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ORIGINAL ARTICLE

Trophic level and fatty acids in harp seals compared with common minke whales in the Barents Sea

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ABSTRACT

The objectives of this study were to explore trophic levels and possible diet overlap between harp seals (*Pagophilus groenlandicus*) and common minke whales (*Balaenoptera acutoroostrata*) in the Barents Sea using stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) and fatty acid analyses, and to explore the energy pathways from the plankton to the top predators. Blubber and muscle samples from 93 harp seals and 20 minke whales were collected in the southern Barents Sea in May 2011. The study showed that harp seals were at a higher trophic level than minke whales during spring. This supported previous diet studies suggesting a more fish-dominant diet for seals, as compared with the whales, at this time of the year. The stable isotopes and fatty acids indicated niche separation between the seals and the whales, and between different age groups of the harp seals. Older seals had fatty acid profiles more equal to minke whales as compared with younger seals. Furthermore, while the fatty acid profiles suggested that krill were of particular importance for the young seals, the profiles from older seals and whales suggested that fish dominated their diets.

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Introduction

The Barents Sea ecosystem is an important feeding area for apex predators such as harp seals (*Pagophilus groenlandicus* (Erxleben, 1777)) and common minke whales (*Balaenoptera acutorostrata* Lacépède, 1804) (Wassmann et al. 2006). Both species exploit several trophic levels of prey in the area, and because of their body sizes, high metabolic demands and abundance, they are thought to have an important top-down effect on the structure and function of the food web (Bowen 1997; Wassmann et al. 2006; Kovacs et al. 2009; Skern-Mauritzen et al. 2011; Bogstad et al. 2000, 2015).

Harp seals are migratory and generalist top predators. The Barents Sea population whelps and moults on the pack ice in the White Sea and south-eastern Barents Sea (Lavigne & Kovacs 1988; Sergeant 1991). After moulting, the stock disperses in small herds to feed along the extended ice edge in the northern Barents Sea. The southward movement of the seals towards the breeding areas in the White Sea begins in November–December (Haug et al. 1994; Nordøy et al. 2008). Although harp seals remain in association with sea ice during much of the year (Sergeant 1991), they spend long periods (particularly in June–October) in open water without access to sea ice on which they can haul out to rest from time to time (Folkow et al. 2004; Nordøy et al. 2008). Harp seals feed upon a variety of species; however, the bulk of their diet is comprised of relatively few species, such as capelin (*Mallotus villosus* (Müller, 1776)), polar cod (*Boreogadus saida* (Lepechin, 1774)), herring (*Clupea harengus* Linnaeus, 1758), krill (*Thysanoessa* spp.) and the pelagic hyperiid amphipod *Themisto libellula* (Lichtenstein in Mandt, 1822) (Lindstrøm et al. 2013; Nilssen et al. 2000).

In contrast to the harp seals, which primarily reside in the Barents Sea, minke whales perform long-distance migrations between breeding areas in temperate waters and feeding areas in boreal and arctic waters. They migrate into feeding areas in the Barents Sea during early spring, whereas in autumn (September–October) they return southwards to breeding areas at lower latitudes (Jonsgård 1951). However, old catch

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statistics reveal that minke whales have been caught in Norwegian waters nearly all year around, indicating that some animals remain in the northern areas throughout the winter (see Haug et al. 2011). Like harp seals, minke whales have a very flexible foraging behaviour, and commonly switch among prey species. Consequently, their diet varies greatly in time (seasonally and annually) and space due to spatio-temporal variation in prey concentrations. Hence, whales exploit a variety of species and sizes of fish and crustaceans (Haug et al. 2002; Windsland et al. 2007; Meier et al. 2016), although they appear to prefer capelin, herring and occasionally krill (Lindstrøm & Haug 2001).

Both harp seals and minke whales increase their fat deposits during the feeding period in summer and autumn, and thereby store energy reserves for wintering and breeding when their feeding activity is assumed to be low (Nilssen et al. 1997; Næss et al. 1998). Food limitation, which is one of the most common population regulators, seems to have affected both harp seals and minke whales recently in the Barents Sea (Bogstad et al. 2015; Haug et al. 2017). Harp seal body condition, modelled from samples taken during the commercial hunts in spring during 1992–2011, exhibited a slow increase from 1992 to 2001 followed by a significant decrease to a minimum in 2011 (Øigård et al. 2013). Concurrently, the body condition of minke whales taken in the commercial hunts during 1993–2013 has declined more or less continuously over the entire period (Solvang et al. 2017). The Barents Sea population of harp seals has shown signs of low production capacity, presumably driven by density-dependent factors, since the 1990s, and the current estimate for the total population is approximately 1.4 million seals (ICES 2014). North-east Atlantic minke whale abundance seems to have been relatively stable over the most recent 25 years (Haug et al. 2011), and now counts approximately 90,000 animals (IWC 2015).

Some degree of spatial overlap has been observed between harp seals and minke whales in the Barents Sea (see Øien et al. 1987; Skaug et al. 2004; Skern-Mauritzen et al. 2011). It should be emphasized that predators may also compete for food despite a lack of spatio-temporal overlap between them if they feed on the same stocks of prey. No direct diet comparisons between harp seals and minke whales have been performed earlier, but because they share preferred prey, such as krill, capelin and herring, interspecific competition probably exists. A recent study by Durant et al. (2014), which analysed the competition among several top predators in the Barents Sea, showed that there was a significant diet overlap between Atlantic cod (*Gadus morhua* Linnaeus, 1758) and minke whales. Harp seals were not included in their study, but another recent study (Bogstad et al. 2015) suggested competition between harp seals and minke whales on the one hand, and Atlantic cod on the other, for shared resources such as krill. They even suggested that cod might outperform the mammal stocks in the competition for food.

Knowledge of predator–prey relationships is essential for understanding energy flow as well as competition in marine ecosystems. Fatty acid analysis combined with stable isotopes are powerful and complementary tools, as they integrate dietary intake and assimilation over longer time periods compared with traditional analysis of intestinal contents and faeces (e.g. Dahl et al. 2003; Dalsgaard et al. 2003; Falk-Petersen et al. 2004, 2009; Petursdottir et al. 2012; Aurioles-Gamboa et al. 2013; McMeans et al. 2013; Querouil et al. 2013). The stable isotopes (SIs) of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) are enriched, in a predictable manner, in consumers relative to their prey, and reveal information about food carbon sources as well as the trophic position of the species in food webs (Peterson & Fry 1987; Hobson & Welch 1992; Søreide et al. 2006a; Newsome et al. 2010). Lipids have been used as biomarkers in marine ecosystems to follow energy transfer and to study predator–prey relationships in harp seals from other geographic areas (e.g. Newfoundland 1994–2004; see Tucker et al. 2009a, 2009b). The use of fatty acid trophic markers (FATM) to trace such transfer of energy from phytoplankton to top predators is based on the observation that primary and some secondary producers synthesize characteristic fatty acids (FAs) and that the FA signals are conservatively transferred through food chains (Dalsgaard et al. 2003; Falk-Petersen et al. 2004, 2009). Previous studies of harp seals and minke whales have shown that both species have high endogenous lipid metabolism and thereby induce some modification of the digested FAs before storage into the blubber (Grahl-Nielsen et al. 2011; Meier et al. 2016). This includes chain-shortening products of 22:1(n-11), 20:1(n-11) and 18:1(n-11) as well as 22:5(n-3), which is an elongation product of 20:5(n-3), and this should be taken into consideration when using fatty-acid profiling as FATMs.

The purpose of this paper is to use SI and FA analyses to assess dietary overlap between harp seals and minke whales in the Barents Sea. Key questions asked are whether:

(1) Trophic positions of harp seals and minke whales indicate shared niche space based on SIs.

(2) Different age groups of harp seals share the same resources, i.e. have similar muscle SIs and blubber FA composition.

Material and methods

Sampling

The harp seal data used included a total of 93 animals from three age groups (1–6 years, 7–15 years and >15 years) sampled during Norwegian commercial sealing on the East Ice (south-eastern Barents Sea, close to Cape Kanin in Russia, see Figure 1), on 5–6 May 2011 (i.e. during time of moult). We assumed that the youngest age group included all immature seals (see Frie et al. 2003), and divided the mature fraction in two (ages 7–15, >15). All seals were shot on ice floes and immediately brought on-board for dissection. Dorsal blubber cores, approximately 5×5 cm, were taken through the full depth of the blubber at the mid-line between the flippers. A piece of muscle was taken underneath the blubber sample. The cores and muscles were immediately wrapped in aluminium foil, packed in plastic bags and frozen at −20°C until subsequent analyses. Lower jaws with teeth were collected for age determinations of the seals. From a canine tooth, a 10–12 mm transverse section was mounted on a glass slide and examined under transmitted light, and the seal's age was estimated from counts of growth layers in the tooth (Bowen et al. 1983).

Entire blubber cores (from skin to muscle) and a muscle sample, both taken dorsally on each whale immediately behind the blowhole, were obtained from 20 minke whales taken in Norwegian commercial whaling on the coast of Finnmark, southern Barents Sea (Figure 1), during 1–15 May 2011. Collection of subsamples from the cores was performed while the blubber was still frozen to avoid 'lipid bleeding'. The surface (1 mm) of inner blubber from the muscle side was removed to avoid oxidation or tissue breakdown and small subsamples weighing 20–50 mg were taken from the inner blubber. Further details are given in Meier et al. (2016), including all results from fatty acid analyses of whale blubber. In addition, a muscle sample to be analysed for stable isotopes was taken from each whale, packed in aluminium foil and plastic bags before it was frozen and kept at –20°C until analysis.

The prey selected for the analyses were selected carefully, based on published information on diet for the two predators (Nilssen et al. 1995a, 1995b; Lindstrøm et al. 1998, 2013; Haug et al. 2002). The FA

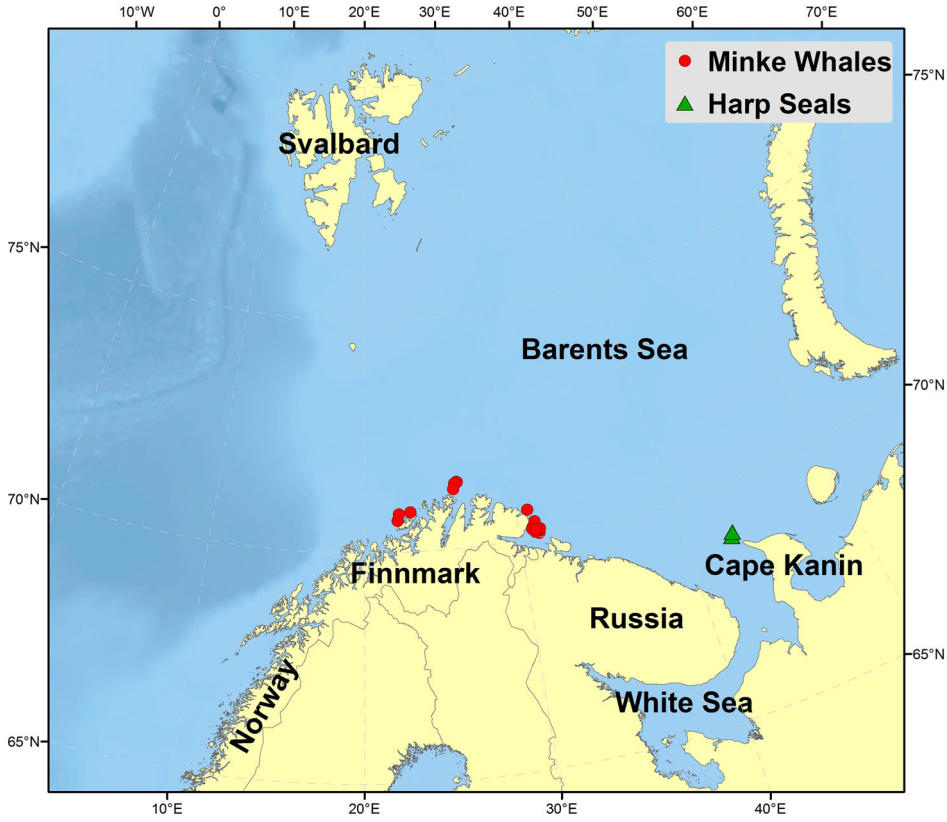

Figure 1. Map showing the sampling positions of harp seals and minke whales in the Barents Sea in 2011.

data, used in the analysis of potential prey, were taken from previous studies of harp seal blubber and prey by Grahl-Nielsen et al. (2011) and minke whale blubber by Meier et al. (2016). The same material was used as a basis for the SI analyses, which included krill (*Meganyctiphanes* sp. and *Thysanoessa* sp.), the amphipod *Themisto libellula*, adult polar cod, capelin and herring, juvenile Atlantic cod and haddock (*Melanogrammus aeglefinus* (Linnaeus, 1758)). Even though the prey organisms were collected in May–June, i.e. comparable in season with the current seal and whale samples, their geographic origin was from the north-western Barents Sea, and the sampling years were also different. Thus, spatial and annual variations in FAs and SIs for prey organisms are not accounted for. This may have introduced some bias into our analyses, presumably small, however, given that sampling months were similar to those for the seals and whales, and assuming a fairly stable diet of the fish and zooplankton.

Stable isotope analyses

Samples analysed for stable isotopes included a subset of samples from harp seal (30), minke whale (20) and the following prey species: polar cod (10), Atlantic cod (10), capelin (10) haddock (5), *Thysanoessa* sp. (10), *Meganyctiphanes norvegica* (M. Sars, 1857) (5) and *Themisto libelulla* (3). Samples of muscle tissues of harp seals, minke whale and fish prey were dried at 60–70°C to constant weight and homogenized. For zooplankton, whole animals were dried at the same temperatures and homogenized. To reduce variability among prey with different lipid and carbonate content, these were removed prior to analyses (Søreide et al. 2006b). Lipids have a higher turnover and are depleted in ^{13}C relative to other tissues (van Dongen et al. 2002). The removal of lipids will also make the C:N ratios more comparable among species with large variation in lipid content (Hobson & Welch 1992). Inorganic carbonates, which are typically isotopically heavier than organic carbon, do not reflect the diet and, thus, are removed (Søreide et al. 2006b). Lipids were removed by Soxhlet extraction, with CH_2Cl_2:7% CH_3OH for approx. 2 h, and carbonates by washing with 2M HCl and distilled water to neutral pH, prior to analyses. Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of the residual material were analysed at the Institute of Energy Technology (IFE), Kjeller, Norway on a Micromass Optima, Isotope Ratio Mass Spectrophotometer. In order to calculate the trophic level (TL) we used a relationship by Hop et al. (2002) with trophic enrichment factor for the European Arctic (Søreide et al. 2006a): $TL_{consumer} = 2 + (\delta^{15}N_{consumer}/\delta^{15}N_{Calanus}/3.4)$, where $TL_{consumer}$ is the trophic level of an organism, $\delta^{15}N_{Calanus}$ is our baseline scaling value (8.5‰) for TL2 and 3.4‰ is the trophic enrichment factor. The baseline scaling is based on an average for *Calanus* spp. for all seasons combined (Søreide et al. 2006a).

Fatty acid analyses

Collection of subsamples was performed while the blubber was still frozen to avoid 'lipid bleeding' from the blubber tissue when thawing. Small subsamples weighing 20–50 mg were taken from the inner blubber, 1 mm from the muscle side. The reason for such small subsamples from the inner blubber was to avoid the effect of stratification. It is well known that the FA composition changes a lot through the blubber and that the inner blubber contains the lipids most influenced by the diet (see Grahl-Nielsen et al. 2011; Meier et al. 2016). All samples were methylated and the respective fatty acid methyl esters (FAME) were analysed on a HP-7890A gas chromatograph (Agilent Technologies, USA) with a flame-ionization detector (GC-FID) according to a method described in Meier et al. (2006), with the fatty acid 19:0 added as an internal standard. As a methylation reagent, 2.5 M dry HCl in methanol:toluene (4:1 v/v) was used. The FAMEs were extracted using 2×2 ml of hexane. The extracted hexane was diluted or concentrated to obtain a suitable chromatographic response. One microlitre was injected splitless (the split was open after 2 min) and the injection temperature was set to 270°C. The column was a 25 m × 0.25 mm fused silica capillary, coated with polyethylene glycol of 0.25 µm film thickness, CP-Wax 52 CB (Varian-Chrompack, Middelburg, the Netherlands). Helium (99.9999%) was used as carrier gas at 1 ml min^{-1}. The temperature of the flame ionization detector was set at 300°C. The oven temperature was programmed to hold at 90°C for 2 min, then from 90°C to 165°C at 30°C min^{-1} and then to 225°C at 2.5°C min^{-1} and held there for 20 min. Total analysis time was 48.5 min. Well-defined peaks in the chromatogram were selected (42), and identified by comparing retention times with a FAME standard (GLC-463 from Nu-Chek Prep., Elysian, MN, USA) and retention index maps and mass-spectral libraries (GC-MS) (http://www.chrombox.org/index.html) performed under the same chromatographic conditions as the GC-FID (Wasta & Mjøs 2013). Chromatographic peak areas were corrected by empirical response factors calculated from the areas of the GLC-463 mixture. The chromatograms were integrated

using the EZChrom Elite software (Agilent Technologies, USA).

Statistical analyses

Ordinations of the FA profiles were achieved using correspondence analysis (CA) and canonical correspondence analysis (CCA) – for recent accounts, see Greenacre & Primicerio (2013) and Greenacre (2016a) – using the ca package (Nenadić & Greenacre 2007) and own code in R (R Core Team 2014). The chi-square distance inherent in CA and CCA has been shown to be more suitable for analysing compositional data than the Euclidean distance used in principal component analysis (PCA), from the viewpoint of so-called 'subcompositional coherence' (Greenacre 2011). This implies that CA is more robust to the choice of FAs and the changes in the data values imposed by the constant-sum constraint of the FA compositions (i.e. profiles), which are always renormalized to sum to 1. In PCA, spurious correlations are induced by this constraint (Aitchison 1986). In addition, CA assigns weights to the FAs proportional to their overall mean values, so that FAs with small percentages are naturally downweighted.

Ordinations were obtained to show: (a) differences between the three age-groups of harp seals in terms of FA profiles of inner blubber (n = 93 seals in total), using CA; (b) comparison of FA profiles between harp seals, minke whales (n = 20) and seven prey species, using CA; and (c) differences between the harp seals, constraining the ordination space to be correlated with the isotope variables (δ^{15}N and δ^{13}C) as well as with age, weight and length, using CCA. The CCA was performed on a subset of 30 seals containing a full set of the explanatory variables. In the case of the first two CA ordinations, 95% confidence ellipses for the mean FA profile in each group (i.e. age groups for the first ordination, species groups in the second) were superimposed on the plot to indicate which groups probably have different mean profiles from the others; see Greenacre (2016b) for an explanation of the properties of confidence ellipses. The ellipses were established by bootstrapping within each group (1000 bootstrap samples in each case) and projecting the bootstrap samples onto the ordination space, called a 'partial bootstrap' because of the projection (Greenacre 2016a). A similar approach, but not needing projection, was used in the scatterplot of the two stable-isotope variables, showing 95% confidence ellipses for their bivariate mean points. In all ordinations, the contribution biplot scaling was used (Greenacre 2013), which simplifies the interpretation by eliminating variables (in this case FAs) that make lower than average contributions to the ordination. In the plots, only those FAs that have a higher than average contribution to the construction of the ordination axes or that have a higher than average correlation with the ordination axes are shown. Univariate tests of inter-age-group differences were performed with a distribution-free permutation test, using the package coin (Hothorn et al. 2008) in R. Permutation tests were preferred in these cases since FA data are clearly non-normal. Since many FA variables were being individually tested, the step-up procedure of Benjamini & Hochberg (1995) was used to control the false positive rate, maintaining an overall significance level of 0.05 over the set of multiple tests. In this approach the *P*-values for all the tests, say *m* tests, are sorted in ascending order and compared to the arithmetic series $\{1/m, 2/m, 3/m, \ldots, m/m = 1\} \times \alpha$, where α is the significance level, usually 0.05. Only those *P*-values less than the corresponding values in the series are judged significant; see Greenacre (2016b) for an example. For testing the differences between pairs of species in the bivariate isotope data, MANOVA tests were performed after confirming that the data were compatible with the bivariate normal distribution. Again, the false positive rate was controlled using the Benjamini–Hochberg procedure.

Results

Stable isotopes

Harp seals were at a higher mean trophic level (3.93; SD = 0.19) than minke whales (3.45; SD = 0.29) in the marine food web (Table I, Figures 2 and 3); the difference was highly significant, $P < 0.0001$, using a permutation test. For the seals, the mean age group (7–15 year olds) was at a slightly higher trophic level than the younger and older animals (Figure 2). The variation in δ^{15}N and, hence, trophic level was slightly larger among the minke whales (ranging from 11.8 to 15.5‰). Whales had slightly higher δ^{13}C values (mean −18.80‰) than seals (mean −19.37‰) (Table I). The δ^{13}C of the prey ranged from − 22.5‰ in *Themisto libelulla* to − 19.8‰ in *Meganyctiphanes norvegica*, and fishes were around − 20.7‰. The main fish prey (cod, polar cod, haddock and capelin) of these two marine mammal species were at intermediate trophic levels, ranging from 3.08 (SD = 0.18) to 3.30 (SD = 0.17), while the zooplankton prey (*Thysanoessa* sp., *T. libelulla* and *M. norvegica*) were at the lowest trophic level, ranging from 1.88 (SD = 0.03) to 2.65 (SD = 0.13). *Thysanoessa* sp. showed the lowest (1.88)

Table I. Stable isotopes (δ^{13}Carbon and δ^{15}Nitrogen) and trophic level of harp seals (*Phoca groenlandica*), minke whales (*Balaenoptera acutorostrata*), and some of their main prey species, given as means and standard deviation. The species codes given are used as denotation of the species in Figures 3 and 5.

Species	Species code	*N*	δ^{13}Carbon		δ^{15}Nitrogen		Trophic level	
			Mean	(SD)	Mean	(SD)	Mean	(SD)
Harp seals (*Pagophilus groenlandicus* (Erxleben, 1777))	Pg	29	−19.37	(0.29)	15.07	(0.64)	3.93	(0.19)
Minke whale (*Balaenoptera acutorostrata* Lacépède, 1804)	Ba	20	−18.80	(0.27)	13.43	(0.98)	3.45	(0.29)
Atlantic cod (*Gadus morhua* Linnaeus, 1758)	Gm	10	−20.39	(0.26)	12.90	(0.59)	3.30	(0.17)
Polar cod (*Boreogadus saida* (Lepechin, 1774))	Bs	10	−20.97	(0.31)	12.80	(0.60)	3.27	(0.18)
Haddock (*Melanogrammus aeglefinus* (Linnaeus, 1758))	Ma	5	−20.66	(0.34)	12.17	(0.61)	3.08	(0.18)
Capelin (*Mallotus villosus* Müller, 1776))	Mv	10	−20.78	(0.13)	12.32	(0.30)	3.12	(0.09)
Thysanoessa sp. (20–30 mm)	Th	6	−21.02	(0.18)	10.70	(0.45)	2.65	(0.13)
Thysanoessa sp. (10–20 mm)	Th	4	−20.33	(0.28)	8.11	(0.09)	1.88	(0.03)
Themisto libellula (Lichtenstein in Mandt, 1822)	Tl	3	−22.25	(0.33)	10.02	(0.16)	2.45	(0.05)
Meganyctiphanes norvegica (M. Sars, 1857)	Mn	5	−19.78	(0.09)	8.44	(0.13)	1.98	(0.04)

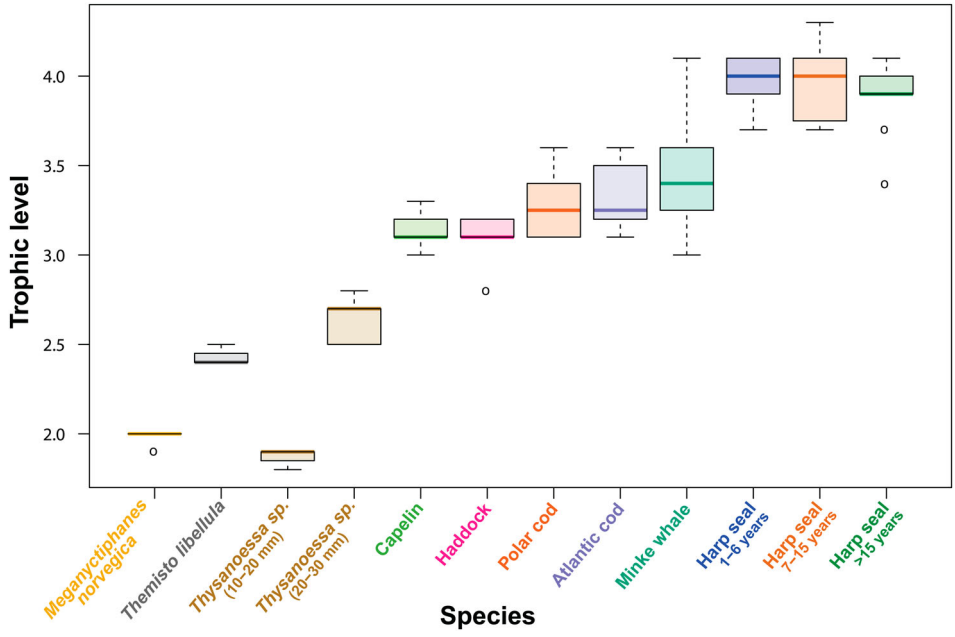

Figure 2. Trophic levels of harp seals (three age groups), minke whales and some of their main prey species. Boxes display median and quartiles, whiskers indicate the distance to the largest and smallest observed values and the circle indicates an outlier, except for the small samples (see Table I), where circles indicate the extreme values.

and highest (2.65) mean values for zooplankton, reflecting trophic levels for juveniles and adults, respectively. On average, fish (3.19) was one trophic level higher than zooplankton (2.24). The MANOVA tests confirmed the separations in Figure 3, namely that all species in the plot are pairwise significantly different, except for the pairs haddock (Ma) and capelin (Mv), and haddock (Ma) and cod (Gm), the only pairs whose confidence regions overlap.

Fatty acids

The FA profiles in the blubber of harp seals were strongly correlated with age (Table II, Figure 4). From the 51 FAs identified, 31 differed significantly between the three chosen age groups; the same was true for the ∑SFA, ∑MUFA and ∑PUFA (Table II). The correspondence analysis (CA) showed separation with regard to age groups, with the first two axes of the biplot explaining 80% of the total variation in the dataset (horizontal dimension 1 = 68% and vertical dimension 2 = 12%; Figure 4). The young seals (1–6 years old) differed particularly from the older ones by having higher levels of the two short-chained monounsaturated FAs (MUFA), 16:1 (n-7) and 18:1 (n-7), and the polyunsaturated FA (PUFA), 20:5 (n-3). The FA profiles in the two older age groups had higher relative levels of long-chained MUFAs (20:1, 22:1 and 24:1 (n-9)) and the long-chained PUFAs (22:5 (n-3) and 22:6 (n-3)). A similar pattern was found for the differences between

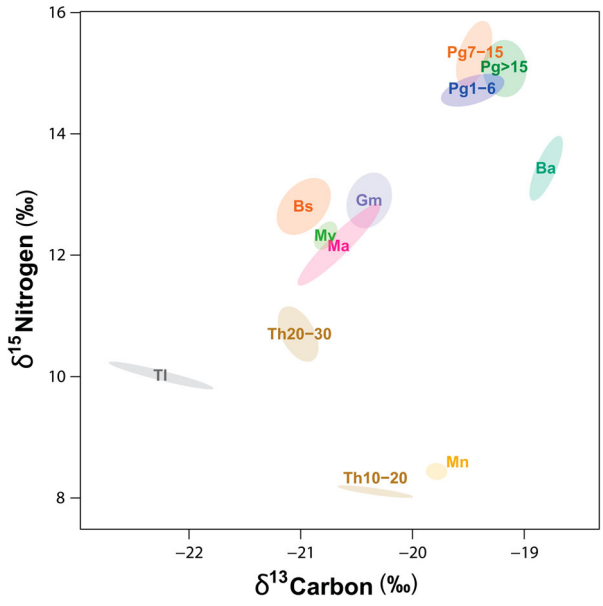

Figure 3. Stable isotopes (δ^{13}Carbon and δ^{15}Nitrogen) of harp seals (Pg), minke whales (Ba), and from seven potential prey species: haddock (Ma), cod (Gm), polar cod (Bs), capelin (Mv), *Meganyctiphanes norvegica* (Mn), *Themisto libellula* (Tl) and *Thysanoessa* sp. (Th-small = 10–20 mm; Th-large = 20–30 mm). Species codes refer to Table I.

the middle-aged seals (7–15 years old) and the oldest ones (>15 years old), although the differences were less pronounced as compared with the juveniles.

Harp seals and minke whales differed considerably from their prey species. Both seals and whales had high levels of FAs that originate from endogenous lipid metabolism, such as 18:1 (n-11) and 22:5 (n-3) (see Figures S1 and S2, supplementary material). To emphasize the diet signal from prey FA profiles, these two FAs were removed from the analyses and the data were normalized and reanalysed (Figure 5). The first two axes in the CA then explained 75% of the total variation in the dataset (horizontal dimension 1 = 44% and vertical dimension 2 = 31%). The biplot showed that both harp seals and minke whales separated from the prey species along CA dimension 1, by having relatively lower levels of the two saturated FAs 16:0 and 18:0 and the long-chained PUFAs 20:4 (n-6), 20:5 (n-3) and 22:6 (n-3), but higher levels of the MUFAs, especially 20:1 (n-9) and 22:1 (n-11) compared with the prey. Along CA dimension 2, the minke whales were located at the same position as the fishes, polar cod, capelin and haddock, while the seals grouped with zooplankton (amphipods and krill).

The age gradient among harp seals was also apparent in Figure 5, in that the young seals were closely associated with *Thysanoessa* sp. which had an FA profile very rich in 16:1 (n-7) (18%) and 20:5 (n-3) (18%); these were also the FAs that were most important in creating the differences between juvenile and adult seals. Older seals are located along the second dimension close to the *Meganyctiphanes norvegica* and *Themisto libellula*, but also in the direction towards the fish prey. Even though the FA profiles in the blubber of older seals were more similar to the minke whale FA profiles than those from younger seals, there are still clear differences between the whales and seals. Harp seals had higher levels of the (n-7) MUFAs (16:1 (n-7), 18:1 (n-7)), but lower levels of the (n-9) and (n-11) MUFAs (18:1 (n-9), 20:1 (n-9), 22:1 (n-9), 24:1 (n-9), 20:1 (n-11), 22:1 (n-11)) as compared with minke whales. Harp seals also had higher levels of the long-chained PUFAs (20:5 (n-3), 22:5 (n-3), 22:6 (n-3)) than minke whales.

The CCA analysis revealed that 56.5% of the total variance of the fatty acid composition of a subset of 30 seals, which contained data of both lipids and isotopes, could be explained within the space of the constrained variables. Almost all (97%) of the constrained variance is shown by these two CCA dimensions (Figure 6). The main part of the variance was explained along the first canonical axis (93.5%), with age and length explaining most of the variance in the fatty acid composition among the seals. However, these two variables were highly correlated.

Discussion

Typically, δ^{13}C values are slightly enriched ($\Delta_C = 0.6‰$) with trophic levels (Søreide et al. 2006a), but in our case, harp seals had significantly lower δ^{13}C values, even if they were at higher trophic levels than minke whales (3.93 and 3.45, respectively). Thus, the isotopic signals in mike whales indicated that they had fed on organisms lower in the food web that were less depleted in δ^{13}C, or that they feed closer to the coast, where the isotopic δ^{13}C tends to be enriched because of higher influence from benthic production and carbon of detrital origin (Hobson et al. 1994; France 1995). Evidently, our sampling of minke whales and harp seals did not occur from sympatric populations of the two species. The minke whales were caught on the coast of Finnmark, where they presumably had fed on prey along the coast, whereas harp seals were caught in the east ice near Cape Canin. The Norwegian coastal current weakens as it moves eastwards into the southern Barents Sea and this area may be more influenced by river run-off from large rivers, such as the Pechora River. Thus, the carbon signal probably varies between the two areas and geographic location is probably responsible for differences

Table II. Fatty acids (FAs) in the inner blubber layer of 92 harp seals (*Pagophilus groenlandicus*).

	1–6 years (n = 20)	7–15 years (n = 44)	>15 years (n = 28)	*P*-values
Weight (kg)	65 (13)	86 (11)	89 (11)	
Length (cm)	147 (9)	171 (7)	176 (8)	
Age (year)	3 (1)	11 (2)	20 (4)	
14:0	5.10 (0.51)	5.26 (0.60)	5.32 (0.42)	0.38
i-15:0	0.23 (0.06)	0.27 (0.05)	0.29 (0.05)	**0.001**
ai-15:0	0.06 (0.02)	0.08 (0.01)	0.09 (0.02)	**<0.0001**
15:0	0.26 (0.03)	0.27 (0.04)	0.28 (0.03)	0.17
i-16:0	0.08 (0.02)	0.09 (0.02)	0.09 (0.02)	**0.008**
16:0	8.91 (1.79)	8.12 (1.30)	7.44 (1.28)	**0.003**
i-17:0	0.19 (0.04)	0.23 (0.03)	0.23 (0.04)	**0.003**
ai-17:0	0.09 (0.02)	0.11 (0.01)	0.11 (0.02)	**0.002**
17:0	0.07 (0.02)	0.09 (0.02)	0.10 (0.02)	**0.0002**
18:0	0.87 (0.16)	0.93 (0.13)	0.88 (0.13)	0.22
20:0	0.06 (0.01)	0.07 (0.01)	0.08 (0.01)	**<0.0001**
∑SFA	**15.93 (2.17)**	**15.49 (1.96)**	**14.94 (1.59)**	**<0.0001**
14:1 (n-5)	1.03 (0.39)	0.99 (0.23)	1.03 (0.22)	0.80
16:1 (n-11)	0.12 (0.05)	0.12 (0.03)	0.12 (0.03)	0.82
16:1 (n-9)	0.20 (0.05)	0.24 (0.04)	0.25 (0.04)	**0.0008**
16:1 (n-7)	17.54 (2.68)	13.36 (2.17)	11.47 (2.15)	**<0.0001**
16:1 (n-5)	0.30 (0.03)	0.28 (0.03)	0.26 (0.03)	**0.0003**
17:1 (n-8)	0.23 (0.04)	0.24 (0.03)	0.25 (0.04)	0.10
18:1 (n-11)[b]	1.07 (0.31)	1.40 (0.54)	1.50 (0.58)	**0.018**
18:1 (n-9)	16.88 (1.98)	16.96 (1.53)	17.06 (1.09)	0.92
18:1 (n-7)	5.37 (0.72)	4.56 (0.50)	4.10 (0.50)	**<0.0001**
18:1 (n-5)	0.42 (0.07)	0.45 (0.06)	0.46 (0.05)	0.11
20:1 (n-11)	1.10 (0.33)	1.51 (0.32)	1.84 (0.43)	**<0.0001**
20:1 (n-9)	7.69 (2.29)	10.69 (1.93)	12.24 (2.31)	**<0.0001**
20:1 (n-7)	0.36 (0.07)	0.43 (0.07)	0.45 (0.08)	**0.0001**
22:1 (n-11)	2.35 (1.07)	3.72 (1.04)	4.57 (0.98)	**<0.0001**
22:1 (n-9)	0.45 (0.16)	0.68 (0.16)	0.81 (0.19)	**<0.0001**
22:1 (n-7)	0.06 (0.02)	0.09 (0.02)	0.10 (0.02)	**<0.0001**
24:1 (n-9)	0.15 (0.05)	0.24 (0.07)	0.30 (0.08)	**<0.0001**
∑MUFA	**55.31 (2.33)**	**55.99 (1.77)**	**56.73 (2.14)**	**0.0004**
16:2 (n-4)	0.76 (0.08)	0.66 (0.11)	0.56 (0.09)	**<0.0001**
16:3 (n-4)[a]	0.29 (0.03)	0.28 (0.05)	0.25 (0.04)	0.003
18:2 (n-4)[a]	0.11 (0.02)	0.12 (0.01)	0.13 (0.01)	**0.005**
16:4 (n-1)	0.36 (0.03)	0.35 (0.06)	0.33 (0.06)	0.10
18:4 (n-1)[a]	0.13 (0.03)	0.14 (0.02)	0.14 (0.02)	0.21
16:2 (n-7)[a]	0.04 (0.00)	0.04 (0.00)	0.03 (0.00)	0.29
18:2 (n-7)[a]	0.07 (0.01)	0.07 (0.01)	0.07 (0.01)	0.68
18:2 (n-6)	1.43 (0.24)	1.54 (0.17)	1.64 (0.14)	**0.001**
18:3 (n-6)[a]	0.13 (0.02)	0.12 (0.01)	0.11 (0.01)	**0.001**
20:2 (n-6)	0.24 (0.03)	0.26 (0.03)	0.28 (0.03)	**0.0004**
20:3 (n-6)[a]	0.09 (0.01)	0.10 (0.01)	0.10 (0.01)	**0.0003**
20:4 (n-6)	0.25 (0.04)	0.24 (0.03)	0.23 (0.05)	0.20
22:5 (n-6)	0.07 (0.01)	0.09 (0.01)	0.11 (0.02)	**<0.0001**
16:4 (n-3)[a]	0.04 (0.02)	0.05 (0.04)	0.05 (0.03)	0.16
18:3 (n-3)	0.59 (0.12)	0.58 (0.07)	0.64 (0.10)	0.053
18:4 (n-3)	2.27 (0.39)	2.25 (0.4)	2.26 (0.43)	0.98
20:3 (n-3)	0.07 (0.01)	0.07 (0.01)	0.07 (0.02)	0.38
20:4 (n-3)	0.48 (0.09)	0.48 (0.05)	0.47 (0.07)	0.941
20:5 (n-3)	8.55 (1.61)	6.15 (1.44)	4.90 (1.46)	**<0.0001**
21:5 (n-3)	0.48 (0.03)	0.50 (0.05)	0.49 (0.05)	0.315
22:4 (n-3)[a]	0.07 (0.03)	0.11 (0.02)	0.12 (0.03)	**<0.0001**
22:5 (n-3)[b]	4.09 (0.57)	4.83 (0.79)	5.20 (0.84)	**<0.0001**
22:6 (n-3)	8.13 (1.39)	9.50 (0.98)	10.08 (1.18)	**<0.0001**
∑PUFA	**28.76 (1.48)**	**28.51 (1.26)**	**28.32 (1.28)**	**0.0004**

Data are mean relative amounts, % of sum and SD. SFA = saturated FA; MUFA = monounsaturated FA; PUFA = polyunsaturated FA. The *P*-values come from distribution-free permutation testing of differences between regions, where bold values show significant differences at $P < 0.05$ across all FAs and FA groups tested. The letter *a* (minor FA < 0.5% in both seals, whales and prey organism) indicates fatty acids that are excluded in the CA analysis in Figures 4 and 5. The letter *b* (FA dominated by metabolic mechanism) indicates fatty acids that are additionally excluded in the CA analysis in Figure 3.

in $\delta^{13}C$ between harp seals and minke whales. Geographic gradients in stable isotopes have also been observed along the coasts on the Pacific side of the Arctic (Dunton et al. 1989; Schell et al. 1989).

The observed trophic level of harp seals is higher than previously reported, e.g. harp seals from the open drift ice along the east of Greenland had a trophic level of 3.5 based on the same trophic enrichment factor of 3.4‰ (Falk-Petersen et al. 2009). In another food web modelling study, Blanchard et al. (2002) reported higher trophic-level estimates in both harp seals (4.7) and minke whales (4.3). It is worth noticing that whereas harp seal diets are particularly characterized by pelagic crustaceans during summer

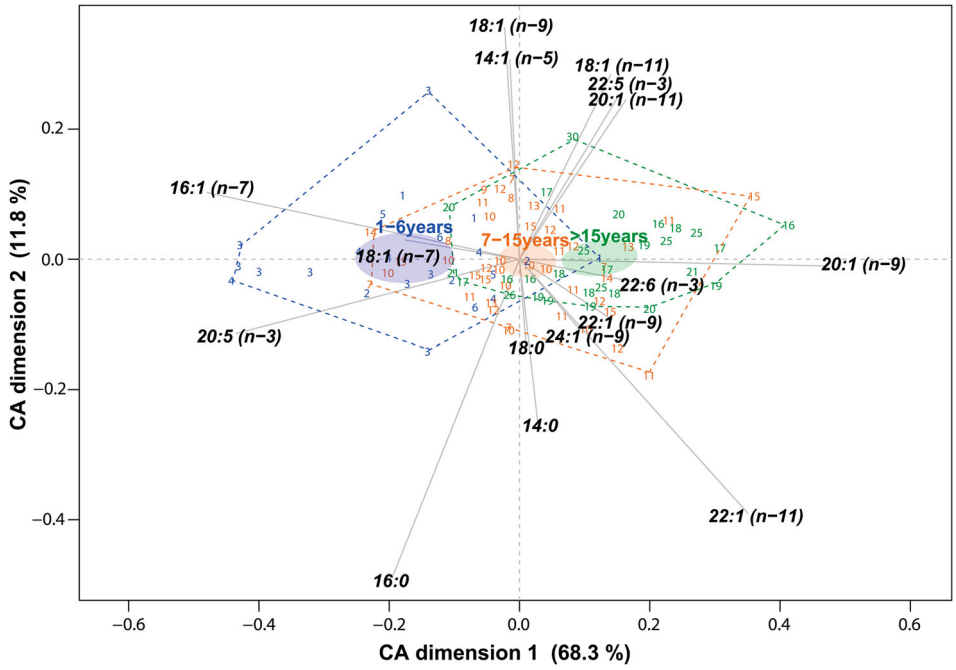

Figure 4. Contribution biplot of correspondence analysis (CA) of FA profiles from inner blubber of 92 harp seals. The positions of the seals are marked with a number giving the ages. The seals are divided into three groups according to ages, 1–6 years (blue), 7–15 years (brown) and >15 years (green), contained by convex hulls around the individuals of the respective groups The shaded ellipses show 95% confidence regions for the mean of each age group. The first two axes explain 80% of the total variance in the dataset (axis 1 = 68%, axis 2 = 12%). FAs with low contributions or low correlations in the ordination are omitted.

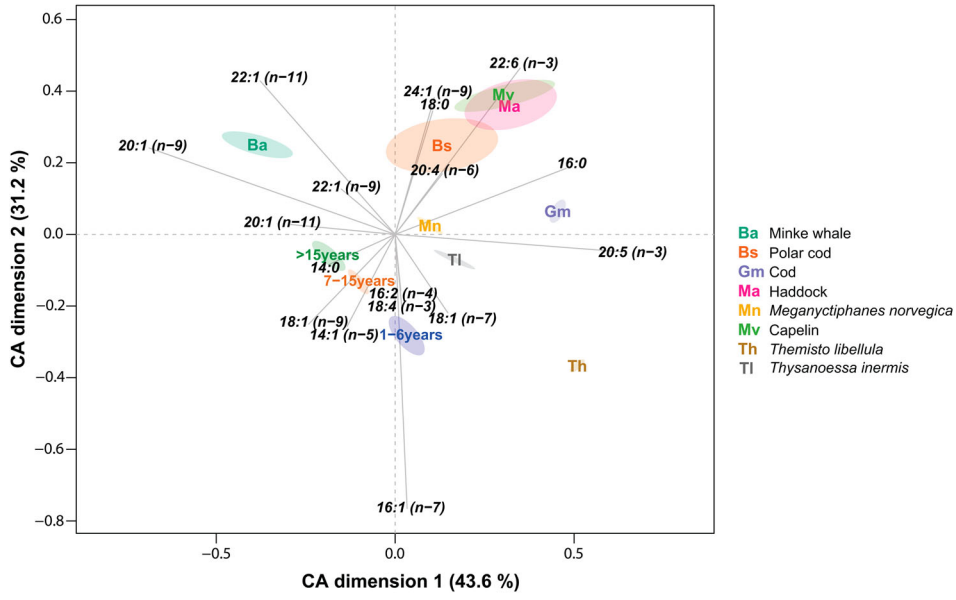

Figure 5. Contribution CA biplot of FA profiles from the inner blubber of 92 harp seals and 20 minke whales (*Balaenoptera acutorostrata* – Ba) sampled in 2011 from the Barents Sea and from seven potential prey species: haddock (Ma), cod (Gm), polar cod (Bs), capelin (Mv), *Meganyctiphanes norvegica* (Mn), *Themisto libellula* (Tl) and *Thysanoessa* sp. (Th). FAs with low contributions or low correlations in the ordination are omitted. The seals are divided into three groups according to ages: 1–6 years (blue), 7–15 years (brown) and >15 years (green). Species codes refer to Table I.

and autumn in their northern feeding grounds, their diet changes to mainly fish, and to some extent also benthic decapods, during winter and spring in the southern Barents Sea and the White Sea (Nilssen et al. 1995a, 1995b; Lindstrøm et al. 1998, 2013; Svetocheva & Svetochev 2015). This may have contributed to

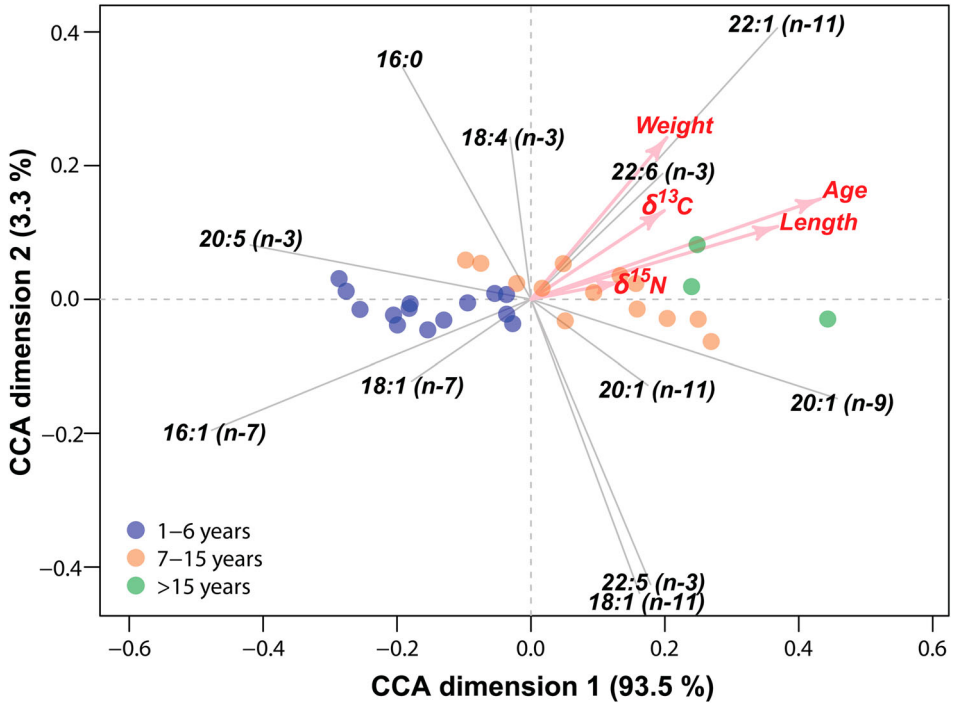

Figure 6. CCA of harp seals, constrained by age, weight, length, $\delta^{13}C$ and $\delta^{15}N$. Only seals with complete data from stable isotopes and lipids are analysed (n = 29), and shown for three age groups: 1–6 (blue), 7–15 (brown) and >15 years (green). Of the total inertia, 56.5% is in the space of the constrained variables, of which almost all (97%) is shown by these two CCA dimensions. The contribution scaling is again used for the FAs, and those with low contributions or low correlations in the ordination are omitted.

the elevated trophic levels observed in harp seals captured well into their southern feeding activity. Although the evidence is restricted, it has been suggested that the isotopic turnover times in mammal muscles are quite rapid, probably on the scale of a week to a couple of months (Hobson 1999; Newsome et al. 2010).

The observed variation in trophic level was slightly larger among minke whales, which may indicate that they have a more diverse diet than harp seals or that earlier feeding influenced the isotopic signal. Gavrilchuk et al. (2014) observed isotopic differences related to gender in North-west Atlantic minke whales; the current material included both males (2) and females (18) that may have contributed to the observed variations. We know that the diets of our 20 minke whales at the time of capture included krill, capelin, sand lance (*Ammodytes* sp.), cod and haddock (Meier et al. 2016). The fish prey was at intermediate trophic levels (3.08 – 3.30), while the zooplankton was at a lower trophic level and with a larger span (1.98 – 2.65). A diet with a larger fraction of zooplankton could result in a lower trophic level and, likely, with larger variation. In a previous study, Born et al. (2003) observed that trophic levels in minke whales varied in the range from 2.9 to 3.4 among sampling areas in the North-east Atlantic, with lowest values in the northernmost areas where crustaceans are known to be of particular importance as prey (Haug et al. 2002; Windsland et al. 2007). Based on diet composition, Pauly et al. (1998) calculated a trophic level of 3.8 for harp seals and 3.4 for minke whales, using a compilation of dietary information from the literature, which is comparable to the results in the present study. However, higher trophic levels (4.1) have been determined for minke whales in the North-west Atlantic (Ostrom et al. 1993), which may reflect regional differences in diets.

The CCA showed that length and age were the main factors explaining the variation in FA composition among harp seals. Old seals had an FA profile more similar to that of minke whales, as compared with younger seals. Some differences between whales and seals were apparent with regard to FAs. In particular, harp seals had higher levels of the MUFA 16:1 (n-7) and long-chained PUFAs than minke whales. High levels of 16:1 (n-7) have also been observed in previous studies of harp seals (Jangaard & Ke 1968; Ackman et al. 1971; Falk-Petersen et al. 2004, 2009; Tucker et al. 2009b; Grahl-Nielsen et al. 2011) and may be characteristic for this species. This MUFA also varied considerably among the age groups of harp seals, and when

compared with prey group FAs this indicates that krill *Thysanoessa* sp. are of particular importance for younger seals. Krill are known to be rich in 16:1 (n-7) and 20:5 (n-3) fatty acids; both probably originate from high-latitude diatom blooms (Falk-Petersen et al. 2004). This is in contrast to *Themisto* amphipods from Norwegian fjords as well as from Arctic waters, which are characterized by very high levels of *Calanus* fatty acid trophic markers 20:1 and 22:1, involving both fatty acids and fatty alcohols (Falk-Petersen et al. 1987, Kraft et al. 2015). These fatty acid trophic markers therefore suggest a short and efficient food chain leading from diatoms (phytoplankton) via krill to young harp seals in the south-eastern Barents Sea. The increase in *Calanus* fatty acid trophic markers in the adult seal (from *c*. 10 to 19%), indicates that *Themisto*, capelin or herring, all part of *Calanus* food chains, are becoming increasingly important as food for adult seals.

The bulk of harp seal diets is comprised of relatively few species, especially capelin, polar cod, herring, krill and the pelagic amphipod *T. libellula* (Lindstrøm et al. 2013; Nilssen et al. 2014). Crustaceans appear to be particularly important as food for harp seals during summer and autumn (July–October), when they are feeding in the northern parts of the Barents Sea. As the sea-ice cover expands southwards in early winter, the southward migrating seals appear to take more fish such as capelin, polar cod and herring (Nilssen et al. 1995a, 1995b; Lindstrøm et al. 1998). The spring diet in their breeding and moulting areas inside the White Sea is a varied mixture of crustaceans (benthic as well as pelagic) and fish (Nilssen et al. 1995b; Svetocheva & Svetochev 2015). The current results, with an apparent size-dependent diet, support previous studies of summer diets of harp seals in the Barents Sea, where both sub-adult (<1.50 m) and adult seals were associated with pelagic crustaceans (particularly krill) and adult seals were mainly associated with fish (capelin, gadoids and flatfishes) (Lindstrøm et al. 2013). Similar observations have been made both in Arctic Canada (Sergeant 1973; Finley et al. 1990) and in Greenland waters (Kapel 2000). Crustaceans (krill and amphipods) are important prey for both juvenile and adult harp seals in the northern Barents Sea during autumn (Nilssen et al. 1995a).

From previous information on the spatial distribution of harp seals during spring (Nordøy et al. 2008) and minke whales (Øien et al. 1987; Meier et al. 2016), it is evident that the two species must overlap spatially, at least temporarily, in the southern Barents Sea. The diving behaviours of both species are consistent with animals primarily exploiting schooling fish or high concentrations of zooplankton (Blix & Folkow 1995; Nordøy et al. 2008). Minke whale diets varied greatly in time and space, reflecting changes in prey availability (Haug et al. 2002; Windsland et al. 2007). Previous dietary studies of minke whales have shown that the importance of krill increases with latitude, and krill dominate the diet composition in the northern areas, whereas capelin dominate the diet in the south, followed by herring and haddock. Minke whales in this study had high levels of MUFAs, especially 20:1 (n-9) and 22:1 (n-11). These fatty acids originate in *Calanus* copepods, the main prey for capelin and herring (Dalpadado et al. 2012). This indicates a food chain from diatoms via *Calanus* copepods and pelagic fish to whales (see Falk-Petersen et al. 1990, 2007), whereas krill seem to be of minor importance as food for minke whales along the coast in the southern Barents Sea. These findings are supported by stomach analyses of the whales in the present study, showing that capelin was the most important food (Meier et al. 2016).

The use of SI and FA analyses to address potential competition between harp seals and minke whales in the Barents Sea has enabled us to draw the following conclusions to our original key questions:

- Harp seals were at a higher trophic level than minke whales; this has also been found in other studies, for instance from West Greenland (Linnebjerg et al. 2016). This may indicate that harp seals include more fish prey in their diets, but even though their trophic levels were significantly different, the harp seals were only 0.5 TL higher than minke whales. Both species have mixed diets, with likely overlap in prey. Capelin and sand lance are important prey for both minke whales and harp seals in West Greenland (Linnebjerg et al. 2016) and these species were also found in stomachs from minke whales included in our study (Meier et al. 2016). Some overlap in diet likely exists in the southern Barents Sea, although competition for resources is reduced by geographic separation and seasonal migrations. At the time of sampling, early May 2011, the two species occurred in different geographic areas, with little potential for direct overlap.
- Both harp seals and minke whales seem to be at the top of a food chain from diatoms via *Calanus* copepods and pelagic fish.
- Different age groups of harp seals exhibited significant variation in blubber fatty acid composition, suggesting age-based differences in diet. Compared with younger seals, older seals had fatty acid compositions in their blubber that were more similar to minke whales, thus indicating similarities in diets.

Disclosure statement

No potential conflict of interest was reported by the authors.

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