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Marine mammals in a warming Arctic: Connections with ecosystem,
environment and Inuit in Inglefield Bredning, northwest Greenland

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Abstract

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The Arctic is one of the most rapidly warming regions on Earth, raising concerns about cascading effects on the interconnected relationships among the environment, marine ecosystems and their apex predators – marine mammals – and Indigenous communities that depend on them as vital resources. To assess and predict the impacts of climate change across this entire network, particularly on marine mammals and local people, which are at the top of this chain, I peered into these connections during the open-water season in Inglefield Bredning, home to Greenland's northernmost Inuit communities, by combining analyses of biological samples with interviews with Inuit people who possess deep knowledge of the local nature and animals. During summer, four species of marine mammals, including ringed seal (*Pusa hispida*), harp seal (*Pagophilus groenlandicus*), bearded seal (*Erignathus barbatus*) and narwhal (*Monodon monoceros*) inhabit this area and are important targets for Inuit hunters.

In chapter 2, I report on their feeding ecology and niche overlap among marine mammals revealed by stomach contents and stable isotope of livers and muscles collected between 2022 and 2024 to provide insights into the relationships between marine mammals and their prey. Polar cod (*Boreogadus saida*), the most abundant fish in the Arctic, was the dominant prey for marine mammals. Red fish (*Sebastes fasciatus*), an Atlantic fish typically found in more southern waters, was found from the stomachs for the first time in this region, and the composition of zooplankton showed a shift toward Atlantic species compared to previous studies, suggesting that climate change is driving changes in the marine ecosystem in this area. It was suggested that the narwhal has the narrowest dietary niche, making them the most vulnerable marine mammals in this region to environmental changes.

In chapter 3, I combined the stomach contents revealed in chapter 2 with location data of where each animal was hunted to conduct a spatial analysis of stomach contents to identify where they feed on polar cod. The results indicated that bearded seals establish a unique feeding niche in shallow waters, while the other mammals mitigate competition by adjusting their feeding areas based on the distance to glaciers. The glacial retreat due to climate change is potentially altering predator-prey interactions and interspecific competition, but the extent of these impacts may vary depending on their feeding areas and the degree of competition, even among sympatric species depending on the same prey.

In chapter 4, I focused on the foraging ground of ringed seals, which particularly uses glacier front as foraging grounds. By comparing data collected in 2003 with the results of this

study, we investigated changes in foraging areas over the past 20 years and examined the impact of glacier retreat on their foraging ecology. Over the past two decades, seals have been foraging closer to glaciers, likely due to increased glacial runoff enhancing marine productivity around glacier fronts.

In chapter 5, I reported the trophic levels of organisms in the food web, from zooplankton to marine mammals, and the contaminant levels in the marine mammals which is accumulated through the food web. Contaminant concentrations were highest in narwhals, suggesting that they are a primary source of contaminant exposure for local people.

In chapter 6, I conducted interviews with local Inuit to incorporate knowledge beyond animal sample analysis, including their deep knowledge built from their lived experiences over the past decades, as well as intergenerational knowledge passed down generations. The most significant change which has been recognized by people was the melting glaciers, sea ice, and ice bergs, which have particularly impacted dog sled hunting, making it increasingly difficult to carry out traditional marine mammal hunting methods. Moreover, what became clear through listening to their stories is that global societal changes may have indirectly, yet significant impacts on their culture and marine ecosystems – Inuit people in this area are struggling in the midst of two changes, a changing environment and societal transformations.

This study comprehensively reveals the connections between the marine ecosystem, environment, and people in the region for the first time with a focus on marine mammals, and provides crucial insights for evaluating and predicting potential impacts of climate change. Results of the study clearly revealed that for both marine mammals and the Inuit people who rely on them as vital resources, climate change is indeed a threat, and there is an urgent need to strengthen resilience to environmental changes in the region. In this study, I focused on the summer period when the only season the sea opens in this region. However, since climate change has been found to particularly affect sea ice condition, it is also necessary to investigate the conditions during the period when the sea freezes. I emphasize that, as the impacts of climate change on the environment, marine ecosystems, marine mammals, and local communities are interconnected, multifaceted, and complex, it is essential to approach the issue from multiple perspectives and interdisciplinary ways in devising effective strategies.

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CHAPTER 1

Background

“The discovery of an animal’s Umwelt and its elucidation require great patience and experimental ingenuity, a free exchange of information among different observers, hours of direct observation, and a reluctance to summarize the animal. This, in my experience, is the Eskimo hunter’s methodology. “

-- Barry Lopetz, Arctic Dreams, 1986

The Arctic environment and ecosystem

The Arctic, defined as the region north of 66.5 degrees latitude, can be described as an extreme environment with dynamic seasonal . In winter, it experiences polar nights when the sun does not rise, while in summer, the sun does not set, known as the midnight sun. The sea ice covering the Arctic varies by nearly a factor of two between summer and winter, reaching its maximum extent in March, and minimum in September. As the sun light returns in early spring, a algae bloom takes place under sea ice. With the emergence of these phytoplankton, predators such as zooplankton and fish follow, and their top predator marine mammals begin to gather. Arctic marine ecosystems also vary spatially throughout the year, as each species undergo seasonal migration, and change their habitats in response to annual changes in marine productivity and environment differently.

It is not only the animals that change dynamically with the season. Unlike the Antarctic, which is also am polar region that undergoes dynamic seasonal changes, the Arctic is home to Inuit communities, and we cannot go without including them as part of the marine ecosystem. The Inuit people have a long history intertwined with the marine ecosystem, particularly with marine mammals, influenced each other in a reciprocal manner. Inuit in the high Arctic currently engage in traditional hunting of marine mammals using boats during open-water season, and dog sleds during winter, and hunt available marine mammals according to the season. They possess a deep knowledge of the habitats and migration patterns of the animals, utilizing the land accordingly (Gryba et al., 2021; Huntington et al., 2017). There is also a history where overhunting led to a drastic decline in marine mammal populations (Garde et al., 2022).

The Arctic marine ecosystem and the lives of Inuit have adapted to the dramatically changing seasonal environment, mutually influencing each other and existing in harmony over time. Therefore, even minor deviations can amplify through interconnected changes in sea ice, primary production, and the entire marine food web, leading to cascading impacts on marine mammals, which are the top predators in the marine ecosystem, and on Inuit communities who rely on them as a vital resources – Indeed, the Arctic is one of the regions on Earth experiencing the most rapid warming.

2024 marked the first year that the global average temperature increase since the pre-industrial era exceeded the 1.5 degree target set in the Paris Agreement of 2015 (). The fact serves as a global wake-up call about climate change, highlighting the need for even stronger measures to curb warming. In the scenario with the global average temperature exceeds 1.5 degrees, extreme weather events, sea-level rise due to glacier melt, and impacts on ecosystems are expected to become more severe, potentially causing significant disruptions to human society. To assess and predict the impacts of climate change on ecosystem and people in the Arctic, long-term monitoring is necessary. However, conducting such continuous survey is often challenging in the Arctic regions, which are remote, and are difficult to assess due to its harsh environments, and there are many areas where scientific data at local level is lacking. Inglefield Bredning in northwest Greenland is one such region, where I focus on this study.

Study area

Inglefield Bredning is known as the fjord home to one of the northernmost Inuit communities in the world. There are three Inuit settlements — Qaanaaq, Qeqertat, and Siorapaluk—where approximately 700 people live (Fig. 1-1). The region is one of the most active for traditional marine mammal hunting in Greenland (Greenland statistics 2023), and is the only area where the traditional narwhal hunting culture using kayaks still remains. At the same time, due to the preservation of a subsistence-based lifestyle, this region has one of the lowest household incomes in Greenland (Greenland statistics 2023), highlighting how crucial marine mammals are as a resource for the local people. During the limited summer period when the sea is open and boats can be used, they hunt marine mammals from boats or kayaks. During the winter when the ocean freeze, hunting is carried out using dog sleds.

In this region, drastic glacier retreat and rising sea temperatures have been revealed, same as other areas in the Arctic (Sugiyama et al., 2015; Wang et al., 2021;Chambault et al., 2020),

rising concerns about changes in the marine ecosystem and the potential impacts on the hunting lifestyles of local Inuits. However, as is often the case in the Arctic, scientific data in this regions is significantly lacking, and changes in the marine ecosystem have never been investigated. In addition to the inaccessibility of the area as the area is covered in sea ice for much of the year and is many icebergs, as the area is important hunting ground for local people, making it difficult to conduct large-scale scientific research using research vessels.

Marine mammals in Inglefield Bredning

During open water season in Inglefield Bredning, four marine mammals coexist in the area, three kinds of seals: ringed seal (*Pusa hispida*), harp seal (*Pagophilus groenlandicus*), bearded seal (*Erignathus barbatus*), and an Arctic cetacean, narwhals (*Monodon monoceros*). These marine mammals consume variety of prey including fish, crustaceans and benthos. Also, they are important resources for local people and predators such as polar bear (*Ursus maritimus*), killer whale (*Orcinus orca*) and walrus (*Odobenus rosmarus*) in this area.

Ringed seals are the most abundant pinniped in the Arctic. Their ability to make and maintain breathing holes on the sea ice allows them to spread out in ice covered ocean where other marine mammals have limited access, and they inhabit this area throughout the year. They are among the smallest of seals, with their body size is approximately 150 cm. Moreover, ringed seals are the most frequently hunted marine mammal in the Inuit communities of northern Greenland for various purposes such as food, sled dogs feed, and for fur, positioning them as a central species for Greenland culture identity, food security and socioeconomic system. There are no available statistics specific to this region, but approximately 30 thousands individuals are harvested annually across Greenland (Piniarneq 2023).

Bearded seals are another marine mammal inhabit the area year-round, who gets its name from the long whiskers on their face. They are the largest seals in the Arctic, with they can be 240 cm and about 360 kg. Due to their large size and thick skin, their skin is used for making dog sled whips and ropes by Inuit people. Approximately 700 individuals are harvested annually across Greenland (Piniarneq 2023).

Different from ringed seal and bearded seal, harp seal and narwhal are migratory species, which coming to this area during summer. Harp seals are named after the black mark on their back, which looks like a harp. There are three populations of harp seals in the world depend on the winter breeding areas: one that breed in the White Sea, Greenland sea, and in

Newfoundland. Harp seals that comes to this area during summer is from Newfoundland, the Gulf of St. Lawrence, Labrador. Approximately 30 thousands individuals are harvested annually across Greenland, but mainly in southern areas (Piniarneq 2023), and fewer than 100 are harvested in this region (Ogawa, pers. obs.).

Narwhal is the most northerly cetacean in the world, known for their unicorn-looking tusk, which can sometimes exceed 3 m. There are three populations of narwhals in the world: Baffin Bay (BB), Northern Hudson Bay (NHB), and East Greenland (EG), and the narwhal that comes to this area is from the BB population. Each population exhibits extremely high site fidelity, and undergo annual migrations in response to sea ice extension. Inglefield Bredning is one of the key summering grounds of narwhals, where they come to the fjord from around July when the ice melts, until October, when the ice forms again. During winter, they are expected to spend time in the North Water Polynya, located in the northern Baffin Bay, outside Inglefield Bredning. Narwhals are one of the most important resources for people in the area during summer both traditionally and economically, hunted for meat, tusks and mattak (skin). The narwhal was included in CITES Appendix 2 in 1979, and quota system was introduced in Greenland in 2004. Currently, there is an annual catch quota of approximately 100 individuals per year in the area.

Seals generally give birth in spring, and undergo moulting from late spring to early summer, during which they engage in minimal feeding (Hammil et al., 1991). Both breeding and moulting seasons are energetically costly, resulting in significant body mass loss during spring (Carlens et al., 2006). To replenish their fat depositions, seals feed most intensively during summer. There is limited information on what narwhals are doing in this region, but it has been suggested that the area play an important role in nursing.

Objectives

In the area where continuous monitoring is technically difficult, apex predator can be used as sentinels for local marine environment and ecosystem. Marine mammals are ideal indicators of monitoring the local marine ecosystem, as they respond to bottom-up changes in the ecosystem and integrate its information over various time scale. Moreover, considering that marine mammals serve as important resources for local communities in this region, understanding the relationships between the environment, the marine ecosystem, and the local people, with marine mammals as their core, is key to grasping the entire interconnected of the area.

Despite the holistic understanding of this interconnected relationships is essential for predicting the impacts of climate change and strengthening resilience, its importance is often overlooked. One reason is that the methodological divide between sociological approaches, which focus on humans, and scientific approaches, which focus on marine ecosystems, makes this comprehensive investigation challenging. In this study, I unraveled these connections by integrating both scientific and sociological approaches. Additionally, by collaborating with local Inuit across the research, I aim to obtain insights that would not have been accessible through researchers alone or scientific investigations alone.

In chapter 2, I report on the feeding ecology and niche overlap among marine mammals revealed by stomach contents and stable isotope, which can provide detailed insights into the relationships between marine mammals and their prey. In chapter 3, I will clarify where they are foraging by using a novel method, spatial analysis of stomach contents, which provide insights into the relationship between marine mammals and the environment. In chapter 4, focusing on the foraging ground of ringed seals, which particularly uses glacier front as foraging ground, I will report on how foraging areas of ringed seals have changes amid the climate change. In chapter 5, based on the predator-prey relationship revealed in chapter 2, I report on the structure of the food web by using stable isotope analysis, and show the results of contaminants levels accumulated in the marine mammals through this food web. In chapter 6, I conducted interviews with local Inuit people to gather information about the environment and marine ecosystem in this region, including their deep knowledge built from their lived experiences over the past decades, as well as intergenerational knowledge passed down generations, which finally allowed us to uncover the structure of the interconnected relationships between environmental, ecosystem, and cultural changes in this area.

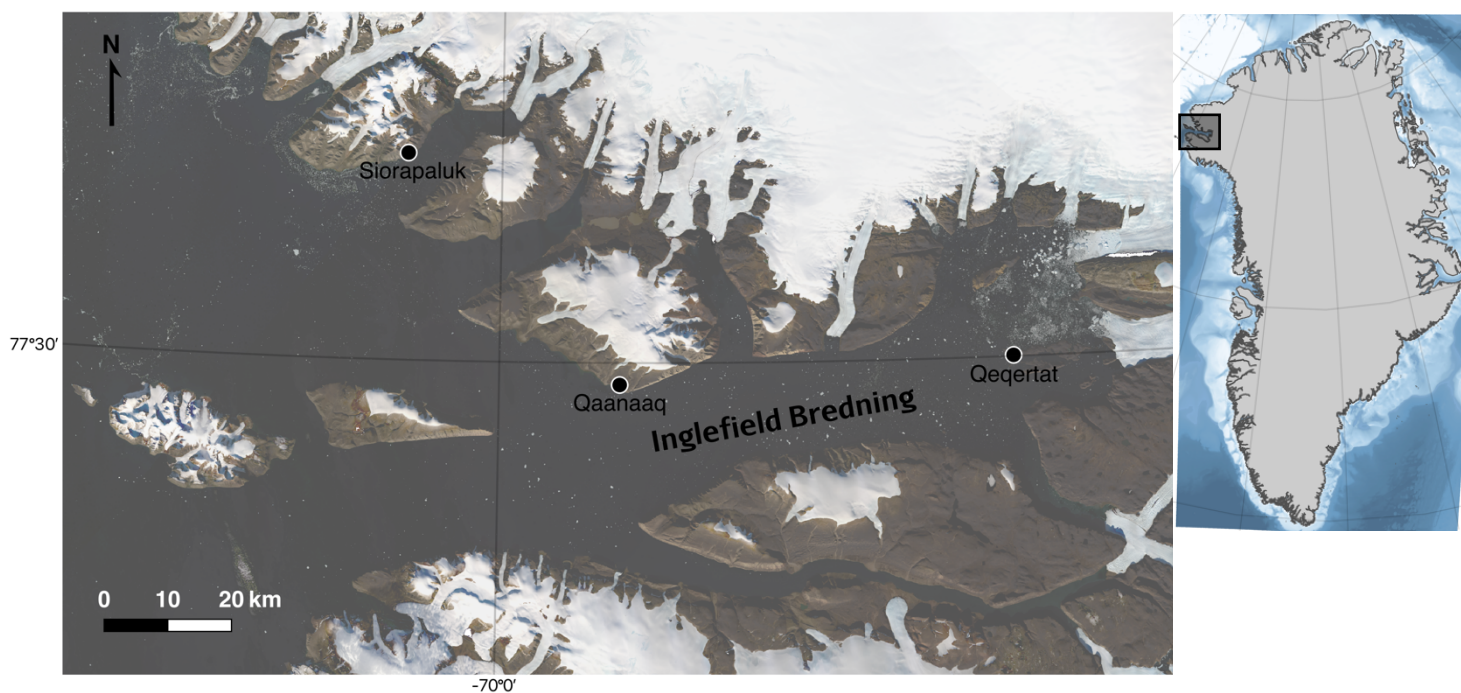


Fig. 1-1 Study site near the Inuit communities of Siorapaluk, Qaanaaq and Qeqertat in the Inglefield Bredning region, northwest Greenland.

CHAPTER 2

Summer diet of marine mammals in Inglefield Bredning

Introduction

Even among animals living in the same space, the impact of environmental and marine ecosystem changes varies between species, depending on the presence and degree of competition (Lowry 2000; Hamilton et al., 2019). Moreover, most theoretical studies of resource use including interspecific competition, predator-prey interaction, and food web model consider conspecific individuals as ecologically similar, and individual-level niche variation have been underappreciated, as it is believed to have an trivial impact in the models (Bolnick et al., 2003). However, individual niche variation is an important factor affecting the population's capacity to stability, intraspecific competition, and it can sometimes be a main factor of the population's niche width (Bolnick et al., 2003; Svanbäck and Bolnick 2006; Johst et al., 2008). Therefore, to understand and predict the impacts of environmental and marine ecosystem changes on marine mammals, it is essential to understand inter and intraspecific niche overlap and individual-level diversity (Gavrilchuk et al., 2014; Fossette et al., 2017; Laidre et al., 2008).

In the Inglefield Bredning, located in northwest Greenland, there are four marine mammals co-occurring during summer, ringed seals (*Pusa hispida*), harp seals (*Pagophilus groenlandicus*), bearded seals (*Erignathus barbatus*) and narwhals (*Monodon monoceros*). There are very few studies on the diet of marine mammals in this area (Ringed seal; Holst et al., 2001, Bearded seal; Vibe 1950, Harp seal; Kapel 2000, and Narwhal; Heide-Jørgensen 1994, Laidre and Heide-Jørgensen 2005), and there is no recent dietary information. Furthermore, there have been no studies to quantitatively investigate and compare the food resources utilized by these sympatric animals. To obtain insight into competition and sharing of prey, it is necessary to compare all sympatric species inhabiting the marine area over the same study period, and here I reports one of the few such results.

Stomach contents analysis is a fundamental method for directly examining the type, quantity, and size of prey, providing detailed insights into dietary ecology (Nielsen et al., 2017), while stable isotope analysis allow us to examine their feeding ecology in longer time scales and provide more broadly quantify and summarize their diet which stomach contents analysis can either overestimate or underestimate. Stable isotope of carbon and nitrogen has been used to get quantitative insights into the foraging ecology, food web structures and niche partitioning over a

specific periods depends on tissues. Carbon isotope ($\delta^{13}\text{C}$) reflects the feeding area (offshore versus inshore, pelagic versus benthic), and nitrogen are used to investigate trophic levels ($\delta^{15}\text{N}$).

A niche can be considered along at n-dimensional hypervolume, including spatial, temporal and trophic axes (Hutchinson 1957; Schoener 1974). Here, I combined stomach contents analysis, which reflects short-term diet, and stable isotope analysis, which represents long-term diet, to compare the feeding ecology of all marine mammals living in the same area. With focusing on interspecific competition and intraspecific dietary diversity, I report resource utilization among marine mammals to provide the insights to predict the impacts of climate change and associated marine ecosystem change on marine mammals in this area.

Materials and methods

Sampling collection

During open water seasons in 2022 to 2024, I worked with local Inuit communities of Siorapaluk, Qaanaaq and Qeqertat to collect stomach, liver and muscle samples of ringed seal, harp seal, bearded seal and narwhal around Inglefield Bredning, northwest Greenland (Fig. 1-1). All samples were collected by local hunters or biologists from the Inuit subsistence hunting. During butchering the hunted animals, the esophagus and the duodenum were tied shut, and the whole stomachs were carefully removed from the carcasses. All stomachs were examined shortly after the animals were caught without being frozen as it may destroy preys and make it difficult to identify species. Sex was recorded based on the reproductive organs. Additionally, age was estimated for several seals using canine teeth on under jaws when the teeth samples were available. Although precise age estimation was not performed for narwhals since an established method for accurate age determination has not been developed, all individuals were categorized as subadult or adult by hunters based on the body size or tusk length (Table S2-1).

Stomach contents analysis

Stomachs were cut open, and their contents were poured to a 15 L buckets. Stomach contents were weighed, washed onto a series of 4.75 mm, 1.7 mm and 0.5 mm sieve. Fleishy pieces and remaining hard part on the sieve such as cephalopod beaks, otoliths of fish, skeleton of invertebrate and crustacean, were collected and rinsed with water. Collected items were

counted and identified to the lower possible taxonomic level using identification references (Frandsen and Wieland 2004; Squires 1990; Keast and Lawrence 1990) and collection of otoliths from fish caught around Greenland, provided by Greenland Institute of Natural Resources (GINR), Nuuk, Greenland. All species identification were conducted under a stereomicroscope (Micronet, YS03C) with micrometer.

Length of all collected otolith with minimal or no erosion were measured using ImageJ software along their longest axis to the nearest 0.01mm (Finley and Gidd 1982; Härkönen 1986). From the measured otolith length, original fork length (*FL*) and wet mass (*WM*) of fish were calculated by using regressions from previous studies, including polar cod (*Boreogadus saida*), Arctic cod (*Arctogadus glacialis*), snailfish (*Liparis* sp.), sculpin (*Cottidae* sp.) and cephalopod (see Table S2-2). For other species with no regressions available, mean weight from previous study (Finley and Evans 1983) or mean weight of all specimens of that species found and measured in this study were used. The number and total biomass of fish were determined by dividing these number by two, as the teleost fish has two sagittal otoliths.

Data analysis on diet

Several indexes were calculated for each prey items (*i*) to examine the dietary composition and the importance of each species; (1) Frequency of occurrence (*FO_i* %), (2) relative frequency of occurrence by number (*N_i* %), (3) relative frequency of occurrence by biomass (*B_i* %), and (4) index of relative importance (*IRI_i*) (Chambellant et al., 2013; Moreno and Castro 1995; Holst 2001; Bengtsson et al., 2020). Each indices were calculated as follows:

$$(1) FO_i(\%) = (S_i/S_t)*100,$$

where *S_i* represent the number of seals or narwhals that consumed prey type *i*, and *S_t* represent the total number of seals or narwhals;

$$(2) N_i(\%) = (n_i/n_t)*100,$$

where *n_i* represent the total number of prey type *i*, and *n_t* represent the total number of all prey samples from stomachs;

$$(3) B_i(\%) = (b_i/b_t)*100,$$

where b_i represent the total biomass of prey type i consumed by seals and narwhals, and b_t represent the total biomass of all estimated prey;

These three different indicators provide the information of importance of each prey in difference aspect. However, each index has limitation, as N_i (%) may overestimate the small prey eaten by mammals in large numbers, and B_i (%) may overestimate large prey, even if the prey species are eaten in small numbers. Therefore, to mitigate these limitation and make it possible to compare the importance of each prey species, Index of Relative Importance (IRI_i) for each prey items (i) was estimated to integrate the different index into one single parameter as follows:

$$(4) IRI_i = (IN + IW) / 2,$$

with IN (indices of importance by number) and IW (indices of importance by biomass) were calculated as follows:

$$IN = (PO_i * N_i)^{1/2}$$

$$IW = (PO_i * B_i)^{1/2}$$

Empty stomachs were not included in calculating these indexes.

For statistical analysis, as some species were represented in small number and/or were found only from a few stomachs, they were grouped into the taxonomic level of Family as follows. For fish; sea snail (Liparidae), eelpout (Zoarcidae), Sculpin (Cottidae), Sea Poacher (Agonidae), and Prickleback (Stichaeidae), and other fish. For Gadidae, I analyzed polar cod (*Boreogadus saida*) and arctic cod (*Arctogadus glacialis*) separately, as they were represented in great number, and considered as one of the main prey of marine mammals in this area. For shrimp, I grouped into following Family level; Cragonidae, Thoridae, Pasiphaeidae, Pandalidae, and unidentified shrimp. For cephalopod, zooplankton and benthos, I analyzed data with lowed possible taxonomic level.

Based on the information above, variation in the diet between and within species were examined by using Schoener's proportional similarity index, following Ogloff et al. (2019) and Araújo et al (2009). Variations in the diet between species (PS_{xy}) were calculated on IRI value as follows:

$$PS_{xy} = 0.5 \sum (| P_{xi} - P_{yi} |),$$

where P_{xi} and P_{yi} represent the proportion of *IRI* value of prey type i in the diet of marine mammal x and y , and PS_{xy} is the diet similarity value between x and y . Variation in the diet within species was also examined with Schoener's Index on percent abundance ($N_i \%$) and percent biomass ($B_i \%$) separately. Now, equation is modified to $PS_{ai} = 0.5 \sum_i | P_{ai} - Q_i |$, where P_{ai} is the proportion of prey type i in individual a 's diet, and Q_i represent the proportion of prey type i in the species' total prey abundance or biomass. Therefore, PS_{ai} value indicates the overlap between an individual a 's diet and the species' diet as a whole, and can quantify the degree to which individuals are specialized to their population. PS_{ai} value was calculated for each individual, and the mean PS_{ai} of each species represent the individual-level dietary similarity within species (PS_a). PS_{xy} and PS_a value vary from 0 to 1, with 0 represent a total similarity, and 1 represent a total difference in prey selection. Similarity is considered ecologically meaningful if index show a value below or equal to 0.40 (Wallace 1981). Detailed on this index can be found in Bolnick et al. (2002).

The total niche width of species (TNW) was calculated by using Simpson's diversity index on the number of prey, following Chambellant et al (2013). TNW value represents the diversity of prey types eaten by each species, and hence I can measure the degree of diet specialty of each species. TNW value was calculated for each species as follow:

$$TNW = 1 - D, \quad D = \sum (n_i / n_t)^2,$$

where n_i represent the number of prey type i , and n_t represent the total number of prey samples from stomachs, same as I calculated N_i values (2). This index will show a value of 0 when all individuals within species use only single type of prey, and increasing with both the number of prey types and the evenness with which they feed (Magurran 2003). Therefore, larger value suggest that the species prey on a large variety of prey, and less dietary specialty.

Difference in size of ingested polar cod (*Boreogadus saida*) and arctic cod (*Arctogadus glacialis*) between species were tested with a Mann – Whitney U test. Since ringed seals and bearded seals consumed very little arctic cod, I present the results for arctic cod only for harp seals and narwhals. Additionally, I compared the size differences of polar cod among different age classes of seals. All the statistical analyses were performed by using R statistical software (version 4.0.0; R Core Team, 2020).

Age estimation analysis

Age of each seal was estimated by counting growth layers in the cementum of canine teeth. The teeth were decalcified with 5% HNO₃ solution for at least 48 hours, and kept in water for 24 hours afterward. Decalcified teeth were cut in 14-μm slices with a freeze-microtome (Leica CM 1520 or Yamato Kouki FX-801). Sliced teeth were dyed with a toluidine blue/NaHCO₃ solution, and the number of dyed layers in the cementum were counted to estimate the age of each seal following Stewart et al. (1996). Seals were grouped into age classes as follows, *pup*; 0-year individuals born in the spring, *juvenile*; seals 1 to 5 years old, *adult*; 6 years old and older which are sexually mature (Holst et al., 1999; Chambellant et al., 2013).

Stable isotope analysis

Muscle and liver tissues of marine mammals and muscle or whole body of prey found from their stomachs were oven-dried at 60°C for 24 h, homogenized for 48 h using a mortar and pestle and lipid-extracted using 2 : 1 chloroform : methanol following the methods of McMeans et al. (2009). After drying lipid-extracted samples at 60°C for 24 h, 0.04 – 0.07 mg of tissue were weighted into tin cuspules and values of δ¹³C and δ¹⁵N were measured by at Kyoto University. Stable isotope ratios were expressed in per mil (‰) in delta (δ) ratios as calculated using the following equation:

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

where X is ¹³C or ¹⁵N, R_{sample} is the ration (¹³C/¹²C or ¹⁵N/¹⁴N) in the sample, and R_{standard} is the ration in the standard. A triplicate was run for every 12th sample. Different organs represent different duration of food. Liver, a high turnover rate organ represent food ingested within days or weeks, whereas muscle, lower turnover rate, integrated value of the diet over several months.(Kurle and Worthy 2002).

To compared isotopic niche width among four marine mammals, Bayesian standard ellipses areas (SEA_B) were estimated using Bayesian inference in the package SIBER and rjags in R v. (Jackson et al., 2011). I estimated SEA_B using 10⁵ iterations, 10³ burn-in and a thinning of 10.

Results

Diet composition

A total of 54 ringed seal, 17 harp seal, 23 bearded seal and 32 narwhal stomachs were collected during the study period (Table S2-1). A total of 62 prey taxa were found as a prey, including 27 types of fish, 3 types of cephalopods, 19 types of shrimp, 8 types of zooplankton and 5 types of benthos.

- *Ringed seal*

Fourteen out of 54 stomachs (26 %) were empty. In total, fifteen types of prey were found from ringed seal (Table S2-3). Mean weight of stomach contents was 168.9 g (Max 669 g, Min 7 g). Polar cod (*Boreogadus saida*) was the most dominant species in terms of *IRI*, PO_i , and B_i value ($IRI = 65.7$, $IRI \% = 49.5$), found from 77.5 % of the seals, and accounted for 82.1 % of total biomass (Fig. 2-1, Table S2-3). Zooplankton was the second most important prey group ($IRI = 39.3$, $IRI \% = 35.6$), made up 62.7 % of the prey items numerically (Fig. 2-1, Table S2-3). More than half of the ringed seal fed at least one kind of zooplankton ($PO_i \% = 57.8$), but due to their small size, contribution to the total biomass was small ($N_i \% = 6.0$).

- *Harp seal*

Three out of 17 stomachs (18 %) were empty. A total of fifteen types of prey were found from harp seal, eight of these were identified to the species level (Table S2-4). Mean weight of stomach contents was 821.3 g (Max 2028 g, Min 10 g). Polar cod was the most dominant and important species in terms of every indices, found from 86.7 % of harp seals, and accounted for 74.0 % in number, and 71.9 % on biomass (Table S2-4). *IRI* value was 79.5, made up 57.8 % of total *IRI* (Table S2-4, Fig. 2-1). Although zooplankton occupied only 0.3 % of total biomass (Table S2-4), *IRI* value suggests that zooplankton is the second most important prey species for harp seal ($IRI = 18.1$, $IRI \% = 22.5$), as it fed quite often by harp seals (Table S2-4, Fig. 2-1).

- *Bearded seal*

Six out of 23 stomachs (26 %) were empty. A total of fifty two types of prey were found from bearded seal, thirty one of these were identified to the species level, mostly benthic inhabitants (Table S2-5). Mean weight of stomach contents was 1485.1 g (Max 5367 g, Min 79 g). In terms of all indices, sculpin (Cottidae) was the most dominant species, eaten by 82.4 % of seals, and accounted 23.3 % for N_i , 50.0 % for B_i (Table S2-5). *IRI* value was 54.0, made up

23.6 % of total *IRI* (Table S2-5, Fig. 2-1). Polar cod was the second most dominant prey, also in terms of all indices. Benthos, e.g. bivalves and snails, were frequently found ($PO_i \% = 70.6$), which were not found from any other marine mammals (Table S2-5).

- *Narwhal*

Three out of 32 stomachs (9 %) were empty. A total of twenty three types of prey were found from narwhals, eleven of these were identified to the species level (Table S2-6). Mean weight of stomach contents was 3080 g (Max 8710 g, Min 250 g). Polar cod was the most important prey in term of number ($N_i \% = 77.0$) and *IRI* value ($IRI = 72.9$), but as arctic cod is larger than polar cod, arctic cod contributed the most in terms of total biomass ($B_i \% = 56.0$) (Table S2-6). Alone with these two Gadidae species, they occupied 93.0 % in total biomass, and 91.8 % in number (Table S2-6). Cephalopod was also fed frequently by narwhal, which were found from 88.9 % of narwhals (Table S2-6).

Variations in the diet between and within species

Based on the Schoener's similarity index on *IRI* value, similarity in diet between ringed seals and harp seals (Schoener's Index 0.3096), and harp seals and narwhals (Schoener's Index 0.3734) were ecologically meaningful (Table 2-1). However, diet of ringed seals and narwhals was below the threshold of 0.4 (Schoener's Index 0.5113), indicated less similarity. Only bearded seal showed no ecologically meaningful similarity to any species (Table 2-1).

In terms of diet similarity within species, Schoener's similarity index showed ecologically meaningful value only for narwhal both based on abundance and biomass (Schoener's Index 0.2416 and 0.2760, respectively), suggests that they have considerably less diverse feeding habit compared to other species (Table 2-2). Based on the abundance, ringed seals showed the highest value (Schoener's Index 0.7799), whereas bearded seals showed the highest in biomass (Schoener's Index 0.5447; Table 2-2). Bearded seal showed extraordinary high TNW value among the four marine mammal species (TNW = 0.9), suggested that they feed variety of species (Fig. 2-1). Ringed seal was the second (TNW = 0.71), followed by narwhal (TNW = 0.53). Harp seal showed the lowest value, suggested that they utilize relatively less diverse preys.

Age specific difference in prey composition was observed for seals (Fig. 2-2). Overall, adults depend highly on polar cod regardless of species, and there were species-specific

differences in the primary prey in younger groups. In ringed seals, there is a tendency for main prey items to shift from zooplankton to polar cod as they mature (Fig. 2-2). Harp seals tend to consume a wide variety of fish and plankton during their younger age, but they become heavily reliant on polar cod in adult stage. Main prey of pups and juveniles of bearded seals was sculpins, and their reliance on polar cod and benthic organisms increases as they get old (Fig. 2-2).

Range of estimated size of polar cod and Arctic cod eaten by marine mammals were shown in Fig. 2-3. Size of the consumed polar cod was the biggest for bearded seal (178.6 ± 26.4 mm, $n = 1109$; Fig. 2-3). Harp seal was 175.8 ± 22.5 mm ($n = 598$), and ringed seal was 163.2 ± 42.4 mm ($n = 520$). Narwhals consumed significantly smaller size polar cod among four marine mammals ($P < 0.01$, 118.8 ± 28.7 mm, $n = 4072$; Fig. 2-3). Polar cod eaten by pups were significantly smaller than juvenile (ringed seal; $W = 8020$, $P < 0.001$, harp seal; $W = 2749$, $P < 0.001$; $W = 1467$, $P < 0.005$) and adult ($W = 26524$, $P < 0.001$, $W = 5450$, $P < 0.001$, $W = 5514$, $P < 0.001$, respectively) regardless of species (Fig. 2-3). No significant difference was observed between juveniles and adults (Fig. 2-3). The mean size of arctic cod was 208.7 ± 40.1 mm for harp seal ($n = 99$) and 187.3 ± 54.4 mm for narwhal ($n = 1761$), respectively, and narwhals consumed significantly smaller size of arctic cod than harp seal ($P < 0.01$, Fig. 2-3).

Stable isotope niche of marine mammals

Narwhal had the narrowest SEA_B in both liver and muscle (Table S2-7), and showed complete niche overlap with harp seals and ringed seals in liver tissues, and heavily overlapped (95.9 %) with harp seals (Fig. 2-4a, b, Table S2-8). Bearded seal occupied the highest $\delta^{13}C$ range, and their isotope niches were significantly different from other mammals in both tissues (Fig. 2-4a). Ringed seal occupied the highest $\delta^{15}N$ range in muscle, whereas narwhals were highest in liver (Fig. 2-4a). In the result of liver samples, reflecting the feeding ecology over the past few weeks which may since the two migratory mammals, narwhals and harp seals arrived in this area, stable isotope niches showed substantial overlap among marine mammals except the bearded seals (Fig. 2-4a).

Discussion

Variation in the diet and insight into habitat use

It was found that the main prey is polar cod, which is not particularly surprising, as it is the same as in other regions in the high Arctic (Siegstad et al., 1998; Labansen et al., 2022; Matley et al., 2015). Still, the unique point of this study is that by comparing the diet of all sympatric marine mammals inhabiting this area for the first time, quantitatively revealing the overlap in their diet niches. It is revealed that the diet of harp seal, ringed seal and narwhal showed an ecologically significant similarities, both in stomach contents (Table S2-1) and stable isotope (Fig. 2-4 a). Since the harp seal, which seasonally occupies the Arctic, has been suggested to extend its geographic range into more northern latitudes and remain there longer due to climate change, our study suggests that this may potentially lead to competition for prey with native species, ringed seals and narwhals in the future (Moore and Huntington 2008; Laidre et al., 2008).

Although polar cod was the main source of energy for all marine mammals (Fig. 2-1, Table S2-3 – 6), the size of cod consumed by each animal was varied (Fig. 2-3). Narwhal fed relatively small size of polar cod, and ringed seals, harp seals and bearded seals fed similar range (Fig. 2-3). This may reflect the vertical differences in foraging zones, as small cod usually occupy shallow area, whereas adult cod tend to inhabit deeper area (Falk-Petersen et al., 1986). During summer, narwhal occupy shallow water (~ 48 % of time at < 8 m) than in winter (Laidre et al., 2004). Therefore, the differences in the size of the consumed polar cod suggest that narwhals may be foraging in shallower waters compared to other animals. The size of polar cod preyed by seals was different depend on age, with pups consumed significantly smaller cods than juveniles and adults (Fig. 2-3). This also likely reflects age – related differences in foraging areas and is consistent with previous studies showing that younger individuals tend to use shallowed waters more frequently (Born et al., 2004). The difference in polar cod *IRI* % among age groups may also be attributed to the fact that younger individuals were consumed smaller polar cod, leading to a lower proportion of cod in total biomass (Fig. 2-2).

Moreover, in the area where information on the abundance and distribution of prey is lacking, it is challenging to assess the diet preferences of marine mammals. In our study, by investigating and comparing the diets of all marine mammals utilizing this area during the open-water season for the first time, I could provide insights into specie-specific dietary preferences.

There are several species which were fed almost exclusively by bearded seal, including

sculpin, sea poacher, pricklebacks and benthos such as snails (Fig. 2-1). Also, bearded seal was the only species did not show any diet similarity to other marine mammals both in stomach contents (Table 2-1) and stable isotope analysis (Fig. 2-4 a). The prey species actively consumed primarily by bearded seals were mostly benthic organisms, suggesting that bearded seals rely relatively heavily on the benthic food web. Ringed seal also found to eat sculpin in some region including northwestern Spitsbergen (Gjertz and Lydersen 1986), eastern Canada (McLaren 1958), Canadian high arctic (Ross et al., 2022) and Easter Greenland (Siegstad et al., 1998). This difference in feeding on sculpin was thought due to the availability of sculpin in each region (Siegstad et al., 1998). However, considering the fact that bearded seals fed great amount of sculpin in this area while ringed seal and harp seal did not, absence of sculpin from ringed seals is either due to prey preference or competition, than just due to an availability. To clarify which of these is the case, further investigation is needed to understand the prey distribution and biomass.

Shrimp were relatively important prey for narwhals and bearded seals ($IRI = 11.5$ and 22.1 , respectively), consumed by more than 66 % and 64 % of all individuals (Table S2-5, 6). However, interestingly, the main types of shrimp differed between narwhals and bearded seals, were hardly overlapped. Cragonidae, the main shrimp taxa of bearded seal's diet, is a benthic shrimp and occur most frequently from mud to rock in sea floor (Saint-Marie et al., 2006; Williams and Wigley, 1977), whereas Pasiphaea, the main shrimp taxa of diet of narwhal, usually found in deep area with vertical migration (Simão et al., 2014). Therefore, these difference in the types of shrimp preyed on may also reflect differences in foraging ecology and habitat use – bearded seals may choose areas with easily accessible to the sea floor, while narwhals may be found in deeper water.

Insight into marine ecosystem change

The diet composition of ringed seal, which is relatively more dependent on zooplankton among four species, suggested changes in zooplankton composition in this area. In the previous study conducted in 1998 in the same area, amphipod (*Themisto libellula*) was the most dominant type of zooplankton in (Holst et al., 2001). On the other hand, in our study, the dominant type of species was replaced by krill (*Thysanoessa* sp. (*T. longicaudata*, *T. longipes*, *T. inermis* or *T. raschii*); Table S2-3), which have never been found from the stomach of marine mammals in Inglefield Bredning (Holst et al., 2001; Laidre and Heide-Jørgensen 2005; Kapel

2000). While amphipod is a typical Arctic cold-water species, usually absent from the warm water ($> 2^{\circ}\text{C}$) (Dunbar 1957; Dalpadado et al., 2001; Sameoto 1984), all possible krill species (*T. longicaudata*, *T. longipes*, *T. inermis* or *T. raschii*) can be found warmer water (Dalpadado and Skjoldadal 1996; Saunderson et al., 2013), which is recognized as a species expanding their habitat northward due to sea temperature rise in the arctic (Buchholz et al., 2012; Daase et al., 2021). This result indicating that the zooplankton community might be changing in the area due to the rising temperature, same as several other arctic oceans (Buchholz et al., 2012; Dalpadado et al., 2012). Moreover, redfish (*Sebastes* sp.) was found from bearded seal, which is considered as boreal fish consumed by seals in more southern area (Siegstad et al., 1998; Kapel 2000). Redfish is now expanding their habitat range northward attribute to the temperature rise as well, started to appear in regions where it was not observed before (Hollowed et al., 2013; Fossheim et al., 2015), and the results suggest that the area also be one of those regions. If the water temperature continues to rise, there may be an increase in Atlantic species and a decline in native species such as polar cod and arctic cod, and subsequent changes in the diets and habitat use of marine mammals may occur.

Vulnerability to the environmental changes

Understanding the specialization in feeding is important to assess the sensitivity responses to climate and marine ecosystem change (Laidre et al., 2008; Watt et al., 2013). Our results showed that bearded seals are likely to be the most resilient species to the environmental change, as they have the greatest feeding variation (Table 2-2, Fig. 2-4 b), and use the widest range of resources (TNW = 0.9, Fig. 2-1). Narwhal showed less diverse feeding habit than other marine mammals living in the area (Table 2-2, Fig. 2-4 b), and also utilize less diverse resources (TNW = 0.53, Fig. 2-1). Narwhal has been considered as one of the most vulnerable Arctic marine mammals to environmental change, as they have narrow prey selection, strict migratory patterns and site fidelity (Chambault et al., 2020, 2022). Recent study, on the other hand, shown that narwhal have higher intra-population and annual inter-individual variability in feeding niches than previously thought (Dietz et al., 2021; Watt et al., 2013; Watt et al., 2015). Considering that they still have relatively narrow dietary niche by comparing to other marine mammals, my study support the previous findings that narwhals are relatively vulnerable to environmental changes. Given their narrow prey selection and the potential overlap with the dietary niches of harp seals, which are expected to increase in number in high-Arctic due to

climate change, future environmental and marine ecosystem changes may particularly have negative impacts on narwhals.

In conclusion, our study compared the diet among four marine mammals inhabiting around Inglefield Bredning for the first time, and provided insights into how sympatric marine mammals share prey resources. Comparison with previous diet suggested that the marine ecosystem in this area is undergoing changes due to climate change. As the utilized prey resources varied among species and age classes, even within the same area, the degree of impact of environmental and ecosystem changes may differ. Further study is needed to investigate seasonal feeding ecology of marine mammals to better understand the impacts of accelerating climate change on them in this area.

Table 2-1. Dietary similarity between species. Schoener's similarity Index of dietary variation between species on *IRI* value shown in Table S3, 4, 5 and 6. Index values below or equal to 0.40 are considered dietary similarity is ecologically meaningful, and are shown in bold font.

	Ringed seal	Harp seal	Bearded seal
Harp seal	0.3096		
Bearded seal	0.7389	0.6963	
Narwhal	0.5113	0.3734	0.7070

Table 2-2. Dietary similarity within species. Schoener's similarity Index of dietary variation within species of ringed seal, harp seal, bearded seal and narwhal. For Schoener's similarity Index, values below or equal to 0.40 are considered ecologically meaningful and are shown in bold font.

Species	Abundance	Biomass
Ringed seal	0.7799	0.4695
Harp seal	0.4824	0.5221
Bearded seal	0.6265	0.5447
Narwhal	0.2416	0.2760

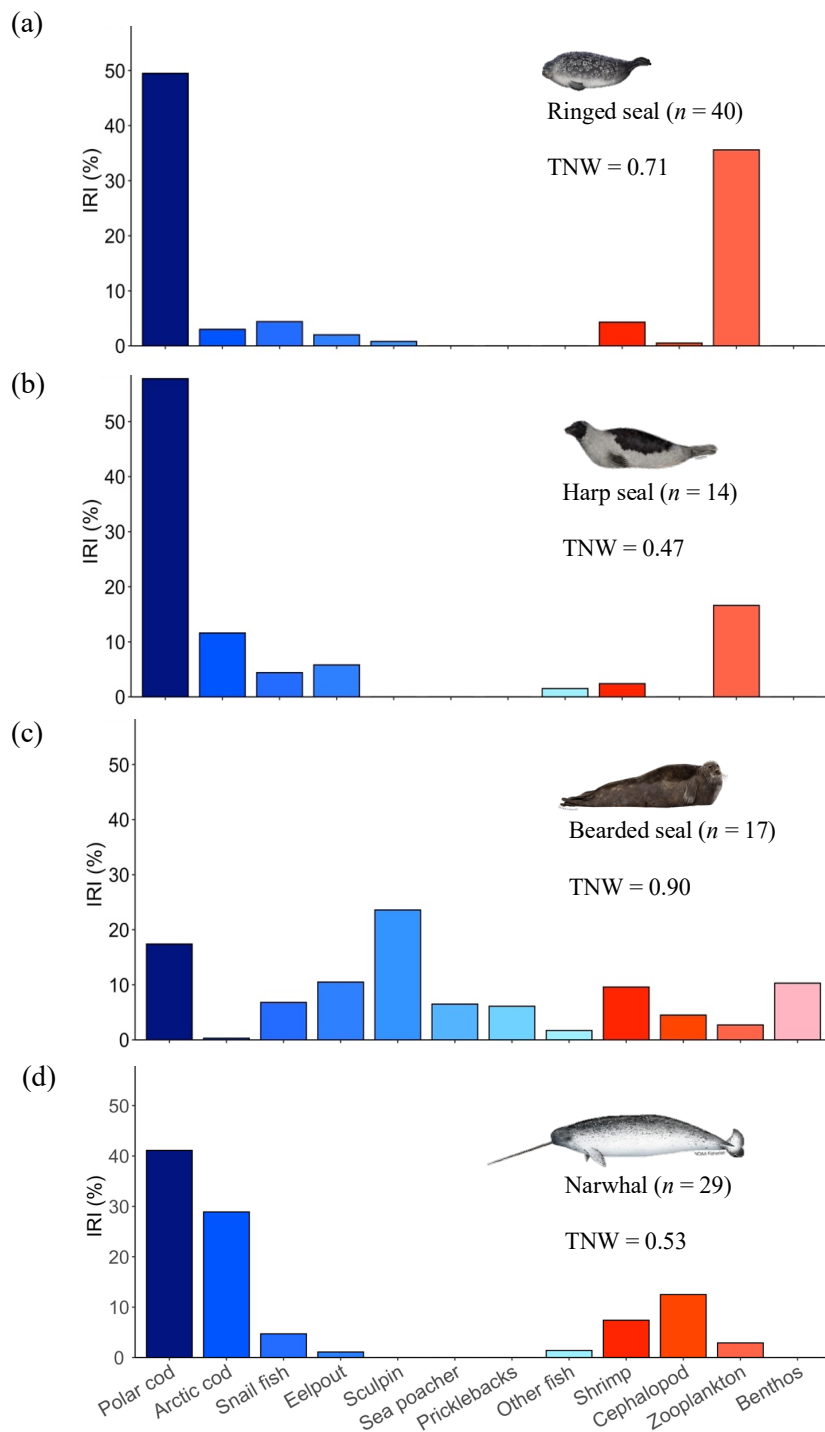


Fig. 2-1 Percent of *IRI* value of prey groups found in the stomachs and total niche width (TNW) of (a) ringed seals, (b) harp seals, (c) bearded seals and (d) narwhals in Inglefield Bredning during summer in 2022 to 2024. Fish species were shown in blue, and invertebrates were in red.

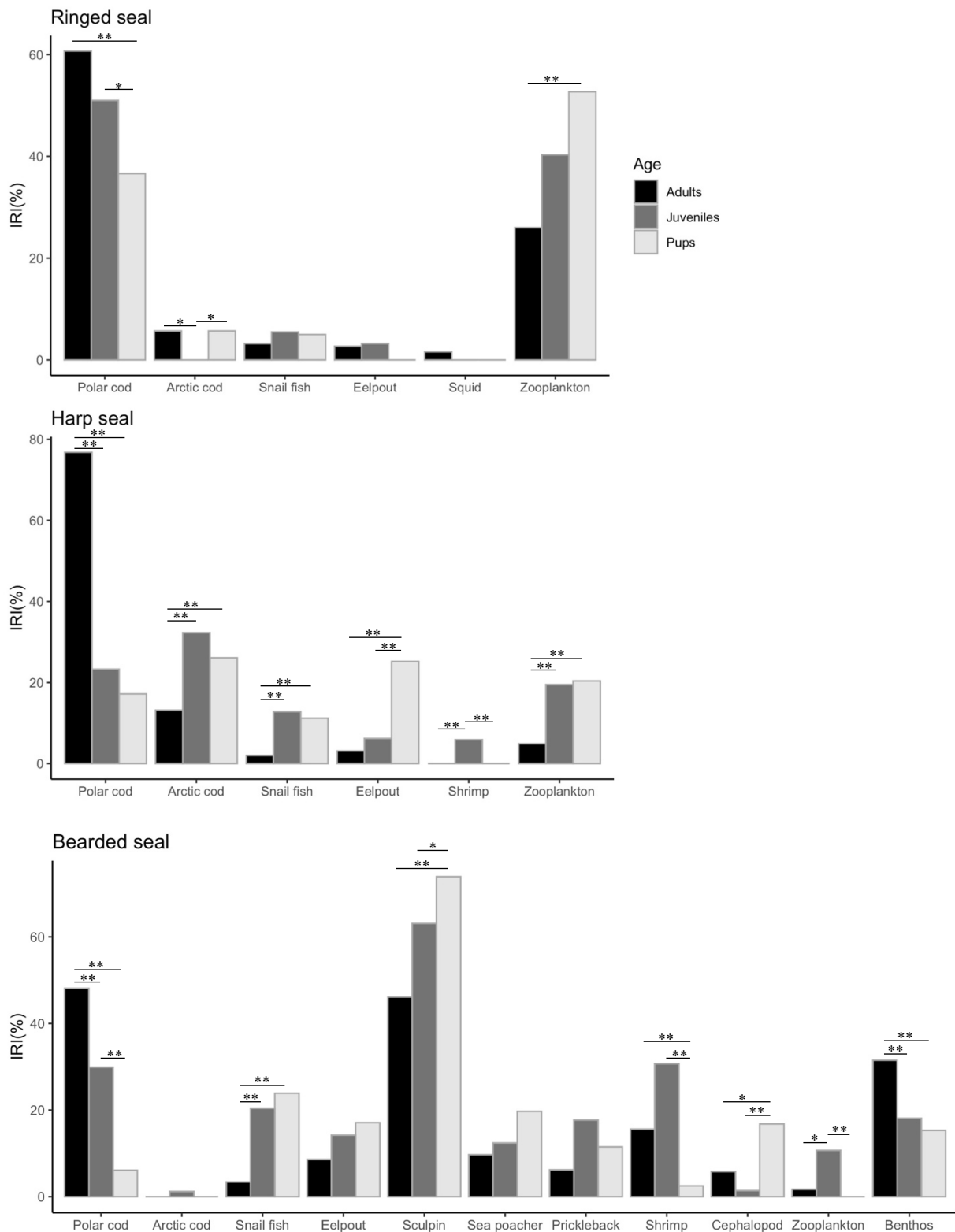


Fig. 2-2 Comparison of the percent of *IRI* among age groups. *IRI* % of prey groups found in the stomachs of ringed seals, harp seals and bearded seals. Proportions are compared among different age groups, pups (light grey), juveniles (grey) and adults (black). Significant differences were analyzed with Fisher's exact test (*=0.05, **=0.01).

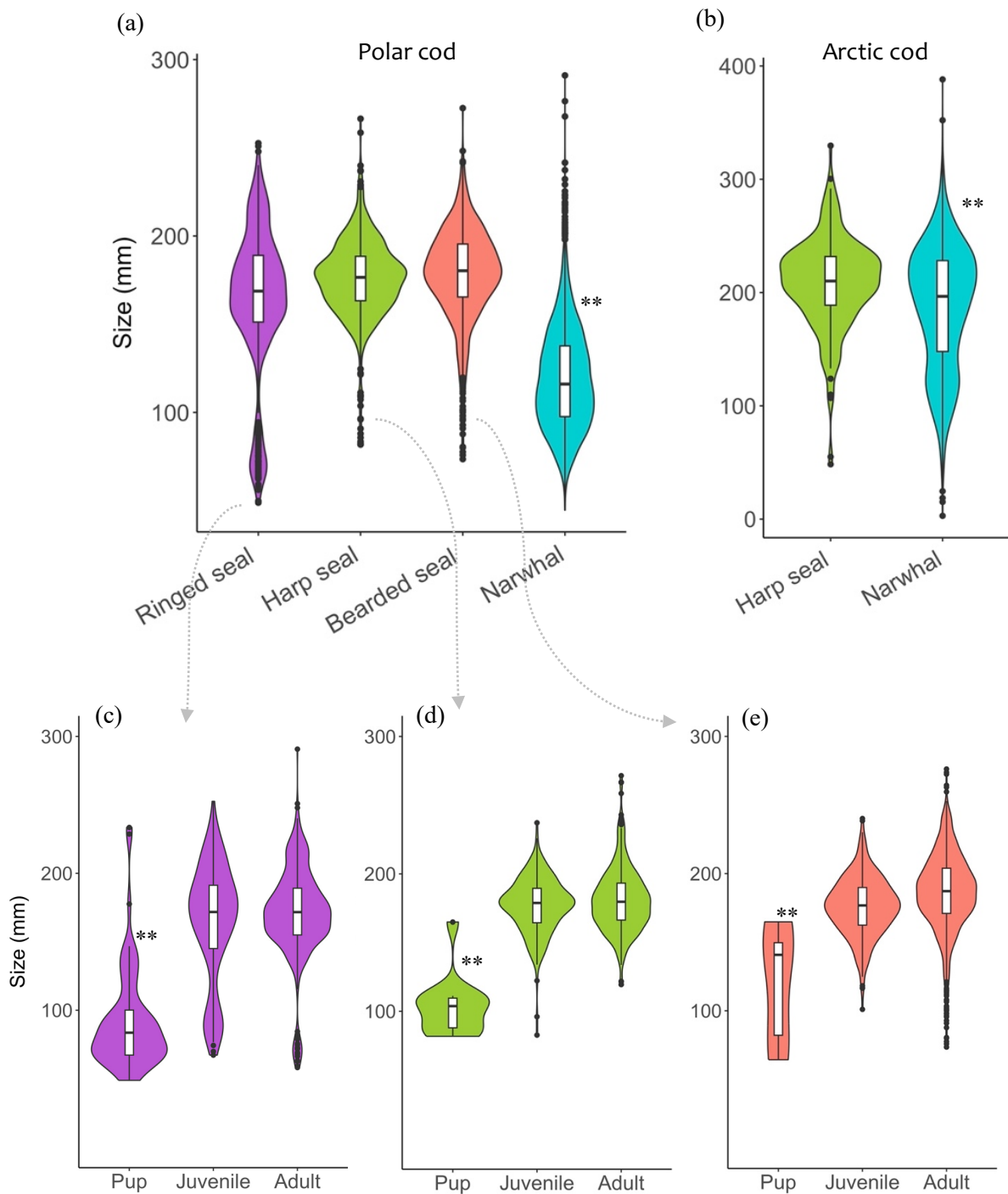


Fig. 2-3 Estimated size of polar cod and arctic cod. Violin plot showing the estimated size of polar cod (a) and arctic cod (b) found from the stomach of ringed seal (purple), harp seal (green), bearded seal (red) and narwhal (blue). Differences in size of polar cod between age groups of ringed seal (c), harp seal (d) and bearded seal (e) are compared with Mann – Whitney’s U test (**=0.01).

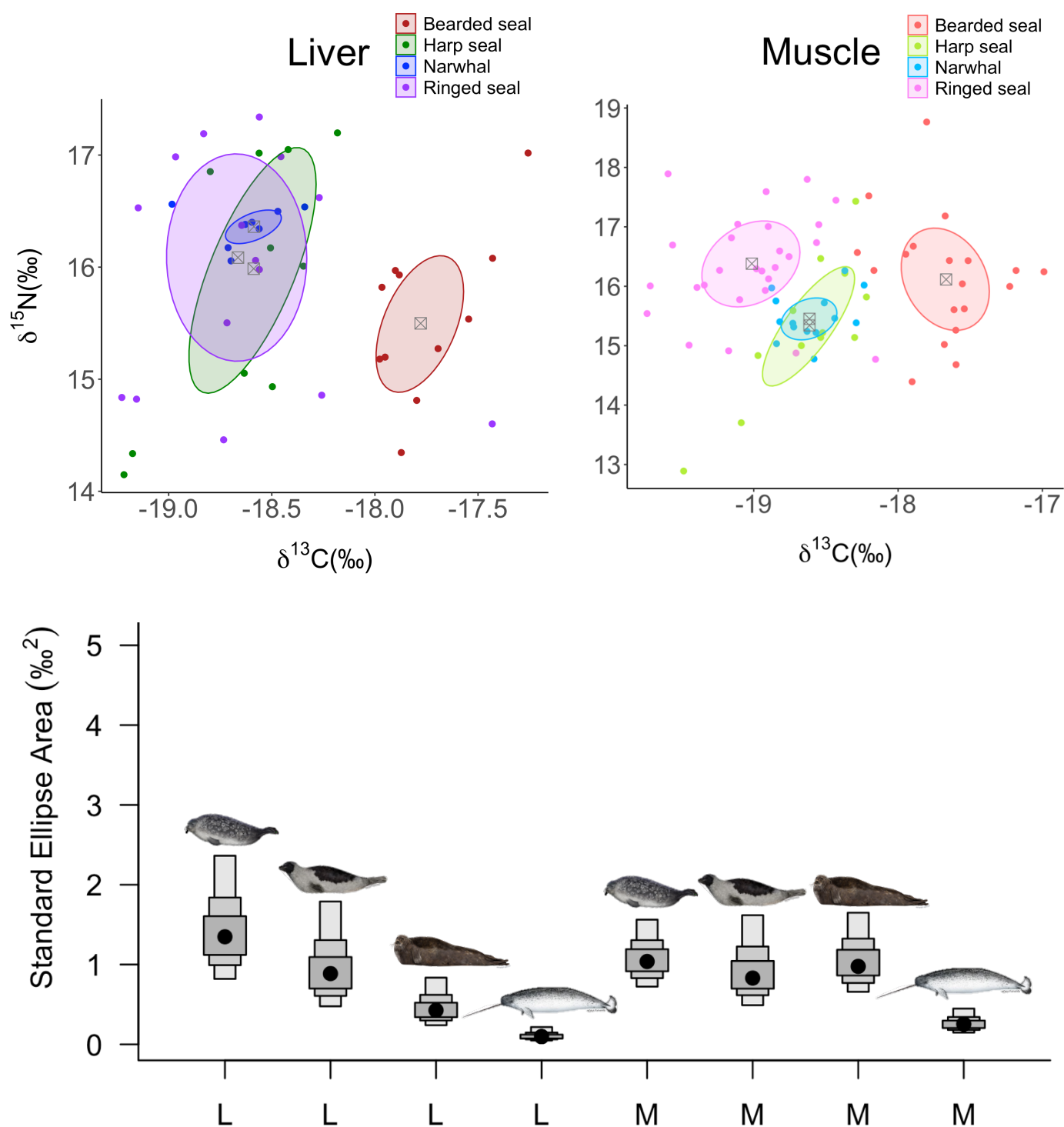


Fig. 2-4 Size of liver and muscle standard ellipse areas (SEAB ,) for marine mammals. (a) Solid circles indicate Bayesian standard ellipse areas (SEAB). (b) SEAB for liver samples of ringed seal ($n = 15$), harp seal ($n = 10$), bearded seal ($n = 11$) and narwhals ($n = 8$), and muscle samples of ringed seal ($n = 27$), harp seal ($n = 12$), bearded seal ($n = 19$) and narwhals ($n = 14$). Boxes indicating the SEAB at 50, 75 and 95 % credible intervals.

Table S2-1. Numbers of marine mammal stomachs collected In the Inglefield Bredning, 2022-2024. Some seals are recorded as unknown as tooth could not be collected, or age estimation is not conducted.

	male				female				
	pup	juvenile	adult	unknown	pup	juvenile	adult	unknown	Total
Ringed seal	8	8	4	14	3	6	3	8	54
Harp seal	5	2	4	5	0	1	0	0	17
Bearded seal	5	6	5	0	1	5	0	1	23
Narwhal	-	-	-	24	-	-	-	8	32
									126

Table S2-2. Estimate regression of prey.

Prey taxon	Wet mass (g)	Mean mass	r ²	n	Energy (kJ g ⁻¹)	source
Gadidae						
<i>Boreogadus saida</i>	WM = 0.1475*OL ^{2.7320}		0.90	192	4.7	(1), (2)
<i>Arctogadus glacialis</i>	WM = 0.0089454*OL ^{4.2543}		0.96	178	-	(1)
Liparidae						
<i>Liparis sp.</i>	WM = 0.0065*BL ^{3.1802}		0.96	39	2.84	(3)
Zoarcidae						
<i>Lycodes sp.</i>	80 g					(4)
<i>Cottidae</i>	WM = 7.37*(BL/10) ^{2.57}				4.57	(7)
Cephalopod	WM = -0.655 + 3.33 ln (LRL)					(5)
Shrimp	4.3 g				4.87	
Zooplankton	0.2 g				4.18	(2), (6)
Benthos					3.03	

Table S2-3 Stomach contents of ringed seal. 15 types of prey were found; 8 of these were identified to the species level. Taxa in bold indicate the key groups used in the analyses. Groups in bold letters

	N prey	POi	Ni	Bi	IRI
FISH					
Cod (Gadidae)	1808	77.5	34.6	86.1	66.7
<i>Boreogadus saida</i>	1792	77.5	34.3	82.1	65.7
<i>Arctogadus glacialis</i>	16	10.0	0.3	4.0	4.0
Snail fish (Liparidae)	45	25.5	0.9	2.0	6.0
<i>Liparis fabricii</i>	25	12.5	0.5	1.1	3.1
<i>Liparis sp.</i>	20	12.5	0.4	0.9	2.8
Eelpout (Zoarcidae)	7	10.0	0.1	1.9	2.7
<i>Lycodes vahlii</i>	5	5.0	<0.1	1.4	1.6
<i>Lycodes sp.</i>	2	5.0	<0.1	0.5	1.0
Sculpin (Cottidae)	2	5.0	<0.1	0.4	1.1
INVERTEBRAT					
Shrimp (Decapoda)	87	12.5	1.7	3.5	5.6
Pandalidae					
<i>Pandalus sp.</i>	1	2.5	<0.1	<0.1	0.5
Thoridae					
<i>Eulalus gaimardii</i>	75	5.0	1.4	3.1	3.3
Pasiphaeidae					
<i>Pasiphaea sp.</i>	9	2.5	0.2	0.4	0.9
Cragonidae					
<i>Sabinea sarsii</i>	1	2.5	<0.1	<0.1	0.5
Unknown decapoda	1	2.5	<0.1	<0.1	0.5
Cephalopod					
<i>Gonatus fabricii</i>	1	2.5	<0.1	0.1	0.5
Zooplankton	3274	57.5	62.7	6.0	39.3a
<i>Mysis sp.</i>	841	20.0	16.1	1.5	11.7
<i>Gammarus setosus</i>	8	2.5	0.2	<0.1	0.6
<i>Gammarus sp.</i>	1	2.5	<0.1	<0.1	0.5
<i>Themisto libellula</i>	743	32.5	14.2	1.2	13.9
<i>Thysanoessa sp.</i>	1487	20.0	28.5	3.1	15.9
<i>Calanus sp.</i>	194	17.5	3.7	0.1	4.7

Table S2-4 Stomach contents of harp seal. 15 types of prey were identified, 8 of these were identified to the species level.

	N prey	POi	Ni	Bi	IRI
FISH					
Cod (Gadidae)	1360	86.7	79.9	94.1	86.8
<i>Boreogadus saida</i>	1261	86.7	74.0	71.9	79.5
<i>Arctogadus glacialis</i>	99	20.0	5.8	22.2	15.9
Snail fish (Liparidae)					
<i>Liparis sp.</i>	33	26.7	1.9	0.9	6.0
Eelpout (Zoarcidae)	13	33.3	0.8	2.9	7.5
<i>Lycodes vahlii</i>	3	6.7	0.2	0.7	1.7
<i>Lycodes seminudus</i>	6	13.3	0.4	1.4	3.3
<i>Lycodes sp.</i>	4	20.0	0.2	0.8	3.0
Other fish					
<i>Reinhardtius hippoglossoides</i>	2	6.7	0.1	1.7	2.1
INVERTEBRATE					
Shrimp (Decapoda)	5	6.7	0.3	0.1	1.1
Pandalidae	2	6.7	0.2	<0.1	1.0
<i>Pandalus borealis</i>	1	6.7	0.1	<0.1	0.8
<i>Pandalus montagui</i>	1	6.7	0.1	<0.1	0.8
Pasiphaeidae					
<i>Pasiphaea sp.</i>	1	6.7	< 0.1	<0.1	0.8
Unknown decapoda	2	6.7	0.1	<0.1	0.8
Zooplankton	290	60.0	17.0	0.3	18.1
<i>Mysis sp.</i>	12	13.3	0.7	<0.1	2.1
<i>Boreomysis sp.</i>	2	6.7	0.1	<0.1	0.8
<i>Calanus sp.</i>	104	26.7	6.1	0.1	7.2
<i>Themisto libellula</i>	172	53.3	10.1	0.1	12.8

Table S2-5 Stomach contents of bearded seal. 52 types were found, 31 of these were identified to the species level.

	N prey	POi	Ni	Bi	IRI
FISH					
Cod (Gadidae)	1111	82.4	18.7	20.1	40.0
<i>Boreogadus saida</i>	1109	82.4	18.7	20.0	39.9
<i>Arctogadus glacialis</i>	2	5.9	<0.1	0.1	0.8
Sea snail (Liparidae)	424	52.9	7.1	2.6	15.6
<i>Liparis fabricii</i>	205	23.5	3.5	1.2	7.2
<i>Liparis gibbus</i>	5	5.9	0.1	<0.1	0.8
<i>Liparis</i> sp.	209	35.3	3.5	1.3	8.9
<i>Careproctus reinhardti</i>	5	5.9	0.1	<0.1	0.8
Eelpout (Zoarcidae)	290	64.7	4.9	14.0	24.0
<i>Lycodes seminudus</i>	23	17.6	0.4	1.1	3.5
<i>Lycodes vahlii</i>	7	5.9	0.1	0.4	1.2
<i>Lycodes</i>	4	5.9	0.1	0.2	0.9
<i>eudipleurostictus</i>					
<i>Lycodes</i> sp.	256	64.7	4.3	12.3	22.4
Sculpin (Cottidae)	1384	82.4	23.3	50.0	54.0
<i>Myoxocephalus scorpius</i>	60	58.8	1.0	2.2	9.5
<i>Gymnecanthus tricuspis</i>	342	58.8	5.8	12.4	22.7
<i>Artediellus uncinatus</i>	2	5.9	<0.1	<0.1	0.8
<i>Triglops pingeli</i>	4	5.9	0.1	0.1	0.8
<i>Triglops</i> sp.	47	29.4	0.8	1.7	6.0
Unidentified Cottidae	929	82.4	15.6	33.6	44.2
Sea poacher (Agonidae)	384	52.9	6.5	2.3	14.8
<i>Ulcina olriki</i>	7	23.5	0.1	<0.1	1.5
Unidentified Agonidae	377	52.9	6.3	2.3	14.6
Prickleback (Stichaeidea)	331	58.8	5.6	1.6	13.9
<i>Lumpenus</i>	51	11.8	0.9	0.3	2.6
<i>lampraetiformis</i>					
<i>Lumpenus</i> sp.	219	35.5	3.7	1.0	8.7
<i>Leptoclinus maculatus</i>	6	5.9	0.1	<0.1	0.8
<i>Eumesogrammus praecisus</i>	15	5.9	0.3	0.1	1.0
Unidentified Stichaeidea	40	11.8	0.7	0.2	2.2
Other fish	29	41.2	0.5	0.3	4.0
<i>Eumicrotremus spinosus</i>	26	35.3	0.4	<0.1	2.8
<i>Sebastes</i> sp.	2	5.9	<0.1	0.2	0.9
Unidentified fish	1	5.9	<0.1	<0.1	0.8
INVERTEBRATE					

Cephalopod	106	70.6	1.8	1.3	10.4
Bathypolypus arcticus	76	64.7	1.3	0.9	8.4
Gonatus sp.	30	47.1	0.5	0.4	4.6
Decapoda	572	64.7	9.6	5.7	22.1
Cragonidae					
<i>Argis dentata</i>	139	52.9	2.3	1.3	9.7
<i>Cragon septemspinosa</i>	7	11.8	0.1	<0.1	1.1
<i>Sabinea septemcarinatus</i>	52	11.8	0.9	0.5	2.8
<i>Sabinea sarsii</i>	38	17.6	0.6	0.4	3.0
<i>Sclerocrangon boreas</i>	57	35.3	1.0	0.6	5.3
Thoridae					
<i>Lebbeus groenlandicus</i>	30	17.6	0.5	0.3	2.6
<i>Lebbeus polaris</i>	68	17.6	1.1	0.7	4.0
<i>Spirontocaris spinus</i>	36	11.8	0.6	0.4	2.4
<i>Spirontocaris phippisii</i>	1	5.9	<0.1	<0.1	0.8
<i>Spirontocaris lilljeborgi</i>	13	5.9	0.2	0.1	0.9
<i>Spirontocaris sp.</i>	27	17.6	0.5	0.3	2.6
<i>Eulalus gaimardii</i>	76	11.8	1.3	0.8	3.5
<i>Eulalus sp.</i>	1	5.9	<0.1	<0.1	0.8
Pandalidae					
<i>Pandalus borealis</i>	3	5.9	0.1	<0.1	0.8
<i>Pandalus sp.</i>	1	5.9	<0.1	<0.1	0.8
Unidentified decapoda	23	5.9	0.4	0.2	1.3
Zooplankton	252	23.5	4.2	0.2	6.1
<i>Stegocephalus sp.</i>	4	5.9	0.1	<0.1	0.8
<i>Gammarus sp.</i>	2	11.8	<0.1	<0.1	1.1
<i>Themisto libellula</i>	246	11.8	4.1	0.2	4.2
Benthos	1055	70.6	17.8	1.9	23.5
Buccinum sp.	824	64.7	13.9	1.5	19.9
Margarites sp.	155	35.3	2.6	0.3	6.4
Holothuroidea	6	11.8	0.1	<0.1	1.1
Bivalve	65	17.6	1.1	0.1	2.9
Eudistoma sp.	5	5.9	0.1	<0.1	0.8

Table S2-6 Stomach contents of narwhal. 23 types were found, 11 of these were identified to the species level.

	N prey	FOi(%)	Ni(%)	Bi(%)	IRI
FISH					
Cod (Gadidae)	13023	93.8	91.8	93.0	93.1
<i>Boreogadus saida</i>	10925	96.3	77.0	37.0	72.9
<i>Arctogadus glacialis</i>	2098	81.5	14.8	56.0	51.1
Sea snail (Liparidae)					
<i>Liparis</i> sp.	198	66.7	1.4	0.7	8.2
Eelpout (Zoarcidae)					
<i>Lycodes</i> sp.	66	7.4	0.5	0.5	1.9
Other fish	27	25.9	0.2	0.3	2.5
<i>Benthoosema glaciale</i>	25	22.2	0.2	0.1	1.8
<i>Reinhardtius hippoglossoides</i>	2	3.7	<0.1	0.2	0.7
INVERTEBRATE					
Cephalopod	485	88.9	3.4	3.5	17.5
<i>Bathypolypus bairdii</i>	69	37.0	0.5	0.5	4.3
<i>B. arcticus</i>	28	33.3	0.2	0.2	2.6
<i>Gonatus</i> sp.	388	85.2	2.7	2.8	15.3
Shrimp (Decapoda)	301	66.7	2.1	1.9	11.5
Pasiphaeidae					
<i>Pasiphaea multidentata</i>	33	18.5	0.2	0.2	1.9
<i>P. tarde</i>	68	22.2	0.5	0.5	3.3
<i>P. sp.</i>	26	18.5	0.2	0.1	1.6
Pandalidae					
<i>Pandalus borealis</i>	15	3.7	0.1	0.1	0.6
<i>P. motague</i>	9	3.7	0.1	0.1	0.6
<i>P. sp.</i>	55	3.7	0.4	0.3	1.1
Thoridae					
<i>Eualus</i> sp.	6	7.4	<0.1	<0.1	0.9
Unknown shrimp	89	14.8	0.6	0.6	3.0
Zooplankton	82	29.6	0.6	0.1	3.0
<i>Mysis</i> sp.	45	22.2	0.3	<0.1	2.0
<i>Boreomysis</i> sp.	3	3.7	<0.1	<0.1	0.6
<i>Thysanoessa</i> sp.	2	3.7	<0.1	<0.1	0.6
<i>Themisto libellula</i>	20	11.1	0.1	<0.1	1.1
<i>Gammarus</i> sp.	12	7.4	0.1	<0.1	0.9

Table S2-7. Summary of (median $\pm$ s.d.), and median Bayesian standard ellipse area (SEA_B) of stable isotope.

species	Age	n	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
Liver				
Ringed seal	all	15	15.94 ± 0.25	-18.64 ± 0.11
	pups	8	15.58 ± 0.37	-18.67 ± 0.14
	juveniles	4	16.19 ± 0.4	-18.63 ± 0.09
	adults	2	16.91 ± 0.20	-18.55 ± 0.07
Harp seal	all	10	15.56 ± 0.21	-17.75 ± 0.07
	pups	5	15.36 ± 0.23	-17.79 ± 0.09
	juveniles	-		
	adults	3	15.93 ± 0.52	-17.65 ± 0.16
Bearded seal	all	11	15.88 ± 0.35	-18.63 ± 0.10
	pups	6	15.70 ± 0.43	-18.59 ± 0.13
	juveniles	-		
	adults	3	16.42 ± 0.56	-18.46 ± 0.11
Narwhals	all	14	16.37 ± 0.06	-18.62 ± 0.06
Muscle				
Ringed seal	all	27	16.34 ± 0.16	-19.02 ± 0.08
	pups	8	16.46 ± 0.26	-19.06 ± 0.14
	juveniles	12	16.26 ± 0.27	-18.99 ± 0.12
	adults	4	16.33 ± 0.53	-19.07 ± 0.17
Harp seal	all	11	16.18 ± 0.23	-17.69 ± 0.08
	pups	4	16.98 ± 0.39	-17.86 ± 0.24
	juveniles	2	16.17 ± 0.46	-17.70 ± 0.09
	adults	3	15.78 ± 0.31	-17.47 ± 0.12
Bearded seal	all	19	15.30 ± 0.36	-18.67 ± 0.11
	pups	2	15.24 ± 0.82	-18.74 ± 0.26
	juveniles	8	15.07 ± 0.05	-18.60 ± 0.05
	adults	3	15.97 ± 0.31	-18.48 ± 0.04
Narwhals	all	8	15.50 ± 0.10	-18.60 ± 0.06

Table S2-8. Percentage of overlapping SEA_B of marine mammals in liver and muscle tissue.

Liver SEA_B (%)

	Ringed seal	Harp seal	Bearded seal
Harp seal	51.1	-	-
Bearded seal	0	0	-
Narwhal	100.0	100.0	0

Muscle SEA_B (%)

	Ringed seal	Harp seal	Bearded seal
Harp seal	0	-	-
Bearded seal	0	0	-
Narwhal	0	95.9	0

CHAPTER 3

Sympatric marine mammals adjust feeding areas to share resource

Introduction

Same as in other Arctic regions, all of the marine mammals in the Inglefield Bredning rely heavily on polar cod (*Boreogadus saida*) as a main energy resource, revealed by stomach contents in chapter 2. Polar cod is the most ubiquitous fish in the High Arctic, and they can be found throughout the circumpolar waters in a variety of habitats, including deep waters (Geoffroy et al., 2011), shallow coastal waters (Welch et al., 1993; Hop et al., 1997), and sea ice (Gradinger and Bluhn 2004; David et al., 2016). They are small (less than 30 cm), and short-lived fish (rarely 7 years), reaching sexual maturity at two to three years of age (Bradstreet et al., 1986). Polar cod spawns under sea ice in the late fall and early winter (Bouchard and Fortier 2011), and their vertical distribution is surface-oriented during the larval stages, shifting to deeper waters by the end of the first year of life (Geoffroy et al., 2016). Water temperature is the most important factor affecting polar cod abundance, and they were most commonly found at temperatures below 2°C (Astthorsson 2016; Marsh and Mueter 2019).

Although there is a wealth of knowledge regarding the ecology of polar cod, and it has long been known that marine mammals in the Arctic heavily rely on polar cod as a prey, there is very little information regarding where marine mammals forage on them. Foraging is a key driver that determine species' energetic efficiency, reproductive success, and the behavior and distribution patterns (Swingland and Greenwood 1983; Stephens et al., 2007). Therefore, understanding where they forage on the key prey, polar cod, is essential not only for predicting future competition over habitats and prey between sympatric animals, but also for predicting impacts on environmental changes on them. Moreover, stomach contents analysis of marine apex predators have been proposed as a potential method to investigate the distribution of marine organisms in areas that are difficult to access and poorly understood. Previous studies have gained insight into prey distribution by, for example, combining habitat use data collected through satellite transmitters with stomach contents (Xavier et al., 2006), or by comparing the stomach contents of predators from different habitat ranges (Lansdell and Young 2007). In most places, except for the Arctic, stomachs of marine mammals are collected from stranded individuals, making it impossible to identify the specific location and date of their death. In this study, I collaborated with the Inuit communities around Inglefield Bredning to collect stomachs

of marine mammals with a detailed site of capture. Such comprehensive data collection is only possible in collaboration with the Arctic communities where seal hunting is practiced.

It has been considered as the drawback of stomach contents analysis which providing only snapshot foraging historied until digestion complete. In this study, I turn this shortcoming into an advantage, leverage their rapid digestion rate to compare and clarify habitat use and diet within a short timeframe. Stomach content records represent feeding history within approximately 2.5 h for narwhals (Heide-Jørgensen et al., 2014), and 4 h for seals (Helm et al., 1984; Pierce and Boyle 1991). The motivation of my study was to gain new insight into the relationship between marine mammals – prey relationship in the Arctic through a novel approach of spatial analysis of stomach contents, and to understand how sympatric species coexist or compete for the same prey.

Materials and methods

Potential feeding and habitat areas of each species were modeled using Maxent software. As response variables, all hunting location data were used for estimating the habitat probability, while data of individuals which had a trace of feeding on polar cod were used for estimating potential feeding area, with water depth, slope, distance to coast and the nearest glacier fronts as explanatory variables (Fig. S3-1). Taking into account the margin of error between the locations where animals were spotted and captured, each explanatory variable was averaged in 2.5 km grids using QGIS. Still, as hunters rarely chase animals over long distances after spotting them, there is little difference between the locations where the animals are spotted and where they are hunted. Bathymetric data was obtained from IceBridge BedMachine Greenland, Version 5 from the National Snow and Ice Data Center, and slope was calculated from the water depth.

Each model was run with a background data set to a maximum of 10,000 randomly generated points. The models were repeated 100 times using bootstrapping to account for variation in sampling, and I used 30 % of the data as test data to assess model performance. Maps were created using the logistic output. The performance of each model was evaluated using the area under the curve (AUC), which measures accuracy on a scale from 0 to 1; with a value between 0.5 – 0.7 representing a low accuracy, 0.7 – 0.9 representing a good fit and a value over 0.9 being an excellent fit (Manel et al., 2001).

To compare the model values with the observed values, I also examined whether there were differences in the four environmental factors (water depth, slope, distance from coast and

distance from the nearest glacier fronts) between presence/absence of polar cod in the stomachs using Wilcoxon rank sum. I inferred that the factors showing significant difference were likely to influence the selection of feeding areas. Furthermore, to test the hypothesis that interspecific overlaps should be reduced in predicted feeding area than in habitat area if each mammals adjust feeding areas for resource partitioning, a spatial niche overlaps between species were calculated as Schoener's *D* index (Schoener 1968) using the R package ENMTools (Warren et al., 2008) in both predicted habitat area and feeding area. Values vary from 0 (completely distinct) to 1 (completely overlapping). The binomial test was conducted to evaluate whether there were significant decreases in overlap values (Schoener's *D*) between habitat area and feeding area.

Results

The hunted locations of ringed seals ($n = 48$), harp seals ($n = 16$), bearded seals ($n = 22$) and narwhals ($n = 31$) are shown in Fig. S3-2. A trace of feeding on polar cod was found from 65 % of ringed seals ($n = 31$), 75 % of harp seals ($n = 12$), 64 % of bearded seals ($n = 14$) and 84 % of narwhals ($n = 26$).

The results of Maxent indicated that the most important environmental factor for predicting feeding areas was the distance to glaciers for ringed seals and narwhals, the distance to the coast for harp seals, and the water depth for bearded seals (Table. 3-1, Fig. S3-3). The feeding areas of ringed seals showed high probability in areas close to glaciers throughout the study area, while those of narwhals exhibited high probability concentrated on the east side of the fjord (Fig. 3-1). The feeding areas of harp seal were near the coast throughout the area, whereas bearded seals were expected to feed in shallow waters, with almost no feeding occurring at depths greater than 200m (Fig. 3-1, Fig. S3-3).

A comparison of the environmental factors at hunted locations between presence and absence of polar cod found in the stomachs is shown in Fig. 3-2. Consistent with the model's results, ringed seals and narwhals with polar cod found in the stomach were hunted significantly closer to glaciers than those without ($p < 0.001$; Fig. 3-2). An opposite pattern was observed in harp seals, where individuals with polar cod in the stomachs were hunted farther from glaciers than those without ($p < 0.05$, Fig. 3-2). This significant difference suggests that distance to the glacier is an important factor in determining feeding areas for them. On the other hand, the distance to the coast, which was suggested as an important environmental factor in the model,

showed no significant difference based on the presence and absence of polar cod (Fig. 3-2), revealing a discrepancy between the model's predictions and the observed data. For bearded seals, consistent with the model's result indicating that water depth was an important factor, they were actually hunted only in shallower areas than other species regardless of the presence and absence of polar cod (Fig. 3-2).

The spatial overlap of the predicted habitats and the feeding areas between species are shown in Table 2. The highest overlap was observed between harp seals and ringed seals in both parameters, and bearded seals showed relatively low overlap to others (Table. 3-2). Significant reductions of overlaps in feeding area than in habitat area were observed between harp seals and ringed seals ($p < 0.01$), and harps seals and narwhals ($p < 0.01$, Table3- 2).

Discussion

In our study, we tried to model and compare the feeding areas of all sympatric marine mammals, and provided new insights into how they share and coexist while feeding on the same key prey, polar cod. We focused on the predator-prey relationship between marine mammals and polar cod, one of the most important relationships in the High Arctic marine ecosystem. Our study enhances the understanding of the environment-prey-predator relationship in this region, and contributes to predicting how accelerating climate change may impact their feeding ecology and interspecific competition.

Both ringed seals and narwhals were suggested to feed on polar cod near glaciers by both models and stomach content (Table 3-1, Fig. 3-2). This suggests that they use the area near glaciers as an important feeding grounds for polar cod. The previous studies have also suggested that the ringed seals frequently utilize areas in front of glacier, and are important feeding grounds for them (Ogawa et al., 2025, submitted, Born et al., 2004, Sakuragi et al., 2024, Lydersen et al., 2014). The inner part of the fjord, predicted to be feeding areas for narwhals (Fig. 3-1), are surrounded by glaciers, making them potentially ideal feeding grounds of species that feed near glaciers. Unlike seals, which feed intensively during the summer, narwhals do not eat as much in this season (Laidre et al., 2005). However, in our study, the proportion of empty stomachs was low, and 84% of the individuals had consumed polar cod. Therefore, even if narwhals may feed less in the summer compared to winter, they still could be competitors for food resources with sympatric marine mammals. For harp seals, there was a discrepancy between the model results which showed that distance to “coast” was important, and stomach

contents results, which indicated that distance to “glaciers” was important (Table 3-1, Fig. 3-2). This may be influenced by factors which could not be taken into account in the model, such as the presence of sympatric competitors.

In front of tidewater glaciers are highly productive, and considered as suitable foraging areas for marine top predators (Lydersen et al., 2014; Meire et al., 2017). In other words, competition here could be intense. As the ringed seal, harp seal, and narwhal all rely heavily on polar cod as the main prey, feeding in the same location may lead to interspecific competition, requiring them to differentiate their feeding niches to reduce competition. Stomach content data suggested that the distance to glaciers may play a key role in the areas where these three species feed on polar cod, as a significant difference in distance to glaciers was observed between the presence and absence of polar cod in the stomachs (Fig. 3-2). Our results suggest that harp seals establish a strategy to feed farther from glaciers to avoid presumably crowded areas. Indeed, when comparing interspecific overlap in habitat and feeding areas, harp seals significantly reduced niche overlap with narwhals and ringed seals in feeding areas, indicating they adjust their feeding locations to mitigate food competition (Table 3-2). Moreover, although the gray range representing the interquartile ranges of all samples shows considerable overlap among the three species, the fact that the interquartile ranges for individuals with polar cod in their stomachs is clearly segregated between species – ringed seal (2.1 – 6.7 km), narwhals (7.0 – 15.3 km), and harp seals (15.7 – 51.9 km) (Fig. 3-2) – further supports this hypothesis.

The bearded seal, which did not show a significant relationship with glacier and polar cod feeding, exhibit minimal overlap with other mammals (Fig. 3-2, Table 3-2). Both the model and the stomach contents results suggested that bearded seals feed on polar cod in shallow waters, and the preferred depth suggested by the model (< 200 m) and the depth range where individuals feeding on polar cod were hunted (< 100 m) hardly overlap with other species (Fig. 3-2, S3-3). This suggests that bearded seals establish a unique habitat niche to mitigate competition with other species by feeding in shallow waters. Bearded seals are known to prefer to feed on benthic organisms such as sculpins and snails, in addition to polar cod (Finley et al., 1983). Therefore, foraging in shallow areas may not only help mitigate competition over polar cod with other species, but also serve as a strategy to efficiently forage on other benthic prey by selecting locations where they can easily access to the seafloor.

Our study provided new insights into how sympatric species partition the foraging area to coexist, which is essential for enhancing our understanding of climate changes at the species-

specific level. It suggests that the relationship between marine mammals and their primary prey, polar cod, may be crucially linked to tidewater glaciers, at least in this fjord during summer. The ongoing reduction of glaciers due to accelerating climate change is likely to alter the distribution of prey (Kortsch et al., 2015; Cheung et al., 2009; Hollowed et al., 2013), which may consequently lead to change in predator-prey relationships (Kovac and Lydersen 2008; Chambellant et al., 2013), and competitions between sympatric marine mammals. This could also affect the diet, distribution and habitat use of marine mammals. To evaluate the cascading impacts of climate change on the High Arctic marine ecosystem, it would be key to further investigate the relationship between glaciers and marine organisms. Understanding these connections will provide insight into how environmental changes affect prey distribution and predator behavior, which are crucial for assessing ecological dynamics in a changing climate. Moreover, our results suggested that the extent to which they are affected by climate change may vary depending on their feeding areas, even among sympatric marine mammals that rely on the same prey. In this region, for example, while ringed seals, harp seals and narwhals whose feeding areas were suggested to be strongly influenced by their relationship with distance to the glaciers may experience greater impacts, while bearded seals, for which depth – a more ubiquitous factor – was a key parameter, may be relatively less affected by environmental and marine ecosystem changes in terms of feeding and interspecific competition.

Table 3-1. Results of Maxent mapping. AUC (Area Under the Curve) is a metric to evaluate the performance of models, and PC (Percent Contribution), PI (Permutation Importance) is a measure of how each environmental variable contributed to the model. The most important environmental variables suggested by the model for each species are highlighted in gray.

	Ringed seal (AUC 0.901)		Harp seal (AUC 0.804)		Bearded seal (AUC 0.925)		Narwhal (AUC 0.968)	
	PC	PI	PC	PI	PC	PI	PC	PI
Glaciers	49.6	30.7	11.6	14.4	9.8	11.0	51.0	65.3
Coast	30.6	26.9	62.2	45.4	16.4	33.0	4.0	10.0
Depth	7.6	23	25.1	39.0	63.0	44.0	31.0	18.4
Slope	12.3	19.4	1.2	1.2	10.8	12.0	14.0	6.3

Table 3-2. Overlaps of habitats (HU) and feeding area (FA) between species predicted by maxent. Overlap values were measured using Shoener's *D*, and significant decrease in overlap between habitat and feeding areas was evaluated using a binomial test. Species pairs that showed a significant decrease in overlap area indicated in bold (* $p < 0.05$, ** $p < 0.01$).

	Ringed seal			Harp seal			Bearded seal	
	HU	FA		HU	FA		FA	FA
Ringed seal								
Harp seal	0.78	0.66	**					
Bearded seal	0.41	0.45	*	0.37	0.39			
Narwhal	0.51	0.48		0.45	0.37	**	0.15	0.13

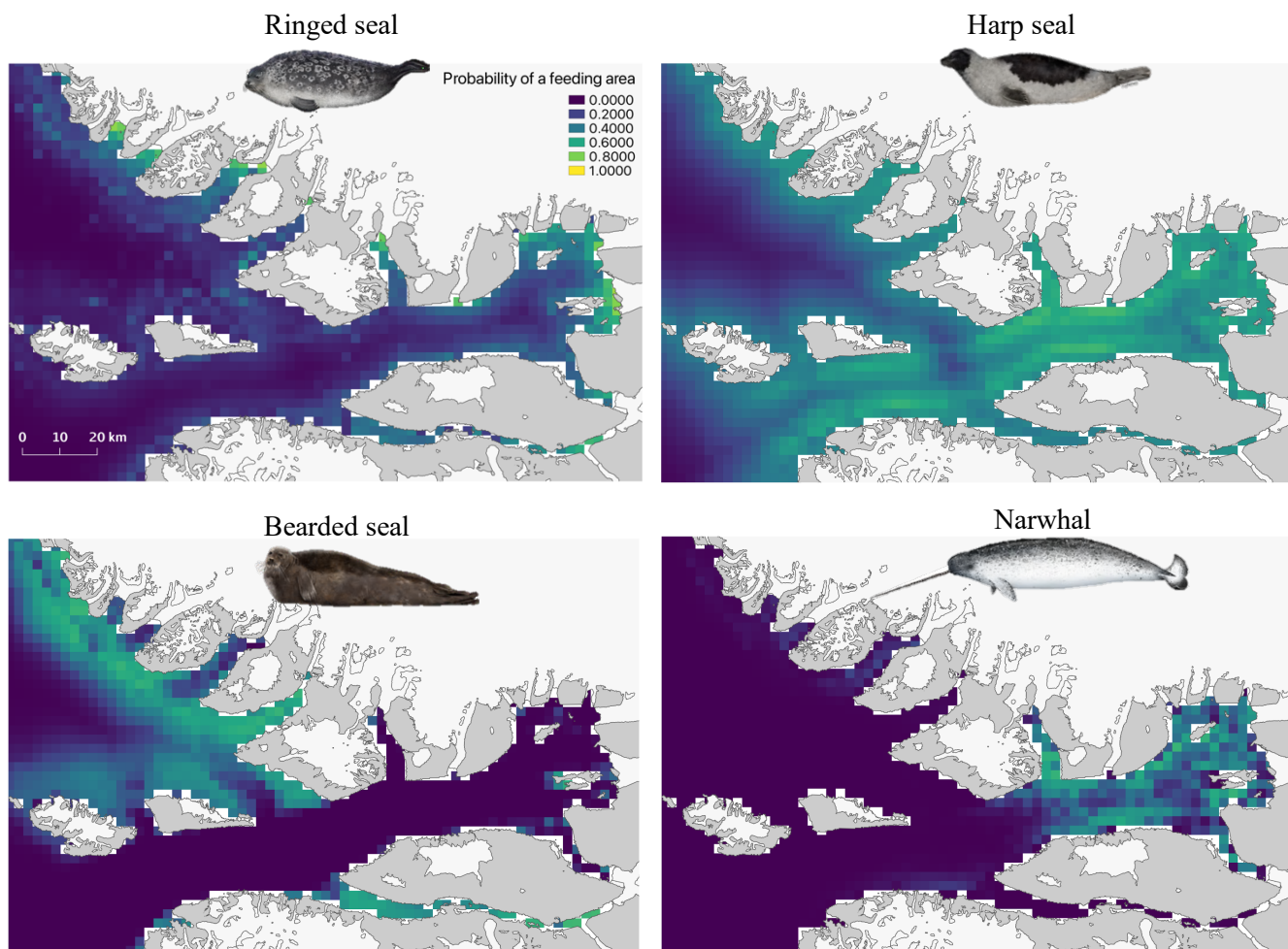


Fig. 3-1 Predicted feeding areas. Feeding areas of ringed seals, harp seals, bearded seals and narwhals predicted using Maxent based on the hunted location data of individuals in which polar cod was found in the stomach.

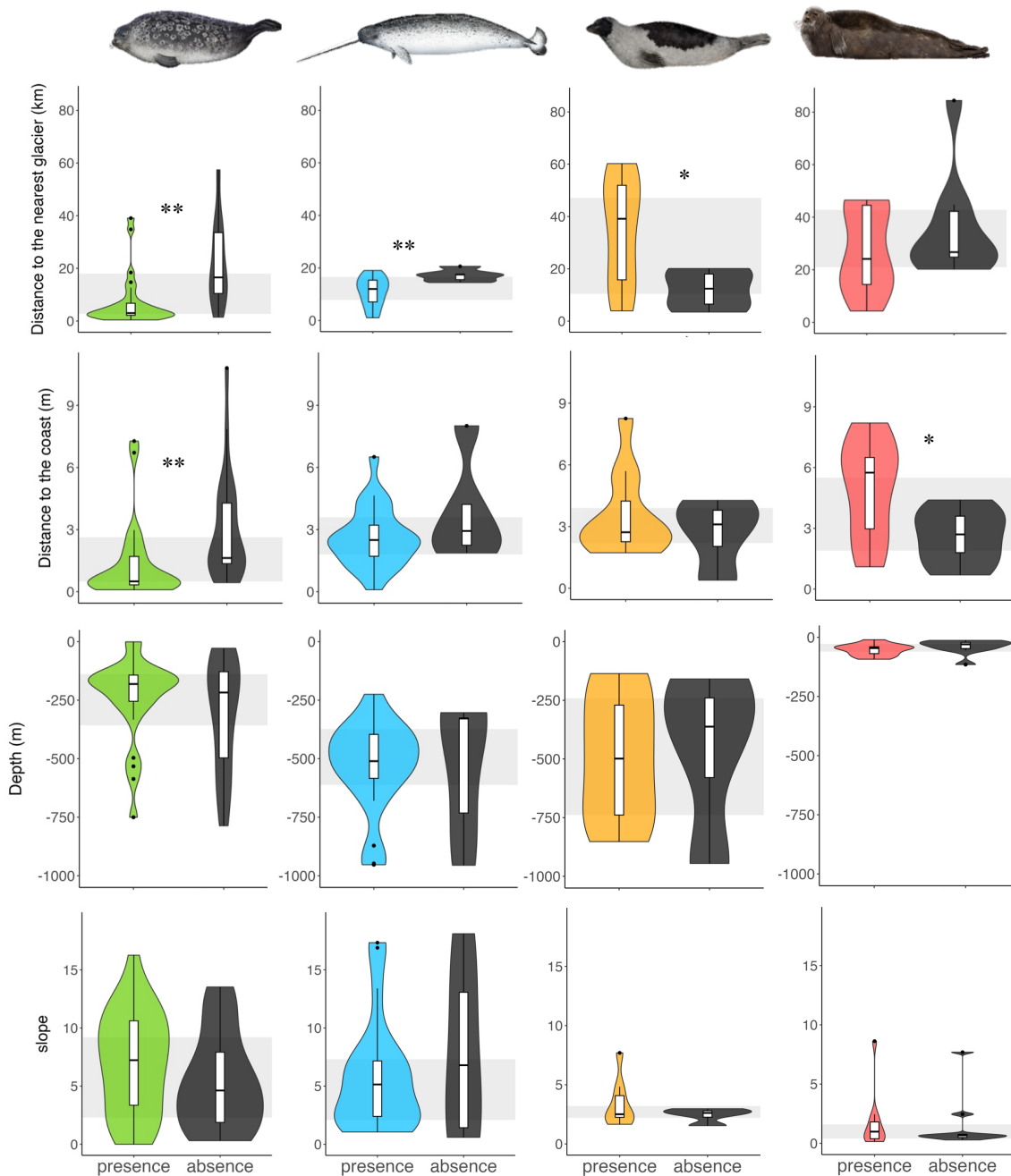


Fig. 3-2 Comparison in environmental parameters based on the presence and absence of polar cod in the stomach. The colored violin plots represent the distribution of individuals in which polar cod was found in the stomach, while the black violin plots represent those without polar cod. The gray shaded areas indicate the interquartile range of all hunted individuals. The difference in distribution of environmental variables between presence and absence of polar cod was tested using Wilcoxon rank sum test (** $p < 0.01$, * $p < 0.05$).

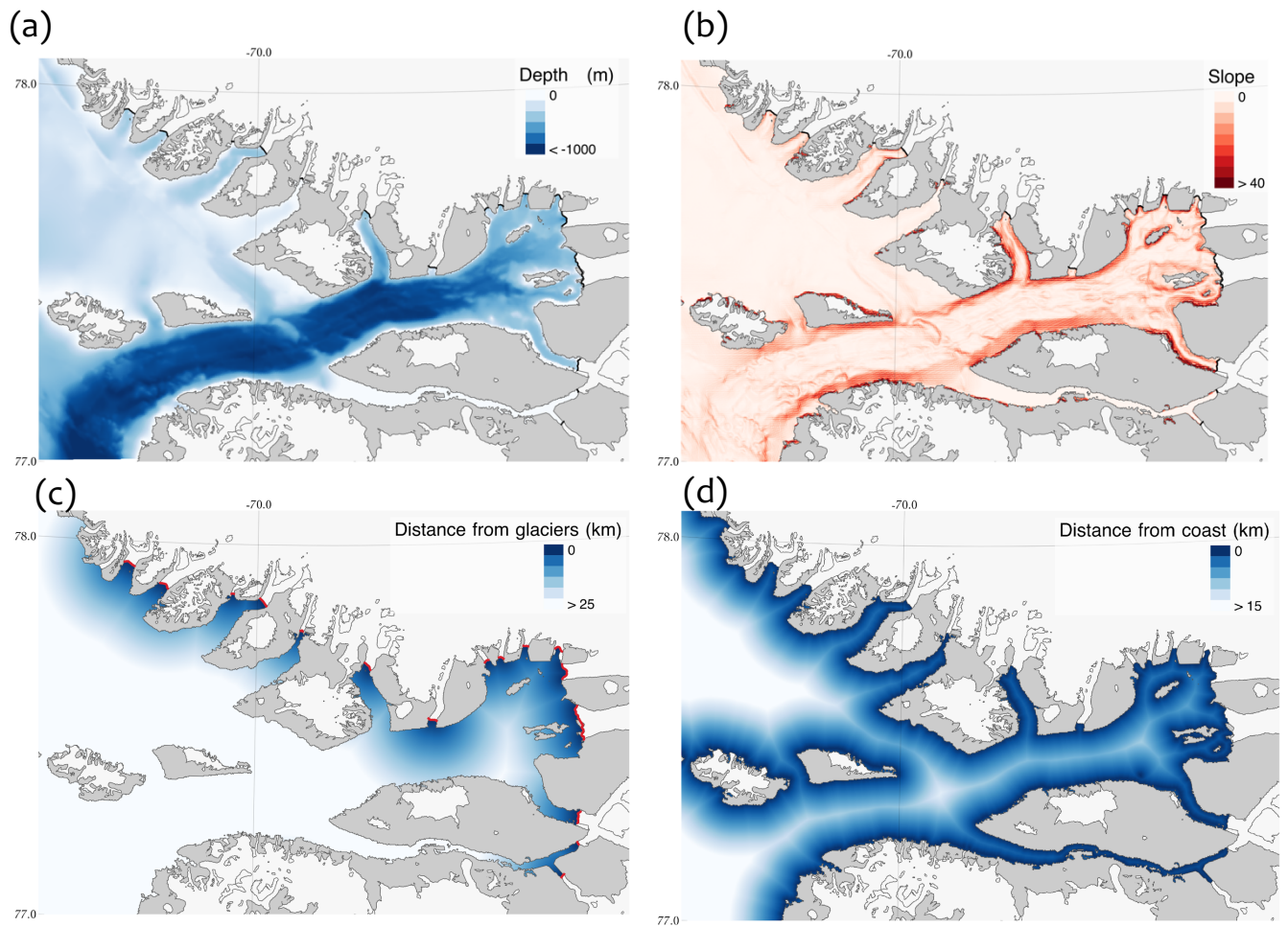


Fig. S3-1 Environmental parameters of the study area used in the Maxent model. (a) Water depth, **(b)** slope, **(c)** distance to the glaciers (red line), and **(d)** distance to the coast line around Inglefield Bredning.

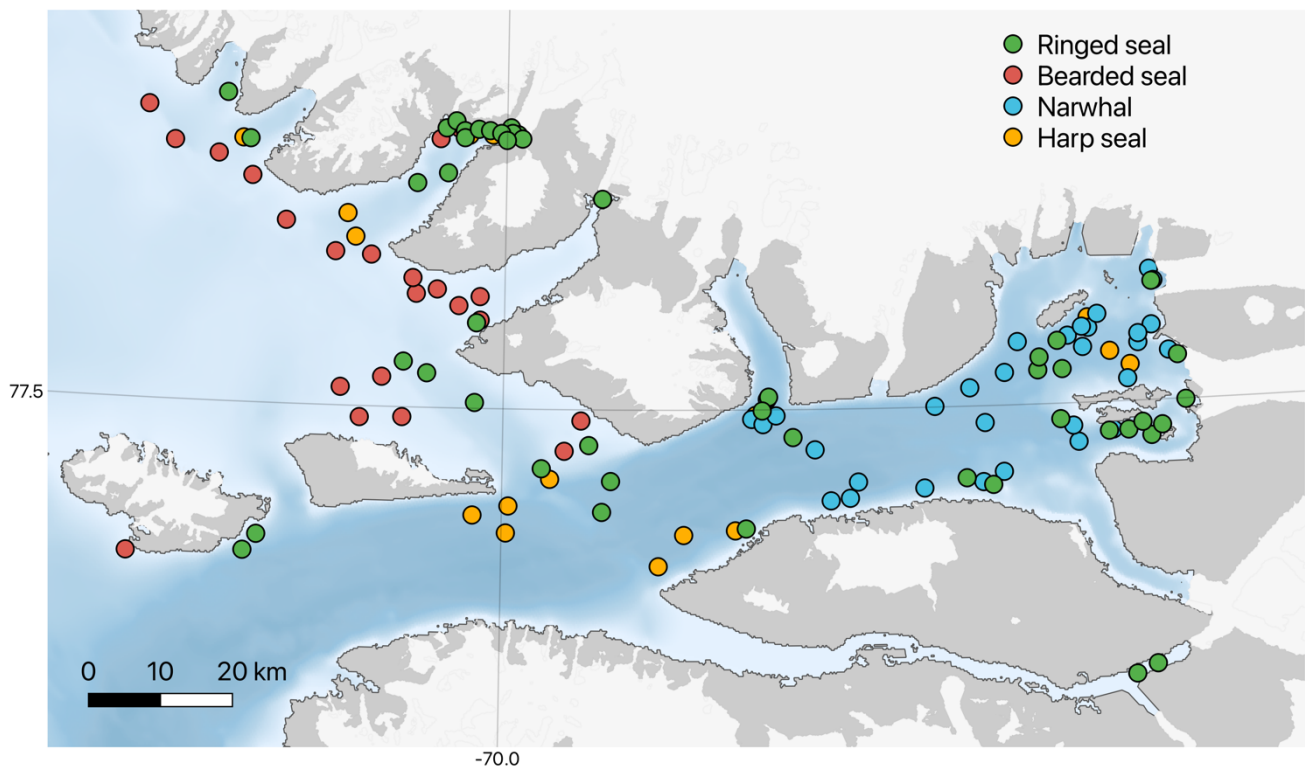


Fig. S3-2 Hunted locations of marine mammals collected during open water season in 2022-2024 around Inglefield Bredning.

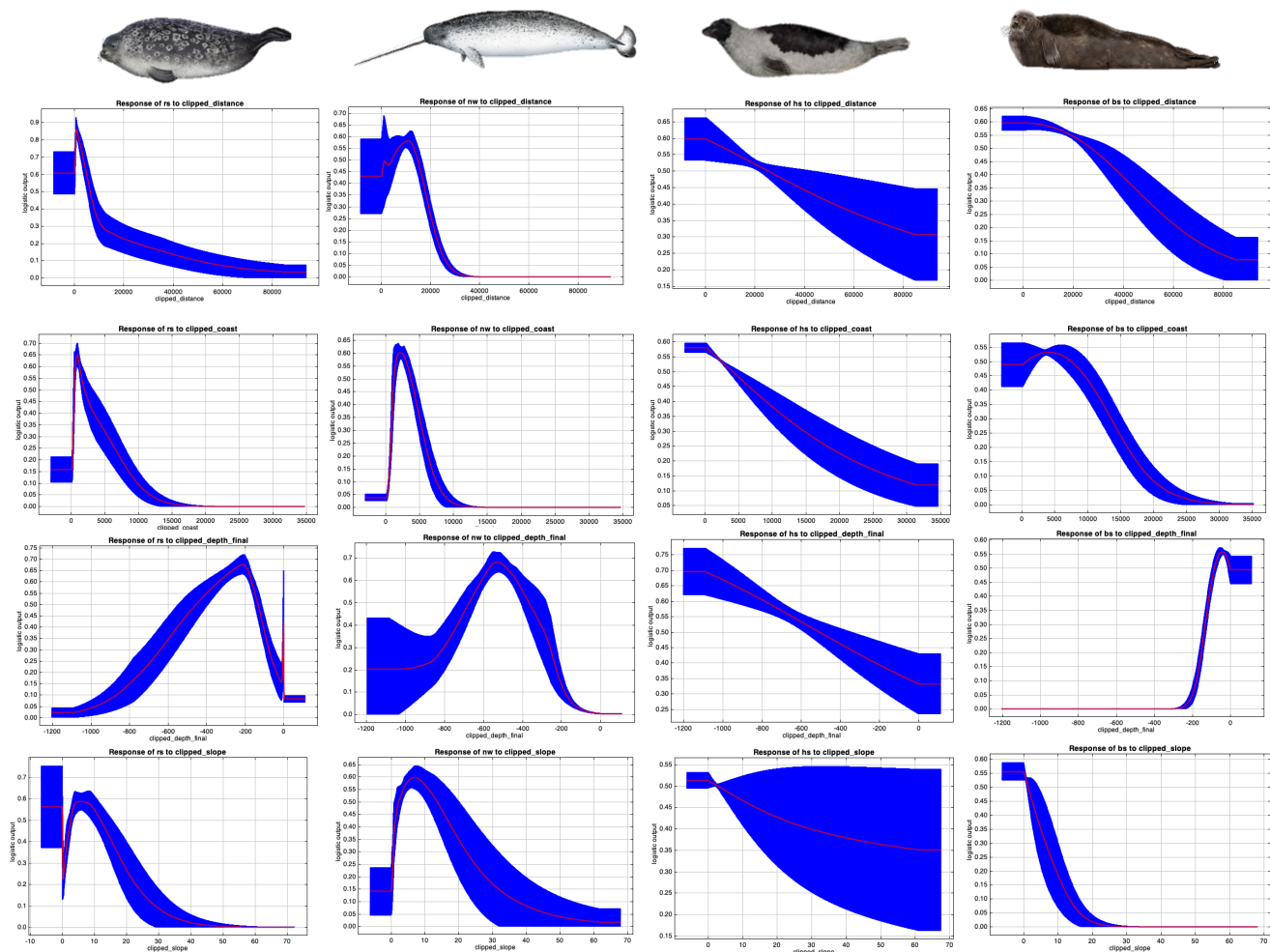


Fig. S3-3 Relationship between the feeding area probability and distance to the glacier, distance to coast, water depth and slope using Maxent. Red lines represent the average, and blue areas show ranges ± 1 SD of 100 Maxent models.

CHAPTER 4

Glacier fronts as key foraging grounds for ringed seals

Introduction

In Chapter 2, we found that marine mammals in this region rely heavily on polar cod, and in Chapter 3, we identified where each species feeds on polar cod. The results revealed that ringed seals typically use glacier fronts, which have been rapidly retreating in recent years due to climate change, as important foraging grounds. This chapter delves deeper into the relationship between ringed seals and the glaciers.

During the open-water season in the Arctic, it is common to observe brownish, murky spots spreading in areas where glaciers meet the sea. At the front of tidewater glaciers, the subglacial discharge of low-density, buoyant freshwater creates upwelling water flows along the calving front. This strongly upwelling glacial meltwater, typically released at the depths of several hundred meters, delivers nutrients, plankton, and sometimes fish from the bottom of the sea all the way to the surface (Lydersen et al., 2014; Meire et al., 2017; Kanna et al., 2018; Podolskiy et al., 2021). This process creates biomass-rich water zones at the glacier fronts, and provides easily available prey for predators, thought to make these areas foraging hotspots during the summer months (Apollonio 1973). Indeed, large gathering event of marine predators including sea birds, seals, and whales have been observed at glacier fronts in various parts in the Arctic (Lydersen et al., 2014; Rink 1862; Hartley et al., 1936; Balance et al., 2001; Urbanski et al., 2017), including in our study area, Inglefield Bredning (Nishizawa et al., 2020; Podolskiy et al., 2020; Sakuragi et al., 2024). At these hotspots, biologging studies suggested that marine top predators engage in frequent dives that are expected to involve foraging (Lydersen et al., 2016, 2001; Freitas et al., 2008; Hamilton et al., 2016; Everett et al., 2018).

Climate change has accelerated since 2000, and the Greenland glaciers have experienced an increase in melting speed particularly since around 2003 (Velicogna and Wahr 2006; Wang et al., 2021), and the increased glacial discharge has been suggested to affect the primary productivity of marine ecosystems (Kanna et al., 2022; Meire et al., 2023). However, it is unclear how this ultimately affects the foraging ecology of marine top predators. The motivation of our study was to fill these knowledge gaps through spatial analysis of ringed seal (*Pusa hispida*) stomach contents as a model case, for which glaciers play a particularly important role in determining foraging area, as revealed in Chapter 3.

For ringed seal stomachs collected in 2002 – 2003 and 2022 – 2023, the percentage of empty stomachs, and the presence or absence of polar cod (*Boreogadus saida*) and zooplankton were recorded, which were thought to be the most important prey in this area as revealed in Chapter 2 and in the previous study (Holst et al., 2001). I then carried out spatial analysis of stomach contents collected during two study periods to investigate the importance of glacier fronts as foraging grounds. Hydroacoustic survey was also conducted in 2023 to document the prey field available for seals in the region.

Materials and methods

Spatial and statistical analysis

In addition to the sample collection in 2022-2023, stomachs of ringed seals collected between July and September in 2002 (n = 11) and 2003 (n = 12) in the previous study were also used to compare (Rosing-Asvid, unpublished data). Since age information is not available for the previous samples, maturity was not considered in this chapter. The sites of capture were mapped, and the shortest distance from each site of captures to the nearest glacier were calculated. As the locations of glacier front has changed significantly over the past two decades (Fig. S4-1), the distances to the glaciers were measured based on the glaciers on the same years of seal capture (Landsat 7, July 26, 2003; Landsat 9, September 7, 2023).

The diversity of prey types eaten by each individual was calculated using Simpson's diversity index based on the number of prey, following Chambellant et al (2013) as follows:

$$\text{Prey diversity} = 1 - D, \quad D = \sum (n_i / n_t)^2,$$

where n_i represents the number of individuals of prey type i , and n_t represents the total number of prey found from the stomachs. This index yields a value of 0 when the individual feeds on only a single type of prey, and increases with both the number of prey types and the evenness with which they are consumed (Magurran 1955). Therefore, larger values suggest that the individual preys on a greater variety of prey.

All statistical analyses were performed using R 4.3.2 in RStudio. To examine the importance of glacier fronts as feeding grounds, I compared the median distance to the nearest glacier fronts from the site of capture (DNG) between stomach with prey and empty stomach and presence / absence of zooplankton and polar cod in the stomach (Wilcoxon rank sum test). I also investigated whether there were differences in the weight of stomach contents between seals caught closer to the glacier than the median DNG (= 4 km) and those caught further away

(Wilcoxon rank sum test). A generalized linear model (GLM) based on gamma distribution (log link) was performed on stomach contents weights and consumed prey diversity to examine the potential effects of age, sex, date and DNG (km) on feeding behavior (Table 4-1). Since DNG was the only variable with a significant effect, subsequent analyses focused on this factor. Furthermore, as the preliminary analysis revealed no sex, age, and date differences in stomach contents, all individuals were grouped together in further analyses.

Acoustic survey

An exploratory survey was conducted between 1 and 12 of September 2023 in Inglefield Bredning. All investigation and data analysis used in this study were performed by Greenland Institute of Natural Resources and National Institute of Aquatic Resources. Acoustic data were collected from 5 to 700 m depth using a Simrad EK80Portable (Simrad ES38-18/200-18C, produced by Kongsberg Maritime) with a dual-frequency transducer mounted on a pole at the side of a 7-meter dinghy at an approximate depth of 1 meter. The transducer emitted a 38 kHz and a 200 kHz continuous wave (CW) pulse every second with a pulse duration of 1.024 ms and a beam opening angle of 18°. The 38 kHz signal was received as a split beam with three sectors, while the 200 kHz was received as a single beam.

Due to practical reasons, data were only collected during the day and in good weather and sea conditions. The survey was segmented into a series of 9 transects that subsampled various parts of the fjord, as it was not practically possible to cover the entire area completely with a speed varying between 2.5 and 5.0 kts (speed over ground measured by GPS) and 8 days at sea. The acoustic data were scrutinized using MAREC LSSS v.2.16.0, where layers of fish and zooplankton were detected using the relative frequency response between the two frequencies. Swim-bladdered fish have a higher acoustic backscatter from the 38 kHz signal compared to the 200 kHz, whereas it is the opposite for zooplankton (Korneliussen et al., 2002). Therefore, I used a threshold ratio of 1:1 (38kHz:200kHz) between the two to assign acoustic layers to one of the two groups. Calibration of the echosounder was performed off site in Øresund, Denmark at approximately 6 m depth using a 38.1 mm tungsten carbide sphere according to standard methods (Demer et al., 2015).

Visual ground truthing of the acoustic registrations was performed 1-2 times per day in areas where high densities of acoustic back-scatterers were observed. The equipment for ground truthing included cameras mounted on a Remotely Operated Vehicle (ROV, "Trident" from

Sofar Technology) down to 100 m depth and a mini-camera (Waterwolf Underwater Fishing Camera) on a fishing line that could be deployed down to 150 m water depth.

Results

Ringed seal caught in 2002 – 2003

A total of 24 ringed seal stomachs were collected by Inuit hunters during the summer in 2002 ($n = 12$) and 2003 ($n = 12$). Five out of 24 stomachs (21%) were empty, and there were no sex difference in the percentage of empty stomachs (Wilcoxon rank sum test, $W = 78$, $p = 0.652$). Polar cod were found in 79% of the seals, and zooplankton were found in 25% of the stomachs. The DNG was 17.2 km (range: 1.1 – 42.6 km), and DNG did not differ significantly between sex (Wilcoxon rank sum test, $W = 76$, $p = 0.843$). The median DNG for seals with history of feeding was 21.2 km, and for seals with an empty stomach was 16.1 km. The median DNG did not differ between the two groups (Wilcoxon rank sum test, $W = 192$, $p = 0.972$).

Ringed seal caught in 2022 – 2023

Half of the seals were harvested within 4 km of glacier fronts (range: 0.5 – 73.6 km; Fig. 4-1 a-c), and no significant difference was found between sex (Wilcoxon rank sum test, $W = 194$, $p = 0.471$) and among age groups (Kruskal-Wallis rank sum test, chi-squared = 0.41795, $df = 2$, $p = 0.811$). The median DNG was significantly shorter for seals with history of feeding: 2.4 km for seals with prey found in their stomach, and 7.8 km for seals with empty stomachs (Wilcoxon rank sum test, $W = 98$, $p < 0.05$; Fig. 4-1 b). In comparison based on the median DNG (= 4 km), seals caught closer to the glaciers had significantly heavier stomachs (Wilcoxon rank sum test, $W = 269$, $p < 0.05$, Fig. 4-1 c, d). The DNG had a significant effect on stomach content weight and consumed prey diversity ($p < 0.01$, respectively), with stomach content weight decreasing and prey diversity increasing as distance to the glacier increased (Table 4-1).

Distance to glacier vs feeding on polar cod

In 2002 and 2003, seals with traces of polar cod in the stomach were caught across a wide range of the fjord (range: 1.1 – 42.6 km), and significant difference in DNG was observed in the presence and absence of polar cod (Wilcoxon rank sum test, $W = 192$, $p = 0.972$; Fig. 4-2 a, b).

On the other hand, during 2022 and 2023, seals with traces of feeding on polar cod were hunted significantly closer to the glacier than those without (Wilcoxon rank sum test, $W = 382$, $p < 0.001$), with the median DNG was 1.6 km (with polar cod) and 18.9 km (without polar cod), respectively (Fig. 4-2 c, d). Except for two individuals, all seals with polar cod in the stomach were caught within 3.3 km from the nearest glacier (Fig. 4-2 c, d). This range is significantly skewed closer to the glaciers compared to the catch range of all samples for those years (Wilcoxon rank sum test, $W = 197.5$, $p < 0.005$; Fig. 4-2 c, d). Seals with no trace of polar cod were captured over a wide range (range: 2.5 – 73.6 km), and were more broadly distributed farther from the glacier compared to the range of all samples (Wilcoxon rank sum test, $W = 602.5$, $p < 0.01$; Fig. 4-2 c, d)

Distance to glacier vs feeding on zooplankton

In 2002 and 2003, the median DNG was 25.5 km for seals with traces of feeding zooplankton, and 13.1 km for those without (Fig. 4-2 e, f), and statistically different (Wilcoxon rank sum test, $W = 91$, $p < 0.05$). Comparing to the sample range for those years, seals with zooplankton in the stomachs were captured significantly farther from the glaciers (Wilcoxon rank sum test, $W = 35$, $P < 0.05$, Fig. 4-2 f).

Similarly, seals collected in 2022 and 2023 showed a trend where seals with traces of feeding on zooplankton were caught relatively further to the glacier than those without (Fig. 4-2 g, h). While no statistical difference was observed between the presence and absence of zooplankton in DNG (Wilcoxon rank sum test, $W = 128$, $p = 0.177$), the trend that seals with trace of feeding were caught relatively farther from the glacier fronts contrasts with the results for polar cod in this period.

Distribution of potential prey in Inglefield Bredning

Acoustic registrations on all 9 transects surveyed in Inglefield Bredning (Fig. 4-3 a) were generally characterized by a diffuse but dense layer of scatterers in the upper 50 m, occasionally extending down to 100 m depth (Fig. 4-4). The relative frequency response in the upper 50 m was mostly around 1:1.5 between 38 and 200 kHz, indicating a predominance of zooplankton. This was corroborated by ground truthing, where a range of invertebrate zooplankton groups (e.g *Limacina helicina*., *Thysanoessa* sp., *Mysis* sp, *Themisto* sp.) and age-0 fish were observed.

Additionally, several dense patches with stronger reflections on 38 kHz (up to 1:0.7) were observed, likely representing loose aggregations of small swim-bladdered fish such as polar cod, which is an only pelagic fish aggregating in large schools in this region and the high-Arctic (Snøeijis-Leijonmalm et al., 2022). Only three distinct dense aggregations of backscatters with a high 38:200 ratio were observed (Fig. 4-3 b). These aggregations or schools were approximately 3 meters high, 10-30 meters long, and were observed near the surface from 6 to 13 m depth, in proximity to large icebergs near a glacier where the bottom depth was 280 m. The relative frequency response of these registrations was 1:0.2, indicating that these registrations were schools of swim-bladdered fish such as polar cod.

Discussion

Monitoring marine mammals as indicators of marine ecosystem change

In this chapter, based on the findings from Chapter 2 that identified polar cod as a key prey species for marine mammals in this region, and the findings from Chapter 3 that showed the distance to glaciers influences the foraging locations of each marine mammal, we focus on ringed seals, which forage predominantly near glaciers. By comparing the data with those from 20 years ago, we examined changes in their foraging locations. Additionally, using acoustic data, we investigated the distribution of polar cod and zooplankton, the primary prey of ringed seals. Monitoring marine mammals, apex predators in marine ecosystems, can be used as indicators of changes in the marine environment and marine ecosystems (Laidre et al., 2008). In the context of rapid glacier decline due to accelerating climate change, assessing the role of glaciers in marine ecosystems is essential to predict its impact in the future. Since 1863, gathering and active diving behaviors of marine predators in front of glaciers, likely associated with feeding activities, have been reported, and remained to be explained with evidence (Rink 1862). By combining the stomach contents analysis and site of capture records, our study provided the first direct evidence that glacier fronts, which are gaining increased attention due to accelerating climate change, serve as vital foraging ground for seals. Furthermore, this study highlight that their significance may have increased over the past two decades.

Insight into prey distribution

In both periods, the most commonly eaten prey was polar cod. While the result was consistent with those from other high-arctic regions including northern Greenland (Holst et al., 2001; Siegstad et al., 1998), southern Greenland (Siegstad et al., 1998; Lebanese et al., 2011), Svalbard, and the Canadian High Arctic (Matley et al., 2015; Ross et al., 2022), our study reveals for the first time the hotspots where the polar cod were actually eaten (Fig. 4-2). Our methodology is applicable to other regions in the Arctic to investigate and compare foraging sites.

Although polar cod was consumed throughout the fjord in 2002 and 2003, seals fed on polar cod intensively at glacier fronts in 2022 and 2023, the only place in the fjord where fish schools were found, almost certainly polar cod (Fig. 4-3). The shift in the locations where polar cod were consumed may reflect changes in primary productivity in front of the glaciers due to the increase meltwater discharge. The previous study conducted in this area reports that in years with greater glacier melt, the marine productivity in front of the glaciers increases compared to typical years (Kanna et al., 2022). Based on the hypothesis, it is predicted that marine productivity was higher during the period of 2022 – 2023 when glacier melt was expected to be greater than in 2002 – 2003, and led the higher polar cod abundance in front of the glaciers.

These changes in the distribution of prey species may have consequently altered the foraging locations of seals (Hamilton et al., 2016; Yurkowski et al., 2016). Indeed, although tagged seals were not utilizing glacier front very often in Inglefield Bredning around 2000's (Teilmann et al., 1999; Born et al., 2004), they now spend significantly more time near glacier fronts during open-water season (Sakuragi et al., 2024). The shift of habitats towards glacier fronts has also been observed in other regions in the Arctic, where arctic prey presumably still concentrate (Hamilton et al., 2016). Our study suggested a chain of impacts, that climate change may affects the distribution of prey species, which in turn influences the behavior of marine mammals, the apex predators in marine ecosystem.

Polar cod, the most ubiquitous fish in the High Arctic, can be found in a variety of habitats including deep waters (Geoffroy et al., 2011), coastal shallow waters (Welch et al., 1993; Hop et al., 1997), and under sea ice (Gradinger and Bluhm 2004; David et al., 2016). Glacier fronts have been suggested as potential habitats during the summer (Hamilton et al., 2019; Bouchard et al., 2023). However, due to the extreme difficulty and danger to conduct observation near the glacier front, with the risk of calving, these areas have been the least studied habitat of polar

cod. Indeed, in our acoustic survey, only a short passage was possible to approach the glacier. In that perspective, stomach contents from the ringed seals that easily swim very close to the glaciers provided a rare opportunity for investigating the importance of the glacier fronts as habitat for polar cod. Our results show that these areas are of high importance, which calls for future studies on the functional role of these areas in the life cycle of polar cod, especially under warming climate.

Prey-specific feeding areas

Interestingly, while polar cod were consumed significantly closer to the glaciers in 2022 and 2023, such a tendency was not observed for zooplankton. Rather, individuals “without” zooplankton were caught closer to the glaciers (Fig. 4-2), despite it was available throughout the fjord regardless of the distance to the glacier (Fig. 4-4, 5). Furthermore, consumed prey diversity increased with greater distance to the glacier (Table 4-1), which can be attributed to the fact that seals fed almost exclusively on polar cod near the glacier. This difference in foraging areas may reflect the seal’s feeding preference for polar cod near glaciers, driven by the energy contents, foraging costs, and distribution of each prey. Data from satellite transmitters mounted on ringed seals in the area indicated that seals spend most of their time in water shallower than 50 m (Sakuragi et al., 2024), where the dominant zooplankton found in the stomachs (*Themisto libellula*, *Mysis* sp. and *Thysanoessa* sp.) are distributed (Buchanan and Sekerak 1982; Saunders et al., 2013). As polar cod was also detected shallower than 50 m (Fig. 4-3), foraging costs to dive to target specific prey may not be different between zooplankton and polar cod. Moreover, although energy content per gram of polar cod and zooplankton are similar, considering the size of each prey, it is likely more efficient to eat one polar cod than to eat a lot of zooplankton (e.g. one polar cod provides equivalent energy as more than 30 *Themisto* sp. or 1000 copepods; Bradstreet 1982). Therefore, in front of the glaciers which have relatively abundant polar cod biomass, there would be no need for seals to actively consume zooplankton. On the other hand, in areas where polar cod biomass is not abundant, seals possibly feed on zooplankton or other prey instead. Therefore, it is reasonable that seals consumed polar cod significantly closer to the glacier fronts, while zooplankton is relatively less consumed in the area. Our study supports the hypothesis that marine mammals target aggregations of fish for high energy potential with low foraging costs, which has been suggested in many studies (Born et al., 2004; Weich et al., 1993; Craeford et al., 1996; Harwood et al., 2015).

My study also suggest that the results of diet compositions can vary depending on the sampling locations, and this should be taken into account in future dietary research. For example, in the High Arctic, samples collected only in front of glaciers are likely to show a dietary bias towards polar cod.

Urgent need to investigate the role of glacier fronts in marine ecosystems

As a consequence of global warming, glaciers all over the Arctic are rapidly melting (Noël et al., 2018; Khan et al., 2022; Jakob and Gourmelen 2023; Kochtitzky and Copland 2022), resulting in increasing amount of freshwater discharge into the ocean (Bamber et al., 2018; Mougint et al., 2019). Glaciers in our study site are also experiencing increased melting in the last decades (Sugiyama et al., 2015; Wang et al., 2021), and several glaciers have reduced in area to the extent that they no longer reach the sea. Glaciers have a significantly different effect on marine productivity depending on whether they extend into the sea or retreated onto land, and seals prefer a marine-terminating glacier over the land-terminating glacier even if the glaciers are adjacent to each other (Everett et al., 2018). If tidewater glaciers further retreat beyond the coastline, important foraging ground for marine mammals disappears and may consequently alter their habitat use.

In conclusion, our spatial analysis of stomach contents provides a comprehensive understanding of the diet, habitat use, foraging strategies, and the distribution of prey. Here, I provide the first direct evidence to show the importance of tidewater glacier front as a foraging ground for marine predators, and suggest that glacier fronts are becoming increasingly important as foraging sites under a warming climate, until the glacier further retreat and terminate on land. Ringed seals are now feeding intensively at glacier fronts, especially on polar cod, which corresponded to the distribution of fish aggregations from our acoustic survey. This highlights the importance of the glacier fronts for polar cod, which is one of the least studied habitat of the species. Although seals with polar cod in their stomachs were caught significantly closer to the glacier compared to those without, opposite tendency was found between the presence and absence of zooplankton. This finding provides a clue to understand the foraging strategies of seals depending on the distribution of prey. In a broader context, my results emphasize that glacier retreats induced by recent warming is likely to deprive the seals of their important foraging grounds, and may result in a change in their diet, behavior, and distribution.

Table 4-1. Results of generalized linear model (GLM). (a) Stomach contents weight and (b) consumed prey diversity, including age, sex, distance to glacier, and date as variables.

(a) Stomach contents weight (Model 2)

variable	Regression estimate	Standard error	t value	p value
Distance to the glacier	-0.02801	0.01104	-2.536	0.0158 *
Date	0.46848	0.36641	1.279	0.2095
Sex	0.78356	0.41631	1.882	0.0682
Age	-0.05145	0.24476	-0.210	0.8347

AIC:394.14

Model 1: Stomach contents weight ~ Distance to the glacier + Sex + Age + Date + Sex-Age (AIC: 397.98)

Model 2: Stomach contents weight ~ Distance to the glacier + Sex + Age + Date (AIC: 396.12)

(b) Prey diversity (Model 2)

variable	Regression estimate	Standard error	t value	p value
Distance to the glacier	0.012237	0.004207	2.909	0.0079*
Date	-0.051913	0.122076	-0.425	0.6746
Sex	0.049217	0.148253	0.332	0.7429
Age	0.056317	0.070902	0.794	0.4351

AIC:-54.121

Model 1: Prey diversity ~ Distance to the glacier + Sex + Age + Date + Sex-Age (AIC: 26.732)

Model 2: Prey diversity ~ Distance to the glacier + Sex + Age + Date (AIC: 24.798)

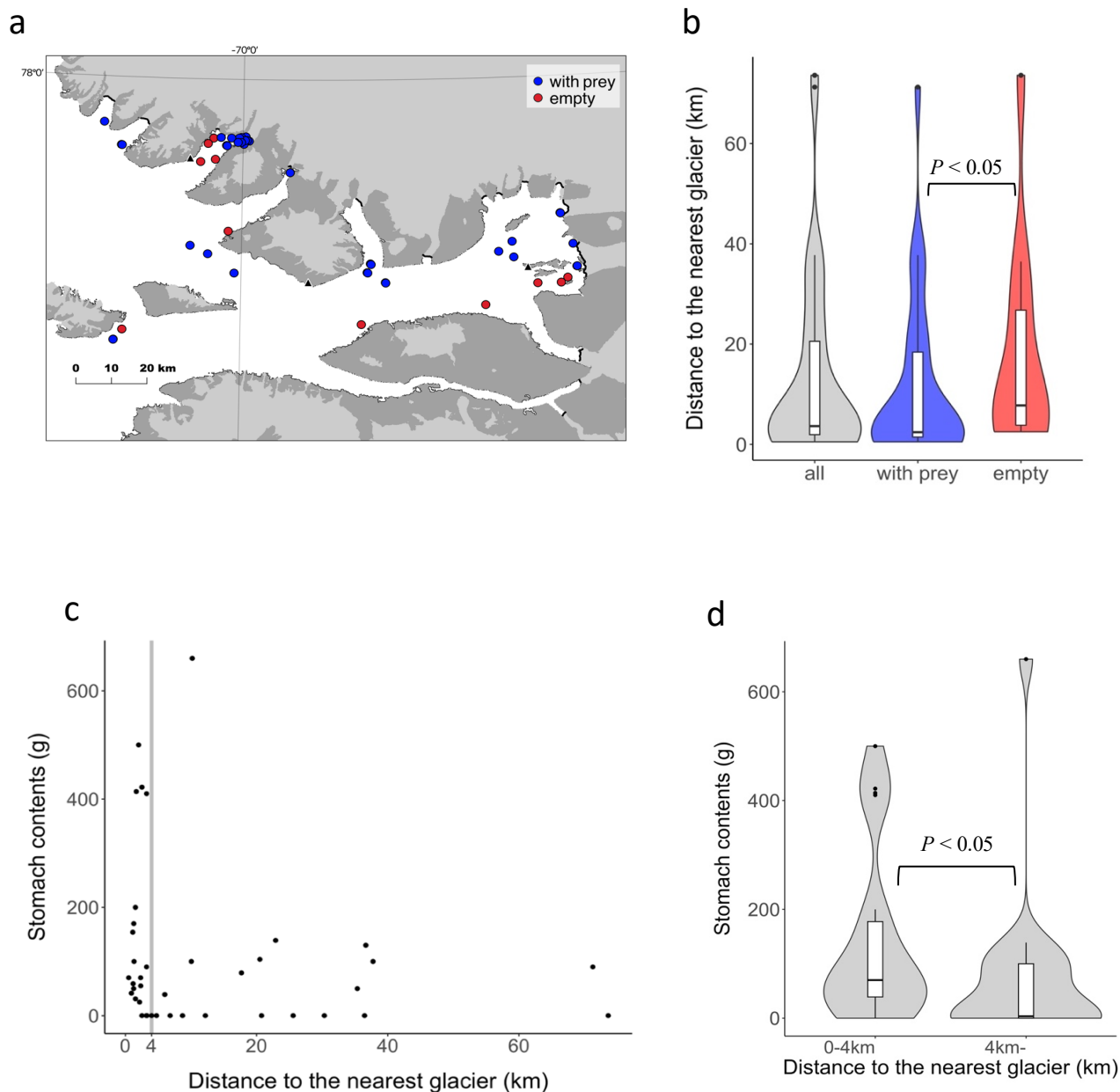


Fig. 4-1. Relationship between stomach contents and the distance to the nearest glacier from site of capture in 2022 and 2023. (a) Site of capture of seals collected during open-water season in 2022 and 2023. Glacier fronts are shown as black lines. (b) Boxplots and violin plots show the comparison of distance to the nearest glaciers (km) between all individuals (gray box), individuals with prey in the stomach (blue box) and with empty stomach (red box). The box edges enclose the first and third quartiles, and median distance to the glacier of each group is shown in central solid line. The upper and lower whiskers show the range of maximum and minimum values, excluding outliers. Significance was calculated using Wilcoxon rank sum test. (c) Distance to the glacier in relation to weight of stomach contents (g). A grey line drawn at 4 km shows a criterion for dividing the samples into two groups based on the median DNG (= 4 km). (d) Boxplots and violin plots show the comparison of the stomach contents weight between seals caught closer to the glacier front than the median DNG and those caught further away.

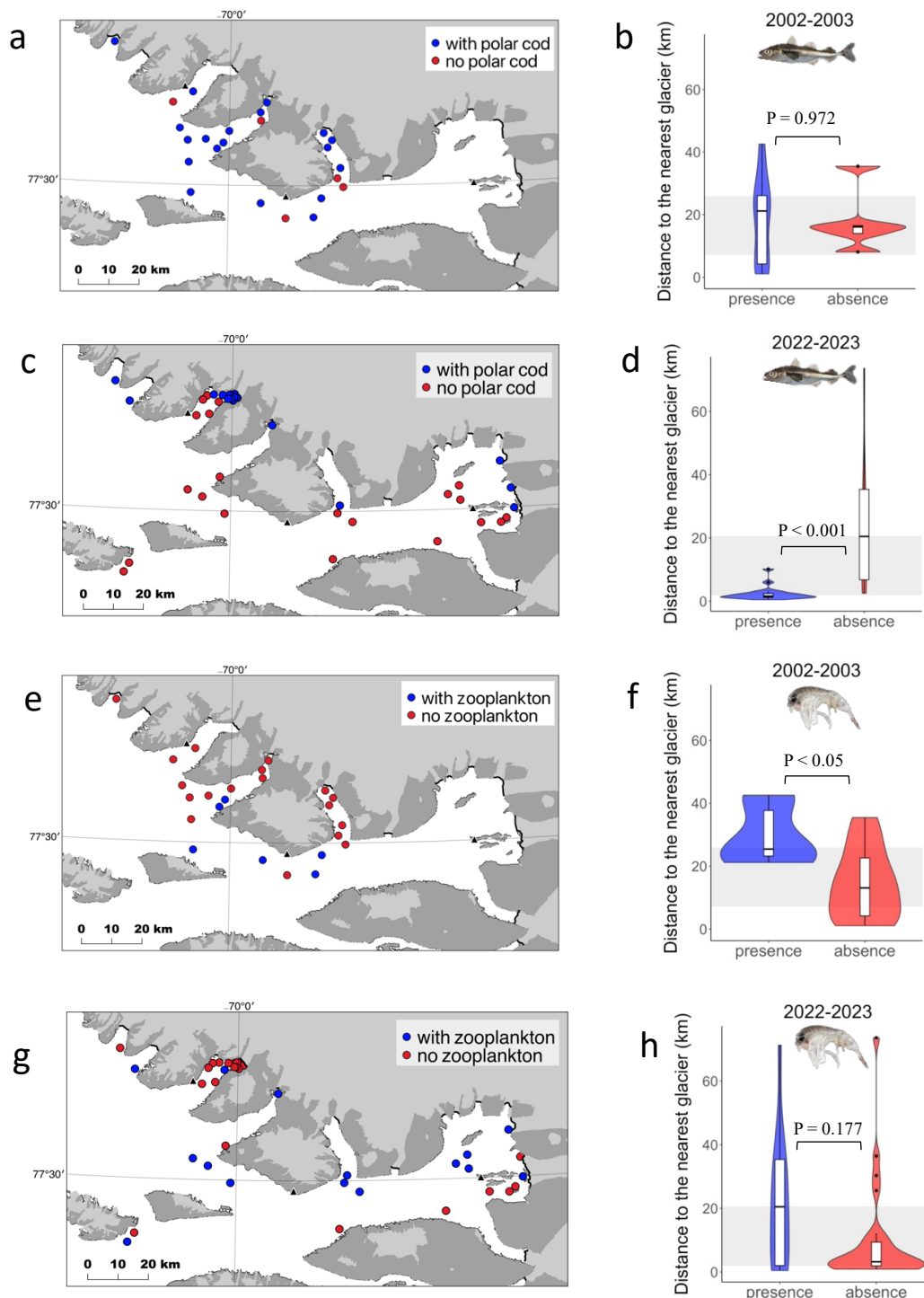


Fig. 4-2. Comparison of distance to the nearest glacier from site of capture by prey species and study period. Site of capture of seals based on the presence (blue dot) and absence (red dot) of polar cod in their stomachs collected during open water season in 2002 and 2003 (**a to b**), and in 2022 and 2023 (**c to d**) with comparison of the distance to the nearest glacier (km) in the boxplots and violin plots. The gray colored area behind the boxplots represent the interquartile ranges of all samples for each study period. Significance was calculated using Wilcoxon rank sum test. Site of capture of seals based on the presence and absence of zooplanktons in their stomachs collected in 2002 and 2003 (**e to f**), and in 2022 and 2023 (**g to h**).

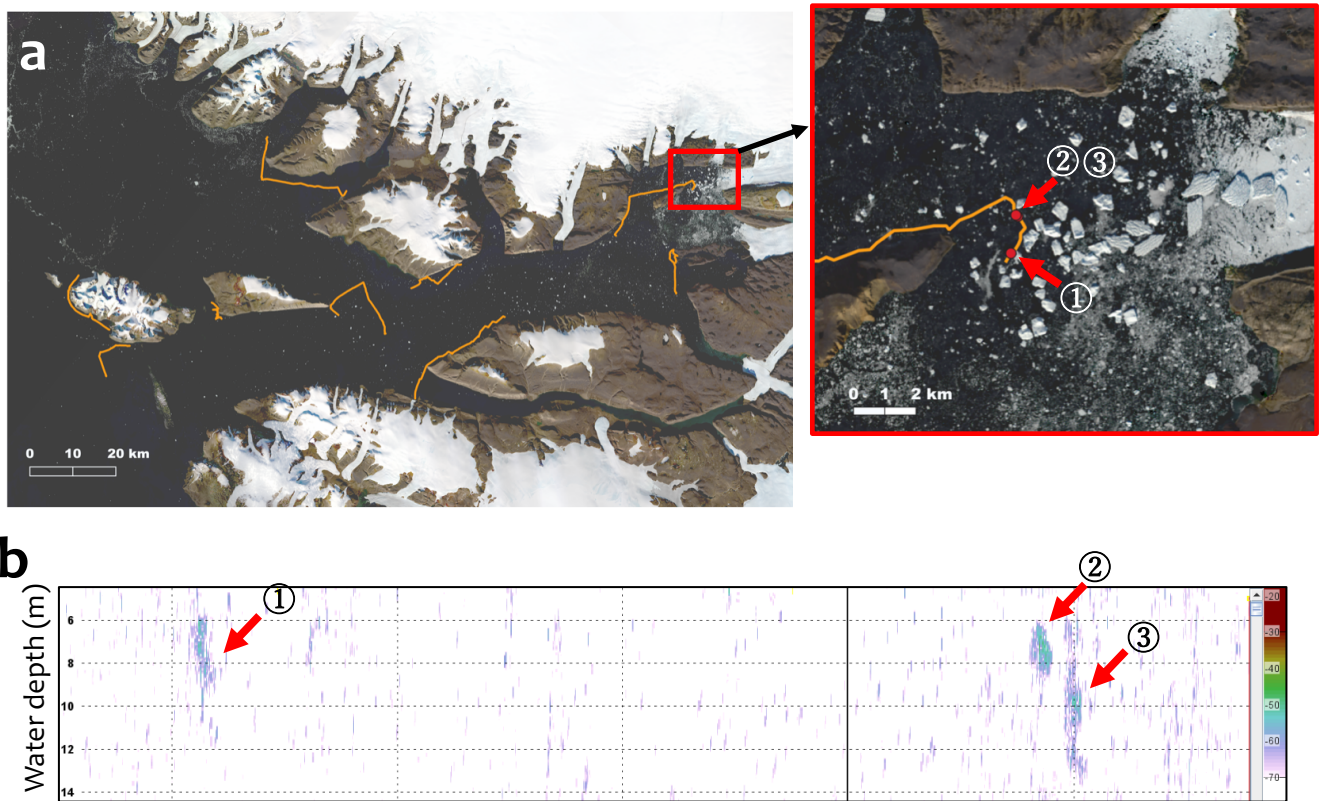


Fig. 4-3. Distribution of potential prey. (a) Hydroacoustic survey transects (satellite imagery by LANDSAT8 , 7th September, 2023). Red dots with arrows show the positions where fish school was detected. **(b)** Echogram of the three fish schools detected in front of the tidewater glaciers.

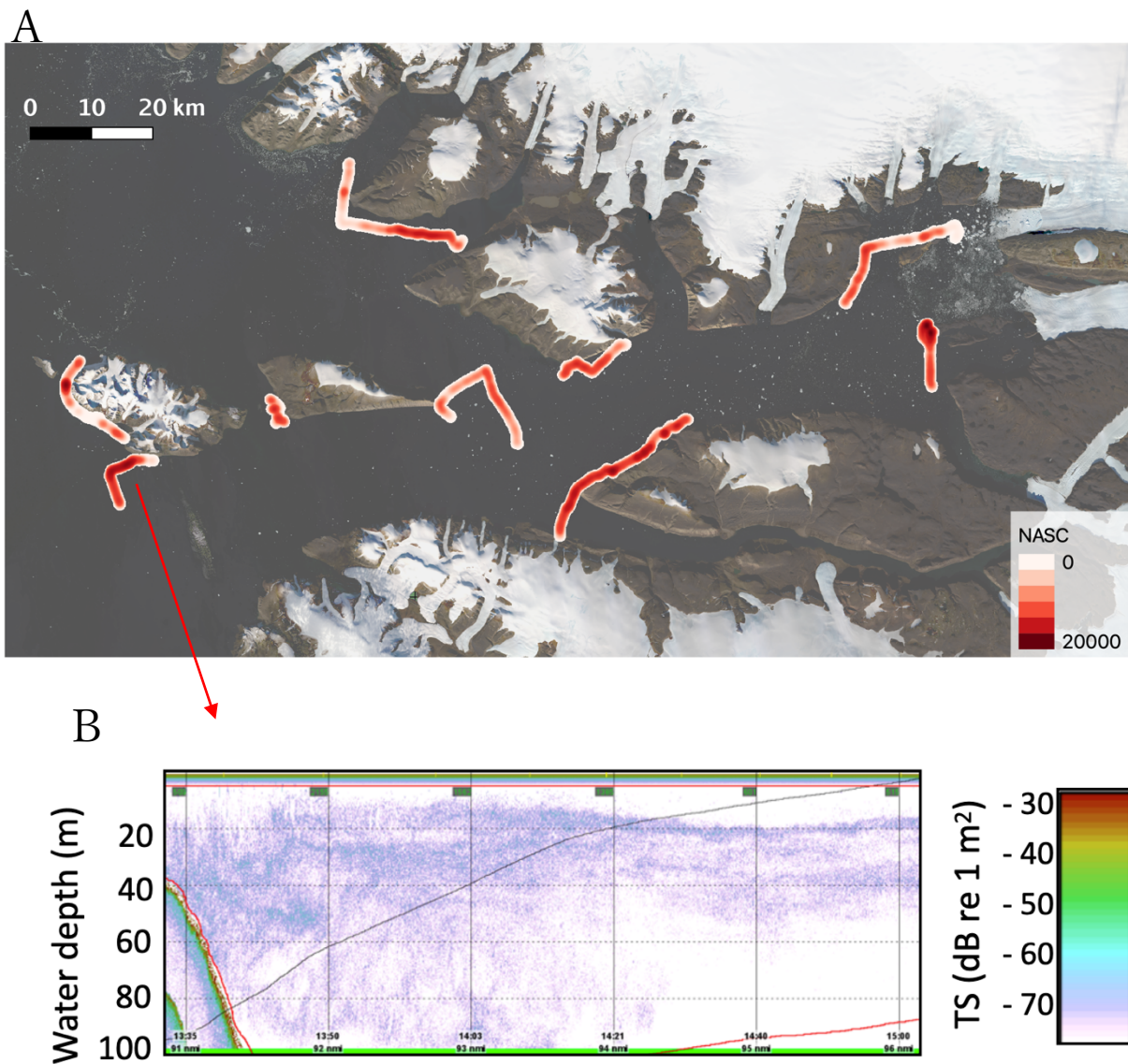


Fig. 4-4. Distribution of zooplankton. (a) Map of the acoustic backscatter along the survey transects which represent the zooplankton distribution. The color of transect indicate the Nautical Acoustic Scattering Coefficient (NASC) in 1 km grid. (b) Example of dense zooplankton aggregations found in the water column from 7-nim transect around 72.1 W, 77.29 N.NASC

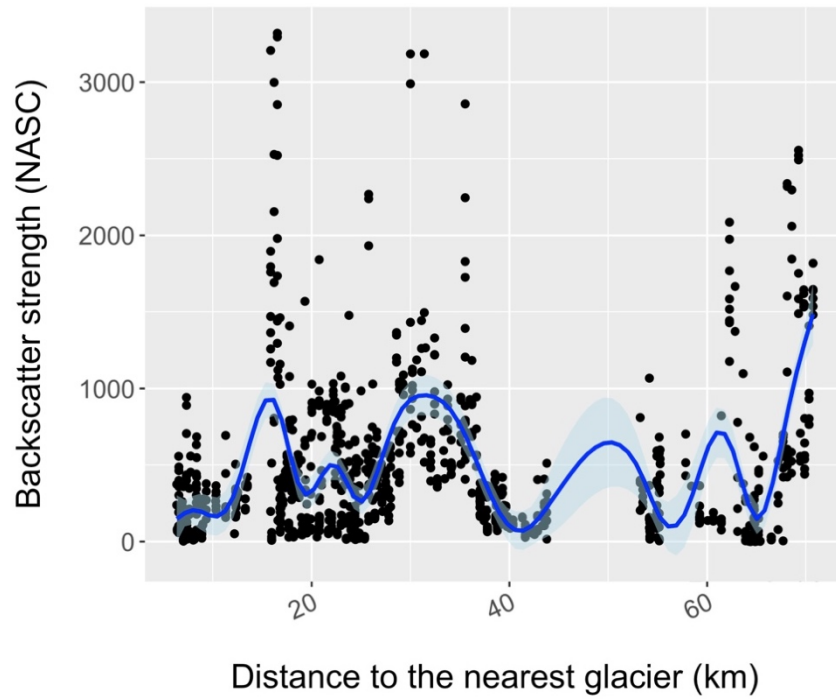


Fig. 4-5. Relationship between zooplankton abundance (acoustic backscatter (NASC)) and distance to the nearest glacier. Black dots represent the observation values, and blue line represents predictions by GAM with 95 % confidence interval.

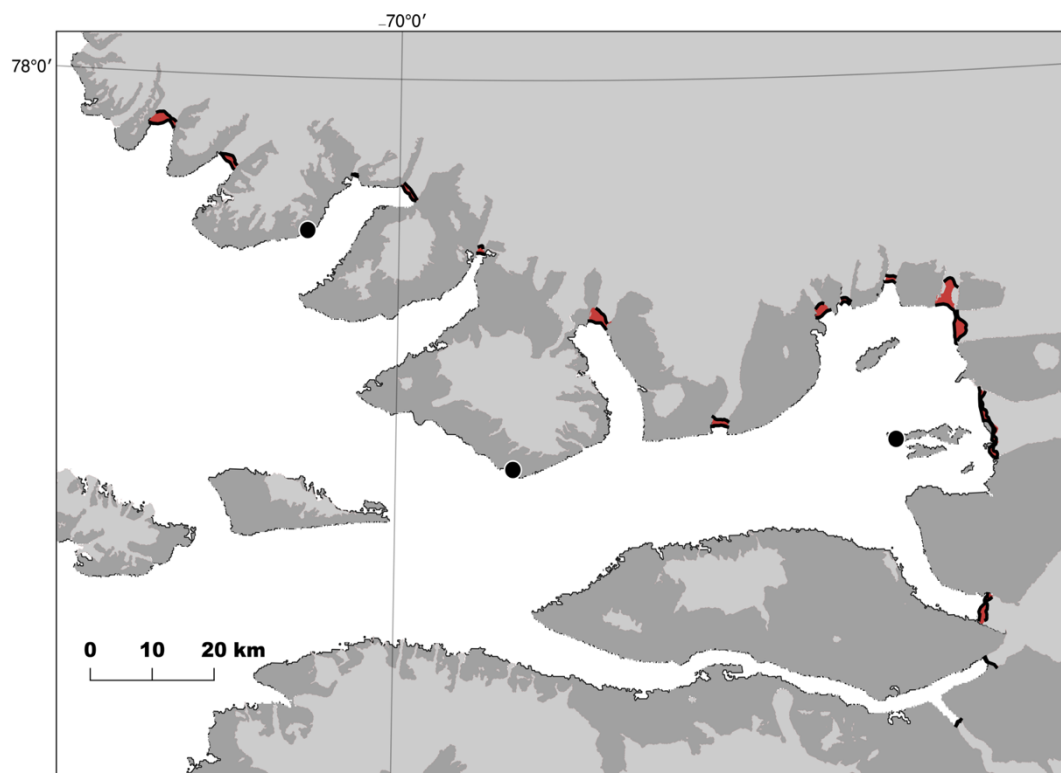


Fig. S4-1. Changes in the glacier fronts during the study period. Red colored spots represent the retreated areas.

CHAPTER 5

Persistent organic pollutants accumulated in marine mammals

Introduction

In the previous chapters, I have focused on the feeding ecology of marine mammals and their interactions with the environments to investigate and predict the future impacts of climate change on them. From this chapter, I will broaden the scope to see the impacts on local people who rely on these marine mammals for their livelihood – Inuit.

In 1992, the United Nations Framework Convention on Climate Change (UNFCCC) was signed the goal, “to prevent dangerous human interference with the climate system“, at the Earth Summit in Rio de Janeiro, Brazil. After the Protocol of Rio de Janeiro, the Millennium Development Goal (MDGs) came in 2000, which a set of 8 specific targets aimed by 2015. Building on the lessons of the MDGs, the Sustainable Development Goals (SDGs) were adapted in 2015, which outline 17 goals part of the 2030 Agenda for Sustainable Development. The SDGs emphasized inclusivity, sustainability, and a commitment to “leave no one behind” for achieving a more sustainable future for all (United Nations 2015). One of the main topics at the intersection of climate change and sustainable development goals is “food security” (Hsieh and Yeh 2024), including key dimensions of availability, access, utilization, stability and quality which is also affecting livelihoods of Inuit (Wesche and Chen 2010).

In the Arctic, Inuit rely heavily on marine mammals as daily food, and they are concerned about contaminants in their consumption of marine mammals (Wesche and Chen 2010). It has been shown in the number of studies the possible effects of climate change on the distribution and accumulation of chemical contaminants in the Arctic marine ecosystem, which is attributed to the changes in water mass distribution, temperature, as well as food web structures (Braune et al., 2019; Rigét et al., 2019). Although Persistent organic pollutants (POPs) have never been used in the Arctic region, these chemicals are transported to the Arctic through atmospheric and oceanic circulation. In water column, the highly chlorinated POPs such as DDTs and PCBs are associated with particles, while more water-soluble chemicals such as HCH are mainly in the dissolved phase (Muire et al., 1999). POPs are characterized as the chemicals which show high persistence and bioaccumulation properties, and long-range transportation (Ellis et al., 2004). Therefore, the impact on marine mammals, which is the top predators in the marine ecosystem, and Inuit who consumed marine mammals are particularly severe (Dietz et al., 2018). Despite the

manufacture and use of POPs have been banned, these chemicals are still detected in the marine mammals in the Arctic (Vorkamp et al., 2011; Routti et al., 2008), which require a continuous monitoring on the chemical distribution and concentration within the ecosystem.

In regards to the contaminant concentration, it is important to understand the food web structure, as it not only represent the flow of energy, but also the flow of contaminants. Here, I revealed the food web structure in the Inglefield Bredning using stable isotope, which represent the energy and contaminants flow within the marine ecosystem. I also measure the POPs concentration in the marine mammals as sentinels in ecological risk assessment (Bjurlid et al., 2018; Routti et al., 2008, 2010).

Typically, stable isotope analysis involves collecting various prey species through net sampling and using them for samples (Hobson et al., 2002). However, since the area is an important hunting ground for Inuit, large-scale sampling, such as the zooplankton or fish sampling using trawl net, cannot be conducted as it can disturb hunting activities. Furthermore, since there is no fishing culture in this region, it is difficult to ask villagers to collect fish samples. Therefore, by making the most of the advantage of the study site being able to collect a large number of stomachs, I directly used fresh prey items collected from the stomachs for analysis. While this method is not yet common in marine mammal studies, if its validity is proven, it is expected to significantly expand the potential for future research that combines stomach contents and stable isotope analysis.

This study highlights the interconnectedness between pollutant concentration in marine mammals and food web structures which marine mammals belong to, providing critical insights into how ecosystem change and pollutants impact the marine ecosystem and the Inuit communities that depend on it.

Materials and methods

Sample collection

From July to August in 2022, and from July to September in 2023, blubber samples of ringed seal, harp seal, bearded seal and narwhal were collected in Inglefield Bredning during summer for contaminants analysis. Freshly remaining prey found from their stomachs were also collected for stable isotope analysis for stable isotope analysis. Results of stable isotope analysis of marine mammals are shown in chapter 2. Collected samples were stored at -20°C until further analysis.

Contaminant analysis

Contaminant analysis was conducted at Ehime University Center for Marine Environmental Studies, Japan. Blubber samples were thawed before the analysis, and subsamples (2 g) were prepared after outer layers were removed. Analysis of legacy POPs including polychlorinated biphenyls (PCBs), dichlorodiphenyltrichloroethane (DDT), polybrominated diphenyl ethers (PBDEs) and hexabromocyclododecanes (HBCDs) was performed following (Kunisue et al., 2021). In brief, samples were homogenized before extraction with dichloromethane (DCM) using a high-speed solvent extraction apparatus. Extracts were then purified and fractionated using gel permeation chromatography and activated silica gel chromatography. The fractionated solution obtained from fractionation was qualitatively and quantitatively analyzed using a gas chromatograph or liquid chromatograph mass spectrometer, and the POPs concentration per gram of sample (seal blubber or whole body of prey) was calculated. A generalized linear mixed model (GLM) was performed to examine the potential effects of age, sex, species on contaminants levels.

Food web construction

Trophic levels (TL) of each species were calculated from their $\delta^{15}\text{N}$ values relative to zooplankton (*Themisto libellula*). Assuming that *Themisto libellula* occupy TL 2.5 around our study site (Hobson et al., 2002), and a constant 3.8 ‰ enrichment (Fisk et al., 2001; Hobson et al., 2002), I calculated the relative TL as follows;

$$\text{TL} = 2.5 + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{T. \text{libellula}}) / 3.8$$

For the marine mammal samples, since narwhals and harp seals are migratory species and may have arrived in the area recently, and because many of the seals were pups that may have been consumed their mother's milk up until a few months ago, the calculation of TLs was based on liver isotope ratios that reflect recent dietary intake over a period of days to weeks. Also, since the values of $\delta^{15}\text{N}$ for the different shrimp taxa (Thoridae, Pasiphaeidae, Pandalidae, Cragonidae) were almost the same (14.0 ± 0.1 , 14.5 ± 0.1 , 14.6 ± 0.1 , 14.6 ± 0.1 , respectively), the TL was calculated by combining all species.

Based on the results of the previous study on stomach contents analysis of marine mammals presented in chapter 2, I made predator-prey relationship groups for each marine mammals, and compared the isotope range among these food webs.

Results

Our result provides a very reasonable assessment of TL consistent with previous study conducted in the adjacent area (Hobson et al., 2001), with ringed seal and harp seal at TL 4.2, bearded seal at TL 4.1 and narwhal at TL 4.3 (Table 5-1, Fig. 5-1). Polar cod, the main prey of ringed seal, harp seal and narwhal in this area were at TL 3.9, and sculpin, the main prey of bearded seals, were at TL 3.8 (Table 5-1, Fig. 5-1). The results suggest that fresh prey collected from the marine mammal stomachs can be used for stable isotope analysis, which is applicable for future studies.

Assumed bearded seal food web was relatively benthic compared to other marine mammals, corresponding to the results of stomach contents in chapter 2 (Fig. 5-1). Regarding the $\delta^{13}\text{C}$ values of shrimps, it is interesting to note that the two families of shrimp which is frequently consumed by bearded seals (Cragonidae and Thoridae; Ogawa et al., unpublished data) showed high $\delta^{13}\text{C}$ values (= benthic), while the two families of shrimp eaten by narwhals (Pasiphaeidae and Pandalidae; Ogawa et al., unpublished data) showed lower $\delta^{13}\text{C}$ values, which is corresponding to the foraging areas of these predators.

POPs levels of marine mammals were shown in (Table 5-2). Across all species, DDTs was found to be the most prevalent, followed by PCBs. For all contaminants measured in this study, the higher concentrations observed in narwhals compared to other marine mammals. Except HCHs, age influenced significantly on the contaminant levels of marine mammals (Table 5-3). In addition to age, $\delta^{15}\text{N}$ value of liver also influenced the contaminant level for DDTs.

Discussion

One of the reason that DDTs and PCBs were that most prevalent in marine mammals may be attribute to its characteristics of chemicals. DDTs and PCBs are hydrophobic organics, which not easily be metabolized and are highly bioaccumulative (Muire et al., 1999). Given that the congeners of PCBs and DDT have water solubility's (10^8 to 10^{10}g l), it is two to three orders of magnitude lower than values for HCH (Tanabe and Tatsukawa, 1983). Therefore, the impact of PCBs and DDTs on marine mammals, which are higher predators and are affected by bioaccumulation, will be greater than that on water-soluble HCHs.

The reason why the highest POPs values were found in narwhal may likely be due to their higher trophic level (Fig. 5-1). Since they position at a higher trophic level in the food web compared to other marine mammals, they may be more strongly affected by biomagnification.

Additionally, in regard to age, it is possible that the narwhal samples included older individuals compared to the seal samples. This is because seals are considered “tastier” when they are young, leading to a frequent sampling of younger individuals (Table 5-2), while narwhal hunt do not show a preference of younger individuals – rather, it is more likely that older individuals with larger tusks can be preferred. Therefore, both ecological factors and hunting culture could explain the relatively high levels of contaminants observed in narwhals. Among five individuals of narwhal, narwhal 1 showed contaminant levels about one-tenth lower than the other individuals (Table 5-2). The individual was a female with a calf, and it is possible that great amount of contaminants accumulated her were transferred to the calf through lactation (Noren et al., 2024), which could explain the lower values seen in this individual. The results suggests that contaminants particularly affect the calved of narwhals.

Contaminants tend to accumulate more in fish species which occupy higher trophic level. For example, this include redfish, which was suggested to start coming to this area due to climate change as discussed in Chapter 2. As climate change progresses, and if redfish become more common as a prey, there is concern that the contaminants levels in marine mammals in this area may increase (McKinney et al., 2012).

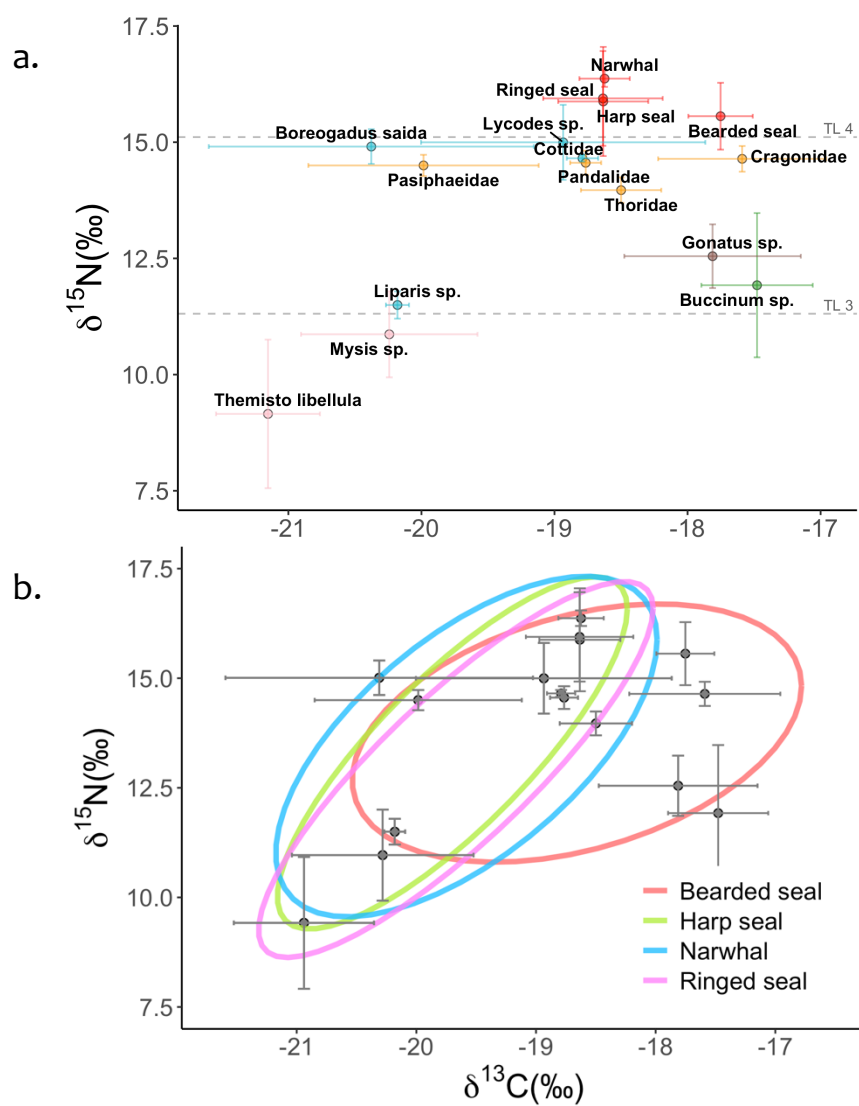


Fig. 5-1 Assumed trophic levels of marine mammals and food webs.

Table 5-1. Stable isotope ratios of marine organisms in Inglefield Bredning.

species	n	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	TL
Marine mammal				
Ringed seal	15	16.0 ± 0.3	-18.6 ± 0.1	4.2
Harp seal	11	15.9 ± 0.4	-18.6 ± 0.1	4.2
Bearded seal	10	15.6 ± 0.2	-17.8 ± 0.1	4.1
Narwhals	14	16.4 ± 0.1	-18.6 ± 0.1	4.3
Fish				
Polar cod	10	15.0 ± 0.1	-20.3 ± 0.4	3.9
Sculpin	4	14.7 ± 0.03	-18.8 ± 0.1	3.8
Sea poacher	2	16.7 ± 0.02	-18.8 ± 0.01	4.4
Snailfish	3	11.5 ± 0.1	-20.2 ± 0.04	3.0
Eelpout	3	15.0 ± 0.4	-18.9 ± 0.5	3.9
Shrimp	14	14.5 ± 0.1	-18.5 ± 0.2	3.8
<i>Thoridae</i>	3	14.0 ± 0.1	-18.5 ± 0.1	-
<i>Pasiphaea</i> sp.	2	14.5 ± 0.1	-20.0 ± 0.4	-
<i>Pandalus</i> sp.	4	14.6 ± 0.1	-18.8 ± 0.1	-
<i>Cragonidae</i> sp.	5	14.6 ± 0.1	-17.6 ± 0.3	-
Cephalopod	3	12.5 ± 0.3	-17.8 ± 0.3	3.3
Benthos				
Buccinum sp.	3	11.9 ± 0.7	-17.5 ± 0.2	3.1
Zooplankton				
Mysis sp.	4	11.0 ± 0.4	-20.3 ± 0.3	2.9
Themisto sp.	5	9.4 ± 0.6	-20.9 ± 0.2	2.5

Table 5-2. Concentrations of POPs in the blubber of marine mammals (ng / g, lipid basis).

Species	ID	sex	age	PCB	DDT	HCH	CB
Harp seal	1	male	44	2400	2700	56	260
Harp seal	2	male	8	110	47	23	18
Harp seal	3	male	1	78	80	5.9	18
Bearded seal	1	male		910	570	10	5.2
Bearded seal	2	male	10	440	560	13	7.4
Bearded seal	3	male	11	660	2100	15	21
Bearded seal	4	male	18	1400	1900	9.4	11
Ringed seal	1	female	2	-	390	67	30
Ringed seal	2	male	4	-	590	39	34
Ringed seal	3	male	1	560	760	77	60
Ringed seal	4	male	0	170	1100	160	17
Ringed seal	5	male	0	610	780	92	89
Ringed seal	6	female	2	250	240	40	27
Narwhal	1	female		130	120	15	51
Narwhal	2	male		1900	2200	170	550
Narwhal	3	male		1600	1700	88	370
Narwhal	4	male		670	620	66	290
Narwhal	5	male		1300	1500	120	360

Table 5-3. Results of generalized linear model (GLM) on the contaminants levels.

PCBs

Variable	Regression estimate	Standard error	t value	p value
sex	-128.09	30.2.92	-0.423	0.7135
age	62.33	6.96	8.954	0.0122 *
species	485.72	162.34	2.992	0.0959
$\delta^{13}\text{C}$ (muscle)	781.89	546.68	1.430	0.2889
$\delta^{15}\text{N}$ (muscle)	153.82	143.18	1.074	0.3951
$\delta^{13}\text{C}$ (liver)	-1002.00	708.57	-1.414	0.2929
$\delta^{15}\text{N}$ (liver)	-81.47	129.56	-0.629	0.5937

AIC: 138.14

DDTs

Variable	Regression estimate	Standard error	t value	p value
sex	-628.97	317.34	-1.982	0.11853
age	74.95	10.47	7.161	0.00201 **
species	363.16	232.51	1.562	0.19333
$\delta^{13}\text{C}$ (muscle)	-93.00	685.90	-0.136	0.89869
$\delta^{15}\text{N}$ (muscle)	116.37	207.22	0.562	0.60439
$\delta^{13}\text{C}$ (liver)	198.96	930.66	0.214	0.84117
$\delta^{15}\text{N}$ (liver)	-503.36	171.16	-2.941	0.04235 *

AIC: 178.21

HCHs

Variable	Regression estimate	Standard error	t value	p value
sex	-35.267	33.676	-1.047	0.354
age	1.064	1.111	0.958	0.392
species	23.692	24.674	0.960	0.391
$\delta^{13}\text{C}$ (muscle)	-29.673	72.788	-0.408	0.794
$\delta^{15}\text{N}$ (muscle)	0.110	21.991	0.005	0.996
$\delta^{13}\text{C}$ (liver)	-7.619	98.762	-0.077	0.942
$\delta^{15}\text{N}$ (liver)	-21.077	18.164	-1.160	0.310

AIC: 124.38

CBs

Variable	Regression estimate	Standard error	t value	p value
sex	-4.916	51.307	-0.096	0.928
age	5.705	1.692	3.371	0.028 *
species	21.804	37.592	0.580	0.593
$\delta^{13}\text{C}$ (muscle)	-7.260	110.895	-0.065	0.951
$\delta^{15}\text{N}$ (muscle)	20.452	33.503	0.610	0.575
$\delta^{13}\text{C}$ (liver)	-34.539	150.468	-0.230	0.830
$\delta^{15}\text{N}$ (liver)	-7.655	27.674	-0.277	0.796

AIC: 134.48

$P < 0.05^*$, 0.01^{**}

CHAPTER 6

The situation of Inuit communities in the continuously changing Arctic revealed by interview

Introduction

The Arctic is warming nearly four times faster than any other places on earth (Rantanen et al., 2022), and as a result, glaciers are losing mass (Khan et al., 2022; Kochtitzky and Copland, 2022), marine ecosystems are changing (Drinkwater, 2005; Hop and Gjørseter, 2013; Lowther et al., 2017), affecting traditional cultures of Inuit people living in the Arctic (Schiøtt et al., 2021). While it is clear that climate change is altering the Arctic environment and affecting local people, knowledge about the changes and impacts at the local level is still lacking. The Arctic communities are culturally diverse, with varying interactions among people, nature, and the environment across different areas. Therefore, impact assessment should be conducted at the local levels (Hayashi and Walls 2019).

Areas surrounding Inglefield Bredning, are home to the northernmost Inuit communities in Greenland, where about seven hundred people live. This is one of the regions where a subsistence lifestyle based on marine mammal hunting has been particularly preserved (Greenland statistics 2022). This area has also been experiencing considerable increase in sea surface temperature in the last decades (Chambault et al., 2020), and the great mass loss in glaciers (Sakakibara and Sugiyama, 2018; Wang et al., 2021), rising concerns about changes in the marine ecosystem and impacts on local communities. However, since the fjord is difficult to approach due to high density of icebergs and sea ice, scientific assessments on the environment and marine ecosystem have been scarce until recently. To investigate the changes in environment and their impact on society, Japanese research projects have been operated in this region since 2012 (Sugiyama 2019; Sugiyama et al., 2021).

There is increasing recognition that traditional knowledge of Indigenous people complement “scientific” observation (ACIA 2005; Usher, 2000), as they have place-based immense knowledge, which has been accumulated and passed through generations. Traditional ecological knowledge (TEK) is “*the knowledge, knowhow, skills and practices that are developed, sustained and passed on from generation to generation within a community, often forming part of its culture or spiritual identity*” (World Intellectual Property Organization, 2015), and it has provided important scientific insights in various regions around the world (Ens et al., 2015; Smith et al., 2021; Schmidt et al., 2021). Moreover, especially in the Arctic, the Arctic Council has repeatedly recommended incorporating the TEK in environmental and ecological survey

where scientific knowledge is scarce due to inaccessibility (Danielsen 2014; Meltøfte 2013). Accordingly, our study aims to investigate the environmental and ecological changes occurring in this area, as well as the impacts of these changes on the local communities, based on the experience of the Indigenous people who have an immense knowledge of their land and ocean.

The study was conducted in August and September, 2023 in the indigenous communities around Inglefield Bredning. Approximately 600 and 40 people are living in Qaanaaq and Siorapaluk, respectively. The villagers in both areas are using the entire fjord as a hunting ground on a daily basis, and they often travel back and forth between each village by boat in summer, and by dogsled in winter.

Materials and methods

The semi-structured interviews were conducted in Qaanaaq and Siorapaluk to document the perception and the knowledge on the marine ecosystem and changing climate in the areas. The questions were predetermined, and focused on changes in 1) environment, 2) marine ecosystem, 3) culture, and 4) whether, and how these changes are affecting their life. The questions were open-ended to learn more about an informant's experience, and to deliver new and unexpected insights (Adams 2015). At the beginning of each interview, I explained them the aim of this study, and asked permission to record the conversation. I requested informant to point and draw out areas on a printed map where they mention. All the interviews asked in English were translated into Greenlandic by a Greenlandic translator. Each interview lasted between 40 – 90 min. In this study, I define the “past” before 2000.

I transcribed all the conversations based on the recorded data. After that, I conducted a manual coding process using extensive notetaking, identifying potential themes and categories for each of the four questions (Seidman 2006). I then calculated the frequency of those themes mentioned during the interview as an indicator of their significance.

A total of 22 informants participated in the survey, including 17 men and 5 women (Table 6-1). One man was a retired hunter, and all other men were active hunters with hunting license. All male informants had started hunting at a young age, learned hunting skills from their fathers while accompanying on hunts. As hunting is primarily a male activity, most of the female participants were not hunters. One woman was a hunter, while others were wives of local hunters. Still, they frequently accompanies their husband on hunting.

They hunt ringed seal and bearded seal throughout the year in the fjord, narwhals and harp seals in open water season, and walruses and polar bears during winter. They also fish halibut in

the winter. Although it is not their main activity, they occasionally catch Arctic char in the summer and Arctic cod in the winter.

Results

Changes in environment

A variety of environmental changes were recognized by local people, including changes in sea ice, glaciers, ocean conditions and climate (Table 6-2). Although these environmental parameters are known to show significant year-to-year variations, people have perceived rapid climate change in recent years, notably since 2000. These changes appear to have accelerated.

- *Ice*

Sea ice conditions have changed drastically and are the most concerned environmental change in this region. Every interviewee recognized drastic changes in the thickness, size, and timing of the sea ice melting and formation (Table 6-2). They say “*everything is melting*” due to rising temperatures.

Compared to the 1990s, the area of sea ice coverage during winter has decreased. Previously, the ice extended from the coast of Qaanaaq to the *Kiatak* island, located on the west side of the fjord, and as far north as Cape Alexander (Fig. 6-1). However, in recent years, it only extends to several tens of kilometers north of Siorapaluk and as far as *Qeqertarssuaq* island outside the fjord (Fig. 6-1). The duration of sea ice formation in the region has reduced since melting occurs earlier and freezing later than in previous decades. Until the 1990s, sea ice began forming around Qeqertat, inside the fjord, from late September, and it became thick enough for dogsledding throughout the entire fjord by the end of October. Nowadays, sea ice formation is delayed by approximately two to three months compared to 1990s. Sea ice thickness has also decreased, making it more easily broken by wind. Sea ice surface becomes irregular and bumpy as a result of break up and refreezing processes, which leads to more physically demanding conditions for traveling by dogsled. Moreover, as sea ice becomes thin and fragile, cracked and fragmented sea ice have increasingly spread along the ice edge. In such areas, villagers can use neither dogsleds nor boats, which hinders their hunting activities. Local people have also noticed that the sea ice contains more freshwater than before. They have observed this change, for example, when drilling holes in the sea ice for halibut fishing in winter. It has been observed that the upper layer of the ice, which is particularly hard as it contains freshwater from the glacial discharge, has become relatively thicker than before, suggesting the increasing amount of meltwater from the glaciers.

Glaciers are also melting in the region, and some of marine-terminating glaciers have retreated so that they no longer reach the sea (Fig. 6-2a). Icebergs in the ocean are smaller than before, while their number has increased. Same trends in iceberg size and number have also been noticed as an environmental change by villagers in Ilulissat ice fjord in central western Greenland (Schiøtt et al., 2021).

- *Ocean*

The ocean currents and waves have become stronger in this region, affecting fishing and hunting activities. It increasingly difficult to properly set up gillnets for Arctic char in summer and for seal in winter, as a net gets swept away by strong currents. People have also noticed that the waves have become higher, and they think it is probably due to increased wind intensity and stronger currents.

- *Climate and weather*

Air temperature is rising, liquid precipitation and wind speed are increasing. A few decades ago, temperature frequently dropped to -40°C in winter, but it rarely happens recently. Winds have intensified, particularly the easterly winds blowing from inside the fjord. The easterly winds often push sea ice out of the fjord, preventing rigid ice cover formation. Additionally, since around 2000, the amount of rain has increased. It used to start snowing around the end of August, but now it can rain at this time of year. In fact, during the fieldwork for this survey in 2024, it sometimes rained even in late September. The increased rainfall, combined with increased glacier meltwater, has caused river flooding and resulting in the destruction of the crucial bridge in the village which connects it to the airport (Fig. 6-2b) (Kondo et al., 2021).

Moreover, the weather is becoming increasingly unpredictable and more erratic. When people go hunting, they rely on traditional knowledge passed down through generations to predict the weather, determine hunting locations and timing (e.g. When there is fog around Cape Alexander, the wind is usually blowing from the northwest, which often creates ocean swells. In such case, they avoid going out to sea and hunt near the coast instead. When traveling on the sea ice with dogsled, they try to pass near icebergs embedded in the sea ice. By listening to the sound of icebergs rubbing against the sea ice, they assess the ocean swell; the louder the sound, the stronger the swell. If the swell is strong, they turn back or hunt in area where the ice is safe). However, in recent years, unexpected and sudden weather changes are more frequently happening and affecting hunting activities in the region. Overall, the timing of seasonal changes

are shifting as represented by extension of the period that people perceive as “summer”. Traditional knowledge and experience have been essential to understand seasonal cycles and weather conditions for ensuring a safe hunt. Nevertheless, villagers are now encountering natural phenomena that do not fit their traditional knowledge, rising concerns about safety.

Changes in marine ecosystem

- Fish

As Inuit communities around Inglefield Bredning traditionally rely heavily on marine mammal resources, fisheries have not flourished much in this region. Still, Arctic char fishing with gill nets occurs during summer, and halibut fishing on sea ice takes place in winter. In addition to these activities, people sometimes enjoy fishing from the coast in summer and from the ice edge in winter. Through these fishing activities, they have observed subarctic fish starting to enter the fjord. Villagers recognize at least five fish species: Greenland cod (*Gadus macrocephalus*), Atlantic cod (*Gadus morhus*), capelin (*Mallotus villosus*), wolffish (*Anarhichas minor*), and redfish (*Sabineia* spp.). These species have become more common in the area since around 2010. During winter fishing from the ice edge, it has become common to catch redfish and subarctic cod (Fig. 6-2c). Recently, wolffish sometimes occupies most of catch during halibut fishing (Fig. 6-2d). Since these kinds of fish are not familiar in this area, people are not used to prepare them. Nonetheless, when they catch these fish, they often try to find ways to eat them. Cod are also used as bait to catch halibut.

People have recognized a decline in the size of Greenland halibut over the last few years in Inglefield Bredning. They also believe that the population of halibut may be declining, based on the increasing number of wolffish catch instead of halibut. As they experienced a significant decline in halibut catches after the bountiful catch in 2019, it is possible that the booming halibut fishery in this area is contributing to the decrease in both halibut size and stocks.

- Marine mammal

Some people have recognized that the blubber of marine mammals has become thinner, a change also observed in other Arctic? Indigenous communities (Huntington et al., 2016). Changes in population have also been noticed in some species. The species identified as “increasing” are the narwhals, harp seals and the walruses. Regarding walruses, both their distribution and the timing of their migration to the area are changing. As sea ice reduced and the ice edge recedes closer to the villages, the walruses’ distribution range has extended right up

to the settlements, making it easier for hunters to access them to catch. Walrus used to arrive near Siorapaluk typically in October until the 1990s, whereas their arrival has recently shifted later in November.

Except for walrus, changes in distributions of marine mammals are not recognized by the interviewees. (Fig. 6-3). Seals can be found throughout the fjord, but bearded seals, in particular, are observed in large numbers in the shallow areas on the western side of the fjord (Fig. 6-3a). Ringed seals are the most abundant pinniped in this area, and they are mostly hunted in areas easily accessible from the villages. They are also often observed in large number near the front of marine-terminating glaciers (Fig. 6-3b). Harp seals only migrate in the area in summer and are not hunted very often, but people sometimes observe them feeding in a group of several dozen individuals (Fig. 6-3c). Narwhals start entering the fjord when sea ice melts. They are most often found in the inner part of the fjord, near the glaciers around Qeqertat (Fig. 6-3d). People have frequently seen narwhals diving near the front of the glaciers presumably for feeding.

While the number of walrus is recognized as increasing near Siorapaluk, seals has been observed decreasing during the migration season of walrus season. People suspect that seals are avoiding this area to evade walrus, which can be a predator of seals. Moreover, people have noticed changes in the molting timing and fur quality of seals through the seal fur tanning process. Seals usually molt in spring, but some seals recently molt in summer and some others even do not molt at all. They report tanning fur of seals is more difficult than before because hair roots are more frequently stiffer or softer than usual. People believe that the change in the fur quality is due to rising temperature and reduced availability of sea ice for resting and molting on.

Sightings of killer whale (*Orcinus orca*) has increased in this area. They have been observed during open water season almost every year since around 2015, whereas rarely seen in the previous period. People believe that when killer whales migrate into the fjord, seals and narwhals become very sensitive and escape to the inner part of the fjord. According to the villagers, when killer whales hunt a narwhal in this region, they have the habit of eating only meat but skin (*Mattak*). People presume that the increase in killer whale sightings may be attributed to the decline in sea ice, as it helps their access to the fjord.

- *Seabird*

The migration timing of little auks (*Alle alle*) is changing; they arrive the study area earlier and leave later than before. The timing of their migration varies from year to year. For example,

in 2022 and 2023, they arrive in Siorapaluk three weeks earlier compared to previous years, and they remained in the area longer. No differences in abundance, timing of migration or distribution were recognized for other seabirds.

Changes in culture

There were two main cultural changes observed during the Our interview revealed two important changes in cultural aspects: increasing difficulty in practicing and acquiring traditional hunting skills, and growing importance and dependence on halibut fishing.

There are many traditional hunting methods that have become difficult to practice due to environmental changes driven by climate change, especially changes in sea ice, as mentioned above. Until about 10 years ago, stable sea ice formed by mid-October before polar night began, which provided occasions to practice how to walk on sea ice to hunt seals– *Quijelinaq*. However, as the sea ice now forms later, this hunting methods is not as common as it once was, and the opportunities to pass down methods to younger generations are decreasing. Moreover, many hunters have stopped hunting walrus on ice because it is not stable enough. One hunter mentioned, “*It was around 2000, while we were hunting walrus on sea ice, the ice cracked, and we drifted out to the sea - we almost died. This never used to happen before. Since that experience, I have become afraid of hunting walrus on ice.*” - People in this area are shifting walrus hunting from on-ice dogsled hunting to boat-based hunting. The same change applies to other target species. Until just about 20 years ago, dogsled hunting was conducted from October to early July. However, it is now only possible from late November or December to June, shortening the period by about three months. People in this area have traditionally used dogsled routes passed down through generations to travel between villages safely and efficiently (Fig. 6-4a). However, due to the retreat of glaciers and the unsafe conditions of sea ice, it is necessary to change these routes (Fig. 6-4a) – The glacier fronts which terminate in the sea during the summer serving as an essential transportation network for Inuit people during the winter. When traveling across the fjord, people take shortcuts by going over the mountains. Since the mountains in this area are steep, they must use the glacier fronts as slopes to navigate these crossings. Thus, If the glaciers retreat and the fronts become unstable with crevasses, these routes become inaccessible. Additionally, since more frequent break off and refreezing process, sea ice surface is bumpy, and traveling over with a dogsled is getting more demanding. Fig. 6-4b shows “dangerous spots” in the fjord where the ice can breaks up more frequently. According to the interview, sea ice in these areas is recently getting thinner and more fragile under the influence of strong ocean currents. When traveling with dogsleds, people avoid these areas and travel on the landfast ice – *Quaingoq* – which is more stable and is considered safer. In this way,

traveling between villages requires more time and energy compared to before. While hunting with dogsled was once predominant, hunting from boats is now becoming more common in this region due to the decrease and instability in sea ice.

Not only environmental changes, but also social changes, such as the introduction of modern vehicles has also brought changes to their cultures. For example, dogsleds are abandoned not only because of weakening sea ice conditions, but also because snow mobiles are available for faster and easier winter travel. Traveling from Qaanaaq to the inner parts of the fjord takes a couple of days by dogsled, while the same travel can be completed within a day using a snowmobile. Nonetheless, hunters mentioned that snowmobiles would not completely replace dogsled because sled dogs can avoid dangerous areas by smelling water while running on ice. Dogs can also find a way back home even if the operator get lost in a snowstorm. Moreover, polar bear hunting is impossible without them, as they need the help of dogs to drive the polar bears in to catch. Therefore, they believe that the dogsledding culture persists as an essential part of the community's culture.

Unlike the other declining traditional hunting methods, the more active halibut fishing is affected by changes in society rather than climate. The most important social change affecting the community was the introduction of a quotas system for narwhal and walrus hunt, which was enforced 2006. Due to the introduction of quotas system and the ban on international trade in narwhal and walrus tusks that were previously the main sources of income, income of hunters from these hunting has decreased. On top of that, income from fur products has significantly decreased as well because of the shift to synthetic clothing and the decline of the global leather trade.. Consequently, winter halibut fishing is now an important source of income for local people. Several hunters said their biggest concerns in life was the loss of incomes due to restrictions on narwhal hunting.

Discussion

The experiences shared by local people revealed an inseparable interconnections among changes occurring in the environment, society and culture. By connecting the changes recognized by locals with causal relationships, our study shows that none of these changes occur in isolation (Fig. 6-5).

The rise in air and ocean temperature has caused a wide range of impact on natural environments, including glacier retreat, shrinking icebergs, alterations in sea ice thickness, extent, duration, surface roughness and stability, changes in seals' molting patterns, and the introduction of Atlantic species (Fig. 6-5). As mentioned by local people, changes in seals'

molting may be attributed to rising temperature and the sea ice loss. To identifying the specific causes, behavioral observations during molting period and comparisons with environmental factors is required. Observed major environmental changes such as instability in sea ice, shrinking icebergs, strong ocean current, high waves and strong wind, recognized by more than half of the subjects (Table 6-2), are likely to mutually influence each other (Fig. 6-5). It has been scientifically confirmed that the increase in wave height and wind in polar regions under climate change (Casas-prat et al., 2024), along with the reduction in sea ice and shrinking icebergs, makes the ocean more prone to wave formation, and vice versa (Squir 2020). In the fjord experiencing sea ice thinning and shrinking icebergs, A vicious cycle may be occurring in the fjord, where waves are more likely to form under the influence of reducing sea ice and shrinking icebergs and the waves further contribute to sea ice break up.

All these cascading series of environmental changes and unpredictable weather end up to impact on the cultures and hunting practices in the communities. Environmental changes in the Arctic regions have altered local cultures, particularly those associated with hunting. Buijs (2010) reported that increase in fish populations resulting from rising water temperatures led shift from marine mammal hunting to fishing. Boats are more commonly used than dogsled for hunting and transportation (Schiøtt et al., 2021) as the use of dogsled on increasingly unstable sea ice is dangerous. Centuries-old traditions of the Inuit communities, passed through generations to generations, are on the verge of being lost due to climate change in just a few decades. People exchange information within the community to adapt the changes in their hunting grounds, routes, and timing. Amidst such intense environmental fluctuations, it is not easy to maintain traditional hunting practices by securing safety and the importance of the connections among people is growing.

As the sign of a marine ecosystem change, people have recognized an introduction of the Atlantic fish including Greenland cod, Atlantic cod, capelin, wolffish, and red fish. These species are supposed to distribute further southern areas (Bengtsson et al., 2020; Carscadden et al., 2013; Higdon et al., 2009), and their presence in this region has not yet been reported by scientific data (Table 6-2, Fig. 6-2). If northward migration of Atlantic fish continues, biomass and distribution of native species may be affected due to competition for food and habitat with newcomers (Brand and Fischer 2016). For example, the habitat of polar cod (*Boreogadus saida*), the major source of energy for marine mammals and sea birds in this region (Holt et al., 2001; Laidre and Heide-Jorgensen, 2005), would be threaten by competition with Atlantic and Greenlandic cods. Although capelin has not been observed to be fed by predators in this region so far (Chapter 2), if their population increase, they can be an alternative prey for marine mammals, as they serve as a primary prey species for marine top predators in southern areas

(Cambellant et al., 2013; Kapel 2000). Therefore, changes in fish communities due to environmental changes have a potential to affect the distribution and diet of marine mammals and seabirds, which are important resources for the local communities in the regions. On the other hand, the increase in Atlantic fish population may provide more fishing opportunities for local people. Consequently, as observed in other Arctic regions, fishing may play more important role in cultural practice in the future (Buijs 2010). Our study strongly suggested that changes in environment and marine ecosystems in the study region have already given impact on the traditional hunting culture, leading to even greater cultural shift in the community in the future.

Finally, I emphasize that cultures and ecosystems are affected by not only environmental changes occurring in the region, but also by global social changes. Hunting of narwhals and walrus have been important source of income in the community, but nowadays it is restricted due to the prohibition of international trade in these animals and the introduction of quota systems. Furthermore, the trade of seal fur products has also declined, as introduction of synthetic clothes and ban of commercial trading of seal products by EU (EC 2015). People are facing the dual impact of reduced hunting opportunities due to environmental changes and insufficient income due to social factors, resulting in need to replenish for these income reductions through alternative ways for instance by halibut fishing.

Although catch volume data of halibut are unavailable in this region, people have mentioned that they are becoming more dependent on halibut fishing as a source of income than before. Since the increase in halibut fishing, they have noticed a decrease in fish size and catch per unit effort (Table 6-2). The observed decrease in the size of halibut in recent years may indicate a decline in its population, similar to the situation in the Disko Bay where decrease in population and mean length of halibut has already confirmed, probably due to overfishing (Nygaard, 2019; Fredenslund 2022). While population assessments have never been conducted in the study area, our study suggests urgent need to conduct halibut population survey to ensure sustainable fisheries in the region. Reducing or regulating fishing quotas is one of the effective counterplans for sustainably fishery (Fredenslund 2022). However, we also have to take it into account that implementing fishing restrictions in this area could strain local economy, since they are already struggling with the decrease in income opportunities. Balancing the livelihoods of local residents, regional fisheries resources, and the protection of marine mammals poses a complex challenge. No matter how effective a method may be for the ecosystem, it cannot be considered “sustainable” if it imposes pressure on the local community. Therefore, it is crucial to incorporate perspectives from natural science, sociology, and the local community to address the multifaceted issues efficiently.

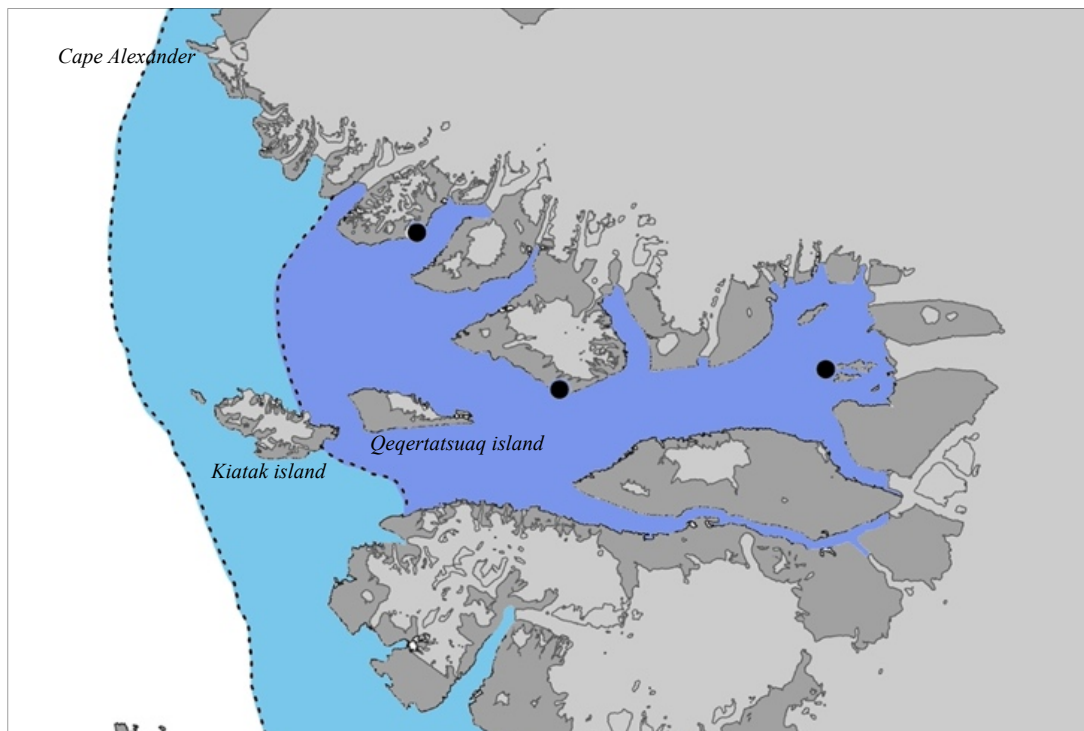


Fig. 6-1 Sea ice extent in Inglefield Bredning, northwest Greenland in the past and present. Light blue colored area represents the ice extent before 1990s, and blue colored area represent recent ice extent. Black dots line represents the ice edge. Even outside area of the ice edge, there are often ice foots along the coast line, and it is possible to travel via ice foots. Gray colored area represent the land, and the light grey showed the glacier covered area.

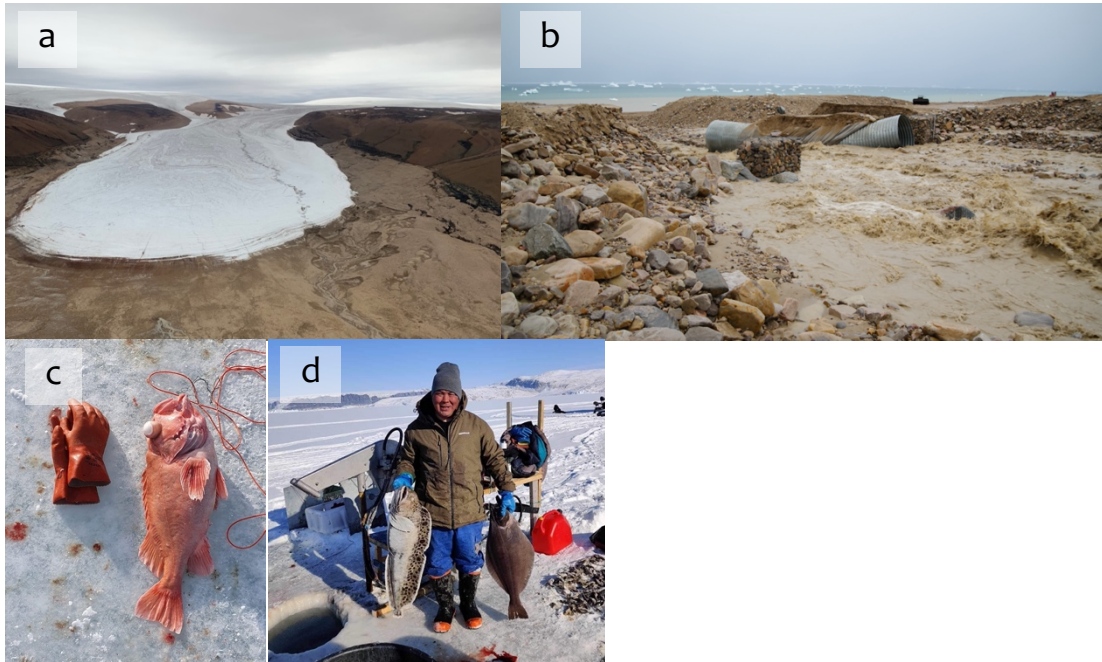


Fig. 6-2 Observed changes in the environment. (a) Land terminating glacier (Fan Glacier) which was terminated into the ocean before (Photo: M. Ogawa, August 2022). **(b)** Destroyed bridge in the village (Photo: R. Kusaka, August 2023). **(c)** A red fish caught by a local (Photo: K. Nielsen, May, 2024). **(d)** A wolffish (left side) caught during halibut fishing (Photo: K. Nuka, Feb, 2020).

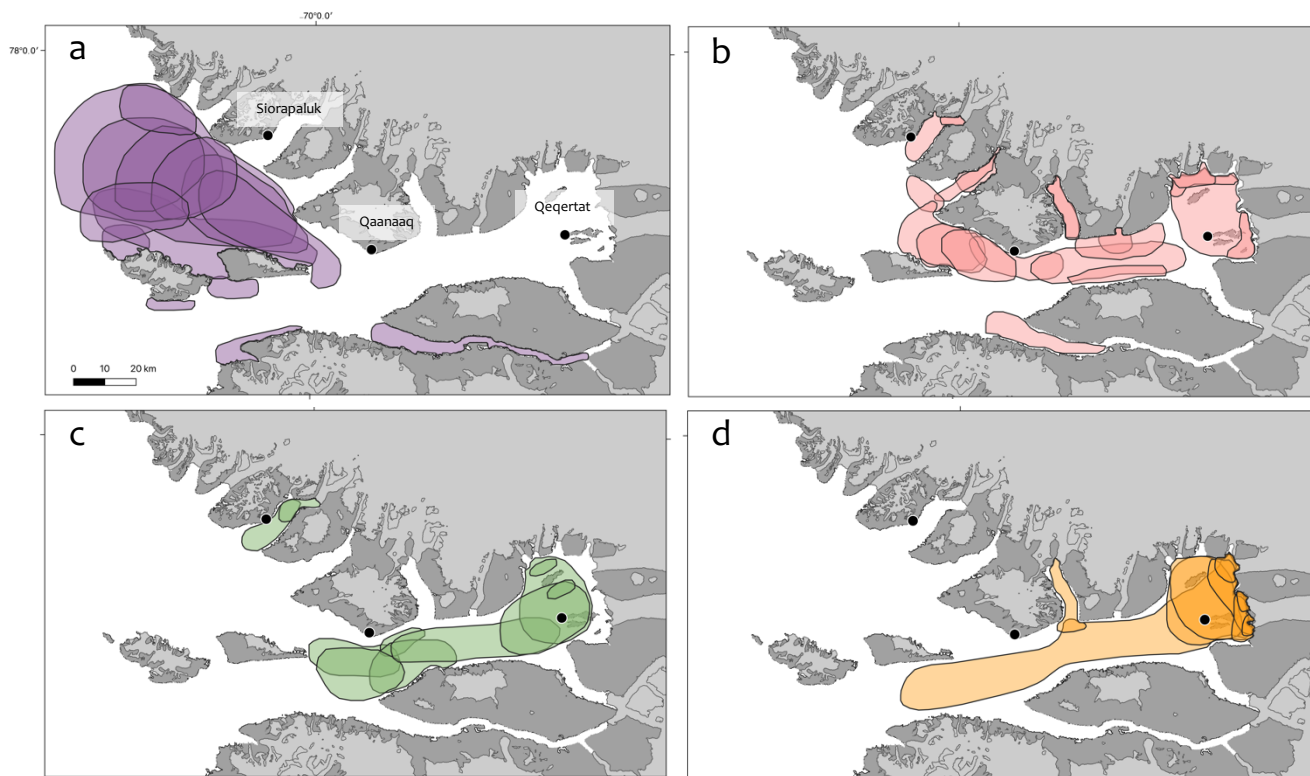


Fig. 6-3 Marine mammal hotspots in Inglefield Bredning based on the traditional ecological knowledge of villagers (a)Distribution of bearded seal, (b) ringed seal, (c) harp seal and (d) narwhal. The density of the color represents the degree of overlapping area.

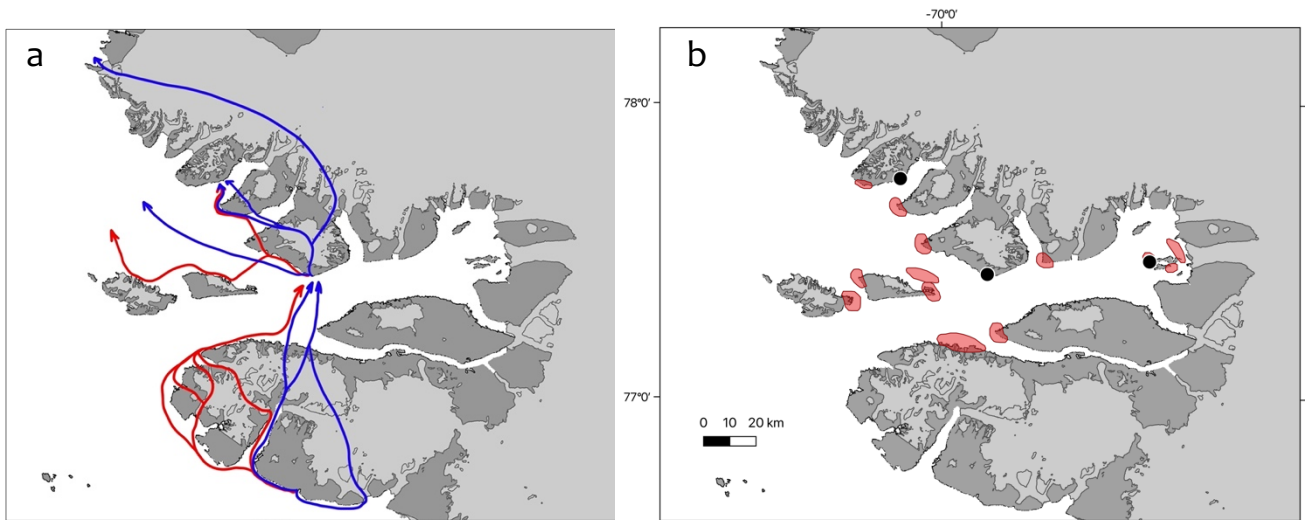


Fig. 6-4 The status of sea ice and the changes in dogsled routes. (a) The blue lines indicate the dogsledding routes that were used by villagers until around 2000 which are now dangerous and rarely used. The red lines indicated the route used recently instead of the traditional routes. **(b)** Red colored areas represent the dangerous spots mentioned by villagers.

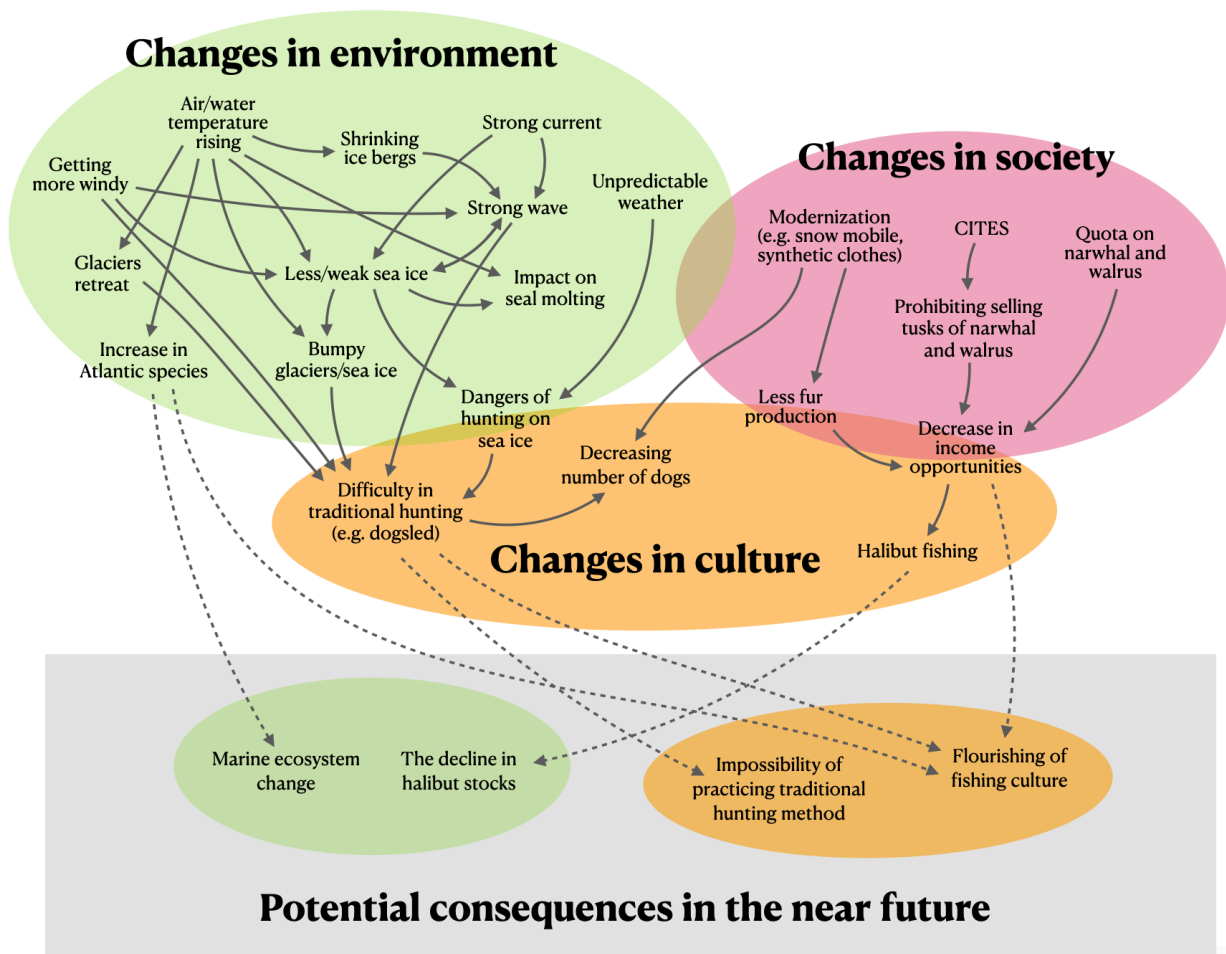


Fig. 6-5 Observed chain of impacts. We categorized the observed changes into three groups: environment, society, and culture. We then connected the interactions between these impacts with grey arrows, and linked the anticipated future impacts with dotted arrows.

Table 6-1. Overview of informants based on gender and age groups. Age ranged from 43 to 76 year old.

	Total	40 - 49	50 - 59	60 - 69	70 -
Male	17	4	9	3	1
Female	5	2	2	1	0

Table 6-2. Overview of the observed changes in environment and marine ecosystem in the northwest Greenland. Mentioned rate (%) shows the percentage of villagers (out of 22) who mentioned each topic during the interviews with a color code, grey (<50%), blue (50 – 75%), and red (> 75 %).

	Topic	Comments	Mentioned rate (%)
Environment	Sea ice, glacier	Decrease in thickness of sea ice	100
		Decrease in the extent of sea ice	100
		Earlier melting and delayed formation of sea ice	100
		Growing instability and fragility of sea ice	100
		Growing roughening of the surface of icebergs and sea ice	45
	Ocean conditions	Glacial retreat	70
		Icebergs are shrinking while their numbers are increasing	65
		Increase in the strength of ocean currents	55
		Increase in wave height	100
		Increase in rainfall	100
	Climate	Rising temperature	40
		Unpredictable whether	80
		Intensification of winds	30
		Changes in the moult of birds	100
Marine ecosystem	Fish	Increase in number of subarctic fish	40
		Decrease in sizes and numbers of Halibut	40
	Marine mammal	Decrease in the blubber thickness of marine mammals	35
		Changes in the seals' fur quality	35
		Changes in the moulting period of seal	40
		Decrease in the number of seals	80
		Increase in number of narwhal	75
		Increase in number of walrus	85
	Seabird	Changes in distribution and migration timing of walrus	20
		Changes in the breeding season of seabirds	100

CHAPTER 7

Conclusion and general discussion

The aim of this study was to examine the interconnected relationships between the environment, marine ecosystems, and Inuit in the northernmost Indigenous community in the world to contribute to predicting the impacts of climate change across the Arctic region in the future. In this region, environmental changes such as glacial retreat driven by climate change, as well as marine ecosystem change such as increase of southern species, were identified as threats to the interconnected relationships between the environment, ecosystem, and Inuit.

In Chapter 2 to 5, I conducted a detailed analysis of the relationships between marine mammals, the marine ecosystem, and the environment in this region using biological samples from marine mammals. This investigation is part of the first comprehensive marine ecosystem survey in this area, and our findings suggest that changes in the marine ecosystem are underway in this region. Specifically, redfish, which are typically found in southern waters, were detected in the stomach contents of seals for the first time, and the composition of zooplankton also showed indications of shifting toward a more southern-type assemblage. Furthermore, a key feature of this study is the integration of scientific research and sociological survey methods. By integrating the analysis of biological samples with interviews, the evidence for changes in the marine ecosystem was further strengthened. The stories of indigenous people's life collected in this study clearly showed that environmental and ecological changes are actually occurring in this region, which extends beyond data reported in scientific research. Although not have been detected from marine mammal stomachs, it was found that southern fish species such as capelin and Atlantic cod are also expanding into this region. It was also reported by local hunters during the interview that the population of the harp seal is also increasing, probably due to climate change. Since the niche comparison in this study showed the dietary niche of harp seal overlap with both ringed seal and narwhal, the continued increase in harp seal population may lead to competition among marine mammals in this region.

The contaminants levels observed in marine mammals in this study did not reach harmful levels. However, as southern fish species contain higher levels of pollutants, the ongoing changes in the marine ecosystem—specifically, the “borealization” in the ecosystem—raise concerns that this could lead to an increase in the concentration of pollutants in the tissues of marine mammals in the future.

The novel approach of spatial analysis of stomach contents employed in this study has provided various new insights into the foraging areas of marine mammals that were previously unattainable.

Specifically, it shed light on how sympatric species partition their foraging habitats, revealing where and what each species feeds on. The results highlighted the importance of glaciers as foraging areas for marine mammals, while interviews revealed that these glaciers are retreating at an acceleration rate. As long as glaciers terminate at the ocean, increased glacial melt is suggested to enhance marine productivity in this spot, providing more prey for marine mammals, as described in chapter 4. However, if glaciers retreat entirely onto land, these crucial foraging grounds for marine mammals will be deprived.

In my study, the traditional ecological knowledge of Inuit provided a unique opportunity to access the environment and ecological change, which require a long-term monitoring to obtain in scientific methods. It also suggested the importance of cooperation with local people for impactful research, and for effective and sustainable management – because they are the “specialist” with immense knowledge of local nature, which is not known by scientists.

In response to recent climate change, one woman stated, *“It is natural for the environment to change, and we have adapted our lives to these changes.”* While people in this region have long adapted to harsh environment which fluctuates in various temporal scales, our research indicates that the rapid acceleration of climate change in the Arctic poses unprecedented challenges to the Indigenous community. The currently occurring climate change and its impact on environments not only require the “adaption”, but could also lead to the “disappearance” of traditional culture. It highlights the urgent need to implement policies to enhance the region’s resilience to climate change.

Through the experience of three years of fieldwork in Greenland, working together with Inuit hunters, I came to realize that even if the changes in the connections between the environment, ecosystems, and people in the Arctic are inevitable in the face of accelerating climate change, what is now required of us as researchers – and the future we should strive for – is one where each can continue to coexist in harmony, even in changing forms, while maintaining ecological, social, and cultural well-being.

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