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Harp seal body condition and trophic interactions with prey in Norwegian high Arctic waters in early autumn

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ABSTRACT

In September 2016, a marine ecosystem survey covered all trophic levels from phytoplankton to seals in the Arctic Ocean to the west and north of Svalbard. At the ice edge, 26 harp seals were sampled to assess whether recent environmental changes had affected their diets and body condition by comparing our current results with previous investigations conducted 2–3 decades ago in the northern Barents Sea, when the ice edge was located much further south. Our results suggest that the body condition was slightly but significantly lower for one year and older seals in 2016 compared with seals sampled in the early 1990s. Furthermore, we confirmed previous findings that polar cod (*Boreogadus saida)* and the pelagic hyperiid amphipod *Themisto libellula* still dominate the seal diet. One consequence of current ice edge localisation north of Svalbard is that the water depth underneath is now 500 m and deeper, which probably explains the absence of bottom associated species, and the presence of species such as Atlantic cod (*Gadus morhua)* and blue whiting *(Micromesistius poutassou)* as alternative species in addition to polar cod and *T. libellula* in the seal diets. Stable isotope data also suggest possible long-term importance in the seal diet of *T. libellula* and of low trophic level benthopelagic prey such as the squid *Gonatus fabricii* over mid-trophic level pelagic fishes, but with a strong component of small, benthopelagic fish such as blue whiting. The long-term importance of pelagic crustaceans was also suggested from the fatty acid analyses. Assessment of the abundance of prey showed that *T. libellula* was by far the most abundant prey species in the upper water layers, followed by krill (mainly *Thysanoessa inermis*), Atlantic cod and polar cod. Prey-preference analyses indicated that polar cod was the most preferred prey species for the seals.

1. Introduction

The harp seal (*Pagophilus groenlandicus)* is the most important top predator in the Barents Sea ecosystem after the northeast Atlantic cod (*Gadus morhua)* (Bogstad et al., 2015). Harp seals are pagophilic and prefer to be near sea ice at virtually all times of the year. They are also highly mobile predators that undertake extensive seasonal migrations, from breeding and moulting areas in the White Sea (southeast of the Barents Sea) in February-May to seasonally ice-covered areas in the northern Barents Sea, following the biological productivity of the ecosystem (e.g., Haug et al., 1994; Nilssen et al., 1995a, b; Nordøy et al., 2008; Lindstrøm et al., 2013). They use the sea ice edge as a platform from which they conduct extended foraging trips into open waters.

Previous studies suggest that harp seal diets vary in time and space, probably due to the seasonal changes in their habitat use and food availability (Nilssen et al., 1995a, b; Lindstrøm et al., 1998, 2013). Fish, mainly capelin (*Mallotus villosus)* and herring (*Clupea harengus*), dominate the diet in the southern Barents Sea during winter and early spring whereas various crustacean species (mainly krill *Thysanoessa* sp. and amphipods *Themisto libellula*) and polar cod (*Boreogadus saida)* dominate the diet along the drift ice in the northern Barents Sea during summer and autumn. From observed seasonal variation in the harp seal body condition, it is evident that the June-September period is when harp seals have the greatest increase in blubber mass, presumably due to increased food intake combined with increased energy content of prey (Nilssen et al., 1997, 2000). The availability of high-energetic food, such as krill and amphipods in the northern areas in summer and autumn presumably provide the energetic advantage necessary to account for

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the long migrations of harp seals from their more sub-Arctic winter and spring distributions (Lindstrøm et al., 2013).

Recent decades have seen substantial environmental changes in the Barents Sea, particularly the warming of water and retreating sea ice in the northern parts (Divine and Dick, 2006; Haug et al., 2017a) and changed distributions of zooplankton, fish and marine mammal species, harp seals included (Fossheim et al., 2015; Kortsch et al., 2015; Vikingsson et al., 2015; Eriksen et al., 2017; Haug et al., 2017a; Vacquie-Garcia et al., 2017; Storrie et al., 2018). The climatic changes are associated with a marked shift in the distribution of water masses, and as a result, the favourable thermal habitat for boreal zooplankton has expanded northwards whereas Arctic zooplankton have retreated further north (see Eriksen et al., 2017). Not surprisingly, the changes have led to changes in spatial distribution of demersal fish communities, with boreal communities expanding northwards with associated food web shifts (Fossheim et al., 2015; Kortsch et al., 2015; Haug et al., 2017a). Given these major environmental changes, previous diet studies of harp seals during autumn in the northern Barents Sea area (Lydersen et al., 1991; Nilssen et al., 1995a), which were conducted 2–3 decades ago, may not describe recent seal diets.

Surveys in the northern Barents Sea, as well as fisheries catches, show recent northwards expansion of key boreal species such as Atlantic cod, haddock (*Melanogrammus aeglefinus)* and capelin (Haug et al., 2017a). Invasion of such species into the northern area has resulted in increased predation pressure on zooplankton and forage fish stocks such as capelin and the endemic polar cod, and also on the Arctic benthic fish community that has retracted north- and northeast-wards to deeper areas bordering the deep polar basin (Fossheim et al., 2015). Competition for food by the currently large and more northerly distributed cod stock may also have affected body conditions of marine mammals

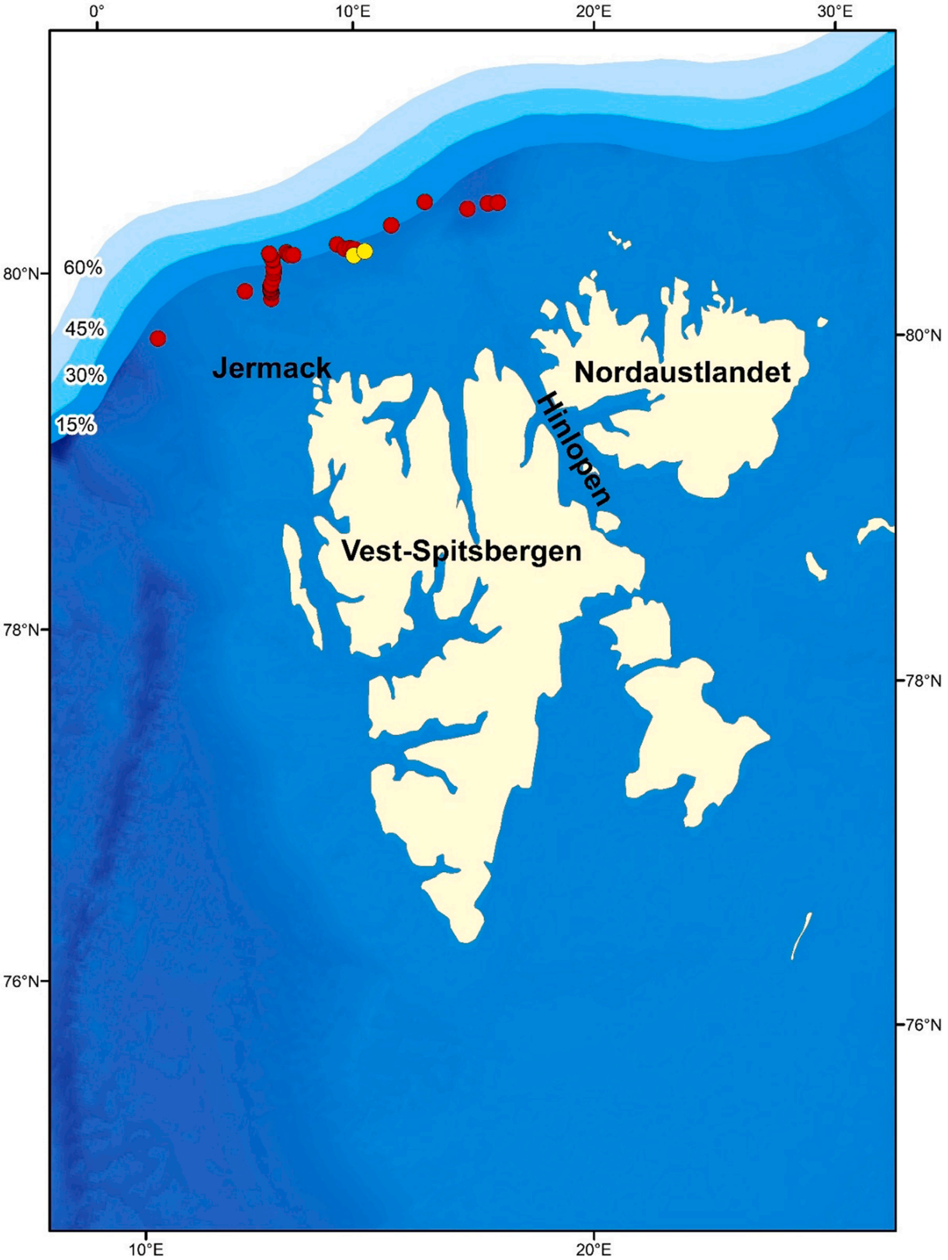

Fig. 1. Map showing where harp seals were observed (red dots) and sampled (yellow dots) along the ice edge north of Svalbard 2–16 September 2016. Ice concentrations from 15% to 60% during the sampling period are indicated. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Bogstad et al., 2015), including harp seals (Øigård et al., 2013).

Given their pagophilic nature, it is evident that harp seals are likely to follow any receding of the ice edge if sufficient food resources become available in the region (Haug et al., 2017a). Variation in ice-cover in the areas north of Svalbard has occurred on decadal as well as on longer time scales with heavy sea ice more or less continuously from 1790 to 1920, and with summer ice for most of the years from 1920 to 2010 (Falk-Petersen et al., 2015; Mörner et al. 2020). These areas, once an important whaling ground (named "The Whalers Bay") where feeding bowhead whales (*Balaena mysticetus*) were intensively hunted with sailing ships in virtually open waters from around 1680 to 1790, is currently being characterized as highly productive (Søreide et al., 2008; Falk-Petersen et al., 2015; Menze et al. 2020). During the years 2014–2017, ecosystem surveys were performed in August-September in the Arctic Ocean both to the west and north of Svalbard. These surveys examined all trophic levels from phytoplankton to whales (see Solvang et al., 2020), as well as chemical and physical properties of the water masses in the area and was conducted as part of a project (SI_ARCTIC, see Ingvaldsen et al., 2017) that aimed to develop a knowledge base on the state and variability of the present and future Arctic Ocean ecosystems. One of the survey years (2016) was devoted particularly to areas at or adjacent to the ice edge, with the option to sample harp seals for ecological investigations. The aim was to gain updated information about current feeding ecology and body condition in the pack ice areas in the northmost parts of the distributional area for the species. We particularly wanted to assess whether recent environmental changes had affected their diets and condition by comparing new results with previous investigations conducted along the ice edge in the northern Barents Sea (i.e., southeast of Hinlopen and Nordaustlandet, see Fig. 1) in September in 1988 (Lydersen et al., 1991), 1990 and 1991 (Nilssen et al., 1995a). Certainly, we acknowledge that there are challenges in distinguishing changes that are true long-term trends, from changes that may be more about random variation from one year to the next. Nevertheless, by using complementary methods, we were able to assess the seal diet both in short-term (morphological analyses of digestive tract contents) and long-term (natural tissue chemical markers: stable isotopes and fatty acids) prey use by the seals. Since the abundance of prey species was assessed concurrently with the seal sampling, it was also possible to address questions related to possible resource preferences by the seals.

2. Materials and methods

2.1. Sampling of harp seals

During the survey from 2 to 16 September 2016, harp seals were observed in the water adjacent to the ice edge north of Svalbard throughout the entire period (Fig. 1). In one harp seal hot spot (between 11°E and 12°E), where the seals had hauled out on pans in the open drift ice, 26 animals were shot on the ice and taken onboard for scientific sampling. Sampling included measurements of weight, length and blubber thickness. Additionally, teeth were taken for age determination, stomach/intestines for diet studies, and muscle and blubber samples (frozen) for studies of stable isotopes and fatty acids, respectively.

2.2. Body condition

All measurements followed the procedures described by Nilssen et al. (1997). Standard body length of seals was measured to the nearest cm in a straight line from the tip of the snout to the tip of the tail, with the animal laying on its back. Ventral and dorsal blubber thickness were measured to the nearest mm (excluding the skin), in a knife-cut on the sternum or at the dorsal mid-line between the front flippers.

Due to the highly biased age and size (body length) distribution of seals collected in 2016 (see results), it was difficult to directly compare the condition of seals in different years using simple condition indices including length and blubber thickness directly. We instead calculated a size-corrected condition index by:

1) Fitting a simple linear regression of dorsal blubber thickness as a function of body length
2) Calculating the residuals (i.e. remaining variation not explained by the linear regression model)
3) Performing a Wilcoxon rank sum test on these residuals between periods of sampling (1990–91 vs. 2016).

For smaller seals (i.e. those with a body length <145 cm, see results), the number of samples obtained were more balanced across the time periods, and we used a Wilcoxon rank sum test on 1) dorsal blubber thickness and 2) the ratio of blubber thickness to body length to test for difference between the two time periods.

2.3. Analyses of gastro-intestinal contents

In the laboratory the stomachs and intestines (colon only) were cut open after thawing. Contents were weighed and flushed with fresh water, then fish and crustaceans were separated. Prey organisms were identified to the lowest possible taxonomic level, preferably species, and numbers and biomass of the different species were estimated as described by Nilssen et al. (1995a) and Lindstrøm et al. (2013). To avoid pseudo-replication, the reconstructed prey biomass of stomachs and colons were pooled and treated as one sample (gastrointestinal contents). Squid was omitted from the biomass calculations because we were not able to reconstruct the weight at the time of ingestion due to lack of a reliable squid beak size-weight relationship. Diet data were presented in terms of frequency of occurrence (F_i) and relative biomass (B_i):

$$F_i = \frac{n_i}{n_t}$$

$$B_i = \frac{b_i}{\sum_{j=1}^{k} b_j}$$

where n_i is number of gastro-intestinal tracts containing species i, n_t is total number of gastro-intestinal tracts, b_i is the biomass of species i and b_t is biomass of all species ($j = 1, \ldots, k$).

2.4. Stable isotope analyses and mixing models

Approximately 2 cm^3 of the frozen muscle tissue was taken from each seal, dissected to remove obvious blood vessels and connective tissue, then rinsed in deionized water to remove as much blood and other mobile compounds as possible. Potential prey species (blue whiting (*Micromesistius poutassou*), juvenile Atlantic cod, squid *Gonatus fabricii*, juvenile haddock, and hyperiid amphipods *T. libellula* were collected on the same ecosystem survey, dissected under a binocular light microscope to sample muscle tissue, and rinsed with deionized water. The samples were subsequently refrozen at −20 °C, then freeze-dried to a constant mass at −80 °C for 48 h. Samples were then homogenized to a fine powder using a pestle and mortar. Stable isotope compositions of carbon and nitrogen were analyzed with a Thermo EA1110 elemental analyzer linked to a Sercon 2020 isotope ratio mass spectrometer by Elemtex Ltd (UK). Measured precision was 0.2‰ for both isotopes, based on USGS40 and USGS41 international standards, and in-house bovine liver standard (BLS).

The measured isotopic compositions of prey sources were used to mathematically estimate the proportional contributions of each prey to the measured isotopic composition, i.e. assimilated diet, of each predator seal using Bayesian stable isotope mixing models (Phillips et al., 2014). These estimates and their associated uncertainty were calculated using the simmr package (Parnell, 2019) in R software (R Core Team, 2017). The diet source isotope data are shown in Table 2. Tissue enrichment factors of 1.3‰ for carbon and 2.4‰ for nitrogen isotopes were taken from a study of captive harp seals by Hobson et al. (1996) and used consistently for all prey types.

2.5. Fatty acid analyses

Blubber cores, approximately 5 × 5 cm, were taken through the full depth of the dorsal 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.

Collection of subsamples was performed while the blubber was still frozen to avoid "lipid bleeding". Small subsamples of blubber weighing 20–50 mg were taken from the inner blubber, 0.1 cm in from the muscle side. Similar small samples were taken of the seal muscle. Different prey organisms (Atlantic cod, haddock, polar cod and amphipods *T. libellula)*, caught in the same area where the seals were sampled*,* were homogenized and subsamples (50–100 mg) were collected for fatty acids analysis.

All samples were methylated and the respective fatty acid methyl esters (FAME) were analyzed on a HP-7890A gas chromatograph (Agilent, USA) with a flame ionization detector (GC-FID) according to a method described in Meier et al. (2006) and further details are given in Meier et al. (2016).

As the amphipods samples contain large amount of wax esters, the FAME and the fatty alcohols (FAOH) were separated on solid phase column (500 mg aminopropyl-SPE, Supelco) and analyzed individually on GC-FID to avoid coelution. The amphipods samples were first methylated and the resulting hexane extracts from the direct metanolysis were added nonadecanol (19:0 alk) as internal standard for the FAOHs. The hexane extract were loaded on to the SPE column and the FAME fraction was eluted with 3 ml hexane + 2 ml hexane:ethyl acetate (9:1 v/v) and the fatty alcohols were eluted with 4 ml chloroform.

The FAOHs or wax esters are not found in the lipids of the seals as the FAOHs are oxidized very fast to the corresponding FAs in the digestion process. The FAOHs does therefore also contribute to predator's fatty acids pool, and when looking at fatty acids trophic markers (FATM), both the FA and the FAOH from the prey should be considered (Budge and Iverson, 2003). In the present work we have therefore added the quantitative amount of the different corresponding FAs and FAOHs (eg. 22:1 (n-11) FA + 22:1 (n-11) FAOH) before normalized to 100%.

2.6. Estimation of prey abundance and biomass

Acoustic data for estimation of the distribution and abundance of pelagic plankton and fish were collected with calibrated EK60 echosounder split beam systems at the acoustic frequencies 18, 38, and 120 kHz at 1 ms pulse duration. The echosounders were connected to transducers mounted on a protruding instrument keel with transducer faces ~3m below the hull, usually ~8.5 m below the sea surface, hence reliable data acquisition from ~15 m depth. The lower working threshold in terms of volume backscattering strength (S_v) in dB was set to −82 dB re 1 m^{-1}.

Multi-frequency scrutinizing of the echograms was conducted with the Large-Scale Survey System (LSSS) acoustic post processing system, as described by Korneliussen et al. (2006, 2016). The processing involved manual removal of noise (acoustic, electric, bubble, temporal noise from e.g., trawl sensors during trawl operations), and correction of erroneous bottom detections. The remaining acoustic values, termed Nautical Area Scattering Coefficient [NASC, s_A (m^2 nmi^{-2}), MacLennan et al., 2002] are a proxy for the density of organisms (fish, zooplankton etc.) in the sea. The NASC values at 38 kHz frequency (optimal for fish) and at 120 kHz (optimal for the krill-amphipod component (KRIAM see below) were allocated values to various species or species groups and stored in the database following long established standards developed at the Institute of Marine Research (IMR), Norway. The LSSS post-processing software (Korneliussen et al., 2006, 2016) was utilized to scrutinize the acoustic data. The process was guided by the frequency response (the backscattering coefficient s_v at 18 and 120 kHz relative to that at 38 kHz), sequential thresholding (see Knutsen et al., 2017), appearance of the echograms, and target strength distribution. Trawl data were used to corroborate the interpretation of the acoustic data. The NASCs for each nautical mile along the cruise tracs were integrated from the upper integration limit (about 15 m depth) to 800 m depth (or to the sea floor where shallower) for 38 kHz and down to 300 m for 120 kHz. Here, only data for those species and groups considered relevant as prey for the harp seals are used, viz Atlantic cod, polar cod, capelin, blue whiting and macro-zooplankton.

For fish species, the target strength/length relationships normally used at IMR for stock size estimation were applied (Table 6). For pelagic species (capelin, polar cod and blue whiting) the s_A-values were averaged over the whole surveyed area north of 79°N, while for Atlantic cod, which is mainly associated with the shelf, the surveyed area shallower than 500 m was used. These areas were considered to be the local feeding areas for the harp seals in the present study. Average densities of the prey species were calculated according to MacLennan et al. (2002), using average standard lengths of each species taken in the study area.

For the macro-zooplankton krill and amphipods, acoustic data were retrieved from the 120 kHz echosounder and we used a simple approach where the total NASC between the volume backscattering strength (S_v, dB re 1 m^{-1}) thresholds −82 dB and −65 dB was accepted to represent macroplankton. The 120 kHz data was scrutinized to 300 m depth, somewhat less than the maximum range recommended by Korneliussen et al., (2020). However, see also Supplementary material II and the considerations on the interpretation of echograms presented in Figs. S2–S4. As for pelagic fish, the derived NASCs were averaged over the surveyed area north of 79°N.

Biological data on macroplankton and micronekton were collected by a Macroplankton trawl (Krafft et al., 2010; Heino et al., 2011), with 36 m^2 opening and an identical mesh size (3 mm square, 8 mm stretched) from the opening to the cod end using the same methods as described in Knutsen et al. (2017). The majority of hauls were V-hauls or oblique hauls (Wiebe et al., 2015). The trawl was sampling from the surface to around 1000 m depth and back up again, although on the slope and shelf maximum depths were shallower, with sufficient safety distance to the seafloor. It was assumed equal opening area and 100% filtration efficiency throughout each haul (Wenneck et al., 2008).

The acoustic category KRIAM is a composite category of the elongate crustaceans, euphausiids and hyperiid amphipods. In order to estimate the abundance and biomass of these organism types we adopted methods used by CCAMLR to estimate the abundance and biomass of Antarctic krill (Reiss et al., 2008; CCAMLR, 2010; Laidre et al., 2010; Fielding et al., 2014). For details, see Supplementary material II. The krill species are the following: *Meganyctiphanes norvegica*, *Thysanoessa inermis* and *Thysanoessa longicaudata,* while the amphipods were the hyperiids *T. libellula* and *Themisto abyssorum.*

The NASCs allocated to KRIAM were split further to krill and amphipods (see Results) and converted to biomass density (g m^{-2}) using the SDWBApackage2010 (CCAMLR, 2010; Calise and Skaret, 2011) according to the CCAMLR protocol and adjustments detailed in Supplementary material II.

2.7. Analyses of prey preferences

Prey preference was analyzed by estimating the relative difference in prey composition between the seal diet (C_i) and the abundance of the prey species in the sea (R_i):

$$D_i = C_i - R_i$$

where C_i and R_i are the relative importance of prey i in the seal diet and in the ocean, respectively. To test whether harp seals have prey preference (positive or negative), the difference measure (D_i), calculated for krill, amphipods, polar cod, Atlantic cod and blue whiting was tested for significant deviance from random feeding (zero). This was accomplished by constructing 95% confidence intervals (95% CI) for the difference measure of each prey species. The confidence intervals were constructed by generating 1000 bootstrap replicates of the diet data and the resource data. The bootstrapping of diet and resource data were performed in R statistical software (R Core Team, 2017). The definition of positive and negative prey preference is when a prey has been consumed in higher and lower proportions than observed in the environment, respectively. Random feeding or random preference is when a prey has been consumed in the same proportions as observed in the environment i.e. when the error bars (95% CI) overlap zero.

3. Results

3.1. Body condition

Not unexpectedly, there was a strong linear relationship between body length (BL) and dorsal blubber thickness ($\widehat{b}_D$). For the combined sample of seals of all sizes, the relationship was best described by the regression equation $\widehat{b}_D = 0.76BL - 57.6$ ($p < 0.001$, $R^2 = 0.77$ (Fig. 2a). However, as indicated by the R^2 there was also substantial remaining variation unexplained after applying the regression. There was a small but significant difference in the distribution of these residuals between the early (1990–91) and late (2016) samples, with predominantly positive residuals in the early period and negative residuals during the late period (Fig. 2b, Wilcoxon Rank Sum W = 1108, p = 0.0058). The difference appeared to be mostly explained by thin blubber layers in seals with a body length above about 120 cm (representing 1 + seals, i.e. excluding pups of the year).

For seals with a body length $L < 145$ mm, the dorsal blubber layer was significantly thinner in 2016 compared to the earlier sampling period (Fig. 2c; 1990–91: 36 ± 5.9 mm, 2016: 27.5 ± 4.9 mm; Wilcoxon Rank Sum W = 392.5, $p < 0.0001$). This difference was also significant for the ratio of blubber thickness to body length (Wilcoxon rank Sum W = 378, p = 0.0004), which controls for potential size biases in the sample of small seals.

3.2. Diet

In terms of frequency of occurrence, polar cod (61.5%) and the pelagic hyperiid amphipod *T. libellula* dominated the diet (Table 1), followed by blue whiting (26.9%) and northeast Arctic (NEA) cod (15.4%). In terms of overall biomass (not shown), amphipods (72.6%) completely dominated the diet composition, followed by polar cod (23.4%), blue whiting (2.8%) and Atlantic cod (1%). Fig. 3 shows the diet composition of the 23 seals with food in their gastro-intestinal tract. Amphipods and polar cod dominate in 15 and 7 harp seals respectively, and one seal had exclusively fed on blue whiting. Interestingly, polar cod was almost exclusively consumed by young (age group 0) animals, with only one 1 + seal having a small proportion of polar cod in its recent diet. In contrast, amphipods were consumed by both young and older individuals, but occurred more frequently and in higher proportions in older individuals. A few beaks from small (mantle length < 50 mm) squid (*G. fabricii*) were found in two seals.

Table 1
Frequency of occurrence of prey in the gastro-intestinal tracts of harp seals. n_t and n_e denotes total and empty number of gastro-intestinal tracts.

	Percentage occurrence
	$n_t = 26$
Prey species	$n_e = 3$
Amphipoda	
Themisto libellula	46.2
Cephalopoda	
Gonatus fabricii	7.7
Pisces	
Gadidae	
Gadus morhua	15.4
Boreogadus saida	61.5
Micromesitius poutassou	26.9
Unid. Codfish	7.7

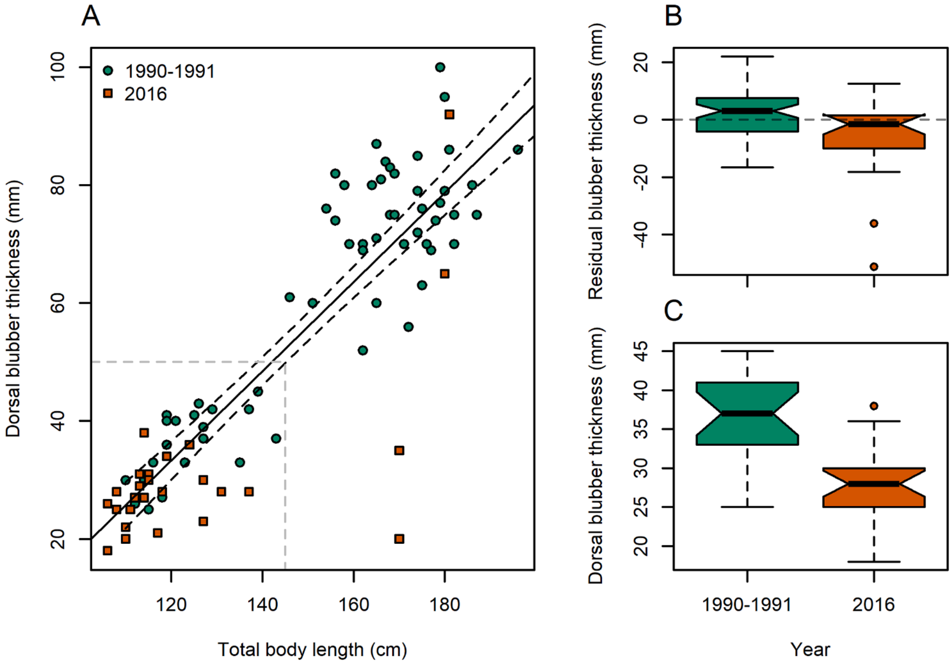

Fig. 2. A: Relationship between body length and dorsal blubber thickness in harp seals sampled in 1990–91 (green) and 2016 (orange). The solid and dotted lines represent the fitted linear regression model and its confidence intervals, respectively. This was based on the total sample of animals. Points within the grey box represents seals with a body length <145 cm; B: Boxplot of the distribution of residuals from the regression model of all samples, split by period. C: Boxplot of the dorsal blubber thickness for seals <145 cm. See text for more details. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

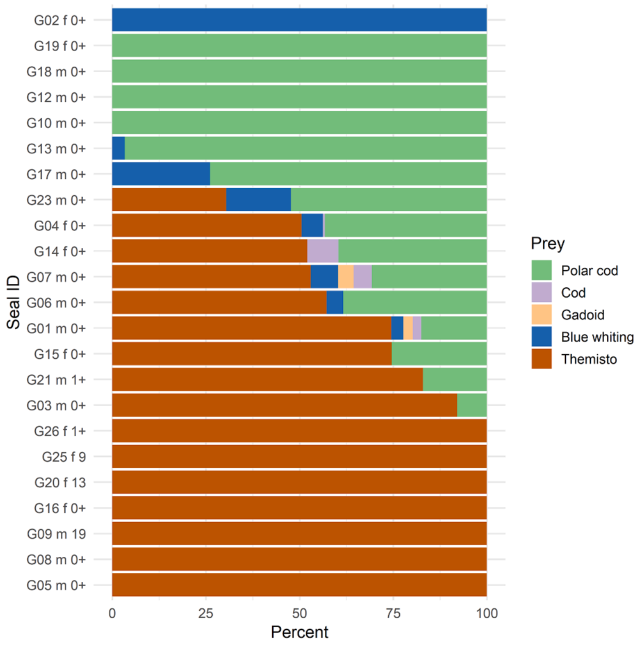

Fig. 3. Relative prey importance, in terms of prey biomass, in 23 harp seals sampled in Svalbard waters in September 2016. In the seal ID, m and f denotes males and females, respectively, 0+ and 1+ denotes 0 age and 1+ age individuals, and a greater positive number represents known age.

3.3. Stable isotope analyses and mixing models

Stable isotope measurements ranged from −21.9 to −20.2‰ for δ^{13}C' (SD 0.42), and from 10.9 to 13.7‰ (SD 0.76) for δ^{15}N; full data are given in Supplementary material I, Table S1. There was a strong, linear correlation between carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope values ($R^2 = 0.44$, $p < 0.0001$). We also found strong, loglinear relationships between values of each isotope and mass, with a slightly stronger relationship between mass and δ^{13}C values (δ^{15}N: $R^2 = 0.46$, $p < 0.001$; δ^{13}C: $R^2 = 0.58$, $p < 0.0001$). These relationships were, however, driven mostly by the four large, adult seals in the sample. We found positive, linear relationship between values of each isotope and both chest and back blubber thickness, again with stronger relationships between blubber thickness and δ^{13}C values (δ^{15}N-chest: $R^2 = 0.20$, $p < 0.05$, δ^{15}N-back: $R^2 = 0.24$, $p < 0.05$; δ^{13}C-chest: $R^2 = 0.17$, $p < 0$ 0.05, δ^{13}C-back: $R^2 = 0.29$, $p < 0.005$). These results should be interpreted with caution, however, as they were largely driven by two individuals with blubber thicknesses at the chest ≥50 mm, and ≥65 mm at the back. No difference was found in stable isotope composition between females and males.

Seals were grouped into five diet types based on stomach contents analysis: blue whiting, polar cod, mixed, *T. libellula,* and unknown. Diet type was classified based on the predominant (>80%) species in each stomach, individuals were classified into the mixed category when no single species occupied over 80% of the stomach contents by mass, or into unknown when stomachs were empty. We found no significant difference between the carbon and nitrogen stable isotope compositions of the seals when grouped by diet type (Fig. 4).

The proportions of prey types in the diet were predicted by Bayesian stable isotope mixing models from the carbon and nitrogen stable isotope compositions of the prey and of the seal tissues, grouped based on their seals' primary stomach contents; summary statistics for prey data are shown in Table 2. The most important prey types are predicted as blue whiting (between 13 and 48%), the squid *G. fabricii* (between 11 and 20%), and the hyperiid amphipods *T. libellula* (between 9 and 29%) see Table 3 and Figs. 4 and 5 for details. The proportion of benthopelagic, low to mid-trophic level prey represented by the squid, *G. fabricii*, and predicted by the mixing models was higher than expected based on stomach contents analyses.

We found no relationship between carbon to nitrogen percent elemental ratio, a good indicator of fat content in muscle tissue (Post et al, 2007), and either maturity stage or blubber thickness at either the chest or the back.

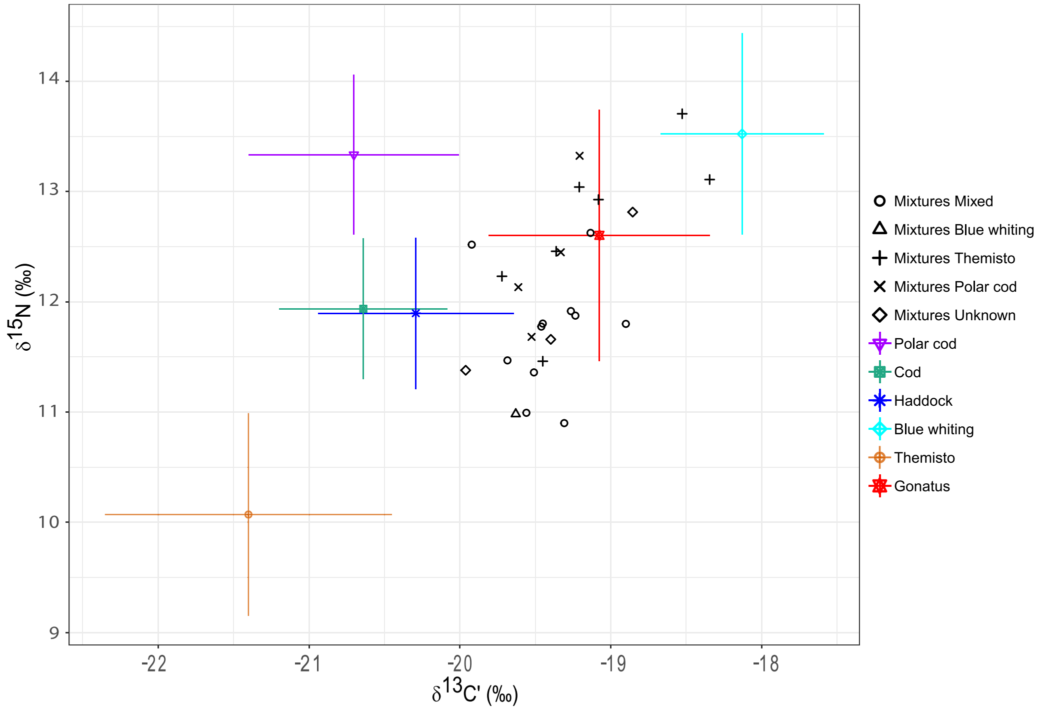

Fig. 4. Carbon and nitrogen isotope values of harp seals (black symbols show individual seal stable isotope composition, grouped by stomach contents-based diet category, classed as mixtures), symbols represent diet type classified from stomach contents analysis, against stable isotope values of potential prey (coloured symbols, ±SD.

Table 2
Carbon and nitrogen stable isotope data for potential prey types (mean and standard deviation values).

Source	Mean $\delta^{13}C$ ‰	SD $\delta^{13}C$	Mean $\delta^{15}N$ ‰	SD $\delta^{15}N$	n
Blue whiting	−20.8	0.23	11.1	0.69	3
Juvenile Atlantic cod	−23.6	0.30	9.5	0.22	3
Gonatus	−23.1	0.97	10.2	0.97	14
Juvenile haddock	−23.4	0.42	9.5	0.33	3
Polar cod	−23.8	0.51	10.9	0.41	4
Themisto libellula	−25.4	1.09	7.7	0.70	33

3.4. *Fatty acids*

All results from analyses of harp seal blubber and muscle are given in Table 4. Results from the fatty acid analyses of prey species are given in Supplementary material I.

Fig. 6 shows a strong linear relationship in the seal blubber lipids between *Calanus* copepod Fatty Acids Tropic Markers (FATMs); the monounsaturated fatty acids (MUFAs) 20:1 (n-9) and 22:1 (n-11) ($R^2 = 0.86$, $P < 0.0001$). This FATM is very high in amphipods and polar cod (which are feeding directly on *Calanus* copepods) (Table S2 in Supplementary material I).

However, matching the sampled seals with their observed stomach content show no grouping against a constant preference for this observed prey, as all diet types show large variation in the *Calanus* FATMs (Fig. 6). There was a small but significant increase in the long-chain 22:1 MUFA in the blubber and both 20:1 and 22:1 in the muscle of the old seals (7–19 years) compared with the young seals (young of the year and 1 year old) (Table 4). Higher levels of the polyunsaturated FA (PUFA), 20:4 (n-6) were found in the young seals (age group 0) compared with the 1 years and older (1+) seals (Table 4). However, when looking at the total

Table 3
Predicted diet proportional composition from Bayesian stable isotope mixing models for each dietary group as defined from ≥80% of stomach contents; mixed denoted no single prey group ≥80%, unknown are seals with empty stomachs.

Diet group	Blue whiting		Atlantic Cod (juv.)		Haddock (juv.)		*Gonatus fabricii*		Polar cod		*Themisto libellula*	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Blue whiting	0.13	0.10	0.14	0.15	0.18	0.19	0.20	0.19	0.07	0.06	0.29	0.19
Mixed	0.38	0.12	0.14	0.11	0.16	0.13	0.11	0.09	0.07	0.05	0.14	0.09
Polar cod	0.42	0.10	0.14	0.10	0.14	0.11	0.13	0.10	0.09	0.07	0.09	0.06
Themisto	0.48	0.09	0.11	0.09	0.12	0.09	0.12	0.10	0.08	0.06	0.09	0.06
Unknown	0.21	0.15	0.17	0.15	0.17	0.15	0.17	0.15	0.13	0.11	0.14	0.11

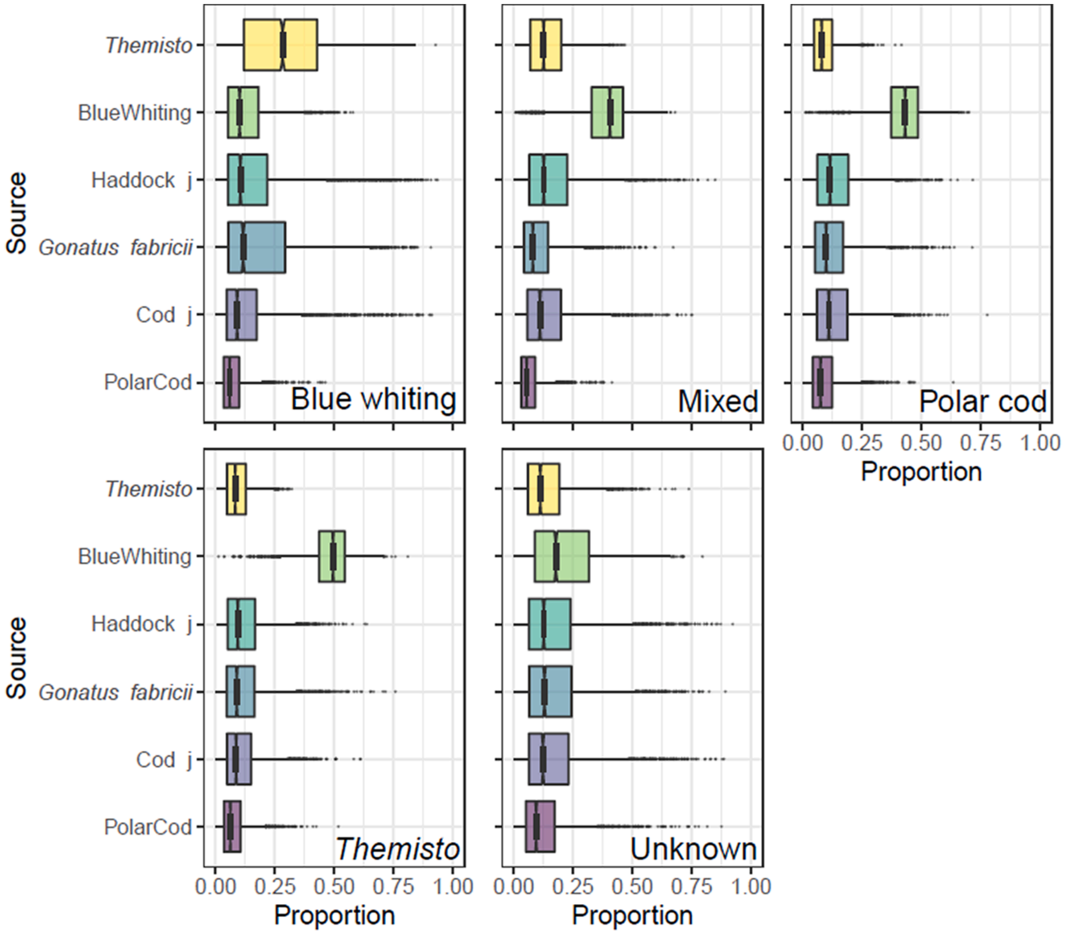

Fig. 5. Proportions of potential prey predicted by simmr stable isotope mixing models (each model run shown as a point) from $\delta^{13}C$ and $\delta^{15}N$ values of prey and seal predators for each dietary group (based on stomach contents).

Table 4
Fatty acids (FAs) in the inner blubber layer and the muscle of 25 harp seals (*Pagophilus groenlandicus*).

	Blubber			Muscle		
	Age = 0 (n = 19)	Age = 1 (n = 3)	Age = 7–19 (n = 4)	Age = 0 (n = 19)	Age = 1 (n = 3)	Age = 7–19 (n = 4)
Weight (kg)	**34 ± 7**	**43 ± 10**	**129 ± 41**	–	–	–
Length (cm)	**114 ± 7**	**127 ± 10**	**175 ± 6**	–	–	–
Relativ amount of FA (mg/ 100 mg sample)	**84.2 ± 4.5**	**86.4 ± 2.9**	**80.2 ± 8.7**	**1.4 ± 0.3**	**1.4 ± 0.2**	**1.4 ± 0.3**
14:0	5.32 ± 0.65^{b}	5.53 ± 0.19^{ab}	6.47 ± 0.37^{a}	2.07 ± 0.43^{c}	2.64 ± 0.04^{b}	3.30 ± 0.24^{a}
Iso 15:0	0.30 ± 0.10	0.24 ± 0.04	0.38 ± 0.05	0.13 ± 0.04^{b}	0.14 ± 0.02^{b}	0.20 ± 0.04^{a}
Antiso 15:0	0.09 ± 0.03	0.07 ± 0.02	0.10 ± 0.02	0.06 ± 0.03	0.07 ± 0.01	0.08 ± 0.05
15:0	0.31 ± 0.05	0.28 ± 0.04	0.36 ± 0.05	0.25 ± 0.05	0.27 ± 0.03	0.26 ± 0.06
Iso 16:0	0.09 ± 0.03	0.06 ± 0.03	0.12 ± 0.03	0.11 ± 0.02	0.11 ± 0.01	0.12 ± 0.05
16:0	9.48 ± 1.60	10.39 ± 1.27	10.53 ± 1.03	15.07 ± 0.91	15.01 ± 0.74	14.44 ± 0.52
Antiso 17:0	0.10 ± 0.03	0.08 ± 0.03	0.09 ± 0.01	0.29 ± 0.06	0.35 ± 0.02	0.25 ± 0.07
17:0	0.12 ± 0.05	0.11 ± 0.05	0.11 ± 0.02	0.25 ± 0.08	0.25 ± 0.05	0.17 ± 0.06
18:0	1.18 ± 0.22	1.18 ± 0.28	1.20 ± 0.14	8.94 ± 2.59	8.71 ± 1.26	7.94 ± 1.06
20:0	0.06 ± 0.02	0.07 ± 0.03	0.08 ± 0.02	0.15 ± 0.03	0.15 ± 0.03	0.14 ± 0.03
∑SFA	**17.29 ± 1.76^{b}**	**18.24 ± 096^{ab}**	**19.69 ± 0.92^{a}**	**27.71 ± 2.85**	**28.05 ± 1.34**	**27.18 ± 1.14**
14:1 (n-5)	0.70 ± 0.22	0.66 ± 0.14	0.43 ± 0.16	0.13 ± 0.10	0.13 ± 0.02	0.19 ± 0.04
16:1 (n-11)	0.14 ± 0.04	0.13 ± 0.03	0.13 ± 0.06	0.29 ± 0.06	0.41 ± 0.05	0.28 ± 0.08
16:1 (n-9)	0.25 ± 0.05	0.23 ± 0.06	0.20 ± 0.02	0.38 ± 0.06^{b}	0.48 ± 0.002^{a}	0.34 ± 0.12^{b}
16:1 (n-7)	12.15 ± 3.30	12.64 ± 3.52	10.94 ± 3.00	5.27 ± 1.67	5.38 ± 0.48	6.62 ± 0.41
16:1 (n-5)	0.28 ± 0.02	0.30 ± 0.02	0.30 ± 0.03	0.31 ± 0.05	0.31 ± 0.02	0.30 ± 0.08
17:1 (n-8)	0.26 ± 0.09	0.24 ± 0.08	0.19 ± 0.02	0.21 ± 0.08	0.20 ± 0.04	0.17 ± 0.04
18:1 (n-11)	1.45 ± 0.39	1.52 ± 0.46	1.38 ± 0.53	0.52 ± 0.20^{b}	0.98 ± 0.18^{a}	0.95 ± 0.30^{a}
18:1 (n-9)	16.13 ± 2.79	15.70 ± 0.86	12.87 ± 2.40	15.93 ± 2.10	15.61 ± 1.01	15.91 ± 1.34
18:1 (n-7)	4.13 ± 1.05	4.43 ± 1.18	3.68 ± 1.37	5.65 ± 1.11	5.13 ± 0.20	4.61 ± 1.22
18:1 (n-5)	0.49 ± 0.10	0.44 ± 0.08	0.51 ± 0.08	0.27 ± 0.06	0.27 ± 0.01	0.33 ± 0.10
20:1 (n-11)	1.22 ± 0.33	1.52 ± 0.27	1.12 ± 0.36	0.65 ± 0.22^{b}	0.83 ± 0.04^{ab}	1.19 ± 0.67^{a}
20:1 (n-9)	7.51 ± 3.59	7.27 ± 1.88	11.16 ± 4.08	2.16 ± 0.74^{b}	2.33 ± 0.37^{b}	4.72 ± 2.54^{a}
20:1 (n-7)	0.33 ± 0.09	0.33 ± 0.03	0.38 ± 0.05	0.12 ± 0.03^{b}	0.11 ± 0.01^{b}	0.20 ± 0.08^{a}
22:1 (n-11)	3.45 ± 1.90^{b}	4.35 ± 1.72^{ab}	6.34 ± 2.52^{a}	0.63 ± 0.22^{b}	0.74 ± 0.14^{b}	2.12 ± 1.41^{a}
22:1 (n-9)	0.54 ± 0.26^{b}	0.62 ± 0.14^{ab}	0.92 ± 0.25^{a}	0.13 ± 0.04^{b}	0.14 ± 0.02^{b}	0.32 ± 0.18^{a}
22:1 (n-7)	0.06 ± 0.03^{b}	0.08 ± 0.02^{ab}	0.12 ± 0.04^{a}	0.06 ± 0.02	0.04 ± 0.01	0.08 ± 0.03
24:1 (n-9)	0.23 ± 0.11	0.19 ± 0.18	0.29 ± 0.09	0.44 ± 0.12	0.37 ± 0.04	0.43 ± 0.06
∑MUFA	**49.32 ± 3.57**	**50.66 ± 1.20**	**50.96 ± 2.15**	**33.16 ± 3.49^{b}**	**33.47 ± 0.31^{ab}**	**38.74 ± 4.99^{a}**
16:4 (n-1)	0.38 ± 0.11	0.44 ± 0.18	0.47 ± 0.15	0.10 ± 0.22	0.01 ± 0.00	0.18 ± 0.35
16:2 (n-4)	0.54 ± 0.17	0.53 ± 0.13	0.53 ± 0.07	0.23 ± 0.10	0.22 ± 0.05	0.31 ± 0.03
18:2 (n-6)	1.82 ± 0.35	1.69 ± 0.53	2.07 ± 0.18	6.52 ± 0.94	6.25 ± 0.92	5.26 ± 1.15
20:2 (n-6)	0.30 ± 0.05	0.30 ± 0.08	0.31 ± 0.02	0.33 ± 0.07^{a}	0.30 ± 0.03^{ab}	0.23 ± 0.11^{b}
20:4 (n-6)	0.33 ± 0.04^{a}	0.33 ± 0.05^{ab}	0.26 ± 0.06^{b}	7.55 ± 1.18^{a}	7.60 ± 0.90^{a}	4.57 ± 2.02^{b}
22:5 (n-6)	0.12 ± 0.03	0.10 ± 0.04	0.10 ± 0.01	0.15 ± 0.05	0.17 ± 0.02	0.13 ± 0.05
18:3 (n-3)	0.97 ± 0.28	0.93 ± 0.22	0.72 ± 0.14	0.41 ± 0.16	0.40 ± 0.10	0.39 ± 0.15
18:4 (n-3)	3.28 ± 0.66	2.99 ± 0.93	3.82 ± 0.70	0.37 ± 0.23^{b}	0.35 ± 0.20^{b}	1.24 ± 0.64^{a}
20:3 (n-3)	0.10 ± 0.04	0.11 ± 0.03	0.07 ± 0.01	0.15 ± 0.10	0.10 ± 0.03	0.16 ± 0.11
20:4 (n-3)	0.73 ± 0.20	0.67 ± 0.15	0.78 ± 0.17	0.25 ± 0.08	0.24 ± 0.05	0.36 ± 0.17
20:5 (n-3)	7.63 ± 2.02	8.81 ± 3.75	6.57 ± 1.94	13.18 ± 1.95	13.17 ± 0.91	11.50 ± 2.44
21:5 (n-3)	0.51 ± 0.05	0.49 ± 0.01	0.47 ± 0.04	0.09 ± 0.05^{b}	0.16 ± 0.04^{a}	0.21 ± 0.07^{a}
22:5 (n-3)	4.64 ± 0.98	3.96 ± 1.05	3.52 ± 0.83	1.65 ± 0.46	1.56 ± 0.14	2.08 ± 0.18
22:6 (n-3)	12.02 ± 2.93	9.75 ± 3.68	9.65 ± 1.33	8.15 ± 2.86	7.95 ± 0.48	7.46 ± 2.17
∑PUFA	**33.38 ± 3.34**	**31.10 ± 2.12**	**29.35 ± 1.87**	**39.13 ± 3.85**	**38.49 ± 1.58**	**34.08 ± 5.65**
∑PUFA (n-6)	**2.57 ± 0.40**	**2.42 ± 0.68**	**2.74 ± 0.24**	**14.56 ± 1.98^{a}**	**14.32 ± 1.82^{a}**	**10.20 ± 2.48^{b}**
∑PUFA (n-3)	**29.89 ± 3.41**	**27.71 ± 1.80**	**25.61 ± 1.69**	**24.25 ± 3.59**	**23.93 ± 0.26**	**23.39 ± 4.18**

Note: Data are mean relative amounts (% of sum ± SD). SFA = saturated FA; MUFA = monounsaturated FA; PUFA = polyunsaturated FA. The letters indicate significant differences between the three groups (ANOVA followed by pairwise comparisons for Group (Tukey (HSD) p-values < 0.05).

FA profiles using correspondence analysis (CA) in Fig. S1 (Supplementary material I), no clear clustering with ages between the FAs in the blubber were found. The CA clustering showed the highest similarity in FA profiles between seal blubber and the polar cod but there were clear differences in FA composition between the blubber and the four prey items. This implies high metabolic modification of the FAs from the diet during the storage process into the blubber. The seals blubber have high levels of the two short chain MUFAs 16:1 (n-7) and 18:1 (n-9) which are synthetized by Δ9-desaturse from 16:0 and 18:0. Likewise, the levels of 22:5 (n-3) were much higher in the seal blubber that in any of the prey, indicating high elongation activity on 20:5 (n-3).

As expected, seal blubber and muscle samples showed large differences in FA profiles (Table 4). The blubber is very lipid rich (the FAs contribute with 80–86% of the wet weight) and totally dominated by the storage lipids, triacylglycerides (TAG), while the muscles are lean (1.4% FAs relative to wet weight) and contain mainly membrane phospholipids (PL). The PL have higher relative levels of the saturated FAs (SFA) and the (n-6) PUFAs, but lower levels of MUFAs and (n-3) PUFAs compared with the TAGs in the blubber (Table S2, Fig. S2 in Supplementary material I).

3.5. *Prey abundance*

Possible prey identified in the water column included the fish species polar cod, capelin, redfish *Sebastes* spp, Atlantic cod, and blue whiting,

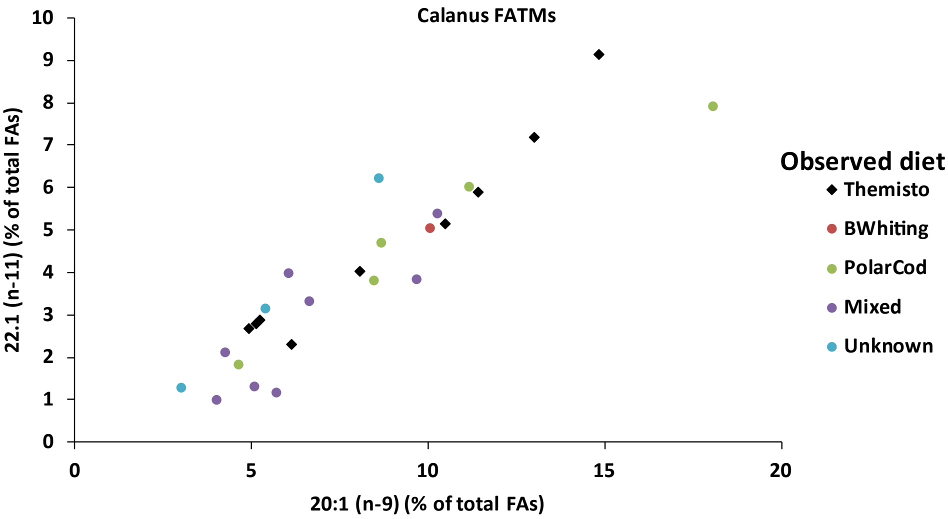

Fig. 6. Relationship in the seal blubber lipids between *Calanus* copepods-Fatty Acids Tropic Markers (FATMs); the MUFAs 20:1 (n-9) and 22:1 (n-11). The samples are marked with the diet observation from the stomach analysis.

0-group fish of various species, and krill/amphipods (Table 5). Average acoustic backscattered energy (NASC) from the fish species polar cod, capelin, Atlantic cod, and blue whiting was generally low, with average NASC in the ranges ~$0.4\cdot10^{-3}$–1.53 m^2nmi^{-2} above 200 m and $0.7\cdot10^{-1}$–34.7 m^2nmi^{-2} below 200 m depth (Table 5). There was, however, considerable variation, with coefficients of variation (CV) from about 200–2000, showing that the distributions of fish were highly patchy within the surveyed area. These average NASC correspond to from about 5 (blue whiting) to about 10 600 (polar cod) individuals per square nautical mile and from about 16 tons (capelin) to 6200 tons (polar cod) of fish in the total surveyed area above 200 m, but considerably more below 200 m depth (Table 6). Neither redfish, mesopelagic fish or 0-group fish were found in the stomachs of seals, although for instance 0-group fish was the most abundant group found in the area (Table 5). Only those species or groups found in seal stomachs were converted from NASCs to abundance and biomass (Table 6), and their geographical distribution shown (Figs. 7–11).

The geographical distributions of relevant prey shown in Figs. 7–11 clearly demonstrate the high patchiness in the acoustic observations (Table 5), and the variation is seen both on a local scale and a larger geographic scale. Capelin (Fig. 8) was almost absent in the area, apart from a limited concentration north of the Hinlopen Strait. Atlantic cod (Fig. 9) was found distributed over larger areas, but mainly below 200 m depth. Polar cod (Fig. 10) was also found in most of the area, but in low concentrations (NASC mainly below 10) and mainly deeper than 200 m. Blue whiting (Fig. 11) was confined to the areas outside the continental shelf with dense concentration below 200 m.

The lowest NASCs from the krill-amphipod category in the upper 100 m was observed in the south-western part of the surveyed area, generally increasing towards the north and east (Fig. 7A). The highest NASCs from the krill-amphipod category along the cruise track were observed deeper than 100 m depth, and mostly east of 15°E, including in the Hinlopen Strait (Fig. 7B). In both depth strata there were clearly indications of patchy distributed backscattering of krill and amphipods which can also be clearly observed from Figs. S2 and S3 in Supplementary material II. The relative abundances of krill and amphipods in

Table 5
Prey abundance: Average water column integrated s_A, Nautical Area Scattering Coefficient in units of (m^2 nmi^{-2}) and associated statistics at 38 kHz (fish) and 120 kHz (krill/amphipods) north of 79°N. A) Above 200 m depth. B) Below 200 m depth. $^{1)}$ Krill and amphipods to 300 m depth. var: variance, std: standard deviation, STE: standard error, CV: Coefficient of variation (%); N = Number of 1-nmi units sailed.

A. Species/group ABOVE 200 m	s_A_mean	s_A_max	var	std	ste	cv	n
0-group fish	91.316	3948.429	66854.469	258.562	7.705	283.152	1126
Plankton	0.003	1.084	0.002	0.043	0.001	1381.433	1126
Polar cod	1.191	120.815	47.590	6.899	0.206	579.129	1126
Capelin	0.000	0.270	0.000	0.009	0.000	2050.865	1126
Redfish	0.012	1.339	0.006	0.080	0.002	694.606	1126
Atlantic Cod	1.531	443.156	218.074	14.767	0.440	964.542	1126
Blue whiting	0.015	2.094	0.013	0.114	0.003	782.729	1126
Mesopelagic fish	0.041	8.331	0.152	0.389	0.012	939.612	1126
Krill/Amphipods ≤100 m	18.464	110.650	327.357	18.093	0.526	97.992	1184
Krill/Amphipods >100 m and ≤200 m	8.808	169.872	273.026	16.524	0.480	187.588	1184
Krill/Amphipods ≤200 m	27.272	197.013	764.121	27.643	0.803	101.359	1184
B. Species/group BELOW 200 m	s_A_mean	s_A_max	var	std	ste	cv	n
0-group fish	0.376	81.234	17.027	4.126	0.123	1097.589	1126
Plankton	0.000	0.025	0.000	0.001	0.000	3355.592	1126
Polar cod	13.561	571.507	1880.166	43.361	1.292	319.750	1126
Capelin	0.071	19.041	1.141	1.068	0.032	1511.281	1126
Redfish	0.402	15.716	1.776	1.333	0.040	331.683	1126
Atlantic Cod	34.715	685.689	6212.054	78.817	2.349	227.042	1126
Blue whiting	0.557	16.480	3.536	1.880	0.056	337.394	1126
Mesopelagic fish	0.439	25.324	3.737	1.933	0.058	439.915	1126
Krill/Amphipods >200 m $^{1)}$	43.425	232.859	990.568	31.473	0.915	72.477	1184

Table 6

Prey abundance: Calculated density, abundance (# = numbers) and total biomass (in tons) of the most relevant fish and crustacean prey species for the harp seals. Calculations, based on results from acoustic surveys (see Table 5), were made for depth layers above and below 200 m depth for the fish species, and above 100 m, between 100 and 300 m for the crustaceans. Std = Standard deviation. The abundance and biomass estimates for cod are within an area of 4340 nmi^2, while the estimates for the other acoustic scatterers are within an area of 12,878 nmi^2, see text for explanation.

Species/group	Depth layer	Density [#/nmi^2]	Abundance [#]	Total biomass (t)*	std (t)
Polar cod	Above 200 m	10 595	136 439 764	1 064	6 163
Polar cod	Below 200 m	120 617	1 553 258 933	12 115	38,739
Capelin	Above 200 m	7	94 647	1	16
Capelin	Below 200 m	1 237	15 930 650	129	1 943
Atlantic Cod	Above 200 m	254	1 101 695	2115	20,403
Atlantic Cod	Below 200 m	5 756	24 979 994	47,962	108,893
Blue whiting	Above 200 m	5	69 230	9	70
Blue whiting	Below 200 m	205	2 648 818	344	1 161
Species/group	**Depth layer**	**g/m2**	**std (g/m2)**	**Total biomass (t)***	**std (t)**
Hyperiid amphipods	Above 100 m	7.6248	7.4717	336 785	330 022
Euphausiids	Between 100 and 200 m	1.6920	3.1741	74 736	140 197
Euphausiids	Below 200 m	8.3417	6.0458	368 450	267 041

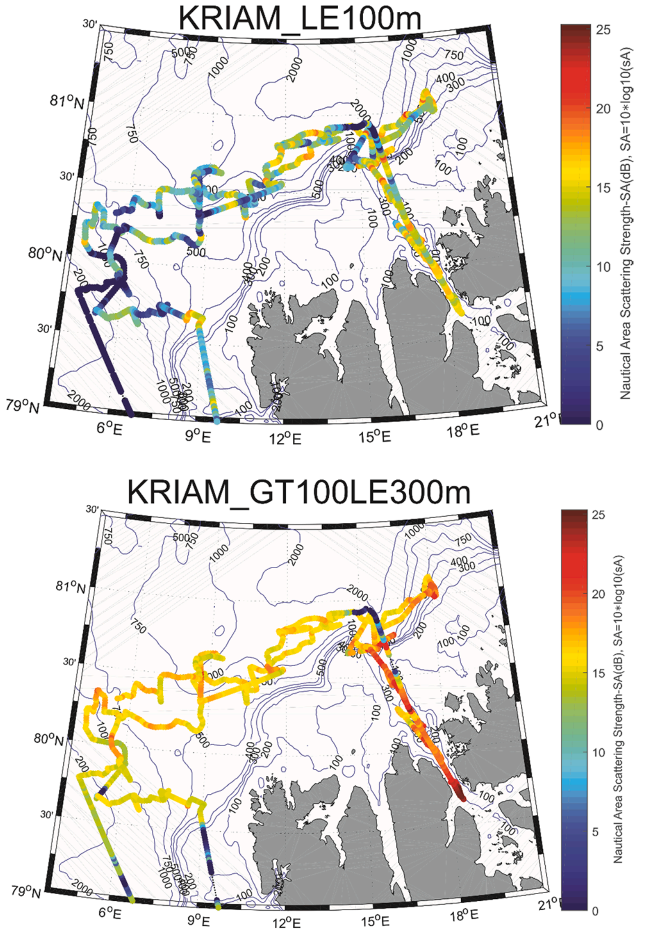

Fig. 7. Acoustic registrations per 1 nmi scrutinized as krill and amphipods along cruise tracks during September 2016 with RV Helmer Hanssen west and north of Svalbard. Upper panel: Integrated values of NASC (m^2·nmi^{-2}) at 120 kHz between ~15 and 100 m depth. Lower panel: Integrated values of NASC (m^2·nmi^{-2}) at 120 kHz between 100 and 300 m depth. Data presented as nautical area scattering strength [S_A, dB re 1 m^2 · nmi^{-2}), S_A = 10log10(s_A)]. Black stippled lines represent along-track locations where integrated NASCs for the given category were originally 0.0. However, a small value of 0.0001 was added to all data in the linear domain so that log-transformation and visualization could be undertaken.

the region from trawl catches taken during the survey, show the importance of various krill species including the Arctic hyperiid *T. libellula* (von Weissenberg, 2018).

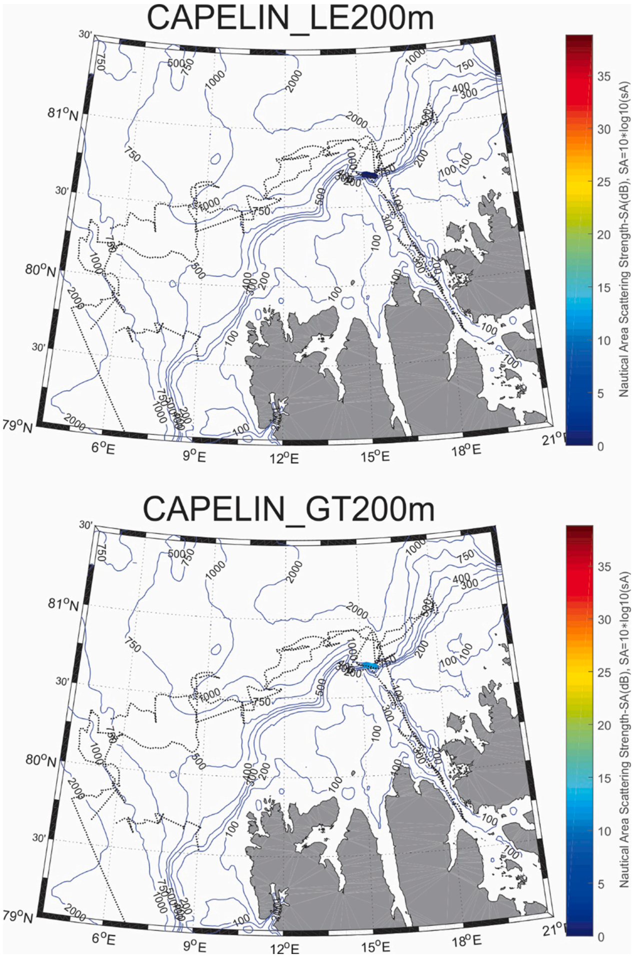

Fig. 8. Acoustic registrations per 1 nmi scrutinized as capelin along cruise tracks during September 2016 with RV Helmer Hanssen west and north of Svalbard. Upper panel: Integrated values of NASC (m^2·nmi^{-2}) at 38 kHz between ~15 and 200 m depth. Lower panel: Integrated values of NASC (m^2·nmi^{-2}) at 38 kHz between 200 m and bottom. Data presented as nautical area scattering strength [S_A, dB re 1 m^2 · nmi^{-2}), S_A = 10log10(s_A)]. Black stippled lines represent along-track locations where integrated NASCs for the given category were originally 0.0. However, a small value of 0.0001 was added to all data in the linear domain so that log-transformation and visualization could be undertaken.

The average NASCs from the category krill-amphipods in the upper 100 m was ~18.46 m^2 nmi^{-2} north of 79°N (Table 4). However, average

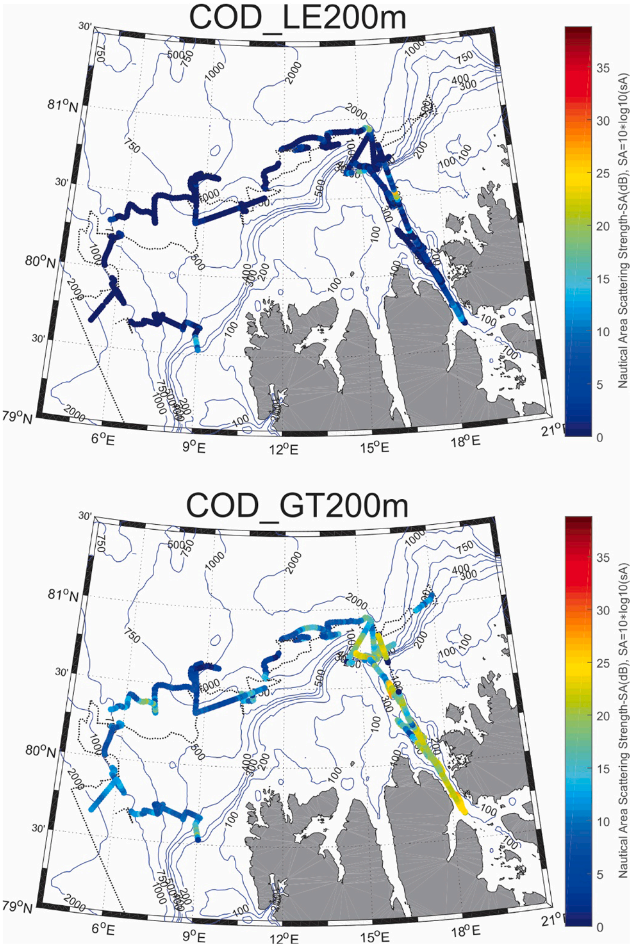

Fig. 9. Acoustic registrations per 1 nmi scrutinized as Atlantic cod along cruise tracks during September 2016 with RV Helmer Hanssen west and north of Svalbard. Upper panel: Integrated values of NASC ($m^2 \cdot nmi^{-2}$) at 38 kHz between ~15 and 200 m depth. Lower panel: Integrated values of NASC ($m^2 \cdot nmi^{-2}$) at 38 kHz between 200 m and bottom. Data presented as nautical area scattering strength [S_A, dB re 1 $m^2 \cdot nmi^{-2}$), $S_A = 10\log10(s_A)$]. Black stippled lines represent along-track locations where integrated NASCs for the given category were originally 0.0. However, a small value of 0.0001 was added to all data in the linear domain so that log-transformation and visualization could be undertaken.

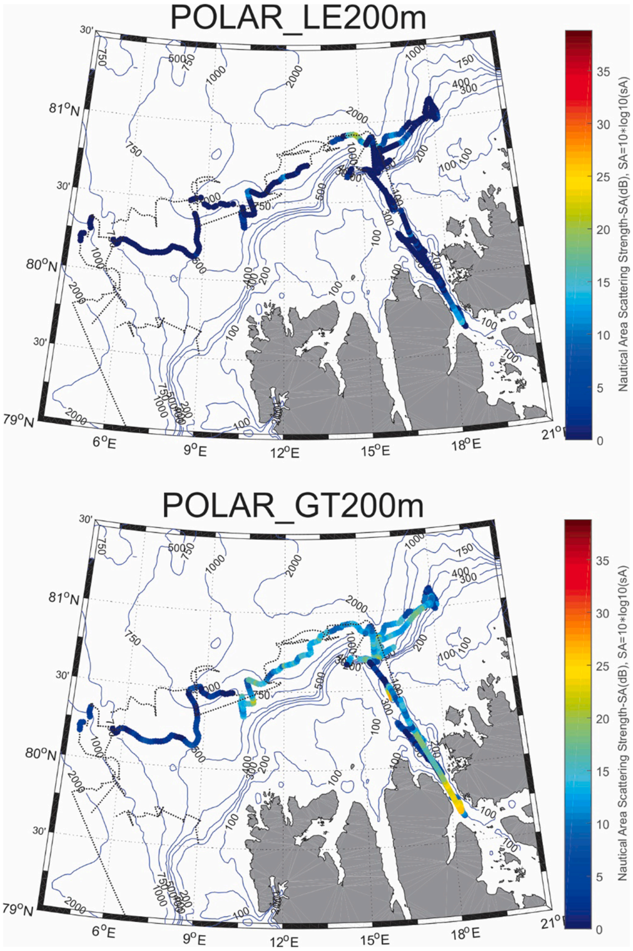

Fig. 10. Acoustic registrations per 1 nmi scrutinized as polar cod along cruise tracks during September 2016 with RV Helmer Hanssen west and north of Svalbard. Upper panel: Integrated values of NASC ($m^2 \cdot nmi^{-2}$) at 38 kHz between ~15 and 200 m depth. Lower panel: Integrated values of NASC ($m^2 \cdot nmi^{-2}$) at 38 kHz between 200 m and bottom. Data presented as nautical area scattering strength [S_A, dB re 1 $m^2 \cdot nmi^{-2}$), $S_A = 10\log10(s_A)$]. Black stippled lines represent along-track locations where integrated NASCs for the given category were originally 0.0. However, a small value of 0.0001 was added to all data in the linear domain so that log-transformation and visualization could be undertaken.

NASCs were clearly lower, ~8.81 m^2 nmi^{-2} for the depth range 100–200 m. For the depth stratum deeper than 200 m it is also clear that the average NASCs were considerably higher, with a mean NASC of 43.43 ± 31.47 m^2 nmi^{-2}. These differences support the understanding that there was a clearly layered distribution of scatterers in the investigated region. The coefficient of variation (CV) is between ~72 and 101% for the krill-amphipod category in the depth strata considered in Table 5, indicating definite variability over the area for this composite category, but lower than for the other scrutinized species categories.

The hyperiid amphipod *T. libellula* generally prefer the cold Arctic surface waters. Hence, the krill-amphipod acoustic backscatter in the upper 100 m (Table 5) have been assigned entirely to be hyperiid amphipods amounting to a total biomass estimated to ~336 785 tons (cf. Table 6). In the depth range 100–200 m, where the krill-amphipod NASCs were not prominent, they were assigned entirely to krill (see Supplementary material II, Fig. S1) and amounted to a biomass of 74 736 tons (Table 6). The acoustic backscatter of crustacean origin were seemingly larger below 200 m depth, which on the shelf could be seen as scattered schools below 200 m and in denser layers close to the bottom at around 300 m (Fig. S2A–B in Supplementary material II), the latter registrations in the outskirts of the detection range of 120 kHz echosounder. These layers were also assigned to krill and their total biomass in the depth range 100–300 m, was estimated to 443 186 tons (Table 6). The difference in vertical distribution of the dominant hyperiid amphipod *T. libellula* and what was more certainly krill (cf. Fig. S2A–B in Supplementary material II), was also supported by results from trawl hauls. In a Macroplankton-trawl V-haul at station 98 (Seriesnr. 2026) north of the Hinlopen Strait to about 223 m depth on the slope to the Arctic Ocean, and a bottom depth of 949 m, the amphipod *T. libellula* was the dominant elongate crustacean and about 40 times more abundant in the catch than the sum of the two krill species *M. norvegica* and *T. inermis*. Similar distribution patterns were found also on the eastern side of Svalbard in a Norwegian-Russian ecosystem survey in 2019 (Supplementary material II, Fig. S4) where one trawl catch in the upper 0–60 m at station 692, gave a total catch of 14.725 kg of the amphipod *T. libellula*, but no krill.

3.6. *Prey preferences*

The lower and upper 2.5% percentiles of the confidence intervals are given in parentheses. Harp seal prey preference varied substantially

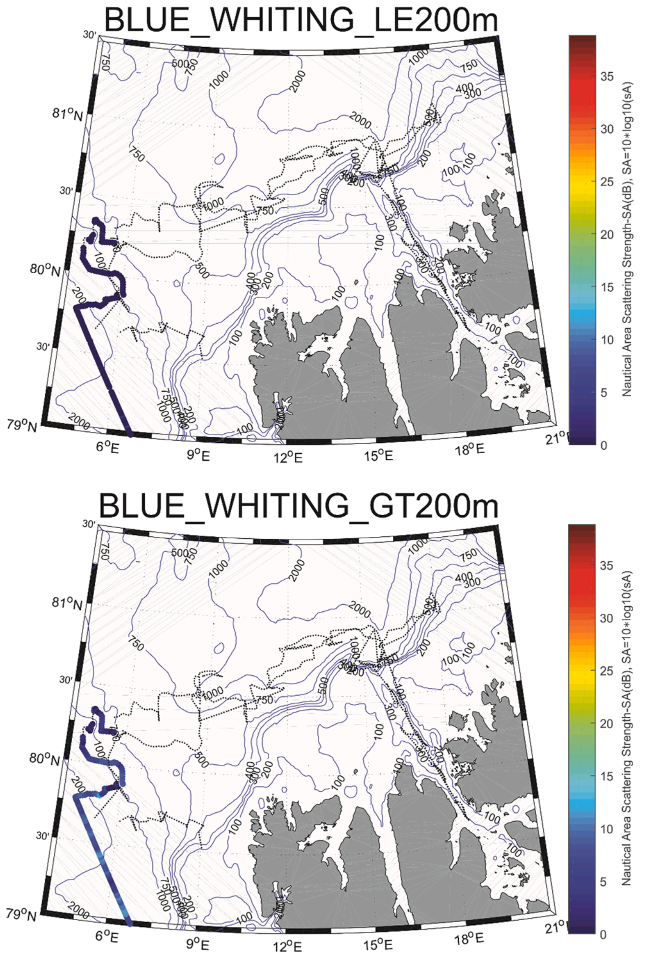

Fig. 11. Acoustic registrations per 1 nmi scrutinized as blue whiting along cruise tracks during September 2016 with RV Helmer Hanssen west and north of Svalbard. Upper panel: Integrated values of NASC ($m^2 \cdot nmi^{-2}$) at 38 kHz between ~ 15 and 200 m depth. Lower panel: Integrated values of NASC ($m^2 \cdot nmi^{-2}$) at 38 kHz between 200 m and bottom. Data presented as nautical area scattering strength [S_A, dB re 1 $m^2 \cdot nmi^{-2}$), $S_A = 10\log10(s_A)$]. Black stippled lines represent along-track locations where integrated NASCs for the given category were originally 0.0. However, a small value of 0.0001 was added to all data in the linear domain so that log-transformation and visualization could be undertaken.

among prey species and less between depth strata (Fig. 12). Polar cod was the overall most preferred prey ($CI_{<200m}$ = [0.14, 0.34], $CI_{0\text{-bottom}}$ = [0.13, 0.33]) followed by amphipods ($CI_{<200m}$ = [0.20, 0.44], $CI_{0\text{-bottom}}$ = [−0.22, 0.02]) and blue whiting ($CI_{<200m} = CI_{0\text{-bottom}}$ = [0.01, 0.06]). Despite amphipods completely dominating the diet (72,6%) and resource composition ($B_{<200m}$ = 81% and $B_{0\text{-bottom}}$ = 40%), seals showed no clear preference with respect to this species in the upper 200 m ($CI_{<200m}$ = [−0.22, 02]), but there was a positive preference when considering the entire water column ($CI_{0\text{-bottom}}$ = [−0.31, −0.07]),. Krill was completely absent from the seal stomach samples, despite being the second most abundant prey in the upper 200 m (18%) and, by far the most abundant prey below 200 m (86%). This led to seals showing random feeding with respect to krill in the upper 200 m ($CI_{<200m}$ = [−0.18, −0.18]) and negative preference when considering the entire water column ($CI_{0\text{-bottom}}$ = [−0.53, −0.53]). There was random preference for capelin in both depth strata whereas Atlantic cod, dominated by large individuals (>30 cm), were exploited randomly in the upper 200 m but when considering the entire water column, seals displayed negative preference for this species. Finally, seals showed positive preference for blue whiting in both depth strata ($CI_{<200m} = CI_{0\text{-bottom}}$ = [0.01, 0.05]).

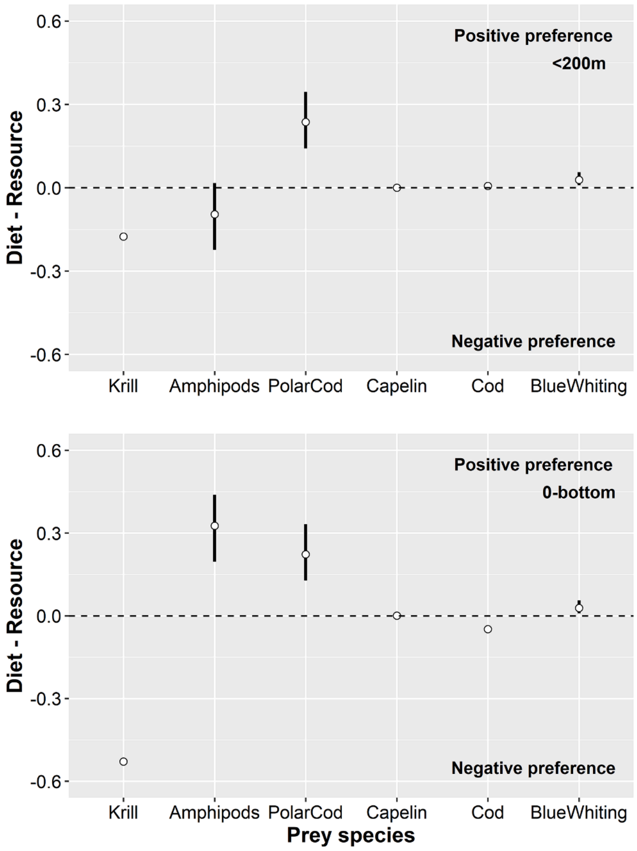

Fig. 12. Harp seal prey preference north of Svalbard September 2016. The preference was calculated in the upper 200 m (upper panel) and in the entire water column (lower panel). The error bars (95% CI), determined from 1,000 bootstrap replicates of the diet and resource data (see text for explanation), is plotted. The dotted line, when the difference in prey composition in the diet equals that in the ocean, indicate random feeding (no preference). Positive and negative preference occur if the error bar is above and below this line, respectively.

4. Discussion

4.1. Body condition

Despite our inability to directly compare the body condition of seals of all ages/sizes between the two sampling periods of 1990–1991 and 2016, the model residuals were significantly lower in 2016 compared to in the earlier sampling period. This was also supported by the thinner blubber layer among small seals in 2016 compared to the earlier sample. This suggests that overall body condition of seals may have declined over the past 25 years. However, this decline may not have been continuous throughout the entire period. Øigård et al. (2013) presented data on the condition of harp seals from commercial and scientific catches between 1992 and 2010, showing that body condition (blubber thickness) in April-May increased gradually from ~40 mm in 1992 to ~50 mm in 2000, before declining to ~30 mm in 2006 and declining further to ~20 mm in 2011. Blubber thickness in the 2016 sample for small seals was comparable to that reported in Øigård et al. (2013). It has been suggested that competition for food by the currently large and more northerly distributed Atlantic cod stock may have contributed to the recent body condition decline in harp seals (Bogstad et al., 2015).

4.2. Diet

The pelagic amphipod *T. libellula* and polar cod were the most prominent prey species in terms of biomass for the harp seals in the current autumn study in the Arctic Ocean, as also observed for harp seals on their northern feeding grounds in the Barents Sea during autumn (September) in 1987 (Lydersen et al., 1991), 1990 and 1991 (Nilssen et al., 1995a),. The localisation of the ice edge in the current sampling year (2016) was considerably further to the north than 2–3 decades ago when the seals were abundant and sampled to the east of the Svalbard archipelago where bottom depths varied between 100 m and 350 m (Nilssen et al., 1995a). In those areas the seal diets also included additional items such as prawns (*Pandalus borealis*) and Arctic bottom fishes such as flatfish, sculpins (Cottidae) and snailfishes (Liparidae). A consequence of current ice edge localisation north of Svalbard is that the bottom depth underneath is now 500 m and deeper. Since harp seal diving depths only very seldom exceeds 500 m (Nordøy et al., 2008), this probably explain the absence of any bottom associated prey species, and the presence of Atlantic cod and blue whiting as alternative species in addition to the dominant amphipods and polar cod. Both Atlantic cod and blue whiting are typically boreal fish species that, under current water warming, have expanded their northward distribution (Fossheim et al., 2015; Haug et al., 2017a).

Our observations of prey abundance indicated that the amphipods *T. libellula* were particularly concentrated in the upper 100 m of the water column, while krill was generally found in deeper (100–300 m) layers. During harp seal diet studies in September in 1990 and 1991 in the northern Barents Sea, Nilssen et al. (1995a) also observed that *T. libellula* was the most abundant prey in the upper layers. A satellite telemetry study of harp seals conducted in 1995 and 1996 (Nordøy et al., 2008) showed that harp seal habitat use corresponded quite well with the vertical distribution of amphipods observed during the resource survey in this study; the majority of dives performed by the seals in autumn were in the upper 100 m. Studies of harp seal diet in summer (May–August) in the northern Barents Sea in 1996, 1997 and 2004–2006 concluded that krill was the dominant crustacean prey along with polar cod which was the prominent fish prey species then as now (Lindstrøm et al., 2013). Later in the year (October), however, a shift to a diet dominated by fish (mainly capelin and polar cod) occurred (Nilssen et al., 1995b; Lindstrøm et al., 1998).

It is well known that both polar cod and the pelagic amphipod *T. libellula* are key forage species for birds and mammals in the Arctic marine food chain (Bradstreet and Cross, 1982; Finley et al., 1990; Nilssen et al., 1995a; Hop and Gjøsæter, 2013). The current dietary study concurs with previous findings that these two species still dominate the diet of harp seals when they are on their northern feeding grounds in the northeast Atlantic during early autumn. Similar observations have been made for harp seals in the Greenland Sea (Haug et al., 2004; Enoksen et al., 2017) and in the Arctic parts of the northwest Atlantic (Finley et al., 1990; Ogloff et al., 2019). The polar cod is known to be an important key prey species for the harp seals also at other times of the year (see Lindstrøm et al., 2013). Since the continuing Atlantic Arctic sea ice retreats may be challenging for the existence of polar cod in the Atlantic Arctic Ocean (Huserbråten et al., 2019), harp seals seeking their usual food resources in northern waters may run into problems in the future.

Seemingly, the most abundant potential prey found in the surveyed area, 0-group fish, seemed to be totally neglected as prey by the seals. This is surprising, given that the typical size of the 0-group fish found in this area (mostly consisting of redfish, Atlantic cod, polar cod and capelin) are in the same size range or a bit larger than krill and amphipods, and are mainly found in the upper 50 m of the water column. The behaviour of small fish may of course make them more difficult to capture as compared with crustaceans. Amphipods such as *T. libellula* are probably the most densely packed high energy lipid zooplankton species (e.g., Noyon et al. 2011), forming dense swarms that might be more attractive than fish aggregations. Also, the small fishes presumably contain less energy per gram wet weight than for instance the plankton species. Also, the lack of 0-group fish in the harp seal diet could be due to difficulties in detecting these small fishes in the stomach and intestine content analyses, which were mainly based on recovering and identifying hard parts such as fish otoliths. 0-group fishes have very small otoliths and they can easily be eroded by the stomach acid (see Lindstrøm et al., 2013). This might underestimate possible contribution of this fish group in the seal diet.

4.3. Stable isotopes

In the marine ecosystem, nitrogen and, to some extent, carbon isotope values usually increase with trophic level, while there is usually a stronger increase in carbon isotope values associated with an increase of benthic nutrients (e.g., Woodland and Secor, 2013). The correlation of both $\delta^{15}N$ & $\delta^{13}C$ isotopes with size and age suggest increases in trophic level, and/or offshore or benthic nutrient-fuelled feeding with age/size in the sampled harp seals. According to the mixing models, the oldest and largest seals in the sample group were more likely to feed on greater proportions of blue whiting, a mid-trophic level fish with a more benthic-origin nutrients than other measured prey types (Lassalle et al., 2014). It is possible that these more experienced seals can exploit prey at greater depths than smaller, younger seals. Also, there could be some difference in onshore-offshore foraging (e.g. Lawson et al., 1998) related to age/size, although the small number of seals sampled that were older than one year ($n = 4$) makes it difficult to draw robust conclusions.

Hobson et al. (1996) showed that harp seal muscle tissue turnover time is approximately one month, so the diet is reflective of the month before capture. This longer-term diet, based on stable isotope composition, is reflected relatively well in frequency-based short-term stomach contents composition, being dominated by the amphipod *T. libellula*, although less well in mass-based composition. Interestingly, the squid *G. fabricii,* or prey with similar isotopic composition and therefore feeding ecology, is suggested as an important resource in long-term diet. *G. fabricii* is known as the most abundant squid in northern waters, and the species is previously observed to be consumed by both harp and hooded (*Cystophora cristata*) seals in the Greenland Sea (Haug et al., 2004, 2007; Enoksen et al., 2017). Juvenile squid (mantle length <50 mm) usually lives in shoals in the uppermost 80 m of the water column (Kristensen 1984), but in the current study remains from only a very few juvenile squid were observed in two seal stomachs. In the Barents Sea and Arctic Ocean areas sampled in the present study, carbon and nitrogen isotope compositions in the marine ecosystem tend to increase with trophic position, and from pelagic to benthic nutrient input (Hobson and Welch, 1992; Tamelander et al., 2006; Sokołowski et al., 2014). As such, it is perhaps better to view the results of the mixing models as harp seals showing greatest reliance on highly pelagic, low trophic level (e.g., *Themisto* spp.) and low to mid-trophic level, mostly pelagic prey that have some benthic-origin nutrients (e.g., blue whiting and *G. fabricii*), but feeding less on mid-trophic level, highly pelagic prey fishes, such as juvenile Atlantic cod, juvenile haddock, and, surprisingly, polar cod. It is worth noting that the isotope-based models suggest that blue whiting is the main component of the seals' diet, while in the stomach contents-based analyses the prevalence of blue whiting is much lower. Caution must be noted in the interpretation of these results, however, as they are based on relatively few fish prey source individuals, and recent prey consumption may not be reflected in muscle isotope values. Additionally, prey samples were sourced over a wide area with some baseline isotopic variation (de la Vega et al., 2019), although relatively close to the origin of the seal samples, but foraging areas of these individual seals are unknown. It is therefore not possible to account for baseline changes altering the isotope composition of prey in the interpretation of the mixing models. Finally, in both stomach content and stable isotope analyses in this study, capelin was not included due to lack of availability in both abundance and seal diet, despite being an important prey type for harp seals in other studies (Nilssen et al., 1995a, b; Lindstrøm et al., 1998, 2013; Hammill and Stenson, 2000; Haug et al., 2004). Capelin and *G. fabricii* have relatively similar isotopic composition, however, being low- to mid-trophic level animals with largely pelagic nutrient sources (e.g. Matley et al., 2015). This similarity means that the mixing model predictions of higher levels of squid in the diet than predicted from stomach contents could equally suggest higher levels of capelin than recorded in stomachs. In short, the mixing models suggest that there was likely a greater amount of low to mid-trophic level, largely pelagic to benthopelagic prey in the seals' long-term diet than in the short-term contents of the stomachs.

Our isotope results broadly correspond with those of Lawson and Hobson (2000), who used stable isotopes to study harp seal diet off Newfoundland, where they inferred that the seals were largely eating low trophic level pelagic animals, and the squid *G. fabricii*, although they observed dominance of polar cod in the diet. The harp seal data measured by Ogloff et al. (2019) in the Canadian Arctic and by Hammill et al. (2005) in the St Lawrence River estuary had similar ranges in both carbon and nitrogen isotope values, despite including some benthic fishes (Cottidae, Lipariidae) in the stomach contents. This similarity indicates likely correspondence in both predominant nutrient sources, i.e. largely pelagic crustacea and fishes, and in the range of prey types that were important components of the harp seal diet, and the Hammill et al. (2005) study also suggested great importance of invertebrate prey.

Interestingly, the mean δ^{15}N value of seals in this study was 12.09‰, which was 2.98‰, or approximately one trophic level, lower than the 15.07‰ measured in harp seals sampled in the southern Barents Sea in May 2011 (Haug et al., 2017b), and the mean δ^{13}C values were also lower (−21.07‰ in this study, −19.37‰ in the southern Barents Sea). In the May 2011 study, the most likely seal prey sources were prawns *Pandalus borealis* and small fishes such as capelin, herring, juvenile Atlantic cod and saithe *Pollachius virens*, sculpins and flatfishes (Nilssen et al., 1995b; Lindstrøm et al., 1998), while the prey of seals in this study were approximately a trophic level lower.

There is some indication that seals with greater blubber thickness feed at slightly higher trophic level, and/or on prey with more benthic carbon compositions, e.g. bentho-pelagic feeding fishes. This may be an effect of increasing blubber thickness with size of the seals due to greater prey catchability (predation experience etc.), or due to greater energetic value of higher trophic level and/or more benthic prey leading to greater fat storage capability.

Seals with lower blubber thicknesses tended to have lower carbon isotope values, potentially indicating a higher proportion of dietary lipids used in protein synthesis (Newsome et al., 2014; McMahon et al., 2015).

4.4. Fatty acids (FA)

FA analysis has been used in several diet studies of harp seals (Ackman et al., 1971; Engelhardt and Walker, 1974; Jangaard and Ke, 1968; Falk-Petersen et al., 2004, 2009; Brunborg et al., 2006; Tucker et al., 2009a,b, Grahl-Nielsen et al., 2011; Haug et al., 2017b). As also observed in our studies of gastro-intestinal contents, the FA analyses of blubber and muscle indicated no clear variations between the different age classes of seals. However, a small increase in the relative levels of Calanus FATMs was observed, suggesting that the old seals might be eating more amphipods than young seals. The amphipod *T. libellula,* is a high energy prey, rich in lipids and contain large amounts of wax ester, obtained from feeding on *Calanus finmarchicus* (Auel et al., 2002; Kraft et al., 2015). Also, they are often found in dense swarms (Havermans et al., 2019) and therefore represent a very attractive high energy prey for the harp seals.

Both previous (Lydersen et al., 1991; Nilssen et al., 1995a) and the current study of harp seal summer feeding along the ice edge north in the Barents Sea show that both sub-adult and adult seals were strongly associated with pelagic crustaceans, particularly the amphipod *T. libellula.* When feeding further south in the Barents Sea during late winter and spring, however, the seals were targeting various fish species to a much larger degree (Nilssen et al., 1995b; Lindstrøm et al., 1998). For this reason, we have compared the FA analysis based on the northern September sampling in 2016 (this study) and the southern May sampling in 2011 (Haug et al., 2017b) (Figs. S3 and S4, Supplementary material I). Even though there was higher internal variation in each dataset (CA dimension 1, explaining 57%) than between them, the CA dimension 2 (explaining 16% of the total variance) separate the different sampling location/years into two clusters. The seals in the north (2016) had especially higher relative levels (% of total FAs) of 22:1 (n-11) (*Calanus* FATMs), 3.6 ± 1.9 (0–1 years) and 6.3 ± 2.5 (>7 years) compared with the southern seals (2011); 2.3 ± 1.1 (1–7 years) and 4.1 ± 1.1 (>7 years). The FATM analysis therefore confirm previous and current instant short-term observations based on gastro-intestinal contents that harp seals feed much more on pelagic crustaceans, particularly amphipods, at their northern feeding grounds than in the south. Higher consumption of amphipods was also observed in harp seals from East Greenland when compared with seals further south around Newfoundland (Tucker et al., 2009a). The comparison of the FA profiles between the 2011 (May) and 2016 (September) seal samples also reveal a general seasonal change in the food web, where the seals caught in May had higher levels of diatom related FATM (16:1 (n-7) and 16 PUFA), while the seals from September were higher in flagellates FATM (18:4 (n-3) and 22:6 (n-3)). This agrees with seasonal changes in primary production in the Arctic from abundance of diatoms in spring and flagellates in fall and winter (Geoffroy et al., 2019).

It is well known that harp seals, like many other marine mammals, have a very active lipid metabolism (Δ9-desaturase and elongation activity) in the blubber, which induces a strong stratification in the FA profile from the inner to the other blubber (Strandberg et al., 2008; Grahl-Nielsen et al., 2011). In the most active inner blubber samples it is also clear that the seals modify the FA composition, both by Δ9-desaturase; 16:0 to 16:1 (n-7) and 18:0 to 18:1 (n-9) and elongation activity; 20:5 (n-3) to 22:5 (n-3). It has been suggested that the appearance of new dietary FAs is probably evident within 1 to 2 weeks of a switch in diet, and it is important to consider endogenous metabolism when using FA profiling in diet studies (Kirsch et al., 2000; Grahl-Nielsen et al., 2011).

The seal muscles are very lean, and the FA profiles differs strongly from the blubber by having high levels of n-6 PUFAs (10–14% of the total FAs in muscle and 2.4–2.7% in blubber). This is in strong agreement with the few others reports about muscle samples in addition to blubber (Engelhardt and Walker, 1974; Brunborg et al., 2006).

4.5. Prey abundance and distribution

Amphipods *T. libellula* were by far the most abundant prey observed in the resource survey in the present study, followed by krill (primarily *T. inermis*), Atlantic cod and polar cod. In general, the amphipods were confined to the depth layers above 200 m while krill and the mentioned fish species were most abundant in the deeper layers.

According to the acoustic registration the amount of fish in the feeding area was rather low and patchy, with densities from about 200–130 000 individuals nmi^{-2} for the relevant harp seal prey species. Consequently, the average densities are not necessarily the most interesting parameter, since the seals probably seek for higher concentrations. For instance, the capelin was mainly encountered in the Hinlopen Strait area, east of where the seals were sampled, while Atlantic cod were mainly found at the shelf and partly pelagically just off the shelf edge. Taking account of the extremely small sampling volume of the echosounder, in particular in the upper water column, compared to the water volume searched by the seals when diving, and the far from optimal survey strategy (if estimates of stock sizes of fish was aimed at) when the ship was moving along the ice edge, the absence of a particular prey in the acoustic data may not necessarily be representative for the seal feeding area as such. In the upper 200 m the maximum values of NASC (Table 5) is typically from around 25 (macroplankton) to 650 (capelin) times higher than the average. Knowing that the acoustic data are scaled to 1 nautical mile before entering into these calculations, the density of fish seen on a scale more relevant for seal feeding will be much higher, in particular for schooling species like capelin, polar cod and blue whiting. In addition, the patchiness in the vertical scale adds to that in the horizontal scale, making average density estimates even less relevant for feeding studies.

The shelf and slope region on the west coast of Svalbard is considerably influenced by Atlantic water that flows northwards along the Svalbard shelf, turning eastward around 80°N, one branch following the rim of the Yermack plateau and another closer to the Svalbard shelf break (e.g., Knutsen et al., 2017; Pérez-Hernández et al., 2017; Menze et al., 2020). The large hyperiid amphipod *T. libellula* is a truly Arctic cold-water species (e.g., Dale et al., 2006; Noyon et al., 2011; Schröter et al., 2019) that are hardly traced in the comparatively warmer northwards flowing Atlantic water. It's considerably smaller congener, *T. abyssorum,* is however regular inhabitant of Atlantic water. In the region north-west and north of Svalbard the Atlantic water subducts below the colder fresher water of Arctic origin (Pérez-Hernández et al., 2017), which means that the two congeners might be caught simultaneously in a net or trawl that pass through both types of water masses, although *T. libellula* is much more abundant in the regions influenced by cold Arctic water (Dalpadado et al., 2001; Dalpadado, 2002). *T. libellula* is a significantly larger species than *T. abyssorum,* thus easier to detect by scientific echosounders at the acoustic frequencies normally used in research vessels (see Supplementary material II). From investigations in May and July in the marginal ice zone east of Svalbard, *T. libellula* was considered "a relatively epipelagic species (<50 m)" (see Dalpadado et al., 2008a). This statement was clearly supported by the vertical distribution of *T. libellula* which was highly associated with Polar Front waters and Arctic Water masses at depths above ~150 m in September 1996 (see Dalpadado et al., 2001). These observations are in accordance with observations from trawl catches and acoustic registrations, both in the present and other (cf. Knutsen et al., 2017) investigations north and east of Svalbard (cf. Figs. S2–S4 in Supplementary material II).

Regarding krill, it is particularly *T. inermis* that is the important species abundant in the shelf and slope waters around Spitzbergen (see Dalpadado et al., 2008b; Knutsen et al., 2017). Dalpadado et al. (2008a) suggest that krill in the Marginal Ice Zone (MIZ) east of Spitzbergen prefer the warmer deep waters, thus avoiding the colder Arctic waters in the upper layer. This was supported by a statement in Dalpadado et al. (2008b), that krill in the period May to September seem to be restricted mostly to Atlantic waters in the deeper layers (>100 m), irrespective of time of the day. However, both studies mentioned above were undertaken during the midnight sun period, where high ambient light conditions may have restricted vertical migration (cf. Gjøsæter et al., 2017). Many authors have over the years used acoustic data (from echosounders and ADCPs) to examine the vertical migration pattern of macroplankton and other organisms in the near Svalbard waters at various times of the year (Cottier et al., 2006; Falk-Petersen et al., 2008; Berge et al 2009; Berge et al., 2014, 2015; Last et al., 2016). It is however difficult, based on these, sometimes limited observations, to derive more generic patterns on the vertical distribution on the macro-zooplankters in the shelf, slope and deeper waters where the harps seal are foraging.

The current investigations were conducted during the period 2–16 September, immediately after the termination of the midnight sun period (~1 September at about 80°30′N), where the daylength and sunheight rapidly decreases towards the onset of the polar night around 22 October. The ambient *in situ* light conditions are considered a key factor driving the diurnal vertical migration of many types of organisms (Norheim et al., 2016) and krill in particular (Simmard et al., 1986; Kaartvedt, 2010), and is certainly a factor to consider in addition to preference for slightly warmer waters. Thus, krill might exhibit increased vertical migration as a response to a changing light climate, migrating to the surface layers for brief periods of time during darkness hours. However, there were few if any signs of such behaviour affecting the epipelagic domain during our investigations in the same area and nearly the same period in 2015 (17 August–7 September, cf. Gjøsæter et al., 2017). According to Russian studies the krill abundance in the Barents Sea is monitored during the autumn–winter period (October–March) by a macroplankton net attached to the bottom trawl. This period was chosen because "most of the species have reduced vertical migration and are found in more confined habitats at depths than what is true for the spring and summer period" (Zhukova et al., 2009). The vertical separation of amphipods and krill might not follow the described pattern during this study over the period of these investigations, but own data and additional studies as mentioned above, suggest that amphipods are confined to the near surface region while krill most of the time stay somewhat deeper in the water column. A separation of the two groups at about 100 m depth, thus seems reasonable. Telemetric studies have shown that there is a major variation in diving behaviour of harp seals on a seasonal time scale (Folkow et al., 2004; Nordøy et al., 2008). The seals tend to perform shallower dives during summer and autumn than during winter, and this may explain why they seemingly feed on amphipods in the upper layers rather than on krill in the deeper layers.

4.6. Prey preferences

From an optimal foraging point of view the seals should select prey which maximize their net energy intake rate (Charnov, 1976), which in our study would appear to be amphipods because they were the most abundant prey (ca. 81%) in the upper 200 m followed by krill, cod and polar cod. Instead, the seals displayed a positive preference for polar cod, i.e. the seals had been consuming polar cod in greater proportions than observed in the environment, and no and negative preference for amphipods and krill, respectively. The latter implies that amphipods and krill had been consumed in less proportions than observed in the sea. These results are partly in line with two previous harp seal preference studies (Lindstrøm et al., 1998, 2013) where krill was negatively preferred by the seals during summer and autumn whereas amphipods and polar cod appeared to be randomly exploited by the seals during autumn but negatively preferred (amphipods) or positively preferred (polar cod) during summer. The negative preference for Atlantic cod is most likely a consequence of not splitting the species into groups of small (<=30 cm) and large (>30 cm) individuals. Given that small Atlantic cod only comprised ca. 0.2% of cod biomass (assuming that the trawl catches of cod are representative for the true length distribution in the sea) and all the Atlantic cod consumed by the harp seals in this study (1.2%) was less than 30 cm, the harp seals appears to have a weak positive preference for small Atlantic cod.

Harp seals, like other marine mammals, are probably not 'ideal' foragers but appear to settle for a 'sufficiently profitable' rather than 'globally optimal' foraging strategy (e.g. Matthiopoulos et al., 2008) because they are not able to perfectly track spatio-temporal changes in prey availability, especially over wide areas. Although harp seals seek to exploit areas of high prey biomass, the fundamental exploitable unit of prey to them is probably more related to some function of patch size and density rather than the average number of individual preys in an area (e.g., Murphy et al., 1988; Piatt and Methven, 1992). The fact that harp seals did not find amphipods as attractive as polar cod, given the abundance, may be explained by differences in the density of prey at small spatial scales (patchiness). If we consider the standard deviation of the prey density estimates (Table 6) as a measure of patchiness, then polar cod is much more patchily distributed in the area than amphipods, independent of depth. This may mean that small high-density patches of cod are energetically more rewarding to seals when they are foraging, while amphipod patches are less concentrated and therefore less rewarding. From an energy point of view the two prey items appeared quite similar with the percentage of fat being 6.0 ± 0.8 mg/100 mg wet weight in polar cod and 6.1 ± 1.3 mg/100 mg wet weight in the amphipods (Table S2, Supplementary material I).

5. Conclusions

The pelagic amphipod *T. libellula* and polar cod were the most prominent prey species by mass for the harp seals in the current study in the Arctic Ocean, as also observed for harp seals on their northern feeding grounds in the Barents Sea during autumn nearly 3 decades ago. The interim ice retreat from the shallow (100–350 m) areas to the east of the Svalbard archipelago in the early 1990s to the current position over the deep polar basin further north explains the absence of any bottom-associated prey species, and the presence of Atlantic cod and blue whiting as alternative species in addition to the dominant amphipods and polar cod in the present seal diet. Despite our inability to directly compare seals of all ages/sizes between the early 1990s and 2016, there are some indications that the overall body condition of the seals may have declined in early autumn over the past 2–3 decades.

By using complementary methods in the diet studies, we were able to compare the short-term (morphological analyses of digestive tract contents) and long-term (natural tissue chemical markers, i.e. stable isotopes and fatty acids) prey use by the seals. Long-term diet, based on stable isotope composition, was reflected relatively well in the short-term stomach contents composition, being dominated by the hyperiid amphipods *T. libellula*. Interestingly, the mean $\delta^{15}N$ value of seals in this study was approximately one trophic level lower than measured in harp seals sampled in the southern Barents Sea in May 2011. In that study, the most likely prey sources were prawns and small fishes such as capelin, herring, juvenile Atlantic cod and saithe, sculpins and flatfishes while the seal prey in the present study were a trophic level lower. This was related to a move away from benthic foraging due to a change in the ice edge position. Also, the current fatty acid analyses were compared with similar analyses performed on the seals from May 2011. These comparisons confirmed previous and current instant short-term observations based on gastro-intestinal contents that harp seals feed much more on pelagic crustaceans, particularly amphipods, when they are on their northern feeding grounds than when they are in the south.

Results from the acoustic and trawl surveys confirmed that amphipods *T. libellula* were by far the most abundant prey observed on the assumed harp seal feeding grounds, followed by krill (primarily *T. inermis*), Atlantic cod and polar cod. In general, the amphipods were confined to the depth layers above 200 m while krill and the mentioned fish species were most abundant in the deeper layers. From an optimal foraging point of view the seals should select prey which maximize their net energy intake rate, which in our study would appear to be amphipods because they were the most abundant prey. Instead, the seals displayed a clear positive preference for polar cod whereas amphipods and krill were consumed in less proportions than observed in the environment.

Author contributions

TH, KTN, HG and TK conceived the study and conducted the field work. In subsequent analyses and interpretation of data, MB was responsible for the body condition and diet studies of the seals, SM for the fatty acid studies, KMM for the stable isotope studies, HG and TK for the prey abundance studies and UL for the prey preference studies. All authors contributed to the preparation of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2020.102498.

References

Ackman, R.G., Epstein, S., Eaton, C.A., 1971. Differences in fatty acid compositions of blubber fats from Northwestern Atlantic fin whales (*Balaenoptera physalus*) and harp seals (*Pagophilus groenlandica*). Comp. Biochem. Physiol. 40B, 683–697.

Auel, H., Harjes, M., da Rocha, R., Stübing, D., Hagen, W., 2002. Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. Polar Biol 25 (5), 374–383. https://doi.org/10.1007/s00300-001-0354-7.

Berge, J., Cottier, F., Last, K.S., Varpe, Ø., Leu, E., Søreide, J., Eiane, K., Falk-Petersen, S., Willis, K., Nygård, H., Vogedes, D., Griffiths, C., Johnsen, G., Lorentzen, D., Brierley, A.S., 2009. Diel vertical migration of Arctic zooplankton during the polar night. Biol. Lett. 5 (1), 69–72. https://doi.org/10.1098/rsbl.2008.0484.

Berge, J., Cottier, F., Varpe, Ø., Renaud, P.E., Falk-Petersen, S., Kwasniewski, S., Griffiths, C., Søreide, J.E., Johnsen, G., Aubert, A., Bjærke, O., Hovinen, J., Jung-Madsen, S., Tveit, M., Majaneva, S., 2014. Arctic complexity: a case study on diel vertical migration of zooplankton. J. Plankton Res. 36, 1–19. https://doi.org/10.1093/plankt/fbu059.

Berge, J., Daase, M., Renaud, P., Ambrose Jr., W., Darnis, G., Last, K., Leu, E., Cohen, J., Johnsen, G., Moline, M., Cottier, F., Varpe, Ø., Shunatova, N., Bałazy, P., Morata, N., Massabuau, J.-C., Falk-Petersen, S., Kosobokova, K., Hoppe, C.M., Węsławski, J., Kukliński, P., Legeżyńska, J., Nikishina, D., Cusa, M., Kędra, M., Włodarska-Kowalczuk, M., Vogedes, D., Camus, L., Tran, D., Michaud, E., Gabrielsen, T., Granovitch, A., Gonchar, A., Krapp, R., Callesen, T., 2015. Unexpected levels of biological activity during the polar night offer new perspectives on a warming arctic. Curr. Biol. 25 (19), 2555–2561. https://doi.org/10.1016/j.cub.2015.08.024.

Bogstad, B., Gjøsæter, H., Haug, T., Lindstrøm, U., 2015. A review of the battle for food in the Barents Sea: cod vs marine mammals. Front. Ecol. Evol. 3, 29. https://doi.org/10.3389/fevo.2015.00029.

Bradstreet, M.S.W., Cross, W.E., 1982. Trophic relationships at high arctic ice edges. Arctic 35, 1–12.

Brunborg, L.A., Julshamn, K., Nortvedt, R., Frøyland, L., 2006. Nutritional composition of blubber and meat of hooded seal (*Cystophora cristata*) and harp seal (*Pagophilus groenlandicus*) from Greenland. Food Chem. 96 (4), 524–553.

Budge, S.M., Iverson, S.J., 2003. Quantitative analysis of fatty acid precursors in marine samples: direct conversion of wax ester alcohols and dimethylacetals to FAMEs. J. Lipid Res. 44 (9), 1802–1807. https://doi.org/10.1194/jlr.D300009-JLR200.

CCAMLR, 2010. Report of the fifth meeting of the Subgroup on Acoustic Survey and Analysis methods. SC-CCAMLR 29/5, 147–171.

Calise, L., Skaret, G., 2011. Sensitivity investigation of the SDWBA Antarctic krill target strength model to fatness, material contrasts and orientation. CCAMLR Sci. 18, 97–122.

Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. Theor. Popul. Biol. 9 (2), 129–136. https://doi.org/10.1016/0040-5809(76)90040-X.

Cottier, F.R., Tarling, G.A., Wold, A., Stig, F.-P., 2006. Unsynchronized and synchronized vertical migration of zooplankton in a high arctic fjord. Limnol. Oceanogr. 51 (6), 2586–2599.

Dale, K., Falk-Petersen, S., Hop, H., Fevolden, S.-E., 2006. Population dynamics and body composition of the Arctic hyperiid amphipod *Themisto libellula* in Svalbard fjords. Polar Biol. 29 (12), 1063–1070. https://doi.org/10.1007/s00300-006-0150-5.

Dalpadado, P., Borkner, N., Bogstad, B., Mehl, S., 2001. Distribution of *Themisto* (Amphipoda) spp. in the Barents Sea and predator-prey interactions. ICES J. Mar. Sci. 58, 876–895.

Dalpadado, P., 2002. Inter-specific variations in distribution, abundance and possible life-cycle patterns of *Themisto* spp. (Amphipoda) in the Barents Sea. Polar Biol. 25 (9), 656–666. https://doi.org/10.1007/s00300-002-0390-y.

Dalpadado, P., Ellertsen, B., Johannessen, S., 2008a. Inter-specific variations in distribution, abundance and reproduction strategies of krill and amphipods in the Marginal Ice Zone of the Barents Sea. Deep Sea Res. Part II: Top. Stud. Oceanogr. 55 (20-21), 2257–2265. https://doi.org/10.1016/j.dsr2.2008.05.015.

Dalpadado, P., Yamaguchi, A., Ellertsen, B., Johannessen, S., 2008b. Trophic interactions of macro-zooplankton (krill and amphipods) in the Marginal Ice Zone of the Barents Sea. Deep Sea Res. Part II: Top. Stud. Oceanogr. 55 (20-21), 2266–2274. https://doi.org/10.1016/j.dsr2.2008.05.016.

de la Vega, C., Jeffreys, R.M., Tuerena, R., Ganeshram, R., Mahaffey, C., 2019. Temporal and spatial trends in marine carbon isotopes in the Arctic Ocean and implications for food web studies. Glob Change Biol. 25 (12), 4116–4130. https://doi.org/10.1111/gcb.14832.

Divine, D.V., Dick, C., 2006. Historical variability of sea ice edge position in the Nordic Seas. J. Geophys. Res. 111 (C1) https://doi.org/10.1029/2004JC002851.

Engelhardt, F.R., Walker, B.L., 1974. Fatty-Acid Composition of Harp Seal, *Pagophilus groenlandicus (Phoca groenlandica*). Comp. Biochem. Physiol. 47 (1B), 169–179.

Enoksen, S., Haug, T., Lindstrøm, U., Nilssen, K.T., 2017. Recent summer diet of hooded *Cystophora cristata* and harp *Pagophilus groenlandicus* seals in the drift ice of the Greenland Sea. Polar Biol. 40 (4), 931–937. https://doi.org/10.1007/s00300-016-2002-2.

Eriksen, E., Skjoldal, H.R., Gjøsæter, H., Primicerio, R., 2017. Spatial and temporal changes in the Barents Sea pelagic compartment during the recent warming. Prog. Oceanogr. 151, 206–226. https://doi.org/10.1016/j.pocean.2016.12.009.

Falk-Petersen, S., Haug, T., Nilssen, K.T., Wold, A., Dahl, T.M., 2004. Lipids and trophic linkages in harp seal (*Phoca groenlandica*) from the eastern Barents Sea. Polar Res. 23 (1), 43–50. https://doi.org/10.3402/polar.v23i1.6265.

Falk-Petersen, S., Haug, T., Hop, H., Nilssen, K.T., Wold, A., 2009. Transfer of lipids from plankton to blubber of harp and hooded seals off East Greenland. Deep Sea Res. Part II: Top. Stud. Oceanogr. 56 (21-22), 2080–2086. https://doi.org/10.1016/j.dsr2.2008.11.020.

Falk-Petersen, S., Leu, E., Berge, J., Kwasniewski, S., Nygård, H., Røstad, A., Keskinen, E., Thormar, J., von Quillfeldt, C., Wold, A., Gulliksen, B., 2008. Vertical migration in high Arctic waters during autumn 2004. Deep Sea Res. Part II: Top. Stud. Oceanogr. 55 (20-21), 2275–2284. https://doi.org/10.1016/j.dsr2.2008.05.010.

Falk-Petersen, S., Pavlov, V., Berge, J., Cottier, F., Kovacs, K.M., Lydersen, C., 2015. At the rainbow's end: high productivity fueled by winter upwelling along an Arctic shelf. Polar Biol. 38, 5–11.

Fielding, S., Watkins, J.L., Trathan, P.N., Enderlein, P., Waluda, C.M., Stowasser, G., Tarling, G.A., Murphy, E.J., 2014. Interannual variability in Antarctic krill (*Euphausia superba*) density at South Georgia, Southern Ocean: 1997–2013. ICES J. Mar. Sci. 71, 2578–2588.

Finley, K.J., Bradstreet, M.S.W., Miller, G.W., 1990. Summer feeding ecology of harp seals (*Phoca groenlandica*) in relation to arctic cod (*Boreogadus saida*) in the Canadian high arctic. Polar Biol. 10 (8), 609–618. https://doi.org/10.1007/BF00239372.

Folkow, L.P., Nordøy, E.S., Blix, A.S., 2004. Distribution and diving behaviour of harp seals *Pagophilus groenlandicus* from the Gtreenland Sea stock. Polar Biol. 27, 281–298.

Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R.B., Aschan, M.M., Dolgov, A. V., 2015. Recent warming leads to a rapid borealization of fish communities in the Arctic. Nature Clim. Change 5 (7), 673–677. https://doi.org/10.1038/nclimate2647.

Grahl-Nielsen, O., Haug, T., Lindstrøm, U., Nilssen, K.T., 2011. Fatty acids in harp seal blubber do not necessarily reflect their diet. Mar. Ecol. Prog. Ser. 426, 263–276. https://doi.org/10.3354/meps09011.

Geoffroy, M., Daase, M., Cusa, M., Darnis, G., Graeve, M., Hernandez, N.S., Berge, J., Renaud, P.E., Cottier, F., Falk-Petersen, S., 2019. Mesopelagic sound scattering layers of the High Arctic: seasonal variations in biomass, species assemblage, and trophic relationships. Front. Mar. Sci. 6, 18. https://doi.org/10.3389/fmars.2019.00364.

Gjøsæter, H., Wiebe, P.H., Knutsen, T., Ingvaldsen, R., 2017. Evidence of diel vertical migration of mesopelagic sound-scattering organisms in the Arctic. Front. Mar. Sci. 4, 332. https://doi.org/10.3389/fmars.2017.00332.

Hammill, M.O., Lesage, V., Carter, P., 2005. Problems associated with determining diet composition in harp seals by reconstruction of stomach contents or faecal samples. Can. J. Zool. 83, 1365–1372.

Hammill, M.O., Stenson, G.B., 2000. Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. J. Northw. Atl. Fish. Sci. 26, 1–23. https://doi.org/10.2960/J.v26.a1.

Haug, T., Bogstad, B., Chierici, M., Gjøsæter, H., Hallfredsson, E.H., Høines, Å., Hoel, A. H., Ingvaldsen, R.B., Jørgensen, L.L., Knutsen, T., Loeng, H., Naustvoll, L.-J., Røttingen, I., Sunnanå, K., 2017a. Future harvest of living resources in the Arctic Ocean of the Nordic and Barents Seas: a review of possibilities and constraints. Fisheries Res. 188, 38–57.

Haug, T., Falk-Petersen, S., Greenacre, M., Hop, H., Lindstrøm, U., Meier, S., Nilssen, K. T., Wold, A., 2017b. Trophic level and fatty acids in harp seals compared with common minke whales in the Barents Sea. Marine Biol. Res. 13 (9), 919–932. https://doi.org/10.1080/17451000.2017.1313988.

Haug, T., Nilssen, K.T., Lindblom, L., 2004. Feeding habits of harp and hooded seals in drift ice waters along the east coast of Greenland in summer and winter. Polar Res. 23 (1), 35–42. https://doi.org/10.3402/polar.v23i1.6264.

Haug, T., Nilssen, K.T., Lindblom, L., Lindstrøm, U., 2007. Diets of hooded seals (*Cystophora cristata*) in coastal waters and drift ice waters along the east coast of Greenland. Mar. Biol. Res. 3, 123–133.

Haug, T., Nilssen, K.T., Øien, N., Potelov, V., 1994. Seasonal distribution of harp seals (*Phoca groenlandica*) in the Barents Sea. Polar Res. 13, 161–172.

Havermans, C., Auel, H., Hagen, W., Held, C., Ensor, N.S., Tarling, G.A., 2019. Predatory zooplankton on the move: *Themisto* amphipods in high-latitude marine pelagic food webs. Adv. Mar. Biol. 82, 51–92.

Heino, M., Porteiro, F.M., Sutton, T.T., Falkenhaug, T., Godø, O.R., Piatkowski, U., 2011. Catchability of pelagic trawls for sampling deep-living nekton in the mid-North Atlantic. ICES J. Mar. Sci. 68, 377–389.

Hobson, K.A., Schell, D.M., Renouf, D., Noseworthy, E., 1996. Stable carbon and nitrogen isotopic fractionation between diet and tissues of captive seals: implications for dietary reconstructions involving marine mammals. Can. J. Fish. Aquat. Sci. 53 (3), 528–533. https://doi.org/10.1139/f95-209.

Hobson, K.A., Welch, H.E., 1992. Determination of trophic relationships within a high Arctic marine food web using d^{13}C and d^{15}N analysis. Mar. Ecol. Prog. Ser. 84, 9–18.

Hop, H., Gjøsæter, H., 2013. Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. Mar. Biol. Res. 9 (9), 878–894. https://doi.org/10.1080/17451000.2013.775458.

Huserbråten, M.B.O., Eriksen, E., Gjøsæter, H., Vikebø, F., 2019. Polar cod in jeopardy under the retreating Arctic sea ice. Commun. Biol. 2 (1) https://doi.org/10.1038/s42003-019-0649-2.

Ingvaldsen, R.B., Gjøsæter, H., Ona, E., Michalsen, K., 2017. Atlantic cod (*Gadus morhua*) feeding over deep water in the high Arctic. Polar Biol. 40 (10), 2105–2111. https://doi.org/10.1007/s00300-017-2115-2.

Jangaard, P.M., Ke, P.J., 1968. Principal fatty acids of depot fat and milk lipids from harp seal (*Pagophilus groenlandica*) and hooded seal (*Cystophora cristata*). J. Fish. Res. Bd. Can. 25 (11), 2419–2426. https://doi.org/10.1139/f68-209.

Kaartvedt, S., 2010. Chapter 9: Diel vertical migration behaviour of the northern krill (*Meganyctiphanes norvegica* Sars). Adv. Mar. Biol. 57, 255–275. https://doi.org/10.1016/S0065-2881(10)57009-3.

Kirsch, P.E., Iverson, S.J., Bowen, W.D., 2000. Effect of a low-fat diet on body composition and blubber fatty acids of captive juvenile harp seals (*Phoca groenlandica*). Physiol. Biochem. Zool. 73 (1), 45–59. https://doi.org/10.1086/316723.

Knutsen, T., Wiebe, P.H., Gjøsæter, H., Ingvaldsen, R.B., Lien, G., 2017. High latitude epipelagic and mesopelagic scattering layers—a reference for future arctic ecosystem change. Front. Mar. Sci. 4, 334. https://doi.org/10.3389/fmars.2017.00334.

Korneliussen, R.J., Gjøsæter, H., Ona, E., Skaret, G., Salthaug, A., Knutsen, T., 2020. Prosedyre for tolkning av data fra ekkolodd. Havforskningsinstituttet: Versjon 1.0, 2020.01.01. pp. 1–55.

Korneliussen, R.J., Heggelund, Y., Macaulay, G.J., Patel, D., Johnsen, E., Eliassen, I.K., 2016. Acoustic identification of marine species using a feature library. Methods Oceanogr. 17, 187–205. https://doi.org/10.1016/j.mio.2016.09.002.

Korneliussen, R.J., Ona, E., Eliassen, I., Heggelund, Y., Patel, R., Godø, O. R., Giertsen, C., Patel, D., Nornes, E., Bekkvik, T., Knudsen, H.P., Lien, G., 2006. The large scale survey system – LSSS. In: Proceedings of the 29th Scandinavian Symposium on Physical Acoustics, Ustaoset, Norway, 29 January – 1 February 2006, 6 pp.

Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A.V., Aschan, M., 2015. Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. Proc. R. Soc. B. 282 (1814), 20151546. https://doi.org/10.1098/rspb.2015.1546.

Kraft, A., Graeve, M., Janssen, D., Greenacre, M., Falk-Petersen, S., 2015. Arctic pelagic amphipods: lipid dynamics and life strategy. J. Plankton Res. 37 (4), 790–807. https://doi.org/10.1093/plankt/fbv052.

Krafft, B.A., Melle, W., Knutsen, T., Bagøien, E., Broms, C., Ellertsen, B., Siegel, V., 2010. Distribution and demography of Antarctic krill in the Southeast Atlantic sector of the Southern Ocean during the austral summer 2008. Polar Biol. 33 (7), 957–968. https://doi.org/10.1007/s00300-010-0774-3.

Kristensen, T.K., 1984. Biology of the squid *Gonatus fabricii* (Lichtenstein, 1818) from West Greenland waters. Meddr Grønl. Biosc. 13, 3–17.

Laidre, K.L., Heide-Jørgensen, M.P., Heagarty, P., Cossio, A., Bergstrøm, B., Simon, M., 2010. Spatial associations between large baleen whales and their prey in West Greenland. Mar. Ecol. Prog. Ser. 402, 269–284.

Lassalle, G., Chouvelon, T., Bustamante, P., Niquil, N., 2014. An assessment of the trophic structure of the Bay of Biscay continental shelf food web: comparing estimates derived from an ecosystem model and isotopic data. Prog. Oceanogr. 120, 205–215. https://doi.org/10.1016/j.pocean.2013.09.002.

Last, K., Hobbs, L., Berge, J., Brierley, A., Cottier, F., 2016. Moonlight drives ocean-scale mass vertical migration of zooplankton during the arctic winter. Curr. Biol. 26 (2), 244–251. https://doi.org/10.1016/j.cub.2015.11.038.

Lawson, J.W., Hobson, K.A., 2000. Diet of harp seals (*Pagophilus groenlandicus*) in nearshore northeast Newfoundland: inferences from stable carbon (δ^{13}C) and nitrogen $^{(}\delta^{15}$N) isotope analyses. Mar. Mamm. Sci. 16, 578–591.

Lawson, J.W., Anderson, J.T., Dalley, E.L., Stenson, G.B., 1998. Selective foraging by harp seals (*Phoca groenlandica*) in nearshore and offshore waters of Newfoundland, 1993–94. Mar. Ecol. Prog. Ser. 163, 1–10.

Lindstrøm, U., Harbitz, A., Haug, T., Nilssen, K.T., 1998. Do harp seals *Phoca groenlandica* exhibit particular prey preferences? ICES J. Mar. Sci. 55, 941–953.

Lindstrøm, U., Nilssen, K.T., Pettersen, L.M.S., Haug, T., 2013. Harp seal foraging behaviour during summer around Svalbard in the northern Barents Sea: diet composition and the selection of prey. Polar Biol. 36 (3), 305–320. https://doi.org/10.1007/s00300-012-1260-x.

Lydersen, C., Angantyr, L.A., Wiig, Ø., Øritsland, T., 1991. Feeding habits of northeast Atlantic harp seals (*Phoca groenlandica*) along the Summer Ice Edge of the Barents Sea. Can. J. Fish. Aquat. Sci. 48 (11), 2180–2183. https://doi.org/10.1139/f91-257.

MacLennan, D.N., Fernandes, P.G., Dalen, J., 2002. A consistent approach to definitions and symbols in fisheries acoustics. ICES J. Mar. Sci. 59, 365–369. https://doi.org/10.1006/jmsc.2001.1158.

Matley, J.K., Fisk, A.T., Dick, T.A., 2015. Foraging ecology of ringed seals (*Pusa hispida*), beluga whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in the Canadian High Arctic determined by stomach content and stable isotope analysis. Polar Res. 34 (1), 24295. https://doi.org/10.3402/polar.v34.24295.

Matthiopoulos, J., Smout, S., Winship, A.J., Thompson, D., Boyd, I.L., Harwood, J., 2008. Getting beneath the surface of marine mammal—fisheries competition. Mamm. Rev. 38, 167–188.

McMahon, K.W., Polito, M.J., Abel, S., McCarthy, M.D., Thorrold, S.R., 2015. Carbon and nitrogen isotope fractionation of amino acids in an avian marine predator, the gentoo penguin (*Pygoscelis papua*). Ecol. Evol. 5 (6), 1278–1290.

Meier, S., Falk-Petersen, S., Gade-Sørensen, L.A., Greenacre, M., Haug, T., Lindstrøm, U., 2016. Fatty acids in common minke whale (*Balaenoptera acutorostrata*) blubber reflect the feeding area and food selection, but also high endogenous metabolism. Mar. Biol. Res. 12, 221–238.

Meier, S., Mjøs, S.A., Joensen, H., Grahl-Nielsen, O., 2006. Validation of a one-step extraction/methylation method for determination of fatty acids and cholesterol in marine tissues. J. Chromatogr. A 1104, 291–298.

Menze, S., Ingvaldsen, R.B., Nikolopoulos, A., Hattermann, T., Albretsen, J., Gjøsæter, H., 2020. Productive detours – Atlantic water inflow and acoustic backscatter in the major troughs along the Svalbard shelf. Prog. Oceanogr. 188, 102447 https://doi.org/10.1016/j.pocean.2020.102447.

Mörner, N.-A., Solheim, J.-E., Humlum, O., Falk-Petersen, S., 2020. Changes in Barents Sea ice edge positions in the last 440 years: a review of possible driving forces. Int. J. Astron. Astrophys. 10, 97–164. https://doi.org/10.4236/ijaa.2020.102008.

Murphy, E.J., Morris, D.J., Watkins, J.L., Priddle, J., 1988. Scales of interaction between Antarctic krill and the environment. In: Sahrhage, D. (Ed.), Antarctic Ocean and resources variability. Springer, Berlin, pp. 120–130.

Newsome, S.D., Wolf, N., Peters, J., Fogel, M.L., 2014. Amino acid δ^{13}C analysis shows flexibility in the routing of dietary protein and lipids to the tissue of an omnivore. Int. Comp. Biol. 54, 890–902. https://doi.org/10.1093/icb/icu106.

Nilssen, K.T., Haug, T., Grotnes, P.E., Potelov, V., 1997. Seasonal variation in body condition of adult Barents Sea harp seals (*Phoca groenlandica*). J. Northw. Atl. Fish. Sci. 22, 17–25.

Nilssen, K.T., Pedersen, O.P., Folkow, L.P., Haug, T., 2000. Food consumption estimates of Barents Sea harp seals. NAMMCO Sci. Publ. 2, 9–27.

Nilssen, K.T., Haug, T., Potelov, V., Stasenkov, V.A., Timoshenko, Y.K., 1995a. Food habits of harp seals (*Phoca groenlandica*) during lactation and moult in March-May in the southern Barents Sea and White Sea. ICES J. Mar. Sci. 52, 33–41.

Nilssen, K.T., Haug, T., Potelov, V., Timoshenko, Y.K., 1995b. Food habits and food availability of harp seals (*Phoca groenlandica*) during early summer and autumn in the northern Barents Sea. Polar Biol. 15, 485–493.

Nordøy, E.S., Folkow, L.P., Potelov, V., Prischemikhin, V., Blix, A.S., 2008. Seasonal distribution and dive behaviour of harp seals (*Pagophilus groenlandicus*) of the White Sea-Barents Sea stock. Polar Biol. 31, 1119–1135.

Norheim, E., Klevjer, T.A., Aksnes, D.L., 2016. Evidence for light-controlled migration amplitude of a sound scattering layer in the Norwegian Sea. Mar. Ecol. Prog. Ser. 551, 45–52. https://doi.org/10.3354/meps11731.

Noyon, M., Narcy, F., Gasparini, S., Mayzaud, P., 2011. Growth and lipid class composition of the Arctic pelagic amphipod *Themisto libellula*. Mar. Biol. 158, 883–892. https://doi.org/10.1007/s00227-010-1615-1.

Ogloff, W.R., Yurkowski, D.J., Davoren, G.K., Ferguson, S.H., 2019. Diet and isotopic overlap elucidate competition potential between seasonally sympatric phocids in the Canadian Arctic. Mar. Biol. 166, 103. https://doi.org/10.1007/s00227-019-3549-6.

Øigård, T.A., Lindstrøm, U., Haug, T., Nilssen, K.T., Smout, S., 2013. Functional relationship between harp seal body condition and available prey in the Barents Sea. Mar. Ecol. Prog. Ser. 484, 287–301.

Parnell, A., 2019. Simmr: A Stable Isotope Mixing Model. R package version 0.4.1. https://CRAN.R-project.org/package=simmr.

Pérez-Hernández, M.D., Pickart, R.S., Pavlov, V., Våge, K., Ingvaldsen, R., Sundfjord, A., Renner, A.H.H., Torres, D.J., Erofeeva, S.Y., 2017. The Atlantic Water boundary current north of Svalbard in late summer. J. Geophys. Res. Oceans 122, 2269–2290. https://doi.org/10.1002/2016JC012486.

Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., Semmens, B.X., Ward, E.J., 2014. Best practices for use of stable isotope mixing models in food-web studies. Can. J. Zool. 92, 823–835. https://doi.org/10.1139/cjz-2014-0127.

Piatt, J.F., Methven, D.A., 1992. Threshold foraging behaviour of baleen whales. Mar. Ecol. Prog. Ser. 84, 205–210.

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., Montana, C.G., 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152, 179–189.

R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Reiss, C.S., Cossio, A.M., Loeb, V., Demer, D.A., 2008. Variations in the biomass of Antarctic krill (*Euphausia superba*) around the South Shetland Islands, 1996–2006. ICES J. Mar. Sci. 65, 497–508.

Schröter, F., Havermans, C., Kraft, A., Knüppel, N., Beszczynska-Möller, A., Bauerfeind, E., Nöthig, E.-M., 2019. Pelagic amphipods in the eastern Fram Strait with continuing presence of *Themisto compressa* based on sediment trap time series. Front. Mar. Sci. 6, 311. https://doi.org/10.3389/fmars.2019.00311.

Simmard, Y., Lacroix, G., Legendre, L., 1986. Diel vertical migrations and nocturnal feeding of a dense coastal krill scattering layer (*Thysanoessa raschi* and *Meganyctiphanes norvegica*) in stratified surface waters. Mar. Biol. 91, 93–105.

Sokołowski, A., Szczepańska, A., Richard, P., Kędra, M., Wołowicz, M., Węsławski, J.M., 2014. Trophic structure of the macrobenthic community of Hornsund, Spitsbergen, based on the determination of stable carbon and nitrogen isotopic signatures. Polar Biol. 37, 1247–1260. https://doi.org/10.1007/s00300-014-1517-7.

Solvang, H.K., Haug, T., Knutsen, T., Gjøsæter, H., Bogstad, B., Hartvedt, S., Øien, N., Lindstrøm, U., 2020. Distribution of rorquals and predatory fish in relation to prey in the Norwegian high Arctic. Polar Biol. In subm.

Søreide, J.E., Falk-Petersen, S., Hegseth, E.N., Hop, H., Carroll, M.L., Hobson, K.A., Blachowiak-Samolyk, K., 2008. Seasonal feeding strategies of *Calanus* in the high-Arctic Svalbard region. Deep-Sea Res. II 55, 2225–2244.

Storrie, L., Lydersen, C., Andersen, M., Wynn, R.B., Kovacs, K.M., 2018. Determining the species assemblage and habitat use of cetaceans in the Svalbard Archipelago, based on observations from 2002 to 2014. Polar Res. 37, 1–22. https://doi.org/10.1080/17518369.2018.1463065.

Strandberg, U., Kakela, A., Lydersen, C., Kovacs, K.M., Grahl-Nielsen, O., Hyvarinen, H., Kakela, R., 2008. Stratification, composition, and function of marine mammal blubber: the ecology of fatty acids in marine mammals. Physiol. Biochem. Zool. 81, 473–485.

Tamelander, T., Renaud, P.E., Hop, H., Carroll, M.L., Ambrose Jr., W.G., Hobson, K.A., 2006. Trophic relationships and pelagic–benthic coupling during summer in the Barents Sea Marginal Ice Zone, revealed by stable carbon and nitrogen isotope measurements. Mar. Ecol. Prog. Ser. 310, 33–46.

Tucker, S., Bowen, W.D., Iverson, S.J., Stenson, G.B., 2009a. Intrinsic and extrinsic sources of variation in the diets of harp and hooded seals revealed by fatty acid profiles. Can. J. Zool. 87, 139–151.

Tucker, S., Bowen, W.D., Iverson, S.J., Blanchard, W., Stenson, G.B., 2009b. Sources of variation in diets of harp and hooded seals estimated from quantitative fatty acid signature analysis (QFASA). Mar. Ecol. Prog. Ser. 384, 287–302.

Vacquié-Garcia, J., Lydersen, C., Marques, T.A., Aars, J., Ahonen, H., Skern-Mauritzen, M., Øien, N., Kovacs, K.M., 2017. Late summer distribution and abundance of ice-associated whales in the Norwegian High Arctic. End. Spec. Res. 32, 59–70.

Vikingsson, G.A., Pike, D.G., Valdimarsson, H., Schleimer, A., Gunnlaugsson, T., Silva, T., Elvarsson, B.û., Mikkelsen, B., Øien, N., Desportes, G., Bogason, V., Hammond, P.S., 2015. Distribution, abundance, and feeding ecology of baleen whales in Icelandic waters: have recent environmental changes had an effect? Front. Ecol. Evol. 3, 6. https://doi.org/10.3389/fevo.2015.00006.

von Weissenberg, E.W., 2018. Spatial structures of a high-Arctic macro-zooplankton community. Master Thesis, University of Helsinki, Faculty of Biological and Environmental Sciences. Helsinki October 2, 2018. pp. 1–32, + Appendixes A-C.

Wenneck, T.d.L., Falkenhaug, T., Bergstad, O.A., 2008. Strategies, methods, and technologies adopted on the R.V. G.O. Sars MAR-ECO expedition to the Mid-Atlantic Ridge in 2004. Deep Sea Res. II 55, 6–28. https://doi.org/10.1016/j.dsr2.2007.09.017.

Wiebe, P.H., Allison, D., Kennedy, M., Moncoiffé, G., 2015. A vocabulary for the configuration of net tows for collecting plankton and micronekton. J. Plankt. Res. 37, 21–27. https://doi.org/10.1093/plankt/fbu101.

Woodland, R.J., Secor, D.H., 2013. Benthic-pelagic coupling in a temperate inner continental shelf fish assemblage. Limnol. Oceanogr. 58 (3), 966–976. https://doi.org/10.4319/lo.2013.58.3.0966966.

Zhukova, N.G., Nesterova, V.N., Prokopchuk, I.P., Rudneva, G.B., 2009. Winter distribution of euphausiids (*Euphausiacea*) in the Barents Sea (2000–2005). Deep-Sea Res. II 56, 1959–1967. https://doi.org/10.1016/j.dsr2.2008.11.007.