Reindeer turning maritime: Ice-locked tundra triggers changes in dietary niche utilization

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Abstract.   The rapid warming of the Arctic may not only alter species' abundances and distributions, but likely also the trophic interactions within and between ecosystems. On the high-arctic tundra, extreme warm spells and associated rain-on-snow events in winter can encapsulate the vegetation entirely in ground-ice (i.e., basal ice) and directly or indirectly affect plants, herbivores, and carnivores. However, the implications of such extreme events for trophic interactions and food-web ecology are generally far from understood. Here, we show that wild Svalbard reindeer populations increasingly isolated by lack of sea-ice respond to rain-on-snow and ice-locked pastures by increased kelp consumption. Based on annual population surveys in late winters 2006–2015, the proportion of individual reindeer feeding along the shoreline increased the icier the winter. Stable isotope values (δ^{34}S, δ^{13}C, δ^{15}N) of plants, washed-ashore kelp, and fresh reindeer feces collected along coast-inland gradients, confirmed ingestion of marine biomass by the reindeer in the shoreline habitat. Thus, even on remote islands and peninsulas increasingly isolated by sea-ice loss, effects of climate change may be buffered in part by behavioral plasticity and increased use of resource subsidies. This marine dimension of a terrestrial herbivore's realized foraging niche adds to evidence that global warming significantly alters trophic interactions as well as meta-ecosystem processes.

Key words: adaptation; Arctic; behavior; caribou; diet; ground-ice; herbivore; meta-ecosystem; niche; rain-on-snow; *Rangifer tarandus platyrhynchus;* ungulate.

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INTRODUCTION

The most rapid climate change occurs in the Arctic, where huge ecological impacts are already evident across terrestrial and aquatic communities (Post et al. 2009, 2013, Wassmann et al. 2011, Ims and Ehrich 2013). It is now well recognized that gradual loss of sea-ice, changes in seasonal phenology, and enhanced primary production fueling the ecosystems may alter the abundance and distribution of a multitude of species. Some of these abiotic and biotic changes are likely to even impact meta-ecosystem processes (Loreau et al. 2003) by altering habitat availability and landscape connectivity, and thereby also the trophic linkages within and between Arctic ecosystems (Post et al. 2009, 2013).

On the Arctic tundra, the warming trend has been especially pronounced during winter. On top of a steady increase in mean ambient temperatures, more frequent extreme warm spells (Moore 2016) and rain-on-snow (ROS) events (Bintanja and Andry 2017) cause dramatic changes in snow-pack characteristics (Kohler and Aanes 2004, Rennert et al. 2009, Hansen et al. 2014, Peeters et al. 2019). At such high latitudes where permafrost prevails, heavy ROS percolating through the snow may generate thick solid ground-ice (i.e., basal ice), entirely encapsulating the short-growing vegetation across large areas (Peeters et al. 2019). Ground-icing directly affects vital rates in lichens (Bjerke 2011), plants (Milner et al. 2016), soil micro-arthropods (Coulson et al. 2000), and small and large herbivores (Hansen et al. 2013, Albon et al. 2017), with further implications for the abundance and distribution of carnivores (Hansen et al. 2013, Sokolov et al. 2016). In particular, ice-locked pastures contribute to the population fluctuations of caribou and wild reindeer (Rangifer tarandus) in high-arctic islands (Miller and Gunn 2003, Kohler and Aanes 2004, Hansen et al. 2011) by causing body mass loss, starvation, and reduced survival and fecundity (Albon et al. 2017). However, unlike a wide range of other taxa and biomes where evolution or phenotypic plasticity has been shown to buffer such negative impacts of climate change (Boutin and Lane 2014, Franks et al. 2014, Schilthuizen and Kellermann 2014), the ability of Arctic ungulates to adapt to altered winter feeding conditions still remains poorly understood.

Extreme weather events are expected to have the strongest impact on populations that are isolated and inhabit the edge of the species' geographical range (Easterling et al. 2000, Parmesan et al. 2000). Accordingly, population crashes in Arctic ungulates following extreme events have been most frequently reported in isolated and non-migratory (i.e., typically island) populations at high latitudes (Klein 1999, Miller and Gunn 2003, Kohler and Aanes 2004), where lack of dispersal opportunities may constrain movement and foraging behavior. However, recent GPS technology and individual-based data indicate that even in such isolated high-latitude systems, behavioral adjustments on small spatial scales (i.e., only a few km) may reduce negative effects of harsh winters. For instance, individuals of wild Svalbard reindeer (R. t. platyrhynchus) can respond through seasonal migrations between semi-isolated valleys or peninsulas (Hansen et al. 2010, Stien et al. 2010, Loe et al. 2016), with an apparent positive net fitness effect despite the potential costs involved along the migration routes. This indicates that individual behavioral plasticity and adaptive landscape use can—at least in part—buffer environmental change (Loe et al. 2016). However, the rapid loss of Arctic sea-ice, a potentially important dispersal corridor (Post et al. 2013), now increases the level of isolation and places further constraints on Arctic island ungulates' ability to respond to changing winters.

Most of non-alpine tundra is essentially a maritime biome, that is, located close to the coast (Walker et al. 2005). Indeed, several species of terrestrial large herbivores have occasionally or regularly been observed "outside their habitat" feeding on kelp or seaweed (e.g., island sheep Ovis aries, Hall 1975; red deer Cervus elaphus on the Isle of Rum, Conradt 2000; black-tailed deer Odocoileus hemionus, Parker et al. 1999; and reindeer, including an introduced population in South Georgia, Leader-Williams 1988; and wild populations in Svalbard, Hansen and Aanes 2012). However, what ultimately triggers an individual to include marine biomass as an exotic supplement to its plant-based diet is not well understood (Carlton and Hodder 2003). A change in utilization of the dietary niche can be a result of optimal foraging choices (e.g., a beneficial effect of nutrients or mineral supplements) yet, at the same time, a last resort to avoid starvation. For instance, during the rainy and icy 2009–2010 winter in the Ny-Ålesund area (79° N, 15° E) on the northwestern coast of Spitsbergen, Svalbard, we observed that isolated wild reindeer (i.e., populations on peninsulas surrounded by year-round open water, steep mountains, and large glaciers) were often feeding on kelp and seaweed as a resource subsidy (Hansen and Aanes 2012). The reindeer are in general stationary year-round but may disperse between neighboring, semi-isolated ranges when winter feeding conditions are harsh (Hansen et al. 2010, Stien et al. 2010, Loe et al. 2016). However, while land-fast sea-ice or drift-ice often covers fjords and bays during parts of the winter, such a potential dispersal corridor has been virtually absent on Western Spitsbergen

since the mid-2000s. In this study, we utilize long-term population monitoring time-series from the same study area (Hansen and Aanes 2012) combined with stable isotope analysis (SIA) of reindeer feces and forage, to explore the possible linkage between, and discuss implications of, marine biomass in reindeer winter diets and changes in winter feeding conditions. In particular, because of the strongly restricted dispersal opportunities among coastal sub-populations, we predicted an increase in marine biomass consumption as a response to increased winter severity, as indexed by ground-icing.

MATERIALS AND METHODS

Svalbard reindeer are solitary and characterized by a stationary and energy-saving behavior, enabled by the virtual lack of predation (Tyler 1987). Through the long Arctic winter, they rely in part on fat reserves built up during summer, but approximately three-quarters of the total energy must be obtained through active feeding (Tyler 1987). Winter forage availability and density dependence are the main drivers of population fluctuations (Kohler and Aanes 2004, Hansen et al. 2011). In particular, ground-icing due to ROS causes loss of body mass and reduced fecundity and survival in late winter (Albon et al. 2017). The areas close to Ny-Ålesund, our main study area (Fig. 1), represent a circumpolar hotspot for such ROS events (Kohler and Aanes 2004, Rennert et al. 2009) due to the recent rapid winter warming (Hansen et al. 2014) and the oceanic climate along the western coast of Spitsbergen.

We applied ground-ice data and reindeer population monitoring data from the Ny-Ålesund area to test our prediction (Hansen and Aanes 2012) that the probability of reindeer utilizing marine biomass increases the more severe the winter. This study area is characterized by coastal plains surrounded by calving glaciers, steep mountains, and the sea. Nine years (2006–2008,
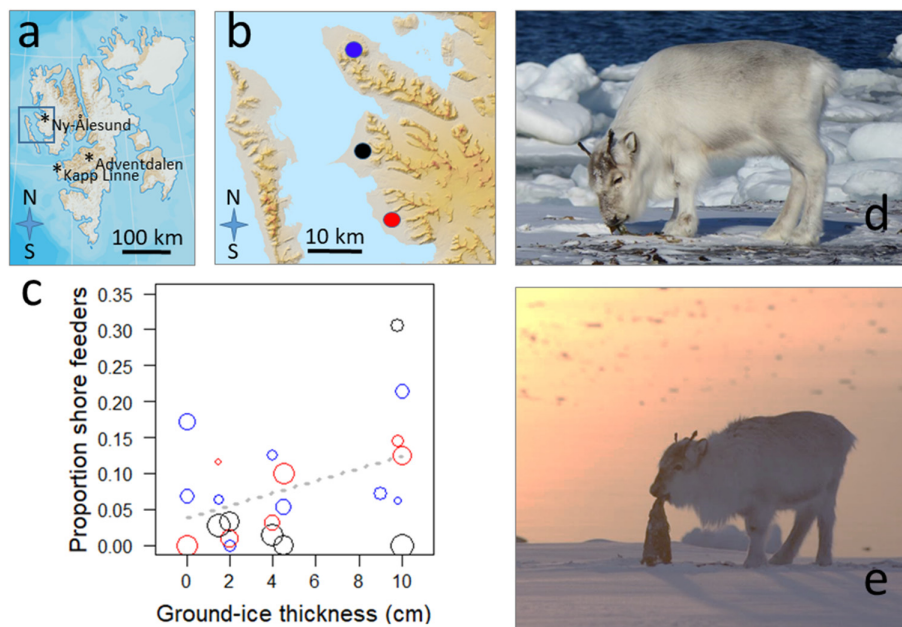

Fig. 1. (a) Location of the study areas in Spitsbergen, Svalbard. (b) Topographic map of the main study area close to Ny-Ålesund, with populations marked in blue (Brøggerhalvøya), black (Sarsøyra), and red (Kaffiøyra). (c) Annual proportion of Svalbard reindeer in the Ny-Ålesund study area feeding on the shoreline in late winter, as a function of the respective winter's average ground-ice thickness. Circle sizes are proportional to sample size. For illustration, we show the regression line from a linear mixed effects regression model with ground-ice thickness as fixed effect and population (color codes as in [b]) and year as random intercept effects. (d, e) Reindeer feeding on washed-ashore seaweed and kelp in late winter. Photographs: Malin Daase.

2010–2015) of data were available of ground-ice thickness measurements and the spatial distribution of the reindeer during a snapshot in late winter (April). Every detected reindeer was mapped and plotted on a 1:50,000 topographic map during total population counts performed by two persons on snowmobiles (see Hansen et al. 2011), covering the entire peninsulas of Brøggerhalvøya, Sarsøyra, and Kaffiøyra. Note that no survey was done in Sarsøyra in 2013–2015 or Kaffiøyra in 2014–2015. In total, $n = 2199$ reindeer were located (on average 244 [range: 83–362] per winter). From these survey data, we calculated the distance to the shoreline for all individual reindeer and classified them as shoreline or terrestrial feeder using a threshold distance of 250 m from the shoreline. This threshold was chosen based on direct field observations combined with locations of GPS-marked reindeer (see Fig. 2). Based on these classifications, we ran a generalized linear mixed effects regression model (function glmer in R
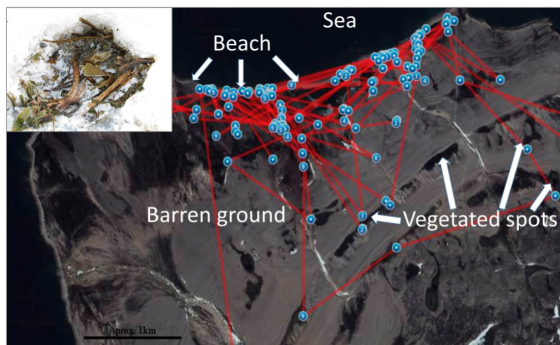

Fig. 2. Satellite photograph (taken in summer) of the NW corner of Brøggerhalvøya, showing winter relocations for n = five GPS-collared female reindeer (out of ten in total) during the first two weeks of March 2015, with three relocations per individual per day. Feeding conditions were harsh due to several rain-on-snow events earlier that winter, and associated ground-ice. Gray areas on the map are characterized by rocky, vegetation-free polar desert. The movements shown here reflect that the reindeer typically move back and forth between the beach (i.e., the shoreline, with kelp and seaweed feeding) and some vegetated ridges further inland (normal plant diet). Inset photograph shows a reindeer feeding crater on the shoreline, with washed-ashore kelp (*Laminaria* sp.) fragments. Photograph: B. B. Hansen.

Package lme4, binomial family with a logit link) of habitat used by individual reindeer (binary model with 0 = terrestrial, 1 = shoreline) during the snapshot in time covered by the population surveys. Year was included as a random intercept effect (factor) to account for dependency in the data within year, and fixed effects were population (Brøggerhalvøya, Sarsøyra, Kaffiøyra) and yearly average ground-ice thickness, which was obtained from two different data sets (see also Hansen et al. 2011, Peeters et al. 2019). In the first ground-ice data set (2006–2007, 2010–2012), $n = 17–31$ snow pits were measured in late March to April in a fixed grid plot design (900 × 1800 m) in vegetated areas below 120 m a.s.l. in Brøggerhalvøya (see Hansen et al. 2011). The measurements were taken during the same period as the spatial reindeer population survey (i.e., late March–mid April). Because the plots were unmarked, their approximate positions were located by the use of GPS. We used a shovel to remove the snow, and ground-ice thickness up to maximum 10 cm depth was measured to the nearest 0.5 cm with a thumb ruler after the ground (or 10 cm depth) was reached by the use of an electric drill or an axe. From 2013 onwards, the Brøggerhalvøya ground-ice data were collected based on a spatial hierarchical design covering the main reindeer winter habitat (ridge and sub-ridge vegetation; see Loe et al. 2016) along an elevational gradient (range: 3–475 m a.s.l.). In total, $n = 40$ pits were measured each year (2013–2015), following the same procedures as described above. No ground-ice measurements were available from Brøggerhalvøya in the winter of 2008, for which ground-ice was predicted based on a linear regression of annual median ice thickness in Brøggerhalvøya against annual median ice thickness in Sarsøyra (data available for 2005–2008 and 2010–2012, see Hansen et al. 2011), with an $R^2 = 0.42$ (analyses not shown). Note that, because of the 10 cm depth threshold for ground-ice measurements, we used the annual median as measure of central tendency, that is, annual average thickness, in the binomial model of reindeer habitat use described above.

Because of different carbon sources for photosynthesis and different carbon acquisition mechanisms in marine algae vs. terrestrial plants, ungulate feeding on seaweed may be distinguished using carbon isotope ratios, which are

expected to be enriched following marine biomass consumption (cf. Balasse et al. 2006). In addition, diets including marine biomass are expected to have enriched $\delta^{15}N$ and enriched $\delta^{34}S$ values compared with purely terrestrial diets (Connolly et al. 2004). We recognize that fecal samples are not as ideal for diet determination as blood, where marine as opposed to terrestrial diets (and mixtures thereof) can be more confidently ascertained (Stanek et al. 2017). However, the real-time collection of the fecal samples and the strong differences in these marine and terrestrial diet isotopic values make use of feces an option when animal captures and blood draws are not possible. Thus, to test whether reindeer that were observed on the shoreline consumed marine biomass, we collected and analyzed stable isotopes in fresh reindeer fecal samples along coast-inland gradients in late winters (i.e., February–April) 2014 and 2015. Because feces were not collected as direct part of the reindeer population monitoring surveys described above, we used samples collected opportunistically in Ny-Ålesund (i.e., Brøgger-halvøya), Adventdalen, and Kapp Linné (Fig. 1a), as part of a parallel study. Kapp Linné largely resembles the feeding conditions around Ny-Ålesund, with coastal plains surrounded by substantial dispersal barriers, and an apparent access to washed-ashore kelp and seaweed. In contrast, Adventdalen is a valley in central Spitsbergen where reindeer are generally distributed far from the sea, and marine biomass is therefore unlikely to be consumed. Fresh fecal samples were collected opportunistically during observational studies. We sampled directly from observed defecations or in the tracks of observed reindeer, ensuring that pseudo-replication was avoided, that is, no individual was sampled more than once. Collected fecal samples were classified into four categories according to habitat and location: Ny-Ålesund shoreline feeders (i.e., feces collected from reindeer on the shoreline; $n = 13$), Kapp Linné shoreline feeders ($n = 7$), Adventdalen terrestrial feeders ($n = 57$), or Kapp Linné terrestrial feeders ($n = 46$).

We also collected reference material from common food items close to Longyearbyen, Adventdalen. Washed-ashore fragments of kelp, predominantly *Laminaria* spp., and seaweed were collected in winter 2014 ($n = 9$). The dwarf shrubs *Salix polaris* ($n = 4$) and *Dryas octopetala* ($n = 4$), grasses and sedges (*Graminoidae* spp, $n = 4$), and mosses *Bryophyta* spp. ($n = 4$) were sampled from inland reindeer feeding craters in March 2013.

Feces and forage samples were stored in plastic bags and kept frozen until dried at 60°C for 24 h. Samples were crushed into a fine homogenous powder using pestle and mortar, which was rinsed with 100% ethanol (ANALAR) between each sample. Approximately 4.0–4.5 mg sample powder was then packed in 3.5 × 5 mm tin sample cups (Costech, Valencia, California, USA) for analysis. The samples were analyzed using a Costech ECS 4010 elemental analyzer, (Costech, Valencia, California, USA), which gives the proportion of C and N, coupled with a ThermoFinnigan Delta^{Plus} XP continuous-flow isotope ratio mass spectrometer (CF-IRMS; Thermo Scientific, Bremen, Germany). $\delta^{13}C$ and $\delta^{15}N$ values were 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). A subset of kelp/seaweed (hereafter referred to as kelp) and fecal samples were also analyzed for $\delta^{34}S$. All values were referenced to Vienna Pee Dee Belemnite (VPDB) for $\delta^{13}C$, air for $\delta^{15}N$, and Vienna Cañon Diablo Troilite (VCDT) for $\delta^{34}S$. We expected a priori that inclusion of marine biomass in the reindeer diet should lead to fecal isotopic values that—compared with a diet with no marine biomass—would be more similar to kelp values, and vice versa for terrestrial plants. Thus, if shoreline feeders included marine biomass in the diet (and terrestrial feeders did not), their feces should also have isotopic values that were enriched in $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values compared to those feeding only on terrestrial vegetation. To test this, we analyzed for differences in $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ between kelp, plants (four plant groups/species), and the four classes of fecal samples, running separate linear regression models for each isotope. All statistical analyses were done in R version 3.3.1 (R for Windows 2016).

RESULTS

The annual proportion of reindeer classified as shoreline feeders during monitoring surveys in

the Ny-Ålesund area (i.e., Brøggerhalvøya, Sarsøyra, and Kaffiøyra) in late winter ranged between 1.6% and 18.9% on the study area level, and 0% and 30.5% on the population level (Fig. 1c). As predicted, the probability of using shoreline habitat increased the thicker the ground-ice, that is, the harsher the feeding conditions (Fig. 1c, Table 1).

Fine-resolution positioning data from GPS-marked females in the Ny-Ålesund area indicated that reindeer found at or near the shoreline tended to switch between shoreline habitat and terrestrial feeding spots further inland (Fig. 2). Accordingly, fecal SIA suggested that animals classified as shoreline feeders tend to mix marine biomass with terrestrial food. $\delta^{13}C$ values were higher in kelp samples than in all other sample categories (Fig. 3a, Table 2), and feces from shoreline feeders in both Kapp Linné and Ny-Ålesund had significantly higher $\delta^{13}C$ values than plants and other fecal sample categories, indicating a strong influence of kelp. The range of $\delta^{13}C$ values for shoreline feeders' feces from Ny-Ålesund was not overlapping the distribution for terrestrial feces/plant sample categories, while shoreline feeders' feces from Kapp Linné overlapped the distribution of terrestrial feeders' feces from the same study site but not those from Adventdalen. Overall, $\delta^{13}C$ in feces from terrestrial feeders did not differ from the terrestrial plant sample categories, except for the evergreen shrub *D. octopetala*, which had significantly lower $\delta^{13}C$ values than terrestrial feeders' feces in Kapp Linné (Table 2).

Table 1. Effects of population and annual ground-ice thickness on the probability of reindeer being found along the shoreline.

Parameter	Parameter estimate ($\beta \pm$ SE)	z	P
Intercept (Brøggerhalvøya)	-2.81 ± 0.29	-9.70	<0.01
Kaffiøyra	-0.51 ± 0.20	-2.51	0.01
Sarsøyra	-0.95 ± 0.23	-4.21	<0.01
Ground-ice	0.113 ± 0.045	2.52	0.01

Notes: Parameter estimates ($\beta \pm$ SE) are shown from a generalized linear mixed effects model (logit link) of the assigned feeding strategies of individual reindeer (binary response: 0 = terrestrial, 1 = shoreline habitat) mapped during population censuses in late winter ($n = 2199$ reindeer observations over 9 winters). Year was included as random intercept effect (variance explained = 0.19). SE, standard error.

$\delta^{15}N$ values exhibited more overlap between sample categories (Fig. 3b, c), possibly due to a combination of diet and endogenous contributions. Nonetheless, feces from shoreline feeders in Ny-Ålesund had statistically higher $\delta^{15}N$ values than all other sample categories (Table 2). This included feces from shoreline feeders in Kapp Linné and kelp itself, both of which had higher $\delta^{15}N$ values than all other sample categories (marginally non-significant difference from graminoids). The lowest $\delta^{15}N$ values were found in *D. octopetala*, the dwarf shrub *S. polaris*, and mosses. The values of $\delta^{34}S$ are known to be particularly enriched in marine samples (Connolly et al. 2004) and did not differ statistically between kelp and feces from shoreline feeders (Fig. 3d). Both sample categories had significantly higher $\delta^{34}S$ values than (and did not overlap with) feces of terrestrial feeders.

DISCUSSION

Despite being encouraged for more than a decade (Parmesan 2006), studies investigating behavioral adaptations to extreme events are still rare. Here, we have demonstrated that environmental perturbations linked to climate can trigger changes in the winter diet of the world's northernmost ungulate, the wild Svalbard reindeer. Since the late 1990s, the high-arctic archipelago of Svalbard has been increasingly often surrounded by open water in winter (Onarheim et al. 2014). Marooned by such recent lack of sea-ice as dispersal corridor, coastal reindeer populations responded to an icier tundra by increasing their use of shoreline habitat (Fig. 1). GPS-data and SIA of kelp, plant, and reindeer feces collected along a coast-inland gradient confirmed the observations that animals found in shoreline habitat during late winter population surveys were indeed feeding on marine biomass as a supplement to their normal terrestrial diet (Figs. 2, 3). Such increased use of marine biomass—an allochthonous food resource subsidy (Polis and Hurd 1996)—may have implications for meta-ecosystem dynamics through a strengthened coupling between the marine and terrestrial ecosystems under Arctic climate change and sea-ice loss (Post et al. 2013, Prop et al. 2015).

Reindeer and caribou are known as generalists (Skogland 1984) that browse or graze on a
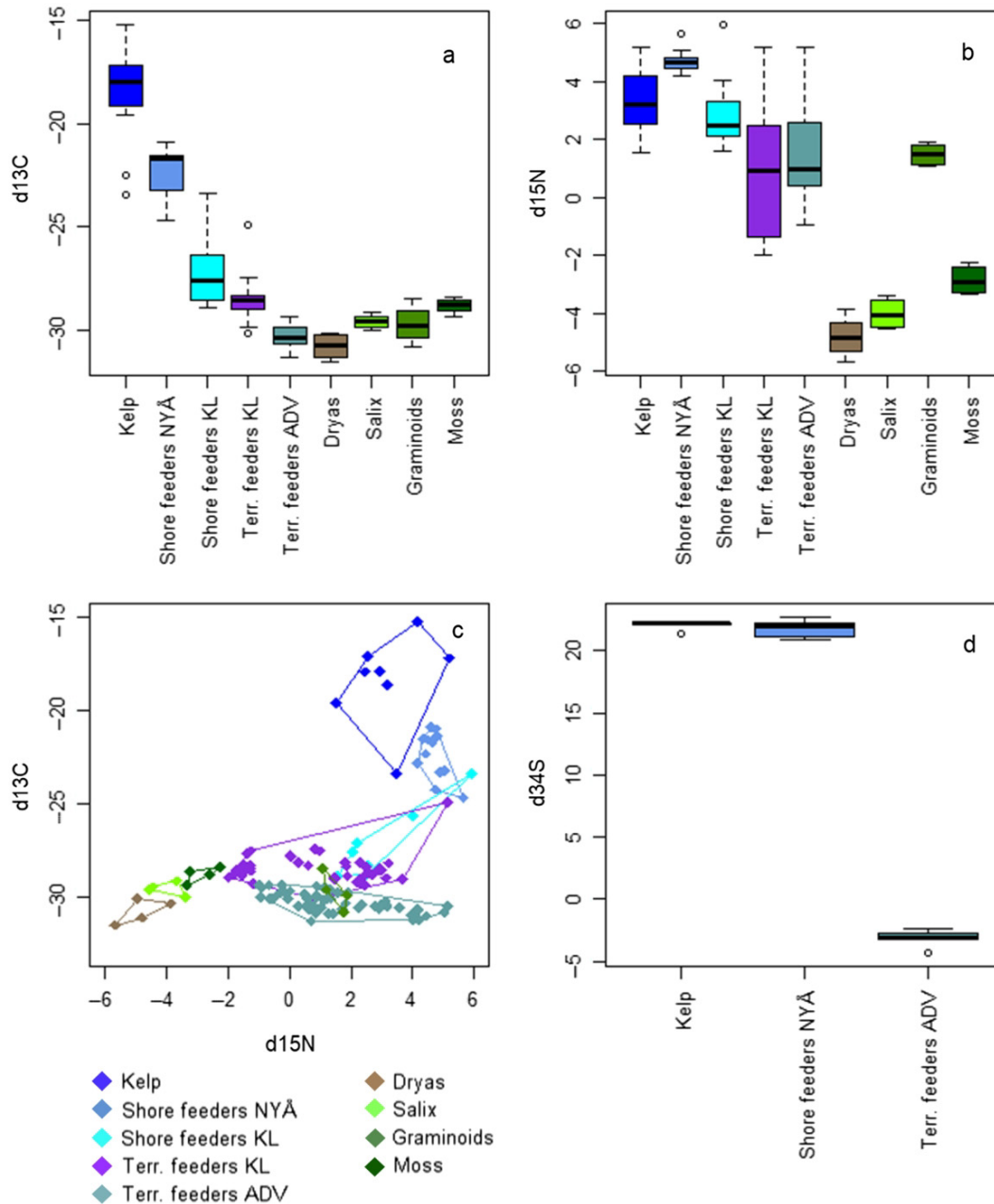
Fig. 3. Distribution of stable isotope values of (a) $\delta^{13}C$, (b) $\delta^{15}N$, (c) $\delta^{13}C$ vs. $\delta^{15}N$ (with similar color codes as in a and b), and (d) $\delta^{34}S$ in samples of kelp/seaweed, plant, and Svalbard reindeer feces from shoreline feeders and terrestrial (terr.) feeders in different study areas (NYÅ, Ny-Ålesund; KL, Kapp Linné; ADV, Adventdalen). Box plots show median (thick solid line), interquartile ranges (box), 10th/90th percentiles (whiskers), and outliers (open circles). Colored lines in (c) are the convex polygons of the $\delta^{13}C$–$\delta^{15}N$ isotopic values for the respective sample category.

variety of vascular plants, bryophytes, and lichens. However, the Svalbard reindeer stands out from most other *Rangifer* subspecies by including large amounts of bryophytes (with overall very low nutritious value) in their winter diet (Staaland 1986). This is assumedly an adaptation to the virtual absence of mat-forming lichens, the otherwise preferred winter food by

Table 2. Differences in stable isotope values between sample types of plants, kelp/seaweed, and reindeer feces.

Sample type	δ^{13}C ($n = 147$)			δ^{15}N ($n = 146$)			δ^{34}S ($n = 14$)		
	$\beta \pm$ SE	t	P	$\beta \pm$ SE	t	P	$\beta \pm$ SE	t	P
Intercept (kelp/seaweed)	-18.8 ± 0.3	-55.4	<0.01	3.19 ± 0.56	5.7	<0.01	22.0 ± 0.3	64.4	<0.01
Shoreline feeders									
Ny-Ålesund	-3.49 ± 0.44	-7.9	<0.01	1.51 ± 0.72	2.11	<0.05	-0.18 ± 0.46	-0.39	0.71
Kapp Linné	-8.3 ± 0.5	-16.1	<0.01	-0.21 ± 0.82	-0.25	0.80			
Terrestrial feeders									
Kapp Linné	-9.7 ± 0.4	-26.0	<0.01	-2.43 ± 0.61	-3.99	<0.01			
Adventdalen	-11.5 ± 0.4	-31.3	<0.01	-1.69 ± 0.60	-2.80	<0.01	-25.1 ± 0.46	-54.9	<0.01
Terrestrial plants									
Dryas octopetala	-11.9 ± 0.6	-19.5	<0.01	-8.0 ± 1.0	-8.2	<0.01			
Salix polaris	-10.7 ± 0.6	-17.5	<0.01	-7.2 ± 1.0	-7.4	<0.01			
Graminoids	-10.9 ± 0.6	-17.7	<0.01	-1.70 ± 0.98	-1.75	0.08			
Mosses	-10.0 ± 0.6	-16.3	<0.01	-6.0 ± 1.0	-6.2	<0.01			

Notes: Feces from shoreline feeders were expected to have isotopic values that—compared with feces from terrestrial feeders—were overall closer to kelp/seaweed values, and vice versa for terrestrial food plants. Parameter estimates ($\beta \pm$ SE) are shown from linear regressions of differences in stable isotope values between kelp/seaweed (intercept), plants, and fresh reindeer winter feces sampled along the shoreline or in terrestrial habitat further inland. n = total sample size. SE, standard error.

Rangifer. The extraordinary digestive capability associated with high moss ingestion likely reflects a strong ability in Svalbard reindeer to adapt to the sparse—and stochastic—feeding conditions characterizing high-arctic island tundra. This prompts the question why the coastal reindeer do not eat kelp every winter throughout, like the sheep on some Orkney islands (Hansen et al. 2003). The nutritious value of marine biomass (for ungulates) is not well known—and probably not well informed by SIA of whole feces—but appears overall comparable to terrestrial plants. The N content (generally 1–2%) and the in vitro dry matter digestibility (e.g., up to 59% for *Laminaria* sp.) of seaweed and kelp on the Isle of Rum were close to red deer's terrestrial food plants (Conradt 2000), and relatively high compared with the typical winter forage vascular plants (N content 1–2%, in vitro dry matter digestibility ~30–50%) of reindeer and caribou (Klein 1990). Seaweed (*Fucus* sp.) consumed by black-tailed deer was found to represent low to moderate levels of digestible energy, but high levels of protein (Parker et al. 1999). However, a seaweed-supplemented diet in sheep ewes caused increased offspring mortality due to reduced passive immunity (Novoa-Garrido et al. 2014), and Orkney sheep subsisting on seaweed suffered from inadequate nutrition and dental diseases rarely observed in sheep on more conventional diets (Britt and Baker 1990). Likewise, we observed disproportionately high frequencies of diarrhea

among Svalbard reindeer feeding on kelp in our study area (Hansen and Aanes 2012), possibly related to high salt content. Accordingly, in spite of a rather stable availability of kelp from year to year, the use of these resources seems to occur mainly when access to terrestrial food plants appears to be limited by ice or exceptionally deep snow. This is consistent with traditional knowledge among Sami reindeer herders in Finnmark, northern Norway, which semi-domesticated reindeer occasionally move to the coast and ingest seaweed under poor winter feeding conditions (J. V. Smuk, *personal communication*).

Because feces collected along the shoreline had isotopic values that—compared with feces from terrestrial feeders—were overall closer to kelp values, δ^{34}S and δ^{13}C were shown to be very effective in detecting the presence of marine biomass in the reindeer diet. This methodology also confirmed the GPS-collar data (Fig. 2) and indicates that kelp is used as a subsidy rather than constituting the entire diet. The largest variation in δ^{13}C was found among feces from Kapp Linné, where both marine biomass and terrestrial biomass were readily available for both shoreline feeders and terrestrial feeders. In contrast, feces sampled from the more inland valley Adventdalen had distinct terrestrial isotope values and no sign of marine influence. This, combined with distinct values of different plant groups (see also Nadelhoffer et al. 1996), advocates for SIA of feces (or other tissues) as a potentially useful tool

for monitoring diet of Arctic herbivores in response to environmental change (Mosbacher et al. 2016, Schmidt et al. 2018). However, SIA of whole feces requires cautious interpretation, for instance, due to the effects of variation in assimilation rates and endogenous contributions, of which the latter could explain part of the large overlap in δ^{15}N between sample categories.

Some have raised doubt regarding the future viability of Arctic ungulates under global warming and other anthropogenic impacts (Vors and Boyce 2009). High-latitude populations are expected to be particularly vulnerable to environmental perturbations (Parmesan et al. 2000), and the increasingly common phenomenon of extreme warm spells, ROS, and ice-locked pastures (Rennert et al. 2009, Hansen et al. 2011, Bintanja and Andry 2017) may indeed cause population crashes in Arctic ungulates (Miller and Gunn 2003, Kohler and Aanes 2004, Forbes et al. 2016). However, there is now increasing evidence that such negative impacts are buffered by warmer and longer summers, which increase the forage production and carrying capacity (Albon et al. 2017), but also in part by spatial (e.g., small-scale dispersal; Stien et al. 2010, Loe et al. 2016), behavioral (Hansen et al. 2010), and dietary plasticity, as shown in this study. Furthermore, these observed changes occur at the meta-ecosystem level (Loreau et al. 2003). Parallel with sea-ice loss and warmer and rainier terrestrial climates, the marine ecosystem is now changing toward richer near-shore benthic communities with more abundant macro-algae, including kelp (Körtsch et al. 2012, Krause-Jensen et al. 2012, Scherrer et al. 2019). In coastal tundra areas, the reindeer use of such allochthonous resource subsidies from the marine system may not only represent an increasingly important lifeline to prevent starvation at the individual level, but also contribute to the altered interactions and energy fluxes between marine and terrestrial ecosystems.

Acknowledgments

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