Long term environmental monitoring using locally-relevant indicators: muskrat (*Ondatra zibethicus*) population dynamics in Old Crow and recreational ecosystem services in Ottawa

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April 2017

A thesis submitted to McGill University in partial fulfilment of the requirements of the degree of
DOCTOR OF PHILOSOPHY

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Abstract

Multi-decade environmental monitoring is necessary to understand many of the effects of anthropogenic activities, yet the success of many long term monitoring programs has been limited and sporadic. In this thesis, I demonstrated the strengths of participatory approaches and locally-relevant environmental indicators as a solution for long term monitoring. In Chapter 1, I described the limited success of many long term monitoring programs, and outlined the current understanding of best practices in monitoring. In Chapter 2, I analyzed the impact of participatory approaches, together with innovative portable digital technologies, in a sample of publications and case studies describing environmental monitoring programs. I found the use of digital data entry can increase a program's management relevance while participatory adaptive monitoring, i.e. the collaborative definition of program questions, objectives, conceptual models, and approaches, improved program sustainability. I applied these principles in Chapter 3 by monitoring the environmental determinants, and cyclicity, of muskrat (*Ondatra zibethicus*) population dynamics in the Old Crow Flats (OCF), Yukon. I interpreted local ecological knowledge (LEK) in the development of questions, conceptual models, and interpretation of results. I found that LEK identified advancing ice phenology as a concerning source of environmental change, Landsat imagery confirmed 0.26 days/year of more open water over the past 31 years, and aerial and field surveys found a negative association between the open water season and muskrat densities. In Chapter 4 I compiled 219 time series of up to 8 years of muskrat abundance in the OCF to describe the first traveling wave of abundance in muskrats. Using spatial patterns of landscape resistance to muskrat movement, genetic relatedness, and population synchrony, I found this wave was likely caused by a combination of landscape obstacles and directional dispersal. In Chapter 5, I identified a parallel indicator that is locally-relevant for Ottawa, recreational ecosystem services on the

Rideau Canal Skateway, and projected the availability and use of those services under climate warming. I found Ottawa's ice phenology to be shifting twice as rapidly as Old Crow's (0.5 days/year), and found this to be linked to an accelerated decline in the use of this cultural ecosystem service. Whether ice or animal, for most people the most recognizable and memorable forms of environmental change will occur in locally-relevant indicators. These indicators are the 'low hanging fruit' of environmental monitoring; with little resources they can form the basis of monitoring programs that stand the test of time.

Résumé

Les programmes de suivis environnementaux sur plusieurs décennies sont nécessaires pour comprendre la plupart des effets anthropiques sur l'environnement, mais le succès de ces programmes est limité est sporadique. Dans cette thèse j'ai tenté de démontrer comment des méthodes participatives et des indicateurs localement pertinents peuvent servir de solutions aux défis des programmes de suivis à long terme. Mon premier chapitre décrit, à ce jour, le succès limité des suivis environnementaux à long terme et notre compréhension des meilleures pratiques. Mon deuxième chapitre est une analyse de l'impact des approches participatives et les technologies numériques portables sur des programmes de suivis environnementaux décrits dans un échantillon de publications et d'études de cas. J'ai trouvé que l'utilisation des technologies numériques portables peut augmenter la pertinence d'un programme de suivis utilisé en gestion environnementale, tandis que les approches participatives améliorent la durabilité des programmes. Ces approches comprennent des questions, objectifs, modèles conceptuels, et méthodes qui sont tous définies de façon collaborative. Dans mon troisième chapitre j'ai appliqué ces principes en étudiant les déterminants environnementaux, et la cyclicité, d'une population de rats musqués (*Ondatra zibethicus*) dans la plaine d'Old Crow au Yukon. J'ai interprété les connaissances écologiques locales dans mon développement des questions, des modèles conceptuels, et l'interprétation des résultats. Les experts locaux ont identifié l'avancement de la phénologie de glaces comme une source de changement environnemental significative, et les images Landsat ont confirmé une augmentation de la saison d'eau libre de 0,26 jour/an au cours des 31 dernières années. Des suivis aériens et *en situ* ont trouvés une association négative entre la saison d'eau libre et la densité des rats musqués. Dans mon quatrième chapitre j'ai compilé 219 séries chronologiques d'abondance de rats musqués sur 8 ans pour décrire pour la première fois

une onde d'abondance progressive chez le rat musqué. En estimant la structure spatiale de la résistance du paysage au mouvement des rats musqués, de leurs relations génétiques, et de la synchronie des leurs populations, j'ai trouvé que l'onde a été causée par une combinaison d'obstacles dans le paysage et de dispersion directionnelle. Dans mon cinquième chapitre, j'ai identifié un indicateur similaire qui est pertinent localement pour Ottawa, les services écosystémiques de loisirs sur la patinoire du canal Rideau. J'ai projeté la disponibilité et l'utilisation de ce service dans des conditions de réchauffement climatique. J'ai trouvé que la longueur des saisons glaciales diminuait deux fois plus rapidement à Ottawa (0,5 jour/an) qu'à Old Crow, et que cela était lié à une réduction accélérée de l'utilisation de ce service. Que ce soit de la glace ou des animaux, les formes les plus reconnaissables et mémorables de changements environnementaux s'opèreront à travers des indicateurs qui sont pertinent localement. Ces indicateurs sont ceux qui peuvent facilement constituer la base de programmes de suivis environnementaux qui persistent à travers des générations.

Acknowledgements

As I write these acknowledgements on my 29th birthday, it is humbling to consider the enormous array of people who have contributed to my life thus far and, in particular, to the work contained in this thesis. First I would like to thank my supervisor, Murray Humphries, who has guided me, offered sage advice, and humoured my many detours on the long path I have taken following the completion of my bachelors. I thank him for trusting me, for re-directing me from my most egregious mistakes while allowing me to stumble on the more the constructive ones.

Over the years my many lab mates have shaped the man and the researcher I am today. It is difficult to consider who I would have become without the ideas, criticisms, laughter, and support provided by Alec, Ally, Amy, Ana, Bertrand, Colin, Devan, Dylan, Elad, Eliot, Elise, Emily ("Studdley"), Guillaume, Jason, Jennifer, Joël, Karine, Luke, Manuelle, Marianne, Meghan, Melanie, Paul, Quinn, Sébastien, Victoria, and Xavier ("Rat Tail"). Xavier, there are few people I would rather have by my side when I'm hungry, stuck in the bush, and wrestling bears. Alec, Ana, Colin, Elise, Jennifer, Karine, and Luke, I have been lucky to work with you on my many projects. Much of this thesis grows out of your efforts. Guillaume, thank you for being there for long conversations and bang on technical advice for the duration of my studies. I credit much of my development of any technical expertise to you setting me on the right track from day one. You get the credit, or the blame depending on one's perspective, for my stab at anisotropy in Chapter 4.

This thesis would not have been possible without the numerous people who began as community partners, and who I would now consider friends. First off, the trappers who took a greenhorn in the bush and taught me how Gwich'in and Dabeeyou hunt, trap, and fish: Dennis Frost, Peter Frost, Stephen Frost, Elmer Georgekish, James Itsi, Irwin Linklater, and Joel Peter.

Next, the many people in the communities who supported me either with housing, food, equipment, knowledge, kind words, or a sympathetic ear: Louis Allain, Allen Benjamin, Martha Benjamin, Billy Bruce, Robert Bruce Jr., Dougie Charlie, Fanny Charlie, Stringer Charlie, Betty Frost, David Frost, Donald Frost, Freddy Frost, Harold Frost, Theresa Frost, Anna Grey, Nick Grey, Peter Josie, William Josie, Danny Kassi, Harvey Kassi, Elizabeth Kaye, John Joseph Kaye Robert Kaye, Roger Kaye, Brandon Kyikavikchik, Norman Linklater, David Lord, Jeremy McCulloch, John MacDonald, Kathryn MacDonald, Georgie Moses, Mary Jane Moses, Florence Netro, Essau Schaeffer, Stanley Nijootli sr., Stanley Grafton Nijootli, Frances Ross, Erika Tizya, Mary Tizya, Kenji Welch, and Megan Williams. I would particularly like to thank Nick and Anna for frequently welcoming me into their home, and John and Kathryn for literally and frequently offering up their home to a wayward and unwashed researcher. These friendships are some of the happiest consequences of my thesis.

Finally, I would be nothing without the love and support of my family. Thank you Andrew, Bill, Helen, Laurie, Lise, Mikki, and Sue for always being there for me. A special thank you to my parents Jane and Tony. You have picked me up and set me straight all my life, and I would literally be nothing without you. I dedicate this thesis to you.

Contribution of authors

All chapters were conceived and written by me and are a result primarily of my research efforts. Supervisor Dr. Murray M. Humphries provided guidance, ideas, critiques, and reviews of all my work. I conceived, gathered data, conducted the meta-analysis, and wrote Chapter 2 with extensive reviews and ideas, particularly regarding the case studies, from a team of co-authors (Drs. Nicolas D. Brunet, A. Cole Burton, Alain Cuerrier, Finn Danielsen, Thora Martina Herrmann, Rod Kennett, Guillaume Larocque, Monica Mulrennan, Arun Kumar Pratihast, Marie Saint-Arnaud, Colin Scott; and Kanwaljeet Dewan and Micha V. Jackson). Notably, Dr. Larocque created Figures 2.1 and 2.5 based on my instructions and Dr. Danielsen provided some of the raw data for the meta-analysis. Chapter 2 has been accepted for publication in Conservation Biology (Brammer et al. 2016). I provided the ideas, gathered most of the data, conducted much of the analysis, and wrote Chapters 3 and 4. Some of the muskrat carcass and aerial pushup survey data were gathered by Dr. Humphries and Manuelle Landry Cuerrier prior to my arrival as a M.Sc. student in 2009. For Chapter 4, Alec Robitaille provided assistance regarding Google Earth Engine coding for the analysis of Landsat imagery; Valerie Hayot programmed the Circuitscape simulations with a land cover map provided by Dr. Trevor Lantz; and Xavier Giroux-Bougard assisted me with muskrat collection and dissections, conducted the genetic analyses of tissues, and assisted with the statistical analysis. I provided the ideas, conducted the analysis, and wrote Chapter 5 using data provided by Alain Nantel at the National Capital Commission and simulated weather data from Dr. Jason Samson. This chapter was published in Nature Climate Change (Brammer et al. 2014).

Preface and contributions to knowledge

Throughout this thesis I endeavoured to develop a framework for long term environmental monitoring using participatory methods and locally relevant indicators. I believe this thesis has made several original contributions to knowledge by: (1) describing the current state of, and best practices in, environmental monitoring; (2) highlighting the advantages of participatory methods and locally-relevant indicators in monitoring; (3) developing an approach for interpreting local ecological knowledge (LEK) in wildlife biology; (4) measuring the decadal rate of change in ice phenology of the Old Crow and Ottawa regions; (5) modeling how these phenological changes are influencing locally-valued ecosystem services; and (6) demonstrating how directional patterns in a particular indicator, time series of animal abundances, can be used to differentiate between various mechanisms driving population dynamics.

Chapter 1 briefly summarized the current state and best practices in the field of environmental, and particularly ecological, monitoring. Chapter 2 analyzed the successes of monitoring programs based on a quantitative review of the literature and a qualitative review of 6 case studies. Both chapters contributed by explicitly defining, compiling, and analyzing a field of inquiry that has primarily been the subject of general discussion: what constitutes successful long-term environmental monitoring and what lessons can be learned from the successes and failures of past programs? Specifically, Chapter 1 contributed an array of evidence to support an often stated, though rarely tested, claim that, notable exceptions aside, effective long term monitoring programs remains a rarity despite being the subject of more than three decades of scientific discussion. In addition, Chapter 1 contributed a detailed summary of published best practices in environmental monitoring that can serve as a condensed guide for future programs. Chapter 2 built on this summary using quantitative and qualitative methods to examine two features of monitoring programs that are increasing in prominence: participatory methods and portable digital devices (e.g. smartphones). This chapter contributed one of the first analyses explicitly linking participatory approaches with management actions and program sustainability. This analysis also contributed one of the few balanced examinations of the utility of innovative digital technologies in environmental monitoring. This chapter contributed to environmental monitoring by arguing that, innovative digital tools notwithstanding, programs should have an established foundation of clear, often collaboratively-defined, questions, protocols, and outputs before they can benefit from data entry technologies.

The contribution of Chapter 3 is the unique combination of satellite imagery, aerial photography, ground surveys, and local ecological knowledge (LEK) interpretation to study the effects of environmental change on a wildlife population. Understanding the ecosystem context of a wildlife population is important for understanding its dynamics. Chapter 3 contextualized research into the ecology of Old Crow Flats muskrats through the interpretation of LEK to identify and determine the implications of important trends of environmental change. In this chapter, LEK was interpreted during the conceptualization of ecosystem models *a priori*, and it was again interpreted during the comparison and discussion of quantitative models based on field surveys, aerial photography, and satellite imagery. This novel approach to LEK was combined with a novel approach to remotely estimating lake ice phenology. Chapter 3 contributed an adaptation of the SNOMAP algorithm, designed for large scale (i.e. 1000 km^2) estimates of snow cover, for the remote sensing of individual lake freeze-up and break-up dates within the Old Crow Flats, Yukon. This unique combination of Landsat-based ice cover estimates and multi-level modeling using hundreds of lakes could be adapted to any region and time covered by Landsat imagery. From my understanding, this approach combining a quantitative analysis of multi-scale field data and LEK is unique, and represents one option for wildlife biologists interpreting LEK.

Chapters 3 and 5 demonstrated multi-decade rates of change in ice phenology in the Old Crow and Ottawa regions respectively, and highlighted the influence of these changes on local ecosystem services. In particular, Chapter 5 contributed one of the few analyses of the environmental determinants of a cultural ecosystem service, a form of ecosystem services that has been neglected due to the difficulty of measuring and quantifying their often intangible benefits. This chapter highlighted the opportunity presented by outdoor recreational services like the Rideau Canal Skateway; they can demonstrate the biophysical requirements of culturally important activities and how these are influenced by environmental change. This analysis adapted Holling's functional responses of resource consumption to describe the use of this recreational service in response to its availability. The combination of this nonlinear functional response and projected rates of warming suggested that the use of this locally-relevant service will experience an accelerating decline. Highlighting the impacts of warming on both the availability and use of a cultural ecosystem service is unique to my knowledge.

Finally, in Chapter 4, I documented the first recorded instance of a traveling wave of abundance in muskrats and provided the first explicit comparison of the four mechanisms currently known to generate waves in any population of wildlife. This analysis is a particularly unique contribution due to its combination of the spatial distributions of landscape resistance inferred from circuit theory, genetic relatedness inferred from tissue specimens, and population synchrony inferred from lake level time series of abundance. This combination allowed for a quantitative test of the mechanisms underlying traveling waves, and for the identification of landscape obstacles and directional dispersal as potentially key drivers. Inferring directional dispersal from directional population synchrony, landscape resistance, and genetic relatedness is an exciting development for population biology that will require more study to fully exploit.

Ranging across remote sensing, aerial surveys, *in situ* measurements, handheld digital data entry, and local knowledge interviews, this thesis employed a wide variety of tools to address an array of environmental phenomena. This thesis demonstrated how locally-relevant indicators and participatory methods can be used to monitor and understand phenomena of interest locally (e.g., muskrat trapping and outdoor skating) and of interest to a broader community (e.g. latitudinal variation in changing ice phenology, traveling waves of animal abundance). It has shown that we can combine multiple decades of satellite imagery, fur returns from local trappers, and local ecological knowledge to conduct environmental monitoring that is both technically accurate and ecologically contextualized. Overall I hope this thesis established that the combination of technical and participatory approaches to monitoring locally-relevant indicators is one solution for environmental monitoring that is informative, useful, and sustainable.

1 Introduction

"Monitoring is science's Cinderella, unloved and poorly paid." (Nisbet 2007)

The processes underlying ecological associations occur across an enormous range of time scales, from fractions of a second to millions of years. Humans are well adapted to observing phenomena at particular scales (e.g. minutes to years), but depend on innovative approaches to expand our observational abilities beyond this narrow band of times. In many fields these efforts have met with great success. For example, we can describe changes in fossilized animal communities around the world in response to millions of years of climate change (Blois and Hadly 2009); meanwhile we can observe turnover of complete communities over a matter of days in the microbiome (Schmidt 2007). We have struggled, however, with documenting phenomena that operate on the scale of several lifetimes (Brammer and Humphries 2016); this is too fine a resolution for many paleoecological records (but not all, see: Smol 1995), whereas it is too long for most ecological time series (but not all, see: Hill and Carey 1997). Unfortunately, many anthropogenic influences, like climate and land use changes, affect ecosystems at this poorly documented time scale. Addressing these challenges will require a careful consideration of the many obstacles to establishing, contributing to, and maintaining records of environmental phenomena over multiple lifetimes. While Krebs (1991) may have exaggerated in arguing "that we have by now completed the major analyses of short-term problems in ecology", he is correct in that greater emphasis must be placed on the "neglected… long-term ecological processes".

In the next section, I will briefly review the published literature describing the advantages of long term monitoring, the surprisingly limited success of these programs to date, general approaches to monitoring and their best practices, and the opportunity presented by participatory monitoring and locally-relevant environmental indicators. I will subsequently describe the two case studies that form the bulk of this thesis, (1) locally-relevant muskrat (*Ondatra zibethicus*) populations of the Old Crow Flats, Yukon, and (2) outdoor recreational opportunities at the Rideau Canal Skateway in Ottawa. Finally, I will describe my objective of demonstrating the benefits of participatory monitoring and locally relevant indicators, and outline my approach to reaching this objective.

1.1 Literature review

1.1.1 The benefits of long term environmental monitoring

The benefits of long term environmental monitoring have been well described and range from contributing to basic scientific research to evaluating the application of management interventions. Generally, long term environmental monitoring, which I define as the process of gathering information about state variables (e.g. animal abundance, forest cover, water pH, etc.) to assess the state of the ecosystem and draw inferences about system change over at least ten years (Yoccoz et al. 2001, Lindenmayer and Likens 2010*a*, Jones et al. 2013), has been the subject of ongoing discussions, debate, and political controversy for decades (Berkowitz et al. 1989, Krebs 1991, Keeling 1998, Legg and Nagy 2006, Haughland et al. 2010, Lindenmayer and Likens 2010*b*). Most authors acknowledge that long term environmental monitoring confers numerous benefits for both basic science and applied environmental management (Yoccoz et al. 2001), and is necessary to understand and address ongoing changes in climate, atmospheric pollution, water pollution, land use, and biodiversity (Parr et al. 2003). Whatever the application, datasets from long term monitoring programs can be used to generate new questions, test current theory, and provide context for experimentation (Krebs 1991, Lovett et al. 2007, Lindenmayer and Likens 2010*a*). This context is particularly valuable, as many ecological phenomena vary along temporal scales far greater than a 3 year graduate research project (Tilman 1989, Krebs 1991). It is important to use data of an appropriate scale to understand the dynamics of 'slower' phenomena (e.g. succession, evolution, climate systems, etc.) and to not confuse correlations with a phenomenon's short term[1] variability and the mechanisms underlying its dynamics (Wolfe et al. 1987, Krebs 1991).

Long term monitoring is often described as beneficial in defining 'baseline' or 'natural' conditions, but it is important to be clear what these terms mean. Disentangling natural from anthropogenic drivers of variability in ecosystems can be challenging as many ecosystems have been influenced by human activities for millennia (Willis and Birks 2006). As a result, baseline conditions are often arbitrarily determined by the initiation date of the monitoring program, or are based on value judgements of the desired system state (Legg and Nagy 2006). Following an explicit decision of what constitutes a baseline, long term monitoring is useful, first, in recording baseline values, variances, rates of change, trends, and periodicities in the dynamics of state variables (Wolfe et al. 1987, Yoccoz et al. 2001, Parr et al. 2003, Legg and Nagy 2006, Lindenmayer and Likens 2009, Carpenter et al. 2011). When this frame of reference is established, long term monitoring is useful, second, in detecting unusual changes from the baseline (Lovett et al. 2007). These changes can be anthropogenic or not (e.g. change in land use vs. recurring forest fires), and intentional or not (e.g. experimental vs. inadvertent lake eutrophication), but all provide an opportunity to test one's mechanistic understanding of the system by evaluating its responses

[1] The use of 'long term' and 'short term' are highly relative, what is considered short term will depend on the phenomenon in question. For example, if one used organism's generation time as the distinction between what constitutes long and short term, the definitions would vary 7 orders of magnitude between bacteria and elephants (Schmidt 2007).

to change (Wolfe et al. 1987, Legg and Nagy 2006, Lindenmayer and Likens 2009, Magurran et al. 2010, Metzger et al. 2013). Well documented examples of this process include the discovery of acid rain and its impacts on the biogeochemistry of forest ecosystems (Likens et al. 1972, 1996), trends in atmospheric carbon dioxide associated with climate change (Keeling et al. 1976, Karl and Trenberth 2003), and the importance of phosphorus in lake eutrophication (Schindler et al. 2008). In fact, Lindenmayer et al. (2010) argue that long term monitoring is critically important because it increases the probability of unexpected ecological discoveries, or 'surprises'. Finally, long term baselines could also be used to predict ecological regime shifts based on declining rates of return from perturbations and increases in the variances of state variables (Carpenter et al. 2011).

Long term monitoring and improved understanding of ecosystem dynamics can contribute to informing environmental management, policy, and legislation. First, monitoring is necessary to document ecosystem status and whether this status is changing (Hewitt and Thrush 2007). These data allow for the definition of conditions for, and the dissemination of, alerts in cases of rapid deterioration in environmental conditions (e.g. declining raptor fertility in response to DDT, the International Union for the Conservation of Nature's Red List of Threatened Species; Ratcliffe 1970, Magurran et al. 2010). Second, monitoring allows for quantitative management objectives and tracking progress towards these objectives (Lindenmayer et al. 2012, Metzger et al. 2013). Third, long term monitoring programs can be used to evaluate the effectiveness of historical management actions, policies, or programs, and to predict the impacts of future interventions (Harremoës et al. 2001, Parr et al. 2003, Legg and Nagy 2006, Lindenmayer et al. 2012). Fourth, information from monitoring programs can be used to develop new legislation in response to documented changes (Lovett et al. 2007, Lindenmayer and Likens 2010*a*). Fifth, while assumed to be costly, monitoring programs can prevent costly deteriorations in environmental states (Lovett et al. 2007). Finally, monitoring can engage the public in environmental management, thus increasing awareness and consideration of these issues (Jones et al. 2013).

1.1.2 The limited success of long term environmental monitoring to date

While there are considerable advantages associated with long term environmental monitoring, many have argued that effective and ongoing monitoring programs are surprisingly uncommon (Wolfe et al. 1987, Krebs 1991, Lindenmayer et al. 2012). This issue was identified 25 years ago in ecological research, where a review of 623 papers published over a decade in the journal *Ecology* found 40 % described datasets that lasted less than 1 year, 80 % lasted 3 or fewer years, and projects lasting more than 10 years were dominated by paleoecological reconstructions (Tilman 1989). Similarly, Smol (1995) surveyed 111 papers in *Limnology and Oceanography* and found less than 30 % were based on more than one year's data, while the number of sites monitored in the Canadian Ice Database has varied dramatically over the years with only 4 % of the freeze-up/break-up sites of 1985-86 still being monitored in 2001 (Figure 1.1; Lenormand et al. 2002). A similar shortage of monitoring makes it difficult to assess the effectiveness of management interventions, such as those of the 37,099 projects of the US National River Restoration Science Synthesis database. These projects represented approximately 15 billion USD spent on river restoration efforts, yet only 10 % of projects reported any form of monitoring to assess the effectiveness of restoration actions (Bernhardt et al. 2005). This shortage of monitoring data also influences decision-making in management agencies. For example, a review of 1000 Australian protected areas found 60 % of management decisions were based on the experience of managers rather than any form of monitoring data (Cook et al. 2010). Similarly, Sutherland et al. (2004)

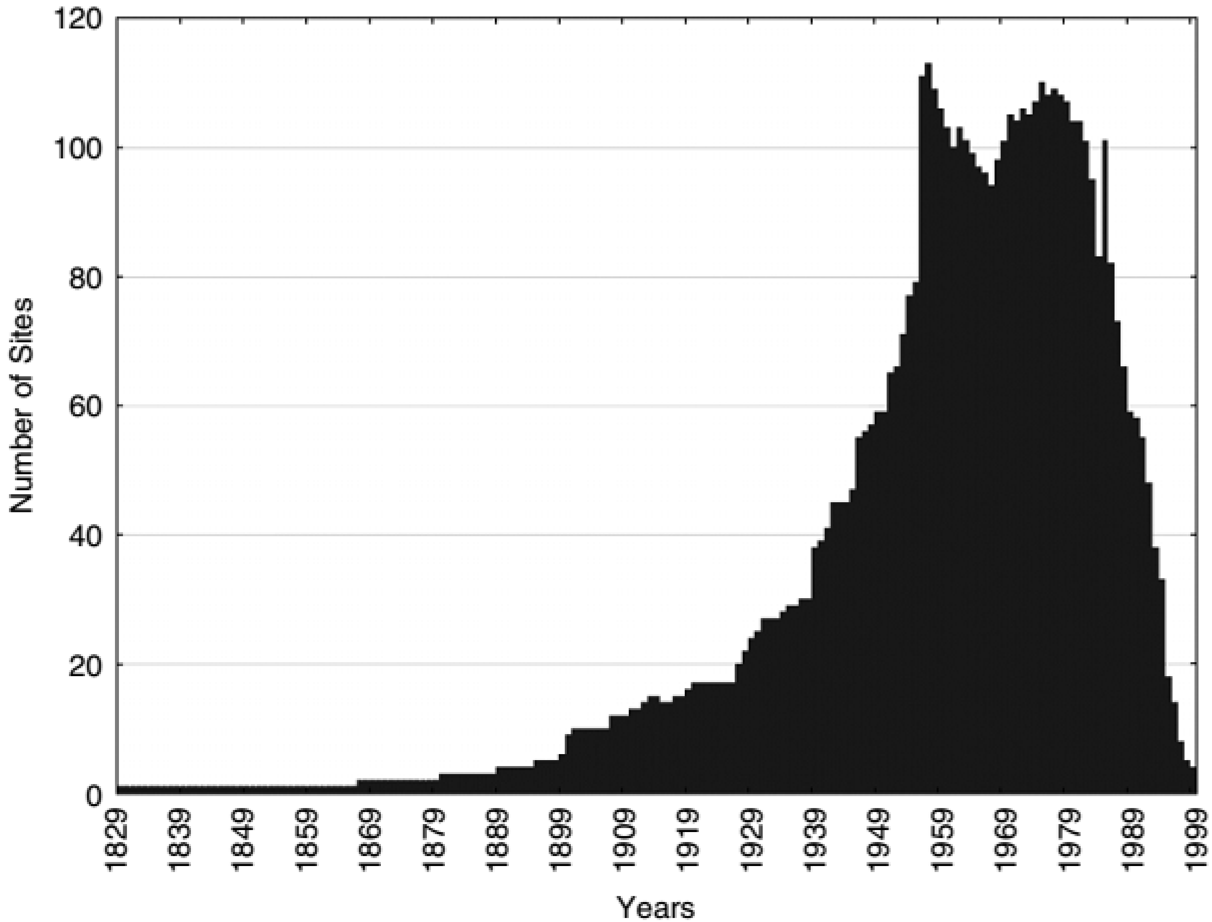


Figure 1-1: Changes in the number of sites where lake ice observations are recorded within the Canadian Ice Database (adapted from Duguay et al. 2006).

found that only 2.4 % of 170 sources used to inform management actions in an English wetland were based on scientific data, and that habitat responses to management actions were generally not monitored. The adaptive management philosophy, aiming to improve ongoing practices in environmental management, emphasized the importance of conducting management experiments, monitoring the results, and ultimately 'learning by doing' (Walters and Holling 1990). Yet, in a review of 61 adaptive management programs (out of 1336 publications using the term!), only 13 projects were supported by published monitoring data, and only 4 of these had lasted longer than 10 years (Westgate et al. 2013).

To explain the spotty record of long term ecological monitoring, Lindenmayer & Likens (2010*a*) offer a number of commonly encountered weakness in monitoring programs. These include: (1) lack of explicit questions; (2) failure to agree on what to monitor and why it is important to monitor those entities; (3) poor study design; (4) monitoring too many things poorly rather than a few things well; (5) disengagement of scientists from the monitoring program; (6) loss of integrity of the dataset; (7) loss of personnel; and (8) loss of funding (Lindenmayer and Likens 2010*a*). They argue that monitoring is too often "planned backwards on the collect now (data), think-later (of a useful question) principle" (Roberts 1991), and that this lack of explicitly-defined questions at the outset exacerbate many of the weaknesses above. Specifically, if monitoring objectives are vague (1), it is more difficult to define precisely what should be monitored (2), contributing to disagreements about what to monitoring and the selection of a "laundry list" approach that is more likely to result in many entities being monitored poorly (3-4; Lindenmayer and Likens 2010*a*). This laundry list approach is often more complicated to implement, and to ensure statistical rigour (3), compared to targeted approaches. Weaknesses in the designs of long term ecological studies have been discussed prior to Lindenmayer and Likens (Krebs 1991), and it is commonly argued that programs should devote more time and resources to their study design to avoid collecting data that are uninformative or biased (Yoccoz et al. 2001, Legg and Nagy 2006, Martin et al. 2007). Common statistical considerations often omitted from monitoring programs include: calculating the power needed to detect a biologically significant trend, measuring the detectability of state variables, optimizing field protocols, establishing contrasting treatments, and considering different sampling regimes like rotating sampling (Krebs 1991, Yoccoz et al. 2001, Legg and Nagy 2006, Lindenmayer and Likens 2010*a*). An alternative to the difficulties of the laundry list approach is to use indicator species, but there is little agreement regarding what species should be indicators, what these taxa are exactly indicative of, and under what circumstances these are, and are not, appropriate indicators (Lindenmayer and Likens 2010*a*). The use of either a laundry list of state variables or few indicator species can be linked to a lack of focus in monitoring questions and objectives (1), which can often lead to an unfocused and inefficient use of monitoring funds (Lindenmayer and Likens 2010*a*). Ultimately, programs that are costly and unfocused have greater difficulty surviving inevitable periods of financial compression compared to targeted programs (8).

The rarity of successful long term monitoring programs is perhaps not surprising considering the organizational, physical, and academic contexts in which these programs operate. Monitoring programs are implemented by organizations whose structures are likely to change over decades of monitoring. Reorganizations can result in change and loss of personnel, associated loss of expertise, interruptions of data collection or the loss of archived data, the loss of a project champion, or the loss of key partnerships within and between organizations (Lindenmayer and Likens 2010*a*, Williams and Brown 2012, Westgate et al. 2013). Organizational rules can be impediments, like when overly strict or unclear intellectual property rights inhibit the sharing of monitoring data. This in turn severely limits general awareness, and the utility, of the program (Lindenmayer and Likens 2010*a*). Perhaps the most clear-cut impediment to long term monitoring program is the occurrence of physical disasters (e.g., fires and floods) that can destroy experimental designs, monitoring infrastructure, or data (Lindenmayer and Likens 2010*a*, Westgate et al. 2013). While less dramatic, the system of rewards within academia likely has a stronger influence impeding long term monitoring. The advancement of academic careers is driven to a large extent by publications and citations, and the longer publication times associated with monitoring is a strong disincentive towards the establishment of long duration time series (Wolfe et al. 1987, Nisbet 2007, Westgate et al. 2013; although for the publication advantages of long term monitoring see: Clutton-Brock and Sheldon 2010). Similarly, there are often strong rewards for new work, as opposed to the continuation of ongoing programs, making it difficult to present multi-decade monitoring programs as opportunities for early career researchers (Lindenmayer and Likens 2010*a*, Westgate et al. 2013).

These academic disincentives are exacerbated considering the frequency of changes in political and funding priorities. Monitoring is an ongoing expense, as a result it is often the last activity to be funded and the first to be cut (Lindenmayer and Likens 2010*a*). Considering that most granting programs operate on a 3-5 year funding cycle, there are frequent opportunities for monitoring programs to lose political relevance and associated funding (Wolfe et al. 1987, Tilman 1989, Russell-Smith et al. 2003, Lindenmayer and Likens 2010*a*, *c*, Westgate et al. 2013). The story of the Keeling curve is telling. Beginning in 1958, Keeling and colleagues started what would become the world's longest continuous record of atmospheric CO_2 at Mauna Loa (Nisbet 2007). This dataset would discover the links between trends in CO_2 associated with seasonal productivity, El Nino/La Nina, and anthropogenic emissions associated with climate change (Keeling 1998, Nisbet 2007). While Mauna Loa contributed to a major advancement of environmental science in the twentieth century, it spent much of its existence under threat of closure due to lack of funds, something that actually occurred for one year in 1964 (Keeling 1998). During a particular funding crisis, Keeling was required to justify his Mauna Loa time series by proposing two anticipated discoveries per year arising from the data (Keeling 1998). It is important to realize, as Keeling (1998) did, that "environmental time series programs have no particular priority in the funding world, even if their main value lies in maintaining long-term continuity of measurements".

1.1.3 Approaches to long term environmental monitoring

A variety of approaches exist to monitoring environmental change over different time scales including paleoecological records, remote sensing, and *in situ* measurements. Paleoecological records (e.g., layers in tree, lake sediment, and ice cores) offer monitoring data that cover the largest temporal extent, and are particularly useful for examining environmental changes occurring over many decades and longer (Smol 1995, Parr et al. 2003). Meanwhile remote sensing imagery are increasing in availability, resolution, coverage, frequency, and cost effectiveness, and are particularly useful for tracking land use, habitat structure, disturbance, and visible phenological events (e.g. trees leafing out; ice breaking up; Parr et al. 2003, Muchoney 2008). These remote and paleoecological approaches are ideally calibrated with *in situ* measurements. Approaches to *in situ* monitoring vary enormously; any brief categorization of their diversity will fall short and debate is ongoing regarding the advantages of different approaches (for more see: Haughland et al. 2010, Lindenmayer and Likens 2010*b*). Generally *in situ* monitoring varies from those typically larger-scaled programs applying a standardized survey protocol observing diverse environmental variables (e.g. the Alberta Biodiversity Monitoring Institute; http://www.abmi.ca/) to typically smaller-scaled monitoring programs targeting particular ecosystems and their dynamics (e.g. the Hubbard Brook Experimental Forest; www.hubbardbrook.org/). The former has been classified as surveillance or omnibus (Nichols and Williams 2006), passive or mandated (Lindenmayer and Likens 2010*a*), and cumulative effects (Boutin et al. 2009) monitoring, while the latter has been classified as hypothesis-driven (Lindenmayer and Likens 2010*a*), stress-oriented (Boutin et al. 2009), strategic (Metzger et al. 2013), and targeted or focused monitoring (Nichols and Williams 2006).

Proponents of surveillance monitoring argue that large scale approaches are necessary to track environmental variables, and how these are influenced by stressors, at scales relevant to managers (i.e. 100-1000 km^2). In particular, Boutin et al. (2009) argue that monitoring biodiversity change in relation to forestry management in Canada requires an approach that moves beyond the geographical and temporal scale of local monitoring initiatives. They found previous approaches, including private companies monitoring in forest management areas, governmental monitoring of priority species, and various volunteer initiatives, were incapable of providing timely, rigorous, and consistent description of biodiversity in Canada due to a lack of standardization of approaches, a heavy bias towards vertebrate and threatened species, and a deficiency of data of sufficient quality[2] to accurately assess trends in abundance (Boutin et al. 2009). To address this, the Alberta Biodiversity Monitoring Institute (ABMI) built a program based on standardized biodiversity surveys at a 20 km by 20 km grid of 1,656 survey sites that are visited on a rotating basis once every five years (Figure 1.2; Nielsen et al. 2009). This distribution is intended to expose correlative relationships between biodiversity indicators and multiple stressors, making it capable of tracking progress towards “maintaining biodiversity” and addressing new stressors as they arise (Boutin et al. 2009). Similar programs include the UK’s Countryside survey, initiated in 1978 and designed to quantify the state or health of the UK countryside (Metzger et al. 2013), and the National Inventory of Landscapes in Sweden (Ståhl et al. 2011).

Proponents of targeted monitoring argue that a focused approach, built around predefined questions, conceptual models, and statistical designs, is necessary to identify and address the mechanisms underlying environmental change (Nichols and Williams 2006, Lindenmayer and

[2] For example, the authors of Canada’s Wild Species Reports documented shifts in species’ status between 2000 and 2005, but point out that 94% of these shifts were a result of changes in data quality or methodology rather than true trends (Boutin et al. 2009).

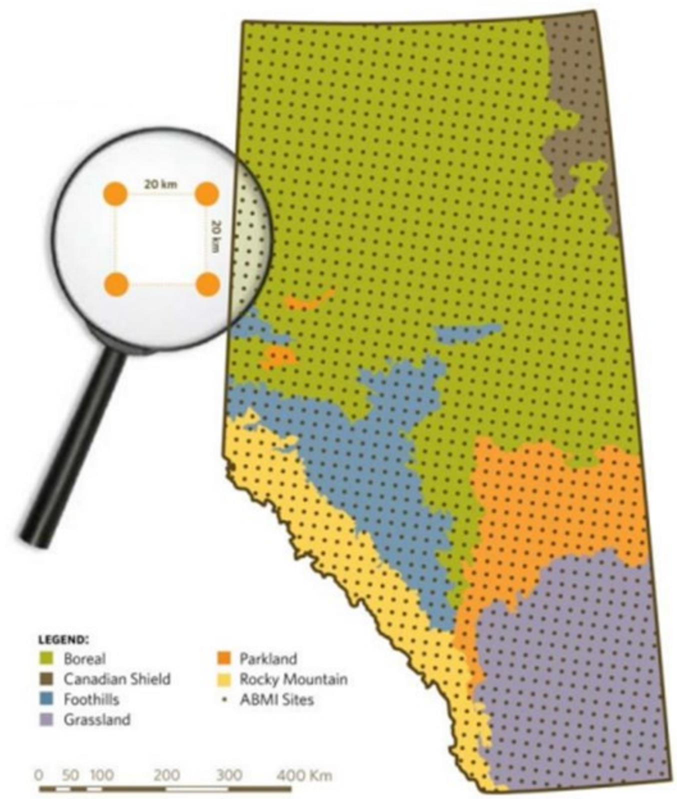


Figure 1-2: The sampling grid of the Alberta Biodiversity Monitoring Institute consisting of 1656 sampling sites at 20km intervals (reproduced from: Bayne et al. 2015).

Likens 2009). This approach is epitomized in Lindenmayer and Likens' (2009) Adaptive Monitoring framework (Figure 1-3), which contends that effective monitoring programs should (1) address well defined, *a priori*, questions; (2) be designed statistically, ideally with experimental manipulations; (3) be based on a preconceived conceptual model of the ecosystem; (4) and be driven by human need to understand the system and stressors (i.e. it should "pass the test of management relevance"; Russell-Smith et al. 2003). This approach is similar to the Adaptive Management framework (Walters 1986) in that question setting and experimental manipulations will often be structured around management interventions (Lindenmayer and Likens 2010*a*). It is argued that this approach is the most capable of generating strong inferences regarding the mechanisms underlying environmental changes of importance to managers in a cost-effective manner (Lindenmayer and Likens 2009). While this framework could theoretically be applied at any spatial scale, it is typically associated with smaller scale, long term, study sites such as the Experimental Lakes Area in Ontario and the Hubbard Brook Experimental Forest in New Hampshire (Likens et al. 1996, Schindler et al. 2008).

The relative merits of surveillance and targeted monitoring have been the subject of constructive debate (e.g. Haughland et al. 2010, Lindenmayer and Likens 2010*b*) and it appears that a combination of these approaches is ideal for monitoring environmental change at a scale and in a manner capable of informing management decisions. On the one hand, small scale targeted monitoring programs have not delivered large scale assessments of environmental trends (e.g. none of the US's Long-Term Ecological Research (LTER) sites, costing ~$US23 million/year, were included in The State of the Nation's Ecosystems report; Lindenmayer and Likens 2010*a*). On the other hand, large scale surveillance monitoring programs are focused on correlational analysis stratified by space or ecosystem, with little capacity for experimental manipulation (Nichols and Williams 2006, Lindenmayer and Likens 2010*b*). Environmental monitoring is likely best situated where it can be targeted, and ideally experimental, at smaller scales within the context of a broad surveillance network (Platt 1964, Krebs 1991, Clutton-Brock and Sheldon 2010). Given the difficulties in maintaining long term funding for monitoring (see section 1.2), supporting multiple levels of monitoring will be challenging. A focus on a few core characteristics, like the importance of well-defined questions, conceptual models of the system monitored, and statistically rigorous study design (Lindenmayer and Likens 2010*a*), should contribute to improving environmental monitoring programs of all types.

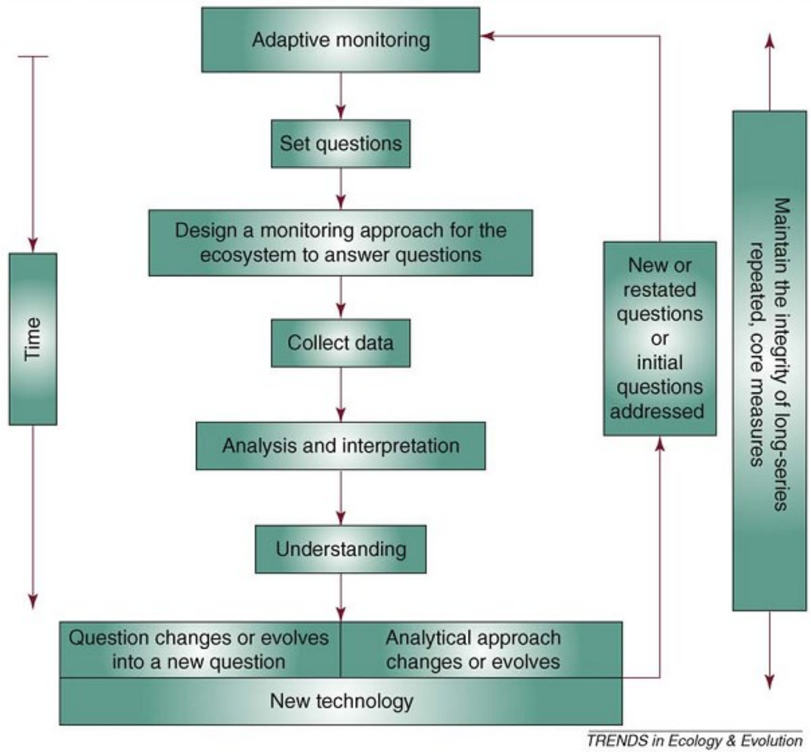


Figure 1-3: The Adaptive Monitoring framework of Lindenmayer and Likens (2009), where programs are built on a foundation of tractable questions, rigorous statistical design, a predefined conceptual model of the monitored entity, and are driven by human need to understand the system (reproduced from: Lindenmayer and Likens 2009)

1.1.4 Characteristics of effective monitoring programs

The Adaptive Monitoring framework (Figure 1-3) is perhaps the most formal of many descriptions of the characteristics of effective monitoring programs (for more see: Yoccoz et al. 2001, Legg and Nagy 2006, Nichols and Williams 2006, Lovett et al. 2007, Lindenmayer and Likens 2010*a*, *c*). Generally, these characteristics can be categorized as effective project initiation, implementation, and dissemination of results. As stated above, any monitoring program should be initiated around an evolving question-setting process leading to clear and quantifiable objectives (Wolfe et al. 1987, Legg and Nagy 2006, Nichols and Williams 2006, Lovett et al. 2007, Lindenmayer and Likens 2010*a*). These questions and objectives can vary in the degree to which they advance scientific versus management priorities, but they are most strongly advanced when testing explicit and *a priori* hypotheses and predictions (Krebs 1991, Yoccoz et al. 2001) based on an explicit conceptual model of the ecosystem(s) monitored (Legg and Nagy 2006, Nichols and Williams 2006, Lindenmayer and Likens 2009). When question setting is motivated by management priorities, monitoring can be ideally situated within an adaptive management framework where it is recording ecosystem responses to alternative management actions that are being evaluated as policy options for governing agencies (Walters 1986, Lindenmayer and Likens 2010*a*).

Effective implementation of a monitoring program requires careful consideration of sampling, statistical power, and uncertainty in the study design and the curation of methods, samples, and data so they are accessible to future generations of scientists. Study design should consider sampling principles by explicitly defining the target population and developing a probability sampling protocol (often stratified by eco-region) that is as flexible and simple as possible (Yoccoz et al. 2001, Boutin et al. 2009, Metzger et al. 2013). The variability (both spatial and temporal) and detectability of the monitored entities should be estimated, and the desired power specified, so the sampling design can be based on an explicit power analysis (Krebs 1991, Yoccoz et al. 2001, Legg and Nagy 2006, Jones et al. 2013). Subsequent data collection should aim to maximize the signal-to-noise ratio of monitored entities through the use of detailed protocols, well trained technicians, and consistent survey timing (Legg and Nagy 2006, Boutin et al. 2009). Survey results must always be presented with quantifications of uncertainty in the models (Harremoës et al. 2001, Nichols and Williams 2006, Magurran et al. 2010). To ensure effective implementation of the program over the long term, methods, samples, and data need to be published, archived, and made available for future use by others (Krebs et al. 2001, Legg and Nagy 2006, Lovett et al. 2007, Lindenmayer et al. 2012). This can facilitate periodic review and adaptation of the study design, ideally through peer review of the project, its funding proposals, and its publications (Legg and Nagy 2006, Lovett et al. 2007). Any modified protocols need to be implemented in parallel with previous protocols for at least a year to calibrate new approaches with historical data (Lindenmayer and Likens 2010*a*).

Monitoring programs are more likely to remain effective across generations if monitoring data is frequently used and disseminated to program partners, peers, and the public. All stakeholders with an interest in monitoring are ideally program partners, providing complementary skills and knowledge associated with their backgrounds (e.g., university and government scientists, statisticians, resource managers, policy makers, residents; Lindenmayer and Likens 2010*a*, Lindenmayer et al. 2012). Building partnerships that are as wide and deep as possible ensures that monitoring methods and data are both well designed and useful for stakeholders so that the program 'passes the test of management relevance' (Russell-Smith et al. 2003, Lindenmayer and Likens 2010*c*). The process of continually examining, interpreting, and presenting program data to peers, ideally as part of a larger research project, should provide frequent opportunities for peer review and feedback that can be used to adapt the design of the monitoring program and its products (Lovett et al. 2007). Finally, outreach efforts should be aimed towards raising the public profile of the program, highlighting the advantages of monitoring, the disadvantages of not monitoring, and the cost effectiveness of the program overall (Legg and Nagy 2006, Lindenmayer et al. 2012, Westgate et al. 2013). Lindenmayer et al. (2012) argue that, overall, the public case for environmental monitoring has been made poorly and would benefit from greater emphasis on the costs of not monitoring. For example, they cite the case of the early detection and eradication of the economically damaging and invasive black stripe mussel (*Mytilopsis sallei*) in Darwin Harbour, a prevention campaign that likely saved millions of dollars (Bax et al. 2002, Lindenmayer et al. 2012).

This focus on the public consequences of monitoring allows for a consideration and communication of the cost effectiveness of a monitoring program. Likely the greatest challenge to long term monitoring is maintaining funding across changing budgets, governments, and public opinion (Strayer et al. 1986, Keeling 1998, Boutin et al. 2009, Clutton-Brock and Sheldon 2010). This requires programs be designed to minimize costs while still gathering sufficiently powerful data to detect relevant trends (Lovett et al. 2007). In many cases monitoring costs can be matched to particular land uses (e.g. monitoring linked to logging should not cost more than the economic benefits of logging; Lindenmayer and Franklin 2002, Hockley et al. 2005). In cases where monitoring benefits are outweighed by costs, the best use of resources could be to not monitor at all (Jones et al. 2013). If monitoring is necessary, many models exist to fund projects over the long term (e.g., trusts, foundation support, lottery proceeds, etc.), although these are rarely used (Lindenmayer et al. 2012). A broad array of funding sources and cost reductions should be considered, because ultimately it is likely the cost of a program will be the strongest determinant of its long term sustainability.

1.1.5 The opportunity of participatory monitoring, locally-relevant indicators, and local ecological knowledge

Given the difficulty of securing long term financial support and the scale of ongoing environmental changes, some have argued more locally administered monitoring programs are necessary (Danielsen et al. 2005, Dickinson et al. 2010, Burton 2012). Participatory monitoring[3]

[3] Various terms have been used to describe the participation of either non-professionals or non-scientists in scientific research and monitoring (e.g. citizen science, community-based monitoring, participatory monitoring and management, community science, participatory action research, public participation in scientific research; for more details of various typologies see: Bonney et al. 2009, Danielsen et al. 2009, Shirk et al. 2011)

programs that engage non-professionals or non-scientists can take many forms (for detailed typologies of participatory monitoring see: Bonney et al. 2009, Danielsen et al. 2009, Shirk et al. 2011) and engage a variety of stakeholders (e.g., concerned citizens, government agencies, industry, academia, community groups, local institutions, and Indigenous peoples; The Ecological Monitoring and Assessment Network and Canadian Nature Federation 2003). The degree to which these programs engage stakeholders can vary from participants only contributing observations to participants leading program design, implementation, and use of monitoring data. Danielsen et al. (2009, 2014*a*) categorize local participation in monitoring as a spectrum ranging from those that are entirely locally administered to those with no participation:

A. *autonomous local monitoring*: no formal affiliations with professional scientists;

B. *collaborative monitoring with local data interpretation*: local stakeholders are involved in data collection, interpretation, or analysis, and management decision-making, although external scientists may provide advice and training ;

C. *collaborative monitoring with external data interpretation*: local stakeholders are involved only in data collection and decision-making emanating from the monitoring;

D. *externally-driven monitoring with local data collectors*: local stakeholders are only involved in data collection (commonly called citizen science); and

E. *scientist-executed monitoring*: external scientists manage all aspects of the project and local stakeholders are not involved.

Participatory approaches to monitoring are believed to have several advantages including the reduction of costs, creation of a monitoring process that is more relevant to stakeholders, and strengthening of associations between monitoring and management. Cost reductions result from stakeholders taking monitoring responsibilities that would require hired personnel to perform otherwise (Danielsen et al. 2005). These are particularly apparent in remote regions (Luzar et al. 2011, Burton 2012, Johnson et al. 2015) and in large scale citizen science projects where, for example, Schmeller et al. (2009) found the participants reduced costs by 2/3 through the contribution of 148,690 person-days to the monitoring of European biodiversity, while Theobald et al. (2015) estimated the contributions of ~1.3 million participants in 388 citizen science projects to be worth $2.5 billion. While there are some concerns regarding data quality in participatory monitoring, clear protocols and data validation appear capable of addressing these concerns without increasing costs dramatically (Newman et al. 2003, Danielsen et al. 2005, Carvalho et al. 2009, Bonter and Cooper 2012). Meanwhile, increased stakeholder engagement in monitoring will frequently lead to a process that is of greater value to stakeholders. This can be from monitoring variables that are more useful to stakeholders (i.e. passing the test of local relevance; Russell-Smith et al. 2003, Eamer 2006, Wolfe et al. 2011, Kouril et al. 2015), building social capital and trust between stakeholder groups through collaborative objective-setting and project implementation (Bliss et al. 2001, Fernandez-Gimenez et al. 2008), or a monitoring process that is more aligned to stakeholder interests (e.g., providing educational or employment opportunities; Brook et al. 2009, Carvalho et al. 2009, Garnett et al. 2009, Brunet et al. 2016). Finally, participatory monitoring programs, particularly those than engage local resource managers, appear to increase the speed of management interventions at a local level (Danielsen et al. 2010). These advantages generally occur due to complementarities between stakeholder and monitoring priorities when programs fulfill a number of key elements (Kouril et al. 2015).

The use of locally-relevant environmental indicators is a particular example of developing monitoring programs that complement the interests of local stakeholders. Indicators with local relevance have provided what is likely the longest and most widespread environmental dataset, one that is so common that it appears banal: weather data. Other locally-relevant indicators are often ecosystem services (i.e. the benefits people obtain from ecosystems; Millennium Ecosystem Assessment 2005), and can be either provisional (e.g. timber cut, fishing catch, wildlife harvested, water quality) or cultural (e.g. catch and release fishing, wildlife viewing, hiking, boating, skiing). These services represent an opportunity to develop indicators that 'piggy-back' on existing activities and are immediately relevant to a segment of stakeholders (Westgate et al. 2013). This could take the form of building experiments around resource extraction activities (e.g. logging; Lindenmayer et al. 2010) or by recording the use of a resource as an index of its availability (e.g. animal fur returns; Estay et al. 2011). This approach dramatically simplifies and reduces the costs of collecting monitoring data, and it is no surprise that some of the longest ecological datasets are derived from these kinds of ecosystem services, like: 40 years of macropod surveys in Australia (Lundie-Jenkins et al. 1999), 125 years of Christmas Bird Counts in North America (Dunn et al. 2005), 160 years of hay production at Rothamsted (Hill and Carey 1997), 200 years of lynx fur returns in Canada (Schaffer 1984), 640 years of grape harvest days from France (Chuine et al. 2004), 1200 years of cherry blossom dates in Japan (Primack et al. 2009), and 3500 years of locust outbreaks in China (Tian et al. 2011).

These kinds of indicators are also complementary with local ecological knowledge (LEK)[4], which is particularly attuned to the availability of provisioning and cultural ecosystem services,

[4] Numerous terms exist to describe the ecological knowledge possessed by groups with a long history of extensive interactions with their environment (e.g., indigenous knowledge, traditional knowledge, local knowledge; sometimes in combination with the qualifier ecological or environmental; Agrawal 1995, Huntington et al. 2004, Moller et al. 2004, Gilchrist et al. 2005, Bohensky and Maru 2011). Here I use the term local ecological knowledge to emphasize that this knowledge is not exclusive to aboriginal groups, and to place less emphasis on its 'traditional', what is often perceived as historical, component (Houde 2007). I define LEK as: "*A cumulative body of knowledge, practice and belief, evolving by adaptive processes, regarding relationships both between organisms and between organisms and their environment that is based on a prolonged interaction with the environment*"(Fernandez-Gimenez et al. 2006,

sometimes across generations (Ferguson and Messier 1997, Ferguson et al. 1998). Interest in documenting LEK and developing partnerships with resource user groups, like Indigenous peoples, has been growing (Brook and McLachlan 2008, Bohensky and Maru 2011). This LEK can contribute to monitoring by contextualizing results and informing management actions (Berkes et al. 2000, Huntington et al. 2004, Moller et al. 2004, Murray et al. 2008, Gagnon and Berteaux 2009). However, interpreting LEK is challenging (Brook and Mclachlan 2005, Fernandez-Gimenez et al. 2006, Wohling 2009, Bohensky and Maru 2011), and there are many possible barriers to its inclusion in monitoring programs, including power imbalances between stakeholders (Nadasdy 1999, Cruikshank 2004); the misidentification of LEK experts (Davis and Wagner 2003); differences in scales, both spatial and temporal, between monitoring and LEK (Duerden and Kuhn 1998, Huntington et al. 2004, Gagnon and Berteaux 2009); a lack of trust between stakeholders (Fernandez-Gimenez et al. 2006, Houde 2007, Moller et al. 2009); and fundamentally different perceptions of local ecology (Huntington et al. 2004). Overcoming these barriers requires monitoring programs that encourage trust between stakeholders, effective communication, equitable decision-making powers, adequate monetary support for participants, and mutual respect (Fernandez-Gimenez et al. 2006, Moller et al. 2009). While participatory methods, locally-relevant indicators, and local ecological knowledge are not appropriate for all environmental variables of interest, they do represent ‘low hanging fruit’ for monitoring by building on already established activities, interests, and knowledge.

Berkes 2012). This definition recognizes that the knowledge element of LEK is not independent of its cultural context; instead LEK is structured as a knowledge-practice-belief complex (Berkes 2012).

1.1.6 Locally-relevant case one: muskrat (*Ondatra zibethicus*) population dynamics in Old Crow Flats, Yukon

Arctic regions, and particularly the Canadian western Arctic, are warming and are expected to continue warming faster than the global average (ACIA 2004, IPCC 2014). Here annual average temperatures have increased 2-3 ºC between 1954 and 2003, compared to a global change of approximately 0.6 ºC over the same period (ACIA 2004, IPCC 2014). This rapid warming is resulting in various environmental changes including more frequent lakes drainages, more unpredictable weather, longer ice free seasons, thinner ice, less snow, and more erosion (Riedlinger 2001, Bonny and Berkes 2008, Carmack and Macdonald 2008, Ford and Pearce 2010). In the community of Old Crow, Yukon, Canada, residents of the Vuntut Gwitchin[5] First Nation (VGFN) have expressed growing concerns regarding the effects of these changes on their traditional territory and foods (Gordon et al. 2008). Members of the VGFN have reported observing more frequent retrogressive thaw slumps, lake drainages, overflows of water on ice, increasing shrub growth, and shifting ice phenologies (Allen et al. 2003, Tetlichi et al. 2004, Gordon et al. 2007, 2008):

> *"Out on the land I see a lot of landslides and permafrost melting. Climate change has changed my life in the way I do things out on the land"* (Gordon et al. 2008)
>
> *"I see a lot of landslides and a lot of lakes drying up."* (Gordon et al. 2007)
>
> *"The water level in rivers, lakes and creeks are all low. It's warming up more."* (Gordon et al. 2007)

[5] The term "Gwitchin" comes in several orthographies. Most recently, the term has switched spelling from Gwitchin to Gwich'in. In this thesis I have used the modern spelling, except in cases referring to formal organizations whose name was established using the older spelling Gwitchin.

"[T]hat trail, you can't follow it anymore, it opens up where it never opened up before, right at the mouth of the Bluefish… water comes over." (Allen et al. 2003)

"The weather is getting warmer and warmer. Plants are growing faster, especially the willows." (Gordon et al. 2008)

"The weather is getting warmer. [The] freeze-up is slow." (Gordon et al. 2008)

These concerns led to the establishment of the International Polar Year research program *Yeendoo Nanh Nakhweenjit K'atr'ahanahtyaa* ("Taking care of the land for the future", hereafter YNNK; Wolfe et al. 2011) with the objectives of assessing the distribution of wildlife in relation to physical changes in the territory of the VGFN and of developing a locally-relevant environmental monitoring program for long term (Wolfe et al. 2011). Of particular concern is the muskrat (*Ondatra zibethicus*), a locally relevant indicator as it is the focus of the Vuntut spring trapping season (Willner et al. 1980, VGFN and Smith 2010).

Muskrats are both a provisional and cultural ecosystem service for the VGFN, as they provide fur, food, and a sense of cultural continuity for a nation who historically spent four months of the spring trapping muskrats in the Old Crow Flats (OCF; VGFN and Smith 2009). This territory, while at the northern edge of muskrats' distribution, is highly productive muskrat habitat and VGFN trappers have traded more than 50,000 muskrat pelts following a single trapping season (Murphy 1986). Previous estimates of muskrat abundance in the OCF have been up to 490,000 animals (Simpson et al. 1989), but there have been no estimates since 1986 and VGFN members have expressed concerns regarding how this indicator will be affected by ongoing environmental change. Previous research suggests that stable water regimes are a prerequisite for dense muskrat populations as variable water levels can increase predation risk and nutritional stress, ultimately reducing survival and recruitment (Bellrose and Brown 1941, Errington 1963, Donohoe 1966, Clark and Kroeker 1993, Virgl and Messier 1996). Still, a large degree of variation in muskrat density can exist within relatively stable wetland habitats (e.g. Clark and Kroeker 1993) often due to the distribution of stands of preferred emergent vegetation (e.g., *Typha*, *Equisetum*, *Potomageton*, *Schoenoplectus*; Danell 1978, Clark 1994) or preferred bank morphologies (Jelinski 1989). A comparison of muskrat populations in the OCF and Ontario found that Ontario muskrats with a longer open water season and access to *Typha* produce more litters and attain larger body sizes (Simpson and Boutin 1993). However there is no evidence that these temperate conditions improve overwinter survival (Simpson and Boutin 1993). Muskrat populations in northern regions have been observed to cycle (Elton and Nicholson 1942, Erb et al. 2000), likely in relation to mink predation (*Neovison vison*; Haydon et al. 2001, Estay et al. 2011).

Muskrats in the OCF occupy a landscape composed of approximately 2700 shallow thermokarst lakes surrounded by tall shrub, spruce forest, and tundra vegetation (Figure 1.4; Turner et al. 2014). Located in the northern Yukon Territory (68º 05’ N, 140º 05’ W), the OCF are a Ramsar wetland of international importance situated 200 km west of the Mackenzie Delta (Brock et al. 2007). The majority of lakes in the OCF are small, flat bottomed, and shallow (<2 m; Labrecque et al. 2009). Formerly a large glacial lake, the long axis of the Old Crow Basin is oriented northwest to southeast and the basin itself is surrounded by the British, Richardson, and Old Crow mountains. The basin is composed of two physiographic units: the Old Crow Flats and Old Crow River valley, the latter being 40-50 m lower than the former based on its continuous incision into the surrounding sediment following the last glacial maximum (Labrecque et al. 2009).

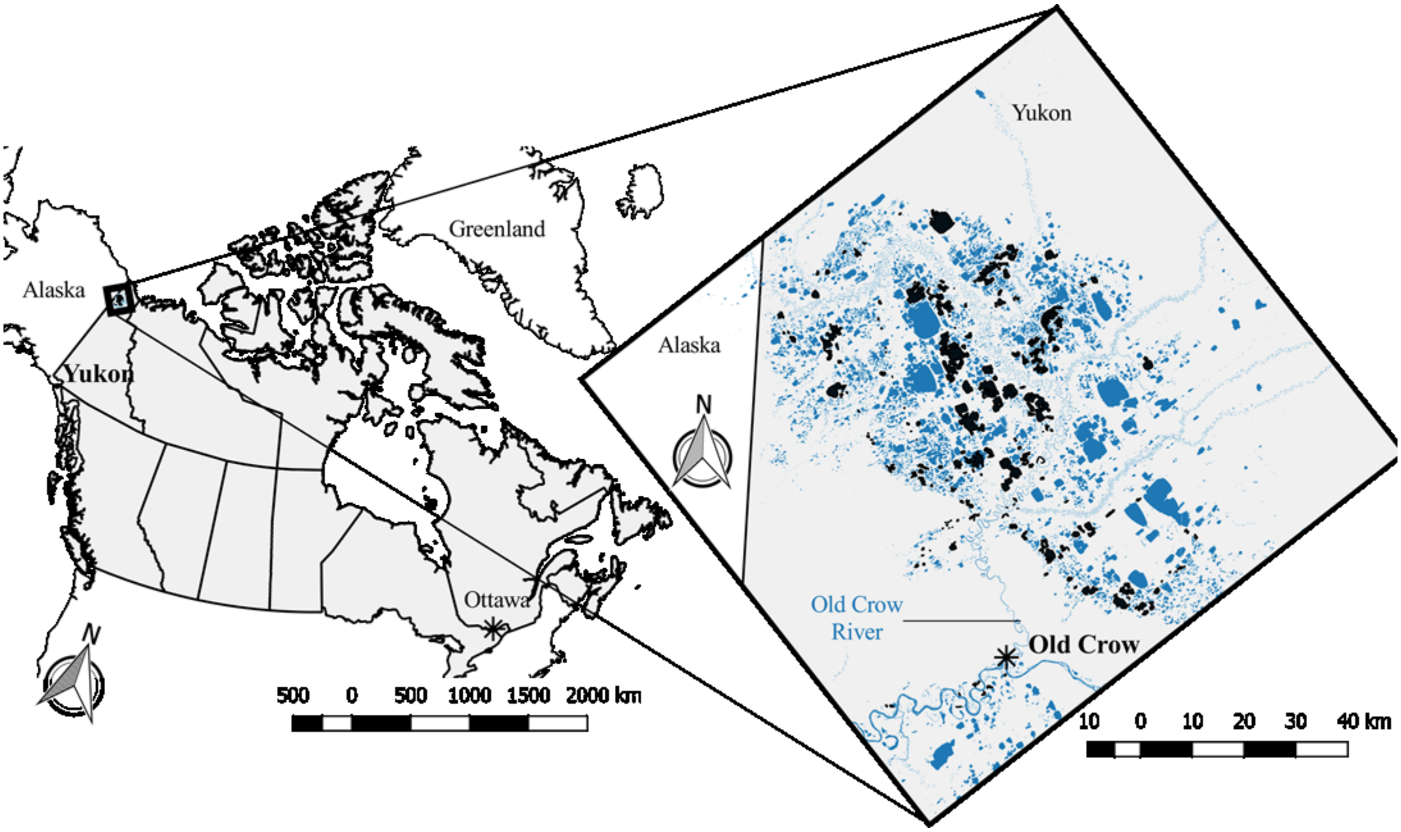


Figure 1-4: The location of the community of Old Crow and the Old Crow Flats (68º 05’ N, 140º 05’ W) in Yukon Territory, Canada. Our 219 study lakes are indicated with black grills.

These river and creek valleys contain the denser stands of terrestrial vegetation, including black and white spruce (*Picea mariana* and *P. glauca* respectively); while white birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*), and trembling aspen (*Populus tremuloides*) are common in successional stands near lakes; and shrub birch (*Betula glandulosa*) and willow (*Salix spp.*) tend to be found towards the tundra (Simpson et al. 1989). The ecotone between boreal forest and tundra crosses the Flats, with the forest transitioning to tundra from SW to NE (Turner et al. 2014). The growing season within the OCF is short due to its northern latitude, with an average of 72.6 ± 5.7 frost free days (Simpson and Boutin 1993). Lakes of the OCF are dominated by submergent vegetation, particularly *Potamogeton* spp. and *Myriophyllum* spp., and contain little emergent vegetation preferred by muskrats as forage and lodge building material, so here muskrats exclusively construct bank burrows rather than lodges (Ruttan 1974). The OCF represents a highly productive region of the traditional territory of the VGFN, and is used for harvesting caribou (*Rangifer tarandus*), waterfowl, mink (*Neovison vison*), marten (*Martes americana*), snowshoe hare (*Lepus americanus*), beaver (*Castor canadensis*), wolverine (*Gulo gulo*), and muskrat (VGFN and Smith 2009).

1.1.7 Locally-relevant case two: recreational ecosystem services of the Rideau Canal Skateway in Ottawa, Ontario

Ecosystem services can be categorized as provisioning, regulating, supporting, or cultural services. By definition, these must be linked to biophysical characteristics of their ecosystem while generating human benefits that contribute to well-being (Millennium Ecosystem Assessment 2005, Daniel et al. 2012). Cultural ecosystem services, or "non-material benefits people obtain from ecosystems", include aesthetic, spiritual, educational, and recreational benefits. These are considered intangible, subjective, and difficult to quantify, hindering their integration into ecosystem service-based research and decision-making (Millennium Ecosystem Assessment 2005, Chan et al. 2012, Daniel et al. 2012, Norton et al. 2012, Milcu et al. 2013). These difficulties are exacerbated when quantifying human benefit, which is often accomplished using monetary metrics (Daniel et al. 2012). As a result, cultural ecosystem services are underrepresented within ecosystem service research (Gee and Burkhard 2010, 2013), and climate change projections (Schröter et al. 2005). For example, Milcu *et al.* (2013) found that only 5 of 84 publications mentioning cultural ecosystem services focus exclusively upon them. Yet cultural ecosystem services are amongst the most recognizable and relatable ecosystem services that affect our daily lives (Chan et al. 2012, Daniel et al. 2012, Milcu et al. 2013).

Of particular interest is outdoor recreation. As a cultural ecosystem service, outdoor recreation is more amenable to quantification, and can help overcome the challenges of intangibility and incommensurability. Outdoor recreation provides employment, improves physical and emotional health, strengthens identities, and is widely recognized and appreciated (Millennium Ecosystem Assessment 2005, Tzoulas et al. 2007, Southwick et al. 2009, Bowler et al. 2010, Daniel et al. 2012, Kettunen et al. 2012). One example of outdoor recreation is winter ice skating. These activities feature prominently in numerous countries (Visser and Petersen 2009, Corder 2012, Damyanov et al. 2012), making them a recognizable and widely appreciated cultural ecosystem service. This is the case for the Rideau Canal Skateway in Ottawa, Canada (Figure 1-5); it is the world's largest outdoor skating surface, a UNESCO world heritage site, and a popular cultural ecosystem service for up to 1.3 million users annually. The Skateway provides a locally-relevant environmental indicator that is responsive to variations in climate specifically through its

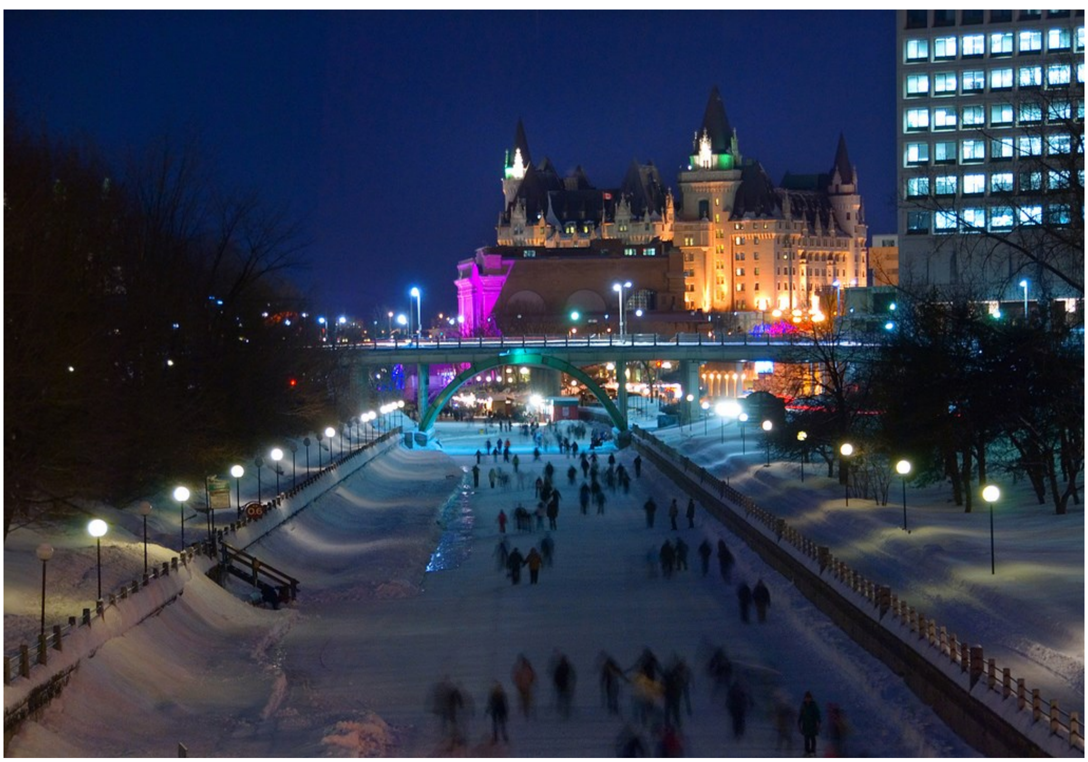


Figure 1-5: Photograph of the Rideau Canal Skateway looking towards the Château Laurier. Courtesy of the National Capital Commission – Commission de la capitale nationale.

opening date, closing date, season length, and number of users, characteristics that have been locally monitored since 1971.

1.2 Objectives and outline

My thesis objective is to develop tools for, and demonstrate insights from, participatory monitoring and locally-relevant environmental indicators. This begins with an examination of the potential of participatory environmental monitoring using portable digital data entry technologies (e.g. smartphones). Chapter 2 evaluates the advantages and disadvantages of the combination of this technology and participatory methods through both a quantitative meta-analysis and six case studies of monitoring programs distributed around the world, and has been published in Conservation Biology (Brammer et al. 2016). Following this methodological analysis, Chapters 3, 4, and 5 examine the dynamics of the two locally-relevant environmental indicators described above: muskrat population dynamics for the Vuntut Gwich'in of Old Crow, Yukon (Chapters 3 & 4), and outdoor recreation for the residents of Ottawa, Ontario (Chapter 5). Chapter 3 quantifies a rapid form of environmental change in the Old Crow Flats, advancing ice phenology, and examines how this change could influence muskrat abundance and body condition using a combination of remote sensing, aerial surveys, field surveys, and local ecological knowledge. Chapter 3 has been prepared for submission to Ecological Applications. Chapter 4 builds on this analysis and documents the first recorded instance of a traveling wave of abundance in muskrats, while demonstrating the importance of landscape characteristics and dispersal in driving this emergent pattern. Chapter 4 has been prepared for submission to Ecological Monographs. Chapter 5 examines the importance of ice phenology to another culturally-relevant indicator: outdoor recreation at the Rideau Canal Skateway in Ottawa. This chapter quantifies the availability of this service, links its availability and use to weather, and projects these over the coming century. Chapter 5 has been published in Nature Climate Change (Brammer et al. 2014). Chapter 6 summarizes the previous chapters and their lessons for other long term environmental monitoring programs.

2 The role of digital data entry in participatory environmental monitoring

2.1 Abstract

Many argue that monitoring conducted exclusively by scientists is insufficient to address ongoing environmental challenges. One solution entails the use of mobile digital devices in participatory monitoring (PM) programs. But how digital data entry affects programs with varying levels of stakeholder participation, from non-scientists collecting field data to them administering every step of a monitoring program, remains unclear. We reviewed the successes, in terms of management interventions and sustainability, of 107 monitoring programs described in the literature (hereafter programs) and compared these with case studies from our PM experiences in Australia, Canada, Ethiopia, Ghana, Greenland, and Vietnam (hereafter cases). Our literature review found participatory programs were less likely to use digital devices, and 2 of our 3 more participatory cases were also slow to adopt digital data entry. Programs that were participatory and used digital devices were more likely to report management actions, which was consistent with cases in Ethiopia, Greenland, and Australia. Programs engaging volunteers were more frequently reported as ongoing, but those involving digital data entry were less often sustained when data collectors were volunteers. For the Vietnamese and Canadian cases, sustainability was undermined by a mismatch in stakeholder objectives. In the Ghanaian case, complex field protocols diminished monitoring sustainability. Innovative technologies attract interest, but the foundation of effective participatory adaptive monitoring depends more on collaboratively defined questions, objectives, conceptual models, and monitoring approaches. When this foundation is built through effective partnerships, digital data entry can enable the collection of more data of higher quality. Without

this foundation, or when implemented ineffectively or unnecessarily, digital data entry can be an additional expense that distracts from core monitoring objectives and undermines project sustainability. The appropriate role of digital data entry in PM likely depends more on the context in which it is used and less on the technology itself.

2.2 Introduction

It is widely acknowledged that more effective environmental monitoring is needed to support management in the face of rapid global change (Lindenmayer and Likens 2009). However many have argued that, based on currently available resources, monitoring executed exclusively by professional scientists is insufficient to address these ongoing challenges (Danielsen et al. 2005, Dickinson et al. 2010). Thus various forms of participatory monitoring (PM) are being used to increase the extent and resolution of monitoring data. The degree to which PM engages stakeholders including resource users, local residents, Indigenous peoples, and interested citizens, varies from participants solely collecting data to participants leading monitoring design, implementation, and subsequent management interventions. Danielsen et al. (2009, 2014*a*) identified a spectrum of participation in monitoring, including:

- *Type A autonomous local monitoring*, no formal affiliations with professional scientists;
- *Type B collaborative monitoring with local data interpretation*, where local stakeholders undertake data collection, interpretation, or analysis, and management decision making, although external scientists may provide advice and training;
- *Type C collaborative monitoring with external data interpretation*, local stakeholders are involved only in data collection and decision making based on monitoring results;

- *Type D externally driven monitoring with local data collectors*, local stakeholders are involved only in data collection (commonly called citizen science); and
- *Type E scientist executed monitoring*, external scientists manage all aspects of the project and local stakeholders are not involved.

For much of recorded history, knowledge generation has been the domain of non-professionals (Miller-Rushing et al. 2012). However, over time studying the environment has become the sphere of an increasingly professional and exclusive scientific community (Miller-Rushing et al. 2012, Hård and Jamison 2013). The result was a field that privileged science and excluded other ways of understanding the environment, such as local ecological knowledge (LEK; Berkes 2012). However, interest is increasing in multiple knowledge systems and in participatory approaches to science, particularly in environmental monitoring (Raymond et al. 2010, Tengö et al. 2014). Concurrently the advent of mobile devices (including: smartphones, personal digital assistants [PDAs], tablets, digital cameras, data loggers, and Global Positioning System (GPS) units) could reinforce this trend toward environmental sciences that are more participatory and inclusive (Dickinson et al. 2012, Newman et al. 2012). In particular, monitoring programs engaging LEK holders could benefit from digital data entry. Ensuring that these benefits are realized by all stakeholders will likely depend on the program's extent of participation (e.g., Types A - D; Danielsen et al. 2014*a*).

Currently, monitoring that is externally driven, with participants collecting data (e.g., type D, most citizen science), is the most frequently documented form of PM (Theobald et al. 2015). This form of PM should benefit from digital data entry because it can increase the potential pool of participants; simplify data collection, transcription, and management; offer immediate feedback to data collectors; improve data diversity (e.g., photos, videos, GPS) and quality; and facilitate data dissemination (Newman et al. 2012, Teacher et al. 2013, Kim 2014). For many the outlook for digital data entry in PM is positive when used to support type D citizen science (Newman et al. 2012, Bonney et al. 2014).

Less clear is how digital data entry contributes to monitoring projects that are more participatory (e.g., types A-C; Johnson et al. 2015), particularly those seeking to engage LEK holders. Among these projects, many currently rely on limited technology (e.g., pen and paper; Stuart-Hill et al. 2005, Ansell and Koenig 2011, but see Gearheard et al. 2011, Riseth et al. 2011, Parry and Peres 2015). This could reflect a lack of access to newer digital technologies, but it may also reflect common concerns such as their high costs, training requirements, and complexity compared to paper-based protocols (Gearheard et al. 2011, Danielsen et al. 2014, Kim 2014) and problems associated with monitoring programs that are highly participatory (e.g., data privacy, limited technical capacities, incompatibilities of LEK and digital data formats; Ellis 2005, Fernandez-Gimenez et al. 2006, Bonny and Berkes 2008).

Given the commitment, in terms of resources and time, necessary for programs to adopt digital tools for data collection, there is a need to explore how this technology has benefited, or detracted from, monitoring programs across the PM spectrum. Here we reviewed monitoring successes, in terms of management actions and project sustainability, of a sample of PM programs described in the literature (hereafter programs) to determine how success was related to project characteristics such as stakeholder participation and use of digital data entry. We compared this general analysis with a detailed examination of multiple case studies based on our PM experiences with Indigenous communities in Australia, Canada, Ethiopia, Ghana, Greenland, and Vietnam (hereafter cases). These parallel analyses allowed for a comparison of broad trends and specific, contextual experiences to determine how digital devices have, and have not, contributed to the success of PM.

2.3 Methods

2.3.1 Meta-analysis

We expanded on Danielsen et al.'s review of 107 environmental monitoring programs (2014*a*) extracted from 3,454 monitoring publications from 1989 to 2012. The terms *monitoring* and *conservation* were queried in BIOSIS Previews 2004-2012, Biological Abstracts 1990-2000, and Biological Abstracts, Reports, Reviews, and Meetings 1989-2003. Publications were selected if they described monitoring species, populations, habitats, ecosystems, or resource use. We evaluated each publication for one monitoring method, use of digital devices for data collection, and two proxies of monitoring success, (1) did monitoring lead to management action, and (2) was monitoring ongoing at the time of publication (indicator of project sustainability).

To explain these outcomes we used 9 contextual elements, four of which were coded by Danielsen et al. (2014a) and the remainder by J.R.B., grouped into 4 categories of explanatory variables: scale and tenure (spatial extent [1-4,999 ha, 5,000 – 9,999 ha, etc.] and local tenure system [national park, locally managed protected area, unprotected area]); cost (funding source [entirely internal, village level; >50% internal; etc.] and amount of funding [in U.S. dollars per hectare per year] and payment of field workers [yes or no]); monitoring duration and diversity (log-transformed years monitored and number of taxonomic groups monitored [single taxon vs. multiple taxa]); public participation (level of participation [types A-E] and use of digital devices for data collection relative to whether monitoring led to management action and was ongoing; Table 2.1). For models of each outcome variable, we omitted publications if any variables were missing values (Table 2.1). We ranked how these categories explained each outcome using logistic models and Akaike's corrected information criterion (AIC_c; Burnham & Anderson 2002). We based inferences on the top model if no competing models were within 2 ΔAICc, and on estimates from the top two models otherwise. Uncertainty was presented as 95% CIs.

Many PM programs are unpublished or their characteristics go unreported. Our sample likely underrepresents smaller and younger programs, and as a result the recent emergence of digital data entry. In addition, management actions and project sustainability may not be consistently reported in academic literature. Due to our small sample, we did not differentiate between the effects of different forms of digital data entry (i.e., smartphones, PDAs, tablets, digital cameras, data loggers, GPS units) and omitted contextual elements of potential importance (e.g., level of training or support provided, education or socioeconomic status of participants). Nonetheless, we believe our quantitative analysis provides an informative snapshot of the environmental monitoring literature with which to compare our multiple cases.

2.3.2 Case studies

We examined 6 PM cases from 6 different nations that involved monitoring projects across the PM spectrum (Figure 2-1). These were selected based on our experiences through our respective research and capacity-building programs. We categorized 3 cases as type B participation: Greenland, community-based monitoring of wildlife harvests and natural resources among local communities in Disko Bugt and adjacent areas (Danielsen et al. 2014); Canada, consultations regarding, and trials of, wildlife- and forestry-monitoring protocols conducted with digital data entry by Inuit, Gwich'in, Cree, and Anicinapek communities; and Australia, natural

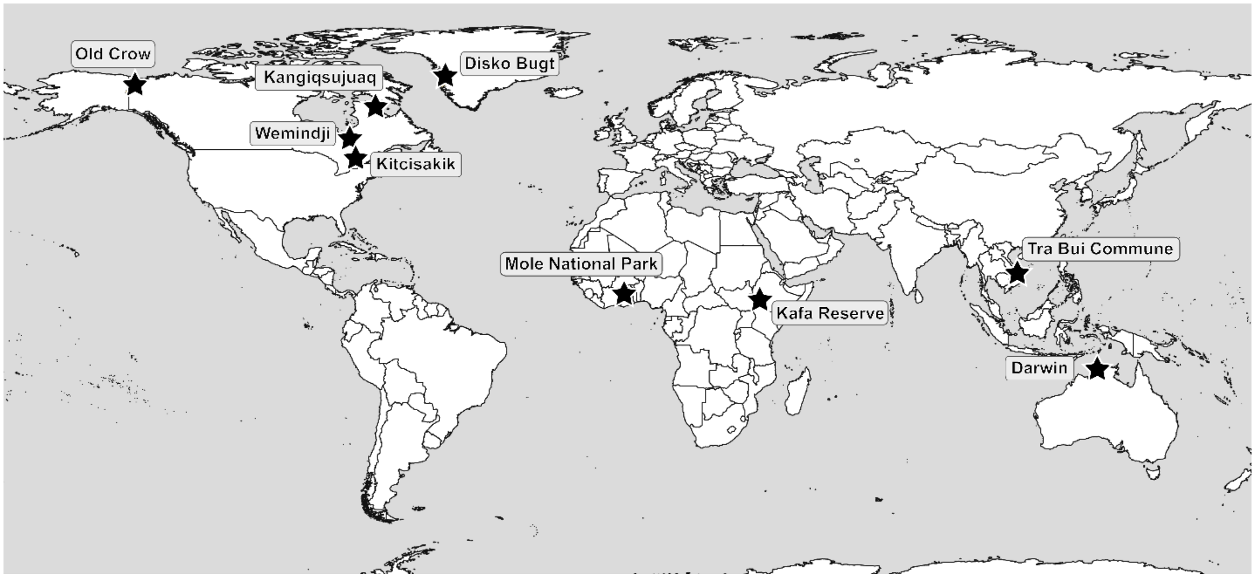


Figure 2-1: Location of 6 case studies. Cases from Australia and Greenland had participants from multiple communities but are represented with just one.

resource monitoring and management (e.g., biodiversity, fire, cultural sites, wildlife, invasive plants and animals, marine debris, tourists) by numerous Indigenous communities in Northern Australia (Kennett et al. 2010). We classified 1 case as type C - Vietnam, forestry monitoring by the Ca Dong community in the Tra Bui commune (Pratihast et al. 2013) - and 2 cases as type D: Ethiopia, forestry monitoring in the Kafa Biosphere Reserve of southwestern Ethiopia by local community members (Pratihast et al. 2014), and Ghana, wildlife monitoring by local indigenous community members employed by Mole National Park (Burton 2012). Detailed descriptions of each program can be found in the Supplementary material.

These programs were established independently with no universally applied protocol. They represent a heterogeneous set of national contexts where digital data entry was evaluated for PM. Each program used various interaction strategies to solicit participant feedback on the strengths and weaknesses of digital data entry, including: participant observations, conversations, public presentations, community meetings, field trials, and interviews (Brunet et al. 2014). Because participation in the assessment was voluntary, sampling of local participants was purposive (Sue and Ritter 2012). We cannot generalize our findings beyond these cases (Yin 2014). Nevertheless, we saw value in documenting these as a heterogeneous sample of international PM projects because they highlight a variety of contexts within which these programs evolve. We believe this strategy supported both the internal and the external validity of our multiple case study (Boeije 2002, Eisenhardt and Graebner 2007). Comparing and contrasting this qualitative approach with our quantitative meta-analysis allowed us to maximize construct validity and test the repeatability of our findings (Stake 2005).

2.4 Results

2.4.1 Use of digital data entry in participatory monitoring

Our meta-analysis found digital devices were more frequently used in less participatory, scientist-driven programs (i.e., Types C-E; model coefficient $\beta = -0.49$ [-0.94, -0.04]; $p = 0.03$; n = 88; Figure 2-2; model selection tables in Supplementary material). Similarly, the slowest adoption of digital data entry occurred in some of our most participatory cases (type B). In the Greenlandic communities, harvesters reported wildlife sightings and harvests at meetings of their Natural Resource Committees (NRC). At these quarterly meetings, individual sightings were compiled into summary reports, results were compared from the same area and season in previous years, interpreted by community members, and management actions were discussed. Participants had the option of reporting observations verbally, on paper data sheets, or with smartphones or body cameras. The majority of the 33 participants favoured oral reporting. The proportion of observations documented digitally increased over time, however, particularly as the number of

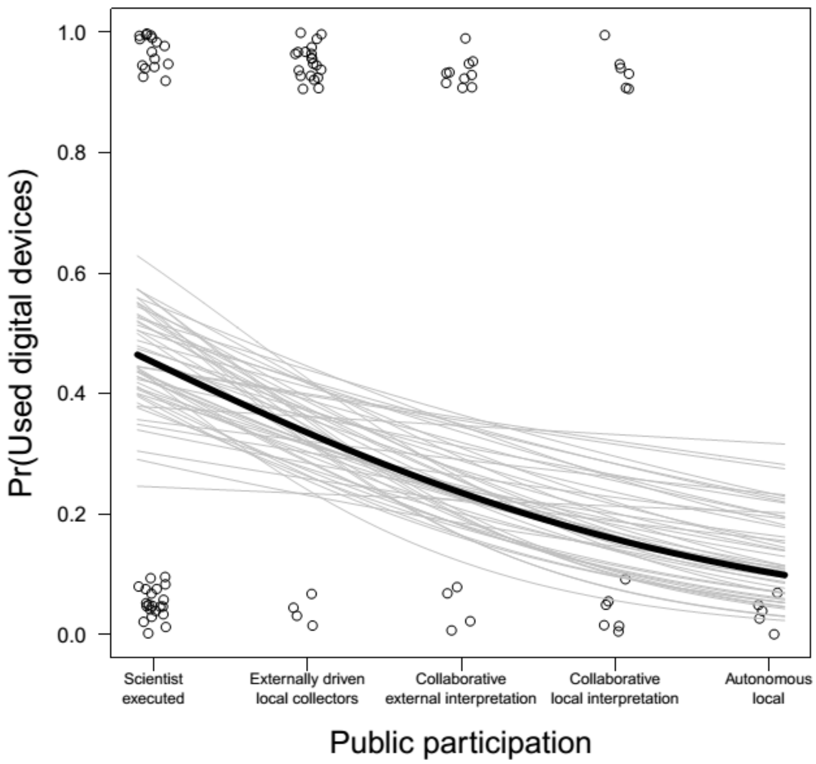


Figure 2-2: The probability (Pr) of a monitoring program using digital devices as a function of the degree of public participation in the program (participation levels from Danielsen et al.[2009]). The thick line represents the mean predicted probability from the participation model; the gray lines 50 simulations of possible models based on estimated model coefficients and their standard errors (Gelman and Hill 2007). Simulations represent the range of possible outcomes that agree with model estimates within a 95% CI. Data points (n = 88) were jittered to improve density visualization.

younger participants increases. Participants suggested digital data entry could contribute to engaging more youth in environmental monitoring and activities on the land. Two Canadian participants said: "[This digital device] is not useful for me because I know my territory. But for our youth, it is useful when a young hunter [is] lost" (Kitcisakik elder) and "[i]t was easy to fire up the [digital device]…" for recording stories (Old Crow youth).

Still, many of the Canadian participants found digital devices complicated to operate in the field and slow to record data, and they had difficulty viewing the screen, using the keyboard, reviewing data once entered, operating the device while cleaning fish, and interpreting the unilingual English interface: “[This digital device] is not so simple to use”” (Kitcisakik professional) and “The GPS was not able to record a place while in a moving boat on water, no matter how slow we were moving” (Old Crow participant).

This reticence was not universal among type B cases. The Indigenous Tracker (I-Tracker) program has successfully coordinated PM frameworks with a customised CyberTracker digital data-entry platform in multiple Indigenous communities in northern Australia (previously summarized in Commonwealth of Australia 2009, Kennett et al. 2010, NAILSMA 2014). Run by the North Australian Indigenous Land and Sea Management Alliance Ltd (NAILSMA), the I-Tracker program engaged Indigenous people, LEK holders, and professional Indigenous rangers in land and sea management and monitoring activities, planning, and decision making in their communities. A most-significant-change evaluation of I-Tracker, involving 66 semi-structured interviews with participants and scientists (Bessen 2013), showed that I-Tracker’s digital tools facilitated the reporting of monitoring data and the transfer of LEK between elders and rangers. However, it also highlighted that one key to program success was the provision of ongoing training and technical support for rangers and the highly participatory approach used to develop monitoring protocols and the digital data-entry platform. One ranger said, “…NAILSMA staff have been ... [b]ringing a lot more training and a lot more I-Trackers. What suits us and what doesn’t suit us and we talk about it.” Overall this case highlighted the importance of digital tools that are adaptable to local settings and changing community needs over time.

2.4.2 Digital data entry, participatory monitoring, and management actions

In our meta-analysis programs were more likely to report management actions if they were more participatory ($\beta = 0.6$ [0.1, 1.1], $p = 0.03$, n = 88) and used digital devices ($\beta = 1.5$ [0.2, 2.8], $p = 0.03$; n = 88; Figure 2-3). Management action was best explained by combining the top two categories of explanatory variables (public participation and duration and diversity). This maintained the positive association between management actions, and participation and digital devices. In our type D case in the Kafa Biosphere Reserve of Ethiopia, the Bureau of Agriculture and Rural Development (Pratihast et al. 2014) hired 30 local community members to document forest change (alongside other responsibilities). Participants used two protocols to document forest degradation, deforestation, and reforestation: paper data sheets and handheld GPS; and smartphones with integrated GPS, camera, and an Open Data Kit (ODK) interface. Participants reported that digital devices simplified data entry in the field and facilitated rapid communication of monitoring results with other community members, particularly when using social media. For example, Facebook reporting of illegal firewood extraction has drawn the attention of enforcement officials and led to the revocation of forest use certification.

The type B cases from Greenland and Australia also showed a relationship between participation and management actions. At the NRC meetings in Greenland, management decisions (e.g., change in quota, hunting season, gear restriction, etc.) were discussed in response to monitoring results (Danielsen et al. 2014). Any management actions recommended by the NRCs were presented to the local government authority. At the time of publication, this NRC-based monitoring system contributed to 14 management recommendations, including: setting quotas (2 proposals), changing hunting seasons (5), identifying research needs (3), altering fishery bylaws (2), and others (2). The local municipal authority responded to 11 of these proposals. In these cases, there was no detectable effect of digital reporting on management activities, but in the

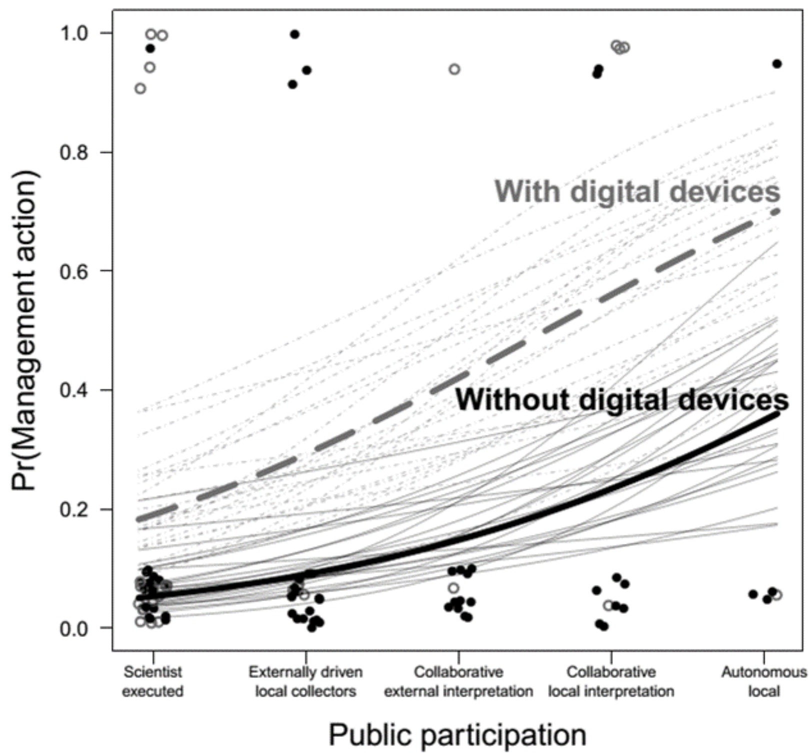


Figure 2-3: The probability (Pr) of a publication describing specific management actions that resulted from monitoring as a function of the level of public participation (participation levels from Danielsen et al.[2009]) and the use of digital data collection. The thick lines represent the predicted probability derived from the top model; thinner lines represent 50 simulations of possible models based on estimated model coefficients and their standard errors (Gelman and Hill 2007). Programs using digital devices were represented with solid circles and lines; projects operating without digital devices were represented with open circles and dashed lines. Data points (n = 88) were jittered to improve density visualization.

Australian case the benefits of digital data entry were more apparent. I-Tracker began as a program that supported monitoring of marine and coastal management issues, then expanded to support over 30 ranger groups to monitor and manage a wide range of natural and cultural resources belonging to their communities. Digital data entry improved the capacity of rangers to record and report the results of their diverse surveillance and management activities, for example enabling them to negotiate fee-for-service contracts with Australian Customs and Northern Territory Fisheries (NAILSMA 2014) and implement locally driven scientific research (e.g. Jackson et al. 2015).

2.4.3 Digital data entry, participatory monitoring, and project sustainability

In our meta-analysis program sustainability was best explained by combining the public participation and cost explanatory variables, which highlighted how more participatory programs, particularly those that engaged volunteer data collectors, were more frequently sustained (β = [0.3, 3.7], p = 0.01; n = 84). Digital devices were negatively associated with project sustainability when data collectors were volunteers (β = [-5.6, -2.0]; n = 84) but not when they were paid (β = [-0.8, 1.0]; n = 84; Figure 2-4). Digital data entry appeared not to enhance program sustainability. In the Vietnamese case, sustainability was entirely unrelated to the degree of participation or the data-entry protocol. Community members contributed to the design of a forest monitoring protocol using digital data entry on XLS forms and ODK. This approach had lower monitoring costs relative to professionally implemented alternatives and provided employment for community members. Nonetheless, the program was not sustained because the local Ca Dong community, an ethnic minority, were displaced from their traditional territory due to the construction of the Sông Tranh 2 hydroelectric dam and this fostered distrust between participants and the national government. Participants, including the Tra Bui commune president, reported an interest in protecting the integrity of their forests, but monitoring objectives did not coincide with their economic priorities and increased financial support was required to mitigate lost farming opportunities.

In the Canadian cases, community objectives also appeared not to coincide with those of PM, particularly due to the use of digital data entry. In most communities, suspicion was expressed regarding PM and the use of digital data entry and how these could facilitate the unauthorized access and use of LEK. It was repeatedly expressed that traditional methods of monitoring were sufficient to address local needs. For example, participants said, ”Inuit know their land and do not need this technology” [Kangiqsujuaq] and, “The one thing…I did not do [or] like is the GPS of

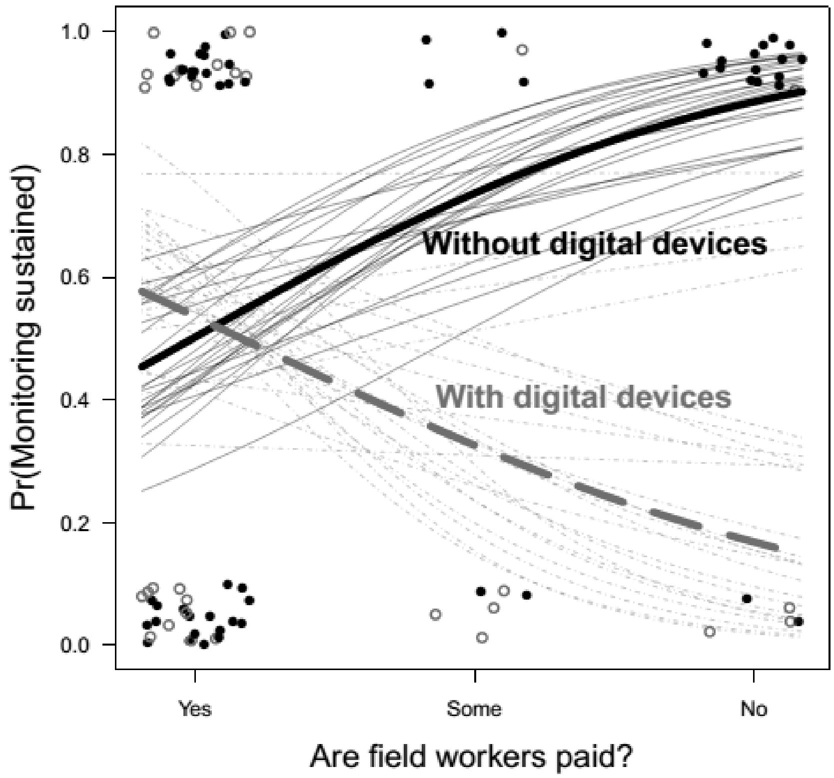


Figure 2-4: The probability (Pr) of a publication explicitly stating that its monitoring program is ongoing as a function of whether field workers were paid and the use of digital data collection. Thicker lines represent the predicted probability derived from the combined public participation and duration and complexity model with all other predictors at their means. Thinner lines represent 50 simulations of possible models based on estimated model coefficients and their standard errors (Gelman and Hill 2007). Programs using digital devices were represented with solid circles and lines; projects operating without digital devices were represented with open circles and dashed lines. Data points (*n* = 84) were jittered to improve density visualization).

the area.…others might come around" [Wemindji]. As a result of these suspicions and a lack of collaboratively agreed-upon objectives, these pilot projects had not led to sustained PM.

While a dearth of broadly accepted monitoring objectives detracted from PM in some contexts, in others the complexity of field protocols may have diminished monitoring sustainability. In Mole National Park (MNP), Ghana, sightings of larger mammals have been recorded since the late 1960s during enforcement patrols of local wildlife guards (Burton 2012). In this type D case, indigenous wildlife guards with little formal education or training collect data for use by park managers and external scientists (Danielsen et al. 2009). In 2006, handheld GPS units were integrated into the monitoring protocol to supplement wildlife sightings with digital records of locations and patrol effort. Simultaneously, the effectiveness of this system was compared with results from a survey with digital camera traps; portions of the survey were implemented by local wildlife guards (Burton 2012). While patrol surveys had poor detectability of some species, low repeatability of observations, and uneven sampling effort, they were financially and organizationally more sustainable than the camera-trap surveys, which are no longer being operated by wildlife guards in the park. Both GPS and camera traps increased equipment costs, upkeep costs (e.g., batteries, memory cards, unit replacement), and training and technical support requirements, but cameras did so to a greater degree. When deployed properly, camera traps were more capable of reliably detecting mammals, particularly small, nocturnal, carnivorous ones. But wildlife guards had greater success using GPS in the field, and overall the cameras' greater complexity, costs, and technical requirements made them less sustainable in this case. The use of GPSs required less training and oversight, cost less than camera traps, and enabled the quantification of patrol effort for standardizing observations. In this case the GPS protocol, not the camera traps, was sustained due to its greater operational simplicity.

Table 2.1: Outcome and predictor variables, including predictor variable categories, used in logistic models based on 107 environmental monitoring programs described in the literature.

Variable	Program characteristics
Method	
use of digital device	Was a digital device (e.g., GPS, still camera, video camera, smartphone, PDA, data logger, handheld computer, or radio transmitter) used for field data collection? 1. yes 2. no
Outcome	
management action	Has the monitoring project explicitly led to specific management actions? 1. yes 2. no
sustainability	Was monitoring ongoing at the time of publication? 1. yes 2. no
Predictor	
category 1 scale and tenure	
spatial extent	Total size of area monitored ≥100,000 ha 50,000-99,000 ha 10,000-49,999 ha 5,000-9,999 ha 1-4,999 ha
land-tenure system	Dominant land-tenure system of area monitored protected area under government authority protected area managed (partially or fully) by the local communities outside protected areas
category 2 cost	
source of funding	Who paid for monitoring? entirely external (national or international) >50% external >50% internal (village or district level) entirely internal
paid field workers	Were field workers paid? yes some no
monitoring cost	How much does the monitoring program cost in US$/ha/year?
category 3 duration and diversity	
project duration	How long has the project been monitoring in years?
taxonomic diversity	Does the scheme monitor >1 taxonomic group or resource 1 taxonomic group or resource (e.g., fish)
category 4 public participation	
level of public participation	What category best describes the projects level of public participation? scientist-executed monitoring externally driven monitoring with local data collectors collaborative monitoring with external data interpretation collaborative monitoring with local data interpretation autonomous local monitoring
use of digital devices	Was a digital device used for field data collection? yes no

2.5 Discussion

Our meta-analysis and case studies suggested that the role of digital data entry in PM depends strongly on the structure and capacity of the monitoring program and the socioecological context in which it occurs. We found programs that were more participatory used digital data entry less frequently; similarly, Wiggins and Crowston found programs focused on specific actions (e.g. opposing development of an electrical generating station) used digital tools less than programs investigating a research question (2011). More participatory programs may have less capacity for, or interest in, investing in and supporting technological infrastructure (Olson et al. 2014, Will et al. 2014); and fewer participatory projects may occur in more affluent (e.g. North American, European) societies with relatively easier access to digital technologies. When digital data entry was used, we found ongoing, staff-intensive, participant training and support were important to sustain its use and evolution. In both our literature review and our cases, stakeholder participation and digital data entry were positively associated with management actions, but their relationships with monitoring sustainability were less clear. Participatory monitoring frequently engages local decision-makers, and has been found to lead to more rapid management interventions at this level (Danielsen et al. 2010). The association of digital data entry and management actions could result from reduced delays between recording observations and reporting results, or it could improve the quality of results making them more useful and compelling for decision makers.

We propose that the advantages and disadvantages of digital data entry in PM can be best understood using Lindenmayer and Likens' (2009) adaptive-monitoring framework. This general framework states that environmental monitoring is most effective when it incorporates a number of features, including explicit and evolving questions, a clear conceptual model of the ecosystem, statistical design of the sampling protocol, and strong partnerships with policy makers and resource managers (Lindenmayer and Likens 2010*c*). These partnerships are important to ensure that monitoring "passes the test of management relevance" (Lindenmayer and Likens 2010*c*). We propose that, to conduct adaptive monitoring that is participatory, these partnerships must be expanded to include stakeholders like local residents, resource users, and Indigenous peoples (Brunet et al. 2016). The role these stakeholders play in the different steps of an adaptive monitoring program will vary (Figure 2-5), but their inclusion should ensure that monitoring programs are relevant to scientists, policy makers, and resource users. In this participatory adaptive-monitoring framework, technology is not central to the process of monitoring. Implemented effectively, technologies like digital data entry allow collection of more data of higher quality by reducing data-entry errors, transcription errors, and processing time; improving the accuracy of location data; and, most importantly, quantifying survey effort (e.g., Inman-Narahari et al. 2010; Olson et al. 2014; Will et al. 2014;). These data are subsequently more useful for analysis, interpretation, and decision making. Implemented ineffectively, or in projects where it is unnecessary, digital data entry can be an additional expense whose costs and upkeep distract from core monitoring objectives and undermine a project's long-term sustainability (Lindenmayer and Likens 2010*c*). Implementing innovative technologies is not a determinant of effective environmental monitoring; rather, effective monitoring depends more on collaboratively defined questions and objectives, conceptual models, and monitoring approaches determined through effective partnerships between relevant stakeholders. Digital data entry can frequently improve programs built on these strong foundations, but it is no remedy if these foundations are weak.

In conclusion, our meta- and multiple case study analyses suggested both stakeholder participation and digital data entry can contribute to environmental monitoring success by linking results and management actions. However digital data entry can be a detriment to PM sustainability

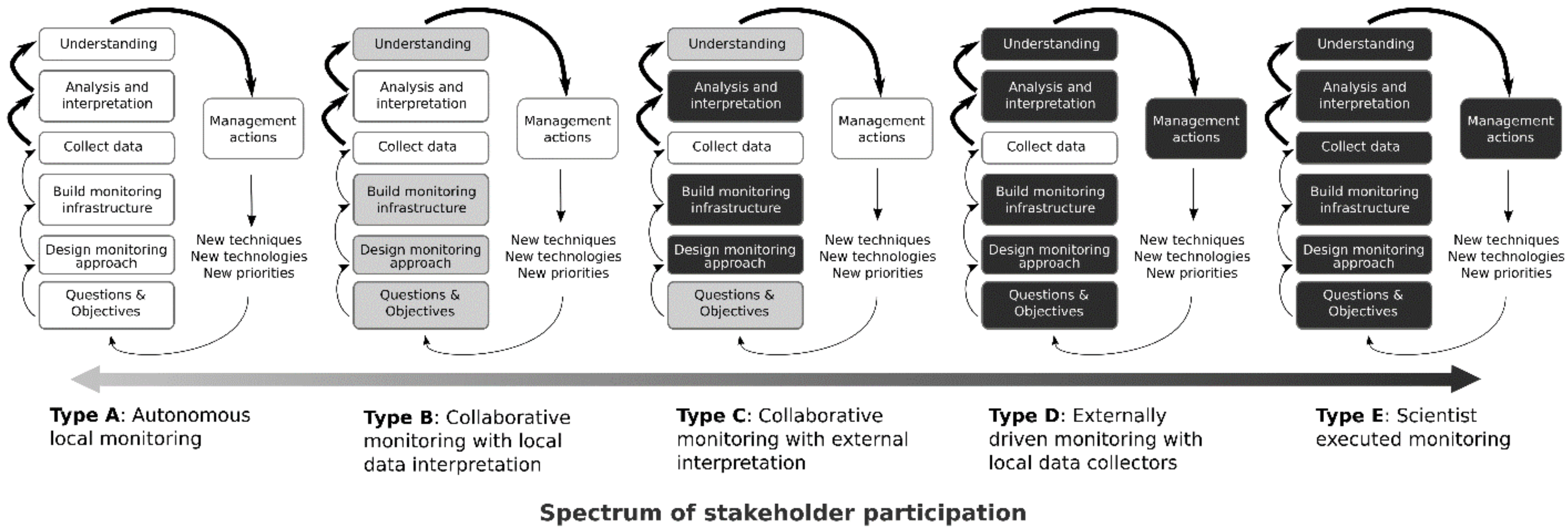


Figure 2-5: The participatory adaptive monitoring framework, including a spectrum of stakeholder participation in monitoring approaches (Danielsen et al. 2009, 2014*a*) mapped onto a modified adaptive-monitoring framework (Lindenmayer and Likens 2009). Contributions by government and university scientists external to the local community (e.g. government and university scientists) are indicated by black, local community contributions are in white, and a combination of the two in grey. Bold arrows represent instances where digital data entry may facilitate the monitoring process.

depending on the context and structure of the program. If it engages stakeholders in its design, a PM program can benefit from the advantages of digital data entry (e.g., high data quality). Yet even if the program is amenable, digital data entry may not be necessary. Knowing program objectives, structure, and capacity allows for an explicit weighing of the two-sided implications of digital data entry. For example, technology can engage youth and other technophiles but may discourage technophobes. Whether digital data entry simplifies fieldwork depends on the user, protocol, interface, device, and environmental conditions (e.g., cold, wet, etc.). Digital data can be more easily shared, but it can also be more difficult to keep private, a particular concern when data are sensitive. Digital data entry can increase program capacity to record, standardize, and share observations, but it can also increase the dependency of PM programs on outside technology, expertise, and support (Danielsen et al. 2005, Constantino and Carlos 2012, Funder et al. 2013). Thus, whether digital data entry contributes or detracts from PM depends on factors related to the technology, the organizational structure of the monitoring program, and the socioecological context in which it occurs. In most cases, the appropriate role of digital data entry in PM depends more on the context in which it is used and less on the technology itself.

2.6 Linking statement

In this chapter I examined the potential of stakeholder participation and new digital technologies to contribute to the success of environmental monitoring programs based on experiences from a broad set of coauthors and literature. I found participatory programs were more frequently associated with management interventions, and that this relationship was strengthened when using digital data entry. I also found that participatory programs were more sustainable when they were built on a foundation of effective partnerships and collaboratively defined questions, objectives, conceptual models, and monitoring approaches. The use of digital data entry appeared to contribute little to the sustainability of monitoring programs. I applied these insights in the design of our collaborative muskrat monitoring program in Old Crow, Yukon, (Chapters 3 & 4) which is based on locally defined research objectives, hypotheses derived from local ecological knowledge, field survey protocols requiring cooperation with Vuntut trappers, and external data interpretation. While I piloted a digital data entry system for trappers to record field survey data, I placed greater emphasis on ensuring the monitoring program is based on collaborative questions, conceptual models, and methods. As a result, Chapter 3 describes the results of monitoring a locally identified form of environmental change, ice phenology, and its potential effect on Old Crow Flats muskrats.

3 Local knowledge and environmental monitoring of ice phenology and muskrat ecology in the Old Crow Flats, Yukon

3.1 Abstract

The western Canadian Arctic is changing: increasing thaw slumps, lake drainages, overflows, shrub growth, and shifting ice phenologies have been observed by the Vuntut Gwich'in, and have led to a community-researcher partnership to determine how change will affect species of cultural importance like muskrats (*Ondatra zibethicus*). We established the baseline periodicity of muskrat populations in the Old Crow Flats (OCF) by interpreting a > 90 year time series of fur returns, a 10 year time series of aerial pushup surveys, and local ecological knowledge (LEK) interviews. We documented shifts in 31 years of freeze-up and break-up dates using Landsat imagery and related these to muskrat density and body condition. We interpreted the LEK of Vuntut trappers to develop hypotheses explaining muskrat density and body condition as a function of habitat characteristics. We found periodicity at 23-34 and 13.3-13.8 year intervals in fur returns, and at 9 years in pushup densities. LEK holders identified local cyclicity that ranged from 1.5 to 11 years, while our 210 lake time series varied from 2 to 8 years. The 1985-2015 Landsat record saw earlier ice break-up (0.20 days/year), later freeze-up (0.07 days/year), and an increase in open water season duration (0.26 days/year). Multi-model comparison suggested open water duration and lake depth were important predictors of muskrat density and body condition with 8 more ice free days associated with a 60% decline in predicted muskrat densities. Both model comparison and LEK suggested that evaporation influences the suitability of OCF lakes for muskrats. While we found little evidence of a long term muskrat decline, we found evidence that the length of the open water season is both an important predictor of muskrat abundance and advancing in the OCF.

We believe this is the first attempt to combine local knowledge, multiple abundance time series, and remote sensing data to examine the impact of environmental change on a traditionally important population of wildlife. Considering rates of environmental change in Arctic wetlands, all available knowledge should be integrated to understand how this change affects ecosystem components of importance to Arctic residents.

3.2 Introduction

The western Canadian Arctic has been one of the fastest warming regions of the world, a pattern that has been consistently reported by its residents (ACIA 2004, Gordon et al. 2007, IPCC 2014). Here annual average temperatures have increased 2-3 ºC between 1954 and 2003 (ACIA 2004). In the community of Old Crow, Yukon, Canada, residents of the Vuntut Gwitchin First Nation (VGFN) have expressed growing concerns regarding the effects of this warming on their traditional territory (Gordon et al. 2008). As a result they initiated the International Polar Year research program *Yeendoo Nanh Nakhweenjit K'atr'ahanahtyaa* ('Taking care of the land for the future'; hereafter YNNK). This community-researcher partnership incorporated multiple locally defined objectives including the evaluation of climate change impacts on the biological and physical environment of the VGFN with a particular focus on traditional foods (Wolfe et al. 2011).

Muskrats (*Ondatra zibethicus*) were identified as a species of concern for the VGFN due to their cultural importance as a source of both fur and food. Historically the Vuntut Gwich'in would move in the spring to trap muskrats in the Old Crow Flats (OCF; VGFN and Smith 2009), a 5,600 km^2 wetland of approximately 2,700 shallow lakes (< 2m; Labrecque et al. 2009), to trap muskrats (VGFN and Smith 2009). This territory, while at the northern edge of muskrats' distribution, is highly productive muskrat habitat and VGFN trappers have traded more than 50,000 muskrat pelts following a single trapping season (Murphy 1986). Previous estimates of muskrat abundance in the OCF have been up to 490,000 animals (Simpson et al. 1989), but there have been no estimates since 1986 and VGFN members have expressed concerns regarding how these populations will be affected by ongoing environmental change.

Members of the VGFN have reported observing a number of ongoing environmental changes, including more frequent retrogressive thaw slumps, lake drainages, overflows of water on ice, increasing shrub growth, and shifting ice phenologies (Allen et al. 2003, Tetlichi et al. 2004, Gordon et al. 2007, 2008):

> *"Out on the land I see a lot of landslides and permafrost melting. Climate change has changed my life in the way I do things out on the land" (Gordon et al. 2008)*
>
> *"I see a lot of landslides and a lot of lakes drying up." (Gordon et al. 2007)*
>
> *"The water level in rivers, lakes and creeks are all low. It's warming up more." (Gordon et al. 2007)*
>
> *"[T]hat trail, you can't follow it anymore, it opens up where it never opened up before, right at the mouth of the Bluefish… water comes over." (Allen et al. 2003)*
>
> *"The weather is getting warmer and warmer. Plants are growing faster, especially the willows." (Gordon et al. 2008)*
>
> *"The weather is getting warmer. [The] freeze-up is slow." (Gordon et al. 2008)*

Some of these trends have also been documented in this region using remote imagery, which demonstrated a 64 % increase in slump area in the Peel region between 1950 and 2008 (Segal et al. 2016), a decline of approximately 6000 ha of lake area (i.e. 5.1 %) driven in large part by a five-fold increase in the frequency of catastrophic lake drainage events in the OCF between 1951 and 2007 (Lantz and Turner 2015), and a significant increase in the mean primary productivity of the north Yukon between 1986 and 2005 (using a regional mean Normalized Difference Vegetation Index [NDVI]; Henry et al. 2012). However no trend was detected in OCF ice phenologies between 1988 and 2001 when estimated using a thermodynamic lake model and data from the Old Crow weather station (Labrecque et al. 2009).

Given conflicting reports of changing ice phenologies from local observers and thermodynamic modelling (Gordon et al. 2008, Labrecque et al. 2009), it is unclear to what degree spring break-up and fall freeze-up have shifted in the OCF, and whether these shifts could affect muskrat population dynamics. Other Arctic regions have seen phenological shifts resulting in one to three weeks more open water over the preceding 50 years (ACIA 2004), while a small sample of lakes across northern Canada experienced earlier average break-up (0.99 days/year) and later freeze-up (0.76 days/year) between 1985 and 2004 (Latifovic and Pouliot 2007). Shifting ice phenologies could influence muskrat dynamics as the longer open water seasons in southern regions enable greater primary productivity and the establishment of preferred species of emergent vegetation (e.g. *Typha*; Errington 1963), allowing muskrats to produce more litters and attain larger body sizes (Simpson and Boutin 1993). However there is no evidence that more temperate conditions improve overwinter survival (Simpson and Boutin 1993), and longer open water seasons in the OCF could be linked to more variable water levels as evaporative forces increase (Labrecque et al. 2009). Stable water levels are a key habitat feature for muskrats, as variable water levels can increase predation risk and nutritional stress, ultimately reducing survival and recruitment (Errington 1963, Virgl and Messier 1996).

To observe the magnitude of shifts in the ice phenology of the OCF, and to explore whether this shift could affect muskrat populations, we used satellite imagery to quantify the timing of freeze-up and break-up and related these to muskrat density and body condition. We established the baseline dynamics of muskrat populations in the OCF by examining a 93 year time series of fur returns. We expanded on weather-based estimates of break-up and freeze-up dates (Labrecque et al. 2009) by using Landsat imagery capturing freeze-up and break-up in the OCF between 1985 and 2015. We compared these remotely-sensed habitat characteristics to landscape variation in muskrat densities and body condition estimated from aerial surveys of pushup construction (Figure 3-2) and trapper carcass collection surveys respectively. As a participatory research project with locally defined objectives (e.g. type C; Danielsen et al. 2014*a*), we documented local ecological knowledge (LEK) of muskrat population dynamics and its ecological drivers during collaborative project planning, field work, and semi-directed interviews. We interpreted this LEK to develop hypotheses regarding cyclicity in OCF muskrat populations, as well as for multi-level models explaining mean muskrat density and body condition as a function of various remotely-sensed habitat characteristics. To our knowledge, this is the first attempt to combine local knowledge, multiple population time series, and remote sensing data in an examination of the impacts of environmental change on a traditionally important population of wildlife.

3.3 Materials and methods

3.3.1 Study area

The Old Crow Flats (OCF), located in the northern Yukon Territory, Canada (68º 05' N, 140º 05' W; Figure 3-1), are a Ramsar wetland of international importance situated 200 km west of the Mackenzie Delta (Brock et al. 2007). The OCF contain over 2,700 thermokarst lakes, the majority of which are small, flat bottomed, and shallow (< 2m; Labrecque et al. 2009). Formerly a large glacial lake, the long axis of the Old Crow Basin is oriented northwest to southeast and the basin itself is surrounded by the British, Richardson, and Old Crow mountains. The basin is composed of two physiographic units: the Old Crow Flats and Old Crow River valley, the latter being 40-50 m lower than the former based on its continuous incision into the surrounding sediment following the last glacial maximum (Labrecque et al. 2009). These river and creek valleys contain the denser stands of terrestrial vegetation, including black and white spruce (*Picea mariana* and *P. glauca* respectively); while white birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*), and trembling aspen (*Populus tremuloides*) are common in successional stands near lakes; and shrub birch (*Betula glandulosa*) and willow (*Salix spp.*) tend to be found towards the tundra (Simpson et al. 1989). The ecotone between boreal forest and tundra crosses the Flats, with the forest transitioning to tundra from SW to NE (Turner et al. 2014). The growing season within the OCF is short due to its northern latitude, with an average of 72.6 ± 5.7 frost free days (Simpson and Boutin 1993). Lakes of the Old Crow Flats are dominated by submergent vegetation, particularly *Potamogeton* spp. and *Myriophyllum* spp. and contain little emergent vegetation preferred by muskrats as forage and lodge building material, so here muskrats exclusively construct bank burrows rather than lodges (Ruttan 1974). The OCF represents a highly productive region of the traditional territory of the Vuntut Gwitchin First Nation (VGFN), and is used for harvesting caribou (*Rangifer tarandus*), waterfowl, mink (*Neovison vison*), marten (*Martes americana*), snowshoe hare (*Lepus americanus*), beaver (*Castor canadensis*), wolverine (*Gulo gulo*), and muskrat (VGFN and Smith 2009).

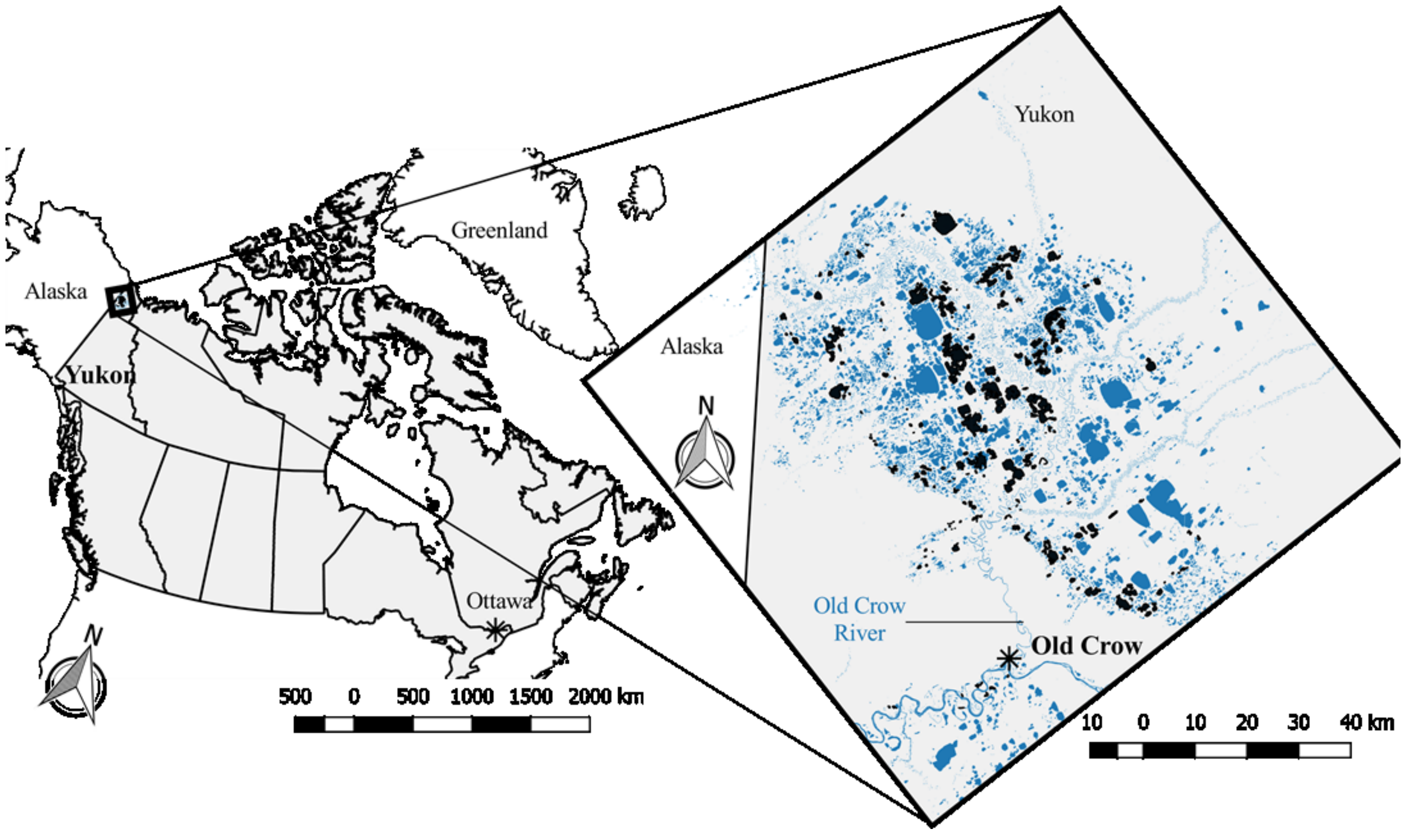


Figure 3-1: The location of the community of Old Crow and the Old Crow Flats (68º 05' N, 140º 05' W) in Yukon Territory, Canada. Our 219 study lakes are indicated with black grills.

3.3.2 Examining trends and cyclicity in OCF muskrat population dynamics (1919-2015)

To determine whether any long term trend or periodicity exists in the population dynamics of OCF muskrat, we examined two time series of indices of muskrat abundance over time: fur returns (1919-2012) and pushup surveys (1984-1986, 2006-2015). We compared the cyclicity of these time series with observations from LEK holders to describe the baseline characteristics of inter-annual variation in OCF muskrat densities

3.3.3 Muskrat abundance using fur returns (1919 – 2012)

We compiled muskrat fur returns for the Yukon and Old Crow from a variety of historical reports and Yukon Environment (Suitor, personal communication; Elton and Nicholson 1942, Slough 1982, Murphy 1986, Simpson et al. 1989). These combined records were complete between 1919 and 2015 for the whole Yukon Territory and included 43 years of Old Crow muskrat returns (Figure 3-3a). Since the Old Crow muskrat harvest represented the majority of the Yukon harvest (54% in years with both), we estimated the Old Crow harvest in the missing years as 54 % of the Yukon harvest. While quantifying harvest effort would improve the utility of fur returns, previous research suggests fur returns alone provide reasonable estimates of relative abundance (Stenseth et al. 1998, Viljugrein et al. 2001, Estay et al. 2011) and periodicity (Turchin, 2003). Nonetheless, we attempted to minimize the influence of market fluctuations in fur prices on trapper effort by dividing fur returns by average muskrat value during the harvest year in inflation-corrected 2016 dollars (Supplementary Figure 7.4b). This generated an index of muskrats harvested per dollar of pelt value. Results were similar using both the unmodified fur returns and the harvest per dollar index. We removed the overall declining trend in fur returns by fitting a cubic smoothing spline with a smoothing parameter of 0.9 (Supplementary Figure 7.4c) and calculated the ratio of the residual and the predicted value of this model (Figure 3-3b). Overall these steps isolated inter-annual variation in muskrat harvests that were independent of variations in muskrat price and the overall decline in the fur trade between 1919 and 2012. We determined the dominant periodicity of this corrected time series using a randomized Lomb-Scargle periodogram, where the significance of the dominant periods is established by scrambling and resampling the original data (Nemec and Nemec 1985). Since fur returns declined significantly in 1989 (Figure 3-3a) we calculated two periodograms: one for the whole dataset and one for the period preceding the decline (1919-1988).

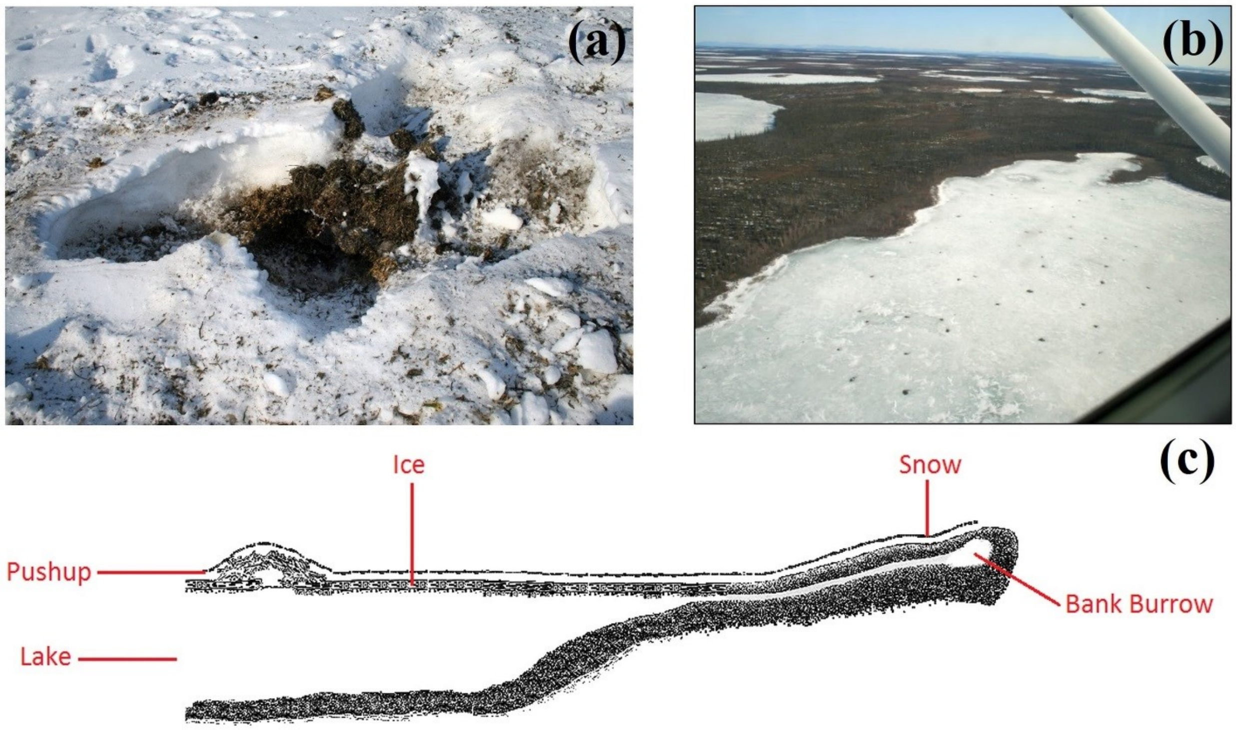


Figure 3-2: Muskrat pushup (a) when opened by a wolverine, (b) when visible from the air, and (c) when visualised from the side. During the spring melt pushups can serve as an index of muskrat density (Diagram adapted from: Aleksiuk 1987).

3.3.4 Muskrat abundance using pushup densities (1984-1986, 2006-2015)

To generate an estimate of muskrat abundance in the OCF that is less dependent on the activities of fur harvesters we used the density of pushups muskrats construct on lake ice. Pushups are domed structures of frozen vegetation that muskrats pile over holes in lake ice and use as winter breathing, resting, and feeding stations (Figure 3.2; Stevens 1955). These structures can be identified by the presence of dark vegetation and a plunge hole. When the lake ice melts, pushups sink. As a structure that is constructed and destroyed annually, pushups respond to annual variations in muskrat abundance (Simpson et al. 1989). While not as precise as estimates derived from intense live capture surveys, counting pushups enables the rapid (2-3 days) estimation of relative muskrat abundance in hundreds of lakes across the 5,600 km^2 OCF.

In 1984-86 and 2006, Yukon Environment conducted aerial pushup counts based on a series of 18 transects (Simpson et al. 1989). Since 2008, we have been flying annual surveys of the Old Crow Flats during the spring melt counting muskrat pushups on, depending on ice conditions, up to 219 study lakes (Figure 3-1). In the years 1984-2012, surveys were conducted by two observers recording counts from a Cessna 206 at an average flight speed of 125 kph and an average altitude of 350 ft. In the years 2012-2015, surveys were conducted based on aerial photographs collected using a window mounted camera on a Cessna 172 with a ground separation distance of 20 cm. During the overlap year of 2012, photography counts were compared to aerial counts and correlated strongly ($r = 0.92$). The number of muskrats per pushup has been estimated from previous live trapping studies in the region, and includes 2.1 (Ruttan 1974), 2.2 (Simpson et al. 1989), and 3.4 in the OCF (Martin 1974); and 1.0 (Stevens 1955), 1.7 (EPEC Consulting Western Ltd. 1976), 2.4 (Hawley 1964*a*, *b*), and 2.9 in the Mackenzie Delta (McEwan 1955). The variability of this relationship, particularly its density-dependence and inter-annual variability, would benefit from more detailed investigation. Nonetheless all evidence suggests this correlation is monotonic (i.e. more pushups means more muskrats), and since pushups per km^2 can vary across four orders of magnitude they are useful coarse indicators of relative densities of muskrat. Observed pushup densities were lognormally distributed with frequent zeros, and so were square root transformed for analysis.

Similar to the fur returns, we examined this time series of overall pushup density in the OCF for long term trends and cyclicity. Specifically, we analyzed the survey estimates from post 2006 using a linear approximation to estimate the 2007 abundance. Considering local knowledge regarding the presence and periods of cyclicity in OCF muskrat population, we also calculated periodograms for our 8 year time series of our 219 study lakes.

3.3.5 Measuring muskrat body condition

In addition to abundance estimates, we recorded muskrat body condition across the Old Crow Flats through 549 carcass specimens collected from 19 VGFN trappers. These carcasses were trapped from March 1st to June 15th between 2007 and 2012. We took a variety of measurements on these specimens, including skinned body mass and total body length. Muskrats can be territorial, particularly approaching the May breeding season when they distribute themselves most closely according to an ideal despotic distribution where the strongest individuals monopolize the best territories (Messier et al. 1990). This assumption is supported by some LEK:

[In a slough that is poor muskrat habitat] "I probably wouldn't even take the time to set up traps, unless we're doing nothing… Because the rat would be poor and small."

"These two, these lakes here. They get pretty thin rat and they're small… So those lakes are not very good for, you just use them when it's hunting time eh?"

"Oh, maybe they got kicked out of their house or something. Maybe another big male moved into their territory and made them move away"

OCF muskrats are on average smaller than muskrats from southern populations, potentially as an adaptation to periods of more severe nutritional limitation (Simpson and Boutin 1993). Therefore we assumed muskrat total body size should, on average, be larger in lakes that experience less nutritional limitation where larger, dominant, individuals would establish territories (Pankakowski 1983). Previous research and LEK suggest muskrats increase their body mass and fat composition during the winter, but that these decline with the onset of breeding (Virgl and Messier 1992). As a result of this trend, in conjunction with sexual dimorphism in muskrats, we included Julian day and sex as explanatory variables in all body condition models.

3.3.6 Modeling break-up and freeze-up dates using LANDSAT imagery

To relate inter-annual changes in muskrat abundance and body condition to ice phenology, we estimated the timing of spring break-up and fall freeze-up in our 219 study lakes across the OCF. We first used Google Earth Engine (GEE) to estimate the proportion of study lakes that were ice covered in scenes taken by the Landsat 5 TM, 7 ETM+ (SLC off and on), and 8 OLI sensors between April 15th and July 15th, and August 15th and November 30th, 1985-2015. Google Earth Engine uses Google's cloud computing capabilities to process large volumes of remotely sensed imagery. Using GEE's coding environment (https://code.earthengine.google.com/), we obtained the top of atmosphere corrected reflectances (TOA; Chander et al. 2009) of Landsat scenes from the United States Geological Survey repository. We filtered these image collections to the paths (65-68) and row (12) that corresponded to the Old Crow Flats, and the dates that correspond to seasonal thaw and freeze (April 15th to July 15th; August 15th to November 30th). We removed scenes that had more than 80 % cloud cover. Within this subset of images, we identified pixels as ice, water, or other using a decision tree of band cut-offs modified from Hall *et al.* (1995; see Supplementary Methods). We digitized our study lakes using Quantum GIS (QGIS Development Team 2016) and a Landsat 5 TM scene mosaic (acquisition dates July – August 2007). We calculated the number of pixels in each of our 219 study lakes that were ice covered in 908 images. This resulted in 92,273 lake ice phenology observations after removing lakes with 80% cloud cover. We identified misclassified images that had escaped our previous filters through clearly erroneous estimates of ice cover (e.g. if numerous lakes were "ice covered" July 5th, or August 20th). In 92 images we manually corrected their classifications, 47 images were omitted for having greater than 80 % cloud cover, and 24 misclassified lakes were removed from the dataset (see supplementary material for lists).

To generate predictions of break-up and freeze-up dates, we used these ice cover estimates to build multi-level logistic models with two varying intercepts: one for inter-lake variation in ice cover ($\alpha_{j(i)}^{lake}$), and the other for inter-annual variation in ice cover ($\alpha_{k(i)}^{year}$). This model is a simplification of actual lake ice phenologies because it assumes each lake behaves similarly every year (i.e. early thawing lakes will always be early thawers) and that all lakes behave similarly in particular years (i.e. all lakes freeze earlier during early freezing years). However these assumptions allow for the estimation of break-up and freeze-up dates for all lakes even if they are frequently cloud covered in a season, a common challenge with Landsat imagery, based on the order in which that lake freezes/thaws in other seasons (e.g. a larger $\alpha_{j[i]}^{lake\ ID}$ indicates a lake tends to have more ice than the lake average, and therefore is a late thawer or early freezer) and whether a particular season is early or late (e.g. a larger $\alpha_{k[i]}^{year}$ indicates a year has more ice than the annual average, and therefore is a late thawing or early freezing year; see Supplementary Methods). To determine each lake's break-up date, freeze-up date, and open water season we used these models to calculate the date that corresponded to a 50 % probability of a lake pixel being ice covered in a particular year. To quantify the temporal trend in break-up and freeze-up, we modeled their occurrence as a linear function of time.

3.4 Evaluating environmental determinants of muskrat density and body condition derived from LEK

To compare potential environmental determinants of muskrat pushup density and body condition in the OCF, we developed a set of multi-level models based on hypotheses derived from LEK. We conceptualized these models *a priori* (Burnham et al. 2011) with the benefit of LEK as we understood it from an eight year period spent working in partnership with LEK holders during collaborative project planning, fieldwork, data interpretation sessions, and during recorded and transcribed semi-directed interviews. We worked with 23 LEK experts identified by the North Yukon Renewable Resource Council and the Vuntut Gwitchin Government Heritage Department. See results for these LEK-derived hypotheses and Supplementary materials for interview guidelines and model structures. We ranked all models using Akaike's corrected Information Criterion (AICc; Burnham and Anderson 2002). All these models used standardized explanatory variables, included year as an explanatory variable to control for linear temporal trends, and were weighted by the lake area. Reported parameter estimates include 95% Wald confidence intervals (CI).

3.5 Results

3.5.1 Examining trends and cyclicity in OCF muskrat population dynamics (1919-2012)

Between 1919 and 2012 the VGFN, who typically numbered around 200 individuals (Murphy 1986), had estimated harvests of between 23 and 50,194 muskrats (Figure 3-3a) over a period where average muskrat prices varied between 3.17 and 32.56 in 2016 CDN$ (Supplementary Figure 7.4b). Overall and price-corrected muskrat returns declined through the time series, with particularly sharp declines in 1989 (Figure 3-3a). As a result, detrended muskrat returns (Figure 3-3b) show increasing variability in later years when the absolute number of furs harvested decreased. Depending on whether you include the final 26 years of the time series, the

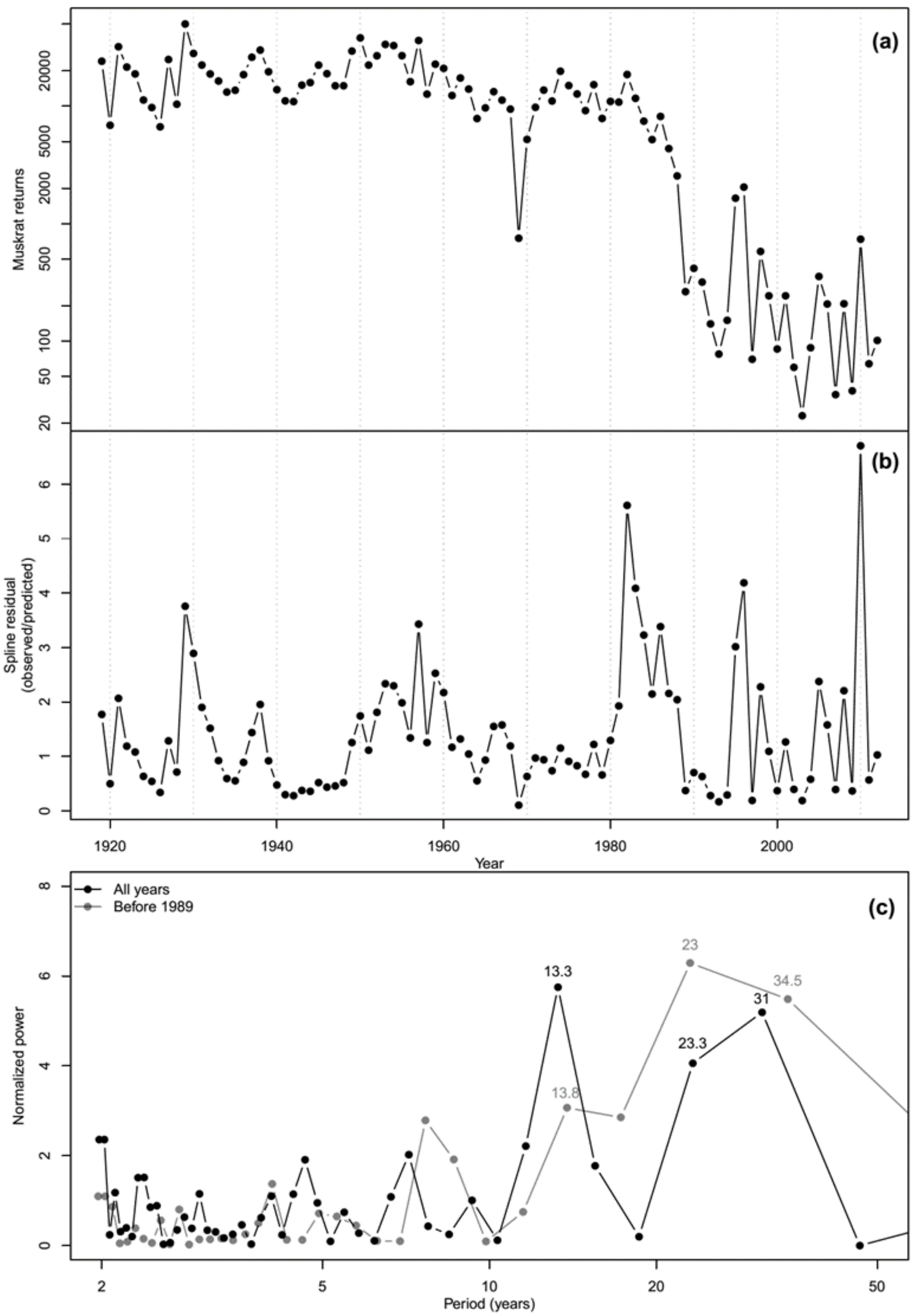


Figure 3-3: Time series of estimated Old Crow muskrat returns (a), the detrended harvest (b), and the dominant periods of this detrended time series (c). The y axes of (a) and the x axis of (c), are logarithmic. The curves in (c) represent the dominant period of all years (black) and pre 1989 (gray).

dominant period occurs either at 13.3 years ($p = 0.06$) or at 23 years ($p = 0.03$). However, in either case periodicity appears to recur at 7.2-7.7, 13.3-13.8, and 23-34 years (Figure 3-3c).

Estimates of muskrat pushup abundance in the Old Crow Flats was highly variable inter-annually, from a maximum of ($CI_{95\%}$ = [190,000, 280,000]) in 2010 to a minimum of ($CI_{95\%}$ = [61,000, 94,000]) pushups in 1984 (Figure 3-4). Using Simpson *et al.*'s (1989) ratio of 2.19 muskrats per pushup, this corresponded to minimum and maximum muskrat abundance estimates of ($CI_{95\%}$ = [410,000, 610,000]) and ($CI_{95\%}$ = [134,000, 206,000]) respectively. There was no linear trend in these estimates over time (β^{year} = [-7000, 7600]; 95% CI). Between 2008 and 2015, estimates of lake pushup density varied from a minimum of 0 to a maximum of 1232 pushups/km^2. While still a short time series, a periodogram of the post-2005 portion of Figure 3-4 produces a dominant peak at 9 years (p = 0.04). This overall time series is composed of 219 individual time series of lake pushup densities, 210 of which have an estimate of dominant periodicity ranging

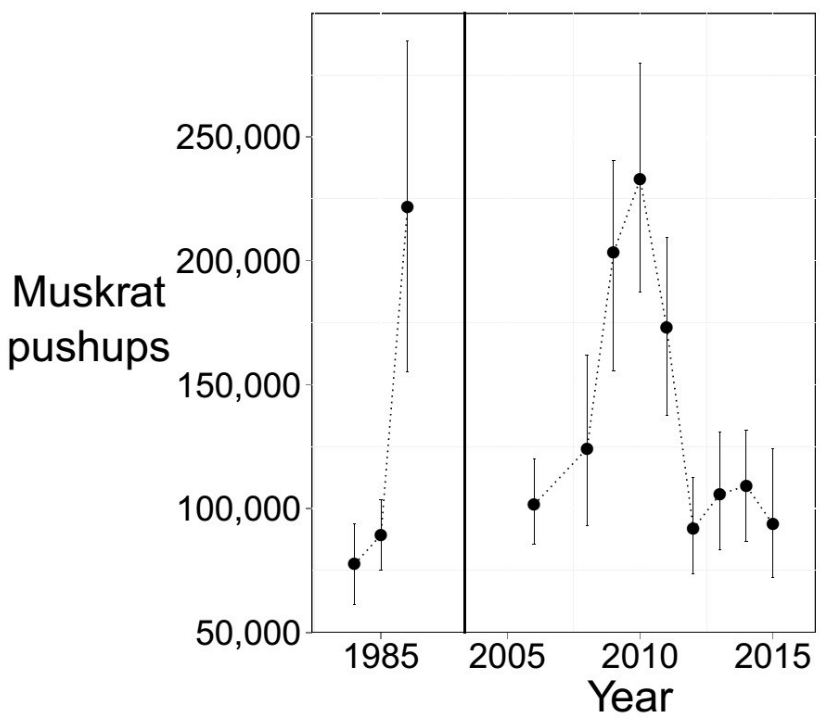


Figure 3-4: Estimates of the abundance of muskrat pushups in the Old Crow Flats based on annual spring aerial surveys. Surveys from 1984-2006 were based on a transect method (Simpson et al. 1989), while those of 2008-2015 were based on a sample of lakes.

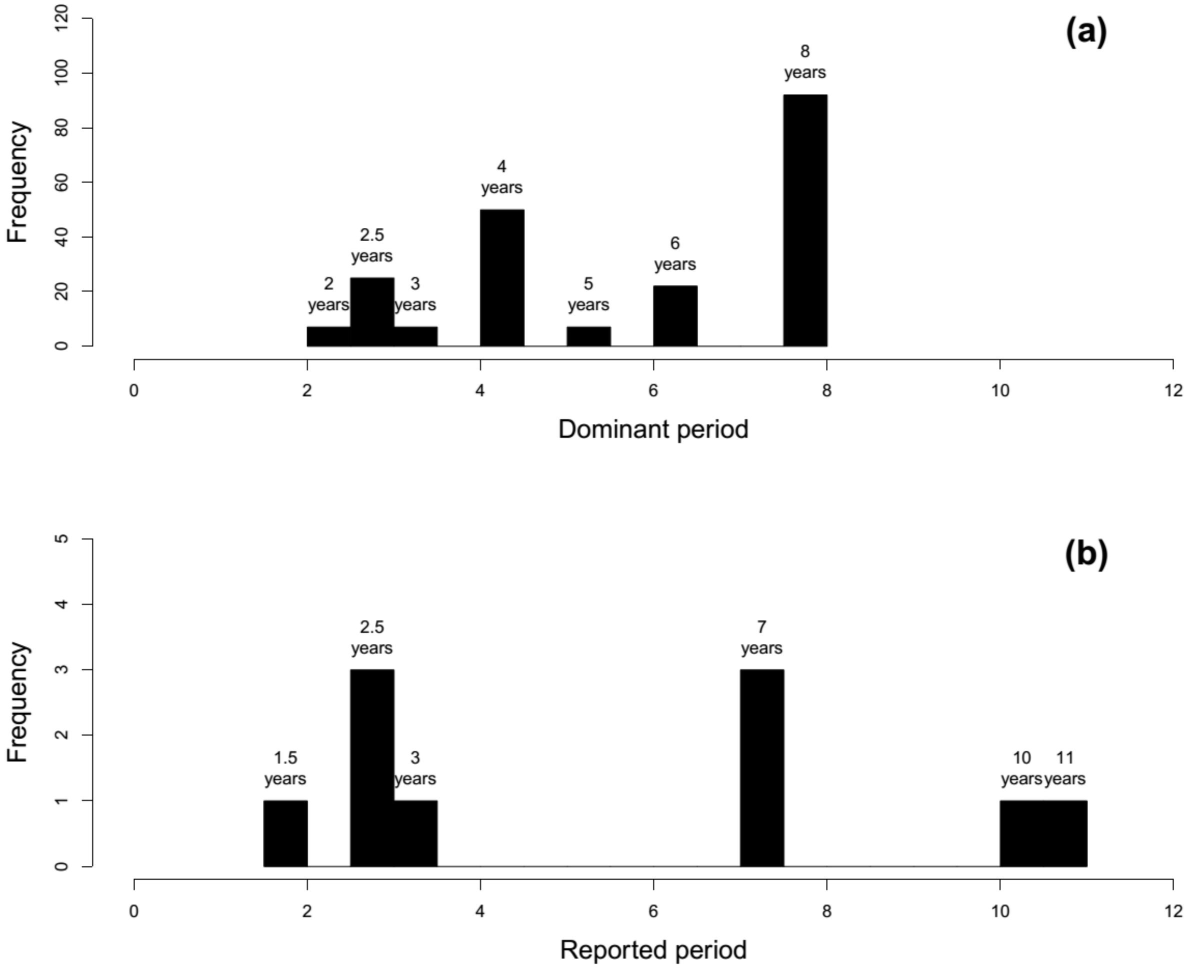


Figure 3-5: Histograms of dominant cycle periods as determined by aerial pushup surveys (a) and LEK interviews (b). Period estimates in (a) were derived from 210 of our time series of lake pushup density with a minimum of 4 years of data, while those of (b) were derived from 10 LEK experts who reported an opinion regarding the presence and duration of cycles in muskrat populations.

from 2 to 8 years (Figure 3-5a). Similarly, local periodicity in muskrat populations as reported by LEK holders varied from 1.5 to 11 years (Figure 3-5b). Three participants were unsure and ten expressed no opinion.

3.5.2 Modeling break-up and freeze-up dates using LANDSAT imagery

The 1985-2015 Landsat record contained a marginally significant advance in the timing of break-up (0.20 ± 0.14 days/year [SE]; n = 602 images), and a non-significant advance in freeze-up timing (0.07 ± 0.12 days/year [SE]; n = 332 images) leading to an increase in the length of the open water season (0.26 ± 0.19 days/year [SE]) in the OCF. These trends corresponded to a shift between 1985 and 2015 of 6 days in break-up (80% prediction interval [PI] shifting from May 22–June 9 to May 16 – June 4), 2 days in freeze-up (80% PI shifting from Sept 23 – Oct 10 to Sept 25 – Oct 12), and an open water season that is 8 days longer (80% PI shifting from 110 – 136 to118 – 144 days; Figure 3-6). Within individual years, estimated thaw dates, freeze dates, and open water seasons varied between lakes by up to 21, 3, 20 days respectively.

"It's a lot quicker melt. Even May is a lot warmer. Snow is gone by the end of May"

"The past we used to trap pretty right near to the end of May… on ice. And now it's not really safe anymore. It get rotten quick"

"Like the 2010 spring, I went up on May 25th and got up there on May 26 morning, picked up Billy and Joseph I was planning to walk on the ice and shoot some muskrat and here it was clear water. I've never seen that in my life."

3.5.3 Evaluating environmental determinants of muskrat density and body condition derived from LEK

Combining our experiences with LEK from Old Crow trappers, we identified the following hypotheses regarding ecological determinants of muskrat abundance and body condition. In order of importance:

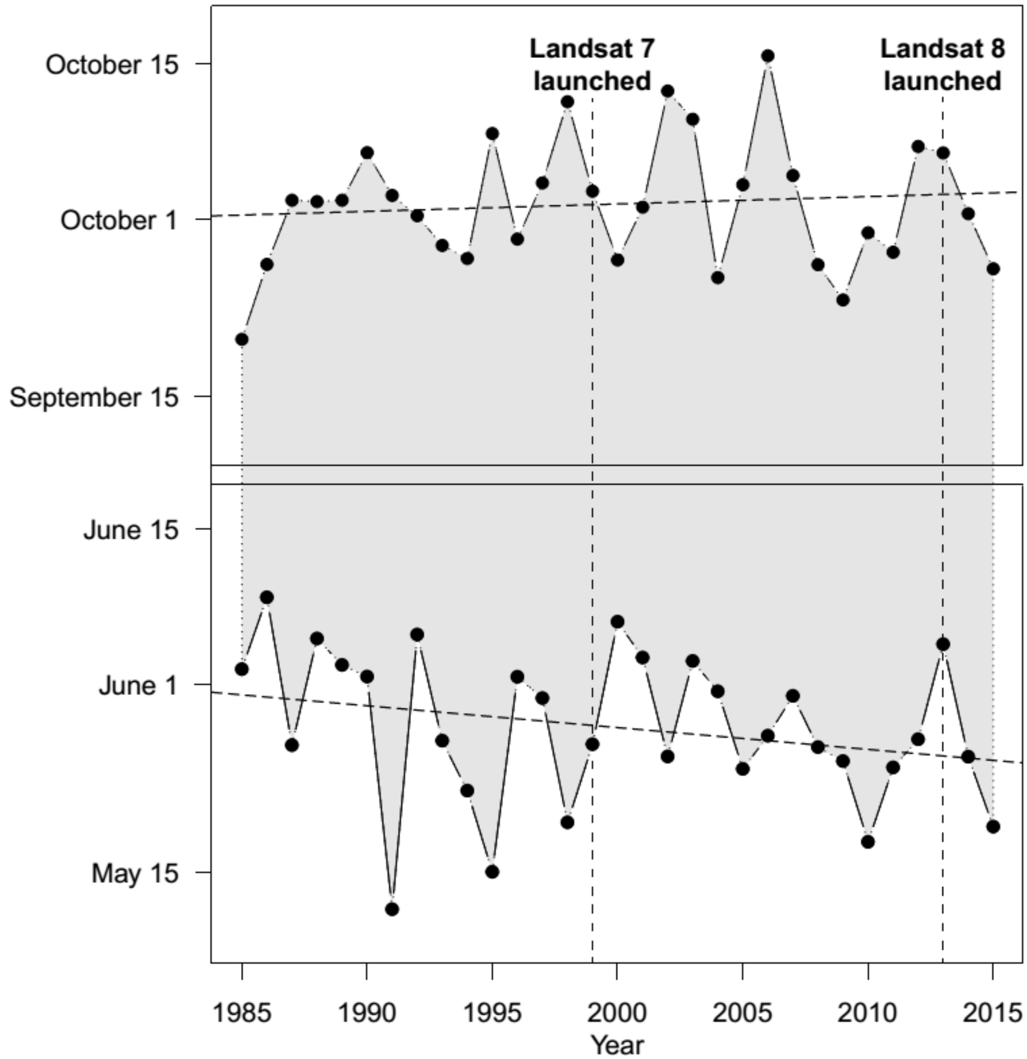


Figure 3-6: Estimated break-up and freeze-up dates for median-sized lake (JER19) in the Old Crow Flats based on Landsat imagery. The length of the open water season is indicated with the shaded zone. During the first 14 years of the time series only Landsat 5 was operating, so these estimates are based on the fewest images. This was a factor in estimates of freeze-up when daylight hours are limited, and as a result inter-annual variability in freeze-up dates is likely underestimated between 1985 and 1999. Estimated break-up, freeze-up, and open water season lengths advanced 0.20 ± 0.14, 0.07 ± 0.12, and 0.26 ± 0.19 days/year respectively (SE).

H1: Open water season

In a landscape where the growing season is short (average 73 frost free days in 1981-85; Simpson and Boutin 1993), an extension of the growing season of several weeks could increase macrophyte primary productivity, increasing the availability of nutrition for muskrats and support greater muskrat densities.

H2: Grassy lakes

Local experts frequently reported the importance of macrophyte growth:

“Lots of food in the bottom of that lake I guess… Lots of vegetation”

“Well food, very important is food…. [Muskrats] go portage, search around, well that’s what my grandfather said to me. And then when they find lots food, that’s where most of the rats go to. That’s why you see some lakes with less rat house on it, and some lakes with a lot of rat house. Food.”

“Some lakes you get a moss, bottom that’s not very good to a lake. For a rat. You gotta have to have food, muskrat foot, the muskrat root. Rat root.”

“They go to their own place so they know what lakes are good. Which means good food, deeper water…”

“It's, they got good vegetation there, that's why there's so much muskrat around there”

We used the mean normalized difference vegetation index (NDVI) from Landsat 5, 7, and 8 images as a measure of aquatic vegetation cover in our shallow study lakes (Liira et al. 2010). Sensors across these platforms are comparable when used to calculate vegetative indices (Li et al. 2014). We based NDVI values on images taken during the summer (July 1st – August 30th) prior to our spring pushup surveys (i.e. summer 2008 for spring 2009) that contained less than 80% cloud cover. Generalized additive models of individual lake NDVI values as a function of Julian day found no significant seasonal trend in NDVI over July and August (e.g. at Schaeffer Lake Julian day smoother $p = 0.54$).

H3: Deeper lakes

Similar to above, local experts often reported the importance of lake depth and its connection to productivity:

"It's good so the deep lakes are the ones that's holding the muskrat I'm pretty sure. They got more food and better growth I think."

"Lots of water is good for them, in the fall when they're cut off. They don't have to make too deep a tunnel if it's high water. And right now water is low so they have to dig that tunnel probably deeper."

"In the fall, you know those dry [lakes] where there's lot of grass and shallow water, there's lots of muskrat in the fall. Then damn muskrat they head to big deep lake in the winter, they know it [will freeze to the bottom] ... you see that slough back there, there's no rat house in it"

"Since I was grown up a lot of people were talking about deep lakes were the best lakes to go trapping"

We estimated lake depth in our 219 study lakes using field measurements collected in comprehensive 100 m x 100 m grids in 9 of our study lakes, together with mean depth measurements collected by colleagues in 54 other lakes (Wolfe et al. 2011). Previous work suggests lake depth is linked with lake morphology in this region, where lakes with more irregular shorelines are deeper (Roy-Léveillée, Laurentian University, personal communication). We combined this association with the tendency of deeper lakes to freeze and thaw later to model mean lake depth as a linear function of the log transformed lake surface area and perimeter, coordinates, thaw and freeze order (varying intercept $\alpha_{j(i)}^{lake}$ from eq. [2]; Supplementary material), and the lake perimeter to surface area ratio. This model ($r^2 = 0.44$) was used to roughly estimate mean depths for all study lakes (Supplementary material). We used estimated lake depths to model lake pushup density as a quadratic relationship, as trappers reported lakes beyond an optimal depth were poor habitat.

H4: Early thaws

Less frequently, local experts identified early thawing lakes as advantageous for muskrat:

> *"[S]ome lake I think open up early. That's my understanding. When you talk to people, Timber Hill is same. Water come in from mountain early, some lakes get water quick. So they go up there and they get a lot of muskrat. Up here it's like that too… get about four, five hundred rat one night there."*

We estimated the annual relative thaw order of our study lakes using lake residuals from a pooled model of seasonal thaw across all study lakes (see Supplementary materials). We calculated mean annual residuals for each study lake relative to this pooled model, and used these mean residuals as an index of annual relative thaw order. This index is positive in years when lakes have more ice cover than the average lake on an average year, and negative in the reverse scenario.

H5: Bigger is better

Occasionally, experts identified lake size as an important habitat feature for muskrats in the OCF:

> *"If it's lots and lots of muskrat, they would use those little lakes I guess. But they prefer the big lake. If it's not too many."*

We used the natural logarithm of lake surface area as a predictor of muskrat pushup density and body condition.

3.5.4 Comparing hypotheses for pushup density and body condition

Individually the length of the open water season was the best predictor of muskrat pushup density, outperforming its nearest competitor lake depth (ΔAICc = 6.3; Table 3.1). However individually these variables explained a small proportion of the variation in pushup density, with more variation explained by varying lake intercepts (just fixed effects: $R^2_{marginal} = 0.09$ & 0.10 respectively; fixed and random effects: $R^2_{conditional} = 0.39$ & 0.38 respectively; Nakagawa and Schielzeth 2013). Both open water season and lake depth were negatively correlated with pushup density ($\beta^{open\ water\ season}$ = [-1.23, -0.27]; $\beta^{mean\ depth}$ = [-1.56, 0.02]; $\beta^{mean\ depth^2}$ = [1.25, 0.08]; 95 % CI). The remaining models did not improve on the null model of a negative trend with time (β^{year} = [-6.29, -4.58]; 95 % CI). A post-hoc combination of all explanatory variables (i.e. the length of the open water season, estimated mean lake depth, mean lake NDVI, lake area, the annual thaw residual [indicator of annual thaw order]) improved the model ($AIC_c^{posthoc}$ = 6450 vs. $AIC_c^{openwater}$ = 6485) and marginally increased its explanatory power ($R^2_{marginal} = 0.12$; $R^2_{conditional} = 0.42$; Table 3.1; Figure 3-7). The combined model increased the strength of the negative effects of open water season and mean lake depth ($\beta^{open\ water\ season}$ = [-9.98, -4.14]; $\beta^{mean\ depth}$ = [-1.94, -0.31]; $\beta^{mean\ depth^2}$ = [-1.29, 0.05]; 95 % CI), while adding negative associations with thaw order ($\beta^{lake\ thaw\ residual}$ = [-0.84, -0.37]; 95 % CI) and lake area ($\beta^{\ln(surface\ area)}$ = [-1.37, 0.29]; 95 % CI), and a positive association with lake productivity ($\beta^{mean\ NDVI}$ = [0.16, 1.32]; 95 % CI). Due to a minor correlation between the length of the open water season and the year (r = [0.17, 0.28]; 95 % CI), we included an interaction term between these variables in the combined model that was significantly positive ($\beta^{open\ water\ season:year}$ = [1.79, 6.76]; 95 % CI). As result the magnitude of the negative effect of the open water season declined as time progressed.

Similarly, the length of the open water season was one of the top predictors (all ΔAICc < 0.5) of muskrat body mass, together with lake productivity and surface area (nearest competitor ΔAICc = 4.9; Table 3.2). However neither of these habitat characteristics individually explained much more variation than the null model including sex and Julian day (null $R^2_{marginal}$ = 0.20; open water $R^2_{marginal}$ = 0.21; productivity $R^2_{marginal}$ = 0.22; area $R^2_{marginal}$ = 0.23). Muskrat body mass was negatively correlated with open water season ($\beta^{open\ water\ season}$ = [-0.42, -0.08]; 95 % CI) and lake productivity ($\beta^{mean\ NDVI}$ = [-0.46, -0.10]; 95 % CI), and positively correlated with lake surface area ($\beta^{\ln(surface\ area)}$ = [0.08, 0.50]; 95 % CI). A post-hoc combination of all habitat variables marginally improved the explanatory power of the fixed portion of the model (ΔAICc = 5.2; $R^2_{marginal}$ = 0.30; $R^2_{conditional}$ = 0.38; Figure 3-8) by explaining some variation previously incorporated in the varying lake intercept. This model maintained a similar effect open water season length ($\beta^{open\ water\ season}$ = [-0.39, 0.05]; 95 % CI), reduced the importance of lake productivity ($\beta^{mean\ NDVI}$ = [-0.25, 0.28]; 95 % CI), and added a quadratic relationship with lake surface area ($\beta^{\ln(surface\ area)}$ = [0.16, 0.70]; $\beta^{\ln(surface\ area)^2}$ = [-0.31, 0.03]; 95 % CI) and depth ($\beta^{\mathrm{mean}\ depth}$ = [0.05, 0.57]; $\beta^{mean\ depth^2}$ = [-0.49, 0.00]; 95 % CI). The control variables Julian day ($\beta^{julian\ day}$ = [0.25, 0.49; 95 % CI]) and sex (β^{sexM} = [0.37, 0.71; 95 % CI]) were also positively associated with body mass.

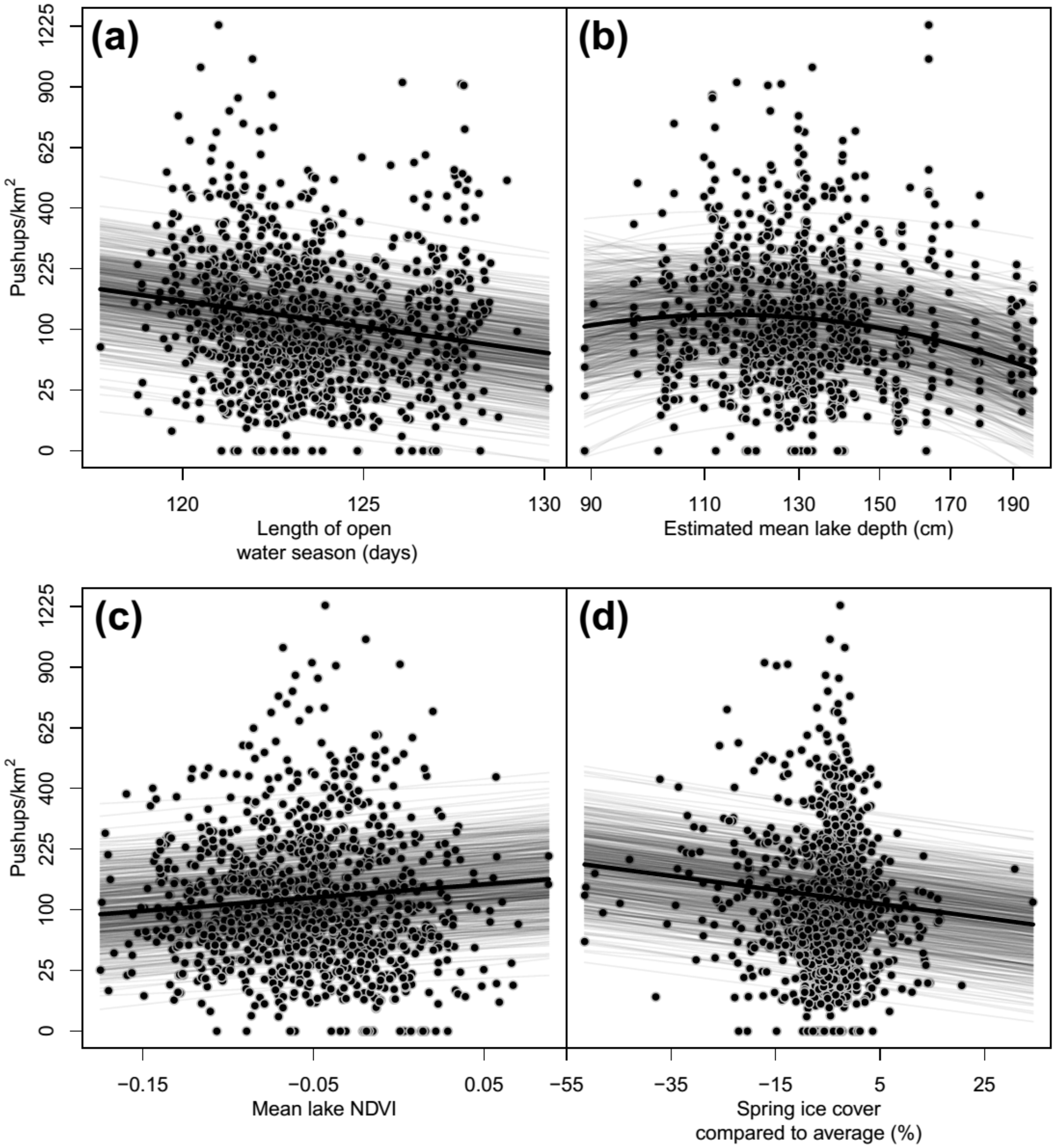


Figure 3-7: The density of muskrat pushups per km^2 based on the optimal multi-level model following model selection and post-hoc combination. Each axis is in the original units of measurement. In the model pushup densities were square root transformed while estimated lake depths were ln transformed. The thick line represents the predicted pushup density from the optimal model assuming a median value for all other co-variables. The thinner lines represent 500 simulations of plausible models sampling the distribution of estimated fixed and random model coefficients given their variances (Gelman and Hill 2007). These represent the range of possible outcomes assuming median values for co-variates and random selections of lakes that agree with model estimates within a band of 95 % confidence.

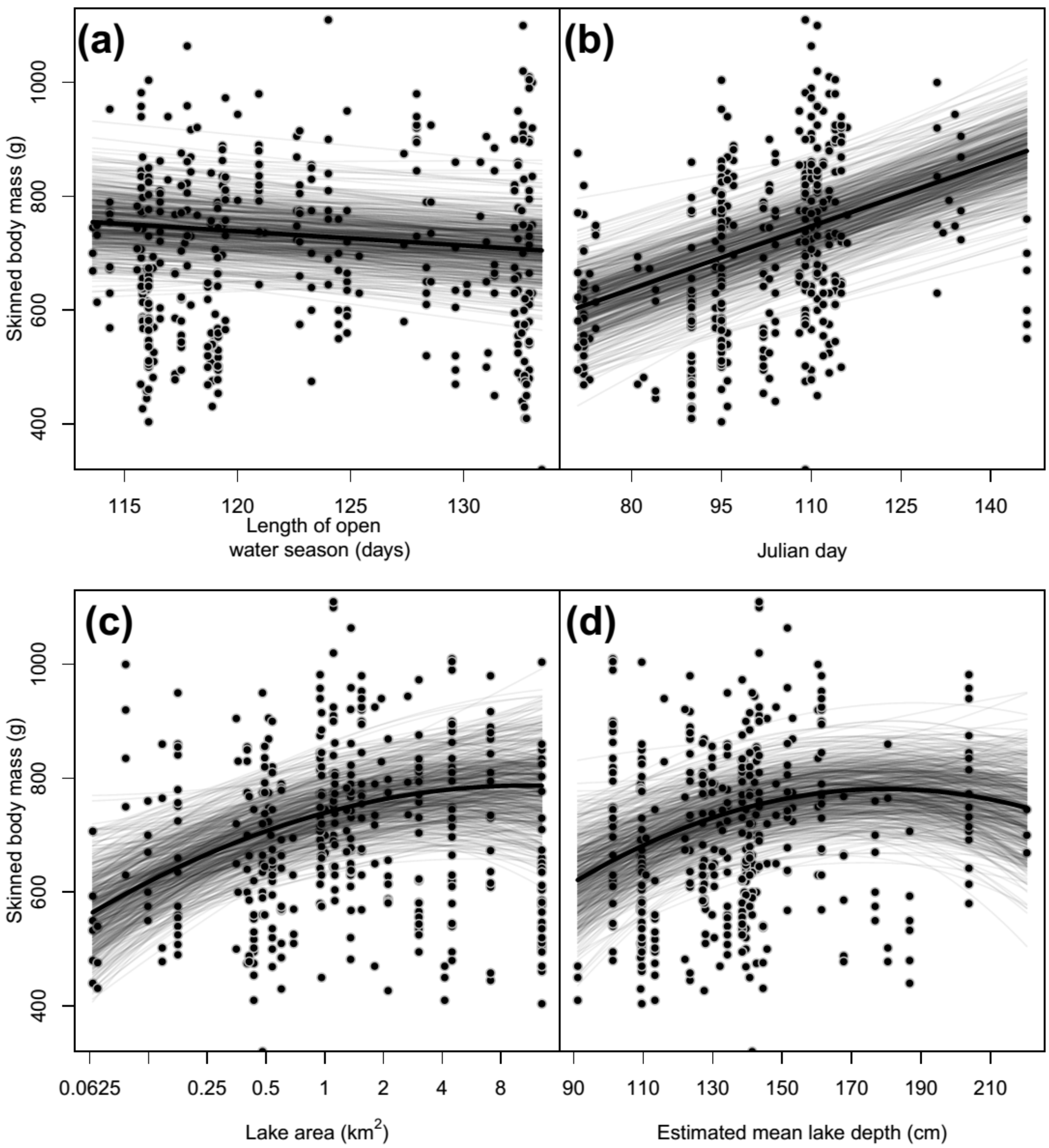


Figure 3-8: Muskrat total skinned body mass as a function of open water season, Julian day, lake surface area, and estimated mean lake depth based on the optimal multi-level model following model selection and post-hoc combination. Each axis is in the original units of measurement. The thick line represents the predicted pushup density from the optimal model assuming a median value for all other co-variables. The thinner lines represent 500 simulations of plausible models sampling the distribution of estimated fixed and random model coefficients given their variances (Gelman and Hill 2007). These represent the range of possible outcomes assuming median values for co-variates and random selections of lakes that agree with model estimates within a band of 95 % confidence.

Table 3.1: Model selection, including coefficient estimates, for muskrat pushup density.

Model name	**year**	**open water**	**NDVI**	**depth**	**depth^2**	**thaw**	**area**	**open water:year**	**AICc**	**delta**	**weight**
Post-hoc	-3.4	-7.06	0.74	-1.13	-0.62	-0.61	-0.54	4.27	6450.1	0.0	1
Open water	-5.12	-0.75							6485.3	35.2	0
Deeper lakes	-5.45			-0.77	-0.59				6491.6	41.5	0
Null	-5.44								6492.5	42.4	0
Early thawers	-5.40					-0.12			6492.7	42.6	0
Bigger	-5.41						-0.48		6493	42.9	0
Grassy	-5.43		-0.05						6494.5	44.4	0

Table 3.2: Model selection, including coefficient estimates, for muskrat furred body mass

Model	julian	sex	open water	NDVI	depth	depth^2	thaw	area	area^2	AICc	delta	weight
Post-hoc	0.37	+	-0.17	0.02	0.31	-0.23	0.03	0.61	-0.14	921.20	0.00	0.83
Grassy	0.44	+		-0.28						926.40	5.19	0.06
Open water	0.42	+	-0.25							926.90	5.66	0.05
Bigger	0.39	+						0.29		926.90	5.67	0.05
Null	0.38	+								931.80	10.60	0.00
Early thawers	0.38	+					0.00			933.90	12.68	0.00
Deeper	0.37	+			0.10	-0.10				935.00	13.80	0.00

3.6 Discussion

Overall we found little evidence for a decline in muskrat populations of the OCF. However, we found some evidence that ice phenology is both an important environmental determinant of muskrat abundance, and that both break-up and freeze-up dates are advancing in this Arctic landscape. While long term records of muskrat fur returns declined, this pattern likely does not reflect a decline in their abundance as fur trapping activities declined during this period (Murphy 1986). The first explicit estimates of muskrat abundance across the OCF in 1984-86 were similar to current estimates (Figure 3-4), suggesting there has been no long term trend in abundance over time. While not strong evidence of a trend, the fur returns provide the first evidence of cyclicity in Old Crow muskrat populations with a combination of long (23-31 year) and medium (13 year) periods. The 10 year pushup time series, while still too short to be convincing, also provides support for short period cyclicity overall (Figure 3-4) and for cyclicity that varies from lake to lake (Figure 3-5a). Interestingly cyclicity has also been observed at a local level, with periods that vary based on individual trapping experiences (Figure 3-5b). There would be value in further exploring the spatial distribution of patterns of cyclicity in the OCF as observed through pushup surveys and LEK experts.

Similarly, our analysis of Landsat imagery supports local observations that ice phenology of the OCF has been changing in conjunction with warming temperatures. Between 1985 and 2015 we observed advances in the timing of both average spring melt (0.2 days/year) and average fall freeze (0.07 days/year) resulting in an average increase in the open water season of 0.26 days/year. These rates of change for melt and freeze are slower than those found between 1985 and 2004 in 6 Canadian high Arctic lakes (0.99 and 0.76 days/year) or in Sitdigi lake 290 km east of the OCF

(0.57 and 0.82 day/year; Latifovic and Pouliot 2007). Changing phenologies in the OCF are likely driven by warming temperatures, where average summer temperatures have warmed approximately 1.2 ºC over the same period. It is important to note that these annual estimates of break-up and freeze-up dates have yet to be ground-truthed and are dependent on the number of cloudless images taken during these periods. The accuracy of estimates increased as new sensors began collecting images of phenological events in 1999 and 2013. Similarly, estimates of freeze-up suffer from fewer available images due to the reduced hours of daylight in the fall, particularly during early years when only the Landsat 5 satellite was operating. As a result, some freeze-up estimates regress to the time series mean (see 1987-89; Figure 3-6). Nonetheless our remote sensing analysis supports local observations that changing ice phenologies, particularly during spring melt, are one of the major observed impacts of climatic warming in the Old Crow region.

"It's a lot quicker melt. Even May is a lot warmer. Snow is gone by the end of May."

Following discussions with LEK holders, we compared various hypotheses regarding environmental determinants of muskrat abundance and found that changing ice phenology could influence muskrat population dynamics in the OCF. While, unsurprisingly, much variability in muskrat densities and body conditions remained unexplained, our evidence supported several LEK-derived hypotheses regarding ecological determinants of these variables. Our estimated lake depths covaried with both muskrat pushup density and body condition. The direction of these relationships differed, but this is consistent with local interpretations of seasonal habitat use by muskrats. Deeper lakes provide larger accessible overwintering habitat in a landscape where mean lake depth is approximately 150 cm and mean ice thickness is 130 cm (Roy-Leveillee and Burn 2016, Ruttan 1974). Muskrats trapped in the spring (March – May) from deeper lakes (mean depth

150-210 cm) tended to be larger, potentially due to increased overwinter growth rates from effectively larger habitats with more accessible nutrition (Simpson and Boutin 1993). Muskrats in the Mackenzie Delta select for deeper habitats in winter (Stevens 1955, Jelinski 1989), and muskrat overwinter growth rates are larger in selected-for habitats containing preferred vegetative assemblies (Clark 1994). In contrast, we found pushup densities were maximized at intermediate mean depths (110-150 cm) and declined as depths subsequently increased. As depth increases, light attenuation will reduce macrophytic productivity. Likely the deepest lakes of the OCF contained the greatest proportion of overwinter habitat, but also had the lowest macrophytic productivity per hectare. This hypothesis was supported by the model prediction that mean muskrat body mass began to decline at depths > 190 cm (Figure 3-8). Seasonal shifts in optimal depths is also supported by LEK that suggests muskrats select shallow lakes for summer use before dispersing to deeper lakes for overwintering.

> *"[T]his little slough back here, because the water will be in there first [in spring], it's shallow and lots of grass, muskrat will go to there from other places … And then the fall time, it work absolutely the other way. In the fall…muskrat they head to big deep lake in the winter, they know it… because if they stay in [the slough]… a lot of that will freeze straight to the bottom. That rat, you know it, he take long range weather forecast."*

Trappers frequently discussed the relationship between depth and productivity, and interestingly mean lake NDVI did increase with muskrat density when controlling for other variables (Figure 3-7; Table 3.1). Lake NDVI did not covary strongly, however, with either pushup density or body mass. This could be because mean lake NDVI poorly represented lake macrophyte production, which could occur from the water column scattering the signal of submerged vegetation or from algae-dominated lakes also reflecting high NDVI values. Lake NDVI could also be conflating the growth of vegetation and turbid water. Alternatively, it is possible muskrat selection for more productive habitats occurred only during the summer and was not captured by either of our response variables. We also found some support for other hypotheses discussed, albeit less frequently, by LEK experts: early thawing and bigger lakes (Figure 3-7; Table 3.1 & Table 3.2). Specifically, we found early thawing lakes to be associated with greater pushup densities, and larger lakes to be both positively (body condition) and negatively (pushup density) associated with muskrats. Larger lakes may provide a greater diversity of depths for overwintering muskrats, but could be less productive per hectare than smaller lakes.

While we found varying levels of support for hypotheses derived from LEK, our data also demonstrated an unexpected relationship with open water season. We assumed our estimates of open water season, which varied in length by up to 22 days between lakes, to represent the length of the growing season available to macrophytes. Thus we hypothesized a positive association between open water season and muskrat density and body condition. We assumed this relationship had not been observed by LEK holders as seasonal harvesting patterns involved Vuntut Gwich'in leaving the OCF in late June and not observing the duration of the open water season (VGFN and Smith 2009). In fact, we found the open water season to be negatively correlated with both our responses. The combined importance of depth and open water suggested evaporation could significantly influence the suitability of lakes for muskrats. Monitoring by Parks Canada and Turner together with LEK suggested lake water levels can vary substantially over the summer (range Parks: -110 to + 110 cm; Turner: -18 to -53 cm; I. McDonald, Parks Canada; K. Turner, Brock University, unpublished data):

"[Before it] finished melting … and the water is level with the [beaver] dam and it stays that way all summer. Now all summer the water evaporates and pretty soon you are down."

Lakes experiencing similar climatic conditions will have longer open water seasons when receiving a greater throughput of water. The combination of higher levels of inflow and outflow, together with a longer season for evaporation, could lead to more unstable water levels that are known to increase muskrat predation risk and nutritional stress, often due to being frozen or flooded out of safer and productive habitat (Errington 1963, Clark 1994, Virgl and Messier 1996). In both the OCF and the Mackenzie Delta water level fluctuations at freeze up are particularly detrimental due to the thickness of lake ice and high overwinter mortality (McEwan 1955, Hawley 1964*b*, Ruttan 1974, Simpson and Boutin 1989).

While we found open water season to covary with both pushup density and muskrat body mass, a good deal of inter-lake variation remained unexplained and there is reason to believe that this correlation may not be causal. The significant interaction of open water season and year in explaining pushup density suggested that the negative effect of open water season was reducing with time. This could reflect how pushup densities have increased and then declined over ten years of monitoring (Figure 3-4), while simultaneously warmer summers have resulted in longer open water seasons (Figure 3-6). The importance of this correlation could decline if OCF muskrat populations return to a cyclic high while open water seasons continue to increase. Longer landscape level monitoring, together with detailed live trapping and experimental manipulations are necessary to determine the strength of this inference. Nonetheless current evidence supports open water season as an important predictor of both muskrat density and condition, even when linear temporal trends are included in the model, and our top model predicted the addition of 8 more ice free days is associated with a 60% decline in mean muskrat densities. Current weather projections suggest that the OCF will experience longer, warmer summers that will undoubtedly lead to longer open water seasons. If the negative association of muskrat abundance and the length of the open water season is maintained, climatic conditions resembling muskrat's core range could, counter-intuitively, have a negative impact on OCF muskrats.

In addition to changing ice phenologies, residents of the OCF are observing changes in its hydrology, raising additional concerns regarding the outlook of various culturally important components of this ecosystem.

"[S]he said the water is dropping, and then I heard that there's a lot of water been losing from lakes and muskrats not coming out like normal… One day I came across a tree, with these lines on it and I marked that water level, next 2 years I came back and it got much lower."

"that lake in 2 years it was… just dry, we could just go cross in skidoo, just grass! Now it's just dried right out, and now what's going on there?"

"So then we, that last time about two, three years ago we went there [to the lake]…. Water drop and water drop, and that two big island in front of there never used to be right there."

"And then these last two lakes to river, they both dried out. They were big lakes too. They were really good for rat, [now] they [are] both dried out."

Similar trends have been identified from aerial and satellite imagery (Lantz and Turner 2015), where the surface area of water in the OCF has declined by approximately 6,000 ha between 1951 and 2007 as lakes drain and form (Lantz and Turner 2015). These drainage events, as well as the thermokarst slumps that drive them, are increasingly being witnessed by Vuntut Gwich'in.

The position of LEK holders to observe multi-decade trends in ecosystem variables, together with their knowledge of ecological processes, places them in a unique position to contribute to global understanding of various climate change impacts (Riedlinger and Berkes 2001). Here we compiled our interpretation of Vuntut Gwich'in LEK and various multi-decade, multi-annual, landscape-level, and lake-level datasets to examine ongoing changes in the OCF, and how these may influence muskrat populations. While we have not observed a long term decline in muskrat populations of the OCF, residents of the neighbouring Mackenzie Delta have observed a multi-decade decline in their muskrats whose driver is not clear (Brietzke 2015). Considering rates of environmental change in Arctic wetlands, all available knowledge should be integrated to understand how this change affects ecosystem components of importance to Arctic residents.

3.7 Linking statement

In this chapter I developed a multi-faceted program for monitoring a population of Arctic muskrats. This program was built on a foundation of research objectives, conceptual models, methods, and analyses developed collaboratively with muskrat trappers from the Vuntut Gwitchin First Nation. Based on this foundation, I developed a series of long term datasets, including 100 years of fur returns, >30 years of satellite imagery, 10 years of aerial surveys, 5 years of field surveys, and local ecological knowledge interviews with trappers whose experience covers decades. These allowed for a multi-decade analysis of changing ice phenology in the Old Crow Flats with estimates of rates of change and how these will influence muskrats within the context of their cycles. While longer monitoring will almost undoubtedly shed more light on the long term ramifications of warming for muskrats, this chapter represents a monitoring result of relevance to Vuntut Gwich'in. But this monitoring program is not only producing insight of use locally, it can also contribute to a growing literature of emergent spatiotemporal properties in geographic dispersed time series of animal abundance. In Chapter 4 I demonstrate the presence of one such phenomenon in muskrats of the Old Crow Flats, a traveling wave of abundance, and evaluate various theoretically and empirically derived hypotheses to explain this emergent pattern.

4 Using demographic, genetic, and land cover data to evaluate the drivers of a traveling wave of abundance in Arctic muskrats

4.1 Abstract

Spatial patterns in time series of animal abundance, like traveling waves, offer insight into the ecology of those populations. Traveling waves of abundance are believed to be caused by four mechanisms: boundaries with hostile obstacles, invasions, epicentres of more productive or connected habitat, and directional dispersal. We used 219 populations of muskrat (*Ondatra zibethicus*) in the Old Crow Flats (OCF), Yukon, to evaluate these mechanisms. Based on 8 years of abundance estimates, we documented the first instance of a traveling wave of muskrat abundance moving from the south-south-west to the north-north-east of the OCF ($CI_{95\%}$ = [14, 36 º]) at a speed of 21.5 km year^{-1} ($CI_{95\%}$ = [18.7, 32.9 km year^{-1}]). By comparing the directionality in the wave, the genetic relatedness of 327 muskrat specimens, and the estimated landscape resistance to muskrat dispersal using Circuitscape, we found the strongest support for the boundary hypothesis in conjunction with the directional dispersal hypothesis. The boundary hypothesis was supported by the traveling wave moving away from the Old Crow Mountain range in the southwestern OCF. The directional dispersal hypothesis was supported by the maximum genetic structure (θ = 160º, Mantel's R = 0.43, $p < 0.001$), and minimized landscape resistance (125º), perpendicular to the wave. This suggested dispersal was minimized along the wave and maximized perpendicular to it. A challenge with this interpretation is that lack of genetic structure can be interpreted as either highly connected or almost entirely disconnected populations. This assumption must be tested. Knowing that obstacles and directional landscapes are the global norm

rather than the exception (e.g. mountain ranges, river valleys), traveling waves should be commonly observed in cyclic populations. Quantifying the extent, direction, and frequency of these waves, and of the synchrony that underlie them, should increase the ability of programs monitoring animal abundance to distinguish between the influence of Moran effects and dispersal. At the appropriate scale dispersal patterns should be directional, while Moran effects should not.

4.2 Introduction

Spatial patterns in time series of animal densities have long been the subject of both theoretical (e.g. Blasius et al. 1999), and empirical (e.g. Lambin et al. 1998) research, and determining what mechanisms drive these dynamics remains a fruitful source of ecological insight. A commonly documented spatiotemporal dynamic is the synchronous fluctuation in density of separate populations (Buonaccorsi et al. 2001). This spatial synchrony has been observed in viruses (Viboud et al. 2006), fungi (Thrall et al. 2001), arthropods (Klemola et al. 2006), birds (Cattadori et al. 2005), and mammals (Post and Forchhammer 2002); and is believed to result from three mechanisms: (1) dispersal of the population of interest, (2) trophic interactions with populations that are themselves synchronized, and (3) density-independent environmental perturbations (i.e. Moran effects; Liebhold et al. 2004). To a degree the spatial pattern of synchrony can indicate which of the three mechanisms is operating; a Moran effect with a sufficiently large extent (e.g. sunspots) should produce a pattern of synchrony that does not decline with increasing distance between populations (Koenig 1999, Gouhier and Guichard 2014). In contrast, synchrony that declines with distance can result from a variety of mechanisms like: the dispersal of the species of interest, dispersal of trophic interactants, or environmental variation that is itself spatially autocorrelated (e.g. temperature; Koenig 1999). For the most part, these three mechanisms work in concert (Bjornstad et al. 1999, Estay et al. 2011), complicating the task of generating ecological insight from patterns of spatial synchrony.

We can also generate ecological insight from another emergent form of spatiotemporal dynamics: traveling waves of abundance. These involve peaks of population density that travel across a spatial gradient over time and frequently occur in cyclic populations (Johnson et al. 2006, Sherratt and Smith 2008). In these cases, populations do not cycle uniformly across the landscape; instead those ahead of the wave front will be earlier in their cycle, and those behind will be later (Johnson et al. 2006, Sherratt and Smith 2008). This results in the synchronization of populations being anisotropic (i.e. directional), because populations perpendicular to the wave will be in phase while those along the wave will not. Periodic traveling waves have been documented in several systems including: field voles (*Microtus agrestis*; Lambin et al. 1998), European water voles (*Arvicola amphibius*; Berthier et al. 2014); red grouse (*Lagopus lagopus scoticus*; Moss et al. 2000), and larch budmoth (*Zeiraphera diniana*; Johnson et al. 2004). Simulations generated traveling waves in regularly oscillating populations when exposed to two mechanisms: boundaries with hostile landscape features (Sherratt et al. 2002), and invasion (Sherratt et al. 2000, Sherratt 2001). The obstacle hypothesis requires hostile landscape features that are fatal if visited by the species in question (e.g. mountains to water voles; Sherratt et al. 2002, Berthier et al. 2014). These features should generate traveling waves that travel either away, or towards, the obstacle perpendicularly (Sherratt et al. 2002). This was believed to be the driver of traveling waves of European water voles in the Jura Plateaus of France (Berthier et al. 2014). The invasion hypothesis consists either of a distinct dispersal event of the species in question (Sherratt et al. 2000), or of its trophic interactants (Sherratt 2001), and can generate waves traveling either towards or away from the invasion front (Sherratt and Smith 2008). Empirical research has revealed two additional mechanisms that can generate traveling waves. First, the epicentre hypothesis, where outbreaks spread outwards from regional foci of more productive, or more connected, habitat (Bjornstad 2002, Johnson et al. 2004, 2006). This was believed to drive outbreaks of larch budmoth in the European Alps (Bjornstad 2002, Johnson et al. 2004). Second, the directional dispersal hypothesis, where traveling waves move towards areas, or along orientations, with lower connectivity where the landscape is more resistant to dispersal (Berthier et al. 2014). Like synchrony, these hypotheses are not necessarily mutually exclusive, and differentiating among them is an ongoing challenge to better understand the drivers of spatiotemporal dynamics in animal populations.

Muskrat (*Ondatra zibethicus*) populations of the Old Crow Flats (OCF), Yukon Territory Canada (Figure 4-1), are an excellent model to study the mechanisms driving patterns in spatiotemporal dynamics. Muskrats are a wide ranging (Willner et al. 1980), well studied (Boyce 1978, Boutin and Birkenholz 1987, Simpson and Boutin 1993) species with a propensity to cycle (Elton and Nicholson 1942, Erb et al. 2000), likely in relation to mink (*Neovison vison*) predation (Haydon et al. 2001, Estay et al. 2011). Muskrats in the Old Crow Flats occupy the northernmost edge of the species' range in North America, a landscape composed of approximately 2700 shallow thermokarst lakes surrounded by tall shrub, spruce forest, and tundra vegetation (Turner et al. 2014). Given the danger associated with overland dispersal for muskrat, these shallow lakes represent thousands of semi-discrete populations. Muskrat populations of the Old Crow Flats are simple to monitor as they den exclusively in bank burrows, their only visible building activity being the construction of temporary feeding structures on lake ice (Figure 4.2; Simpson et al.

1989). These pushups are composed of macrophytic vegetation built over holes in lake ice, sheltering the open water for use as breathing and resting stations throughout the winter. As snow melts in the spring exposing lake ice, pushups are visible from an aircraft; when the ice melts, pushups collapse ensuring no evidence of this index remains in subsequent years. Capture-mark-recapture studies confirm that pushups can serve as an index of relative muskrat density, although quantifying the precise ratio of muskrats to pushups and its inter-annual variability would benefit from further investigation (McEwan 1955, Stevens 1955, Martin 1974, Ruttan 1974, EPEC Consulting Western Ltd. 1976, Simpson et al. 1989). We have been monitoring changes in this index of muskrat density for 8 years (2008-2015) in 219 lakes located across this 5600 km^2 landscape. This simple metric of mammal abundance represents an ongoing opportunity to empirically test the predictions of established hypotheses regarding population synchrony and traveling waves.

The dynamism of the Old Crow Flats landscape also contributes to its utility for testing these hypotheses. Dramatic changes in this thermokarst landscape provided quasi-experimental manipulations to better explore predictions of traveling wave theory. In June 2007 Zelma Lake, a ~12km^2 lake in the centre of our study area, catastrophically drained losing 80% of its volume over several days when its banks were breached and connected to a nearby creek (Turner et al. 2010). This dramatic reduction presumably resulted in a mass dispersal of muskrats who previously occupied Zelma. This invasion front provided an opportunity to distinguish between the theoretical drivers of traveling waves. The invasion hypothesis predicts that major dispersals of single species (Sherratt et al. 2000) or multi-trophic systems (Blasius et al. 1999) can result in regular waves of abundance traveling along the axis of the invasion (Sherratt and Smith 2008), which was presumably radiating out from Zelma Lake. But the Old Crow Flats is also surrounded by the Old Crow, Richardson, and British mountain ranges which give the Flats a NW-SE orientation (Figure 4-1). According to the obstacle hypothesis, these hostile landscape features could produce waves traveling perpendicularly to the orientation of the landscape (e.g. SW-NE; Sherratt et al. 2002). The epicentre hypothesis predicts that a traveling wave should emanate from lakes with higher connectivity, higher maximum growths rate, and lower minimum growth rates; and travel towards lakes with less connectivity (Johnson et al. 2006). Finally, the directional dispersal hypothesis predicts that habitat connectivity in the Old Crow Flats should be greater along the axis of propagation of a traveling wave than its orthogonal.

To date, few studies has been able to empirically compare the above hypotheses (Sherratt and Smith 2008). To do so, we used our time series of muskrat pushup densities and land cover maps of the Old Crow Flats to: (1) document the landscape-level synchrony of muskrat population dynamics; (2) test for the presence of travelling waves of abundance, particularly unidirectional waves and radial waves emanating from Zelma Lake; (3) map the distribution of maximum, median, and minimum lake muskrat productivity in relation to any travelling waves; and (4) quantify lake connectivity and landscape resistance and determine whether they are anisotropic. In addition, we analysed the genetic relatedness of muskrat tissue samples collected across the Old Crow Flats (Figure 4-1) to determine whether gene flow, and by extension dispersal, was directional. We expected to detect a traveling wave driven by the invasion hypothesis, due to a major dispersal event extending radially from the area of Zelma Lake. We predicted this would create strong regional synchrony, weak global synchrony, and a circular traveling wave. If the invasion of Zelma muskrats, and/or their predators, was the driver of a traveling wave, we expected habitat productivity, connectivity, landscape resistance, and muskrat genetic relatedness to have no relation to the direction of wave flow.

4.3 Methods

4.3.1 Study site

The Old Crow Flats, located in the northern Yukon Territory, Canada (68º05’ N, 140º05’ W; Figure 4-1), is a 5600km^2 Ramsar wetland of international importance situated 200 km west of the Mackenzie Delta (Brock et al. 2007). The OCF contain over 2700 thermokarst lakes, the majority of which are small, flat bottomed, and shallow (< 2 m deep) (Labrecque et al. 2009). Formerly a large glacial lake, the long axis of the Old Crow Basin is oriented northwest to southeast and the basin itself is surrounded by the British, Richardson, and Old Crow mountains. The basin is composed of two physiographic units: the Old Crow Flats and Old Crow River valley, the latter being 40-50m lower than the former based on its continuous incision into the surrounding sediment following the last glacial maximum (Labrecque et al. 2009). These river and creek valleys contain the denser stands of terrestrial vegetation, including black and white spruce (*Picea mariana* and *P. glauca* respectively); while white birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*), and trembling aspen (*Populus tremuloides*) are common in successional stands near lakes; and shrub birch (*Betula glandulosa*) and willow (*Salix spp.*) tend to be found towards the tundra (Simpson et al. 1989). The ecotone between boreal forest and tundra crosses the Flats, with the forest transitioning to tundra from SW to NE (Turner et al. 2014). The growing season within the OCF is short due to its northern latitude, with an average of 72.6 ± 5.7 frost free days (Simpson

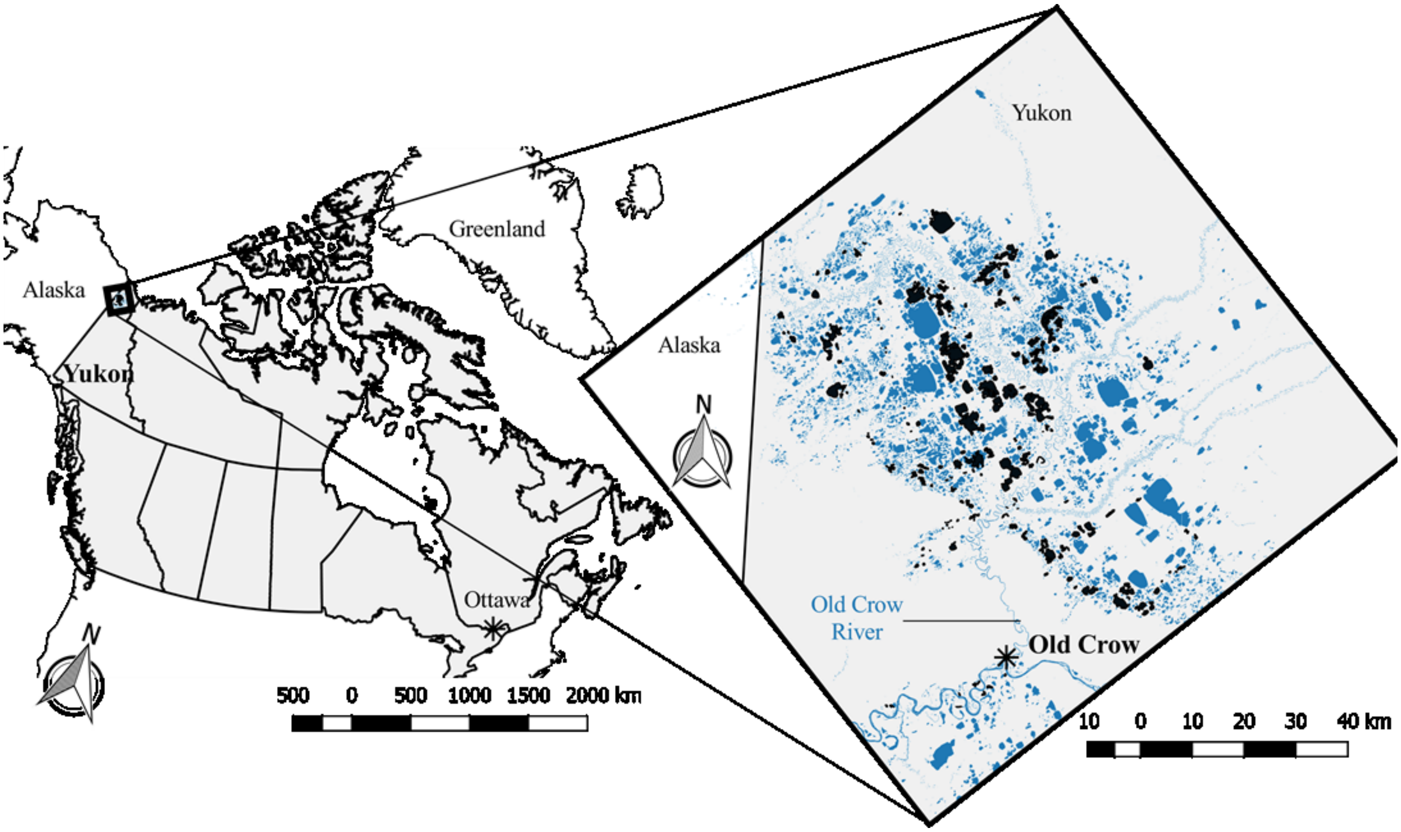


Figure 4-1: The location of the community of Old Crow and the Old Crow Flats (68º05' N, 140º05' W) in Yukon Territory, Canada. Our 219 study lakes are indicated with black grills.

and Boutin 1993). Lakes of the Old Crow Flats dominated by submergent vegetation, particularly *Potamogeton* spp. and *Myriophyllum* spp. It contains little emergent vegetation, which is preferred by muskrats as a forage and lodge building material, so here muskrats exclusively construct bank burrows rather than lodges.

4.3.2 Index of muskrat density

We used the density of muskrat pushups constructed on ice as an index of muskrat density in lakes of the Old Crow Flats. Pushups are domed structures of frozen vegetation that muskrats will pile over holes in the winter lake ice (Figure 4.2; Stevens 1955). Pushups can be identified by the presence of vegetation and a plunge hole. When the lake ice melts, pushups sink. As a structure that is constructed and destroyed annually, pushups respond to annual variations in muskrat abundance (Simpson et al. 1989). Since 2008, we have been flying annual surveys of the Old Crow Flats during the spring melt counting muskrat pushups on, depending on ice conditions, up to 219 study lakes (Figure 4-1). While not as precise as estimates derived from intense live capture surveys, counting pushups enables the rapid (2-3 days) estimation of relative muskrat abundance in hundreds of lakes across the 5600 km^2 OCF. In the years 2008-2012, surveys were conducted by two observers recording counts on a lake-by-lake basis from a Cessna 206 at an average flight speed of 125 kph and an average altitude of 350 ft. In the years 2012-2015, surveys were conducted based on aerial photographs collected using a window mounted camera on a Cessna 172 with a ground separation distance of 20 cm. During the overlap year of 2012, photography counts were compared to aerial counts and correlated strongly ($r = 0.92$). The number of muskrats per pushup has been estimated from previous live trapping studies in the region, and includes 2.1 (Ruttan 1974), 2.2 (Simpson et al. 1989), and 3.4 in the OCF (Martin 1974); and 1.0 (Stevens 1955), 1.7 (EPEC Consulting Western Ltd. 1976), 2.4 (Hawley 1964*a*, *b*), and 2.9 in the Mackenzie Delta (McEwan 1955). The variability of this relationship, particularly its density-dependence and inter-annual variability, would benefit from more detailed investigation. Nonetheless all evidence suggests this correlation is monotonic (i.e. more pushups means more muskrats), and since pushups per km^2 can vary across four orders of magnitude they are useful coarse indicators of relative muskrat densities. Pushup densities were lognormally distributed, and were ln transformed for analyses. We found pushup densities in small sample lakes (i.e. $< 0.1 km^2$) to be highly variable, and so limited our analyses to the 139 largest (> 0.1 km^2) lakes to best represent regional changes in muskrat densities across the Old Crow Flats between 2008 and 2015.

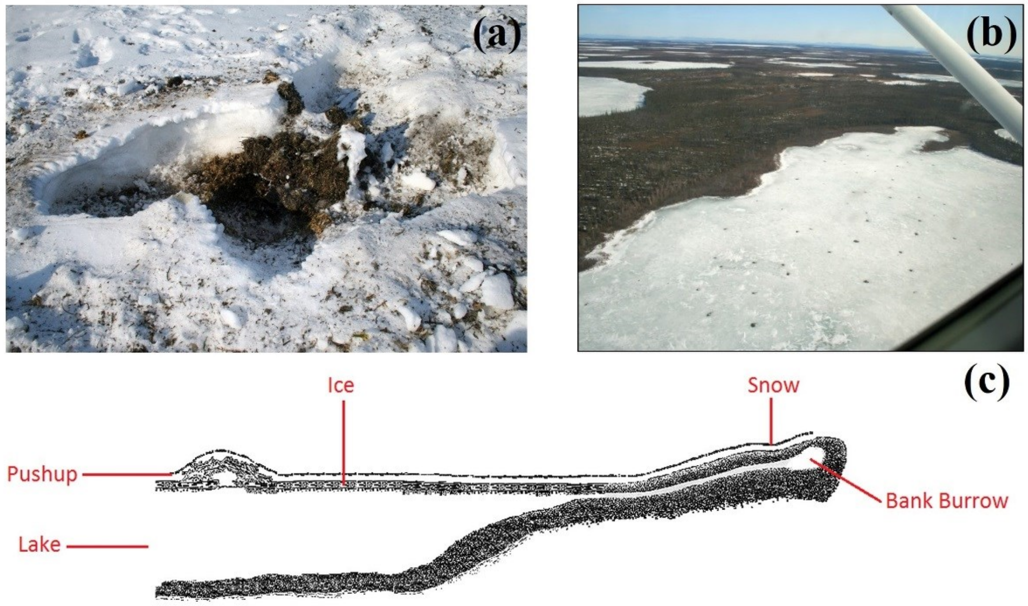


Figure 4-2: Muskrat pushups (A) when opened by a wolverine (B) when visible from the air, and (C) when visualised from the side. In the spring pushups can serve as an index of muskrat density (diagram adapted from: Aleksiuk 1987).

4.3.3 Landscape-level synchrony of muskrat populations

We estimated the total number of pushups in the Old Crow Flats by calculating the overall pushup density in our study lakes, and multiplying this by the surface area of water in the Flats. The total area of water was estimated using a supervised land cover classification based on SPOT satellite imagery. We estimated 95 % confidence intervals of the total pushup abundance by bootstrapping individual lake densities over 10,000 iterations. We estimated lake-to-lake synchrony of muskrat population dynamics by calculating a Pearson correlation coefficient between population growth rates ($r_t = \log[N_T + 1] - \log[N_{T-1} + 1]$) for each lake pair (Bjornstad et al. 1999, Buonaccorsi et al. 2001). We also measured the overall synchrony of muskrat populations by taking a mean Pearson correlation coefficient, and calculated its significance with 9999 Monte

Carlo randomizations (Gouhier and Guichard 2014). To examine the spatial scale of synchrony between lakes, we used multivariate variograms and identified the nugget (max synchrony), range (distance synchrony levels out), and sill (base synchrony level) of synchrony in muskrat population dynamics.

To examine how synchrony varies along different orientations in the Old Crow Flats, we followed the methods of Lambin *et al.* (1998) and calculated distances between lake pairs along 360 single dimensional axes projected at angles of 0 to 359 degrees from the north. These axes pass through the centroid of all study lakes, and reduce the two dimensional Euclidean distance between lake pairs to a single dimension (e.g. at 0 º rotation, the pairwise distance between lakes will be their north-south distance; at 90 º rotation, it would be their east-west distance). The axis where synchrony declined most rapidly with increasing geographic distance represented the orientation where space presented the largest obstacle to the movement of muskrats and/or their predators (Berthier et al. 2014). We tested whether the range of synchrony differed along different orientations by calculating spline correlograms for 72 different bearings from 0 º to 360 º north, and by estimating the x intercepts of these correlograms as the mean bin distance of the first bin where synchrony was zero or less. All reported intervals are 95 % confidence intervals.

4.3.4 Modeling travelling waves

Following the methods of Lambin *et al.* (1998) and Berthier *et al*. (2014), we tested whether a traveling wave could better explain the spatial distribution of muskrat density in the Old Crow Flats between 2008 and 2015. As a frame of reference we calculated a location-independent, general additive model (GAM) for all our study lakes:

$$D(i,t) = m + s[t] + e(i,t) \tag{4.1}$$

Where $D(i,t)$ is the estimated pushup density of lake i in year t, m is the mean pushup density of all lakes, $s[t]$ is the smoothing spline modeling the change in pushup density through time, and $e(i,t)$ is the error associated with each lake at each time point. We compared this model to a GAM that incorporated either (a) a radial front, constant speed, traveling wave moving away from Zelma Lake, or (b) a linear front, constant speed, traveling wave moving towards an angle of θ from north. These traveling waves build upon the base GAM by advancing or retreating a lake's density estimate based on its location. In the case of the radial wave, lake pushup density was modeled as:

$$D(i,t) = m + s[t + rd(i)] + e(i,t) \tag{4.2}$$

Where r is the inverse speed of the wave and d is the radial distance of site i from the centroid of Zelma Lake. Similarly, in the case of the unidirectional wave front, lake pushup density was modeled as:

$$D(i,t) = m + s[t + rd(i,\theta)] + e(i,t) \tag{4.3}$$

Where d is the uni-dimensional distance of site i from the centroid of the Old Crow Flats after a rotation of θ. For more details see (Bjornstad et al. 1999).

We selected the smoothing spline with degrees of freedom (d.f.) that minimized the Akaike Information Criterion (AIC) in the base model (equation 4.1) for the traveling wave models (equations 4.2 & 4.3). We selected from 18,000 traveling wave models whose wave speeds varied from 1 to 40 km/year, and whose orientation varied from 0 º to 360 º by two degree increments. We calculated maximum likelihood estimates of wave speed and orientation by minimizing the

AIC of these models, and compared the AIC of the two traveling wave models and the base GAM with no wave.

4.3.5 Mapping lake productivity and aquatic connectivity

We mapped lake muskrat productivity by taking the maximum, median, and minimum growth rates on a lake-by-lake basis. We quantified lake connectivity by mapping a 500 m buffer around each study lake and by calculating the proportion of this buffer that was water. We compared how lake muskrat productivity and connectivity varied along the axis of any modelled travelling waves.

4.3.6 Spatial genetic pattern

Between 2008 and 2012 we collected tissue samples for 327 individual muskrats originating from 21 different lakes within the OCF, and assigned each of these individuals the geographic coordinates of the centroid of its lake of origin (Figure 4-3). We extracted DNA from muscle tissue using the QIAGEN DNeasy tissue kit and amplified 9 microsatellite loci developed for muskrats (Oz06, Oz08, Oz16, Oz17, Oz27, Oz34, Oz41, Oz43, and Oz44) following the procedure described by Laurence et al. (2009). Genome Quebec sequenced our PCR products using an ABI-3730 capillary sequencer. We scored each locus up to three times using GeneMarker v2.4.2 (SoftGenics), and removed locus Oz08 because it was monomorphic in our sample (Giroux-Bougard 2014).

To quantify spatial similarities in genetic patterns we computed pairwise genetic distances between lakes using the proportion of shared allele distance (*Dps*; Bowcock et al. 1994) and correlated these genetic distances with Euclidean distances between lakes using a Mantel

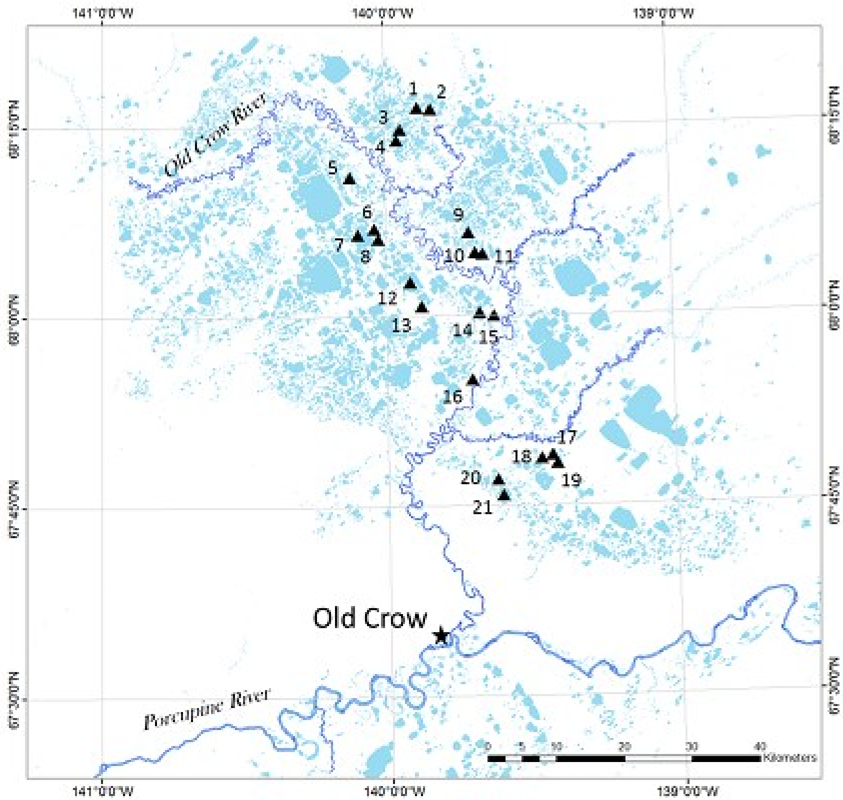


Figure 4-3: The sample distribution of muskrats used for the estimation of genetic distances. Lakes are in light blue while rivers and creeks are in blue (Giroux-Bougard 2014).

correlogram. We estimated the significance of the Mantel coefficient in each distance category using 9999 permutations. We interpreted the minimum distance of the first distance class where the Mantel coefficient was not significantly different from zero as representing the spatial extent of genetic structure in the Old Crow Flats. Beyond this distance, any pair of muskrats were, on average, as genetically related as any randomly selected pair of muskrats from the Old Crow Flats (Vekemans and Hardy 2004). In effect, this spatial extent indicated the distance at which muskrat dispersal still has some sort of homogenizing effect, whether through stepping stone or long-distance dispersal events (Berthier et al. 2014). We examined the directionality of this gene flow as well using Mantel correlograms based on inter-lake geographic distances that were weighted using the degree of alignment of the lake pair with an axis of rotation. Similar to above, we calculated overall Mantel coefficients, and the spatial extent of genetic structure. This directional analysis determined angles of rotation in the Old Crow Flats where gene flow is more or less distance-dependent. Orientations where genetic relatedness is not distance-dependent suggest that either populations along this axis are highly connected by gene flow irrespective of the distance between them, or they are essentially unconnected by gene flow and differences emerge via genetic drift (Berthier et al. 2014). The Old Crow Flats is greater than 50 km wide at its narrowest point, and muskrats in the OCF have demonstrated genetic autocorrelation up to a distance of 9 km (see section 4.4). As a result we believe that lack of distance dependence likely indicates isolation rather than complete homogenization.

4.3.7 Landscape resistance

We used Circuitscape 4.0 to model the resistance of the Old Crow Flats to muskrat dispersal along different orientations (e.g., west to east, north to south; Shah and McRae 2008). Circuitscape applies electrical circuit theory to model the connectivity of habitat patches in a matrix of various land cover types. Each habitat patch, composed of a contiguous set of cells with the same land cover classification, is treated as a node in an electrical circuit; and connections between adjacent habitat patches are treated as electrical resistors. The magnitude of the resistance of these resistors is analogous to the degree to which that habitat type is a barrier to dispersal. Once a land cover map is converted to an electrical circuit composed of a grid of various resistors, Circuitscape simulates the application of a voltage differential from one grid edge to the other (e.g., west-east, north-south). In effect, this models the resistance between lake pairs based on a random-walk disperser; effective resistance increases with the frequency and value of resistors that are crossed, but decreases with the number of additional pathways between lakes (McRae et al. 2008). This

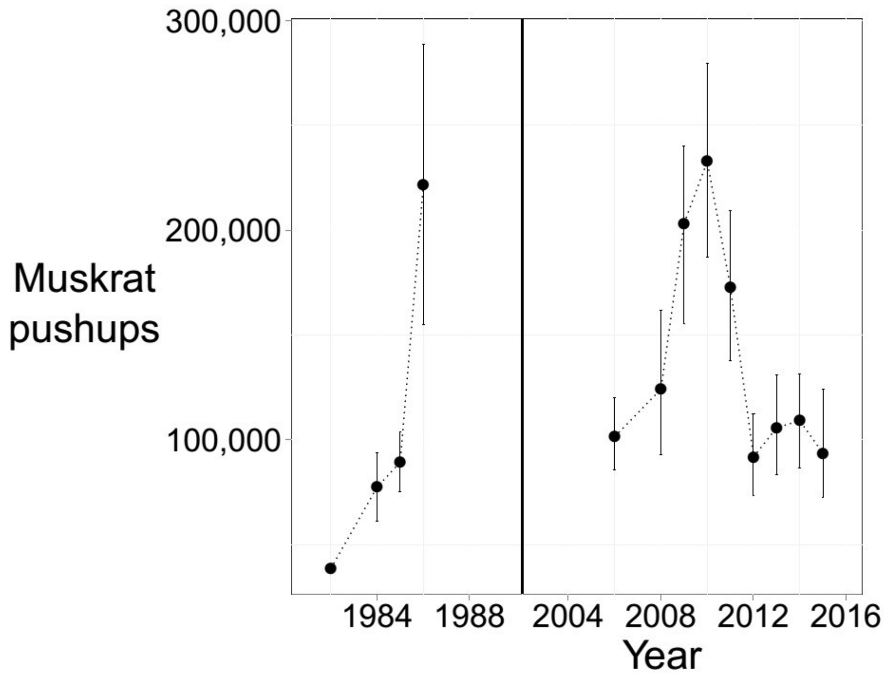


Figure 4-4: Estimates of the abundance of muskrat pushups in the Old Crow Flats based on annual spring aerial surveys. Surveys from 1984-2006 were based on a transect method (Simpson et al. 1989), while those of 2008-2015 were based on a sample of lakes.

method is particularly adept at identifying pinch-points, where many dispersers must travel to cross the landscape (Shah and McRae 2008). To parameterize our Circuitscape analysis, we used a land cover map of the Old Crow Flats generated through supervised classification based on aerial, LANDSAT, and SPOT imagery (for more details see: Turner et al. 2014). We estimated the resistance values of the different land cover types (i.e. forest, water, etc.) through PEST optimization using Circuitscape (see: Giroux-Bougard 2014). To determine whether the Old Crow Flats is more resistant to muskrat dispersal in some orientations versus others (e.g. west to east vs. north to south), we calculated an average resistance value for crossing the whole landscape along 180 orientations. We created 180 resistance maps by rotating the original land cover raster clockwise a degree at a time. We processed each raster in Circuitscape by simulating a current traveling through the map moving from left to right, and top to bottom. This produced two mean resistance values reflecting these two axes of travel. We added a-5293 x 5293 pixel buffer with a resistance value of 40,000 to the original map to spread out the current before it reached any landscape features of the OCF.

4.4 Results

Estimates of muskrat pushup abundance in the Old Crow Flats was highly variable inter-annually, from a maximum of ($CI_{95\%}$ = [190,000, 280,000]) in 2010 to a minimum of ($CI_{95\%}$ = [70,000, 110,000]) pushups in 2012 (Figure 4-4). Using Simpson *et al.*'s (1989) ratio of 2.19 muskrats per pushup, this corresponded to minimum and maximum muskrat abundance estimates of ($CI_{95\%}$ = [410,000, 610,000]) and ($CI_{95\%}$ = [160,000, 250,000]) respectively. From 2008 to 2015, estimates of lake pushup density varied from a minimum of 0 to a maximum of 1232 pushups/km^2 (Figure 4-5). The mean synchrony of muskrat growth rates for all lake pairs was 0.11 ($p < 0.0001$). According to the isotropic Pearson correlogram of synchrony in growth rates (Supplementary Figure 7.5), the spatial range of this synchrony was approximately 10 km, with a nugget synchrony value of 0.3. There was evidence of directionality in both the range of synchrony between muskrat growth rates, and synchrony's rate of decline as inter-lake distance increased. Synchrony declined most rapidly with inter-lake distance after projecting lakes onto an axis 35 º from north (Mantel's R: -0.13), and did not decline at all after projecting lakes onto an axis 104 º from north (Mantel's R: 0.01). The spatial extent of synchrony was greatest, 18.3 km ($CI_{95\%}$ = [2.9, 23.3]), at 25 º from north. The extent of synchrony was at its minimum extent, 5.4 km, at 125 º from north, although at this orientation synchrony essentially did not decline with distance between lakes so estimates

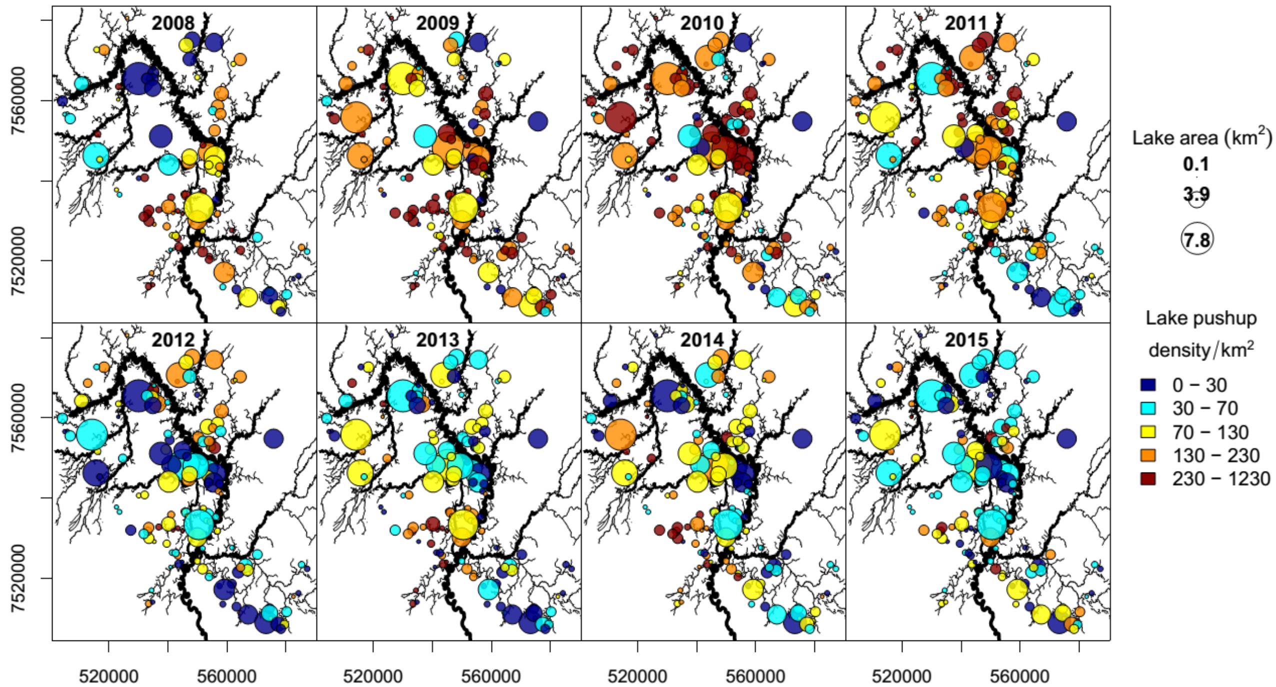


Figure 4-5: The density of pushups in lakes of the Old Crow Flats, by year, from spring aerial surveys. Colours represent density and are lognormally scaled. Circle area is proportional to lake area. Number of survey lakes vary by year (n = 99, 118, 139, 136, 139, 136, 136, 138). Only the river and creeks of the Old Crow Flats are displayed as a background.

of its extent were highly variable ($CI_{95\%}$ = [0, 40.9]; Figure 4-6).

We did not find support for a traveling wave emanating from Zelma Lake (base GAM AIC = 3542; radial wave AIC = 3583), but we did find support for a unidirectional traveling wave (best AIC = 3477; Δ65AIC). The best GAM without a traveling wave used a smoothing spline with 5 d.f. with an adjusted r^2 of 0.15. The GAM that included the unidirectional traveling wave also had 5 d.f., and an adjusted r^2 of 0.21 (Supplementary Figure 7.6). The maximum likelihood estimates of the angle of the traveling wave was 28 º ($CI_{95\%}$ = [14, 36 º]) from the north with a speed of 21.5km year^{-1} ($CI_{95\%}$ = [18.7, 32.9 km year^{-1}]). The direction of the wave was SSW to NNE,

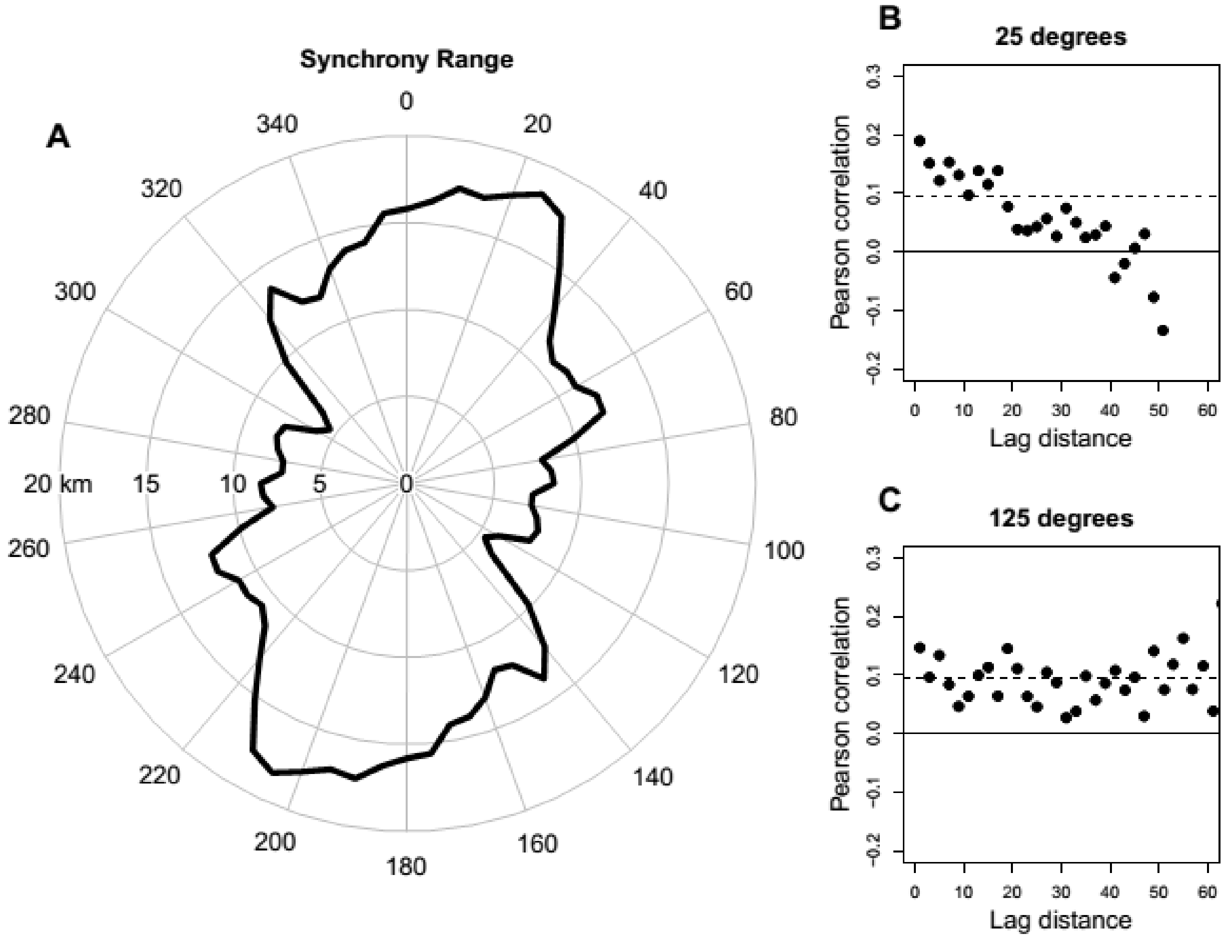


Figure 4-6: The spatial extent of synchrony in muskrat growth rates was greatest between 20º and 40º from north, and smallest between 100 and 130º. Distances are in kilometres. The range of synchrony is the x intercept of the spline correlogram using unidimensional lake distances along 72 axis rotated 360º by 5º intervals. A) A polar plot of the range of synchrony in km along single axes; B) the maximum synchrony range occurs along an axis 25º from north; and C) does not decline with distance along an axis 125º from north.

traveling approximately perpendicular to the long axis of the Old Crow Flats, originating in the Old Crow Mountain range and dissipating in the British and Richardson Mountains.

We found no relationship between a lake's position along this traveling wave and its muskrat growth rates (maximum $CI_{95\%}$ = [-0.17, 0.16]; median $CI_{95\%}$ = [-0.13, 0.20]; minimum ($CI_{95\%}$ =

[-0.07, 0.26]). Lake connectivity was positively correlated with lake position along the traveling wave ($CI_{95\%}$ = [0.23, 0.54]), i.e. lakes NNE had more water around them than lakes in the SSW of the Old Crow Flats. This pattern however was primarily driven by study lakes within 20 km of the centre of the Flats and not by those in the extreme NNE (Supplementary Figure 7.7). We found the genetic distance of muskrat populations in the Old Crow Flats increased with increasing distance between lakes overall (Mantel's $R = 0.40$, $p = 0.0001$); but when examined by distance category this genetic structure was only present up to ~8.7 km ($R = 0.12$, $p = 0.02$); beyond that distance genetic similarity did not change with increasing inter-lake distance. This spatial structure of genetic relatedness of muskrats also varied based on orientation. Non-significant Mantel coefficients indicated that there was no spatial structure in the genetic relatedness of muskrats along axes rotated between 15 - 65 º and 195 – 245 º from north. Approximately orthogonal to these orientations were the strongest indications of genetic structure, including the largest Mantel coefficients ($\theta = 160$ º, $R = 0.43$, $p < 0.001$) and the largest spatial extents of structure ($\theta = 140$ º, 10.8 km; Figure 4-7). According to 180 Circuitscape simulations, the mean resistance for a muskrat traveling across the Old Crow Flats landscape was maximized along an axis 36 º from north, and minimized along an axis 125 º from north. This orientation of maximum landscape resistance coincided with the most rapid decline in the synchrony of muskrat growth rates and the least structure in muskrat genetic similarity (Figure 4-8).

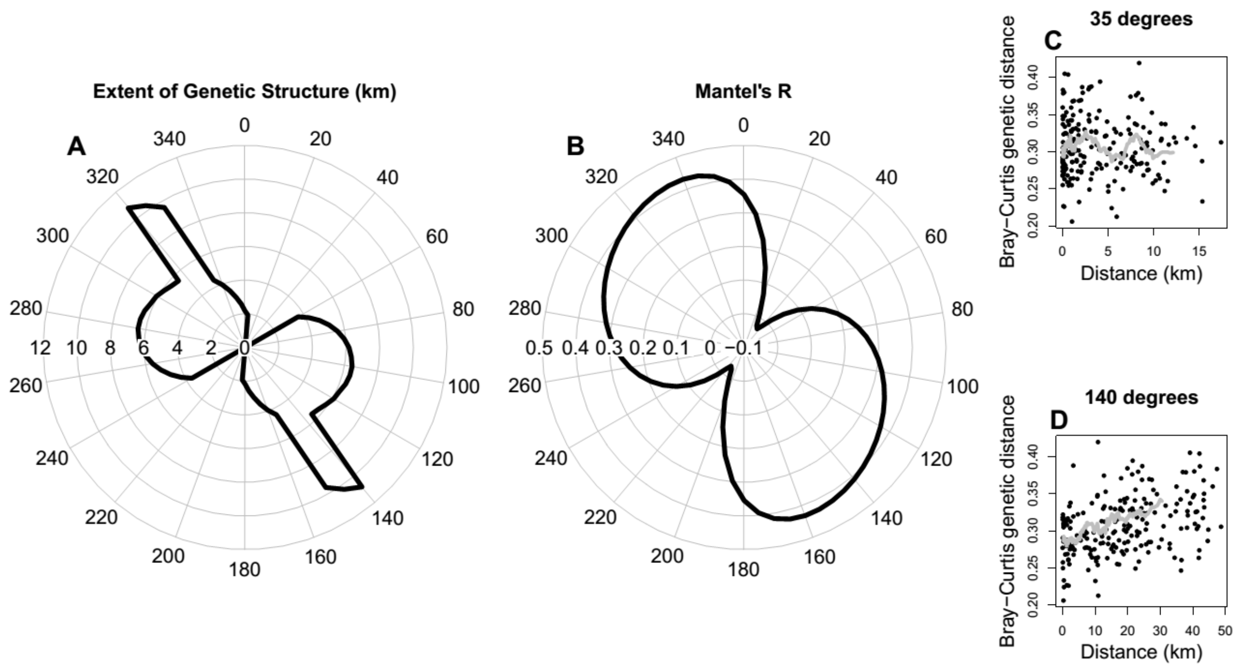


Figure 4-7: Directionality in the extent of genetic structure, and the Mantel's R between genetic relatedness and inter-lake distance, in the Old Crow Flats. The extent of genetic structure was calculated as the minimum distance of the first distance class where the Mantel coefficient was not significantly different from zero. Unidimensional Mantel correlograms were calculated based on inter-lake geographic distances that were weighted using the degree of alignment of the lake pair with 72 axes of rotation, beginning at north (0º) and increasing by 5º increments. A) A polar plot of the extent of muskrat genetic structure in km; B) the Mantel's R between genetic distance and inter-lake distance; C) muskrat genetic distance does not increase with geographic distance along an axis 35º from north; but (D) it does increase along an axis 140º from north.

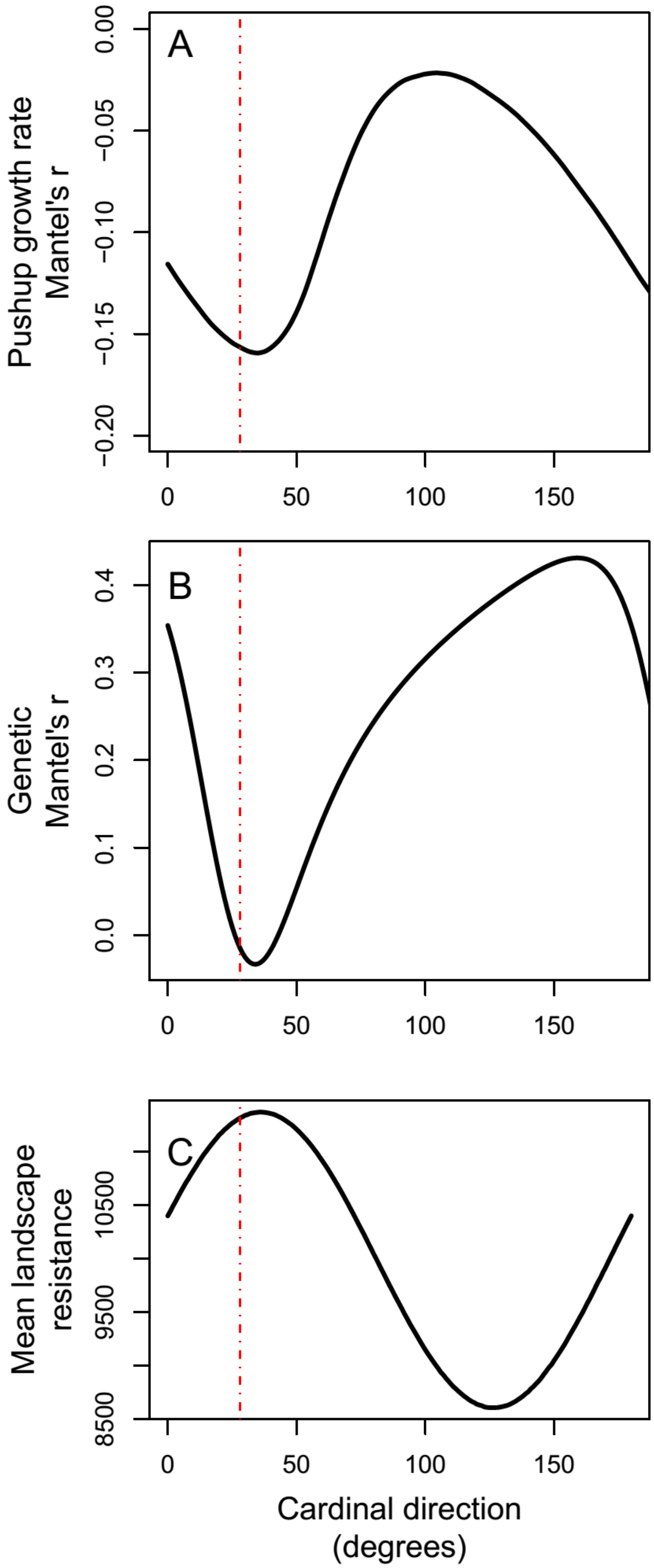


Figure 4-8: The degree that synchrony declines with distance varies according to the cardinal direction considered, and synchrony declines most quickly in directions where landscape resistance is greatest. Panels include: Mantel correlations between synchrony of (A) muskrat pushup densities growth rates and geographic distances; (B) Mantel correlations between genetic distances (Dps) and geographic distances; and (C) mean landscape resistance of the Old Crow Flats after projecting lake locations onto an axis that rotates clockwise up to 180 degrees from north (0 = north). Red vertical lines indicate the orientation of the maximum likelihood estimate of the traveling wave

4.5 Discussion

Here we found evidence for the presence of a traveling wave of muskrat abundance moving from the south-south-west to the north-north-east of the Old Crow Flats at a speed of 21.5km year^{-1}. This analysis explicitly considered a variety of theoretically and empirically derived hypotheses for the generation of traveling waves, and found the boundary hypothesis in conjunction with the directional dispersal hypothesis, to be the most strongly supported at present. This analysis applied novel approaches to quantifying landscape connectivity to quantify a congruence of directionality in demographic, genetic, and landscape resistance patterns. This provided the strongest evidence to date for the importance of directional dispersal in the generation of traveling waves, with limited animal dispersal in the direction of propagation of the wave.

We found several lines of evidence supporting the presence of a traveling wave in muskrat growth rates in the OCF. While overall synchrony pattern indicated low levels of synchrony across the OCF as a whole, we found lakes within 10 km of another to be more synchronized (Supplementary Figure 7.5). This suggested that there are at least two scales of synchronizing factors in the OCF, one operating weakly across the landscape and one operating more locally (Liebhold et al. 2004). The presence of anisotropy in the decline and scale of synchrony (Figure 4-6) suggested some directional pattern associated with these local synchronizing factors. We found this directionality of synchrony in growth rates (35 º) corresponded approximately with the direction of our optimal traveling wave (28 º) as predicted by traveling wave theory (Bjornstad et al. 1999). However (Berthier et al. 2014) predicted that the spatial extent of synchrony will be smallest in the direction of the wave, while we observed the opposite (Figure 4-6A). This is likely because we did not observe any decline in synchrony in growth rates along the axis perpendicular to the wave (Figure 4-6C). As a result, it is difficult to distinguish local synchrony from regional synchrony and could be interpreted as local synchrony having spatial extents approaching 0 or ∞ (Bjornstad et al. 1999). Regardless we are cautious in interpreting this wave as our model described a single wave in an animal population that could be cyclic (Figure 4-4). Assuming muskrat populations of the Old Crow Flats are cyclic (as seen in Chapter 3 and regionally in: Elton and Nicholson 1942), traveling waves could also be periodic and should be expected to occur 13-31 years following the first. Multi-decade monitoring is necessary to test this prediction.

In our comparison of hypothetical mechanisms driving this traveling wave we found little support for the invasion or epicentre hypothesis. Following the catastrophic draining of one of the largest muskrat trapping lakes in the OCF, Zelma Lake, we expected to observe a circular wave emanating from Zelma. In fact, the radial wave model performed poorly compared to the base model with no wave, and particularly compared to the unidirectional wave model. This uni-directional wave, visible among the significant inter-lake variation in Figure 4-5, does not correspond to the invasion hypotheses. Similarly we found no support for the predictions of the epicentre hypothesis, specifically that muskrat growth rates should vary along the direction of propagation of the wave (Johnson et al. 2004, Berthier et al. 2014). This suggests that it is neither a one-off event of muskrat dispersal, nor a region of highly productive muskrat habitat, that are driving the traveling wave in the OCF. We did find that lake connectivity, in terms of surrounding water, varied along the axis of wave propagation; but it behaved contrary to our prediction. We found habitat connectivity was highest at the end of the wave, rather than its origin, further weakening the epicentre hypothesis (Johnson et al. 2006).

We did find support for hypothesis that landscape obstacles could drive this traveling wave. Specifically, we found the traveling wave moved perpendicularly away from the Old Crow Mountain range in the southwestern edge of the OCF. Traveling waves moving away from landscape obstacles have been observed before (Moss et al. 2000, Berthier et al. 2014), suggesting this mechanism could be more common. Simulations identifying the obstacle hypothesis suggest that obstacles should represent a sink for the animal in question (i.e. individuals should be lost to that habitat, and not simply avoiding it; Sherratt et al. 2003). Examining these assumptions requires habitat specific survival based on live trapping surveys.

In addition, we combined both genetic relatedness and landscape resistance to dispersal to find stronger evidence that directional dispersal is driving this traveling wave. While directional dispersal has been suggested to be important for the generation of linear traveling waves (Sherratt et al. 2000), to our knowledge Berthier *et al.* (2014) have been the only ones to empirically link directional dispersal and a traveling wave. They used genetic relatedness to show directional dispersal in European water voles with greater genetic structure in the direction of wave propagation. We found genetic structure to be greatest in the direction perpendicular the traveling wave, suggesting dispersal was greater along this axis than in the direction of the wave. A challenge with this interpretation is that lack of genetic structure can be interpreted as either lakes being highly connected by gene flow regardless of the distance between them, or as lakes being mostly disconnected with genetic differences being driven primarily by drift rather than dispersal (Berthier et al. 2014). It is important to test this assumption more closely through additional genetic samples to improve our confidence in this interpretation.

Here we have documented, to our knowledge, the first recorded instance of a traveling wave of muskrat abundance. This adds to the list of waves in other species, including: field voles, European water voles, red grouse, and larch budmoth (Lambin et al. 1998, Moss et al. 2000, Johnson et al. 2004, Berthier et al. 2014). These emergent patterns of population dynamics provide insight into the mechanisms driving animal ecology at a landscape scale, and should become increasingly visible with the growing number of spatially dispersed time series of animal abundances available (e.g. http://livingplanetindex.org/). Using a combination of demographic, genetic, and land cover data we found the primary driver of traveling waves of muskrat abundance was most likely directional dispersal as a result of landscape obstacles, both impermeable (e.g. mountains) and of varying permeability (e.g. wetlands to shrubs to forests). Based on this premise, and knowing that directional landscapes are the global norm rather than the exception (e.g. mountain ranges, river valleys), we believe traveling waves should be a commonly observed pattern in cyclic animal populations. Quantifying the extent, direction, and frequency of these waves, and the directional patterns of synchrony that underlie them, should increase the ability of passive monitoring schemes of animal abundance to differentiate between synchrony patterns that are driven by Moran effects and those that are driven by dispersal. At the appropriate scale dispersal patterns should be anisotropic while Moran effects should not.

4.6 Linking statement

This chapter combined data from satellite imagery, aerial surveys, and a community carcass collection program to contribute to our understanding of the spatiotemporal dynamics of muskrat populations. It documented the first recorded instance of a traveling wave of abundance in muskrats, and found the strongest support for a combination of obstacles and directional dispersal as mechanisms causing the wave. Locally relevant environmental indicators like muskrats provide an opportunity to generate spatially distributed time series of abundance that can contribute to the development of population biology. A noteworthy synergy from participatory monitoring is the combination of spatial structure in abundance estimates and genetic relatedness, the latter being accessible through the participation of interested hunters, trappers, and fishers. While economically or recreationally harvested wildlife offer one locally relevant environmental indicator, recreational ecosystem services in general provide numerous other potential indicators. These are particularly applicable in urban regions, where residents will more frequently interact with their local ecosystems in non-consumptive rather than consumptive activities. These indicators provide another method of quantifying environmental change in a manner that is compelling for residents. This is the case in Chapter 5, where I examined historical and projected impacts of climate warming on recreational opportunities on the Rideau Canal Skateway in Ottawa.

5 Declining availability and use of outdoor recreation on the Rideau Canal Skateway in Ottawa, Canada

Climate change is, and will continue, altering the supply of ecosystem services (Millennium Ecosystem Assessment 2005, Schröter et al. 2005). Cultural ecosystem services provide important societal benefits but are challenging to operationalize (Millennium Ecosystem Assessment 2005, Chan et al. 2012, Daniel et al. 2012, Milcu et al. 2013). The impact of warming on these cultural activities, such as ice skating, are likely to be among the most broadly obvious and compelling impacts of climate change (Visser and Petersen 2009). Here we report that the availability and benefits of skating on the world's largest outdoor ice skating facility: declined from 1972 to 2013, were strongly dependent on weather, and are projected to continue declining with an accelerated rate between 2020-2090.

Ecosystem services, or the "benefits people obtain from ecosystems", can be categorized as provisioning, regulating, supporting, or cultural services (Millennium Ecosystem Assessment 2005, Daniel et al. 2012). Cultural ecosystem services, or "non-material benefits", include aesthetics, spirituality, education, and recreation. These are often intangible, subjective, and difficult to quantify (Millennium Ecosystem Assessment 2005, Gee and Burkhard 2010, Chan et al. 2012, Daniel et al. 2012, Norton et al. 2012, Milcu et al. 2013), particularly in the context of human benefits (Daniel et al. 2012). Cultural ecosystem services are generally underrepresented within ecosystem service research (Gee and Burkhard 2010, 2013), and climate change projections (Schröter et al. 2005). Yet these services are amongst the most recognized and acknowledged by the general public (Visser and Petersen 2009, Chan et al. 2012, Daniel et al. 2012, Milcu et al. 2013).

We projected local weather-mediated declines in the availability and benefit of a recreational cultural ecosystem service: outdoor ice skating. Clearly ice (Weyhenmeyer et al. 2011), and by extension, ice-based recreation (Visser and Petersen 2009, Damyanov et al. 2012), will be impacted by a changing climate. The Rideau Canal in Ottawa, Canada, is the world's largest outdoor ice skating surface and a UNESCO heritage site, with up to 1.3 million visitors annually (Figure 1-5). We used season length, or the days between opening and closing, to represent ecosystem service availability, and user number to represent service benefit (Daniel et al. 2012). We evaluated weather as a predictor of availability, and fitted ecological models to the relationship between use and availability (Holling 1959). Treating user numbers as analogous to resource consumption, and skating days as analogous to resource density, we compared three responses: (**type I**) constant increase in use with more skating days; (**type II**) saturating increase in use with more skating days; and (**type III**) accelerating increase in use initially, followed by saturating increase in use with more skating days (Supplementary Figure 7.6; Holling 1959). Combining these models with MarkSim weather projections (see Supplementary methods; Jones and Thornton 2013), we projected the availability and use of this cultural ecosystem service to 2090.

Unsurprisingly, service availability was highly weather dependent. From 1972-2013, season length varied substantially year-to-year (35 – 90 days) with an overall decline (-5.2 ± 2.9 days/decade; 95% CI; Figure 5-1; Supplementary Table 7.6) driven by later opening dates (6.3 ± 2.0 days/decade), not earlier closing dates (1.0 ± 2.6 days/decade). Among top models (R^2_{max} = 0.53), the most important explanatory variable was mean daily temperatures of the 100 coldest days of the year (Supplementary Methods). Using skating days (season length minus within-season closures) as the response variable had the same result (Supplementary Table 7.7).

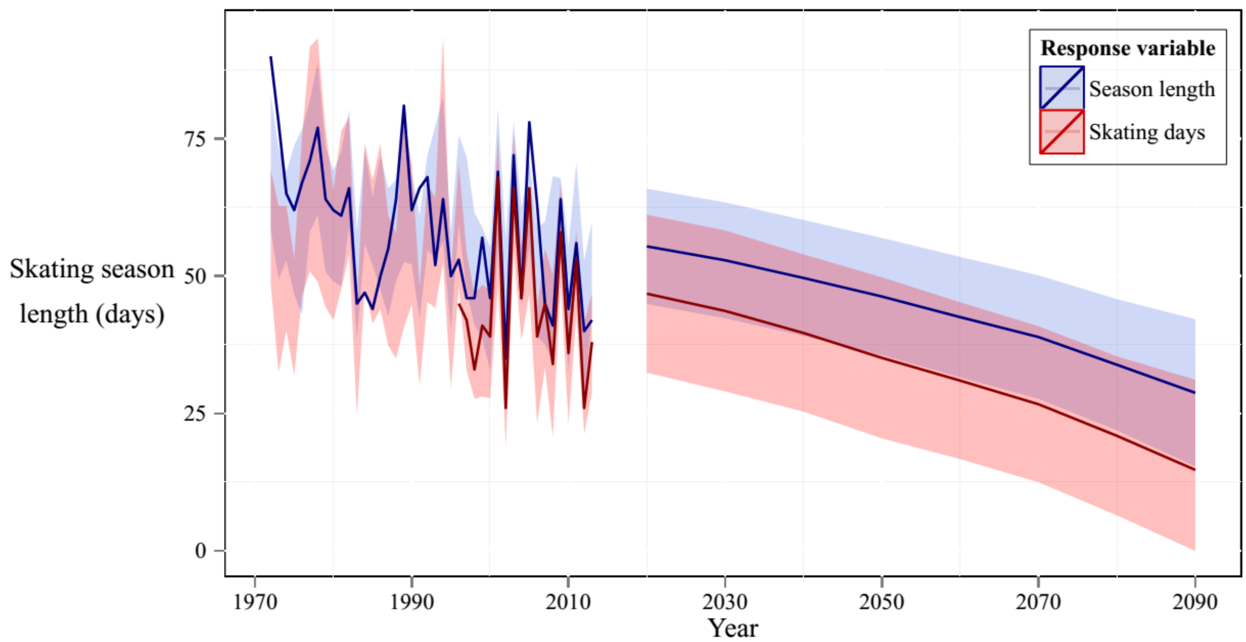


Figure 5-1: Historical and projected season length (opening to closing; n = 42) and skating days (opening to closing minus within season closures; n = 18) at the Rideau Canal Skateway in blue and red respectively. Prediction intervals (80%) for the model and projections are shaded. Projections were based on simulated weather from the MarkSim Weather Generator using an average of 6 IPCC general circulation models and the A2 emissions scenario (see Supplementary Methods; Jones and Thornton 2013).

Like availability, use varied substantially inter-annually (400,000 – 1,300,000 users), and declined overall from 1992 to 2013 (-84,000 ± 187,000 users/decade, 95% CI; Figure 5-2a). User numbers were non-linearly related to availability ($R^2_{max} = 0.82$), with use increasing marginally in long seasons but decreasing dramatically in short seasons (Figure 5-2a). Use also depended on opening date with late opening seasons having fewer users than early opening seasons, independent of season length. Including both skating days and opening date, the relationship between use and availability was either: type III (AICc = 478.4; $R^2 = 0.82$), or type II (AICc = 480.3; $R^2 = 0.80$), but likely not type I (AICc = 483.5, $R^2 = 0.77$; Figure 5-2a). Types II and III are

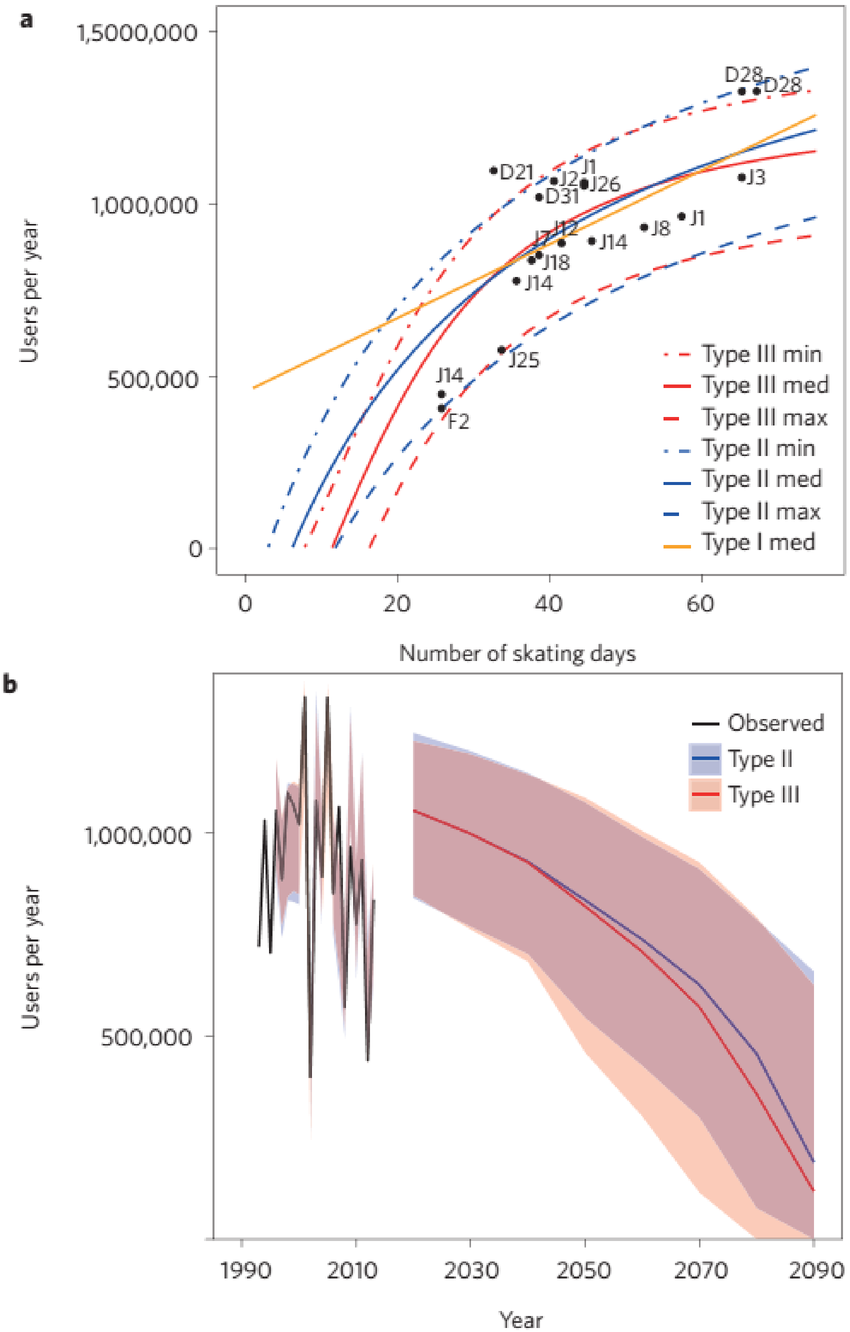


Figure 5-2: Comparing different models of cultural ecosystem service benefit in terms of user numbers. Use is plotted against availability (number of skating days; n = 18) (*a*), and time (*b*). All models include opening date. Points in (*a*) are labelled with their opening date (e.g. J1 = January 1st). Model types are: I ($f(x) = ax + b$), II ($f(x) = \frac{ax}{b+x}$), and III ($f(x) = \frac{ax^2}{b^2+x^2}$; see legends). The three curves in (*a*) plotted for types II and III represent earliest (*min*), median (*med*), and latest (*max*) opening dates. Projected user numbers using types II and III are plotted in (*b*) with 80% prediction intervals.

not strongly differentiated (III is 2.6 times more likely) due to few data from very short seasons. Regardless, in either model benefits are compromised more by short seasons than they are enhanced by long seasons.

Combining models of availability and use with MarkSim weather projections based on the high emission, business-as-usual, A2 scenario (Supplementary methods; Jones and Thornton 2013), we forecasted the availability of this service to decline with shorter seasons (-3.8 ± 2.0 days/decade; 95% CI), later opening dates (2.6 ± 1.5 days/decade), but not earlier closing dates (-0.6 ± 0.7 days/decade). In 1972-2013, the mean season at the canal was 58.4 ± 3.9 days (95% CI). For the 2040 horizon, all else being equal, we projected seasons of 49.7 ± 10.6 days (80% PI); for 2090, 28.8 ± 13.4 days. Incorporating within-season closures, mean skating days at the canal was 44.5 ± 6.5 days (95% CI) for 1996-2013. We projected 39.6 ± 14.0 days (80% PI) skating days for the 2040 horizon, and 14.7 ± 16.4 days for 2090. How use will be impacted by this reduced availability depends on the form of the use:availability relationship Figure 5-2b: all else being equal, initial declines are identical between types II and III (-5.4% ± 1.4% mean decline in users/decade; 95% CI), but type III is more pessimistic later in the century (-67.0% ± 9.1% vs. -58.5% ± 8.3% mean decline in 2080-2090). Alternatively, if measures are taken to limit global mean temperature increase to 2˚C, the projected use and availability of the canal would correspond to approximately the 2040 time horizon.

In our projections based on the high-emission, business-as-usual A2 scenario, the declines are likely underestimated. Since 1970, the Rideau Canal has experienced an accelerating rate of warming with mean winter temperatures increasing 0.51˚C/decade between 1970 and 1990 and 1.3˚C/decade between 1991 and 2013 (Supplementary Figure 7.10). Similarly, other analyses of ice-based recreation have found accelerating rates of warming, leading to accelerating declines in ice skating indicators persisting since the 1970s (Visser and Petersen 2009, Damyanov et al. 2012). Meanwhile, the general circulation models used by MarkSim have consistently underestimated the accelerating rate of global warming since 1983 (Supplementary results & discussion; Peters et al. 2012). As a result, our temperature projections appear optimistic given the historical trend (Supplementary Figure 7.10). Since season length and use are highly sensitive to errors in temperature, an underestimation of warming will lead to overly optimistic projections in both. Projections of use in particular appear discontinuous with the historical trend (Supplementary Figure 7.9b). Simple extrapolation suggests a more rapid decline in both is possible.

Here we presented a case study of the importance of weather in determining recreational cultural ecosystem service availability and use historically, and projected an accelerating decline in both due to warming. Recreation is a more readily quantified cultural ecosystem service (Milcu et al. 2013); as such it represents an opportunity to quantify the linkages between physical drivers, cultural ecosystem services, and human well-being (Millennium Ecosystem Assessment 2005, Norton et al. 2012). Many other cultural ecosystem services are not so easily quantified (e.g. spirituality; Milcu et al. 2013), and their connections with human well-being and the physical environment are complex (Millennium Ecosystem Assessment 2005). In this case, however, visitor numbers provided a quantitative index of human benefit (Daniel et al. 2012), and enabled the demonstration of a nonlinear relationship between service benefits and availability. Other recreational ecosystem services may also have low availability thresholds below which their use rapidly declines, and high availability thresholds above which their use saturates. Cultural ecosystem services that are responsive to weather may emerge as among the most compelling indicators of long term climate trends.

6 Summary and conclusions

It is likely that, for most people, the most recognizable and memorable forms of environmental change will occur in locally-relevant indicators, whether they be ice or animal. These relatable indicators are the low hanging fruit of environmental monitoring; with little resources they can form the basis of monitoring programs that stand the test of time. It was my objective here to develop tools for, and demonstrate insights from, these locally-relevant indicators and the participatory methods they often require. In Chapter 2, I found that participatory monitoring programs had greater management relevance and sustainability. I also found these programs can benefit from new digital data entry technologies through improved data quality. but that program success depended more on collaboratively defined questions, objectives, conceptual models, and monitoring approaches rather than technology. This collaborative approach formed the basis of the participatory adaptive monitoring framework (Figure 2-5). In Chapter 3 I endeavoured to apply these principles in monitoring muskrat populations of the Old Crow Flats with the Vuntut Gwitchin First Nation. I found these muskrat populations demonstrated their strongest periodicities at multiple decades at a landscape scale, but that lake-level periodicity appeared to more closely correspond to local knowledge. I found LEK of shifting ice phenology corresponded to an average increase in the open water season, according to Landsat imagery, of 0.26 day per year. Local knowledge also suggested that evaporation during this season lead to the open water season's negatively association with both muskrat densities and body condition. In Chapter 4 I used time series of muskrat abundance from 219 lakes to document the first recorded instance of a traveling wave of abundance in that species. Chapter 4 also provided the first, to my knowledge, quantification of directional dispersal as a mechanism to explain this phenomenon.

Finally, Chapter 5 applied the principle of locally-relevant indicators to identify outdoor ice skating as a useful indicator of winter weather conditions in Ottawa, and found this indicator to be declining approximately 0.5 days a year with a potentially accelerating decline in use associated with warming.

The participatory adaptive monitoring framework forms the foundation of my solution to long term environmental monitoring. I applied this framework in Chapter 2 where I examined the utility of innovative digital technologies for environmental monitoring. I found these innovative technologies can improve data quality and dissemination when used in programs with clear questions, protocols, and outputs. I also found participatory programs that collaboratively designed these questions, protocols, and outputs were most frequently successful at generating management actions (Figure 2-3) and at being sustained (Figure 2-4). Both Russell-Smith et al. (2003) and Lindenmayer & Likens (2010*c*) emphasize the importance of "passing the test of management relevance" for monitoring programs to be sustained. I believe the iterative process of collaboratively defining questions, conducting monitoring, reviewing results, and defining new questions, places far greater emphasis on monitoring programs that pass this test, or the related test of "stakeholder relevance". The application of this approach led to my examination of the impacts of changing ice phenology in the Old Crow Flats (Chapter 3) and at the Rideau Canal Skateway (Chapter 5).

Changes in the timing of clear seasonal events, like the freezing and thawing of waterways, offers a widely recognized indicator of environmental conditions. Changing ice phenology formed the basis of both Chapters 3 and 5 as phenology affected particular ecosystem services, namely muskrat trapping and outdoor skating. Interestingly, both analyses differed in the observed rates of changing phenologies. I expected the Old Crow Flats to have experienced more rapid changes in their freezing and thawing dates due to their higher latitude. Instead, it was the freezing of the Rideau Canal that appeared to be advancing more quickly, with ice free seasons increasing by approximately 0.5 days/year, compared to 0.3 days/year in the Old Crow Flats. This latitudinal difference in rates of ice phenology change has been observed elsewhere (Weyhenmeyer et al. 2004, 2011), and suggests that residents of more temperate regions may in fact experience more rapid changes in ice related ecosystem services due to warming. This problem could be exacerbated by the nonlinear relationship between service availability (Figure 5-2), where declines in already short ice covered seasons could lead to accelerating declines in the use of these ecosystem services. I believe these kinds of cultural ecosystem services represent a highly relatable indicator for communicating environmental change.

Another advantage often associated with these locally-relevant indicators is that they are frequently well understood by local ecological knowledge holders. In Chapter 3 I generated hypotheses, statistical models, and interpreted results based on my understanding of LEK. This contextualized my analyses of satellite imagery, aerial photography, and *in situ* surveys, and led to my identification of evaporation during the open water season as a potential limiting factor of OCF muskrat populations. While local ecological knowledge is now well established in the literature (Bohensky and Maru 2011), it is still infrequently used in wildlife research (Gilchrist and Mallory 2007). I hope Chapter 3 demonstrated that engaging with and interpreting local ecological knowledge can contextualize and improve essentially every step of a biology student's graduate research program.

While Chapters 3 and 5 demonstrated that locally relevant indicators are responsive to multi-decade climatic change, Chapter 4 highlighted the use of spatially distributed time series of animal abundance to test theoretical population biology. In many regions fish and wildlife are an important ecosystem service, and local stakeholders can often be engaged to help generate time series of animal abundance indices. If these indices can be well calibrated, they allow for the observation of spatiotemporal dynamics of various wildlife populations. In Chapter 4 I combined abundance estimates, genetic distances (determined from locally collected tissue samples), and land cover characteristics of the Old Crow Flats, to identify landscape obstacles and directional dispersal as possible drivers of a traveling wave of muskrat abundance. Quantifying the scale and directionality (i.e. anisotropy) of synchrony in time series of animal abundance, and in genetic distances between populations, represents a largely untapped opportunity for surveillance monitoring programs to differentiate between the synchronizing effects of dispersal and Moran effects (e.g. Marjomäki et al. 2004). Population biology would benefit from future work combining spatiotemporal patterns from large scale surveillance monitoring, genetic patterns from carcass collection programs, and experimental manipulations from targeted programs.

Overall my thesis examined the organization, tools, results, and broader implications of a variety of environmental monitoring programs. I found participatory monitoring of locally relevant indicators to have management relevance, sustainability, sensitivity to environmental change, and applicability to population biology. Future research should consider: the nature of partnerships and the structure of programs underlying effective environmental monitoring, how local ecological knowledge can be interpreted at various stages of an effective biological research program, the accuracy and reliability of commonly-used indices of relative animal abundance (e.g. fur returns, harvest statistics; track, sign, and house surveys), how various forms of environmental change influence locally-valued ecosystem services (particularly Old Crow muskrats), and the 'smoking gun' that is anisotropic patterns in population synchrony and genetic similarity. There are many avenues to establishing and maintaining useful environmental monitoring programs over the long term. Participatory monitoring of locally-relevant environmental indicators offers one such avenue.

7 Supplementary material

7.1 Supplementary material for Chapter 2

7.1.1 Case studies

Canada

In selected Indigenous communities in northern Canada, CyberTracker^{TM} interfaces (NAILSMA 2014) were collaboratively designed to address local monitoring objectives, and trialed with potential users to evaluate the strengths and weaknesses of the devices. Each community identified monitoring priorities for trials, ranging from ongoing land-use, to wildlife observations and forestry inventories.

These consultations were the first stage of a Type B (*collaborative monitoring with local data interpretation*) monitoring framework. On eight occasions between 2011-2013, we held formal meetings in four Canadian communities: Wemindji, Kangiqsujuaq, Kitcisakik, and Old Crow to discuss PM and/or trial field protocols using digital data entry. We recorded participant feedback during informal conversations, public presentations, community meetings, field trials, and/or semi-directed interviews.

Participant observations of the digital devices varied within and between communities, but generally the technology was perceived less favourably after it had been tested in the field. Some participants found digital devices were simple and efficient to use, led to fewer input errors, and had less risk of physical damage (e.g. water).

“[This digital device] is ideal…. If it rains the paper is wet, [the digital device is] not.” [Kitcisakik participants]

Several suggested this could improve data quality through fewer input errors, and more data types (e.g. photographs, audio/video recordings), while providing a multi-functional bush tool (e.g. GPS, satellite communication, games) that could engage youth in monitoring, recording TEK, and activities on the land:

“[This digital device] is not useful for me, because I know my territory. But for our youth it is useful, when a young hunter [is] lost” [Kitcisakik elder]

“It was easy to fire up the [digital device] when we were all sitting around a fire listening to stories.” [Old Crow youth]

Others found digital devices complicated to operate; slow to record data; and had difficulty viewing the screen, using the keyboard, reviewing data once entered, operating the device while cleaning fish, and interpreting the unilingual English interface. *“[This digital device] is not so simple to use. It needs further refinement”* [Kitcisakik professional]

“The GPS was not able to record a place while in a moving boat on water, no matter how slow we were moving” [Old Crow participant]

Users had concerns with operating in cold temperatures and under heavy canopies; short battery life; resistance to damage; and poor flotation. Participants were concerned about who would pay to manage these devices, and questioned the need for digital technology or centrally-administered PM entirely:

”Inuit know their land and do not need this technology” [Kangiqsujuaq participant]

The latter concerns were frequently the result of the belief that both PM and digital technology could enable unauthorized access to and use of TEK.

> *"The one thing that I did not do/like is the GPS of the area.… others might come around"* [Wemindji fisherperson]

PM projects using digital devices have not been established in these communities at the time of publication.

Vietnam:

In 2012, digital devices were used in a forestry PM program among the Ca Dong community, an ethnic minority, in the Tra Bui commune of Vietnam. This forestry monitoring project, designed through household surveys, semi-directed interviews with commune leaders, and a workshop with 80 participants, aimed to monitor forest carbon stocks as part of the Reduced Emissions from Deforestation and Forest Degradation program (REDD+). This project used a digital data entry system based on XLS forms and the Open Data Kit (ODK) interface. Training materials were written in the local language, and sampling was purposive to facilitate participation. Participatory monitoring results on above ground forest biomass and disturbances were compared with those of professional surveyors (local, regional, and national) and high resolution SPOT-5 imagery (Pratihast et al. 2013).

Participants recorded above ground forest biomass and disturbance data of similar quality to experts at a much reduced cost. Overall 15 community members (aged 22-40 with elementary education) monitored 17 biomass and 48 disturbance plots, and collected results that agreed entirely with expert observations when a digital drop down list was used, but agreed less when data were manually written (72 %; n = 65). Participatory monitoring reduced the costs to external agencies from 6.4 to 1.2 USD/hectare while, at the same time, providing payments of 288 USD to each participant. Participants were better and faster at identifying small scale forest disturbances compared to remote sensing, which only identified 18 % of observed forest degradation events (n = 9) and often after a delay of 1-2 years. Overall, digital data entry simplified data processing, enabled more data types (e.g. location, date, text, audio, video, images), and reduced the delay between data collection and use. However, the digital devices were difficult to keep powered in the field, limited in compatibility with Android phones, susceptible to loss and water damage, still led to data entry errors (which selection lists or checkboxes reduced), more costly than the paper alternative (but still cheaper than experts), and required continued technical supervision.

Greenland:

The Department of Fisheries, Hunting, and Agriculture established a Type B PM program with fishermen, hunters, and others to inform adaptive management of Greenland's natural resources (Danielsen et al. 2014b; www.pisuna.org). Between 2009-2011, natural resource committees (NRCs) were established in the three communities of Kitsissuarsuit, Akunnaq and Qaarsut, and the town of Ilulissat. NRC members reported their field observations and harvests, either after returning from each trip using a paper calendar, or verbally at NRC meetings. At quarterly meetings, individual sightings are compiled into summary reports, results are compared from the same area/season as previous years and interpreted by community members, and management possibilities are discussed. Smartphones and GoPro cameras are regularly used to record and share video and still images on the project's Facebook page. Any management decisions (e.g. change in quota, hunting season, gear restriction, etc.) proposed by the NRCs are presented to the Local Government Authority, and the NRC hosts a public meeting approximately annually. At these meetings, monitoring results and decisions for the year are discussed with the entire community to validate the findings and obtain broader support for management proposals.

Assessment of the management recommendations and sustainability of this program was based on conversations with participants and staff of the Local Government Authority, and review of reports from the NRC meetings (Danielsen et al. 2014b). This simple approach to participatory monitoring has proven sustainable with locally available human and financial resources, while increasing local involvement in natural resource management. During the first three years, 33 participants recorded 24 variables including sea ice, shipping, three fish, nine mammals, and nine bird populations. Eight participants used paper datasheets; the remainder contributing observations orally or occasionally with digital devices. Early on, digital devices were used infrequently, but their use has increased slowly with the 2012 establishment of the project's Facebook page. The NRC monitoring system has contributed to 14 management recommendations, including: setting quotas (2 proposals), changing hunting seasons (5), identifying research needs (3), altering fishery bylaws (2), and others (2). The local municipal authority responded to 11 of these proposals.

Since 2011 the project has been abandoned in the town of Ilulissat but is spreading elsewhere in the communities of Disko Bugt, although its use of digital technology, or even paper datasheets, has varied by community and user. Younger users are most interested in digital technologies; older participants (i.e. > 40 years) prefer analog methods. A key motivation for many participants is knowledge sharing between generations (Nordic Council of Ministers 2015). More young participants will likely increase the adoption of digital tools and media, like Facebook, to disseminate monitoring results and engage more community members.

Ghana:

Between 2006 and 2009, the effectiveness of participatory mammal monitoring in Mole National Park (MNP), Ghana was evaluated. Since the late 1960s, MNP has documented sightings of larger mammalian wildlife during law enforcement patrols (Burton 2012). This program is an example of Type D participatory monitoring, in which local wildlife guards with little formal education or training collect data for use by park managers and external scientists (Danielsen et al. 2009). The program's longevity in a resource-limited region is remarkable, but its accuracy had not been assessed. Beginning in 2006, MNP integrated handheld GPS units into their monitoring protocol to supplement wildlife sightings with digital records of locations and patrol effort. The effectiveness of this system was compared with results from a simultaneous survey using digital camera traps, with portions of the survey implemented by local wildlife guards (Burton 2012).

We evaluated the effectiveness of the participatory monitoring methods, including incorporation of digital technologies (GPS, cameras), by assessing the quality of resulting data and through informal discussions with participants. Overall, patrol-based monitoring was cheaper and simpler than monitoring with camera traps, and patrols more frequently detected instances of illegal hunting. Integrating GPS units into patrols improved the quality of recorded data by spatially quantifying the survey effort and the distribution of wildlife sightings. Patrols and camera traps provided similar results for larger, social, and diurnal mammals, but camera traps detected smaller and nocturnal mammals that went undetected by patrols. Patrols were also more prone to observation error and variable effort (e.g. species misidentification, variable counts, patrols concentrated near park headquarters) compared to camera traps (Burton 2012).

While patrol surveys had poor detectability of some species, low repeatability of observations, and uneven sampling effort, they were more financially and organisationally sustainable than camera traps, which are no longer being operated by wildlife guards in the park. Both GPS and camera traps increased purchase and upkeep costs (e.g. batteries, memory cards, unit replacement), and training and technical support requirements; but camera's did so to a greater degree. When deployed properly, camera traps were more capable of reliably detecting mammals, particularly small, nocturnal, carnivorous ones. But wildlife guards had greater success using GPS in the field; and overall the camera's increased complexity, costs, and technical requirements made them less sustainable in this context. The use of GPS's required less training and oversight, cost less than camera traps, and enabled the quantification of patrol effort for standardizing observations. This patrol-based monitoring system with GPS units is ongoing, but it could be improved with more consistent effort; measurements of observation error (e.g. distance sampling); focusing on particular species and questions; and periodic calibrations with more intense monitoring methods (Burton 2012).

Ethiopia:

In 2011 participatory forestry monitoring was established in the Kafa Biosphere Reserve of southwestern Ethiopia by community members working together with the Kafa Zone Bureau of Agriculture and Rural Development (BoARD; Pratihast et al. 2014). The BoARD hired 30 knowledgeable local community members to document forest change in the Reserve (alongside other responsibilities). Participants used two protocols to document forest degradation, deforestation, and reforestation; one using paper datasheets and handheld GPS, the other smartphones with integrated GPS, camera, and ODK interface. In total, 755 sites were monitored by participants. Within these sites, 140 sites were randomly selected, and their results were compared with parallel monitoring by professional foresters and SPOT/RapidEye imagery.

Participant observations were complementary to remote sensing, and comparable to professional foresters' observations with some caveats. Frequently participants, who had at least a secondary level of education, identified forest degradation events before remote sensing (54 % of instances, n = 60), but detected deforestation events after (45 % of instances, n = 40). Participant assessment of forest presence and change type corresponded to professional foresters' in 93 % and 83 % cases respectively (n = 140; n = 140). However, there was less agreement (71 %, n = 140) in determining the drivers of forest change. Observations of community members were biased to occur near roads (53 % within 1 km; n = 140) and in the dry season (>80 %; n = 140). However, community members were more capable of detecting small scale forest changes (< 2 ha), particularly forest degradation, and determining with reasonable accuracy the drivers of changes compared to reference datasets (Pratihast et al. 2014).

Mobile devices contributed to PM success by facilitating data collection and communication. Participants reported digital devices simplified data entry in the field, and reduced entry errors. Using smartphones, community members collected data in multiple forms (e.g. photographs), could visualize their results immediately, and easily communicate these results, particularly using social media like Facebook. Notably, one participant reported the illegal extraction of firewood on Facebook, which drew the attention of government agents. PM has promoted the transparent use of forest resources, as participants are present throughout the Reserve monitoring more than 1500 forest plots. This PM system is ongoing and could be integrated into a national REDD+ monitoring system.

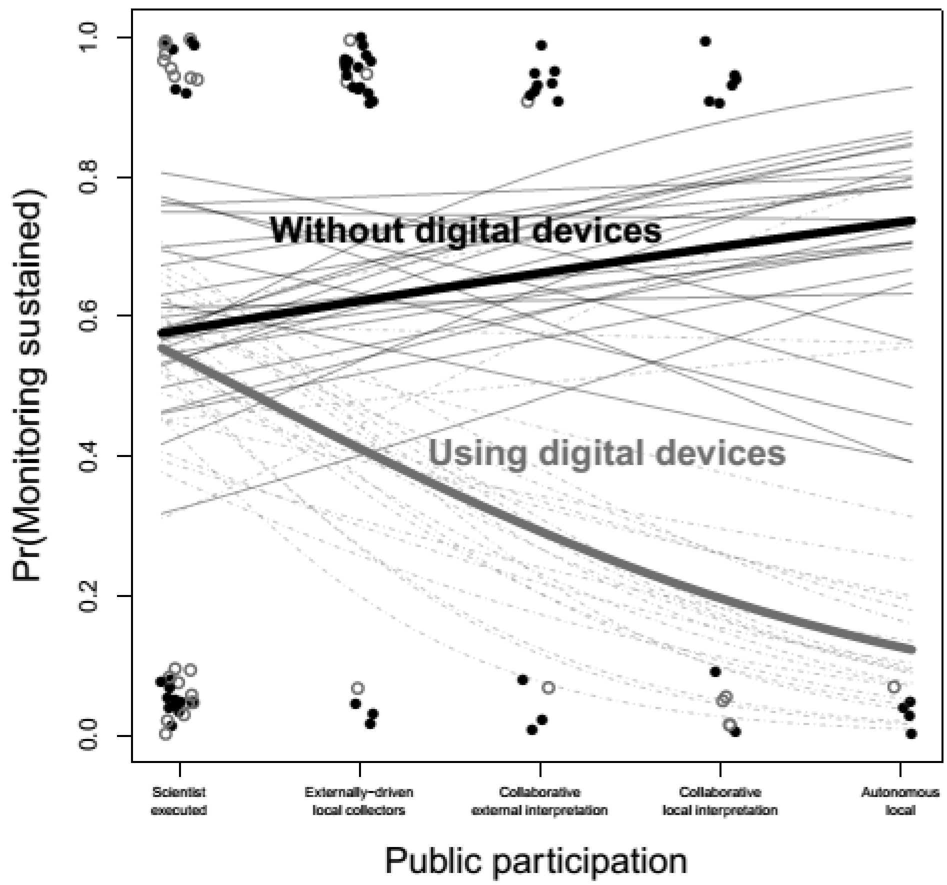
Australia:

To support the growing movement of locally-driven Indigenous land management in Australia the North Australian Indigenous Land and Sea Management Alliance Ltd (NAILSMA), based in Darwin, NT initiated the Indigenous-Tracker (I-Tracker) program in 2008. I-Tracker pairs digital devices with customised CyberTracker™ applications collaboratively developed by Indigenous resource managers, scientists, and other experts to meet local, regional, and national monitoring priorities. It supports Type B participatory monitoring frameworks being established in many Indigenous communities in northern Australia through the engagement of TEK holders in land and sea management and monitoring activities, planning and decision-making (Kennett et al. 2010). I-Tracker commenced as a program that supported monitoring of marine and coastal management issues, then expanded to support over 30 Indigenous ranger groups to collect and manage data on a wide range of issues including biodiversity, fire management, cultural site maintenance and monitoring, species monitoring, invasive plant and animal management, marine debris removal and visitor management (NAILSMA 2014). To support uptake and use, the I-Tracker program includes training, technical support, and regular fora for rangers to meet (NAILSMA 2014).

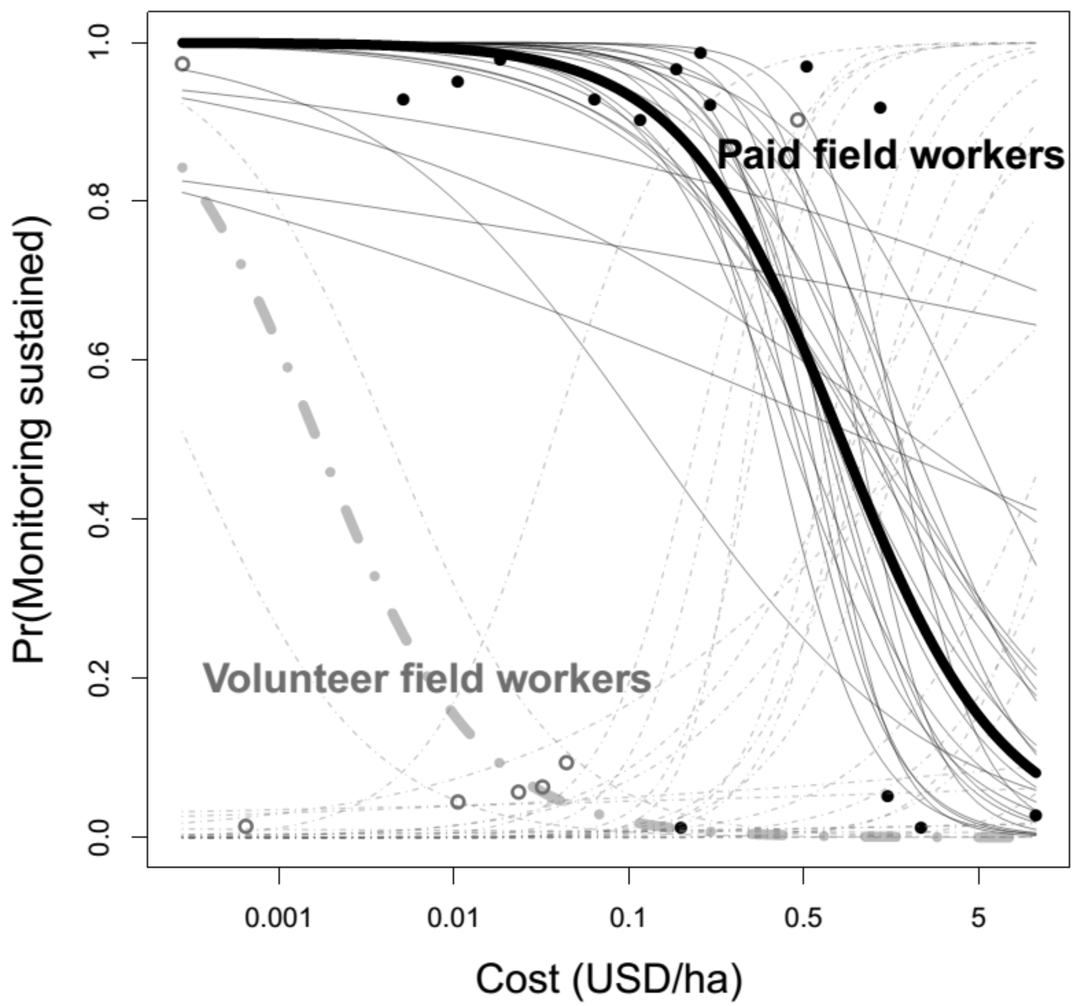
I-Tracker tools have also been applied in locally-driven scientific research projects for specific species. For example, marine turtles are of high cultural and conservation significance in Australia. In Western Australia, the Wunambal Gaambera Aboriginal Corporation's Uunguu Rangers, NAILSMA, and CSIRO (a leading science agency) worked collaboratively to design and implement a boat-based survey approach for local populations of marine turtles, particularly green turtles *Chelonia mydas*, using I-Tracker tools (Jackson et al. 2015). The project has facilitated scientific monitoring by Uunguu Rangers and increased local mapping and documentation of turtle populations (Jackson et al. 2015). In another example, Indigenous rangers, NAILSMA, and BirdLife Australia collaboratively developed I-Tracker tools for local surveys of shorebird species by Indigenous rangers in north Australia that can be aggregated nationally (NAILSMA 2014: pp. 142-149). In the Mapoon community in Queensland, these tools support wider efforts by local Indigenous people to manage and protect shorebirds, reflected in their community-developed natural and culture resource management plan (Mapoon Land & Sea Program 2013). For both of these examples, monitoring activities are ongoing within local environmental monitoring regimes despite the completion of development funding for I-Tracker tools.

A *Most Significant Change* (Dart and Davies 2003) evaluation of I-Tracker involving 66 semi-structured interviews with participants and scientists (Bessen 2013) concluded that I-Tracker's digital tools were effective for Indigenous ranger work – particularly in improving monitoring over the huge geographic areas that Indigenous ranger groups are generally responsible for. I-Tracker tools facilitated the reporting of monitoring data, and the transfer of Indigenous Ecological and Cultural knowledge between generations. Touchscreen interfaces with images and icons assisted users with limited literacy and numeracy. However the report also highlighted that key to program success was the provision of ongoing training and technical support for participants, and the highly participatory approach that was used to develop program tools. Maintaining these aspects is staff-intensive and requires ongoing resourcing to be successful. *Looking After Country: The I-Tracker Story* (NAILMA 2014) includes a summary of experiences from almost 20 Indigenous ranger groups, who voluntarily provided stories and data for collation. The book illustrates the wide variety of ways that I-Tracker tools have contributed to management goals for different communities. This highlights another aspect, which is the importance of adaptability of tools to local settings and the need for tools to remain responsive to changing community needs over time. Again, this reinforces the need for ongoing resourcing to support use of digital tools.

7.1.2 Additional figures



Supplementary Figure 7.1: The probability of a publication explicitly stating that its monitoring program is ongoing as a function of the level of public participation (levels from: Danielsen et al. 2009) and the use of digital data collection. Thicker lines represent the predicted probability derived from the public participation model. Thinner lines represent 50 simulations of possible models considering the estimated model coefficients and their standard errors (Gelman and Hill 2007). These represent the range of possible outcomes that agree with model estimates within a 95% confidence interval. The black line is for projects using paper based methods; the blue one for those using digital devices. Individual data points were jittered to better visualize their density.



Supplementary Figure 7.2: The probability of a monitoring program being ongoing at the time of publication as a function of the program cost in USD per hectare per year and the use of volunteer field workers. This top model is based on a reduced sample of 21 monitoring programs that explicitly reported monitoring costs. Thicker lines represent the predicted probability derived from the cost model. Thinner lines represent 50 simulations of possible models considering the estimated model coefficients and their standard errors (Gelman and Hill 2007). These represent the range of possible outcomes that agree with model estimates within a 95% confidence interval. Black solid values are for projects using paper based methods, grey open values for those using digital devices. Individual data points were jittered to better visualize their density.

7.1.3 Model selection tables

Supplementary Table 7.1: A list of models that explain the use of digital devices in a sample of 107 published environmental monitoring projects. Explanatory variables were organized into four categories of model. Models were ranked using Akaike's corrected Information Criterion (AICc). Model coefficient estimates are presented as 95% confidence intervals.

Model category	Coefficients (95%CI) and variables	AICc	ΔAICc	Weight
Participation	[-0.95, -0.04] level of public participation	110.44	0	0.85
Scale & tenure	[-3.5, 1.1] locally protected + [-1.9, 0.0] unprotected + [-0.4, 0.16] extent of monitoring region	115.38	4.94	0.07
Cost	[-1.6, 1.0] source of funding + [-1.7, 0.7] volunteer field workers + [0.97, 5.6] funding:volunteer	115.6	5.17	0.06
Duration & diversity	[-0.7, 0.2] duration + [-1.4, 0.5] single taxon + [-0.7, 1.1] duration:single taxon	118.04	7.6	0.02

Supplementary Table 7.2: A list of models that explain the occurrence of management actions in a sample of 107 published environmental monitoring projects. Explanatory variables were organized into four categories of model. Models were ranked using Akaike's corrected Information Criterion (AICc). Model coefficient estimates are presented as 95% confidence intervals.

Model	Variables	AICc	ΔAICc	Weight
Participation + duration & diversity	[0.1, 1.2] level of public participation + [0.2, 3.1] Use of digital devices + [-3.0, 0.4] Single taxon + [-0.2, 1.4] Duration + [0.0, 3.0] Single taxon:duration	76.35	0	0.71
Participation	[0.1, 1.1] level of public participation + [0.2, 2.8] digital technology	79.57	3.22	0.14
Duration & diversity	[-0.4, 1.0] duration + [-3.3, 0.1] single taxon + [0.0, 2.9] duration:single taxon	80.19	3.84	0.10
Scale & tenure	[-1.8, -0.2] nationally protected + [-1.4, 2.6] locally protected + [-2.5, 0.0] unprotected + [-0.2, 0.5] extent of monitoring region	82.73	6.38	0.03
Cost	[-1.8, 1.1] source of funding + [-0.2, 1.5] volunteer field workers + [-2.2, -1.0] paid field workers	83.10	7.61	0.02

Supplementary Table 7.3: A list of models that explain the sustainability of monitoring in a sample of 107 published environmental monitoring projects. Explanatory variables were organized into four categories of model. Models were ranked using Akaike's corrected Information Criterion (AICc). Model coefficient estimates are presented as 95% confidence intervals.

Model	Variables	AICc	ΔAICc	Weight
Participation + cost	[-0.5, 0.5] level of public participation + [-2.0, 0.1] digital technology + [0.4, 3.7] volunteer field workers + [-0.9, 1.1] local funding source + [-6.7, -0.8] digital:volunteer field workers	114.96	0	0.63
Participation	[-0.3, 0.7] level of public participation + [-2.0, 0.1] digital technology + [-1.6, 0.2] public participation:digital	118.04	3.07	0.13
Cost	[-0.8, 0.8] local funding source + [-0.2, 2.0] volunteer field workers + [-0.1, 0.7] paid field workers	120.32	3.18	0.13
Duration & diversity	[-0.9, 0.9] single/multi-taxa	118.88	3.91	0.09
Scale & tenure	[-0.4, 1.1] nationally protected + [-2.4, 1.9] locally protected + [-1.0, 0.9] unprotected + [-0.1, 0.5] extent of monitoring region	120.91	5.94	0.03

Supplementary Table 7.4: A list of models that explain the sustainability of monitoring in a sample of 21 published environmental monitoring projects that include descriptions of project costs. Explanatory variables were organized into four categories of model. Models were ranked using Akaike's corrected Information Criterion (AICc). Model coefficient estimates are presented as 95% confidence intervals.

Model	Variables	AICc	ΔAICc	Weight
Cost	[-1.4, 0.1] amount of funding + [-13.5, 0.4] volunteer field workers + [-0.5, 5.0] volunteers:funding	28.23	0	0.86
Participation	[-0.6, 1.8] level of public participation + [-4.2, 0.4] digital technology + [-3.6, 0.1] digital:public participation	32.2	3.98	0.12
Duration & diversity	[-0.1, 0.2] duration + [-1.8, 1.9] single taxon	35.55	7.33	0.02
Scale & tenure	[-0.7, 2.1] nationally protected + [-3.1, 1.8] locally protected + [-2.7, 1.3] unprotected + [-0.4, -.6] extent of monitoring region	38.46	10.23	0.01

7.2 Supplementary material for Chapter 3

7.2.1 Model averaged coefficients for depth prediction

Supplementary Table 7.5: The model averaged coefficients used to estimate mean lake depth based on its location, morphology, and ice phenology.

(Intercept)	$\alpha_{j[i]}^{thaw}$	ln(lake area)	ln(lake perimeter)	longitude	perimeter/lake area	(perimeter/lake area)^2	latitude
7.64	0.30	-0.31	0.35	7.6E-6	4.13E-5	-6.11E-10	-3.09E-6

7.2.2 Local ecological knowledge interview consent form and guidelines

Muskrats, Environmental Change and Traditional Use of the Old Crow Flats

Muskrat Traditional Knowledge Interview Guide

Prepared by Murray Humphries, McGill University
in consultation with
Dorothy Cooley, Yukon Environment and
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General Information on Muskrat Traditional Knowledge Research:

As part of the larger YNNK [Yeendoo Nanh Nakhweenjit K'atr'ahanahtyaa (Taking care of the land for the future) - Environmental Change and Traditional Use of the Old Crow Flats (OCF) in Northern Canada] IPY (International Polar Year) Project, we are conducting research on muskrat ecology.

In collaboration with Yukon Environment and Vuntut Gwitchin Government Hertitage Department, one objective of the muskrat research component is to gather traditional knowledge on muskrat ecology and harvest in OCF. Particularly, we are interested in collecting local ecological knowledge on lake-to-lake and year-to-year differences in muskrat abundance and health across OCF, as well as information on local harvest practices.

The purpose of the traditional knowledge aspect of the muskrat research is to 1) formally document some of the traditional knowledge that has already been informally contributed by community members, 2) broaden the scope of the traditional knowledge contribution to the muskrat component of the YNNK IPY Project, by incorporating the knowledge of a broader range of people (for example elders in addition to trappers who have guided us in the field) across a broader range of questions, and 3) create a transcript of these interviews to contribute to the legacy of the YNNK IPY Project. All muskrat traditional knowledge gathered will be owned and managed by VGG Heritage Department, who would be responsible of granting access to Yukon Environment and other researchers or organizations involved in the YNNK IPY Project.

Your Participation in Muskrat Traditional Knowledge Research:

You have been identified by VGG Heritage Committee as a local muskrat expert and are invited to participate in the traditional knowledge aspect of the muskrat research. At the time and place of your convenience, you will be shown a map of Crow Flats and asked a few questions on muskrat abundance, health and harvest practices (*see Interview Questionnaire below*). You will have the choice of your interviewer: Erika Tizya from Old Crow and/or another member of the muskrat research team from McGill (Murray Humphries, Jeremy Brammer or Manuelle Landry-Cuerrier). The duration of the interview will also be at your convenience and will be video or audio recorded (your preference) in its entirety (unless you do not want to be recorded) to allow the interviewer to actively participate in the interview rather than always be taking notes. Recordings of the interview will be transcribed by the interviewer and data gathered through the interviewing process will be compiled and administered within VGG Heritage traditional knowledge database. Recordings will not be publicly presented.

Your participation is voluntary and you may choose not to participate, not to answer any question or to withdraw at any time and have your data removed. Anything you say will only be attributed to you with your permission; otherwise the information will be reported in such a way as to make direct association with yourself impossible. You will receive $50 in compensation for your time. Check boxes below serve to indicate your interview preferences and your signature below serves to signify that you agree to participate in this study.

Consent Form:

I wish to be identified in the report: □ YES □ NO

I agree to be recorded: □ YES □ NO

I agree to be video recorded: □ YES □ NO

I agree that the audio recordings may be given to VGG Heritage: □ YES □ NO

I agree that the video recordings may be given to VGG Heritage: □ YES □ NO

I agree to being directly quoted in presentations and publications: □ YES □ NO
□ With attribution to my name
□ Without attribution to my name

I have read the above information and I agree to participate in this study: □ YES

If you have any questions about your rights as a research participant, or if you would like to verify the ethical approval of this study, please feel free to contact any of the following:

Research Ethics Board
Faculty of Agricultural and Environmental Sciences
McGill University, Tel: (514) 398-8716
Email: research.macdonald@mcgill.ca

Participant's signature________________________ Researcher's signature __________________

Participant's printed name _____________________________ Date ____________________

Interview Questionnaire
Identify interviewer, interviewee, date and location.

Q1. Extent of muskrat experience

a) When were you born? Where were you born?
b) How long have you been trapping muskrat?

Q2. Spatial Variation in Muskrat Number:

- a) Where are your trapping camps?
- b) Which lakes do you usually trap for muskrats?
  - a. What makes these lakes good for trapping?
    - i. Food? Ice? Size? Shoreline? Water level? Beaver? Wind?
- c) What lakes are bad for trapping?
  - a. Why are they bad?
- d) Do muskrats travel between lakes?

Q4. Temporal Variation in Muskrat Number

a) Did you trap this year? How many muskrats did you get? From what lakes? Were they healthy? Fat?
b) How about last year? The year before that? The year before that?...
c) Are good muskrat lakes always good muskrat lakes? Why or why not?
d) Do you notice any cycles in muskrat numbers between years? What causes this?
e) How long does it take for muskrats to come back after their population crashes?

Q5. Muskrat Health

a) How do you tell if muskrats are healthy?
b) What do you do if they are not healthy?
a) Are there lakes where muskrats are more or less healthy? Why
b) How often do muskrats breed in a year?

Q6. Muskrat Trapping and Harvest

a) What happens to muskrat populations when you don't trap them?
b) When is the best time to trap muskrats?
c) When do you stop trapping at a given lake?
d) Where on the lake (distance from shore or from burrow) do you find pushups? Which ones do you trap?
e) How many push-ups per lake do you trap at?
f) How many muskrats per push-up do you trap?
g) Have you seen caribou eating muskrat pushups? How often do you see that?

Q7. Muskrat Trapping Today

a) Are people trapping muskrats like they used to? If not, why not?
b) What do you wish young people knew about muskrat trapping?

Q8. General

- a) Are there any lakes in your country that always thaw early or thaw late? Or lakes that always have lots of vegetation growing in them?
- b) Have you noticed changes in the weather over your lifetime?
  - a. Do you remember years that were very hot or very cold?
  - b. Do you remember years that were very snowy or rainy?
- c) Who else in town would you consider a muskrat expert that we should talk to?
- d) Are there other things about muskrats and muskrat trapping that you think we should know?

7.2.4 Modeling break-up and freeze-up dates using LANDSAT imagery

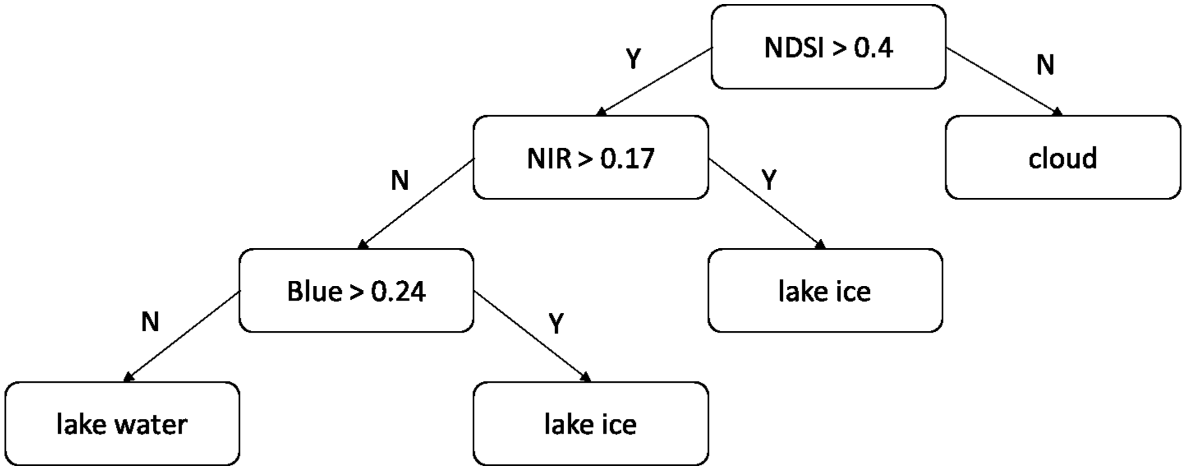
To relate inter-annual changes in muskrat abundance and body condition to ice phenology, we estimated the timing of spring break-up and fall freeze-up in our 219 study lakes across the OCF. We first used Google Earth Engine (GEE) to estimate the proportion of study lakes that were ice covered in scenes taken by the Landsat 5 TM, 7 ETM+ (SLC off and on), and 8 OLI sensors between April 15th and July 15th, and August 15th and November 30th, 1985-2015. Google Earth Engine uses Google's cloud computing capabilities to process large volumes of remotely sensed imagery. Using GEE's coding environment (https://code.earthengine.google.com/), we obtained the top of atmosphere corrected reflectances (TOA; Chander et al. 2009) of Landsat scenes from the United States Geological Survey repository. We filtered these image collections to the paths (65-68) and row (12) that corresponded to the Old Crow Flats, and the dates that correspond to seasonal thaw and freeze (April 15th to July 15th; August 15th to November 30th). We removed scenes that had more than 80 % cloud cover. Within this subset of images, we identified pixels as ice, water, or other using a decision tree of band cut-offs modified from Hall *et al.* (1995). Specifically, we calculated the Normalized Difference Snow Index (NDSI) as:

Landsat 8: Landsat 5 and 7:

$$NDSI = \frac{B3 - B6}{B3 + B6} \qquad NDSI = \frac{B2 - B5}{B2 + B5} \tag{7.1}$$

and omitted any cloudy pixels with NDSI values of < 0.4 (Hall et al. 1995, Kour et al. 2015). Both clouds and snow have high reflectance in green (Landsat 5/7: B2; Landsat 8: B3), the reflectance of snow declines in short-wave infrared (Land 5/7: B5; Landsat 8: B6) but that of most clouds remains high (Hall et al. 1995). This approach has the greatest difficulty in removing cirrus clouds, but is advantageous for its computational simplicity. Subsequently, we designated all pixels with a reflectance in the near infrared (NIR) band (Landsat 5/7: B4; Landsat 8: B5) > 0.17 as ice because water has low reflectance in NIR compared to snow (Hall et al. 1995). However, some pixels with NIR < 0.12 were lake ice in the shadow of clouds, as cloud shadow reduced snow NIR. We used a 0.24 threshold in the visible spectrum, specifically blue (Landsat 5/7: B1; Landsat 8: B2), because lake ice in the shadow still had greater blue reflectance than water (Supplementary Figure 7.3). We digitized our study lakes using Quantum GIS (QGIS Development Team 2016) and a Landsat 5 TM scene mosaic (acquisition dates July – August 2007). We calculated the number of pixels in each our 219 study lakes that were ice covered in 908 images. After removing lakes that were up to 80 % cloud covered, we were left with 92,273 lake ice phenology observations. We identified misclassified images that had escaped our previous filters through their generation of clearly erroneous estimates of ice cover (e.g. if numerous lakes were "ice covered" July 5th, or August 20th). In 92 images we manually corrected their classifications, 47 images were omitted for having greater than 80% cloud cover, and 24 misclassified lakes were removed from the dataset (see S4 for lists).

To generate predictions of break-up and freeze-up dates, we used these ice cover estimates to build multi-level logistic models with two varying intercepts: one for inter-lake variation in ice cover ($\alpha_{j(i)}^{lake}$), and the other for inter-annual variation in ice cover ($\alpha_{k(i)}^{year}$). This model is a simplification of actual lake ice phenologies because it assumes each lake behaves similarly every year (i.e. early thawing lakes will always be early thawers) and that all lakes behave similarly in particular years (i.e. all lakes freeze earlier during early freezing years). However these assumptions allow for the estimation of break-up and freeze-up dates for all lakes even if they are frequently cloud covered in a season, a common challenge with Landsat imagery, based on the



Supplementary Figure 7.3: Decision tree classifying Landsat pixels as cloud, lake ice, or lake water within predefined study lakes of the Old Crow Flats, Yukon.

order in which that lake freezes/thaws in other seasons (e.g. a larger $\alpha_{j[i]}^{lake\ ID}$ indicates a lake tends to have more ice than the lake average, and therefore is a late thawer or early freezer) and whether a particular season is early or late (e.g. a larger $\alpha_{k[i]}^{year}$ indicates a year has more ice than the annual average, and therefore is a late thawing or early freezing year). Specifically we modeled the proportion of a lake's pixels that are classified as ice covered in individual Landsat images as a function of the standardized $julian\ day_i$ of the satellite image:

$$P(pixel\ ice_i = 1) = logit^{-1}\left(\alpha_{j(i)}^{lake} + \alpha_{k(i)}^{year} + \beta^{julian\ day} \times julian\ day_i + \varepsilon\right)$$

$$\alpha_{j(i)}^{lake} \sim N\left(\mu_{\alpha_{j(i)}}, \sigma_{lake}^2\right), \text{for j = 1, 2... 219 lakes} \qquad 7.2$$

$$\alpha_{k(i)}^{year} \sim N\left(\mu_{\alpha_{k(i)}}, \sigma_{year}^2\right), \text{for k = 1, 2... 31 years}$$

Where $P(pixel\ ice_i = 1)$ is the probability of a pixel being ice covered, $\alpha_{j(i)}^{lake}$ the varying lake intercept, $\beta^{julian\ day}$ the coefficient estimate for Julian day, $julian\ day_i$ the value of predictor Julian day for observation *i*, ε the normally distributed error, μ_α the mean lake intercept value, σ_{lake}^2 the variance of that intercept, $\mu_{\alpha_{k(i)}}$ is the mean year intercept, and σ_{year}^2 is the variance of that intercept. To determine each lake's break-up date, freeze-up date, and open water season we used our coefficient estimates and equation (1) to calculate the Julian day that corresponded to a 50 % probability of a pixel being ice covered in a lake in a particular year. To quantify the temporal trend in the above phenological characteristics, we modeled the estimated break-up date, freeze-up date, and open water season length as a linear function of time.

7.2.5 Evaluating environmental determinants of muskrat density and body condition derived from LEK

To compare potential environmental determinants of muskrat pushup density and body condition in the OCF, we developed a set of multi-level models based on hypotheses derived from LEK. We conceptualized these models *a priori* (Burnham et al. 2011) with the benefit of LEK as we understood it from an eight year period spent working in partnership with LEK holders during collaborative project planning, fieldwork, data interpretation sessions, and during recorded and transcribed semi-directed interviews. We worked with 23 LEK experts identified by the North Yukon Renewable Resource Council and the Vuntut Gwitchin Government Heritage Department. All multi-level models had the following general structure:

$$\begin{gathered} y_i = \alpha_{j(i)}^{lake} + \beta^{variable} \times variable_i + \beta^{year} \times year_i + \varepsilon \\ \alpha_{j(i)}^{lake} \sim N(\mu_\alpha, \sigma_\alpha^2) \text{ for j = 1, 2, 219 lakes} \end{gathered} \tag{7.3}$$

where $y_i = \sqrt{pushup\ density}$ or $skinned\ total\ body\ mass$, $\alpha_{j(i)}^{lake}$ is the varying lake intercept, $\beta^{variable}$ the coefficient estimate for the explanatory variable, and $variable_i$ the value of predictor variable for observation i. We ranked models using Akaike's corrected Information Criterion (AICc; Burnham and Anderson 2002). All these models used standardized explanatory variables, included year as an explanatory variable to control for linear temporal trends, and were weighted by the lake area. Body condition models included a varying intercept by year to account for multiple specimens being removed from one lake on the same year. Reported parameter estimates include 95 % Wald confidence intervals (CI).

7.2.6 Determining early thawing lakes

We estimated the annual relative thaw order of our study lakes using lake residuals from a pooled model of seasonal thaw across all study lakes:

$$y_i^{logit\ ice\ cover} = \alpha + \beta^{julian\ day} \times julian\ day_i + \ \varepsilon \qquad 7.4$$

We calculated mean annual residuals for each study lake relative to this pooled model, and used these mean residuals as an index of annual relative thaw order. This index is positive in years when lakes have more ice cover than the average lake on an average year, and negative in the reverse scenario.

7.2.7 Landsat images manually removed or edited

The following images or data points were removed after manual diagnostics revealed they were cloud covered:

"LT50660122008183PAC01", "LE70650122002167PAC00", "LE70660122004196EDC01", "LC80650122013189LGN00", "LC80660122016157LGN00", "LE70660122000169AGS00", "LC80650122014176LGN00", "LC80670122015193LGN00", "LT50660122007164PAC00", "LE70670122001162PFS00", "LT50650122008192PAC01", "LT50650121991161XXX01", "LE70660122010180EDC00", "LE70660122012186EDC00", "LE70660122011167EDC00", "LE70660122013172EDC00", "LE70670122012177EDC00", "LE70660122009177EDC00", "LT50670122006168PAC01", "LE70660122002174EDC00_32", "LE70680122014189ASN00", "LE70670122001178PFS00", "LE70660122002174EDC00_41", "LE70680122002172EDC00", "LE70660122002174EDC00_53", "LT50660121997168PAC00", "LE70660122002174EDC00_42", "LE70660122002174EDC00_35") "LT50650121994249PAC00_1126", "LT50650121990254PAC00_1126", "LE70670122015233ASN00", "LT50670122005229PAC00_1129", "LE70650122014248EDC00_1129", "LE70660122014239ASN00_1129", "LE70670122014230ASN00_1129", "LC80660122014231LGN00_1129", "LT50650122003242PAC03", "LE70650122002247EDC00", "LT50650122004261PAC00_1027", "LT50660121986234XXX03", "LE70650122014248EDC00_32", "LT50650122006250PAC01_47", "LE70650122004237PAC00_1033", "LE70660122004228EDC02_1129", "LE70660121999246AGS00", "LC80670122015257LGN00", "LC80670122014238LGN00", "LT50650122010229PAC01", "LC80680122014245LGN00", "LT50680121985325XXX03_1111", "LT50650121999247PAC03", "LT50650122010229PAC01", "LE70650122001244PAC00_32", "LC80680122014245LGN00", "LT50640121990247PAC00_1003", "LC80660122013292LGN00", "LE70670122012241EDC00", "LE70670122001258EDC00", "LE70660122014239ASN00", "LT50650121986243XXX03", "LC80660122014231LGN00_32", "LC80680122013258LGN00_32", "LE70650122002263PAC00", "LT50670122004227PAC00_1126", "LC80680122015264LGN00","LE70680122009255EDC00_1024", "LE70650122012259EDC00", "LT50680122010234GLC01", "LE70660122012250EDC00", "LE70680122001249EDC00", "LC80670122013283LGN00"

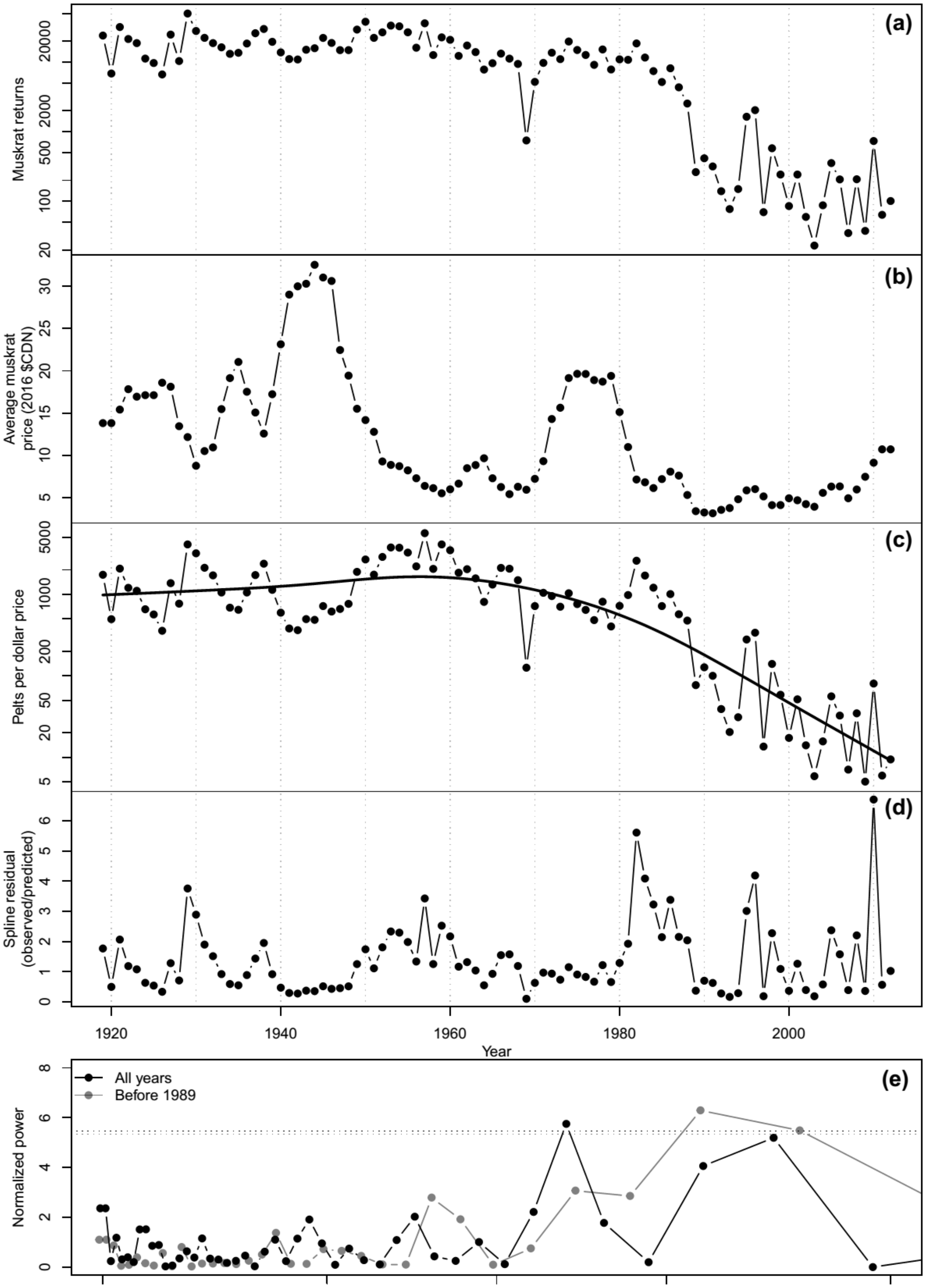
The following images were set to zero ice cover as they contained instances of misclassifications but were taken during periods of no ice cover.

"LT50650122007173PAC00", "LC80670122013187LGN00", "LT50640122008185PAC01", "LT50650122007189PAC00", "LT50670121995186PAC00", "LT50670122009192PAC01", "LE70650122013181EDC00", "LE70660122002190EDC00", "LE70670122004187EDC01", "LT50670121990188PAC00", "LE70670122006176EDC00", "LE70680122001185PFS02", "LT50660122005190PAC00", "LE70670122009184EDC00", "LE70680122004194PAC00", "LT50660121993189PAC00", "LE70650122006194EDC00", "LT50650121994185PAC00", "LE70660122008191EDC00", "LT50660121998171PAC00", "LE70650122012195EDC00", "LT50680121990179PAC00", "LE70650122001180PFS00", "LC80670122014174LGN00", "LC80660122014183LGN00", "LC80650122015195LGN00", "LT50660121995195XXX00", "LT50670122006184PAC01", "LE70650122012179EDC00", "LE70680122006183EDC00", "LE70650122011192EDC00", "LE70650122014184ASN00", "LE70680122012184EDC00", "LT50680121988174PAC00", "LT50670121996173PAC00", "LE70670122011190EDC00", "LE70680122002188EDC00" "LT50650121998260PAC00", "LT50680122004234PAC01", "LE70650122004253PAC00", "LE70670122014246ASN00", "LE70660122010260EDC00", "LT50650121993262PAC00", "LT50680122008229PAC01", "LT50680122008245PAC01", "LC80670122015241LGN00", "LE70680122000247AGS00", "LC80670122013267LGN00", "LC80670122014270LGN00", "LE70680122014269ASN00", "LE70670122007243EDC00", "LT50680122003247PAC02", "LT50680122003231PAC02", "LT50680122007242PAC01", "LT50680122009247PAC00", "LT50660122011239PAC00", "LT50660122010268GLC01", "LT50660122011255PAC02", "LT50670122010227PAC00", "LT50670122010243GLC01", "LT50670122011230PAC00", "LT50680122004250PAC01", "LE70650122011256EDC00", "LE70660122010228EDC00", "LE70660122011231EDC00", "LE70660122013236EDC00", "LE70670122011238EDC00", "LT50670122003256PAC02", "LT50650121992228PAC00", "LT50650121989235PAC00", "LT50650121992244PAC00", "LT50650121993230PAC00", "LT50660121986250AAA03", "LT50660121990229PAC00", "LT50660121991232PAC00", "LT50670121986257XXX03", "LT50670121990236PAC00", "LT50670122006232PAC00", "LE70670122009232EDC00", "LT50660122003249GNC03", "LC80650122015259LGN00", "LE70650122013245ASN00", "LT50650121987230XXX01", "LE70670121999237AGS00", "LE70680122002252EDC00", "LT50680121990227PAC00", "LC80670122014254LGN00", "LE70670122011254EDC00", "LT50660122006241PAC00"

The following images or data points were set to full ice cover as they contained instances of misclassifications but were taken during periods of full ice cover.

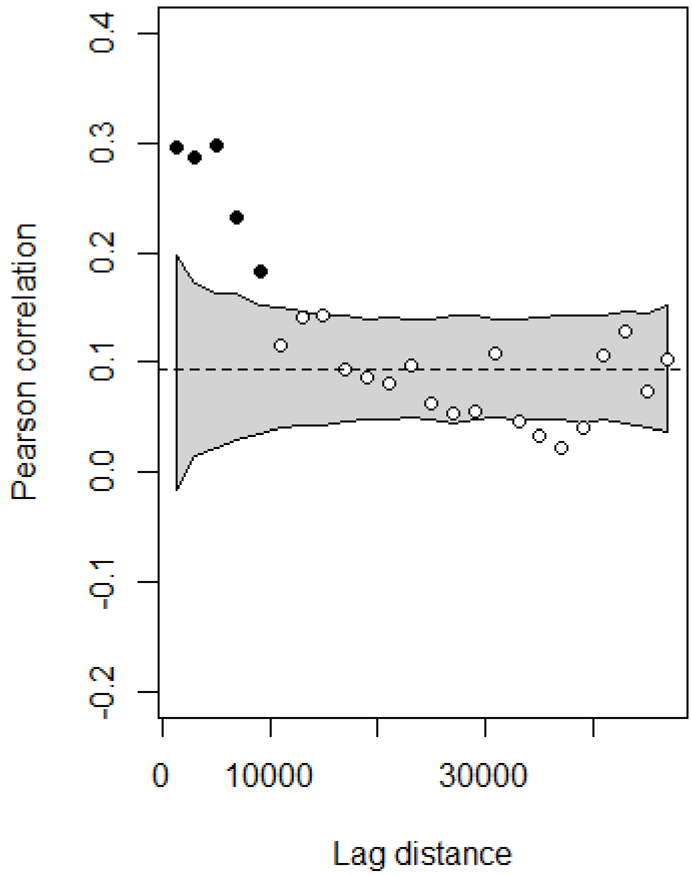
"LE70650122015139ASN00_1093" "LT50680121985325XXX03", "LC80670122013299LGN00"

7.2.8 Supplementary results

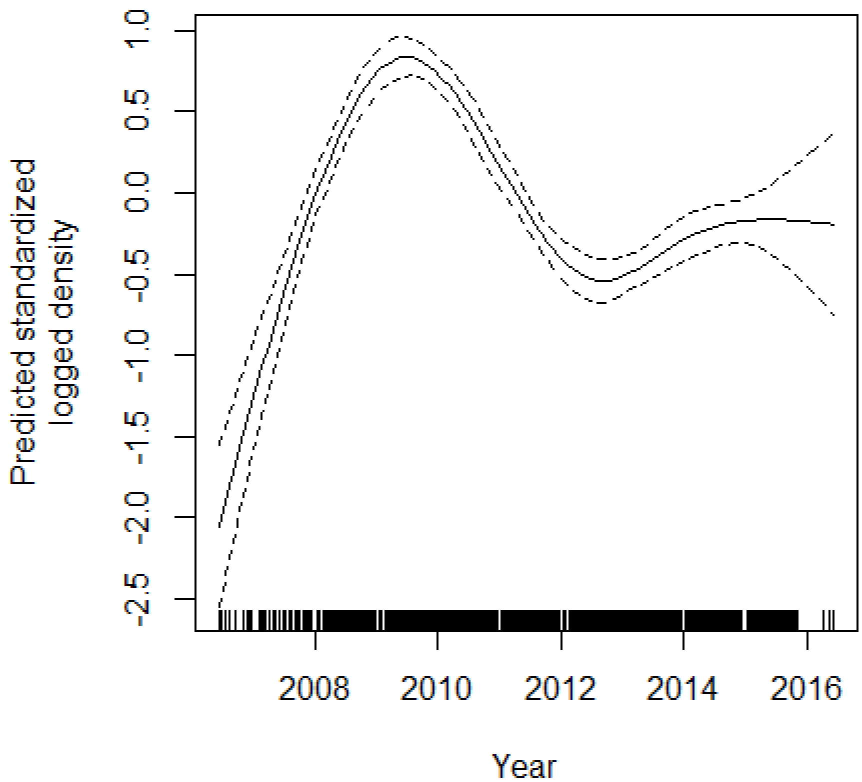


Supplementary Figure 7.4: Time series of estimated Old Crow muskrat returns (a), the inflation-adjusted mean muskrat price (b), price corrected harvest (c), detrended harvest (d), and the dominant periods of this detrended time series (e). The y axes of (a) and (c), and the x axis of (e), are logarithmic. The curve in (c) is the cubic smoothing spline used to detrend fur returns using the ratio of observed harvests to predicted harvest (d). The curves in (e) represent the dominant period of all years (black) and pre 1989 (gray). Dotted lines indicate significant periods ($\alpha = 0.1$).

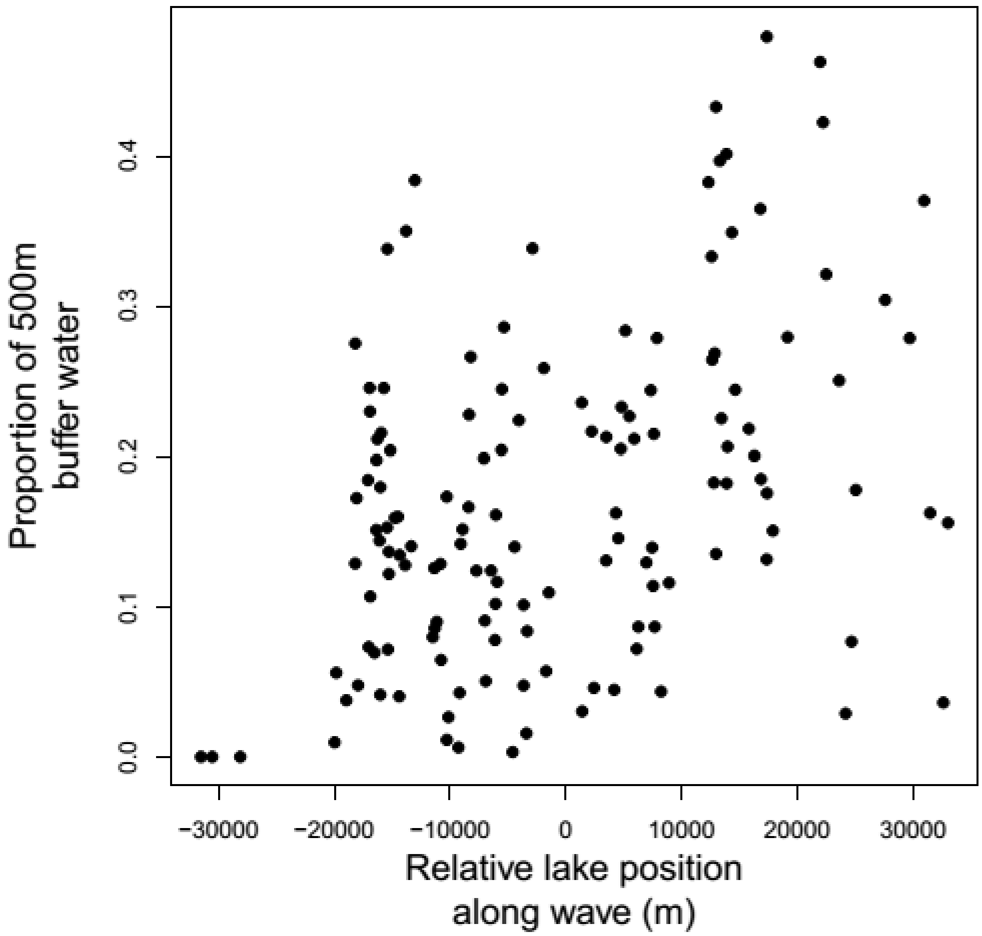
7.3 Supplementary material for Chapter 4



Supplementary Figure 7.5: Synchrony declines with distance, but average includes isolated populations. The Mantel correlogram for growth rates in logarithmically transformed muskrat pushup densities demonstrates a decline of synchrony with distance. The range of above average synchrony extends approximately 10km. The mean synchrony of the whole set corresponds to that of isolated Porcupine basin lakes, 0.12.

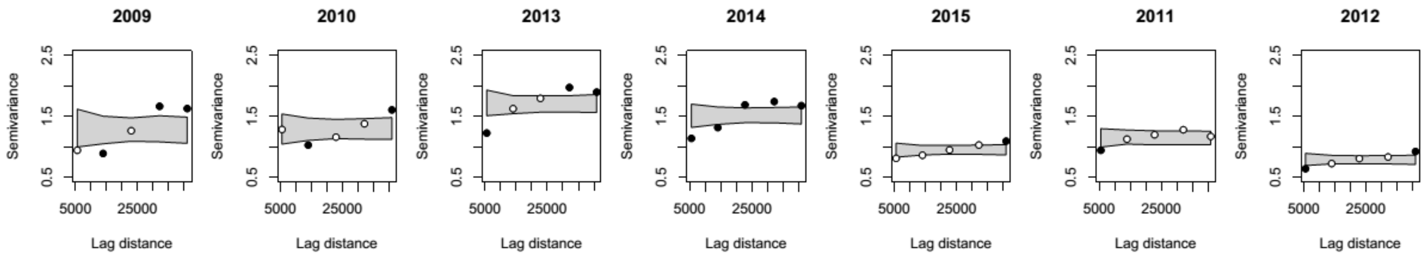


Supplementary Figure 7.6: Optimal generalized additive model of change in mean pushup density through time for sample lakes in the Old Crow Flats that includes a traveling wave.

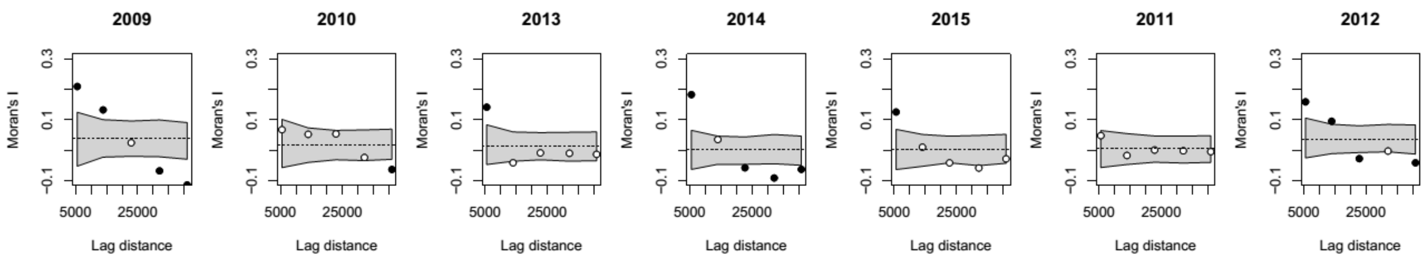


Supplementary Figure 7.7: Water in 500 m lake perimeter buffer as a function of lake position along the axis of the optimal unidirectional travelling wave. Note how the positive correlation is primarily driven by lakes between 10000 and 20000 m from the centroid and that lakes in the extreme NNE of the Flats (i.e.> 20000 m from the centroid) had less water in their buffers.

(a)



(b)



Supplementary Figure 7.8: Spatial variability in growth declines as growth itself declines. (a) Semivariograms of annual growth in logarithmically transformed pushup densities in the Old Crow Flats. Years are organized from largest positive growth to largest negative growth. Note the decline in overall variability in negative growth years. (b) Mantel's I correlograms of same. Note the range of autocorrelation, and negative autocorrelation in extreme years.

7.4 Supplementary material for Chapter 5

7.4.1 Methods: Availability & use

Similar to Jones et al. (2006), we compiled skating records for the Rideau Canal Skateway from the National Capital Commission. These begin in 1971-72 and include: *date opened*; *date closed*; *season length* (open date to close date); since 1992-93, number of *users*; and, since 1995-96, number of *skating days*. The latter is equivalent to the season length minus the number of days the canal was closed due to poor weather. We used season length, skating days, date closed, and date opened as response variables representing ecosystem service availability. We employed number of users as an index of cultural ecosystem service benefit, and modeled it as a function of skating days, date opened, date closed, and the proportion of days open. The first year of the season length time series was omitted because it is an outlier (Bonferroni outlier test $p = 0.03$) likely because, in that year, the canal was cleared for skating by hand rather than by tractor as was the case subsequently.

7.4.2 Model selection:

We obtained weather records from Environment Canada's Climate Data Online. For weather variables, previous research used freezing degree days, mean temperature of the 15 coldest consecutive days, and the number of days below -5°C (Visser and Petersen 2009, Damyanov et al. 2012). We elaborated upon these approaches by calculating mean daily temperature across a variety of time window length (e.g. 25 days) for all such time windows in that year (e.g. Dec. 1 to Dec. 25, Dec. 2 to Dec. 26, etc.). We assessed time window lengths of 10, 25, 50, 75, 100, 125, 150, 175, and 200 days. For each window length, we selected the window that minimizes mean daily temperature (e.g. the coldest 10 days of the year, coldest 25, etc.), and calculated all other weather variables based on that window. This avoids using artificial designations of winter weather based on calendar months. In addition to daily mean temperatures (T_{mean}), we calculated: coefficient of variation of daily mean temperatures (T_{CV}), total precipitation (P_{tot}), and the number of days with mean temperature below -5°C (D_{-5C}). The time window length across which each variable was calculated is expressed as a subscript (e.g. $T_{mean-10}$, $T_{mean-25}$, etc.) We square root transformed P_{tot-10} and P_{tot-25}. All other variables were approximately normally distributed.

To model season length, skating days, opening date, and closing date, we selected from linear models that contained at most one explanatory variable for temperature (T_{mean}/D_{-5C}), precipitation (P_{tot}), and temperature variability (T_{CV}). For users, we compared models containing Holling's three functional responses (Supplementary Figure 7.9) with respect to skating days and proportion of days open, and linear responses with respect to opening and closing date (Holling 1959). Holling's functional responses were selected, where any increasing mathematical function would have sufficed, as they reflect a situation analogous to our case study namely: the rate of consumption of a resource while varying its density (Holling 1959). We used the software R and the package MuMIn to conduct multi-model comparison (Bartoń 2013). We ranked models using Akaike's Corrected Information Criterion (AICc; Burnham and Anderson 2002). For models of availability, we did not expect to find one strongly supported model due to the similarity of explanatory variables and the large number of possible models. We calculated projections based on the weighted averages of regression coefficients from all models to reduce biases due to overreliance on a single "best" model (Burnham and Anderson 2002).

7.4.3 Projection

We used the MarkSim Weather Generator (Jones and Thornton 2013) to forecast daily weather conditions in the Ottawa region for each year between 2019 and 2091. This uses an ensemble forecast of six general circulation models (GCMs; ECHam5, BCCR_BCM2.0, CNRM-CM3, CSIRO-Mk3.5, INMCM3.0, MIROC3.2) to simulate stochastic localized weather patterns with a long-term average corresponding to the GCM forecasts while reflecting regional weather characteristics based on historical observations (Jones and Thornton 2013). We used the business-as-usual, high emission A2 scenario for all models. We generated 990 unique weather forecasts to calculate means and confidence intervals for season length, skating days, opening date, and closing date over decadal time horizons.

7.4.4 Results & Discussion: *Weather projections*

We identified 14 top models for the weather-dependency of season length (Supplementary Table 7.6) and 28 top models for skating days (Supplementary Table 7.7). From 1972-2013, season length varied substantially year-to-year with an overall decline (-5.2 ± 2.9 days/decade, 95% CI; Figure 5-1) driven by later opening dates (6.3 ± 2.0 days/decade), not earlier closing dates (1.0 ± 2.6 days/decade). Incorporating temporary closures within the season to estimate skating days more precisely between 1996 and 2013, we found a non-significant negative trend over time (-1.9 ± 12.8 days/decade; 95% CI; Figure 5-1) driven by the shorter time series and inter-annual variability.

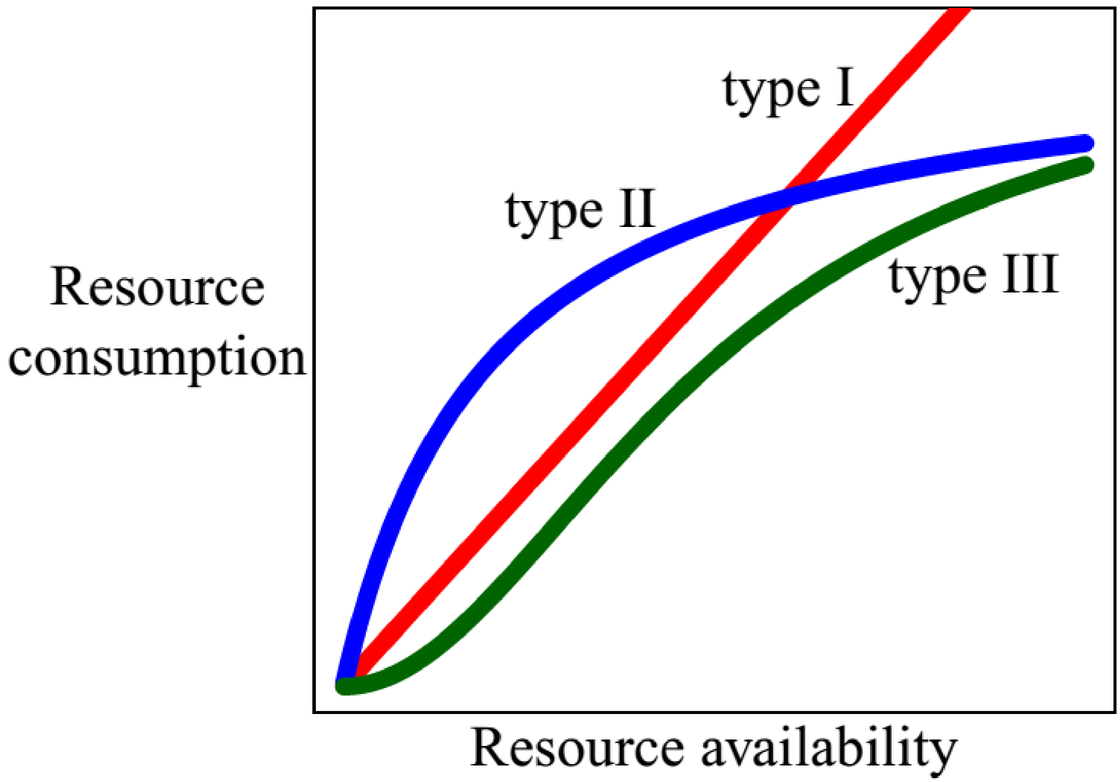
For season length the most important explanatory variables were $T_{mean-100}$ (relative variable importance = 0.67), T_{CV-200} (0.47), and P_{tot-10} (0.21). For skating days, the most important variables were $T_{mean-100}$ (0.79), $P_{tot-125}$ (0.38), and T_{cv-50} (0.19). Using the MarkSim Weather Generator (Jones and Thornton 2013), we projected a continuation of historical trends in weather variables for the Ottawa region, including: a warming trend in multi-month temperature averages $T_{mean\cdot100}$ (0.67 ± 0.39 °C/decade historically vs. 0.59 ± 0.39 °C/decade projected; 95% CI; Supplementary Figure 7.10a); no trend in winter precipitation P_{tot-10} (0.1 ± 2.3 cm/decade historically vs. 0.02 ±

0.6 cm/decade projected, 95% CI; Supplementary Figure 7.10b); and large inter-annual fluctuations with a minor negative trend in daily temperature variability T_{CV-200} ($-7.0 \pm 6.4 \times 10^{-4}$ /decade historically vs. $-3.3 \pm 7.6 \times 10^{-4}$ /decade projected, 95% CI; Supplementary Fig. 3c). In the context of the global target of 2°C warming, this corresponds approximately to the 2040 horizon of our projections. However, the uncertainty in projected global mean temperatures based on the six GCMs used in our projections (e.g. in 2050: 2.38 ± 0.32 °C; SD) highlights the need for caution in such an assessment.

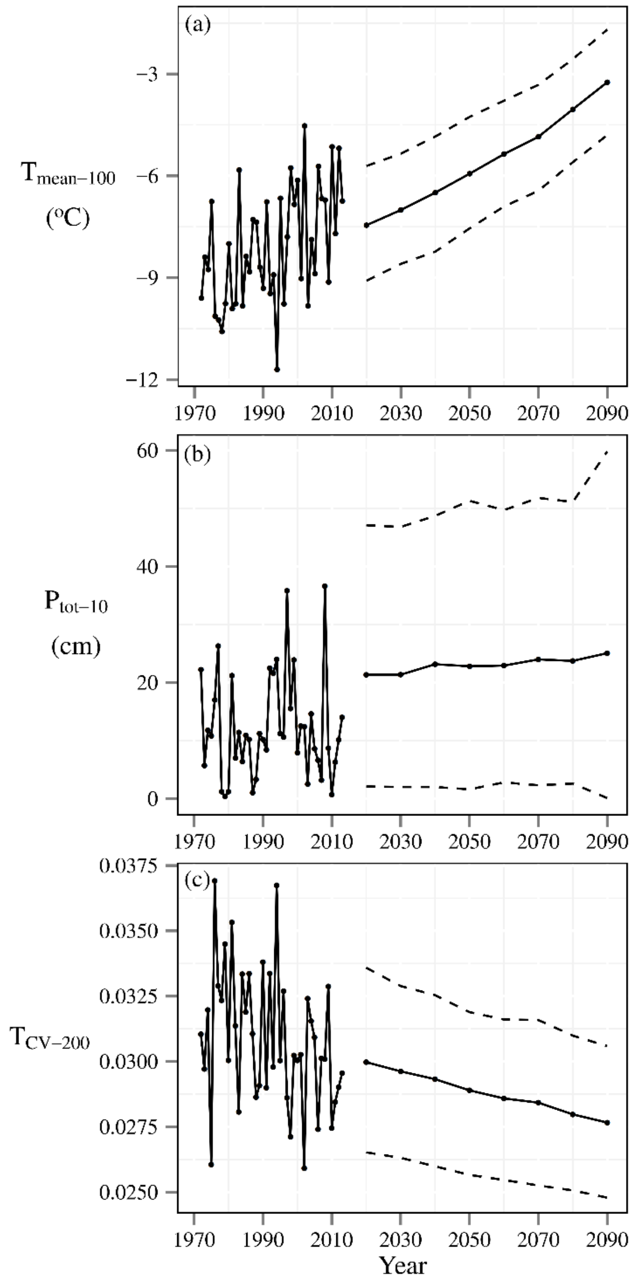
The reliability of these projections depends on MarkSim, a downscaled, ensemble weather forecaster using GCMs from the IPCC AR4 report (Jones and Thornton 2013). MarkSim is one of the only available tools to generate daily weather conditions that are generally in agreement with local weather observations. While MarkSim projections are based on a robust climate typing with 701 unique weather clusters depicting different weather temporal dynamics at the local scale, future localized weather may differ from historical weather as climate changes. While the ensemble of GCMs used to forecast future weather is limited to six simulations, these simulations are centered upon the average of all the GCMs found in the AR4. We chose a high-emission, business-as-usual, scenario (A2) even though the emissions scenarios used in the IPCC report describe the range of possible socio-economic development in the next decades. The reason we chose the most pessimistic scenario is that, to date, CO_2 emissions have coincided with the most pessimistic scenarios from the first to the fifth IPCC report (Peters et al. 2012). While this is currently the case, future emissions could follow an alternate path. Still, basing ourselves on the assumptions of the most pessimistic emissions scenario, our MarkSim projections appear to *underestimate* the increase and variability in temperature when compared to the historical record (Supplementary Figure 7.10). Since a single temperature variable ($T_{mean-100}$; Supplementary Table

7.6; Supplementary Table 7.7) was consistently selected as the most important driver of service availability in our models, our projections of availability and benefits are likely conservative due to this underestimated warming.

7.4.5 Figures & tables



Supplementary Figure 7.9: Conceptual examples of Holling's three functional responses relating resource consumption to resource availability. Types I, II, and III are in red, blue, and green respectively.



Supplementary Figure 7.10: Plots demonstrating historical time series and projected values with 80% prediction intervals for the top three importance weather variables modeling skating season length at the Rideau Canal Skateway (n = 990 per decade). Variable abbreviations are as follows: (*a*) $T_{mean-100}$ = mean daily temperature for the coldest 100 days; (*b*) P_{tot-10} = total precipitation for the 10 coldest days; and (*c*) T_{CV-200} = coefficient of variation of mean daily temperature for the 200 coldest days.

Supplementary Table 7.6: Comparison of weather models for the skating season length of the Rideau Canal Skateway. Models within 4 ΔAICc (Akaike's corrected information criterion (Burnham and Anderson 2002)) are presented, representing 48.9% of model weights. For each explanatory variable, values are calculated over time windows that represent the coldest consecutive days of a particular year. These time windows varied from 10 to 200 days and are indicated by the number associated with each variable. SL = skating season length, P_{tot} = precipitation, T_{mean} = mean daily temperature, T_{CV} = coefficient of variation of mean daily temperature. Projections of season length are weighted based on all models.

formula	**AICc**	**ΔAICc**	**weight**	**R^2**
SL ~ T_{CV-200} + $T_{mean-100}$	311.7	0.0	0.0905	0.51
SL ~ T_{CV-200} + $T_{mean-100}$ + P_{tot-10}	312.4	0.8	0.0622	0.53
SL ~ T_{CV-200} + $T_{mean-100}$ + $P_{tot-200}$	312.8	1.1	0.0514	0.53
SL ~ T_{CV-200} + $T_{mean-100}$ + P_{tot-50}	312.9	1.2	0.0495	0.53
SL ~ T_{CV-200} + $T_{mean-100}$ + $P_{tot-175}$	313.7	2.0	0.0327	0.52
SL ~ T_{CV-200} + $T_{mean-100}$ + $P_{tot-150}$	313.9	2.2	0.0294	0.52
SL ~ T_{CV-200} + $T_{mean-100}$ + $P_{tot-100}$	314.0	2.3	0.0281	0.52
SL ~ T_{CV-200} + $T_{mean-100}$ + P_{tot-75}	314.0	2.4	0.0276	0.52
SL ~ T_{CV-200} + $T_{mean-100}$ + $P_{tot-125}$	314.1	2.5	0.0263	0.52
SL ~ T_{CV-200} + $T_{mean-100}$ + P_{tot-25}	314.2	2.6	0.0249	0.51
SL ~ T_{CV-175} + $T_{mean-100}$ + P_{tot-10}	314.3	2.6	0.0243	0.51
SL ~ T_{CV-175} + $T_{mean-100}$	315.0	3.4	0.0168	0.47
SL ~ T_{CV-175} + $T_{mean-100}$ + $P_{tot-200}$	315.6	3.9	0.0129	0.50
SL ~ T_{CV-100} + $T_{mean-100}$	315.6	4.0	0.0123	0.47

Supplementary Table 7.7: Comparison of weather models for the number of skating days at the Rideau Canal Skateway. Models within 4 ΔAICc (Akaike's corrected information criterion; Burnham and Anderson 2002)) are presented representing 61.9% of model weights. For each explanatory variable, values are calculated over time windows that represents the coldest consecutive days of a particular year. These time windows varied from 10 to 200 days, and are indicated by the number associated with each variable. SD = skating days, P_{tot} = precipitation, T_{mean} = mean daily temperature, T_{CV} = coefficient of variation of daily minimum temperature. Projections of skating days are weighted based on all models.

formula	AICc	ΔAICc	weight	R^2
$SD \sim T_{CV-50} + T_{mean-100} + P_{tot-125}$	122.3	0.0	0.0663	0.86
$SD \sim T_{CV-50} + T_{mean-100} + P_{tot-10}$	123.0	0.6	0.048	0.85
$SD \sim T_{CV-100} + T_{mean-100} + P_{tot-125}$	123.4	1.0	0.0396	0.85
$SD \sim T_{CV-75} + T_{mean-100} + P_{tot-125}$	123.4	1.1	0.0384	0.85
$SD \sim T_{CV-25} + T_{mean-100} + P_{tot-150}$	123.6	1.3	0.0354	0.85
$SD \sim T_{mean-100} + P_{tot-125}$	123.8	1.4	0.0324	0.81
$SD \sim T_{CV-125} + T_{mean-100} + P_{tot-125}$	124.2	1.8	0.0264	0.84
$SD \sim T_{mean-100} + P_{tot-10}$	124.5	2.2	0.0225	0.80
$SD \sim T_{CV-50} + T_{mean-100} + P_{tot-150}$	124.5	2.2	0.0224	0.84
$SD \sim T_{CV-25} + T_{mean-100} + P_{tot-125}$	124.6	2.2	0.0219	0.84
$SD \sim T_{CV-100} + T_{mean-100} + P_{tot-10}$	124.6	2.2	0.0217	0.84
$SD \sim T_{CV-200} + T_{mean-100} + P_{tot-125}$	124.6	2.3	0.0211	0.84
$SD \sim T_{CV-25} + T_{mean-100}$	124.9	2.6	0.0183	0.79
$SD \sim T_{CV-10} + T_{mean-100} + P_{tot-10}$	125.0	2.6	0.0177	0.83
$SD \sim T_{mean-125} + P_{tot-125}$	125.0	2.7	0.0174	0.79
$SD \sim T_{CV-150} + T_{mean-100} + P_{tot-125}$	125.0	2.7	0.0171	0.83
$SD \sim T_{CV-25} + T_{mean-100} + P_{tot-200}$	125.1	2.8	0.0165	0.83
$SD \sim T_{CV-175} + T_{mean-100} + P_{tot-125}$	125.2	2.8	0.016	0.83
$SD \sim T_{CV-75} + T_{mean-100} + P_{tot-10}$	125.3	3.0	0.0149	0.83
$SD \sim T_{CV-10} + T_{mean-100} + P_{tot-125}$	125.3	3.0	0.0148	0.83
$SD \sim T_{CV-25} + T_{mean-100} + P_{tot-175}$	125.6	3.2	0.0131	0.83
$SD \sim T_{CV-200} + T_{mean-100} + P_{tot-10}$	125.7	3.3	0.0126	0.83
$SD \sim T_{CV-25} + T_{mean-100} + P_{tot-10}$	125.7	3.3	0.0124	0.83
$SD \sim T_{mean-100} + P_{tot-150}$	125.7	3.4	0.0122	0.78
$SD \sim T_{CV-50} + T_{mean-100}$	126.0	3.7	0.0107	0.78
$SD \sim T_{CV-100} + T_{mean-50}$	126.0	3.7	0.0105	0.78
$SD \sim T_{CV-125} + T_{mean-100} + P_{tot-10}$	126.2	3.9	0.0095	0.82
$SD \sim T_{CV-50} + T_{mean-100} + P_{tot-100}$	126.3	3.9	0.0092	0.82

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