Progress in Oceanography 224 (2024) 103267

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Trophic interactions between common minke whales (*Balaenoptera acutorostrata*) and their prey during summer in the northern Barents Sea

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ARTICLE INFO

Keywords:
Common minke whales
Diet
Fatty acids
Stable isotopes

ABSTRACT

Global warming is causing rapid change in marine food webs, particularly at northern latitudes where temperatures are increasing most rapidly. In this study, the diet of common minke whales *Balaenoptera acutorostrata* was assessed both in terms of short-term (morphological analyses of digestive tract contents) and longer-term (tissue chemical markers: fatty acids and stable isotopes) prey use in the northern Barents Sea to see if they are prey shifting. Samples (blubber cores, muscle, and stomach contents) were obtained from 158 common minke whales taken during Norwegian commercial whaling operations during summer over the period 2016–2020. Two prey items, capelin *Mallotus villosus* and krill (primarily *Thysanoessa* sp.), dominated the stomach contents in the entire period of investigation, which included sampling both in June and in August, similar to findings from earlier studies. A few gadoids were also observed in the whale stomachs. Lower blubber fatty acid (FA) contents in 2016/2017 as compared with 2018/2019 were observed. This is most likely explained by differences in sampling time (June in 2016/2017 vs August in 2018/2019, i.e., after a longer feeding period during the summer in the latter case). This explanation also fits with the fact that FA profiles of the 2018/2019 whales were more similar to the FA profiles of the potential prey, presumably reflecting the two months longer assimilation time for these whales. Multidimensional mixing models based on carbon and nitrogen isotope composition of the most likely prey groups suggested that the whales ate mostly krill in four of the five sampling years. In 2018 there were indications of a higher proportion of gadoid fish, showing some dietary flexibility. The trophic level of the whales' feeding, as interpreted from the nitrogen isotope values, was positively correlated with blubber thickness suggesting that fish-eaters tended to assimilate more energy than whales that focused more exclusively on lower trophic prey. The variation suggested by different dietary analyses methods – stomach contents, fatty acids, and stable isotopes – most likely reflects different turnover times, with muscle stable isotopes likely representing several months of dietary integration, while lipid stores are more dynamic and may represent weeks, and stomach contents represent feeding events during the last few hours. The change in diet of minke whales from small pelagic fishes (in the past) to a greater quantity of krill and demersal fish (seen in this study) suggests that the whales are responding to the ongoing borealization of the Barents Sea ecosystem.

1. Introduction

Recent warming in the Barents Sea has led to a marked shift in the distribution of water masses and, as a result, changes in the spatial distribution of both zooplankton and fish (Gerland et al., 2023). Boreal pelagic communities have expanded northward (Eriksen et al., 2017; Fossheim et al., 2015; Ingvaldsen et al., 2021). Scientific surveys as well as fisheries catches in the northern Barents Sea show recent northward expansions of boreal fish species such as Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus* and capelin *Mallotus villosus*, and of temperate marine mammal species such as common minke whales *Balaenoptera acutorostrata* (Haug et al., 2017a; Storrie et al., 2018; Bengtsson et al., 2022). These climate-driven poleward shifts of boreal communities have led to changes in food web structure of the northern

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https://doi.org/10.1016/j.pocean.2024.103267

Available online 3 May 2024

Barents Sea (e.g., Kortsch et al., 2015; Pecuchet et al., 2020), that are likely to impact ecosystem function and services.

North Atlantic common minke whales undertake seasonal migrations from mid-latitude/tropical regions, where they breed and overwinter, to sub-Arctic and Arctic regions in the summer months for feeding (Jonsgård, 1951, 1966). The feeding grounds range from the east coast of Canada to the Novaya Zemlya region in the western Russian Arctic (Stewart and Leatherwood, 1985; Horwood, 1990). The most recent Norwegian sightings surveys for minke whales, conducted in 2014–2019, estimated the abundance of the regional population to be circa 104 700 (CV = 0.17), making common minke whales the most abundant baleen whale in the Northeast Atlantic by far (Solvang et al., 2021). The species has been commercially exploited in Norwegian waters since the 1920 s (see Haug et al., 2011; Glover et al., 2012).

Along with Atlantic cod and harp seals *Pagophilus groenlandicus*, common minke whales are among the main consumers of biomass in the Barents Sea (Skern-Mauritzen et al., 2011, 2022; Bogstad et al., 2015), although they also feed extensively in areas off the west coast of Svalbard and to a lesser extent in the Norwegian Sea (Haug et al., 2011). While they are considered to be a generalist predator, with a very flexible foraging behaviour that allows them to exploit a variety of species and sizes of fish and crustaceans (Haug et al., 2002), minke whales show a preference for capelin, herring and occasionally krill (Lindstrøm and Haug, 2001). During extreme events, such as the simultaneously low abundance of capelin and herring in 1995–1996, minke whales switched to feeding more on krill and gadoid fishes (Atlantic cod and haddock), which was associated with a reduction in their body condition (Haug et al., 2002). More recent studies (2000–2004 and 2010–2011) confirmed previous findings of significant differences in diet composition of minke whales between areas and some differences between years as well (Windsland et al., 2007; Bogstad et al., 2015; Meier et al., 2016). The importance of krill for common minke whales in the Barents Sea increases with latitude and dominates the diet of the species around Svalbard, while capelin dominates the diet around Bear Island and contributes significantly to the diet along the coast of northern Norway. In the latter area, herring and haddock are also important prey for minke whales.

The northern parts of the Barents Sea have been important feeding grounds for common minke whales in recent years (Skern-Mauritzen et al., 2011; Haug et al., 2017). These areas are part of the study area for the large-scale Norwegian research program "The Nansen Legacy", aimed at providing a cross-disciplinary scientific basis for long-term, holistic, and sustainable management of marine ecosystems and human presence in the northern Barents Sea and adjacent Arctic Ocean (Reigstad et al., 2021; Gerland et al., 2023). The Nansen Legacy program has primarily addressed questions related to lower trophic levels, but it has also contributed to the exploration of food webs through to high trophic feeders in order to provide comprehensive inputs to the many modelling work-programmes undertaken within the Nansen Legacy that aim to provide systems forecasting. We have chosen to focus on the common minke whale because it is a key migratory species in the Barents Sea system. In this study we use complementary methods to assess the diet of the common minke whale from short-term (morphological analyses of digestive tract contents) to longer-term (tissue chemical markers – fatty acids and stable isotopes) prey use.

Using this range of methods, we aim to build a current picture of minke whale diet in a rapidly changing sea area, updating the available information on the dietary habits of this key biomass predator, not only at the time point of sampling but also in the preceding weeks to months. This paper also provides a temporal gradient of prey consumption by Barents Sea minke whales across years. This information can be used for comparisons with previously published dietary studies and with analyses of ecosystem conditions to aid predictions of future biomass transfer within the Barents Sea ecosystem in a management and conservation context during a time of rapid change.

2. Material and methods

2.1. Whale samples and stomach contents

Samples (blubber, muscle, and stomach contents) were obtained from 137 common minke whales taken during Norwegian commercial whaling operations in the northern Barents Sea during summer in the period 2016–2019 (Fig. 1). In 2020, stomach content data were obtained from an additional 21 whales. Samples from 2016 (N = 27), 2017 (N = 58) and 2020 were taken in June, whereas samples from 2018 (N = 21) and 2019 (N = 31) were taken in August (Table S1).

Harvested whales were processed onboard the whaling vessels. The complete digestive tract was removed, and an inspection of the forestomach was conducted to assess the dominant prey species. The intensive summer feeding by minke whales at high latitudes results in seasonal deposition of blubber, and the thickness of the blubber layer is used as a measure of the general body condition of the animals (Solvang et al., 2022). Blubber thickness was therefore measured dorsally just behind the blowhole (see Næss et al., 1998), and a full-depth blubber core was removed from the same area for subsequent analyses. In 2016, a piece of muscle was also collected from beneath the blubber core. Both muscle and blubber samples were packed in aluminum foil and placed in plastic bags before being frozen at –20 °C until analyses.

2.2. Prey samples

Samples of potential prey species were obtained (and frozen at −20 °C) during the joint Norwegian-Russian ecosystem survey from trawl hauls in the northwestern Barents Sea in September 2016 and August-September 2019 (Michalsen et al., 2013; Protozorkevich and van der Meeren, 2020). Potential prey species were selected based on information on the diet composition of common minke whales in the Barents Sea in previous studies (Haug et al., 2002; Windsland et al., 2007; Bogstad et al., 2015; Meier et al., 2016). The prey library included krill (*Meganyctiphanes* sp. And *Thysanoessa* sp.), the amphipod *Themisto libellula*, polar cod (*Boreogadus saida*), capelin (*Mallotus villosus*), herring (*Clupea harengus*), blue whiting (*Micromesistius poutassou*), Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). The prey organisms were collected in the same areas and seasons as the whale samples, but only in one of the years (2019) for fatty acids and only in 2016 and 2019 for stable isotopes.

2.3. Fatty acid analyses

The fatty acid content and profiles were analysed in the blubber of 80 (of the 137) minke whales sampled in the period 2016–2019 (20 in each year), and in muscle samples from 18 minke whales from 2016 (Table 1). In addition, samples from potential prey sampled in 2019 were analysed (Table S7). Small subsamples of blubber weighing 20–50 mg were taken from the inner blubber, 0.1 cm in from the muscle side while the blubber was still frozen to avoid "lipid bleeding". Muscle samples were homogenized and freeze-dried, and subsamples (50–100 mg) were collected for fatty acids analyses. Different prey organisms were homogenized as whole animals, then freeze-dried, and subsamples (50–100 mg) were collected for fatty acids analyses. The samples were weighed into 16 ml glass tubes and a known amount of nonadecanoic acid (19:0) was added as an internal standard, before all FAs were converted to fatty acid methyl esters (FAME) with the methanolysis reagent (2.5 M HCl in anhydrous methanol) (Meier et al., 2006). FAME were extracted with hexane before being analysed on a HP-7890A gas chromatograph (Agilent, USA) with a flame ionization detector (GC-FID). One microliter sample was injected in puls-splitless mode (25 psi in 2 min). Injector and detector temperature were 280 and 300 °C, respectively. The column was a CP-WAX 52CB with length 25 m, internal diameter 0.25 mm, and film thickness of 0.2 μm (Agilent p/n CP7713I). The temperature program was: total run time 75 min, initial

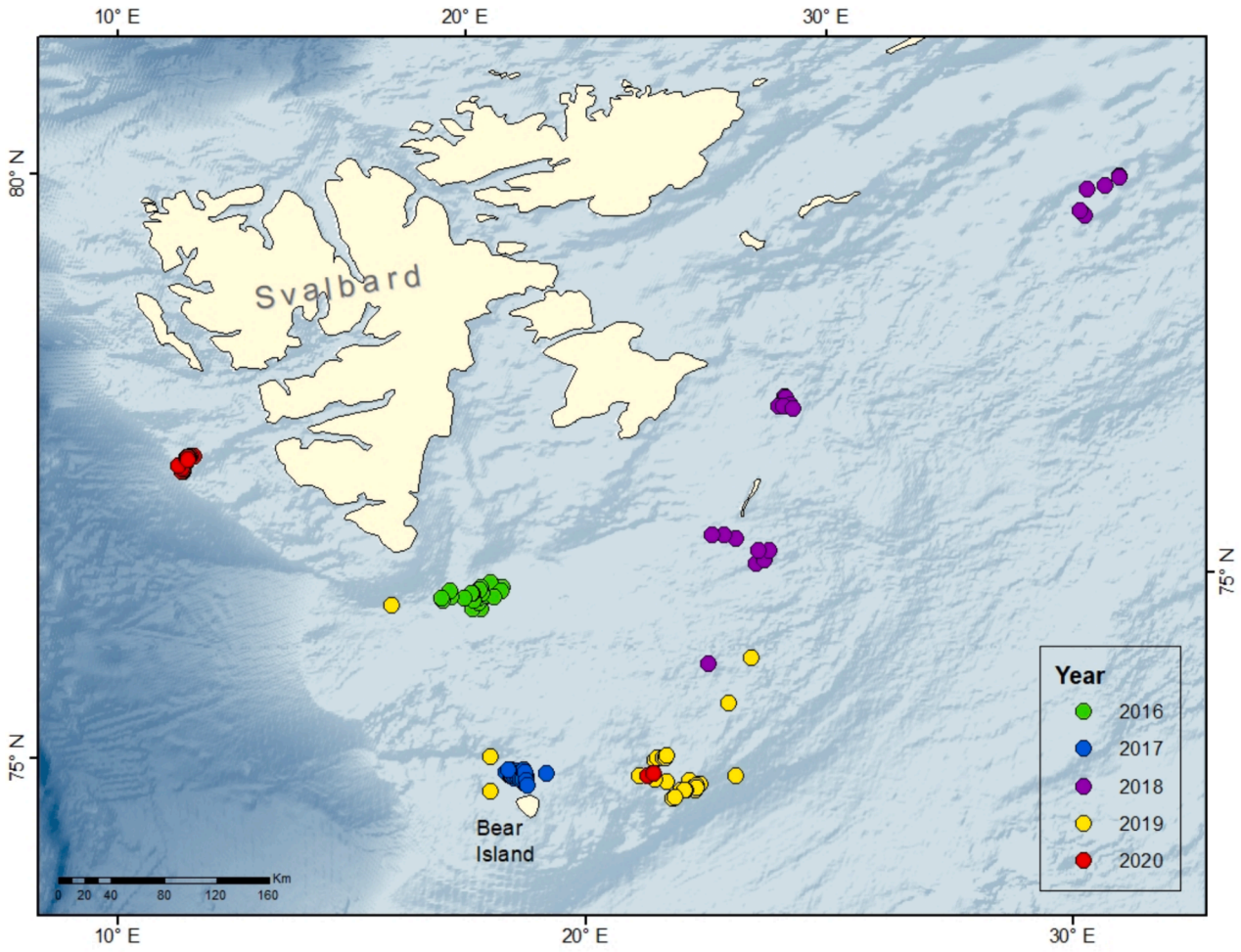

Fig. 1. Catch positions of minke whales sampled during Norwegian whaling in the northwestern Barents Sea in 2016–2020.

temperature 90 °C, increased to 150 °C (30 °C/min), hold time 0 min, increased to 240 °C (2.5 °C/min), and hold time 35 min. Helium (99.9999 %) was used as mobile phase at 1 mL/min for 45 min, followed by a flow increase to 3 mL/min which was held for 30 min. The method can distinguish between 97 different FAs that are identified based on comparison of retention time with standard mixtures of FAME, retention index card, and mass spectrum library (GC–MS) (http://www.chrombox.org). However, only the 60 FAs that contribute with more than 0.1 % of the total FAs are included in the data analysis. The data are presented either as FA profiles (% of total FAs) or normalised to tissue weight (mg/100 mg wet weight) (Tables S3, S6, and S7).

The normalised FA data are mean relative amounts (% of sum FA ± SD). We analysed 60 different FAs, but only the 21 FAs that contribute more than 0.5 % of the total FA are shown in the table. The sum of the minor FAs are given in the table. All FAs are shown in table S5. The letters show significant differences between the years analysed by Kruskal-Wallis test followed by pairwise comparison for Groups (Steel-Dwass-Critchlow-Fligner procedure / Two-tailed test), p-value < 0.05).

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

FAOHs or wax esters are not found in the lipids of minke whales because they are oxidized very rapidly into the corresponding FAs in the digestion process. The FAOHs therefore also contribute to the predator's fatty acid 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 sum of the quantitative amount of the different FAs and FAOHs (especially 22:1n-11 FA + 22:1n-11 FAOH in *T. libellula* and 14:0, 16:0 and 16:1n-7 in *Thysanoessa* sp.) before normalizing to 100 %. The FAOH compositions of the samples are given in the supplementary information, Table S8.

2.4. Stable isotope analyses

Stable isotope compositions of carbon and nitrogen were analysed in muscle samples from 66 of the 137 minke whales taken in 2016–2019, and in their potential prey species. For the prey, *Themisto* spp. amphipods (2016 & 2019) and krill (2016 & 2019) were sampled whole, while dorsal muscle was sampled from capelin (2019), herring (2019), polar cod (2016 & 2019), juvenile haddock (2016 & 2019), blue whiting (2016 & 2019) and Atlantic cod juveniles (2016) and adults (2019). These samples were freeze-dried for 48 h at −80 °C before being homogenised with a ball mill grinder. We then removed lipids from half of each sample using a cyclohexane extraction (Chouvelon et al., 2011), then thoroughly washed the samples in deionised water, before drying and weighing the powders into tin capsules for analyses.

Samples from the whales and the potential prey were analysed in duplicate, using lipid-extracted samples for $\delta^{13}C$ and unextracted

Table 1
Fatty acids (FAs) in the inner blubber layer of minke whales captured around Svalbard/Bear Island in the Barents Sea in 2016–2019.

Year	Blubber 2016	2017	2018	2019	Muscle 2016
	(n = 20)	(n = 20)	(n = 20)	(n = 20)	(n = 18)
FA (%*)	36 ± 23^{bc}	31 ± 20^{c}	65 ± 10^{a}	49 ± 14^{b}	4.0 ± 1.7
Blubber thickness (cm)	3.3 ± 0.8^{b}	3.5 ± 0.6^{ab}	3.8 ± 0.5^{ab}	3.9 ± 0.4^{a}	–
14:0	4.99 ± 0.65^{c}	5.20 ± 0.60^{c}	5.89 ± 0.43^{b}	6.35 ± 0.60^{a}	3.37 ± 1.52
16:0	9.90 ± 2.45	9.69 ± 2.01	11.10 ± 0.92	10.92 ± 1.10	16.85 ± 2.05
18:0	2.48 ± 0.66^{a}	2.38 ± 0.39^{a}	1.94 ± 0.32^{b}	2.05 ± 0.39^{b}	7.56 ± 2.10
∑SFA	**19.43 ± 2.40^{b}**	**19.33 ± 2.42^{b}**	**20.79 ± 1.01^{ab}**	**21.34 ± 1.33^{a}**	**29.96 ± 2.08**
16:1n-7	5.91 ± 2.27^{b}	5.72 ± 1.49^{b}	9.05 ± 1.81^{a}	6.36 ± 0.95^{b}	4.59 ± 2.21
18:1n-11	1.27 ± 0.49^{ab}	1.43 ± 0.34^{a}	0.97 ± 0.21^{b}	1.16 ± 0.23^{b}	0.40 ± 0.29
18:1n-9	17.89 ± 2.74^{a}	16.53 ± 2.44^{a}	11.42 ± 1.48^{b}	11.96 ± 1.77^{b}	25.23 ± 1.93
18:1n-7	4.03 ± 1.06^{a}	3.51 ± 0.63^{ab}	3.17 ± 0.58^{b}	2.53 ± 0.49^{c}	5.40 ± 0.82
18:1n-5	0.47 ± 0.08^{b}	0.47 ± 0.05^{b}	0.54 ± 0.03^{a}	0.48 ± 0.03^{b}	0.23 ± 0.07
20:1n-11	1.90 ± 0.86^{ab}	2.02 ± 0.59^{a}	1.03 ± 0.23^{c}	1.50 ± 0.33^{b}	0.65 ± 0.34
20:1n-9	17.50 ± 4.90^{a}	18.88 ± 4.43^{a}	13.61 ± 2.13^{b}	13.35 ± 2.46^{b}	3.07 ± 2.55
20:1n-7	0.55 ± 0.16^{a}	0.58 ± 0.11^{a}	0.43 ± 0.07^{b}	0.33 ± 0.10^{c}	0.14 ± 0.07
22:1n-11	9.63 ± 2.78^{b}	10.15 ± 2.56^{ab}	9.66 ± 1.87^{b}	11.49 ± 1.83^{a}	1.24 ± 0.93
22:1n-9	1.44 ± 0.36^{a}	1.50 ± 0.39^{a}	1.11 ± 0.15^{b}	1.07 ± 0.19^{b}	0.20 ± 0.17
24:1n-9	0.71 ± 0.26^{a}	0.75 ± 0.15^{a}	0.55 ± 0.07^{b}	0.67 ± 0.09^{ab}	0.46 ± 0.20
∑MUFA	**62.93 ± 5.91^{a}**	**63.08 ± 5.28^{a}**	**53.15 ± 3.22^{b}**	**52.51 ± 3.71^{b}**	**43.29 ± 4.63**
18:2n-6	1.82 ± 0.32	1.69 ± 0.17	1.59 ± 0.18	1.69 ± 0.21	2.59 ± 0.66
20:4n-6	0.29 ± 0.11	0.28 ± 0.09	0.26 ± 0.03	0.30 ± 0.05	3.07 ± 1.57
18:3n-3	0.59 ± 0.17^{b}	0.52 ± 0.12^{b}	0.62 ± 0.15^{b}	0.96 ± 0.18^{a}	0.34 ± 0.10
18:4n-3	1.43 ± 0.43^{c}	1.46 ± 0.50^{c}	2.36 ± 0.49^{b}	2.79 ± 0.51^{a}	0.54 ± 0.29
20:4n-3	0.77 ± 0.19^{b}	0.75 ± 0.17^{b}	1.08 ± 0.18^{a}	1.18 ± 0.16^{a}	0.30 ± 0.08
20:5n-3	3.47 ± 1.79^{b}	3.06 ± 0.98^{b}	6.89 ± 1.05^{a}	6.33 ± 1.29^{a}	12.23 ± 3.29
22:5n-3	2.16 ± 0.54	2.07 ± 0.41	2.28 ± 0.39	2.08 ± 0.29	1.40 ± 0.39
22:6n-3	4.13 ± 1.52^{b}	4.86 ± 1.48^{b}	7.28 ± 1.23^{a}	7.45 ± 1.00^{a}	4.33 ± 1.12
∑PUFA	**17.64 ± 4.10^{b}**	**17.59 ± 3.06^{b}**	**26.06 ± 2.50^{a}**	**26.15 ± 2.89^{a}**	**26.75 ± 5.38**
∑PUFA (n-6)	**3.03 ± 0.31^{a}**	**2.85 ± 0.23^{ab}**	**2.66 ± 0.25^{b}**	**2.78 ± 0.29^{b}**	**6.40 ± 1.71**
∑PUFA (n-3)	**13.66 ± 4.05^{b}**	**13.75 ± 3.04^{b}**	**21.65 ± 2.41^{a}**	**22.03 ± 2.82^{a}**	**19.63 ± 4.01**
∑Minor FAs	**6.38**	**6.24**	**6.94**	**6.86**	**5.40**

Note: *The quantitative data are given as amount FA (mg) / 100 mg wet weight blubber and amount FA (mg) / 100 mg dry weight muscle.

samples for $\delta^{15}N$ values. Isotope compositions were measured at the CLIPT Lab (University of Oslo) using a Delta V Advantage Continuous Flow Isotope Ratio Mass Spectrometer (Thermo Scientific, Bremen, Germany) coupled to a Flash Elemental Analyzer (Thermo Scientific, Bremen, Germany). Analytical precision was 0.03 ‰ for $\delta^{15}N$ and 0.05 ‰ for $\delta^{13}C$, as measured in glycine, L-glutamic acid and L-alanine internal standards, calibrated against NBS19 and LSVEC for $\delta^{13}C$, and USGS40 and USGS41 for $\delta^{15}N$. Data for each individual sample are included in Table S10.

2.5. Statistical analyses

Correspondence analysis (CA) using all 60 FAs was executed in the software SIRIUS 11.5 (Pattern Recognition Systems, Bergen, Norway). The FA values were transformed by ln (x + 1), and the means were centred before performing the CA. These transformation methods level out the quantitative differences among FAs and ensure that the variation in the minor FAs counts as much as for the dominating FAs.

For whale samples, differences in blubber thickness, FA concentration and relative composition between years (both sexes are tested together) were tested by One-Way ANOVA and Tukey-Kramer multiple comparison post-hoc tests. Statistical differences were examined using the XLSTAT software (Addinsoft, US), and significance was assigned to p-values < 0.05. A *t*-test of sex differences for each year was also conducted. These latter results are given in supplementary information, Table S4, S5.

The SI data were analysed in R (R Core Team, 2022), using the packages rstatix (Kassambara, 2023), vegan (Oksanen et al., 2022), MixSIAR (Stock and Semmens, 2016; Stock et al., 2018), rjags (Plummer et al., 2022) and ggplot2 (Wickham, 2016). Data were first tested for normality, by taxon and by year and age-class. As multiple groups were found to be non-normal, non-parametric permutational multivariate analysis of variance were applied using distance matrices (adonis2 function in the vegan R package), followed by post-hoc testing (pairwise adonis test) to compare the isotopic differences between minke whale data by year and between prey taxa (results are given in supplementary information, Table S9). Following these preliminary analyses of prey isotope compositions, four groups were formed based on dual isotope similarities: 1. krill (*Thysanoessa* sp. and *Meganyctiphanes* sp., n = 53), 2. *Themisto* spp. amphipods (n = 44), 3. small pelagic fishes (capelin, juvenile cod, juvenile haddock, herring, and polar cod, n = 55), and 4. demersal fishes (adult Atlantic cod and blue whiting, n = 19). No statistical differences were found between years within these groups, so data from 2016 and 2019 were combined for further analyses. Mixing models were run, overall and by year, to determine the relative contribution of these four prey groups to the isotope composition of the minke whales. Predator-prey diet-muscle isotopic discrimination values from fin whales (Borrell et al., 2012) were used, as these values are not currently available for minke whales in the literature. The models were run under the "long" ($3x10^5$ chain length, burn = $2\ x10^5$, thin = 100, chains = 3) setting for three parallel Markov Chain Monte Carlo (MCMC) runs. Convergence was assessed using the default MixSIAR diagnostic Gelman-Rubin and Geweke tests.

3. Results

3.1. Stomach contents

The stomach content inspections revealed that krill (primarily *Thysanoessa* sp.) dominated the diet of minke whales sampled in June 2016 (Fig. 2). In the three following years, which included samples both from June and August, the whales had primarily eaten capelin, while in June 2020 the diet was a mixture of capelin and krill. Gadoid fish were found only in very small amounts in any of sampling years. No significant differences were observed between the sexes in stomach contents.

3.2. Fatty acids

The sampled whales were heavily biased towards females whales in most years (17 out of 20 whales in 2016, 2017 and 2018). But in 2019 there were 10 females and 10 males. However, no sex differences were found in the amount of lipid or in the FA profiles (Tables S3 and S4 in the Supplementary information), so both sexes were pooled for further analyses.

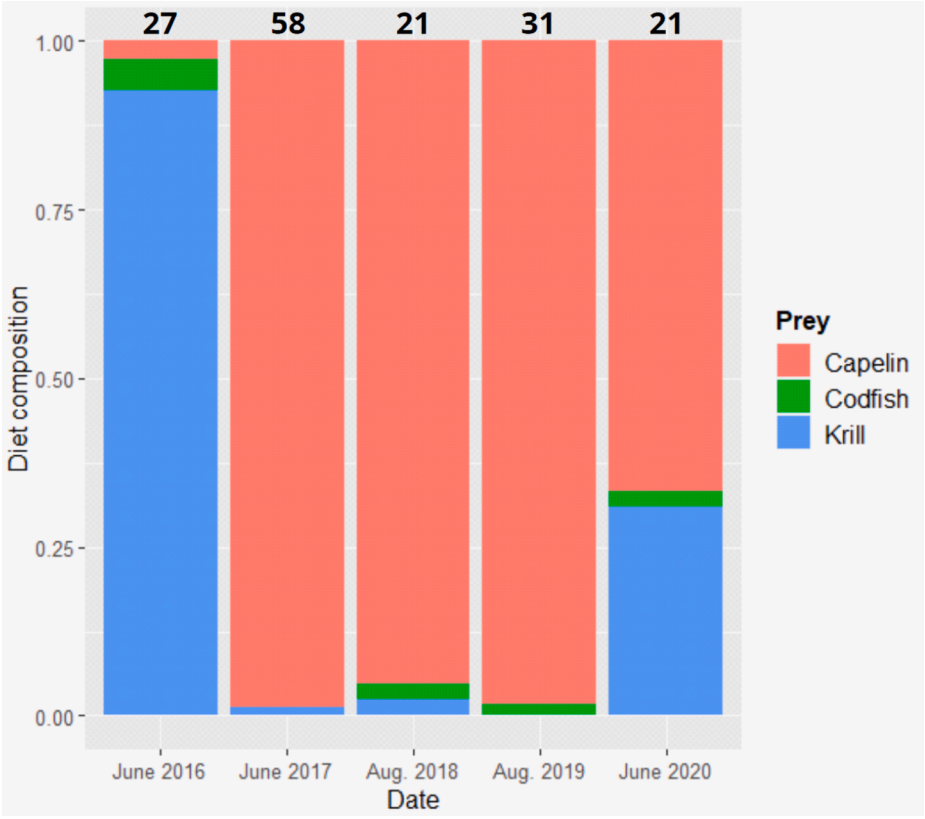

Fig. 2. Diet composition in minke whales – June and August – in the northwestern Barents Sea in 2016–2020. Numbers above columns indicate numbers of stomachs inspected.

There were annual differences in blubber lipid concentrations (measured as FA mg/100 mg wet weight) (Kruskal-Wallis test ($P < 0.0001$) (Fig. 3A), with high blubber lipid contents (more than 50 %) in 90 % of the whales in 2018 and in 55 % of the whales in 2019 (Table S4). None of the whales had below 20 % FAs in the blubber. In contrast, several whales had very low lipid levels in the blubber in 2016 and 2017, with 25–30 % having below 20 % FAs in the blubber. Additionally, only 35 % (2016) and 10 % (2017) of the whales, respectively, had more than 50 % FAs in the blubber in these years.

Blubber thickness was greater in 2019 compared with 2016, while 2017 and 2018 were intermediate and did not differ significantly from the other years (Kruskal-Wallis test, $p = 0.004$) (Fig. 3B). Even though both the blubber thickness and lipid concentration in the blubber were variable, no significant correlation was found between blubber thickness and FA content in the blubber ($R^2 = 0.003–0.06$).

Clear inter-annual differences were found in the blubber FA profiles (see Fig. 4 and Tables 1 and S5). Whales sampled in 2016 and 2017 had relatively lower levels of short-chain saturated FAs (SFAs): 14:0, iso15:0, 15:0, iso16:0 and 16:0, higher levels of monounsaturated FAs (MUFAs):18:1n-9, 20:1n-9, 20:1n-7 and lower levels of polyunsaturated FAs (PUFAs): 16:4n-1, 18:4n-1, 16:2n-4, 16:3n-4, 18:2n-4, 16:2n-7, 18:4n-3, 20:4n-3, 20:5n-3 and 22:6n-3 compared with whales sampled in 2018 and 2019.

Muscle FA profiles (only analyzed in 2016) were different from blubber FA profiles, having higher levels of 16:0, 18:0, 18:1n-9, 20:4n-6 and 20:5n-3, and lower levels of the long-chain MUFAs (20:1n-9 and 22:1n-11) (Table 1).

Correspondence analysis (Fig. 5) showed that FAs profiles from whale blubber were separated from prey samples along CA dimension 1 (explaining 38 % of the variance), with blubber samples from 2016/

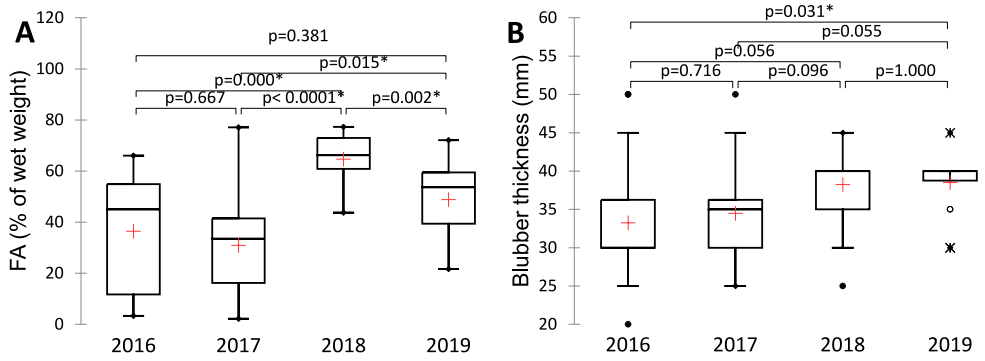

Fig. 3. Box plot (min–max, inter quartile. Median and mean (marked in red)) of FA concentrations in the inner blubber of minke whales (**A**) and blubber thickness (**B**). The data from each year represent samples from 20 whales. The letters show significant differences between the years analysed by Kruskal-Wallis test followed by pairwise comparison for Groups (Steel-Dwass-Critchlow-Fligner procedure / Two-tailed test), p-value < 0.05).

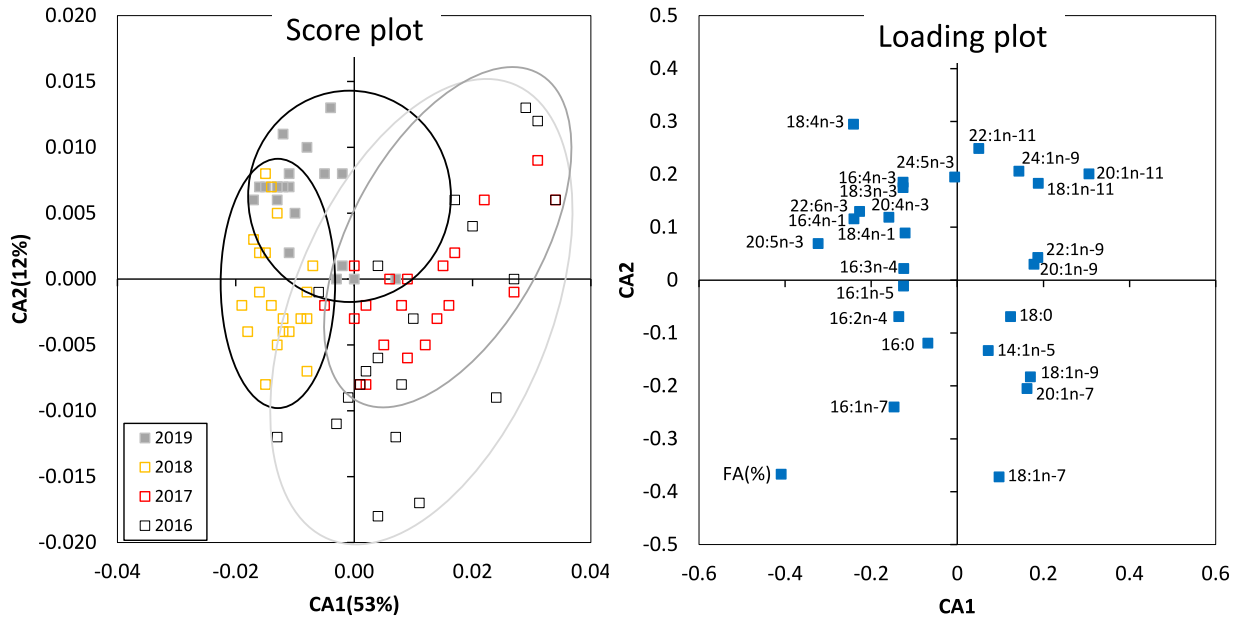

Fig. 4. Score and loading plots from correspondence analysis (CA) of FA profiles (60 FAs) from inner blubber of 40 minke whales captured around Svalbard/Bear Island in the Barents Sea in 2016–2019. The first two axes explain 65 % of the total variance in the dataset (axis 1 = 53 %, axis 2 = 12 %). FAs that had low correlations with the ordination are omitted.

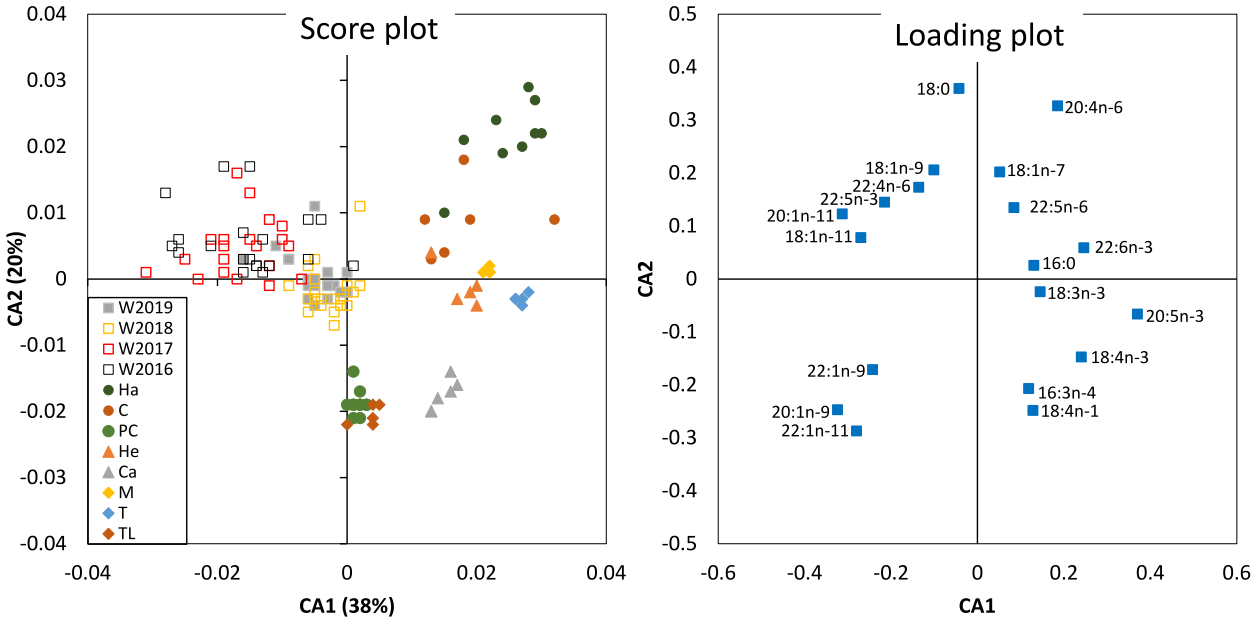

Fig. 5. Score and loading plots from CA of FA profiles (60 FAs) from the inner blubber of 40 minke whales captured around Svalbard/Bear Island in the Barents Sea in 2016–2019 and from 8 potential prey species: haddock (Ha), Atlantic cod (C), polar cod (PC), herring (He), capelin (Ca), *Meganyctiphanes* sp. (M), *Thysanoessa* sp. (T) and *Themisto libellula* (TL). The first two axes explain 58 % of the total variance in the dataset (axis 1 = 38 %, axis 2 = 20 %). FAs with low correlations with the ordination are omitted.

2017 being most different from the prey samples. The loading plot shows that FAs involved in endogenous metabolism; peroxisomal β-oxidation and chain shortening (18:1n-11, 20:1n-11), elongation (22:4n-6, 22:5n-3) and *de novo* synthesis (18:0, 18:1n-9) were responsible for this separation along CA dimension 1. The highest similarity between whale blubber and prey was found for small pelagic fish (polar cod and capelin) and amphipods, *T. libellula*, because of the high relative levels of long-chain MUFAs (20:1 and 22:1). The other potential fish prey species (Atlantic cod, haddock and herring) had much higher levels of PUFAs compared with the whale blubber.

3.3. Stable isotopes

Full stable isotope results of minke whales and potential prey species are shown in Table S10. Based on their $\delta^{13}C$ and $\delta^{15}N$ values, minke whales sampled in the Barents Sea in 2016, 2017 and 2019 were not statistically distinguishable, but whales from 2018 formed a distinct group from the other years, largely due to higher $\delta^{15}N$ values (Table 3, Fig. 6). Due to the low number of males in the samples, it was not possible to test inter-annual isotopic differences between sexes, but no significant differences were found between the isotope compositions of

Table 3
Post-hoc results of pairwise adonis tests with Bonferroni corrections for minke whale muscle $\delta^{15}N$ and $\delta^{13}C$ values by year, significant results ($\alpha \leq 0.05$) are shown in bold.

Years	Df	F	R^2	p	p_{adj}
2016 vs 2017	1	0.625	0.02	0.464	1.000
2016 vs 2018	1	10.289	0.22	**0.003**	**0.018**
2016 vs 2019	1	1.688	0.07	0.215	1.000
2017 vs 2018	1	6.262	0.14	**0.012**	0.072
2017 vs 2019	1	2.826	0.10	0.089	0.534
2018 vs 2019	1	9.541	0.28	**0.002**	**0.012**

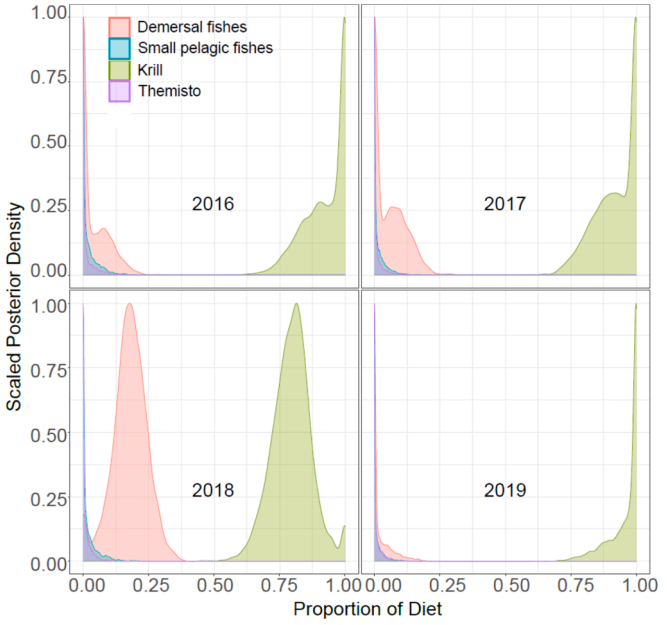

Fig. 6. Density of estimations of diet proportions for each study year for minke whales based on nitrogen and lipid-extracted carbon isotope compositions of minke muscle and prey muscle from MixSIAR.

female versus male whales (post-hoc pairwise adonis test for $\delta^{13}C$ and $\delta^{15}N$ values from male and female whales, df: 1, F: 0.338, R^2: 0.005, p: 0.644).

The results of Bayesian MixSIAR mixing models for minke whale diet, based on nitrogen and lipid-extracted carbon stable isotope compositions of the whales and their potential prey (Fig. 6), were relatively consistent for 2016, 2017 and 2019, with between 92 to 96 % krill (±0.06—–0.08 SD), 2 to 5 % demersal fishes (±0.02–0.05 SD), 1 to 2 % small pelagic fishes (±0.04—–0.06 SD), and *c.* 1 % *Themisto* amphipods (±0.02–0.03 SD). Modelled proportions were, however, very different in 2018, with c. 80 % krill (±0. 08 SD), and c. 18 % demersal fishes (±0.07 SD), while proportions of small pelagic fishes and *Themisto* were similar to the diet in other years, at c. 2 % (±0.03 SD) and 1 % (±0.02 SD), respectively.

We found a significant positive correlation (df: 1, 64; F: 5.349; p = 0.024) between muscle $\delta^{15}N$ values and whale dorsal blubber layer thickness (for all years), while no relationship was found for blubber thickness and $\delta^{13}C$ (Fig. 7).

4. Discussion

4.1. Stomach contents

Common minke whales are known to exhibit spatial, seasonal, and temporal heterogeneity in their feeding habits in Norwegian and adjacent waters (Haug et al., 1996, 2002; Bogstad et al., 2015). Two prey

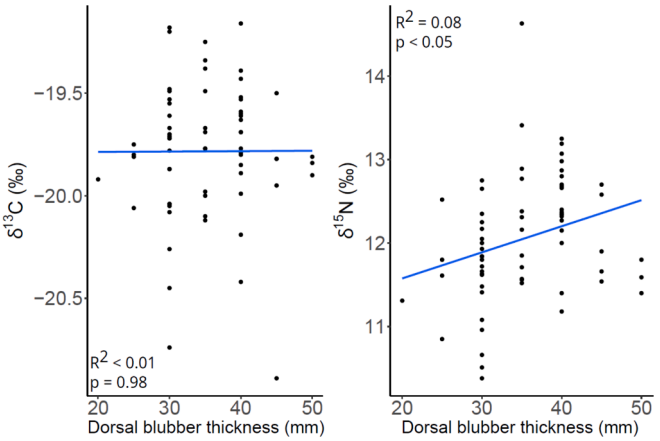

Fig. 7. Relationships between dorsal blubber thickness (mm) and a) lipid-extracted $\delta^{13}C$ values, b) $\delta^{15}N$ values for muscle of all sampled minke whales.

items, capelin and krill, dominated stomach contents throughout the current period of investigation in the northern Barents Sea, spanning the years 2016–2020, regardless of the month of sampling. A few gadoids were also observed in the whale's stomachs. These results are similar to previous studies conducted around Bear Island and in waters around the Svalbard Archipelago in the summer period from around 1950 to 2010. Capelin tends to dominate the diet of minke whales around Bear Island but the importance of krill increases with latitude towards Svalbard, where krill becomes the most important prey for minke whales, particularly on the western side of the archipelago (Jonsgård, 1951, 1982; Nordøy and Blix, 1992; Haug et al., 1996, 2002; Windsland et al., 2007; Meier et al., 2016).

The diets observed for minke whales in this study showed considerable variability inter-annually and by location of sampling. However, there is considerable evidence that capelin, if sufficiently abundant, is the preferred prey of common minke whales, but they are clearly plastic enough in their dietary choices to replace capelin with krill and other prey types when necessary (Lindstrøm and Haug, 2001; Haug et al., 2002). During our study period, the capelin stock was estimated to be below the long-term average, but nevertheless quite abundant in 2017, 2018 and 2020; abundances of capelin were low in 2016 and 2019 (Protozorkevich and van der Meeren, 2022). Krill biomass was close to the long-term average for the area in 2017, above this level in 2019, and below this level in 2016, 2018 and 2020 (ICES, 2022). Clearly, there are some finer-scale patterns in availability that appear to effect what prey is chosen by minke whales in a given area. The latter, and presumably also the general prime preference for capelin by the whales (Lindstrøm and Haug, 2001), may have contributed to the dietary dominance of this species in 2019 which was otherwise a year with a general low capelin and high krill abundance in the Barents Sea.

4.2. Fatty acids

There were clear differences in FA contents of the minke whales between years: in 2016 (36 ± 23 %) and 2017 (31 ± 20 %), most of the whales had low lipid contents in the blubber compared with 2018 (65 ± 10 %) and 2019 (49 ± 14 %). Solvang et al. (2022) studied the blubber thickness in minke whales from 1993 to 2020, and they detected a u-shaped trend with a minimum blubber thickness i.e. low energy reserves around 2015 before it started to increase again in 2020. The low FA content in the blubber seen in 2016/2017 followed by higher FA content in 2018/2019 is in general agreement with these previous findings. This difference might also be explained partly by differences in sampling time, as the samples in 2016/2017 were collected in June and the samples from 2018/2019 were collected in August. The greater lipid reserves in 2018/2019 could be the result of the longer feeding period

during the summer in the most recent years (Næss et al., 1998; Solvang et al., 2022). This explanation also fits with the fact that the FA profiles of the 2018/2019 whales were more similar to the FA profiles of the potential prey species, which fits with the two-month longer assimilation time that these whales had within the Barents Sea, compared to the whales sampled in 2016/2017.

The FA profiles in the common minke whale blubber were most similar to the FA profiles of the small pelagic fish, polar cod and capelin, having high levels of long-chain MUFA (20:1n-9, 22:1n-9 and 22:1n-11). However, there were also clear differences between the FA profiles in the whale blubber and the different prey types. As stated by Meier et al. (2016), minke whale blubber is relatively high in FAs that are likely the products of endogenous metabolism. For example, elongation of 16:0 to 18:0, Δ9-desaturation of 18:0 to 18:1n-9, elongation of 20:5n-3 to 22:5n-3 and 20:4n-6 to 22:4n-6 and chain shortening by peroxisomal β-oxidation of 22:1n-11 to 20:1n-11 and 18:1n-11 can take place within the whales. On the other hand, the levels of long-chain PUFAs 20:5n-3 and 22:6n-3 are much lower in the whale blubber than in the fish and zooplankton, which suggests selective mobilisation of these PUFAs from triacylglycerol in the blubber for use in phospholipids in cell membranes of muscle and other organs (Meier et al., 2016).

In the present study, FA profiles in common minke whale muscle showed high levels of long-chain PUFAs compared with the corresponding blubber samples, especially 20:4n-6 (10 times higher) and 20:5n-3 (3.5 times higher), but not 22:6n-3 (similar levels in both muscle and blubber). This suggests that these long-chain PUFAs (20:4n-6 and 20:5n-3) are especially important for maintaining homeostasis of membrane lipids in common minke whales. Selective mobilisation of 20:5n-3 has been found in several marine mammals during lactation, e.g. hooded seal (*Cystophora cristata*) (Iverson et al., 1995), Weddell seals (*Leptonychotes weddellii*) (Wheatley et al., 2008), and elephant seals (*Mirounga angustirostris*) (Fowler et al., 2014), while selective mobilization of both 20:5n-3 and 22:6n-3 is reported only in grey seals (*Halichoerus grypus*) (Grahl-Nielsen et al., 2000; Arriola et al., 2013).

4.3. Stable isotopes

The stable isotope composition of minke whale muscle was relatively consistent in most years in this study, differing only in 2018, with higher nitrogen isotope values in that year, which suggests higher trophic level feeding. However, there was no difference in carbon isotope compositions between any of the years studied, suggesting that the carbon source supporting the prey did not differ between years, despite different months of sampling. Carbon isotope compositions are related to geographic location of feeding, the degree of pelagic versus benthic and marine versus terrestrial nutrients, as well as the trophic level at which feeding takes place (MacKenzie et al., 2011; Magozzi et al., 2017; Carpenter-Kling et al., 2020). It is known that common minke whale diets can vary throughout the season but, on a longer-term than the dietary and fatty acids measurements (Haug et al., 1995). The sampled whales appear to have integrated prey from similar locations and similar sources of production in all years, and do not appear to have carbon sources recently imported to the Barents Sea. The differences between the longer-term stable isotope results and the diet and FAs analyses have the potential to originate from the integration of isotope signals from areas outside of the Barents Sea. However, if this were the case it would be expected that the isotope values should be higher from more southerly feeding areas (e.g., Trueman et al., 2019), which might be interpreted in the mixing models as being more similar to benthic prey species and less similar to low trophic level pelagic krill, in opposition to the data seen here.

Groups of whales with different stomach contents did not show isotopic differentiation, suggesting similar longer-term diets among year groups of whales.

The mixing models applied to whale samples, using the carbon and nitrogen isotope composition of their most likely prey groups, suggested a predominance of krill in the diet during all years. However, in 2018 there were indications of a higher proportion of demersal fishes (e.g., Atlantic cod and blue whiting), which are relatively high trophic level prey. This was also the year with the highest FA concentrations in the inner blubber, suggesting a positive link between the trophic level of the longer-term diet and the condition of minke whales in the Barents Sea. This explanation is also consistent with the positive relationship between dorsal blubber thickness and nitrogen isotope values. Interestingly, small pelagic fishes were not found to be a significant part of the integrated recent dietary history of these whales based on their isotopic composition, contrary to the results of previous studies (Haug et al., 1996, 2002; Sivertsen et al., 2006; Windsland et al., 2007; Meier et al., 2016). The possible change in diet from small pelagic fishes-dominated diets in these previous studies to a greater quantity of krill and demersal fishes integrated into the muscle of the whales studied here may be a result of observed borealization of the Barents Sea ecosystem (Fossheim et al., 2015; Eriksen et al., 2017). This result might represent a northward continuation of the trend observed by Víkingsson et al. (2014) for common minke whales in Icelandic waters.

4.4. Short- to longer-term trophic behaviour

Overall, the results of the diet and fatty acids analyses indicate that feeding in the hours to weeks leading up to capture was most likely dominated by small pelagic fishes, while the stable isotope compositions suggest that feeding over the prior months may be dominated by krill. Only in 2016 do the very short- and longer-term trophic analyses agree, where krill dominated in both diet and stable isotope composition mixing model probabilities, although there is dissimilarity with the fatty acid measurements. It has previously been observed that minke whales in the northern Barents Sea sequentially prey on krill followed by small pelagic fishes during the feeding season (Haug et al., 1996), similarly to haddock and Atlantic cod in this area, which have been seen to move from high-krill diets in the spring to more fish-dominated diets in summer and autumn (Eriksen et al., 2021).

5. Conclusions

In this study, the different dietary analyses methods, stomach contents, stable isotopes, and fatty acids analyses, gave somewhat different results. However, it must be noted that both the blubber thickness and fatty acid composition (%) were both greatest in 2018, the year in which both the fatty acid and the stable isotope compositions were also the most distinct. This suggests agreement in inter-annual results between the fatty acids and stable isotope data, in particular the $\delta^{15}N$ values and the mixing-model dietary predictions. The differences seen between the different analytical methods are most likely a result of different turnover times, with stomach contents representing the most recent feeding events (hours), whereas the lipid stores likely represent recent weeks of feeding, and stable isotopes in the muscle tissue reflect feeding over periods of months. The differences seen between the analytical results from the three methods might also be related to the availability of krill (which are fatty) earlier in the season, followed by consumption of higher trophic level prey such as fish, as a natural consequence of succession in ecosystems, with plankton biomass probably responding first, and more rapidly, to spring phytoplankton blooms, and higher trophic levels lagging behind (Næss et al., 1998; Haug et al., 2002). This could be misinterpreted as feeding on lower trophic levels when compared to the higher isotope values of prey sampled later in the summer feeding season. However, a change in food chain length between seasons would impact values of both nitrogen and, to a lesser extent, carbon isotopes, but we did not see inter-annual differences in carbon isotope compositions of minke whale muscle. From previous studies, it is known that, in addition to capelin, gadoid fish species such as Atlantic cod and haddock can also be important prey for minke whale early in the season (April-May) around Bear Island (Haug et al., 1996). During their annual spring

migration from south to north (Jonsgård, 1951, 1966) minke whales pass through and feed in southerly areas where herring and gadoid species can be important food sources (Haug et al., 1996, 2002; Windsland et al., 2007; Meier et al., 2016). To achieve the most comprehensive and robust understanding of the diet of minke whales in the Barents Region, it would be necessary to sample the whales and their potential prey and prey abundance dynamics throughout the entire feeding season.

Author contributions

TH, KMMacK, KMK and CL conceived the study. LL conducted the field work. For analyses and statistical interpretation of the data, LL and UL were responsible for the stomach contents studies, SM for the fatty acid studies and KMMacK for the stable isotope studies. All authors contributed to the preparation of the manuscript.

CRediT authorship contribution statement

T. Haug: Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **M. Biuw:** Writing – original draft, Investigation. **K.M. Kovacs:** Writing – review & editing, Writing – original draft, Validation, Investigation, Conceptualization. **L. Lindblom:** Writing – review & editing, Formal analysis, Data curation. **U. Lindstrøm:** Writing – review & editing, Investigation, Formal analysis, Data curation. **C. Lydersen:** . **K.M. MacKenzie:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **S. Meier:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation.

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.

Data availability

The data will be given open access status and be available in the SIOS data access portal (as all other Nansen Legacy data).

Acknowledgements

The authors thank Nils-Erik Skavberg, Michael Poltermann and the crews onboard MS *Reinebuen* and MS *Kato* for all their help during the collection of the whale samples. The Research Council of Norway provided financial support through the project “The Nansen Legacy” (AeN, RCN 276730).

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2024.103267.

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