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Multi-decadal trends in biomarkers in harp seal teeth from the North Atlantic reveal the influence of prey availability on seal trophic position

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Abstract

Arctic food webs are being impacted by borealisation and environmental change. To quantify the impact of these multiple forcings, it is crucial to accurately determine the temporal change in key ecosystem metrics, such as trophic position of top predators. Here, we measured stable nitrogen isotopes (δ^{15}N) in amino acids in harp seal teeth from across the North Atlantic spanning a period of 60 years to robustly assess multi-decadal trends in harp seal trophic position, accounting for changes in δ^{15}N at the base of the food web. We reveal long-term variations in trophic position of harp seals which are likely to reflect fluctuations in prey availability, specifically fish- or invertebrate-dominated diets. We show that the temporal trends in harp seal trophic position differ between the Northwest Atlantic, Greenland Sea and Barents Sea, suggesting divergent changes in each local ecosystem. Our results provide invaluable data for population dynamic and ecotoxicology studies.

KEYWORDS
amino acids, Barents Sea, Greenland Sea, harp seals, Labrador Sea, multi-decadal trends, stable nitrogen isotopes, trophic position

1 | INTRODUCTION

Marine ecosystem-based management is crucial for effective marine conservation and resource management (Pikitch et al., 2004). Top predators can act as indicators of ecosystem change, reflecting the status of the ecosystem on which they depend (Sydeman et al., 2015). Trophic position of marine top predators, which can be used as an expression of food chain length, is a fundamental property of ecological communities, reflecting direct and indirect effects of changes in food web dynamics (Post, 2002a; Post & Takimoto, 2007). Trophic position, reflecting the trophic ecology of predators, is also utilised in population dynamic studies, as body

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condition and reproduction of marine predators are linked to their diet (Arnould et al., 2011; Øigård et al., 2013; Ronconi et al., 2014). In addition, trophic position is one of the key drivers of contaminant burdens (Borgå et al., 2004; Braune et al., 2015; Brown et al., 2016; Carravieri et al., 2014) and trophically derived parasite loads (Couch et al., 2022; Vestbo et al., 2019) in predators. It is therefore crucial to accurately detect decadal changes in trophic position of marine predators in order to understand how food webs are being reshaped and the consequences of these modifications on population dynamics and contaminant bioaccumulation, which could, in turn, be used in ecosystem-based management.

Here, we examined multi-decadal trends in trophic position of a generalist near-top marine predator, the harp seal (*Pagophilus groenlandicus*), across three locations in the North Atlantic. The North Atlantic food web is under a period of tremendous changes, including ocean warming, change in ocean circulation and change in fisheries, impacting all trophic levels from phytoplankton to predators (Meredith et al., 2019). The Barents Sea, Greenland Sea and Baffin Bay connect the Atlantic to the Arctic Ocean and have undergone several shifts in fish and zooplankton abundance and species composition resulting from fishing and changes in environmental conditions (Dalpadado et al., 2016; Dempsey et al., 2017; Fossheim et al., 2015; Koen-Alonso et al., 2018; Nöthig et al., 2015; Oziel et al., 2020; Pedersen et al., 2017, 2020). These changes in community structure have resulted in changes to predator–prey interactions in recent decades (Dwyer et al., 2010; Haug, Bogstad, et al., 2017; Kortsch et al., 2015; Pecuchet et al., 2020; Stenson, 2012), and are likely to indirectly impact marine top predators, such as harp seals, through changes in foraging ecology (e.g. Hoover et al., 2013; Kovacs & Lydersen, 2008; Laidre et al., 2008).

Stable nitrogen isotopes are commonly used as a biomarker to reconstruct food webs and estimate trophic position of predators. The ratio between heavy (^{15}N) and light (^{14}N) stable nitrogen isotopes in bulk tissue (hereafter $\delta^{15}N_{Bulk}$) undergoes a fractionation between each trophic level estimated to be on average $3.4 \pm 0.2‰$ (Vander Zanden & Rasmussen, 2001), providing a measure of trophic position (Post, 2002b). However, $\delta^{15}N_{Bulk}$ values in consumers are heavily dependent on $\delta^{15}N$ at the base of the food web, or baseline. Nitrate, underpinning the baseline of marine food web (Mariotti et al., 1981), is supplied to the Arctic Ocean by Atlantic water entering through the Barents Sea and Fram Strait, and by Pacific water crossing the Bering Strait (Torres-Valdes et al., 2013). The $\delta^{15}N$ values of nitrate in Atlantic water are depleted in ^{15}N compared to the $\delta^{15}N$ values of nitrate in Pacific water and water masses present in the high Arctic, as a result of the biological processing within the Atlantic, and Pacific oceans (Buchanan et al., 2022; de la Vega et al., 2020; Knapp et al., 2008; Marconi et al., 2015; Somes et al., 2010; Tuerena, Hopkins, et al., 2021). The Arctic is experiencing changes in ocean circulation, including a simultaneous increase in the rates of Atlantic and Pacific inflows (Polyakov et al., 2020; Woodgate, 2018). Thus, spatial trends in water mass influence, alongside temporal changes in circulation, lead to a heterogenous and evolving $\delta^{15}N$ baseline across the Arctic and sub-Arctic, that needs to be accounted for to

reliably detect changes in trophic position of predators (Buchanan et al., 2022; de la Vega et al., 2020, 2022).

Compound-specific stable nitrogen isotopes of amino acids ($\delta^{15}N_{AA}$) can overcome this issue. $\delta^{15}N_{AA}$ is a powerful biomarker approach that disentangles baseline and fractionating trophic effects when using $\delta^{15}N$ values to estimate trophic position. The $\delta^{15}N$ of the 'source' amino acid (AA) phenylalanine ($\delta^{15}N_{Phe}$), can conservatively trace the $\delta^{15}N$ at the baseline as it experiences minimal fractionation (<1‰) during trophic transfer (McMahon & McCarthy, 2016). The $\delta^{15}N$ of 'trophic' AAs ($\delta^{15}N_{Trophic}$), for example, glutamic acid, undergoes significant fractionation (>3‰) resulting in ^{15}N enrichment between each trophic step (McMahon & McCarthy, 2016). This approach simultaneously fingerprints both the $\delta^{15}N$ baseline and trophic information in a predator from the analysis of predator tissue alone. This allows accurate estimation of changes in relative trophic position while accounting for variation in $\delta^{15}N$ baseline, using baseline-corrected $\delta^{15}N_{Trophic}$ (cor-$\delta^{15}N_{Trophic}$; de la Vega et al., 2020).

In this study, we used harp seals as an indicator species of changes in the North Atlantic sub-Arctic food web (Laidre et al., 2008). Harp seals are the most abundant pinniped in the North Atlantic (Stenson et al., 2020). They are found in three populations, in the Barents and White Seas (hereafter, Barents Sea population), in the Greenland Sea (hereafter, Greenland Sea population) and in the Northwest Atlantic off Newfoundland and Labrador (hereafter, Northwest Atlantic population, Figure 1; Carr et al., 2015; Sergeant, 1991). Harp seals undertake substantial annual migrations between sub-Arctic breeding and moulting areas in winter and spring, and Arctic feeding grounds in summer and autumn (Figure 1;

○ Seal sampling sites
▨ Range of harp seal population from the Barents Sea
▨ Range of harp seal population from the Greenland Sea
▨ Range of harp seal population from the Northwest Atlantic
▨ Fish data from the Barents Sea
▨ Fish data from the Newfoundland shelf
▬ Atlantic influenced water
▬ Pacific influenced water
▬ Modified water
IC = Irminger Current
LC = Labrador Current
EGC = East Greenland Current
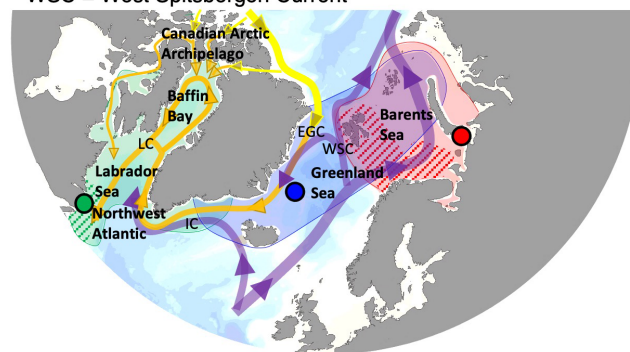WSC = West Spitsbergen Current

FIGURE 1 Map depicting the seal sampling sites, their population range, the areas from which the fish data were taken, and the main ocean circulation.

Folkow et al., 2004; Lacoste & Stenson, 2000; Nordøy et al., 2008; Stenson & Sjare, 1997). Harp seal diets consist of a wide variety of fish and invertebrates, with substantial seasonal and geographical variations in their diet composition associated with changes in local prey availability and abundance (e.g. Bogstad et al., 2000; Enoksen et al., 2017; Lawson et al., 1995; Lawson & Stenson, 1995, 1997; Nilssen et al., 1998; Stenson, 2012). Seal diet is therefore expected to be a strong indicator of variation in prey availability and changes in fish communities. Here, we analysed $\delta^{15}N_{AA}$ in harp seal teeth from 1949 to 2012, from the Barents Sea, the Greenland Sea and the Northwest Atlantic (Figure 1) to assess multi-decadal trends in harp seal relative trophic position across the North Atlantic sub-Arctic. To relate temporal trends in prey availability and harp seal trophic position, we collated published temporal data on biomass of seal's prey species, including fish and invertebrates, from the Barents Sea and Northwest Atlantic. We predicted that: (1) $\delta^{15}N_{Phe}$ values, reflecting the $\delta^{15}N$ baseline, will vary temporally reflecting changes in water mass circulation occurring across the North Atlantic, and (2) cor-$\delta^{15}N_{Trophic}$, representing the relative trophic position of harp seals, will vary temporally reflecting changes in prey species availability across the North Atlantic.

2 | MATERIALS AND METHODS

2.1 | Seal sampling

Teeth of harp seals from the Barents Sea ($n=72$), Greenland Sea ($n=55$) and Northwest Atlantic ($n=48$; Table 1; Figure 1) were taken from archives in the Institute of Marine Research (IMR), Norway and Fisheries and Oceans (DFO) St John's, Canada. The teeth were prepared following the method described in Kershaw et al. (2021). In brief, the teeth were sectioned along two planes: transverse and sagittal using a precision low speed diamond saw (Buehler, Isomet™). The transverse sections were used to identify the different annual growth layer groups (GLGs) based on the structure, width and opacity of individual layers (Bowen et al., 1983). Each GLG corresponds to 1 year of life of the individual. A 700 μm sagittal section was cut as close as possible to the central plane of the tooth and demineralised with 0.25 M HCl for between 12 and 24 h. Once softened, any remaining gum tissue and cementum were cut away from the outer edge of the tooth. The dentine samples representing the individual GLG for the second (GLG2) and third years (GLG3) of life of the seal individuals were freeze-dried and stored in plastic vials prior to stable isotope analysis. Material from GLG2 and GLG3 was combined (GLG2+3) in order to provide sufficient material for compound-specific stable isotope analyses for each individual (Kershaw et al., 2021). Thus, each data point represents the isotopic signal averaged over the second and third year of life of each individual. Knowing the sampling year and the age of the individual, we were able to assign specific years represented by GLG2 and GLG3 for each individual (Supporting Information S1). GLG2+3 of teeth from the Barents Sea and Greenland Sea represented years from 1949–1950 to 2011–2012 and from 1945–1946 to 2007–2008 respectively (Table 1). GLG2+3 of teeth from the Northwest Atlantic covered years from 1975–1976 to 2010–2011 (Table 1).

2.2 | Stable isotope analyses of seal teeth samples

For $\delta^{15}N_{Bulk}$, ~0.5 mg of sample was precisely weighed (±1 μg) and sealed in a tin capsule. For $\delta^{15}N_{AA}$, ~15 mg of dentine was hydrolysed and propylated. Amino acid methyl esters were then acetylated, dissolved in dichloromethane and stored at −20°C until analysis. A detailed outline of the method is provided in Supporting Information S1.

All seal $\delta^{15}N$ analyses were carried out at the Liverpool Isotope Facility for Environmental Research (LIFER), University of Liverpool, and reported in standard δ-notation (‰) relative to atmospheric N_2 (Mariotti, 1983). $\delta^{15}N_{Bulk}$ was determined using a Costech elemental analyser coupled to Thermo Fisher Delta V isotope ratio mass spectrometer (IRMS). Samples were corrected using international reference materials USGS40 and USGS41a, analysed throughout each run with a reproducibility of <0.1‰. An internal standard of ground prawn (*Penaeus vannamei*) with a well characterised $\delta^{15}N$ value (6.8‰) was analysed every 10 samples to monitor precision, which was <0.2‰.

$\delta^{15}N_{AA}$ were determined using a Trace Ultra gas chromatograph (GC) coupled to a Thermo Fisher Delta V Advantage IRMS with a ConFlo IV interface. A liquid nitrogen trap was added after the reduction oven to remove CO_2 from the sample stream. The separation of AA was achieved using a HP Innowax capillary column (Agilent). Samples were analysed in duplicate. A mixed standard prepared from eight AAs with known $\delta^{15}N$ values (University of Indiana and SI Science) was used for calibration and analysed every four injections. Details of methods, precision, accuracy and $\delta^{15}N$ values of all identified AA are provided in Supporting Information S1.

TABLE 1 Stable nitrogen isotopes analyses and sampling site for harp seal teeth; Ranges of the sampling years and ages of seal individuals, and year(s) represented in the tissue analysed for $\delta^{15}N$; n = number of analysed samples (=data points); All $\delta^{15}N$ values represent the years assigned to GLG2 and GLG3, corresponding to the foraging at 2 and 3 years old for all individuals.

Sampling site	Sampling year	Age	Year represented by GLG2+3	n
Barents Sea	1963–2018	3–15	1951–1952 to 2011–2012	72
Greenland Sea	1953–2014	7–12	1945–1946 to 2007–2008	55
Northwest Atlantic	1979–2016	4–6	1975–1976 to 2011–2012	48

2.3 | Seal trophic position estimation

We used the $\delta^{15}N$ values of phenylalanine ($\delta^{15}N_{Phe}$) to track the $\delta^{15}N$ of the base of the food web in seals, and the $\delta^{15}N$ values of two main trophic amino acids (glutamic acid and aspartic acid) to estimate relative seal trophic positions. The uncertainty regarding trophic fractionation factors between source and 'trophic amino acids' across taxa in entire food webs (Nielsen et al., 2015) prevents accurate estimation of an organism's absolute trophic position (Matthews et al., 2020). To estimate the relative trophic position of each seal individual, we used the mean $\delta^{15}N$ values of glutamic acid and aspartic acid ($\delta^{15}N_{Trophic}$), that was baseline corrected using $\delta^{15}N_{Phe}$ (Equation 1), providing baseline-corrected $\delta^{15}N_{Trophic}$ (hereafter Cor-$\delta^{15}N_{Trophic}$).

$$Cor - \delta^{15}N_{Trophic} = \delta^{15}N_{Trophic} - \delta^{15}N_{Phe}. \qquad (1)$$

2.4 | Statistical analyses

Statistical analyses were performed in R version 3.5.1 (R Core Team, 2018). We assessed the relationship between $\delta^{15}N_{Bulk}$, $\delta^{15}N_{Phe}$ and Cor-$\delta^{15}N_{Trophic}$ using simple linear regression models (hereafter linear models). To analyse temporal variation in $\delta^{15}N_{Phe}$ and Cor-$\delta^{15}N_{Trophic}$ in harp seals, linear models and general additive models (GAMs) were fitted with $\delta^{15}N_{Phe}$ and Cor-$\delta^{15}N_{Trophic}$, respectively, as a function of year for each site separately. Model fit was checked by residual analyses (Zuur et al., 2009). Linear models provided best fit for $\delta^{15}N_{Phe}$. GAM using the restricted maximum likelihood estimation method, cubic regression spline smoothing functions and Gaussian error distributions with no data transformation provided the best fit for Cor-$\delta^{15}N_{Trophic}$. Model significance was assessed with p-values, degrees of freedom, R^2 (linear models) and deviance explained (GAM), and F-statistics (linear models).

2.5 | Fish biomass

To qualitatively compare the relative temporal variation of fish biomass and seal trophic position, we collated estimates of fish biomass from the Barents Sea, and fish and invertebrate biomass from the Northwest Atlantic from published sources. There were no time series of fish stock assessments from the Greenland Sea.

For the Barents Sea, biomass of capelin (*Mallotus villosus*; more than 1 year old) and juvenile Atlantic herring (*Clupea harengus*; 1 and 2 years old) from 1972 to 2010, and biomass of Arctic cod (*Boreogadus saida*; more than 1 year old) from 1986 to 2010 were taken from Johannesen et al. (2012). Biomass of Atlantic cod (*Gadus morhua*; more than 3 years old), haddock (*Melanogrammus aeglefinus*; more than 3 years old) and Greenland halibut (*Reinhardtius hippoglossoides*; more than 5 years old) from 1960 to 2020 was taken from ICES (2020). The capelin and Arctic cod biomass were

based on annual acoustic fish stock surveys covering both the Southern and Northern Barents Sea (Figure 1; van der Meeren & Prozorkevich, 2021). The biomass of Atlantic herring, Atlantic cod, Greenland halibut and haddock was from ICES stock assessment (ICES, 2010, 2020; Supporting Information S2). Fish species were grouped into 'demersal fish' (in thousand tonnes), including Atlantic cod, haddock, Greenland halibut and 'pelagic schooling fish' (in million tonnes), including capelin and Atlantic herring. Arctic cod, capelin and juvenile herring are the most abundant pelagic fish, and cod and haddock dominate the biomass of demersal fish in the Barents Sea (Johannesen et al., 2012). These species are important prey species for harp seals in the Barents Sea (Lindstrøm et al., 2013; Nilssen, Haug, Potelov, Stasenkov, et al., 1995; Nilssen, Haug, Potelov, & Timoshenko, 1995), and the interactions between capelin, cod and herring are key processes in the Barents Sea ecosystem (Hamre, 1994; Haug, Bogstad, et al., 2017; Ushakov & Prozorkevich, 2002; Wassmann et al., 2006).

For the Northwest Atlantic, biomass of capelin (in million tonnes) from 1957 to 2018 was taken from Buren et al. (2019). Biomass of planktivore–piscivore and demersal piscivore fish species (in million tonnes) from 1981 to 2017, and crustaceans (in thousand tonnes) from 1995 to 2017 were taken from Koen-Alonso and Cuff (2018). All biomass data were from surveys conducted by the Fisheries and Ocean Canada (DFO) along the Newfoundland shelf (Figure 1; Koen-Alonso & Cuff, 2018; Pepin et al., 2014) in autumn (September to December) and/or spring (May). The biomass of capelin which dominated the biomass of pelagic fish, was determined from acoustic surveys (Buren et al., 2019; Supporting Information S2). The biomass of demersal piscivore and planktivore–piscivore fish species and crustaceans was estimated from multispecies surveys using bottom trawls (Supporting Information S2). Demersal piscivores consisted of 33 species and were dominated by Atlantic cod and Greenland halibut. Planktivore–piscivores consisted of 11 species and were dominated by Arctic cod and redfish (DFO, 2006). Crustaceans included snow crab (*Chionoecetes opilio*) and Northern shrimp (*Pandalus borealis*). Atlantic cod, Greenland halibut, Arctic cod and redfish are important prey species for harp seals on the Newfoundland shelf, in addition to invertebrates such as shrimp (Lawson et al., 1995; Lawson & Hobson, 2000; Lawson & Stenson, 1997; Stenson, 2012; Tucker et al., 2009).

3 | RESULTS

3.1 | Temporal trend in isotopic baseline ($\delta^{15}N_{Phe}$)

$\delta^{15}N_{Phe}$ values in harp seal teeth ranged from 7.9‰ to 13.2‰ in the Barents Sea population (Figure 2a), from 8.3‰ to 12.0‰ in the Greenland Sea population (Figure 2b) and from 10.2‰ to 14.9‰ in the Northwest Atlantic population (Figure 2c).

$\delta^{15}N_{Phe}$ values decreased by -0.036 ± 0.005‰ year^{-1} in harp seals from the Barents Sea population, declining from 11.7 ± 1.0‰ in 1951–1952 to 10.0 ± 0.2‰ in 2011–2012 (linear model: $p < .01$,
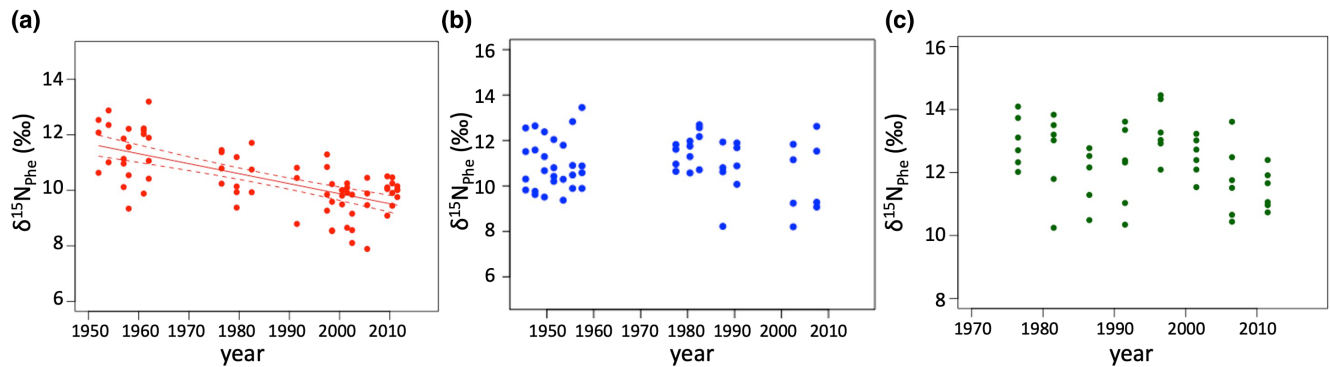
FIGURE 2 $\delta^{15}N_{Phe}$ values per year in harp seals teeth from (a) the Barents Sea, (b) the Greenland Sea and (c) the Northwest Atlantic; Solid line shows linear models fit on the $\delta^{15}N_{Phe}$ values and dashed lines show 95% confidence interval of the linear models; $\delta^{15}N_{Phe}$ values in harp seal teeth from the Barents Sea were already published in de la Vega et al. (2022).

TABLE 2 Statistical parameters of the linear models assessing the temporal trend in $\delta^{15}N_{Phe}$ in harp seal teeth from each Arctic region; df, degree of freedom; n, number of samples; SD, standard deviation, lines in bold are considered significant.

Site	Response variable	Explanatory variable	n	Intercept ($\pm$SD)	p Value	Slope ($\pm$SD)	p Value	R^2 (%)	F value (df)
Barents Sea	$\delta^{15}N_{phe}$	**Year**	**72**	**81.89 $\pm$ 9.66**	**<.01**	**−0.036 $\pm$ 0.005**	**<.01**	**43.1**	**54.8 (70)**
Greenland Sea	$\delta^{15}N_{phe}$	Year	55	18.85 $\pm$ 15.20	.220	−0.004 $\pm$ 0.008	.606	0.0	26.9 (53)
Northwest Atlantic	$\delta^{15}N_{phe}$	Year	48	70.79 $\pm$ 26.94	.012	−0.029 $\pm$ 0.014	.035	7.5	4.7 (46)

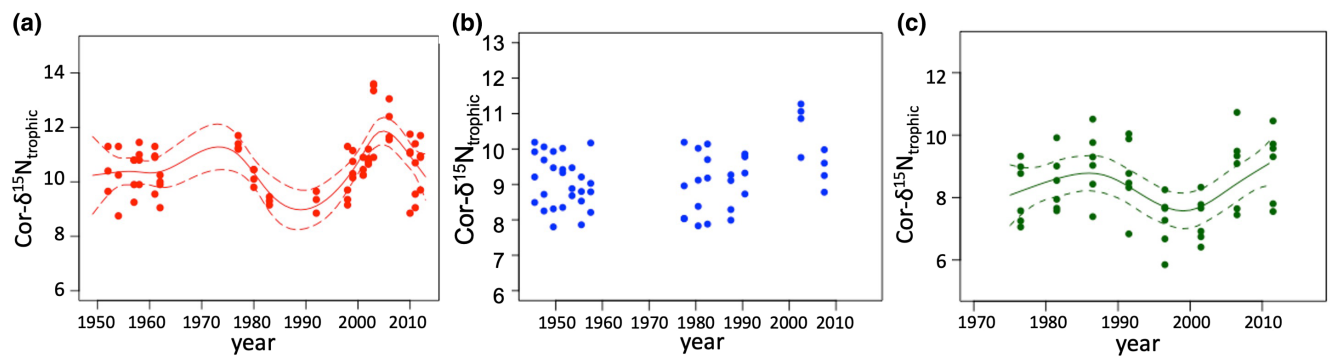**FIGURE 3** Baseline-corrected $\delta^{15}N_{Trophic}$ (Cor-$\delta^{15}N_{Trophic}$) values per year in harp seals teeth from (a) the Barents Sea, (b) the Greenland Sea and (c) the Northwest Atlantic; Solid line shows general additive models (GAMs) fit on $\delta^{15}N_{Trophic}$ values and dashed lines show 95% confidence interval of the GAMs.

$R^2 = 43.1\%$, Figure 2a; Table 2). There was no temporal trend in $\delta^{15}N_{Phe}$ values in harp seals from the Greenland Sea and from the Northwest Atlantic populations (Figure 2b,c; Table 2).

3.2 | Temporal trend in Cor-$\delta^{15}N_{Trophic}$ of harp seals

Cor-$\delta^{15}N_{Trophic}$ values of harp seal teeth ranged from 8.8‰ to 13.6‰ in the Barents Sea population (Figure 3a), 7.8‰ to 11.2‰ in the Greenland Sea population (Figure 3b) and 5.8‰ to 10.7‰ in the Northwest Atlantic population (Figure 3c).

Cor-$\delta^{15}N_{Trophic}$ values of harp seals from the Barents Sea, Greenland Sea and Northwest Atlantic populations varied over time, alternating between periods of increasing and decreasing cor-$\delta^{15}N_{Trophic}$ (Figure 3a–c). In the Barents Sea population, cor-$\delta^{15}N_{Trophic}$ of harp seals decreased in the 1980s to a minimum cor-$\delta^{15}N_{Trophic}$ annual value of 9.3 $\pm$ 0.4‰ in 1983, followed by an increase in the early 2000s of ≈2‰, to a maximum cor-$\delta^{15}N_{Trophic}$ annual value of 12.9 $\pm$ 1.3‰ in 2003, and another decrease in the late 2000s (GAM: effective degree of freedom [edf] = 6.42, s(year): $p < .01$; Figure 3a; Table 3). Cor-$\delta^{15}N_{Trophic}$ of harp seals from the Greenland Sea population did not vary with time (Figure 3b; Table 3). Cor-$\delta^{15}N_{Trophic}$ of harp seals from the Northwest Atlantic population

TABLE 3 Statistical parameters of the general additive models assessing the temporal trend in $\delta^{15}N_{trophic}$ in harp seal teeth from each Arctic region; edf, effective degree of freedom; lines in bold are considered significant.

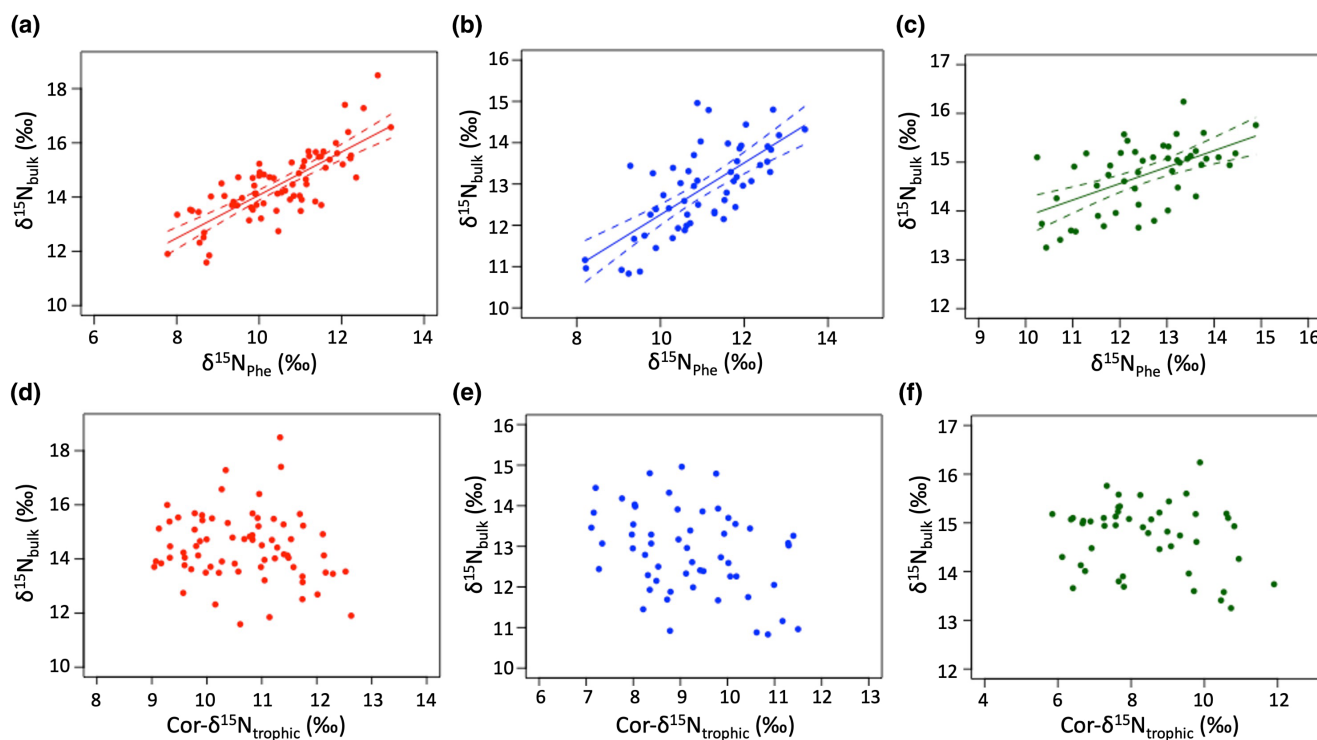| Site	n	Deviance explained (%)	Parametric coefficient		Smooth function, s(year)	
			Intercept	p Value	edf	p Value
Barents Sea	**72**	**43.7**	**10.60**	**<.01**	**6.5**	**<.01**
Greenland Sea	55	16.2	9.18	<.01	1.8	.012
Northwest Atlantic	**48**	**27.6**	**8.37**	**<.01**	**3.4**	**<.01**

FIGURE 4 Relationship between $\delta^{15}N_{Phe}$ in per mil (‰) and $\delta^{15}N_{Bulk}$ in harp seals from (a) the Barents Sea, (b) the Greenland Sea and (c) the Northwest Atlantic, and relationship between Cor-$\delta^{15}N_{Trophic}$ and $\delta^{15}N_{Bulk}$ in harp seals from (d) the Barents Sea, (e) the Greenland Sea and (f) the Northwest Atlantic. Solid lines show linear model, dashed lines show 95% confidence interval of the linear model.

increased slightly from the mid-1970s to mid-1980s of ≈1.5‰, then decreased from the mid-1980s to the early 2000s of ≈2‰, to a minimum cor-$\delta^{15}N_{Trophic}$ annual value of 7.3±0.7‰ in 2002, and increased again from early 2000s to early 2010s of ≈2‰, to a maximum cor-$\delta^{15}N_{Trophic}$ annual value of 9.4±1.1‰ in 2012 (GAM: edf=3.4, s(year): $p<.01$; Figure 3c; Table 3).

3.3 | Relationships between $\delta^{15}N_{Bulk}$ and $\delta^{15}N_{AA}$

There was a strong positive correlation between $\delta^{15}N_{Bulk}$ and $\delta^{15}N_{Phe}$ in harp seals from the Barents Sea (linear model: $p<.01$, $R^2=61.2\%$; Figure 4a), Greenland Sea (linear model: $p<.01$, $R^2=49.3\%$; Figure 4b) and Northwest Atlantic (linear model: $p<.01$, $R^2=30\%$; Figure 4c; Table 4) populations. $\delta^{15}N_{Bulk}$ was not correlated with cor-$\delta^{15}N_{Trophic}$ in all populations studied (Figure 4d–f; Table 4).

3.4 | Temporal variation of fish biomass

In the Barents Sea, the biomass of capelin, dominating the pelagic schooling fish stock, fluctuated with time, with peaks of biomass in 1975, 1980, 1991, 2000 and 2008 (Figure 5a). The years 1980, 1991 and 2000 were followed by the collapse of the capelin stock (Figure 5a). The herring biomass also fluctuated with time, with the highest biomass in 1984, 1993, 2000 and 2004 (Figure 5a). The biomass of Atlantic cod, dominating demersal fish stock, decreased from 1968 to 1983, and increased again in the last decades (Figure 5a). The biomass of Arctic Cod, fluctuated with time, with the lowest values in 1988 and 2003, and the highest values in 2001 and 2006 (Figure 5a).

In the Northwest Atlantic, the biomass of capelin was the highest in 1988, followed by an abrupt collapse of capelin stock (Figure 5b). The capelin biomass slightly increased again after 2010 (Figure 5b).

TABLE 4 Statistical parameters of the linear models assessing the relationships between $\delta^{15}N_{Bulk}$, $\delta^{15}N_{Phe}$ and Cor-$\delta^{15}N_{Trophic}$ in harp seal teeth from each Arctic regions; the response variable was $\delta^{15}N_{Bulk}$ for all models; df, degree of freedom; n, number of samples; SD, standard deviation, lines in bold are considered significant.

Site	Explanatory variable	n	Intercept ($\pm$SD)	p Value	Slope ($\pm$SD)	p Value	R^2 (%)	F value (df)
Barents Sea	**$\delta^{15}N_{Phe}$**	**72**	**6.13$\pm$0.79**	**<.01**	**0.795$\pm$0.075**	**<.01**	**61.2**	**113.2 (70)**
Greenland Sea	**$\delta^{15}N_{Phe}$**	**55**	**5.98$\pm$0.95**	**<.01**	**0.628$\pm$0.086**	**<.01**	**49.3**	**53.6 (53)**
Northwest Atlantic	**$\delta^{15}N_{Phe}$**	**48**	**10.51$\pm$0.92**	**<.01**	**0.338$\pm$0.073**	**<.01**	**30.0**	**21.1 (46)**
Barents Sea	$\delta^{15}N_{trophic}$	72	16.43$\pm$1.69	<.01	−0.187$\pm$0.159	.241	0.0	1.4 (70)
Greenland Sea	$\delta^{15}N_{trophic}$	55	15.66$\pm$1.05	<.01	−0.113$\pm$0.159	.010	10.3	7.2 (53)
Northwest Atlantic	$\delta^{15}N_{trophic}$	48	15.49$\pm$0.56	<.01	−0.092$\pm$0.065	.168	2.0	2.0 (46)

(a) Barents Sea
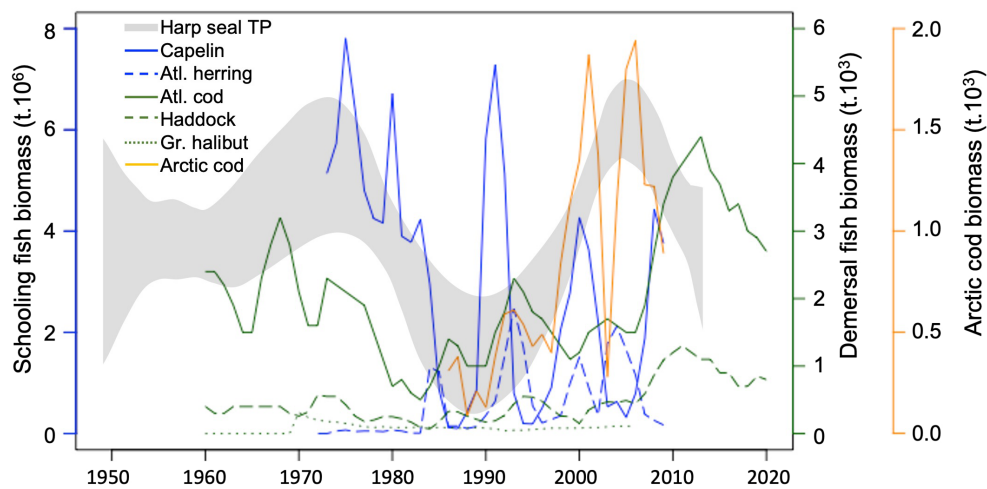
(b) Northwest Atlantic

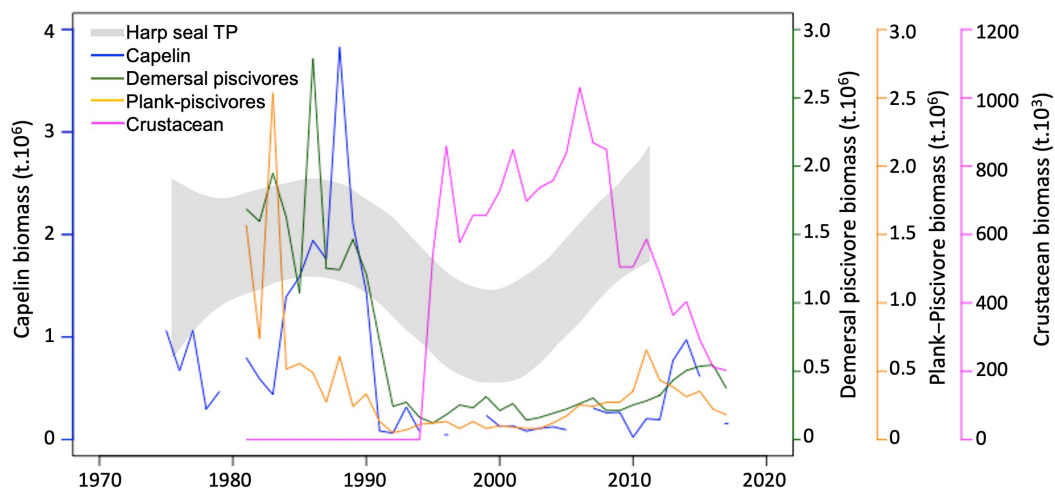**FIGURE 5** (a) Temporal variation of fish biomass in the Barents Sea, as available; Pelagic schooling fish (in million tonnes; t.10^6) from 1972 to 2010, includes capelin and Atlantic herring (Atl. herring) and were taken from Johannesen et al. (2012); Arctic cod (in thousand tonnes; t.10^3) from 1986 to 2010 were taken from Johannesen et al. (2012); demersal fish (in thousand tonnes; t.10^3) from 1960 to 2020 includes Atlantic cod (Atl. cod), haddock and Greenland halibut (Gr. halibut) and were taken from ICES (2020). (b) Temporal variation of capelin biomass (in million tonnes; t.10^6) from 1957 to 2018, biomass of demersal piscivore and planktivore–piscivore (plank-piscivore) fish species (in million tonnes) from 1981 to 2017, and crustaceans biomass (in thousand tonnes; t.10^3) from 1995 to 2017 in the Northwest Atlantic, as available; demersal piscivores are dominated by Atlantic cod and Greenland halibut; planktivore–piscivores are dominated by Arctic cod and redfish; Crustaceans include Northern shrimps and snow crabs; data were taken from Buren et al. (2019) and Koen-Alonso and Cuff (2018). The shaded grey areas represent the 95% confidence intervals of the general additive model shown in Figure 3a,c and indicate the temporal trends in trophic position (TP) of harp seals.

The biomass of demersal piscivore and planktivore–piscivore fish species followed similar temporal variation. Their biomass was the highest in the early and mid-1980s and the lowest in the mid-1990s–early 2000s (Figure 5b). The biomass for both functional groups slowly increased again until the mid-2010s, reaching a biomass values remaining well below the previous high (Figure 5b). The biomass of crustaceans, mainly consisting of shrimp, increased in the 1990s, reaching its maximum value in 2006, and strongly decline after the mid-2000s (Figure 5b).

4 | DISCUSSION

4.1 | Multi-decadal trends in the $\delta^{15}N$ baseline

The Arctic is experiencing simultaneous changes in water mass circulation and in the rate of Atlantic and Pacific inflows (Polyakov et al., 2020; Woodgate, 2018), influencing the $\delta^{15}N$ baseline across the Arctic and sub-Arctic (de la Vega et al., 2022). The overall volume and speed of Atlantic water flowing northward has increased in the last decades (Oziel et al., 2016, 2020), bringing more ^{15}N-depleted water into the Eastern Greenland Sea via the West Spitsbergen Current, and the southern Baffin Bay via the Irminger Current (Figure 1). The inflow of Pacific water through the Bering Strait has increased by more than 50% (Woodgate, 2018), in turn enhancing the export of ^{15}N-enriched water from the Arctic via the East Greenland Current in the Western Greenland Sea (Håvik et al., 2017), and through the Canadian Arctic Archipelago, influencing the surface waters as far South as the Labrador Sea via the Labrador Current (Figure 1; McGeehan & Maslowski, 2012; Rice, 2002). The strong correlations between $\delta^{15}N_{Bulk}$ and $\delta^{15}N_{Phe}$ and the absence of correlations between $\delta^{15}N_{Bulk}$ and $\delta^{15}N_{Trophic}$ in the three harp seal populations demonstrated that variations in $\delta^{15}N_{Bulk}$ were mainly driven by changes in the $\delta^{15}N$ baseline, which were likely impacted by changes in water circulation.

The Barents Sea, which is the main gateway between the Arctic and adjacent Atlantic Ocean in the northeast, is experiencing changes in the rate of Atlantic water inflow, nitrogen sources and in situ biogeochemical processes, influencing the $\delta^{15}N$ baseline. The range of the Barents Sea harp seal population is restricted within the Barents Sea (Haug et al., 1994; Nordøy et al., 2008), harp seals migrating between their breeding and moulting areas in the southern Barents Sea in winter and spring, and Arctic feeding grounds in the northern Barents Sea in summer and autumn (Haug et al., 1994; Nordøy et al., 2008). The decreasing temporal trend in $\delta^{15}N_{Phe}$ values of harp seals from the Barents Sea therefore reflects environmental changes occurring within the Barents Sea, and has been described in de la Vega et al. (2022) as the result of the combination of increased anthropogenic atmospheric ^{15}N-depleted nitrogen deposition in the Atlantic (Buchanan et al., 2022; Duce et al., 2008; Jickells et al., 2017; Yang & Gruber, 2016) and subsequent increased northward transport of ^{15}N-depleted Atlantic water through the Barents Sea Opening (Oziel et al., 2016, 2020).

The absence of temporal trend in $\delta^{15}N_{Phe}$ in the Greenland Sea and Northwest Atlantic harp seal populations could be explained by the combined influences of different water masses having different $\delta^{15}N$ baseline within the range of both harp seal populations. Harp seals from the Greenland Sea gather into large and dense aggregations on the pack ice off the east coast of Greenland during the breeding and moulting periods in winter and spring (Folkow et al., 2004). The Greenland Sea has a complex hydrography hosting multiple water masses from different origins (Brakstad et al., 2019; Tuerena, Mahaffey, et al., 2021). The Western Greenland Sea receives ^{15}N-enriched Pacific origin water exiting the Arctic on the Western side of Fram Strait which is transported southward via the East Greenland Current system, and the Eastern Greenland Sea is influenced by the West Spitsbergen current flowing northward, which consists of ^{15}N-depleted Atlantic Water (Figure 1; Håvik et al., 2017). In summer, most of the Greenland Sea harp seals travel eastward to the Barents Sea, which is mainly influenced by Atlantic water, where the larger parts of the Greenland Sea and Barents populations share feeding grounds during most of the autumn (Folkow et al., 2004). Harp seals from the Greenland Sea population therefore integrate over the year a $\delta^{15}N$ baseline influenced by both ^{15}N-enriched Pacific origin water during the breeding and moulting period, and ^{15}N-depleted Atlantic water during summer and autumn. The absence of trend in $\delta^{15}N_{Phe}$ in the Greenland Sea harp seal population could thus reflect the increased influence of both ^{15}N-enriched Pacific and ^{15}N-depleted Atlantic waters within their migration area.

Harp seals from the Northwest Atlantic are found on both the Canadian and Greenland continental shelves (Stenson et al., 2020). They spend winter and spring on their breeding and moulting grounds on the Labrador shelf, and migrate northward into Arctic waters in the Baffin Bay and across the Labrador Sea to the coast of Greenland in summer and autumn (Stenson & Sjare, 1997). The Canadian shelf is mainly influenced by the Labrador Current flowing southward (Rice, 2002), which transports ^{15}N-enriched Pacific-derived waters exiting the Arctic through the Canadian Arctic Archipelago (Azetsu-Scott et al., 2010; Roy et al., 2015; Woodgate, 2013). The West Greenland shelf receives a mix of East Greenland current and ^{15}N-depleted Atlantic water advected via the Irminger current flowing northward along the East coast of Greenland (Hansen, Nielsen, et al., 2012; Myers et al., 2007). Like Greenland Sea harp seals, harp seals from the Northwest Atlantic therefore integrate a $\delta^{15}N$ baseline influenced by both ^{15}N-enriched Pacific water and ^{15}N-depleted Atlantic water over the year. de la Vega et al. (2021) observed an increasing decadal trend in $\delta^{15}N_{Phe}$ in ringed seals from the Canadian Arctic Archipelago and Baffin Bay, that has been explained by the increasing influence of ^{15}N-enriched Pacific-derived water in these regions, and the effect of increasing primary production and in turn benthic denitrification. The increasing trend in $\delta^{15}N_{Phe}$ in ringed seals from the Baffin Bay was less pronounced than in the Canadian Arctic Archipelago, likely reflecting a dilution effect of the Pacific water influence when reaching southern Baffin Bay (de la Vega et al., 2021). Here, the absence of trend in $\delta^{15}N_{Phe}$ in harp seals from the Northwest Atlantic population could result from the increased

influence of both ^{15}N-enriched Pacific water and ^{15}N-depleted Atlantic water, counterbalancing each other in the migration area of this population.

In addition to changes in water mass influence, other factors, such as increasing primary production and in turn benthic denitrification (Arrigo & van Dijken, 2015), or increasing bacterial activity with increasing temperature (Vaqué et al., 2019) that tend to increase the δ^{15}N baseline (Granger et al., 2011; Morata et al., 2008), might also have influenced the $\delta^{15}N_{Phe}$ in harp seals from these areas. These results suggest that migratory predators, as they forage within different food webs, assimilate spatially varying isotopic baselines, which complicates the use of single-site baselines that are common in analyses of bulk isotope values. Not accounting for this change in the δ^{15}N at the baseline would lead to misestimation of harp seal trophic position using $\delta^{15}N_{Bulk}$ alone (de la Vega et al., 2020). This highlights the power of using cor-$\delta^{15}N_{Trophic}$ values to assess temporal trend in trophic position of harp seals across the North Atlantic, especially when the rates of change in δ^{15}N at the baseline vary spatially.

4.2 | Multi-decadal trends in harp seal trophic position

Harp seal diet consists of various prey items, including invertebrate and fish species. During summer and autumn, their diet is dominated by invertebrate species such as krill (*Thysanoessa* spp.) and sea ice-associated amphipods (e.g. *Themisto libellula*), and Arctic cod (Haug et al., 2021; Lindstrøm et al., 2013; Nilssen et al., 2000; Nilssen, Haug, Potelov, & Timoshenko, 1995; Ogloff et al., 2019). During winter, forage fish, such as Atlantic herring, Arctic cod and especially capelin, are the primary prey, although the proportion of capelin in the diet varies among years reflecting the local abundance of other prey species, such as Atlantic cod, Greenland halibut, haddock, sand eels (*Ammodytes* sp.), sculpins, redfish (*Sebastes* spp.), gadoids, mysids and shrimp (Lawson et al., 1995; Lawson & Stenson, 1995, 1997; Nilssen et al., 2000; Nilssen, Haug, Potelov, Stasenkov, et al., 1995; Ogloff et al., 2019). In general, demersal species such as Atlantic cod, Greenland halibut and haddock are at a higher trophic position, and have higher δ^{15}N values than schooling fish such as capelin and Atlantic herring, which in turn are at a higher trophic position and have higher δ^{15}N values than crustacean species such as amphipods and shrimp (Hansen, Hedeholm, et al., 2012; Haug et al., 2021; Haug, Falk-Petersen, et al., 2017; Lawson & Hobson, 2000; Sherwood & Rose, 2005; Tamelander et al., 2006). However, fish species often undergo ontogenetic shift (Sánchez-Hernández et al., 2019), for example juvenile Atlantic cods are at a lower trophic level and have lower δ^{15}N values than adults (Hansen, Hedeholm, et al., 2012; Haug et al., 2021; Holt et al., 2019). In addition, the δ^{15}N values of fish can vary between inshore and offshore which makes it difficult to differentiate the trophic position of, for example, Atlantic herring, Atlantic cod, capelin and Arctic cod, based on their δ^{15}N values alone (Hansen, Hedeholm, et al., 2012; Lawson & Hobson, 2000; Sherwood & Rose, 2005). Nevertheless, we assumed overall that a

change from a diet dominated by invertebrate species to a diet dominated by fish, or a change from a pelagic to a demersal diet would result in an increase in δ^{15}N values in predators, and conversely.

The multi-decadal trends detected in cor-$\delta^{15}N_{Trophic}$ values in the Barents Sea and Northwest Atlantic harp seal populations likely reflected changes in prey community. In the Barents Sea, historical data on fish stocks showed that schooling fish, such as capelin and Atlantic herring, demersal fish, such as Atlantic Cod, haddock and Greenland halibut, and Arctic cod fluctuated with decadal periodicities during the last 40 years (ICES, 2020; Johannesen et al., 2012; Stenson et al., 2020). The 1960s and 1970s were characterised by high demersal fish (Figure 5a) and Arctic cod stocks (Johannesen et al., 2012), which coincides with the relatively high cor-$\delta^{15}N_{Trophic}$ values in harp seal teeth. In the mid-1980s, 1990s and 2000s, the capelin stock collapsed, and subsequently rebuilt (Figure 5a). In the mid-1980s, Atlantic herring and Arctic cod stocks collapsed simultaneously to the capelin stock, leading to an almost complete collapse of fish stock in the Barents (Figure 5a; Johannesen et al., 2012). This period of low fish biomass corresponds to the low cor-$\delta^{15}N_{Trophic}$ values indicating a decrease in trophic position of harp seals (Figure 5a), which could reflect an increased proportion of invertebrates in their diet. During the capelin collapse in the 2000s, the overall biomass of fish in the Barents Sea remained high and was characterised by high abundance of Atlantic herring and Arctic cod, which increased slowly from the mid-1990s to 2010s, rebuilding the pelagic fish stock (Figure 5a; Øigård et al., 2013). The demersal stock also increased during this period (Figure 5a), mainly driven by the increase in Atlantic cod biomass, and the northward shift of sub-Arctic and temperate species, such as blue whiting (*Micromesistius poutassou*; Johannesen et al., 2012), a process known as borealisation (Dalpadado et al., 2016; Fossheim et al., 2015; Nöthig et al., 2015; Oziel et al., 2020). A change towards an invertebrate-dominated diet during years of low fish abundance might explain the low cor-$\delta^{15}N_{Trophic}$ values indicating a decrease in trophic position in the late 1980s, compared to the high cor-$\delta^{15}N_{Trophic}$ values indicating an increase in trophic position before 1980 and after 2000, that could reflect a diet more dominated by fish (Figure 5a). This is consistent with the higher contribution of amphipods, krill and shrimps in the diet of Atlantic cod in the late 1980s and early 1990s compared to early 2000s (Holt et al., 2019). Overall, the harp seal trophic position was higher during periods of species-rich fish community, that is, in the mid-1970s and mid-2000s when both the demersal and pelagic stocks were high (Figure 5a).

In the Northwest Atlantic, the diets of harp seals before the 1990s were dominated by fish (Lawson & Stenson, 1995). The slight increase in cor-$\delta^{15}N_{Trophic}$ values in harp seals in the mid-1980s could reflect a change from a diet dominated by capelin in the early 1980s, to a diet dominated by Arctic cod in the mid- and late 1980s (Lawson & Stenson, 1995; Stenson, 2012). The decrease in cor-$\delta^{15}N_{Trophic}$ values in harp seals after the late 1980s (Figure 2f) coincides with a shift from an ecosystem dominated by demersal fish species, to an ecosystem dominated by crustaceans such as shrimp and snow crab that occurred in the late 1980s and early 1990s in the Newfoundland

and Labrador shelves (Figure 5b; Dawe et al., 2012; Koen-Alonso & Cuff, 2018; Pedersen et al., 2017; Stenson et al., 2020). This shift in community structure, concomitant with the decline in biomass of capelin (Figure 5b) and multiple demersal species, such as Atlantic cod (Buren et al., 2019; Buren, Koen-Alonso, Pepin, et al., 2014), resulted from a history of overfishing combined with environmental change (Buren, Koen-Alonso, Pepin, et al., 2014; Koen-Alonso et al., 2018; Stenson et al., 2020). A change from a fish-dominated diet to an invertebrate-dominated diet could explain the lower cor-$\delta^{15}N_{Trophic}$ values, indicating a lower trophic position of harp seals in the mid-1990s compared to the mid-1980s (Figure 3c). This is consistent with the increased proportion of invertebrate relative to fish observed in the diet of Greenland halibut, one of the top fish predators in the Northwest Atlantic (Dwyer et al., 2010). Presently, this ecosystem appears to have returned to communities dominated by demersal fish, although the total fish biomass remains very low compared to levels prior the 1990s (Koen-Alonso & Cuff, 2018; Stenson et al., 2020). Harp seals returning to a more fish-dominated diet in the recent years could explain the increase in cor-$\delta^{15}N_{Trophic}$ values from the 2000s to the 2010s, reaching similar values to those before the ecosystem shift (Figure 3c), suggesting that harp seals were feeding on prey species having similar trophic levels in the 1980s and in the 2010s.

The stable cor-$\delta^{15}N_{Trophic}$ values of harp seals in the Greenland Sea since the mid-1940s (Figure 3b) indicate that harp seals remained feeding on prey species having similar trophic levels in the past six decades. Greenland Sea harp seals rely on an Arctic diet dominated by pelagic invertebrates all year long, in contrast to harp seals from the Barents Sea and the Northwest Atlantic. Harp seals from the Barents Sea and the Northwest Atlantic populations rely mainly on pelagic invertebrates, such as krill (*Thysanoessa* spp.) and sea ice associated amphipods (e.g. *Themisto libellula*), and Arctic cods in summer and autumn in Arctic feeding grounds, but fish, such as capelin, dominate their diet in winter and spring in sub-Arctic breeding and moulting areas (Enoksen et al., 2017; Folkow et al., 2004; Lacoste & Stenson, 2000; Lawson & Stenson, 1997; Lindstrøm et al., 2013; Nilssen, 1995; Nilssen, Haug, Potelov, Stasenkov, et al., 1995; Nilssen, Haug, Potelov, & Timoshenko, 1995; Nordøy et al., 2008; Ogloff et al., 2019; Stenson, 2013). Most of Greenland Sea harp seals spend summer and autumn in the northern Barents Sea (Folkow et al., 2004), where they share feeding ground with Barents Sea harp seals, mainly feeding on pelagic invertebrates and Arctic cods. However, unlike the Barents Sea and Northwest Atlantic populations, Greenland Sea harp seals continue feeding on a pelagic invertebrate-dominated diet, mainly consisting of krill and amphipods (*Themisto* sp.), during the breeding and moulting seasons in winter and spring in Arctic ice-filled areas in the Western Greenland Sea (Enoksen et al., 2017; Haug et al., 2002; Potelov et al., 2000). This is supported by the overall lower cor-$\delta^{15}N_{Trophic}$ values of Greenland Sea harp seals (9.2 ± 0.8‰), indicating a lower trophic position, compared to the Barents Sea harp seals (10.6 ± 1.1‰). The absence of temporal trend in relative trophic position of harp seals from the Greenland Sea could reflect their more specialised Arctic

diet dominated by pelagic invertebrates all year long, compared to the two other harp seal populations relying part of the year on boreal diets dominated by fish in more southern areas.

Overall, these results suggest that harp seals modify their diets to adapt to change in prey availability (Buren, Koen-Alonso, & Stenson, 2014; Lawson & Stenson, 1995; Øigård et al., 2013), switching between invertebrate- and fish-dominated diet. The temporal trends in harp seal trophic position agrees with the temporal variations in the main fish stocks in the Barents Sea and the Northwest Atlantic, suggesting that changes in trophic position of harp seals likely reflect decadal changes in the fish community and the entire ecosystem. This would make harp seal trophic position a good indicator of ecosystem status. However, the lack of time series on fish stock at the species level, especially for noncommercial stocks, prevented quantitative exploration of the temporal variation observed in harp seal trophic position. Harp seals can exploit local resources when these are concentrated, even when the fish or invertebrate stock overall is low (Haug et al., 2021; Lawson et al., 1998; Lindstrøm et al., 1998, 2013; Marshall et al., 2010). Long time series on every important prey species, at relevant spatial scales, are therefore needed to improve our understanding about how changes in prey availability influence harp seal diet and in turn trophic position.

The plasticity in harp seal diet could render them less sensitive to borealisation (Clavel et al., 2011) and their flexible response would improve their chances of adapting to abrupt changes in environmental (Ogloff et al., 2019) and prey (McMahon et al., 2015) conditions. However, despite their generalist trophic behaviour, harp seals in the Barents Sea displayed a clear positive preference for Arctic cod and negative preference for amphipods and krill (Haug et al., 2021), and the nutritional content of prey can have an impact on harp seal body condition with consequences for reproduction (Frie et al., 2003; Øigård et al., 2013; Stenson et al., 2016, 2020). For example, in the Barents Sea harp seal population, the mean age at sexual maturity increased and the growth rate decreased from the 1960s to the early 1990s (Frie et al., 2003; Kjellqwist et al., 1995) coinciding with indications of reduced body condition (Frie et al., 2003), and corresponding to the low relative trophic position of harp seals in the late 1980s–early 1990s (Figure 3a). The age at sexual maturity in Greenland Sea harp seals did not vary from the 1960s to the early 1990s, and was lower in the late 1980s-early 1990s than for Barents Sea harp seals (Frie et al., 2003). This suggests that Greenland Sea harp seals had access to higher quality prey items (Frie et al., 2003), and is consistent with the absence of temporal variation in the relative trophic position of harp seals from the Greenland Sea (Figure 3b). In the Northwest Atlantic, Stenson et al. (2016) observed a decrease in harp seal pregnancy rate from the mid-1980s to the early 2000s and an increase in late term abortions correlated with poor capelin years, which corresponds to the decrease in harp seal relative trophic position (Figure 3c). This supports that the temporal variations in body condition and reproduction rates of harp seals from the Barents Sea and Northwest Atlantic observed in the last decades may be associated with changes in

prey availability, in addition to other factors such as population density and environmental conditions, for example, ice cover (Frie et al., 2003; Stenson et al., 2016, 2020).

These results could be included in studies of harp seal population dynamics to improve their predictive power given the known importance of trophic position and diet composition for body condition and reproduction. Population models that can include wider ecosystem effects have much potential to suggest future directions of change for predator populations (Smout et al., 2022). In addition, these results are highly valuable for ecotoxicology studies, as trophic position is a key factor influencing contaminant bioaccumulation (Borgå et al., 2004). This study provides a unique 60-year record of harp seal trophic position across the North Atlantic.

CONFLICT OF INTEREST STATEMENT

We declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in NERC EDS UK Polar Data Centre at https://doi.org/10.5285/6AAA53E8-3D0A-48FE-838E-31C5B5F24CE7.

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SUPPORTING INFORMATION

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