

**Spatial and watercourse influences on Arctic Charr (*Salvelinus alpinus*) migration
in Nunavut**

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A thesis submitted to the Faculty of Graduate Studies of
The University of Manitoba
in partial fulfilment of the requirements of the degree of

Master of Science

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Abstract

Migration is an adaptive mechanism for species to meet life cycle needs in heterogeneous habitats such as the Arctic. The Arctic Charr (*Salvelinus alpinus*) is a northerly-distributed, partially anadromous fish that is culturally and economically important in Nunavut, Canada. Previous studies have investigated charr migratory choices in specific areas of Nunavut, but our understanding is limited of how these vary across the territory's freshwater ecosystems. Understanding environmental influences on charr migratory choices can give insight on population reactions to climate change. To assess the drivers behind and differences in Arctic Charr migratory ecotype distribution across Nunavut, I compiled and cleaned three pre-existing sources—the Arctic Fisheries Stock Assessment database (scientific research), the Nunavut Coastal Resource Inventory (mapped Inuit knowledge) and the Nunavut Wildlife Harvest Study (Inuit fishermen harvest records). I used generalized linear mixed models to compare 691 cleaned Inuit knowledge records of anadromous and resident charr populations to river, lake, and geographic variables. I validated these models using 51 independent scientific records and k-fold cross-validation. Inuit knowledge data had more observations across a broader geographic and environmental space. Both models strongly fit the training data, but the resident model was not transferrable to the independent data. There was substantial overlap between the models. Both anadromous and resident charr are more likely to be found in larger lakes further east, and are more readily detected close to communities. Anadromy is less likely in longer rivers, although the effect is reduced for large lakes. This analysis demonstrates that existing Inuit knowledge data is underutilized for wildlife research and management in Nunavut. Combining two complementary types of records allowed a broader scale analysis than previously. Modelling at the lake level, however, primarily identified distributional drivers for the Arctic Charr species, not migratory types. Large lakes in eastern Nunavut may provide relatively stable refugia for Arctic Charr under climate change, but anadromous charr may be more adversely affected by changes in lake access. This study provides a basis for further exploring charr-habitat relationships using Inuit knowledge—and preferably, Inuit-led research—to support better fisheries management decisions in Nunavut.

Acknowledgements

To my friends and family—first and foremost Laurent—I finally did it! Thank you for supporting me on the journey, this thesis would not have happened without your badgering, cheering squad, and patience.

Thank you to my supervisor, Ross Tallman, for your support and guidance, especially for adapting to the many changes in direction. I especially appreciated you lasting this out with me and my steadily worsening communication. I think you had more faith in me than I did.

Thank you also to my committee – Darren Gillis, Margaret Docker, and Kim Howland. You were understanding of my situation but still challenged me, and it has made me a better scientist.

To my lab mates—Lauren, Gabrielle, and Chris—and all the DFO graduate students, thank you for the fun, the laughs, the tears, the political discussions, and for welcoming me to Winnipeg. The journey would not have been the same without you, and I look forward to seeing you round the north sometime!

To Zoya Martin, Chris Lewis, Simon Wiley—thank you for guiding me through the complexities of federal government administration, and being my ever-patient feet on the ground in Iqaluit and Winnipeg.

Finally, qujannamiik / mat’na / quana to those people and organizations who provided me with data and background for my research: Angela Young, Janelle Kennedy, Corenna Nuyalia, and Teresa Tufts with the Government of Nunavut and Amos Hayes from Carleton University (Nunavut Coastal Resource Inventory); Chris Cahill from the University of Calgary and Ross Tallman at Fisheries and Oceans Canada (Arctic Fisheries Stock Assessment database).

Funding for this research was gratefully received from Fisheries and Oceans Canada, the Government of Nunavut, the Northern Scientific Training Program, a Major G.E.H. Barrett-Hamilton Memorial Scholarship, a Manitoba Graduate Fellowship, the Canadian Society of Zoologists, the University of Manitoba Department of Biological Sciences, the University of Manitoba Graduate Student Association, and the Ocean Tracking Network.

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List of abbreviations

AIC	Akaike information criterion
AFSA	Arctic Fisheries Stock Assessment database
AUROC	Area under the receiver operating curve
CRS	coordinate reference system
DFO	Fisheries and Oceans Canada (Government of Canada)
EPSG	European Petroleum Survey Group (structured dataset of CRSs)
GBIF	Global Biodiversity Information Facility
GIS	geographic information system
GN	Government of Nunavut
GLM	generalized linear model
GLMM	generalized linear mixed model
IHT	Inuit Heritage Trust
NCRI	Nunavut Coastal Resource Inventory study, including associated data
NLCA	Nunavut Land Claim Agreement
NNP	Nunavut Named Places dataset
NPC	Nunavut Planning Commission
NWHS	Nunavut Wildlife Harvest Study, including associated data
NWMB	Nunavut Wildlife Management Board
NWT	Northwest Territories
OBIS	Ocean Biodiversity Information System
QGIS	Quantum Geographic Information System software
SAC	spatial autocorrelation
SDM	species distribution model
SSB	spatial sorting bias
UOM	Use and Occupancy Mapping study, including associated data
UTM	Universal Transverse Mercator
WGS	World Geodetic System

1. Chapter 1: Introduction and literature review

1.1. Habitat selection and anadromy in Arctic Charr

Aquatic habitat is heterogenous across landscapes, varying in the availability of resources (e.g., prey, shelter), and the physiologically acceptable conditions (e.g., light, temperature, dissolved oxygen) that are necessary for survival, reproduction, and persistence of fish species (Krausman 1999; Planque et al. 2011). Variation in, and interaction between, habitat components dictates the quality and types of habitat that are available to be selected by an organism. Habitat affects species distribution, abundance (Krausman 1999; Boyce et al. 2016) and community structure (Jackson et al. 2001). Fish populations are thus non-randomly distributed both spatially and temporally within available habitats (Le Pape et al. 2014).

Individuals select habitat in order to maximise their lifetime fitness, as measured by reproductive success (Planque et al. 2011; Boyce et al. 2016). Habitat selection is a hierarchical process involving a series of innate and learned behavioural decisions made by an animal about what habitat it would use at different spatial and temporal scales (e.g., seasons or life stages). Habitat selection is thereby affected by selective physiological (e.g., dissolved oxygen requirements, temperature tolerances) and behavioural differences (e.g., feeding behaviour, spawning strategies, aggressiveness) between species, mediated by density dependent effects that can reduce fish access to resources or drive movement between habitat patches (Huey 1991; Langeland et al. 1991; Planque et al. 2011; Boyce et al. 2016). The sum of individual habitat selection for a species indicates habitat use, and affects aquatic community structure (Jackson et al. 2001; Hershey et al. 2006), population size (Boyce et al. 2016), and population persistence (Krausman 1999).

One behavioural mechanism for dealing with a heterogeneous environment is movement, or migration, across environmental gradients (Secor 1999). By moving to a more suitable habitat, fish may escape predators, escape density-dependence and have better access to prey, or

increase the probability for survival of their offspring (Kendall et al. 2015). These benefits, however, must be balanced against the energetic costs, and risks of migrating. Migration requires fish to adapt to different water temperatures, flows and salinities, which can have significant physiological costs (Huey 1991; Lans 2010; Chapman et al. 2012). Additionally, predation or other risks (e.g., stranding) can lead to higher mortality for migrants (Gross et al. 1988). Migrations are thus only an energetically and evolutionarily beneficial strategy if the new environment provides greater opportunity for growth and subsequent lifetime fitness (reproductive capacity) (Näslund et al. 1993).

For anadromous fish species, those which spawn in freshwater but migrate to marine environments for portions of their adult life (Secor and Kerr 2009), two ultimate causal mechanisms have been proposed. First, that fish migrate to feed in the more productive marine environment (driving migration to the ocean) (Nordeng 1983; Gross et al. 1988); and second, that freshwater environments provide a safer spawning and rearing environment (driving the return to freshwater) (Secor 1999; Chapman et al. 2012; Reed et al. 2016). Further, in addition to the relative suitability of the connected habitats, the ability to move between them, and the difficulty of (or barriers to) such movement, affects how beneficial migration is as a strategy. Regardless, proximal environmental cues initiate the movements between these environments (Reed et al. 2010). Thus, many species in highly variable environments, such as the Arctic, maintain population viability through facultative (partial) anadromy, whereby a portion of the population is migratory, while the remainder is resident in freshwater year-round. Partial anadromy is thought to promote long term population resilience (Moore et al. 2014b), and be driven by local or even individual factors such as sex (Nordeng 1983; Reist et al. 2013).

Salmonids are well-known examples of anadromous species, of which the Arctic Charr (*Salvelinus alpinus*; or “charr”) has the most northerly distribution. Charr demonstrate substantial variation in morphology, migratory history, dietary niches, and habitat preferences (Reist et al. 2013) – resulting in a series of questions relating to the drivers of this diversity, known as the ‘char problem’ (Nordeng 1983). In particular, charr demonstrate multiple

migratory types, including anadromy, potamodromy (movements between freshwater habitats), residency (remaining in freshwater even in systems that are connected to the ocean), and landlocked forms (unable to reach the ocean due to physical or geographic barriers) (Reist et al. 2013). Arctic Charr are widespread across the Canadian Arctic territory of Nunavut, and are culturally, and economically important to Inuit communities (Nunavut Planning Commission 2016) as well as important to marine and freshwater ecology (Swanson et al. 2010b). The species exhibits diverse life histories across the territory, with populations demonstrating differing proportions and patterns of anadromy (Secor 1999).

1.2. Environmental drivers of anadromy

Migratory history has been examined for Nunavut Arctic Charr stocks in a limited number of areas, particularly the High Arctic (e.g., Ellesmere Island) (Babaluk et al. 1997, 2002; Loewen 2016), and the Cambridge Bay and Kugluktuk areas (Campbell et al. 1999; Kristofferson 2002; Swanson et al. 2010a; Gilbert et al. 2016). These studies found that Nunavut Arctic Charr are variable in the age at which they first migrate (Campbell et al. 1999; Birtwell et al. 2005; Swanson et al. 2010a; Gilbert et al. 2016; Loewen 2016), and the lifetime migratory behaviours that they exhibit (Moore et al. 2017), but the costs and benefits of migration likely change over an individual's life (Bond et al. 2015).

Migration is likely a conditional strategy, the result of interactions between genetics, fish size or dominance at certain developmental stages (i.e., smolting) (Sprules 1952; Reist et al. 2013), and environmental conditions. Anadromous and resident fish often come from the same population, with multiple genes controlling life history expression (Hecht et al. 2013; Sloat et al. 2014) at several junctures in a fish's life (Ferguson et al. 2019). In this model, an underlying and continuous trait either exceeds or falls below a threshold value, and is thereby expressed as a discrete migratory life history type (Dodson et al. 2013). The ability to migrate has therefore been found even in some landlocked populations for some fish (e.g., Rainbow Trout (*Oncorhynchus mykiss*); Hecht et al. 2013), and Moore et al. (2014a) found no genetic

difference between sympatric anadromous and resident Arctic Charr in Cumberland Sound, Nunavut. Limited gene flow among Arctic Charr populations (Moore et al. 2017), however, may result in different population level expressions of anadromy in response to environmental cues, as has been found in Chinook Salmon (*O. tshawytscha*) (Anderson and Beer 2009; Hecht et al. 2015) and other salmonids (Sahashi and Morita 2018). Migratory morphs may even differentiate in threshold traits (Sahashi and Morita 2018) or become more genetically isolated over time (Salisbury et al. 2018, 2020; Turbek et al. 2018). Additionally, other aspects of fish biology may influence anadromy. For instance, female fish are more likely to migrate to access productive feeding areas that support better gonad development (Ohms et al. 2014; Kendall et al. 2015; Kelson et al. 2019). Conversely, males can adopt alternative mating strategies (e.g., sneaking) that make residency more beneficial (Kelson et al. 2019); although Salisbury et al. (2020) suggest that this may not be the case for Arctic Charr. Nevertheless, anadromy appears to have a strong genetic basis, with resident parents more likely to produce resident offspring (Kendall et al. 2015; Kelson et al. 2019).

An individual's life history is also thought to relate to early growth and age-at-maturity (Table 1) (Secor 1999; Dodson et al. 2013). Variability in growth may be related to differential gene expression in some populations, as well as available resources to fuel growth (Rikardsen 1997; Reist et al. 2013), and density-dependence (Benjamin et al. 2013). Fast-growing juveniles more quickly reach a threshold size that allows migration (Finstad and Hein 2012). With access to the more productive marine environment, anadromous fish reach a larger maximum size and are more fecund (Gross et al. 1988; Klemetsen et al. 2003). The energy devoted to this fast growth, however, is unavailable for the development of reproductive organs, so these fish typically mature at an older age (around 12 years) (Richardson et al. 2001). Conversely, slower-growing juveniles generally demonstrate non-migratory behaviour, and have a smaller maximum size, and lower fecundity; however resident charr are usually younger at maturity (Secor 1999). Many of these studies on charr growth and migratory life history, however, were based on captures of larger fish that were already migrating. Less is known about the early growth rates and whether this might influence anadromy, but recent research by Grenier and Tallman (2021)

found that anadromous Arctic Charr grow faster as juveniles, and maintain higher but more variable growth rates over their lives than residents. These growth rates appear to be tied to aquatic productivity (e.g., temperature, growing season; Sinnatamby 2013) so may change over time and affect charr anadromy. A similar relationship between faster growth and migration has been found for Brown Trout (*Salmo trutta*) (Marco-Rius et al. 2013a); but conversely, Gruzdeva et al. (2017) found a complex effect of growth on anadromy in Dolly Varden (*Salvelinus malma*), such that the fastest growers become resident, intermediate growers are earlier migrators, and the slowest growers migrate later (see also Morrison 2017; Gallagher et al. 2019). There are additionally other complicating factors that drive variability in charr morphology and ecology such as diet, which can cause populations to develop bi-modal size distributions (Reist et al. 2013). Consequently, our understanding of the drivers of anadromy in Arctic Charr is constantly developing.

Table 1: Potential costs and benefits for partially anadromous fish species (reproduced from Kendall et al. 2015; permission obtained from Canadian Science Publishing on 26 March 2021)

Life history	Costs	Benefits
Residency	Typically smaller size at maturation: For females, lower fecundity, smaller eggs, producing smaller fry, smaller range of gravel for redds, and shallower redds. For males, decreased chance of competitive dominance and female choice for reproduction.	Reduced mortality with younger age at maturation, avoidance of large marine predators. Reduced cost and length of marine migration. Increased chance of iteroparity.
Anadromy	Increased mortality risk during marine migration. Higher mortality with older age at maturation. Decreased chance of iteroparity.	Reproduction typically at larger size: For females, higher fecundity and access to a larger range of gravel for redds and larger eggs, producing larger fry. For males, increased chance behavioral dominance during mating and female choice.

In addition to the genetic and physiological drivers of partial anadromy, however, climate and habitat factors affect the costs and benefits of migratory strategies. For instance, in their comparison of scientific and Inuit knowledge on Arctic Charr growth in the Inuvialuit Settlement Region, Knopp et al. (2012) found consistent themes of environmental and ecological timing emerged from community knowledge of climate change and fish growth. Inuit saw predictable migration timing and consistent seasonal fishing success as indicators of fish population health. Further, many of the environmental variables that Inuvialuit participants indicated affected charr growth are those that are thought to influence migration timing – including lake

conditions (e.g., water temperature, ice thickness and timing), lake-river connectivity (i.e., water levels) and changes in stream channels or shorelines, precipitation levels, and the presence of other species. Even winter snowfall, as a predictor of spring water levels, consequently influences charr migrations (Brent Nakashook, pers. comm., 2016).

Although Canadian freshwater fish species diversity generally decreases with latitude (Ecological Stratification Working Group 1995; Chu et al. 2003; Abell et al. 2008), globally, the number of anadromous species increases (catadromy is conversely more prevalent in the tropics) (Gross et al. 1988). Freshwater productivity generally decreases towards the poles (Chu et al. 2003), so that the marine environment is comparatively more productive (Nordeng 1983). For fish in low productivity northern lakes, anadromy is thus thought to be more beneficial to access the higher productivity marine environment (Birtwell et al. 2005). This is reflected in higher growth rates in northern compared to southern Arctic Charr populations (Chavarie et al. 2010; Sinnatamby 2013). Residents showed a stronger response to this latitudinal gradient than did anadromous fish (Chavarie et al. 2010), implying that migration helps charr to counteract the effects of decreasing freshwater productivity.

Fewer studies have assessed the effect of longitude on fish distribution, nevertheless, it has been found to influence community structure (Tallman et al. 2016). On a cross-Canadian watershed scale, terrestrial productivity decreases somewhat towards the east, for the same latitude (Chu et al. 2003; Reist et al. 2016). Conversely, marine productivity and diversity should be higher in the eastern Arctic Ocean, which is more directly and openly connected to the Atlantic than the western Northwest Passage is to the north Pacific (Tremblay et al. 2012; Druon et al. 2018). There may therefore be an increasing difference between freshwater and marine productivity, so that anadromy is more likely at more easterly longitudes.

Within these broad productivity gradients, however, landscape features can influence fish community composition (Hershey et al. 2006). The Arctic is a geologically recent landscape, so dispersal and subsequent physiological ability to survive likely dictate composition (Power and

Power 1995) rather than extinction factors. Consequently, watersheds, which influence species distributions (Minns and Moore 1992; Porter et al. 2000; Chu et al. 2003, 2014; Tedesco et al. 2017) and abundance (Samarasin et al. 2014; Jones et al. 2020), may affect the likelihood of anadromy since they integrate information on climate, flow regimes, and landscape connectivity. Patterns of anadromy would be expected to be more similar within than between watersheds as the probability of species presence is often autocorrelated (i.e., higher closer to other presences) (Chu et al. 2005). Although charr can undertake long migrations (Brown and Fast 2012), they tend to stay close to source rivers (Dempson and Green 1985; Finstad and Hein 2012; Spares et al. 2012), so some autocorrelation is expected.

Within a watershed, the amount of available overwintering habitat could affect the likelihood of anadromy. Niche availability has been found to increase the number of morphological and foraging variants (Reist et al. 2013). Larger, deeper lakes have more heterogeneous habitat so may offer a greater amount of stable thermal habitat and more niches, thus reducing the benefit of anadromy (Kristoffersen et al. 1994; Jensen 2013; Murdoch and Power 2013; Samarasin et al. 2014; Reed et al. 2016). In general, smaller lakes have a lower carrying capacity (Samarasin et al. 2014). Density-dependent factors thus play a greater role in smaller lakes, which could be expected to reduce individual marginal fitness and make early anadromy a more beneficial strategy (Kendall et al. 2015); particularly if, as suggested by some Inuit observations, fish in small lakes have better condition (Fisheries and Sealing Division 2017) and are thus more able to migrate. Finally, smaller lakes have more variable environmental conditions, for instance demonstrating lower dissolved oxygen levels in late winter (Leppi et al. 2016), a larger proportional reduction in available lake volume under winter ice that change species spatial requirements (Jackson et al. 2001; Blanchfield et al. 2009; Salonen et al. 2009; Helland et al. 2011), and large seasonal variation in water levels (Fisheries and Sealing Division 2017) so residency may be riskier.

Lake surface area may not fully reflect the available habitat, however, if lakes are small but deep. Lakes in the Qikiqtaaluk are more likely to fit this model, while shallow lakes that freeze

to the substrate may be more common in the flatter Kivalliq and Kitikmeot (Figure 1). Consequently, it may be possible that there is an interaction between the effects of lake surface area and lake shape (shoreline complexity), which influences the types and proportions of lentic habitat. For instance, populations that primarily use productive littoral habitats often demonstrate greater proportions of anadromy (Kristoffersen et al. 1994; Rikardsen 1997; Secor 1999) so lakes with complex shorelines may be more likely to contain anadromous populations, regardless of size.



Figure 1: Nunavut administrative regions (created by Maximilian Dörrbecker, used under Creative Commons license CC BY-SA 2.5¹)

¹ https://commons.wikimedia.org/wiki/File:Map_of_the_Nunavut_regions.png

Finally, the effect of lake morphometry on anadromy likely interacts with effects caused by the presence of other species in the freshwater environment, as landscape factors drive fish community and trophic structure (Hershey et al. 1999). Charr presence and habitat use has been found to depend on which other species occur in the same (Knudsen et al. 2010; Reist et al. 2013) or connected (Spens and Ball 2008) freshwater habitat. In sympatry, charr face greater predation risk (Gross et al. 1988) as well as competition for food (Hershey et al. 2006), making anadromy more beneficial (Secor 1999). This effect would be expected to be more pronounced in smaller lakes that do not have as many refuges from predation (Reed et al. 2016), nor as many opportunities for resource partitioning (Marco-Rius et al. 2013b).

Regardless of lake conditions, however, anadromy isn't possible if fish can't move between the freshwater and marine environments. Consequently, residency is more likely if the access river contains barriers that make migration more difficult and riskier for fish. These may include waterfalls or other sudden elevation changes (Hershey et al. 2006; Spens et al. 2007), fords or other shallow areas that may become impassable (Spens et al. 2007; Golder Associates 2013; Gilbert et al. 2016), or rapids that require too much energy to traverse. The exact effect of such barriers individually is unclear, as charr were able to climb a 1.5m waterfall, but were stopped by a 3.3m fall in the same study (Evans et al. 2002). Similarly, Power and Barton (1987) found that shallow areas without a clear channel can pose a sufficient barrier to migration to affect population abundance, particularly in low water years (Nunavut Tunngavik Inc. 2001; Gilbert et al. 2016) and fish may need to wait for high tides to provide easier passage upstream (Sprules 1952; Spares et al. 2015b). However, Arctic Charr have also been shown to pass through shallows only 10 cm deep (Evans et al. 2002), possibly by swimming on their sides to pass through shallow sections (Fisheries and Sealing Division 2017). Barriers may not completely stop movement but may nevertheless make the ascent more difficult and therefore decrease the likelihood of charr being anadromous.

A steep river gradient may have the same effect by decreasing anadromy (Finstad and Hein 2012), even if no section is steep enough to be considered a fall (Spens et al. 2007). Similarly,

mean elevation, and elevation range within a watershed affected species distribution across Canada (Chu et al. 2003) and the USA (Huang and Frimpong 2015). If a river is accessible by charr, however, river length appears to be a stronger predictor of the degree of anadromy than migration difficulty (represented by river slope or water velocity) (Kristoffersen 1994).

A shorter and easier path between freshwater and marine environments makes migration energetically less costly, particularly if the short open-water season at northern latitudes precludes fish recouping these energy expenditures during marine feeding. In addition to having a physically longer migration to undertake, fish in longer rivers also face greater variability in conditions (e.g., slow-melting river ice, or low water levels that change migration costs and benefits) during the run (Hegg et al. 2013; Ohms et al. 2014). Thus, river length has been found to affect the degree of anadromy in rainbow trout (Ohms et al. 2014), coregonids (Haynes et al. 2014), and Arctic Charr (Kristoffersen 1994; Hershey et al. 2006). Similarly, Loewen (2016) found that Arctic Charr in northern Nunavut lakes with shorter rivers (i.e., easier migration) migrate when younger and smaller than charr from lakes further from the ocean.

1.3. Climate change impacts on migratory behaviour

Improving our understanding of the drivers behind any aspects of Arctic Charr variety has implications for how we define diversity, and consequently manage this concept (Reist et al. 2013). Further, understanding which environmental cues influence Arctic Charr migratory decisions provides insight on population reactions to climate changes or anthropogenic impacts. Environmental changes can increase the patchiness of an environment and have demographic, distribution, and evolutionary effects on populations (Reist et al. 2006; Reed et al. 2010; Hegg et al. 2013). Anadromous species may be particularly affected by climatic change, as they will experience effects in both freshwater and marine environments (Johnson et al. 2012). Further, differing rates of change between the freshwater and marine environments may affect cue reliability and the coupling between components of aquatic systems (i.e., when the consequence of a behaviour is felt shortly after a cue is received, and in

the same environment). When cues are reliable, generalist and plastic species, such as Arctic Charr (Reist et al. 2013), can change quickly in response to environmental cues, particularly through behaviours such as migration, and maintain viable populations. If decoupling is extreme, however, plasticity can lead to maladaptation, and greater extinction probabilities for populations (Reed et al. 2010; Reist et al. 2013).

For instance, in even short, easy to navigate rivers, lower water levels may prevent fish passage (Nunavut Tunngavik Inc. 2001). Consequently, as rivers become more shallow, ice barriers may become more common and block fish passage or cause unusual dispersal into other freshwater environments (Nunavut Tunngavik Inc. 2001). Changes in stream routes (Nunavut Tunngavik Inc. 2001) may affect fish navigation ability and the costs of migration. Or, upstream run timing has been found to be earlier as a response to variable conditions (Gilbert et al. 2016), so fish may need to “hedge bets” with increasing water temperatures and changes in flows (Anderson and Beer 2009; Reed et al. 2016) so that at least part of the population experiences preferred migratory conditions (Ohms et al. 2014). Such direct effects have been noted by communities who have observed increasing difficulty in Arctic Charr migration in multiple locations throughout northern Canada (Power and Barton 1987; Gilbert et al. 2016). In addition to these direct effects, such as possible changes in fish diet (Nunavut Tunngavik Inc. 2001), growth (Lynch et al. 2016), and range expansions by other species (Bilous and Dunmall 2020) may indirectly affect anadromy (Reist et al. 2006). For example, communities have noted increased vegetation in lakes (Nunavut Tunngavik Inc. 2001), which may indicate that freshwater productivity is already increasing, and affecting the availability of both shelter and food. Experimentally raising freshwater food availability has been found to reduce the incidence of anadromous fish within a population (Nordeng 1983), and a similar effect could occur if climate change increases lake productivity.

Further, non-climate related environmental changes such as isostatic rebound (Nunavut Tunngavik Inc. 2001) that alter the availability of freshwater habitats and the ease of access to these, may affect Arctic Charr migration (Power and Power 1995). This study will shed light on

the spatial and environmental factors that affect migratory strategies of Arctic Charr, which can guide both short-term adaptive fisheries management and long-term conservation of the species in Nunavut (Sprules 1952; Secor 1999; Gilbert et al. 2016). Understanding the drivers of and barriers to migration may shed light on possibilities for Arctic Charr habitat enhancement, particularly projects to improve fish passage, as water levels change (Power and Barton 1987; Gilbert et al. 2016); and provide an intraspecific diversity lens through which to identify refugia to protect Arctic fish in the context of climate change (Poesch et al. 2017; Bilous and Dunmall 2020).

1.4. Species distribution modeling

The specific meaning of habitat depends on the species as well as the spatial and temporal scales being considered (Krausman 1999). Ultimately, community structure is the result of a series of selective pressures operating at progressively finer physiological and geographic scales (illustrated in Figure 1 of Jackson et al. 2001; Hershey et al. 2006), whereby broad-scale abiotic influences such as climate, geology, or ecoregion (Maloney et al. 2013; Ptolemy 2013) first dictate species potential niche (available conditions in which a species could occur). The realised niche (areas where the species actually occurs) is then further limited, for instance by access (e.g., connectivity, barriers, fish dispersal capabilities) or competition with co-occurring species, and can depend on life stage or internal population processes such as density dependence. Studies of fish diversity in the Canadian Arctic have often focused on the higher, regional fauna levels (Chu et al. 2003, 2005).

The relationship between these climatic or environmental predictors and species habitat use is commonly evaluated using species distribution models (SDMs) (Elith and Leathwick 2009; Araújo et al. 2019). SDMs—also variously known as ecological niche modeling, habitat suitability models, resource selection functions, or climate envelopes—are models that relate “species distribution data (occurrence or abundance at known locations) with information on the environmental and/or spatial characteristics of those locations” (Elith and Leathwick 2009).

SDMs are generally used to explain the species-environment relationships, to predict distributions in a similar time and place to the model, or to project to a different geography or climate, either past or future (Araújo et al. 2019). SDMs can be used at the species level, but also to explore niches for cryptic species (Zhao et al. 2019), subspecies, or locally adapted populations (Chen et al. 2020).

There are various methods for conducting an SDM including envelope models, regression-based methods (Hijmans 2012), maximum entropy (Fourcade et al. 2014; Chen et al. 2020), machine learning (Olden and Jackson 2001; Hershey et al. 2006), and Bayesian approaches (Ward et al. 2015); with one common one being logistic regression. Logistic regression is an application of generalized linear models (GLMs) used for binary data that have values of either 0 or 1 (in the case of SDMs, absence or presence of a species). A logistic link translates the set of linear explanatory variables into a probability that the response has a value of 1 (i.e., that a species is present).

GLMs been found to be equivalent to other SDM approaches (Pearce and Boyce 2006; Elith and Leathwick 2009), including when used to model citizen science data (e.g., Mengersen et al. 2017). Correlative SDM procedures like GLM are generally used when the focus of the study is environmental drivers of distribution. Conversely, process based SDMs are better for predicting future distributions or transferability to areas outside of the training data domain. GLMs perform best within the environmental and geographic space of the training data, and with easily detected species (Rota et al. 2011). GLMs have been used to model Arctic Charr and other fish distributions in Canada (Chu et al. 2003, 2005) and elsewhere (Finstad and Hein 2012; Hein et al. 2012; Huang and Frimpong 2015). Few of these studies were at high latitudes, however, despite faster environmental changes in the north (Lynch et al. 2016).

GLMs, like most SDM methods, require information on both the presence and the absence of the species throughout the study area. In areas such as the Arctic, however, fieldwork is challenging due to the large area, high costs and difficult access to many sites, and extreme

weather conditions that restrict the sampling season. Such challenges mean that systematic scientific data on fish presence and absence is limited, particularly of non-commercial and migratory freshwater species (Grandmaison and Martin 2015; Huang and Frimpong 2015). In a pan-Canadian analysis of freshwater fish biodiversity and conservation importance (2003), and in an updated analysis 10 years later (2014), Nunavut watersheds were the most data-deficient, missing observations in 38% of watersheds (the Northwest Territories was next, at 26%). Similarly, many Nunavut watersheds were some of the 20% of global drainage basins that had no records during the development of a worldwide freshwater fish database (Tedesco et al. 2017). More recently, WWF Canada (2017) found that all Nunavut watersheds lacked sufficient data to assess any trends in fish presence or abundance (although they noted that this was also the case for most of Canada); and Oceans North Conservation Society et al. (2018) found that data were limited to delineate the Arctic Charr range. This lack of data can falsely represent the true distribution of northern species (Chu et al. 2003) and misdirect management actions.

While research and funding support for Arctic studies is increasing, other existing sources of knowledge remain to be explored. Data collected for specific research projects (Gamble 1984), or for environmental assessments (Baffinland Iron Mines Corporation 2012), could fill in gaps. Most of this data is in hardcopy (Nunami Stantec 2012), however, so would take significant effort to compile. The varying extents, methods, and precision can also require caution when interpreting in habitat studies such as this (Banci and Spicker 2014). Citizen science and global biodiversity databases can provide species observations across broad areas (e.g., the Global Biodiversity Information Facility² (GBIF); Ocean Biodiversity Information System³ (OBIS); eBird⁴) (Amano et al. 2016). Several studies have used this type of data for SDMs (Senay et al. 2013; Fourcade et al. 2014; Mengersen et al. 2017; Fletcher et al. 2019; Chen et al. 2020; Florence et al. 2020; Higgins et al. 2020). While there can be some constraints in species identification and the amount of detail that can be obtained per observation, these can be offset by the greater spatial and temporal coverage. Citizen science information is limiting when exploring

² <https://www.gbif.org/>

³ <https://obis.org/>

⁴ <https://ebird.org/home>

intraspecies diversity using SDMs, however, as identification is generally only to a species level or higher.

Instead, more specific local or Indigenous knowledge has the potential to fill this gap, extend the spatial and temporal scope of studies (Fraser et al. 2006; Gagnon and Berteaux 2009), and illuminate species-habitat relationships (López-Arévalo et al. 2011; Polfus et al. 2014; Sánchez-Carnero et al. 2016; Misiuk et al. 2019). Fishermen, who spend all seasons, and many years, working with a species, and whose livelihoods depend on it, often have unrecognized but accurate and detailed knowledge of the species and ecosystems in their area. Documenting such information, although often considered a colonial process that writes down an oral form of knowledge, can nevertheless provide practical benefits not only for governance organizations but also for communities and individuals, for instance in search and rescue (Peplinski 2014). Further, documentation also records information that may otherwise be lost as Elders pass away, and maintains the Inuit connection to the land, their language, and cultural practices (Peplinski 2014). Inuit and other Indigenous knowledges have been used to explore fish-habitat relationships for other northerly distributed species in Alaska (Robinson 2005; Brewster et al. 2010), Quebec (Fraser et al. 2006), Nunavik (Dubos 2020), and the Northwest Territories (VanGerwen-Toyne 2002; Howland et al. 2004; Winbourne 2004; Thompson and Millar 2007; GRRB 2010; Knopp et al. 2012). In Nunavut, the use of Inuit Qaujimajatuqangit—Inuit knowledge, beliefs, behavioural mores, and worldview—remains a substantially unexplored source of insight for fisheries management (Wenzel et al. 2008).

1.5. Inuit Qaujimajatuqangit

Inuit, as a nomadic people, lived on and with huge areas of land. Inuit knowledge of the land and the environment is highly accurate in many contexts, particularly when relating to geographic locations and relationships between these (Rundstrom 1990; Peplinski 2009). Their knowledge needed to be detailed, practical, and adaptable to survive and thrive in an extreme environment.

For instance, Inuktitut place names are still preferred by many Elders or land experts (Peplinski 2014) as they describe Inuit relationships to the land that they travelled, lived upon, and used. Inuit knowledge is thus place-based and consequently specific to an individual's known area, despite incorporating broader community knowledge and traditional or historic information (Omura 2005).

Although sometimes considered “traditional”, and by inference potentially historical or out-of-date, Inuit knowledge is a continually evolving and currently used knowledge system. The Inuit worldview (Inuit Qaujimajatuqangit) is a holistic and adaptive system of beliefs, behaviours, and knowledge that integrates new information in the context of and with reference to pre-existing understanding. Consequently, although they are often used interchangeably in the literature, Inuit knowledge is only one component of Inuit Qaujimajatuqangit, and an understanding of these other cultural and contextual aspects should inform Inuit knowledge use within a traditionally scientific context.

For instance, from a wildlife management perspective, Inuit Qaujimajatuqangit emphasizes the connections between environmental components, and species even within the Inuit taxonomic system, which uses behavioural and habitat traits rather than genetic relatedness to group species (Randa 2002). As with vernacular English names, fish species are known by various names in Inuktitut (the collective term for Inuit language dialects). These names often include specific names or terms for different life stages or morphs, including a variety of names for different migratory ecotypes and habitat associations (Table 2). By naming intraspecific diversity rather than clarifying descriptions, Inuit demonstrate the importance they place on this diversity, which can sometimes lead to conflict with scientific generalization (Polfus et al. 2016).

Table 2: Inuktitut names and terms for selected fish species

Inuktitut name	English name or definition
Ikaliviit⁵; Erlakupik, Kaloarpok, Ivatarak, Ivitagok, Ikalopik, Ekalupik, Eqaluk, Ekalluk, Eekallûk, Equaluk, Ekaluppik, Kaïtilik, Ihkaluk, Iqalukpik, Iqalukpik, Iqaluppik, Iqalukpiaryuk, Ekalluk, Eekalook, Iqaluk, Irkaluk, Angmalook, Hiwiterro, Tisuajuk, Suvaliviniq, Aupalijaat, Aopalayâk, Aoparktulâyoq, Tادلulik⁶; Ikalukpik^{6, 7}; Ekalukpik; Ekaluk⁸	Arctic Charr
Ivitaaruq, Ivitaroq, Ivitaruk, Ivisaruk⁶; Evitagok⁷	Red charr / spawning charr
Nutilliajuk ⁶	Land-locked charr
Ehokketak ⁷	Inland charr with a hooked lower jaw (older term) ⁷
Aniaq⁶; Aniak⁷	Skinny charr from lakes ⁷
Hanimoyok ⁷	“Fish that migrate down river (from the lakes to the ocean)” ⁷

⁵ (Banci and Spicker 2012)

⁶ (Priest and Usher, 2004)

⁷ (Nunami Stantec 2012)

⁸ (Sprules 1952)

Mayoaktok ⁷	“When the charr go up river (from the ocean to the lakes to over-winter)” ⁷
Panmoktok ⁷	“When charr migrate to the ocean from the lakes (downstream) after spawning” ⁷
Ikaluit ⁵	Fish (unspecified)
Eektok ⁷	“Any large fish from lakes” ⁷
Hugtook ⁷	“Big fish from lakes” ⁷
Hukton ⁷	“Big fish” ⁷
Tahinikikaluit ⁵	Freshwater fish (unspecified)
Tagiumiikaluit ⁵	Ocean fish (unspecified)

As seen in the above names, Inuit Qaujimajatuqangit of common and culturally important species, such as Arctic Charr, is generally detailed and specific. However, Idrobo (2008) demonstrates that Inuit knowledge of even unharvested and little known species such as the Greenland Shark (*Somniosus microcephalus*) can be greater than anticipated and wholly integrated into the larger worldview.

Although I don’t know of any studies that have specifically documented Inuit knowledge on Arctic Charr migration, the holistic nature of Inuit Qaujimajatuqangit means that, for instance, other information such as the diet of Arctic Charr (Idrobo 2008) and the Inuit understanding of seasons—based not on calendar dates but rather annual patterns in environmental events,

including wildlife migrations (Government of Nunavut 2005; Brewster et al. 2010)—may indicate drivers of migration. Similarly, place names can indicate species locations, as well as habitat relationships, areas of abundance, and population conditions (Byam 2013; Dedats’eetsaa: Tlicho Research and Training Institute 2014; Peplinski 2014). Consequently, when investigating temporal and spatial movement patterns (migrations), Inuit knowledge can provide insights into potential spatial and habitat influences.

Multiple existing sources have documented such Inuit knowledge and species observations for other purposes, but this information has generally not been explored beyond the original objectives. Like museum and herbarium records, such sources offer potential knowledge about species habitat associations and distributions. Older projects that supported land claim processes such as the Inuit Land Use and Occupancy Study (Milton Freeman Research Limited 1976; Freeman 2011) and subsequent Nunavut Atlas (Riewe 1992) contain detailed information on both community and commercial fisheries locations; however, the information has not been digitized and is difficult to access. More recent consultations, for instance to identify Ecologically and Biologically Significant Areas in Nunavut (Dept. of Fisheries and Oceans Canada 2011; Grandmaison and Martin 2015), documented areas of charr abundance. This information has been used for land use planning (Nunavut Planning Commission 2013, 2016), but is at a too broad a scale to provide insight on charr habitat selection, let alone migratory life history choices. I know of three possible digital sources that are at a reasonable scale for species distribution modeling: the Nunavut Wildlife Harvest Study (NWHS; Priest and Usher 2004); use and occupancy mapping (UOM) conducted by the Nunavut Planning Commission (NPC) between 2004 and 2010 (described in Kowalchuk 2010; Dillon Consulting Limited 2012; Kowalchuk and Kuhn 2012); and the ongoing Nunavut Coastal Resource Inventory (NCRI; Fisheries and Sealing Division 2017).

1.6. Towards an integrated understanding of Arctic Charr migration

By exploring already documented data, I exclude many of the social, economic, or cultural aspects of Inuit Qaujimajatuqangit. This approach ignores the true complexity, depth, and interconnectedness of Inuit Qaujimajatuqangit as I employ a purely scientific approach to the compilation and analysis of the knowledge that's been shared. Nevertheless, even this limited approach can improve insights into Arctic Charr ecology. In the Inuit view species are integrated into a broader system; taxonomy revolves around species habitat, ecology, and relationships with other wildlife and people (Randa 2002). Using Inuit knowledge in management-relevant studies inherently considers both human and wildlife needs and interactions, and can better support adaptive co-management than scientific data alone (Moller et al. 2004; Kristofferson and Berkes 2005).

Currently, fisheries management is conducted on a stock-by-stock basis, and stock mixing is not well understood. Changes in Arctic Charr migration patterns may impact subsistence and commercial fisheries, many of which take place during charr runs, or target anadromous fish in either the ocean or overwintering lakes (Boudreau and Fanning 2015). For instance, land use planning in Nunavut considers "Special management or mitigation measures...on activities and/or timing of these activities in critical [arctic char] habitat areas as well as during periods of char migration...[and] the maintenance of natural water flows in char river systems" (Nunami Stantec 2012). Similarly, the Nunavut Regional Wildlife Priorities include research (particularly research incorporating Inuit viewpoints and community-based monitoring) on Arctic Charr habitat and movement and the impacts of hydrological and climate changes, to support fishery development (Nunavut Wildlife Management Board 2017). Further, for communities, which rely on Arctic Charr as a key food source, understanding and predicting fish distributions, movements, and response to changes is essential (Knopp et al. 2012).

For such reasons, "Healthy fisheries" are the first component of the vision for the Nunavut Fisheries Strategy 2016-2020 (Department of Environment 2016). Under this Strategy, healthy

fisheries are those that “allow fish to have healthy places to live, feed, and reproduce, and healthy corridors to migrate between these places”. Meeting such a vision, however, requires information on which corridors are used by fish, and what environmental components impact their use, i.e., make them “healthy” (Evans et al. 2002). This study can help to illuminate a basis of existing knowledge against which evolving Inuit Qaujimagatuqangit can record changes.

1.7. Objectives

My thesis aims to explore the patterns of anadromy and residency in Arctic Charr populations across Nunavut. I had three objectives:

1. To combine pre-existing observations of Arctic Charr anadromous and resident life histories across Nunavut from scientific studies, harvest reports, and Inuit knowledge mapping;
2. To develop species distribution models to describe the presence of anadromous and resident Arctic Charr populations across Nunavut in relation to geography, river length and difficulty, lake morphology, and regional productivity; and
3. To compare the overlap of the predicted anadromous and resident distributions and driving factors to assess whether habitat factors affect the life history decisions of Arctic Charr in Nunavut.

1.8. Predictions

Given the paucity and specificity of scientific data from studies of Arctic Charr in Nunavut, I expect that harvest records and Inuit knowledge will provide records of Arctic Charr populations across a larger spatial and environmental gradient than scientific data alone.

Genetics, fish growth, and environmental thresholds interact to drive anadromy. If migration to the ocean is an attempt to access more productive feeding areas (Nordeng 1983; Gross et al. 1988), then anadromy may be more likely where freshwater resources are limited or fish have to compete for them. I thus expect the probability of anadromous populations to be higher in areas of greater relative marine productivity (i.e., higher latitudes and further east), in smaller lakes, and when sympatric competitor or predator species are present in the freshwater environment. If, however, anadromy helps fish to access safer freshwater spawning (Secor 1999; Chapman et al. 2012; Reed et al. 2016), then lakes with shorter and easier (less steep) ocean access would also be more likely to contain anadromous populations.

Since Arctic Charr is a partially anadromous species and populations in the same lakes may exhibit both migratory forms, I expect that there will be overlap between the projected distributions of anadromous and resident presences. Lake characteristics may thus represent the conditions that can support charr survival, while anadromy will only persist where the costs of migration are sufficiently low. I thus expect that the greatest differences in projections will be due to differences in habitat access (e.g., river length, gradient and obstacles) rather than in overwintering habitat (e.g., lake size and shoreline complexity).

1.9. Thesis organization

This thesis is arranged in three chapters. This first chapter reviewed the background literature on habitat selection and drivers of anadromy, to introduce the study justification and overall objectives. Chapter 2 describes my methods and results for the species distribution models. The final chapter summarises my conclusions.

2. Chapter 2: Geography and waterbody morphometry drive the distribution of anadromous and lake resident Arctic Charr populations in Nunavut

2.1. Introduction

Habitat, the sum of the necessary resources and physiologically acceptable conditions that allow the survival and persistence of an individual, population, or species, directly affects distribution and abundance (Krausman 1999; Boyce et al. 2016). Aquatic habitats are heterogeneous across landscapes and over time, so many species develop unique functional and behavioural mechanisms that allow individual fish to select habitat to maximise their lifetime fitness (Secor 1999). One such behavioural mechanism is migration.

For anadromous fish, migration both gives access to the more productive marine environment, and allows safer spawning and rearing in freshwater (Railsback et al. 2014; Kendall et al. 2015). Migrations can have significant physiological and osmoregulatory costs, however, and present greater mortality risks (e.g., predation, stranding). The difficulty of moving between habitats thus affects how beneficial migration is as a strategy. Thus, many species in highly variable environments, such as the Arctic, maintain population viability through facultative (partial) anadromy, whereby a portion of the population is migratory, while the remainder is resident in freshwater year-round (Kristoffersen et al. 1994; Carlsen et al. 2004).

Partial anadromy is thought to buffer populations against environmental changes (Secor 1999; Moore et al. 2014b); however, such intraspecific diversity is not usually considered in assessments of species distributions (e.g., Chu et al. 2014; Samarasin et al. 2014).

Consequently, improving our understanding of anadromous fish habitat use is necessary for fisheries management (Bégout Anras et al. 1999; Krausman 1999), especially in the context of anticipated environmental changes (Birtwell et al. 2005).

Most studies investigating species distributions or the impacts of climate change on freshwater (including diadromous) fish have focused on the continental United States and southern Canada (Samarasin et al. 2014; Lynch et al. 2016). Few have assessed impacts on Arctic species (Poesch et al. 2017), even though the Arctic environment appears to be changing at a faster rate than watersheds in southern Canada (Chu et al. 2014), and winter-adapted, long-lived species such as salmonids may be more severely impacted (Samarasin et al. 2014; Poesch et al. 2017).

The Arctic Charr (*Salvelinus alpinus*; or “charr”) is a well-known partially anadromous Arctic species. Arctic Charr is the world’s northern-most distributed freshwater fish species (Helland et al. 2011) and the most wide-spread freshwater fish in Nunavut. Charr are culturally important to Nunavummiut as well as forming the primary subsistence, recreational, and commercial fisheries across the Territory. Nunavut charr populations exhibit diverse life histories with differing proportions and patterns of anadromy (Secor 1999), which may be partly driven by differences in the freshwater and marine environments across the three regions of Nunavut.

Nunavut communities are already noticing both short- and long-term changes (Nunavut Tunngavik Inc. 2001) in the freshwater and marine environments across the territory, although the direction of change may be different in different regions (Chu et al. 2014). Observed changes include less predictable weather patterns, lower water levels (Power and Barton 1987; Fisheries and Sealing Division 2017), more rapid ice breakup, increased turbidity, thinner ice, decreased precipitation, warmer air and water temperatures, changes in seasonal timing and length, increased lake vegetation (Nunavut Tunngavik Inc. 2001; Government of Nunavut 2005), erosion (Power and Power 1995; Nunavut Tunngavik Inc. 2001; Government of Nunavut 2005), and species range expansions (Poesch et al. 2017). Such changes may alter fish population dynamics, competition or predation, the availability of marginal habitats (particularly in river ecosystems (Power and Power 1995)), and the ability of fish to move between habitats (Lynch et al. 2016; Fisheries and Sealing Division 2017 Arctic Bay and Cambridge Bay interviews);

thereby affecting charr migration patterns (Reist et al. 2006; Lynch et al. 2016; Poesch et al. 2017).

With such broad-scale environmental changes occurring, a similarly broad understanding is needed of what drives charr anadromy. Previous studies have investigated charr migratory choices in specific systems or areas of Nunavut, with few expanding this to a regional scale (Dempson and Kristofferson 1987; Loewen 2016). Such studies are usually based on telemetry or mark-recapture approaches, so provide detailed movement data, but are often expensive and difficult to implement. Most have been conducted in the High Arctic (Babaluk et al. 1997, 2002; Loewen 2016), the Cambridge Bay area (Kristofferson et al. 1984; Gyselman and Gould 1992; Campbell et al. 1999; Kristofferson 2002; Swanson et al. 2010a; Gilbert et al. 2016; Moore et al. 2016), and south-eastern Baffin Island (Moore 1975; Spares et al. 2012, 2015a). Nunavut, with a land area of over 2,000,000 km², thus presents an excellent opportunity to examine Arctic Charr migratory patterns across a spectrum of environments, including in mainland parts of Nunavut that have rarely been examined (i.e., the Kivalliq; but see MacDonell 1989).

I therefore explored Arctic Charr migration across Nunavut, using existing fishing, harvest, and Inuit knowledge data in a generalized linear model to compare the important factors driving the distributions of anadromous and resident charr. I combined two sources of presence observations (harvest records and mapped Inuit knowledge) to explore the effect of river length, lake area, regional productivity, and geographic position (Spens et al. 2007; Spens and Ball 2008; Kowalchuk and Kuhn 2012) on the probability of presence of anadromous or resident populations. While this is a comparatively coarse measure of anadromy, this analysis can define the landscape limits of anadromy for Nunavut Arctic Charr (i.e., barriers to migration; Hershey et al. 2006; Spens et al. 2007). Further, the analysis may indicate areas where Arctic Charr migratory strategies could be most vulnerable to changes in lake productivity (Näslund et al. 1993; Finstad and Hein 2012).

Several previous studies have taken a similar approach to analyzing charr distribution in Norway (Finstad and Hein 2012) and Sweden (Hein et al. 2012). The Nunavut context, however, expands the habitat types under consideration from the Scandinavian environment, which in general includes many small lakes, comparatively shorter rivers, and a fiord environment with steeper topography. The Baffin region of Nunavut shares these traits, but this study can assess whether the relationships found in Scandinavia remain true in northern Canada, while extending the assessment to the flatter, larger river systems of the Kivalliq and Kitikmeot.

If migration is driven by access to marine feeding areas (Gross et al. 1988), I expect anadromy to be more common further north (Jensen 1981; Stephenson and Hartwig 2010; Finstad and Hein 2012; Hein et al. 2012; Bilous and Dunmall 2020) and east, where the ocean is comparatively more productive than freshwater (Tremblay et al. 2012; Druon et al. 2018). However, nearshore marine productivity is likely to be the most influential on anadromy, since Arctic Charr generally stay in coastal waters less than 30 kilometres from shore, and spend much of their time in estuarine waters (Moore 1975; Ulvund 2011; Spares et al. 2012, 2015b; Jensen et al. 2016; Loewen 2016; Moore et al. 2016). Consequently, the nearshore presence of recurrent open water areas (polynyas), which are areas of higher biodiversity in the marine environment (Hannah et al. 2008; Banci and Spicker 2012; Brown and Fast 2012; Fisheries and Sealing Division 2017), may increase in the probability of anadromous charr presence.

Further, if the within-lake environment offers more habitat niches and productive food resources, as well as a safer environment for charr, then anadromy might be less beneficial. Larger lakes generally have more heterogeneous habitat, more species (Jackson et al. 2001) and greater biomass of fish, regardless of latitude (Samarasin et al. 2014). Consequently, I expect that increasing lake area will decrease the probability of anadromous charr presence.

Larger lakes, however, tend to have more complex fish communities, and the presence of other species, particularly predators, can drive Arctic Charr distributions (Spens and Ball 2008; Hein et al. 2012). Since charr habitat use and niche can be plastic in sympatry, the presence of key

predators such as Lake Trout (*Salvelinus namaycush*) and Northern Pike (*Esox lucius*) is thus expected to increase the probability of anadromy, particularly in small lakes.

These drivers need to be balanced against the increased energy costs and mortality risks during migration. Longer migrations can expose charr to warmer thermal environments, greater predation risk, and uncertain hydrological conditions. Consequently, anadromy is expected to be less likely in longer rivers (Finstad and Hein 2012) with steep gradients or other barriers along the migratory route (Power and Barton 1987).

Finally, river characteristics are expected to have a greater influence on the likelihood of migration than lake features, since Arctic Charr in the north primarily use rivers as migratory rather than overwintering habitat (Evans et al. 2002). Further, landscape factors are expected to have a larger influence on whether populations are anadromous than ecological factors, since Arctic stream characteristics, including fish community, are most heavily influenced by abiotic factors (Power and Power 1995). The relationship may be less pronounced at lower latitudes, however, where overall productivity is generally higher and biotic influences are greater, particularly in river environments (Power and Power 1995).

2.2. Methods

2.2.1. Study area

Nunavut (meaning “our land” in Inuktitut) is the easternmost of Canada’s three northern territories. The territory covers just over two million square kilometres (Statistics Canada 2012), spanning latitudes from 55°N to 83°N and longitudes from 61°W to 110°W (Figure 2). The predominantly Inuit population (estimated at 35,944 people in the 2016 census (Statistics Canada 2017)) is spread across 26 communities in three administrative regions: five communities in the north-westerly Kitikmeot region, including communities both on the mainland and some islands of the Arctic Archipelago, seven communities in the south-central Kivalliq on western Hudson Bay, and 13 communities in the easterly Qikiqtaaluk (Baffin) region.

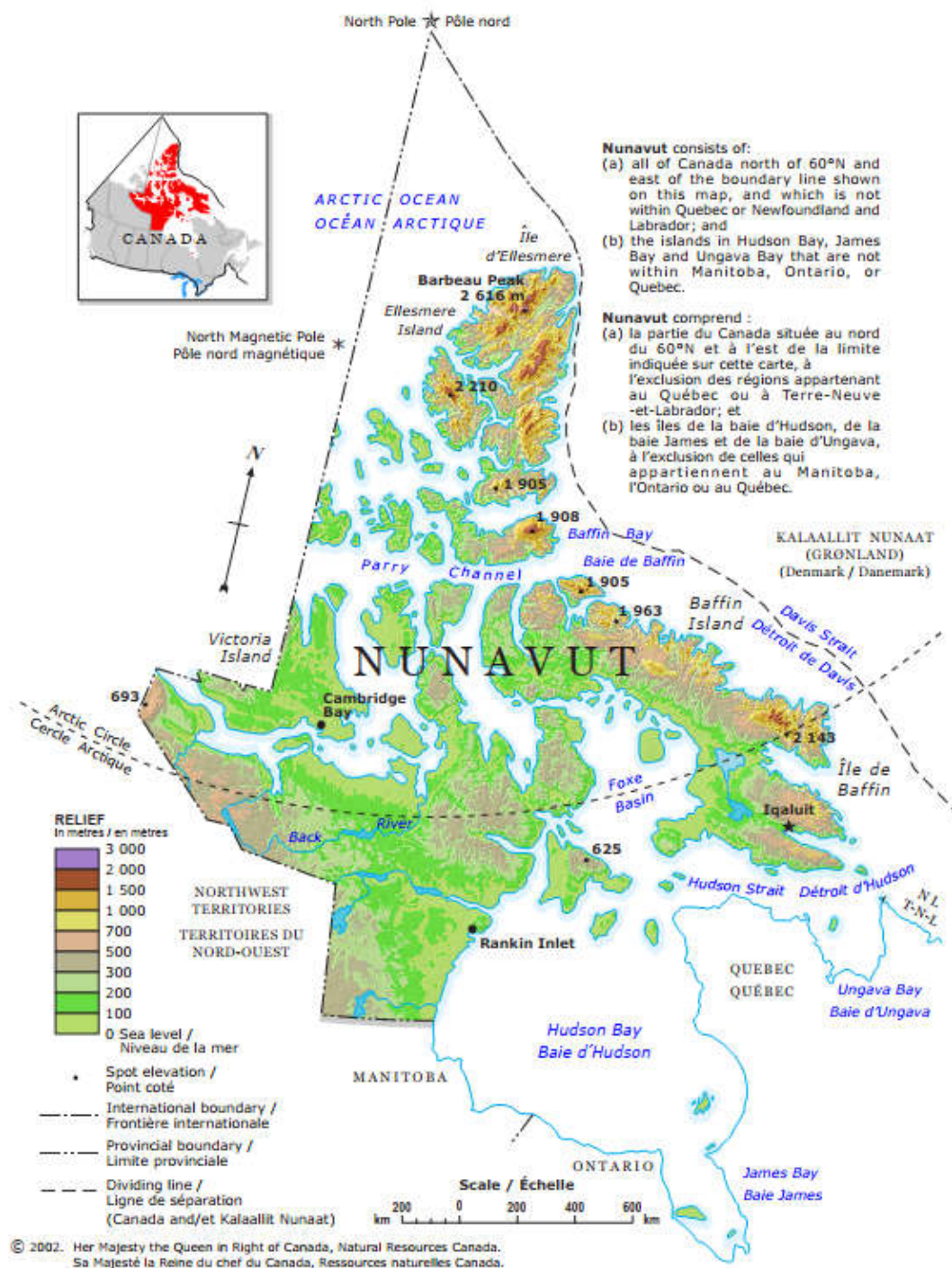


Figure 2: Map of Nunavut showing key communities, watercourses, and topography (Natural Resources Canada 2002, used according to Government of Canada's Open Government License⁹)

⁹ <https://open.canada.ca/en/open-government-licence-canada>

Most of the territory is above the treeline, so the vegetation is primarily tundra herbs and mosses, with scattered low shrubs. Approximately 7% of the Nunavut land mass is covered by fresh water (Statistics Canada 2012). Nunavut overlaps three freshwater ecoregions, which reflect the broad underlying geology, topography, terrestrial and freshwater environments (Poesch et al. 2017). The Kivalliq region is a comparatively flat sub-arctic and tundra region in the Western Hudson Bay freshwater ecoregion, while the Central Arctic Coastal freshwater ecoregion encompasses the mainland portion of the Kitikmeot. Both these ecoregions have continental influences, with the treeline running through inland portions of both regions, high volume seasonal freshwater transfer from the Barrenlands through large lakes and long river systems, and greater climate variability seasons (Ecological Stratification Working Group 1995; Reist et al. 2016). By contrast, the Qikiqtaaluk region is comprised primarily of islands in the eastern Arctic Archipelago, many of which have convoluted fjorded shorelines and mountains, continuous permafrost or ice covered areas, and low precipitation (Ecological Stratification Working Group 1995; Abell et al. 2008). While lakes overall appear to be smaller and rivers shorter, the Qikiqtaaluk also contains Nunavut's two largest lakes, Netilling and Amadjuak.

These freshwater ecoregions drain into three marine ecozones, each with their own oceanographic conditions (Poesch et al. 2017). The Northwest Atlantic marine ecozone transitions from warmer southern waters to colder Arctic temperatures, and includes habitats ranging from offshore depths to a fjorded coastline with large tidal fluctuations in some locations. In contrast, the Arctic Archipelago is more varied and less open, consisting of interconnected bays and passages surrounding the Arctic islands, and extending south into Hudson Bay (Ecological Stratification Working Group 1995). Finally, the most northerly marine ecozone, the Arctic Basin, describes those areas of the Arctic Ocean that are permanently ice-covered (Ecological Stratification Working Group 1995).

2.2.2. Fish observations

I used three pre-existing sources of information on fish species distributions across Nunavut, the Nunavut Wildlife Harvest Study (NWHs; harvest records), Nunavut Coastal Resource Inventory (NCRI; mapped Inuit knowledge), and the Arctic Fisheries Stock Assessment database (AFSA; fisheries research). Data approvals and licenses are listed in Appendix 1: Data licenses. For all sources, anadromous and resident fish were distinguished morphologically either by samplers in the field (AFSA) or by interviewees (NCRI and NWHs). In general, resident fish are smaller, with relatively larger eyes, longer fins, and longer upper jaws for their size (Loewen et al. 2009), and sometimes different colouration (Klemetsen et al. 2003).

Nunavut Wildlife Harvest Study

The NWHs was conducted by the Nunavut Wildlife Management Board (NWMB) as mandated by the Nunavut Land Claim Agreement (NLCA) Article 5, Part 4. Between July 1996 and June 2001, community coordinators interviewed harvesters each month and recorded the date of harvest, species, and number of individuals harvested. The study attempted to census all harvesters in 21 communities, and interview all intensive harvesters in seven of the largest communities (Arviat, Baker Lake, Cambridge Bay, Cape Dorset, Gjoa Haven, Kugluktuk, and Rankin Inlet).

6,018 Inuit hunters were registered in the study throughout its duration, but not all were interviewed; nevertheless, the study had an average territory-wide response rate of 82% (of those who were eligible to be interviewed). Interviewees were Inuit (plus, in some communities, some non-Inuit with assigned rights), over 16 years of age, and participated in hunting, fishing or trapping at any time in the past year. Interviewees thus included occasional (occasionally participates in short-term hunting activities), active (regularly participates in major harvesting activities), and intensive (repeatedly and regularly participates in (almost) all harvesting activities) hunters. Interviewees generally continued to be interviewed even if their

status changed, or they moved communities; only four communities had consistent non-response rates over 5%, indicating that overall observation bias in the study was low.

Under the NLCA Article 5 (Wildlife), a “species” is defined as “any particular species or any distinct sub-group within a species such as a stock or population”. Consistent with this definition, the NWHS distinguished between anadromous and resident life-histories for Arctic Charr, where harvesters were able to identify these; although community harvest estimates in the study’s final report combined these. Most other fish species were identified to species level (e.g., in the NWHS, the term “Whitefish” represented *Coregonus clupeaformis*), with a few to genus or family (e.g., “Cod”, as used in the NWHS, included *Gadus ogac*, *Boreogadus saida*, and *G. morhua*). The NWHS gathered data on a total of 15 aquatic species, plus several observations of species not on the coordinators’ lists (e.g., described in the NWHS as “Capelin”, “Herring”, and “Flounder”).

Community harvest reports in some cases included species not found in the immediate area around the reporting community (e.g., Clyde River harvesters reported catches of Arctic Cisco (*C. autumnalis*) made during trips to the Kivalliq, even though this species is not found in the Clyde River area). Further, since the NWHS is used to calculate total allowable harvest and basic needs levels, which are calculated “for each stock or population”, location information was important, and in fact required as part of presenting the study results graphically. Location information (place name, map code, and a Universal Transverse Mercator (UTM) grid location on a 1:250,000 National Topographic System map, however, was gathered only for certain species, which for fish were Arctic Charr (“sea-run” populations only) and Lake Trout. In general, the location information is accurate to one kilometre; however, in some cases hunters indicated only a general area, or gave only a place name, after which the fieldwork identified the grid location.

For the NWHS, “harvest” was defined as those animals that were struck and retrieved. This definition should not impact the distribution of recorded Arctic Charr locations, as most Inuit

fish for Charr using nets (Boudreau and Fanning 2015); fishermen may therefore either catch or not catch fish, but are less likely to catch and then lose fish that are there. The NWHS focused on harvest only for local (not commercial) use, but this is not expected to bias results, as there is often overlap between commercial and community fishing locations (Milton Freeman Research Limited 1976); in fact, Priest and Usher (Priest and Usher 2004) notes that in some communities it was impossible to distinguish commercial harvest so it was included.

Data was verified during the NWHS both statistically (e.g., by comparison to government data from commercial or managed harvests), and through community consultations throughout the study (i.e., during design, data collection, and post data-processing), but may still have some reliability issues (2004).

Missing study periods and hunter under-enumeration should minimally affect my analysis given the temporal repetition and large overall number of interviewees. Community feedback indicates that under-reporting was more common than over-reporting, but mostly affected fish species that were perceived as unimportant or incidental catches (e.g., Least Cisco (*C. sardinella*), sculpins (*Myoxocephalus* spp.)). Further, this issue more likely affects harvest quantity estimates than the number of observed locations.

Low response rates, however, may lead to a non-response bias in the observed locations (e.g., if a non-responding family are the only ones to fish in a location, or if sampling rates between communities/regions are highly uneven). The inland area of the mainland, and Southampton Island, are most likely underrepresented, due to the low response rates and consistent high intentional non-response rates in Baker Lake, Rankin Inlet, and Coral Harbour throughout multiple years (Priest and Usher 2004). This may not greatly affect my analysis, however, as in most communities, response rates were lowest in spring or summer when hunters were on the land. Since migratory charr would be in the rivers or ocean at this time of year, overwintering lake locations may still have been reported.

Longer recall periods may result in more inaccurate location information; however, longer recall periods were generally only an issue in one or two years in a community, so that the temporal repetition of the study likely minimizes the extent of any bias. Again, recall periods in Baker Lake and Coral Harbour were the longest in the study, so locations in the interior Kivalliq and on Southampton Island may be more uncertain.

I downloaded the NWHS data from the NWMB website¹⁰ on January 31, 2018.

Nunavut Coastal Resource Inventory

The NCRI is run by the Fisheries and Sealing Division, Department of Environment, Government of Nunavut (GN). The project records observations of coastal species, which are published in community-specific reports. Between 2007 and 2018, 207 interviews were conducted in 22 communities, resulting in 16,209 observations of 333 species, and 4,462 place records.

Between six and 12 individual or pair interviews are conducted in each community, with interviews lasting between 1.5-7 hours. Interviews may be conducted in either English or Inuktitut in conjunction with a local interpreter. Interviews are semi-structured, documenting distribution and ecological information on 504 potential species (including some not known to be in Nunavut). In some interviews when there were time constraints, however, less-common species or categories (e.g., aquatic plants) were not asked.

Correct species identification is supported by photos, species descriptions, and local species names; nevertheless some species are still prone to confusion (e.g., Dolly Varden with spawning Arctic Charr, Arctic Cisco with Least Cisco, Broad Whitefish (*C. nasus*) with Lake Whitefish; Fisheries and Sealing Division 2017). Over time, however, project documentation has improved, and additional species and questions have been added to the survey—so later inventories may include more accurate observations and more species than earlier interviews. Fish, however, are the first category asked, and the core focus of the NCRI, so changes or additions to this

¹⁰ <https://www.nwmb.com/en/resources/publications>

category have been less substantial than for other groups such as aquatic invertebrates and plants. Fish data from early interviews in Igloodik, Kugluktuk and Chesterfield Inlet (the three regional pilot communities) does appear to be less precise (i.e., more, larger polygons), however.

Shared knowledge is recorded on paper maps and notebooks, with audio and/or video recordings as backup if approved by the interviewee. The base data used to create the interview maps was at a 1:250,000 scale, however the maps were printed at much smaller scales ranging from 1:1,350,000 (Arctic Bay) / 1:2,350,000 (Qikiqtarjuaq) to reflect the common areas traveled by hunters in that community.

Spatial data is subsequently digitized into a geographic information system (GIS), with attributes for each observation including species, life stage (e.g., feeding, migration, breeding), timing of observation (e.g., season, year), unique characteristics (e.g., abundant), and other observations (e.g., feeding ecology, habitat associations) if shared. Attributes are created from interviewer notes, as the recordings are not currently transcribed.

The NCRI data was provided by Amos Hayes, Technical Manager, Geomatics and Cartographic Research Centre as a geoJSON from the project's online atlas¹¹ on July 20, 2018.

Arctic Fisheries Stock Assessment database

Fisheries and Oceans Canada maintains the AFSA Microsoft Access database, which contains catch and biological data for exploratory and select research projects from 1947 to 2005, across the Canadian Arctic. This database compiles 400,000 catch records of 38 species from multiple projects and reports, including creel surveys, tagging studies, weir enumerations, and commercial or exploratory fisheries. The disparate records are linked to waterbodies using names and locations that appear to be from the Northwest Territories Fisheries Regulations,

¹¹ <https://ncri.gcrc.carleton.ca>

Schedule V. The level of detail in each record varies by study; and although there is some within-database information on source and gear types, detailed methodological information is lacking. There is similarly no metadata on how the database was compiled and is maintained. Chris Cahill provided me with a copy of the AFSA database on November 19, 2016.

2.2.3. Environmental variables

I used a variety of data sources that used different coordinate reference systems (CRS). CRSs represent the globe in a flattened plane in a GIS, but distort some aspect of the data's geometry, i.e., shape, area, and/or Euclidean (straight line) distance. Data sources were reprojected to a consistent CRS for analyses. I used different CRSs that were consistent with the extent of the analysis and minimised distortion for each calculation type (Šavrič et al. 2016):

- For equal area calculations: ESRI's Canada Albers Equal Area Conic (EPSG 102001);
- For equal distance calculations: ESRI's North America Equidistant Conic (EPSG 102010);
- For conformal (shape-preservation) needs e.g., overlays and mapping: Canada Lambert Conformal Conic (EPSG 102002); and
- For modeling, so that location coordinates were in decimal degrees rather than metres: World Geodetic System 1984 (WGS 84).

All data cleaning, statistical analyses, and plots were prepared using R version 4.0.1 (R Core Team 2013) unless stated otherwise (Appendix 2: R code). Key packages used for data access and manipulation included `odbc` (Hester and Wickham 2018), `sf` (Pebesma 2018), `dplyr` (Wickham et al. 2017), and `ggplot2` (Wickham 2016).

Most environmental variables were calculated from CanVec data that I downloaded from the Government of Canada's Open Data Portal¹² on November 20, 2017 in file geodatabase format.

¹² <http://open.canada.ca/data/en/dataset/8ba2aa2a-7bb9-4448-b4d7-f164409fe056>

CanVec data is produced by Natural Resources Canada, and comes in Lambert Conformal Conic projection (EPSG 42304). The datasets downloaded included:

- NU Hydro 250K¹³:
 - polygons of waterbody shorelines
 - lines of smaller linear watercourses
 - points, lines, and polygons of hydrological barriers
- NU Hydro 50K¹⁴, specifically:
 - polygons of waterbody shorelines
 - points, lines, and polygons of hydrological barriers
- NU Admin 250K, specifically:
 - Geopolitical region polygons
- NU Elevation 50K
 - Elevation contour polylines

I used waterbody and watercourse data at the 250K scale, since all observation datasets were collected on maps of that scale or smaller. In particular, although the NCRI data used a 250K waterbody dataset to create the interview maps, these maps were printed at smaller scales (i.e., over larger extents with less detail than the original data). Many of the lakes from the 50K waterbody dataset would therefore not have been visible to the interviewees to mark and needed to be avoided during overlay analyses. For instance, where NCRI interviewees used polygons to indicate observations in multiple waterbodies (instead of points in a waterbody), overlaying these on 50K waterbody data would also select any surrounding, smaller waterbodies. If interviewees didn't intend to select these lakes (which were not visible on the maps they were annotating), this could bias my results.

The 250K dataset was nevertheless too large to load or use in R directly. Prior to calculating environmental variables, I used QGIS version 3.12.3 (QGIS Association 2020) for initial data

¹³ Where 250K represents the scale of the dataset, 1:250,000

¹⁴ Where 50K represents the scale of the dataset, 1:50,000

exploration and interactive mapping, and PostGIS bundle 3.0 (Ramsey et al. 2019) for PostgreSQL 11 to manipulate the large vector files. I clipped waterbodies (lakes) from watercourse (river) polygons in the 250K dataset, dissolved features along shared borders, subsetting to the Nunavut territorial boundaries, and noded the river network using PostGIS.

Some environmental variables were not available through CanVec, so other data sources included:

- Locations of Nunavut communities, downloaded as a .csv from the Government of Canada's Open Data Portal¹⁵ on May 25, 2018.
- National Hydrographic Network watershed polygons (created from Water Survey of Canada Sub-Sub-Drainage Areas (WSCSSDAs), and equivalent to quaternary watersheds) were downloaded as a shapefile from Government of Canada's Open Data Portal¹⁶ on May 25, 2019.
- Community observations of notable environmental features recorded by the Nunavut Planning Commission (NPC) during consultation tours to develop the Nunavut Land Use Plan in 2014. It's unclear exactly how this data was gathered, but it's likely that information was shared in group consultations. I downloaded the shapefiles from the NPC website¹⁷ on January 16, 2017; note that these are no longer available following website restructuring¹⁸.
- Nunavut Named Places (NNP) points recorded by the Inuit Heritage Trust (IHT). The IHT was created under the NLCA to manage Inuit archaeological, ethnographic and cultural resources; including documenting and reviewing traditional place names to become official (Tungavik Federation of Nunavut and Hon. Tom Siddon, P.C., M.P. 1990, S33.9.1). Over 8,000 place names (Peplinski 2014) were collected through interviews in each community, usually with three or four Elder-experts (Peplinski 2009). Elders share

¹⁵ <https://open.canada.ca/data/en/dataset/2bcf34b5-4e9a-431b-9e43-1eace6c873bd>

¹⁶ <https://open.canada.ca/data/en/dataset/a4b190fe-e090-4e6d-881e-b87956c07977>

¹⁷ <https://lupit.nunavut.ca/portal/registry.php?public=docs>

¹⁸ Display only at

<https://nunavut.maps.arcgis.com/apps/Viewer/index.html?appid=a9af182ca44e4cffafe61e1956144d34>

names for known locations including permanent (e.g., lakes) and recurring (e.g., ice cracks) features. The NNP dataset also includes some Kitikmeot place names that were collected as a part of the Naonaiyaotit Traditional Knowledge Project¹⁹ run by the Kitikmeot Inuit Association. I downloaded 19 community datasets in keyhole markup language format (which always has a CRS of WGS84) from the IHT Google MyMaps website²⁰ (Inuit Heritage Trust 2016) on January 22, 2017. These were combined in R to create consistent variables (where available) for Inuktitut place names, Qallunaatitut (English) place names, latitude, longitude, feature type, and place name meaning.

Environmental covariates were calculated as follows:

- EPSG 102001 has units in metres, so lake surface area was calculated in square metres (m²) and subsequently converted to square kilometres (km²).
- Lake perimeter was calculated in metres (m), the units used by EPSG 102010, and subsequently converted to kilometres (km).
- Shoreline development is a commonly used morphometric measure of the relative amount of littoral area in a lake (Hutchinson 1957; Reeves 1968; Hershey et al. 2006). Shoreline development was calculated as lake perimeter/(2 * (pi * lake area)^{1/2}) (km / km²).
- River length was calculated from each waterbody in each system, using an undirected network graph created from the 250K waterbody and watercourse lines, since charr tend to follow lake and river shorelines while migrating. Some systems, particularly in the Kivalliq and Kitikmeot, have two exit rivers, for instance leaving Meliadine Lake (Meliadine and Diane Rivers) and Maguse Lake (Maguse River splits); I assumed that the shortest river was the easiest migration path. I created migration start points by snapping lake polygons to the adjacent streamflow vertices, and river mouths (migration end points) by intersecting the Nunavut border polygon with the streamflow lines. I used the tidygraph package (Pedersen 2020) to calculate the distances along the

¹⁹ <https://www.ntkp.ca/>

²⁰ <http://ihti.ca/eng/place-names/pn-goog.html>

streamflow lines between all combinations of the migration start and end points, and selected the minimum distance for each waterbody.

- Average river gradient was calculated by dividing the elevation of the closest contour line to the source lake by the river length (Power and Barton 1987). Sections of rivers may be steeper than this average gradient calculation, but as barriers to migration can take many forms unrelated to steepness, these were calculated by other methods (see below) (Torgersen et al. 2006).
- The location of falls, fords and rapids were extracted from CanVec 50K and 250K data. Some additional barriers were extracted from the NNP and NCRI data using search terms “waterfall”, “rapids”, “shallow”, “block”, “barrier”, “stop”, “can’t”. The barriers were assigned to the closest river segment and then summed along the shortest route from each lake.
- The polynya data was generally coarser than the other environmental covariates as locations were extracted from NPC, NNP and NCRI data using the search terms “polynya” and “open water”. The resulting distribution generally matched previous reports of major polygons in Nunavut (Hannah et al. 2008), with some differences due to my inclusion of shore leads and other open water (WWF-Canada 2015). The greatest differences were regional: polynyas ran along most of the Hudson Bay coast, whereas the Kitikmeot had fewer, smaller, discrete polynyas (see Appendix 3: Polynya data). I calculated the Euclidean distance between each river mouth and the closest polynya within five kilometres of shore, where charr are most active (Moore et al. 2016).
- Latitude and longitude were calculated as the on-polygon centroid of each lake, initially in EPSG 102001, but subsequently transformed to WGS84 to put the coordinates on a scale more consistent with other covariates.
- Lake centroids were spatially joined to the watershed polygons to assign a watershed name to each waterbody.

2.2.4. Data combination

Observations were extracted from each dataset including species (with anadromous and resident charr being considered as separate “species” for this analysis), location, community of observation, and date of observation. Data was tidied to remove or repair invalid geometries, and standardize formats (e.g., units, CRS). For instance, the NWHS database has no associated metadata, so after initial exploration, some locations appeared in a grid pattern. Consequently, locations were replaced with the coordinates in the “Modification” table in the database, which visually appeared to be more accurate (e.g., the coordinates for adjacent points were not identical), and which matched with corrected Kivalliq regional data from the Kivalliq Inuit Association (provided by Maria Serra, GIS Coordinator, Kivalliq Inuit Association, in shapefile format on November 24, 2016).

Species codes and names were converted to match that used in the NCRI (as downloaded on 21 April, 2018), as this dataset had the most extensive species list (although this was updated to include any additional species from the AFSA and NWHS datasets) (Tedesco et al. 2017). Marine species, as identified by FishBase (Froese and Pauly 2018), were removed from further analysis, as were species with uncertain identifications. Observations of unexpected species (i.e., where identification could be more unreliable), such as Inconnu (*Stenodus leucichthys*) in the NWHS (Priest and Usher 2004) and AFSA databases, were removed. “Landlocked Char” observations from the Igloodik NCRI were excluded from analysis, as this community’s report (and personal communications with the GN), noted that the incorrect Inuktitut term (ivitaaruq, meaning male spawning charr) was used to describe a photo of landlocked charr. Observations might thus represent a mix of both landlocked and spawning charr, and the migratory type could not be reliably determined.

Observations were clipped to the extent of the Nunavut land boundaries, then point geometries were linked to the lake polygons using a point-in-polygon overlay to remove observations that were made in watercourses (rivers, streams) and the ocean, and to estimate

the minimum area of lakes occupied by fish. Lakes below this minimum area were assumed to be unable to support fish populations, as either ephemeral waterbodies that dry up throughout the summer (Power and Power 1995), or shallow lakes that freeze to the bottom in winter (Haynes et al. 2014). Waterbodies smaller than this threshold were thus excluded during subsequent overlays with the line and polygon NCRI observations to ensure that I wasn't overestimating fish presences due to the small scales used in the NCRI mapping. For the same reason, I also excluded any NCRI polygons or lines that intersected multiple waterbodies, a process similar to removing observations with a spatial impression greater than the raster cell size in raster-based species distribution modelling (Labay et al. 2011; Konowalik and Nosol 2021).

The environmental variables and observation data were considered temporally congruent (Labay et al. 2011), since the covariates were unlikely to have changed in the approximately 40 years since the NWHS data was collected. To avoid pseudo-replication, however, environmental and occurrence data were integrated to the same spatial scale, i.e., the waterbody. Fish observations were summarized by waterbody number, with anadromous and resident charr and Lake Trout designated as present or absent, and the number of other species summed for that waterbody. I reviewed observations in combination with the calculated environmental variables and several were removed as too uncertain or biologically highly unlikely (e.g., anadromous fish observations in lakes that had access gradients of over 40 m/m).

Finally, various methods have been proposed to accommodate spatial bias in SDMs. Species observations from citizen science data (e.g., incidental observations or interview responses), or surveys with non-random site selection (e.g., fisheries development studies), are often spatially biased particularly towards areas with easier access (e.g., roads, communities, rivers). Such a bias is clear in the NCRI data, which records areas traveled and used by the interviewees (Fisheries and Sealing Division 2017). For GLMs, incorporating spatial covariates (Allouche et al. 2008; Mendes et al. 2020) has generally been shown to be more effective at dealing with spatial bias than background selection methods such as target group background (Phillips et al.

2009). I thus included a distance to closest community covariate in my model that reflects spatial bias in the presence records (i.e., ease of travel), as well as latitude and longitude.

An example of the final dataset is provided in Appendix 4: Data sample. Ranges for variables were reasonably consistent across the datasets used in model training, validation, and prediction (Table 3).

Table 3: Variables created from fish observation and environmental datasets, and explored as possible covariates for SDMs of anadromous and resident Arctic Charr in Nunavut (see section 2.2.6 for which variables were ultimately retained in model construction). Value ranges are provided for the data used to train each model, as well as the external dataset and prediction region used to validate both models.

Variable name	Variable definition	Variable type	Set of waterbodies			
			Anadromous model training	Resident model training	External validation	Prediction
Char	Presence / absence of anadromous charr	Binary	518 present 8,805 absent	N/A	43 present, 8 absent	N/A
LLC	Presence / absence of resident charr	Binary	N/A	235 present, 9,114 absent	8 present, 43 absent	N/A
Xdd	Latitude in decimal degrees (WGS84)	Continuous	-120.20 — -61.68	-120.08 — -61.86	-110.87 — -63.97	-120.20 — -61.58
Ydd	Longitude in decimal degrees (WGS84)	Continuous	55.82—79.33	55.85—79.91	56.16—72.62	55.82—79.91
WShed	Watershed in which the waterbody is located	Categorical	51 watersheds	51 watersheds	19 watersheds	51 watersheds
Area_km	Lake area (km ²)	Continuous	0.023— 4,853.719	0.023— 4,853.719	0.192— 4,853.719	0.022— 4,853.719
Perim_km	Lake perimeter (km)	Continuous	0.556— 6,341.597	0.555— 6,341.597	1.672— 6,341.597	0.554— 6,341.597

SDI_km	Shoreline development index (km / km ²)	Continuous	1.015—25.678	1.017—25.678	1.076—25.678	1.015—25.678
RivDist_km	Shortest distance between waterbody and river mouth (km)	Continuous	0.0015—153.6070	0.0015—179.3820	0.022—51.563	0.001—190.502
Gradient	Average gradient of the access river (unitless)	Continuous	0.0002—85.0000	0.00013—200.00000	0.00067—1.81818	0.00013—Inf
nObst	Number of obstacles along the shortest river route	Integer	0—23	0—20	0—3	0—23
PresObst	Presence / absence of obstacles along the shortest river route	Binary	910 present, 8,413 absent	885 present, 8,464 absent	4 present, 47 absent	5,137 present, 49,746 absent
PolynyaDist_km	Distance from river mouth to closest polynya	Continuous	0.0014—430.0854	0.0014—379.2116	0.3786—320.0825	0.0014—430.0854
CtOthSpp	Number of other species in the lake	Integer	0—4	0—4	0—5	0—5
PresOthSpp	Presence / absence of other species in the lake	Binary	137 present, 9,186 absent	137 present, 9,186 absent	10 present, 41 absent	454 present, 54,429 absent
LKTR	Presence / absence of Lake Trout in the lake	Binary	124 present, 9,199 absent	124 present, 9,199 absent	9 present, 42 absent	425 present, 54,458 absent

Pred	Presence / absence of predator species (Lake Trout or Northern Pike) in the lake	Binary	124 present, 9,199 absent	124 present, 9,199 absent	9 present, 42 absent	425 present, 54,458 absent
CommDist_km	Euclidean (straight-line) distance to the closest community	Continuous	0.8011—342.2852	0.8011—396.0905	12.53—162.70	0.4383—396.0905

2.2.5. Background point selection

I modeled the probability of anadromous and resident presence in response to spatial and environmental covariates using a generalized linear model (GLM) with a binomial distribution and a logit link. GLMs are fitted on both presence and absence species information; however, the NCRI and NWHS data is presence-only, based on observations. It was thus necessary to select background points (sometimes known as pseudo-absences) that represent the available environmental space (i.e., they're not true absences). I randomly selected 20,000 background waterbodies (Wisz and Guisan 2009; Barbet-Massin et al. 2012) from watersheds containing charr presences. Selection was constrained in this way to account for some of the spatial bias in the records (Lobo et al. 2010; Finstad and Hein 2012; Stolar and Nielsen 2015) and to make river network calculations computationally feasible.

2.2.6. Data exploration

Data was explored following the protocols outlined in Zuur et al. (2010). Lake area, lake perimeter, river length, and river gradient were all log-transformed (using natural logarithms) to reduce the influence of outliers on the high end of each scale. Locations with infinite values in both river length and river gradient (representing lakes without rivers connecting them to the ocean), as well as corresponding infinite values for the number of obstacles and distance to polynyas, were dropped since they were inaccessible to anadromous charr (i.e., the habitat is not available for selection), and to avoid later errors in model fitting (e.g., dropped observations during stepwise model selection).

River distance and gradient were highly collinear, so gradient was removed from further analysis. Similarly, lake area, lake perimeter, and shoreline development were highly collinear; variance inflation factors suggested removing lake area and lake perimeter from the modeling. Lake perimeter was removed, as shoreline development was expected to better represent lake littoral habitat; however, lake area was expected to influence anadromy so was retained

despite the collinearity (De Marco and Nóbrega 2018). Model results were interpreted while considering the potential for unstable coefficient estimates and lower statistical power resulting from this collinearity (De Marco and Nóbrega 2018).

Likewise, the presence of Lake Trout, presence of predators, and both the presence and number of other species in the waterbody were all highly correlated (~ 0.9). 468 waterbodies contained observations of other species. A breakdown of species counts showed that only 33 waterbodies contained observations of species that weren't Lake Trout; consequently, presence of Lake Trout was retained, and the collinear variables dropped. Comparing charr presence / absence and Lake Trout presence / absence, however, showed that only 307 background locations (of 20,000) had any information about other species presence (with another 40 observations of other fish species from watersheds where charr were not observed, i.e., outside the watersheds being used in my model). Since this could cause issues with model convergence and parameter estimation, Lake Trout presence (and consequently the presence of any other species) was dropped as a model covariate.

Finally, during model development, the residuals showed some patterns with the number of obstacles in a river. I thus created and modeled a binary covariate for the presence or absence of obstacles on a river.

2.2.7. Species distribution modeling

I fitted separate SDMs for anadromous and resident charr using R packages lme4 (Bates et al. 2015) and dismo (Hijmans et al. 2020). The presence-absence of anadromous ("Char") or resident ("LLC") populations was assumed to follow a binomial distribution with probability π_i (Equation 1).

Equation 1: The binomial distribution (presence or absence), expected value, and variance for the presence of anadromous charr in lake j of watershed i. I used the same distribution to model resident charr, in which case the variable "Char" was replaced by "LLC".

$$\begin{aligned} Char_{ij} &\sim Bin(\pi_{ij}) \\ E(Char_{ij}) &= \pi_{ij} \\ var(Char_{ij}) &= \pi_{ij} \times (1 - \pi_{ij}) \end{aligned}$$

I used a logistic link and included all covariates in my initial model. I included interactions that might be expected biologically, but only if the main terms were not correlated (Equation 2). Variables were scaled and centred to allow model convergence. I modeled watershed as a random intercept z_i , as lakes and their species composition within the same watershed are expected to be more similar to each other than to lakes from other watersheds (Samarasin et al. 2014), and can affect species distribution models for freshwater fish (Porter et al. 2000). My models were thus more properly termed generalized linear mixed models or GLMMs.

Equation 2: Logistic link, covariates, and random watershed intercept for my initial model

$$\begin{aligned} \text{logit}(\pi_{ij}) &= \eta_{ij} \\ \eta_{ij} &= \beta_1 + \beta_2 \times Xdd_{ij} + \beta_3 \times Ydd_{ij} + \beta_4 \times PolynyaDist_km_log_{ij} + \beta_5 \times Area_km_log_{ij} + \beta_6 \\ &\times SDI_km_log_{ij} + \beta_7 \times RivDist_km_log_{ij} + \beta_8 \times nObst_{ij} + \beta_9 \times CommDist_km_{ij} + \beta_{10} \times \\ &RivDist_km_log_{ij}:nObst_{ij} + \beta_{11} \times RivDist_km_log_{ij}:Area_km_log_{ij} + z_i \\ z_i &\sim N(0, \sigma_{WShed}^2) \end{aligned}$$

When model assumption checks identified patterns in the residuals for the number of obstacles (nObst), nObst was replaced by the binary presence of obstacles variable (PresObst) in both the main term and interaction. Model selection followed the modified protocol for mixed effects models as described in Zuur, Hilbe and Ieno (2015). I found the most parsimonious model from a backward stepwise model selection using Akaike's Information Criterion (AIC) and likelihood ratio tests. However, SDM techniques can bias model comparison towards more complex, and

potentially over-fitted, models (Jiménez-Valverde et al. 2008). All competitive models within 2 AIC of the most parsimonious model were thus also considered and investigated for uninformative parameters per Arnold (2010). More complex competitive models were retained if the additional variables improved coefficient stability. Model coefficients that had 95% confidence intervals that did not overlap zero were considered to have an impact on probability of presence. I verified model assumptions graphically following Zuur, Hilbe and Ieno (2015).

Even after accounting for spatial bias in the presence data, SDMs can have residual spatial autocorrelation (SAC). SAC reflects the greater similarity of close locations compared to those further apart, and occurs when an important covariate is not modeled, a species exhibits spatial clumping in its distribution, or environmental covariates have an underlying geographical distribution. SAC violates the assumption of independence for the residuals and can result in models with less precise parameter estimates, more Type I errors where the null hypothesis is incorrectly rejected, and biased model selection (Dormann et al. 2007). Residual SAC was assessed via mapping and variograms to look for patterns in the residuals across space. Variogram distances were calculated along the river network, as this better represents spatial connectivity in freshwater systems than Euclidean distance (Ganio et al. 2005; Ladle et al. 2017).

SDM performance can vary depending on the input data, environmental variables used, geographic space, and model type, and thus needs to be evaluated carefully. Model validation using an independent dataset (external validation) is considered superior to k-fold cross-validation (a common method of internal validation), which tends to overestimate model accuracy (Newbold et al. 2010), particularly when projecting results to a novel spatial or temporal space. With three data sources available, I used the smallest dataset (AFSA) as an independent test set containing both presence and absence information, against a presence-only training set created by combining the other two sources (NCRI and NWHS). The AFSA dataset is small (51 waterbodies containing 43 anadromous and 8 resident presences), but small datasets can nevertheless provide model validation (Allouche et al. 2008; Newbold et al.

2010). In addition, I used 10-fold cross-validation to divide the NCRI-NWHS observations and background into 10 random groups, which were sequentially used to test a model built from the other nine subsets; test results were averaged for all runs. K-fold cross-validation, however, can give overly optimistic model evaluations if spatial sorting bias (SSB) is present. SSB is the ratio of the geographic distance between test presences and training presences to the distance between test background and training presence, and can upwardly bias model evaluations (Hijmans 2012). I found SSB in my dataset after internal validation, so additionally conducted a spatially blocked cross-validation by using spatial blocks (in my case, watersheds (Chu et al. 2005; Hein et al. 2012)) instead of random assignment to create the training and test folds. Model performance was evaluated using the area under the receiver operating curve (AUROC), with higher values indicating a model that reliably predicts a higher probability at presence locations than at absence locations, when locations are randomly compared in pairs. An AUROC of 0.5 is no better than random. Further, a smaller difference in AUROC values between internal and external validations demonstrates that a model is more transferable (Higgins et al. 2020).

Additionally, the classification accuracy of the models was assessed from confusion matrices for all lakes, and for the 307 lakes where charr were not observed but other species were (i.e., likely charr absences; Huang and Frimpong 2015). Confusion matrices provide information on the overall classification accuracy (number of correctly predicted presences and absences), sensitivity (correctly predicted presences), specificity (correctly predicted absences), and kappa (which compares the classification accuracy to that expected by chance). A poorly fitting model has a kappa value less than 0.4, while a value over 0.75 implies an excellent fit. Additionally, I plotted response curves for variables in the final models. Finally, the best model was applied to 54,883 waterbodies in the target group background region (Phillips et al. 2009; Hein et al. 2012) to predict the expected probability of presence of anadromous and resident charr populations across Nunavut. These were converted to expected presence and absence using the maximum specificity-sensitivity threshold from the internal, spatially blocked, and external validations (Olden and Jackson 2001).

2.3. Results

2.3.1. Fish observations

The smallest lakes that were occupied by fish were just over 27,000 m². Only 0.7% of available waterbodies were smaller than this. After data cleaning and combination, 1,284 fish observations remained in 986 waterbodies (Figure 3). Anadromous charr observations were the most common (561), followed by Lake Trout (439), resident charr (255), and all other species (29). 21.4% of these observations overlapped between species or ecotypes (Figure 4).

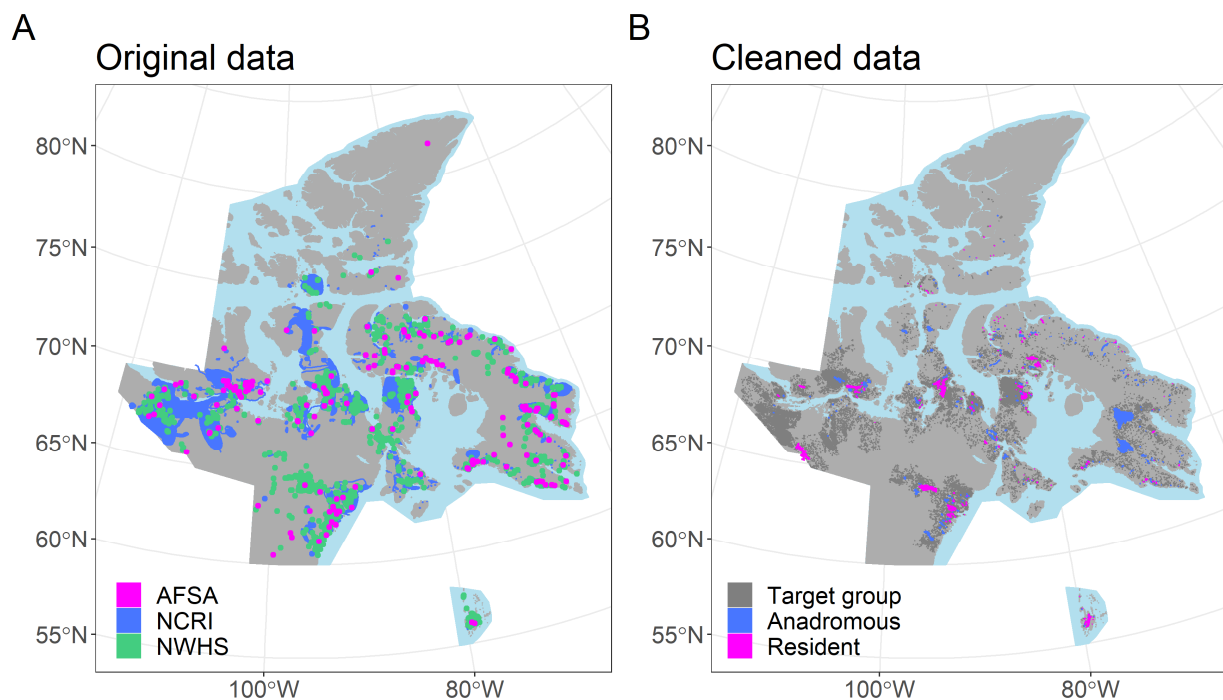


Figure 3: The distribution of the A) original and B) cleaned observation datasets. Sources of original data include the Arctic Fisheries Stock Assessment database (AFSA), Nunavut Coastal Resource Inventory (NCRI), and Nunavut Wildlife Harvest Study (NWHS). Cleaned data shows the distribution of target group background waterbodies (i.e., intersecting with any fish observations from the original data), and those containing at least one observation of anadromous or resident charr.

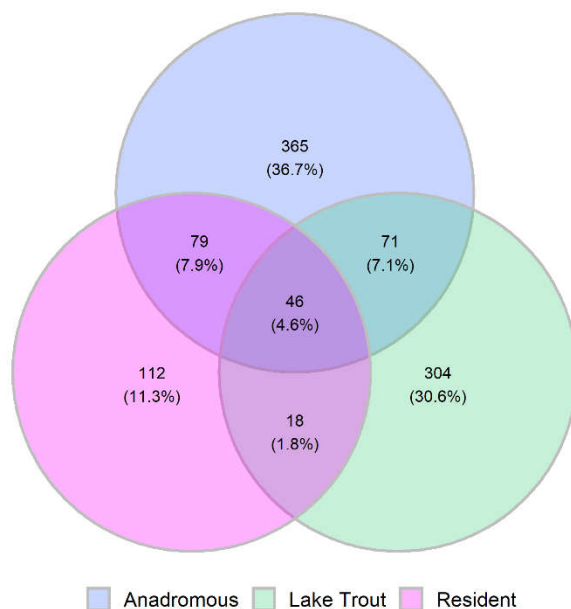


Figure 4: The number (and percentage) of fish observations occurring in each waterbody.

41% of waterbodies intersected with only one observation. Multiple observations in one waterbody were mostly from the same source (e.g., separate NCRI interviews, AFSA catches over multiple years, or NWHS harvests from several locations in a lake). Between sources, there was greater overlap between NCRI and NWHS observations than with AFSA records (Figure 5). More observations of anadromous charr overlapped (15.3%) than resident charr (8.7%) or Lake Trout (5.4%).

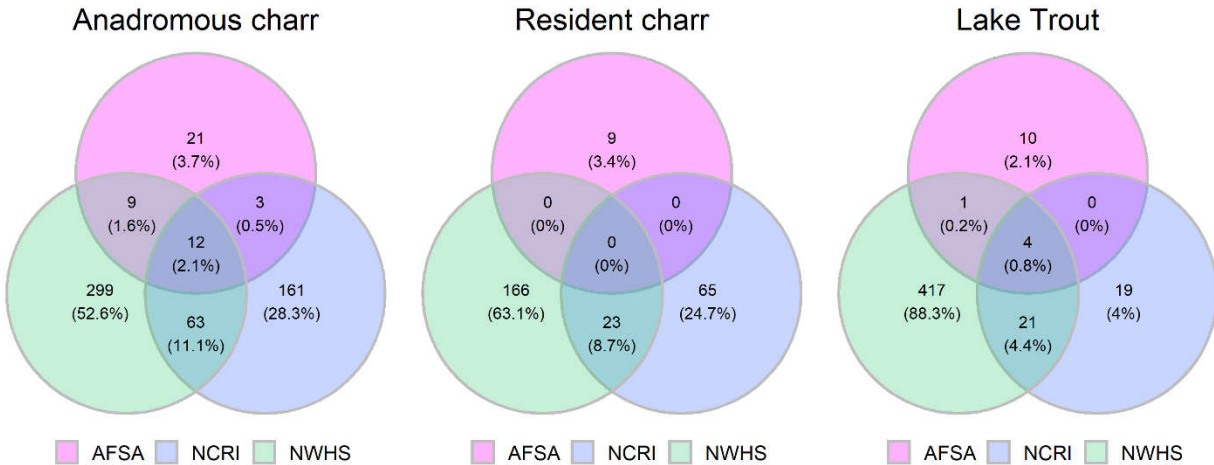


Figure 5: Number (and percentage) of waterbodies intersecting with different sources of fish observations in Nunavut. Sources include the Arctic Fisheries Stock Assessment database (AFSA), Nunavut Coastal Resource Inventory (NCRI), and Nunavut Wildlife Harvest Study (NWHS).

2.3.2. Model selection

The full model including a random watershed intercept had a lower AIC than the full model with only fixed effects, and was used for subsequent model selection. I conducted stepwise selections on the full model using either PresObst or nObst, which both resulted in the same minimum parsimonious model that lacked a barrier covariate. The coefficient estimate for river length halved when the Area_km_log:RivDist_km_log interaction was dropped. The model containing the interaction was thus considered the best model, as it was within 2 AIC of the parsimonious model and all coefficient estimates were stable (Table 4).

Table 4: Comparison of GLMMs fitted to describe the distribution of anadromous charr populations in Nunavut. Models used a binomial distribution as described in Equation 1 and Equation 2, and differed only in the covariates that were included in the logistic link function for each model.

Model	Covariates	AIC	Δ AIC
Full	$\eta_{ij} = \beta_1 + \beta_2 \times Xdd_{ij} + \beta_3 \times Ydd_{ij} + \beta_4 \times$ $PolynyaDist_km_log_{ij} + \beta_5 \times Area_km_log_{ij} + \beta_6 \times$ $SDI_km_log_{ij} + \beta_7 \times RivDist_km_log_{ij} + \beta_8 \times nObst_{ij} + \beta_9 \times$ $CommDist_km_{ij} + \beta_{10} \times RivDist_km_log_{ij}:nObst_{ij} + \beta_{11} \times$ $RivDist_km_log_{ij}:Area_km_log_{ij} + z_i$	2198.786	6.586
Best	$\eta_{ij} = \beta_1 + \beta_2 \times Xdd_{ij} + \beta_3 \times Ydd_{ij} + \beta_4 \times Area_km_log_{ij} + \beta_5 \times$ $RivDist_km_log_{ij} + \beta_6 \times CommDist_km_{ij} + \beta_7 \times$ $RivDist_km_log_{ij}:Area_km_log_{ij} + z_i$	2192.7	0.5
Parsimonious	$\eta_{ij} = \beta_1 + \beta_2 \times Xdd_{ij} + \beta_3 \times Ydd_{ij} + \beta_4 \times Area_km_log_{ij} + \beta_5 \times$ $RivDist_km_log_{ij} + \beta_6 \times CommDist_km_{ij}$	2192.2	0

Like for anadromous charr, including a random watershed intercept in the full resident model lowered the AIC. Model selection using either PresObst or nObst resulted in two similar models differing only in this variable. The model containing nObst was the most parsimonious with the lowest AIC, and higher log likelihood (Table 5).

Table 5: Comparison of GLMMs fitted to describe the distribution of resident charr populations in Nunavut. Models used a binomial distribution as described in Equation 1 and Equation 2, and differed only in the covariates that were included in the logistic link function for each model.

Model	Covariates	AIC	Δ AIC
Full	$\eta_{ij} = \beta_1 + \beta_2 \times Xdd_{ij} + \beta_3 \times Ydd_{ij} + \beta_4 \times$ $PolynyaDist_km_log_{ij} + \beta_5 \times Area_km_log_{ij} + \beta_6 \times$ $SDI_km_log_{ij} + \beta_7 \times RivDist_km_log_{ij} + \beta_8 \times nObst_{ij} +$ $\beta_9 \times CommDist_km_{ij} + \beta_{10} \times RivDist_km_log_{ij}:nObst_{ij} +$ $\beta_{11} \times RivDist_km_log_{ij}:Area_km_log_{ij} + z_i$	1153.084	11.184
Competitive	$\eta_{ij} = \beta_1 + \beta_2 \times Xdd_{ij} + \beta_3 \times Area_km_log_{ij} + \beta_4 \times$ $CommDist_km_{ij} + \beta_5 \times PresObst_{ij} + z_i$	1143.2	1.3
Parsimonious	$\eta_{ij} = \beta_1 + \beta_2 \times Xdd_{ij} + \beta_3 \times Area_km_log_{ij} + \beta_4 \times$ $CommDist_km_{ij} + \beta_5 \times nObst_{ij} + z_i$	1141.9	0

2.3.3. Model parameters

The probability of occurrence for anadromous Arctic Charr was best explained by a mix of environmental and spatial covariates: the log of lake area, longitude, distance to the closest community, and the log of river distance (Table 6). Although the positive interaction between lake area and river distance was not significant, it was included since the estimate for log of river distance was inconsistent and changed sign without the interaction. Latitude was not significant (Appendix 5: Response curves for insignificant variables), but removing it increased model AIC.

The probability of anadromous charr presence increases with lake area and longitude, but decreases with distance to communities and river length (Table 6). As shown by the partial residuals, the model generally slightly overpredicts charr presence, and but the less frequent underpredictions are larger (Figure 6).

Table 6: Coefficient estimates and 95% confidence intervals (CI) from the best GLM predicting the probability of anadromous charr presence in Nunavut.

Covariate	Estimate	Lower CI	Upper CI
Intercept	-4.65	-5.05	-4.26
Xdd	1.16	0.83	1.49
Ydd	0.14	-0.02	0.30
Area_km_log	1.14	1.04	1.24
RivDist_km_log	-0.14	-0.27	-0.002
CommDist_km	-1.04	-1.19	-0.89
Area_km_log:RivDist_km_log	0.05	-0.02	0.11

Variable response curves for the resident model echo the relationships in the anadromous model (Figure 7), but are slightly weaker (except for distance to community; Table 7). Like for anadromous charr, the probability of occurrence for resident fish increased with the log of lake area and longitude, but decreased further from communities. The number of obstacles in the access river was not significant, but showed a positive trend in the response curve (Appendix 5: Response curves for insignificant variables). Partial residuals (both positive and negative) are smaller for all predictors in the resident model as compared to the anadromous model, particularly for longitude and distance to community (Figure 7).

Table 7: Coefficient estimates and 95% confidence intervals (CI) from the best GLM predicting the probability of resident charr presence in Nunavut.

Covariate	Estimate	Lower CI	Upper CI
Intercept	-5.99	-6.82	-5.17
Xdd	1.07	0.41	1.74
Area_km_log	0.92	0.82	1.02
nObst	0.12	-0.004	0.26
CommDist_km	-1.68	-1.94	-1.41

The random intercept by watershed appeared to be capturing spatial patterns in both the anadromous and resident models, as adjacent watersheds often had similar random effect estimates (Appendix 6: Spatial patterns, Figure 14). The groupings appeared to approximate the higher-level watersheds outlined as Water Management Areas in Schedule 4 of the Nunavut Waters Regulations (Government of Canada 2013).

2.3.4. Habitat suitability

The predicted probability of presence for both anadromous and resident charr across Nunavut reflects the model covariates that differed from zero. The mapped probability of presence is higher in the larger lakes, further east, and close to communities. 90% of lakes were common to both anadromous and resident charr (i.e., joint absence or joint presences). Overall, the predicted probability of presence was higher for anadromous charr than resident charr in Nunavut lakes (Figure 9). The predicted probability of presence was inversely related to the distance to the nearest charr observation for both anadromous and resident charr (Appendix 6: Spatial patterns, Figure 17).

When these probabilities were converted to presences and absences, both internal validations also predicted anadromous charr more often than resident charr (Figure 10). The two internal validations for each model resulted in very similar predictions. The spatially blocked validations had SSB close to one, however, so were considered more robust than the random internal validations. The spatially blocked validations for both the anadromous and resident models strongly fitted the data, with an AUROC of 0.903 and 0.928, respectively (Table 8). Both models had poor fit as estimated by the kappa values, but high prediction accuracy. The resident model performed slightly better than the anadromous model for all spatially blocked internal validation metrics.

Conversely, the external validations predicted more resident than anadromous populations (Table 9, Figure 10). The anadromous model was transferrable to the AFSA dataset (AUROC

0.741), but underpredicted anadromous presences (sensitivity = 0.61). External validation of the resident model, however, gave an AUROC of 0.314 (i.e., worse than random; see Figure 8: Performance of the anadromous and resident models as described by receiver operating curves. Figure 8). This validation underpredicted resident absences (specificity = 0.78), resulting in low accuracy (0.79) and 9,141 more predicted presences than the resident spatial internal validation across the target group background lakes.

Table 8: Performance statistics and confusion matrices resulting from spatially blocked internal validation of the anadromous and resident charr models. Confusion matrices were calculated for all training lakes, and for the 307 lakes where other fish, but not charr, were observed.

Anadromous model			
AUROC		0.903	
Accuracy		0.87 (0.860 - 0.874)	
Kappa		0.37	
Sensitivity		0.89	
Specificity		0.87	

		All data	
		Absent	Present
Predicted	Absent	7,626	57
	Present	1,179	461

		“Not found” lakes	
		Absent	Present
Predicted	Absent	69	N/A
	Present	238	N/A

Resident model			
AUROC		0.928	
Accuracy		0.91 (0.908 - 0.919)	
Kappa		0.32	
Sensitivity		0.91	
Specificity		0.91	

		All data	
		Absent	Present
Predicted	Absent	8,330	22
	Present	784	213

		“Not found” lakes	
		Absent	Present
Predicted	Absent	132	N/A
	Present	175	N/A

Table 9: Performance statistics and confusion matrices resulting from external validation of the anadromous and resident charr models. Confusion matrices were calculated for all training lakes, and for the 307 lakes where other fish, but not charr, were observed.

Anadromous model	
AUROC	0.741
Accuracy	0.95 (0.950 - 0.958)
Kappa	0.57
Sensitivity	0.61
Specificity	0.97

Resident model	
AUROC	0.314
Accuracy	0.79 (0.777 – 0.794)
Kappa	0.15
Sensitivity	0.96
Specificity	0.78

		All data	
		Absent	Present
Predicted	Absent	8,576	200
	Present	229	318

		All data	
		Absent	Present
Predicted	Absent	7,117	9
	Present	1,997	226

		“Not found” lakes	
		Absent	Present
Predicted	Absent	173	N/A
	Present	134	N/A

		“Not found” lakes	
		Absent	Present
Predicted	Absent	54	N/A
	Present	253	N/A

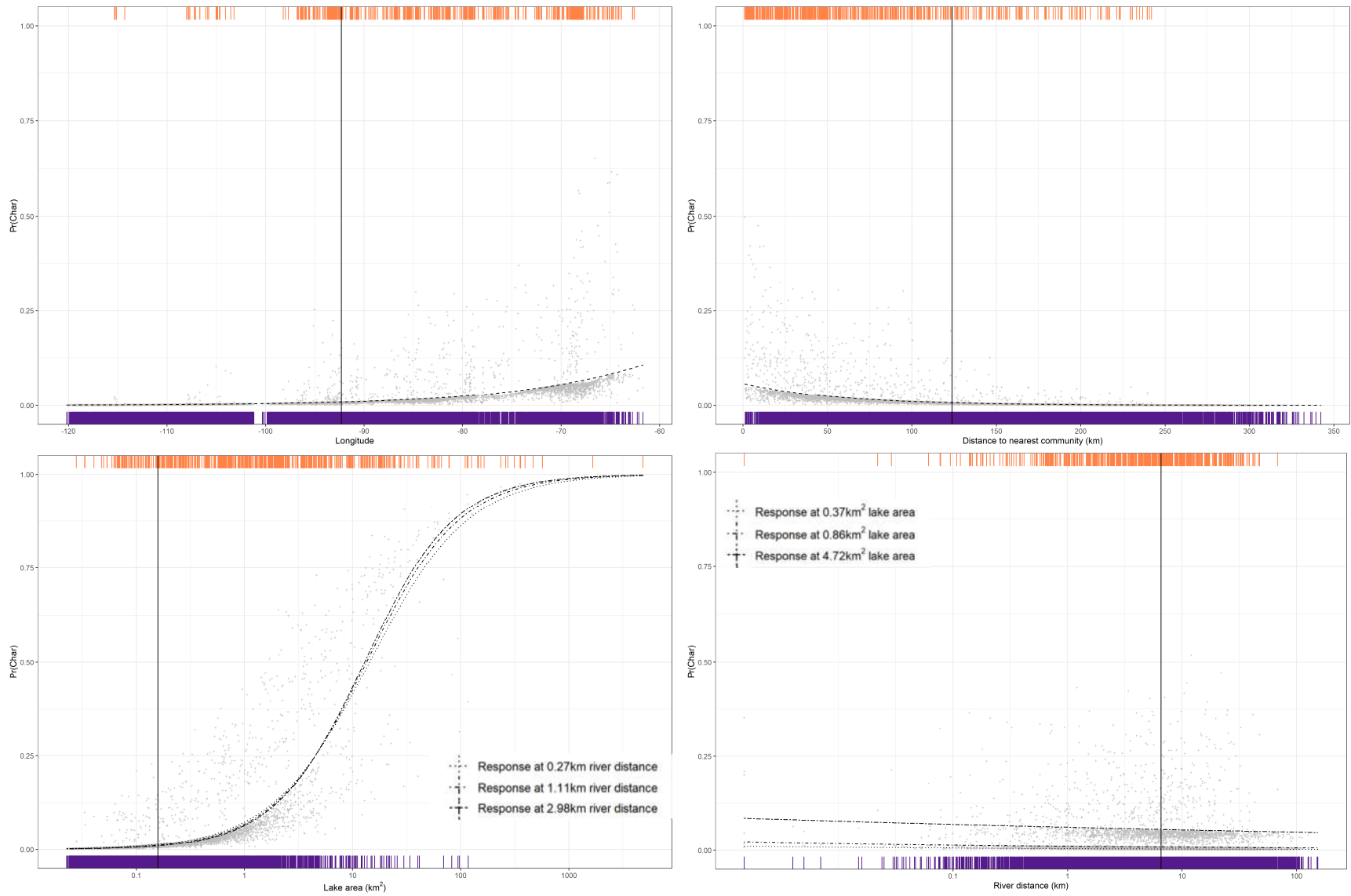


Figure 6: Response curves for the best anadromous GLM, plotted against the training dataset. Variables other than the focal are held at their median values to calculate fitted values (dashed lines). Partial residuals (grey crosses), mean variable values (solid lines), and actual presence (orange) and background (purple) values are illustrated, for comparison.

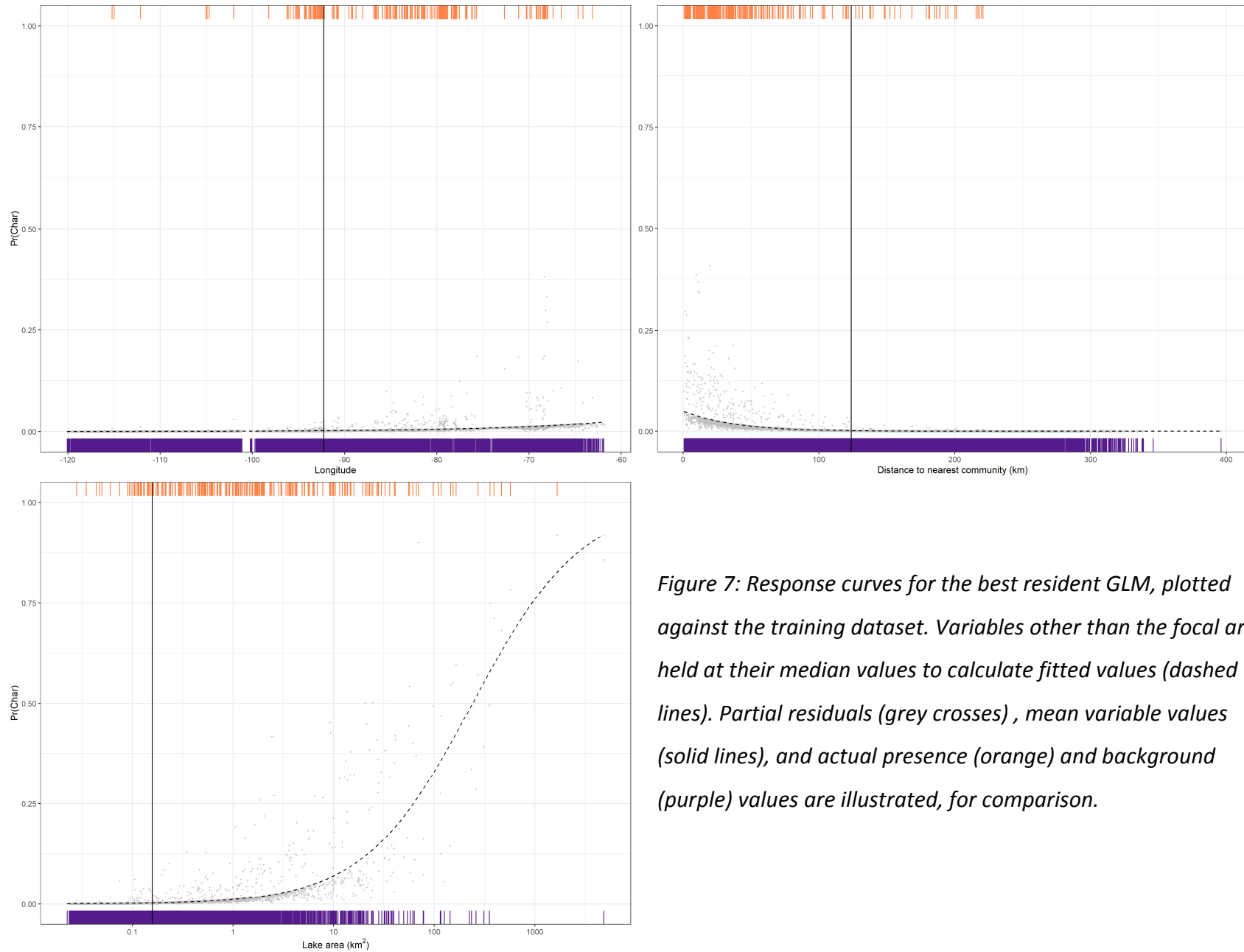


Figure 7: Response curves for the best resident GLM, plotted against the training dataset. Variables other than the focal are held at their median values to calculate fitted values (dashed lines). Partial residuals (grey crosses), mean variable values (solid lines), and actual presence (orange) and background (purple) values are illustrated, for comparison.

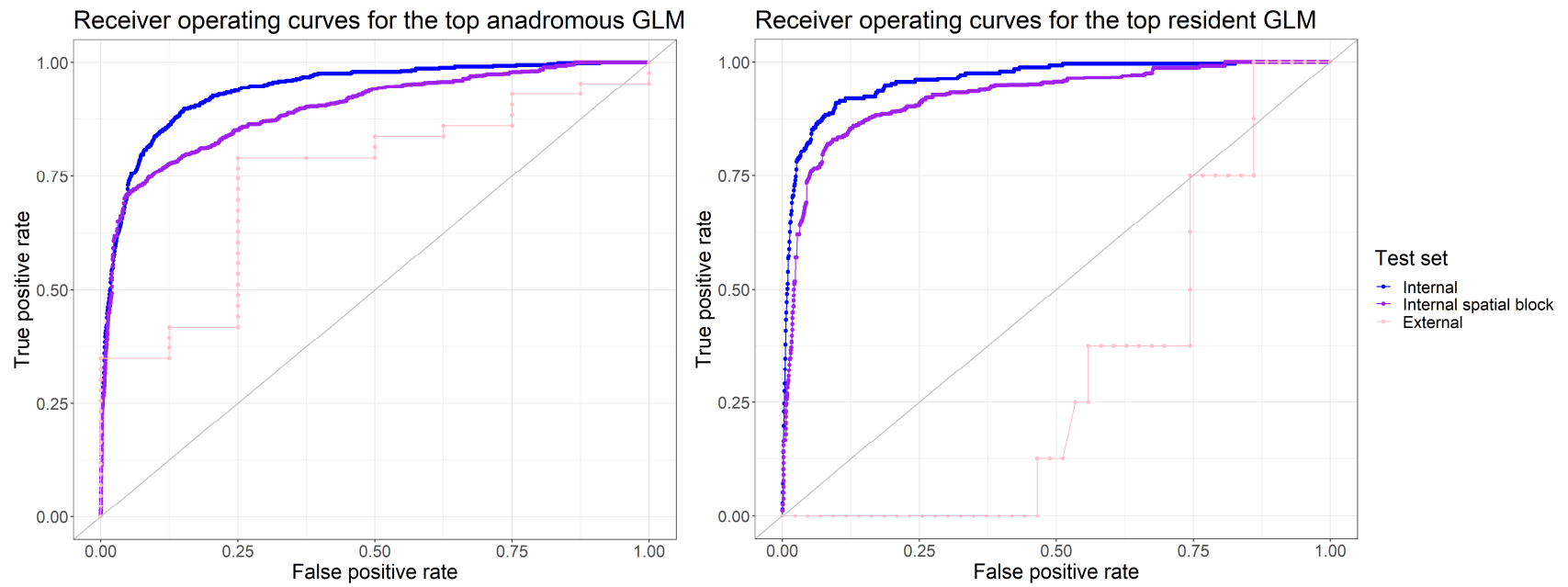


Figure 8: Performance of the anadromous and resident models as described by receiver operating curves.

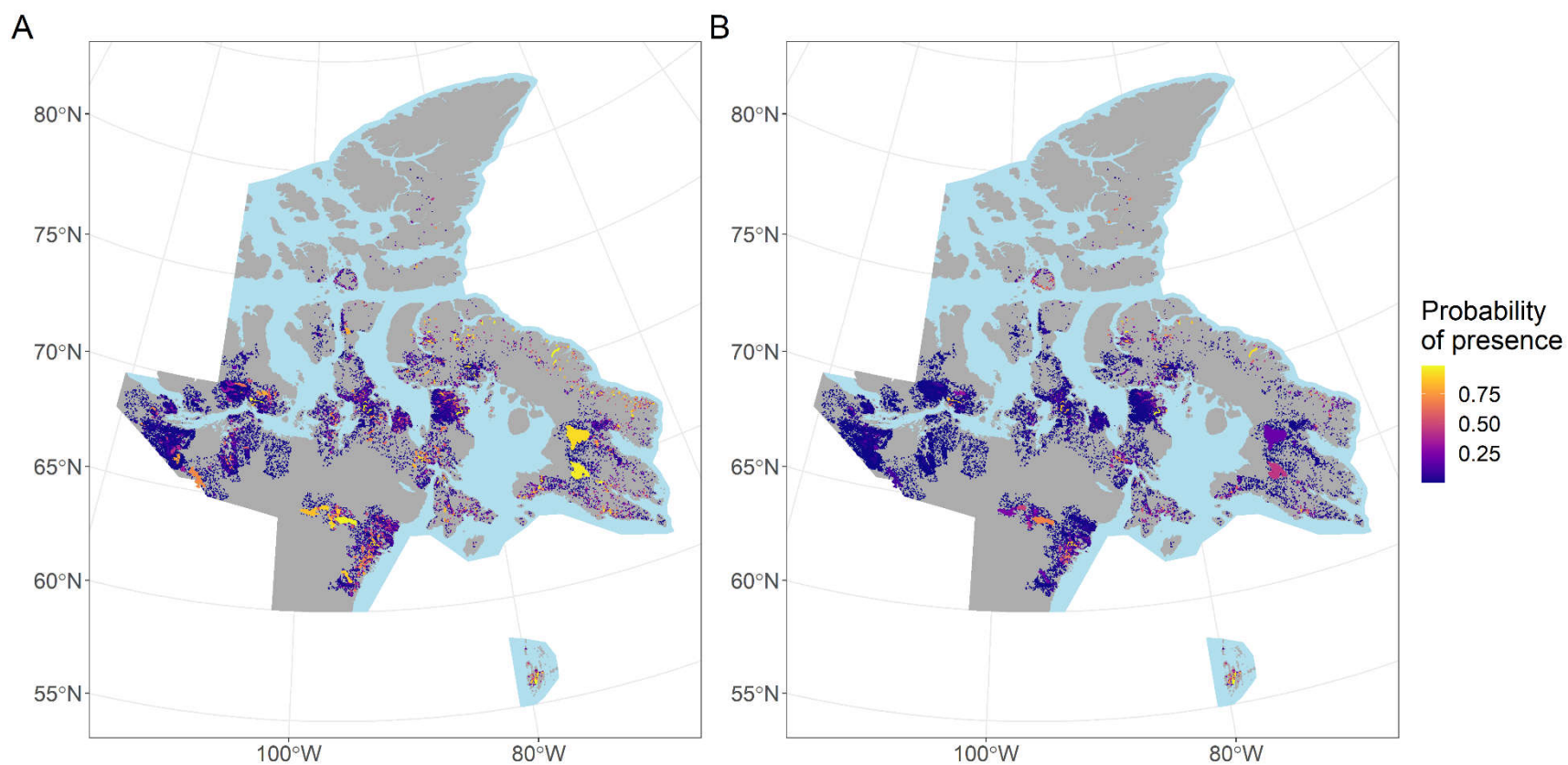
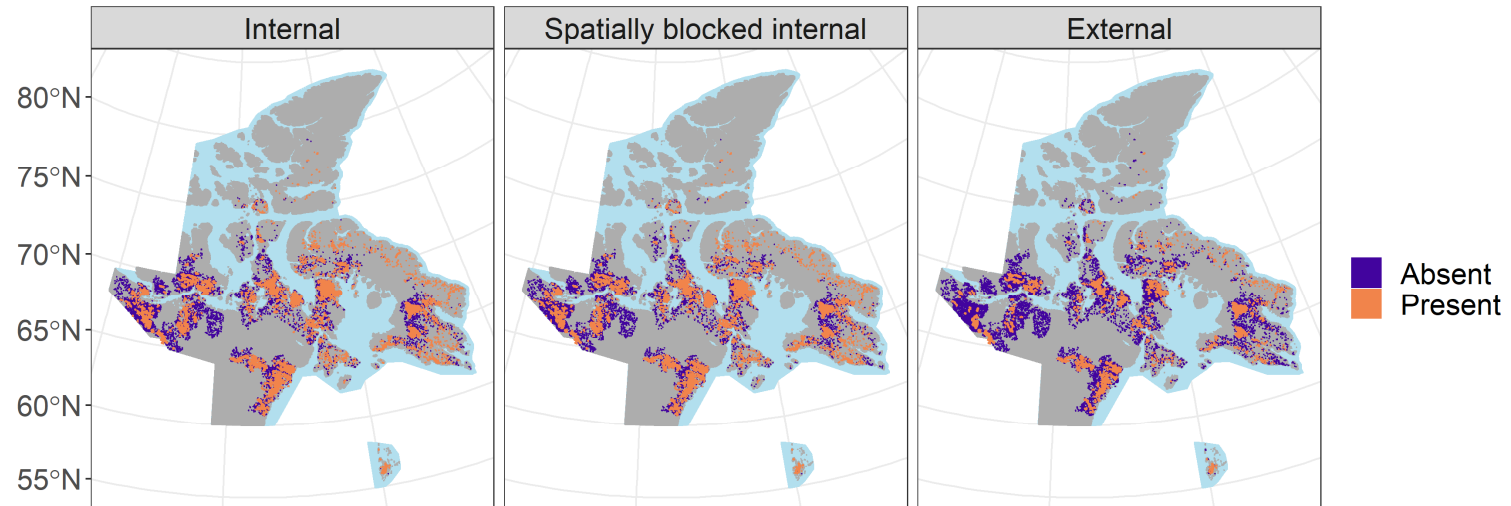


Figure 9: Probability of charr life history types in lakes across Nunavut, predicted by the best A) anadromous and B) resident GLMs.

A

Anadromous charr



B

Resident charr

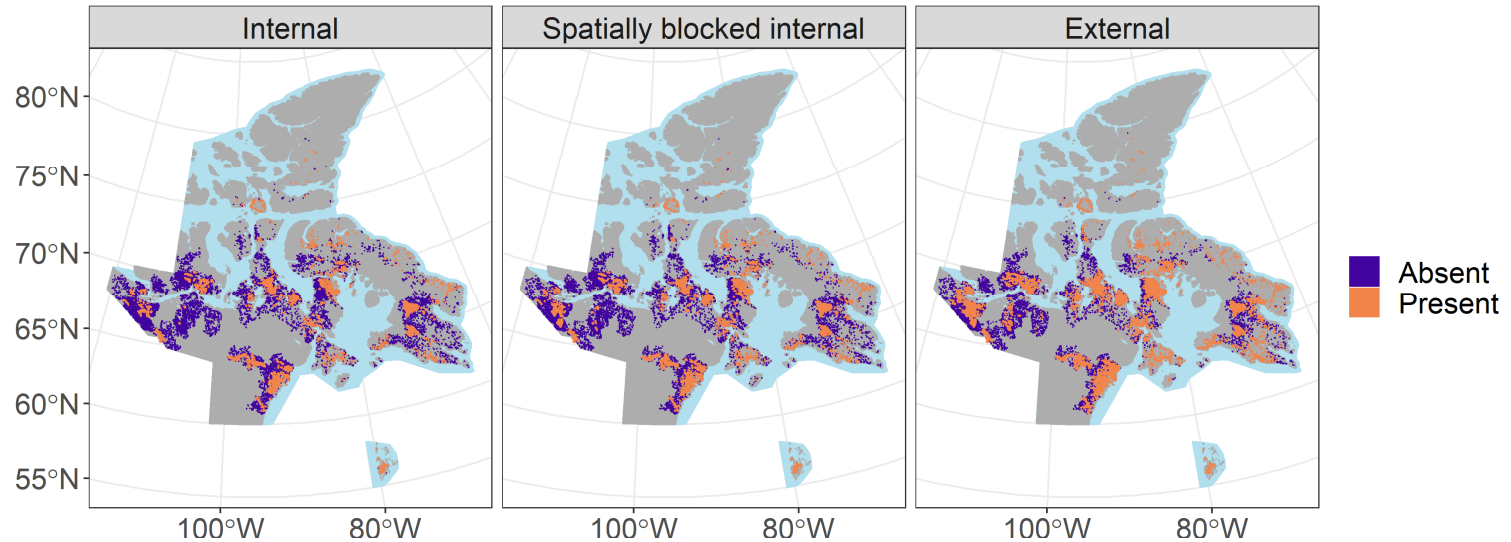


Figure 10: Predicted presence of charr life history types in lakes across Nunavut using thresholds from internal and external model validations

2.4. Discussion

2.4.1. Fish observations

As expected, incorporating Inuit knowledge and harvest records greatly expands the extent of Arctic Charr observations across Nunavut, particularly in the High Arctic. Previous regional work by Chu, Minns and Mandrak (2003) that investigated fish distributions in Nunavut were missing observations in 23 tertiary watersheds. Visually, it appears that their data reflects the scientific (AFSA) records, and that many of the watersheds missing records would be filled by Inuit knowledge observations from the NCRI and/or NWHS. The situation was similar compared to other freshwater fish databases that I explored. OBIS, for example, has over 1,000 records for Arctic Charr in Nunavut; but only 85 records intersected with waterbodies (i.e., all other observations were in rivers or the marine environment). Consequently, these two Inuit knowledge sources substantially increase the number of observations of variation within the Arctic Charr species (i.e., morphs) in Nunavut.

There are nevertheless some areas that still lack records, notably around Ukkusiksalik (Wager Bay), the inland Kivalliq, the far western Kitikmeot, the south-central Qikiqtaaluk coast, and the northern Arctic Archipelago. Missing records around Kugluktuk are likely due to the imprecision of the NCRI data in this region (mean polygon size was 625 km², with the largest being over 26,000 km²), combined with minimal research (as documented by the AFSA database) in the region. The other areas are likely sparsely recorded due to their further distance and relative inaccessibility from communities. Other more focused studies such as the Ukkusiksalik Inuit Knowledge Working Group (2012) could provide records to fill in these remaining gaps. The inland Kivalliq, which had low response rates in the NWHS Baker Lake interviews and has had less focus from DFO as an inland region, should be recorded in the future, when an NCRI occurs in Qammanituaq (Baker Lake) and Arviat. Some of the remaining spatial patterns (e.g., in random intercept estimates) may be due missing data from these regions.

Despite the lack of data from these areas, the patterns in my dataset reflect those in previous studies of fish distribution in Nunavut. I found that fish were present in lakes larger than 27,000m², which is within the range previously found to support charr (10,000m² (Hein et al. 2012) to 300,000m² (Harris et al. 2013)). The number of species was highest in Kivalliq lakes, then the Kitikmeot, and lowest in the Qikiqtaaluk, a pattern that reflects the analysis in Chu, Minns and Mandrak (2003). Occupied lakes in my dataset contained between 1-6 species (including charr). This is likely an underestimate in mainland areas, since previous studies found up to eight species in Northwest Territories (NWT) Barrenland lakes (Samarasin et al. 2014) and southern and central Nunavut watersheds (Chu et al. 2003; Brown and Fast 2012). In particular, large lakes may contain as many as 16 species (Reist et al. 2016). The lower species richness in my dataset may be due to spatial errors that removed observations during overlays, as well as inherent biases in the source data.

For instance, the NWHS only recorded locations for Arctic Charr and Lake Trout but not other species. Further, difficulty distinguishing between species with similar appearances or the same Inuktitut name may underrepresent species diversity, particularly in the NCRI (e.g., if two similar coregonid species are conflated; Lukyanenko et al. 2011; Fisheries and Sealing Division 2017). Finally, not all species may have been detected; even the AFSA data came from a variety of survey methods, which may have incompletely sampled lakes (e.g., gillnets, angling, trap nets). Such issues may be why there were fewer resident charr observations, since these fish are often smaller, darker, and harder to catch than their anadromous counterparts.

My final dataset had double the number of anadromous charr observations than resident charr. Further, while 50% of resident charr populations in the training dataset coexisted with anadromous fish, only 22% of anadromous populations had sympatric resident charr, possibly due to lower detectability of residents. Finally, resident charr observations declined more quickly with increasing distance from communities than did anadromous observations. If resident charr are harder to see or catch, they may be more likely to be observed in more frequently used areas, i.e., closer to communities. On the other hand, fishermen may be more

willing to travel further to catch the more sought-after than “sea-run” fish, resulting in more observations of anadromous populations further from communities.

Additionally, both resident charr and Lake Trout were often reported in the NCRI as present “everywhere” or in “every lake in this area” throughout large polygons (e.g., Arctic Bay, Chesterfield Inlet; Fisheries and Sealing Division 2017). Consequently, although NCRI observations initially covered the greatest extent, the imprecision of much of this polygon data meant that it was removed during data cleaning (i.e., I excluded any NCRI polygons or lines that intersected multiple waterbodies). The mismatched scale was particularly problematic close to communities, where a higher number of observations combined with a more cramped map can make precision difficult. Consequently, observations of resident charr and other species were more likely excluded from analysis than anadromous charr, which was usually explicitly and precisely mapped. This is supported by the high prevalence of resident charr in the AFSA data. My data cleaning choices (e.g., excluding polygon records that intersected multiple waterbodies) aimed to maximise observation certainty, which may have further reduced resident charr prevalence in the training data. Some background points may thus be false absences. Modeling approaches that explicitly include a measure of observation certainty (Mengersen et al. 2017) or use multiple data sources to infer non-detection rates (Dorazio 2014; Fletcher et al. 2019) might better account for such false absences without overinflating the false presence rate.

While the NCRI attempted to clarify “everywhere” observations of species by delineating interviewee travel areas, the designation is still difficult to interpret. From an analysis perspective, future NCRIs should avoid recording large polygons that include many waterbodies. This could, however, violate interviewee preferences or impose a cultural bias (scientific lens) on the knowledge shared. Instead, interviewers can query the habitat relationships such as lake size, depth, morphometry, or other environmental correlates. In some cases, the NCRI could also record known absences in any large polygons. For instance when Arctic Bay an interviewee described landlocked charr as present in “every lake...unless

the lake is so shallow that it freezes entirely to the bottom” (Fisheries and Sealing Division 2017), my suggested approach could have identified the lakes where landlocked charr were absent. If done retroactively for previously collected NCRI data, the large polygons that I excluded could potentially provide observations in areas that had fewer records, like the western Kitikmeot. This would both improve mapping precision and better incorporate broader Inuit Qaujimajatuqangit into the interview process.

Similarly, if species identification is unclear, interviewers can elicit further information on species attributes (e.g., appearance, habitat, behaviour, common Inuktitut or English names) rather than forcing a single identification (Lukyanenko et al. 2011). This could improve the certainty of identifications and highlight congruencies and differences between scientific and Inuit views of wildlife (Polfus et al. 2016). For instance, Inuit see spawning charr—ivitaaruit—as a separate species. Such approaches would make the NCRI even more of a resource for fisheries research and management. The NCRI has previously been used for broad GN development initiatives (e.g., fisheries, tourism), impact assessment (Baffinland Iron Mines Corporation 2012), land use planning and marine protected area designation (Dept. of Fisheries and Oceans Canada 2011; Byam 2013). This is the first study to use NCRI data for hypothesis-based research at such a precise scale (although see Misiuk et al. 2019 for a broader marine habitat study).

Although the above discussion might imply that broad observational data like the NCRI is less reliable than harvest records (Kowalchuk 2010), this depends on the scale of the study (Gagnon and Berteaux 2009). The NWHS was designed to provide the NWMB with information to determine basic needs levels and harvest limits, and has mostly been used for this purpose. Otherwise, the data has been used in historical catch analysis (Booth and Watts 2007), and the spatial data reviewed for land use planning (Nunami Stantec 2012) and environmental assessments (e.g., Baffinland Iron Mines Corporation 2012). Kowalchuk and Kuhn (2012), however, used NHWS and UOM data in a formal approach to assess marine mammal distribution for species at risk management planning. They found that the point geometries of this data underestimated the area of occupancy for all species compared to scientific

movement studies considered in the previous species assessments. They proposed that future work include measures of species movement, a finding congruent with other studies recommending that SDMs include measures of dispersal (Allouche et al. 2008; Mendes et al. 2020). The NCRI can provide such data, complementary to the NWHS and AFSA harvest information, and increase the spatial or temporal extent of our species knowledge (Gagnon and Berteaux 2009).

My dataset highlights how combining multiple diverse sources provides comprehensive and detailed information. The observations in my dataset were spread across the territory. My final sample sizes were comparable or better than many previous studies exploring regional lacustrine fish distributions (e.g., ranging from 53 to 1,309 lakes; Power and Barton 1987; Hershey et al. 2006; Spens and Ball 2008; Finstad and Hein 2012; Hein et al. 2012; Samarasin et al. 2014). Waterbodies with multiple observations (from a single or multiple sources) are more certain to be true presences (Power and Barton 1987; Mengersen et al. 2017); this constitutes nearly 60% of my dataset. The converse (i.e., waterbodies with single observations) does not always imply uncertainty, however. Rather, such differences may reflect differences in the data collection methods. For instance, the AFSA database describes commercial or exploratory fishing locations, which are documented to some extent in the NCRI, but not the NWHS (except incidentally where they overlap with domestic harvest locations; Priest and Usher 2004; Kowalchuk 2010). Further, changes in land use patterns, or possibly temporal changes in species distributions could result in single, uncorroborated observations. Among the multiple observations, however, 69% spanned two or more years (and up to 23 years), indicating that there are few spurious points, and that temporal changes may have been limited.

The low overlap between AFSA and NCRI / NWHS observations may explain the generally poor classification performance of the external validations, particularly for the resident model. AFSA locations (recorded as degrees and minutes) were less precise than the NWHS and NCRI data, so a large proportion were lost during waterbody intersections. This resulted in a small independent test set (51 waterbodies), when larger samples are usually recommended

(Vaughan and Ormerod 2005). The characteristics of the AFSA waterbodies generally fell within the ranges of the training environmental covariates. AFSA lakes, however, were further from communities (e.g., if subsistence rather than commercial harvest is prioritized near communities), had fewer obstacles along their access rivers and higher prevalence (proportion of presences) of both charr and Lake Trout. Since these are all important covariates in the models, the differences between the training and test sets may have resulted in the poor validations. Additional work could compare the performance of models constructed using other combinations of my data sources (e.g., AFSA and NWHS as a larger training set validated by the NCRI data; or subsets of all three sources) (Eddings 2020).

2.4.2. Drivers of anadromy

Charr are a generalist species, which can be more difficult to model using SDMs, particularly when using GIS-derived rather than field-measured covariates (Porter et al. 2000). The three most influential variables—lake area, longitude, and distance to community—were common to both the anadromous and resident SDMs, and showed similar response curves when plotted against the training data. Consequently, there was almost complete overlap in the lakes predicted as having both resident and anadromous populations, or having neither. It's therefore likely that the assessed variables reflect basic ecological limits on Arctic Charr distribution rather than drivers of migratory behaviour. Previous work supports this possibility, since charr species presence in Sweden increased with increasing lake area (Hein et al. 2012) but there was no correlation with anadromy in Norway (Finstad and Hein 2012). The premise could be further investigated using additional, independent observations across Nunavut to assess whether the identified relationships hold at the species level.

Additionally, my results may not fully reflect drivers of charr distribution or migratory choice since the model was constrained by a political boundary (the Nunavut territory)(Koen et al. 2010). While necessary because the NWHS and NCRI were conducted only in Nunavut communities, the environmental covariates may be artificially limited. The AFSA database

contains records for Arctic Charr in the Northwest Territories, so this or other data could be used to extend the model to additional regions (e.g., the NWT, Nunavik, Labrador).

This could further illuminate some of the spatial patterns in my data. For instance, longitude was the second most important variable driving anadromous and resident charr distributions. Both migratory types are more likely to be present further east, but the effect is stronger for anadromous populations. This may reflect distributional patterns across northern North America, as most charr populations in Alaska and the NWT are resident (Hershey et al. 1999; Sawatzky et al. 2007). This distribution is likely a result of freshwater colonization following the glacial retreat towards the northeast (Moore 2012). Arctic Charr distribution in Canada is expected to contract towards the north and east under future climate scenarios (Chu et al. 2005, their Figure 6). Although this may not be happening as fast as predicted—Chu, Minns and Mandrak (2003) study predicted charr as absent along the mainland Kitikmeot coast in 2020, but the NCRI recorded observations in that area as recently as 2015 (Fisheries and Sealing Division 2017)—the effect of longitude may become more pronounced over time.

Neither model supported my hypothesis that anadromy would increase with latitude, although it was still important in the anadromous model (with a non-significant positive effect). Samarasin et al. (2014) also found that species diversity and abundance was less affected by latitude than expected, when comparing two groups of lakes in the central Northwest Territories and southern Ontario. In particular, Lake Trout biomass was not influenced by latitude, but did increase with lake size (Samarasin et al. 2014); a result echoed in my models for charr presence. Samarasin et al. (2014) suggested that the lack of a latitudinal effect could be due to the comparative scarcity of data in their northern study lakes. My data similarly had relatively fewer observations at both the northern (high Arctic Archipelago) and southern (Belcher Islands) extremes. Additional observations at these latitudes (e.g., on Ellesmere Island, or in Nunavik (Power and Barton 1987) and the northern Manitoba coast) might provide enough contrast and power to detect an effect.

Further, previous findings that charr populations are more likely to be found further north didn't account for spatial patterns in the data (Hein et al. 2012; see their Figure 1). Conversely, any latitudinal effect in my model may have been captured by the random watershed intercept. This possibility is supported by the fact that latitude changed from a positive effect to insignificant when the random intercept was added to the full anadromous model. Similarly, shoreline development index changed from a negative effect to insignificant. Watersheds may thus be integrating information on the freshwater-marine productivity difference. Any effect of freshwater productivity may also have been assimilated by the lake area covariate, which was strongly colinear with both lake perimeter and shoreline development (i.e., morphological measures that can represent lake productivity). Future work using a more complex analytical approach—such as spatial random fields in R-INLA—might better separate any conflated effects.

Additionally, other more direct measures of this productivity gradient might more strongly predict differences in charr anadromous behaviour. My proximity to polynyas covariate did not appear to reflect marine productivity as expected, possibly because the effect of open water features depends on the mechanisms that form them (Grandmaison and Martin 2015). Further, Arctic Charr are generalist feeders and populations of their marine prey species (e.g., Arctic Cod (*B. saida*), shrimp, and Capelin) fluctuate spatially and temporally. If charr prey are not closely associated with the upwelling or current areas that form polynyas, then polynya locations may not drive migration over long periods of time. Estuaries could be an alternate nearshore feature of more productive areas that is associated with migratory charr populations (Grandmaison and Martin 2015; Spares et al. 2015b; Moore et al. 2016); however they may be more difficult to define from remotely sense or GIS data than polynyas. Otherwise, climate-driven productivity correlates such as sea surface temperature, air temperature, growing degree days, and growing season length have elsewhere been found to influence fish distributions and charr anadromy (Chu et al. 2005; Finstad and Hein 2012; Kovach et al. 2015).

Alternatively, residual spatial patterns and unexplained model fit can be caused by missing covariates if data is unavailable or can't be calculated (Renner et al. 2015). I was unable to evaluate the effect of Lake Trout presence on Arctic Charr migratory choices, as there were insufficient Lake Trout records in the background lakes. In general, studies of fish distributions over large geographic extents—like mine—tend to find stronger relationships with abiotic than biotic variables (Jackson et al. 2001). Only 21% of my anadromous populations and 25% of resident populations coexist with Lake Trout, however. Conversely, data exploration prior to modeling indicated that habitat variables generally overlapped between charr morphs and Lake Trout. My models may thus be missing a Lake Trout covariate. This possible species interaction could be investigated using additional Lake Trout records (for instance from GBIF; Amano et al. 2016), or a joint species distribution modelling approach (Wagner et al. 2020). If resident and anadromous charr respond differently to the presence of Lake Trout, the relative distributions of the migratory types could change across their range in response to any climate-induced expansion in Lake Trout distribution. For instance, resident charr populations could better persist if protected by barriers that prevent Lake Trout from colonizing new lakes, while conversely anadromous populations may not be able to reach suitable new habitat (Hershey et al. 1999; Hein et al. 2012; Lynch et al. 2016). Such different reactions might also occur or be exacerbated by climate-driven range expansions of other competitors, such as Atlantic Salmon (*Salmo salar*) (Bilous and Dunmall 2020).

Anadromous and resident fish do appear to respond slightly differently to some lake and river characteristics. For instance, relationships were weaker than expected between the presence of charr migratory types and river distance; in fact, river length was not related to the presence of resident charr. Gallagher et al. (2019) also observed that residency in Dolly Varden females may be unrelated to access route length, although their sample size was small. Anadromous charr, were less likely to be found in lakes with longer access rivers, but this effect lessened with increasing lake size. Conversely, the positive effect of lake area on the probability of presence was stronger for anadromous charr, especially for longer rivers. Both these interactions imply that fish trade off the costs and benefits of migration. Migration in longer rivers is only worth it

if fish can be reasonably assured of reaching usable spawning and overwintering habitat—which is more likely in larger lakes due to their greater size, heterogeneity, and stability (Jackson et al. 2001). Hein et al. (2012) found that charr populations in larger lakes were more likely to persist in future climate scenarios, particularly if predator (in their study, Northern Pike) ranges expand (see also Spens and Ball 2008). 121 Nunavut lakes are larger than Hein et al. (2012)'s six refuge lakes ($> 29\text{km}^2$), so charr populations in Nunavut may be better buffered than those in Sweden from climate change effects (Spens and Ball 2008; Hein et al. 2012). The relationship may also be complicated, however, by terrestrial and climate factors that interact with lake size to influence productivity. Finstad and Hein (2012) found that anadromous charr populations in less productive Norwegian lakes were more likely to undertake longer migrations, while differences in lake productivity were less important if migration distances were short.

Further, the effect of river distance may in fact be driven by river gradient, with which it is negatively correlated. Since elevation in Nunavut varies more regionally than locally, rivers with lower average gradients are likely to be longer. Maximum spot gradient, if considered as another type of barrier, may thus better indicate river difficulty and connectivity. Steepest spot gradient restricts anadromy in Norwegian charr (in conjunction with river length; Finstad and Hein 2012), and Northern Pike ability to colonize lakes (Spens et al. 2007). Further, the number of barriers along a river was an insignificant, but still important variable in my resident model (i.e., model fit improved when it was included). Thus, residency may be the “default” situation for charr populations in all lakes that were colonized after glacial retreat (including “landlocked” populations that were excluded from my analysis). When a lake is connected to the marine environment, however, anadromy may be preferable, particularly in short rivers.

Almost all the barriers (97%) in my dataset were rapids, however, so barriers to charr movement may be more physiological than physical (i.e., fish are able to move through them, but the energetic cost is too high). Similarly, discharge has been found to better indicate migration cost than river slope (Power and Barton 1987; Kristoffersen 1994). Effects of higher

discharge, however, can be mitigated in wider rivers that offer alternative low-flow routes or resting areas out of the river current (imaogatnait) (Brewster et al. 2010; Banci and Spicker 2012; Clark 2012). Further, charr migration likely has a bimodal response to discharge, with extremely low flows also preventing migration (Power and Barton 1987). For instance, Arctic Bay NCRI interviewees suggested that land-locked charr are found in all High Arctic lakes that don't freeze to the substrate, but anadromous charr occur only where water flow is sufficient for upstream migration (Fisheries and Sealing Division 2017). Conversely, shallow rivers can cause stranding and increased mortality (Golder Associates 2013), freeze and block movement, or create patinnik (frozen pools where fish die from lack of oxygen) (Brewster et al. 2010; Banci and Spicker 2012). Thus, if climate change reduces discharge in Nunavut rivers, the barrier effect of rapids may be substituted for low water barriers. I would expect this shift to increase residency (Branco et al. 2017).

Such differences in the limits on dispersal between migratory types may be important in predicting the impacts of future changes to charr distribution (Hein et al. 2012), as incorporating dispersal improves the predictive ability of SDMs (Allouche et al. 2008; Mendes et al. 2020). Other studies have also emphasised the importance of connectivity variables over lake characteristics in driving distributions of migratory species (Haynes et al. 2014). Additional work could consider more specific connectivity measures such as lake order (Hershey et al. 2006); the number of river inlets / outlets from each lake (makhakheek) (Brewster et al. 2010; Banci and Spicker 2012); the up or down-stream distance to other charr populations in the same watershed; or the coastal distance to other charr rivers (Dempson and Kristofferson 1987; MacDonell 1989; Harris et al. 2013). Connectivity might also be related to within-lake or within-river habitats that can promote charr movement and presence (Harwood and Babaluk 2014; Reed et al. 2016). Other documented Inuit knowledge identified recurring deep pools (Banci and Spicker 2012), areas that remain ice-free in winter (Kugluktuk interviews; Fisheries and Sealing Division 2017), and river widenings (Sprules 1952; Inuit Heritage Trust 2016) as important migratory and overwintering habitat. I've personally seen winter community fisheries in such small chains of river widenings. Such locations are excluded from my analysis, however,

by the 1:250,000 scale and the pre-defined “waterbody” and “watercourse” designations used in the CanVec data. Inuit, and even fish views of available habitat may thus occur at a different scale from the waterbody scale and the presence-absence response variable that I used.

I expected overlap between resident and anadromous habitat requirements, since a single lake can contain both migratory forms. Ultimately, however, modeling presence-absence may have obscured any distinctive responses of anadromous and resident charr to the environmental covariates. The binary response variable doesn’t fully reflect the continuum of facultative and variable Arctic Charr migratory behaviour, since even designating fish as “anadromous” or “resident” isn’t straightforward. For instance, resident charr (Loewen 2016; Ulrich and Tallman 2021) and pre-spawning females (Kristofferson 2002), may make short migrations to estuarine areas; while anadromous fish can skip migrations (Gilbert et al. 2016; Loewen 2016). Further, migratory runs can consist of fish from multiple spawning stocks (Kristofferson and Berkes 2005) since non-spawning charr may overwinter in non-natal, easier-to-access waterbodies (Beddow et al. 1998; Nunavut Tunngavik Inc. 2001; Gilbert et al. 2016; Moore et al. 2017) or in the ocean (Jensen and Rikardsen 2012; Fisheries and Sealing Division 2017), and undertake long-distance migrations (Dempson and Kristofferson 1987; Fisheries and Sealing Division 2017). Additionally, although fish life history choices were originally believed to be lifelong (Secor 1999), recent research shows that the costs and benefits may change over a fish’s life (Bond et al. 2015). My results imply that the cost-benefit balance of migration may vary by individual (Näslund et al. 1993) rather than by population.

Additionally, differences in migratory life history may manifest as behavioural changes that are not reflected at the population level, but are nevertheless driven by lake or river characteristics. For instance, charr in lakes with shorter access rivers tend to first migrate at a younger age (Loewen 2016), or the proportion of anadromous and resident fish may differ by system (Klemetsen et al. 2003). Additionally, migration timing can be driven by climate factors and accessibility (Morin et al. 1992; Anderson and Beer 2009; Kovach et al. 2015; Quinn et al. 2016)(Morin et al. 1992), age (Quinn et al. 2016), size (Dempson and Green 1985) or sex

(Kristoffersen et al. 1994; Rikardsen 1997) of the fish. Such factors can outweigh environmental drivers of anadromy, including river length (Ohms et al. 2014). Future work could explore such patterns for Nunavut charr using my data sources, which variously contain information on ecotype proportions, migration timing and spawning locations.

2.4.3. A broader understanding of Arctic Charr migration for fisheries management in Nunavut

This study emphasizes that existing Inuit knowledge data is underutilized for wildlife research and management in Nunavut. Combined, the NCRI and NWHS provided more than 10 times the number of observations than the AFSA. These observations covered more habitat types (e.g., smaller lakes) across a greater extent of the territory. Both the AFSA database and NCRI are ongoing projects, so the volume of data will continue to increase. I've suggested several methodological changes to the NCRI and AFSA that could reduce some sources of error and bias as data is added in the future.

My analysis demonstrates how researchers and managers can take advantage of this growing information base to explore aquatic species distribution and population changes across the territory. While my analysis explained more about the species distribution than Arctic Charr migratory choices, my results nevertheless represent an important step forward in understanding charr distribution in the territory. No other studies have analysed Nunavut charr distribution at a precise scale over such a large extent. Understanding charr preferred habitat characteristics supports land use prioritization and regional fisheries management decisions.

Using these observations in a SDM identified large lakes in eastern Nunavut as the most likely habitat for Arctic Charr, with populations more likely to be observed closer to communities. Several of my hypotheses were not supported by my results, particularly that the wider difference between marine and freshwater productivity at northern latitudes would increase anadromy. Nevertheless, aquatic productivity is likely still important for charr distribution, since

watersheds—which integrate climate and river network information—explained much of the variability in both models, and latitude also improved the fit of the anadromous charr model. Consequently, smaller charr lakes in mainland Nunavut are likely most vulnerable to future climate change, as increasing water temperatures, decreasing water levels will reduce the suitability of already lower quality habitat.

The greatest differences between the anadromous and resident models related to river characteristics. Anadromous charr are less likely to be found in long rivers, although more available lake habitat can mitigate this effect. The number of the obstacles in a river appeared to be more important than river length in explaining resident charr presence, although there was not a clear response. Consequently, while the core charr habitat indicated by my model may provide relatively stable refugia for Arctic Charr under climate change (Kelly et al. 2020), anadromous and resident populations are likely to respond differently to changing river conditions. Decreased river flows may increase barriers to charr movement, especially if compounded by channel changes caused by post-glacial rebound on the mainland. Resident populations may persist across their current distribution, but anadromous populations would likely become more strongly associated with the coast (i.e., shorter rivers).

Any impacts from climate change may be exacerbated by Lake Trout range expansions, although I was unable to assess how charr respond to Lake Trout presence. The datasets I used offer opportunities to further explore this and more detailed hypotheses of Arctic Charr migration using more recently developed SDM approaches. I compiled the three sources into a single dataset at the same waterbody scale and thereby lost more detailed information such as NWHS catch numbers, or AFSA biological measurements. Spatial data integration (Fletcher et al. 2019; Isaac et al. 2020), however, can simultaneously model multiple types of information including presence-absence, abundance, condition, ecological linkages, and value judgements.

It remains challenging to find information on environmental covariates at a comparable scale to the data (i.e., at the lake/river level across all of Nunavut). This should improve with

technological advances, and as Inuit participation in and control of research is prioritised. For instance, the NWMB's Community Based Monitoring Program²¹, ArctiConnexion²² programs, or the Arctic Eider Society's SIKU²³ app, all simultaneously document Inuit knowledge and scientific measurements. The NCRI is starting to be used in this integrative fashion, since it forms one component of the Atlas of Arctic Ocean Perspectives²⁴, alongside Inuktitut place names, OBIS data, and management perspectives such as DFO's Ecologically and Biologically Significant Areas (EBSA). Not only do such projects equalize these different types of information, but they support joint hypothesis development, results interpretation, and management decision-making.

The NCRI and NWHS were designed to gather information for management purposes, but have not been used to their full potential. My research not only identifies key charr habitat relationships, but I am using these sources for the purposes for which they were gathered – for research that supports the sustainable management of a culturally, economically, and socially important species across Nunavut.

²¹ <https://www.nwmb.com/en/382-english/cbmn>

²² <https://arcticonnexion.ca/>

²³ <https://siku.org/about>

²⁴ https://aoa.gcrc.carleton.ca/index.html?module=module.aoa_ncri_nunavut_communities

3. Chapter 3: Study conclusions

Migration is an adaptive mechanism for species to meet life cycle needs in heterogeneous habitats, such as the Arctic. The Arctic Charr (*Salvelinus alpinus*) is a northerly-distributed, partially anadromous fish that is culturally and economically important in Nunavut, in Canada's eastern Arctic. Previous studies have investigated charr migratory choices in specific areas of Nunavut, but we have a limited understanding of how these vary across the territory's freshwater ecosystems. Understanding environmental influences on charr migratory choices can give insight on population reactions to climate change.

To assess the drivers behind and differences in Arctic Charr migratory ecotype distribution across Nunavut, I compiled and cleaned three pre-existing sources—the Arctic Fisheries Stock Assessment database (scientific research), the Nunavut Coastal Resource Inventory (mapped Inuit knowledge) and the Nunavut Wildlife Harvest Study (Inuit fishermen harvest records). I used generalized linear mixed models to compare 691 cleaned Inuit knowledge records of anadromous and resident charr populations to river, lake, and geographic variables. I validated these models using 51 independent scientific records and k-fold cross-validation.

Using Inuit knowledge data increased the quantity and extent of freshwater fish observations across Nunavut in both geographic and environmental space. Despite different scales, precision, and bias in my three sources, combining complementary information allowed a broader scale analysis than has previously been possible from scientific studies alone.

I successfully used this information to build species distribution models relating anadromous and resident charr presence to river, lake, and geographic variables. Modelling at the lake level, however, primarily identified distributional drivers of the Arctic Charr species, rather than migratory types. As expected, there was significant overlap between the models. Both anadromous and resident charr are more likely to be found further east in larger lakes, and be observed close to communities.

River characteristics had different effects on charr migratory types. Anadromy is less likely in longer rivers, although the effect is reduced for large lakes. Latitude and the number of river obstacles further captured variation in presence for anadromous and resident charr, respectively. Resident charr appear to occur in most suitable habitat regardless of connectivity. In lakes that connect to the ocean, however, anadromy may be the preferred choice as long as the benefit of marine feeding outweighs the cost of long-distance movement. My study demonstrates how existing Inuit knowledge can provide insights into the ecology of Arctic species, expand the spatial and temporal scope of such research, and help develop new hypotheses.

Historically, fisheries management decisions in Nunavut have been made primarily based on data from a comparatively limited set of locations where fishery-dependent or independent sampling has occurred. Inuit knowledge has mostly used to only a limited extent, for instance to set harvest levels or in stock assessments that were initiated in response to community concerns about harvest or fish condition (Read 2004). Nunavut fisheries management organizations, however, are required by the NLCA to incorporate Inuit knowledge and values in their respective processes and decision-making (Government of Nunavut 2013). Recent management approaches are thus moving to be more collaborative (Nunavut Wildlife Management Board 2014; Boudreau and Fanning 2015).

Studies like mine can help to bridge the gap, and provide a basis from which to explore more detailed mechanisms of change through dual perspectives. Inuit knowledge, for instance, indicates that environmental change is impacting fish condition and population size distribution (Fisheries and Sealing Division 2017; Knopp 2017), and that ongoing monitoring using both science and Inuit knowledge is needed (Knopp 2017). My results indicate that smaller lakes with longer rivers in western Nunavut are more marginal habitat for anadromous Arctic Charr populations. Such areas may thus be better early indicators of change. Similarly, these key

habitat characteristics could be considered when prioritising habitat restoration options or locations for fisheries development.

This study provides a basis for further exploring charr-habitat relationships using Inuit knowledge to support better fisheries management decisions in Nunavut. It is nevertheless important to recognise the constraints of my data, and that it is only a limited portion of the comprehensive ecological understanding in Inuit Qaujimajatuqangit. Although I used Inuit knowledge in my study, I reduced the data to observations and did not account for all the information documented during NCRI interviews, let alone the cultural attitudes and practices inherent in Inuit Qaujimajatuqangit. A more comprehensive partnership to develop hypotheses on the drivers of and barriers to charr migration and interpret results through an Inuit lens would further explore the patterns shown here, and likely result in stronger conclusions (Fraser et al. 2006; Gagnon and Berteaux 2009; López-Arévalo et al. 2011; Sánchez-Carnero et al. 2016; Skroblin et al. 2020). Ultimately, employing both science and Inuit knowledge will lead to stronger management decisions and more strongly implement the Nunavut Land Claim Agreement.

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Appendix 1: Data licenses

Nunavut Coastal Resource Inventory

I submitted a data release request to the Government of Nunavut to use the then-available NCRI data on January 26, 2017. Approval was provided via email by Angela Young on January 27, 2017.

Nunavut Wildlife Harvest Study

The NWMB maintains an open data approach following s.5.2.38(a) of the NLCA, which states “the NWMB shall: (a) establish and maintain an open file system for all raw and interpreted data and information regardless of its source”. More specifically, s5.4.6 of the NLCA specifies that “Raw and interpreted data produced from the Study shall be fully and freely available to the Government of Canada, the Territorial Government and Inuit”. This has been achieved by making the NWHS data and report available for download on the NWMB [website](#). Use of the data from the website is subject to the NWMB [disclaimer](#).

Arctic Fisheries Science Database

Permission to use the AFSA for the purpose of this study was received from my supervisor, Dr. Ross Tallman.

CanVec / NHN watersheds / Nunavut communities

CanVec data is available from open.canada.ca and is subject to the Government of Canada’s [Open Government License](#).

Appendix 2: R code

R code can be requested from the author. R files were run in the following order:

1. dbSetup.R: Creates the PostGIS database used for later analysis.
2. CommonFiles.R: Creates and tidies files that are used in later code including species and community lists, Nunavut land boundaries, coastline.
3. MignDataClean.R: Extracts and tidies freshwater fish observations from the AFSA, NCRI and NWHS data sources.
4. WBDDataClean.R: Extracts and tidies waterbody information from CanVec data.
5. MignDataCombine.R: Combines waterbody and fish data to create the modeling dataset.
6. WCDataClean.R: Extracts and tidies watercourse and related information (watersheds, barriers, river mouth locations) from CanVec data.
7. NetwkCreate.R: Creates a topologically valid, undirected network from the watercourse information.
8. LdscapeDataCalc.R: Calculates river distance, barriers, and gradient along the network.
9. MignDataComp.R: Compares final dataset between species and sources.
10. MignDataExplore.R: Explores the modeling dataset to check assumptions, identify bias, and spatial autocorrelation.
11. MignModel.R: Runs and verifies a GLM on the anadromous charr dataset.
12. LLCModel.R: Runs and verifies a GLM on the resident charr dataset.

Appendix 3: Polynya data

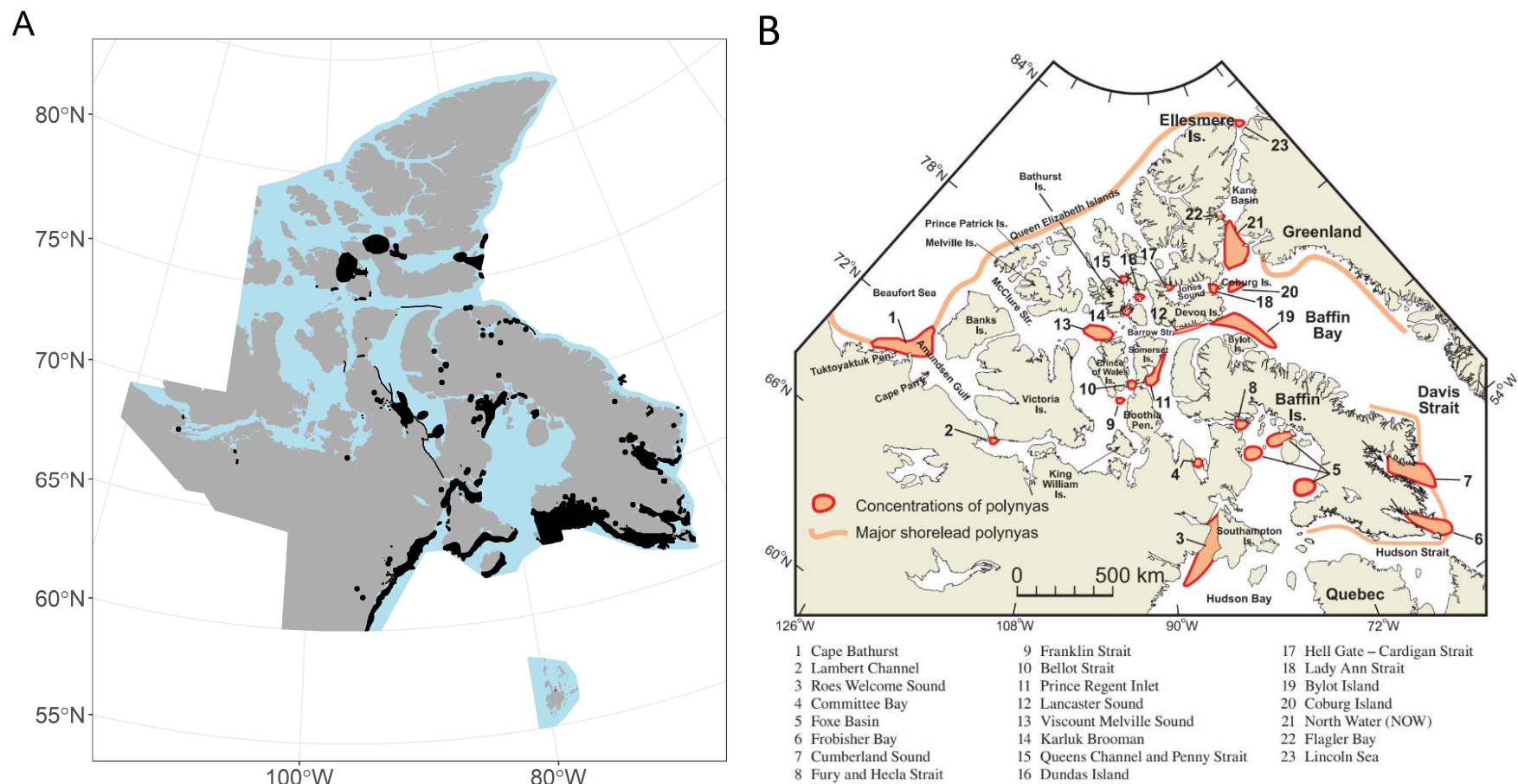


Figure 11: Polynyas in Nunavut as reported in the NCRI and NPC data, compared to those identified from remote sensing [149]

Appendix 4: Data sample

Table 10: The first 50 rows of the cleaned and summarized fish observation data after calculating environmental covariates.

WBID	Xdd	Ydd	Area_km	Perim_km	ShoreDens_km	Char	LLC	Set.Anad	Set.LLC	LKTR	Pred	CtOthSpp	PresOthSp	CommDist_km	WShed	RivDist_km	Gradient	nObst	PolynyaDis_t_km
60901	-94.36734013	61.31500109	0.024296359	0.599857299	24.68918508	NA	0	NA	Training	NA	NA	NA	NA	29.24703308	Western Hudson Bay - Maguse	3.718	0.010758472	0	61.74706107
68635	-95.21861959	61.51013976	0.024379975	0.606050549	24.85853838	NA	0	NA	Training	NA	NA	NA	NA	77.44247111	Western Hudson Bay - Maguse	2.563	0.031213422	0	86.35552552
70988	-94.39485531	61.57730287	0.02512212	0.627370162	24.97281905	NA	0	NA	Training	NA	NA	NA	NA	56.45801744	Western Hudson Bay - Maguse	0.151	0.397350993	0	34.26899031
81005	-94.43648324	61.85112922	0.024840316	0.612418907	24.6542315	NA	0	NA	Training	NA	NA	NA	NA	86.46596467	Western Hudson Bay - Ferguson	21.481	0.003724221	0	0.00144912

WBID	Xdd	Ydd	Area_km	Perim_km	ShoreDens_km	Char	LLC	Set.Anad	Set.LLC	LKTR	Pred	CtOthSpp	PresOthSp	CommDist_km	WShed	RivDist_km	Gradient	nObst	PolynyaDis_t_km
86173	-93.69296612	61.97092889	0.02482322	0.585899833	23.60289391	NA	0	NA	Training	NA	NA	NA	NA	65.49045921	Western Hudson Bay - Ferguson	22.671	8.82E-04	0	5.385222272
95565	-93.51398904	62.23626364	0.024541485	0.592807255	24.15531344	0	NA	Training	NA	NA	NA	NA	NA	48.40825666	Western Hudson Bay - Ferguson	10.743	0.003723355	0	36.51989351
131838	-93.22924257	63.35573639	0.025115527	0.595925303	23.72736579	NA	0	NA	Training	NA	NA	NA	NA	85.09531563	Chesterfield Inlet - Mouth	14.067	0.005687069	0	190.0537757
164306	-93.07425183	64.37324446	0.022904186	0.555665131	24.26041784	0	NA	Training	NA	NA	NA	NA	NA	148.9076857	Chesterfield Inlet - Mouth	6.582	0.01519295	0	12.90482923
181621	-95.47238119	64.74625575	0.025179729	0.592739384	23.54034031	0	NA	Training	NA	NA	NA	NA	NA	55.19376867	Baker Lake	12.238	0.011439778	0	157.3041842

WBID	Xdd	Ydd	Area_km	Perim_km	ShoreDens_km	Char	LLC	Set.Anad	Set.LLC	LKTR	Pred	CtOthSpp	PresOthSp	CommDist_km	WShed	RivDist_km	Gradient	nObst	PolynyaDis_t_km
185805	-97.78689601	64.82261544	0.024614492	0.587150836	23.85386815	NA	0	NA	Training	NA	NA	NA	NA	104.9688841	Lower Thelon - Mouth	1.523	0.091923835	0	4.709755421
205821	-108.2664057	65.1585633	0.022664902	0.557335023	24.59022396	0	NA	Training	NA	NA	NA	NA	NA	187.6654147	Upper Back	3.808	0.105042017	0	1.711153858
218771	-109.7044311	65.37689199	0.02391373	0.58440334	24.43798327	0	NA	Training	NA	NA	NA	NA	NA	181.5892056	Upper Back	1.065	0.450704225	2	33.67210432
332615	-114.3167039	67.06577165	0.024586141	0.614355638	24.987884	NA	0	NA	Training	NA	NA	NA	NA	91.89827224	Coronation Gulf - Tree	16.138	0.028504152	0	32.73894537
354239	-102.1019084	67.28782368	0.024877183	0.593870879	23.87211136	NA	0	NA	Training	NA	NA	NA	NA	245.974733	Queen Maud Gulf - Simpson	14.43	0.006930007	0	165.8199751

WBID	Xdd	Ydd	Area_km	Perim_km	ShoreDens_km	Char	LLC	Set.Anad	Set.LLC	LKTR	Pred	CtOthSpp	PresOthSp	CommDist_km	WShed	RivDist_km	Gradient	nObst	PolynyaDis_t_km
367 677	- 114.810 3779	67.4298 5676	0.02534 7849	0.61644 2891	24.3193 3732	NA	0	NA	Training	NA	NA	NA	NA	45.5434 5979	Coronation Gulf - Tree	15.0 23	0.02529 4548	0	0.00144 912
374 635	- 114.458 3534	67.5001 4942	0.02261 1285	0.55532 5934	24.5596 8063	NA	0	NA	Training	NA	NA	NA	NA	47.1459 9453	Coronation Gulf - Tree	45.0 59	0.00710 18	0	21.2082 3455
425 398	- 85.6210 6001	63.7402 4878	0.02439 4046	0.59964 0976	24.5814 4785	NA	0	NA	Training	NA	NA	NA	NA	132.563 2385	Southern Southampton Island	10.3 88	0.00192 5298	0	0.00144 912
433 630	- 83.6556 7159	63.8678 315	0.02426 6325	0.60616 3124	24.9796 0095	0	NA	Training	NA	NA	NA	NA	NA	38.6982 2625	Southern Southampton Island	21.8 16	9.17E- 04	0	64.6027 7705
444 609	- 71.2948 1916	64.0291 3552	0.02403 6702	0.58292 8097	24.2515 8386	NA	0	NA	Training	NA	NA	NA	NA	145.215 7151	Baffin Island - Hudson Strait	38.2 65	0.01045 3417	0	3.71782 3405

WBID	Xdd	Ydd	Area_km	Perim_km	ShoreDens_km	Char	LLC	Set.Anad	Set.LLC	LKTR	Pred	CtOthSpp	PresOthSp	CommDist_km	WShed	RivDist_km	Gradient	nObst	PolynyaDis_t_km
456143	-70.70586877	64.23444916	0.024938575	0.598475733	23.99799222	0	NA	Training	NA	NA	NA	NA	NA	123.9888999	Foxe Basin - Baffin - Koukdjuak	21.113	0.009472837	0	17.04301602
460138	-71.16592397	64.3141483	0.024946622	0.61097871	24.49144021	NA	0	NA	Training	NA	NA	NA	NA	148.8314639	Foxe Basin - Baffin - Koukdjuak	10.106	0.019790224	0	69.11684983
472051	-71.32194622	64.51476582	0.02497142	0.59992881	24.02461772	NA	0	NA	Training	NA	NA	NA	NA	166.0792205	Foxe Basin - Baffin - Koukdjuak	106.718	0.001499278	3	48.99881988
481523	-72.00246292	64.65173507	0.023448915	0.581210531	24.78624378	0	NA	Training	NA	NA	NA	NA	NA	203.3291255	Foxe Basin - Baffin - Koukdjuak	1.259	0.127084988	0	15.28907629
482876	-73.0583598	64.67100222	0.024041514	0.59910708	24.91968984	NA	0	NA	Training	NA	NA	NA	NA	181.9575218	Baffin Island - Hudson Strait	11.938	0.011727257	0	2.127364819

WBID	Xdd	Ydd	Area_km	Perim_km	ShoreDens_km	Char	LLC	Set.Anad	Set.LLC	LKTR	Pred	CtOthSpp	PresOthSp	CommDist_km	WShed	RivDist_km	Gradient	nObst	PolynyaDis_t_km
485 438	- 73.7427 0058	64.7092 7153	0.02378 4853	0.59456 455	24.9976 13	NA	0	NA	Train ing	NA	NA	NA	NA	150.448 4655	Baffin Island - Hudson Strait	10.2 77	0.00389 2186	0	4.07324 3395
488 791	- 73.7535 4612	64.7667 6536	0.02360 7668	0.58279 2752	24.6865 8716	NA	0	NA	Train ing	NA	NA	NA	NA	152.233 4873	Baffin Island - Hudson Strait	8.31 3	0.00962 3481	2	53.5198 9781
545 526	- 70.0363 7338	65.8213 031	0.02501 3138	0.57973 9195	23.1773 8718	NA	0	NA	Train ing	NA	NA	NA	NA	212.299 0707	Foxe Basin - Baffin - Koukdjuak	12.8 12	0.01561 0365	0	24.5394 6204
555 908	- 70.2327 1749	66.0343 3704	0.02533 1624	0.60667 5924	23.9493 5023	NA	0	NA	Train ing	NA	NA	NA	NA	218.553 1562	Foxe Basin - Baffin - Koukdjuak	22.2 94	0.00538 2614	0	15.3341 7241
560 879	- 87.6104 2312	66.1808 6849	0.02302 3281	0.57265 3344	24.8727 9446	0	NA	Train ing	NA	NA	NA	NA	NA	79.5174 6605	Western Hudson Bay - Wager Bay	18.9 23	0.01162 6064	0	25.3408 1298

WBID	Xdd	Ydd	Area_km	Perim_km	ShoreDens_km	Char	LLC	Set.Anad	Set.LLC	LKTR	Pred	CtOthSpp	PresOthSp	CommDist_km	WShed	RivDist_km	Gradient	nObst	PolynyaDis_t_km
576 218	- 87.8755 3286	66.6620 835	0.02515 8584	0.59693 7677	23.7269 9833	0	NA	Train ing	NA	NA	NA	NA	NA	81.5161 7879	Repulse Bay	14.8 43	0.02021 1548	0	45.5314 8282
621 195	- 106.962 3933	67.6671 1237	0.02446 7559	0.60881 3639	24.8824 8322	NA	0	NA	Train ing	NA	NA	NA	NA	46.0914 2175	Bathurst Inlet - Burnside	0.02 4	5	0	19.1240 6277
623 035	- 106.517 0344	67.6913 6159	0.02461 9963	0.59397 9711	24.1259 3883	0	NA	Train ing	NA	NA	NA	NA	NA	66.6587 4844	Bathurst Inlet - Burnside	2.41 8	0.03308 5194	0	18.8640 8652
653 123	- 98.4182 0275	68.3794 4862	0.02537 1966	0.61719 1921	24.3257 426	NA	0	NA	Train ing	NA	NA	NA	NA	119.977 7011	Queen Maud Gulf - Kaleet	19.4 01	0.00103 0875	6	73.3853 6147
661 822	- 110.795 5047	68.6207 1512	0.02511 279	0.60147 0699	23.9507 7167	NA	0	NA	Train ing	NA	NA	NA	NA	166.456 5603	Southern Victoria Island	2.40 5	0.01663 2017	0	6.92309 1764

WBID	Xdd	Ydd	Area_km	Perim_km	ShoreDens_km	Char	LLC	Set.Anad	Set.LLC	LKTR	Pred	CtOthSpp	PresOthSp	CommDist_km	WShed	RivDist_km	Gradient	nObst	PolynyaDis_t_km
662 411	- 117.136 4459	68.6359 6704	0.02399 8473	0.57387 0864	23.9128 0701	0	NA	Train ing	NA	NA	NA	NA	NA	129.405 3986	Rae	12.4 86	0.01441 6146	0	13.0618 8051
674 791	- 109.265 1005	68.9067 33	0.02293 2797	0.57187 1424	24.9368 3749	0	NA	Train ing	NA	NA	NA	NA	NA	148.315 4947	Southern Victoria Island	21.8 38	0.00732 6678	0	275.588 5224
697 907	- 95.6132 3621	69.4489 8125	0.02524 3533	0.62143 9726	24.6177 7928	NA	0	NA	Train ing	NA	NA	NA	NA	91.3513 0818	King William Island	0.77 2	0.02590 6736	0	6.87536 3605
803 733	- 88.6233 6526	68.4651 0948	0.02465 8323	0.60733 889	24.6301 7777	NA	0	NA	Train ing	NA	NA	NA	NA	55.0789 0953	Pelly Bay	3.28 7	0.04867 6605	0	22.5734 1044

Appendix 5: Response curves for insignificant variables

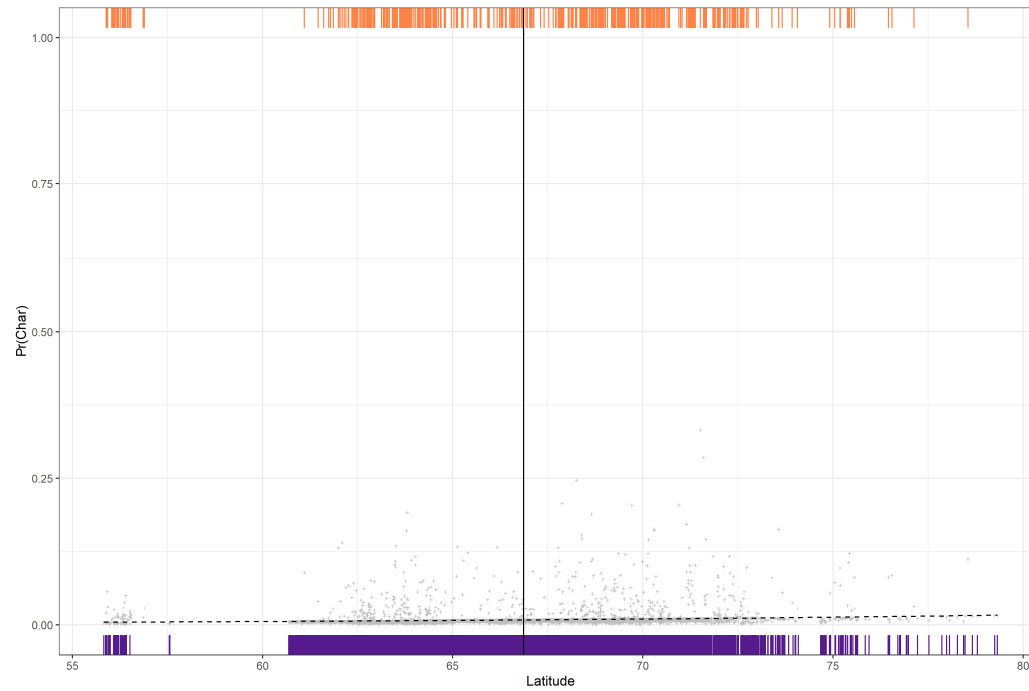


Figure 12: Response curve for the insignificant variable (latitude) in the anadromous model

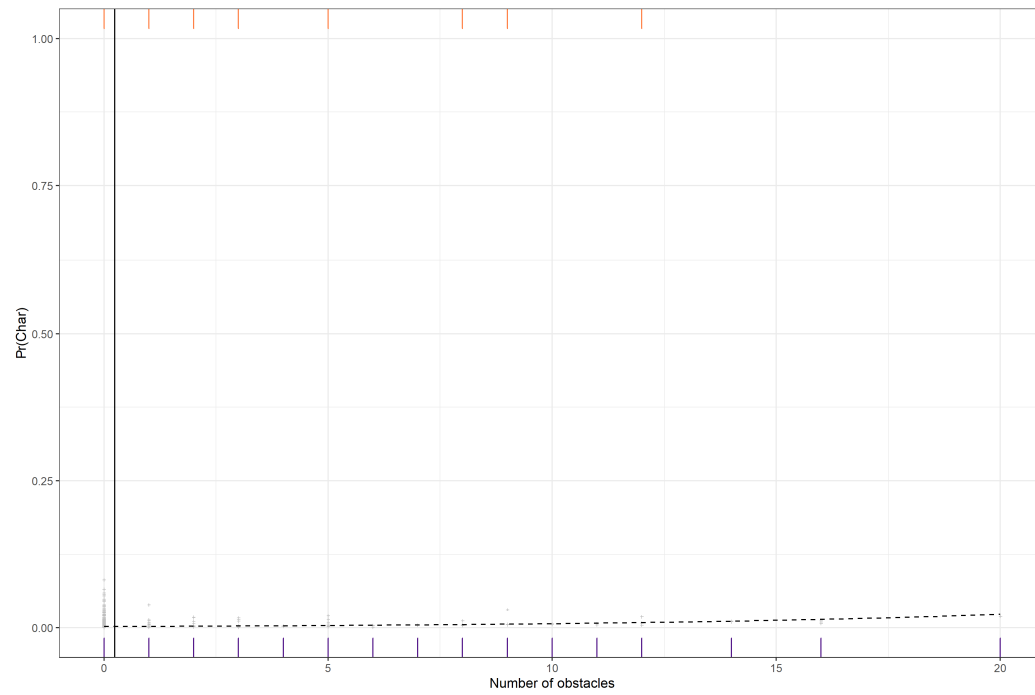


Figure 13: Response curve for the insignificant variable (number of obstacles) in the resident model

Appendix 6: Spatial patterns

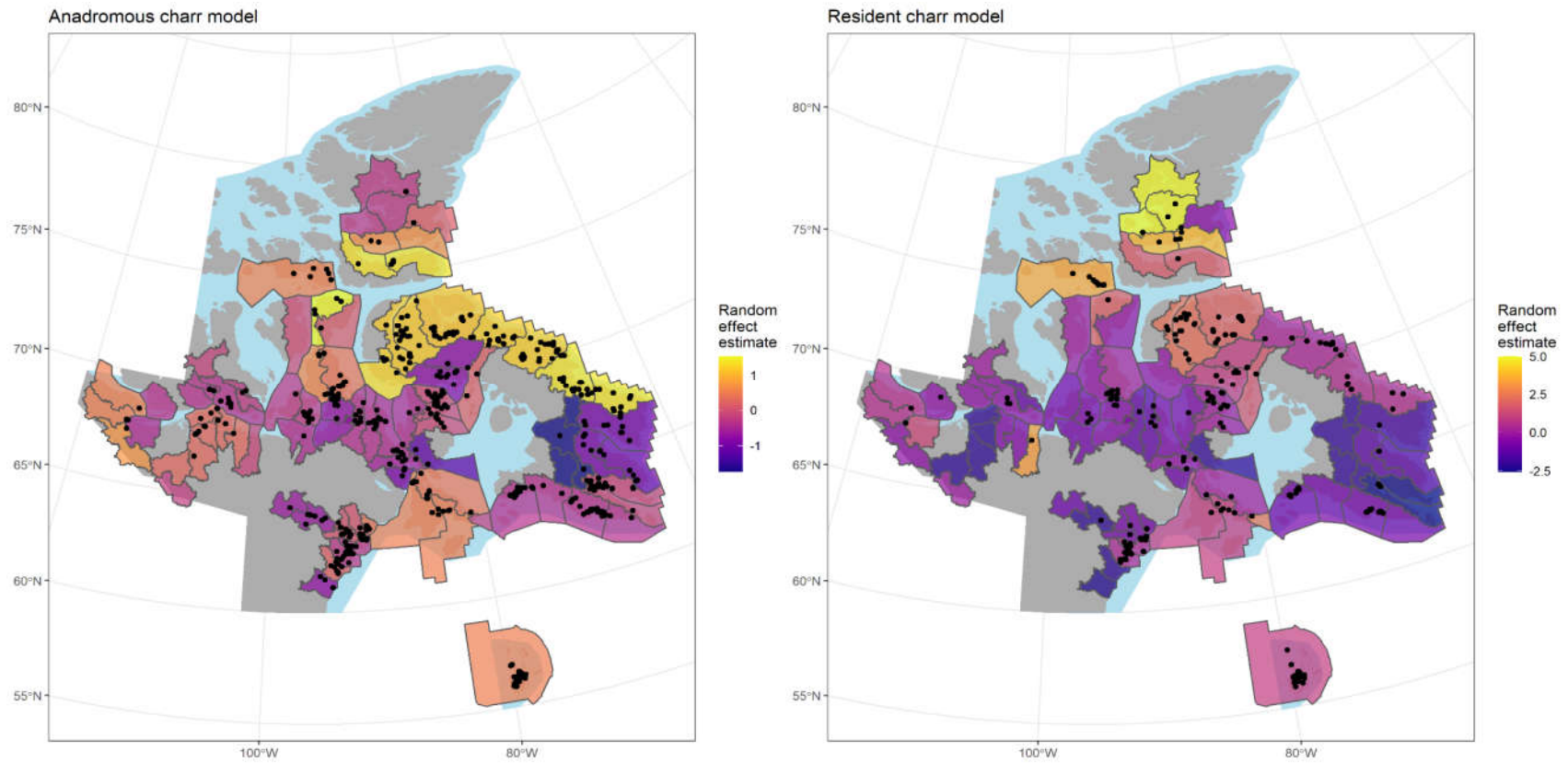


Figure 14: Random intercept estimates by Nunavut watersheds for the anadromous and resident models

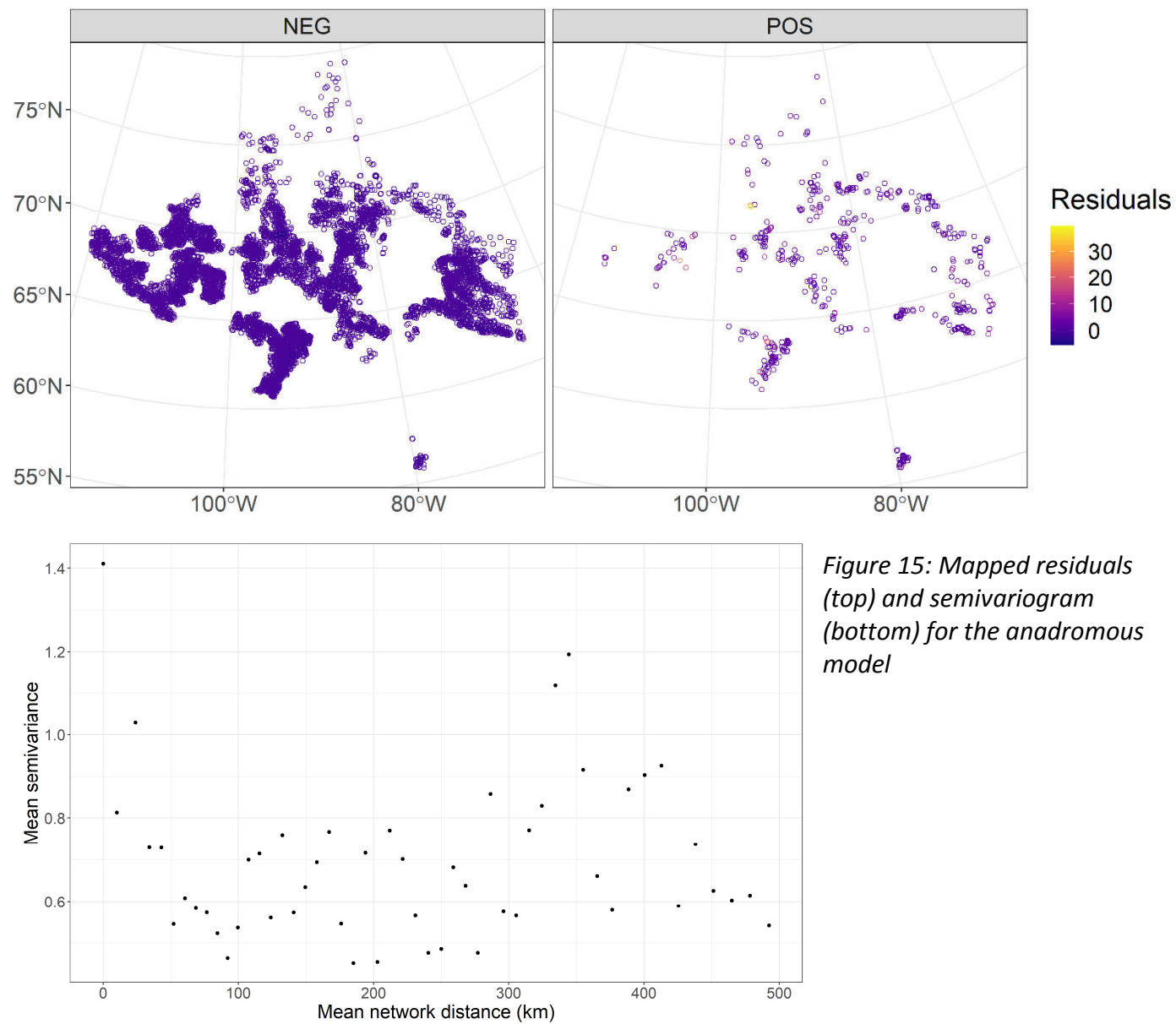
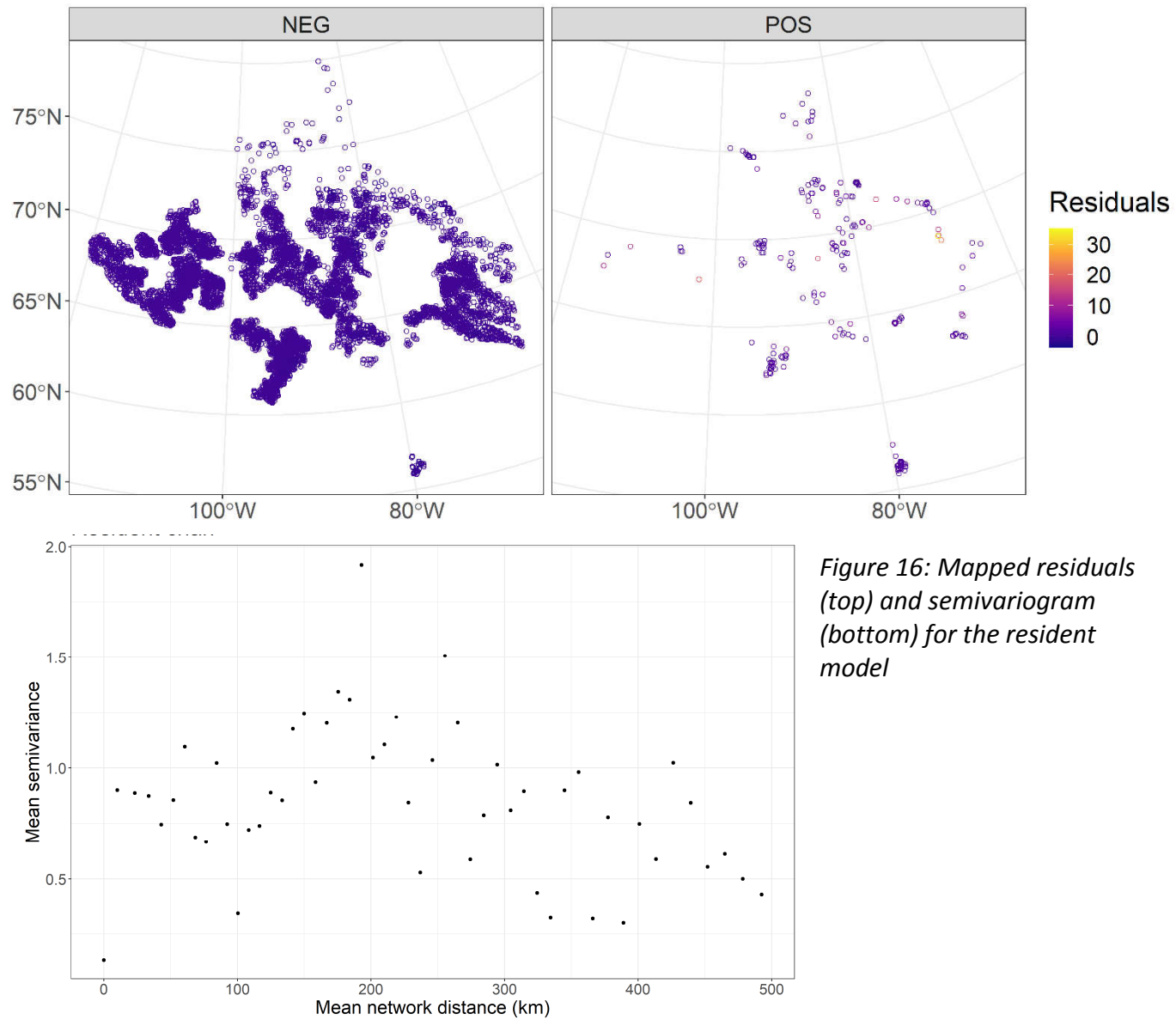


Figure 15: Mapped residuals (top) and semivariogram (bottom) for the anadromous model



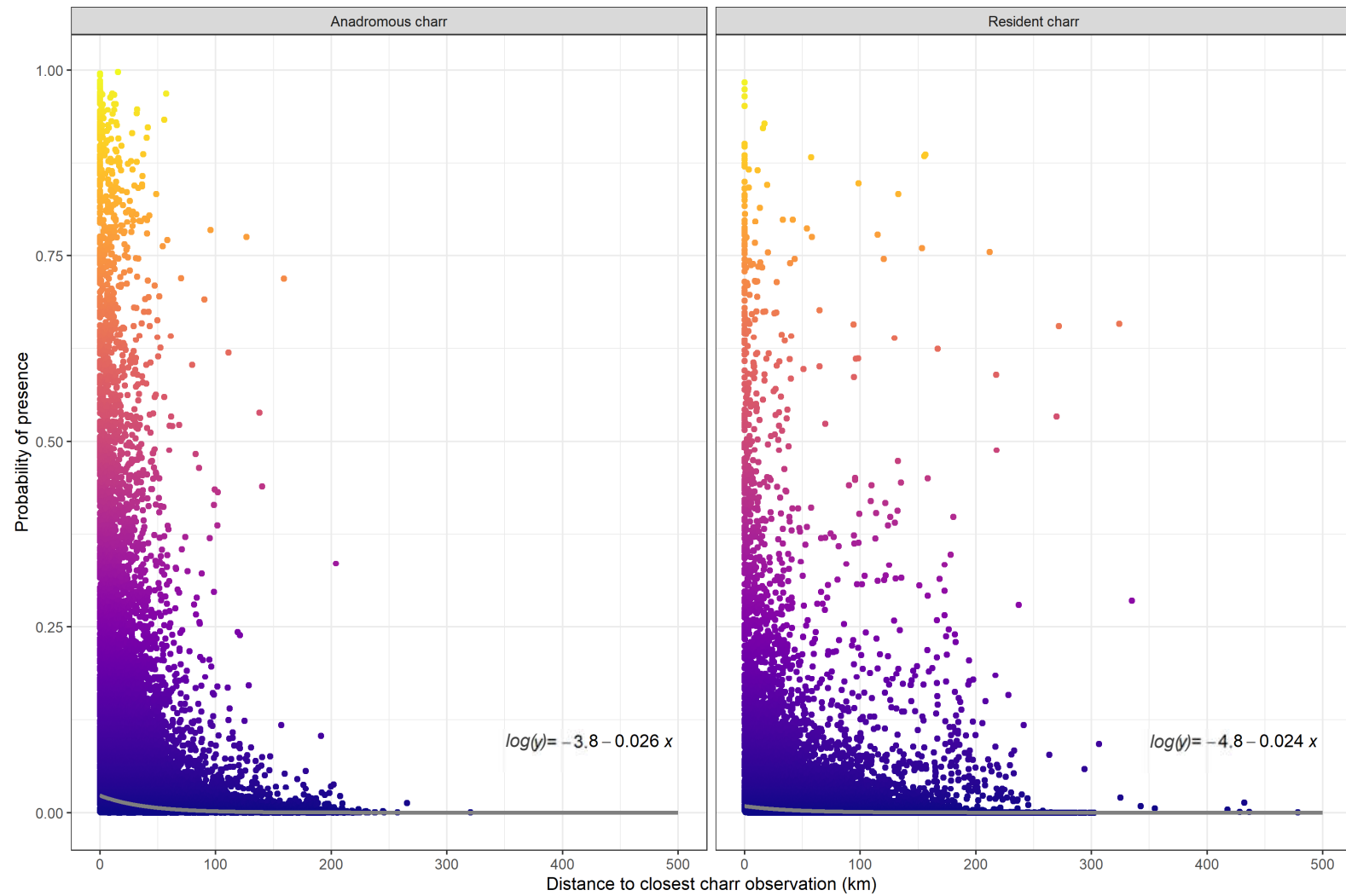


Figure 17: Inverse linear relationships between the distance to closest observation and predicted probability of presence for anadromous and resident charr