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Ecological niche partitioning between baleen whales inhabiting Icelandic waters

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ABSTRACT

The highly productive waters off Iceland are an important feeding ground for baleen whales. Five balaenopterid species coexist there during the summer feeding season: the blue whale, the fin whale, the sei whale, the humpback whale and the common minke whale. For capital breeders such as baleen whales, niche partitioning and reduced interspecific competition during their stay in the feeding grounds may be critical for the completion of their annual cycles and the long-term stability of populations. Coexistence often entails spatio-temporal or trophic segregation to avoid competitive exclusion. With the aim of studying how these species share habitat and trophic resources, we analyzed the δ^{13}C, δ^{15}N and δ^{34}S values in skin samples. Bayesian stable isotope mixing models to calculate compositional mixture of food sources showed that most species segregate by consuming different prey. Segregation was further enhanced by some degree of spatio-temporal exclusion. Overall, clear ecological niche partitioning was apparent between all species except between blue and fin whales. All the species consumed krill and, except for the common minke whale, this was the dominant prey. Among baleen whales, common minke whales and humpback whales were the major predators of sand eel, capelin and herring. In humpback whales, a strong reliance on krill may explain the apparently low rates of local entanglement in fishing nets as compared to other areas. Except for the blue whale, all species have shown evidence of adapting to shifts in prey availability and thus suggested capacity to cope with variability. However, in a scenario of increasing environmental variability associated to global warming, the overlap between ecological niches may have to decrease to allow long-term coexistence.

1. Introduction

The ecological niche of a species can be understood as a multi-dimensional volume whose axes represent environmental and trophic variables and in which every point corresponds to a state of the environment which permits the survival of that species (Hutchinson 1957). Overlap between niches of species that co-exist in a given ecosystem should be necessarily limited to avoid an excessive competition (MacArthur and Levins 1967, Schoener 1983) that may end up with the exclusion of one of the competing species (Hardin 1960, Pianka 1974).

Marine organisms show consistently higher frequencies of competition than terrestrial ones, as do large-sized organisms compared to smaller ones (Connell 1983). Baleen whales or mysticetes are marine organisms and include the largest animals on Earth. They are filter feeders and all of them, except the gray whale (*Eschrichtius robustus*), which mostly preys on benthic crustaceans, exploit prey that thrive in the water column, a fact that inevitably involves some degree of interspecific competition (Mori and Butterworth 2006). After centuries of exploitation, once protection came into force the recovery of the various species and populations has been heterogeneous (Best 1993, Clapham et al., 2008, Thomas et al., 2016) and this has triggered debate on the potential effect of interspecific competition for food and its interplay with the long-term demographic trajectory of populations (Clapham and Brownell 1996, Friedlaender et al., 2009, Konishi et al., 2008). Similar debate has been raised with regards to the competition of baleen whales with commercial fisheries, and this has led in some instances to the proposal that a reduction in whale biomass may translate into a corresponding increase in the species consumed by whales which would then

become available to fisheries (Schweder et al., 2000). This has become an argument to support whaling independently of their direct economic exploitative benefits (Morissette et al., 2012, Ruzicka et al., 2013).

All this demands for a more precise delineation of the ecological niches of baleen whales. Although both diet and ecological niche are dynamic and may vary ontogenetically and between seasons and years responding to environmental shifts (Gómez-Campos et al., 2011, Fleming et al., 2016), niche delineation shall permit a better understanding of the place of baleen whales in ecosystems. In particular, it should allow an accurate integration of these organisms as functional groups in trophic web models (Jusufovski et al., 2019) and in this way contribute to the in-depth assessment of potential competition between baleen whales and fisheries (Stefánsson et al 1997). Moreover, projections on the impact that climate change may have on baleen whales point to population declines as a consequence of reduced prey from warming and increasing interspecific competition between whale species or between whales and fisheries (Tulloch et al., 2019; Bogstad et al., 2015). In this scenario, the need for reliable information on diet composition and habitat use is particularly urgent in polar ecosystems, where both the ecosystems and their marine mammal populations are expected to experience substantial environmental pressures caused by the foreseen climate shifts (Huntington 2009, Moore et al 2019).

Traditional methods for determining feeding ecology, such as fecal analysis, stomach contents analyses, or observations of feeding behavior provide only information of the most recently consumed prey, and thus yield an incomplete picture of overall diet, and can be biased by differences in the digestibility of prey and in the easiness of species-identification of body parts (Bowen and Iverson 2013, Trites and Spitz 2018). The stable isotope composition of the tissues of an individual contains the label of both the assimilated diet and the environment in which the individual lives. Consequently, tissue stable isotope analysis has become a useful complementary tool to investigate the place of wild animals in their ecosystems (Kelly 2000, Newsome et al., 2010). The use of tissues with relatively high turnover, such as skin with a turnover of a few months (Busquets-Vass et al., 2017), can be used to draw stable isotope niches that reflect the bionomic elements sustaining organisms in a given area and season, and thus infer the ecological niches of cohabiting species (Newsome et al., 2007, Pinela et al., 2010, Gavrilchuk et al., 2014). Although most studies of this nature rely on the application of stable isotope biplots (usually $\delta^{13}C$ and $\delta^{15}N$), the strength of the assessment increases if the stable isotopes of further elements (e.g. $\delta^{34}S$) are incorporated into the analysis because the various elements contribute different information (Connolly et al., 2004; Swanson et al., 2015). Thus, while all isotope ratios reflect baseline levels (McMahon et al., 2013), $\delta^{15}N$ and, to a lesser extent, $\delta^{13}C$ values vary with trophic level. $\delta^{13}C$ values also provide general information about spatial distribution because they mirror the primary C sources and thus tend to be higher in coastal or benthic primary producers than in offshore or pelagic primary producers. Finally, $\delta^{34}S$ values decrease with freshwater inputs and therefore also vary with proximity to coast (e.g. Borrell et al., 2021).

Iceland (63–66°N) is located just at the Arctic Circle, at the juncture of Arctic and North Atlantic oceans, and the high productivity of its waters makes them an important foraging area for baleen whales during the summer (Sigurjónsson, 1995). The most common species there are the common minke whale (*Balaenoptera acutorostrata*), the fin whale (*Balaenoptera physalus*), the sei whale (*Balaenoptera borealis*), the humpback whale (*Megaptera novaeangliae*) and the blue whale (*Balaenoptera musculus*). Although a small part of the population of some or all of these species may remain around Iceland throughout the year, the largest component of all species undertakes annual migrations and alternate low-latitude breeding grounds in winter with the high-latitude Icelandic feeding grounds in summer (Sigurjónsson and Víkingsson 1997, Magnusdottir and Lim 2019, Lydersen et al., 2020). The coexistence of these five species with similar ecological requirements in Iceland is intriguing, and leads to questioning how they share the available

resources to avoid competitive exclusion. In-depth studies on diet have been conducted on the two species that have been exploited commercially until recent times, the common minke whale (Sigurjónsson et al., 2000, Víkingsson et al., 2014) and the fin whale (Víkingsson 1997), but information on the diet composition and ecological niche of the other species is scant or absent. In addition, in the last decades the effects of global warming have become apparent in the oceanic ecosystem off Iceland (Sarafanov et al., 2007, Pálsson et al., 2012b) and this has led to changes in the composition, distribution and abundance of numerous species that constitute baleen whale prey (Stefansdottir et al., 2010, Silva et al., 2014, Víkingsson et al., 2014; Gíslason et al., 2009; Astthorsson et al., 2012). These changes necessitate continuous re-evaluation of feeding and habitat-use parameters.

Here we present results of a study conducted through the stable isotope analyses of three elements (nitrogen, carbon and sulfur) in skin samples from the five baleen whale species inhabiting Icelandic waters. While our first objective was to investigate the diet composition and potential overlap in trophic niches of these species in Iceland, the study also allowed to gain some perspective on their interaction with the local fisheries as well as on plausible trends in their ecology in a scenario of global warming.

2. Material and methods

2.1. Sample collection and preparation

Details about the sampling of skin from the baleen whale species are shown in Table S1. The skin samples from humpback and blue whales were collected using biopsy darts shot to free-ranging individuals during the summer, while for sei and fin whales they were obtained from individuals caught off West Iceland, and for common minke whales from individuals taken by different boats around Iceland, all of them also collected during the summer. In all cases, skin was obtained from the dorsal region of the central portion of the body trunk. Although some variation may exist in the precise body location sampled, this is not expected to affect the study as skin has been shown to be a homogeneous tissue with regards to its stable isotope composition (Borrell et al., 2018b). Krill samples were obtained from fresh stomach contents from fin whales caught off W Iceland in 2018 and flensed at the Hvalur H/F station. All samples were preserved at −20 °C. The stable isotope values from other prey consumed by the whales were obtained from the literature.

Prior to analyses, the samples were dried for 24 h at 50 °C, and ground to powder using a mortar and pestle. To avoid the decrease of $\delta^{13}C$ values produced by lipids (DeNiro and Epstein 1977), the lipidic fraction was removed by soaking the skin samples in a chloroform/methanol (2:1) solution following the Folch method (Folch et al., 1957) and shaking them with a rotator for 24 h . This process was sequentially repeated three times, and samples were dried before analysis.

2.2. Stable isotope analyses

For carbon and nitrogen analyses, powered samples of approximately 0.3 mg of skin and 1 mg of krill were weighed into tin capsules. Samples were loaded and combusted at 1000 °C and analyzed using a continuous flow isotope ratio mass spectrometer (ThermoFinnigan Flash 1112 elemental analyzer; CE Elantech, Lakewood, NJ, USA), coupled to a Delta C isotope ratio mass spectrometer via a ConFlo III interface (both from ThermoFinnigan, Bremen, Germany). For sulfur analyses, powered samples of approximately 2 mg of skin were weighed into tin capsules. Samples were loaded and combusted at 1030 °C and analyzed with an Elemental Analyzer (Carlo Erba 1108) coupled to a Delta Plus XP isotope ratio mass spectrometer via a ConFlow III interface (both from Thermofisher).

The analytical results are presented according to the delta (δ) notation, where the relative variations of stable isotope ratios are expressed

in parts-per-thousand (‰) compared to predefined standards:

$$\delta X = [(R\ sample/R\ standard) - 1] * 1000$$

where X is ^{13}C, ^{15}N or ^{34}S, and R sample and R standard are the heavy-to-light isotope ratios (^{13}C/^{12}C, ^{15}N/^{14}N and ^{34}S/^{32}S) in the sample and in the reference standards, respectively. These standards are the Vienna Pee Dee Belemnite (V-PDB) calcium carbonate for ^{13}C, atmospheric nitrogen (air) for ^{15}N, and Vienna Canyon Diablo Troilite (V-CDT) for ^{34}S. The accuracy of measurements for δ^{13}C, δ^{15}N and ^{34}S were 0.1, 0.3 and 0.2 ‰, respectively.

For δ^{13}C and δ^{14}N, international isotope secondary standards of known isotope ratios in relation to V-PDB and air, respectively, were used. These were: polyethylene (IAEA-CH-7; δ^{13}C = -31.8‰), sucrose (IAEA-CH$_6$; δ^{13}C = -10.4‰), ammonium sulfate (IAEA N1; δ^{15}N = $+0.4$‰ and IAEA N2; δ^{15}N = $+20.3$‰), potassium nitrate (USGS 34; δ^{15}N = $- 1.7$‰), L-glutamic acid (USGS 40; δ^{15}N = $- 4.6$‰; δ^{13}C = -26.2‰) and caffeine (IAEA 600; δ^{15}N = 1.0‰; δ^{13}C = $- 27.7$‰). For δ^{34}S, secondary standards of known isotope ratios in relation to V-CDT were: barium sulfate (IAEA SO-6; δ^{34}S = -34.1‰ and IAEA SO-5; δ^{34}S = $+0.5$‰) and YCEM (δ^{34}S= $+12.8$‰).

The reference materials used for the analysis were obtained from the International Atomic Energy Agency (IAEA). The analyses were carried out in the Centres Científics i Tecnològics of the University of Barcelona (CCiT-UB).

2.3. Statistical analyses

Because of the occurrence of the Suess effect, which is a significant decrease of ^{13}C in atmospheric CO_2 caused by the burning of fossil fuels (Keeling 1979), before conducting any statistical analysis the δ^{13}C values from both the baleen whale samples and the prey samples were converted to values corresponding to 2013 by considering a decrease of 0.027 ‰ yr^{-1} (Borrell et al., 2018a).

Data were tested for normality (Shapiro–Wilk test) and homoscedasticity (Bartlett test), and means and standard deviations were calculated for each baleen whale species. A Kruskal-Wallis test was performed for each stable isotope ratio to look for significant differences between species, followed by a post-hoc test (Dunn Test) adjusted with the Holm method (Ogle et al., 2020). Bayesian mixing models were applied to stable isotope data to estimate the prey contributions to the diet of each whale species, following the MixSiar model framework (Stock and Semmens 2016). We performed a separate model for each baleen whale species.

Parameters included in these models were: the δ^{15}N and δ^{13}C individual values of whales, those of their prey sources (Table S2), and the predictable shift between whale skin and diet (trophic discrimination factors) that had been previously estimated for fin whales as 2.82 ± 0.30‰ for δ^{15}N and 1.28 ± 0.38‰ for δ^{13}C (Borrell et al., 2012). The potential prey considered in the model for each whale species were identified according to previously available information on stomach content analyses conducted on whales from the North Atlantic (Table S3). Because for fin and minke whales there was detailed information on diet composition off Iceland (Víkingsson 1997; Víkingsson et al., 2014), for these two species we incorporated priors into the model. For the fin whale these were: krill: 80%, capelin: 15%, sand eel: 2.5%, and copepods: 2.5%. For the minke whale, krill: 10%, sand eel: 45%, capelin: 12.5%, herring: 12.5%, and gadoids: 20%. All models were run with the following Markov Chain Monte Carlo (MCMC) settings: length chain: 300,000–3,000,000, burn-in: 200,000–1,500,000, thin: 100, chains: 3. To ensure that all models converged we used the Gelman-Rubin and Geweke tests (see Table S4).

The δ^{13}C, δ^{15}N and δ^{34}S values were used to run the probabilistic method that allows defining niche region and pairwise niche overlap with three dimensions (Swanson et al., 2015) using the R package "nicheRover" (Lysy et al., 2015). For conducting the analyses, the species niche region was defined as the region with a 95% probability of finding a specific individual of that particular species and denoted as NR$_{95}$. For each species of baleen whale and every pair of isotopes, posterior distributions were obtained. The size of the niche and the niche overlap, defined as the probability that an individual from a particular species is found in the niche of another species (Swanson et al., 2015), were calculated. Posterior means of niche overlap and 95% credible intervals were obtained. For plotting the 5 random elliptical projections for each of the posterior distributions, the alpha value was set as 0.4 (denoted as NR$_{40}$) and 0.95 (denoted as NR$_{95}$). While NR$_{40}$ depicts the niche core similarly to the widely used bivariate Standard Ellipse Areas (Jackson et al., 2017), NR$_{95}$ provides the 95% probability region of the tridimensional stable isotope niche and is thus considered a more accurate measure of actual overlap. We performed 10,000 runs for all analyses.

3. Results

Table 1 shows summary statistics of the stable isotope ratios of the baleen whale species analyzed in this study. Kruskal-Wallis test showed that δ^{13}C, δ^{34}S and δ^{15}N values were significantly different among species (p.value < 0.001 for all of them). The Post-hoc Dunn test indicated that all species showed significant differences for at least one of the three stable isotope ratios, except between the blue and fin whales which did not present significant differences for any of the isotope ratios.

Table S2 details the stable isotope values of potential prey of baleen whales sampled in summer. *Calanus finmarchicus* was considered to be representative species of the copepod group and *Meganyctiphanes norvegica* of krill because these two species are the major components of their respective zooplankton groups in the region and constitute a main prey for whales (Planque and Fromentin, 1996; Víkingsson, 1997; Prieto et al., 2012). Fig. 1 shows the stable isotope ratios of both potential prey and baleen whales. Results of Bayesian mixing models indicated that krill represents the major contribution to the diet of blue (mean ± SD: 95% ± 4), fin (94% ± 7), humpback (67% ± 7) and sei (66% ± 5) whales, while it has a lower contribution in the diet of common minke whales (23% ± 10). Sand eel was the main prey for common minke whales (54% ± 15), and contributed marginally to the diet of humpback whales (7% ± 6). *C. finmarchicus* was an important prey for sei whales (34% ± 5) and had a marginal contribution in the diet of blue (5% ± 4) and fin whales (1% ± 0,4). Capelin contributed to 15% (±9) of the diet of humpback whales and to less than 10% to that of common minke

Table 1

Number of samples analyzed, mean and standard deviation of δ^{15}N, δ^{13}C and δ^{34}S values and niche size for each species. Values obtained from samples collected before 2013 were corrected for the Suess effect (see text). Within a column, superscript letters indicate that, according to the post-hoc Dunn test, differences between species noted with the same letter are non-significant (p > 0.05); e.g δ^{15}N values showed non-significant differences between sei and fin whales (both noted with "a"), between blue and fin whales (both noted with "b"), between blue and humpback whales (both noted with "c"), and between humpback and common minke whales (both noted with "d").

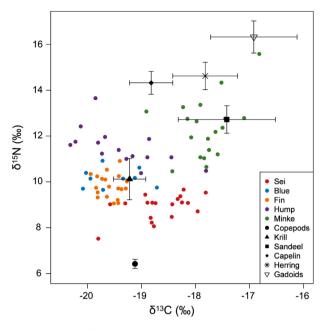| Species	n	δ^{15}N (‰) mean ± SD	δ^{13}C (‰) mean ± SD	δ^{34}S (‰) mean ± SD	Niche size (‰^{3}) (α = 0.95)
Sei whale	19	8.9 ± 0.6 [a]	−18.7 ± 0.5 [a]	18.8 ± 0.3 [a]	4.7 ± 1.3
Blue whale	9	10.2 ± 0.4 [bc]	−19.5 ± 0.5[b]	19.2 ± 0.3 [a]	3.7 ± 1.6
Fin whale	19	9.8 ± 0.5 [ab]	−19.6 ± 0.2 [b]	18.8 ± 0.4 [a]	3.4 ± 1.0
Humpback whale	15	11.5 ± 0.8 [cd]	−19.4 ± 0.7[b]	18.3 ± 0.5[b]	15.6 ± 5.1
Common minke whale	19	12.4 ± 1.3 [d]	−17.8 ± 0.5[c]	18.3 ± 0.4[b]	12.9 ± 3.7

Fig. 1. Individual stable isotope ratios of N and C in the skin of baleen whales analyzed in this study, and mean (±SD) of the six potential groups of prey included in the MixSiar models corrected with the discrimination factors calculated by Borrell et al. (2012).

whales (6% ± 7). Finally, gadoids and herring accounted for less than 10% of the contribution to the diet of all the species (Fig. 2). In total, fish species contribution was the highest for common minke whales (77%), followed by humpback (34%) and fin whales (2%).

Fin whales had the smallest niche size, although it was very close to that of blue and sei whales, while common minke and humpback whales exhibited larger niche sizes (Table 1 and Fig. 3 and S1). Overlap in isotopic niches between baleen whale species was high for δ^{34}S, medium for δ^{13}C, and small for δ^{15}N, but the result of combing the three values resulted in most cases in a moderate overlap between them. Thus, in all cases the estimated NR$_{95}$ overlap between whale species was below 25% except between fin and blue whales, in which overlap values were between 50 and 60% (Table 2, Fig. S1).

4. Discussion

4.1. Diet composition

The stable isotope ratios determined in both the skin of the whales and in their prey are discrete measures taken from a complex scenario influenced by different variables and processes. The samples of both the whales and their prey were collected in different years, and tissue turnover, migration, the erratic movement of the whales, temporal and the geographical variation of local oceanographic conditions all interact to determine the stable isotope signal that is eventually found in organisms (e.g. Hobson and Wassenaar, 2019). As such, stable isotope ratios should be taken only as a proxy of diet and trophic interactions, and considered at the light of the knowledge on the biology of species.

Bayesian mixing models showed that sei whales primarily fed on krill, as previously reported in Iceland (Sigurjónsson 1995). *C. finmarchicus* was the second most common prey, contributing to the 34% of the diet. This highlights the importance of this species for the sei whales as it appears to be the rule in most areas of the North Atlantic, where *C. finmarchicus* or other copepods are the most abundantly consumed prey (Hjort, 1933, Flinn et al., 2002, Prieto et al., 2012, Silva et al., 2019).

The mixing models also showed that the diet of both blue and fin whales was mainly composed of krill. Although the diet of blue whales

summering off Iceland has not been previously studied, our results concur with those found in other areas of the North Atlantic, such as the Estuary and Gulf of St. Lawrence or Norway (Christensen et al., 1992, Sears and Perrin 2018, Guilpin et al., 2019). In the case of the fin whale, the diet predicted by the mixing models showed that the species barely consumes fish. However, the individuals sampled were all taken during the summer, and previous studies have shown that later in the year the species also feeds on capelin (MFRI unpublished observations), coincidentally with results from other geographical regions where a significant part of the diet is composed of schooling fishes like capelin, herring, mackerel, blue whiting, and secondarily, copepods (Jonsgård 1966, Kawamura 1980, Gavrilchuk et al., 2014, Aguilar and García-Vernet 2018).

According to the mixing models, humpback whales also largely consumed krill, with fish contributing about 34% of their diet. Although there is no direct data on stomach contents from this species in Iceland (Sigurjónsson and Víkingsson 1997), this balaenopterid is usually considered a generalist species (Wright et al., 2016, Clapham 2018) and has been reported to be associated with areas of high capelin density (Pike et al., 2019). It is noteworthy that the contribution of krill in the diet of Icelandic humpback whales is much higher than that estimated for other feeding areas in the northern hemisphere, such as the Gulf of St. Lawrence (Gavrilchuk et al., 2014), Newfoundland (Piatt and Methven 1992), Norway (Christensen et al., 1992), Alaska (Wright et al., 2016) or the California current (Fleming et al., 2016). Although this difference may be reflecting the large abundance of krill during the summer in Icelandic waters and ignoring the stronger reliance of humpback whales on capelin during autumn and winter, it may also be a consequence, at least partially, of the reduction in the capelin stocks that in the last decades has taken place in these waters (Vilhjálmsson 2002, Pálsson et al., 2012a).

With regards to common minke whales, the mixing model showed that krill was still a significant component of the diet (23% of the assimilated diet) but the largest component were fish, with sand eel being the major prey and a much lower contribution of capelin, herring and gadoids. However, it should be noted that in more recent years the proportion of sand eel in the diet of common minke whales appears to have decreased, with a corresponding increase in herring and haddock purportedly by the effect of an increase in sea surface and bottom temperatures caused by global warming (Víkingsson et al., 2014). Whatever the case, the trophic level exploited by the species off Iceland is clearly higher than that of blue and fin whales, and in the upper range determined in other localities, where reliance on krill appears comparatively higher (Born et al., 2003). The composite results confirm that the common minke whale feeds on a broad range of different prey (Perrin et al., 2018) and is the most piscivorous among all baleen whale species (Skaug et al., 1997, Windsland et al., 2007).

4.2. Niche partitioning and interspecific competition

Being located at the northernmost end of the propagating wave of high productivity associated to the North Atlantic spring bloom (Visser et al., 2011), the waters off Iceland are a main summering feeding area for all the baleen whale species here examined. Baleen whales are capital breeders that migrate to temperate, low-productivity waters for reproduction (Lockyer, 1984). As a consequence, a significant portion of their annual energy budget, and in particular that required to provision their offspring during lactation, depends on the lipid reserves accrued during the intensive feeding conducted in the summering grounds (Lockyer, 1984). Trophic network analyses indicate that baleen whales are very sensitive to competition, a hypothesis that appears confirmed by the episodic appearance of emaciated individuals caused by food shortage (Moore et al., 2001, Ruzicka et al., 2013, Ribeiro et al., 2018). Niche partitioning and reduced interspecific competition while their stay in the Icelandic feeding grounds is therefore critical for the completion of their annual cycles and the long term stability of
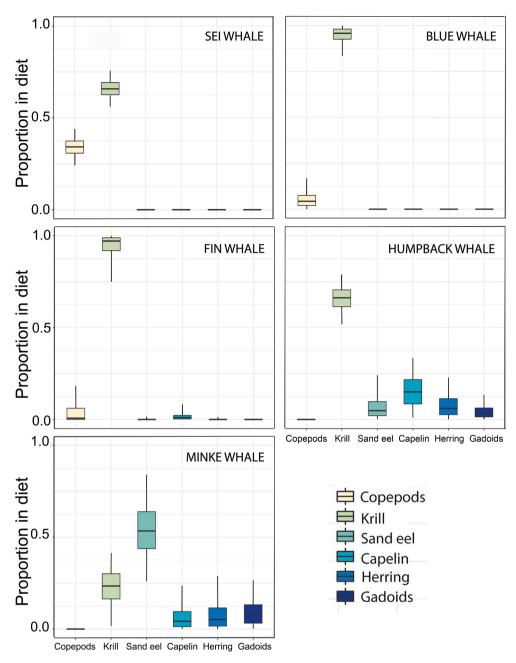
Fig. 2. Boxplot showing the estimated diet composition of the five baleen whale species studied. Proportions of the different prey are shown as 50% (inner box), 75% (outer box) and 95% credible intervals (whiskers).

populations.

The overlap in distribution, as indicated by the niches drawn by the $\delta^{13}C$ and $\delta^{34}S$ axes, is substantial and might in principle lead to a situation of diffuse competition between the various species. This would be a hindrance to coexistence because coexisting species must differ in their ecological requirements by at least some minimal amount to avoid competitive exclusion (Pianka 1974). A strong diffuse competition, as observed here, requires great average niche separation among coexisting species. This appears resolved by the niches participated by the $\delta^{15}N$ value (a trophic indicator) which separates the various species. The splitting becomes particularly clear in the niches drawn with the combination of the $\delta^{15}N$ and $\delta^{13}C$ axes, which integrate both the trophic signal with the habitat signal. The only exception to this splitting are the niches of blue and fin whales, which do not separate significantly under any combination of axes of stable isotope values.

All the species here studied consumed krill, which was always the

most common prey group. This shows the strong reliance of baleen whales on this resource, as it has been previously reported in this and other areas in the North Atlantic (Jonsgård 1966, Kawamura 1980, Víkingsson 1997, Laidre et al., 2010). Indeed, the lack of distinguishability between the ecological niches of fin and blue whales is explained by their overwhelming dependence on krill. Conversely, the other species also relied substantially on other prey and their overlap in diet composition decreased to some extent.

However, diet composition is not the only factor determining ecological niche overlap. Trophic competition between sympatric species can be mitigated by segregating through other niche dimensions, either spatial and/or temporal; this is, two species may consume the same prey but forage on different size classes of the same prey (Santora et al., 2010), or forage in different locations, seasons or depths in the water column (Clapham and Brownell 1996). For example, in the Gulf of Maine both humpback whales and fin whales consume sand eel, but
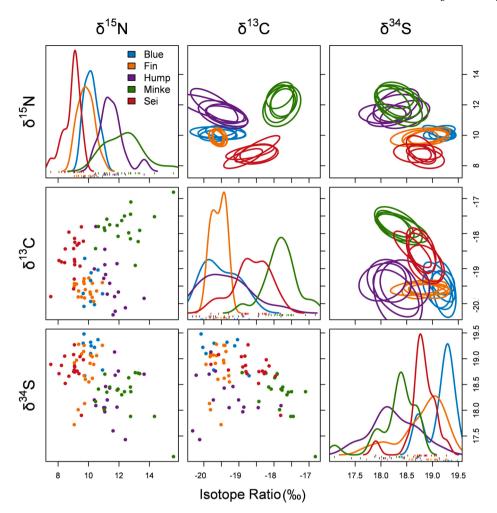
Fig. 3. NicheRover plots for the baleen whale species analyzed in this study. Top-right: five random elliptical projections at 40% niche region (NR_{40}) for each pair of isotope ratios. Diagonal: One-dimensional density plots. Bottom-left: Scatterplots of raw data for each pair of isotopes.

Table 2
Pairwise percentages of directional overlap between NR_{95} calculated using nicheROVER: posterior mean (95% credible intervals).

	Sei whale	Blue whale	Fin whale	Humpback whale	Common minke whale
Sei whale		8.1	5.5	6.1	23.5
		(0.2–37.1)	(0.3–19.0)	(0–35.2)	(0.6–69.8)
Blue whale	9.2		57.8	18.9	10.9
	(0.2–35.9)		(31.8–84.1)	(0.5–66.2)	(0.1–44.7)
Fin whale	8.2	50.2		14.3	1.2
	(0,5–29.6)	(27.7–78.0)		(0.3–57.4)	(0–12.5)
Humpback whale	1.1	4.6	2.4		11.3
	(0–5.6)	(0.1–20.1)	(0.1–9.7)		(1.8–29.4)
Common minke whale	3.9	2.4	0.2	18.1	
	(0.4–12.5)	(0.1–10.8)	(0–1.2)	(2.3–43.5)	

Note: The table is to be read across each row, e.g. 8.1 % of the sei whale niche overlapped the blue whale niche, and 9.2 % of the blue whale niche overlapped the sei whale niche.

hydroacoustic scans show that they exploit patches of different size or located at different depths (Clapham and Brownell 1996).

In this respect, $\delta^{34}S$ values give a clue to spatial segregation because $\delta^{34}S$ values decrease with freshwater inputs, this is, with proximity to the coast (Barros et al., 2010, Nehlich 2015). The $\delta^{34}S$ values found in blue, fin and sei whales were all relatively high and not statistically different between them, indicating that these species all forage in offshore waters. The apparent lack of difference between the blue whale and the other two balaenopterids is difficult to interpret and to a certain degree contradicts results from surveys conducted in Icelandic waters, which showed that common minke, humpback and, to less extent, blue

whales are largely confined to the shelf areas, while fin and sei whales are most abundant close to the shelf slope and further out (Pike et al., 2009b, 2019; Sigurjónsson 1995). However, in other areas in the North Atlantic Ocean blue whales have been seen to forage both pelagically, over seamounts and other deep ocean structures, as well as on relatively inshore waters, such is the case of the St. Lawrence Estuary and the northwestern Gulf of St. Lawrence (Silva et al., 2013; Lesage et al., 2017). It is likely that, despite skin has a turnover rate of only few months (see above) the blue whale skin analysed still retained some of the $\delta^{34}S$ signal from previous occupancy of more offshore waters as most of the samples were taken shortly after their presumed arrival to coastal

waters. Moroever, in the last decades their distribution off Iceland has apparently experienced a northward shift that has been associated to changes in oceanographic variables and prey distribution (Víkingsson et al 2015). In such changing scenario, the matching of the evidences obtained from surveys and from stable isotope analyses may become difficult if the studies are not temporally coincidental.

Common minke whales and humpback whales presented the lowest $\delta^{34}S$ values, which indicates a more inshore distribution of these two species as compared to the rest, a finding supported by sighting studies both in Iceland and in other North Atlantic locations where all these species also co-exist (Frankel et al., 1995, Clapham 2000, Doniol-Valcroze et al., 2007, Pike et al., 2009a, 2019). Such spatial segregation again tends to reduce interspecific competition, which may be further strengthened by the differences in foraging behavior mentioned above. It is noteworthy that the niche size of common minke whales and humpback whales were the largest among all the baleen whale species here studied. This reflects the ability of these two balaenopterids to exploit a wider range of resources and habitats, something which is particularly true in the case of common minke whales, a species whose diet is well known to have pronounced spatial and temporal variation (Víkingsson et al., 2014).

A further element that strengthens resource partitioning is the timing of residence at the feeding grounds. Although the five species here examined visit Icelandic waters in the summer, their presence shows some temporal segregation. Stable isotope niches do not through light on this variable, but sightings and catch data do. Thus, Sigurjónsson and Vikingsson (1992, 1997) found that the first species arriving to the Icelandic feeding grounds are the humpback, fin and minke whales, followed by blue whales, and finally by sei whales. A similar migratory sequence has been observed off Northwestern Spain in the summer, where the peak of abundance of fin whales preceded for about 2–4 weeks the sightings of blue whales and by about 4 weeks the peak of abundance of sei whales (Aguilar and Sanpera 1982, Aguilar 1985). In other areas the same species also segregate temporarily, but the sequence may be different. At the Azores Islands in spring, the peak of abundance of blue whales preceded those of fin and sei whales (Visser et al., 2011, Silva et al., 2019), as it also happened in the North Pacific and the Antarctic, where call detections of blue whales preceded those of fin whales (Risting, 1928, Stafford et al., 2009). Taking this into account, we cannot discard that some degree of temporal segregation between the species actually occurs and slightly alleviates interspecific competition. This temporal and spatial segregation may be particularly relevant for the coexistence of blue and fin whales given the severe overlap observed in their respective stable isotope niches.

4.3. Interaction with fisheries

Some studies have suggested that marine mammals require 2–10% of the net primary production of their ecosystem, and this has triggered proposals for culling based on the alleged competition of the whales with commercial fisheries (Morissette et al., 2012, Ruzicka et al., 2013). Our results show that in Icelandic waters common minke whales and humpback whales are major predators of capelin, herring, sand eel and to a less extent of gadoids, and with little doubt, also of other species of commercial fishes that have not been included in the mixing models. This is consistent with previous estimates of food consumption by these whale species in Icelandic waters (Sigurjónsson and Víkingsson 1997) as well as from similar studies conducted in other areas of the North Atlantic (Markussen et al., 1992). Blue, fin and sei whales may also occasionally prey on fish, although their consumption rate, and therefore their direct incidence on the commercial fish stocks, appears much smaller. The abundance of each component of the trophic web is strongly interrelated and explains the observation by Víkingsson et al. (2014) that the reduction in the local stock of sand eel during the period 2003–2007 (Bogason and Lilliendahl 2008) rapidly translated into a decline in the contribution of this fish species to the diet of minke whales

during the same years.

Moreover, all the baleen whale species here examined are major pelagic predators of euphausiids, and sei whales -and marginally fin and blue whales- also consume copepods, and these two groups of organisms are central elements of the macroplanktonic community in the cold waters of the Northeast Atlantic Ocean. Copepods and euphausiids feed on phytoplankton or small zooplankton and are thus at the basal levels of the trophic web which, in one way or another, sustain most commercial fish species in the region (Mauchline 1980, Astthorsson and Gislason 1997). This should be highlighted because trophic network analysis (Ruzicka et al., 2013) shows that the impact on commercial fisheries of the indirect competition for zooplankton by baleen whales is understood as being more intense than if the whales were directly preying on fish or cephalopods. Indeed, baleen whale grazing is considered to have a greater and broader potential effect on upper trophic levels and on fisheries than the specific predation by the fully piscivorous pinnipeds or odontocetes (Trites et al., 1997, Ruzicka et al., 2013). The other side of the coin is that, beyond their role and importance as macro-zooplankton or fish consumers, baleen whales also benefit fisheries by acting as food web structuring agents (Essington 2006, Willis 2007, Jusufovski et al., 2019), a fact that is valued positively for the maintenance of commercial fish stocks (Morissette et al., 2012). For example, albeit small, the segment of the baleen whale population that overwinters in Iceland (Magnusdottir and Lim 2019, Lydersen et al., 2020) may play a role of nutrient recyclers in periods of low productivity (Nicol et al., 2010, Roman and McCarthy 2010).

Interaction with fisheries involves another undesired effect, which is the potential entanglement of the whales in nets or in other fishing gear. The consequences of entanglement range from death by drowning, to stress, impaired foraging and starvation, systemic infection of unresolved entanglement wounds, and hemorrhage or debilitation due to severe gear-related damage to tissues (Cassoff et al., 2011). Even though any of the species studied here is susceptible of becoming entangled in fishing gear, the one that in other areas appears to be more strongly affected by this problem is the humpback whale due to its coastal distribution and relatively high piscivorous diet. Thus, quantification of entanglement rates using standardized scar-based techniques in the Gulf of Maine, Alaska and the Arabian Sea indicated that well over 50% of the individuals in these areas show signs of having experienced entanglements in the past (Robbins and Mattila 2004, Neilson et al., 2009, Robbins 2009). However, Basran et al. (2019) found that in Iceland the prevalence of entanglement marks in humpback whales was about half the above figures, this is, within the range 24,8–50,1%. They suggested a number of reasons to explain the difference, such as a different risk of entanglement caused by variations in the fishing gear used locally, a lower fishing pressure in the wintering or summering destinations of the whales or, because juveniles entangle more frequently than adults, geographical dissimilarities in the demographic composition. Although the question remains open, we should highlight that targeted preying on fish has been in the past associated with high entanglement rates of whales (Whitehead and Carscadden 1985). It is likely that the comparatively strong dependence on krill of the humpback whale in Iceland by may contribute, at least partially, to reduce its entanglement risk in these waters.

4.4. Evolution of interspecific relationships

A main question is how these ecological interrelationships will evolve in the future. In humpback whales, which were sampled during 2009–2013, capelin represented only 12% of the assimilated diet, a contribution that, as seen above, is much lower than what has been observed in other feeding areas of the species (Whitehead and Carscadden 1985). Without discarding the potential interaction of other factors, a possible explanation for the difference between geographical regions is the progressive warming of seawater that appears to have caused off Iceland a lower recruitment of capelin during the last decades

(Vilhjálmsson 2002, ICES 2018). To this, it should be added the northward shift in distribution of the 0-group of capelin and the westward shift of old capelin reported in the last years (Pálsson et al., 2012a), all which have resulted in a decrease of this resource off coastal Iceland during summer. In this scenario, the capelin consumers, mainly the humpback and the common minke whales, may have increased their dependence on krill and/or on other fish species not included in our analysis, a shift that has already been observed in the common minke whale of the Barents Sea (Haug et al., 2002). Such shift has been demonstrated for common minke whales in Icelandic waters with decreased krill and capelin consumption between around 1980 and after 2000, and increased proportions of herring and gadoids after the collapse of sand eel around 2005 (Víkingsson et al 2014, 2015). Also, a warming-induced mismatch in the phenology of reproduction with the peaks of oceanic productivity may have major implications on the reproductive success of some other prey species such as the sand eel, another species which is in decline in Icelandic waters (Wright et al., 2017) and that has reduced its contribution to the diet of whales (Víkingsson et al., 2014). Very likely, the changes in distribution and abundance observed in the different balaenopterid species in the region during the last decades may be a functional feeding response to the changes in the marine environment (Víkingsson et al., 2015).

The more generalist balaenopterids, particularly humpback and minke whales, have shown great plasticity to adapt in the past to varying environments (Kasamatsu and Tanaka 1992, Haug et al., 2002, Víkingsson et al., 2014, Fleming et al., 2016) and should be expected to react promptly to future changes. In recent decades there has been a significant shift in relative abundance of humpbacks whales and common minke whales in the Icelandic shelf area. While the abundance of common minke whales has drastically declined since 2001 (Pike et al., 2020), humpback whales have increased in abundance so that they have now taken over the role as the dominant baleen whale species in this area (Víkingsson et al 2015). The overlap in these two species ecological niches could indicate that inter-specific competition may have contributed to this shift. On the contrary, the more stenophagous species, like the blue whale and, to a lesser extent, the fin whale, may face difficulties if krill, their overwhelmingly basic prey, declines in abundance or varies its phenology, distribution or pattern of occurrence. Anyway, it is difficult to guess the directions that the dynamic equilibrium between the various baleen whale species will follow in a scenario of climate change. Theory predicts (Pianka 1974) that the upper limit on the permissible degree of niche overlap between species shall tend to reduce with the increasing environmental variability that it is expected to accompany global warming (Vasseur et al., 2014, Vázquez et al., 2017). This implies that, irrespective of the shifts in diet and distribution that the different species opt to, their ecological overlap will have to further reduce to allow long-term successful coexistence.

5. Conclusions

The Bayesian mixing models developed with the stable isotope data showed that, with the exception of minke whales, all baleen whales primarily fed on krill, with a variable contribution of copepods and fish depending on the species. Because baleen whales are capital breeders, the high krill availability characteristic of the feeding grounds off Iceland appears critical for these species for the completion of their migratory cycle and population maintenance. In these feeding grounds, the distribution of the various whale species substantially overlaps. This triggers strong diffuse competition which is partially mitigated by some degree of splitting in trophic niches. The only exception to this are fin and blue whales, which largely overlapped in diet and coincide in the feeding grounds during most of the feeding season. The strong dependence on krill of all species may contribute to reduce the risk of entanglement in fishing gear, particularly of humpback whales. It is unclear how the interspecific ecological relationships will evolve in the future taking into account the environmental changes observed in Icelandic

waters. It has been observed some variation in the distribution of the various baleen whale species as a functional feeding response to sea water warming and salinity changes, but it is expected that the overlap in their ecological niche will have to reduce to continue allowing coexistence.

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.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2021.102690.

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