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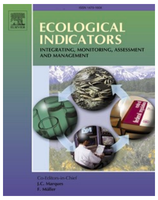

Original Articles

Niches of marine mammals in the European Arctic

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ABSTRACT

The Arctic is warming rapidly, with concomitant sea ice losses and ecosystem changes. The animals most vulnerable to Arctic food web changes are long-lived and slow-growing such as marine mammals, which may not be able to adapt rapidly enough to respond to changes in their resource bases. To determine the current extent and sources of these resource bases, we examined isotopic and trophic niches for marine mammals in the European Arctic using skin carbon (δ^{13}C) and nitrogen ($\delta\ ^{15}$N) stable isotope (SI) compositions from 10 species: blue, fin, humpback, minke, sperm and white whales, bearded and ringed seals, walruses and polar bears, and dietary fatty acids (FAs) in polar bears, walruses and most of the whale species listed here. SI values showed clear species separation by trophic behaviour and carbon sources. Bearded seals, walruses and white whales had the smallest isotopic niches; these species are all resident High Arctic species and are likely to be particularly vulnerable to changes in Arctic ecosystems. We found clear separation between FA groupings driven by pelagic, benthic and planktonic/algal sources: pelagic FAs in all whales, benthic FAs in walruses, and copepod/algae/dinoflagellate FAs in polar bears, with some polar bear compositions approaching those of the whales and walruses. There is strong niche partitioning between study species with minimal functional redundancy, which could impact Arctic ecosystem structure and connectivity if populations of these large nutrient vectors are reduced or lost.

1. Introduction

Marine mammals in the High Arctic cover the trophic spectrum from planktivores to apex predators, pelagic to sympagic to benthic **feed**ers, and from dietary generalists to specialists (Bluhm and Gradinger 2008). All the marine mammal species are K-selected, with relatively slow growth and reproduction, long life-spans and large maternal investments, and may therefore be affected by rapid change in prey resources (Simmonds and Isaac 2007; Kovacs et al. 2011). Such changes can lead to e.g. lower availability of preferred resources, extended migrations or shorter foraging seasons (Víkingsson et al. 2015; Choy et al. 2017; Choy et al., 2020; van Weelden et al. 2021). Quantifying feeding ecology in terms of food-web position, carbon sources and dietary specialisation is important to assess how these species may respond to current and future stressors.

The marine mammal species assemblage of the Barents Sea is currently experiencing the combined effects of intense warming (the Arctic water mass around Svalbard warmed by around 0.9 °C between 2005 and 2016 (Barton et al. 2018), and up to 4.5 °C of warming is projected for the Barents Sea by 2100 (Albouy et al. 2020)) and large reduction in sea ice duration, extent and thickness in the Arctic (Comiso and Hall 2014; Laidre et al. 2015) with concomitant increases in human activities (Kovacs et al. 2011; Stocker et al. 2020). Direct impacts on ice-reliant species such as reduction in breeding habitats can be identified easily, but impacts of changes in marine mammal prey bases and nutrient sources are more difficult to ascertain (Bluhm and Gradinger 2008; Kovacs et al. 2011).

To assess future ecological impacts from changes in prey and nutrient

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sources, it is necessary to determine trophic and isotopic niche baselines. An isotopic niche is defined by an organism's interactions with its environment, including its trophic position, nutrient sources and space use (Newsome et al. 2007; Shipley and Matich 2020). Carbon and nitrogen stable isotope (SI) niche spaces and compositions of fatty acids (FAs) within an ecosystem can be used to assess the ecological niche of species or groups of organisms (Rossman et al. 2016). In the Barents Sea area, the isotope niche space axes are largely defined in a simple, linear way, with nitrogen isotope values (δ^{15}N) increasing with relative trophic position and carbon isotope (δ^{13}C) values increasing from pelagic towards benthic, from terrestrial towards marine and, in some areas, pelagic towards sympagic nutrient sources (Hobson et al., 1995; Hop et al., 2006; Søreide et al., 2013; Tamelander et al., 2006). Comparison of how niches are positioned relative to known species ecologies can allow detection of trophic function, cryptic, i.e. difficult to directly observe, ecology and ecological change (Rossman et al. 2016), and can be used to monitor ecosystem changes and predator-prey relationships over time.

Specialist adaptation to a particular food source can be a successful strategy in stable environments, while animals in variable environments or animals that move over large distances benefit from more generalist foraging strategies (Isaac 2009; Berta and Lanzetti 2020). In a rapidly changing Arctic, it is likely that dietary specialisation and local residency may increase species' vulnerability.

Arctic-resident marine mammals are likely to be more strongly impacted by changes in their local marine ecosystem than migratory, non-resident species, because they are less likely to shift to new areas if local prey resources and environmental conditions become less optimal (Learmonth et al. 2006; MacLeod 2009). This vulnerability is greatest for ice-reliant animals, such as ringed (*Pusa hispida*) and bearded seals (*Erignathus barbatus*) and polar bears (*Ursus maritimus*) (Kovacs et al. 2011; Laidre et al. 2015), which can potentially be forced into suboptimal habitats, e.g. areas where access to preferred prey is diminished, leading to greater metabolic foraging costs (e.g. Laidre et al. 2008; Kovacs et al. 2011; Pagano et al. 2018).

The degree of redundancy in a system defines to a large degree how prone the system will be to collapse or cascading impacts if individual species are extirpated (Sanders et al. 2018); redundancy is low in Arctic ecosystems (Murphy et al. 2016; Blanchet et al. 2019).

In this study, we measure current trophic and isotopic niche properties for the marine mammal species of the European Arctic. The studied species span the full range of ecosystem macrofauna, from obligate planktivores to apex carnivores, and include sympagic, pelagic, benthic and deep-sea feeding species, representing:

Low-trophic level: pelagic zooplanktivores, blue whales (*Balaenoptera musculus*) (Christensen et al. 1992; Gavrilchuk et al. 2014; Tartu et al. 2020); zooplanktivores and piscivores, fin whales (*Balaenoptera physalus*) (Christensen et al. 1992; Víkingsson 1997; Gavrilchuk et al. 2014; Víkingsson et al. 2015; Das et al. 2017; Tartu et al. 2020);

Mid-trophic level: opportunistic species that feed on fish and invertebrates from pelagic and benthopelagic sources, humpback (*Megaptera novaeangliae*) and minke whales (*Balaenoptera acutorostrata*) (Haug et al. 2002; Gavrilchuk et al. 2014; Víkingsson et al. 2015); benthic bivalve specialists that occasionally feed on pinnipeds, walrus (*Odobenus rosmarus*) (Lowry and Fay 1984; Scotter et al. 2019); individual dietary specialists on zooplankton and fish making a generalist population, ringed seals (*P. hispida*) (Yurkowski et al. 2016; Bengtsson et al. 2020); and

High-trophic level: benthic to benthopelagic fish and invertebrate specialists, bearded seals *(E. barbatus)* (Hjelset et al. 1999)*;* benthopelagic, Arctic fish and invertebrate specialists, white whales (*Delphinapterus leucas*) (Dahl et al. 2000; Yurkowski et al. 2016; Loseto et al. 2018; Choy et al. 2020); deep water squid and fish specialists, sperm whales (*Physeter macrocephalus*) (Martin and Clarke 1986; Christensen et al. 1992; Mendes et al. 2007); and polar bears (*U. maritimus*) that preferentially feed on Arctic seal species' blubber but are opportunists, taking any available resources including small odontocete whales, whale carcasses and terrestrial food such as birds/eggs and reindeer, and even plants (Derocher et al. 2000; Derocher et al., 2002; Grahl-Nielsen et al. 2003; Iversen et al. 2013; Prop et al. 2015; Tartu et al. 2016a).

Aside from narwhals, white and bowhead whales, the majority of the whales present in the Barents Sea are long-range migrants that spend the winter at lower latitudes in breeding areas and migrate north to their primary feeding grounds in nutrient-rich, high latitude waters in the spring and summer (Wassmann et al. 2006; Goldbogen et al. 2011; Avgar et al. 2014). Here in the colder waters, they feed on the abundant fish and crustacean populations, such as capelin and krill, to grow and replenish reserves used during breeding and migration, where feeding occurs to a much lesser extent and fasting is common (Brodie 1975; Oftedal 1993; Nash et al. 2013; Aguilar et al. 2014; Christiansen et al. 2014; Aguilar and García-Vernet 2018; Bannister 2018). Blue and fin whales do feed during migration and a lower latitudes as well (Goldbogen et al. 2011; Lydersen et al. 2020), despite reduced availability of prey and increased metabolic costs of foraging. However, lower latitude foraging events are relatively brief compared to feeding in higher latitude, cold-water areas (Bailey et al. 2010; Silva et al. 2013; Silva et al., 2019; Lydersen et al. 2020). These seasonal fasting and feeding patterns may, however, change opportunistically or with altered productivity (De Sá et al., 2009; Bortolotto et al. 2016; Findlay et al. 2017; Baines et al. 2017; Romagosa et al. 2020).

White whales are ecologically different from the other whales studied here as they are smaller, coastal and locally resident around Svalbard year-round (Lydersen et al. 2001; Vacquié-Garcia et al. 2018); bowheads and narwhal are also Arctic endemics that live in the Barents Region but these species are dependent on sympagic drift ice ecosystems and were not included in this study.

Aside from orcas, polar bears are the apex predator in the Arctic marine ecosystem. The Barents Sea polar bear population is comprised of two ecotypes: one that tends to remain resident on Svalbard year-round, and the other that hunts on the progressively diminishing offshore drift ice (Mauritzen et al. 2001; Tartu et al. 2016a; Blanchet et al. 2020).

The Barents Sea pinniped species studied herein are year-round Arctic residents. Walrus and bearded seals prefer shallow, coastal waters for feeding, while ringed seals also dive for prey in deep waters (Lowther et al. 2015; Hamilton et al., 2018; Hamilton et al., 2019). Sea ice decline is reducing the direct transfer of sympagic nutrients to the benthos (Grebmeier et al., 2006; McMahon et al., 2006), with potential for negative effects on benthic productivity levels and thus also impacts on benthic feeders such as walrus and bearded seals. All of the Arctic pinnipeds use ice for hauling out to rest and for pupping, nursing etc., with ringed seals being particularly reliant on ice edges and glacial fronts for feeding, and special snow-on-ice conditions for breeding (Kovacs et al. 2011).

For each marine mammal species in this study, we investigate relative food-web position, degree of specialization in terms of isotopic niche space, functional redundancy by niche overlap, and carbon sources (i.e. pelagic, benthopelagic, benthic or terrestrial). Through these metrics we investigate species-specific resource use and discuss possible impacts of climate change.

2. Methodology

We measured the trophic sources and isotopic niches of marine mammals around Svalbard and surrounding areas of the Barents Sea using carbon and nitrogen SI compositions of skin, and individual dietary-origin FA compositions (Iverson et al. 2004) in blubber or subcutaneous fat. We used Bayesian stable isotope standard ellipse area, corrected for small sample size; SEAc (Jackson et al. 2011), as a metric of diversity and overlap in sources of nutrients.

2.1. Sampling

Samples of skin and blubber were taken from blue, fin, humpback and sperm whales, using a custom-built biopsy dart launched from either an airgun or from a crossbow (see Tartu et al. (2020) and Lydersen et al. (2020) for full details) using a small boat or a helicopter to approach the whales. Samples from white whales were taken from physically restrained animals, captured for tracking studies (Vacquié-Garcia et al. 2018). Ringed and bearded seal samples were collected from animals shot during the annual sport hunt in Svalbard (Bengtsson et al. 2020). Minke whale samples were taken during the Norwegian commercial harvest. Samples from polar bears and walruses were taken from chemically immobilised individuals, according to the methods described in Scotter et al. (2019) and Tartu et al. (2016a). Sampling was approved, where relevant, by the National Animal Research Authority, the Norwegian Animal Care Authority and the Governor of Svalbard (Tartu et al., 2016a, 2020; Villanger et al., 2011; Scotter et al. 2019).

2.2. Stable isotope analyses

Stable isotope compositions of carbon and nitrogen were analysed in 152 skin samples (21 blue, 27 fin, 6 humpback, 17 minke, 5 sperm and 10 white whale samples, 5 bearded and 12 ringed seal samples, 37 walrus samples, and 12 polar bear samples, see Table 1 for sampling by years). We freeze-dried these samples for 48 h at −48 °C before homogenisation. We removed lipids using a 2:1 chloroform-methanol solvent extraction, then thoroughly washed samples in deionised water, before drying and weighing into tin capsules for analysis. Isotope compositions were measured using a Delta V Advantage Thermo-scientific Continuous Flow Mass Spectrometer (Thermo Scientific, Bremen, Germany) coupled to a 4010 Elemental Combustion System (Costech Instruments, Valencia, CA, USA), with analytical precision of 0.2 ‰ for both δ^{15}N and δ^{13}C, as measured in NIST 1577c, tilapia muscle, USGS40 and urea standards.

Table 1

Stable isotope summary statistics by species and year of sampling, with sample numbers for fatty acids, in order of relative trophic position (rTP), with Bayesian ellipse area metrics (‰ squared); TA: total area, SEA: standard ellipse area, SEAc: standard ellipse area corrected for small sample size (Jackson et al. 2011).

Name	SI n	Year	Mean δ^{13}C ± sd	Mean δ^{15}N ± sd	rTP	TA	SEA	SEAc	FA n
Blue whale	3	2014	−18.8 ± 0.2	8.9 ± 0.3					4
	5	2015	−19.0 ± 0.8	9.2 ± 0.2					3
	4	2016	−16.7 ± 0.7	9.6 ± 0.6					5
	4	2017	−19.6 ± 1.6	9.6 ± 0.7					
	4	2018	−18.9 ± 0.7	9.7 ± 0.7					
	1	2019	−19.7	10.0					
All blue	21		−18.7 ± 1.3	9.4 ± 0.6	3	8.25	2.43	2.54	12
Fin whale	2	2012	−20.3 ± 0.4	10.1 ± 0.9					
	3	2014	−19.6 ± 0.5	9.9 ± 0.7					2
	1	2015	−19.7	11.1					2
	2	2016	−17.6 ± 1.1	11.3 ± 1.0					1
	6	2017	−20.1 ± 0.2	10.5 ± 0.6					
	1	2019	−19.4	11.1					
	12	2020	−19.4 ± 0.6	10.8 ± 0.7					
All fin	27		−19.5 ± 0.8	10.7 ± 0.7	3.4	6.08	1.75	1.82	5
Minke whale		2009							9
		2010							84
		2011							20
		2016							20
		2017							27
		2018							20
	17	2019	−19.4 ± 0.4	12.2 ± 1.3					20
All minke	17		−19.4 ± 0.4	12.2 ± 1.3	3.9	3.63	1.48	57	200
Walrus	18	2014	−16.8 ± 0.5	12.7 ± 0.2					31
	19	2015	−16.6 ± 0.5	12.1 ± 0.6					
All walrus	37		−16.7 ± 0.5	12.4 ± 0.5	4.0	2.89	0.71	0.73	31
Humpback whale	1	2013	−20.4	12.0					
	2	2015	−20.2 ± 0.6	11.3 ± 1.7					2
	1	2016	−17.9	13.9					1
	2	2018	−18.9 ± 0.6	13.8 ± 0.9					
All humpback whales	6		−19.4 ± 1.1	12.7 ± 1.5	4.1	3.27	2.25	2.81	3
Sperm whale	5	2020	−16.9 ± 1.4	13.8 ± 0.3	4.4	1.45	1.21	1.62	
Bearded seal	5	2019	−18.6 ± 0.4	15.7 ± 0.5	5.1	0.45	0.42	0.57	
Ringed seal	9	2014	−18.4 ± 0.7	17.1 ± 0.6					
	3	2016	−18.8 ± 1.5	17.0 ± 0.7					
All ringed seals	12		−18.5 ± 0.9	17.1 ± 0.6	5.6	4.11	1.81	1.96	
White whale	1	2013	−16.9	17.8					3
	6	2014	−17.2 ± 0.5	17.5 ± 0.6					5
	2	2015	−17.0 ± 0.2	17.4 ± 0.3					2
	1	2016	−18.1	18.0					5
All white whales	10		−17.2 ± 0.5	17.5 ± 0.5	5.7	1.45	0.71	0.80	15
Polar bear		2012							40
		2013							43
	1	2014	−18.2	18.6					
	4	2015	−19.1 ± 1.1	17.2 ± 1.4					
	5	2016	−18.6 ± 0.9	18.1 ± 1.9					
	1	2017	−18.29	17.96					
	1	2018	−17.90	19.67					
All polar bears	12		−18.6 ± 0.9	18.0 ± 1.5	5.8	4.62	2.12	2.33	83

2.3. Fatty acid analyses

We analysed fatty acid compositions from 349 frozen blubber (12 blue, 5 fin, 3 humpback, 200 minke and 15 white whale samples, and 31 walrus samples) and subcutaneous fat samples (83 polar bear samples), see Table 1 for sampling by years. Samples were methylated, and fatty acid methyl esters analysed by gas liquid chromatography, according to the methods in Meier et al. (2016) for minke whales and Tartu et al. (2016a) for other samples.

We screened all FA data from blue, fin, humpback, and white whales, polar bears and walruses to remove FAs that were not measured in all species, along with any *in-vivo* altered FAs, leaving only dietary source FAs, and then to remove FAs comprising <1 % of dietary FA compositions by mass in all samples (Mayzaud and Ackman 1978; Iverson et al. 2004; Falk-Petersen et al. 2004; Linder et al. 2010; Parrish 2013; Chavarie et al. 2016; Chavarie et al., 2020; Kohlbach et al. 2018). We then renormalized data on the compositions of the remaining 23 dietary FAs to 100 % within each animal to facilitate comparisons.

2.4. Statistical analyses

We performed all statistical analyses in R statistical programming language (R Development Core Team, 2011). We calculated and compared the Bayesian stable isotope niche of 95% ellipses and their overlaps (proportion of overlap relative to non-overlapping area), including standard ellipse areas corrected for small sample numbers (SEAc), using the SIBER package (Jackson et al., 2011). We use these SEAc values throughout in comparative discussions of niche sizes. We tested nitrogen and carbon isotope data for normality by Shapiro-Wilks test using the RVAideMemoire package, and found δ^{13}C data for fin and white whales, bearded seals and polar bears and δ^{15}N data for white whales to be non-normal, so we compared isotope compositions between species pairs using Wilcoxon signed rank tests (Hervé 2021) with Bonferroni correction ($\alpha = 0.025$) (Rice 1989).

We investigated prevailing dietary FA compositions by correspondence analysis to determine groupings of animals and which FAs were driving the groupings (Fig. 2). We performed analyses and made plots using ggplot, FactoMineR and factoextra packages in R (Lê et al. 2008; Wickham 2016; Kassambara and Mundt 2020), and then edited the plots for aesthetics and labelling in InkScape Vector Graphics Editor (Inkscape Developers, 2020).

We calculated relative trophic position (rTP) for each species using the following equation:

$$rTP = \left(\frac{\delta^{15}N_{Sp} - \delta^{15}N_{base}}{\Delta^{15}N_{T-D}}\right) + rTP_{base}$$

where $\delta^{15}N_{Sp}$ and $\delta^{15}N_{base}$ are the mean δ^{15}N values of the species of interest and of the species used as a proxy baseline, respectively, $\Delta^{15}N_{T\text{-}D}$ is the tissue-diet fractionation value (change in δ^{15}N between each trophic level) and rTP_{base} is the relative trophic position of the proxy baseline species. Here, we assigned blue whales as the rTP_{base} with a value of 3, and $\Delta^{15}N_{T\text{-}D}$ a value of 3 as this is a reasonable estimate across highly variable marine animals and, for the purposes of this work, is simply a relative scaling factor (Hobson and Welch 1992; Hobson et al. 1996; Hoekstra et al. 2002; e.g. Matthews et al. 2020).

2.5. Data

Data are available from MacKenzie et al., (2022). All walrus, and some blue ($n = 18$) and fin ($n = 12$) whale SI data have been published previously (Routti et al. 2019; Scotter et al. 2019; Tartu et al. 2020), as have FAs data from minke whales (Meier et al. 2016) and polar bears (Tartu et al. 2016a; Tartu et al., 2016b).

3. Results and discussion

Summary SI statistics are in Table 1.

There was some species overlap in trophic level (δ^{15}N) or in carbon source (δ^{13}C), but the greatest overlap in Bayesian SI ellipses, between blue and fin whales, was only 32% (Table 2), although blue whales have significantly more variable δ^{13}C values (Table 1, F-test $F = 2.7693$, $df = 20$, $p < 0.05$).

3.1. Isotopic niche

Table 2 shows statistical comparisons between species SI values and Bayesian ellipses. Despite relatively small sample sizes in several species, mean δ^{15}N values broadly followed expected patterns based on previously published feeding ecologies (Gavrilchuk et al. 2014; Linnebjerg et al. 2016; Das et al. 2017), increasing from zooplanktivorous blue whales to the apex predator, polar bears (Table 1). We show relative trophic positions (rTP) for the species investigated (Fig. 1, Table 1).

Fin whales had slightly higher δ^{15}N values compared to blue whales (Table 2b), consistent with both blue and fin whales feeding on pelagic crustacea such as krill and amphipods, while the fin whales also feed on fishes such as herring and capelin (Christensen et al. 1992). Contrary to Blanchet et al. (2019), the present study found minimal niche overlap between fin and humpback whales (Table 2a). Our results are therefore in agreement with previous studies that suggest that both target small, lipid-rich fishes (Gavrilchuk et al. 2014), but fin whales are more constrained to lower trophic level prey while humpback whales have a larger isotopic niche, extending to relatively higher trophic level prey (Løviknes et al. 2021). The range of δ^{15}N values within humpback and minke whales and polar bears confirm previous studies suggesting that these species are flexible, generalist feeders across multiple trophic levels or regions of different isotopic baselines (Christensen et al. 1992; Tartu et al. 2016a; Silva et al. 2019; Cade et al. 2020). The diverse feeding strategies in polar bears, demonstrated by their range of stable isotope compositions (Fig. 1), reflect a typical polar bear diet, with most individual bears likely feeding on marine mammals, but with some individuals having lower SI values, suggesting that they fed lower in the trophic chain on more terrestrial prey, perhaps reindeer (*Rangifer tarandus platyrhynchus*), consistent with previous studies (Tartu et al. 2016a; Hansen et al. 2019). Active predation on reindeer by polar bears in Svalbard has been reported on several occasions (Derocher et al. 2000; Stempniewicz et al. 2021), and in recent years bears have increasingly plundered bird colonies, eating eggs and chicks (Prop et al. 2015). The observed polar bear dietary breadth is, to an extent, echoed in FA compositions (Fig. 2, see *3.3 Fatty acids source*, below).

White whales are resident year-round in Svalbard waters and their relatively high δ^{13}C values are consistent with feeding much more coastally and benthically, and on prey with more sympagic carbon contributions compared to the other whales in the Barents Sea ecosystem (see Lydersen et al. 2001; Vacquié-Garcia et al. 2018).

Walrus individuals clustered tightly together; SI values indicated a consistent, population-wide low trophic level benthic diet (Table 1, Fig. 1), in agreement with previous studies (Lowry and Fay 1984; Scotter et al. 2019), that is relatively specialised and separated from other species analysed here (Fig. 1, Tables 1 and 2).

In the Barents Sea ecosystem, the δ^{13}C composition of each species (Table 1) reflects their relative use of pelagic- to benthic-, coastal- to offshore-, and/or terrestrial- or sympagic-source carbon (Hobson et al., 1995; McMahon et al., 2021; Tamelander et al., 2009; Tamelander et al., 2006). Consistent with previous studies (Pauly et al., 1998), mean δ^{13}C values increased from pelagic-feeding fin whales to benthic-feeding walruses (Fig. 1, Table 1), and species with a greater assumed intake of benthic or deep-water prey in their diet: walruses and white and sperm whales, had elevated δ^{13}C values (Table 1). In general, it is thought that the vast majority of food for all the species studied, and therefore the dominant proportion of proteins and fats measured in this

Table 2

a. Bayesian 95% ellipse overlap as a proportion of the non-overlapping area of marine mammal species skin δ^{15}N and δ^{13}C values (Jackson et al. 2011); and 2b. significance of pairwise comparisons (with Bonferroni correction (Rice 1989), $\alpha = 0.025$, Wilcoxon rank test, significant differences in bold) between δ^{15}N values (upper right) and δ^{13}C values (lower left).

2a		Blue whale	Fin whale	Minke whale	Walrus	Humpback whale	Sperm whale	Bearded seal	Ringed seal	White whale	Polar bear
Blue whale	**Proportional ellipse overlap**		0.32	0.09	<0.001	0.08	<0.001	<0.001	<0.001	<0.001	<0.001
Fin whale				0.26	<0.001	0.17	<0.001	<0.001	<0.001	<0.001	<0.001
Minke whale					<0.001	0.26	0.08	0.02	<0.01	<0.001	<0.01
Walrus						0.01	0.05	<0.001	<0.001	<0.001	<0.001
Humpback whale							0.12	0.05	<0.001	0.01	<0.001
Sperm whale								<0.001	<0.001	<0.001	<0.001
Bearded seal									0.15	0.08	0.09
Ringed seal										0.21	0.30
White whale											0.06
2b		**δ ^{15}N p-value**									
Blue whale	**δ^{13}C p-value**	-	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Fin whale		**<0.01**	-	**<0.001**	**<0.001**	**<0.01**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Minke whale		**<0.025**	0.26	-	0.87	0.44	**<0.025**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Walrus		**<0.001**	**<0.001**	**<0.001**	-	0.36	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Humpback whale		0.29	0.95	0.91	**<0.001**	-	0.26	**<0.01**	**<0.001**	**<0.001**	**<0.001**
Sperm whale		**<0.025**	**<0.001**	**<0.001**	0.61	0.028	-	**<0.01**	**<0.001**	**<0.001**	**<0.001**
Bearded seal		0.77	**<0.01**	**<0.001**	**0.001**	0.44	0.026	-	**<0.001**	**<0.01**	0.03
Ringed seal		0.61	**<0.1**	**<0.01**	**<0.001**	0.25	0.04	0.41	-	0.12	**<0.025**
White whale		**<0.01**	**<0.001**	**<0.001**	**0.01**	**<0.01**	0.82	**<0.01**	**<0.001**	-	0.05
Polar bear		0.60	**<0.01**	**<0.01**	**<0.001**	0.26	0.04	0.62	0.97	**<0.001**	-

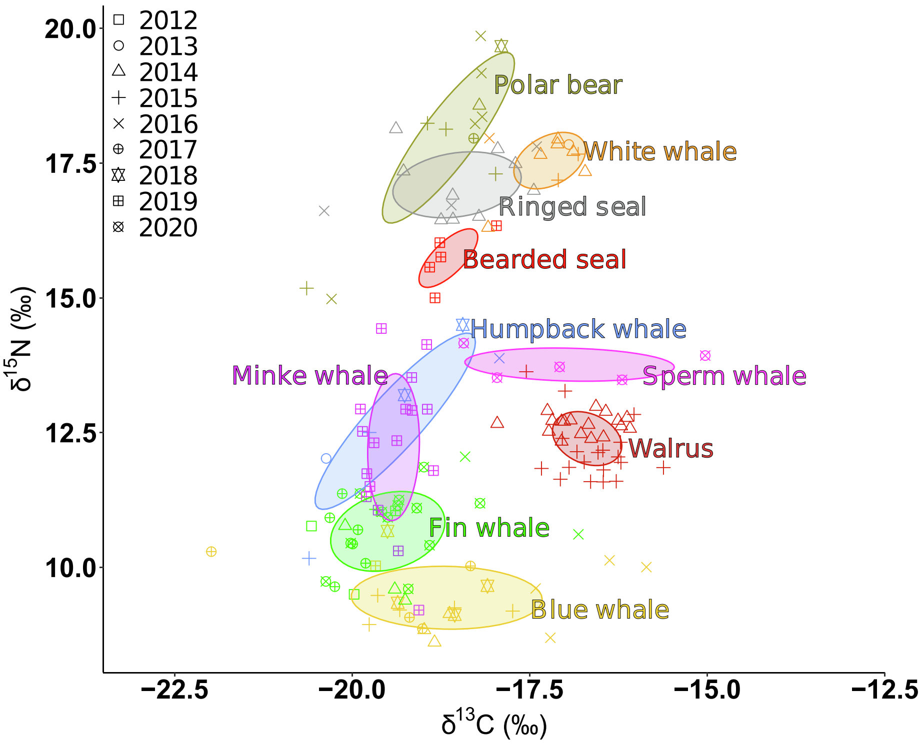

Fig. 1. Carbon and nitrogen SI skin values from blue, fin, humpback, minke, sperm and white whales, walrus, bearded and ringed seals, and polar bears. Colours indicate species, symbol shapes indicate sampling year, ellipses are 40% prediction areas (approximately equal to a standard ellipse (Jackson et al. 2011; Jourdain et al. 2020)) for each species for multivariate normal distribution. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

study, originate in the northern feeding areas (Kshatriya and Blake 1988; Hazen et al. 2015; Guilpin et al. 2019). In 2016, however, blue whales had higher than expected δ^{13}C values for an animal feeding on pelagic prey, particularly krill (*Thysanoessa* and *Meganyctiphanes* spp.) within the Barents Sea, which would place them within the benthic nutrient pathway (Tamelander et al. 2006). Given that this species is a highly migratory pelagic planktivore, the carbon isotope composition measured in 2016 likely originated from warmer waters with an elevated δ^{13}C baseline (Silva et al. 2019). Sperm whales also showed a wide range of δ^{13}C values, where the elevated values may originate either from warmer waters as with the blue whale, or from much deeper feeding on prey in ecosystems with strong depth-based isotopic remineralisation (Cherel et al. 2009). The origin of these elevated carbon isotope values in other ecosystems suggests that these two species may represent large vectors of nutrient transfer in this Arctic ecosystem.

3.2. *Specialisation*

Niche space in carbon and nitrogen SI composition provides a measure of ecological range (Newsome et al. 2007; Fry and Davis 2015).

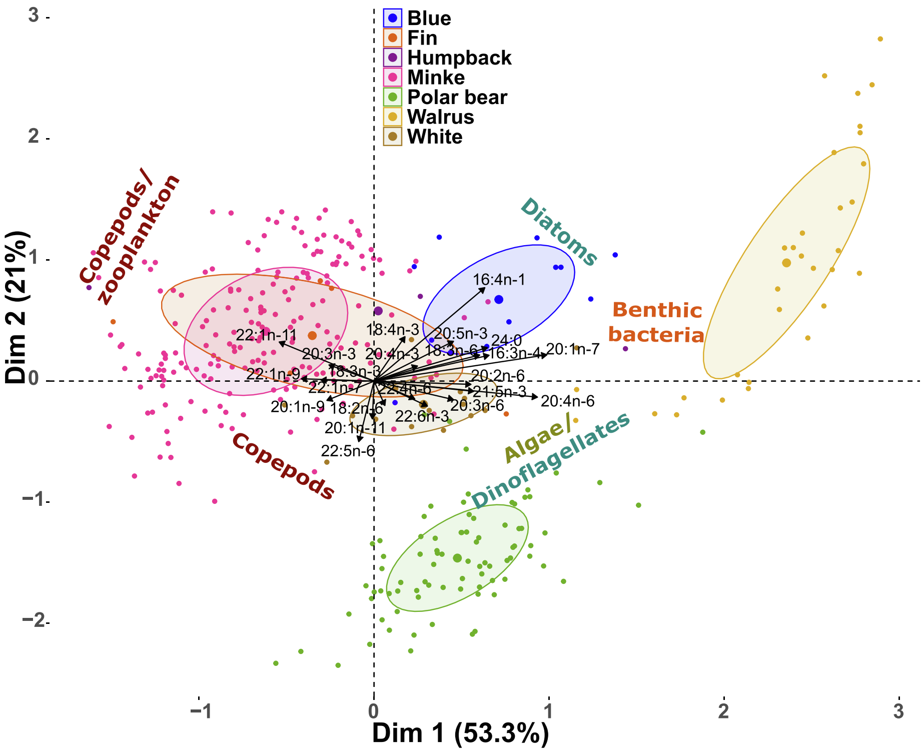

Fig. 2. Correspondence analysis of blubber and subcutaneous fat dietary fatty acids compositions from blue, fin, humpback, minke and white whales, walruses and polar bears; larger symbols are species centroids, ellipses cover 40% of the species data; n.b. there were insufficient humpback whale samples (n = 3) to calculate an ellipse. The main fatty acids driving the groupings (arrow length indicates contribution strength) are labelled according to their origins; individual animal values by contribution to each dimension are in Table S1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Species with smaller isotopic niche area (SEAc) are often more specialised and therefore may be more vulnerable to change (Dulvy et al. 2003; Newsome et al. 2012; Yurkowski et al. 2016). A small isotopic niche could also result from feeding on a wide range of items in consistent proportions among individuals, although this is less likely than feeding on a smaller range of prey types. Isotopic niche area increased from the smallest niche in bearded seals to the largest in the generalist humpback whales (Fig. 1, Table 1). In blue and fin whales, and to some extent also in humpback whales, the niche area was enlarged by high δ^{13}C values in samples taken during 2016 (Fig. 1, Table 1), which might indicate extensive feeding in warmer waters prior to sampling in that year. The larger species niches mostly extended along a single isotopic axis (Fig. 1, Table 1), apart from those of the generalist feeders (humpback whales and polar bears), indicating population flexibility in either trophic level (minke whales) or pelagic-benthic/coastal-offshore/sympagic-open water prey sources (ringed seals, sperm whales).

The specialist species, exemplified by the walrus, tended to have smaller niches (Table 1, Fig. 1). This species in particular may be affected in the long-term by borealisation of the ecosystem, which tends to result in retention and recycling of nutrients in the pelagic component of the food web with less export to the benthos (Bluhm and Gradinger 2008; Fossheim et al. 2015), although Scotter et al. (2019) suggest that the Svalbard population is currently below its carrying capacity. White whales around Svalbard are coastal specialists that are close to the apex of the Barents Sea ecosystem. Their enriched carbon isotope composition may originate from sympagic production fuelling their preferred prey, ice-reliant gadoids (Lydersen et al. 2001; Choy et al. 2017; Choy et al., 2020; Vacquié-Garcia et al. 2018; McMahon et al. 2021), which may confer additional vulnerability to changes from borealization.

Polar bears had the third largest niche of the species assessed here (Table 1, Fig. 1), demonstrating their adaptability in the prey that they can take, but these apex predators are vulnerable to factors such as dwindling sea ice reducing access to their optimal prey, ice-associated seals and whales (Simmonds and Isaac 2007; Pagano et al. 2018; Moore and Reeves 2018).

The more specialized species may be particularly vulnerable to multiple effects of change and disturbance simultaneously, including loss of appropriate habitat and of cold-water specialist prey (Laidre et al. 2008; Kovacs et al. 2011; Descamps et al. 2017). In the Barents Region, this group includes walruses (benthic specialists), bearded and ringed seals (individual specialists) and white whales (narrow dietary and location preferences).

3.3. Fatty acids source

Prevailing (>1%) dietary source FA composition data strongly divided the study species into three groups according to the origins of the FAs (Fig. 2) (Mayzaud and Ackman 1978; Iverson et al. 2004; Falk-Petersen et al. 2004; Linder et al. 2010; Parrish 2013; Chavarie et al. 2016; Chavarie et al., 2020; Kohlbach et al. 2018; Jónasdóttir 2019).

Divisions and groupings of FAs in the correspondence analysis (Fig. 2, Table S1) were largely driven by benthic-origin dietary FAs (originating from benthic bacteria, diatoms and algae) in walruses, versus pelagic-origin FAs (mainly copepods) in all whale species along dimension 1, while dimension 2 separated more diatom-origin FAs from more dinoflagellate- and algae-origin FAs in polar bears and, to a lesser extent, white whales. It is interesting to note that, while most polar bears were quite separate from both whales and walruses, some individual bears also showed values close to both the whales, particularly the white whales, and walruses, sometimes within individual bears sampled repeatedly in different seasons or years. The clustering together of all whale species suggests a relatively common, zooplankton-driven source of prevailing dietary lipids within this group relative to the other groups. The FAs compositions of all whales were grouped together and separated from both walruses and polar bears in their dietary-origin fats, suggesting feeding on fats originating from copepod-based pelagic ecosystems. Blue and white whales were relatively peripheral, although still strongly included within this group, suggesting additional incorporation of dietary fats from other sources than the broad whales group, including those originating in diatoms and algae. As blue whales are obligate feeders on pelagic plankton, particularly krill (Kawamura 1980), this result may indicate incorporation of dietary FAs from producers in different ecosystems, as also suggested by blue whale carbon isotopic composition (Fig. 1, Table 1) (Silva et al. 2019). The results demonstrating dietary lipid sources here echo to a large extent those of the species separations and similarities in carbon sources, as shown by the $\delta^{13}C$ values, with the exception of the polar bears. Our results show that the FAs in these mammals contain information on the ecosystem origin of fats, and may possibly reveal behavioural changes with temporally repetitive sampling.

4. Conclusions

Using combined SI and FA analyses, we have empirically defined the relative structure, trophic function, nutrient sources and degree of specialisation of marine mammals feeding in the Arctic waters around Svalbard. We have also identified a few species that likely feed a significant part of the year in other ecosystems, i.e. the blue and possibly sperm whales, with implications for nutrient transfer to the Arctic region. Echoing results from West Greenland (Linnebjerg et al., 2016), we find strong niche partitioning and minimal between-species functional redundancy, with a maximum niche overlap between any two species of 32%. The patterns found here suggest that potential ecosystem-scale effects could result from reduction or loss of any of these vulnerable species, and that, reciprocally, ecosystem changes could result in reduction or loss of these species in the European Arctic.

Ethics statement

Sampling procedures for blue, fin, humpback, sperm and white whales, polar bears, and walruses were approved by the National Animal Research Authority, the Norwegian Animal Care Authority and the Governor of Svalbard. Ringed and bearded seal samples were collected from animals shot during the annual sport hunt in Svalbard by hunters with "big game" licenses. Minke whale samples were taken from the Norwegian commercial harvest. See references (Villanger et al. 2011; Tartu et al., 2016a; Tartu et al., 2020; Scotter et al. 2019; Bengtsson et al. 2020) for details.

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 data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.108661 and in MacKenzie et al. (2022).

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