LETTER

Arctic seals as tracers of environmental and ecological change

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Scientific Significance Statement

Decadal trends in the trophic position (TP) of marine predators, ascertained through tracers such as stable nitrogen isotopes, have been used to infer the impact of environmental change on ecosystems. Understanding how the environment is altering stable nitrogen isotopes at the base of the food web is key to interpreting these tracers in predators. Here, we demonstrate that the stable nitrogen isotope signatures in harp and ringed seals across the Arctic are directly controlled by the stable nitrogen isotope signature of the water masses they forage in. This has important implications for accurately estimating the TP of predators, as water mass circulation in the Arctic Ocean has been altered during the last decades as a result of climate change.

Abstract

Knowledge of species trophic position (TP) is an essential component of ecosystem management. Determining TP from stable nitrogen isotopes (δ^{15}N) in predators requires understanding how these tracers vary across environments and how they relate to predator isotope composition. We used two seal species as a model for determining TP across large spatial scales in the Arctic. δ^{15}N in seawater nitrate (δ^{15}N$_{NO3}$) and seal muscle amino acids (δ^{15}N$_{AA}$) were determined to independently characterize the base of the food web and the TP of harp and ringed seals, demonstrating a direct link between δ^{15}N$_{NO3}$ and δ^{15}N$_{AA}$. Our results show that the spatial variation in δ^{15}N$_{AA}$ in seals reflects the δ^{15}N$_{NO3}$ end members in Pacific vs. Atlantic waters. This study provides a reference for best practice on accurate comparison of TP in predators and as such, provides a framework to assess the impact of environmental and human-induced changes on ecosystems at pan-Arctic scales.

Marine ecosystems are being modified as a result of multiple stressors, including global environmental change, fish exploitation, pollution, and habitat degradation (IPCC 2019). Determining the resilience of marine ecosystems to perturbations is essential for sustainable management in a changing environment (Silberberger et al. 2018). Food webs interconnect a diverse range of species and body sizes, over large spatial scales and across a variety of different habitats. Food web structure is inherently linked to ecosystem function and resilience (Yen et al. 2016). Trophic position (TP) of top and near-top predators is a fundamental property of ecological communities. It has the general function of reflecting changes in ecosystems overall, and can be used to assess food web structure, food chain length, and functional roles of predators (Post 2002).

Stable nitrogen isotopes are commonly used as a chemical tracer to reconstruct food webs and estimate TP of predators. The ratio between heavy (^{15}N) and light (^{14}N) isotopes of bulk tissue ($\delta^{15}N_{bulk}$) increases by ~ 3‰ at each trophic level, providing a continuous measure of TP (Post 2002). However, $\delta^{15}N_{bulk}$ is influenced by δ^{15}N at the base of the food web, or "baseline." Variation in $\delta^{15}N_{bulk}$ in predators can therefore reflect changes in either (1) TP (Fig. 1a) or (2) δ^{15}N at the baseline (Fig. 1b).

Compound-specific stable nitrogen isotopes of amino acids ($\delta^{15}N_{AA}$) is a powerful approach that disentangles baseline and trophic level effects from the analysis of consumer tissue alone. The δ^{15}N of "source" amino acids experiences negligible fractionation during trophic transfer and conservatively traces the δ^{15}N baseline, whereas significant fractionation of

"trophic" amino acids results in ^{15}N enrichment between each trophic transfer (McMahon and McCarthy 2016). The uncertainty regarding trophic fractionation factors between "source" and "trophic" amino acids across taxa in entire food webs prevents accurate estimation of an organism's absolute TP (Nielsen et al. 2015). However, this approach allows robust estimation of relative TP (TP_{rel}) and is particularly insightful when comparing TP_{rel} of mobile predators, which integrate the biochemical characteristics of their foraging habitats over large spatial scales with potentially different baselines.

Here, we used two key marine predators, the ringed (*Pusa hispida*) and harp (*Pagophilus groenlandicus*) seal, as model species for determining TP_{rel} across large spatial scales and environmental gradients in the Arctic and sub-Arctic. The Arctic Ocean is experiencing unprecedented rates of environmental change compared to the rest of our planet (IPCC 2019). Changes in sea ice extent and thickness, and hydrographic structure have altered the timing and magnitude of primary production (Arrigo and van Dijken 2015). The warming ocean is leading to changes in zooplankton (Dalpadado et al. 2016) and fish (Fossheim et al. 2015) communities. Collectively, these food web alterations are affecting the phenology, behavior, and distribution of top predators in the Arctic (IPCC 2019). Understanding food web structure in the Arctic and sub-Arctic is vital for the development of policies to manage and conserve these unique polar ecosystems.

Phytoplankton underpins marine food webs and their δ^{15}N mainly reflects the δ^{15}N of seawater nitrate ($\delta^{15}N_{NO3}$), an essential nutrient (Mariotti et al. 1981). Nitrate is supplied to the Arctic Ocean by Atlantic water entering through the Barents Sea and on the eastern side of Fram Strait, and by Pacific water crossing the Bering Strait (Fig. 2) (Torres-Valdés et al. 2013). Pacific water $\delta^{15}N_{NO3}$ is enriched in ^{15}N by ~ 3‰ compared to Atlantic water $\delta^{15}N_{NO3}$, as a result of the biological processing within the Pacific and Atlantic oceans (Somes et al. 2010). Pacific and Atlantic waters are further modified by the physical and biogeochemical changes that occur within the Arctic basin, before exiting via the Canadian Archipelago and on the Western side of Fram Strait (Fig. 2; Torres-Valdés et al. 2013). Gradients in $\delta^{15}N_{NO3}$ across the Arctic and sub-Arctic therefore reflect water mass supply, mixing processes and in situ nitrogen cycling. To reliably detect pan-Arctic trends in seal TP_{rel}, it is essential to account for spatial variation in the δ^{15}N at the baseline.

In this study, we used both $\delta^{15}N_{bulk}$ and $\delta^{15}N_{AA}$ to determine the TP_{rel} of harp and ringed seals. Ringed and harp seals are abundant near-top trophic level generalists that have a wide distribution. Generally, their diet consists of a large variety of pelagic invertebrates and forage fish (Wathne et al. 2000; Folkow et al. 2004; Nordøy et al. 2008; Lindstrøm et al. 2013; Ogloff et al. 2019). Given these characteristics, ringed and harp seals are suitable model species with which to quantify spatial variation in food web structure. We specifically focus on δ^{15}N of the source amino acid phenylalanine ($\delta^{15}N_{phe}$),
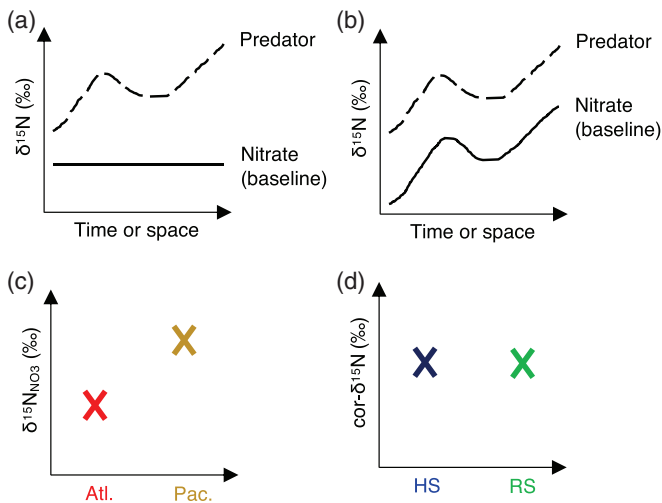
Fig. 1. Examples of variation in the $\delta^{15}N_{bulk}$ observed in a predator caused by (**a**) change in the food chain length or in the predator diet and (**b**) variation in the δ^{15}N at the baseline (e.g., nitrate), and predictions of (**c**) relative δ^{15}N at the baseline (e.g., nitrate) in Atlantic (Atl.) and Pacific (Pac.) influenced Arctic regions and (**d**) relative baseline-corrected δ^{15}N (cor-δ^{15}N) in harp (HS) and ringed (RS) seals in the Arctic.

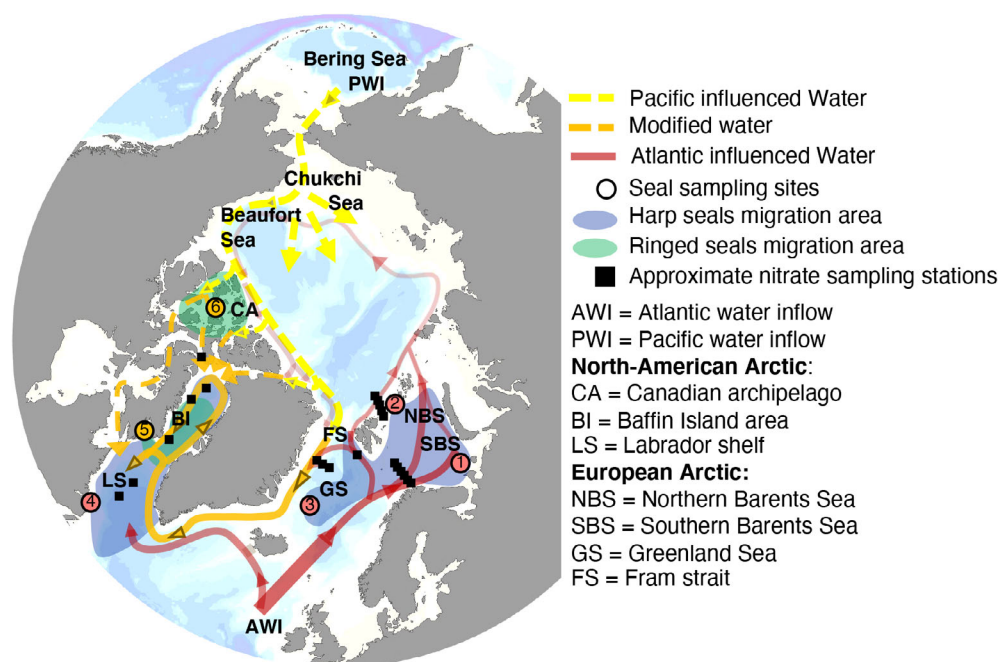**Fig. 2.** Map depicting the seal sampling sites and their migration areas, the approximate location of nitrate sampling stations, and the main Arctic regions and currents.

which reflects variations in the baseline, and $\delta^{15}N$ of three main trophic amino acids (glutamic acid, aspartic acid, and leucine), allowing accurate estimation of TP_{rel} McMahon and McCarthy 2016). In addition, we compared $\delta^{15}N_{phe}$ in seals and $\delta^{15}N_{NO3}$ from the seal foraging areas. We predict that: (1) $\delta^{15}N_{bulk}$ in Arctic seals varies across the Arctic, (2) spatial variation in $\delta^{15}N_{bulk}$ is driven by variation in $\delta^{15}N_{phe}$, (3) spatial variation in $\delta^{15}N_{phe}$ is driven by spatial variation in $\delta^{15}N_{NO3}$ reflecting water mass characteristics (Fig. 1c), and (4) harp and ringed seals are at similar TP (Fig. 1d), which does not vary across the Arctic.

Materials and methods

Seal sampling

A total of 210 muscle samples were obtained from the long-issimus dorsi of adult (older than 6 year old) harp and ringed seals at six sites across the Arctic and sub-Arctic (Southern Barents Sea, Northern Barents Sea, Greenland Sea, Labrador shelf, Baffin Island, and Canadian Archipelago; Fig. 2, Table 1). Harp seals from the Barents Sea were sampled by the Norwegian Institute of Marine Research as part of Norwegian commercial sealing. Permission for the scientific catch of harp seals from the Greenland Sea in 2018 and 2019 was obtained from the Ministry of Foreign Affairs of Denmark (Utenrigsministeriet) in verbal notes (JTHAV sagsnr 2017-4885 and JTHAV sagsnr. 2019-9877) and from the Norwegian Directorate of Fisheries (letter ref. 18/1124 and 18/14793). Ringed and harp seals from the Canadian Archipelago, Baffin Island and Labrador Shelf were collected by trained, licensed hunters following the humane hunting requirements, as part of the Inuit subsistence and commercial harvests. All samples were immediately frozen and stored at −20°C.

Seal sampling design

Muscle tissue, which integrates the $\delta^{15}N$ of the diet over 4–5 months (Vander Zanden et al. 2015), reflected seal foraging over different seasons depending on the sampling month (Table 1; Fig. 3).

The harp seal populations of Greenland and southern Barents Sea (Fig. 2) partially overlap in the northern Barents Sea during the summer and autumn (Folkow et al. 2004; Nordøy et al. 2008). In late November/early December, harp seals migrate back toward their breeding and molting areas in the Greenland Sea and the southern Barents Sea/White Sea. Muscle samples collected in March from harp seals from the Greenland Sea, reflected the diet integrated from late autumn to late winter (Fig. 3), whereas muscle samples collected in spring from the southern Barents Sea (Table 1) reflected the diet integrated from winter to spring (Fig. 3). These seals were foraging within the sampling regions during both periods (Table 1, Fig. 3). Muscle tissue of harp seals from the northern Barents Sea reflected a combination of diets consumed in the Greenland Sea, southern and northern Barents Sea (Table 1, Fig. 3).

Harp seals from Newfoundland spend summer and autumn in Arctic waters (Baffin Island and Davis Strait) and migrate south to the Labrador shelf in early winter (Lacoste and Stenson 2000). Harp seal samples from the Labrador shelf,

Table 1. Seal sampling sites and regions, seal species, total number of seal samples (*N*), number of seal samples selected for $\delta^{15}N$ analyses on amino acids (*n*), seal sampling years, seal sampling months, Arctic regions reflected in seal muscle tissue, mean $\delta^{15}N_{NO3} \pm SD$ (sample number) in the region(s) integrated by seal muscle tissue (*see* Fig. 3); seal and nitrate sampling regions are labeled on Fig. 2.

Sampling sites	Sampling regions	Species	*N**	*n**	Sampled years	Sampling months	Region(s) integrated in muscle	$\delta^{15}N_{NO3} \pm SD$ (*n*)
Cape Kanin	Southern Barents Sea	Harp	17	17	2018	April, May	Southern and northern Barents Sea	5.1 ± 0.1‰ (*n* = 11)
North Svalbard	Northern Barents Sea	Harp	4	4	2016	September	Southern and northern Barents Sea	5.1 ± 0.1‰ (*n* = 11)
Jan Mayen	Greenland Sea	Harp	17	17	2018, 2019	March	Greenland Sea and northern Barents Sea	5.1 ± 0.2‰ (*n* = 4)
Labrador shelf	Labrador shelf	Harp	59	14	2017, 2018	January, February	Baffin Island area and Labrador shelf	5.6 ± 0.3‰ (*n* = 6)[†]
Pangnirtung	Baffin Island	Harp	8	8	2015, 2016	July, September	Baffin Island area and Labrador shelf	5.6 ± 0.3‰ (*n* = 6)[†]
		Ringed	4	4	2015, 2016	September, October	Baffin Bay	6.2 ± 0.2‰ (*n* = 3)[†]
Resolute	Canadian archipelago	Ringed	10	10	2015, 2016	June, July, August	Canadian archipelago	6.8 ± 0.2‰ (*n* = 1)[†]

[*]Total number of females (F), males (M) and unknown sex (U), and number of females (f), males (m) and unknown sex (u) selected for $\delta^{15}N$ analyses on amino acids; Harp seals F/M/U (*f/m/u*): 71/33/1 (*45/14/1*); ringed seals F/M/U (*f/m/u*): 8/5/1 (*8/5/1*).
[†]Data from Lehmann et al. (2019).

collected in winter, and from Baffin Island, collected in summer, reflected both a combination of the diet from the Baffin Island area and the Labrador shelf (Table 1; Fig. 3).

Ringed seal samples from Baffin Island, collected in autumn, and from the Canadian Archipelago, collected in summer, reflected the diet during seasons when seals were foraging within the sampling regions (Yurkowski et al. 2016) (Table 1; Fig. 3).

Stable nitrogen isotopes analyses in seals

Stable isotope ($\delta^{15}N_{bulk}$ and $\delta^{15}N_{AA}$) analysis of seal muscle tissue was carried out at the Liverpool Isotopes for

Environmental Research laboratory, University of Liverpool and results are reported in standard δ-notation (‰) relative to atmospheric N_2 (Hobson and Welch 1992; Hobson et al. 1997; Germain et al. 2013). Details of sample preparation, instrument configuration, and reproducibility are detailed in Supporting Information S1. All samples were analyzed for $\delta^{15}N_{bulk}$ and a subset were selected for $\delta^{15}N_{AA}$ (Table 1; de la Vega 2020).

TP estimation

We used the $\delta^{15}N$ of phenylalanine ($\delta^{15}N_{Phe}$) to track the $\delta^{15}N$ of the baseline and the $\delta^{15}N$ of three amino acids
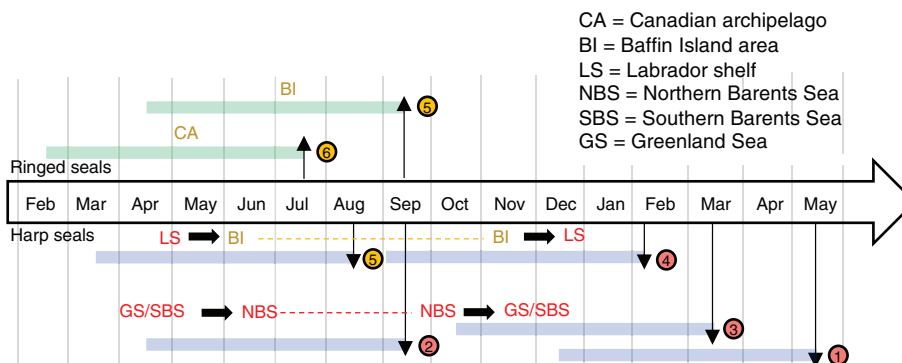

Fig. 3. Schematic diagram of the sampling design. Harp seals (blue) are shown at the bottom and ringed seals (green) are shown at the top of the timeline. Black vertical arrows indicate the median seal sampling month at each site; numbers refer to seal sampling sites in Fig. 2; black horizontal arrows indicate seal migration; colored horizontal bars indicate the period integrated in muscle (~ 5 months; Vander Zanden et al. (2015)). Migration of seals are summarized after Lacoste and Stenson (2000), Nordøy et al. (2008), and Yurkowski et al. (2016).

($\delta^{15}N_{trophic}$; glutamic acid, aspartic acid, and leucine) to estimate TP. The uncertainty regarding trophic fractionation factors between "source" and "trophic" amino acids across taxa in entire food webs prevents accurate estimation of an organism's absolute TP (Nielsen et al. 2015). To compare the relative TP (TP_{rel}) across sampling sites, we subtracted the $\delta^{15}N_{Phe}$ values from $\delta^{15}N_{trophic}$ providing baseline-corrected $\delta^{15}N_{trophic}$ values (cor-$\delta^{15}N_{trophic}$; Supporting Information S2). To prevent variation in the absolute values from overwhelming trends in relationships among AA, cor-$\delta^{15}N_{trophic}$ values were scaled using z-transformation. We applied principal component analysis (PCA) on the scaled cor-$\delta^{15}N_{trophic}$ values (Supporting Information S3) and used the scores of the PCA axis 1 as a proxy for TP_{rel} of harp and ringed seals.

Nitrate

Seawater for nitrate analysis from the European Arctic (Fig. 2) was collected as part of the NERC Changing Arctic Ocean program, from the RRS *James Clark Ross* in July–August 2017 (JR16006) and May–June 2018 (JR17005). Seawater was collected using a 24-position stainless steel rosette equipped with a SBE911*plus* CTD and 20-liter OTE bottles. $\delta^{15}N_{NO3}$ (Table 1; de la Vega 2020) were determined at the University of Edinburgh, UK, using the denitrifier method (Sigman et al. 2001) and following Geotraces protocols (Schlitzer et al. 2018). Samples were corrected using international reference standards N3 and USGS34 and analyzed in duplicate with a reproducibility < 0.2‰. $\delta^{15}N_{NO3}$ data from the North American Arctic (Table 1) were compiled from Lehmann et al. (2019). Mean values were calculated from samples below the mixed layer (mean sampling depth = 202 ± 107 m) and were representing the nitrate isotope end member in a given region prior to biological utilization.

Statistical analyses

Statistical analyses were performed in R v. 3.5.1 (R Core Team 2018), mainly following Zuur et al. (2009*a*) and Zuur et al. (2009*b*).

The effect of species on $\delta^{15}N_{bulk}$, $\delta^{15}N_{Phe}$, and TP_{rel} (scores of the PCA axis 1) was tested through linear models, with model fit being checked by residual analyses with visual inspection of quantile-quantile plots, and residuals and standardized residuals vs. fitted values plots.

As samples for both species were only available at one site, separate models were fitted for harp and ringed seals. Multifactorial linear models were used to investigate the influence of site, individual body length, and sex on $\delta^{15}N_{bulk}$, $\delta^{15}N_{Phe}$, and TP_{rel} (scores of the PCA axis 1) for harp and ringed seals separately. Explanatory variables were not significantly collinear (variance inflation factors [VIFs] < 3). Model selection was based on Akaïke information criterion scaled for small sample sizes (AICc). We compared a list of biologically meaningful candidate models, with the maximal model being: $\delta^{15}N$ = site + length + sex. Model specification was validated via residual analyses of maximal model. For each specific model, we

calculated the AICc, the difference between AICc of the specific model and the best model (ΔAICc), and the AICc weight (normalized weight of evidence in favor of the specific model, relative to the whole set of candidates). Variables included in the best model (lowest AICc) were considered to best explain variation in $\delta^{15}N_{bulk}$, $\delta^{15}N_{Phe}$, and TP_{rel}. For harp seals that were sampled at more than two sites, we applied ANOVAs followed by Tukey pairwise comparison tests on $\delta^{15}N_{bulk}$, $\delta^{15}N_{Phe}$, and TP_{rel} to test the effect of the most accurate explanatory factors derived from the model selection (Supporting Information S4). Significance was considered when the 95% confidence interval of the slopes did not cross zero. *p* values (α = 0.005; Benjamin et al. 2018), R^2, *F*-statistics, and df are reported for each model (Supporting Information S4).

The $\delta^{15}N_{NO3}$ values in seawater were averaged within the seals foraging areas (Table 1). The relationship between $\delta^{15}N_{bulk}$, $\delta^{15}N_{Phe}$ and TP_{rel} in seal tissues and the averaged $\delta^{15}N_{NO3}$ were investigated using linear models and Pearson correlations.

Results

Spatial variation of $\delta^{15}N_{bulk}$ in seals

$\delta^{15}N_{bulk}$ in harp seals ranged from 13.2 ± 0.7‰ (Greenland Sea) to 14.4 ± 0.9‰ (Baffin Island). $\delta^{15}N_{bulk}$ in ringed seals ranged from 16.3 ± 0.1‰ (Baffin Island) to 17.4 ± 0.4‰ (Canadian Archipelago, Fig. 4a). The best models for $\delta^{15}N_{bulk}$ included "site" for both seal species (Tables 2, 4 in Supporting Information S4). In these models, $\delta^{15}N_{bulk}$ varied significantly between sites in both harp (linear model, *p* < 0.005, R^2 = 41.2%, *n* = 105; Tables 2, 3 in Supporting Information S4) and ringed seals (linear model, *p* < 0.005, R^2 = 67.7%, *n* = 14; Table 5 in Supporting Information S4). $\delta^{15}N_{bulk}$ in harp seals from the Greenland Sea was depleted in ^{15}N compared to harp seals from the Southern Barents and Labrador Shelf (Tukey tests following ANOVA: *p* < 0.005; Fig. 4a, Table 3 in Supporting Information S4). The $\delta^{15}N_{bulk}$ in ringed seals from the Baffin Island was depleted in ^{15}N compared to the Canadian Archipelago (Fig. 4a, Table 5 in Supporting Information S4). $\delta^{15}N_{bulk}$ of ringed seals was enriched in ^{15}N compared to harp seals (linear model: *p* < 0.005, R^2 = 41.8%, *n* = 119; Table 1 in Supporting Information S4).

Spatial variation in the baseline

$\delta^{15}N_{NO3}$ of seawater was enriched in ^{15}N by ~ 2‰ in the Pacific influenced Canadian Archipelago water (6.8‰), compared to the Barents Sea (5.1 ± 0.2‰) and Labrador Shelf (5.0 ± 0.3‰; Table 1). $\delta^{15}N_{Phe}$, representing the $\delta^{15}N$ of the baseline in seal tissues ranged from 6.2 ± 0.9‰ (Greenland Sea) to 9.8 ± 0.7‰ (Baffin Island) in harp seals, and from 11.2 ± 0.2‰ (Baffin Island) to 12.1 ± 0.6‰ (Canadian Archipelago) in ringed seals (Fig. 4b,c). The best models for $\delta^{15}N_{Phe}$

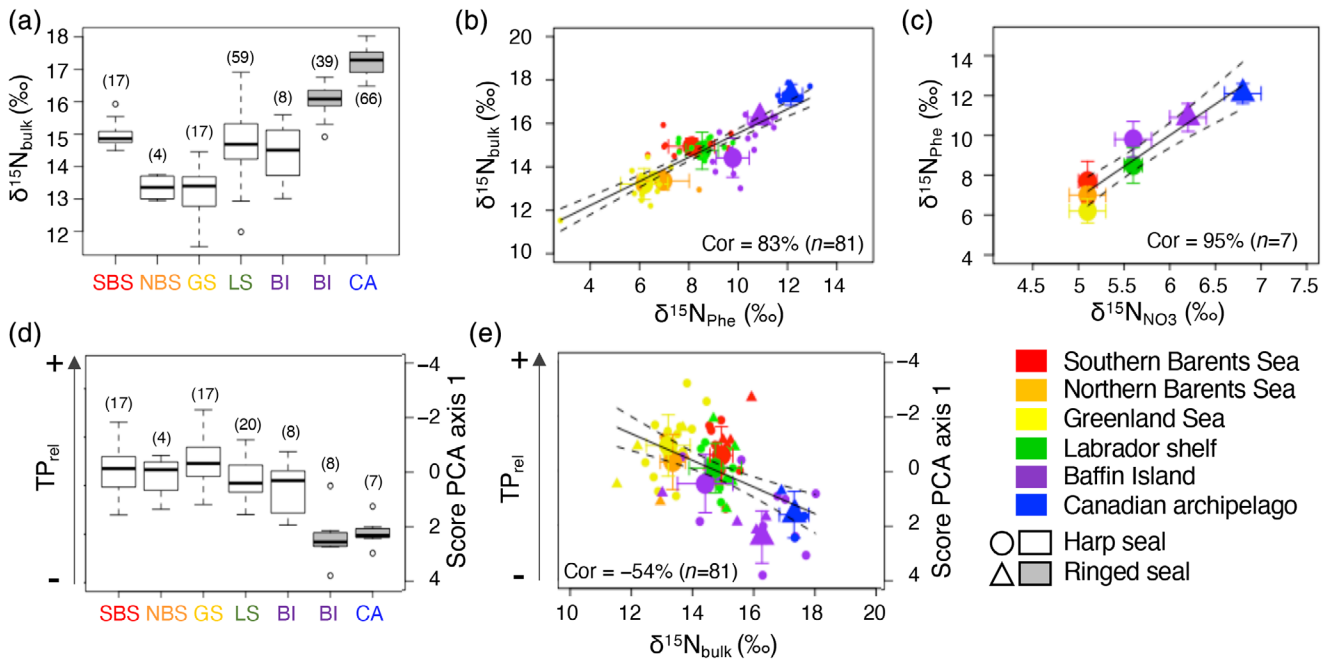**Fig. 4.** (a) $\delta^{15}N_{bulk} \pm$ standard deviation (‰) in harp (white box) and ringed (gray box) seals per Arctic region, (b) $\delta^{15}N_{bulk} \pm$ standard deviation (‰) and $\delta^{15}N_{Phe} \pm$ standard deviation (‰) in harp and ringed seals (circular and triangular point respectively), and linear model (c) $\delta^{15}N_{Phe} \pm$ standard deviation (‰) and $\delta^{15}N_{NO3} \pm$ standard deviation (‰), (d) scores of the PCA axis 1 and $TP_{rel} \pm$ standard deviation per Arctic region in harp and ringed seals and (e) scores of the PCA axis 1, used as proxy for relative trophic position (TP_{rel}) vs. $\delta^{15}N_{bulk}$ in seals; decreasing PCA scores indicates increasing $\delta^{15}N$ values of trophic amino acids and in turn increasing TP_{rel} (Supporting Information S2, S3); Cor, Pearson correlation; n, number of data points used in the correlation; SBS, southern Barents Sea; NBS, northern Barents Sea; GS, Greenland Sea; LS, Labrador shelf; BI, Baffin Island; CA, Canadian archipelago; CI95%, 95% confidence interval; the number of data points per site is indicated between parentheses on the graphs and in Table 1.

included "site" for both seal species (Tables 2, 4 in Supporting Information S4). In these models, $\delta^{15}N_{Phe}$ varied significantly between sites in both harp (linear model, $p < 0.005$, $R^2 = 56.4\%$, $n = 60$; Table 3 in Supporting Information S4) and ringed seals (linear model: $p = 0.020$, $R^2 = 34.5\%$, $n = 14$; Table 5 in Supporting Information S4). $\delta^{15}N_{Phe}$ in harp seals from the Greenland Sea and Northern Barents Sea were depleted in ^{15}N compared to harp seals from the Labrador Shelf and Baffin Island (Tukey tests: $p < 0.005$; Table 3 in Supporting Information S4). $\delta^{15}N_{Phe}$ in ringed seals from the Baffin Island was depleted in ^{15}N compared to ringed seals from the Canadian Archipelago (Fig. 4b,c). $\delta^{15}N_{Phe}$ of ringed seals was enriched in ^{15}N compared to harp seals (linear model: $p < 0.005$, $R^2 = 56.4\%$, $n = 74$; Table 1 in Supporting Information S4). $\delta^{15}N_{Phe}$ were positively correlated with $\delta^{15}N_{bulk}$ (Linear model: $p < 0.005$, $R^2 = 68.9\%$; Pearson correlation: 85%, $n = 74$; Fig. 4b; Table 6 in Supporting Information S4) and with $\delta^{15}N_{NO3}$ from the seals foraging areas (linear model: $p < 0.005$, $R^2 = 88.4\%$; Pearson correlation: 93%, $n = 7$; Fig. 4c; Table 6 in Supporting Information S4).

Seal TP

$\delta^{15}N_{bulk}$ was ~ 3‰ higher in ringed seals than in harp seals, which would indicate that ringed seals occupy a higher TP than harp seals (Post 2002). However, $\delta^{15}N_{bulk}$ was poorly

and negatively correlated with TP_{rel} (linear model: $p < 0.005$, $R^2 = 23.4\%$; Pearson correlation: −49%, $n = 74$; Fig. 4e; Table 6 in Supporting Information S4).

Cor-$\delta^{15}N_{trophic}$ were enriched in ^{15}N by ~ 4‰ in harp seals compared to ringed seals (linear model: $p < 0.005$, $R^2 = 39.9\%$, $n = 74$; Supporting Information S2 and Table 1 in Supporting Information S4) indicating that harp seals are in fact approximately one TP higher than ringed seals (McMahon and McCarthy 2016). These trends are supported by the higher $\delta^{15}N_{bulk}$, but lower TP_{rel} of ringed seals compared to harp seals, specifically at sampling site 5 (Figs. 2, 4a, d), the only site where we were able to compare directly between species. TP_{rel} (as given by PCA axis 1 of Cor-$\delta^{15}N_{trophic}$) did not vary with site for any of the seals species, as the best model for TP_{rel} in harp seals only included length, and none of the models for TP_{rel} in ringed seals was better than the null model (Tables 2, 4 in Supporting Information S4).

Discussion

When using the $\delta^{15}N_{AA}$ approach and correcting for variations in the baseline using $\delta^{15}N_{Phe}$, our results show that: (1) within each seal species, the TP_{rel} does not vary across the Arctic, confirming our prediction and (2) ringed seals are at a

lower TP than harp seals, contradicting our prediction. If the traditional interpretation of $\delta^{15}N_{bulk}$ in predators was applied here, we would conclude that: (1) the TP of seals varies between Arctic regions, as suggested by the spatial variation of $\delta^{15}N_{bulk}$ between sampling sites and (2) ringed seals are one TP higher than harp seals, as evidenced by their ~ 3‰ enrichment in ^{15}N (Post 2002). These findings highlight the power of using $\delta^{15}N_{AA}$ when examining spatial variation in TP of predators and demonstrate the need to account for variation in the $\delta^{15}N$ of the baseline to avoid misinterpretation of $\delta^{15}N_{bulk}$ in consumers.

Harp seals are generally larger than ringed seals (Ogloff et al. 2019). While harp and ringed seals feed on broadly similar prey species, stomach content analysis has shown that ringed seals have a greater reliance on smaller fish and invertebrates in the upper water column compared to harp seals, which rely to a greater extent on larger fish at deeper depths, probably related to differences in body size and habitat preferences (Wathne et al. 2000; Ogloff et al. 2019). This is in agreement with the lower TP_{rel} of the smaller ringed seals compared to the larger harp seals.

Variation in $\delta^{15}N_{bulk}$ in Arctic seals was largely driven by variation of $\delta^{15}N$ of the baseline, as evidenced by the strong positive correlation between $\delta^{15}N_{Phe}$ and $\delta^{15}N_{bulk}$ in seal tissue and supported by the weak and negative correlation between TP_{rel} and $\delta^{15}N_{bulk}$. In turn, despite the small sample size (n = 7), the strong positive correlation between $\delta^{15}N_{Phe}$ and $\delta^{15}N_{NO3}$ confirmed that spatial patterns in $\delta^{15}N_{Phe}$ were driven by the $\delta^{15}N$ of water masses associated with the seal foraging areas. The offset observed between $\delta^{15}N_{NO3}$ in water masses and $\delta^{15}N_{Phe}$ in seal tissues demonstrates that there is some fractionation of phenylalanine from the base of the food web to the upper trophic levels. This has previously been reported as ~ 1.5‰ between each trophic step (Bradley et al. 2014; McMahon and McCarthy 2016), which agrees with observations in this study (1.1 ± 0.5‰, assuming the seals to be at trophic level 3).

For the first time, we demonstrate a direct link between $\delta^{15}N_{NO3}$, $\delta^{15}N_{Phe}$, and $\delta^{15}N_{bulk}$ in predators, using observations of all three properties. Crucially, the ^{15}N-enrichment of $\delta^{15}N_{Phe}$ in seals from the Canadian archipelago and Baffin Island reflects the influence of the $\delta^{15}N_{NO3}$ of the Pacific derived water exiting the Arctic via the Canadian Archipelago (Lehmann et al. 2019), which is ^{15}N enriched by ~ 2‰ compared to the Atlantic water inflow (Somes et al. 2010). Our results show that $\delta^{15}N_{Phe}$ in seals can be used as tracers of spatial variation of environmental gradients across the Arctic. Any future changes in Arctic circulation, such as an increase of Pacific inflow through the Bering Strait (Woodgate 2018) or a weakening of the North Atlantic subpolar gyre (Hátún et al. 2017), will influence the $\delta^{15}N$ baseline of the Arctic Ocean, and in turn the $\delta^{15}N$ in Arctic seals, convoluting the detection of temporal trends in food web structure without baseline correction.

Changes in species composition of Arctic communities have already been observed as a result of environmental change. The northward shift of warmer water zooplankton (Dalpadado et al. 2016) and fish communities (Fossheim et al. 2015) has led to an increased abundance of boreal species at the expense of Arctic species, a process commonly referred to as "borealization." This has implications for Arctic food web structure (Kortsch et al. 2015; Yurkowski et al. 2018) and more specifically, prey availability to mobile predators including ringed and harp seals. With continued climate warming and environmental change, the impact on Arctic and sub-Arctic ecosystems will intensify, potentially having divergent effects on harp and ringed seals due to differences in dietary plasticity as a result of differing life-history strategies (Ogloff et al. 2019). Regional and local rates of borealization could also lead to a different ecosystem response between Canadian and European Arctic (Moore et al. 2019). Decadal assessment of $\delta^{15}N_{AA}$ values in Arctic seals is urgently required to assess past and future impact of environmental and human-induced changes on seal TP over pan-Arctic scales. Our study provides a reference for best practice on accurate comparison of TP_{rel} across large spatial and temporal scales, not only in the Arctic and sub-Arctic but also in other marine and terrestrial environments.

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