



UiT The Arctic University of Norway

Department of Arctic and Marine Biology

Changes in environment cause dietary shifts in the Svalbard Arctic fox

A stable isotope study

Daniel J. Krogh

Master's thesis in Biology BIO-3950, February 2022

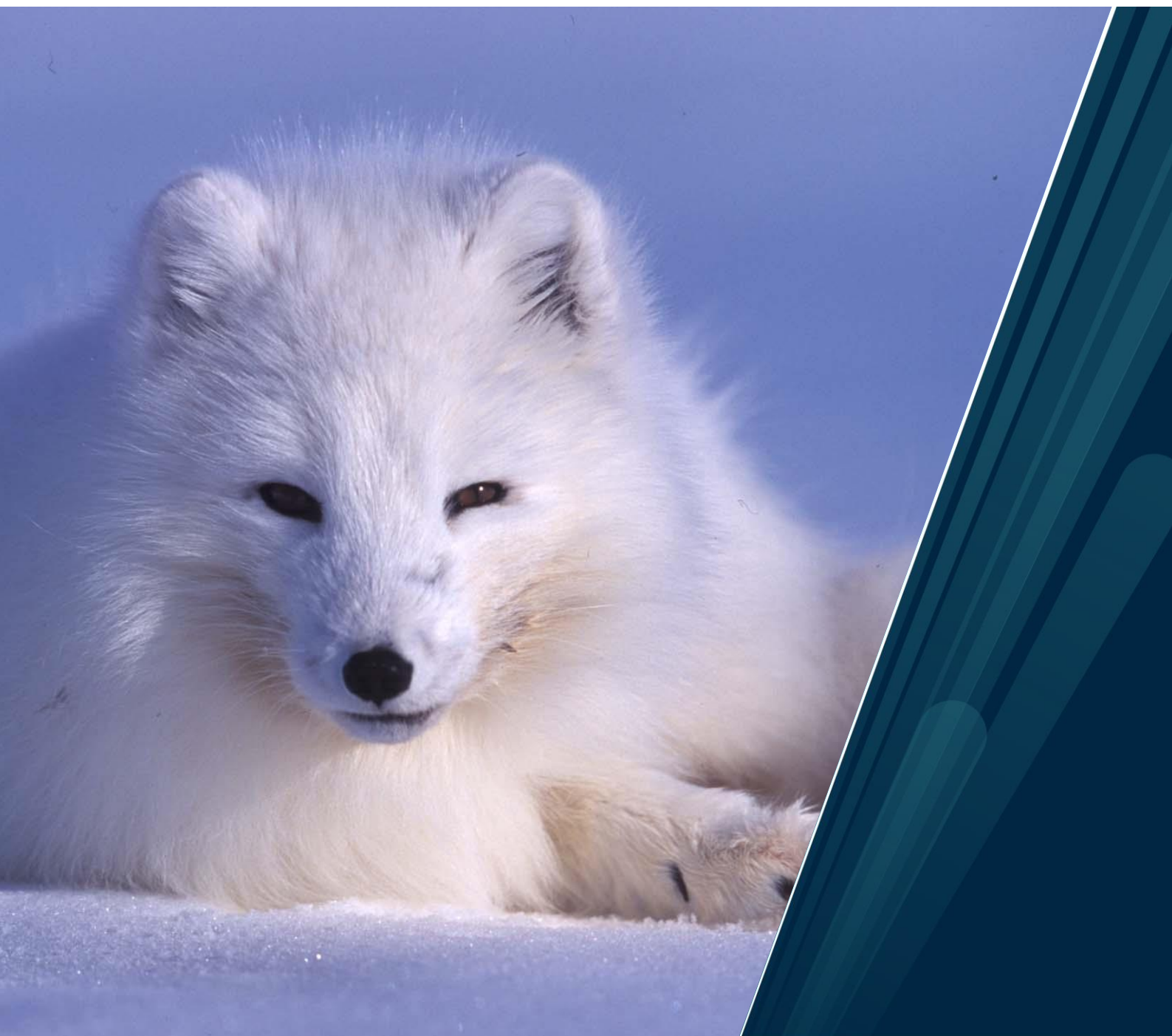


Table of Contents

1	Introduction	1
2	Methods	5
2.1	Study area	5
2.2	Sample collection	7
2.3	Stable isotope analysis	7
2.4	Environmental variables	9
2.5	Data analysis	10
2.5.1	Calculation of distance to coast	11
2.5.2	Prey species isotope plots and discrimination	12
2.5.3	Spatial and temporal trends	12
2.5.4	Determining effects of environmental drivers	13
3	Results	14
3.1	Arctic fox dietary range	14
3.2	Spatial and temporal patterns	15
3.3	Environmental drivers	18
3.3.1	Models based on muscle samples	18
3.3.2	Models based on fur samples	26
4	Discussion	30
4.1	Arctic fox dietary range	30
4.2	Spatial and temporal trends	31
4.3	Impact of environmental drivers and coastal distance	33
4.4	Arctic fox diet in circumpolar coastal Arctic ecosystems	35
4.5	Ecological implications	36
4.6	Concluding remarks	37
	Acknowledgements	38
	References	38

Appendix	43
----------------	----

List of Tables

Table 1 - Estimates of coefficients of untransformed muscle isotope models.....	20
Table 2 - Estimates of coefficients of detrended muscle isotope models.....	21
Table 3 - Estimates of coefficients of untransformed fur isotope models.....	27
Table 4 - Estimates of coefficients of detrended fur isotope models.....	27
Table A - Overview of number of Arctic fox samples, for full dataset.....	43
Table B - Overview of number of Arctic fox samples, for reduced dataset.....	44
Table C - List of prey species and their mean isotope values.....	45
Table D - List of untransformed muscle models.....	46
Table E - List of detrended muscle models.....	47
Table F - List of untransformed muscle models.....	47
Table G - List of detrended muscle models.....	48

List of Figures

Figure 1- Map of Svalbard with Arctic fox trapping locations	6
Figure 2 - Time series of the environmental variables.....	10
Figure 3 - All Arctic fox isotope values plotted after correcting for discrimination.	15
Figure 4 - Boxplots showing isotope value distributions for each of the four regions.	16
Figure 5 - Isotope temporal trend of Arctic fox muscle for the regions.....	17
Figure 6 - Isotope temporal trend of Arctic fox fur for the regions.	18
Figure 7 - Effect plots of the coefficients of the chosen untransformed muscle model.....	23
Figure 8 - Effect plots of the coefficients of the chosen detrended muscle model.	25
Figure 9 – Effect plots of the coefficients of the chosen untransformed fur model.....	28
Figure 10 - Effect plots of the coefficients of the chosen detrended fur model.....	29

Abstract

In this thesis, shift in diet of Arctic foxes on Svalbard over a long time frame was analyzed. The Svalbard Arctic fox is a generalist who links the terrestrial and marine ecosystems. The objectives were 1) investigate whether there are spatial and temporal trends in Arctic fox diet on Svalbard, 2) determine how important the changes in the environmental variables are for dietary shifts of the Arctic fox in different seasons and 3) determine whether other parameters like the distance to the coast and age class have any impact on the diet as inferred from stable isotopes. Stable isotope values of carbon and nitrogen from Arctic fox muscle (representing winter diet) and fur (representing autumn diet) samples over the winter seasons 1997/1998 to 2019/2020 were used to assess dietary shifts. Arctic fox isotope values fitted mainly linearly between marine and resident terrestrial prey (reindeer and ptarmigan). Both negative temporal trends and differences between regions were found, signifying a shift towards more use of terrestrial resources in both winter and autumn. This was also found when analyzing environmental effects, where the number of geese and year to year fluctuations in reindeer carcass number were significant in shifting diet towards more use of terrestrial resources in winter. The distance to the coast also showed significant difference in the diet between coastal and inland Arctic foxes. The value of long time data series was shown in this thesis as these gave significant results, while short time data series usually did not. Continued monitoring and sampling, as well as including other parameters like seabird population estimates and the fox's preference of marine invertebrates are of interest to improve models and give more accurate estimates.

Front page photo: Svalbard Arctic fox in its winter coat (Photo: Jason Roberts).

1 Introduction

An ecosystem is made up by a community of organisms and the environment in which they live (Chapin III et al. 2011). The organisms interact with each other in multiple ways and these direct and indirect interactions can shape ecosystem dynamics and structure (Schmidt et al. 2017). Environmental change can regulate population dynamics and interactions within a system, where impacts can spread across trophic levels through the interaction links (Schmidt et al. 2012, Schmidt et al. 2017). Resilience to these changes can partly depend on the degree of specialization, where a system with many generalists is more interlinked and complex (Schmidt et al. 2017). Complex food webs are more stable than simple food webs, particularly when complexity results of many weak interactions (Rooney & McCann 2012). Food webs often have links to neighboring ecosystems. Subsidies are allochthonous resources (coming from another ecosystem) that can also affect the stability and dynamics of the ecosystem and its consumer populations (Giroux et al. 2012).

The changing climate has generally resulted in warming of the atmosphere, ocean and land around the globe (IPCC 2021). The Arctic is especially experiencing rapid changes, as it has the largest mean temperature increases (Descamps et al. 2017, IPCC 2021). Among predicted changes in the Arctic include increase in precipitation and reduction in sea ice cover (IPCC 2021). The Arctic is attractive for many migratory species that travel to the region in the productive summers for feeding and breeding. As the Arctic is becoming more productive with the continuing warming trend, it will also be impacted by increased subsidies in the form of growing populations of migratory species (e.g., geese population on Svalbard, Descamps et al. 2017).

Different environmental factors might affect an ecosystem in different ways. So how do changes in different factors of environment influence the Arctic ecosystem structure, and which are more impactful and important in driving ecosystem change? The resilience of different Arctic species to the changing environment might depend on their position and role in the food web. If a species is more specialized it might be less resilient to changes as it does not necessarily have alternative resources it can depend on (Schmidt et al. 2012). Generalists are thought to be more resilient to environmental changes, as they are more flexible in their use of resources and habitat (Schmidt et al. 2012, Schmidt et al. 2017, Nater et al. 2021). If predators switch to alternative resources of the ecosystem, then this will lead to a changing impact on the species they prey on. This means that environmental change can alter predator-

prey dynamics. Climate change is also likely to affect the links between neighboring ecosystems resulting for instance from predators that use resources from different ecosystems.

Svalbard is a good location for ecological and environmental change studies, where the link between the marine and terrestrial ecosystems is especially important. The Svalbard ecosystem is simpler than other high Arctic systems (Hansen et al. 2013), because of the presence of only a few residential prey species. The simplicity comes especially from the lack of small rodents (except for a small invasive local population of sibling vole), who are known to influence Arctic predator population dynamics, like how lemmings influence the Arctic fox (*Vulpes lagopus*) population dynamics (Gilg et al. 2006). The simpler food web makes it easier to assess which biotic and abiotic factors affect different components of the ecosystem. Svalbard is interesting in that it experiences dramatic changes in the environment. The Barents Sea and Svalbard experiences the fastest temperature increases and sea ice loss in the Arctic (Descamps et al. 2017). In the last couple of decades there has been a much greater reduction in ice cover than before, with many areas experiencing little to no ice for at least the early winter months (Dahlke et al. 2020, Nater et al. 2021). On Svalbard there is also increase in frequency of rain on snow (ROS) events, which makes the ground vegetation (all vegetation on Svalbard is low growing) less available or completely unavailable for herbivores by the crusting of the snow or icing of the ground (Hansen et al. 2013, Hansen et al. 2014, Descamps et al. 2017). This leads to increased mortality of herbivores in winter, which results in an increase in terrestrial resources (carcasses) for predators. These extreme weather events can synchronize population dynamics (bottom-up climate forcing) of the resident terrestrial herbivores (Hansen et al. 2013, Descamps et al. 2017). The drastic increase in the populations of geese on Svalbard is another increase in terrestrial resources (Descamps et al. 2017, Nater et al. 2021).

The Arctic fox is a good candidate species for studying environmental impacts on coastal predators and the species they are linked to in the food web. The Arctic fox is an Arctic top predator that is known as an opportunistic specialist and scavenger (Elmhagen et al. 2000, Ehrich et al. 2015, Eide et al. 2012). The Arctic fox is generally a lemming specialist in inland areas or where lemmings are abundant, and a generalist in coastal areas with no or low abundance of lemmings (Ehrich et al. 2015, Eide et al. 2012, Fuglei & Ims 2008). Its range expands throughout the circumpolar Arctic and is common in most regions. The coastal variants link terrestrial and marine ecosystems through predation and scavenging, and

depending on prey availabilities, the foxes change prey preferences as a functional response (Eide et al. 2005).

On Svalbard, important food resources of the Arctic fox are carcasses of Svalbard reindeer (*Rangifer tarandus platyrhynchus*), and migratory Arctic breeding geese and seabirds (Eide et al. 2005, Eide et al. 2012, Jepsen et al. 2002). The fox can kill reindeer calves, but carrion is the main resource (Jepsen et al. 2002). They are able to kill adult geese but prefer eggs and chicks (Eide et al. 2005). The migrating preys (i.e., geese and seabirds) are temporally and spatially predictable, and by the availability of these preys, resource areas on Svalbard can be divided into three. These are poor inland areas with only reindeer, rich inland areas with reindeer carcasses in winter and geese available in summer, and coastal areas with seabirds, geese and reindeer carcasses (Eide et al. 2005, Eide et al. 2004, Eide et al. 2012, Jepsen et al. 2002). The Svalbard Arctic fox is quite mobile (Eide et al. 2012, Ehrich et al. 2011a), so it is expected that the foxes are not restricted to one territory or habitat. In the harsh polar winter, the few resident prey resources are important for survival, which for foxes are reindeer carrion and Svalbard rock ptarmigan (*Lagopus muta hyperborea*). The foxes can also venture out on the sea ice, maybe following polar bears (*Ursus maritimus*) to scavenge for seal carcasses, and even kill newborn seal pups in spring (Roth 2002, Roth 2003). The foxes are also known to scatter hoard, where they cache food for storage that they can find later (Frafjord 1993, Samelius et al. 2007, Sklepkovych & Montevecchi 1996), which is also important for winter survival. Rapid environmental change has resulted in increase of terrestrial prey resources on Svalbard, while the access to marine resources may have decreased because of the decline in sea ice extent (Nater et al. 2021). The observed stability of population size of the Arctic fox on Svalbard, despite the importance of the environment and available resources, might be due to the ability of the foxes to alternate between the different types of resources (Nater et al. 2021).

Analyzing stable isotope ratios is a very good way to study dietary shifts in coastal species, since marine and terrestrial prey isotopic values are easily distinguished (Ehrich et al. 2015, Killengreen et al. 2011). Unlike other methods used to study diet that shows snap shots of the diet (like stomach content and scat analysis), the isotope values represent the average use of resources over a certain time period. Through discrimination, different isotopes have varying degrees of being assimilated into tissues (Ben-David & Flaherty 2012), which results in specific ratios of heavy to light isotopes. The saying “you are what you eat”, which in the context of stable isotopes means that the isotopic build is dependent on the isotopic ratios of

the food sources. This results in the predators' isotope values to lie between the preys' isotope values that the diet consists of, after correcting for discrimination (see Lecomte et al. 2011). There will be individual and metapopulation differences in isotope ratios of a species because of differences in consumption and habitat, so one can get a large variety of isotope values within a species. Different species using overlapping niches and feeding on the same type of resources will have overlapping isotope values, making it difficult to distinguish them, which is a problem when analyzing preferences of isotopically alike prey (Ehrich et al. 2015, Killengreen et al. 2011). At a population level, isotope analysis can reveal prey preferences and temporal trends in dietary shifts by looking at how isotope values align with functional resource groups. This can give further inference about changing environmental impacts on different aspects of an ecosystem or food web.

Svalbard has experienced drastic decrease in sea ice extent, and drastic increase in number of migrating geese due to the changing climate (Descamps et al. 2017). The increase of ROS frequency might result in changed availabilities in number of reindeer carcasses over time. Reindeer carcasses are also known to be important winter food for the Svalbard Arctic fox, as between year abundance fluctuations are known to affect fox dynamics (Hansen et al. 2013, Eide et al. 2012, Descamps et al. 2017). Sea ice extent regulates the access to marine food resources in winter and spring, while geese and reindeer carcass numbers represent terrestrial food resources that are important for the Arctic fox. These environmental variables have been shown to impact vital rates of the Svalbard Arctic fox, caused by the transitioning towards higher terrestrial resource availability and lower marine resource availability, though population size remains stable (Nater et al. 2021). A long time series of these resources were used in this thesis, as well as isotopic values of muscle and fur from Arctic foxes on Svalbard covering the period from winter 1997/1998 to 2019/2020. The objectives for this thesis were 1) investigate whether there are spatial and temporal trends in Arctic fox diet on Svalbard, 2) determine how important the changes in the environmental variables are for dietary shifts of the Arctic fox in different seasons and 3) determine whether other parameters like the distance to the coast and age class have any impact on the diet as inferred from stable isotopes. The distance to the coast is included as it may provide information about the degree of fox territoriality.

2 Methods

2.1 Study area

Svalbard is a High Arctic archipelago located in the north-western Barents Sea between 74-81°N and 10-30°E (Jónsdóttir 2005). The archipelago has a land area of about 60000km², with 60% of it glaciated (Jónsdóttir 2005). The rest of the land area can be divided into 3 Arctic bioclimatic subzones, and these are the Arctic polar desert, northern Arctic tundra zone and middle Arctic tundra zone (Jónsdóttir 2005). Svalbard has among the simplest terrestrial food webs (Hansen et al. 2013), with the abundant Svalbard Arctic fox as a generalist apex predator and scavenger found across the archipelago. The main prey of the Svalbard Arctic fox are the Svalbard reindeer and the migratory geese and seabirds (Eide et al. 2005, Eide et al. 2012, Jepsen et al. 2002), with reindeer and food caches available in winter. Svalbard experiences the fastest temperature increases and sea ice loss in the Arctic (Descamps et al. 2017), with the western parts of Spitsbergen having experienced larger changes due to the warmer water currents from the Atlantic (Dahlke et al. 2020). Northern and eastern Svalbard (regions in more contact with colder Arctic oceans) are colder with larger sea ice cover, but these regions are thought to eventually reach similar conditions as the west with the continued warming (Dahlke et al. 2020).

Arctic foxes are harvested annually for their fur by local trappers on Spitsbergen, the main island of Svalbard. The trapping was done across many locations on Spitsbergen as shown in figure 1, from along the coastal shores and fjords to the valleys stretching and branching further inland. Foxes were trapped in the northern and middle Arctic bioclimatic zones. The trapping locations were grouped into four regions on Spitsbergen (Nordenskiöld Land (including both local trappers and one trapping station), Kapp Wijk (trapping station), North-West (including both local trappers and one trapping station) and Wijdefjorden (including two trapping stations), see figure 1). Only samples from Nordenskiöld Land were used in the model analysis. The trapping season lasts from 1. November to 15. March. The annual recreational trappings are performed mainly around Nordenskiöld Land by local trappers (including an area south of Ny-Ålesund), while trappers living in remote trapping stations are more spread across Spitsbergen (in total, 5 such stations on Spitsbergen are Van Mijenfjorden, Kapp Wijk, Farmhamna, Austfjordnes and Mushamna, where not all stations are inhabited every trapping season, see figure 1).

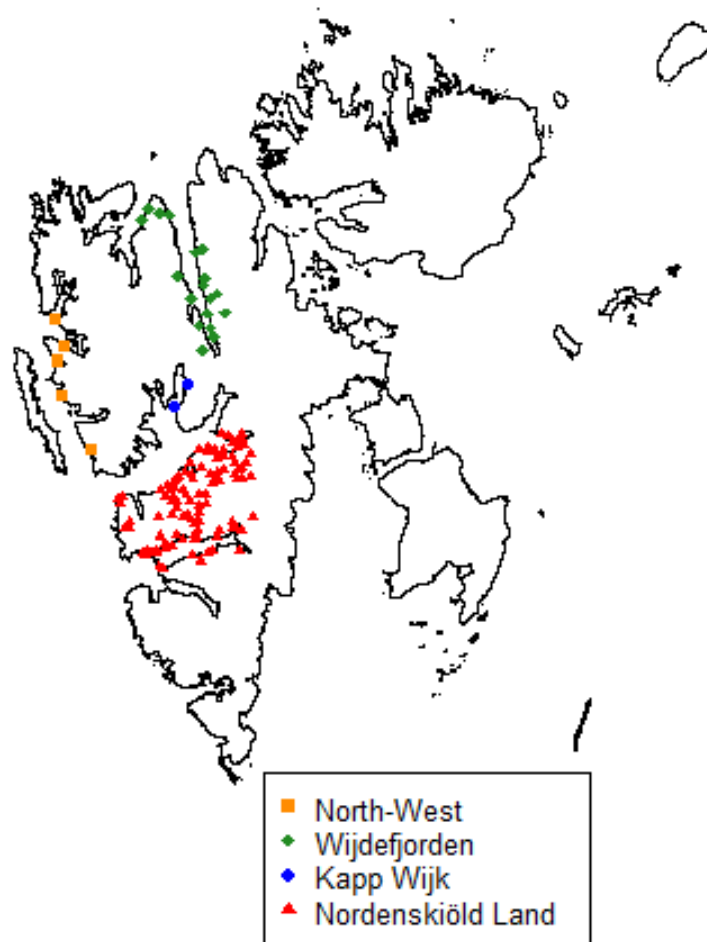
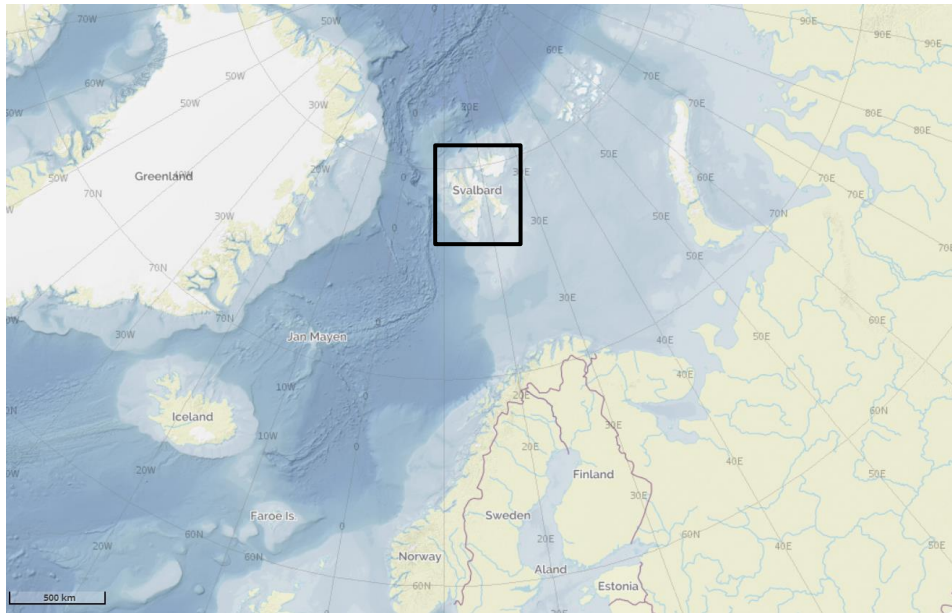


Figure 1- Map on top is showing the location of the Svalbard archipelago in the Barents Sea (from <https://geoportal.arctic-sdi.org>). Map on bottom show Svalbard with trapping locations of all the Arctic foxes from where samples originate. Trapping locations were grouped into four different regions on Spitsbergen (Nordenskiöld Land in red triangles (including both local trappers and one trapping station), Kapp Wijk in blue circles (trapping station), North-West in yellow squares (including both local trappers and one trapping station) and Wijdefjorden in green diamonds (including two trapping stations)). Only samples form Nordenskiöld Land were used in the model analysis.

2.2 Sample collection

The Arctic fox trapping on Svalbard is organized by the Governor of Svalbard (<https://www.sysselmesteren.no/en/hunting-trapping-and-fishing/fox-hunting/>), and since the season 1997/1998 hunters have reported all foxes trapped with dates and trapping location. Carcasses of the foxes are collected from the trappers by the Norwegian Polar Institute and kept frozen at -20°C for further autopsy and analysis. Muscle and fur samples used for stable isotope analysis were collected during autopsy. Muscle samples were available from the trapping season 1997/1998 (start of fox hunt reporting) to 2019/2020, with the seasons 2000/2001 and 2005/2006 not available. Fur samples were available from 2006/2007 to 2011/2012, as well as 2019/2020. The overview of number of muscle and fur samples per trapping season for each region is given in table A in the appendix.

From the collected Arctic foxes, the age was determined based on counts of tooth cementum annuli according to Grue and Jensen 1976 and Bradley et al. 1981 (done by the Norwegian Institute of Nature Research, Trondheim, Norway). The estimated ages were used to assign each fox one of two age classes. One year old Arctic foxes were considered juveniles and the older were classified as adults.

Samples of major prey species have also been collected (see table C in the appendix). Geese and most seabird samples were collected from the North-West part of Spitsbergen, while reindeer, ptarmigan and seals were sampled from the Nordenskiöld Land region. Most samples were collected in 2007 and 2008 (Most samples are from Ehrich et al. 2015).

2.3 Stable isotope analysis

Sample preparations for stable isotope analysis were done according to the protocol from SINLAB (<https://www.isotopeecology.com/collection-prep>). Muscle samples were first dried in a drying closet for two days at 60°C, then ground into powder using a mixer mill. Fur samples were cleaned in distilled water by using a sonicator, then dried, and then cleaned by using 2:1 chloroform: methanol mixture to rinse of fat. Finally, the samples were cut into fine small pieces. Between 1 mg and 1.2 mg of samples were weighed into small tin cups. The tin cups with the samples were packed into small balls and put in each of their own well in a tray. Samples were sent to SINLAB in New Brunswick, Canada, where carbon and nitrogen isotope ratios were determined with a Finnigan Delta Plus Mass spectrometer. Muscle and fur

samples of 2019/2020 and muscle samples of 2004/2005 had to be prepared for stable isotope analysis for this thesis, while isotope analysis for the other years had been done earlier and data were available. Isotope values of the Arctic fox samples reflect the diet 1-2 months before the kill (which results in data ranging from September-February) for muscle samples and the diet during the last molt (here autumn) for fur samples (Killengreen et al. 2011, Newsome et al. 2012).

The isotope ratios are given as isotope values denoted as δX , where X is an element in one isotopic form. These values are calculated by the formula (Ben-David & Flaherty 2012):

$$\text{Eq 1: } \delta X = \frac{R(\text{sample}) - R(\text{std})}{R(\text{std})} * 1000$$

In the formula, $R(\text{sample})-R(\text{std})$ is the difference of the heavy to light isotope ratio between the measured value of the sample and a standard for the element. Dividing this by the standard gives the relative difference of sample's isotopic value to the standard. The isotope value is given in permille (‰). In this thesis, $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) are used, and their standards are the international standards, Vienna Peedee Belemnite for carbon and atmospheric nitrogen for nitrogen.

Since lipids are more depleted in the amount of $\delta^{13}\text{C}$ compared to protein, correction for fat content must be done for isotope values. This can be done arithmetically by normalizing with a model using the carbon to nitrogen ratio as a proxy for fat content of the sample (Ehrich et al. 2011b). Fat correction for muscle samples was done according to Ehrich et al. 2011b, where the non-linear equation 3 from the article was used. The formula is:

$$\text{Eq 2: } \Delta\delta^{13}\text{C} = \text{beta0} + \text{beta1} * \ln\left(\frac{\text{C}}{\text{N}}\right)$$

$\Delta\delta^{13}\text{C}$ is the difference in $\delta^{13}\text{C}$ between $\delta^{13}\text{C}$ depleted samples and what would be non-depleted (or pure protein/no fat) samples. C/N is the ratio of carbon to nitrogen isotopes, which are already given from the isotope analysis from SINLAB, and beta0 and beta1 are standard parameters (see Ehrich et al. 2011b). Fat correction by using equation 2 were done for samples with a C/N ration between 3.5 and 7 (in accordance with Ehrich et al. 2011b). The fat corrections were made by adding the calculated $\Delta\delta^{13}\text{C}$ (equation 2) to the respective $\delta^{13}\text{C}$ values, and corrected values were used in subsequent analyses.

Stable isotope ratios for the major prey samples were determined according to similar protocols as used for Arctic fox muscle samples, including fat correction (Ehrich et al. 2015). Prey isotope data are given in table C in the appendix showing which species are included, their sampled tissue, their average isotopic values and their sample size, location and year.

2.4 Environmental variables

The data of environmental variables used in the analysis of this thesis are the terrestrial prey resources represented by the number of geese and carcasses of Svalbard reindeer and the monthly sea ice extent, which is linked to marine resource availability. The number of geese is yearly November estimates from counts of the Svalbard population of pink-footed geese (*Anser brachyrhynchus*) extracted from the European goose management platform (EGMP) report number 16 (see Johnson et al. 2020, figure 2a). The counts were coordinated by trained observers in Norway, Sweden, Denmark, the Netherlands and Belgium (covering wintering grounds and migration route) in November where flocks were counted on fields or when they arrive or leave roosting sites in the morning and evening respectively (Heldbjerg et al. 2020). There are two other species of geese that migrate to Svalbard (barnacle goose and brent goose), but number of pink-footed geese are used in this thesis as a proxy because it is the most numerous and increasing of the three. The yearly number of geese were aligned with fox samples by the current winter season. The data of reindeer carcass and sea ice extent were provided by the Norwegian Polar Institute. The number of reindeer carcasses are yearly (after winter) carcass counts from the annual reindeer count in Adventdalen (Å.Ø.Pedersen, Norwegian Polar Institute, figure 2b). The yearly number of reindeer carcasses were aligned with fox samples by the last winter season. The sea ice extent is the monthly average sea ice extent, given as at least 90% sea ice concentration (very close drift ice) on Isfjorden and Van Mijenfjorden (see Dahlke et al. 2020, Nater et al. 2021, figure 2c). Data of sea ice extent comes from sea ice charts produced by the Norwegian Meteorological Institute (Dahlke et al. 2020). Because the 1-2 months prior to the foxes' trapping month represent the diet for muscle samples, the average of the sea ice extents between the prior two months were aligned accordingly to each individual fox, making up the proper sea ice extent variable used in model analysis. The time series of the environmental data are shown in figure 2, with the number of geese and sea ice extent showing clear increasing and decreasing trends respectively.

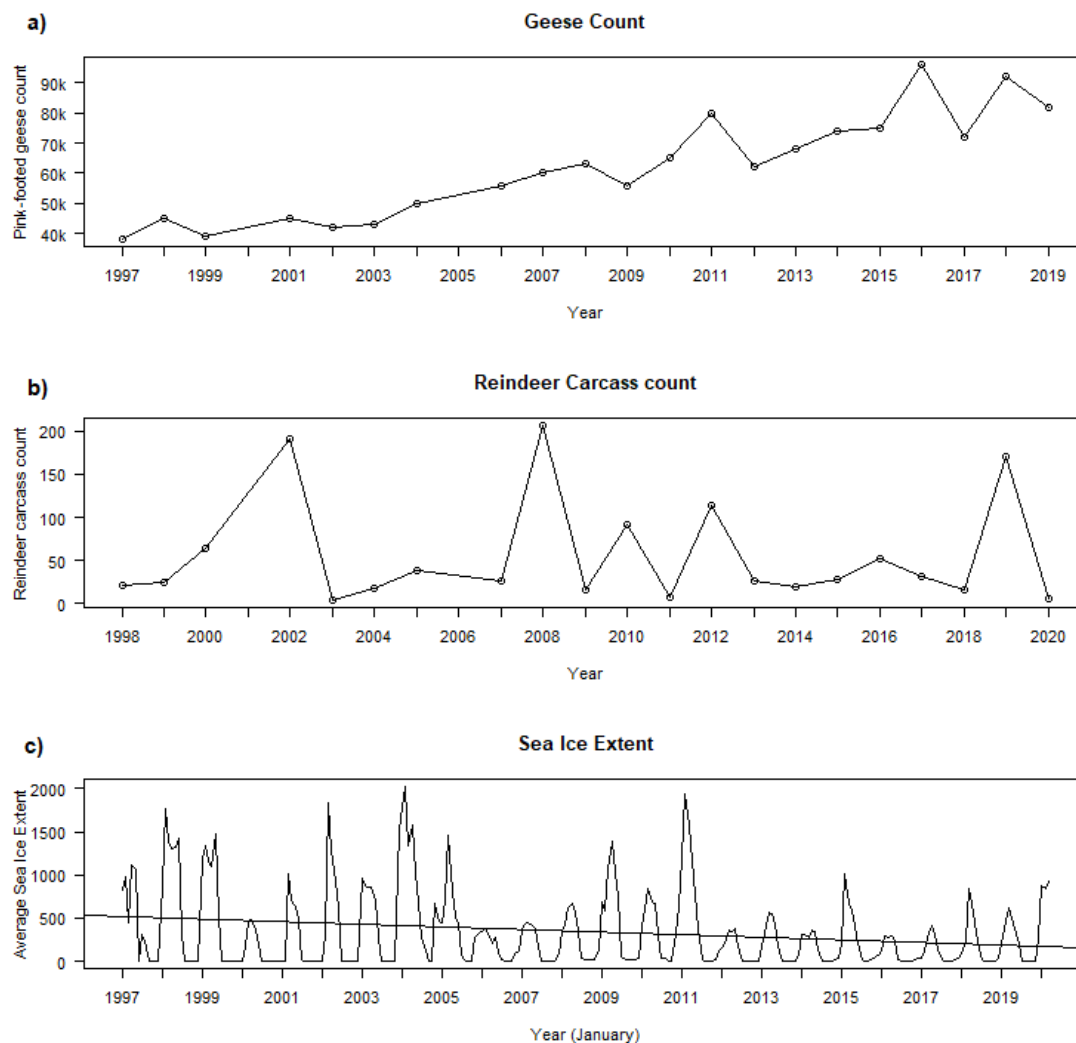


Figure 2 - Time series of the environmental variables used in this thesis. a) shows counts of the Svalbard population of pink-footed geese carried out annually in November (coordinated counts in Norway, Sweden, Denmark, the Netherlands and Belgium), b) shows counts of reindeer carcasses done annually in Adventdalen done after winter and c) shows monthly average sea ice extent given as at least 90% sea ice concentration, with years marked every January. A regression line is added to the sea ice extent plot to clearly show trend over time.

2.5 Data analysis

The total number of samples successfully analyzed for stable isotopes was 1409 (muscle n=1033 and fur n=376). Four fur samples were excluded because they had a C/N ratio above 3.5, which indicates that the tissue contains more fat than clean fur (Ehrich et al. 2011b). Fur is made up by metabolically inactive keratin (Newsome et al. 2012), so this could mean that there is some error, or the samples were not cleaned enough. One fur sample had the same ID as another in season 2006/2007. They had slightly different isotope values, but the same trapping information, so the first sample (the one with lower isotope values) was randomly

chosen to be removed. There were 3 muscle samples in the same trap season that were from the only foxes in the whole dataset trapped in April, so these were also removed. Some outliers identified on the $\delta^{15}\text{N}/\delta^{13}\text{C}$ plot (figure 3) were checked for potential errors, but no obvious errors were found. Removing the errors (red dots in figure 3) reduced the dataset to 1401 samples, of which 1030 are muscle samples and 371 are fur samples (black circles in figure 3). Data preparations and analysis were done using R version 3.6.1 (R Core Team, 2019).

For the analysis addressing the effects of the environmental variables, only data of Nordenskiöld Land were focused on. The environmental variables are assumed to be representative of Nordenskiöld Land, so they would not necessarily match with the other regions, and the data from the regions Kapp Wijk, North-West and Wijdefjorden (see figure 1) were therefore removed for both muscle and fur datasets. Samples with early trapping months (November and December) which account for diet in September-November were also removed from muscle data, because it is in winter (trapping months January-March resulting in the diet representative months November-February) when reindeer carcass numbers and sea ice extent are expected to be more important for the Arctic fox. Samples for which date was missing were also removed from muscle data as it becomes uncertain in which monthly ice data should be aligned. It is possible that some of these are samples taken in early trapping months representing autumn diet. Samples of foxes missing age were also removed. Muscle data had 5 samples with missing age that were removed, while fur data had 4 with missing age that were removed. The resulting datasets were finally reduced to a total of 1030 samples, with 714 samples of muscle and 316 of fur (see table B in appendix for yearly sample distribution for reduced datasets). The reduced data with samples from only Nordenskiöld Land were used in the model analyses (see figure 7 and 8).

2.5.1 Calculation of distance to coast

The distance to the coast for each trapped Arctic fox were determined by calculating the distance from the foxes' trapping coordinates to a shapefile exported from QGIS marking the Svalbard coastline. The shapefile was exported from a base map of Svalbard obtained from the Norwegian Polar Institute Map Data and Services (<https://geodata.npolar.no/>). The shapefile was set with a map projection of UTM 33N, and the longitude and latitude coordinates of the fox data were converted to the same UTM as the shapefile. The fox data

coordinates were corrected if there were any mistakes or missing values. Samples with missing coordinates were given the coordinates of the trapping location given in the data (locations looked up and coordinates found with <https://stadnamn.npolar.no/>). Some coastal sample coordinates were located out in the sea right off the coast (e.g., in bays or sounds). For those samples the coastal distance was changed to 0 km. Based on this, a total of 87 samples had the coastal distance changed to 0 km, and the locations reported for these samples were Bellsund, Engelsbukta, Kaldbukta, Vårsolbukta, Farmhamna, Gipsvika, Mushamna, Tempelfjorden and Slettвика. Data of distance to the coast were checked whether there are uneven distribution or trend over the time series. For both datasets of muscle and fur, the range of the distance to the coast goes from 0 km (at the coast) to 21.3 km away from the coast (inland).

2.5.2 Prey species isotope plots and discrimination

The relationship between Arctic fox isotope values to that of the foxes' prey was represented graphically. First, the fox isotope values were corrected for discrimination, which is the systematic difference in isotope ratios between a resource and a consumer due to assimilation into the consumer's tissue (Ben-David & Flaherty 2012). Mean discrimination factors from Lecomte et al. 2011 were subtracted from the isotope values of the foxes, where the overall mean values for each isotope for muscle (0,37 for carbon and 1,79 for nitrogen) and fur (2,18 for carbon and 3,34 for nitrogen) were used. Isotope values of different prey species from Svalbard were added to the fox $\delta^{15}\text{N}/\delta^{13}\text{C}$ plot as means with standard deviations (figure 3). Isotope values of pink-footed geese and barnacle geese (*Branta leucopsis*) were grouped together, with values of egg and muscle tissue types separated. The list of prey species and their isotope values are given in table C in the appendix.

2.5.3 Spatial and temporal trends

Based on the difference in environment and climate change with Nordenskiöld Land experiencing faster changes compared to the northern regions (see Dahlke et al. 2020), the locations from where data were collected were divided into four regions (see figure 1, see table A in appendix for total muscle and fur sample number per region). Temporal trends in muscle and fur isotope values were assessed by linear regressions. Regressions for regional

temporal trends were only calculated for regions with data available for more than five years, as too few sample years might give biased estimates or coincidental errors. Because distance to the coast varied during the study period, temporal trends per region were also estimated adding distance to the coast as an additive explanatory variable.

2.5.4 Determining effects of environmental drivers

Linear models were used to analyze possible effects of the environmental variables, coastal distance and age class (explanatory variables) on the isotope values (response variables). Several candidate models were built for each isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) as response variable for both muscle and fur data (list of muscle models in table D and E and fur models in table F and G in appendix). All muscle models included geese number, reindeer carcass number and sea ice extent, while all fur models included geese number (as the other resources are only important in winter, the period represented by muscle samples). The distance to the coast is an extra variable that were added, because the inland and coastal environment are different with the coast having stronger marine influence compared to inland. The distance to the coast is also tested as an interacting term with each or all of the environmental variables (only geese number in fur models). Age class is a variable to be included after coastal distance and is added because juvenile foxes might have different isotope values or dietary shifts compared to adults, which might give a model that explains the data better. Because there are strong temporal trends observed in several variables where correlated variables might obscure the effect of each other, new sets of candidate models were built with the variables detrended (i.e., geese number, reindeer carcass number, sea ice extent and isotope values). Detrended values represent the difference from the trend (regression line) of the variable over the time series. The models analyzing detrended variables had the exact same structure as the models described above. Candidate models were ranked based on AICc (Akaike's Information Criterion corrected for small sample sizes) values, where the models within a difference of 2 in AICc from the AICc of the best model had substantial support to fit the data equally well (Burnham & Anderson 2004). Of these models, the simplest among them was selected to analyze the effects of the explanatory variables.

The variables were checked for correlation with correlation factors and variance inflation factors (VIF), but no high correlations were found between the variables, and also geese number and sea ice extent had only low correlation. There were also no high VIFs, with all

values close to no correlation. Because there is no strong or even moderate correlation found between the variables, all variables were included also in the models with untransformed variables. Model fit was assessed graphically for each candidate model by inspecting the distribution of residuals.

3 Results

3.1 Arctic fox dietary range

The full dataset of muscle (1033 samples including errors) and fur (376 samples including errors) isotopes plotted on a $\delta^{15}\text{N}/\delta^{13}\text{C}$ plot shows the distribution of individual Arctic fox diet (figure 3). Prey isotope means with standard deviation (table C in appendix) are also plotted in figure 3 to show the dietary range. The fox isotope values fit between three areas of the plot, to which the functional prey groups can be assigned. These groups are reindeer and ptarmigan as resident terrestrial resources, geese as migrating terrestrial resource and seabirds and seal (and others) as marine resources. The fox isotope values fit linearly between resident terrestrial and marine resources and bends more toward geese in the muscle plot in comparison to the fur plot.

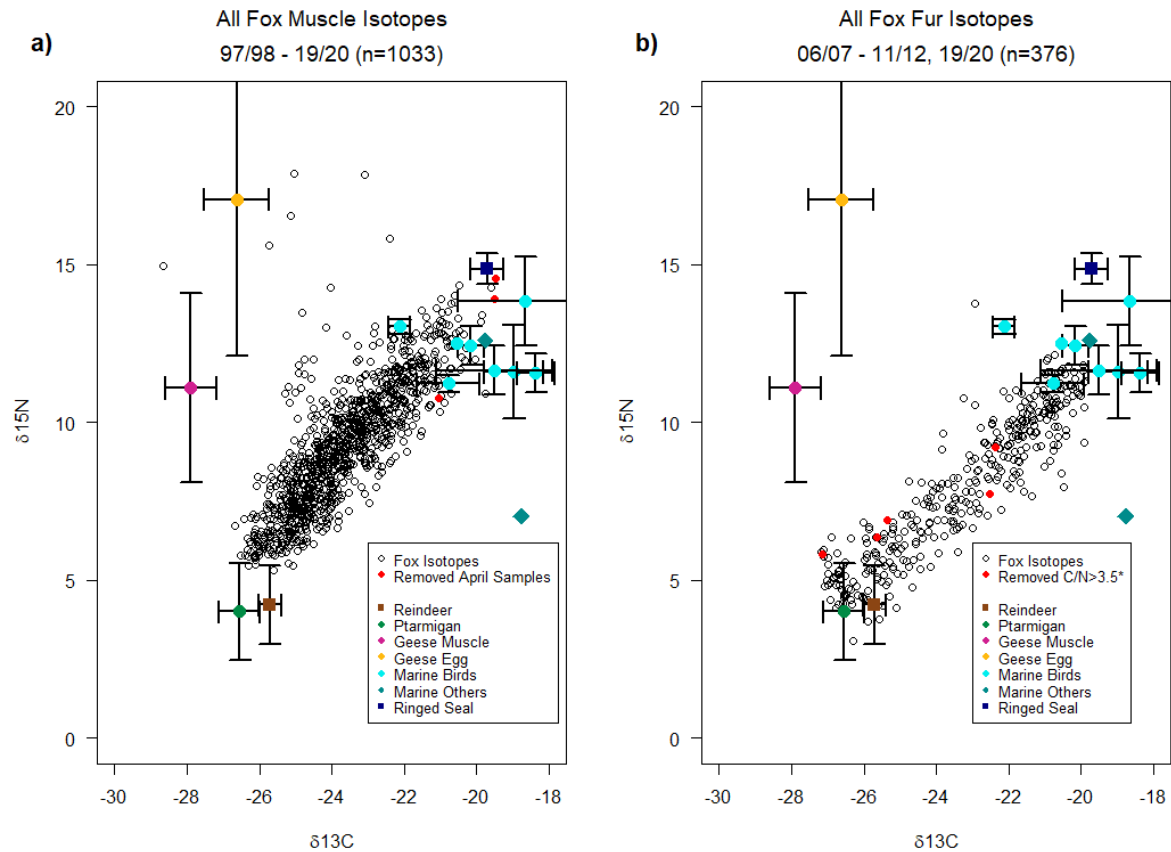


Figure 3 - All Arctic fox isotope values plotted after correcting for discrimination, and prey isotope value means with standard deviation. Muscle samples ($n=1033$) are from trapping season 1997/1998 to 2019/2020, and fur samples ($n=376$) are from 2006/2007 to 2011/2012, including 2019/2020. The removed samples (red dots) are included in the sample numbers in this figure, and removal of these are described in the text (*one removed ID duplicate included as removed fur value). The removed number of samples and from which seasons they are removed from are given in parenthesis in table A in the appendix.

3.2 Spatial and temporal patterns

The difference of the range of Arctic fox muscle and fur isotope values between the regions are shown in figure 4. The isotope interquartile range and median are lower for Nordenskiöld Land (908 muscle and 320 fur samples) compared to the other regions (see figure 4). This suggests a more terrestrial diet on average in Nordenskiöld Land. Though there is overlap, the trend is the same in all boxplots of figure 4. Kapp Wijk (21 muscle and 1 fur sample) and North-West (34 muscle and 9 fur samples) have only samples collected close to the coast, while Wijdefjorden (67 muscle and 41 fur samples) has few inland samples. The coastal bias for these regions could be the reason why values of both isotopes are higher there.

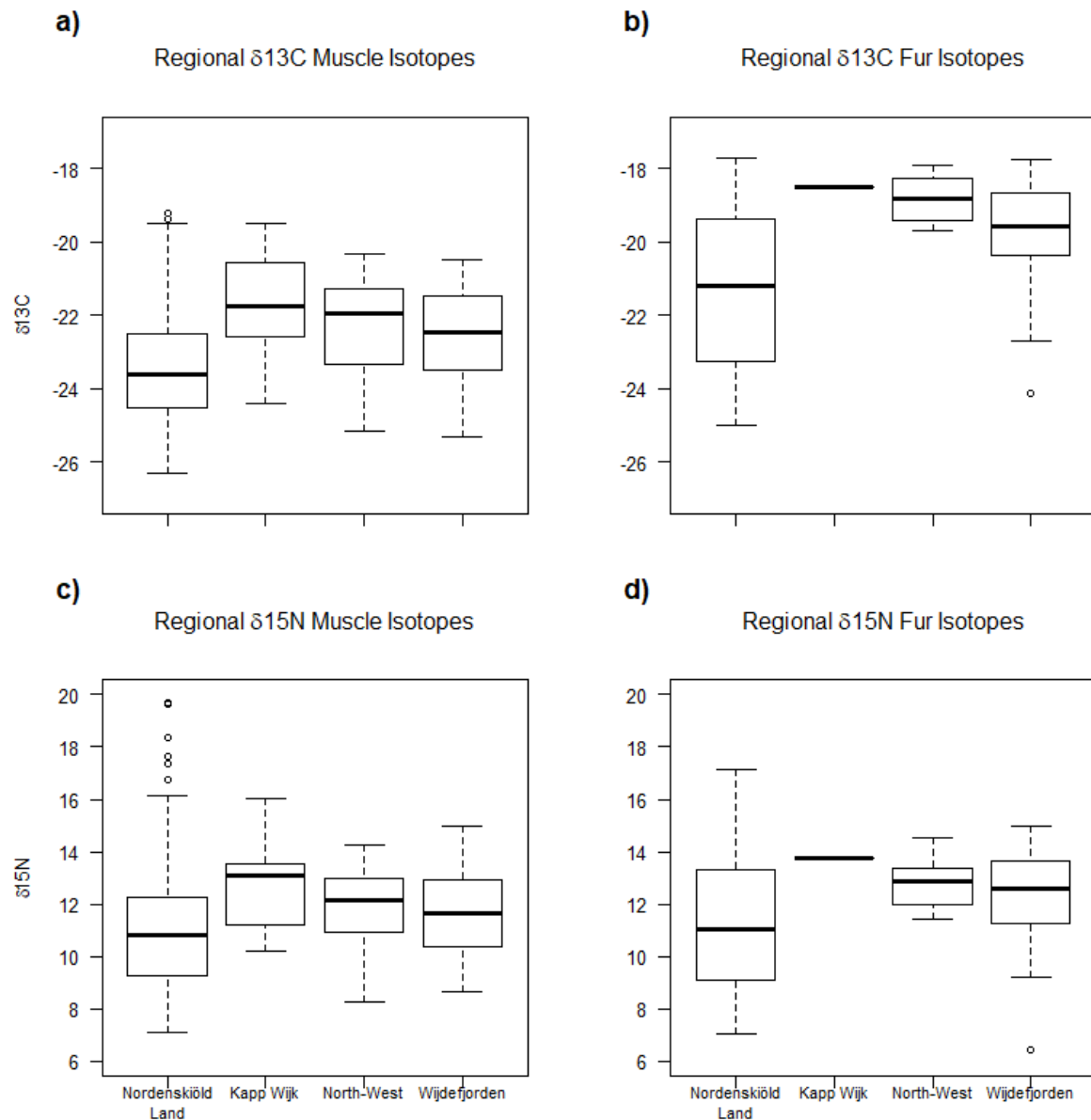


Figure 4 - Boxplots showing isotope value distributions for each of the four regions (Nordenskiöld Land, Kapp Wijk, North-West and Wijdefjorden), where a) show boxplots with muscle carbon isotopes, b) fur carbon isotopes, c) muscle nitrogen isotopes and d) fur nitrogen isotopes. Black lines are the medians of the isotope values, the boxes are the interquartile ranges, the end of the whiskers are the minimum and maximum values, and the circles are outliers.

The temporal trends of regional isotope values are shown in figure 5 (only muscle isotopes) and 6 (only fur isotopes). Carbon isotopes of muscle showed significant negative trends for the regions; Nordenskiöld Land with a reduction of -0.043 ‰ per year ($\text{SE}=0.008$, $p<0.001$), North-West with -0.144 ‰ per year ($\text{SE}=0.036$, $p<0.001$) and Wijdefjorden with -0.092 ‰ per year ($\text{SE}=0.043$, $p=0.037$) (figure 5 a, c and d). The negative trends of North-West and Wijdefjorden were steeper than for Nordenskiöld Land. No significant temporal trends were found for nitrogen isotopes of muscle (figure 5 e, f, g and h). Carbon isotopes of fur showed

significant negative trends for Nordenskiöld Land with a reduction of -0.206 ‰ per year ($SE=0.021$, $p<0.001$), but only when 2019/2020 was included (figure 6 a). Nitrogen isotopes of fur also showed significant trends for Nordenskiöld Land with a reduction of -0.163 ‰ ($SE=0.024$, $p<0.001$), but only when 2019/2020 was included (figure 6 e). Though regressions for North-West and Wijdefjorden are not included in the fur plots because of the lack of data (figure 6 c, d, g and h), these regions do indicate a negative trend, which coincides with the other trends being all negative. Kapp Wijk has only data over the earliest years of the sampling period and has one single sample in 2008/2009, which biases the trend to a positive. Temporal trends of isotopes for the reduced data set of muscle and fur used in model selection were also checked, but not included in figures since their trends are similar to Nordenskiöld Land. Temporal trends were also similar when distance to coast was added as an additive effect to the linear regressions, so differences in distance to the coast cannot explain the observed temporal trends.

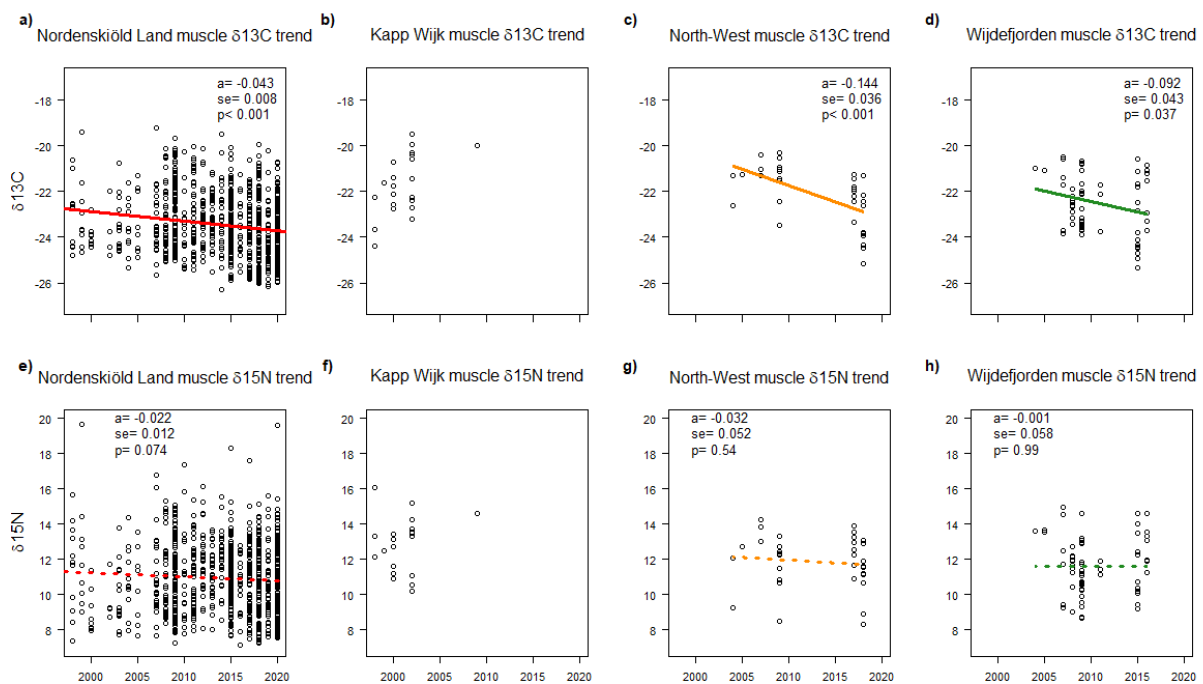


Figure 5 - $\delta^{13}C$ isotope temporal trend of Arctic fox muscle for the regions a) Nordenskiöld Land, b) Kapp Wijk, c) North-West and d) Wijdefjorden. $\delta^{15}N$ isotope temporal trend of Arctic fox muscle for the regions e) Nordenskiöld Land, f) Kapp Wijk, g) North-West and h) Wijdefjorden. a = slope of linear regression, se = standard error of slope, p = p -value of the regression. Solid lines show significant relationships and dashed lines show non-significant relationships at the 0.05 level.

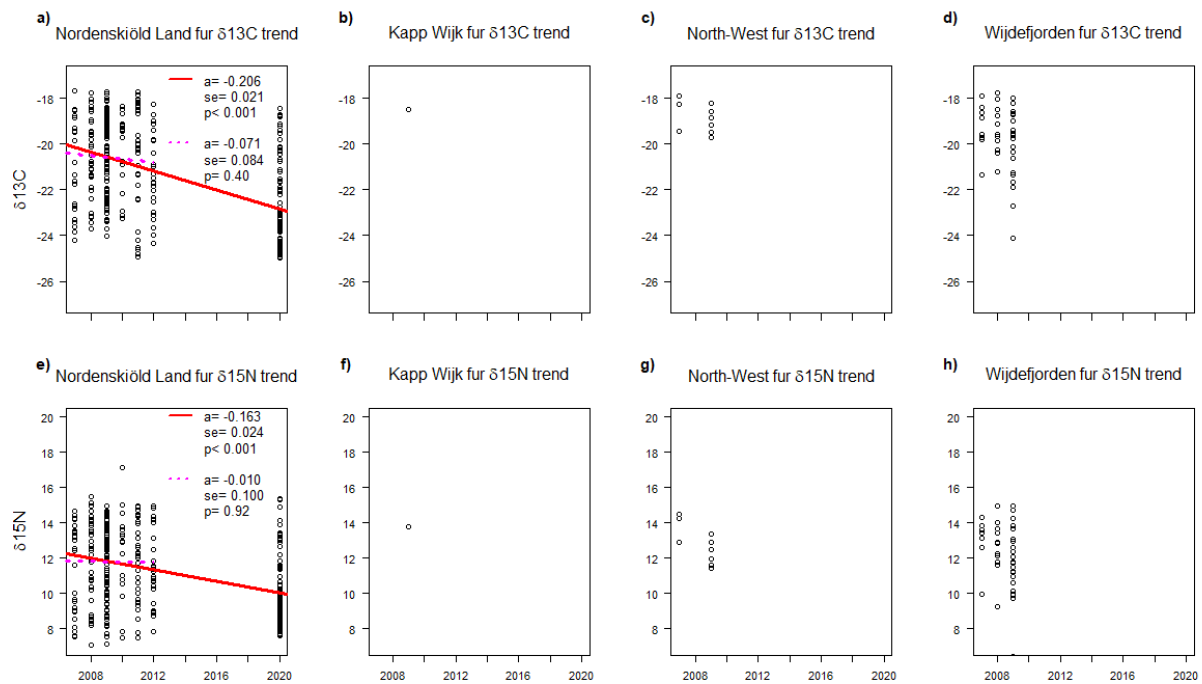


Figure 6 - $\delta^{13}\text{C}$ isotope temporal trend of Arctic fox fur for the regions a) Nordenskiöld Land, b) Kapp Wijk, c) North-West and d) Wijdefjorden. $\delta^{15}\text{N}$ isotope temporal trend of Arctic fox fur for the regions e) Nordenskiöld Land, f) Kapp Wijk, g) North-West and h) Wijdefjorden. a = slope of linear regression, se = standard error of slope, p = p -value of the regression. Because of the gap in years, a second regression for Nordenskiöld Land is given for the period 2006/2007-2012/2012 for each isotope. Solid lines show significant relationships and dashed lines show non-significant relationships at the 0.05 level.

3.3 Environmental drivers

3.3.1 Models based on muscle samples

There was one distinguished far right point in the leverage plot for muscle models with interaction between the distance to the coast and sea ice extent. The sample were identified and had one of the highest distances to coast and ice extent values (one sample in 2010/2011). This is the only sample with such high values for both variables, and very few samples have large or even medium values for both coastal distance and sea ice extent at the same time. Models were checked again without this sample, but estimates remained about the same, so the sample was kept.

For both carbon and nitrogen isotopes of muscle, the best model with untransformed variables according to AICc was the model with geese number, reindeer carcass number, sea ice extent and distance to the coast as additive effects, and no interactions. Other models with age class as additional additive factor or coastal distance interacting with either of the environmental variables were within a difference of 2 in AIC from the best model (see appendix table D).

However, these models had similar effects for the main explanatory variables (geese number, reindeer carcass number, sea ice extent and distance to the coast) to those of the best model, and the interactive terms and age class were not significant. The best model was therefore used alone for effect estimates. Other models with coastal distance interacting with environmental variables together with age class added as an independent term had larger increases in AICc, ranging from about 2.7 to 7 from the best model. Model with just the environmental variables as explanatory variables had very large increases in AICc (about 20.6 for carbon and 37.4 for nitrogen) from the best model. This indicates that these models explain the data much more poorly.

For the muscle model with untransformed variables, the effect of the number of geese is -0.017 ‰ (SE=0.004, $p < 0.001$) on carbon isotopes per 1000 geese. This amounts to a change of -0.986 ‰ on carbon across the range of geese number given for muscle data. Coastal distance had an effect of -0.042 ‰ (SE=0.009, $p < 0.001$) on carbon isotopes and -0.082 ‰ (SE=0.013, $p < 0.001$) on nitrogen isotopes per 1 km away from the coast. This amounts to a change of -0.895 ‰ and -1.747 ‰ on carbon and nitrogen isotopes respectively, across the range of coastal distance. Estimates from the muscle model with untransformed variables are given in table 1. Effect plots for the coefficients are given in figure 7, showing their estimated effects on change in isotope values.

The best muscle model with detrended variables according to AICc had the same structure as the best model with untransformed variables. Similarly, other models with age class added or coastal distance interacting with either of the environmental variables were within or had about a difference of 2 in AICc from the best model (see appendix table E). These models had similar effects for the main explanatory variables (detrended geese number, detrended reindeer carcass number, detrended sea ice extent and distance to the coast) to those of the best model, and the interactive terms and age class were not significant. The best model was kept for effect estimates. Other models with coastal distance interacting with detrended environmental variables together with age class added as an independent term had larger increases in AICc, ranging from about 3.5 to 7.7 from the best model. Models with only the detrended environmental variables as explanatory variables had very large increases in AICc (about 19.5 for carbon and 35.8 for nitrogen) from the best model, again indicating that these models explain the data much more poorly.

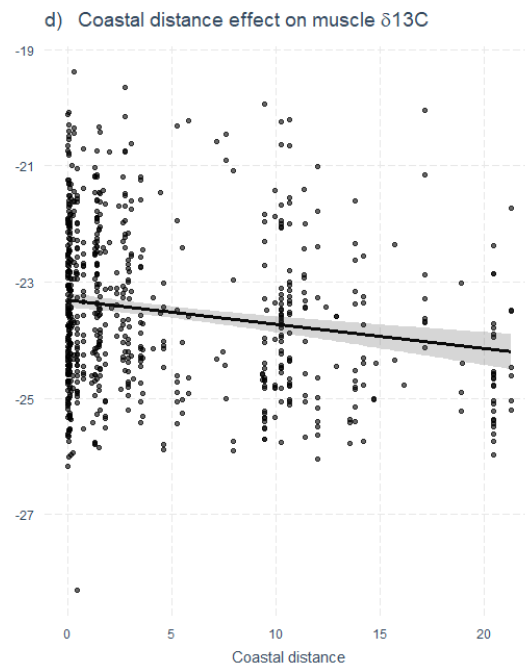
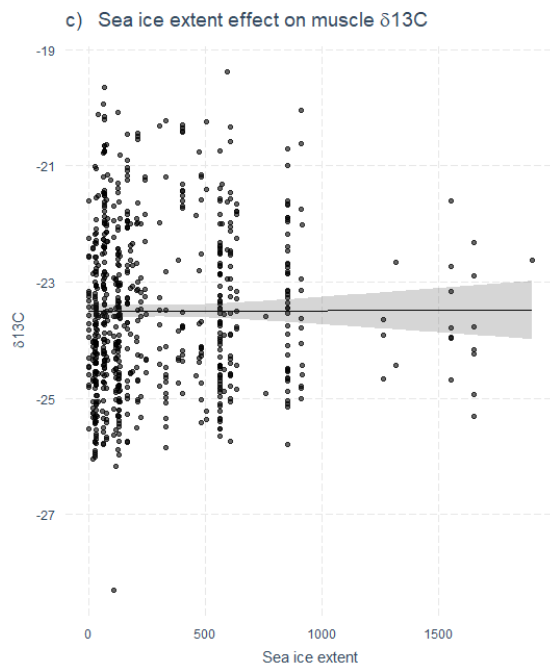
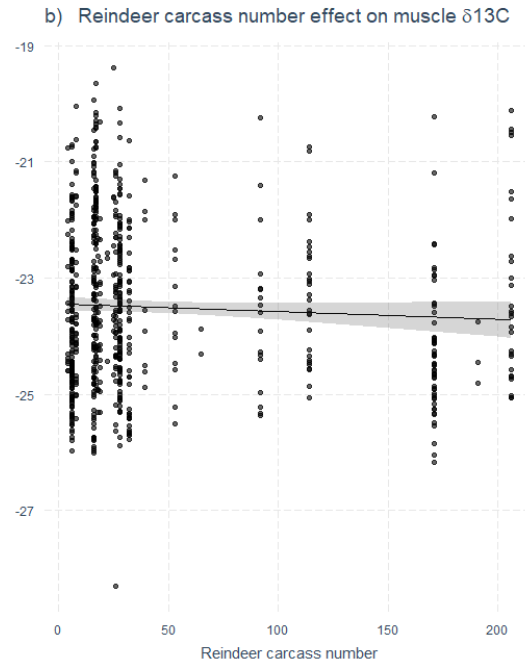
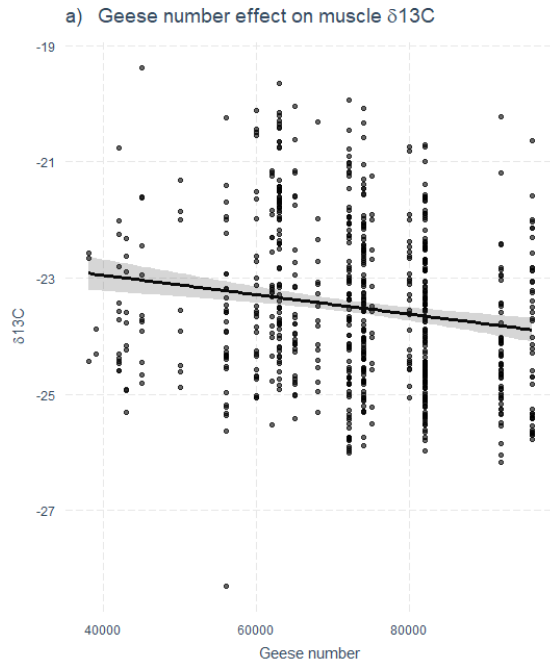
For the muscle model with detrended variables, coastal distance had an effects of -0.040 ‰ (SE=0.009, p<0.001) on detrended carbon and -0.080 ‰ (SE=0.013, p<0.001) on detrended nitrogen per 1 km away from the coast. This amounts to a change of -0.852 ‰ and -1.704 ‰ on detrended carbon and nitrogen isotopes respectively, across the range of coastal distance. Detrended reindeer carcass number had an effect of -0.023 ‰ (SE=0.010, p=0.016) on detrended carbon per 10 carcasses. This amounts to a change of -0.468 ‰ on detrended carbon across the range of detrended number of reindeer carcasses. Estimates from the muscle model with detrended variables are given in table 2. Effect plots for the coefficients are given in figure 8, showing their estimated effects on change in isotope values.

Table 1: Estimates of coefficients of muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ linear models with untransformed variables. Geese number and sea ice extent estimates are multiplied by 1000, and reindeer carcass number estimate is multiplied by 10 to give easier interpretable values. Values rounded to 3 decimals. Significant values are shown in bold.

Muscle models (untransformed):	Estimate	Std. Error	t value	P
$\delta^{13}\text{C}$ model				
Intercept	-22.040	0.305	-72.262	<0.001
Geese number (x1000)	-0.017	0.004	-4.242	<0.001
Reindeer Carcass number (x10)	-0.013	0.009	-1.429	0.153
Sea Ice extent (x1000)	0.011	0.157	0.072	0.942
Coastal distance	-0.042	0.009	-4.775	<0.001
$\delta^{15}\text{N}$ model				
Intercept	-11.610	0.451	25.763	<0.001
Geese number (x1000)	-0.005	0.006	-0.821	0.412
Reindeer Carcass number (x10)	0.004	0.014	0.312	0.755
Sea Ice extent (x1000)	0.028	0.232	0.121	0.904
Coastal distance	-0.082	0.013	-6.348	<0.001

Table 2: Estimates of coefficients of detrended muscle $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ linear models. Geese number (detrended) and sea ice extent (detrended) estimates are multiplied by 1000, and reindeer carcass number (detrended) estimate is multiplied by 10 to give easier interpretable values. Values rounded to 3 decimals. Significant values are shown in bold.

Muscle Detrended models:	Estimate	Std. Error	t value	P
$\delta^{13}\text{C}$ model				
Intercept	0.156	0.065	2.402	0.017
Geese number (x1000)	3.010*10 ⁻⁴	0.008	0.038	0.970
Reindeer Carcass number (x10)	-0.023	0.010	-2.266	0.024
Sea Ice extent (x1000)	0.025	0.156	0.163	0.871
Coastal distance	-0.040	0.009	-4.659	<0.001
$\delta^{15}\text{N}$ model				
Intercept	0.358	0.096	3.719	<0.001
Geese number (x1000)	0.016	0.012	1.363	0.173
Reindeer Carcass number (x10)	-0.008	0.015	-0.557	0.578
Sea Ice extent (x1000)	0.063	0.231	0.274	0.784
Coastal distance	-0.080	0.013	-6.210	<0.001



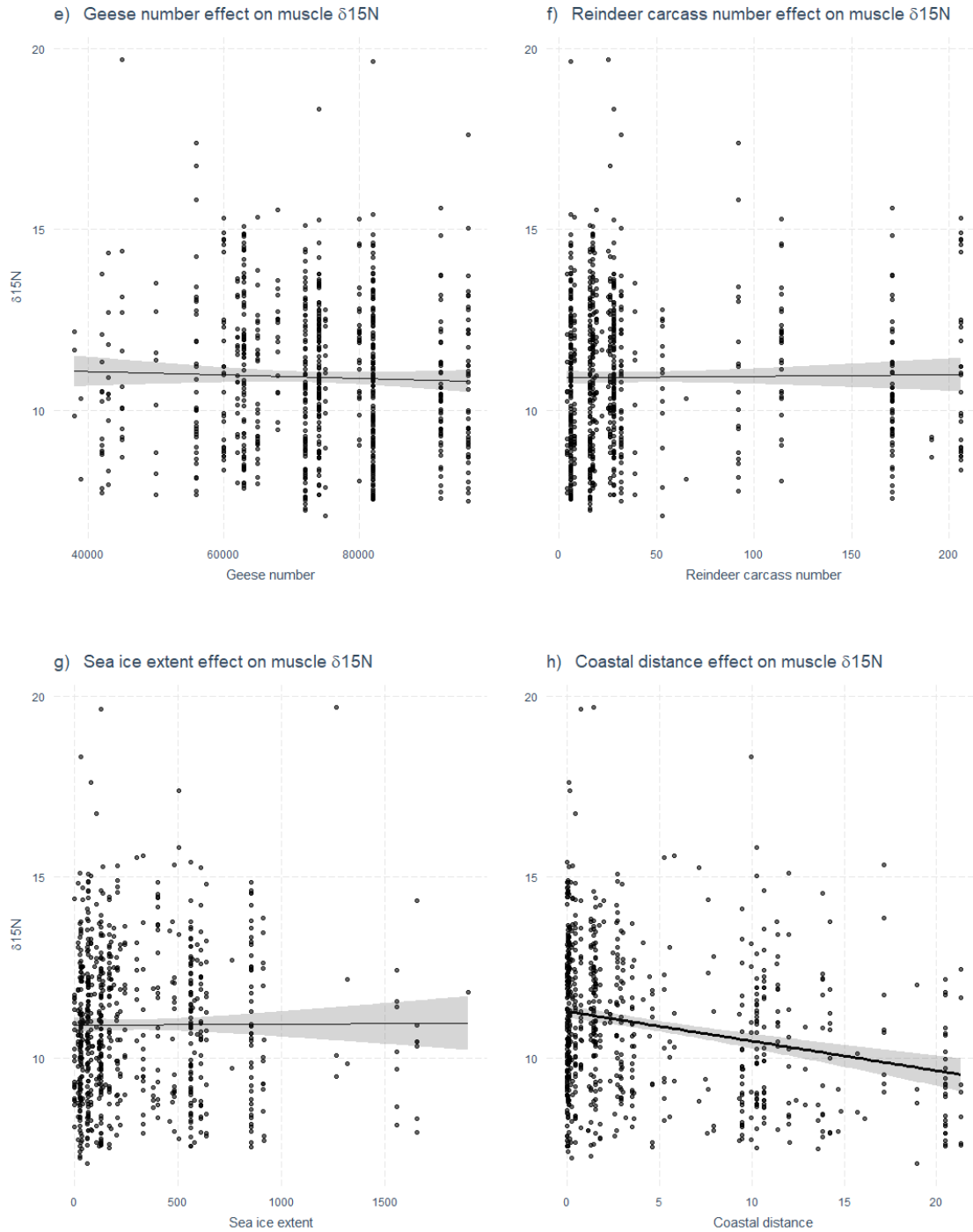
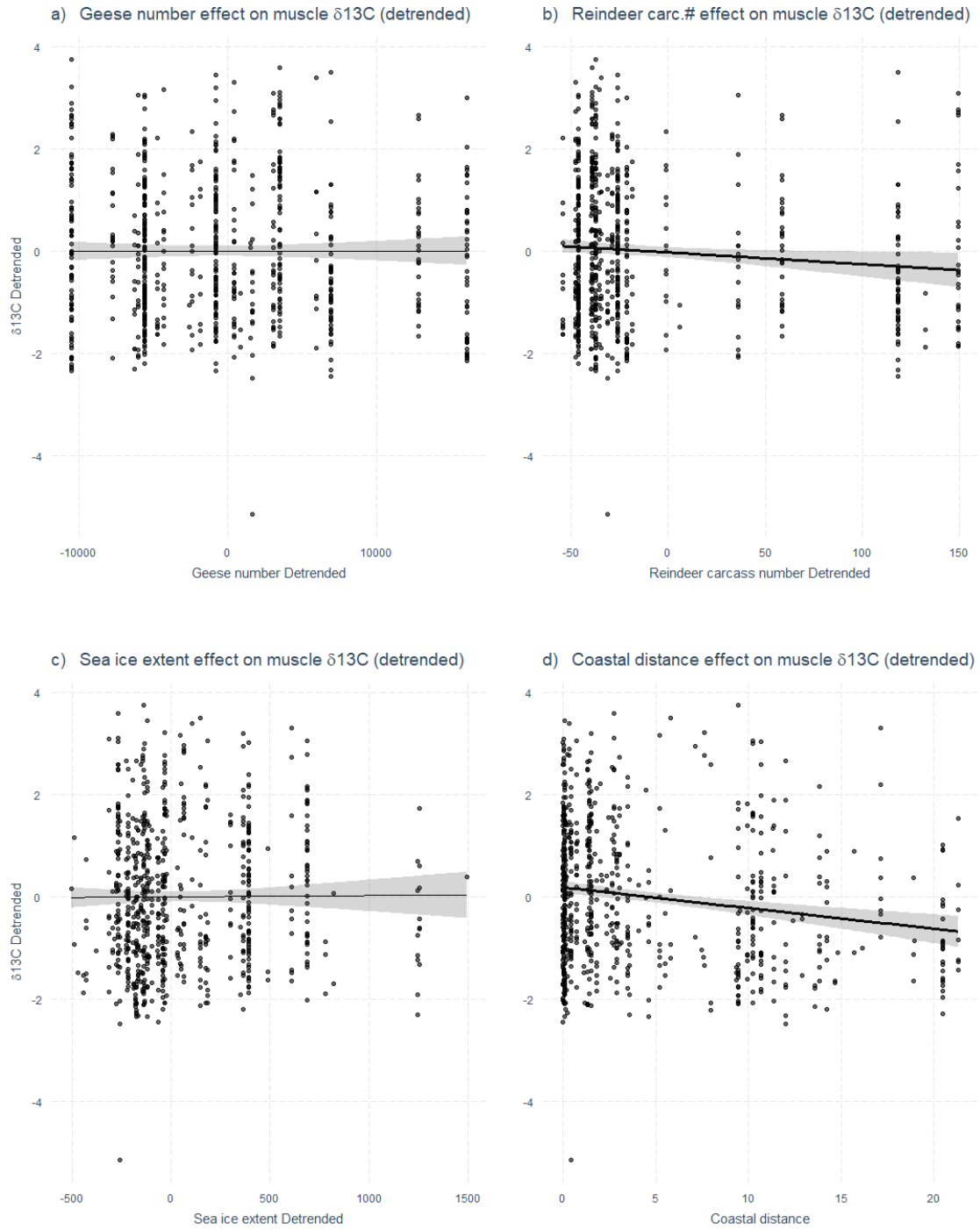


Figure 7 - Effect plots of the coefficients of the chosen untransformed muscle model (see table 1 for estimates) with 95% confidence intervals (gray shaded area). Plots with the data points added show a) geese number, b) reindeer carcass number, c) sea ice extent and d) coastal distance effect on $\delta^{13}\text{C}$, and e) geese number, f) reindeer carcass number, g) sea ice extent and h) coastal distance effect on $\delta^{15}\text{N}$. Thick lines signify significant effect, while thin lines signify non-significant effect.



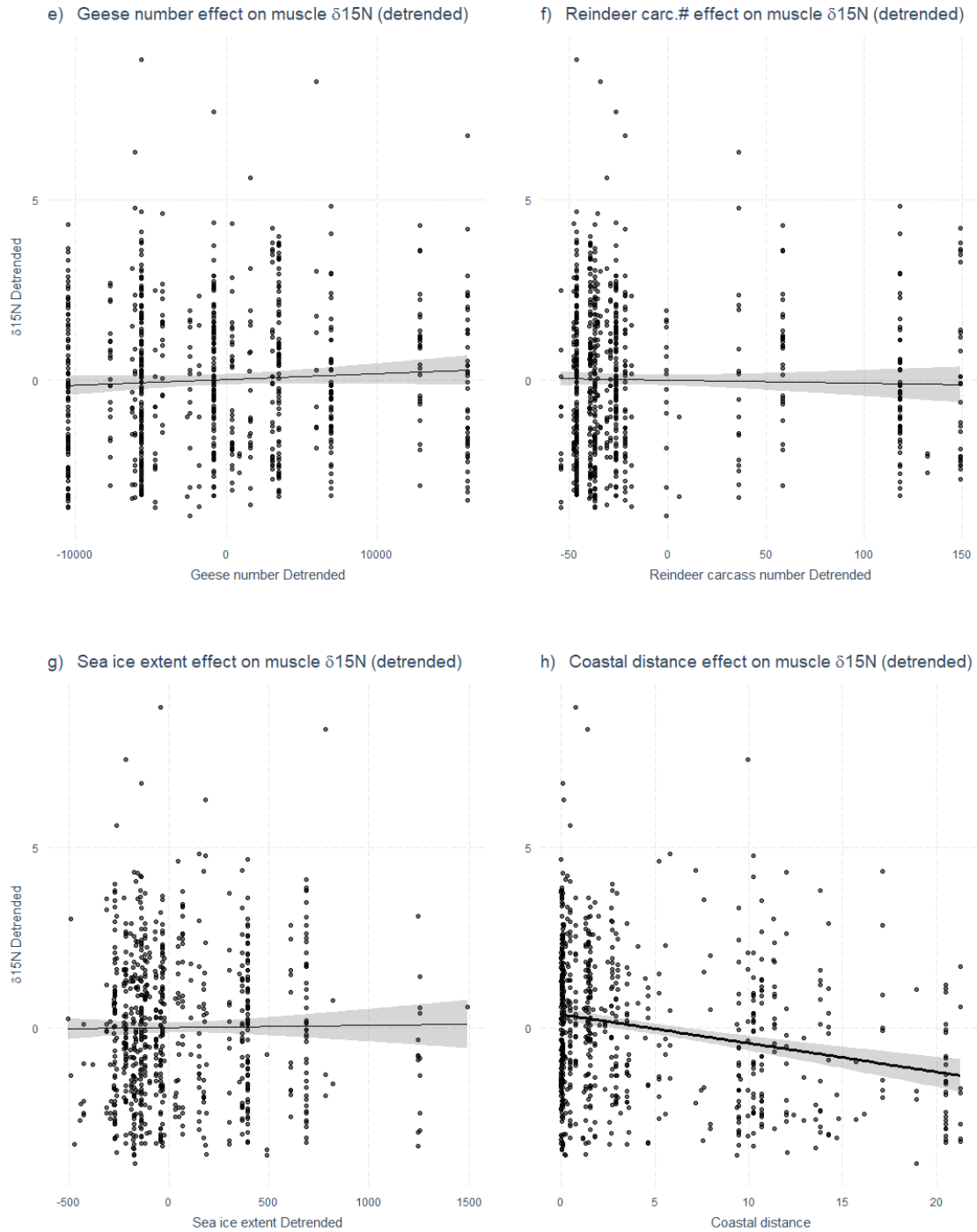


Figure 8 - Effect plots of the coefficients of the chosen detrended muscle model (see table 2 for estimates) with 95% confidence intervals (gray shaded area). Plots with the data points added show a) detrended geese number, b) detrended reindeer carcass number, c) detrended sea ice extent and d) coastal distance effect on detrended $\delta^{13}\text{C}$, and e) detrended geese number, f) detrended reindeer carcass number, g) detrended sea ice extent and h) coastal distance effect on detrended $\delta^{15}\text{N}$. Thick lines signify significant effect, while thin lines signify non-significant effect.

3.3.2 Models based on fur samples

For both carbon and nitrogen isotopes of fur, the best model with untransformed variables according to AICc was the model with geese number and distance to the coast as additive effects, and no interactions. For both isotopes, model with geese number alone as an explanatory variable were within a difference of 2 in AICc from the best model, as were models with age class added or with interaction between geese number and coastal distance when nitrogen is the response variable (see appendix table F). Since the best model includes coastal distance, which is of interest, and that the other models had similar effects for the main explanatory variables (geese number and distance to the coast) to those of the best model, the best model was used alone for effect estimates. Interaction between geese number and coastal distance together with added age class gave the poorest fit to the data, with an increase in AICc of 4.13 for carbon and 3.48 for nitrogen from the best model.

For the fur model with untransformed variables, the effect of the number of geese is -0.092 ‰ (SE=0.011, $p<0.001$) on carbon isotopes and -0.070 ‰ (SE=0.012, $p<0.001$) on nitrogen isotopes per 1000 geese. This amounts to a change of -2.392 ‰ and -1.82 ‰ on carbon and nitrogen isotopes respectively, across the range of geese number given for fur data. Coastal distance is not significant for the models of fur, but do have about the same estimate and low p-values. Estimates are also similar but lower than that of muscle models. Estimates from the fur model with untransformed variables are given in table 3. Effect plots for the coefficients are given in figure 9, showing their estimated effects on change in isotope values.

The best fur model with detrended variables according to AICc had the same structure as the best model with untransformed variables when detrended carbon isotope is the response variable. With detrended nitrogen isotope as the response variable however, the model with geese number alone as the explanatory variable was the best model. The model with coastal distance as an additive effect was used for both isotope variants for effect estimates, because this model is within a difference of 2 in AICc ($\Delta\text{AICc}=0.5$) from the best model for detrended nitrogen (see appendix table G). Also, Coastal distance is of interest and kept for all other chosen models in this thesis. The model with interaction between detrended geese number and coastal distance was also within a difference of 2 in AICc when detrended carbon is the response variable. Again, the model with interaction between detrended geese number and coastal distance with added age class gave the poorest fit to the data, with an increase in AICc of 3.68 for detrended carbon and 4.38 for detrended nitrogen from the best model.

For the fur models with detrended variables, coastal distance has about the same estimate, as well as somewhat low p-value. Estimates are also similar but lower than that of muscle models with detrended variables. The model of fur with detrended variables did not give any significant estimates (see table 4). Effect plots for the coefficients are given in figure 10.

Table 3: Estimates of coefficients of fur $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ linear models with untransformed variables. Geese number estimate is multiplied by 1000 to give easier interpretable values. Values rounded to 3 decimals. Significant values are shown in bold.

Fur models (untransformed):	Estimate	Std. Error	t value	P
$\delta^{13}\text{C}$ model				
Intercept	-14.830	0.735	-20.189	<0.001
Geese number (x1000)	-0.092	0.011	-8.659	<0.001
Coastal distance	-0.029	0.017	-1.694	0.091
$\delta^{15}\text{N}$ model				
Intercept	16.190	0.845	19.162	<0.001
Geese number (x1000)	-0.070	0.012	-5.759	<0.001
Coastal distance	-0.028	0.020	-1.433	0.153

Table 4: Estimates of coefficients of detrended fur $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ linear models. Geese number (detrended) estimate is multiplied by 1000 to give easier interpretable values. Values rounded to 3 decimals. Significant values are shown in bold.

Fur Detrended models:	Estimate	Std. Error	t value	P
$\delta^{13}\text{C}$ model				
Intercept	13.740	0.140	0.984	0.326
Geese number (x1000)	-0.009	0.019	-0.456	0.649
Coastal distance	-0.025	0.017	-1.473	0.142
$\delta^{15}\text{N}$ model				
Intercept	0.132	0.162	0.813	0.147
Geese number (x1000)	-0.003	0.022	-0.128	0.889
Coastal distance	-0.024	0.020	-1.240	0.216

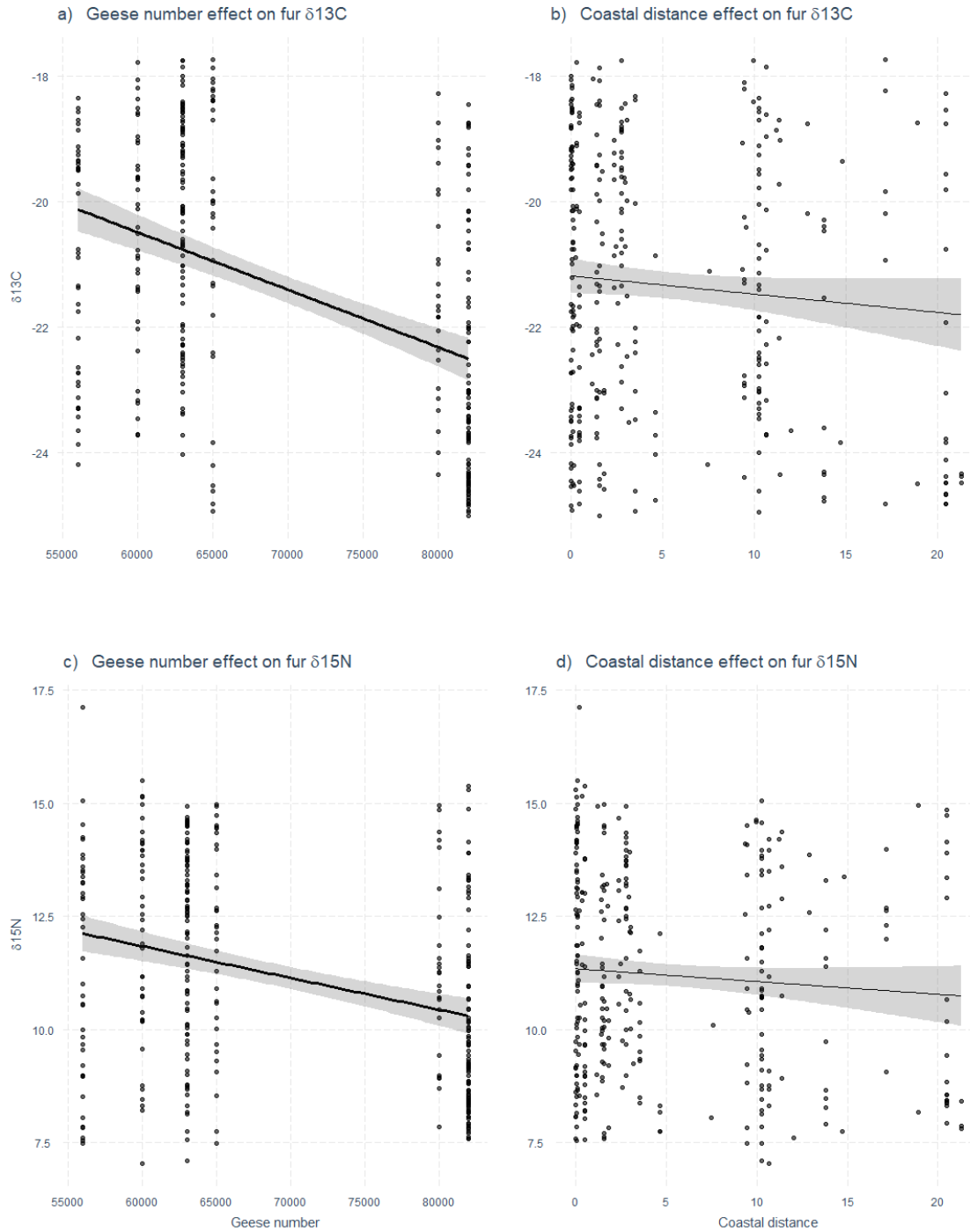


Figure 9 – Effect plots of the coefficients of the chosen untransformed fur model (see table 3 for estimates) with 95% confidence intervals (gray shaded area). Plots with the data points added show a) geese number and b) coastal distance effect on $\delta^{13}C$, and c) geese number and d) coastal distance effect on $\delta^{15}N$. Thick lines signify significant effect, while thin lines signify non-significant effect.

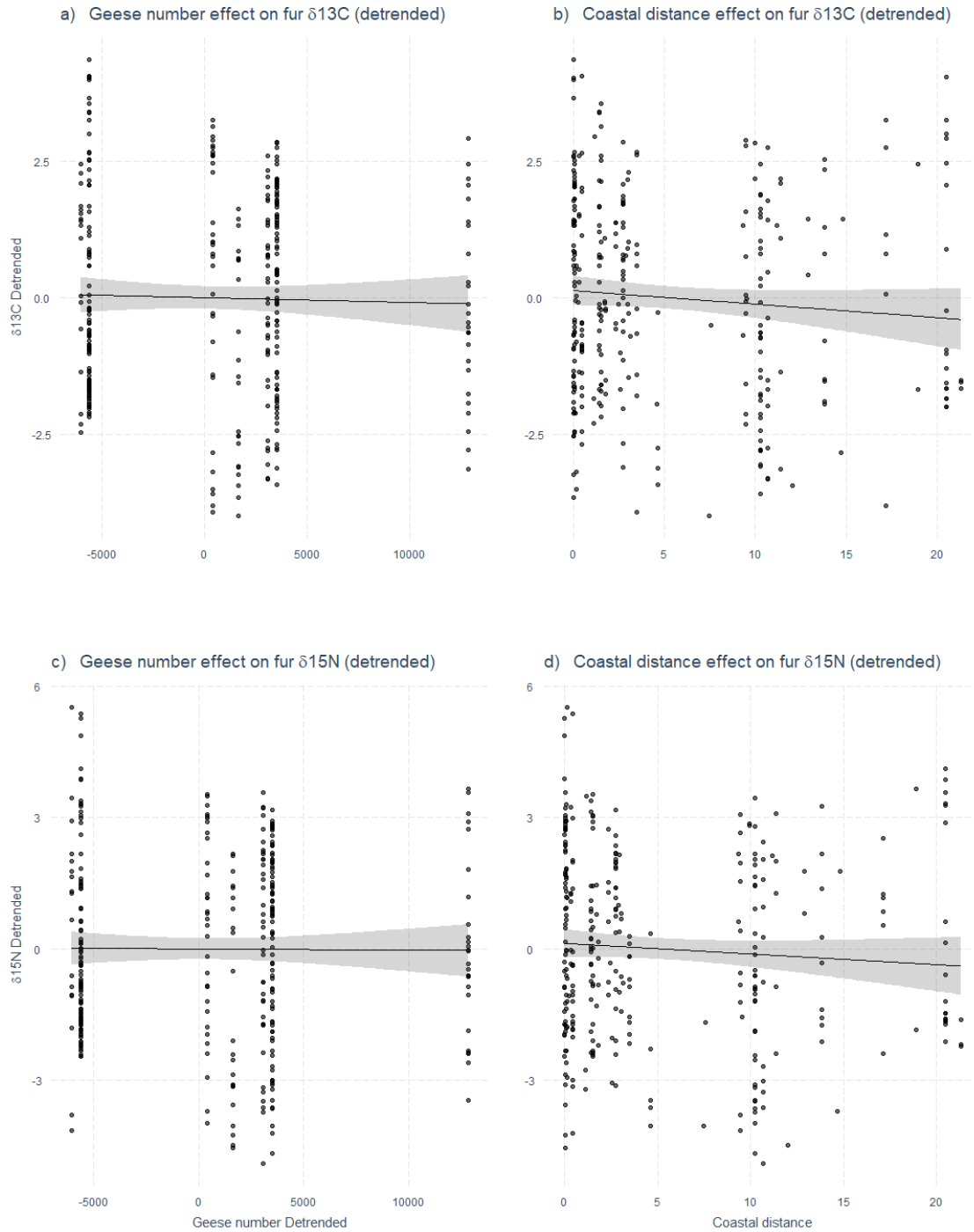


Figure 10 - Effect plots of the coefficients of the chosen detrended fur model (see table 4 for estimates) with 95% confidence intervals (gray shaded area). Plots with the data points added show a) detrended geese number and b) coastal distance effect on detrended $\delta^{13}\text{C}$, and c) detrended geese number and d) coastal distance effect on detrended $\delta^{15}\text{N}$. All effect estimates for this model are non-significant.

4 Discussion

The results of this thesis indicate clear temporal trends showing reduction of carbon isotope values of Arctic fox in the different regions of Svalbard, both in winter and autumn. This reduction means that the diet of Arctic fox on Svalbard has become more terrestrial over the years. In winter, it seems that there might be a faster transitioning towards a more terrestrial diet in northern parts of Svalbard compared to the more southern Nordenskiöld Land.

Between seasons, it also seems that there is stronger reduction of isotope values in autumn (fur) compared to winter (muscle). Results from this thesis indicate that the strong increase in goose population (terrestrial resource) may be the reason for the significantly reduced isotope values, though in autumn it is unclear how much other factors (not accounted for in this thesis) may also explain this effect. There is no trend in number of reindeer carcasses (terrestrial resource) on isotope values over time, but the year-to-year fluctuations of number of carcasses did have a significant impact, where increases in carcass number reduced the carbon isotope values. There was no significant impact of sea ice (proxy of marine resource availability) on isotope values. Surprisingly, the distance from the coast had very high significance on changes in isotope values in winter, implying that there might be less movement of foxes on Svalbard than previously thought.

4.1 Arctic fox dietary range

When considering the isotope values of Arctic foxes in relation to the values of their main prey showed that the isotope values of Arctic foxes were more distant from isotope values of geese in autumn compared to winter (figure 3). This may seem surprising, since geese could be expected to be most important for the fox diet in summer. This pattern might be explained by the presence of seabirds in autumn, as they have isotope values at the same $\delta^{15}\text{N}$ range (trophic position) as geese. Seabirds are one of the important prey resource groups of Arctic foxes on Svalbard, so an impact on the dietary range can be expected when they are present. Foxes are known to cache seabirds as well (Sklepkovych & Montevicchi 1996) and could prey on remaining seabirds, if any, in early winter. Most migratory birds leave Svalbard in August/September, but Northern Fulmar (*Fulmarus glacialis*) leave in October/November (Eide et al. 2005). Seabirds could therefore have some impact on winter diet. Potentially, consumption of marine invertebrates could contribute to the more marine signatures observed in fur as well. Isotope values of the marine benthic fauna of Svalbard are in the marine range

of Arctic fox carbon isotope values (larger than $\delta^{13}\text{C}=-23\text{‰}$) but cover the whole range of Arctic fox nitrogen isotope values (see Søreide et al. 2013). It would be interesting to include isotope values of marine invertebrates that the Arctic fox prey on, as they have been observed digging for them on the beaches (pers. obs. Tommy Sandal, Arctic fox trapper). With reducing sea ice, the shores and beaches might be more accessible for the foxes in winter to search for invertebrates and could therefore counter the reducing effect that sea ice loss possibly could have on carbon isotopes. It is not possible to assess which marine prey resource are influencing the dietary range in figure 3, but more muscle samples have higher $\delta^{15}\text{N}$ values and some of them are closer to seal. Foxes can scavenge for seal carcasses with available sea ice in winter (Roth 2002, Roth 2003), which may explain this pattern.

A few values are located closer towards isotope values of goose eggs in the muscle plot (figure 3). This might indicate that some individuals were very reliant on goose egg caches in winter, a food source they are known to use (Frafjord 1993, Samelius et al. 2007). That there are more isotope values closer to goose eggs in winter than autumn might be because caches might play a bigger role proportionally for some individual foxes, as food is scarce in the harsh polar winter. In Canada, Arctic foxes are known to cache thousands of goose eggs every year close to the goose colonies, which are indeed shown to make up large proportion (at low lemming abundance) of the studied autumn and spring diet (Samelius et al. 2007). This could support the suggestion that a few individuals in this thesis seem reliant on caches of goose eggs. Consumption of Svalbard rock ptarmigan might contribute to a more terrestrial signature, but their importance in fox diet cannot be assessed separately as their isotope values overlap with that of reindeer.

4.2 Spatial and temporal trends

There was a general trend in decreasing carbon isotope values over time, where the temporal trends additionally showed regional variation. The temporal trends for carbon isotope values of muscle (figure 5) are steeper for the northern regions compared to the trend of Nordenskiöld Land. Wijdefjorden shows a weaker temporal trend than North-West (figure 5 c and d), as well as lower positioned isotope value ranges (figure 4). This could be explained by that North-West (and Kapp Wijk) only have samples collected close to the coast, while Wijdefjorden had some inland samples included as well. Being further inland means more likely a higher proportion of terrestrial diet compared to being closer to the coast, resulting in

lower isotope values. Northern areas of Svalbard have not reached the same environmental conditions as Nordenskiöld Land where lack of sea ice is becoming more normal, as the northern parts are colder with smaller influence by the warm Atlantic currents (Dahlke et al. 2020). Though the environmental changes have been larger in Nordenskiöld Land (Dahlke et al. 2020), the northern regions are experiencing sea ice reduction when ice cover is still larger than the southern region. The steeper trends in the north could therefore possibly be explained by northern foxes experiencing a greater reduction in ice cover and marine resource availability in the periods they were sampled.

Fur data do not have the same long time series as the muscle data but do show a significant drop in isotope range in Nordenskiöld Land for season 2019/2020 (figure 6 a and e) after the large gap in years (7 years) due to lack of data. Unlike for muscle, the fur isotope values show a clear negative temporal trend for nitrogen as well. The prediction was that because geese have high nitrogen isotope values, the drastically increasing geese resource would buffer the negative trend on nitrogen caused by a shift to more terrestrial resources due to other factors like reducing sea ice extent. But this was not the case for the temporal trend of nitrogen isotope values of fur. One potential explanation for this could be a possible reduction in population of some species of seabirds on Svalbard. Some species seemed to decrease, while others seemed to increase, with the huge populations of Little Auk (*Alle alle*), Brünnich's Guillemot (*Uria lomvia*) and Northern Fulmar possibly declining since 2009 (Descamps & Strøm 2021). As mentioned above, nitrogen isotope values of the marine benthic fauna on Svalbard range across the same range of nitrogen values of Arctic fox (compared isotope values of benthos from Søreide et al. 2013 with values of figure 3). To assess if marine invertebrates impact the temporal trend of nitrogen isotopes, more knowledge of which species the foxes consume and prefer is needed. Though the temporal trends of fur do seem to also be negative for the North-West and Wijdefjorden regions, the sample size is too small across too few years to be able to conclude their effects (figure 6 c, d, g and h).

Autumn temporal trends (based on fur isotopes) are steeper than winter trends (muscle isotopes) on Nordenskiöld Land for both carbon isotopes (figure 5 a-6 a) and nitrogen isotopes (figure 5 e-6 e). The slope estimate of the temporal trends of fur might be biased as its significance and steepness is caused by the separate 2019/2020 season. If the indication for a stronger trend for fur is valid, this would be consistent with a hypothesized effect of decreasing seabird populations. This could then suggest that decreasing populations of seabirds have a stronger effect on the overall proportion of marine resources in the fox diet

than sea ice reduction in winter, but other factors that could counter the effect of sea ice should be explored.

The results show that long time series of data are highly valuable, and that interpretation is more difficult when there are gaps in the data series. This is because components of an ecosystem are dynamic, where population sizes, climatic factors and isotope values varies within the temporal frame. Samples from only a few years do not necessarily provide enough data for studying a system (Magurran et al. 2010), as indicated by the small sized datasets used in this thesis. There is the risk of the results being influenced by errors or coincidental pulses of biotic or abiotic variables in small datasets, as is seen with the winter temporal trend in Kapp Wijk being influenced by one sample in a separate year (figure 5 b and f). Especially in ecological studies, it is essential to have long time series of data, both of response and explanatory variables. Changes in nature usually happens slowly over time, and one cannot say for sure whether there have been any effects or not by a studied variable in a short time frame (Cusser et al. 2021). Even if there is great between year variability (e.g., with isotope values or prey availabilities), long time frame studies might be able to reveal trends of change, which can then be further used to possibly predict future trends and outcomes.

4.3 Impact of environmental drivers and coastal distance

According to the results, number of geese, reindeer carcass numbers and distance to the coast had significant effect on isotope values in winter (muscle). The full range of geese number had an effect of reducing the carbon isotope values approximately by 1 ‰ (figure 7 a). Isotope values of carbon of Arctic foxes range from about -27 to -20 ‰ (figure 3), so the strong increase in number of geese on Svalbard show a significant change towards a more terrestrial diet in winter. With the continuing warming of the climate on Svalbard resulting in increases of goose populations and reduction of ice cover, the diet and ecological role of Arctic foxes will increasingly become more terrestrial. Results of sea ice extent, which represents marine resource availability (mainly seal carcass) on the ice, did however not indicate any significant effect on isotopes.

In autumn (fur), only the number of geese had significant effect on isotope values. In autumn, the full range of geese number (over the same time frame as fur data) had an effect of reducing carbon isotope values approximately by 2.4 ‰ (figure 9 a) and nitrogen isotope

values by 1.8 ‰ (figure 9 c). Because the number of geese is the only variable other than the distance from the coast included in fur models, it is possible that the effect of geese is confounded with other factors that exhibit similar trends. For example, the negative effect of geese number on nitrogen isotope values is unexpected, as the nitrogen isotope value range of geese is high, similar to marine food resources (see figure 3). Again, other factors like seabirds and marine invertebrates could explain the negative trend reflected in the significant effects of geese, and these are needed in the models to be able to distinguish effects on isotopes in autumn.

The effect of the number of reindeer carcasses was not significant on isotope values in winter, but the fluctuations of the carcass numbers was. The full range of fluctuations in reindeer carcass numbers had an effect of reducing carbon isotope values approximately by 0.5 ‰ (figure 8 b). The number of reindeer carcass did not show any clear temporal trend (figure 2 b), which could explain why it had no significant effect on isotope values. The availability of reindeer carcasses in winter are important for the Arctic fox dynamics (Hansen et al. 2013, Eide et al. 2012), and this is shown by the significance of the carcass fluctuations. Effect might be weak because of the sample timing, as many reindeer die of hunger in late winter, while isotopes cover whole winter (but not as late as April). The effect of the number of reindeer carcasses might be clearer if isotopes reflected diet in late winter. Winters with higher abundance of reindeer carcasses would add to the effect of Arctic fox diet becoming more terrestrial for that winter. In the future, if the number of reindeer carcasses would increase over time due to warmer climate and increased frequency of ROS, its effect on Arctic fox diet could be revealed and add to the diet becoming more terrestrial. It was unexpected to not find a clear relationship between reindeer carcass and isotope values. Maybe the data of reindeer carcasses used in this thesis are not accurate enough to give significant effects, as the data are only from counts in Adventdalen (one valley in Nordenskiöld Land).

The full range of coastal distance had an effect of reducing the values of carbon isotopes approximately by 1 ‰ (figure 7 d-8 d) and the values of nitrogen by 1.7 ‰ (figure 7 h-8 h). Arctic foxes on Svalbard are known to be very mobile (Eide et al. 2012, Ehrich et al. 2011a), but results of this thesis show that there are significant differences in stable isotope values, and therefore diet, between coast and inland, implying that Arctic foxes are more sedentary in winter than previously thought. It could also mean that foxes are still very mobile, but mostly within either coastal or inland habitats. Results of this thesis show fox diet over short periods of time (1-2 months for muscle samples and molting period for fur samples), meaning foxes

could be more residential in smaller temporal frames, but highly mobile over their life cycles. On Bylot Island in Nunavut, Canada when sea ice was present, most Arctic foxes were found to remain residential (Lai et al. 2017). This was especially the case when foxes were in highly predictable resource pulse areas like goose nesting areas or areas with abundance of egg caches (Lai et al. 2017). This supports the significant effect that the distance from the coast has on isotopes, implying that foxes are being even more sedentary than predicted. Foxes are shown to commute on the sea ice (Lai et al. 2017) instead of long-distance migrations, which could also be the case on Svalbard, especially when increases in goose egg caches could lessen the need to do travel long distances. Estimates of the distance to the coast effects from fur models are close to that of muscle models, so maybe coastal distance would show significance if there were more data of fur isotopes, as it is significant in the bigger dataset of muscle models. It seems that coordinates of general, larger scale trapping areas were reported for some samples (not all trappers provided coordinates of each trap) instead of exact locations, though the coordinate data probably still align well with the distance from the coast gradient, since the effect of the distance to the coast were found significant. Still, better reporting of more precise coordinates could improve model estimates.

4.4 Arctic fox diet in circumpolar coastal Arctic ecosystems

For Arctic foxes on Svalbard, a system without cyclic small rodent populations, there is almost no changes in diet between years over a short time frame (Ehrich et al. 2015), which is also seen in this thesis (small changes over few years, as is seen in figure 5-6 for Nordenskiöld Land). Western Greenland also has no rodents, while they are rare in Iceland (Angerbjörn et al. 1994). In Zackenberg (coastal eastern Greenland) and Yamal (north-western Siberia) rodents are present, but their population cycles are more stable and at low abundances (Ehrich et al. 2015). These regions also show stability in diet of Arctic foxes over shorter time frames, and apart from Yamal has larger span in dietary range (Ehrich et al. 2015, Ellgutter et al. 2020). Larger shifts in diet could be expected when cycling small rodent populations are present (foxes act as specialists), as is seen in many systems with cycling lemming populations (Ehrich et al. 2015, Giroux et al. 2012, Roth 2002, Roth 2003). Over longer time frames however, it is revealed that the Arctic fox diet on Svalbard has slowly become more terrestrial due to changes in the environment, as is also the case in Iceland (Ellgutter et al. 2020).

Marine resources are important for Arctic foxes on Svalbard (Ehrich et al. 2015, Eide et al. 2012), as well in Greenland and Iceland (Angerbjörn et al. 1994, Ellgutter et al. 2020). The decline of marine input to diet is happening slowly over time, with marine input still important for Arctic foxes as isotope values still range between marine and terrestrial resources (as seen in this thesis and Ellgutter et al. 2020). Marine resources seem less important in systems with small cyclic rodent populations, showing differing importance of different types of resources in comparison to Svalbard, Iceland and Greenland. A stable isotope study from Iceland suggests that a recent drop in Arctic fox population size might be related to decreasing populations of seabirds (Ellgutter et al. 2020). As mentioned, a possible decline of seabird populations on Svalbard could explain the reducing trend of nitrogen isotope values in autumn in this thesis, indicating the importance of seabirds for both systems. As is shown for Svalbard in this thesis, the Arctic foxes at the coast and in inland areas in Iceland also showed differing isotope values (Angerbjörn et al. 1994, Ellgutter et al. 2020), signifying stronger marine input at the coast and terrestrial in inland areas. The system of Iceland and Greenland seem similar to Svalbard, with Svalbard possibly developing more similarities to Iceland as climate change continues.

4.5 Ecological implications

Nater et al. 2021 showed how changes in the environmental variables goose reproduction, reindeer carcass number and sea ice extent (latter two are same variables used in this thesis) impact Arctic fox population dynamics on Svalbard. Both population size and age structure were stable over time for the foxes (Nater et al. 2021), and population size projections showed population trajectories with neither drastic population extinction or explosion (Nater et al. 2021 supplementary information). According to their analyses, increases in goose reproduction (affecting only juveniles foxes), reindeer carcass availability and sea ice extent reduced fox mortality, and reindeer carcass availability and sea ice extent increased fox pregnancy rate, number of fetuses (sea ice extent only) and denning survival (reindeer carcass availability only). In this thesis, the effect of sea ice extent was not significant on Arctic fox diet, and could potentially be obscured by other factors not accounted for in the present thesis. The effects of terrestrial resources however were significant. The results of the present thesis and Nater et al. 2021 show the importance that the environmental variables have on Arctic foxes on Svalbard, where changes in them significantly impact the foxes numerically (as seen

in Nater et al. 2021) and functionally with increased use of the terrestrial ecosystem (seen as diet shift in this thesis). The Arctic fox as a generalist predator is shown to be able to switch to alternative resources and being resilient to drastic changes in environment and climate.

Arctic foxes are shown to not be as affected by lowering lemming abundance compared to more strictly specialist species, as they can be generalists and are able to make use of alternative resources (Schmidt et al. 2012, Schmidt et al. 2017). Although Arctic interaction webs are known as simple, especially on Svalbard, they are still complex and may have high degree of interaction and generalism where most species are flexible (Schmidt et al. 2017). Because ecosystems are complex with generalists being able to exploit different distinct functional resource groups and ecosystems, the opportunistic generalists and scavengers of the Arctic are thought to be resilient to changes in environment and climate (Nater et al. 2021, Schmidt et al. 2017).

Research on effects of environmental change on more resilient systems, or generalist predators, could be important to be able to understand how the changes influence Arctic ecosystems and what thresholds the systems might have. Sensitive systems and specialist species could give biased or extrapolated estimates and predictions of environmental change. Svalbard is simpler than other coastal Arctic ecosystems, where the fox are generalists linking marine and terrestrial ecosystems. Svalbard is also an isolated island that is not affected by the more dominant red fox migrating from the south as on the Arctic continents, which adds to the simplicity (Killengreen et al. 2011, Ehrich et al. 2015). One can therefore expect that more complex systems are possibly more resilient than the Svalbard system, as they are more interlinked (Rooney & McCann 2012). Keeping this in mind, the Svalbard system with its higher degree of simplicity and isolation is more likely to give significant estimates of climate impact on coastal ecosystems and the interaction between marine and terrestrial systems. Study of the Svalbard system could therefore also give more understanding of the influence the generalist predators have on the changing systems, looking at shifts in the interaction web.

4.6 Concluding remarks

Svalbard Arctic foxes have in this thesis been shown to shift their diet to a higher degree of terrestrial resources over a long time span as a functional response to environmental change, both in winter and autumn. Results from the present thesis showed significant effects of the

number of geese, distance from the coast and fluctuations in the number of available reindeer carcasses on the transition to a more terrestrial diet. Changes in nature happens slowly over time and can have large between year variability. The value of long time series of several variables was clear in this thesis, as long time data series were able to give significant results, while short time data series with few variables usually did not.

Continued monitoring and sampling is valuable in studying the impacts of changes in climate and resource availabilities on a coastal system with generalist predators. Including other parameters might be valuable in adding to the understanding of what influences the dietary change of Arctic foxes and changes in ecosystem structure. Further research on other factors like seabird population estimates and the Arctic fox's preference of marine invertebrates are of interest, as they might improve the models that will provide more accurate estimates.

Acknowledgements

First, I am very grateful to Dorothee Ehrich and Eva Fuglei, my thesis supervisors, for their helpful supervision and feedback throughout my work on this thesis. I thank all the trappers, that allowed for the Arctic fox carcasses to be given for research and sampling after skinning of the fur coat. I thank Åshild Ø. Pedersen for the data of reindeer carcasses and the Norwegian Polar Institute for the data of sea ice extent. I also thank the laboratory workers doing the stable isotope analysis in SINLAB in New Brunswick, Canada.

References

- Angerbjörn, A., et al. (1994). *Dietary variation in arctic foxes (Alopex lagopus) - an analysis of stable carbon isotopes*. *Oecologia*, 99, 226-232.
- Ben-David, M. & Flaherty, E. A. (2012). *Stable isotopes in mammalian research: a beginner's guide*. *Journal of Mammalogy*, 93(2), 312-328.
- Bradley, J. A., et al. (1981). *Age determination in the arctic fox (Alopex lagopus)*. *Can. J. Zool.*, 59(10), 1976-1979. <https://doi.org/10.1139/z81-269>

- Burnham, K. P. & Anderson, D. R. (2004). *Multimodel Inference: Understanding AIC and BIC in Model Selection*. *Sociological Methods & Research*, 33(2), 261-304.
<https://doi.org/10.1177/0049124104268644>
- Chapin III, F. S., et al. (2011). *Principles of Terrestrial Ecosystem Ecology* (2nd ed.). Springer, p. 3-22. <https://doi.org/10.1007/978-1-4419-9504-9>
- Cusser, S., et al. (2021). *How long do population level field experiments need to be? Utilising data from the 40-year-old LTER network*. *Ecology Letters*, 24(5), 1103-1111.
<https://doi.org/10.1111/ele.13710>
- Dahlke, S., et al. (2020). *The observed recent surface air temperature development across Svalbard and concurring footprints in local sea ice cover*. *Int J Climatol*, 1-20.
<https://doi.org/10.1002/joc.6517>
- Descamps, S., et al. (2017). *Climate change impacts on wildlife in a High Arctic archipelago - Svalbard, Norway*. *Global Change Biology*, 23, 490-502, <https://doi.org/10.1111/gcb.13381>
- Descamps, S. & Strøm, H. (2021). *As the Arctic becomes boreal: ongoing shifts in a high-Arctic seabird community*. *Ecology*, 102(11), e03485. <https://doi.org/10.1002/ecy.3485>
- Ehrich, D., et al. (2011a). *Age-dependent genetic structure of arctic foxes in Svalbard*. *Polar Biol*, 35, 53-62. <https://doi.org/10.1007/s00300-011-1030-1>
- Ehrich, D., et al. (2011b). *Stable isotope analysis: modelling lipid normalization for muscle and eggs from arctic mammals and birds*. *Methods in Ecology and Evolution*, 2, 66-76.
<https://doi.org/10.1111/j.2041-210X.2010.00047.x>
- Ehrich, D., et al. (2015). *What Can Stable Isotope Analysis of Top Predator Tissues Contribute to Monitoring of Tundra Ecosystems?* *Ecosystems*, 18, 404-416.
- Eide, N. E., et al. (2004). *Spatial organization of reproductive Arctic foxes *Alopex lagopus*: responses to changes in spatial and temporal availability of prey*. *Journal of Animal Ecology*, 73, 1056-1068.
- Eide, N. E., et al. (2005). *Dietary responses of arctic foxes *Alopex lagopus* to changing prey availability across an Arctic landscape*. *Wildlife Biology*, 11(2), 109-121.

Eide, N. E., et al. (2012). *Reproductive responses to spatial and temporal prey availability in a coastal Arctic fox population*. *Journal of Animal Ecology*, 81, 640-648.

Ellgutter, J. A. C., et al. (2020). *Dietary variation in Icelandic arctic fox (*Vulpes lagopus*) over a period of 30 years assessed through stable isotopes*. *Oecologia*, 192, 403-414.
<https://doi.org/10.1007/s00442-019-04580-0>

Elmhagen, B., et al. (2000). *The arctic fox (*Alopex lagopus*): an opportunistic specialist*. *J. Zool., Lond.*, 251, 139-149.

Frafjord, K. (1993). *Food Habits of Arctic Foxes (*Alopex lagopus*) on the Western Coast of Svalbard*. *Arctic*, 46(1), 49-54.

Fuglei, E. & Ims, R. A. (2008). *Global warming and effects on the arctic fox*. *Science Progress*, 91(2), 175-191. <https://doi.org/10.3184/003685008X327468>

Gilg, O., et al. (2006). *Functional and numerical responses of four lemming predators in high arctic Greenland*. *Oikos*, 113(2), 193-216. <https://doi.org/10.1111/j.2006.0030-1299.14125.x>

Giroux, M., et al. (2012). *Benefiting from a migratory prey: spatio-temporal patterns in allochthonous subsidization of an arctic predator*. *Journal of Animal Ecology*, 81, 533-542.

Grue, H., & Jensen, B. (1976). *Annual cementum structures in canine teeth in arctic foxes (*Alopex lagopus*(L.)) from Greenland and Denmark*. *Vildtbiologisk station*, 10(3), 12 p.

Hansen, B. B., et al. (2013). *Climate Events Synchronize the Dynamics of a Resident Vertebrate Community in the High Arctic*. *Science*, 339, 313-315.
<https://doi.org/10.1126/science.1226766>

Hansen, B. B., et al. (2014). *Warmer and wetter winters: characteristics and implications of an extreme weather event in the High Arctic*. *Environmental Research Letters*, 9, 114021.
<https://doi.org/10.1088/1748-9326/9/11/114021>

Heldbjerg H., et al. (Compilers). (2020). *Svalbard Pink-footed Goose Population Status Report 2019-2020 (*Anser brachyrhynchus*)*. AEW A EGMP Technical Report No. 15. Bonn, Germany.

IPCC. (2021). *Climate Change 2021: The Physical Science Basis: Summary for Policymakers*. Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change [Masson-Delmotte, V. & Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M. I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J. B. R., Maycock, T. K., Waterfeld, T., Yelekçi, O., Yu, R. and Zhou, B. (eds.)]. In Press.

Jepsen, J. U., et al. (2002). *The importance of prey distribution in habitat use by arctic foxes (Alopex lagopus)*. *Can. J. Zool.*, 80, 418-429. <https://doi.org/10.1139/Z02-023>

Johnson, F. A., et al. (Compilers). (2020). *Adaptive Harvest Management for the Svalbard Population of Pink-Footed Geese - 2020 Progress Summary*. AEWG EGMP Technical Report No. 16. Bonn, Germany.

Jónsdóttir, I. S. (2005). *Terrestrial Ecosystems on Svalbard: Heterogeneity, Complexity and Fragility from an Arctic Island Perspective*. *Biology & Environment Proceedings of the Royal Irish Academy*, 105(3), 155-165. <https://doi.org/10.3318/BIOE.2005.105.3.155>

Killengreen, S. T., et al. (2011). *The importance of marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the arctic tundra*. *Journal of Animal Ecology*, 80, 1049-1060.

Lai, S., et al. (2017). *Movement tactics of a mobile predator in a meta-ecosystem with fluctuating resources: the arctic fox in the High Arctic*. *Oikos*, 126(7), 937-947. <https://doi.org/10.1111/oik.03948>

Lecomte, N., et al. (2011). *Intrapopulation Variability Shaping Isotope Discrimination and Turnover: Experimental Evidence in Arctic Foxes*. *PLoS ONE*, 6(6), e21357. <https://doi.org/10.1371/journal.pone.0021357>

Magurran, A. E., et al. (2010). *Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time*. *Trends in Ecology and Evolution*, 25, 574-582. <https://doi.org/10.1016/j.tree.2010.06.016>

Nater, C. R., et al. (2021). *Contributions from terrestrial and marine resources stabilize predator populations in a rapidly changing climate*. *Ecosphere*, 12(6), e03546. <https://doi.org/10.1002/ecs2.3546>

- Newsome, S. D., et al. (2012). *Tools for quantifying isotopic niche space and dietary variation at the individual and population level*. *Journal of Mammalogy*, 93(2), 329-341.
- R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rooney, N. & McCann, K. S. (2012). *Integrating food web diversity, structure and stability*. *Trends in Ecology and Evolution*, 27(1), 40-46. <https://doi.org/10.1016/j.tree.2011.09.001>
- Roth, J. D. (2002). *Temporal variability in arctic fox diet as reflected in stable-carbon isotopes; the importance of sea ice*. *Oecologia*, 133, 70-77.
- Roth, J. D. (2003). *Variability in marine resources affects arctic fox population dynamics*. *Journal of Animal Ecology*, 72, 668-676.
- Samelius, G., et al. (2007). *Prolonging the arctic pulse: long-term exploitation of cached eggs by arctic foxes when lemmings are scarce*. *Journal of Animal Ecology*, 76, 873-880. <https://doi.org/10.1111/j.1365-2656.2007.01278.x>
- Schmidt, N. M., et al. (2012). *Response of an arctic predator guild to collapsing lemming cycles*. *Proc. R. Soc. B*, 279, 4417-4422. <https://doi.org/10.1098/rspb.2012.1490>
- Schmidt, N. M., et al. (2017). *Interaction webs in arctic ecosystems: Determinants of arctic change?* *Ambio*, 46, 12-25. <https://doi.org/10.1007/s13280-016-0862-x>
- Sklepkovych, B. O. & Montevecchi, W. A. (1996). *Food Availability and Food Hoarding Behaviour by Red and Arctic Foxes*. *Arctic*, 49(3), 228-234.
- Søreide, J. E., et al. (2013). *Sympagic-pelagic-benthic coupling in Arctic and Atlantic waters around Svalbard revealed by stable isotopic and fatty acid tracers*. *Marine Biology Research*, 9(9), 831-850.

Appendix

Table A: Overview of number of Arctic fox samples, for full dataset, over trapping seasons (1997/1998 to 2019/2020) per region and tissue type (Muscle and Fur). Trapping seasons 2000/2001 and 2005/2006 have no samples (-). Number of removed samples are not included in number of samples but are given in parenthesis (* means removed sample with same ID as another). Which samples were removed are described in the text. One sample (**) had very high value of both sea ice extent and coastal distance.

Trap season	Nordenskiöld Land		Kapp Wijk		North-West		Wijdefjorden	
	Muscle	Fur	Muscle	Fur	Muscle	Fur	Muscle	Fur
97/98	11		3					
98/99	10		1 (3)					
99/00	8		6					
00/01	-	-	-	-	-	-	-	-
01/02	4		10					
02/03	14							
03/04	11				2		1	
04/05	8				1		2	
05/06	-	-	-	-	-	-	-	-
06/07	26	26 (*1)			3	3	6	8
07/08	43	38					11	11
08/09	97	83	1	1	9	6	23	22
09/10	18	17						
10/11	45**	32 (1)					3	
11/12	30	26						
12/13	33							
13/14	26							
14/15	125						14	
15/16	19						7	
16/17	64				8			
17/18	101				11			
18/19	58							
19/20	157	98 (3)						
Total	908	320 (5)	21 (3)	1	34	9	67	41

Table B: Overview of number of Arctic fox samples, for reduced dataset used in model analysis, over trapping seasons (1997/1998 to 2019/2020) per region and tissue type (muscle and fur). It is a reduced version of Nordenskiöld Land data of table A. How the datasets are reduced are described in the text. Trapping seasons 2000/2001 and 2005/2006 have no samples (-). One sample (*) had very high value of both sea ice extent and coastal distance.

Trap season	Reduced muscle dataset	Reduced fur dataset
97/98	3	
98/99	9	
99/00	2	
00/01	-	-
01/02	3	
02/03	13	
03/04	10	
04/05	8	
05/06	-	-
06/07	17	22
07/08	27	38
08/09	73	83
09/10	17	17
10/11	31*	32
11/12	28	26
12/13	21	
13/14	17	
14/15	102	
15/16	14	
16/17	43	
17/18	83	
18/19	53	
19/20	140	98
Total	714	316

Table C: List of prey species and their mean isotope values and sd=standard deviation (rounded to 2 decimals). Sampled tissue, sample size, locations and years of sampling are also listed.

Species	Tissue	Sample Size	Mean $\delta^{13}\text{C}$ (sd)	Mean $\delta^{15}\text{N}$ (sd)	Location	Year
Svalbard Reindeer (<i>Rangifer tarandus platurhynchus</i>)	Muscle	39	-25.71 (0.32)	4.22 (1.26)	Sassendalen, Colesdalen, unknown	2007, 2008
Svalbard Rock Ptarmigan (<i>Lagopus muta hyperborea</i>)	Muscle	7	-26.55 (0.58)	4.01 (1.53)	Gruve 7	2008
Geese Muscle (<i>Anser brachyrhynchus</i> + <i>Branta leucopsis</i>)	Muscle	7	-27.89 (0.71)	11.10 (2.99)	Ny-Ålesund, Kongsfjorden, Fuglehuken	1997, 2007, 2008
Geese Egg (<i>Anser brachyrhynchus</i> + <i>Branta leucopsis</i>)	Egg membrane/ content	14	-26.62 (0.90)	17.06 (4.96)	Krossfjorden, Fuglehuken	2008
Common Eider (<i>Somateria mollissima</i>)	Muscle	5	-18.36 (0.53)	11.56 (0.62)	Kongsfjorden	2002, 2004, 2010
Little Auk (<i>Alle alle</i>)	Muscle	6	-20.78 (0.88)	11.23 (0.26)	Bjørndalen	2008
Northern Fulmar (<i>Fulmarus glacialis</i>)	Muscle	5	-22.12 (0.30)	13.02 (0.23)	Kongsfjorden	2006
Black-Legged Kittiwake (<i>Rissa tridactyla</i>)	Egg membrane	10	-18.97 (0.82)	11.60 (1.49)	Kongsfjorden	2008
Parasitic Jaeger (<i>Stercorarius parasiticus</i>)	Feather	36	-18.65 (1.87)	13.85 (1.41)	Ny-Ålesund, Kongsfjorden, Longyearbyen, Bjørndalen	2007, 2008

Brünnich's Guillemot Muscle (<i>Uria lomvia</i>)	Muscle	6	-20.15 (0.37)	12.43 (0.63)	Kongsfjorden, Fuglehuken	2006, 2007, 2008
Brünnich's Guillemot Egg (<i>Uria lomvia</i>)	Egg	10	-19.51 (1.61)	11.65 (0.77)	Fuglehuken, Krossfjorden	2008
Clupeid	Whole body	1	-19.77	12.60	Kongsfjorden	2008
Crab	Whole body	1	-18.77	7.03	Fuglehuken	2008
Atlantic Puffin (<i>Fratercula arctica</i>)	Muscle	1	-20.55	12.50	Fuglehuken	2008
Ringed Seal (<i>Pusa hispida</i>)	Muscle	13	-19.71 (0.45)	14.87 (0.49)	Van Mijenfjorden, Tempelfjorden	2007

Table D: List of untransformed linear muscle models used in model selection. *K* (number of parameters), *AICc* and $\Delta AICc$ (difference in *AICc* from the top model) given for the models, for both when $\delta^{13}C$ or $\delta^{15}N$ are set as response variable. *Geese*=geese number, *Rcarcass*=reindeer carcass number, *Ice*=sea ice extent, *DistSea*=coastal distance, *Age*=age class. A + signifies additive effect and a * signifies interaction.

Untransformed muscle model Explanatory variables	K		AICc		$\Delta AICc$	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Geese + Rcarcass + Ice + DistSea	6	6	2457.46	3015.31	0	0
Geese*DistSea + Rcarcass + Ice	7	7	2458.17	3017.23	0.72	1.92
Geese + Rcarcass*DistSea + Ice	7	7	2459.33	3017.14	1.88	1.82
Geese + Rcarcass + Ice + DistSea + Age	7	7	2459.41	3016.60	1.95	1.29
Geese + Rcarcass + Ice*DistSea	7	7	2459.50	3017.30	2.04	1.99
Geese*DistSea + Rcarcass + Ice + Age	8	8	2460.12	3018.53	2.67	3.22
Geese + Rcarcass*DistSea + Ice + Age	8	8	2461.30	3018.45	3.84	3.14
Geese + Rcarcass + Ice*DistSea + Age	8	8	2461.45	3018.58	4.00	3.26
Geese*DistSea + Rcarcass*DistSea + Ice*DistSea	9	9	2462.15	3020.98	4.70	5.67
Geese*DistSea + Rcarcass*DistSea + Ice*DistSea + Age	10	10	2464.12	3022.29	6.66	6.98
Geese + Rcarcass + Ice	5	5	2478.03	3052.75	20.57	37.44

Table E: List of detrended linear muscle models used in model selection. *K* (number of parameters), *AICc* and $\Delta AICc$ (difference in *AICc* from the top model) given for the models, for both when $\delta^{13}C$ or $\delta^{15}N$ are set as response variable. *Geese*=detrended geese number, *Rcarcass*=detrended reindeer carcass number, *Ice*=detrended sea ice extent, *DistSea*=coastal distance, *Age*= age class. *A* + signifies additive effect and *a* * signifies interaction.

Detrended muscle model Explanatory variables	K		AICc		$\Delta AICc$	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Geese + Rcarcass + Ice + DistSea	6	6	2453.69	3011.71	0	0
Geese + Rcarcass*DistSea + Ice	7	7	2455.49	3013.48	1.18	1.77
Geese + Rcarcass + Ice*DistSea	7	7	2455.65	3013.74	1.96	2.03
Geese + Rcarcass + Ice + DistSea + Age	7	7	2455.71	3013.42	2.02	1.71
Geese*DistSea + Rcarcass + Ice	7	7	2455.72	3013.43	2.04	1.72
Geese + Rcarcass*DistSea + Ice + Age	8	8	2457.52	3015.20	3.83	3.49
Geese + Rcarcass + Ice*DistSea + Age	8	8	2457.68	3015.45	3.99	3.74
Geese*DistSea + Rcarcass + Ice + Age	8	8	2457.75	3015.13	4.07	3.42
Geese*DistSea + Rcarcass*DistSea + Ice*DistSea	9	9	2459.37	3017.36	5.69	5.65
Geese*DistSea + Rcarcass*DistSea + Ice*DistSea + Age	10	10	2461.42	3019.07	7.73	7.36
Geese + Rcarcass + Ice	5	5	2473.18	3045.49	19.50	35.78

Table F: List of untransformed linear fur models used in model selection. *K* (number of parameters), *AICc* and $\Delta AICc$ (difference in *AICc* from the top model) given for the models, for both when $\delta^{13}C$ or $\delta^{15}N$ are set as response variable. *Geese*=geese number, *DistSea*=coastal distance, *Age*= age class. *A* + signifies additive effect and *a* * signifies interaction.

Untransformed fur model Explanatory variables	K		AICc		$\Delta AICc$	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Geese + DistSea	4	4	1308.29	1396.60	0	0
Geese	3	3	1309.12	1396.62	0.83	0.01
Geese*DistSea	5	5	1310.34	1398.19	2.05	1.59
Geese + DistSea + Age	5	5	1310.35	1398.50	2.06	1.90
Geese*DistSea + Age	6	6	1312.42	1400.09	4.13	3.48

Table G: List of detrended linear fur models used in model selection. K (number of parameters), AICc and $\Delta AICc$ (difference in AICc from the top model) given for the models, for both when $\delta^{13}C$ or $\delta^{15}N$ are set as response variable. Geese=detrended geese number, DistSea=coastal distance, Age= age class. A + signifies additive effect and a * signifies interaction.

Detrended fur model Explanatory variables	K		AICc		$\Delta AICc$	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Geese + DistSea	4	4	1296.83	1390.19	0	0.50
Geese	3	3	1296.96	1389.69	0.13	0
Geese*DistSea	5	5	1298.44	1392.12	1.61	2.43
Geese + DistSea + Age	5	5	1298.89	1392.11	2.06	2.43
Geese*DistSea + Age	6	6	1300.51	1394.06	3.68	4.38

