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Title	Studies on habitat use of ringed seals (<i>Pusa hispida</i>) in glacial fjords, northwestern Greenland [an abstract of entire text]
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Description	この博士論文全文の閲覧方法については、以下のサイトをご参照ください。 https://www.lib.hokudai.ac.jp/dissertations/copy-guides/
Degree Grantor	北海道大学
Degree Name	博士(環境科学)
Dissertation Number	乙第7218号
Issue Date	2025-03-25
Doc URL	https://hdl.handle.net/2115/95357
Type	doctoral thesis
File Information	SAKURAGi_Yuta_summary.pdf



学位論文内容の要約

博士（環境科学）

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学 位 論 文 題 名

Studies on habitat use of ringed seals (*Pusa hispida*)
in glacial fjords, northwestern Greenland

（グリーンランド北西部の氷河フィヨルドにおける
ワモンアザラシの生息地利用に関する研究）

Chapter 1. General Introduction

The Arctic environment is changing more rapidly than in other areas of the world, and 85% of tidewater glaciers have been retreated in the Northern Hemisphere (Kochtitzky and Copland 2022, Calvin et al. 2023). Climate change is altering abiotic and biotic factors across the globe, leading to widespread changes in species distribution and habitat use. Many species are having difficulty adapting the rapid environmental changes and will instead need to shift their distributions to track suitable environment (Parmesan and Yohe 2003, Root et al. 2003, Parmesan 2006). Glacial fjords and surrounding waters are important habitats for marine mammals because subglacial discharge from the glacier during the open-water period creates biologically productive areas (Lydersen et al. 2014). Marine mammals are top predators in Arctic marine ecosystems and an important resource for local people. Therefore, the impacts of climate change on marine mammals are likely to be even greater due to the interrelationship with ecosystems and society. In order to predict what effects will be felt in the future, it is necessary to understand the relative importance and interactions of abiotic and biotic factors influencing habitat use.

Ringed seals (*Pusa hispida*) play important roles in the ecosystem (Kovacs et al. 2011). With a circumpolar distribution and the most abundant Arctic pinniped, ringed seals are not only important consumers in Arctic food webs, but also they are the main prey for polar bears, and an important resource for humans in coastal communities (Laidre et al. 2008). They primarily inhabit coastal areas, including glacial fjords, where land-fast ice forms during winter. In the open-water period, ringed seals concentrate around tidewater glacier fronts, where abundant prey species are expected to be found. Ringed seals feed opportunistically on sympagic, pelagic and semi-demersal fish and invertebrates (Weslawski et al. 1994, Siegstad et al. 1998, Holst et al. 2001).

Recent retreat of tidewater glaciers will affect coastal marine ecosystems, ocean circulation, and the environment. Rapid glacier melting influences the oceanic environment and the distribution of prey species in fjords (Hamilton et al. 2017, Stempniewicz et al. 2021, Bertrand et al. 2021). When tidewater glaciers continue retreating, this will result in changes of water circulation and ecological function of glacial fjords. Therefore, assessing the impacts of climate change on these species requires understanding the relative importance and interactions of abiotic and biotic factors influencing habitat use.

Greenland is characterized by large area of ice sheet and many glaciers, which covered approximately 80% of the land area (Morlighem et al. 2017). Ice sheet and glacier mass loss in Greenland has greatly accelerated in the 21st century (Mouginot et al. 2019), causing changes in the marine environment and potentially affecting marine mammals. In addition, since local communities hunt and use marine mammals including ringed seals for their important resources, these changes effect on the life of them. To understand the impact of climate change on marine ecosystem in Greenland, the study of the relationship between the habitat use of ringed seals and the environment, including glaciers and oceanographic environments is necessary.

The objective of this study was to characterize abiotic and biotic factors influencing habitat use of ringed seals in glacial fjords, northwestern Greenland. Glacial fjords are usually closed off by large icebergs and sea ice throughout most of the year, it is difficult to conduct surveys from large research vessels inside the fjord system. Recent advances in survey and analytical methods allow us to obtain more detailed information of marine ecosystem, such as environmental DNA (eDNA) metabarcoding (Jensen et al. 2023, Schiøtt et al. 2023) and biologging methods (Boehme et al. 2009). By collaborating with local hunters and using recent advanced approaches, it is possible to investigate various aspects of marine ecosystems in glacial fjords.

Chapter 2. Abiotic and biotic habitat use characteristics of ringed seals in glacial fjords, northwestern Greenland during the open-water period

Species respond differently to changes in the environment that depend on complex relationship to their ecological attributes, such as abiotic tolerances, dispersal capacity, and biotic interactions (Ferrier and Guisan 2006, Algar et al. 2009, Wisz et al. 2013). Biotic interactions affect species' spatial patterns via several mechanisms, such as predation, competition, resource-consumer interactions. Prey species distribution is a primary biotic feature for habitat use of predators (Bluhm and Gradinger 2008), and this largely depend on the physical settings of the habitat of species (Walsh 2008). Co-existing species that have overlapping abiotic or biotic requirements can be in a competitive situation when resources are limiting (Macarthur and Levins 1967). In the Arctic ecosystem, where functional redundancy is low, shifts in species distribution are

likely to have significant impacts. Therefore, understanding the environmental factors that interact with these species is important for predicting the effects of climate change.

In northwestern Greenland, ringed seals and bearded seals (*Erignathus barbatus*) are distributed sympatrically throughout the year (Teilmann and Kapel 1998, Heide-Jørgensen et al. 2013, Grønnow 2016). Only in the open-water period, harp seals (*Pagophilus groenlandicus*) migrate from southward to this area (Kapel 1996, 2000). Thus, glacial melt is active during the open-water period, and many other species of seals are distributed in the habitat of the ringed seal. However, information on the distribution of ringed seals, which seal species occur, and its interspecific relationship with these other sympatric seal species are unknown in this area. For sympatric seal species to co-exist, their distribution or their food sources need to be separated. Therefore, in this study, visual surveys and SI analysis were conducted during the open-water period in the Thule area to investigate abiotic and biotic factors influencing the habitat use of ringed seals and interspecific relationship with sympatric seal species. Visual surveys provide snapshot data on abiotic features related to distribution, including distance to tidewater glacier fronts. SI analysis provides a dietary record integrated over time and was used to assess the dietary niche overlap of sympatric species.

Field surveys were conducted in July and August 2019, 2022 and 2023 in Inglefield Bredning Fjord, Bowdoin Fjord and Murchison Sound in the northwestern Greenland. Visual surveys were conducted from the small boat and record seal species and location. From the visual survey, three species of seals were observed: 12 bearded seals, 73 harp seals, 54 ringed seals and 39 unidentified seals. Ringed and harp seals were found around tidewater glacier fronts, whereas bearded seals were found farther from glaciers, in relatively shallower waters.

All seal samples for SI analysis were collected by inughuit hunters between July to August, 2022, and 2023. All muscle and liver tissues of seals were subsampled (approximately 5–10 g) and used for stable isotope analysis, as these tissues have different turnover rates, reflecting assimilated diet over different periods of time. Muscle has a slower turnover rate than liver, with an isotopic half-life in the range of ~100–130 days (Vander Zanden et al. 2015). On the other hand, liver has a faster turnover rate than muscle, representing the average diet over approximately 1 month (Tieszen et al. 1983, Vander Zanden et al. 2015). Therefore, muscle represents the averaged diet of seals both before and during the open-water period, while liver represents the averaged diet when all seal species are sympatric in the Thule area. As a result, SI indicated that ringed and harp seals mainly fed on pelagic species, whereas bearded seals mainly fed on benthic species. The SI niche size of ringed seals was greater than harp seals, and overlap in SI niche of ringed and harp seals was higher than that of bearded seals. SI supported that physical habitat features of each species of seals

were associated with foraging. Ringed and harp seals used closer to tidewater glacier front areas to feed on pelagic prey species, whereas bearded seals used shallower waters to feed on benthic prey species.

Chapter 3. Spatial distribution of fish fauna revealed by the environmental DNA metabarcoding method in glacial fjords, northwestern Greenland

Arctic seal species use glacial fjords and surrounding waters in the Arctic which contain tidewater glaciers sustain high marine biomass productivity (Meire et al. 2017, Hopwood et al. 2020, Hoshiba et al. 2024). In the Thule area, local people also use the glacial fjord for hunting and fishing. Despite the importance of the glacial fjord for marine ecosystem and local communities, and the rapid changes currently induced by climate change (Sugiyama et al. 2021), few studies have investigated marine environmental and ecological conditions inside the glacial fjord. Because the glacial fjord is closed off by large icebergs and sea ice throughout most of the year, surveys by large research vessel (e.g. trawl surveys) are impossible inside the glacial fjords. Therefore, information about fish fauna and distribution in glacial fjords is limited. Environmental DNA (eDNA) analysis of water samples collected inside the glacial fjord represents an attractive alternative method (Lacoursière-Roussel et al. 2018, Leduc et al. 2019, Jensen et al. 2023, Schiøtt et al. 2023). The objective of the present study was to investigate the spatial distribution of fish fauna in the glacial fjord of the Thule area by using eDNA metabarcoding.

Water samples were collected from a local hunter's boat during July and August in 2022. A total of 10 stations were selected in the Inglefield Bredning and Bowdoin fjord. Seawater samples were collected using Niskin sampling bottles at depths of 10 m, 150 m, and just above the seafloor, with a volume of 2 L for each sample. All water filtration procedures were performed in the house at Qaanaaq. To minimize the risk of contamination, all equipment used for water collection and filtration were decontaminated by soaking in a 2% bleach solution. DNA was extracted from the Sterivex filter units using a DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) in a clean laboratory. Extracted eDNA was amplified and sequenced using MiFish, a universal primer for fish. The obtained sequences were processed using Claident, and fish species were determined by QCaution. As a result, eDNA detected 21 taxa of fish including 9 families, 5 genus, and 4 species. Prey fish species of ringed seals, such as polar cod, sculpins (Cottidae), and snailfish (Liparis) were found. Polar cod were widely distributed throughout the glacial fjord, with relatively higher abundance closer to tidewater glaciers and at depths below 150 m. Sculpins and snailfish were also found in areas closer to tidewater glaciers. These results suggest that tidewater glaciers created biologically productive areas where the prey species of ringed seals were concentrated.

Chapter 4. Seasonal habitat use of ringed seals in the Thule area, northwestern Greenland

The distribution of abiotic and biotic factors for animal habitat use is seasonally dynamic and can change in space and time (Fretwell 1972, Born et al. 2004, Womble et al. 2021, Vacquié-Garcia et al. 2021). The environment of the Thule area is also change seasonally. In the early July, the open-water period began with the breakup of the land-fast ice. Sea ice formation began in October, and the ice-covered period began with land-fast ice formation in November. Subglacial glacial discharge from tidewater glacier usually active during the open-water period (Everett et al. 2018). Understanding how animals interact with their habitat use in response to seasonally changing physical environmental factors is essential for predicting how populations respond to rapidly changing polar ecosystems. Therefore, in this chapter, seasonal habitat use of ringed seals in relation to the environment was investigated by deploying satellite telemetry tags on ringed seals to assess the habitat use of ringed seals in response to the seasonally changing environment in glacial fjords.

Ringed seals were captured in mid-August 2021 at the inside of Inglefield Bredning Fjord, northwestern Greenland. Four seals (three adult females and one subadult male) were tagged with Conductivity-Temperature-Depth Satellite-Relay Data Loggers (CTD-SRDLs, Sea Mammal Research Unit, St Andrews, Scotland). CTD-SRDLs record oceanographic data and the diving behavior of seals, and then transmit the data via Argos satellite system (Boehme et al. 2009, CLS 2016). Each telemetry tags transmitted information on the seals' locations, activity patterns, diving behavior, percentage of time hauled out. Additionally, CTD-SRDLs were configured to collect temperature, salinity and depth (pressure) on the ascending portion of selected dives, and to transmit data from the deepest dive within each 6-hour period. To assess temporal variations in behavior, dive and activity variables were analyzed using a generalized additive model.

Four ringed seals transmitted data for 137 ± 68 days and traveled 1328 ± 858 km. All four seals transmitted data during the open-water period, and two of the seals transmitted data until the ice-covered period. All seals spent most of their time in front of tidewater glaciers during the open-water period. Two seals that continued to transmit after beginning of the ice cover period moved out of glacial fjords due to the formation of land-fast ice and stayed in the shallower water depth area, where sea ice was relatively thin and sparse during the ice-covered period. Additionally, the oceanographic data indicated that ringed seals mainly dove to depths associated with the habitat of polar cod. These findings suggest a strong association between ringed seals and tidewater glaciers during the open-water period, likely linked to the prey species availability.

Chapter 5. General Discussion

The overall objective of my research was to characterize abiotic and biotic factors influencing habitat use of ringed seals in the Thule area, northwestern Greenland. In conclusion, the habitat use of ringed seals was closely associated with tidewater glacier fronts and prey species distribution. The present study showed that polar cod is important species for habitat use of ringed seals during summer in the Thule area. Polar cod is the most abundant forage fish in the Arctic seas. One of the expected impacts of changing environmental variables on the polar cod population in Baffin Bay is the increase in freshwater input. This is related to the melting of the tidewater glaciers. Recent faster retreating of tidewater glaciers in Greenland will lead to increase meltwater discharge. Additionally, increased meltwater discharge will change stratification and mixed-layer depth, which could affect primary production (Oliver et al. 2018).

These abiotic and biotic resources were impacted by climate changes, with shifts in prey distribution under changing climate conditions potentially leading to increased interspecific competition. Species redistribution leads to changes in spatial predator-prey overlap (Carroll et al. 2024). In the situation where predator and prey species occur in the similar environmental niches, spatial overlap is maintained when environmental changes occur. Spatial predator-prey overlap can increase when species undergo different rates or directions of redistribution such that the prey occupies more of the predator's range, whereas can decrease when predators and prey undergo different rates or directions of redistribution such that the prey occupies less of the predator's range. The recent retreat of tidewater glaciers and the northward movement of fish distributions due to climate change, including polar cod, are likely to change the foraging habitat and alter the distribution of ringed seals (Geoffroy et al. 2023). In addition, increasing sea water temperatures affect physiology of fish and change interspecific competition (Seth et al. 2013) and suggest that climate change may alter the fish species composition and distribution in the Arctic.

Continuous monitoring of marine environments and ecosystems is important for detecting changes in them. In particular, glacial fjords are ideal monitoring sites for climate change because these areas are highly sensitive. In the future, if the quantitative interactions between abiotic and biotic factors and ringed seals are revealed, this could not only facilitate the development of SDMs but also contribute to climate change monitoring using ringed seals. Continuous monitoring is essential for detection changes in abiotic and biotic features induced by climate change, and eDNA metabarcoding and biologging were highlighted as valuable tools for monitoring marine environment and ecosystems inside glacial fjords. The present study provides fundamental insights into the habitat use of ringed seals in glacial fjords, and offers essential baseline data for predicting the impacts of future climate change on marine ecosystems.