LINKING INUIT AND SCIENTIFIC KNOWLEDGE IN COASTAL MARINE RESEARCH: ADVANCING OUR UNDERSTANDING OF GREENLAND COD, *OGAC*, (*GADUS OGAC*) NEAR ULUKHAKTOK, NORTHWEST TERRITORIES UNDER A CHANGING CLIMATE

by

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STATEMENT OF OWNERSHIP

The knowledge contained in this thesis was generated and shared by many contributors. Ulukhaktomiut shared their knowledge of Greenland cod, *ogac*, (*Gadus ogac*) with confidence that it would be used for the purposes of this project. The project outcomes are a reflection of this collaborative process that was governed by the Olokhaktomiut Hunters and Trappers Committee (OHTC), who is responsible for ensuring that the knowledge presented and the use of it, is attributed to the appropriate knowledge holders. Any future interest in using the information presented in this thesis must be directed to the OHTC.

ABSTRACT

The Arctic is warming at an unprecedented rate, with implications for the marine ecosystem and species that are important for the tradition, culture, and livelihoods of Indigenous people. Inuit in the western Canadian Arctic have identified a need to better understand the impacts of a changing climate on coastal marine species important for subsistence. Greenland cod, *ogac*, (*Gadus ogac*) are found in the coastal marine ecosystem and are reportedly experiencing changes in population dynamics in recent years. In this thesis, I present findings from Inuit and scientific knowledge of Greenland cod as a means of linking knowledge systems to advance our understanding of this species and discuss the implications for Inuit livelihoods under a changing environment. The objectives of this research were to: (1) investigate the adaptation potential of Greenland cod, (2) document Inuit knowledge of this species, and (3) examine the cumulative findings of Greenland cod research and discuss the potential impacts of shifting marine resources on livelihoods in the Inuvialuit Settlement Region.

I measured individual specialization-generalization of morphological and habitat-trophic traits from Greenland cod collected along the marine coast near Ulukhaktok, Northwest Territories, NT, in the western Canadian Arctic. I then used this information to elicit discussion on their morphology, feeding, and movement behaviour with key knowledge holders in Ulukhaktok. Scientific findings from this project suggest that Greenland cod are overall generalists but display a range in feeding behaviours for two identified morphotypes. These findings highlight the importance of maintaining trait variation to conserve biodiversity while promoting population resilience in wild fish populations. Inuit knowledge holders were able to build a rationale for some of the phenomena observed and identify early signs of ecosystem change. Linking Inuit and scientific knowledge was a two-way process in which the knowledge systems built off one another to inform the next steps in the research process and interpret the findings more holistically. The cumulative findings advance our understanding of the baseline ecology of this species and intend to inform the design of future research using Inuit and scientific knowledge to generate enriched findings. The knowledge gained and lessons learned from this study can serve as a tool for establishing additional conservation efforts that may be required in the future to ensure a sustained Arctic marine ecosystem can continue to support Inuit subsistence and livelihoods.

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ABOUT THE AUTHOR

I came to this project as an early-career researcher with an academic background in environmental sciences and work experience in field-based research projects. I completed an undergraduate degree at McGill University (2015 – 2018), where I developed a deep interest in natural history, wildlife conservation, and climate change issues. Throughout my degree, I was exposed to various wildlife conservation projects across Canada and abroad, where I gained experience handling, monitoring, and researching wildlife through the lens of Western scientific approaches. All these projects were led by women with strong backgrounds in ecology, biology, and environmental research. The mentorship I received from these projects greatly influenced my desire to pursue a career in research while striving to become a competent and independent female in academia.

In 2019, I had the opportunity to conduct fieldwork in Nunavik, Quebec. This work supported a colleague's master's project investigating the effects of beaver borealization on Arctic char migration in the Canadian Arctic tundra. This project took on approaches that were entirely unique from my previous experiences and used scientific methods but also heavily engaged with Inuit knowledge, expertise, and culture. My short exposure to Inuit tradition and culture inspired me to continue working in this area while simultaneously pursuing my interests in fish and wildlife conservation.

Inspired by these previous experiences, I then pursued graduate studies at the University of Northern British Columbia. ArcticNet Project 33 focused greatly on interdisciplinary research which meant that my previous experiences and desire to learn more about these topics made me suitable to embark on this role.

As most of this research was conducted during the COVID-19 pandemic, I was unable to travel to the community for pre-research consultations or attend in-person meetings to establish personal connections with community members and integrate myself into the research group. To help address this, I participated in online meetings (FJMC and Char Working Group) and contributed to summary reports that were distributed to the community, while still acknowledging the fact that travel restrictions would likely impact the trajectory of this project such as timelines and means of communication.

As a non-Inuit researcher working with an Inuit community, I tried my best to remain open-minded and receptive to learning from others. Recognizing that I am a researcher representing an academic institution and possess worldviews that may differ from those of my research partners, I have done my best to handle the knowledge presented in this thesis responsibly while ensuring that the reported outcomes accurately reflect the study area and respective knowledge holders.

CONTRIBUTION OF AUTHORS

This thesis is written in manuscript style, with Chapters 3 and 4 intended for publication. This research is part of ArcticNet Project 33: Using Co-Produced Knowledge to Understand and Manage Subsistence and Marine Harvests in a Changing Climate and the “Ulukhaktok Fish Tagging Project”. These programs are supported by the Fisheries Joint Management Committee (FJMC), the Olokhaktomiuk Hunters and Trappers Committee (OHTC) and the Beaufort Regional Strategic Environmental Assessment (BRSEA).

In 2018, this project began when researchers and Inuit collaborators established research priorities, identified research questions, implemented a research design, and conducted data collection. In 2020, I joined this project as a Master’s student at a later stage, and began with cleaning and analyzing the data, interpreting the results, and communicating these results with research partners. This multi-year research project was co-developed and continues to engage collaborators from start to finish. As the leader of both manuscripts, I completed the initial write-up and received several revisions from co-authors.

Chapter 3, “Intraspecific Variation of Greenland cod (*Gadus ogac*) as a Measure of Climate Change Adaptation Potential in the Arctic” was co-authored by the following individuals, Dr. Harri Pettitt-Wade (University of Windsor and Fisheries and Oceans Canada), Dr. Jack P. W. Hollins (University of Windsor), Dr. Tristan Pearce (University of Northern British Columbia), Dr. Lisa Loseto (Fisheries and Oceans Canada and University of Manitoba), Teah Burke (University of Windsor), and Dr. Nigel Hussey (University of Windsor). All co-authors contributed to manuscript revisions. Additional collaborators that participated in the project design and data collection of this work include Ross Klengenberg and Isaac Inuktalik (Ulukhaktok, NT), Bessie Inuktalik and David Kuptana (OHTC), Hussey Lab, and Department of Fisheries and Oceans (DFO) Canada. Additional support on project approval, research design and methodologies were received from the OHTC and UCWG. This manuscript is in preparation for submission.

Chapter 4, “Linking Inuit and Scientific Knowledge in Coastal Marine Research: Advancing Our Understanding of Greenland cod (*Gadus ogac*) in the Canadian Arctic” was co-authored by the following, Dr. Tristan Pearce (University of Northern British Columbia), Dr. Harri Pettitt-Wade (University of Windsor and Fisheries and Oceans Canada), Dr. Lisa Loseto (Fisheries and Oceans Canada and University of Manitoba), all of which provided manuscript revisions. Co-authorship by specific OHTC members will be identified at a later time. OHTC provided approval of this study and research direction, recommended initial participants for this study, contributed to the interpretation of results, and provided feedback on ongoing research progress. The final version of the manuscript will also be reviewed by specific members of the OHTC to ensure results properly capture details provided by participants. Interviews and workshop sessions were held by myself and Dr. Harri Pettitt-Wade. This manuscript is in preparation for submission.

Dr. Tristan Pearce provided academic supervision and direction. Dr. Nigel Hussey, Dr. Lisa Loseto, and Dr. Harri Pettitt-Wade provided additional guidance and feedback on the development of the research questions, research design, and analytical approaches.

CHAPTER 1: GENERAL INTRODUCTION

Ongoing climate change continues to rapidly transform the Arctic, with severe impacts on the marine ecosystem (Bindoff 2019) and species important for Inuit subsistence and livelihoods (Archer et al. 2017). Changes in the Arctic marine environment will severely affect the distribution, quality, and availability of resources in the marine food-web (Deb and Bailey 2023; Florko et al. 2021). Trends of poleward distribution shifts have been documented in many marine species (Frainer et al. 2017; Kortsch et al. 2015), notably in sub-Arctic Gadids such as Pacific cod (*Gadus macrocephalus*) and walleye pollock (*Gadus chalcogrammus)* (Spies et al. 2020; Stafford et al. 2022). These patterns of northward expansion are projected to continue, with potentially severe consequences on Gadid populations endemic to the Arctic (Geoffroy et al. 2023). Understanding the ecology of these lesser-known species in the Arctic, their potential interactions with northern invaders, and their adaptation potential is critical for managing these species in a rapidly changing climate.

Greenland cod, *ogac*, (*Gadus ogac*) are a species of Gadid broadly distributed in the Arctic Ocean and fished by Arctic Indigenous peoples. In the western Canadian Arctic, Inuit traditions and cultural practices are strongly tied to ancestral land and the biophysical environment (Vincent 2020), making them greatly dependent on healthy ecosystems for their livelihoods (Hovelsrud et al. 2011). More recently, Inuit have reported changes to the marine ecosystem attributed to climate change, with potential impacts on subsistence harvesting practices. Understanding the changes taking place in Greenland cod can provide proximate measures of the overall changes taking place in the marine ecosystem. Addressing these concerns and implications for managing these species requires knowledge of the changes taking place and links to Inuit subsistence harvesting practices.

The intersection between Arctic marine fish species and connections to Inuit harvesting practices under a changing environment provides a unique opportunity of study that requires input from multiple sources of knowledge. Traditional ecological knowledge (used here synonymously with Inuit knowledge) has become increasingly recognized in addressing challenges related to natural resource management, including fisheries co-management (Bouchard et al. 2023; Pettitt-Wade et al. 2020). Scientific knowledge on fish populations combined with knowledge from Inuit harvesters can provide an overall better understanding of the marine environment and capture the changes taking place that are impacting Inuit. The cumulative knowledge can generate enriched findings useful to inform co-management decision-making in the Inuvialuit Settlement Region (ISR).

Understanding changes in the marine environment is critical in sustaining Arctic marine biodiversity and habitats under a changing climate. This project responds to needs identified by Inuit and was designed from a platform of active collaboration between Inuit and scientists to better understand changes in the marine ecosystem and implications for Inuit food systems using a case study of Greenland cod. The process of co-interpretation intends to enhance our understanding of this species within the context of climate change and provide a proximate measure of adaptation potential of the Greenland cod population.

Aim and Objectives

This research aims to examine findings from scientific and Inuit knowledge of Greenland cod as a means of linking knowledge systems to advance our understanding of this species and discuss the implications of a changing environment. The objectives of this research are to:

1. Investigate the adaptation potential of Greenland cod by measuring individual specialization-generalization of morphological and habitat-trophic traits;

2. Document Inuit knowledge of Greenland cod;
3. Examine the cumulative findings of Greenland cod research and discuss the potential impacts of shifting marine resources on livelihoods in the Inuvialuit Settlement Region.

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CHAPTER 2: LITERATURE REVIEW

This chapter summarizes published literature on climate change impacts on the Arctic marine ecosystem, individual specialization in the Greenland cod population, and fisheries co-management in the western Canadian Arctic. These bodies of scholarship will then be reviewed and critiqued to identify knowledge gaps and opportunities for future research.

2.1 Climate Change in the Arctic

The Arctic continues to experience an accelerated rate of warming, with surface air temperatures reported to have increased by more than double the global average over the last two decades (Pörtner et al. 2019). Reductions in arctic sea-ice extent and sea-ice thinning continue to have wide-ranging implications for ecosystems and species inhabiting this region (Box et al. 2019). Regional temperature fluctuations and large-scale changes in ocean and atmospheric circulation patterns will likely persist in the Arctic. These effects will continue over the next century, leading to the ongoing transformation of atmospheric, ice, sea, and land environments.

2.1.1 Observed Physical Changes

Sea ice plays a critical role in the Earth's climate by regulating heat, momentum and moisture exchange between the atmosphere and the polar oceans (Stroeve and Notz 2018). The reduction of highly reflective, high albedo snow or ice cover due to warming temperatures causes a reduction in solar energy reflected into the atmosphere. This results in the increased absorption of heat at the Earth's surface. The continuous reduction in sea ice due to increased warming allows further solar radiation to be absorbed by the ocean surface, generating a positive feedback (Schneider and Dickinson 1974). The link between this positive albedo feedback and the amplified warming of the Arctic has been most prominent in recent decades, with significant contributions of Arctic amplification to the alteration of arctic sea ice dynamics and sea ice decline (Hall 2004; Screen and Simmonds 2010). Observations of reductions in sea ice extent (Stroeve and Notz 2018), thinning of sea ice (Kwok 2018), and a shift from perennial to seasonal sea ice (Stroeve and Notz 2018) are some of the most prominent transformations that have been recorded across the Arctic Ocean, notably in the 21st century.

Changes to atmospheric circulation patterns are a combination of increased greenhouse gas emissions and unexpected natural climate variability (AMAP 2011). Although the basic mechanisms behind global warming are clear, the response of atmospheric circulation at the regional scale is less well-known (Shepherd 2014; Collins et al. 2018). With the continued reduction of summer sea ice over the next decade, changes in atmospheric circulation patterns are expected to occur (Overland and Wang 2010). There is some evidence that arctic atmospheric circulation may already be changing in response to warming and sea ice loss however, the future response of atmospheric circulation over the Arctic to warming and declining sea ice remains highly uncertain (Overland et al. 2016).

Snow cover possesses many important physical properties and plays a role in moderating the effects of climate variability (Cohen and Rind 1991). The low thermal conductivity of snow promotes insulative properties, which affects ice growth rates and ice thickness during the development of seasonally frozen ground and permafrost. Changes in snow cover respond to multiple environmental stressors, such as warming, increased moisture availability, and changing vegetation (Brown et al. 2017). The decrease in snow cover will also result in a lower albedo (reduced reflectivity of incoming radiation) and reduced insulative properties, both of which promote the warming of surface temperatures (Cohen and Rind 1991). Evidence of reduced snow cover in the Arctic has occurred over the last decade and is projected to continue over the near-term (2031–2050) due to increasing surface air temperatures (Meredith et al. 2019).

The physical changes associated with a warming climate have altered many fundamental characteristics of terrestrial and aquatic ecosystems in the Arctic (Meredith et al. 2019). Changes to seasonal activities, and the abundance and distribution of plant and animal species have also resulted in ecological disturbances and ecosystem function. Physical disturbance events, including wildfires and abrupt permafrost thaw are becoming more frequent (Box et al. 2019). Due to these ecological disturbances, biome shifts through the expansion of tall shrubs and trees into the tundra, conversion of terrestrial and aquatic ecosystems, and shift of species distributions will continue to occur. The introduction of non-native species has also been documented across many taxa in the Arctic (Pauchard et al. 2016; Chan et al. 2019). Some studies predict that several mammal and seabird species will also experience habitat shifts, affecting species distributions, migration patterns, behaviour, interspecific interactions, demography, population changes, and vulnerability to extinction (Larsen 2014).

2.1.2 Arctic Marine Ecosystem

One of the most drastic changes associated with climate change in the Arctic is the rapid decline in sea ice, specifically sea ice extent, type, and duration of sea ice cover (Dauginis and Brown 2021). These changes will continue to have cascading effects on biological systems, including marine food webs. With rising temperatures, marine coastal regions are experiencing rapid change through the reduction of sea ice, permafrost degradation, accelerated coastal erosion, and enhanced methane release (Ramesh et al. 2015). Coastal marine ecosystems, in particular, are a primary recipient of increasing carbon flux and nutrients associated with permafrost thaw, and the fate of these materials can impact biogeochemical cycles and overall marine ecosystem functioning (Fritz et al. 2017). These relatively shallow areas of high productivity support the lifecycles of several Arctic fish and wildlife species, many of which also provide ecosystem services and subsistence resources for nearby Arctic communities (Meredith et al. 2019). In the Canadian Arctic, coastal regions within the Beaufort Sea play a fundamental role in ecological systems and support important linkages among freshwater, anadromous, and coastal marine species (Niemi et al. 2019). Fish, in particular, play a fundamental role in the marine food webs through the transfer of energy between lower and upper trophic levels, and across distinct aquatic zones (e.g. benthic-pelagic) (Majewski et al. 2017)

2.1.3 Marine Fish

Due to rapid global warming, some marine fish populations are experiencing northward distribution shifts (Frainer et al. 2017; Kortsch et al. 2015). Sub-Arctic Gadids such as Pacific cod (*Gadus macrocephalus*) and walleye pollock (*Gadus chalcogrammus*) have experienced significant shifts northward (Spies et al. 2020; Stafford et al. 2022). Arctic species, including polar cod (*Boreogadus saida*) and saffron cod (*Eleginus gracilis*), are experiencing habitat contractions that are driving increasing niche overlap with these northern invaders (Baker 2021; Laurel et al. 2016). Chan et al. (2019) argue that the interaction between species of different origins could potentially lead to increased competition and risks of invasion of non-native species in the future. Bluhm et al. (2009) hypothesize that water temperature plays a significant role in the distribution of Pacific epifaunal benthic species and predict the potential northward expansion of these species.

2.1.4 Greenland cod

Greenland cod (*Gadus ogac*) is a northern, medium-sized Gadid distributed in Arctic and sub-Arctic coastal waters. In Canada, they are found along the Atlantic coast, ranging from Nova Scotia, north to Baffin Island, along the mainland coast of the Beaufort Sea, and through Hudson, James, and Ungava bays (Mikhail and Welch 1989). Population estimates and life history parameters of Greenland cod are poorly understood, with studies being relatively outdated or focused on a small number of areas such as Greenland and James Bay (Hansen 1949; Morin et al. 1991; Nielsen and Andersen 2001).

Unlike other Arctic benthic fishes, Greenland cod display activities of rapid growth, high fecundity, low age at maturity and high mortality (Morin et al. 1991). From the 2012, and 2014 to 2016 sampling seasons, the mean total length of Greenland cod from Darnley Bay was 245.1 ± 86.5 mm, with the largest individual being 500 mm. Individuals ranged from age 1+ years to 7+ years. In the Hudson Bay, Greenland cod were observed to be as old as 12+ years (Mikhail and Welch 1989). Age of maturation has also been documented at 2-3 years of age. The high fecundity of cod suggests that allocation to spawning is an important investment. Spawning of *G. ogac* has been reported from April to June (Morin et al. 1991).

In Saqvaqjuac, NT, Greenland cod were reported to feed primarily on fish when available (Mikhail and Welch 1989). In other years when capelin was highly abundant, cod fed on them almost exclusively. In other years when capelin was absent due to migration season, cod shifted their diet to crabs, benthic amphipods and polychaetes. In the James Bay area, Greenland cod reportedly fed on mysids, cumaceans, amphipods, and less frequently on fish (Morin et al. 1991). Differences in diet during the summer and winter months were also observed.

As Greenland cod exhibit a benthic feeding strategy, the availability of food resources does not rely on seasonal variations observed in zooplankton (Dunbar 1982). *G. ogac* benefits from coastal areas, which are generally richer than offshore waters in Arctic and sub-Arctic oceans and may exert selective pressure on Greenland cod for higher reproductive output (Morin et al. 1991). Additionally, glycoprotein production in their blood serum acts as an antifreeze, allowing them to survive in low water temperatures (Van Voorhies et al. 1978). Mikhail and Welch (1989) argue that these key features suggest cod are well adapted to their environment and remain active under a wide range of extreme conditions. *G. ogac* appear to have few predators and are not the primary food of any common top predator (Mikhail and Welch 1989). In the shallow Hudson Bay, they fill the role as the top predator in benthic food chains.

2.2 Individual Specialization

2.2.1 Defining Individual Specialization

The concept of "niche theory" has been used historically to describe the ecology of an entire species, with the underlying assumption that conspecific individuals are ecologically equivalent (Bolnick et al. 2003). Many studies measuring species' niche do not consider the variation in resource use between individuals of the same species (e.g. Colwell and Futuyma 1971; Abrams 1980; Feinsinger et al. 1981). Trait variation at the population-level has been ignored in traditional ecological theory (Bolnick et al. 2010; Violle et al. 2012), and many argue that populations are not homogenous and can differ substantially in resource use across individuals (Bolnick et al. 2003; Araújo et al. 2011). This variation is also known as individual specialization and can be defined as an individual whose niche is substantially narrower than its population's niche for reasons not related to its sex, age, or discrete morphological group (Bolnick et al. 2003). This concept of individual specialization appoints to the overall occurrence of individual specialists in a population or the degree to which individuals' resources are specialized compared to their population. There is a growing body of literature that suggests that individual specialization occurs when individuals use a small subset of a population's resources, and has been documented across many vertebrate and invertebrate taxa (Bolnick et al. 2003; Araújo et al. 2011).

2.2.2 Measuring Individual Specialization

Bolnick et al. (2002) describes four indices to quantify individual specialization in resource use, and describes the major challenges associated with each approach. Indications for individual specialization can be measured through an individual's resource use in comparison to that of the entire population (Bolnick et al. 2003). A quantitative framework developed by Roughgarden (1972; 1974) describes intrapopulation niche variation according to continuous data, such as prey size. The total niche width (TNW) is the variance of the population's resource utilization and equals the sum of the within-individual component (WIC) and the between-individual component (BIC), such that TNW = WIC + BIC. WIC is the average variation of resources found within individual's diets such as food abundance, cost of obtaining various food types, etc. BIC is the variation among individuals and quantifies characteristics related to resource gathering such as jaw size, bill size, etc. The degree of individual specialization can be measured as the proportion of TNW explained by WIC, as such WIC/TNW. As the value of WIC/TNW approaches 1, all individuals utilize the full range of the population's niche, suggesting a strong generalist population. A WIC/TNW value closer to 0 indicates decreasing inter-individual overlap, suggesting stronger incidence of individual specialization.

A similar index proposed by Roughgarden (1979) estimates individual specialization using discrete data, such as the frequency of prey items that fall in a given category. This approach incorporates the Shannon-Weaver index as a proxy for variance and can be described using the equation $TNW_s = WIC_s + BIC_s$, where subscript "s" is used to differentiate from the continuous index. In addition to estimating individual niche specialization, both methods described by Roughgarden hold assumptions about the resource distribution. The continuous approach assumes niches hold a normal distribution, whereas the Shannon-Weaver index assumes the even distribution of resources, and is maximized by having many diet categories and equal utilization of each (Feinsinger et al. 1981). This approach also uses the proportion WIC_s/TNW_s to estimate individual specialization of a population.

Bolnick et al. (2002) also summarizes two different estimates of distribution-overlap that can be used as measures of resource specialization. The mean proportional similarity index (PS) calculates the proportion of overlap between individual and population resource consumption (Feinsinger et al. 1981; Bolnick et al. 2002). This approach provides estimates of specialization for each individual. Individuals who consume resources in direct proportion to their population will carry a PS value equal to 1, and decreases with greater incidence of specialization. The population-wide prevalence of individual specialization can also be measured through the mean of all individual's PS values. A second measure of overlap uses the mean likelihood approach to measure species' niche width (Petraitis 1979; Bolnick et al. 2002). An individual likely to consume resources directly proportional to their population will carry a Wi value of 1, and decreases with greater likelihood of specialization. The population-wide prevalence of individual specialization can be measured through the mean of all individual's Wi values. The advantages of using these overlap measures are that no assumptions about the shapes of the resource distributions are made and provide estimates of specialization at the individual level (Bolnick et al. 2002).

Individuals within a population, each acting strategically towards resource selection, may arrive at different outcomes even within a common environment (Bolnick et al. 2003). The individual's choice to select different resources can be explained by different preferences or resource-use efficiencies, reflected through variable morphological, behavioural, or physiological capacity to handle alternative resources. These choices in resource use are derived from the interaction between resource traits, resource abundance, and the individual's phenotype. Consequently, these interactions will help determine prey availability, escape rates, environmental heterogeneity, and social interactions that best explain the individual's actual resource use. Individual specialization is often reflected in resource use, and can be measured through individual diet variation (Bolnick et al. 2002). Various approaches have been used to quantify dietary individual specialization (Bolnick et al. 2003). Some studies attempt to measure individual specialization by quantifying individual diet variation through observation or analysis of stomach contents (e.g. Dixon et al. 2017; Petta et al. 2020), while others have used indirect methods such as measuring phenotypic variation in traits linked to resource utilization (e.g., Nosil and Reimchen 2005; Eklöv and Svanbäck 2006).

2.2.3 Dietary Variation

Dietary patterns, nobly in fish, vary throughout their lifecycle primarily due to morphological changes linked to growth, habitat use or foraging strategies (Persson and Crowder 1998). Changes in diet and habitat can also be influenced by prey abundance and predation risk, thus affecting species interactions. Some studies have used a single approach to study diet variation however, data from cross-sectional sampling have also been used to strengthen inferences regarding feeding ecology within a population (Araújo et al. 2011).

Stable Isotope Analysis

Stable isotope analysis is a method used to provide insight into ecological processes that would otherwise be difficult or impossible to accomplish (Heady and Moore 2013). Ratios of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes have been applied to examine diet variation over time (Carter et al. 2019). In marine environments, $\delta^{13}C$ serves as a proxy for foraging habitat through sources of organic matter, whereas $\delta^{15}N$ can indicate trophic position since consumers exhibit higher levels of ^{15}N relative to their prey (Michener and Lajtha 2008). Studying changes in stable isotopes across an individual can reflect the nutrients assimilated over multiple feeding events (Futuyma and Moreno 1988). The stable isotope method assumes that different food sources exhibit distinct isotopic signatures (Araújo et al. 2011). As a result, the variance in isotope values among individuals can be used to infer a degree of diet variation.

Isotopic ratios of δ^{13}C and δ^{15}N have also been used as a measure of specialization in animals (e.g., Del Rio et al. 2009; Francois et al. 2016; Voigt et al. 2018; Scholz et al. 2020). Following a diet switch, different tissue types (e.g., muscle, liver) take different amounts of time to turnover, indicating changes in resource use over time (Bearhop et al. 2004). Individuals who consistently feed on the same resources should have similar isotope values in different tissues, and individuals who switch resources over time should show a combination of fast and slow tissues (Heady and Moore 2013). This multi-tissue approach can distinguish feeding habits from different temporal windows, using stable isotope values holding fast and slow turnover rates (Naya and Franco-Trecu 2019). Stable isotopes can provide temporal consistency to diet analysis because they can provide a longer integrative history of feeding compared to other methods such as stomach content analysis (Mantel et al. 2004).

Stomach Content Analysis

Stomach content analysis is a tool that can be used to infer diet specialization at the individual level. This approach provides a snapshot in time of prey ingestion, and reflects only a limited temporal resolution according to digestion rates (Petta et al. 2020). Instead, cross-sectional sampling is applied when stomach content analysis is complemented with another approach such as stable isotope analysis to form a robust understanding of feeding activity.

Grey (2001) used stable isotopes of carbon and nitrogen to complement gut content analysis and otolith aging in brown trout (*Salmo trutta* L.). Using this data, it was possible to infer dietary specialization among individuals in the population. Stomach content, fatty acid, and stable isotope analysis were also used to evaluate the impacts of changing arctic sea ice habitats on Arctic cod (*Boreogadus saida*) (Kohlbach et al. 2017). Diets and carbon sources were examined to quantify and describe the feeding habits of this species. Matley et al. (2015) examined prey selection by mammals in the Canadian High Arctic using stomach contents and $\delta^{13}C$ and $\delta^{15}N$ stable isotopes from liver and muscle tissues. Stable isotope and fatty acid biomarkers were used to assess differences in trophic niche for Arctic Gadid species in the Canadian Beaufort Sea including Arctic cod (*Boreogadus saida*), saffron cod (*Eleginus gracilis*) and Greenland cod (*Gadus ogac*) (Brewster et al. 2018). Matich et al. (2019) used the multi-tissue stable isotope approach to infer dietary specialization in three shark species; spurdogs (*Squalus* spp.), bull sharks (*Carcharhinus leucas*), and blacktip reef sharks (*Carcharhinus melanopterus*). The use of multiple sample types can provide robust indications of specialization but require specific attention to select tissues that are metabolically active with considerably different turnover rates. In these studies, multiple and complementary sampling techniques are advantageous for understanding animal behaviours and foraging techniques under a range of spatial distributions but require careful consideration for the types of samples and methods chosen depending on the species of interest.

Cross-sectional sampling has been applied in many cases to quantify individual specialization. As summarized by Araújo et al. (2011), the application of cross-sectional sampling is subject to four main assumptions:

i. *There are multiple prey items per stomach.* The number of prey items per individual influences statistical power of the analysis. Low sample sizes per individual can artificially inflate estimates of individual specialization. Statistical tests including Monte Carlo resampling procedures or contingency tables can be used to test for the effects of inflation on a small sample size (Bolnick et al. 2002; Araújo et al. 2008). These approaches can test whether or not the observed diet variation exceeds a null distribution, with the null hypothesis being that individuals sample randomly from a single population diet distribution. We would often expect the null distribution to vary, depending on the population being observed.

ii. *Multiple prey items represent independent prey-capture decisions.* If prey samples are non-independent (e.g., if prey are spatially clumped), over-estimation of diet variation can occur. Despite this assumption being the most difficult to assess, independence across samples ensures that results are statistically informative.

iii. *The sampled diet is representative of the overall diet of the individual.* If individuals feed on multiple prey items, the sampled diet must be a reasonable approximation of the overall, long-term diet of the individual. The degree of individual specialization can be overestimated with fewer prey items sampled per individual. The use of a null model can also be used to help overcome this issue.

iv. *Individuals being compared must be drawn from a small spatial range, and a single point in time.* Any spatial or temporal fluctuations observed within the sample population may result in variance in resource availability that artificially inflates measures of individual specialization. Theoretically, the effects of spatial and temporal fluctuations can be removed to calculate individual specialization.

To test against the null hypothesis, Monte Carlo resampling techniques can be used as measures of individual specialization (Araújo et al. 2011). Under the null model, individuals within a population feed from a single diet distribution (e.g., WIC/TNW=1). Individual specialization is first calculated using several indices, as described by Bolnick et al. (2002). Under Monte Carlo resampling, each individual in the sample is reassigned its original number of prey, and randomly drawn from the population diet distribution to calculate the index of diet variation (e.g., WIC/TNW). The sample population undergoes several thousands of iterations to generate a null model. Variation in diet occurs when observed values fall outside the range of the null values. Using this null model, the occurrence of individual specialization can be detected.

The null values generated from Monte Carlo resampling are also accompanied by limitations that may influence the outcome of individual specialization (Araújo et al. 2011). The null models do not test for independence of feeding events or spatial or temporal variability. Additionally, these models can only be applied to discrete data such as prey count, and not prey mass or volume. Another limitation of the null model is that the baseline expectations of individual specialization are not automatically accounted for. When conducting studies between multiple populations, using the mean null values can provide indications of true individual specialization, whereas the raw values can may falsely propose individual specialization due from sampling effects (Bolnick et al. 2007).

2.2.4 Phenotypic Variation

Natural populations are composed of phenotypically diverse individuals (Bolnick et al. 2011). An individual's phenotypes will determine the limits of their performance since the ability to perform a behaviour is directly linked to the design of its functional traits (Wainwright 1994). As a result, differences in performance may be seen within a natural population. The study of phenotypic traits can be used to describe individual specialization within a single population. Morphometrics is one of many techniques that can be used to study shape in biological structures (Slice 2007).

Morphometrics

Individual specialization can be measured by mapping resource utilization directly through morphological variation. Morphometrics is the study of size and shape of living organisms, and has been applied traditionally through linear measurements (e.g. length, width), masses, angles, ratios, and areas (Park et al. 2013). A major limitation of this method is that spatial properties are no longer retained on each structure throughout this type of measurement (Slice 2007). In the 1980s, morphometrics experienced a major revolution through the adoption of coordinate-based methods, allowing for the in-depth visualization of large, high-dimensional data sets (Mitteroecker and Gunz 2009).

This new approach is referred to as "geometric morphometrics" as it preserves the geometric properties of the landmark configurations throughout analysis and allows statistical results to be represented as shapes or forms (Webster and Sheets 2010). Landmarks are defined as points of correspondence on each specimen across a population, or biologically homologous anatomical loci distinguishable on all specimens in the study. They are expressed as both cartesian coordinates (x and y), and distinct anatomical features on a structure. As Webster and Sheets (2010) summarized, homologous landmarks on an organism should be defined according to various factors. First, each landmark must be a homologous anatomical locus recognizable on each specimen in the study. Second, configurations should be selected to represent an adequate summary of morphology. Otherwise, shape variation found between landmarks will not be detected. Third, landmarks should be easily digitized, meaning consistently replicable with high accuracy. Fourth, for 2D data, landmarks should be coplanar (i.e., in the same plane). Finally, landmark topological positions should be conserved relative to other landmarks. Morphometric techniques are generally most effective when comparing biological structures that are quite similar, as opposed to ones that are widely different.

This coordinate-based morphometric approach eliminates the effects of size, position, and orientation, allowing for the retention of shape throughout (Querino et al. 2002). Within the field of geometric morphometrics, various approaches are used to evaluate mathematical and statistical properties, with the most common being the Procrustes method (Mitteroecker and Gunz 2009). This method uses the translation rotation, and scaling of shapes using least-squares estimation, and represents the mean (consensus shape) of all shapes combined. The resulting centered, scaled, and rotated landmarks are referred to as Procrustes shape coordinates (Figure 1).

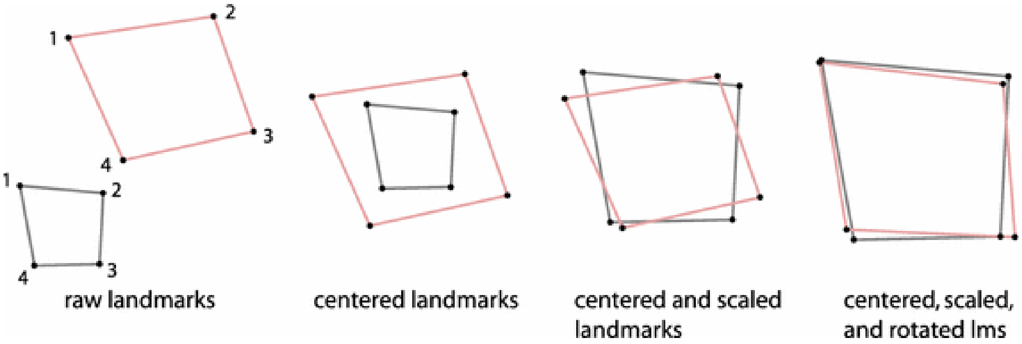

Figure 1: The three steps of Procrustes superimposition: (1) Raw landmarks centered and superimposed upon a common coordinate system. (2) Landmarks are individually scaled to the same unit Centroid Size (the square root of the sum of squared distances of the landmarks in a configuration to their average location). (3) Rotation to minimize the sum of squared Euclidean distances between homologous landmarks (Mitteroecker and Gunz 2009).

The application of geometric morphometrics in various fish taxa has been used to study morphological characteristics of distinct genera, species, populations, morphs, and individuals (e.g., Marcil et al. 2006; Maderbacher et al. 2008; Cabuga 2016). Characteristics of ecological niche use and resources are often reflected in morphology, as form and function are highly correlated (Webb 1984; Wootton 1990), and have the potential to provide proximate measures of trait variation and infer a degree of individual specialization.

2.3 Co-Management

Collaborative or cooperative management can be used to "convey the sharing of rights and responsibilities by the government and civil society" (Plummer and FitzGibbon 2004, 63). Some forms of collaborative management include; integrated conservation and development, participatory natural resource management, participatory appraisal and participatory action research, community-based natural resource management, and co-management (Berkes 2002; Armitage et al. 2010). Co-management has emerged as a formalized management tool that engages with local communities and governmental bodies. Carlsson and Berkes (2005) define co-management as "a power sharing arrangement between a coherent State and a community of resource users." The co-management strategy can benefit community-based economic and social development, decentralize resource management decisions, and act as a mechanism to reduce conflict through participatory democracy (Armitage et al. 2010).

Integrating collaboration and learning within resource management can be described as adaptive co-management (Olsson et al. 2004; Armitage et al. 2010). Olsson et al. (2004, 75) define adaptive co-management as "flexible community-based systems of resource management tailored to specific places and situations and supported by, and working with, various organizations at different levels." Similarly, Ruitenbeek and Cartier (2001, 8) define co-management as "a long-term management structure that permits stakeholders to share management responsibility within a specific system of natural resources, and to learn from their actions." Some features of adaptive co-management include: 1) a shared vision or common goal among parties of interest, 2) a high degree of dialogue, interaction, and collaboration, 3) distributed or joint control across multiple levels, with shared responsibility for action and decision making, 4) a degree of autonomy for different actors at multiple levels, 5) commitment to the pluralistic generation and sharing of knowledge, and 6) a flexible and negotiated learning orientation with an inherent recognition of uncertainty (Armitage et al. 2010). Ayles et al. (2016) also argue that adaptive management techniques of acknowledging uncertainty, learning from experience, feedback, and new actions provide an outcome of an enhanced co-management system. Co-management and adaptive systems have been shown to be successful in many cases but are often accompanied by various challenges and drawbacks. Castro and Nielsen (2001) argue that conflict is often a product of co-management arrangements due to the interactions between individuals and communities with one another in the midst of change. Political challenges within co-management strategies are also difficult to fix and can't be solved by simply gathering or integrating knowledge. Instead, Nadasdy (2003) recommends that the reconstruction of institutions, practices, and underlying assumptions of wildlife management itself is necessary.

The bridging of knowledge has a central focus within co-management activities (Cooke et al. 2020). This bridging can be accomplished in different ways, one of which can be through co-interpretation (Moore and Manuel 2020; Cooke et al. 2020). Co-interpretation can be described as interpreting the meaning and implications of the results among different parties of interest. It is a form of adaptive management, or learning-by-doing, and was developed to deal with uncertainty and complexity (Holling 1978). The co-interpretation step adds meaning to the data, by inclusion of different perspectives from both knowledge systems, and contributes to the generation of knowledge through a more complete output (Dunmall and Reist 2018).

2.3.1 Co-Management in the Arctic

Co-management is an emerging discipline that is being used to bringing together TEK and scientific knowledge for the purposes of resource and wildlife management (Armitage et al. 2011). As described by Berkes et al. (2000), TEK is a cumulative body of knowledge, practice and belief evolving from adaptive processes and handed down through generations by cultural transmission – about the relationship of plants, animals, and humans with one another and their environment.

Scientific and TEK knowledge have been used in several studies to inform management decisions related to Arctic wildlife species. Dale and Armitage (2011) assess the co-management approach using a case study on narwhals in Nunavut, Canada. This study documents the multi-faceted processes of knowledge gathering, sharing, integration, interpretation, and application, all of which play imperative roles within resource management and decision-making. Rather than compartmentalizing the different views of knowledge, this case study demonstrates the value of learning and collaborating to foster better social, ecological, and social-ecological outcomes. Armitage et al. (2011) evaluate the co-management process across three cases in Canada’s Arctic: 1) narwhal (*Monoceros monodon*) co-management in Arctic Bay, Nunavut, 2) co-management of beluga (*Delphinapterus leucas*) entrapment in Husky Lakes, Northwest Territories, and 3) Dolly Varden char (*Salvelinus malma malma*) in the western Canadian Arctic. Each of these co-management cases present opportunities of enhanced social learning for the purposes of increasing resilience in a rapidly changing environment. Idrobo and Berkes (2012) document the process of engaging with Inuit knowledge on the Greenland shark (*Somniosus microcephalus*), a rarely encountered, undesirable, by-catch species. Interactions between Inuit and researchers were used as a forum to generate knowledge and engage with management and conservation decisions.

2.3.2 The Inuvialuit Settlement Region

In 1984, the Inuvialuit Final Agreement (IFA) was signed as the first land claim agreement in the Northwest Territories, establishing the Inuvialuit Settlement Region (ISR). This region of the western Canadian Arctic spans approximately 906 430 km^2 of land and includes distinct regions including the Mackenzie Delta, Beaufort Sea, and Amundsen Gulf (Canada 1984; Fast et al. 2005). Six communities are located within the ISR which include: Aklavik, Inuvik, Paulatuk, Tuktoyaktuk, Sachs Harbour, and Ulukhaktok. Inuit located in the western Canadian Arctic region are referred to as Inuvialuit.

The marine environment in the ISR includes a permanently ice-covered region, a seasonally ice-covered region, and a coastal area connected directly linked to the Mackenzie River (Fast et al. 2005). The continental shelf of the Beaufort Sea is narrow, with an average dept of 65 meters and ranges from 10 meters in the Mackenzie Delta, and 600 meters in the Amundsen Gulf. The shelf seas and ice edges are considered areas of high productivity and a popular spot for Inuit harvesting activity. Inuvialuit benefit from a variety of fish and wildlife subsistence species found in the Beaufort Sea region including: beluga (*Delphinapterus leucas*), bowhead whales (*Balaena mysticetus*), ringed seals (*Pusa hispida*), Arctic char (*Salvelinus alpinus*) and Dolly Varden char (*Salvelinus malma*) as well as land mammals, birds and freshwater fishes (Day 2002; Usher 2002; Ayles et al. 2007). The signing of the IFA provided Inuvialuit with surface title to 30% of their traditional land base, with exclusive rights to harvesting of some wildlife species, co-management of wildlife, fisheries, and the environment, and a cash institutional basis for Inuvialuit economic development (Canada 1984; Usher 2002).

The IFA recognizes a number of co-management boards to manage fish and wildlife through regulation, allocation, enforcement, research, and environmental impact assessment activities (Pinkerton 1989). The five co-management boards responsible for the management of fish and wildlife species recognized under the IFA include: the Wildlife Management Advisory Council (WMAC), Fisheries Joint Management Committee (FJMC), Inuvialuit Game Council (IGC), and Inuvialuit Hunters and Trappers Committees (HTCs) (Canada 1984). Each co-management board is comprised of an equal number of members of government and Inuvialuit. This complex co-management system captures the sharing of power and responsibility between government and local resource users to cover all aspects of renewable resource management (Elias 1995).

2.3.3 Fisheries Management in the ISR

Arctic fisheries play a fundamental role in Inuvialuit subsistence activities and serve as integral parts of culture and tradition (Papik et al. 2003). As recognized under the IFA, the FJMC is the co-management board responsible for fish and mammals in the ISR (Canada 1984). This board is comprised of two Inuvialuit members appointed by the Inuvialuit Game Council, two Canada members appointed by the Minister of Department of Fisheries and Oceans (DFO) and a Chair selected by the four appointed members (Ayles et al. 2016). Prior to the IFA, fisheries were managed exclusively by the DFO. Today, the FJMC works jointly with the Department of Fisheries and Oceans (DFO) and the HTCs to develop integrated fisheries management plans for individual fish stocks or stock complexes to establish conservation, socio-economic, and ecosystem objectives, strategies to support those management objectives, and plans to implement those strategies (Canada 1984; Ayles et al. 2007). The FJMC is responsible for collecting harvest

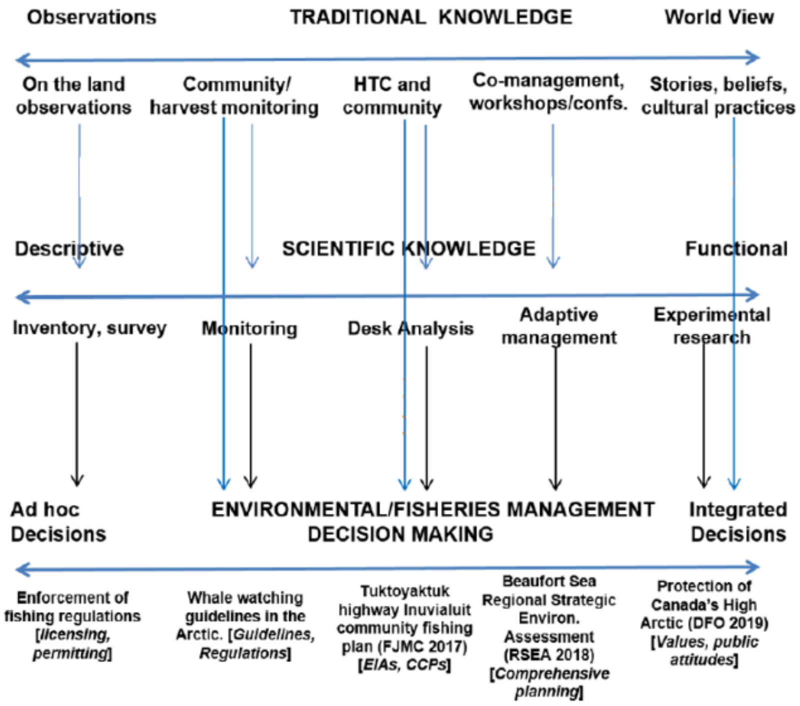

Figure 2: Fisheries co-management framework in the western Canadian Arctic. This model illustrates the relationship between traditional ecological knowledge (TEK), scientific knowledge and environmental/fisheries management decision-making. EIA: Ecosystem Impact Assessment; FJMC: Fisheries Joint Management Committee, IGC: Inuvialuit Game Council (Niemi et al. 2019).

information and making recommendations on subsistence quotas for fish and harvestable quotas for marine mammals.

Under the established land claims, a co-management framework was developed to link knowledge systems (TEK and western science) with environmental and fisheries management decision-making (Figure 2). This structure intends to utilize TEK within fisheries and environmental management by recognizing the value of Inuit understanding of the environment. Functioning under this model should facilitate communication between participants (e.g., harvesters, scientist, politicians) and help focus TEK and western science efforts on specific activities required to improve decision-making. The top row of the model shows a continuum of activities supported through co-management, informed by TEK. The middle horizontal row represents a continuum, from research activities (e.g., species type and location) to functional knowledge (e.g., system relationships such as how char populations will respond to fishing). These activities support the diverse decision-making processes that are commonly practiced in the ISR, as represented by the bottom horizontal row. Vertical blue arrows show linkages and parallels between the TEK and science spectrums, that are also linked to the management spectrum. Vertical black arrows illustrate the link between the scientific knowledge spectrum and the management spectrum. As argued by Rivera et al. (2014), co-management is a promising strategy used to achieve sustainable fisheries and has the potential to strengthen community integration, enhance fishing stocks, empower resource users, adapt to changing conditions and incorporate both fishers; knowledge and scientific information in management strategies.

An example of a collaborative decision-making within the co-management framework includes the Beaufort Sea Integrated Fisheries Management Framework (BSIFMF). The Canadian Beaufort Sea is one of the few marine areas left in the world that has not yet experienced large-scale commercial fisheries (Ayles et al. 2016). However, global climate warming and economic opportunities linked through fish stock failures in other parks of the world's oceans are becoming a deeper concern for ecosystems and communities in the ISR. As a result of these concerns, fisheries management efforts through the BSIFMF were developed among the DFO, the FJMC, the IGC, and the Inuvialuit Regional Corporation (IRC). The BSIFMF aims to achieve ecosystem-based management and compatible sustainable fisheries development (Beaufort Sea Partnership 2009; Ayles et al. 2016). As part of the BSIFMF, working groups within the governance structure are created on an as-need basis (Beaufort Sea Partnership 2009). These groups often work in the following areas: community consultation, traditional knowledge, social, cultural and economic matters, biophysical components, and geographic/spatial components of the planning area. For the BSIFMF to achieve ecosystem-based management and compatible sustainable fisheries development, the co-management approach is fundamental for improving the decision-making processes, while bringing together government and communities to develop resource management processes in the ISR (Ayles et al. 2016).

Fisheries management initiatives have been primarily targeted at key marine subsistence species in the ISR. The Ulukhaktok Char Working Group (UCWG) was developed in response to changes in population fish dynamics and continues to address fisheries management in the region with consideration for community priorities and concerns (Holman Char Working Group 2004).

2.4 Knowledge Gaps and Research Opportunities

Research efforts focused on the Arctic are limited relative to the rest of the world. The Arctic marine ecosystem lacks sustained research efforts in this region (Christiansen et al. 2014), and even more so with recent climate change events (Deb and Bailey 2023). These cascading effects on the marine environment and species supporting Inuit subsistence and livelihoods make them highly vulnerable to ongoing climate change (Ford et al. 2008). To implement the proper management strategies that can support a sustained marine population while supporting Inuit tradition and cultural practices, understanding the changes taking place in the biophysical environment and links to coastal Inuit communities are necessary for anticipating changes that may occur in the near future.

Research on marine fish populations can contribute to the existing baseline data of Arctic ecosystems. Greenland cod can serve as an indicator of the changes taking place in the marine ecosystem. Given the projected northward expansion of many sub-Arctic fish populations in the future (Fossheim et al. 2015), investigating the adaptation potential of Arctic marine populations can provide further knowledge on this ecosystem and connections to the changing Arctic.

Greenland cod are part of Inuit harvesting practices and are currently being co-managed by local, territorial, and government organizations in the ISR (Lea et al. 2023), and should therefore undergo collaborative research efforts and draw from different knowledge sources to inform decision-making. By consolidating various knowledge systems, such as Inuit and scientific knowledge, there is potential to generate a broader range of information that can provide meaningful contributions towards the management and conservation of marine species in the changing environment.

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RESEARCH APPROACH

This research draws upon an integrated approach and will engage with Inuit and scientific knowledge to document and interpret changes being experienced in the Arctic marine ecosystem and implications for Inuit subsistence and livelihoods. Ongoing collaboration between Inuit knowledge holders, OHTC, FJMC, and researchers from academia and DFO are taking place throughout this project. This step is critical for developing strong community-researcher relationships through identifying interested community partners, linking with existing research projects, and communicating research progress and findings in the community (Pearce et al. 2009). In this project, the ongoing community-researcher collaboration entails Inuit involvement in all steps of the research process through problem identification, data collection, and data interpretation.

This study is part of a larger network of research projects, which aims to fill knowledge gaps on coastal fish ecology in the Arctic to better understand climate change impacts and help guide fisheries and ecosystem management in the ISR. This research is part of ArcticNet Project 33: Using Co-Produced Knowledge to understand and Manage Subsistence Marine Harvests in a Changing Climate and the “Ulukhaktok Fish Tagging Project”. These programs are supported by the Fisheries Joint management Committee (FJMC), the Olokhaktomiuk Hunters and Trappers Committee (OHTC) and the Beaufort Regional Strategic Environmental Assessment (BRSEA).

EXPECTED RESEARCH CONTRIBUTIONS

This study intends to provide empirical, methodological, and practical contributions through collaborative efforts between key knowledge holders in Ulukhaktok, OHTC, FJMC, and researchers from academia and DFO. Empirical contributions of this research relate to the ecology of Greenland cod, specifically through the study of intraspecific variation in morphological and feeding traits. Gaining a better understanding of this lesser-known species adds to the existing knowledge of marine fish species in the Arctic. The use of an integrated approach from multiple indices (i.e., morphometrics, stable isotope analysis) can provide a proximate measure of individual specialization-generalization that can infer a level of adaptation potential within individuals and across the population. This research will also link Inuit and scientific knowledge to generate enriched findings that may not be achieved from each knowledge system independently. The process of pairing knowledge can provide methodological contributions and set a foundation for future work that would also benefit from active collaboration and engagement with Inuit and scientific knowledge to address fisheries conservation and management needs in the ISR. The knowledge gained from this study may also serve as a practical contribution used to inform Arctic fisheries adaptive co-management strategies. Gaining a better understanding of the ecology of Arctic fish species can help predict future changes within the marine ecosystem and the consequences of a changing environment. Documenting the connections of coastal fish species to Inuit subsistence and livelihoods can also help contextualize the research and ensure that fisheries co-management can continue to make decisions using a broad range of knowledge while continuing to support community priorities and Inuit-led decision-making.

CHAPTER 3: INTRASPECIFIC VARIATION OF GREENLAND COD (*GADUS OGAC*) AS A MEASURE OF CLIMATE CHANGE ADAPTATION POTENTIAL IN THE ARCTIC

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ABSTRACT

Morphological variation and the presence of distinct morphotypes have been observed in many fish species, however, the ecological consequences of this variation in terms of habitat occupied or prey consumed are rarely studied. Understanding individual specialization through morphological and habitat-trophic variations can provide insight into the ability of Arctic fish species to adapt to ongoing climate change. We estimated morphological variation of Greenland cod (*Gadus ogac*) collected along the marine coast near Ulukhaktok, Northwest Territories (NT), in the western Canadian Arctic (n=45) and compared our morphological assessments to habitat and trophic specialization indices derived from carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes. Principal component analysis (PCA) of linear morphometric measurements indicated significant variation in the morphology of sampled cod, primarily in head shape and body depth posterior. Subsequent kmeans clustering categorized fish into two discrete morphological groups. Comparison of $\delta^{13}C$ and $\delta^{15}N$ values between morphs revealed an overall generalist population with notable variation among individuals, suggesting that morph-specific behaviours can be observed over a gradient rather than distinct groups that may favour generalist populations in the future due to their ability to undergo resource shifts. The integrated approach used here informs our understanding of species' flexibility to competition and resource modification with ongoing borealization. The findings highlight the need to consider individual-level data and the degree to which a population exhibits specialization-generalization in fisheries co-management in the Arctic.

KEYWORDS: Individual specialization, morphometrics, stable isotopes, Greenland cod, Canadian Arctic

INTRODUCTION

Phenotypic variation among individuals of the same species (intraspecific variation) can result in conspecifics exhibiting contrasting ecological traits, with consequences for community structure, and population-level ecosystem function (Bolnick et al., 2011; Des Roches et al., 2018; Ward et al., 2016). In wild animal populations, greater diversity in a given trait may stabilize populations against environmental disturbances (McKenzie et al., 2021; Nati et al., 2021) by buffering against their direct impact (Barabás and D'Andrea, 2016; McKenzie et al., 2021), and enhancing subsequent population recovery (Des Roches et al., 2018). Consequently, it is increasingly recognized that wildlife conservation and management should aim to preserve or promote phenotypic diversity within wild populations (Des Roches et al., 2021; Moran et al., 2016; Ward et al., 2016), to mitigate the deleterious impact of anthropogenetic activities, and maintan ecosystem resilience in an era of ongoing environmental change. In fish, the underlying causes of intraspecific variation are complex, and can be reflected in traits related to physiology, behaviour, habitat use and life history patterns (Burton et al., 2011; Metcalfe et al., 2016), but often correspond to adaptation to local or experienced conditions (Fraser et al., 2011). Of the phenotypic traits known to show significant variation within a fish species, morphology and the presence of distinct morphotypes are among the most widely studied and observed (Andres et al., 2019; Svanbäck et al., 2008).

Intraspecific variation in fish morphology is often associated with adaptations related to prey location, acquisition, and handling (Ferry-Graham et al., 2002). For example, jaw and pharyngeal morphology was observed to be diet-specific in a widespread cichlid fish species (Binning and Chapman, 2010), while traits related to locomotory performance (e.g. body depth/length) and prey detection (e.g. eye diameter) have been found to correlate with individual dietary traits in European minnow (*Phoxinus phoxinus*) (Raffard et al., 2020). These morphological adaptations may also lead to individual fish specializing in the acquisition of certain prey items, such that their diet is dominated by specific prey types which comprise a small proportion of those available to the overall population. As distributions of prey items are often associated with specific environmental variables, and the advantages provided by certain morphological traits may be environment-dependent (Binning and Chapman, 2010; Raffard et al., 2020; Svanbäck and Bolnick, 2007), morphology may therefore also correlate with individual patterns of habitat use and selection (Paz Cardozo et al., 2021; Svanbäck and Bolnick, 2007; Wolff et al., 2023). Individual variation in morphological traits may consequently drive intraspecific variation in both the ‘position’ (i.e. the resource use of that individual) and ‘breadth’ (i.e. the diversity of resources used by that individual, and their proportional importance) of their ecological niche (Paz Cardozo et al., 2021; Winkler et al., 2017).

Importantly, species trait diversity related to habitat and diet coupled with position along the generalist-specialist axis (Bolnick et al., 2002; Svanbäck and Schluter, 2012) and the relative proportion of generalist/specialist phenotypes within a population can impact ecosystem resilience. Given generalist individuals can make use of a broad range of resources, they may be less impacted by the loss of a given habitat or prey type, contributing to population stability (Laske et al., 2018). Where these generalists also exhibit a degree of resource partitioning (Chavarie et al., 2016), the impacts of environmental disturbances may be buffered further. In contrast, species with narrow divergent resource needs are more likely to experience fitness consequences should a specific prey or habitat resource be lost, increasing their vulnerability to certain environmental stressors (Carscadden et al., 2020). However, specialized phenotypes can also enhance the potential for populations to expand into novel environments and niches (Martin and Pfennig, 2009; Sexton et al., 2017), providing an alternative mechanism by which phenotypic diversity can contribute to population resilience. Understanding the diversity of ecological traits and degree of individual generalization/specialization within a population, consequently, provides a more accurate indication of how natural populations will respond to environmental disturbances and their resilience to climate change (Bolnick et al., 2003; Thomson et al., 2018).

Ongoing climate change impacts are transforming marine food-web structure in Arctic ecosystems, changing the distribution, quality, and availability of resources that Arctic consumers depend on (Deb and Bailey, 2023; Florko et al., 2021). Trends of poleward distribution shifts have been documented in marine species (Hastings et al., 2020), notably in boreal fish populations (Frainer et al., 2017; Kortsch et al., 2015). Sub-Arctic Gadids such as pacific cod (*Gadus macrocephalus*) and walleye pollock (*Gadus chalcogrammus)* have experienced significant shifts northward (Spies et al., 2020; Stafford et al., 2022), while Arctic species including Arctic cod (*Boreogadus saida*) and saffron cod (*Eleginus gracilis*) are experiencing habitat contractions that are driving increasing niche overlap with northern invaders (Baker, 2021; Laurel et al., 2016). The range expansion of these boreal generalists are expected to increase the rates of resource competition and predation experienced by Arctic species (Bogstad et al., 2015; Fossheim et al., 2015), and represent stressors likely to have severe impacts on endemic Arctic Gadids (Geoffroy et al., 2023). Additionally, sub-Arctic Gadids have been shown to exhibit high adaptive potential to environmental stressors (Laurel et al., 2016; Leo et al., 2020), potentially exacerbating their competitive impacts on endemic Arctic Gadids as climate change continues.

Variation in ecological niche does not necessarily have a direct relationship with morphological traits (Binning and Chapman, 2010), and so establishing morph-niche relationships using corresponding observations of ecological niche is an important area of continued research. Stable isotope analysis provides a means to quantify several components contributing to variability in ecological niche, including differences in foraging areas (Mumby et al., 2018), prey consumption (Malek et al., 2016), generalization/specialization (Bond et al., 2016), and seasonal variability (Coulter et al., 2019). Comparison of stable isotope ratios of tissues with different turnover rates can reveal variation over short (days – weeks; plasma) to long time scales (weeks – months; red blood cells (RBCs); Vander Zanden et al., 2015) of sampled individuals within a population (Bearhop et al., 2004; Newsome et al., 2007). Carbon stable isotopes ($\delta^{13}C$) are often used as a proxy for habitat use among individuals (Cherel and Hobson, 2007; Matich et al., 2017) through evaluating sources of carbon an organism consumes (DeNiro and Epstein, 1978). Nitrogen stable isotopes ($\delta^{15}N$) define an organism's trophic position, given notable enrichment in ^{15}N with each trophic level (DeNiro and Epstein, 1981; Post, 2002). Variation in stable isotopes has also been linked to distinct morphotypes to provide a complementary assessment of trophic and morphological variability (Senegal et al., 2021). Quantitative assessments of trophic variability can be measured through specialization indices (Bolnick et al., 2002), or further evaluated through linear mixed-effects models (LMEs) to assess relative specialization within and between populations (Newsome et al., 2009). Individuals with variable $\delta^{13}C$ or $\delta^{15}N$ values would therefore indicate more variation in resource use and would be reflected through habitat ($\delta^{13}C$) or trophic ($\delta^{15}N$) specialization.

Greenland cod (*Gadus ogac*) are endemic to the Arctic and northwest Atlantic Oceans and are broadly distributed throughout inshore coastal regions (McNicholl et al., 2017; Mikhail and

Welch, 1989). Subsistence cod fishing plays a role in Inuit tradition and livelihoods (Collings et al., 1998; Hoover et al., 2016; Pearce et al., 2011), with this species currently co-managed by local, territorial, and government organizations (Lea et al., 2023). Changes in fish population dynamics however, have been reported in recent years, including a decrease in abundance and increase in size of Greenland cod (Chan S., Personal Communication, 24 July 2022). Despite these changes, subsistence harvesting has increased observed over time (Lea et al., 2023), making them a focal research species given data deficiencies, community dependence, and year-long presence in coastal areas. Our limited understanding of the behaviour of Greenland cod complicates understanding their interactions within the marine ecosystem and how they will respond to climate change.

To investigate how intraspecific diversity may buffer the impact of environmental disturbance on Greenland cod, we aimed to quantify trait variation in terms of morphology and assess how this variation correlated with individual specialization-generalization in habitat and trophic (i.e. foraging ecology) metrics. Specifically, we (i) quantified morphological variation in a population of Greenland cod, to investigate the occurrence of unique morphotypes, and (ii) quantified the degree of individual specialization-generalization using multi-tissue stable isotope analyses for the derived morphotypes. In the Arctic, where resources are generally limited and biodiversity is reduced compared to lower latitudes (Hillebrand, 2004), individual specializations may occur as a means to maximize fitness and reduce intraspecific competition (Roughgarden, 1972).

MATERIALS AND METHODS

Study area and fish sampling

Fish were captured near the Inuit community of Ulukhaktok, Northwest Territories (NT; 70.59^{o}N, 117.27^{o}E), at the entrance to Safety Channel, a semi-enclosed channel approximately 30 kilometres east of Ulukhaktok on the edge of the Amundsen Gulf in the western Canadian Arctic, Inuvialuit Settlement Region (Figure 3). The study location was determined following consultation and advice from the Olokhaktomiut Hunters and Trappers Committee (OHTC), Ulukhaktok Char Working Group (UCWG) and local Inuit harvesters (R. Klengenberg, I. Inuktalik, and D. Kuptana). Greenland cod were sampled in Safety Channel in 2018 during the summer months (July and August) and in 2019 during the spring and summer months (April, July – August). Fish were caught by angling with a rod and line from shore and from an 18ft vessel in open waters. After capture, individual Greenland cod were assigned a unique

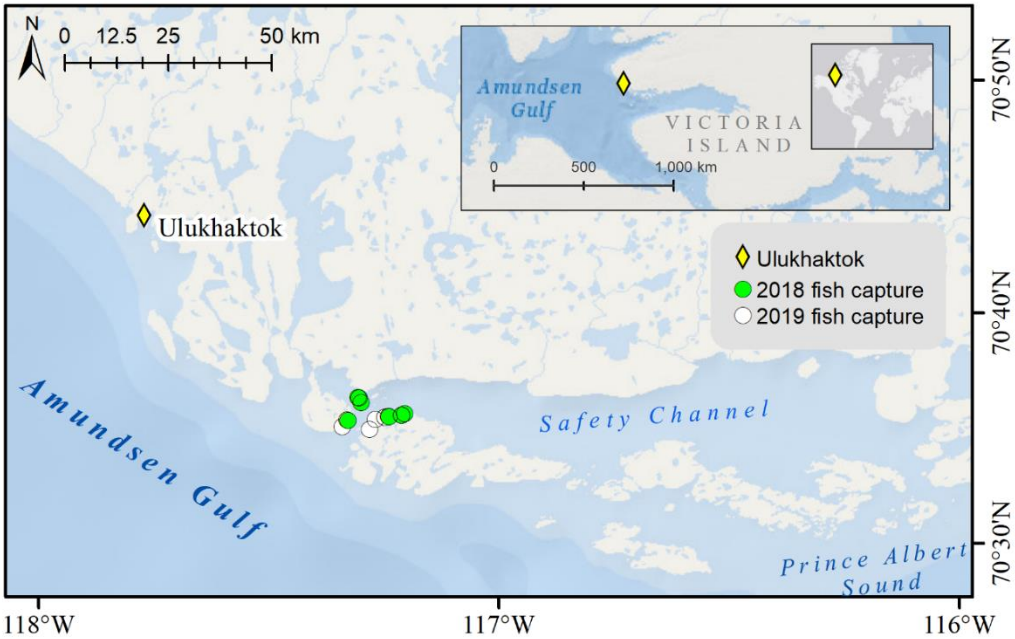


Figure 3: Map showing the study site in the western Canadian Arctic. Greenland cod (*Gadus ogac*) were captured in the semi-enclosed Safety Channel near the community of Ulukhaktok, Northwest Territories (NT). Service layer credits: Esri, Garmin, GEBCO, NOAA.

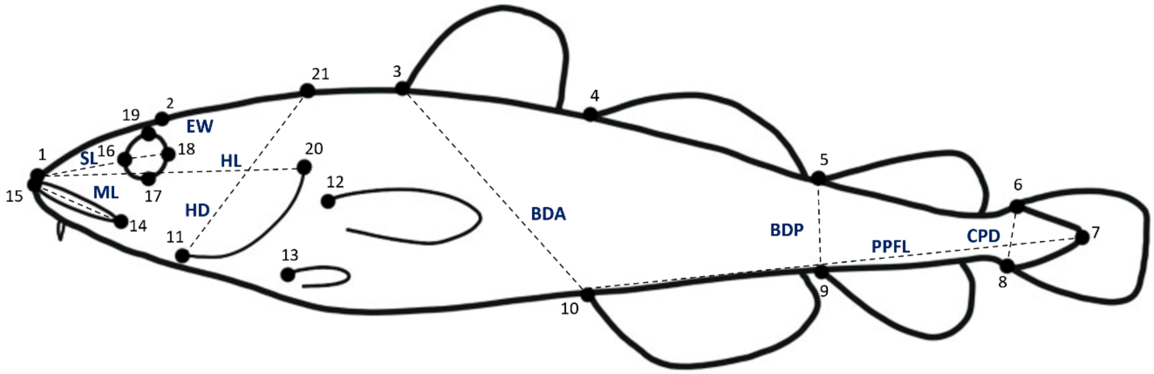
identification number and placed lateral side down on a mesh tray with a ruler and colour chart. Fish were then photographed with a DSLR camera (Canon T2i Rebel) that was positioned above the fish on a fully extended tripod.

Following standardized photographs, blood was collected from the caudal vein of each individual using a 2ml heparinized syringe and separated immediately into plasma and red blood cells (RBC) using a field centrifuge. Samples were stored frozen (-20^{o}C) and later shipped to the University of Windsor, Canada for stable isotope analysis.

Geometric Morphometrics

Data Preparation

Morphometric analyses methods were adapted according to those described in Skoglund et al. (2015) and Burke et al. (2022). Photographs of each fish were converted to a .tps file using the tpsUtil ver. 181 software (Rohlf, 2021) and a total of 21 landmarks were identified to encapsulate head and body shape of the fish (Figure 4). Landmarks were selected according to previous morphometric studies examining the body shape of juvenile Atlantic cod (Marcil et al., 2006) and head shape of Arctic char (Skoglund et al., 2015). Homologous landmarks were digitized on each photograph using the tpsDig2 ver. 2.31 software (Rohlf, 2018). Photographs were scaled with a centimeter ruler before landmark placement. Fork length was measured (mm) as the distance between the tip of the snout and the posterior end of the caudal peduncle. For each photograph, individual landmarks were assigned a ranking of 1-3 for light and focus: (1) representing poor quality, (2) average, or (3) excellent. An identical ranking system was then used to assess the overall quality of photographs, for example, if landmarks could not be easily distinguished on fish or excessive bending of a fish occurred which would otherwise distort



1. Anterior tip of snout
2. Dorsal edge in line with posterior extremeof orbital bone
3. Anterior base of anterior dorsal fin
4. Anterior base of central dorsal fin
5. Anterior base of posterior dorsal fin
6. Dorsal edge at base of caudal fin
7. Posterior point of caudal peduncle
8. Ventral edge at base of caudal fin
9. Anterior base of posterior anal fin
10. Anterior base of anterior anal fin
11. Ventral edge in line with anterior extreme of orbital bone
12. Dorsal extent of pectoral fin
13. Dorsal extent of pelvic fin
14. Posterior extreme of maxilla
15. Anterior extreme of premaxilla
16. Anterior extreme of orbital bone
17. Ventral extreme of orbital bone
18. Posterior extreme of orbital bone
19. Dorsal extreme of orbital bone
20. Dorsal edge in line with posterior extreme of operculum
21. Posterior extreme of operculum

Linear Measurements:
Caudal peduncle depth (CPD): 6, 8
Body depth posterior (BDP): 5, 9
Body depth anterior (BDA): 3, 10
Post pelvic fin length (PPFL): 7, 10
Head depth (HD): 11,21
Head length (HL): 15, 20
Snout length (SL): 1, 16
Eye width (EW): 16, 18
Maxilla length (ML): 14, 15

Figure 4: Locations of landmarks (n=21) and linear measurements (n=9) identified for geometric morphometrics of Greenland cod.

morphological analyses. Photos with a missing landmark or received a ranking of 1 for either category were eliminated from further analysis.

Statistical Analyses

Landmark coordinates were standardized to remove the effects of size, position, and orientation on each image using the gpagen function within the R package geomorph (Adams et al., 2021) to obtain Procrustes coordinates. Principal component analysis (PCA) of Procrustes coordinates was performed using the gm.prcomp function. Minimum and maximum eigenvalues were obtained to create deformation grids outlining cod shape to visualize shape deviations relative to the mean position of each landmark using the plotRefToTarget function.

Nine linear measurements were collected for each fish by calculating the distance between landmark pairs (Figure 4). Linear distances were size-adjusted following Reist (1985):

$$\mathrm{log^{10}Y_i = log^{10}M_i + b(log^{10}L_m - \ log^{10}L_i)}$$

where $\mathrm{Y_i}$ is the size-adjusted linear measurement, $\mathrm{M_i}$ is the measured linear measurement, b is the linear regression coefficient (slope) of the measured linear measurement ($\mathrm{log^{10}M_i}$) against fork length ($\mathrm{log^{10}L_i}$), and $\mathrm{L_m}$ is the average fork length across all fish and $\mathrm{L_i}$ is the measured fork length. Linear measurements were allometrically aligned to the mean fork length of 36.81cm.

PCA was applied to all nine size-adjusted measurements using the PCA function within the R package FactoMineR (Lê et al., 2008). The two principal components (PCs) explaining the most variation in the data were plotted on a two-dimensional plane for data visualization. Using the silhouette method, the optimal number of clusters, *k*, was determined using the function fviz_nbclust function within the R package factoextra (Kassambara and Mundt, 2020). Data were clustered into *k* groups using the kmeans function within R (R Core Team, 2020), such that the sum of squares from points to the assigned cluster centers is minimized. Identified clusters were used to represent cod morphotypes within the sampled population.

A one-way multivariate analysis of variance (MANOVA) was conducted to test for differences in the nine size-adjusted linear measurements across clusters. Assumptions of normality (Shapiro-Wilk test) and equal variances (Levene’s test) were conducted before MANOVA testing. MANOVAs with significant effects were followed up with *post hoc* Student T-tests to determine which size-adjusted linear measurements explained variation between clusters. To reduce the likelihood of Type I error, a Bonferroni correction was applied to the multiple comparisons.

Stable Isotope Analyses

Data Preparation

Plasma and RBC samples were freeze-dried and ground to a homogenous powder. Lipid extraction was conducted using the Solvent Distillation method. In brief, 2:1 chloroform:methanol solution was added to the homogenized powder, agitated and left in a 30°C water bath for 24 hours. The solvent was then decanted, and samples were air-dried using a fume hood. Samples and standards were then weighed into tin cups (5mm x 9mm) and analyzed using a 4010 Elemental Analyzer (Costech Instruments, Italy), coupled to a Delta Plus XL (Thermo-Finnigan, German) continuous flow isotope ratio mass spectrometer (CFIRMS) at the University of Waterloo Environmental Isotope Laboratory. All resulting measurements were expressed in standard delta (δ) notation as parts per thousand differences (‰) relative to international standard reference materials for carbon (Vienna Pee Dee Belemnite; Coplen et al., 2002) and nitrogen (atmospheric nitrogen; IAEA 1995), using the following equation:

$$\delta R\ (‰) = [R_{\text{sample}}/R_{\text{standard}} - 1] \times 1000$$

where R is the ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Analytical precision was ± 0.2‰ and ± 0.3‰ for $\delta^{13}C$ and $\delta^{15}N$ respectively, where reference materials of USGS 40 and USGS 41 from L-glutamic acid were run in duplicates after every ten samples.

Statistical Analyses

To derive information on temporal habitat-trophic shifts at the individual level, analyses of stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) were performed on multiple tissues per individual (RBC and plasma, i.e. slow vs. fast turnover). Prior to analyses, lipid-extracted isotope values were corrected with diet-tissue discrimination factors to standardize values given the difference in turnover rates between tissues. Diet-tissue discrimination factors based on a controlled study of the leopard coral grouper (*Plectropomus leopardus*) were applied (δ^{13}C: plasma; 1.2‰, RBC; 0.1‰ and δ^{15}N: plasma; 0.9‰, RBC; 1.1‰) (Matley et al., 2016). Given the absence of species-specific discrimination factors for Greenland cod, these values were selected based on comparable tissue types (Dalerum and Angerbjörn, 2005), lipid extraction treatment (Murry et al., 2006), environment type (marine; Vanderklift and Ponsard, 2003), and biology (Frisch et al., 2016; Mikhail and Welch, 1989). Discrimination-corrected RBC and plasma values were first compared between cluster groups using Student T-tests for δ^{13}C and δ^{15}N separately. Assumptions of normality (Shapiro-Wilk test) and equal variances (Levene's test) were examined prior to analysis.

Individual Specialization Metrics

Individual specialization metrics using stable isotope values were calculated for cluster groups and the total sample population. Following Newsome et al. (2009), separate LMEs for δ^{13}C and δ^{15}N were used to analyze variance using the lmer function within the R package lme4 (Bates et al., 2015). Variation displayed in δ^{13}C and δ^{15}N of RBC and plasma tissues from individual cod can be explained by a combination of fixed and random effects. Effects included in our final model were based on significant effects on δ^{13}C and δ^{15}N values derived from the full model. Non-significant variables ($p > 0.05$) with a variance of zero were excluded from the final model. In our model, fork length and tissue type were considered fixed effects and individual fish ID was considered a random effect. Models were performed using discrimination-corrected δ^{13}C and δ^{15}N values. The residual variance represents the variance not explained by the identified sources, herein referred to as the within individual component (WIC). Variance between individual fish represents the between individual component (BIC). The sum of BIC and WIC represents the total niche width (TNW) of the population. Diet specialists are broadly defined as having a narrow niche (WIC) relative to the total niche (TNW) (Bolnick et al., 2003). Through analysis of variance from our models, we would expect that diet generalists display greater WIC values from higher residual variance, and diet specialists would display greater BIC values from higher variance between individuals. Specialization indices were calculated and standardized as the proportion of WIC:TNW and allowed for comparison between cluster groups.

To calculate individual WIC values, separate $\delta^{13}C$ and $\delta^{15}N$ predicted linear models were fit against actual RBC versus plasma values. The absolute difference between the predicted and actual values represents residual variance and were thus used to represent individual WIC values. The effects of cluster, fork length, and year on individual WIC values for $\delta^{13}C$ and $\delta^{15}N$, were tested via general linear models (GLMs) using the glm function in R (R Core Team, 2020). Non-significant interaction terms were dropped sequentially, starting with those with the smallest t values, but were retained if their removal resulted in higher AIC values [ΔAIC > 2 (Arnold, 2010)]. Assumptions of normality and multicollinearity of the response variable were checked and WIC values were log10 transformed prior to testing. All statistical analyses were performed using R software, Ver. 4.1.1 (R Core Team, 2020). Significance was tested at $\alpha = 0.05$.

RESULTS

Quantifying Morphological Variation and Establishing Morphotypes

A total of 117 Greenland cod (2018: n = 69, 2019: n = 48) ranging in size from 251.9mm to 578mm (mean 388.58 ± 57.63mm SD, n = 102 where length was available) and weight from 250g to 2000g (mean 882.04 ± 340.93g SD, n = 109 where weight was available), were caught and sampled for geometric morphometric analyses. Of those, 72 were excluded following our assessment criteria, resulting in a final sample size of 45 fish (2018: n=19, 2019: n=26).

For the PCA conducted on the nine size-adjusted linear measurements (Table A1). PC1 and PC2 accounted for 64.7% of the total variation. PC1 accounted for 38% of the total variation, principally from variation in head features, including head length, head depth, snout length and eye width (Figure 5). Through deformation grids, extreme positive PC1 values showed more deformations in the body, resulting in a longer head depth and enlarged body depth anterior (cluster one). Extreme negative PC1 values showed deformations centered around the intersection of the head and body regions, resulting in a shortened head and reduced body depth anterior (cluster two). PC2 accounted for 26.8% of the total variation and was explained mainly by body depth posterior and caudal peduncle depth. Variation in PC2 values was mainly present in the posterior end of the fish. However, the natural bending of the fish during photography may have also contributed to deformations of this nature. Subsequent clustering analysis of PC1 and PC2 data revealed two distinct clusters, with head features explaining the majority of this distinction (Figure 5).

MANOVA indicated that linear measurements significantly differed between cluster groups (Pillai's Trace: F=6.20, $p < .001$; Table 1, Table A1). *Post hoc* Student T-tests showed significant differences between cluster groups for all size-adjusted linear measurements with the exception of the caudal peduncle ($t = -1.3$, $p = 0.19$). This was despite the fact that caudal peduncle contributed the most to variation observed in PC2. Post pelvic fin length (PPFL) had the strongest overall effect on the difference between the clusters ($t = 25.9$, $p < 0.001$), while of all head features (head depth, head length, snout length, eye width, and maxilla length) significantly differed between the two clusters. Of the head features, head length and head depth contributed the most variation ($t = 16.8$, $p < .001$ and $t = 13.4$, $p < .001$, respectively).

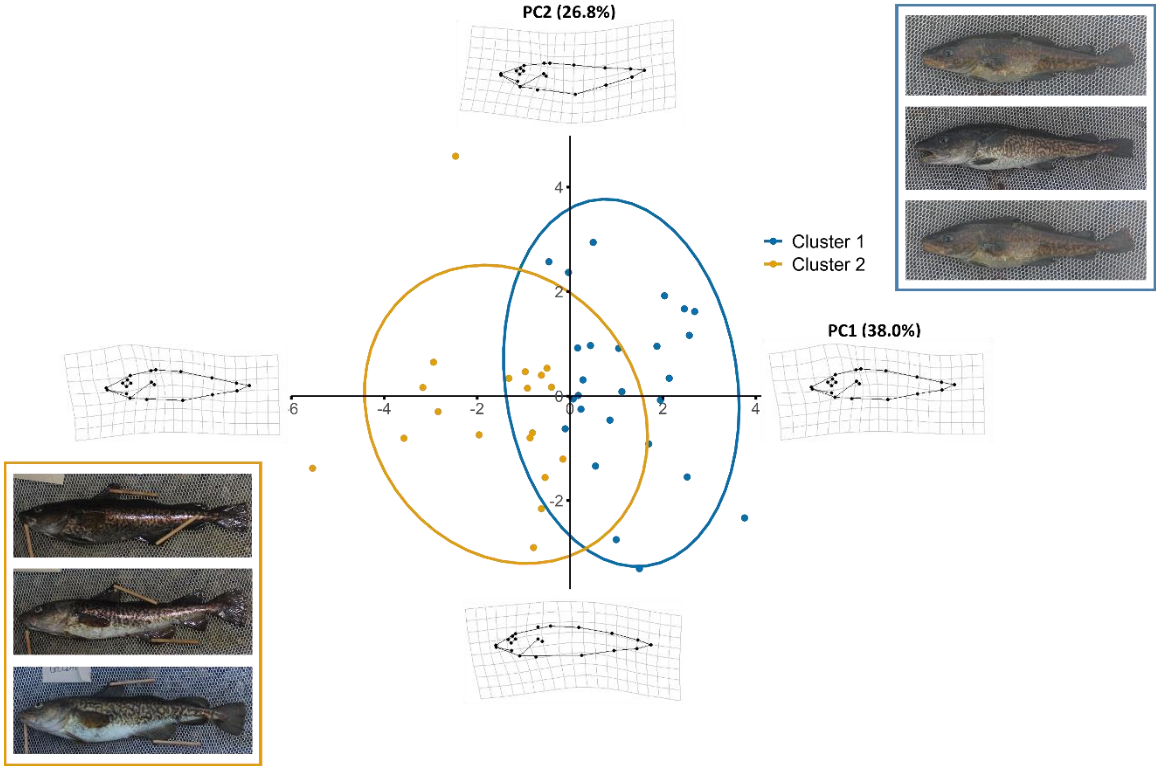


Figure 5: Principal component analysis (PC1 and PC2) of body shape for the two identified cluster groups of Greenland cod using kmeans clustering. Deformation grids represent shape variation along each extreme of the axes (PC1 on X axis, PC2 on Y axis).

Table 1: Summary of size-adjusted linear measurements (mean ± standard error (SE) and range in mm). Post hoc Student T-tests show comparisons between cluster groups 1 (n = 26) and 2 (n = 19) for each linear measurement.

Linear Measurement		**Sample population mean x ± SE Range (mm)**	**Mean measurement (mm)**		**T-test**		
			Cluster 1	**Cluster 2**	***t***	**df**	***p*-value**
CP	Caudal peduncle	1.32 ± .0065 1.25 to -18.03	1.33	1.31	-1.3	44.7	0.19
BDP	Body depth posterior	1.82 ± .011 1.65 to 1.96	1.84	1.78	5.2	46	< .001
BDA	Body depth anterior	2.66 ± .0097 2.50 to 2.79	2.69	2.62	16.5	45.5	< .001
PPFL	Postpelvic fin length	3.37 ± .01 3.18 to 3.49	3.38	3.35	25.9	45.6	< .001
HD	Head depth	2.43 ± .011 2.25 to 2.55	2.47	2.38	13.4	45.9	< .001
HL	Head length	2.69 ± .014 2.42 to 2.91	2.74	2.62	16.8	47.2	< .001
SL	Snout length	1.68 ± .015 1.32 to 1.93	1.72	1.63	3.4	47.6	< 0.05
EW	Eye width	1.25 ± .011 1.04 to 1.41	1.28	1.20	-2.3	45.9	< 0.05
ML	Maxilla length	1.79 ± .017 1.54 to 2.09	1.83	1.74	4.9	48.5	< .001

Quantifying Intraspecific Variation from Stable Isotope Analyses

A total of 31 RBC and plasma samples (cluster one: n = 26, cluster two: n = 19) were analyzed for δ^{13}C and δ^{15}N (Table 2). Discrimination-corrected δ^{13}C values ranged from -22.02‰ to -18.85‰ in RBC and from -24.22‰ to -19.23‰ in plasma. While RBC and plasma δ^{13}C values were slightly higher in cluster two compared to cluster one, no significant difference between cluster groups for RBC (t = -1.5, df = 26, p = 0.15) or plasma (t = -2.0, df = 26, p = 0.06) were observed. Discrimination-corrected δ^{15}N values ranged from 13.66‰ to 17.19 ‰ in RBC and from 13.35‰ to 17.01‰ in plasma. Plasma δ^{15}N values generally displayed greater variation compared to RBC, but there was no significant difference between cluster groups for either RBC (t = -1.5, df = 34, p = 0.13) or plasma (t = -1.8, df = 29, p = 0.08).

Table 2: Summary of discrimination-corrected δ^{13}C and δ^{15}N values (mean ± standard error (SE) and range in ‰) of RBC and plasma for identified cluster groups. Subsequent results from Student T-tests are also shown.

		Cluster 1			**Cluster 2**			**T-test**		
	Tissue	**n**	**Mean x ± SE** **Range (‰)**	**Std dev**	**n**	**Mean x ± SE** **Range (‰)**	**Std dev**	***t***	**df**	**p**
δ^{13}C	RBC	26	-21.05 ± 0.13 -21.71 to -19.18	0.61	19	-20.7 ± 0.20 -22.02 to -18.85	0.76	-1.5	26	0.15
	Plasma	26	-22.46 ± 0.32 -24.22 to -19.61	1.37	19	-21.59 ± 0.32 -23.41 to -19.23	1.14	-2.0	26	0.06
	RBC - plasma	19	1.42 ± 0.32 -2.01 to 2.88	1.41	12	0.86 ± 0.22 -0.16 to 2.19	0.74	1.5	28	0.15
δ^{15}N	RBC	26	15.03 ± 0.20 13.66 to 17.19	0.90	19	15.40 ± 0.15 14.36 to 16.37	0.57	-1.5	34	0.13
	Plasma	26	14.83 ± 0.25 13.35 to 17.01	1.09	19	15.47 ± 0.20 14.39 to 16.57	0.72	-1.8	29	0.08
	RBC - plasma	19	0.22 ± 0.16 -1.71 to 1.63	0.69	12	-0.12 ± 0.20 -1.45 to 1.16	0.70	1.3	23	0.19

To examine habitat and trophic shifts (RBC – plasma; $\delta^{13}C$ and $\delta^{15}N$), individual fish that were missing either RBC or plasma values were removed, providing a total of 31 individuals with paired tissue isotope data (cluster one: n = 19, cluster two: n = 12). While the absolute difference between RBC and plasma $\delta^{13}C$ values from cluster one showed greater variation compared to cluster two, the difference in $\delta^{15}N$ values showed greater variation in cluster two versus cluster one (Figure 6). Student T-tests revealed no significant difference between cluster groups for either $\delta^{13}C$ (t = 1.5, df = 28, p = 0.15) or $\delta^{15}N$ (t = 1.3, df = 23, p = 0.19).

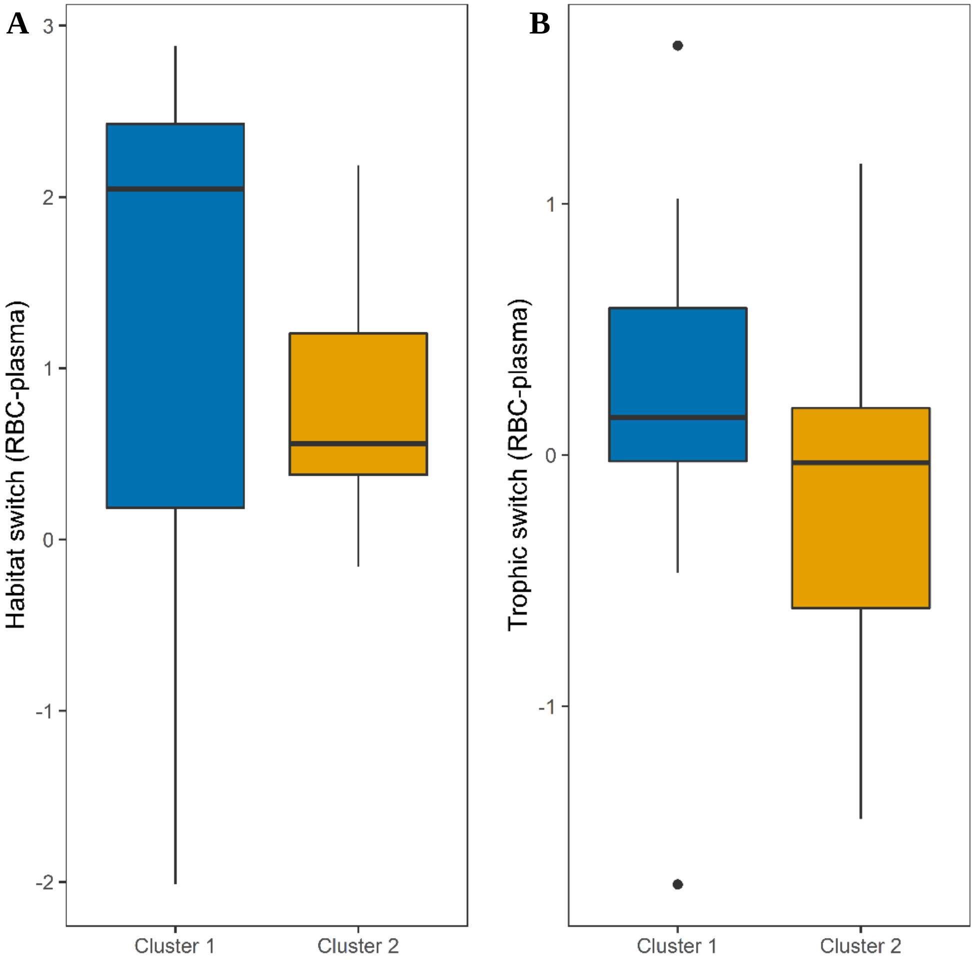


Figure 6: Comparison of discrimination-corrected habitat and trophic switch values between identified cluster groups for lipid-extracted a) $\delta^{13}C$ and b) $\delta^{15}N$ stable isotopes.

Measuring Individual Specialization

The δ^{13}C LME revealed that cluster two tended to be the most specialized in habitat use compared to cluster one and population (WIC:TNW: 1.00 (cluster one), 0.43 (cluster two); 1.00 (population), Figure 7). BIC for cluster two was higher (0.36) in comparison to cluster one (0.00) and population (0.00). WIC was highest in cluster one (0.69) and population (0.66), and lowest in cluster two (0.27). The δ^{15}N LME revealed that cluster one displayed higher trophic specialization compared to cluster two and total population (WIC:TNW: 0.40 (cluster one), 0.92 (cluster two); 0.35 (population), Figure 7). BIC for cluster one was higher (0.36) in comparison

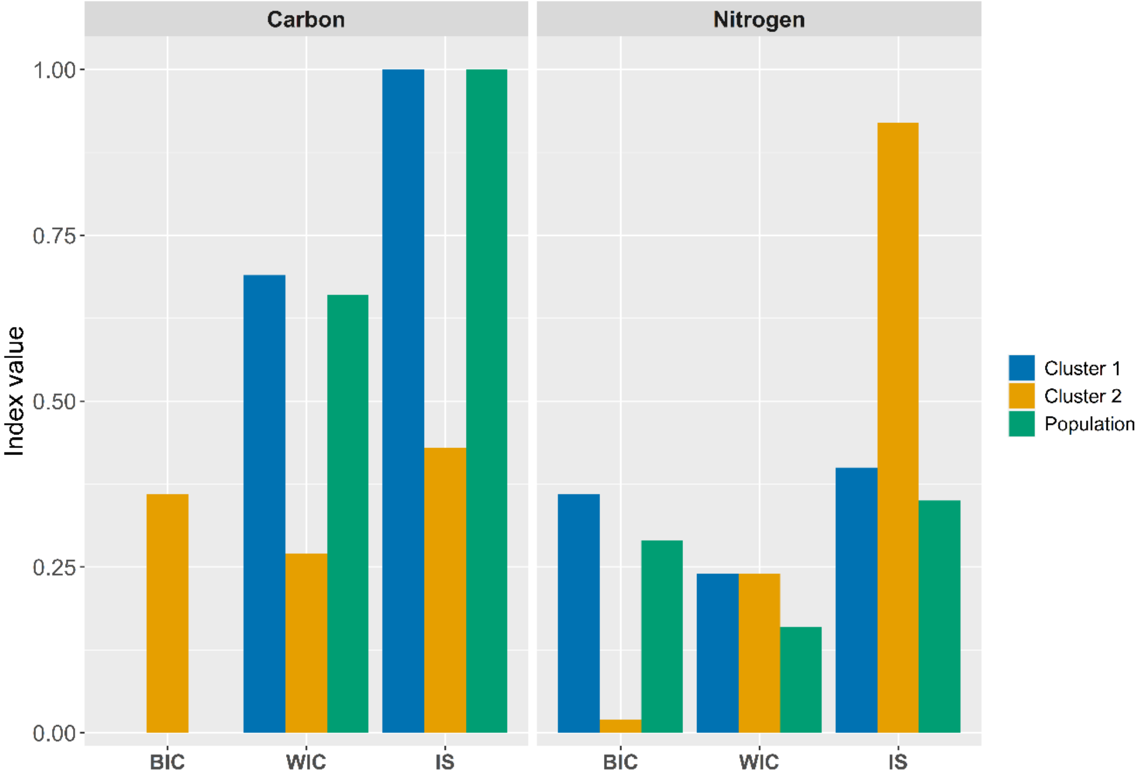


Figure 7: Individual specialization indices derived from discrimination-corrected lipid-extracted δ^{13}C (left panel) and δ^{15}N (right panel) stable isotope values for cluster one, cluster two, and total sample population using linear mixed-effects models (LMEs), previously described in Newsome et al. (2009). Between individual component (BIC), within individual component (WIC) and individual specialization (IS) indices are shown.

to population (0.29) and cluster two (0.02). WIC was higher in both clusters one (0.24) and two (0.24), compared to population (0.16).

Factors Affecting Individual Specialization

Individual δ^{13}C WIC values of cod ranged from 0.035 to 3.15 (mean 1.05 ± 0.57 SD), with 55% of the total sample population having an index value of < 0.5. WIC values for δ^{13}C showed a significant relationship with cluster, fork length, and year ($p > 0.05$; Table 3). Individual δ^{15}N values ranged from 0.013 to 1.72 (mean 0.50 ± 0.47 SD), with 14% of the total sample population having a WIC value of < 0.5. WIC values for δ^{15}N were not associated with cluster, fork length, or year ($p > 0.05$; Table 3).

Table 3: General linear model (GLM) results for the effects of cluster, fork length, and year on δ^{13}C and δ^{15}N within individual component (WIC) values. Note that estimates and standard errors (SE) were back-transformed from their common logarithm ($\log_{10}$). Results are shown for the most parsimonious model (ΔAIC < 2).

	Estimate	**SE**	**p**
δ^{13}C WIC			
Cluster	0.49	1.31	0.01
Fork length	1.00	1.00	0.003
Year	1.92	1.34	0.03
δ^{15}N WIC			
Cluster	1.40	1.79	0.57
Fork length	1.00	1.00	0.48
Year	1.24	1.88	0.73

DISCUSSION

In the current study, we quantified the extent of morphotype correlated habitat-trophic specialization within Greenland cod. We identified two morphotypes of Greenland cod that differed primarily in head length and body depth. Measures of individual specialization indicated that the morph with the smaller head and slender body had lower habitat specialization and higher trophic specialization compared to the morph with the larger head and stockier body.

Stable isotope values of $\delta^{13}C$ and $\delta^{15}N$ from blood tissues showed minimal differences between morphotypes. However, notable variation in specialization was observed across individuals. We postulate that the observed morphotypes linked to a high degree of variation in habitat-trophic diversity metrics can be displayed as a range of generalist-specialist traits rather than distinct morphs to describe individuals and populations. This furthers our understanding of the potential responses of marine fish, such as Greenland cod, in a changing climate.

Intraspecific variation in morphological traits was observed in the Greenland cod population sampled, which can arise from individual differences in resource acquisition (Binning and Chapman, 2010) and habitat use (Winkler et al., 2017). The larger head paired with a stockier body associated with cluster one may be beneficial for consuming multiple or larger-sized prey items and specialized for low-speed maneuvering and navigating complex habitats with precision such as rocky benthic areas (Webb, 1984). Gape size can dictate prey selection, with larger-sized heads selecting larger prey items (Mihalitsis and Bellwood, 2017). Contrastingly, the smaller head and slender body associated with cluster two is better suited for consuming fewer (i.e. in one event) or smaller prey items, but individuals typically exhibit greater speed that improves maneuverability to catch faster and more agile prey (Webb, 1984). These observed differences in morphological specializations could represent performance trade-offs based on handling efficiency linked to mouth size, and encounter rates according to maneuverability and habitat use.

Performance trade-offs linked to morphology can be observed across populations occupying overlapping niches. It was proposed that three distinct morphs of migratory anadromous Arctic char (*Salvelinus alpinus*) that were also sampled in Ulukhaktok, NT and Safety Channel were likely driven by ecological differences linked to resource or habitat use

(Burke et al., 2022). The difference in the number of morphs observed in Arctic char compared to Greenland cod may be a result of contrasting life history patterns, where migratory Arctic char encounter marine, estuarine, or freshwater environments (Hollins et al., 2022; Moore et al., 2016), and can spend proportionally more time in one environment versus another (e.g. long versus short river runs; long versus short sea-run migrations to core foraging habitat). This could promote diversification into different morphotypes as a result of contrasting phenotypes optimized to occupy such environments, encouraging the potential for niche specialization (Hollins et al., 2022). In contrast, non-migratory Greenland cod inhabit marine environments year-round, which may help explain the reduced phenotypic diversity or morphotypes required to adapt to the environments they occupy. It is apparent, however, that the morphs of both species can be displayed over a gradient rather than distinct morphs.

Findings from morphological assessments linked to stable isotope analysis demonstrate that Greenland cod display variation in feeding behaviours across morphotypes. The LMEs revealed that the morph with the elongated head and stockier body (cluster one) displayed higher habitat specialization from $\delta^{13}C$ values (i.e. restricted habitat range or consumption of basal carbon sources) and lower trophic specialization $\delta^{15}N$ values (i.e. feeding across trophic levels). The stockier body associated with cluster one could reflect reduced maneuverability and speed (Webb, 1984), leading to reduced foraging behaviours across different habitats that could result in more generalist individuals. Contrastingly, the morph with the shorter head and slender body (cluster two) displayed lower habitat specialization (i.e. occupied a broader foraging habitat or consumed more diverse basal carbon) and higher trophic specialization (i.e. feeding on prey at a similar trophic level). The slender body could help maneuvering at higher speeds (Webb, 1984) and allow individuals to be selective, or specialize on particular prey. Patterns of functional morphology have been correlated with feeding behaviours in a variety of fish species, where benthivorous feeding has been documented in deeper-bodied fish (cluster one), and limnetic feeding activities have been linked to shallower-bodied fish (cluster two; Hendry, 2009; Robinson and Parsons, 2002). Our variations in specialization indices and absolute δ^{13}C tissue differences across individual cod may be a reflection of habitat segregation among benthic versus pelagic (Hobson et al., 1995) and coastal versus offshore areas (Hobson et al., 1994). The inclusion of spatial movement data of individual fish and baseline isotopic data of the marine environment (Rogers and White, 2007) could help further tease apart causation of morphological differences and observed specialization values and ranges.

Despite the non-significant differences in δ^{13}C and δ^{15}N between morphotypes and less variation when WIC was calculated at the individual level, the observed pattern of variation could reflect a gradient of habitat or trophic segregation among coastal versus offshore areas and benthic versus pelagic feeding (Hobson et al., 1995), respectively. The fact that the distinction was marginal across the two morphotypes could suggest that morphology is not a key factor regulating their occurrence in a specific habitat. Alternatively, morphology may allow greater flexibility whereby individual fish do not undertake distinct movement behaviours but proportionally spend more time in some habitats that others. Our range in individual WIC values and absolute isotope tissue-difference data across the two morphotypes support adaption to high connectivity across habitat types.

While variation in δ^{13}C and δ^{15}N values was observed within clusters, it may be insufficient for individuals to diverge into discrete morphotypes with entirely distinct patterns in resource use, suggesting evidence of cod’s generalist niche. Given that cod were sampled in similar locations characterized by coastal benthic environments, this area may support two morphs through providing a relatively consistent pool of resources suitable for cod that aligns with a generalist feeding strategy. However, intraspecific variation in niche use could occur within the population to alleviate selection pressures and reduce competition among individuals (Skulason and Smith, 1995). Greenland cod consume small fish, crustaceans, and molluscs (McNicholl et al., 2017) and are found in structurally complex areas (Knickle and Rose, 2014). Arctic coastal habitats are also considered highly dynamic and biologically complex (Irrgang et al., 2022), which creates opportunities for fish to occupy such environments year-round for feeding and habitat use (Friedman et al., 2020; Kutti et al., 2015), potentially allowing individuals with a wide range of traits to inhabit and thrive in these mixed environments.

Annual ice breakup can greatly influence the availability of resources in the Arctic, leading to seasonal resources pulses (Yang et al., 2008). In our study, sampling of Greenland cod occurred during the ice-free season following a resource pulse event, where the observed habitat-trophic switches could represent a period of higher activity due to increased productivity and prey availability following ice melt (Hermann et al., 2023; Hop et al., 2011). Seasonal prey shifts documented from stomach content analysis revealed that Greenland cod shifted from higher trophic level feeding in the winter to lower trophic feeding in the summer, likely due to temperature and prey availability (Morin et al., 1991). Therefore, the longer turnover rates of RBCs (weeks – months) in our study may have captured winter pre-ice breakup conditions and could reflect feeding activity on higher trophic level prey. The non-significant difference between habitat and trophic switch values (absolute RBC-plasma) between groups may also show that resource pulses could have little to no impact on feeding activity over time. However, variation in specialist and generalist behaviours via our LMEs potentially indicates that some fish are responding differently to the resource pulse with potentially higher activity rates during consumption of more variable prey (whether from habitat or trophic level specific, i.e. $\delta^{13}C$ and $\delta^{15}N$). Nevertheless, habitat-trophic variation can be viewed as a gradient where individuals have overlapping niches and individuals may co-exist.

Intraspecific differences in habitat-trophic niche derived from $\delta^{13}C$ and $\delta^{15}N$ GLMs showed significant impacts from cluster, fork length, and year on $\delta^{13}C$ WIC values and no impact on $\delta^{15}N$ WIC values. Suggesting that habitat segregation (from $\delta^{13}C$ values) has more impact across the sampled cod population and less from differences in trophic level feeding (from $\delta^{15}N$ values). Cluster groups were primarily defined by distinctions in head and body shape and showed significant effects on individual habitat specialization between morphs. However, the lack of association between cluster and trophic level may occur due to overlapping trophic use between morphs. Ontogenetic patterns were also studied across the same individuals used in our study and showed that cod were generalists across different prey and habitats, regardless of size (Pettitt-Wade et al., 2023) and may help explain the weak association of fork length with trophic level specialization according to our $\delta^{15}N$ GLM. Environmental conditions across sampling years could impact habitat availability or use during feeding activity, but may still offer similar prey types that allow for trophic specialization to remain unaffected. Some the ecological differences observed in our model likely occurred due to factors unmeasured within our study. Additional considerations for the spatial ecology using acoustic telemetry could clarify movement patterns and habitat use among distinct morphotypes (Hawley et al., 2016; Rogers and White, 2007). The inclusion of stomach content data could also provide evidence of specific prey items consumed by individuals over a short time scale and complement feeding data gathered from stable isotopes (Araújo et al., 2011) and could be used to clarify individual feeding choices and specialization in prey items.

The impacts of climate change are expected to produce variable responses across individuals as a result of the observed intraspecific variation in the sampled Greenland cod population. Poleward species distribution shifts have been documented and are projected to continue (Baker, 2021). Among the sub-Arctic Gadids that are expanding northwards, Pacific cod (*Gadus macrocephalus*) are of particular concern given their current range expansion into Pacific Arctic waters and are projected to continue (Spies et al., 2020). Evidence of overlap in the distribution and feeding patterns of Greenland cod and the Atlantic cod has been documented, with strongest occurrence in coastal and shallow areas that would likely result in interspecific competition for food and space (Nielsen and Andersen, 2001). Greenland cod in the western Canadian Arctic could experience increasing occurrences of overlap with sub-Arctic species, potentially causing competition and predation between populations. With the potential for this increased niche overlap, Arctic generalists may be less impacted by competition as they would likely switch to alternative resources (Vázquez and Simberloff, 2002). Arctic specialists that possess a narrower niche may not necessarily experience overlap. However, they may be highly vulnerable in the event that their specialized niche experiences an environmental disturbance (Wilson et al., 2008). The consequences of borealization may also affect food web structure (Fossheim et al., 2015), resulting in changes in prey availability (Florko et al., 2021). Generalist individuals could adapt and shift their diet to other available resources, whereas specialist individuals could be severely affected if their diet is focused on a particular resource that is vulnerable to climate-induced changes. The cumulative impacts of increasing overlap with sub-Arctic species and changes in prey availability could benefit or have minimal effect on generalist individuals, as the introduction of new prey types could increase prey diversity with little consequence on overall resource availability or abundance in their diet. For specialist individuals, the cumulative impacts could result in native prey being outcompeted, limiting their only food source. Further considerations from our study revealed that Greenland cod morphotypes can be displayed as a gradient attributed to different feeding behaviours and may benefit these generalists in the future given their broad niche and ability to adapt to a larger variety of resources.

When considering caveats of this study, fish discrimination factors are influenced by temperature (Britton and Busst, 2018; Canseco et al., 2022), and typically increase with decreasing temperatures (Barnes et al., 2007; Godiksen et al., 2019) due to lower metabolic rates in cold-adapted species (Maitland et al., 2021). The clear differences in environmental temperature between our study species and the conditions from the selected discrimination factors of the leopard coral grouper could therefore have influenced our numerical outcomes. The discrimination factors used, however, were for a species that is most similar in morphology and behaviour, albeit in a tropical environment and were considered the most applicable. Turnover rates would also be slower in Greenland cod due to the lower assimilation rate of stable isotopes from prey consumed that may cause a delay when a diet switch is reflected. Discrimination factors specific to Greenland cod would improve our individual specialization estimates. Finally, landmark identification from morphometrics is difficult in species with low colour contrast in body features. We therefore accept that this may have impacted the accuracy of landmark identification for Greenland cod.

CONCLUSION

As climate change continues to alter Arctic marine ecosystems, the broad niche and spectrum of generalist-specialist behaviours of Greenland cod could create variable responses to environmental disturbances and may be key to their resilience in the future. The ongoing borealization of sub-Arctic species to an arctic environment where resources are inherently limited may favour generalists that may be more capable of shifting their resource use to minimize niche overlap and competition with sub-Arctic species. Further work should focus on potential interactions between native Arctic species and closely related sub-Arctic species. Our findings highlight the importance of maintaining trait variation to conserve diversity and promote resilience under a changing climate. Fisheries management and conservation strategies should be more inclusive towards population-level trait diversity to promote adaptability and resilience to changing environmental conditions. Studying the ecology of Greenland cod serves as a valuable tool to better understand the impacts of climate change on coastal marine ecosystems and can help inform management decisions of subsistence species in the Canadian Arctic.

ETHICAL STATEMENT

Strict ethical guidelines were followed from the Canadian Council on Animal Care for the handling of live animals with approval from the University of Windsor Animal Care Committee; Reference #18-03, and Fisheries and Oceans Canada License to Collect Fish for Scientific Purposes; License # S-19/20-3000-YK. As guided by the Inuvialuit Game Council, the work was completed with full support and approval from the OHTC and with collaborative feedback from the UCWG.

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APPENDIX A

Table A1: Contribution (%) of size-adjusted linear measurements expressed as Principal Components (PC) towards total variation representing Greenland cod morphology.

PC Axis	Eigenvalue	Percent Variance (%)	Cumulative Percent Variance (%)
PC1	3.4	38.0	38.0
PC2	2.4	26.8	64.7
PC3	0.9	10.3	75.1
PC4	0.8	8.6	83.6
PC5	0.6	7.1	90.8
PC6	0.3	3.9	94.6
PC7	0.2	2.6	97.2
PC8	0.1	1.5	98.7
PC9	0.1	1.3	100.0

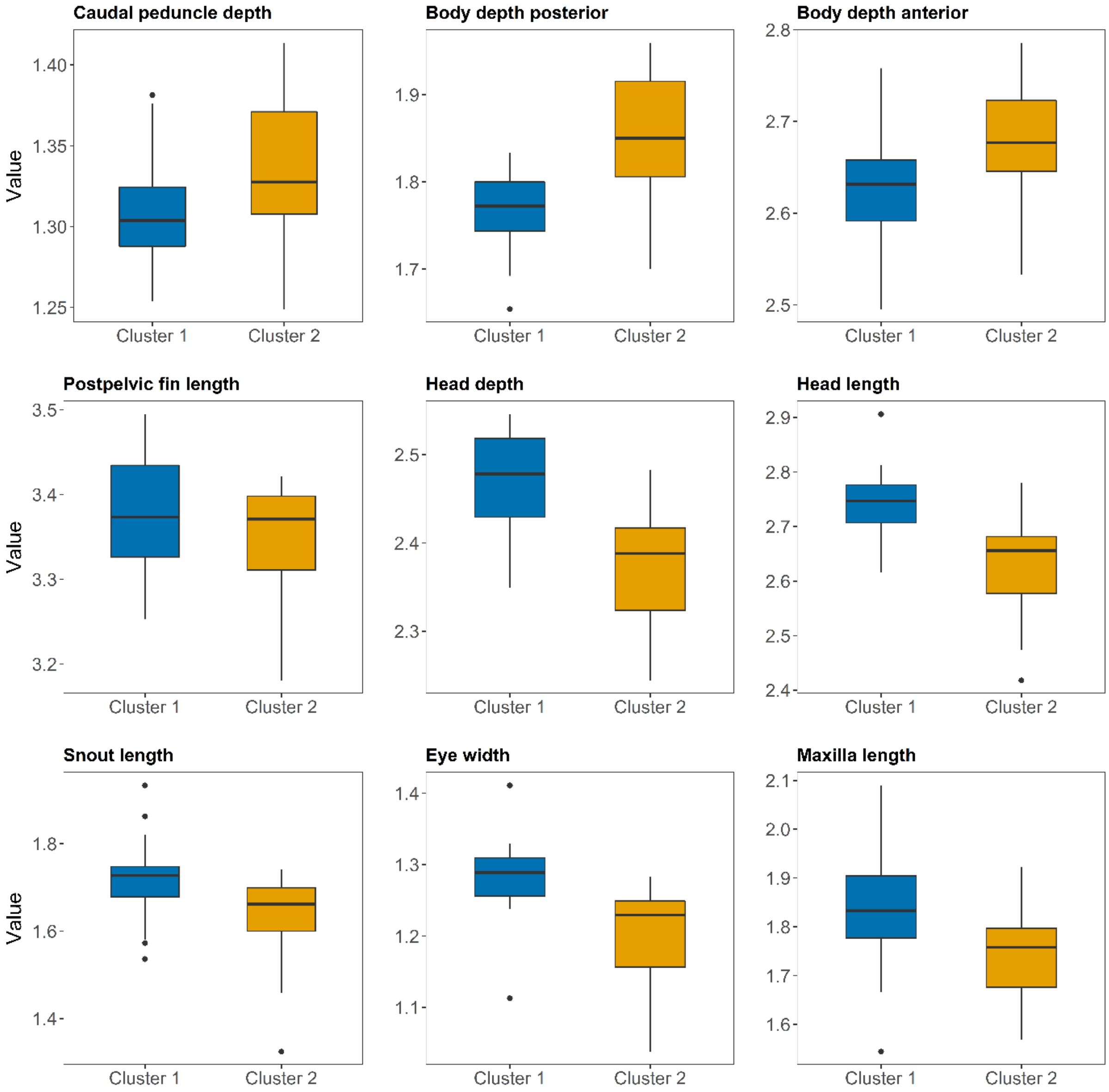

Figure A1: Box plot comparisons of nine size-adjusted linear measurements for identified cluster groups of Greenland cod (cluster 1: n = 26, cluster 2: n = 19).

CONNECTING STATEMENT

The previous chapter adds to the current state of knowledge pertaining to the ecology of coastal marine species in the western Canadian Arctic. Under projected climate change scenarios, Greenland cod generalists may be capable of shifting their ecological niche to reduce competition with sub-Arctic species with ongoing borealization, suggesting a level of adaptation potential under changing environmental conditions. The reported findings document the baseline ecology of this species and potential implications under a changing climate. It is imperative that scientific approaches continue to monitor coastal fish species to properly inform conservation and management decisions in the Arctic. Additional consideration for local knowledge can generate enriched findings that would improve co-management decisions.

In the following chapter, we document Inuit knowledge of Greenland cod and review cumulative knowledge to gain a more comprehensive understanding of this species. Findings from the previous chapter are integrated here to elicit discussion among Inuit and scientists to co-interpret the information and allow for further discussion that may not be captured through scientific interpretations alone. This next chapter chapter intends to build on the previous chapter by considering the needs for Inuit subsistence and harvesting activities that would better inform co-management initiatives of coastal marine species in the region. These manuscript style chapters are stand-alone documents but provide complementary information to generate a more in-depth understanding of this species, its role in the marine environment, and connections to Inuit coastal communities in the western Canadian Arctic.

CHAPTER 4: LINKING INUIT AND SCIENTIFIC KNOWLEDGE IN COASTAL MARINE RESEARCH: ADVANCING OUR UNDERSTANDING OF GREENLAND COD (*GADUS OGAC*) IN THE CANADIAN ARCTIC

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ABSTRACT

This paper links Inuit and scientific knowledge of Greenland cod in the marine ecosystem near Ulukhaktok, Northwest Territories (NT), Canada to better understand their ecology in a changing climate. The project was co-designed with Ulukhaktomiut (Inuit from Ulukhaktok) and used telemetry, biological fish samples, and Inuit knowledge to analyze individual movement, appearance, and health. We conducted 16 interviews with 21 Inuit knowledge holders that involved using photographs of the sampled fish, and the results of morphometric, stable isotope, and telemetry data to elicit discussion on their morphology, feeding, and movement behaviour. Ulukhaktomiut were able to build a rationale for some of the phenomena observed, such as habitat associations among different morphotypes, identify movement locations beyond what was captured by telemetry, and identify early signs of ecosystem change. Linking Inuit and scientific knowledge was a two-way process in which the knowledge systems built off one another to inform the next steps in the research process and interpret the findings more holistically. The results of this research are intended to inform the design of future research on Arctic coastal marine species in a changing climate and advance our understanding of how to link Inuit and scientific knowledge to generate enriched findings.

KEYWORDS: Arctic, Inuit, Greenland cod, knowledge co-production, marine ecosystem, Inuvialuit, Traditional Ecological Knowledge, TEK, Ulukhaktok

INTRODUCTION

Arctic marine ecosystems are experiencing rapid changes due to anthropogenic climate change (Meredith et al., 2019). Changing coastlines (Fritz et al., 2017) and altered spatial distribution and composition of fish populations have been observed (Fossheim et al., 2015; Frainer et al., 2017), with subsequent impacts on the availability of fish species important for Inuit subsistence. These changing conditions are also causing the range expansion of southern fish species into arctic environments (Fossheim et al., 2015). In the Pacific Arctic region, changes in species composition of Gadids have been recorded (Wildes et al., 2022), with observed range expansions of sub-arctic Gadids such as Pacific cod and walleye pollock (Baker, 2021; Spies et al., 2020; Stafford et al., 2022). With the ongoing northward expansion of sub-arctic species into arctic waters (Fossheim et al., 2015; von Biela et al., 2023), baseline information on many arctic fish species is sparse, leaving future interactions between native and non-native species unclear. Subsistence fishing continues to be a valued activity among Inuit in the Canadian Arctic for food production, and has strong economic, dietary, and cultural importance (Condon et al., 1995; Pearce et al., 2011). The paucity of baseline information and long-term data in many arctic marine ecosystems, however, makes management plans difficult to develop. Addressing this challenge requires collaborative efforts across disciplines and consideration for multiple ways of knowing, including Inuit and scientific knowledge.

In the Canadian Arctic, knowledge co-production can be broadly defined as the bridging of local and scientific knowledge to enhance the understanding of the changing environment, intended to inform management and conservation practices (Yua et al., 2022). The process aims to be inclusive and promote equality among all partners at each stage of the research process, ranging from project design, execution, and communication of results (Enquist et al., 2017).

Recent advances in our understanding of fisheries and fisheries co-management in the Canadian Arctic have involved input from multiple knowledge sources, including Traditional Ecological Knowledge (TEK) (used here synonymously with Inuit knowledge) and scientific knowledge, following principles of knowledge co-production (Bouchard et al., 2023; Pettitt-Wade et al., 2020; Roux et al., 2019). Knowledge co-production has become increasingly recognized as a useful tool to understand changes in the Arctic and implications for Inuit (Armitage et al., 2011; Johnson et al., 2020; Yua et al., 2022), and calls for it's continued application to inform sustainable fisheries management practices.

Greenland cod are traditionally harvested along the marine coast in the Amundsen Gulf by Ulukhaktomiut (Inuit from Ulukhaktok). Greenland cod, often in large abundance, and are found year-round but typically harvested during spring and summer (Lea et al., 2023). Residents in Ulukhaktok, Northwest Territories (NT) have expressed climate-related changes to the marine environment, with potential implications for subsistence species. To date, documented knowledge pertaining to the biology and ecology of Greenland cod in the Arctic has been sparse, primarily derived from scientific studies focused on its known eastern distribution ranging from Greenlandic waters to Hudson Bay (Mikhail & Welch, 1989; Morin et al., 1991; Nielsen & Andersen, 2001), with more recent biological surveys extending in the western Canadian Arctic (Brewster et al., 2018; McNicholl et al., 2017; Pettitt-Wade et al., 2023). Further understanding of this species and changes being experienced by their population calls for the contribution of place-based knowledge.

In this paper, we link Inuit and scientific knowledge of Greenland cod in the marine ecosystem near Ulukhaktok, NT, Canada, to better understand their ecology in a changing climate. This project was co-designed with Ulukhaktomiut and used telemetry, biological fish samples, and Inuit knowledge to analyze individual movement, appearance, and health. Specifically, we (i) document Inuit knowledge of Greenland cod through interviews and workshops, (ii) briefly summarize the research findings derived from scientific methodologies, and (iii) examine the cumulative findings of Greenland cod research and implications for fisheries management.

METHODS

Study Area

Ulukhaktok, Northwest Territories, is an Inuit community of approximately 500 people (NWT statistics, 2022), situated on the west coast of Victoria Island in the Inuvialuit Settlement Region (ISR), located in the western Canadian Arctic (Figure 8) (Pearce et al., 2010). Traditional harvesting of fish continues to play an important role for subsistence, culture, and well-being of Ulukhaktomiut (Lea et al., 2023). Fisheries in the ISR are co-managed by the Fisheries Joint Management Committee (FJMC) and is a joint partnership between Inuvialuit and the Department of Fisheries and Oceans Canada (DFO) (Ayles et al., 2016). The FJMC holds decision-making power and is responsible for evaluating fish stocks and developing management plans to meet subsistence needs within the six ISR communities (IFA, 1984). Decision making from co-management partners consider all information collected through harvest surveys, monitoring programs, Indigenous knowledge and observations, and scientific research (Lea et al., 2023). Greenland cod are currently being co-management by the FJMC and were identified as a research priority given their continued dependence on this culturally important subsistence species, and recent accounts for changes in their population.

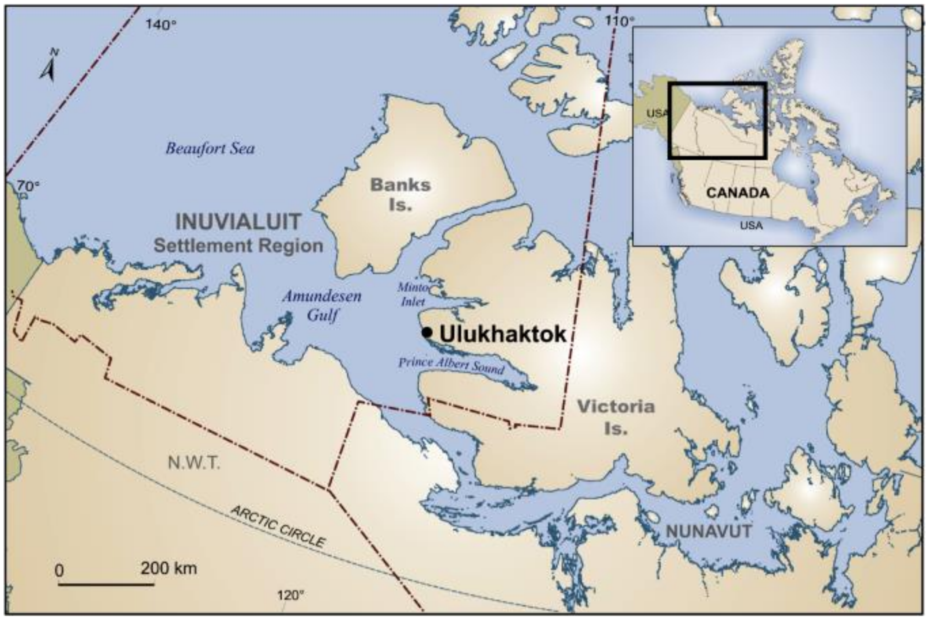

Figure 8: Map showing the study site in the western Canadian Arctic. Greenland cod (*Gadus ogac*) were captured in the semi-enclosed Safety Channel near the community of Ulukhaktok, Northwest Territories (NT) (Pearce et al., 2010).

Research Design

Initial meetings were held in Winnipeg, Manitoba, Canada with the Fisheries Joint Management Committee (FJMC) and Fisheries and Oceans Canada (DFO). An expression of interest was made by representatives from Ulukhaktok in having research conducted in their community given recent accounts of changes in the Arctic marine environment and concerns for subsistence hunting and fishing activities. Research planning meetings were held in Ulukhaktok (two meetings in 2018, one in 2019) with the Ulukhaktok Char Working Group (UCWG) and the Olokhaktomiut Hunters and Trappers Committee (OHTC), during which experienced harvesters and elders identified potential research questions, approaches, and focus species. During these meetings, the process of co-design was initiated between Ulukhaktomiut and scientists. Community priorities, questions regarding fish movement, the best tools and methods for addressing these questions, and the best locations to conduct the work were discussed. Greenland cod was confirmed as a focus species. Tracking the movement of coastal fish species using acoustic telemetry was agreed upon as the appropriate means to conduct the research. From there, researchers and two Inuit community members who are experienced harvesters, tagged fish, and deployed receivers within the identified study area (2018 and 2019). Data were collected on fish movement, and photographs and biological samples were taken for further laboratory analysis. The scientific analyses of photographs and biological samples were conducted by researchers and the findings were synthesized and presented during interviews and workshops to elicit discussion between researchers and key knowledge holders in Ulukhaktok. The results of these discussions are the focus of this paper.

Study protocols were approved by the Human Research Ethics Board at the University of Northern British Columbia. The research was licensed by the Aurora Research Institute (#16767), which oversees research in the Northwest Territories. A letter of support was provided by the OHTC for the research to be conducted in Ulukhaktok on co-producing knowledge of Arctic marine species in a changing climate (Appendix A).

Interview Preparation

On July 19, 2022, university researchers attended the regular OHTC meeting to provide updates on their research and present the goals of their visit. The researchers and OHTC members co-developed interview questions and identified potential informants based on their knowledge of Greenland cod fisheries in the area and changes to the marine environment. Additional informants were also identified by other informants during the interviews using a snow-ball sampling technique (Bernard, 2013). All interviews and workshops were held in English, with Inuinnaqtun translation as needed. A local Inuit research partner comfortable speaking in both Inuinnaqtun and English was available to facilitate interviews where informants were non-English speaking or preferred having translation services. An additional interpreter was hired to participate in the workshop sessions when the local research partner was unavailable.

Interview sessions and photo grouping exercise

A total of 16 interview sessions were held: five sessions had two informants, and 11 sessions had one informant. In total, 21 informants were interviewed: 11 women and 10 men (Appendix B). All informants are current or retired fishers who had fished in Ulukhaktok or the surrounding area. One informant is a retired fisher, while 20 informants continue to fish for subsistence. Greenland cod fishing is done with a fishing rod or by jigging, with some caught indirectly in gill nets set for Arctic char. All informants had started fishing for Greenland cod since childhood and were taught the skills for catching, preparing, and preserving by parents and grandparents. Many informants recalled regularly fishing cod for subsistence during their childhood, many of whom lived primarily on the land in surrounding areas prior to settlement in Ulukhaktok.

Interviews were held from July 13 to July 27, 2022. Interviews sessions followed a consistent format and were held in the order of (1) semi-structured interviews, (2) grouping exercise, (3) sharing of research findings, and (4) discussion. Interviews were held in locations that were most comfortable for informants including their homes, the OHTC boardroom, or the house that the research team was staying at. Interviews lasted between 33 and 96 minutes. All informants were asked for consent to audio record their interviews. Unrecorded sessions were conducted in the same manner and handwritten notes were taken throughout the interview. A total of 15 interviews were audio recorded and one was documented with handwritten notes. An interview guide and supporting documentation were available for reference to facilitate discussion during interviews (Appendix C, Appendix D). Supporting documentation that included visual diagrams and infographics was available for reference. A fish identification guide with images and descriptions of each species was available for reference, along with a 1:250,000 scale map of Victoria Island that includes fishing areas surrounding Ulukhaktok. Interview questions were structured around personal experiences related to cod harvesting, ecology, and informant's concerns related to the changing marine environment and implications for harvesting practices. The following steps were followed for the interview sessions and photo grouping exercise:

1. Interview questions of Greenland cod explored topics of fishing activity, ecology, and environmental change (Appendix C). Interviews were semi-structured to allow informants the opportunity to guide the discussion and share information on interview topics they were knowledgeable about. Each interview began with collecting basic demographic information including gender, age, means of livelihood (i.e. hunter or fisher). This was followed by questions on Greenland cod subsistence fishing activities. Informants were then asked questions focused on the ecology of Greenland cod such as body condition, health, movement, and diet. Next, informants were asked questions pertaining to observed environmental changes that could potentially impact Greenland cod.
2. Following the interview questions, a grouping exercise was conducted. Photographs of individual Greenland cod were presented, and informants were asked to group the photos without any prompts or information provided from the researchers to avoid any biases from scientific interpretations. Informants in group sessions were able to discuss the information together and form a consensus about the groupings. The researchers recorded fish grouping and reasonings.

3. Researchers shared groupings of fish determined through scientific analysis of morphology (body shape), stable isotopes (feeding behaviours), and telemetry data, accompanied by graphs and other supporting information (Chapter 3, Appendix D).
4. The reasonings for the groupings and similarities and differences made by informants and researchers were discussed. Open discussion between local harvesters and researchers were held with the aim of using various knowledge sources to better understand the ecology of this species and how it can impact traditional harvesting activities under a changing climate.
5. Informants and researchers also discussed what information might be missing from the exercise that could help fill knowledge gaps about Greenland cod and other marine species. Informants had the opportunity to provide additional information not covered during interview questions or previous discussions.

Knowledge sharing workshop

All informants from the initial interview sessions were invited back to participate in a knowledge-sharing workshop as a continuation of the interview sessions. Workshops were held on July 25, 2022 and lasted 2 hours each in the OHTC boardroom. Workshops were split into smaller group sizes and held in the format of open discussions to allow informants to share information and build off other responses. Of the 21 total informants, eight individuals returned for the workshop session. Two sessions were held (session 1 = five informants; session 2 = three informants and one interpreter), where one informant attended session 1 and acted as the interpreter for session 2. Workshop sessions were held in a casual open dialogue format. Researchers gave a presentation that covered the research activities conducted over the visit and summarized the information collected from interview sessions. During this time, researchers were able to ask follow-up questions and clarify the gathered information as a form of data validation. Informants were also encouraged to provide additional information that may have been missed during the interviews and correct any information the researchers gathered and interpreted. A 1:250,000 scale map was provided to mark off common fishing areas and sightings of juvenile and adult cod. Inuinnaqtun placenames were also recorded on the map. Feedback from the interviews and workshops was also gathered and intends to be incorporated into future visits to the community that will involve linking knowledge using similar approaches. Informants received a monetary compensation of $40 per hour for each interview and $20 for the workshop session. The local research partner and interpreter were compensated $100 for each interview and/or workshop session.

Interview analysis

Interview data was transcribed in English then coded using thematic analysis (Bernard, 2013) using NVivo 14 qualitative data analysis software (QSR International, 2023). The transcripts underwent deductive coding, where themes identified from the interview guide were recorded, including (1) subsistence and harvest, (2) ecology, and (3) environmental changes. Inductive coding, where additional sub-themes within each of the three themes, were uncovered during analysis. The identified sub-themes was able to capture the cumulative knowledge of Greenland cod into discrete groupings and were more specific to fishing activities and the ecology of Greenland cod, that may be potentially useful for the community afterwards in fisheries management.

RESULTS

Inuit Knowledge

Taste of meat. All informants described the taste of cod as very rich or generally taste the same from one individual to the next. One informant added to this by saying, “Uh, they're similar. But if you get the bigger ones you could taste the old, olderness” (Informant #21). In addition to the meat, many individuals also enjoy eating the livers and stomachs. “Oh yeah, same with the liver too. She likes to fry the stomachs, the liver and the meat together with some butter. Really strong smell though when you cook these cuz they live off the bottom” (Informant #12).

Distribution. Inuit knowledge of Greenland cod was focused along the coast within two marine inlets that lead to the Amundsen Gulf, Prince Albert Sound and Minto Inlet (Figure 9). Cod were most reported at the mouth of Prince Albert Sound, in Safety Channel, which is easily accessed from the settlement. They were also observed at the Southeastern end of Prince Albert Sound and in Minto Inlet, along the shoreline in the cliffs at the mouth of the inlet, and in the estuary at the opening of the Kuujjua River. Informant #8 mentioned that cod are unlikely to be found further

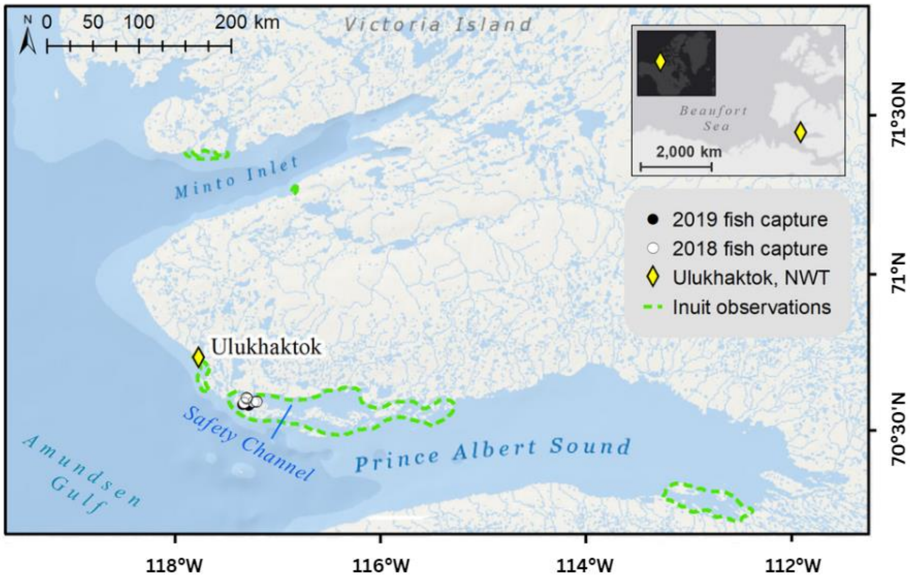

Figure 9: Map showing the study area near Ulukahktok, Northwest Territories with Greenland cod (*Gadus ogac*) capture locations and approximate traditional fishing areas and potential spawning areas highlighted from Inuit observations and traditional knowledge.

in Prince Albert Sound due to the absence of rocky habitat and instead has sandy and flat seabeds. The observations recorded do not represent the full extent of Greenland cod distribution and may only represent areas that are utilized by Ulukhaktomiut that are accessible by boat within their seasonal harvesting radius.

Size and colour. All informants have caught different sizes of cod described as small, medium or large in length. Several informants associated different sizes of cod with factors including habitat, colour, taste, health, season, and years. Many informants said big ones tend to be found in rocky or areas near cliffs. Size was also linked to the health of the fish, with larger fish in length and belly fullness, were perceived to be healthier. Another informant associated size with colour and taste. Small ones were described as more tender, and older, bigger ones were described as tougher and richer. Size was also linked to season, with more big fish caught in the fall.

Shape and health. Several informants recognized differences in shape between cod. Many informants also noticed fin shape to differ between individuals, while one informant asked if the researchers had considered fin spacing as part of the scientific analysis (Informant #18). Many informants had also observed differences in heads (pointy versus rounded), while others noticed fish to be fatter or have fuller bellies. Informants listed indicators of fish health according to size, belly fullness, colour of the outer flesh, colour of the meat, presence of scarring or injuries, liver colour or bruising, or presence of parasites. All informants mentioned that cod were generally healthy, while some informants noticed occasional differences in liver colour or evidence of bruising.

Habitat. All informants said that cod are normally found in rocky areas. Some informants said that the biggest cod can be found by large cliffs along the shoreline. They are mostly found at the bottom, in the deep and cold parts of the water column. They are also fished in bays near Ulukhaktok. During the formation and melting of ice, smaller sized cod can be found in the natural cracks and holes. Some informants also mentioned that cod can also be found in sandy areas, “in the bottom parts of the open leads it's mostly where they cod fish is because there's some sandy spots and there's rocky areas” (Informant #4). The environment or habitat was also linked to the colour of the fish.

Movement and season. All informants said cod perform movement for the purposes of feeding and breeding. Informants #7 and #11 further described cod as being non-migratory. More specifically, described as sedentary opportunistic feeders, “They sit in the rocks waiting for prey to come by. And if you want to drift along with my hook along big rocks, see you come out of the rocks and take the hook. So they're ambush predators. And they don't usually go swimming they’re actively hunting. They're more sit there and wait in between the rocks. When something edible comes by, they come out and get it” (Informant #7). Several informants also speculate that the size of the fish influences how far or deep they go, and may be greater for larger-sized individuals.

Some informants mentioned that changes in season impact movement patterns for feeding purposes. Informants described cod as being active year-round but varies with season. “They probably go feed some place else in different seasons eh. Like in the early spring they probably move somewhere where they could feed and go back in the fall” (Informant #8). One informant also speculates that changes in season triggers movement “They [Greenland cod] move and maybe go deeper water in the summer. Maybe start coming back before ice. I don't know, that's what I think anyway” (Informant #10).

Diet and food-web interactions. Several informants were familiar with cod feeding, where some informants mentioned that they occasionally check their stomachs to see what they are eating. Many informants mentioned that cod often eat sandfleas and sand lance. Informant #20 mentioned that they have seen other Greenland cod, sandfleas, sculpin, capelin, sand lance, and occasionally rocks in their stomach. Many informants have seen cod in the stomachs or mouths of bearded and ringed seal. Others have mentioned seeing sand lance, sculpin, or capelin co-inhabit similar areas to cod. One individual also said, “we notice when there’s lot of shrimp around that’s when the cod are around” (Informant #21).

Reproduction and spawning activity. Most informants seemed unsure with the timing or areas in which Greenland cod spawning occurs. An Elder (Informant #18) mentioned that another family used to share stories with them about cod, “but the other ones that talk about ogac [Inuinnaqtun name for cod] spawning, they go into the deeper or into the rocky areas and go under and spawn that's the knowledge he was given” (translated from Inuinnaqtun to English).

The timeline of events provided by several respondents tells us that young cod were seen in the summer and fall months, which may suggest that cod likely spawn in the spring. Informant #17 shared that cod spawn in shallow rivers during the spring and lay eggs wherever there’s a river. Additional supporting evidence for spring spawning was provided by other respondents that observed young cod following spring. Informants #5 and #20 recalled seeing young cod during the summer. Another informant recalled seeing a bunch of fry in October or November, during the fall season. “There’s a couple of seals and I was walking around with a spotlight and I was getting close to the shore. I thought I was looking at the bottom of the ocean. Shining. And there’s millions of little ogac fry hanging out right where it gets shallow. So I guess they were there to escape from predators cuz there’s big rocks” (Informant #7).

Changes to the marine environment and impacts on Greenland cod

Several informants mentioned that recent climate change events continue to impact marine fish species in the Arctic. Warmer waters are causing the introduction of new species, such as salmon. One respondent also noticed shifts in species composition from capelin to sand lance. “It has gotten a lot warmer the ocean water yeah. I noticed we get we're getting different species of fish. More like I said sand lance never used to be around when I was growing up” (Informant #7). Many respondents also discussed the appearance of tunicates, also referred to as “jellies,” that have created negative impacts on marine mammals and fish that are important for subsistence harvesting. “There were millions of them you know in the ocean, and there was no char, no seals” (Informant #7). Informants also expressed that this unusual event could impact cod populations. “Before that, when there was none of that stuff around, we had seals everywhere, fish [cod] everywhere, but when those things came it's just like they affected the animals… I don't know if that plays into the factor of where cod go, feeding and breeding” (Informant #21).

Most informants shared that Greenland cod are experiencing changes as a result of climate related events, while others shared that fluctuations in numbers are occurring throughout the years. Some informants mentioned that cod are increasing in size. Several informants also mentioned that cod abundance has decreased in recent years. Some informants noted that cod fishing has greatly reduced within the last five years. “There wasn't too many ogac this year, last couple of years. Compared to other years. One year there was a lot where you could look down you couldn't even see the bottom and you're looking at 10, 20 feet of water so you can see the bottom right away. But there were so many at that one year you just couldn't even see the bottom” (Informant #21). Some informants also noticed a difference in cod numbers compared to their childhood. “Right now I see a big difference. There's way less ogac than there used to be. Lots. As kids growing up there used to be a lot of ogac and there used to be lots” (Informant #20).

Some individuals haven’t noticed any changes in climate that have direct impacts on their cod fishing (Informant #12).” One informant mentioned that they continue to fish in the same spots since childhood. When asked if anything significant has changed in the last 20 years the informant said “Uh no. I've just done the same thing for ever since I was growing and went to the same spots” (Informant #10).

Linking Inuit and Scientific Knowledge of Greenland cod

Cumulative knowledge of Greenland cod near Ulukhaktok, NT was derived from both Inuit and scientific knowledge, and was separated into three themes including (1) subsistence and harvest, (2) ecology, and (3) environmental changes (Figure 10). The following sections link existing knowledge of this species to gain a better understanding of the ecology of Greenland cod and links to the changing marine environment.

Distribution and movement

Inuit and scientific knowledge show that Greenland cod in the Amundsen Gulf region are distributed along the coasts within Prince Albert Sound and Minto Inlet. Telemetry data from 2018 and 2019 captured the movement of 91 Greenland cod that were caught and tagged at the mouth of Prince Albert Sound, at the west end of Safety Channel (Pettitt-Wade et al., unpublished data). During the ice-covered months (September and October), larger-sized cod travelled out of range where they could no longer be detected. Similarly, observations from

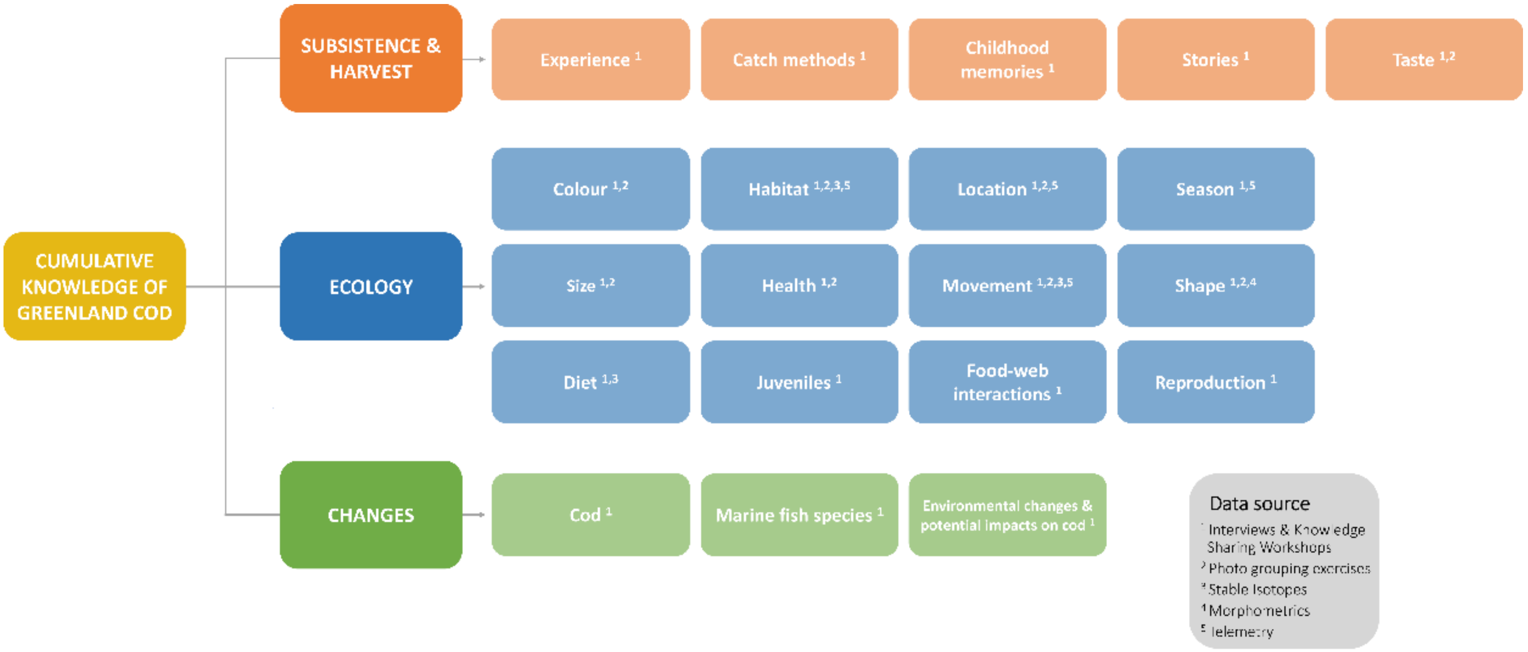

Figure 10: Diagram displaying cumulative knowledge of Greenland cod in Ulukhaktok, NT derived from Inuit and scientific knowledge sources. Gathered cumulative knowledge of Greenland cod is broken into three overarching themes and corresponding sub-themes. Sub-themes are accompanied by the identified data sources used to derive the information.

Ulukhaktomiut indicated that bigger ones likely move further out and smaller individuals stay closer to shore.

Observations from Ulukhaktomiut also tell us that cod are predominately found along the coast in deep, rocky areas. This information is in agreement with the telemetry data, which also showed that of the cod that remained detected within the study region, they spent most of their time in rocky channels at 50 to 70 meters throughout the year. Telemetry also revealed that cod are active year-round, but were most active close to shallow islands in the spring and summer, and moved towards deeper waters during the winter and fall seasons. Information from Ulukhaktomiut harvesters also showed that cod are most often fished during the spring and summer months, when cod are found in natural cracks through the ice. This information reveals that seasonality plays a role in timing of cod movements that likely allow for different resources to be utilized throughout the year, that plays a role in the timing of harvesting practices.

Telemetry data showed that cod spend most of their time in west Safety Channel, however, additional insights from Ulukhaktomiut revealed additional cod distribution within the full extent of Safety Channel. This area harbours rocky channels and may have been where the tagged cod that moved outside of the study area ended up. Cod were also reported in southeastern parts of Safety Channel, and in bays and inlets around Ulukhaktok. Additional sightings of cod were made in Minto Inlet, most notably the larger-sized and darker colour cod in these rockier cliffs. One informant from the photo grouping sessions was able to distinguish individual cod according to their origin. Specifically, they stated that the larger-sized fish with dark skin are found in the rocky cliffs near Minto Inlet.

Morphology

Quantitative assessments showed cod size can be described as fork length (mm) and measured as the distance between the tip of the snout to the edge of the tail. A total of 117 Greenland cod were measured (2018: n = 69, 2019: n = 48) ranging in size from 251.9mm to 578mm (mean 388.58 ± 57.63mm SD, n = 102 where length was available) (Chapter 3). Further understanding of the relationship between size and niche use across individual cod has been measured (Pettitt-Wade et al., 2023). Where fish size was paired with stable isotope data showed that changes in size did not impact the type of trophic niche utilized by individuals, indicative of generalist feeding behaviours.

Ulukhaktomiut made distinctions between individual cod with pointy versus rounded heads that may affect different feeding behaviours. This observation aligns with further analysis that was done, where observed differences in body shape were used to elucidate possible feeding patterns observed within the population (Chapter 3). Results showed minimal difference in habitat or trophic specialization in resource use across individuals. However, the observed intraspecific trait variation observed could allow for variable responses to environmental disturbance by buffering against their direct impact and could possibly enhance population resilience in the future (Barabás & D'Andrea, 2016; McKenzie et al., 2021).

Reproduction and Spawning

The documented Inuit knowledge tells us that cod utilize different areas (different spaces and depths in the water column) for the purposes of movement, feeding, and breeding. Movements detected from telemetry data shows that the larger-sized cod left the study area in winter between the months of January to March, and returned in spring between the months of April to June but were not detected leaving Safety Channel. These movements could relate to potential spawning events that could occur in bays with river mouths in Safety Channel. Some individuals traveled shorted distances and remained in bays during spring between the months of February to April. The energetic costs associated with both movement and spawning activity may explain why these smaller-sized individuals travelled shorter distances during this period. Sightings from Ulukhaktomiut of young cod during the summer and in the stomachs of adult cod provides supporting evidence for spawning activity during the spring.

Cod are known to spawn in a variety of habitats, with evidence in both inshore (Lawson & Rose, 2000) and offshore habitats (Marteinsdottir et al., 2000). The large variation in cod spawning locations is likely to reflect the conditions that would maximize offspring survival under local conditions (Endo et al., 2023). Seabed conditions have also been shown to influence spawning distribution, where the closely-related Atlantic cod (*Gadus morhua*) showed a preference for coarse sandy areas and avoid areas of very high tidal flow (González-Irusta &

Wright, 2016). This may help explain the spawning activity of Greenland cod within bays and inlets that offer sandy substrates and lower tide activity in the study region. The enclosed, narrow channels and reduced tide activity within Safety Channel may also favour suitable spawning grounds in comparison to the more open waters of Prince Albert Sound that is subject to greater tide activity due to the direct influence of the Amundsen Gulf. The timing of spawning may be similar to that of Atlantic cod, which occurs over a three to four month period usually during the spring or winter (Zemeckis et al., 2014).

Diet and Feeding

Stomach contents observed by Ulukhaktomiut during harvesting revealed that Greenland cod consume a variety of prey items found along the coast in the marine environment. The wide range of prey items including shrimp, sandfleas, sculpin, capelin, and sand lance suggest that cod have broad diets. Informants also mentioned that Greenland cod are opportunistic feeders and also display cannibalistic behaviours, which has been extensively observed in other Gadid species such as Atlantic and Arctic cod (Bogstad et al., 1994; Puvanendran et al., 2008; Yaragina et al., 2009).

Stable isotope analysis provided details on cod feeding behaviours, specifically looking at the range in generalist-specialist behaviours across observed morphotypes within the sampled population (Chapter 3). Both knowledge sources are in agreement with each other and tell us that that Greenland cod in the western Arctic can be described as generalists in resource use and prey consumption. Accounts for specific prey items consumed by cod was provided by Inuit knowledge, whereas broader details on the ecology and connections to the environment were further discussed through scientific analysis.

DISCUSSION

Observations from Ulukhaktomiut and telemetry data showed some overlap in information pertaining to the distribution of Greenland cod. However, observations from Ulukhaktomiut clearly covered a larger area that go beyond telemetry methods. Knowledge of cod distribution is gathered throughout an individual's lifetime or shared across generations, and therefore capture a relatively longer period. Observations are also based on opportunistic events and limited to areas accessible by humans along the shoreline and in open waters through boat access and dependent on sea ice conditions. In addition to the existing traditional knowledge held by Ulukhaktomiut, hunting and fishing practices remain active in this community, allowing for the ongoing development of local knowledge. The suggested placement of telemetry receivers deposited in the water for fish tagging was informed by Inuit knowledge following consultation and advice from the Olokhaktomiut Hunters and Trappers Committee (OHTC), Ulukhaktok Char Working Group (UCWG) and local Inuit harvesters (R. Klengenberg, I. Inuktalik, and D. Kuptana) (Hollins et al., 2022). This approach was able to capture fine sale movements of cod and was able to capture specific environmental data that would allow us to further understand the relationships between the environment and potential impacts of cod movement and behaviour (Matley et al., 2023). However, they were limited to a relatively smaller time scale of two years, which may not capture the full extent of changes to the marine environment associated with climate change. While observations from Ulukhaktomiut on Greenland cod covered a larger area and capture a longer time scale, telemetry was able to provide fine-scale movement data that serve as complementary data sources to provide a broader understanding of cod distribution.

Scientific analysis of body shape was conducted using morphometric analysis. Identification of landmark across individuals showed that fish body shape can be categorized in two groups, with one group characterized as having smaller head and slender body and a second group having a larger head and stockier body (Chapter 3). Observations from Ulukhaktomiut also further revealed that cod morphology was intertwined with other variables including habitat, colour, or shape. Larger-sized cod were darker in colour and associated with rocky, deep, and cliff habitats, whereas smaller-sized cod were lighter in colour and associated with shallow, sandy areas. Some informants also noticed differences in fin spacing or shape. Additional insights provided from Inuit knowledge could be integrated into future scientific assessments of coastal fish species. Specifically, additional indicators of morphology including fin shape and spacing, could be considered to elucidate potential morphological distinctions or presence of sub-species. Indictors of fish health linked to belly fullness and diet could also provide additional information on health and diet of individual cod.

Knowledge shared by Ulukhaktomiut was able to provide early indications of environmental change including changes in species composition, with increasing reports on salmon, and shifts from capelin to sand lance that have been attributed to increasing water temperatures. Inuit knowledge was able to provide subtle indications of change over a long time span of approximately 5 to 20 years. These observations can be useful to inform further investigations to complement scientific assessments. Many Ulukhaktomiut noticed an increase in size and decrease in abundance of cod in recent years. The specific mechanisms as to why this is occurring remains unclear. However, Inuit knowledge tells us that adaptation potential can vary within the population based on different traits observed. Informants expressed having to adapt their fishing practices in accordance with these changing environmental conditions. For example, shifts in the timing of harvesting season, fishing areas, and fishing effort have been altered in recent years. Several informants also mentioned that Greenland cod fishing has been reduced, notably in the last two years. Many informants have also noticed changes in species composition, with increasing reports on salmon, and shifts from capelin to sand lance that have been attributed to increasing water temperatures. These reported changes are likely a result of environmental stressors creating variable responses across individuals. Further advancement of knowledge in this area would benefit from long-term monitoring.

CONCLUSION

This paper links scientific and Inuit knowledge of Greenland cod in the marine waters near Ulukhaktok to better understand their ecology in a changing climate. The research was guided by principles of knowledge co-production and generated findings that could only be produced by linking Inuit and scientific knowledge. The sampled Greenland cod population around Ulukhaktok exhibit a range of traits related to feeding, movement, and physical appearance, that can be associated to different morphotypes dispersed in varying areas around Prince Albert Sound and Minto Inlet.

Inuit and scientific knowledge provided several strengths and opportunities that were utilized differently depending on the stage of the research. Much of the information collected from both knowledge systems were complementary and allowed for them to build on one another to inform the next stages of the research process. During the early stages of the research, Ulukhaktomiut identified the research priorities and narrowed down suitable areas for the telemetry study. Scientists were able to support these research initiatives and provide the tools to make quantitative assessments and initial follow-up interpretations. Additional interpretations from interview and workshop sessions with Ulukhaktomiut were able to enrich the findings and provide holistic interpretations of the data. The summarized information in this study captures cumulative knowledge of Greenland cod in the western Arctic under a changing climate and reinforce the deep connections with harvesting activities and importance of coastal marine fish species for Inuit culture and tradition.

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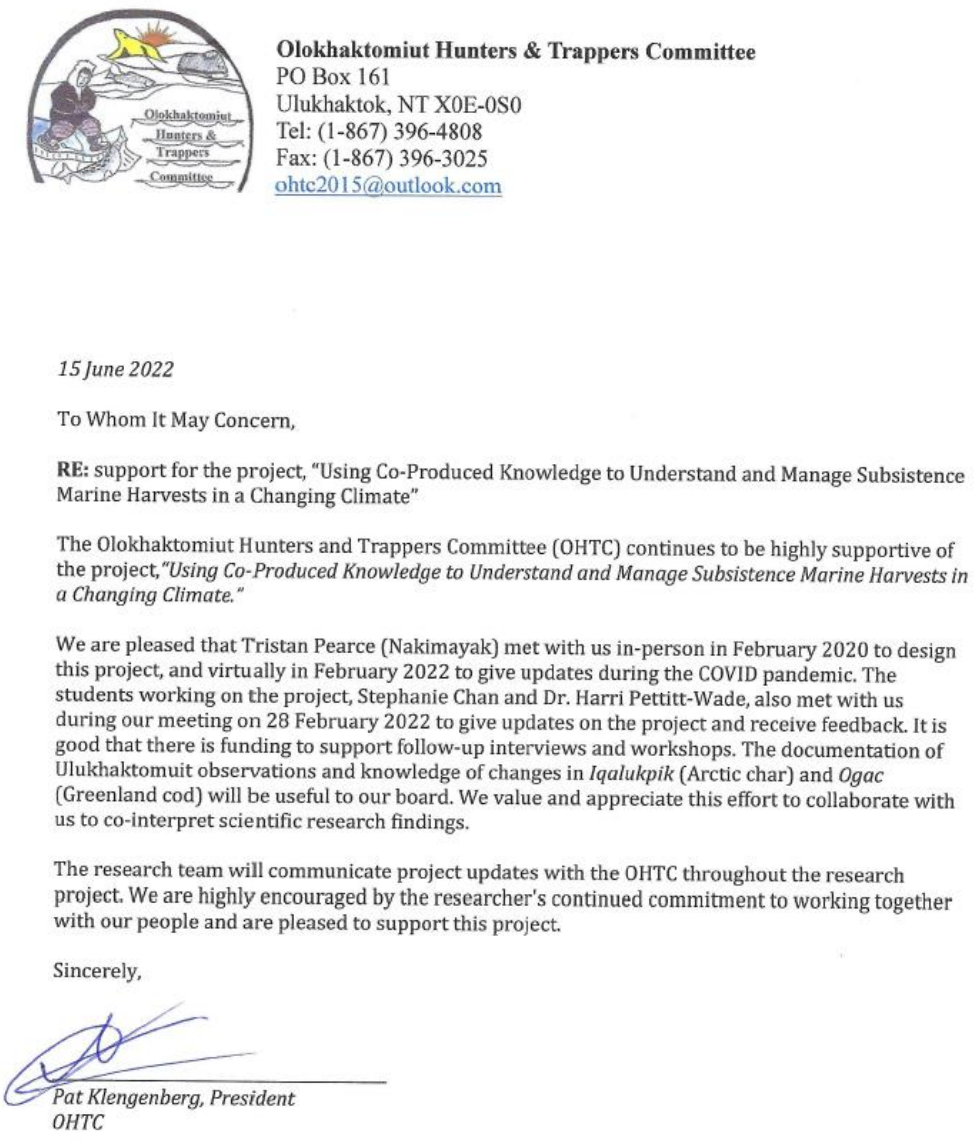
APPENDIX A



Olokhaktomiut Hunters & Trappers Committee
PO Box 161
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Tel: (1-867) 396-4808
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15 June 2022

To Whom It May Concern,

RE: support for the project, "Using Co-Produced Knowledge to Understand and Manage Subsistence Marine Harvests in a Changing Climate"

The Olokhaktomiut Hunters and Trappers Committee (OHTC) continues to be highly supportive of the project,*"Using Co-Produced Knowledge to Understand and Manage Subsistence Marine Harvests in a Changing Climate."*

We are pleased that Tristan Pearce (Nakimayak) met with us in-person in February 2020 to design this project, and virtually in February 2022 to give updates during the COVID pandemic. The students working on the project, Stephanie Chan and Dr. Harri Pettitt-Wade, also met with us during our meeting on 28 February 2022 to give updates on the project and receive feedback. It is good that there is funding to support follow-up interviews and workshops. The documentation of Ulukhaktomuit observations and knowledge of changes in *Iqalukpik* (Arctic char) and *Ogac* (Greenland cod) will be useful to our board. We value and appreciate this effort to collaborate with us to co-interpret scientific research findings.

The research team will communicate project updates with the OHTC throughout the research project. We are highly encouraged by the researcher's continued commitment to working together with our people and are pleased to support this project.

Sincerely,

Pat Klengenberg, President
OHTC

APPENDIX B

Table A2: Demographics of Informants

Category		Number of Informants
Age	18-29	0
	29-39	1
	40-49	2
	50-59	7
	60-69	1
	70-79	5
	80+	5
Gender	Male	10
	Female	11

APPENDIX C

Interview questions on Greenland cod fishing activity, ecology, and environmental changes

Questions on fishing activity

- Would you describe yourself as a hunter, fisher, both, or neither?
- How old when you learned how to fish? Who taught you?
- Would you say you are an active fisher?
- Where do you like to go fishing? Do you fish near other communities?
- Are you familiar with ogac (Greenland cod)?

Subsistence and commercial harvest

- How often do you fish for ogac?
- When is your favourite time to fish ogac?
  - Do you notice any differences depending on when you fish?
- Where do you like to fish ogac?
  - Do you notice any differences depending on where you fish?
- What is the best way to catch ogac?
  - Are there other ways to catch cod depending on where you go?
- How do you decide which ogac are good to catch and which to release?

Body condition and health

- Can you tell if some ogac are healthier than others?
  - Can you describe a healthy looking ogac?
- Do you notice differences in their taste?
  - Do you notice any differences in taste depending on where you catch them?
  - Time of year or longer-term changes / how they look?

Movement and behaviour

- Have you ever looked inside the stomach or seen what ogac eat? Or heard it from others?
- Can you describe the area where you see ogac swimming?
- Do you notice other types of fish that swim near ogac?

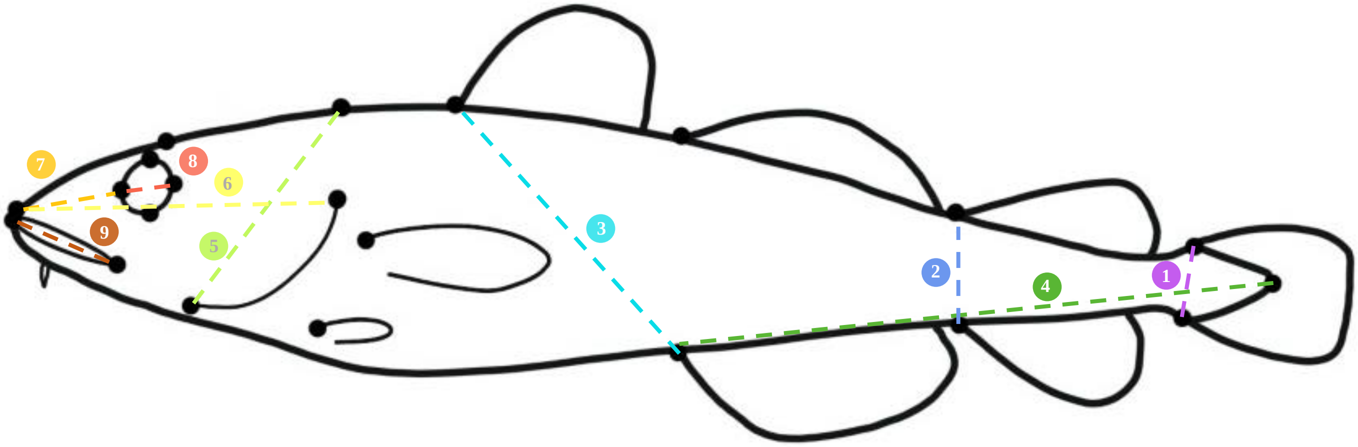
Observed Changes

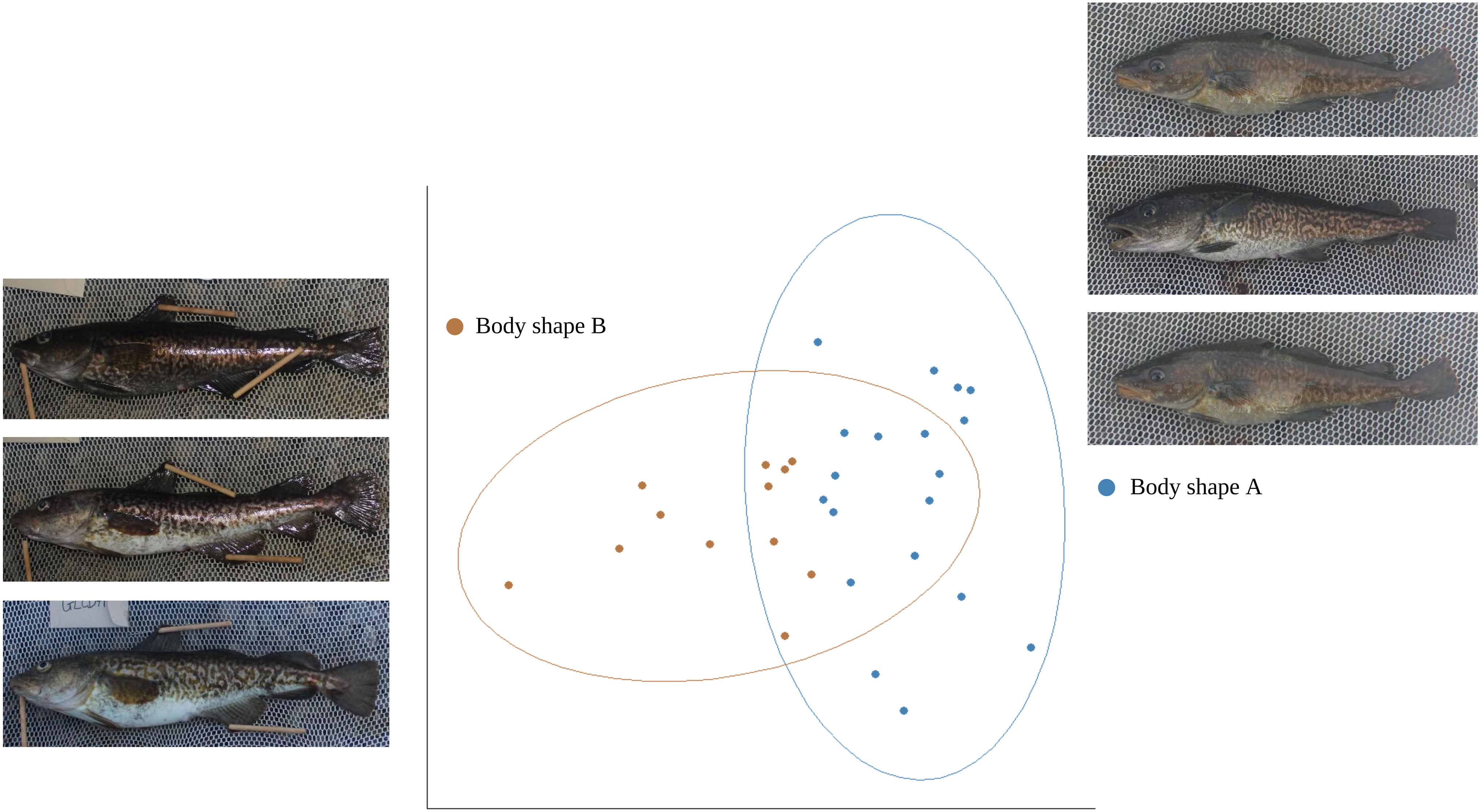
- Have you noticed any changes in ogac? Size? Taste? Colour? Swimming area? Swimming patterns? How many there are in different areas?
  - Over how long? The last 5 years? 10? 20?
- Have you noticed any changes on the marine coast?
  - Over how long you’ve noticed these changes? The last 5 years? 10? 20?
- Is it easier to catch them depending on what method you use?
- Is it easier to catch them at a certain time of year?
- How do you think the environment has changed? How do you think this has affected ogac or how you fish them?

APPENDIX D

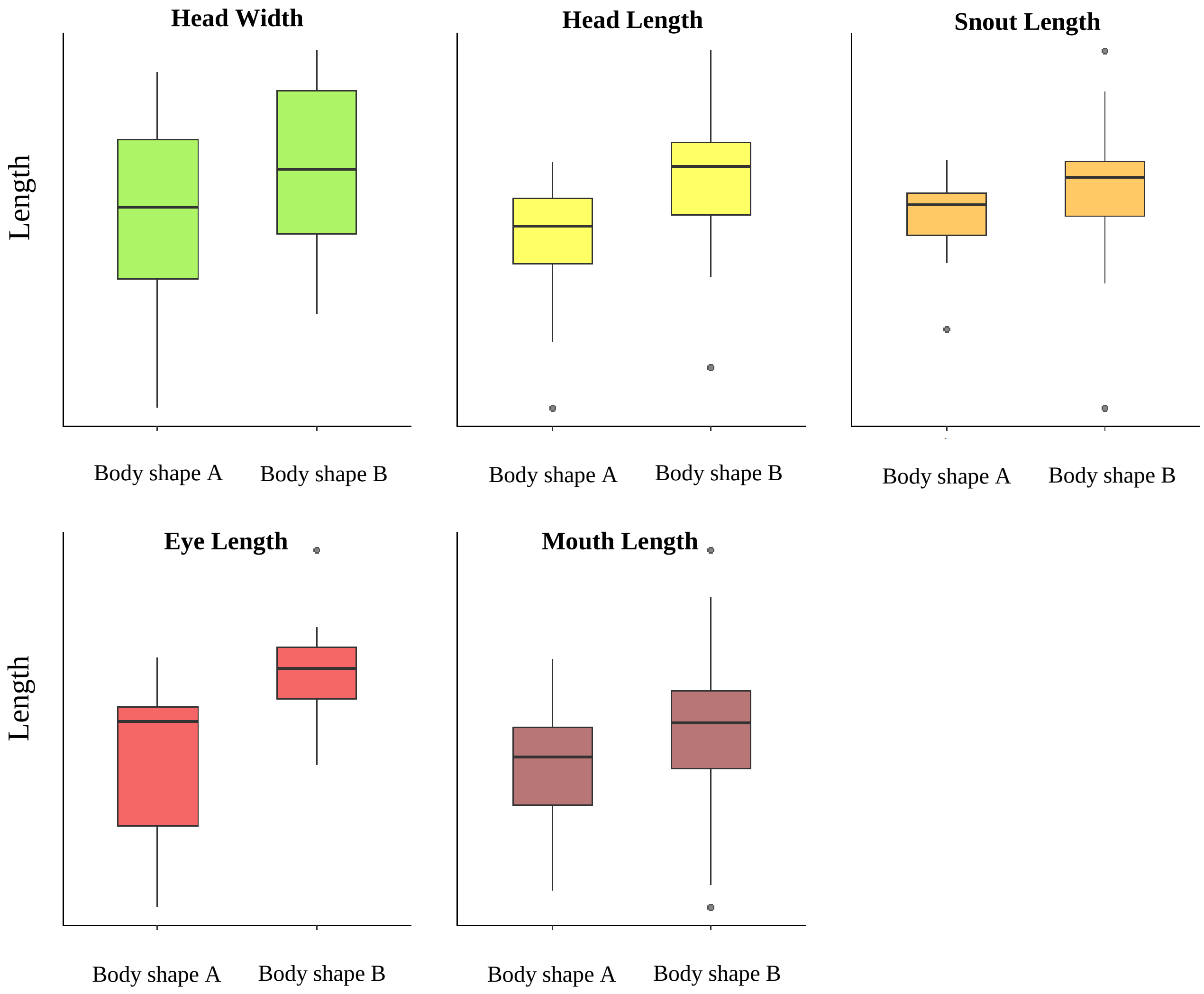
Reference material available for interview sessions

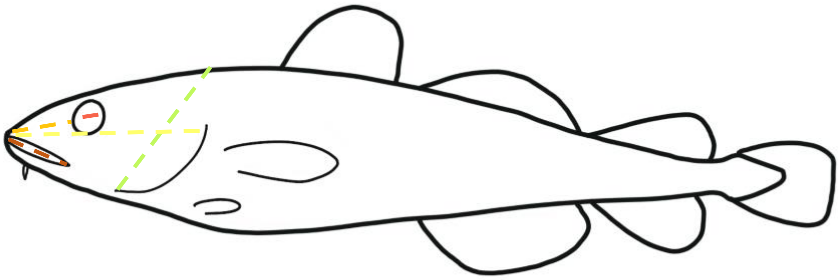
Fish measurements

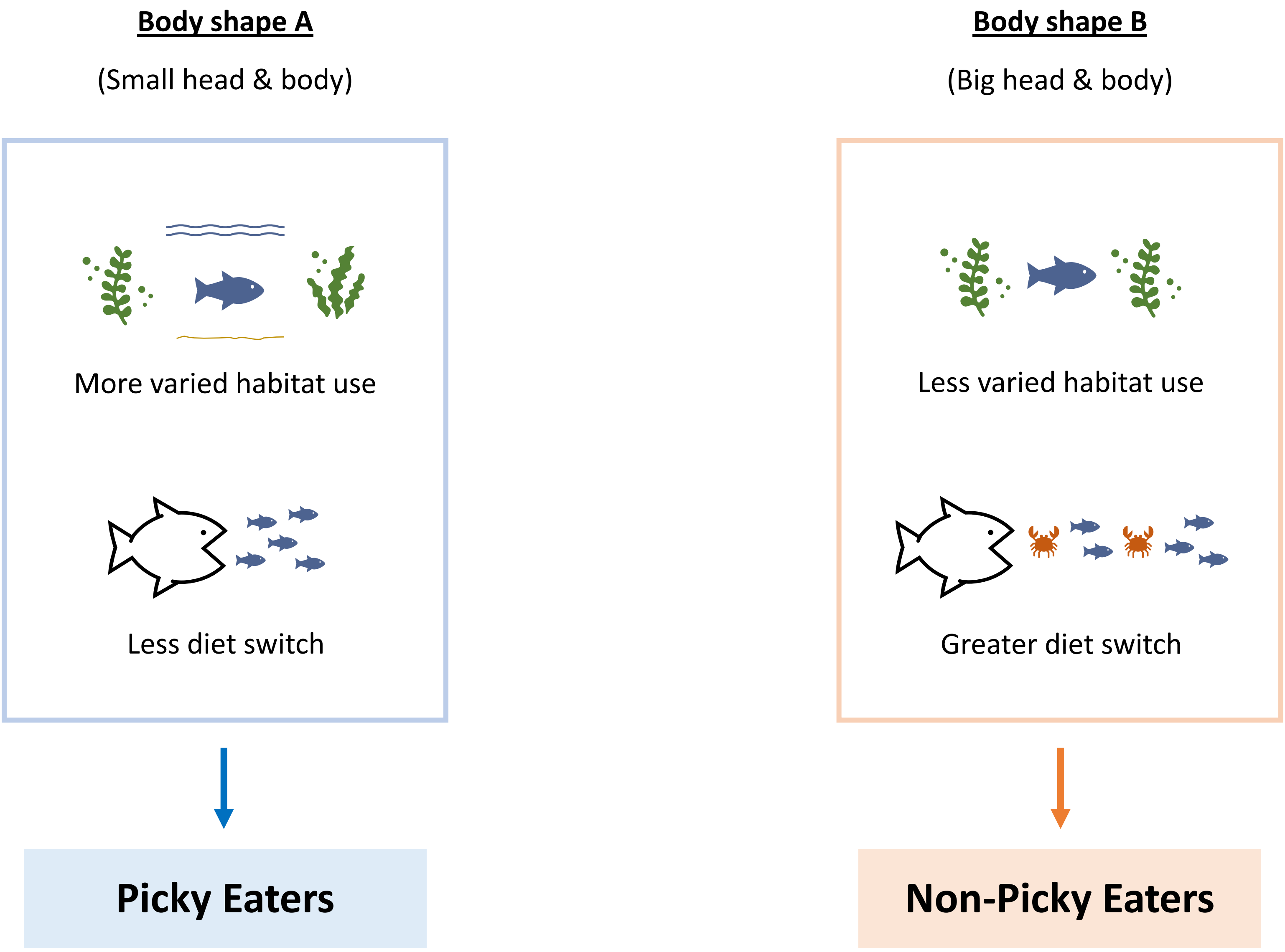



● Body shape B
● Body shape A

Head Measurements







Body shape A

(Small head & body)

More varied habitat use

Less diet switch

Picky Eaters

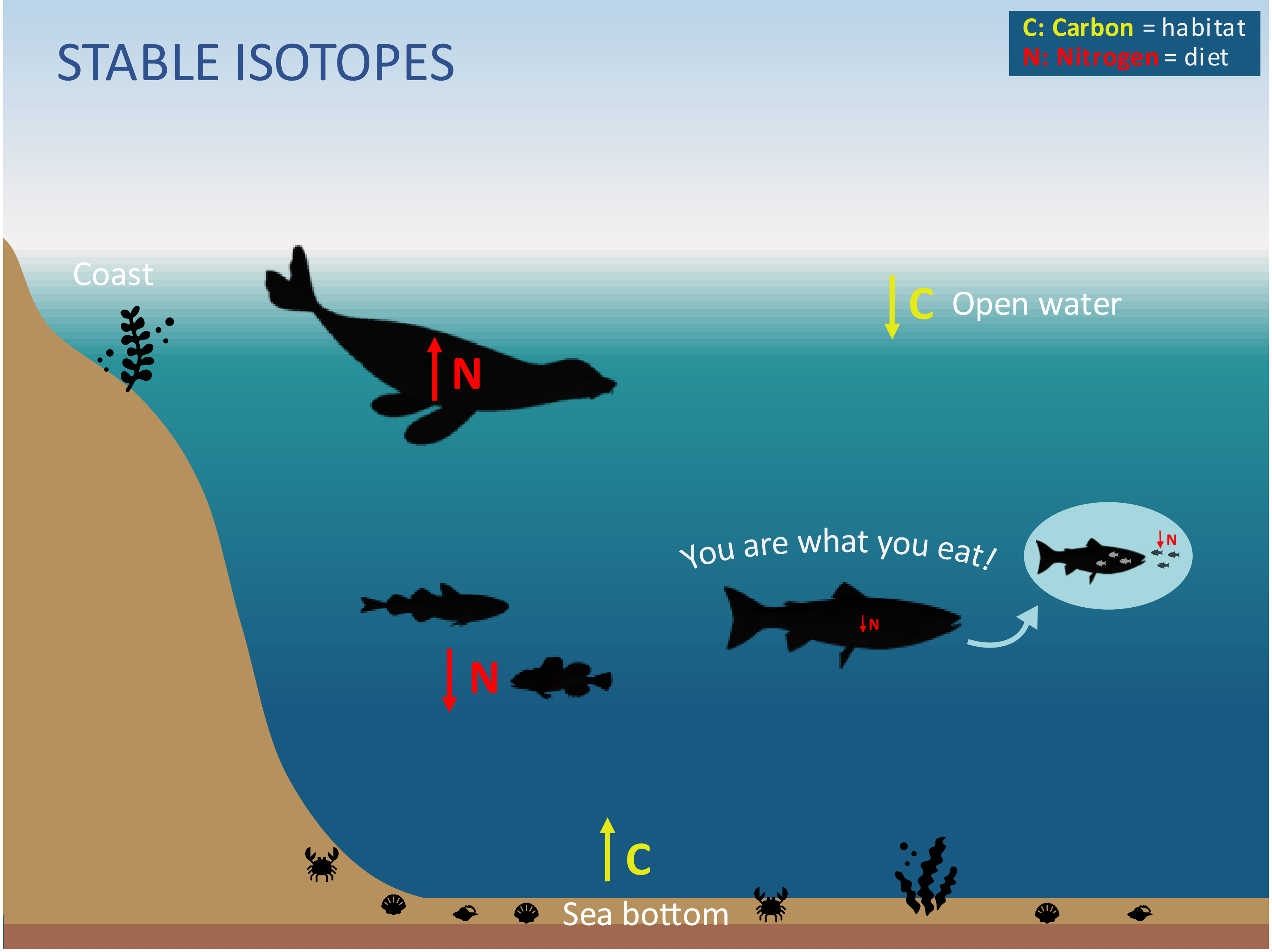
Body shape B

(Big head & body)

Less varied habitat use

Greater diet switch

Non-Picky Eaters



STABLE ISOTOPES

C: Carbon = habitat
N: Nitrogen = diet

You are what you eat!

CHAPTER 5: GENERAL DISCUSSION

This thesis examines findings from Inuit and scientific knowledge of Greenland cod as a means of linking knowledge systems to advance our understanding of this species and the implications of a changing environment. The research methods further suggest that linking Inuit and scientific knowledge is an effective way to advance our understanding of Arctic fish populations while supporting co-management initiatives in the ISR under a changing climate. The intersection between the marine ecosystem and Inuit subsistence harvesting practices demonstrates the need for collaborative efforts across multiple disciplines to address ongoing challenges faced by northern coastal communities. Knowledge linking was done among Inuit knowledge holders, OHTC, FJMC, researchers from academia and DFO, and it allowed us to generate new insights and achieve project milestones that could not be achieved by each of these knowledge systems or groups independently. The described research is built on a foundation of ongoing dialogue between knowledge holders to advance knowledge to inform co-management practices while supporting Inuit-led decision-making. This thesis supports the outcomes of the broader ArcticNet research project that seeks to understand and manage subsistence and marine harvests in a changing climate using co-produced knowledge.

Initial analysis from scientific methodologies investigating Greenland cod morphology and feeding behaviours demonstrate an overall generalist population, with evidence of generalist-specialist traits. These findings highlight the importance of maintaining trait variation to conserve diversity and promote resilience under a changing climate. Investigating the baseline ecology of this lesser-known species can enable improved predictions on potential interactions between Arctic and sub-Arctic species, which may be useful for managing these species in the future.

The methods employed in this research highlight the strengths offered by Inuit and scientific knowledge together, and demonstrate how knowledge systems can build off one another to inform subsequent stages of the research. Observations made by Ulukhaktomiut were able to provide preliminary insights into environmental changes that are taking place. Inuit are deeply connected to their local environment and are often the first to detect environmental changes from extreme events and unusual patterns (Moller et al., 2004). Ulukhaktomiut harvesters were the first to identify early signs of change in this region, such as changes in the abundance and size of Greenland cod, the presence of non-native species, and subtle changes in species composition in the marine food-web. Scientific efforts including fish tracking and biological sampling allowed for these concerns and observations provided by Inuit to be supported and further investigated through a quantitative lens providing measurable outputs. Researchers made initial assessments of the data, which were then shared with Ulukhaktomiut who provided holistic interpretations of the data and drew connections between the observed phenomena and the broader context of ecosystem change. The cumulative understanding of Greenland cod around Ulukhaktok indicate that this population exhibits a range of traits related to feeding, movement, and physical appearance, that can be associated with different morphotypes dispersed around Prince Albert Sound and Minto Inlet. The documented changes potentially taking place in Greenland cod may be an indication of other changes taking place in the marine ecosystem. The presented ecological assessments on Greenland cod may also be useful to understand other Arctic coastal marine species. The methods employed can be used similarly to other species of interest, including Arctic char, a species that is frequently harvested by Inuit. The links between this subsistence species and the changing marine environment also presents opportunities to generate co-produced knowledge to inform fisheries management in the ISR.

The work described in this thesis benefited from several elements of the knowledge co-interpretation, however, the process of co-interpreting knowledge can be challenging in practice. Co-interpretation is considered a relatively new process that continues to evolve in interdisciplinary research (Norström et al., 2020), specifically within the context of Western science and Inuit knowledge (Zurba et al., 2022). The process was initially developed under Western scientific methods and is seemingly an unusual approach to generating knowledge for Inuit. Although we hoped to accomplish an in-depth exchange of knowledge and collaborative interpretations of the findings between researchers and key Inuit knowledge holders, this process was difficult to fully achieve. The level of engagement in the research greatly differed between Ulukhaktomiut and researchers, and was heavily favoured towards researchers with backgrounds in scientific methods. Future research that draws on the knowledge co-production framework should consider the level of engagement between groups and consider the most appropriate means to communicate findings for the targeted audience.

This project addressed research questions that directly affect Ulukhaktomiut and necessitated engagement that went beyond the academic requirements of graduate studies. Individuals appointed to research positions may not always see a project through from start to finish. The real-life implications of ongoing challenges faced by Inuit communities due to climate change are an ongoing challenge that goes beyond the length of a project, and highlights the importance of creating strong community-researcher relationships. This partnership created several opportunities to mobilize the findings useful for decision-making. For these reasons, research activities must be built on a strong foundation of communication and relationships between research partners and community members. The concerns and needs identified by local communities must also be prioritized to ensure that the research remains relevant and provides tangible outputs that can inform Inuit-led decision-making.

Future Directions

This research identified several questions that could guide the development of future research projects. For example, specific questions aimed at further understanding Greenland cod with ongoing climate change include: *Which environmental variables play a role in individual resource use (e.g., distribution, habitat, diet) of Greenland cod? Which traits are most sensitive to climate-induced stressors? Under various climate change scenarios, how would the interaction between Arctic and sub-Arctic cod populations affect Arctic marine food-web composition and dynamics over time? What are the genetic consequences of interactions between Arctic and sub-Arctic closely-related cod species? Which other marine fish species are experiencing environmental changes, and how will they impact Inuit in the future?*

Other areas of future research that require working in Indigenous communities could build on or improve the methods of co-production described in this work. Methods of engagement such as meetings between local collaborators, workshops, or methods of data collection have the potential to be further adapted or utilized in other contexts. For example, modes of data collection, dissemination, and knowledge mobilization can be executed differently depending on community interest. Although the process might differ for each project, initiatives that aim to address concerns under contemporary climate change in the north can be supported by researchers but ultimately, should focus on utilizing Indigenous knowledge to its fullest capacity to support Indigenous-led decision-making.

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CHAPTER 6: CONCLUSION

In this thesis, we present findings from Inuit and scientific knowledge of Greenland cod as a means of linking knowledge systems to advance our understanding of this species and the implications of a changing environment. The objectives of this research were to: (1) investigate the adaptation potential of Greenland cod, (2) document Inuit knowledge of Greenland cod, and (3) examine the cumulative findings of Greenland cod research and discuss the potential impacts of shifting marine resources on livelihoods in the Inuvialuit Settlement Region. These objectives were accomplished by measuring individual specialization-generalization from morphological and habitat-trophic traits of the sampled Greenland cod population, conducting interviews and workshops with key knowledge holders in Ulukhaktok, and linking multiple knowledge systems to enhance our understanding of the ecology of this species and develop a better understanding through consideration for Inuit harvesting and subsistence activities.

This research links Inuit and scientific knowledge to better understand this species, its role in the marine environment, and its connections to Inuit livelihoods. This work responds to the needs and priorities identified by Ulukhaktomiut and was built on a foundation of collaboration at each stage of the research process. The Arctic marine ecosystem is generally data-deficient, and this research advances our understanding of the baseline ecology of this region on a lesser-known species. Advances in ecological research should continue to monitor marine fish and mammal species in the Arctic that remain at the forefront of global climate change impacts. The research approaches carried out in this project set a precedent for future studies that wish to integrate multiple knowledge systems to address conservation issues in an era of rapid climate change, specifically within the context of collaborative research. Active collaboration between local knowledge holders and scientists is imperative to ensure that co-management decisions are adequately formulated to consider a broad range of knowledge that also supports Inuit subsistence and harvesting priorities.