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Marine Biomass Consumption by Wild Svalbard Reindeer: Fecal Stable Isotope Analysis as a Tool to Detect Climate Change Effects

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Abstract

Climate change in the Arctic is becoming evident with increased winter temperatures and changes in precipitation already perturbing Arctic ecosystems. Warm spells with rainfall in winter, also known as rain on snow (ROS) events, allow accumulation of ice on the tundra, hindering arctic herbivores access to preferred forage. Observations of the Svalbard reindeer (*Rangifer tarandus platyrhynchus*) in the high Arctic archipelago of Svalbard might indicate utilization of marine food sources during winters with severe icing conditions. Here I used spatially mapped population monitoring data from nine winters to first test the hypothesis that kelp and seaweed are utilized more frequently during years with heavy ROS and accumulated tundra ice. I find support for the hypothesis based on a positive correlation between proportion of animals foraging along the shore and the amount of tundra ice the respective winter. Second, I do stable isotope analysis (SIA) on fecal and kelp samples to assess new methods for monitoring such changes in the realized foraging niche among high arctic ungulates. $\delta^{13}C$ values were significantly higher for kelp and feces from the two marine feeder groups than feces from the two terrestrially feeding groups. For $\delta^{34}S$, with three analyzed categories, including kelp and the two considered extremes, there were no significant difference between kelp and feces from reindeer feeding on kelp, but significantly lower and non-overlapping values for feces from terrestrial feeders. Large variations in $\delta^{15}N$ values within terrestrial fecal samples and large overlap among sample groups (kelp and the different fecal groups) dismiss Nitrogen as a viable option. Thus, $\delta^{13}C$ and $\delta^{34}S$ values represent the best indicators distinguishing between marine and terrestrial forage origins. These results emphasize the importance of monitoring changes in foraging behavior as a mean to predict effects of the expected increase in ROS-events in circumpolar regions. SIA on feces may provide a cost-efficient, non-invasive tool to better achieve this and could easily be implemented in current and future research and monitoring programs.

Sammendrag

Klimaendringer i arktis begynner å bli beviselig tydligere med økte vintertemperaturer og store endringer i nedbørsmønstre, noe som allerede er med på å forstyrre arktiske økosystemer. Varme perioder med regn om vinteren, kjent som «rain on snow» (ROS) hendelser, fører til akkumulering av is på tundraen som igjen hindrer arktiske planteetere tilgang til foretrukket beite. Observasjoner av Svalbard reinsdyr (*Rangifer tarandus platyrhynchus*) på øygruppen Svalbard har gitt indikasjoner på bruk av alternative matkilder under perioder med kraftig isdannelse på tundraen. I denne oppgaven brukte jeg først posisjonsdata fra ni år med reintellinger på Svalbard for å teste hypotesen om at tang og tare blir brukt oftere i år med kraftige ROS-hendelser og akummulert is. Jeg finner støtte for denne hypotesen basert på en positiv korrelasjon mellom andel beitene dyr langs kysten og mengden av is respektive år. For det andre gjør jeg stabile isotop analyser (SIA) på avføring og tang/tare i et forsøk på å etablere nye metoder for overvåkning av endringer i faktisk beite blant hjortedyr i høyarktiske strøk. δ^{13}C-verdiene viste seg å være signifikant høyere for tang/tare og avføring som stammet fra marint beitene dyr enn for avføringsprøver fra terrestrisk beitende dyr. For δ^{34}S-analysene, med kun tre av fem kategorier analysert, inkludert tang/tare og avføring fra de to antatt ytterlige kategoriene i denne studien, var det ingen signifikant forskjell mellom tang/tare og avføring fra tangbeitende dyr men en signifikant lavere, ikke-overlappende forskjell i verdier fra terrestrisk beitende dyr. Store variasjoner i δ^{15}N-verdier innenfor de terrestriske avføringsprøvene og et stort overlapp blant prøvekategoriene forkaster nitrogen som et brukbart alternativ. Derfor ser det ut til at δ^{13}C og δ^{34}S representerer de beste indikatorene for å skille mellom beite med marint eller terrestrisk opphav. Disse resultatene understreker den betydning overvåkning av beiteadferdsendringer har for å kunne forutsi de fremtidige effektene av økte ROS-hendelser i sirkumpolare strøk. SIA av avføring kan vise seg å være et kostnadseffektivt og lite invaderende verktøy, for bedre å oppnå dette, og kan med enkelthet implementeres i nåværende og fremtidige forsknings- og overvåkningsprogram.

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INTRODUCTION

Climate change and global warming have been predicted to be most pronounced in Arctic regions (Hassol 2004). Today this is becoming more and more evident with an increase in annual temperatures as well as an increase in extreme weather events and abnormal precipitation patterns (Hassol 2004, Walsh, Overland et al. 2011). The biggest contributor to this increased annual temperature is a rise in winter temperature and in some areas this rise is not just an overall increase in temperature but is manifested in shorter periods with above zero temperatures which allows precipitation to fall as rain (Serreze, Walsh et al. 2000), known as Rain on Snow (ROS) events. This type of warm spells with rain during winter allows thick ice layers to form on the tundra and can have a big impact on ecosystems in the Arctic, directly affecting everything from plant community (Bjerke 2011, Cooper 2014) and soil micro arthropod communities (Coulson, Leinaas et al. 2000) to mammalian populations (Kohler and Aanes 2004, Ims, Henden et al. 2008, Hansen, Aanes et al. 2011, Hansen, Grøtan et al. 2013). Details regarding effects of ROS are still not fully understood and further knowledge regarding these events are critical, especially as they effect herbivores in isolated locations where the possibility for long distance migrations are limited.

Ice layer accumulation due to ROS is especially challenging for overwintering arctic herbivores whose survivability primarily is determined by winter snow and ice conditions (Putkonen and Roe 2003, Hansen, Grøtan et al. 2013) Forage paramount for winter survival, normally accessible under soft layers of snow, will now more frequently be covered by thick layers of ice which can strongly affect ungulate population dynamics by reducing reproductive rate (Solberg, Jordhøy et al. 2001, Stien, Ims et al. 2012) and survivability among large herbivores such as muskoxen (*Ovibos moschatus* (Forchhammer and Boertmann 1993) and reindeer/caribou (Peary caribou *Rangifer tarandus pearyi* (Miller and Gunn 2003, Tews, Ferguson et al. 2007); Svalbard reindeer *R. tarandus platyrhynchus* (Solberg, Jordhøy et al. 2001, Kohler and Aanes 2004, Hansen, Aanes et al. 2011); semi-domesticated reindeer *R. tarandus tarandus* (Tveraa, Fauchald et al. 2007).

Demographic responses affected by stochastic environmental events, such as ROS, are increasingly well studied (Helle and Kojola 2008, Gaillard, Mark Hewison et al. 2013) and it is expected that continued increase in future ROS-event frequency could turn out to be devastating for a wide array of herbivores living in the Arctic (Forchhammer and Boertmann 1993, Hansen, Aanes et al. 2011). However, in areas and years with “extreme” weather conditions there have been indications of behavioral adaptations that could help buffer this expected increase, adaptations such as an increase in range displacement (Stien, Loe et al. 2010) and change in foraging niches (Larter and Nagy 2004, Hansen, Aanes et al. 2010, Hansen and Aanes 2012). These indications are mostly based on observational or anecdotal data from single years and little is known about to what degree and to what effect these adaptations might help herbivore sustainability in the Arctic. In order to effectively be able to predict future impacts of climate change on arctic herbivore populations, understanding the effects of foraging behavior adaptations on population sustainability are crucial (Post, Forchhammer et al. 2009).

On Spitsbergen, a part of the high arctic archipelago of Svalbard and Jan Mayen Islands, we find three, year round, resident herbivore vertebrate species; the Svalbard ptarmigan (*Lagopus muta hyperborea),* the Sibling vole (*Microtus levis)* and the Svalbard reindeer (*Rangifer tarandus platyrhynchus*). Here, average annual temperatures have risen approximately 4°C in the last 20 years (Norwegian Meteorological Institute) and warm spells with heavy ROS-events are becoming more and more frequent (Rennert, Roe et al. 2009). Heavy ROS-events have been shown to be especially challenging for the Svalbard reindeer. One population on the Brøgger peninsula near Ny Ålesund experienced, in winter 1993-94, a severe population decline following such an event because of lowered survivability due to ice locked pastures (Aanes, Sæther et al. 2000, Kohler and Aanes 2004). Die offs due to ROS-events as extreme as this are rare but are expected to occur more regularly following global warming (Rennert, Roe et al. 2009). However, several studies indicate that there might be behavioral adaptations among the Svalbard reindeer buffering the negative effects of these events. These include dispersal to other areas (Stien, Ims et al. 2012) such as movement to steeper terrain at higher altitudes which are less prone to thick ground icing, a more active use of olfactory senses in order to detect high value forage under the snowpack (Hansen, Aanes et al. 2010) and foraging on kelp and/or seaweed along the coast (Hansen and Aanes 2012).

There are observations of other ungulates utilizing kelp and seaweed; Red deer (*Cervus elaphus*) on the Isle of Rum (Conradt 2000), white-tailed deer (*Odocoileus virginianus*) on Anticosti Island (Giroux, Valiquette et al. 2015), Reindeer in South Georgia (Leader-Williams 1988), domesticated sheep (*Ovis aries*) (Hall 1975, Levring 1977, Jarvis 1998), reviewed in (Carlton and Hodder 2003). Along parts of the wintery coast of Spitsbergen, kelp and seaweed are often found in abundance, either swept ashore by winter storms or carried on land by scouring sea ice (B.B. Hansen, pers. comm.). This marine food source was observed to be utilized by parts of the Svalbard reindeer population following an episode with severe ground icing (Hansen and Aanes 2012). Little is known about to what degree this is used as an alternative to terrestrial forage and how it correlates with winter conditions. Neither is it known if consumption of marine resources could be a last resort strategy in order to avoid starvation making the Svalbard reindeer able to buffer some of the negative effects of ROS.

The Svalbard reindeer populations do not have any natural predators (Solberg et al. 2008), nor are they suffering noticeable from insect harassment (Hagemoen and Reimers 2002) and they tend to stay in defined populations without any large scale migration due to Spitsbergen topography, with mountains, glaciers and fjords, hard for the animals to traverse (Tyler and Øritsland 1989), with support from a genetic study (Côté, Dallas et al. 2002). Forage availability and animal density are the main factors determining Svalbard reindeer population dynamics (Solberg, Jordhøy et al. 2001) but also tooth wear are contributing to early death among Svalbard reindeer due sand particles ingested together with foraged low-growing plants (Veiberg, Mysterud et al. 2007). Weather and winter severity differ considerably between populations and from year to year making the Svalbard reindeer, including the aforementioned factors, an ideal study species in order to answer questions regarding effects of climate on foraging behavior in a high arctic ungulates.

In this study I will first test the hypothesis that utilization of marine forage increase with an increase in ice locked pastures, proposed in Hansen and Aanes (2012). To do this I will analyze spatially mapped population monitoring data to examine if animals tend to utilize forage available in the littoral zone to a higher degree in years when ROS events are more prevalent in the region and thus restricting forage availability on the tundra. Second, I will conduct stable isotope analysis (SIA) (Peterson and Fry 1987) on feces (Sponheimer, Robinson et al. 2003) collected in geographically distinct populations living under different winter conditions and compare them with SIA conducted on kelp and seaweed samples. SIA on different types of animal tissue are regarded as an effective method in order to investigate diets, both spatially and temporally (Dalerum and Angerbjörn 2005, Adams, Farley et al. 2010). SIA on fecal material will enable me to get a snapshot picture (approx. 24h) of utilized forage under current conditions. Feces are readily available wherever ungulates are found and are easy to obtain without disturbing the animals, already living under strong environmental stress. While SIA on feces might represent a useful method in order to determine variation in the realized niche by this high arctic ungulate undergoing huge environmental changes, the method needs to be tested and verified.

METHOD

Animal locations from annual population counts in the Ny-Ålesund area were provided by the Norwegian Polar Institute (NPI). Data from three subpopulations were included in this analysis, Brøggerhalvøya, Sarsøyra and Kaffiøyra (fig.1), all three regarded as coastal populations situated on the west coast of Spitsbergen. The census` span from 2006 to 2015, conducted in April, but data is lacking from 2009, and there is neither any data from Sarsøyra, 2013 to 2015 and Kaffiøyra, 2014 to 2015 due to logistical difficulties getting to these locations because of surging glaciers and absent sea ice. The counts were done by covering the whole area by snowmobiles, animals were counted and roughly registered with a position on a 1:50000 scaled map based on surrounding topography. It is expected that virtually all individuals in the three census areas were counted and registered (Aanes, Sæther et al. 2000). I analyzed position data by plotting all animal aggregations onto a map. Then each aggregation were measured with regard to distance from shoreline. All aggregations within 250 meters of the shoreline where then regarded as possible kelp/seaweed feeders, accounting for some positioning inaccuracy and the fact that animals feeding on kelp/seaweed partly utilize terrestrial food as well, often swapping between the food sources several times per day (fig.5). As a measure of winter severity two different variables were used; Rain on snow (ROS), based on amount of precipitation when temperatures exceeded 1°C (Stien, Ims et al. 2012), and measured ice thicknesses (Peeters et al. in prep. Hansen et al. 2011).

Feces, and kelp/seaweed were sampled at multiple locations on Spitsbergen, a part of the high Arctic archipelago of Svalbard. Three main areas were chosen for their difference in weather conditions and topography (fig.1) Adventdalen, an inland valley with mountain slopes easily accessible to reindeer and the area South of Kapp Linné, a flat coastal region with harsher climate cut of further inland by steep mountainous terrain hard for animals to traverse. In addition feces were collected from reindeer directly observed feeding on kelp and seaweed in the Ny Ålesund area in April 2014, Samples from Adventdalen and Kapp Linné were collected during 2014 and 2015 between February 17th - May 10th and Mars 12th - 14th respectively. Animals were approached in situ and observed foraging in the area, fecal material could be determined to be fresh from visual examination and from the fact that they lay on top of recent snowfall or observed defecated and thus collected. Nevertheless feces were only sampled if animals were in the immediate vicinity. Sex and age of the animals were not taken into account because it would be too time consuming to actually observe and identify the animal defecate before sampling. All material were put in marked zip-lock bags and stored frozen awaiting processing for analysis.

All samples were dried at 60°C for 24 hours. Fecal pellets were crushed into a fine homogenous powder using pestle and mortar which was rinsed with 100% ethanol (ANALAR) between each sample. Some fecal pellets contained gravel and therefore had to be sieved in order to separate the organic from the inorganic material. Samples were packed into small zip-lock bags before postage to the Environment and Natural Resources Institute Stable Isotope Laboratory at the University of Alaska, Anchorage (http://www.uaa.alaska.edu/enri/labs/sils) where analysis were to be conducted. Pulverized feces with a weight between 4.0 - 4.5 mg were packed into 3.5 x 5 mm tin sample cups (Costech, Valencia, CA) for analysis. Samples were analyzed using a Costech ECS 4010 elemental analyzer, (Costech, Valencia, CA), which gives the total proportion of carbon and nitrogen in a sample, coupled with a ThermoFinnigan Delta^{Plus} XP continuous-flow isotope ratio mass spectrometer (CF-IRMS; Thermo Scientific, Bremen, Germany) for $\delta^{13}C$ and $\delta^{15}N$ which was calibrated against international reference standards from the International Atomic Energy Agency (IAEA-N1, IAEA-CH7, IAEA-C3, and IAEA-600) and the USGS (USGS-25, USGS-40, and USGS-41). Some selected samples were also analyzed for $\delta^{34}S$ to provide additional chemical evidence of marine-derived biomass consumption. All values are referenced to Vienna Pee Dee Belemnite (VPDB) for $\delta^{13}C$, air for $\delta^{15}N$ and Vienna Cañon Diablo Troilite (VCDT) for $\delta^{34}S$.

From the census data both ice thickness and ROS were used to test correlation between winter severity and proportion of animals in the three populations feeding along the shore separately. Animals were classified as potential kelp/seaweed feeders, or not, based on the 250 m threshold proxy. Two generalized linear models, one with ROS and one with ice thickness set as predictor variable, with a binomial family (0 [kelp] or 1 [non-kelp]) and a logit link showed overdispersion with a residual deviance of 157 on 20 degrees of freedom, therefor year was introduced as a random variable in order to simulate stochasticity between years. In this mixed model (function lmer in R Package lme4) model selection were done using the corrected Akaike´s Information Criterion (AICc) and the MuMIn package (Bartoń 2013). ROS and Ice thickness, the two estimates of winter severity, were included in separate models. A total of 6 models where tested (table.2)

Feces and kelp samples were split into a total of five categories as follows; Kelp/seaweed (n=11), animals observed eating on kelp/seaweed at Kapp Linné (n=7) and Ny Ålesund (n=13) and lastly animals foraging on terrestrial forage in Adventdalen (n=60) and Kapp Linné (n=46). A selection of 5 samples from terrestrial feeders, 5 from marine feeders and 5 from kelp itself were selected for $\delta^{34}S$ analysis to be used as a reference for the other samples. All groups were statistically analyzed with regard to whether or not they differed in $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ from the kelp/seaweed samples, using linear regression models. All analyses were done in R version 3.0.2 (R Development Core Team 2013)

RESULTS

I found a strong variation in proportion animals foraging along the shoreline from year to year. In addition there were a minor significant variation between the three different areas. Among the models tested, the model with the best fit, according to AICc, were the model with ROS and area without any interactions between the two, while the second most parsimonious model replaced ROS with ice thickness (delta AICc = 0.2) (table.2). However, seeing that dAICc < 2 I chose to focus on the model with ice thickness seeing that as a more direct measure of actual conditions. Ice thickness were positively correlated with proportion of animals foraging along the shore (fig.2).

$\delta^{34}S$ values shows a clear enrichment of the heavier isotope both in kelp and droppings collected from animals observed feeding on kelp/seaweed, with no significant difference between them. Feces stemming from terrestrially foraging animals were significantly different from the two other groups (fig.3a & table.1).

The $\delta^{13}C$ values of kelp and feces showed large variation between the different categories (fig.3b). Kelp itself had a heavy carbon isotope enrichment significantly higher than any of the feces groups analyzed. The Ny Ålesund fecal material had the highest enrichment of the heavier isotope among the feces. The next group were fecal material collected from animals in Kapp Linné expected to feed on kelp/seaweed close to the shore closely followed by the group of animals from the same population feeding further inland. The feces with the lowest $\delta^{13}C$ values were collected from the inland population in Adventdalen. All groups tested for $\delta^{13}C$ values differed significantly between each other (table.1).

$\delta^{15}N$ values exhibited larger variation within the groups compared to $\delta^{13}C$ values (fig. 3c). Feces collected from Ny Ålesund seems to have the most enriched $\delta^{15}N$ values. Kelp itself had a significantly lower mean $\delta^{15}N$ value but with a variance spanning the Ny Ålesund feces values. Feces collected from Kapp Linné expected to be from animals which had at least partly fed on kelp have coinciding $\delta^{15}N$ values with kelp. Both the Adventdalen and Kapp Linné terrestrial groups have a significantly lower mean than kelp but with a large variance spanning the whole $\delta^{15}N$ spectrum among these samples without any significant difference between them (table.1).

DISCUSSION

Analysis of feces from terrestrial- and marine-foraging Svalbard reindeer showed a clear distinction in isotopic composition between the two, especially sulfur and carbon seems to be good indicators to determine these animals' diet. However, for sulfur, I only examined fifteen samples, five from every chosen group; kelp, feces stemming from animals feeding almost solely on kelp at Ny Ålesund (mar_nya) and feces stemming from animals residing in Adventdalen feeding on terrestrial forage (ter_adv), which can be regarded as the extremes in this study. This were done to add methodological certainty seeing that ^{34}S enrichment is regarded as a strong indicator when trying to distinguish between terrestrial and marine ecosystem origins (Peterson and Fry 1987). And even with this small sample size, SIA on sulfur shows a statistically significant difference between organic material stemming from kelp and material stemming from the terrestrial ecosystem. The small sample size analyzed for sulfur stems from the fact that the cost of analyzing sulfur are considerably higher than analyses of carbon and nitrogen and I had a limited budget for my analyses. Seeing that no samples from any of the intermediary samples were analyzed it is hard to conclude if sulfur is the best way to go but it looks promising and examining this further should not prove particularly hard.

All analyzed categories differed significantly from each other with regard to $\delta^{13}C$ values with pure kelp having the highest enrichment followed successively by the fecal samples according to what were expected through observation of what were digested by the animals and area of sampling. Among the fecal samples the ones collected from Ny Ålesund, in a spatially restricted coastal site (see Fig.1) where almost no terrestrial forage were available, showed the highest $\delta^{13}C$ values. The biggest $\delta^{13}C$ variation observed were from animals feeding along the shore of Kapp Linné, this comes as no surprise seeing that both kelp and plant forage were readily available at this location. The "inland" samples collected from Kapp Linné showed a small heavy carbon isotope enrichment compared to the samples collected from Adventdalen. This can be due to differences in proximity to the ocean and not necessarily an indication that these animals have been utilizing kelp. Seeing that Kapp Linné is a coastal location it is expected a certain heightened influx of $\delta^{13}C$, solely due to proximity to the ocean, mediated through both meteorological and biological processes such as precipitation, sea spray, marine bird deposits etc. Both terrestrial feces groups showed very little variation despite them being the categories with the biggest sample size, further strengthening that $\delta^{13}C$ analysis could be a good indicator in order to differentiate between marine and terrestrial forage.

The Svalbard reindeer is considered a generalist herbivore (Skogland 1989). It is shown that nitrogen isotope composition varies considerably among tundra plant taxa (Nadelhoffer, Shaver et al. 1996). This might explain the large variation in the $\delta^{15}N$ values for the two terrestrial groups which span all the other groups tested. For this reason $\delta^{15}N$ analysis, by itself, might not be a viable option in order to establish marine winter subsidies among tundra living herbivores but can be considered informative when looked at together with $\delta^{13}C$ values seeing the large variation in terrestrial $\delta^{15}N$ values compared to the marine $\delta^{15}N$ values (fig4).

The $\delta^{15}N$ x $\delta^{13}C$ plot clearly shows see the differences in isotopic composition (fig.4). It is interesting to see that two of the samples from the coastal location on Kapp Linné are very similar to the Ny Ålesund samples, indicating that these two individuals mainly has been feeding on kelp. The rest of the coastally foraging animals seems to have corresponding values with inland foraging animals at the same location, seeing that terrestrial forage were available along the coast of Kapp Linné this should be expected. One animal from the inland part of Kapp Linné have similar isotopic values as the Ny Ålesund individuals, suggesting that this individual recently have been foraging along the coast before moving inland. As expected there is no marine isotope signatures among the Adventdalen animals.

Stable isotope analysis on feces in order to establish dietary choice among high arctic ungulates might be considered a novel yet uncertain method. Feces are the remnants after assimilation, the fraction of the forage or consumed material that has passed thru the gut, and thus there are some uncertainty whether the material is something that usually are assimilated by the animals (Tieszen, Boutton et al. 1983). Therefor isotope composition might not give a correct picture of the diet composition if only applied to this type of material. Usually, when determining what an animal has foraged, SIA are conducted on tissue such as blood, hair, bone and/or muscle (Tieszen, Boutton et al. 1983) which of course will give a more correct picture of assimilated food and can even give an estimate on when what type of food was utilized depending on tissue examined, e.g. hair, which can be cut into sections which are analyzed separately in order to establish what the animal has been feeding on during the growth of the hair as done in (Darimont and Reimchen 2002). Feces, however, will only give an indication of what have been ingested a few hours earlier (Tieszen, Boutton et al. 1983). However, in this study I attempted to differentiate between forage with marine and terrestrial origin. It is known that isotope composition differ considerably between marine and terrestrial ecosystems (Balasse, Tresset et al. 2006, Bessa, Baeta et al. 2014) and SIA on feces might therefore be a sufficient tool in order to establish which ecosystem the animal has been feeding from. In addition, the short time resolution given by examining feces could be regarded as an advantage as it allows the researcher to get a snapshot picture of utilized forage under current conditions which can be measured and observed while in the field at the location in question. Also, sex and age of the animals could be included to see if kelp and seaweed are preferred by a certain part of the reindeer population. Observations indicate that it is the younger animals that tend to utilize kelp (Hansen and Aanes 2012). Which again might indicate that the less competitively strong individuals are the ones forced to utilize marine forage.

Analysis of animal positions during snapshots in late winter suggests that the animals are more likely to feed along the littoral zone when plant availability are scarce due to ice building up on the tundra hindering access to normal forage which indicate an increased utilization of marine forage during unfavorable conditions, given that kelp and seaweed are available. This availability of marine forage is very variable in time and space seeing that it depends on a multitude of factors such as tidal movements, winter storms, orientation of the coast, and exposure to wind and waves (Spiller, Piovia-Scott et al. 2010, Lastra, Rodil et al. 2014). In addition, topographical features might hinder animals reaching this food source, such as shore cliffs separating the tundra from the littoral zone. However, these factors can largely be expected to vary independently of climate change, except for potential sea ice effects. Accordingly, my results suggest that warmer wetter winters will induce increased utilization of marine subsidies by the Svalbard reindeer if available. And may also be expected to increasingly become so all over the circumpolar Arctic where kelp and seaweed are available.

CONCLUSION

Understanding how alternative food sources and feeding strategies may contribute to changes in the realized foraging niche of a species is important in order to be able to predict its future, given expected changes in climate and anthropogenic landscape use (Hof, Jansson et al. 2015), especially when predictions already estimate that the drivers for this type of foraging behavior will increase in the future. The west coast of Svalbard might be considered a bellwether location due to warm water being transported via the North Atlantic current increasing the overall temperature in the entire region and also making the effects of climate change more evident here than in other circumpolar regions, regions that in the future might expect an increase in similar climate scenarios with warmer and wetter winters (Hassol 2004). In this study I have shown that utilization of kelp and/or seaweed probably increase with winter severity and that SIA on carbon and sulfur in feces might be used to further investigate and monitor the effects of this foraging behavior. Seeing that utilization of kelp increases in correlation with a weather phenomenon that is expected to increase in frequency all over the circumpolar regions due to global warming, it is of outmost importance to monitor and examine possible effects of this behavior on arctic ungulate populations presently and in the future. The method proposed in this study is a non-invasive, cost-effective way to easily monitor marine subsidy utilization among arctic herbivores and could easily be incorporated in existing monitoring programs and research.

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TABLES

Table 1: Parameter estimates +/- SE and test statistics from linear regression models of $\delta^{34}S$, $\delta^{13}C$ and $\delta^{15}N$ as a function of sample type. All feces groups are compared against kelp/ seaweed values. Explanation of categories: kelp = analyzed kelp samples. mar_nya = analyzed feces from animals expected to only feed on kelp in the Ny Ålesund area. mar_kap = analyzed samples from animals observed feeding where kelp where available at Kapp Linné. ter_adv = analyzed feces from animals expected to feed solely on terrestrial forage in Adventdalen. ter_kapp = analyzed feces from animals feeding further inland at Kapp Linné.

	$\delta^{34}S$	$\delta^{13}C$	$\delta^{15}N$
Intercept (Kelp)	22.0004 +/- 0.2930	-18.4850 +/- 0.3234	3.2929 +/- 0.5191
	t= 75.076, p<<0.01	t= -57.159, p<<0.01	t= 6.343, p<<0.01
mar_kapp	-	-8.6199 +/- 0.5186	-0.3069 +/- 0.8090
	-	t= -16.622, p<<0.01	t= -0.379, p=0.705
mar_nya	-0.2214 +/- 0.4144	-3.8354 +/- 0.4394	1.4089 +/- 0.6905
	t= -0.534, p=0.603	t= -8.729, p<<0.01	t= 2.040, p<0.05
ter_adv	-25.1369 +/- 0.4144	-11.7823 +/- 0.3518	-1.8549 +/- 0.5607
	t= -60.656, p<<0.01	t= -33.492, p<<0,01	t= -3.308, p<0.01
ter_kapp	-	-10.0228 +/- 0.3600	-2.5314 +/- 0.5728
	-	t= -27.842, p<<0.01	t= -4.419, p<<0.01

Table 2: Model selection results from the analysis of the spatially mapped population monitoring data, where all animals were classified as being kelp/seaweed-feeder or not, based on proximity to shore. Models are ranked according to AICc, and parameter estimates +/- SE and test statistics are shown for variables included in the respective model. Ice = Ice thickness (cm) based on measurements and models. ROS = Amount of precipitation (mm) during periods with temperatures exceeding 0°C. Area = Brøggerhalvøya, Kaffiøyra and Sarsøyra.

	Intercept	Ice	lnROS	Area	Ice : Area	lnROS : Area	Year (sd)	AICc	dAICc
Model.1	-3.47 +/- 0.47 z= -7.42, p<<0.01	-	0.29 +/- 0.12 z= 2.43, p<0.05	Kaff: -0.38 +/- 0.22 z= -1.76, p=0.08 Sars: -0.9 +/- 0.24 z= -3.79, p<<0.01	-	-	0.5	207	0
Model.2	-3.01 +/- 0.30 z= -9.97, p<<0.01	0.091 +/- 0.036 z= 2.53, p<0.05	-	Kaff: -0.39 +/- 0.22 z= -10.5, p<<0.01 Sars: -0.88 +/- 0.24 z= -11.4, p<<0.01	-	-	0.47	207.2	0.2
Model.3	-3.08 +/- 0.5 z= -6.16, p<<0.01	-	0.18 +/- 0.13 z= 1.41, p=0.15	Kaff: -1.74 +/- 0.67 z= -2.61, p<0.01 Sars: -1.02 +/- 0.87 z= -1.17, p=0.24	-	Kaff: 0.34 +/- 0.15 z= 2.22, p<0.05 Sars: 0.05 +/- 0.2 z= 0.23, p=0.81	0.5	209.6	2.6
Model.4	-2.76 +/- 0.31 z= -8.9, p<<0.01	0.056 +/- 0.039 z= 1.43, p=0.15	-	Kaff: -0.79 +/- 0.38 z= -2.07, p<0.05 Sars: -1.71 +/- 0.49 z= -3.49, p<<0.01	Kaff: 0.056 +/- 0.04 z= 1.36, p=0.18 Sars: 0.1 +/- 0.05 z= 2.05, p<0.05	-	0.44	210.7	3.7
Model.5	-3.32 +/- 0.29 z= -11.35, p<<0.01	0.085 +/- 0.037 z= 2.32, p<0.05	-	-	-	-	0.47	215.1	8.1
Model.6	-3.71 +/- 0.47 z= -7.84, p<<0.01	-	0.26 +/- 0.12 z= 2.1, p<0.05	-	-	-	0.52	215.3	8.3

FIGURES

Figure 1: Map of Svalbard with the fecal sampling sites (red) and the three census areas (blue). Upper left: Ny Ålesund area (Brøggerhalvøya, Sarsøyra and Kaffiøyra from north to south with fecal sampling site in red which also is the area for the GPS-collared animals in fig.5). Lower left: Nordenskiold coast (Kapp Linné). Lower right: Adventdalen.

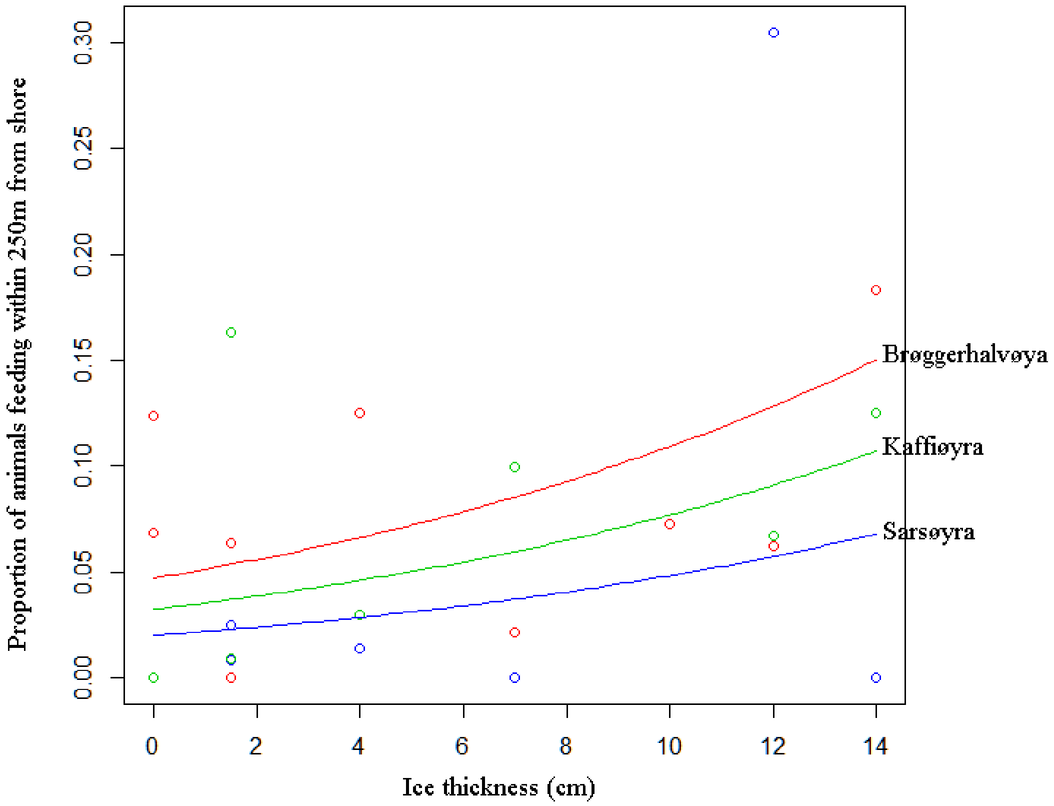

Figure 2: Proportion of animals mapped within 250m from the shore in the three census areas as a function of annual estimated ice thickness.

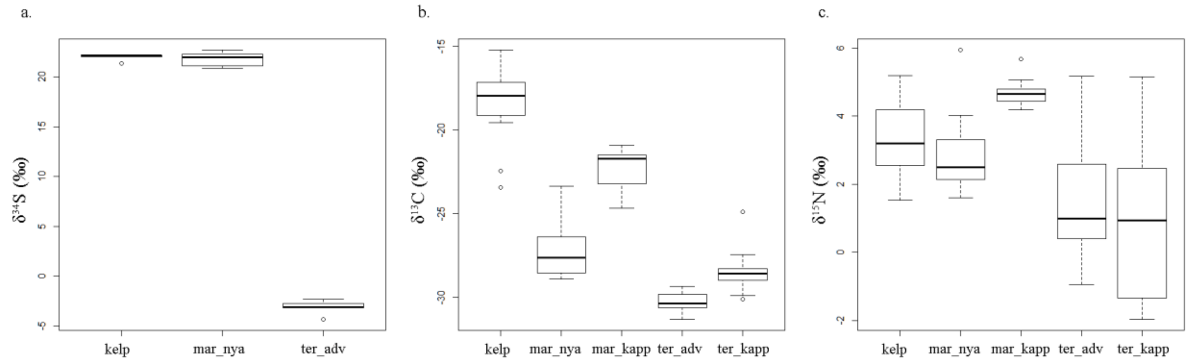

Figure 3: Boxplot of a. $\delta^{34}S$ values, b. $\delta^{13}C$ values and c. $\delta^{15}N$ values. Explanation of categories: kelp = analyzed kelp samples. mar_nya = analyzed feces from animals expected to only feed on kelp in the Ny Ålesund area. mar_kap = analyzed samples from animals observed feeding where kelp where available at Kapp Linné. ter_adv = analyzed feces from animals expected to feed solely on terrestrial forage in Adventdalen. ter_kapp = analyzed feces from animals feeding further inland at Kapp Linné.

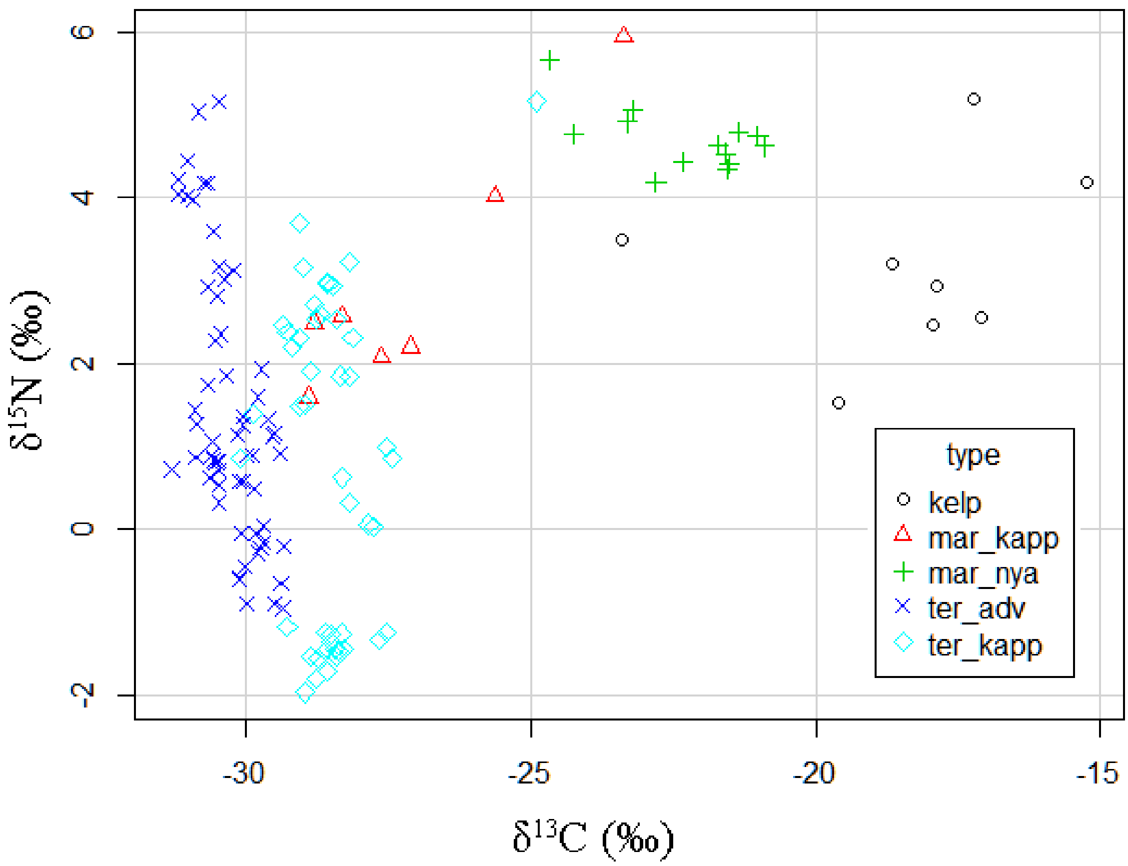

Figure 4: Carbon and Nitrogen isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) for kelp and all fecal samples from Svalbard reindeer. Explanation of categories: kelp = analyzed kelp samples. mar_nya = analyzed feces from animals expected to only feed on kelp in the Ny Ålesund area. mar_kap = analyzed samples from animals observed feeding where kelp where available at Kapp Linné. ter_adv = analyzed feces from animals expected to feed solely on terrestrial forage in Adventdalen. ter_kapp = analyzed feces from animals feeding further inland at Kapp Linné.

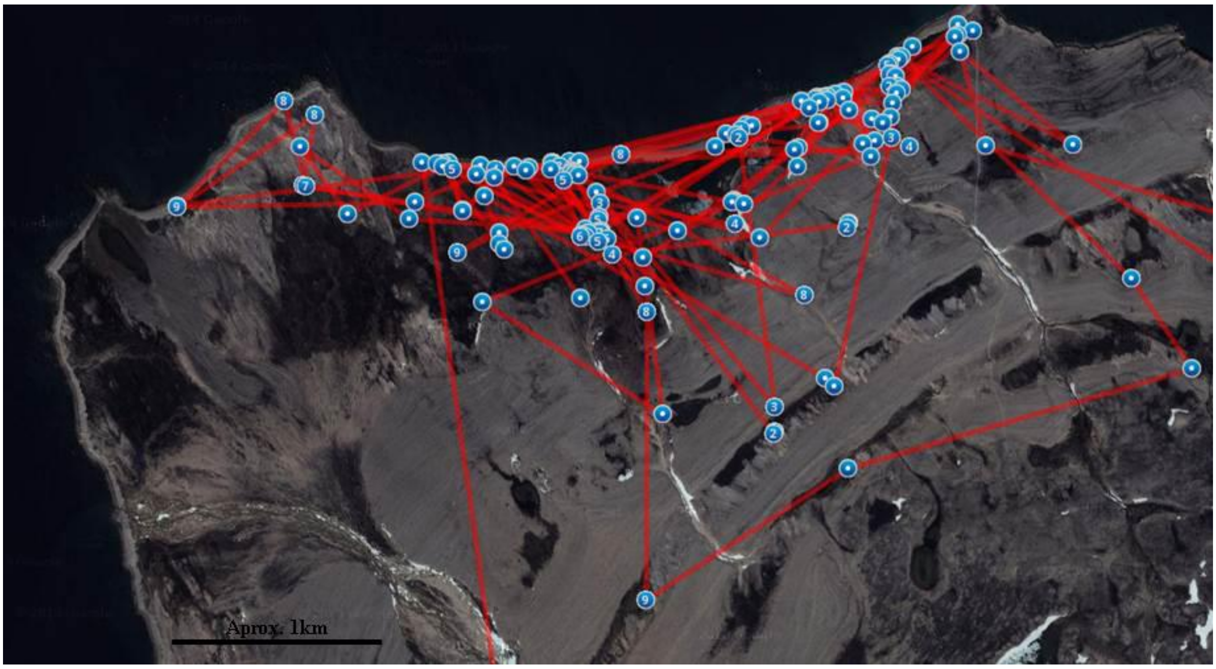

Figure 5: Locations of 5 (out of 10 in total) GPS-collared female reindeer on Brøggerhalvøya (close to Ny-Ålesund, see fig.1) during the first two weeks of March 2015, showing three locations per animal per day. Feeding conditions were icy due to several rain-on-snow events earlier that winter. Virtually no terrestrial forage was accessible in the displayed area on the NW tip of Brøggerhalvøya, an area known for being utilized for kelp and seaweed feeding during winter. The movements shown here reflect that reindeer typically move back and forth between littoral feeding areas and resting areas (possibly combined with some terrestrial feeding) further inland (B.B. Hansen, pers. obs.). Data are shown with permission from the Norwegian Polar Institute (Åshild Ø. Pedersen