The foraging ecology of minke whales (*Balaenoptera acutorostrata*) in Northeast Scottish waters using stable isotope analysis.

Submitted by

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to the University of Exeter as a thesis for the degree of

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I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

Signed:

Ciarán John Dolan

A minke whale lunges for prey in Scotland’s Moray Firth (Credit Eleanor Marwood).

Abstract

The marine environment is undergoing rapid change, impacting the entire food web. Monitoring the ecology of trophic factions that utilise the ecosystem resources is therefore crucial in tracking change and assessing its key drivers. Baleen whales, as mid-trophic level predators, are indicator species that reflect pressure-driven changes at both higher and lower trophic levels. As such, understanding their foraging ecology is critical to informing effective conservation and management during a time of rapid environmental change.

The waters of Northeast Scotland provide rich feeding opportunities for large marine vertebrates, such as cetaceans. Migratory baleen whales exploit these productive areas during the summer months to replenish energy reserves lost over winter. The minke whale (*Balaenoptera acutorostrata*) is the most abundant baleen whale in Scottish waters, yet key aspects of its foraging ecology remain poorly understood. Using bulk minke whale skin tissue, and muscle tissue from their putative prey, stable isotope analysis was conducted to derive $\delta^{13}C$ and $\delta^{15}N$ values.

The aims of this thesis were to: (i) determine the contribution of known prey species to the diet of minke whales in Northeast Scotland and assess prey preferences between adult and juvenile age classes; (ii) establish if age-related dietary differences are reflected in trophic position estimates; (iii) investigate seasonal (spring-summer) variation and overlap in the isotopic niche between adults and juveniles; and (iv) interpret these new findings in the context of emerging threats such as prey stock decline and evaluate their implications for management within the Scottish Marine Protected Area (MPA) network.

Minke whale $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SD) were -17.6 ± 1.4 ‰, and 13.0 ± 1.1 ‰, respectively. Prey $\delta^{13}C$ differed between species (sand eel: -18.27 ± 0.68 ‰; sprat: -18.09 ± 0.2 ‰; herring: -18.25 ± 0.53 ‰; mackerel: -19.02 ± 0.45 ‰; whiting: -18.03 ± 0.78 ‰; zooplankton: -18.79 ± 0.28 ‰) as did their $\delta^{15}N$ values (sand eel: 11.25 ± 1.60 ‰; sprat: 11.98 ± 0.23 ‰; herring: 11.87 ± 0.57 ‰; mackerel: 11.83 ± 1.01 ‰; whiting: 13.52 ± 1.38 ‰; zooplankton: 10.81 ± 0.63 ‰). Mixing model results (median, low–high 95% credibility intervals) revealed that adult and juvenile minke whales primarily consumed sand eel (*Ammodytidae sp.*) (0.34, 0.03 - 0.68 and 0.36, 0.03 - 0.74, respectively). Isotopic niche analysis (SEA_B ‰^{2}, low–high 95% credibility

intervals) showed that adults occupy a smaller niche area than their juvenile counterparts, (1.89, 1.08 – 3.29 ‰^{2}; 4.66, 3.28 – 6.95 ‰^{2}), respectively. The analyses highlight that minke whale foraging behaviour in Northeast Scotland is closely tied to the availability of key prey species, linking their ecology to commercially important fisheries for sand eel.

These findings emphasise the need for adaptive management of the Scottish MPA network to account for seasonal prey availability and to ensure that populations of ecologically important forage fish remain sufficient to meet the energetic demands of minke whales during the summer feeding season.

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Author's declarations

All chapters presented in this thesis were written by Ciarán John Dolan under the supervision of Kristian Metcalfe, Brendan Godley, Richard Inger, and Kevin Robinson. The contributions of each supervisor and intended co-authors of subsequent papers are detailed at the start of each chapter.

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Supervision	KR, BG, RI, KM	KR, BG, RI, KM

Abbreviations and definitions

AIR: Atmospheric nitrogen

BSIMM: Bayesian stable isotope mixing model

Bulk tissue: The entire tissue material; not compound-specific.

CAM: Crassulacean acid metabolism

Cetaceans: Whales, dolphins, and porpoises.

CRRU: Cetacean Research and Rescue Unit

CSIA: Compound-specific stable isotope analysis

DCM: Dichloromethane

DMSO: dimethyl sulfoxide

EEZ: Exclusive Economic Zone.

FFVB: Fixed Form Variational Bayes

Firth: A narrow inlet of the sea; an estuary

Fractionation: The process by which the abundance of elemental isotopes change.

IBTS: International Bottom Trawl Survey

MCMC: Markov Chain Monte Carlo

MeOH: Methanol

MPA: Marine Protected Area

Mysticetes: Cetaceans with baleen plates.

Odontocetes: Toothed cetaceans.

SCA: Stomach contents analysis

SIA: Stable Isotope Analysis

SMASS: Scottish Marine Animal Stranding Scheme

SST: Sea surface temperature.

TDF: Trophic discrimination factor

VPDB: Vienna Peedee Belemnite

δ: Delta

g: Gram

KJ//g WM: Kilojoules per gram of wet mass

m: Metre

mg: Milligram

mm: Millimetre

‰: Permille

Chapter 1: General Introduction

Marine environment of Northeast Scotland

Scottish waters cover an area of 462,315 km^2 which accounts for 63% of the UK Exclusive Economic Zone (EEZ). Scotland also has an extensive coastline of 18,743 km, much of which borders the North Sea on the east coast. Although the North Sea is relatively enclosed by other European countries, its ecosystems are heavily influenced by oceanic currents from the North Atlantic (Fair Isle current) (Turrell *et al.*, 1996). This is a known driver of increasing sea surface temperature (SST) in the northwestern reaches of the North Sea (Schückel *et al.*, 2010). As a result, seasonal stratification often occurs, whereby a warmer surface layer does not mix with the rest of the water column below (Tinker *et al.*, 2020).

The Moray Firth (57°41′ N, 2°40′ W) is a large embayment located in Northeast Scotland (Figure 1.1). Regulated by both terrestrial and marine inputs, it forms an important part of the North Sea and the wider North Atlantic basin (Wright *et al.*, 1998). The dominant marine input comes from the Dooley current which channels cold water down from the north and circulates it in a clockwise direction. In total, 12 rivers feed into the Moray Firth (Wilson, 1995; Holmes *et al.*, 2004), and as an important nutrient source, their freshwater inputs mix with the oceanic waters from the North Sea before getting recycled through the Dooley Current. The Firth's seabed consists mainly of sand or sandy gravel, with some of the deeper areas containing higher volumes of mud (Wilson, 1995). Seabed physiography is highly variable throughout the Moray Firth; where the inner firth only reaches 50 m at about 15 km from shore, the outer Firth reaches depths exceeding 100 m just 8 km from the shore (Eleftheriou *et al.*, 2004).

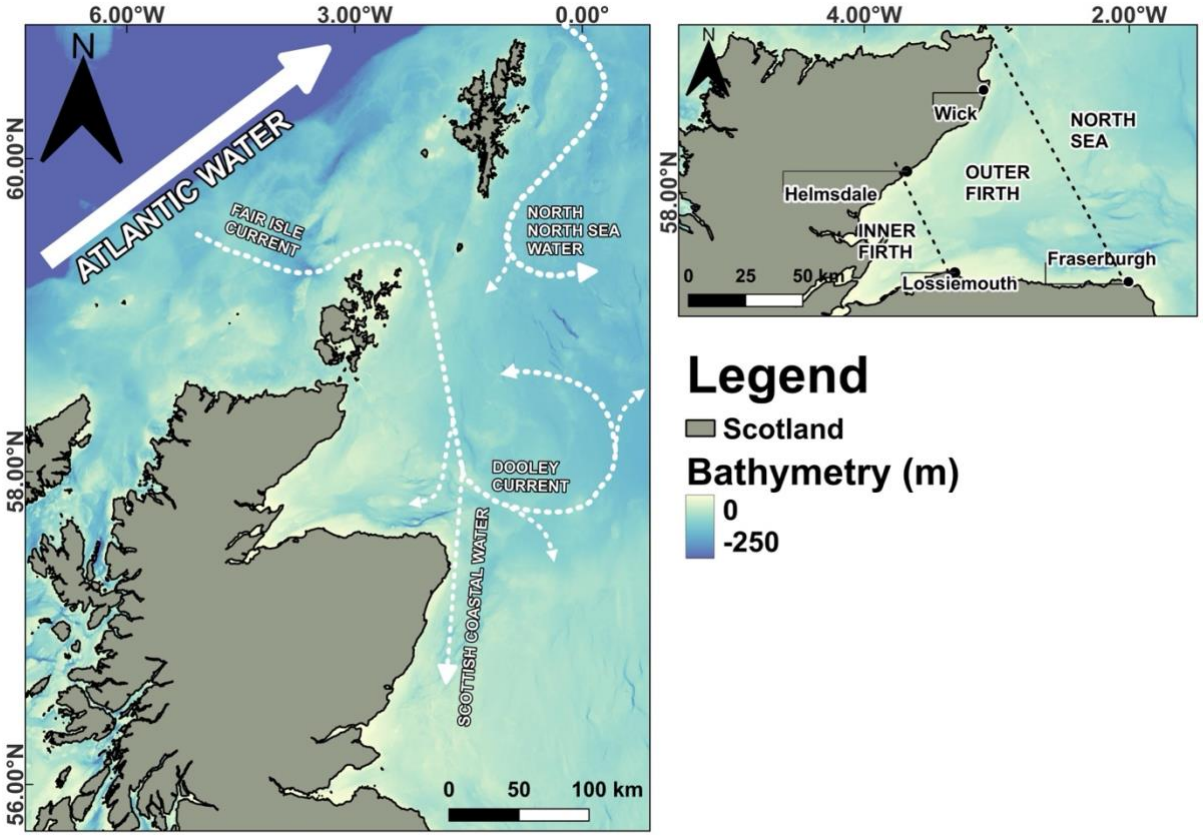

Figure 1.1 The study area and its main oceanographic currents; the Moray Firth and boundary lines dividing the inner and outer firths. Map projection: OSGB36 / British National Grid (EPSG: 27700). Units: kilometres. Data sources: British Iles polygon was sourced from ESRI. Bathymetry was sourced from Geospatial Data Abstraction Library (GDAL).

Ecological importance of Scottish waters

To date, 28 species of cetaceans have been recorded in the UK either through sightings or strandings (JNCC, 2021), comprising both *odontocetes* (toothed whales) and *mysticetes* (baleen whales) (Appendix 1.1, Supplementary material). In Scotland, cetaceans occur throughout its coastal and pelagic waters (Hammond *et al.*, 2017) within which there are multiple habitat types that collectively support the entire marine ecosystem. Coastal habitats such as seagrass meadows offer rich foraging opportunities and safe nursery grounds for a plethora of species (Jackson *et al.*, 2001), which has both ecosystem and commercial benefits. Hard substrate beds such as horse mussel (*Modiolus modiolus*) reefs and maerl or rhodolith beds are fragile habitats known to be biodiversity hotspots. Indeed, maerl grounds are important in the recruitment of valuable gadoids such as cod (*Gadus morhua*) and pollock (*Pollachius*

virens) (Riosmena-Rodríguez, 2017), which play a crucial role in exerting top-down control measures. Horse mussel reefs have also been shown to provide a comparable amount of refuge for a range of species (Kent *et al.*, 2016), as well supporting at least two distinctly different trophic webs, as inferred from stable isotope analysis (SIA) (Kent *et al.*, 2017).

Offshore habitats are typically more ambiguous, however, (Wakefield *et al.*, 2009) defines pelagic habitats using environmental conditions rather than features. For example, differences in temperature between two adjacent water masses, which cause oceanic fronts (Belkin, 2021), have been shown to be significant drivers of marine predator distribution (Gregory Lough and Manning, 2001; Worm *et al.*, 2005). The heterogenous nature of Scottish waters consequently makes them a major hotspot for these fronts. Mapping of frontal systems has established key North Sea front locations and have made a significant contribution to the construction of Scotland's current MPA network (Pingree and Griffiths, 1978).

MPAs of the Scottish seas

MPAs can be found throughout Scotland's territorial waters and as of 2022, the Scottish MPA network consisted of 244 sites (Figure 1.2A), which is made up of a mixture of different types of MPA (Appendix 1.2, Supplementary material) (Strachan *et al.*, 2022). The vast majority of MPAs are located within coastal waters since these regions represent highly productive areas. Of particular interest are the Sea of the Hebrides and Southern Trench sites, for both of which minke whales (*Balaenoptera acutorostrata*) have been identified as a protected feature. The Southern Trench MPA (57° 44.103' N 2° 08.056' W) is located on the southern coast of the outer Moray Firth and covers a total area of 2398 km^2 (Figure 1.2B).

The physical and environmental characteristics of this deep coastal trench play an important role in minke whale ecology. The other protected features include burrowed mud, shelf deeps and fronts. Burrowed mud is a habitat usually located on sandy and muddy substrata in stable conditions and is generally associated with burrowing species (Greathead *et al.*, 2011). Although sand eel (*Ammodytidae sp.*) show a greater affinity for sandier habitats (Macer, 1966), they too are a burrowing species and a known prey item of minke whales. The shelf deeps create complex topography and support an array of habitats that are dependent on this substrate (NatureScot, 2020).

Finally, fronts are highly important to organisms at every trophic level. Through the process of stratification, plankton remain at the surface for a greater amount of time (Kimura *et al.*, 1997), which creates feeding opportunities for consumers throughout the food web.

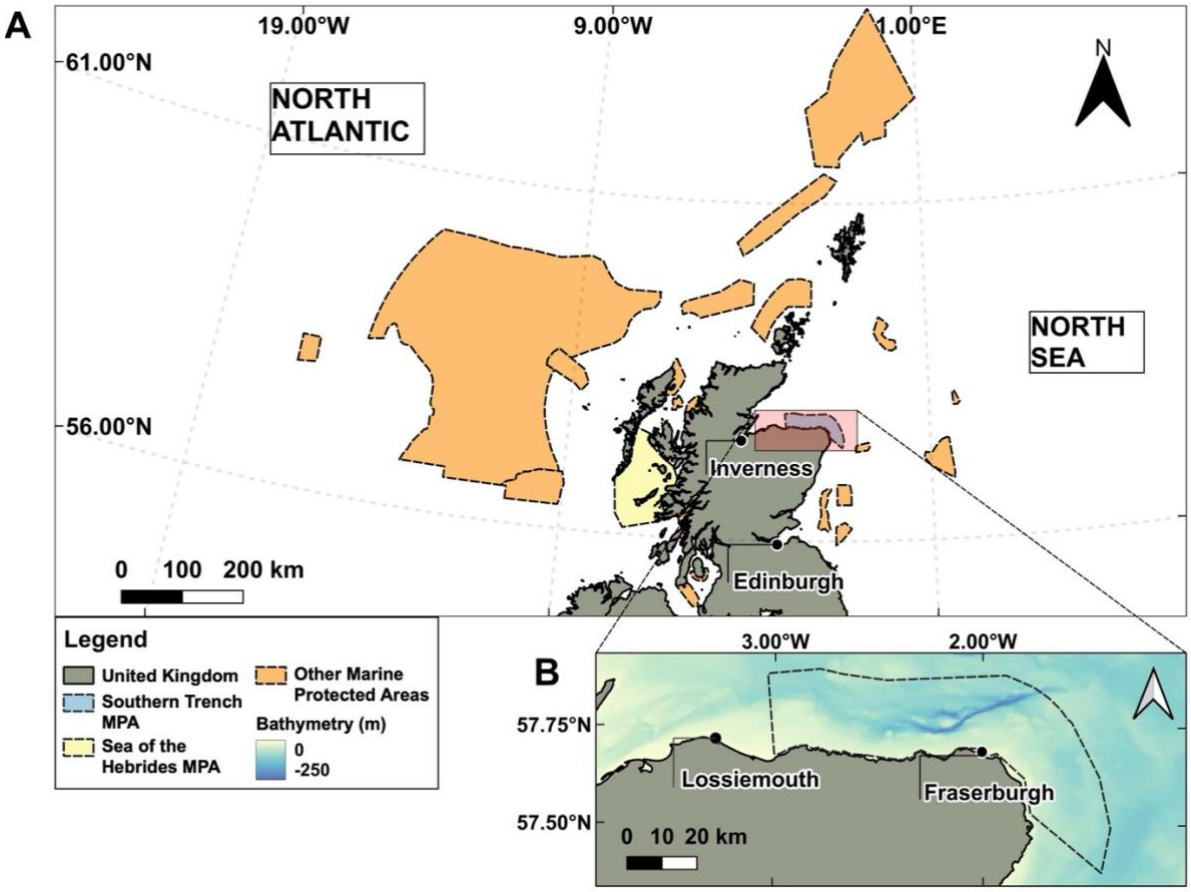

Figure 1.2. A) The extent of Scotland's MPA network as of 2020; **B)** the boundary limits of the Southern Trench MPA. Map projection: OSGB36 / British National Grid (EPSG: 27700). Units: kilometres. Data sources: British Iles polygon was sourced from ESRI. MPA shapefiles were attained from NatureScot. Bathymetry was sourced from Geospatial Data Abstraction Library (GDAL).

Ecology of the minke whale

The minke whale (*Balaenoptera acutorostrata*) Lacepede 1804 is a cetacean belonging to the suborder *mysticeti* and is the smallest member of the *Balaenopteridae* family (Figure 1.3) (Dell *et al.*, 2016). Like other balaenopterids, minke whales

undertake annual migrations between their feeding and breeding grounds that can span long distances (Christiansen *et al.*, 2013).

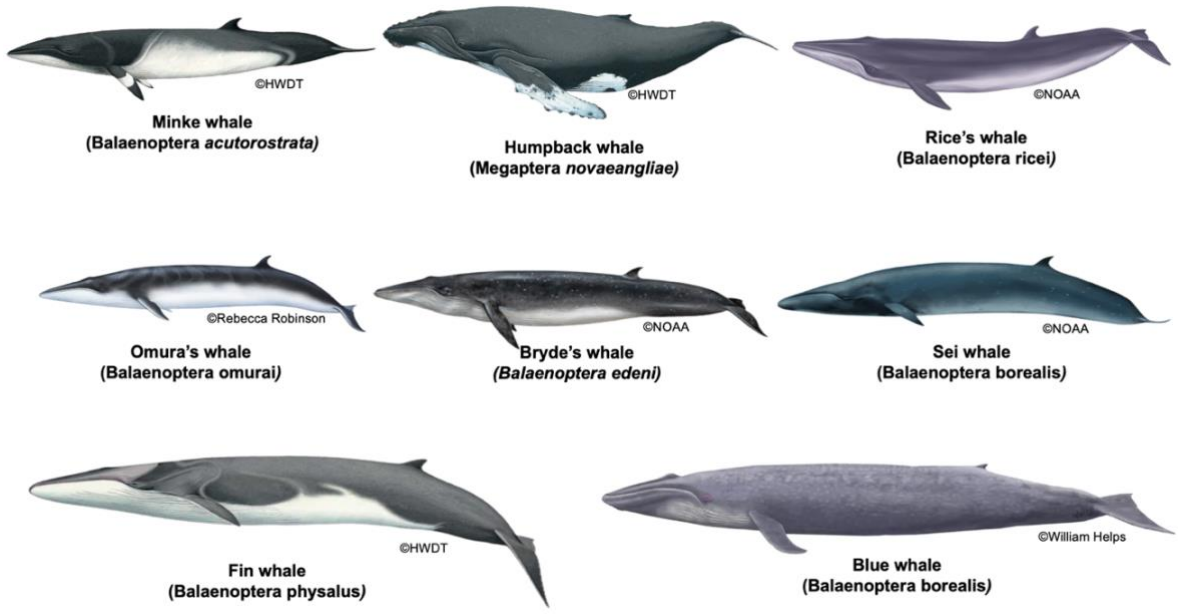

Figure 1.3. Current species in the *Balaenopteridae* family (Credit: Hebridean Whale and Dolphin Trust, National Oceanic and Atmospheric Association, Rebecca Robinson, William Helps).

Distribution

The common minke whale is one of the most widely distributed mysticetes (Figure 1.4) (Risch *et al.*, 2019). The species is regularly seen around the United States (U.S.), Canada, Greenland, Iceland, Norway and the UK (Pampoilie *et al.*, 2008; Christiansen *et al.*, 2015; Lomac-MacNair *et al.*, 2022) and it is well known to travel to extremely high latitudes to feed, with sightings reported as far north as Baffin Bay, Canada and the Barents Sea, Norway (Perrin *et al.*, 2018). Comparatively little is known about their southern extent, although sightings and strandings have been recorded in the West African area (Bamy *et al.*, 2010; Weir and Pierce, 2013; Valente *et al.*, 2019), Macronesia (Freitas *et al.*, 2012; Pampoulie *et al.*, 2013; Silva *et al.*, 2013) and the Mediterranean (Kerem *et al.*, 2013; Fraija-Fernández *et al.*, 2015; Insacco *et al.*, 2016; Maio *et al.*, 2016; Correia *et al.*, 2020; Ibrahim *et al.*, 2020).

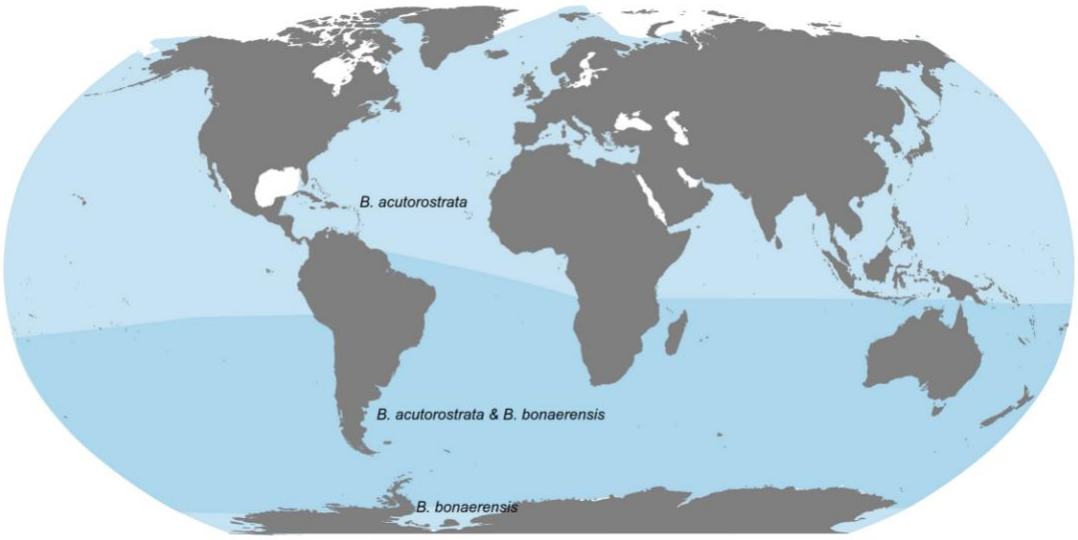

Figure 1.4. Global distribution of all minke whale species (Risch *et al.*, 2019).

In Scotland, high densities are reported in the Hebridean waters of the west coast where their distribution also shifts throughout the season (Macleod *et al.*, 2004). In the outer southern Moray Firth, minke whales are encountered throughout the summer with a peak in sightings from July through August (Robinson *et al.*, 2009). Minke whales have also been recorded in the inner Firth's Special Area of Conservation (SAC) (Bailey *et al.*, 2010). Although its importance to minke whales is not known, the inner firth has been identified as a spawning ground and nursery for herring (*Clupea harengus*) (Heath *et al.*, 1989; Wall *et al.*, 1997) which may be a key driver of minke distribution in the Moray Firth. Furthermore, age-class partitioning of minke whales has been observed in the Moray Firth (Robinson *et al.*, 2023) but more work is needed to conclude the mechanisms driving this partitioning.

Habitat use in foraging areas

On the west coast of Scotland, minke whales have been shown to target prey in different habitats at different times of the year. Where cooler waters (11.5 °C – 12 °C) and shallow slopes (2° - 2.5°) were associated with foraging whales in spring/early summer, warmer waters between 13 °C and 14 °C and depth appeared to be more important in the autumn (Anderwald et al., 2012a). High primary productivity was further noted as being a key predictor of minke whales in the autumn months.

In the Moray Firth, (Tetley *et al.*, 2008) linked areas of high primary productivity to strong minke whale presence concluding that these productive areas are important to the plankton feeding prey of minke whales such as sand eel and clupeids. Recent

work looking into ontogenetic habitat partitioning between age classes reports that juvenile individuals were found to prefer shallow inshore waters, whereas adults were associated with steeper gradients in deeper offshore waters (Robinson *et al.*, 2023). However, these findings should be followed up with further work given the possibility of bias. The study reports roughly 100 more juveniles than adults which may have been a result of small adults being misidentified as juveniles. Here, stable isotope analysis (SIA) would contribute valuable information on the dynamics of partitioning of minkes in the Moray Firth.

Minke whales are often sympatric with other species (Corkeron *et al.*, 1999; Friedlaender *et al.*, 2021), but for there to be coexistence between species, there must be differences in their respective niches, whether that be on trophic, spatial or temporal levels (Schoener, 1968; Friedlaender *et al.*, 2009). Measuring sympatry in cetaceans is often conducted using SIA because this is a useful way of quantifying the degree of overlap between the respective isotopic niches of coexisting species. Such studies have been conducted with sympatric rorquals in the GoSL and found that minke, humpback, fin and blue whales exhibit dietary partitioning (Gavrilchuk *et al.*, 2014). In UK and Irish waters, minke, fin and humpback whales have all been shown to demonstrate resource partitioning (Ryan *et al.*, 2013), highlighting how these sympatric rorquals reduce interspecific competition for recourses. In the Moray Firth, the trophodynamics of cetaceans, let alone minke whales, are poorly understood. However, SIA offers a novel method exploring the trophic ecology of minke whales in this important region.

Foraging ecology

Minke whales have evolved to exploit food resources in the most efficient way possible. Efficiency in this context can be described by the optimal foraging theory (OFT) as continuous foraging decisions made by an individual to maximise the net rate of energetic gain (Krebs *et al.*, 1983). OFT usually focuses on a single currency, whether that be time expenditure, energy gain or efficiency (MacArthur and Pianka, 1966; Houston and Carbone, 1992; Thompson and Fedak, 2001). However, in the case of marine mammals, there is the added pressure of energy gain and oxygen use acting as competing currencies. As such, mysticetes have been shown to adapt their

foraging and feeding techniques to account for this conflict of currencies (Goldbogen *et al.*, 2012).

Minke whales have been described using two different foraging techniques – active and passive foraging (Hoelzel *et al.*, 1989). Where active corralling is more energetically demanding and involves the individual locating and corralling prey by their own efforts (Figure 1.5), passive foraging or bird-associated foraging reduces energy expenditure because the corralling of prey is conducted by birds on the surface as well as predatory fish below (Hoelzel *et al.*, 1989; Robinson *et al.*, 2007).

Figure 1.5. An adult minke whale in the Moray Firth actively lunges for prey with little bird activity (Marwood 2021).

Spatial and temporal dietary trends

Across the North Atlantic, the minke whale diet varies considerably on both spatial and temporal scales (Macleod *et al.*, 2004; Robinson and Tetley, 2007; Gavrilchuk *et al.*, 2014). In the Northwest Atlantic, sand eel and northern krill (*Meganyctiphanes norvegica*) are reported as being the dominant prey species. Furthermore, the proportion of sand eel and northern krill was shown to increase over three years with a correlating decrease in herring and capelin (*Mallotus villosus*) (Gavrilchuk *et al.*, 2014). In Norwegian waters, the minke whale diet varies considerably with latitude. Krill and capelin are vital constituents in northern areas like Bear Island and

Spitsbergen (Haug et al., 1996; 2024); their dietary significance has been known to alternate during years of poor recruitment of the other respective prey species (Haug *et al.*, 2010). However, animals feeding closer to the coast in areas such as Lofoten primarily target fish species like spawning herring, sand eels and 0-group gadoid fish (Skaug *et al.*, 1997; Haug *et al.*, 2010). Minke whales in Iceland also show variability in their diet. SIA has revealed that sand eel is primarily targeted in Icelandic waters, followed by krill. Gadoids, herring and capelin appear to be targeted equally (García-Vernet *et al.*, 2021). These findings are similarly reported in stomach content analysis (SCA) studies (Víkingsson *et al.*, 2013). However, differences between minke whales feeding in the north and south of Iceland were observed, with gadoids being of more importance in the north and sand eel in the south.

In Scottish waters, the minke whale has a completely ichthyophagous diet. SCA of stranded individuals from around the Scottish coastline concluded that sand eel make up 62% of their diet by weight, whilst herring and sprat together make up 32% (Pierce *et al.*, 2004). On the west coast of Scotland, herring, sprat and sand eel are suspected of being the targeted prey species due to the strong correlation of minke whale distribution with their respective habitats and emergence times (Macleod *et al.*, 2004). Minke whale presence in early summer aligns strongly with sand eel distribution, then shifts later in the summer closely aligning with the emergence of spawning herring cohorts. Similar prey species are preyed upon in the Moray Firth (Robinson *et al.*, 2009). However, in the Moray Firth there is evidence to suggest ontogenetic dietary partitioning with juveniles suspected of preferring inshore sand eel and adults of offshore clupeid species (Heath *et al.*, 1989; Wall *et al.*, 1997; Robinson *et al.*, 2023).

These studies that focus on the foraging ecology of minke whales in Scottish waters are costly to run as they generally involve multiple boat-based surveys that require fuel, charter and even salary costs (Williams and Thomas, 2009; Hammond *et al.*, 2021). On the other hand, an effective and relatively inexpensive method of analysing foraging ecology is through SIA using tissue from strandings. With the growing pressures on the marine environment impacting more habitats and species, crucial data such as diet must be updated regularly and precisely if meaningful management of such pressures is to be achieved.

Stable isotope analysis and applications

Isotopes are a form of element that hold the same number of protons but have a different number of neutrons which gives them a different atomic mass (Ben-David and Flaherty, 2012). For example, nitrogen has two stable isotopes: ^{14}N and ^{15}N. Where both have seven protons, only ^{14}N has seven neutrons whilst ^{15}N has eight, making it the heavier isotope (Hashizume, 2011). Typically, throughout nature, the heavier isotopes are less common so when analysing the stable isotopes of tissue, the values are expressed in ratios of the heavier isotope to the lighter one, using the delta notation (δ) (Newsome *et al.*, 2007).

SIA measures the heavy to light isotope ratios of animal tissues that, accounting for metabolic processes, reflect the environment or prey source from where they originated. The ratio of carbon isotopes ($\delta^{13}C$) is used to explore an organism's diet because of how the stable isotopes react in these predictable metabolic processes. From one trophic level to another, ^{13}C has only a slightly higher tissue enrichment rate compared to ^{12}C which is excreted, resulting in little difference between the $\delta^{13}C$ of a consumer, their prey, and the primary producers that initially fixed the carbon (DeNiro and Epstein, 1978). On the other hand, ^{15}N becomes enriched significantly more than ^{14}N (Fry, 2006), leading to higher $\delta^{15}N$ ratios. The greater this value, the higher this organism is in the trophic web (Figure 1.6). These increases are often referred to as trophic discrimination factors (TDFs). It has always been assumed that TDFs between diet and tissue are between 0-1‰ and 3-5‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively (DeNiro and Epstein, 1978), but it has since been shown that these values can differ between tissues, taxa and even individuals, often proving challenging during analysis (Tieszen *et al.*, 1983; Riekenberg *et al.*, 2021).

The varying nature of TDFs is just one limitation. Isotopes have different turnover rates depending on how active the tissue is, metabolically. For example, inert baleen (keratin) will reflect isotope incorporation over a timeframe of years, whereas relatively active skin tissue incorporates isotopic information over months (Teixeira *et al.*, 2022). Coupled with the spatial and temporal variation in baseline isotopic values, across latitudinal gradients for example, SIA is highly sensitive to misinterpretation. This is an important consideration when studying a migratory species such as the minke whale, as their tissues will potentially reflect isotopic assimilation over a large spatial scale.

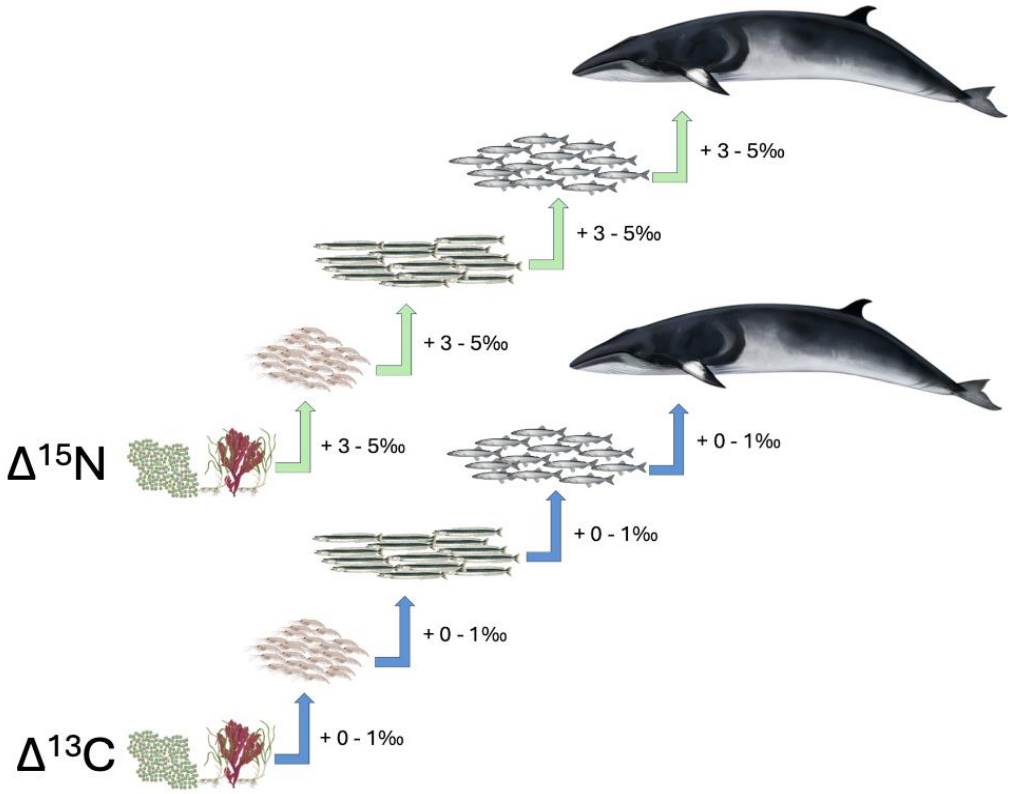

Figure 1.6. Change (Δ) in ^{15}N and ^{13}C at each trophic level.

Isotope mixing models work by comparing the isotopic composition of a consumer and its prey, accounting for uncertainty in the TDFs (Phillips *et al.*, 2014). Using a Bayesian framework, they estimate the proportional contribution, and confidence, of the included prey sources to the diet of the consumer. This allows researchers to quantitively analyse trophic relationships and make probabilistic inferences on diet.

The diet and foraging ecology of minke whales in most other Northeast Atlantic feeding grounds is well established due to ongoing SCA and stable isotope studies (Eerkes-Medrano *et al.*, 2021; García-Vernet *et al.*, 2021; Haug *et al.*, 2024). There is even recent evidence to suggest that the Iberian Peninsula holds some value to foraging whales (Monteiro *et al.*, 2025). Over the past two decades, there have been a few key studies that have explored the foraging ecology of minke whales in Scottish waters (Macleod *et al.*, 2004; Pierce *et al.*, 2004; Robinson *et al.*, 2023), but generally our understanding lacks depth.

A specific gap in our understanding of minke whale ecology is the extent of ontogenetic dietary partitioning and what factors drive it. In the Moray Firth, adults appear to target more clupeid fish species than juveniles who predate mainly sand eel (Robinson *et al.*, 2023), but we do not know how well defined this divergence is or why it happens.

By using SIA to quantitively establish the proportional contributions of these prey species to the diet of adults and juveniles, grounded conclusions can then be made on the behaviour driving any observed partitioning. Temporal shifts in Scottish foraging grounds is a second area that, although having been observed, lacks the fine-scale clarity other parts of the Northeast Atlantic have acquired. On both the east and west Scottish coasts, minke whales shift throughout the spring and summer seasons; their movements closely linked to environmental variables (Macleod *et al.*, 2004; Tetley *et al.*, 2008). Temporally variable tissue assimilated stable isotopes can be used to reliably track the isotopic niche of minke whales throughout the foraging season, opening up further possibilities of assessing dietary plasticity and overlap with conspecifics.

Developing a more well-rounded understanding of minke whale trophic ecology would profoundly advance the management of threats in Scottish waters. Filling these knowledge gaps is crucial to fisheries management and could have significant implications for catch quotas and moratoriums of these commercial prey species.

Threats

Threats towards minke whales have changed through time and have varied in their intensity. Historically, whaling was the only human-imposed threat. However, poorly managed fishing practices and climate change are now amongst the most severe threats to minke whales.

Climate change

In 2023, the North Atlantic Ocean was measured to be roughly 1.4 °C warmer than the average recorded for 1982 – 2011 (Kuhlbrodt *et al.*, 2024). This increasing trend has led to marine heatwaves in recent years (Plecha *et al.*, 2021; Xu *et al.*, 2022), with drastic consequences for marine life such as biodiversity and genetic diversity loss (Smale *et al.*, 2019; Gurgel *et al.*, 2020), and alterations in animal behaviour (Wernberg *et al.*, 2016). This raises concerns for cetaceans as their reproductive success is closely linked with body condition (Christiansen *et al.*, 2014) and shifts in prey emergence times may force migratory species, such as minke whales, to alter their departure north from their breeding grounds (Kebke *et al.*, 2022). A premature departure would reduce the mating time and thus reproductive opportunities, whilst leaving and arriving too late at their respective foraging grounds might result in

intensified competition for depleted resources. North Atlantic fin whale populations stagger their departure and arrival times at common feeding grounds, reducing intraspecific competition (Gauffier *et al.*, 2020), but their delayed arrival at a Northwest foraging ground coincides with that of humpback whales, intensifying interspecific competition for shared prey (Ramp *et al.*, 2015).

North Sea fish communities are exhibiting strong responses to warming waters; fish assemblages are going deeper (Dulvy *et al.*, 2008), and shifting northwards in efforts to find cooler waters (Engelhard, Righton, *et al.*, 2014). Extreme shifts may force minke whales to invest more time foraging and locating prey than feeding, reducing the net energy gain. Furthermore, if the prey have moved into deeper waters, the disparity between energy expenditure and gain could be greater still due to the increased time required for diving recovery at the surface. However, much of this depends on the dietary plasticity of the consumer and minke whales are known to be adaptable to changes in prey availability (Windsland *et al.*, 2007; Eerkes-Medrano *et al.*, 2021). Climate change applies pressure on marine ecosystems from multiple directions and although not a direct physical hazard, it exacerbates other threats that are closely linked to the trophic ecology of minke whales such as the overexploitation of prey.

Unsustainable fishing practices

The northern North Sea alone is responsible for 43% of all UK landings (Akbari *et al.*, 2022). Many of the species targeted by these fisheries are also cornerstones of their ecosystems and major dietary contributors to marine predators. However, industrial fishing in the North Sea has seen many of these populations decline (Ducrotoy and Elliott, 2008). Species targeted in Scottish waters include mackerel (*Scomber scombrus*), cod, whiting (*Merlangius Merlangus)*, but most significantly sand eel, and herring (Dunn, 2021; Holah *et al.*, 2022; Brigden *et al.*, 2025), both of which are overexploited in the North Sea (Wanless *et al.*, 2018; van Deurs *et al.*, 2023; ICES, 2024b). In the case of the Scottish sand eel fishery, a moratorium was put into effect in 2024 (The Scottish Executive, 2023). The overlap of these fisheries with minke whales creates intense competition for resources and exploitation to the point of stopping the fishery altogether is concerning for minke whales. Over exploitation of these populations poses a significant threat to predators like seabirds, seals and cetaceans. For example, when sand eel recruitment has been low, studies have reported seabirds switching to poorer quality prey (Wanless *et al.*, 2018), and reduced

breeding success (Rindorf *et al.*, 2000). Similar impacts could be expected in minke whale populations. As capital breeders, minke whales must consume enough food to sustain themselves and in the case of females, a growing calf, so if they are unable to secure a sufficient amount of food because of over exploitation of key resources, low reproductive success can be expected (Christiansen *et al.*, 2014).

Demersal trawling targets some of the gadoid prey contributing to the minke whale diet, such as cod and whiting. Bottom-trawl fishing is a highly destructive fishing method with effects ranging from disruption and shifts in benthic communities (Sciberras *et al.*, 2018) to complete destruction of habitats (Clark *et al.*, 2016). Although trawling effort in the North Sea was higher 30 to 40 years ago than in recent years (Couce *et al.*, 2020), it is still one of the most intensely bottom-trawled regions, globally (Amoroso *et al.*, 2018). Furthermore, bottom-trawling often takes place within MPAs where minke whales are listed as a protected feature (Porz *et al.*, 2024) (Figure 7). In spite of the management controls put in place for the sand eel and herring fisheries, trawling remains a persistent threat to these key prey species. The destruction of the benthic habitat and the associated sediment displacement (Olsgard *et al.*, 2008) inevitably disrupts benthic communities, particularly those that are highly sensitive to environmental and sediment conditions, such as sand eels (Wright *et al.*, 2000; van der Kooij *et al.*, 2008). Continued trawling within key minke whale foraging areas, and their protective boundaries, could force individuals to search outside the MPA for more reliable food patches which may expose them to other anthropogenic threats such as entanglement and ship strikes.

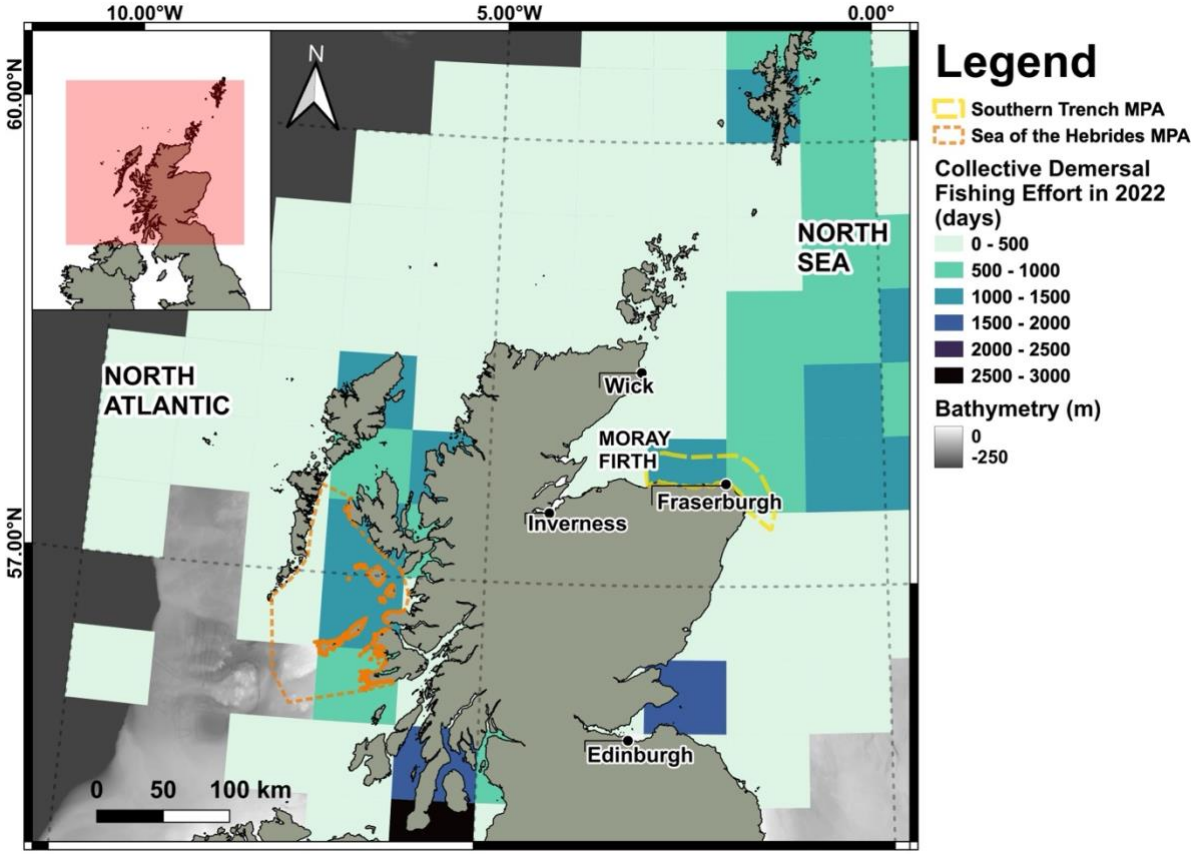

Figure 1.7. Intensity of demersal fishing effort in Scottish waters in 2022, two years after the designation of the Southern Trench and Sea of the Hebrides MPAs, of which minke whales are a protected feature. Map projection: OSGB36 / British National Grid (EPSG: 27700). Units: kilometres. Data sources: British Iles polygon was sourced from ESRI. MPA shapefiles were attained from NatureScot. Fishing data was sourced from Marine Scotland.

In Scottish waters, entanglement is the lead cause of minke whale mortality (Northridge *et al.*, 2010), with fatality rates of up to 84% (Leaper *et al.*, 2022). Both creelers and minke whales share a similar spatial niche in coastal waters so naturally there is likely to be some degree of conflict, particularly during the summer and autumn months when minke whale presence is highest. A growing concern for large baleen whales is the risk of ship collisions (Rockwood *et al.*, 2020). Although globally, ship strikes are an extremely pressing threat to baleen whales, it appears to be less significant in the mortality of minke whales in Scotland compared to other causes (Deaville *et al.*, 2011, 2018).

Noise and chemical Pollution

Increasing levels of pollution cause major issues mainly through disturbance. Whilst plastic pollution is a global issue threatening all marine life, noise and chemical pollution are a specific concern to cetaceans. Vessel noise is thought to be responsible for the increase in low frequency ambient noise from the 1960s to the 1990s (Cholewiak *et al.*, 2018), and although not intense enough to be fatal, vessel noise can be extremely disruptive. The communication space for minke whale pulse trains in the North Atlantic alone has been reduced by about ~80% (Cholewiak *et al.*, 2018), which could have catastrophic ramifications for breeding and possibly feeding. Chemical pollution is perhaps more obscure. In areas of the Northeast Atlantic, mean organochlorine levels in minke whales from two studies conducted six years apart, have shown a declining trend since the early 1990s (Kleivane and Skaare, 1998; Hobbs *et al.*, 2003). However, persistent organic pollutants (POPs) are still of particular concern given their lipophilic properties and tendency to accumulate in the blubber tissue (Williams *et al.*, 2023). Chronic exposure to POPs can have serious adverse effects on reproductive success of baleen whales (Bachman *et al.*, 2014; Muñoz-Arnanz *et al.*, 2019; Simond *et al.*, 2019).

Conservation status, management, and study priorities

The common minke whale is currently listed as “Least Concern” under the International Union for the Conservation of Nature (IUCN) (Cooke *et al.*, 2018). Under the Convention on International Trade in Endangered Species (CITES), they are listed as Appendix I (threatened with extinction) with the exception of the West Greenland stock. Although abundance estimates vary, the regional SCANS IV survey estimated the number of minke whales in the North Sea at just over 7,800 (Gilles *et al.*, 2023). However, because of the different jurisdictions within the North Sea, the status and level of protection for minke whales changes. Inherent inconsistencies in their protection therefore threaten minke whales throughout their summer range, particularly as their range expands further north into other jurisdictional waters such as those of Iceland and Norway (Lambert *et al.*, 2014).

In Europe, minke whales are listed as European Protected Species (EPS) (NatureScot, 2023). This grants them protection from unmitigated injury and disturbance from all anthropogenic marine activities (UK Government, 1994). The Scottish guidance for EPS does not list commercial fishing as an activity with the

potential to disturb. However, impacts on their prey sources and loss of habitat are both listed as associated potential impacts that minke whales, as an EPS, are protected from (Scottish Government, 2020). Further work is needed in order to emphasise the threat posed by commercial fishing activities and accordingly tighten up irregularities within policy at national and international levels.

Scotland's principal management initiative for cetaceans is the MPA network. Within the MPA network, minke whales are listed as protected features of two MPAs: The Southern Trench and Sea of the Hebrides sites (Ryan *et al.*, 2022). However, the extent of protection for minke whales is limited; bottom trawl fishing is still permitted within MPA boundaries as is the use of static gear (Pita *et al.*, 2013) – the main threat to minke whales in Scottish coastal waters (Leaper *et al.*, 2022). Furthermore, the permitted fishing activity in these designated areas target species that are significant components of their ecosystem as well as dietary constituents of the minke whale (Piet *et al.*, 2009; Thorpe *et al.*, 2022), yet protection does not extend to these important species, instead protection is allocated at the feature level. Therefore, minke whales and the wider MPA ecosystem are continually threatened by destructive fishing practices. It is perhaps more appropriate that the management approach to the MPA network is altered so that protection is more ecosystem based rather than feature based. Streamlining the management process in this way could produce more effective protection measures.

Continued and improved monitoring of minke whale foraging ecology is evidently required to inform these significant adjustments and transform the approach to the MPA network. For example, highly focused and thorough monitoring of minke whale habitat use and wider foraging ecology within Scottish MPAs and the surrounding waters would highlight temporal and spatial variability, which management does not currently account for. This is highly important given that minke whales are migratory and highly mobile within their foraging grounds (Anderwald *et al.*, 2012), so the entirety of an MPA is unlikely to be of equal value to monitoring efforts (Hooker *et al.*, 2011).

To date, the MPA network has been informed mostly by transect surveys throughout Scottish waters (Robinson *et al.*, 2009; Anderwald *et al.*, 2012). These have contributed significantly to the establishment of MPAs, and their continuation is vital in informing the adaptative management process. Anecdotal sightings and SCA

underpin our current understanding of minke whale foraging ecology (Pierce *et al.*, 2004; Robinson *et al.*, 2023) and provide strong foundations from which further analysis of minke whale trophic dynamics can be conducted. Indeed, recent eDNA analysis has provided new insights into minke whale foraging behaviour and species interactions in the Moray Firth (Boyse *et al.*, 2024, 2025). In this context, SIA can also be an effective tool in addressing key knowledge gaps within the MPA network.

Primarily, SIA of bulk skin tissue can infer precise dietary proportions of prey species to the minke whale diet over a period of months (Borrell *et al.*, 2012; Giménez *et al.*, 2016). It can also utilise tissue samples from stranded individuals, enabling larger sample sizes that are more representative over temporal and spatial scales. This both compliments and expands the information determined from SCA. Where stomach contents can be used to identify ingested prey species, SIA can be used to assess long-term dietary contributions from prey. This directly addresses a major shortcoming in the MPA network by highlighting the importance of key prey species to protected features such as minke whales and can be used to inform catch quotas for the fisheries that target them.

Over a similar timeframe of months, SIA can also provide clarity on the isotopic niche of minke whales which can be used as a coarse proxy for habitat use (Newsome *et al.*, 2012; García-Vernet *et al.*, 2021). Within Scottish coastal waters where presence/absence analysis has detected changes in minke whale distribution, isotopic niche analysis can provide context on the foraging behaviour that potentially drives such change by detecting overlap and shifts in niche throughout the foraging season. This creates a more rounded picture of temporal habitat use within foraging grounds which can be used to manage fishing practises such as bottom trawling and static gear fishing. The current MPA network, although widespread, lacks detail in its protective measures and in spite of thorough monitoring efforts that have generated datasets >20 years (Robinson *et al.*, 2023), the pursued methods lack the precision that SIA can provide.

In this thesis, entitled '**The foraging ecology of minke whales (*Balaenoptera acutorostrata*) in Northeast Scottish waters using stable isotope analysis**', I focus on two specific aspects: diet and isotopic niche to improve our understanding of minke whale dietary preferences and how it drives seasonal and ontogenetic variation

in isotopic niche. The results of which aim to support the adaptive management process in addressing persistent threats within the Scottish MPA network.

In Chapter 2, '**Identifying prey preferences and trophic position of minke whales (*Balaenoptera acutorostrata*) in Northeast Scottish waters through stable isotope analysis of bulk tissues**', SIA is used to infer dietary proportions of putative prey species to the diet of minke whales through mixing models. Furthermore, the minke whale trophic position is calculated to illustrate how their diet influences their trophic role within the food web. Mixing model analysis shows that sand eel is the primary dietary contributor, with clupeids and krill making up relatively significant proportions in the adult and juvenile diets, respectively. Overall, the derived trophic positions were lower than expected given the predominantly fish diets.

In Chapter 3, '**Niche partitioning between adult and juvenile minke whales (*Balaenoptera acutorostrata*) in Northeast Scottish waters using bulk skin stable isotopes**', the standard ellipse area (SEA) is used to assess isotopic niche partitioning between adult and juvenile minke whales as well as to investigate the extent of overlap between their respective seasonal niches. The results show that adult and juvenile minke whales overlap considerably in the spring months but partition completely by the summer. Additionally, whilst juvenile niche areas overlap and expand slightly from spring and summer, the adult niche areas for the same seasons diverge and constrict in size.

Conclusion

In conclusion, our understanding of minke whales in the Northeast Atlantic is insufficient when compared to other mysticete species. Scotland has highly productive waters that are influenced by oceanic currents at both regional and local scales. During the summer months, this provides rich feeding opportunities for all marine taxa. Minke whales migrate from their unknown breeding grounds to these waters, exploiting the rich feeding opportunities available to them. Although their summer range spans the whole UK coastline, Scottish waters support a proportionally large number. The Moray Firth in Northeast Scotland has been identified as a key foraging ground that hosts above average densities compared to the wider Scottish marine estate, hence the designation of the Southern Trench MPA in 2020, of which the minke whale has been selected as a protected feature. However, more work is needed to fully understand the

role of the minke whale in the Scottish marine ecosystem. A task that comes ahead of NatureScot's new initiative to boost the MPA network with Highly Protected Marine Areas (HPMAs) that will cover 10% of Scotland's seas. Reviewing the selection guidelines that accompany this legislation points to a cure over prevention management system which is high risk given the amount of time some aspects of the marine ecosystem need to recover after damage.

Literature on the feeding ecology of minke whales in the UK is scarce. In the Moray Firth, they are thought to be generalists feeding primarily on sand eel, herring and sprat. Their diet in Scottish waters is based solely on SCA of deceased animals who may have died from illness some time before analysis took place. It is overdue that this data is re-assessed using more accurate methodologies. Precise in-situ tissue sampling presents extremely valuable opportunities to analyse the stable isotopic ratios in the tissues as a means of deriving dietary constituents of live and possibly healthy individuals. Moreover, this line of research will address an area that has not previously been looked at for the Moray Firth - trophic dynamics. The trophic relationships between minke whales and the wider food web have been explored in a number of regions of the Northeast Atlantic, namely Ireland's west coast, the Barents Sea and Iceland but such data remains absent for individuals using the valuable MPA network. The current project aims to address this clear absence of data by placing this highly mobile species in a trophic context. A question pertaining to habitat partitioning between adults and juveniles also remains unclear. It is a core aim to establish any potential isotopic niche partitioning between age classes which may further our current understanding of habitat use in minke whales.

The mass of literature on threats in Scottish waters shows that entanglement is by far the overwhelming cause of death in minke whales. Although, other threats such as unsustainable fishing practices and climate change are also posing serious issues to the species that could have significant ramifications for individual survivability that, with the combined growth of these threats, may have a larger population impact. The MPA network stands as Scotland's primary management initiative, but its effectiveness in safeguarding highly mobile species such as cetaceans is questioned. Indeed, the incoming designations of HPMAs may certainly offer sufficient protection for prey species that could indirectly benefit the wider minke whale population, but any results will not become clear until enough time has passed and the effect of the

upgraded MPA network is measurable. In the meantime, efforts should look to reduce the effect of bottom-trawl fishing and overfishing in Scottish waters so that this understudied species can continue to take advantage of the rich feeding opportunities that are offered by these productive waters.

Thesis Aims

- To apply SIA in assessing the foraging ecology of minke whales in Scottish waters and therefore broaden the current understanding of trophic interactions between predator and prey.
- To determine the contribution of known prey species to the diet of adult and juvenile minke whales using SIA of bulk tissues.
- To investigate seasonal variation and overlap of the isotopic niche between adults and juveniles and use this to infer the extent of partitioning between the two age-classes.
- To interpret these new findings in the context of emerging threats such as prey stock decline and habitat destruction and therefore establish the importance of SIA as an effective monitoring tool for protected features within the MPA network.

Appendices

Appendix 1.1. Species of cetacean observed in UK waters.

Suborder	Common name	Scientific name	Distribution	Occurrence	Reference
Odontocete	Sperm whale	*Physeter macrocephalus*	Throughout the UK and Ireland	Rare. Mainly bachelor groups	(Santos *et al.*, 2002)
Odontocete	Pygmy sperm whale	*Kogia breviceps*	Scotland	Rare	(Kitchener *et al.*, 2012)
Odontocete	Soweby's beaked whale	*Mesoplodon bidens*	Throughout the UK and Ireland	Rare	(Dolman *et al.*, 2010)
Odontocete	Blainville's beaked whale	*Mesoplodon densirostris*	Irish sea	Rare	(MacLeod *et al.*, 2004)

Odontocete	True's beaked whale	*Mesoplodon mirus*	Ireland	Rare	(MacLeod *et al.*, 2004)
Odontocete	Gervais' beaked whale	*Mesoplodon europaeus*	Ireland	Rare	(MacLeod *et al.*, 2004)
Odontocete	Cuvier's beaked whale	*Ziphius cavirostris*	Scotland and Ireland	Rare	(Dolman *et al.*, 2010)
Odontocete	Northern bottlenose whale	*Hyperoodon ampullatus*	Throughout the UK and Ireland	Rare	(Whitehead and Hooker, 2012)
Odontocete	Narwhal	*Monodon monoceros*	Orkney	Extremely rare	(Evans *et al.*, 2003)
Odontocete	Beluga	*Delphinapterus leucas*	Ireland, Scotland and Thames estuary, England	Extremely rare	(Evans *et al.*, 2003)
Odontocete	Harbour porpoise	*Phocoena phocoena*	Throughout the UK and Ireland	Resident	

Odontocete	Long finned pilot whale	*Globicephala melas*	Throughout the UK and Ireland	Seen annually. Migratory	(Gajdosechova *et al.*, 2016)
Odontocete	Killer whale	*Orcinus orca*	Throughout the UK and Ireland	Resident	(Beck *et al.*, 2014)
Odontocete	False killer whale	*Pseudorca crassidens*	Scotland	Rare	(Vicari *et al.*, 2022)
Odontocete	Risso's dolphin	*Grampus griseus*	Throughout the UK and Ireland	Resident	(Hodgins *et al.*, 2014)
Odontocete	White beaked dolphin	*Lagenorhynchus albirostris*	Throughout the UK and Ireland	Resident	(Canning *et al.*, 2008)
Odontocete	Atlantic white sided dolphin	*Lagenorhynchus acutus*	Throughout the UK and Ireland	Offshore resident	(Macleod 2004)
Odontocete	Bottlenose dolphin	*Tursiops truncatus*	Throughout the UK and Ireland	Resident	(Robinson *et al.*, 2012)

Odontocete	Striped dolphin	*Stenella coeruleoalba*	Throughout the UK and Ireland	Offshore resident	(Hammond *et al.*, 2017)
Odontocete	Short beaked common dolphin	*Delphinus delphis*	Throughout the UK and Ireland	Offshore resident	(Robinson *et al.*, 2010)
Odontocete	Fraser's dolphin	*Lagenodelphis hosei*	Outer Hebrides, Scotland	Rare	(Bones *et al.*, 1998)
Mysticete	Blue whale	*Balaenoptera musculus*	West coast of Ireland	Extremely rare. Migratory	(Lavallin *et al.*, 2023)
Mysticete	Fin whale	*Balaenoptera physalus*	Throughout the UK and Ireland	Migratory	(Ryan *et al.*, 2013)
Mysticete	Sei whale	*Balaenoptera borealis*	Throughout the UK and Ireland	Migratory	(Macleod *et al.*, 2003)
Mysticete	Minke whale	*Balaenoptera acutorostrta*	Throughout the UK and Ireland	Migratory	(MacDougall and Robinson, 2025)

Mysticete	Humpback whale	*Megaptera novaeangliae*	Throughout the UK and Ireland	Migratory	(Marwood *et al.*, 2022)
Mysticete	North Atlantic right whale	*Eubalaena glacialis*	Northern Scotland and Ireland	Extremely rare. Migratory	(Reeves, 1982)
Mysticete	Bowhead whale	*Balaena mysticetus*	Southwest England and Ireland	Extremely rare. Migratory	(de Boer *et al.*, 2017)

Appendix 1.2. Types of MPA in the UK's MPA network, and their purpose *(Strachan* et al.*, 2022)*.

Type	Purpose
Highly Protected Marine Area (HPMA)	Prohibiting all damaging human activities and allowing ecosystems to recover and thrive.
Special Areas of Conservation (SACs)	Designated to protect habitats and species of European importance.
Special Protection Areas (SPAs)	Classified to protect bird species of European importance and regularly occurring migratory birds.
Marine Conservation Zone (MCZ) / Nature Conservation Marine Protected Area (NCMPA)	Designated to protect nationally important species, habitats, ecological processes and features of geological/geomorphological importance.
Sites of Special Scientific Interest (SSSIs) / Areas of Special Scientific Interest (ASSIs)	Designated to protect any area of special interest for its flora, fauna, geological or physiographical features. These are coastal (and terrestrial) designations with some sites protecting marine features. ASSIs are designated in Northern Ireland, which are equivalent to SSSIs in England, Scotland and Wales.
Ramsar Sites	Wetlands of international importance designated under the Ramsar Convention. These are coastal (and

terrestrial) designations with some sites protecting marine features.

Chapter 2: Identifying prey preferences and trophic position of minke whales (*Balaenoptera acutorostrata*) in Northeast Scottish waters through stable isotope analysis of bulk tissues.

Authors

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Abstract

The coastal waters of Northeast Scotland are highly productive and provide rich feeding opportunities for both resident and migratory cetaceans. Migratory whales exploit these high latitude areas during the spring and summer to capitalise on the seasonal abundance of prey and replenish energy reserves depleted over the winter. The minke whale (*Balaenoptera acutorostrata*) is the most abundant of baleen whales in this region, yet its dietary composition and feeding ecology remain poorly understood. This study uses stable carbon and nitrogen isotope ratios in minke whale skin tissue, and in the muscle tissue of putative prey species to quantify dietary contributions using Bayesian stable isotope mixing models (BSIMMs). Given the generalist feeding behaviour of this

species, trophic position was also estimated for minke whales in Northeast Scottish waters and compared with published values from elsewhere in the North Atlantic. Mixing model outputs (median, low–high 95% credibility intervals) indicated that sand eels (*Ammodytidae* sp.) (0.34, 0.03 - 0.68) and Clupeidae (0.27, 0.07 - 0.54) comprised the majority of the assimilated diet in adults, but the main dietary constituents for juveniles were sand eel (0.36, 0.03 - 0.74) and krill (0.29, 0.06 - 0.55). However, posterior distributions of these models were diffuse reflecting uncertainty in prey source estimates. These results highlight the need for further research and refinement of dietary models through greater samples sizes potentially sourced from strandings, more appropriate trophic discrimination factors (TDFs) and complementary movement data, such as satellite tracking to better constrain foraging ranges and prey composition. By providing the first isotopic assessment of the minke whale diet in Northeast Scotland, this study contributes valuable baseline information to inform management of Scottish fisheries and Marine Protected Areas (MPA), particularly the recently designated Southern Trench MPA, a recognised feeding ground for this species.

Key words: Minke whale, strandings, age class, diet, stable isotope, mixing models, sand eel, fisheries

Introduction

Prey availability is a key driver of marine predator distribution and abundance (Skern-Mauritzen et al., 2011; Meyer-Gutbrod et al., 2015) and plays a central role in shaping the migratory strategies of baleen whales whose large-scale annual latitudinal migrations are a defining feature of their life histories (Abrahms *et al.*, 2019). During the summer months, whales migrate to seasonally productive high latitude foraging grounds to exploit rich feeding opportunities (Bannister, 2009; Ramp *et al.*, 2015). These periods of intense feeding enable whales to replenish energy reserves depleted during winter months spent in lower latitude breeding grounds – a period often associated with fasting and nursing (Ramp *et al.*, 2015). Consequently, migratory whales are highly sensitive to fluctuations in prey availability, with prey stock collapse and distribution shifts posing serious risks to their reproductive success and population health (Víkingsson *et al.*, 2015; Meyer-Gutbrod and Greene, 2018; Moore *et al.*, 2019; Tulloch *et al.*, 2019). Monitoring the foraging ecology of these sentinel species can therefore provide

valuable insights into ecosystem change and the effectiveness of management measures aimed at maintaining healthy predator-prey dynamics.

Traditional approaches for studying marine predator diets, like stomach contents analysis (SCA) have long been used to identify prey items but are often limited in scope. SCA, which is lethal when applied to elusive, wide-ranging cetaceans can only represent feeding activity over short timescales (Barros and Wells, 1998; Dunshea *et al.*, 2013). In contrast, using ecological tracers such as stable isotopes provides a non-lethal, indirect and powerful approach to investigating foraging ecology over longer temporal scales (DeNiro and Epstein, 1978; Deniro and Epstein, 1981). Over the last two decades, Stable Isotope Analysis (SIA) has become widely adopted in marine mammal research, enhancing understanding of diet (Jackson et al., 2025; Ryan et al., 2014), trophic position (Troina *et al.*, 2021; Paschoalini *et al.*, 2025) and habitat use (Lesage *et al.*, 2010; Wright *et al.*, 2025). SIA can provide an estimate of the proportional contribution of prey sources to the diet of a consumer. This is because stable isotope ratios and their variation are predictably incorporated into consumer tissues, with some amount fractionation (TDF). Therefore, if the prey sources of a given consumer are known, as well as the respective TDFs, then the stable isotope ratios of both the consumer and its prey can be measured and modelled using mixing models to determine the relative contribution of the selected prey sources to the diet. Click or tap here to enter text.Click or tap here to enter text.Click or tap here to enter text.

The minke whale is the most abundant baleen whale in UK waters (Stockin *et al.*, 2001), with more than 7,800 individuals estimated in the North Sea (Gilles *et al.*, 2023). They exploit the rich seasonal prey resources of Scottish coastal and offshore waters during the spring and summer (Macleod *et al.*, 2004; Robinson *et al.*, 2009). In recognition of their ecological importance, two marine protected areas (MPAs) were designated in 2020: the Sea of the Hebrides and the Southern Trench, both listing minke whales as protected features (Figure 1). The Moray Firth, within which the Southern Trench MPA is located, supports some of the highest seasonal densities of minke whales in Scotland (Paxton *et al.*, 2014). Despite this, knowledge of their dietary composition and trophic ecology in these waters remains limited.

Existing dietary information comes primarily from SCA of stranded individuals across the Scottish coastline, which indicates that sand eels (*Ammodytidae sp.*) are the dominant prey by number and weight, followed by the clupeid species sprat (*Sprattus sprattus*) and herring (*Clupea harrengus*) (Pierce *et al.*, 2004). Visual feeding observations similarly suggest a preference for sand eels in the Moray Firth (Robinson and Tetley, 2007). However, these methods offer only short-term insights of feeding activity and cannot easily account for spatial or temporal variation in diet.

To address this knowledge gap, this study analyses $\delta^{13}C$ and $\delta^{15}N$ values from minke whale skin samples (sourced from both live and stranded individuals) and muscle tissue from potential prey species in the waters of Northeast Scotland. Using Bayesian mixing models, the study estimates the contribution of key prey species and establishes baseline data on trophic position. These findings provide valuable insights into the foraging ecology of minke whales and will inform sustainable fisheries management and adaptive conservation within Scotland's MPA network.

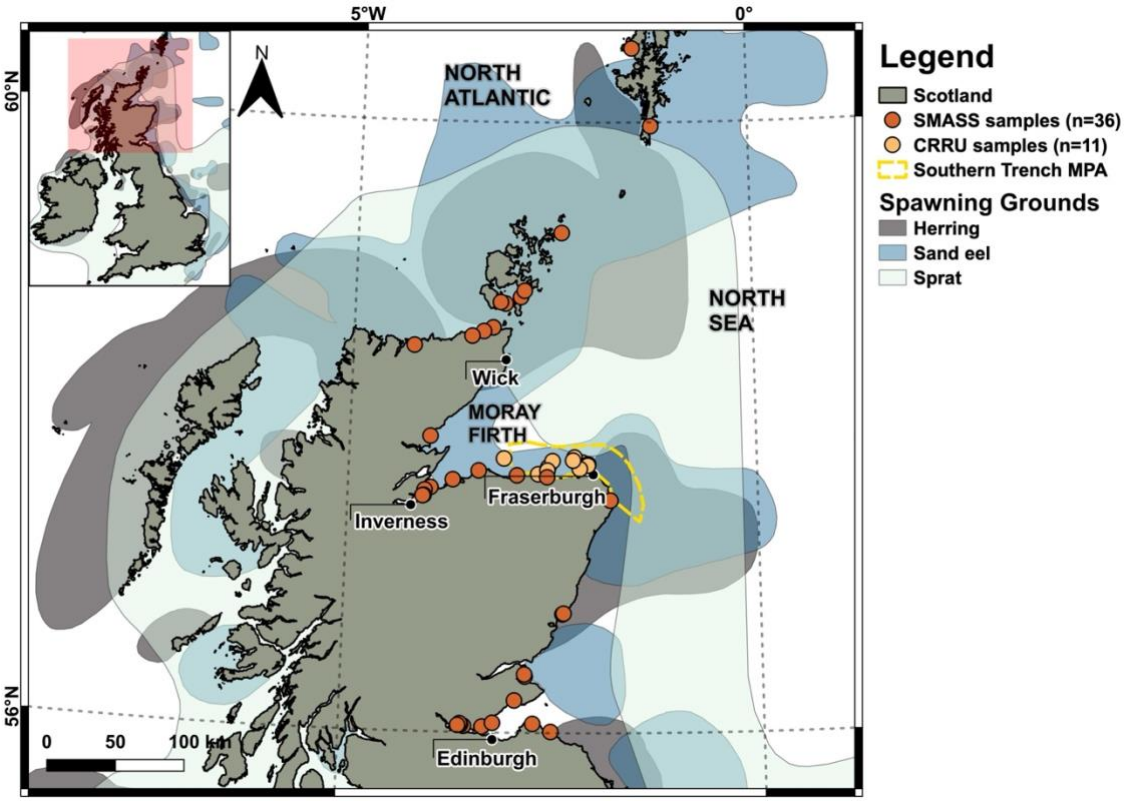


Figure 2.1. Northeast Scotland study area and locations of minke whale samples (Live animals CRRU n=11; Stranded animals SMASS n=36). Map projection: OSGB36 / British National Grid (EPSG: 27700). Units: kilometres. Data sources: British Iles polygon was sourced from ESRI. Spawning ground data sourced from Centre for Environment, Fisheries and Aquaculture Science (CEFAS).

Materials and Methods

Strandings

Minke whale skin samples (n = 36) were acquired from individuals that had stranded from the Firth of Forth to the Islands of Orkney and Shetland (Figure 2.1). The collection of these samples was carried out by the Scottish Marine Animal Stranding Scheme (SMASS) following standard post-mortem protocols outlined in (Kuiken and Hartmann, 1991; Ijsseldijk *et al.*, 2019). Samples were collected between 1993 and 2023, between March and December. The samples were stored at -20 °C, and in the case of particularly decomposed carcases, samples were often retrieved without a formal post-mortem. Individuals ranged between 2.48 – 8.30 m, with age class being determined from a combination of body length and assessments of sexual maturity. Both adults and juveniles were sampled. Samples were assigned a condition code depending on the extent of decomposition (Table 2.1). Previous isotopic studies using skin tissue from stranded individuals have shown that the stage of decomposition had limited impact on bulk $\delta^{13}C$ and $\delta^{15}N$ values (Payo-Payo *et al.*, 2013; Burrows *et al.*, 2014) and so samples were obtained from individuals with decomposition codes 2a (Fresh) – 4 (Advanced Decomposition) (Table 2.1).

Table 2.1. Number of SMASS samples of each condition code (n = 36).

Condition code	Number of skin tissue samples
2a (Fresh)	10 (2 adults, 8 juveniles)
2b (Slight decomposition)	8 (3 adults, 5 juveniles)
3 (Moderate decomposition)	7 (1 adults, 6 juveniles)
4 (Advanced decomposition)	11 (4 adults, 7 juveniles)

Live sampling

Between June and September (2017 - 2022), skin tissue samples of free ranging adult and juvenile minke whales (n = 11) were attained under license by the Cetacean Research and Rescue Unit (CRRU) using the crossbow and dart method (Noren and Mocklin, 2012) (License number 211818) (Table 2.2, Appendix 2.8; Supplementary material). Age class was assigned based on the individual's estimated length relative to the vessel, and their colouration with adults being classed as larger, darker individuals (Mitchell and Kozicki, 1975). A Jandao recurve crossbow with a draw strength of 150 lbs was used to deliver custom made bolts developed by Finn Larsen (CETA-DART®). These bolts were fitted with hollow, stainless-steel tips measuring 6mm in diameter and roughly 40mm in length. Attached to the shaft was a stopper that prevented the bolt from penetrating past the collection tip and kept the bolt afloat for easy retrieval.

The following protocol was strictly adhered to during all sampling attempts: when an individual had been sighted, photographs were taken and cross referenced with a biopsy catalogue to ensure the individual had not been previously sampled. If it had not, the crossbow and bolt would be prepared whilst monitoring of the whale continued. Signs of avoidance, malnourishment or if the animal was thought to be feeding would call for the sampling attempt to be aborted. However, if the animal was healthy and its movements predictable, tracking and sampling efforts could continue. From 2021, this method was aided with the use of a drone which would allow the heading of the whale to be ascertained during dives, when tracking would otherwise be more challenging.

Once the arbalester (crossbow operative) was in place on the bow of the vessel and the final approach to the whale began, all remaining team members would move towards the stern, to minimise human risk. At this point, the crossbow could be drawn, and the bolt knocked. The safety catch always remained on until time of delivery. The coxswain would approach the whale from behind and offset slightly to one side so that the arbalester was positioned directly parallel to the individual at a minimum distance of 10 metres. When the whale surfaced, and if the arbalester was satisfied with the shot, the bolt would be released.

The primary target area for this type of sampling is typically ventral and posterior to the dorsal fin along the upper peduncle flank where there is a larger target area and greater tissue mass. If it was a successful attempt, the bolt would be

collected, and the tip removed for short term storage in a sealed and sterile screw-top container and placed on ice. Once back at the field base, the skin tissue layer was separated from the blubber using a sterilised scalpel and the skin sample was split into two pieces for dual analysis. The skin was stored in an Eppendorf tube with 20% dimethyl sulfoxide (DMSO), saturated with 5 mol/L sodium chloride (NaCl) whilst the blubber was stored in sterilized foil and frozen directly (Gavrilchuk *et al.*, 2014; Durante *et al.*, 2021).

Table 2.2. Number of free ranging minke whale samples attained in each year by CRRU (n = 11).

Year	Number of samples
2017	1 (1 adult)
2018	1 (1 juvenile)
2020	2 (2 adults)
2021	6 (4 adults, 2 juveniles)
2022	1 (1 juvenile)

Prey sampling

A review of the available literature and photographic evidence of feeding encounters was conducted to identify the most likely contributors to the diet of minke whales in the study area (Table 2.3). Prey samples were collected by Marine Scotland during the annual International Bottom Trawl Surveys (IBTS) in January and August 2023. Specimens of sand eel (*Ammodytidae*), sprat (*Sprattus sprattus*), herring (*Clupea harengus*), sardine (*Sardina pilchardus*), mackerel (*Scomber scombrus*), whiting (*Merlangius merlangus*), and zooplankton were attained from throughout the northern North Sea at depths between 59 – 92 m. Samples were bagged individually according to species and age class (adult/juvenile) and frozen whole at -20 ºC for the duration of the survey and then transported, on ice, to the laboratory for sample preparation. Due to differing sample sizes for each species, additional data were sought from the literature to supplement species where sample sizes were <20 individuals (Table 2.3). These species included sand eel, sprat and mackerel.

Table 2.3. Prey samples acquired from Marine Scotland archives and literature.

Prey species	Tissue	Marine Scotland (n)	Literature (n)	Location	Collection year	$\delta^{13}C$ Mean ± SD	$\delta^{15}N$ Mean ± SD	Study
Sand-eel	Muscle	5	15	North Sea	2023	-18.71 ± 0.43	10.48 ± 0.72	(Käkelä *et al.*, 2007; Bean, 2016)
Sprat	Muscle	7	15	North Sea	2023	-17.91 ± 0.47	12.72 ± 0.48	(Bean, 2016; Mahfouz *et al.*, 2017)
Herring	Muscle	20	-	North Sea	2023	-18.25 ± 0.53	11.87 ± 0.57	-
Sardine	Muscle	7	-	North Sea	2023	-18.78 ± 0.31	12.89 ± 0.59	-
Mackerel	Muscle	15	11	North Sea	2023	-18.32 ± 0.45	13.19 ± 0.89	(Das *et al.*, 2003; Bean, 2016)
Whiting	Muscle	19	-	North Sea	2023	-18.79 ± 0.78	13.52 ± 1.38	-

Zoo-plankton	Whole organism	7	-	North Sea	2023	-18.03 ± 0.28	10.81 ± 1.09	-
Krill	Whole organism	-	5, 32, 53	Norway, Iceland, Norway	2011, 2018, 2019	-21.07 ± 0.59	8.32 ± 1.09	(Haug *et al.*, 2017, 2024; García-Vernet *et al.*, 2021)
Capelin	Muscle	-	7, 5, 10	Iceland, Iceland, Norway	2003, 2004, 2011	-21.53 ± 0.66	10.66 ± 0.45	(Sarà *et al.*, 2009; Olafsdottir and Rose, 2013; Haug *et al.*, 2017)

One requirement of the mixing models for accurate determination of source proportions is that all contributing sources are included in the model. Following preliminary exploration of processed data, the isotope biplot indicated that there were contributing prey species, with notably lower $\delta^{13}C$ values (Figure 2.2), not present in the data samples – principally northern krill (*Meganyctiphanes norvegica*) and capelin (*Mallotus villosus*) which have been recorded in the diet of minke whales in the Northeast Atlantic (Haug *et al.*, 2017; García-Vernet *et al.*, 2021). Given that Norway and Iceland are known to be the two prominent foraging areas where both these species are abundant, isotope data were sourced from five studies where the years of data collection ranges from 2002 to 2011 for capelin and 2011 to 2019 for krill (Table 2.3). The weighted mean value of each isotope and the respective standard deviations were then calculated for both krill and capelin.

Zooplankton sampling

A total of seven samples of zooplankton each weighing 1-2 g were collected by Marine Scotland during the 2023 IBTS. All samples were taken from the Moray Firth with each deployment being >10 nautical miles from another. Seasonal variation in zooplankton $\delta^{13}C$ and $\delta^{15}N$ values has been demonstrated (Kürten *et al.*, 2011; Giering *et al.*, 2019) and so samples should be obtained during the same time period as the sampling of minke whales or slightly before, however, this was the only available data at the time. The samples were immediately frozen untreated at -20 ºC and kept frozen until transport could be organized from the Marine Scotland archives.

Lipid extraction

The preparation of all samples was conducted at Heriot Watt's Lyell Centre for Earth and Marine Sciences, Edinburgh, UK. Lipids are relatively depleted in ^{13}C, compared to other biochemical classes, resulting in an overall decrease in their $^{13}C/^{12}C$ ratios, and therefore also $\delta^{13}C$ values, by roughly 4 – 7 ‰, relative to the protein component of the animal (DeNiro and Epstein, 1977; Newsome *et al.*, 2018). Studies using $\delta^{13}C$ values of tissues that contain varying lipid content consequently introduce the possibility of tissue bias (Post *et al.*, 2007). However, chemical extraction of lipids can also alter the $\delta^{15}N$ values of bulk tissues (Newsome *et al.*, 2018). As such, all minke whale samples (n = 49) were divided

in two to allow half of the sample to be subject to lipid extraction and analysed for $\delta^{13}C$, whilst the other untreated aliquot was analysed for $\delta^{15}N$. Due to the small number of zooplankton samples, zooplankton was also dual analysed this way.

The lipid extraction aliquot of samples were solvent lipid extracted in an Accelerated Solvent Extractor (Dionex ASE 350). Sample material was placed in pre-extracted cells packed with clean gravel and exhaustively lipid extracted with 9:1 DCM:MeOH (dichloromethane:methanol), set to 3 cycles at 100 °C (10.3 MPa) with a static extraction time of 5 mins and a rinse volume of 75 % (Magill *et al.*, 2015). The lipid-free tissues were then left to air-dry under a fume hood for about 12 hours. The lipid-free samples as well as the second aliquot were then freeze-dried for 24 hours. Then, using a pestle and mortar, all dried samples were ground to a fine powder and 0.5 – 0.7 mg of material was weighed into tin capsules, flattened, folded and crimped into a rounded pellet for analysis.

Lipid normalisation

To avoid costly and time-consuming dual analysis of prey samples, a lipid normalisation approach was adopted to account for the effect of lipids on bulk $\delta^{13}C$ values. The carbon to nitrogen (C:N) ratio of a sample has been found to act as a reliable indicator of lipid content in aquatic organisms (McConnaughey and McRoy, 1979; Post *et al.*, 2007). Studies have found that lipid-free C:N values of white muscle tissue of clupeid fish species herring and sprat, and whiting are 3.3 ± 0.1 and 3.1, respectively (Kiljunen *et al.*, 2006; Caut *et al.*, 2011; Ryan *et al.*, 2014). Using these values as thresholds for lipid-free material in the respective species, any observed values higher than the threshold indicate that the sample was not free of lipids and that the associated $\delta^{13}C$ values need to be corrected. For cetacean skin, a C:N value of < 4 indicates effective lipid removal (Lesage *et al.*, 2010), but models estimating the $\delta^{13}C$ values of lipid-free balaenopterid skin tissue are unreliable (Ryan *et al.*, 2012). Therefore, any minke whale samples with C:N >4 were excluded from analysis (n=3).

Prey samples were chemically lipid extracted following the same procedure as the minke whale skin samples, to attain a mean lipid-extracted $\delta^{13}C$ value ($\delta^{13}C_{lipid\text{-}free}$). The remainder of the non-lipid-extracted prey samples were analysed and corrected using a non - linear model (Equations 1 and 2). The selected normalisation model was adapted from two equations. The first

calculates the sample's proportional lipid content (McConnaughey and McRoy, 1979):

Equation 1.

$$\mathrm{L} = \frac{93}{1 + (0.246 \times (\mathrm{C{:}N}) - 0.775)^{-1}}$$

where L is the proportional lipid content of the sample, C:N is the sample carbon to nitrogen ratio. The second equation then estimates the lipid-free $\delta^{13}C$ values of the untreated samples (Kiljunen *et al.*, 2006):

Equation 2.

$$\delta^{13}\mathrm{C}' = \delta^{13}\mathrm{C} + \mathrm{D} \times \left(\mathrm{I} + \frac{3.90}{1 + 287/\mathrm{L}}\right)$$

with $\delta^{13}C$' denoting the lipid-normalised $\delta^{13}C$ values, D is the isotopic difference between protein and lipid and was assigned a value of 7.018 ± 0.263. I is a constant and was re-estimated to 0.048 ± 0.013 (Kiljunen *et al.*, 2006).

Stable isotope analysis

All stable isotope analyses were conducted at the University of Exeter's Environment and Sustainability Institute stable isotope facility, Penryn, UK. Samples were analysed for $\delta^{13}C$ and $\delta^{15}N$ using a Sercon Integra 2 continuous flow stable isotope mass spectrometer. Samples were run alongside in-house reference material (bovine liver: $\delta^{13}C$ -28.6 ‰, $\delta^{15}N$ 6.3 ‰; alanine; $\delta^{13}C$ -19.6 ‰, $\delta^{15}N$ -1.9 ‰) which was used to correct for instrument drift and to determine the $\delta^{13}C$ and $\delta^{15}N$ values of the samples. Elemental % (%C and %N) were determined using the beam area relative to the bovine liver standard (%C 47.2, %N 9.3). The values of in-house reference material had been previously determined by running alongside the following certified reference material: IAEA-N-1, IAEA-N-2, IAEA-LSVEC, IAEA-CH-6 and B2155 (protein standard, elemental microanalysis). The reference material, measured to two standard deviations (2SD), were analysed regularly with the samples to obtain instrument precision. Reported values were 0.1 ‰ and 0.2 ‰ for carbon and nitrogen respectively. All ratios were expressed in the standard delta notation (δ) using the equation:

Equation 3.

$$\delta X = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 10^3$$

where X is the stable isotope, R represents the ratio of the heavy isotope to the lighter.

Statistical analysis

All analyses were conducted using the statistical computing platform R v4.2.2 (R Core Team, 2023). Escalated burning of fossil fuels has subsequently led to increases in atmospheric carbon dioxide (CO_2). Industrial CO_2 is depleted in ^{13}C by roughly 2 % per mole, compared to atmospheric CO_2, leading to a process known as the Suess effect (Keeling, 1979) – a steady reduction of $\delta^{13}C$ in organic matter over time. A linear model was fitted to highlight any changes in whale skin $\delta^{13}C$ values over time, which would help inform the decision of using uncorrected $\delta^{13}C$ data, or Suess corrected data ($\delta^{13}C.Cor$) (Appendix 2.1; Supplementary material). Minke whale $\delta^{13}C$ values were corrected using the SuessR package (Clark *et al.*, 2021).

Suess corrected minke whale isotope data were tested for normality. Significant differences in individual isotope values between both age classes were then explored with a one-way ANOVA (Kassambara, 2023). Prey lipid-corrected data were tested for normality, for each isotope using a multivariate normality test, given the multiple species of prey. A PERMANOVA was then used to identify differences in the mean isotope values of each prey species. Finally, post hoc pairwise comparisons (with Bonferroni correction) were conducted to identify differences amongst species (Appendix 2.4; Supplementary material) (Vicente-Gonzalez *et al.*, 2021).

Consumer diet was reconstructed using Bayesian isotopic mixing models utilising the simmr package (Parnell *et al.*, 2023). Mixing models require three key inputs to resolve dietary questions: the isotopic values ($\delta^{13}C.Cor$ and $\delta^{15}N$) of consumers (minke whale), the mean isotopic values (and standard deviations) of selected sources (prey) and a TDF that accounts for fractionation (Teixeira *et al.*, 2022). Simmr accounts for areas of potential uncertainty such as variation in the

source data, covariance between source values, and TDFs (Parnell *et al.*, 2010; Harris *et al.*, 2018).

Mixing model construction

Despite no statistically significant change in whale skin $\delta^{13}C$ values over time, Suess corrected data ($\delta^{13}C.Cor$) were used in the models. Subsequently, consumer input data consisted of skin $\delta^{13}C.Cor$ (corrected for the Suess effect) and $\delta^{15}N$ values. Mean ± 1SD isotope values of the selected sources were included as source input data in the models.

The TDF is a common area of uncertainty in mixing models (Healy *et al.*, 2018). For definitive TDFs, controlled feeding studies are required where the consumer is kept on a constant diet of sources with known isotope values (Kelly, 2000; Caut *et al.*, 2011; Browning *et al.*, 2014; Giménez *et al.*, 2016). This is intractable for baleen whales, and so most studies resort to using TDF's derived from similar taxa. There are currently no species-specific discrimination factors for minke whales. However, diet-tissue discrimination factors for both $\delta^{13}C$ (1.3 ± 0.4) and $\delta^{15}N$ (2.8 ± 0.3) have been established for the genetically similar fin whale (Balaenoptera physalus) skin (Borrell *et al.*, 2012). Furthermore, a computational approach was explored using SIDER – an R package that applies a phylogenetic regression model based on a growing dataset to calculate the TDF of a given consumer (Healy *et al.*, 2018). Ultimately, the TDFs selected for inclusion in the models were values in the range of those generated by SIDER and for fin whales (Borrell *et al.*, 2012) (Table 2.4).

Table 2.4. The TDFs of both stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) used in the models for fish source groups and krill. Δ refers to the difference in isotope values between the consumer (minke whale) and its prey.

Source	$\Delta^{13}C$ ±SD	$\Delta^{15}N$ ±SD	Study
Fish sources	1.0 ± 0.5	2.7 ± 1.0	This study
Krill	1.3 ± 0.4	2.8 ± 0.3	(Borrell *et al.*, 2012)

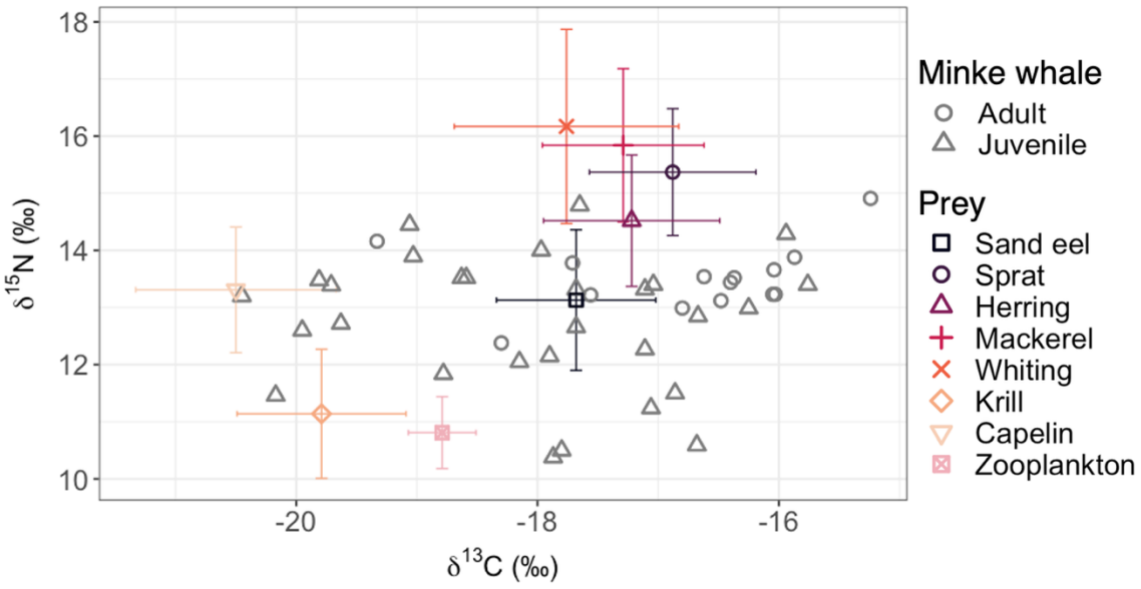


Figure 2.2. Mean ± 1SD $\delta^{13}C$ and $\delta^{15}N$ ratios of prey sources, and individual $\delta^{13}C$ and $\delta^{15}N$ isotope ratios of minke whales, with circles and triangles denoting adults and juveniles, respectively.

Nevertheless, models can still be sensitive to TDFs, even to those derived from controlled feeding studies. Therefore, we carried out sensitivity analysis by altering the mean $\Delta^{13}C$ and $\Delta^{15}N$ values by ± 1SD, one isotope at a time, as has been done previously in dietary studies using uncertain TDFs (Inger *et al.*, 2010). The source inputs remained the same as in the main model, and consumer data consisted of the composite sample of adults and juveniles. Sensitivity analysis was not performed with singular age classes as it was expected that the composite sample approach would provide an accurate representation of model sensitivity, generally. The posterior distributions were then compared with those of the main model to gauge the extent of change in source proportions, and therefore the sensitivity of the model.

A preliminary model was run and a matrix plot showing source proportion histograms, relational contour plots and the correlation between sources was analysed to further evaluate model performance and source interactions. The extent of correlation between sources can be indicative of the model's inability to differentiate between sources and therefore allocate reliable proportions to those sources (Govan *et al.*, 2023). Across 28 pair-wise tests consisting of the original prey sources, two pairs were observed to have high negative correlations. These were sand eel and zooplankton (-0.77), and sand eel and krill (-0.78). Given the

isotopic and trophic difference between sand eel and krill, the decision was made to keep both of these sources in the model. However, considering the purported dominant role of sand eels in the minke whale diet in Scotland (Pierce *et al.*, 2004) and the negligible importance of zooplankton, the decision was made to ultimately exclude zooplankton from the final model.

In the final model run, some sources were highly correlated, suggesting poor source determination. This can result in uncertain and diffuse posterior distributions (Phillips *et al.*, 2014). To address this issue and improve discriminatory power, prey species were grouped. Any number of sources that do not test as statistically different can be grouped (Ben-David *et al.*, 1997; Phillips *et al.*, 2005). However, this invariably depends on the system being studied; it may be more appropriate to group sources that are taxonomically, isotopically or ecologically similar (Phillips *et al.*, 2014). Four prey sources were combined into two groups. Sprat and herring were grouped due to their taxonomical relatedness and isotopic similarity. Mackerel and whiting, despite testing as statistically different in their isotopic ratios, were also grouped due to their similarity in isotopic space and ecologically similar roles as secondary consumers (Table 2.5).

Table 2.5. Grouped source mean $\delta^{13}C$ and $\delta^{15}N$ and standard deviation.

Group name	Prey source	$\delta^{13}C$ ±SD	$\delta^{15}N$ ±SD
Clupeidae (n = 27)	Sprat, herring	-18.2 ±0.5	11.9 ±0.5
Secondary consumers (n = 28)	Mackerel, whiting	-18.4 ±0.8	13.0 ±1.5

Finally, combining sources can be done a priori or a posteriori. A priori can be convenient when two or more sources are known to be related, for example, genetically. However, this approach inevitably leads to greater isotope variability and therefore more uncertainty in contribution estimates (Phillips and Gregg,

2001). Instead, sources were combined a posteriori to improve source determination.

Minke whales were grouped by age class (adult and juvenile) to discern any potential prey preferences between the two groups. To measure the relative importance of individual species in source groups, the source comparison function within simmr was used. This retrieves the probability of one given source having a larger relative contribution than another.

Trophic position

Trophic position was estimated using three methods. The first utilises a Bayesian framework within the R package tRophic Position (Quezada-Romegialli *et al.*, 2018) which accounts for variability within the consumer data. The second and third methods are both arithmetic but differ in their input variables. The first is an equation derived from (Germain *et al.*, 2013):

Equation 4.

$$\mathrm{TP_{bulk}} = \left[\frac{\left(\delta^{15}\mathrm{N_{bulk}} - \mathrm{TDF_{con-prey}}\right) - \delta^{15}\mathrm{N_{base}}}{3.4}\right] + \mathrm{TP_{base}} + 1$$

and the second method is an equation from (Post, 2002):

Equation 5.

$$\mathrm{TP_{bulk}} = \mathrm{TP_{base}} + \left[\frac{\left(\delta^{15}\mathrm{N_{bulk}} - \delta^{15}\mathrm{N_{base}}\right)}{\mathrm{TDF_{con-prey}}}\right]$$

where TP_{bulk} and $\delta^{15}N_{bulk}$ are the trophic position and $\delta^{15}N$ value of the target consumer, respectively, $TDF_{con\text{-}prey}$ and 3.4 are the TDF between the consumer and its prey and a TDF constant, respectively. $\delta^{15}N_{base}$ and TP_{base} are the $\delta^{15}N$ value and trophic position of the baseline organism. For all methods, zooplankton $\delta^{15}N$ values were used to represent the baseline data, and 2 was assigned as baseline trophic position.

Results

Stable isotope ratios

Minke whale

A total of 43 minke whale samples, consisting of 14 adults (8 strandings 6 live samples) and 29 juveniles (25 strandings, 4 live samples), were used in the mixing models. Minke whale mean $\delta^{13}C$ and $\delta^{15}N$ values were -17.6 ± 1.4 ‰ and 13.0 ± 1.1 ‰, respectively. Adult whale mean $\delta^{13}C$ (-16.8 ± 1.3 ‰) and $\delta^{15}N$ (13.5 ± 1.1 ‰) values were higher than those of the juvenile whales (-18.0 ± 1.4 ‰ and 12.8 ± 1.1 ‰, respectively) (Figure 2.3; Appendix 2.2 Supplementary material).

Prey sources

Collectively, prey $\delta^{13}C$ ratios were normally distributed ($\delta^{13}C$ W = 0.974, p = 0.183), whilst $\delta^{15}N$ ratios were not ($\delta^{15}N$ W = 0.938, p = 0.023) (Appendix 2.3 Supplementary material). Interspecies variation was identified among prey (PERMANOVA, $F_{1,71}$ = 112.49, p = <0.001) and post hoc pair wise tests with Bonferroni correction highlighted that whiting was significantly different from sand eel (adjusted p-value = <0.05), herring (adjusted p-value = 0.01), and mackerel (adjusted p-value = <0.05) (Appendix 2.4 Supplementary material).

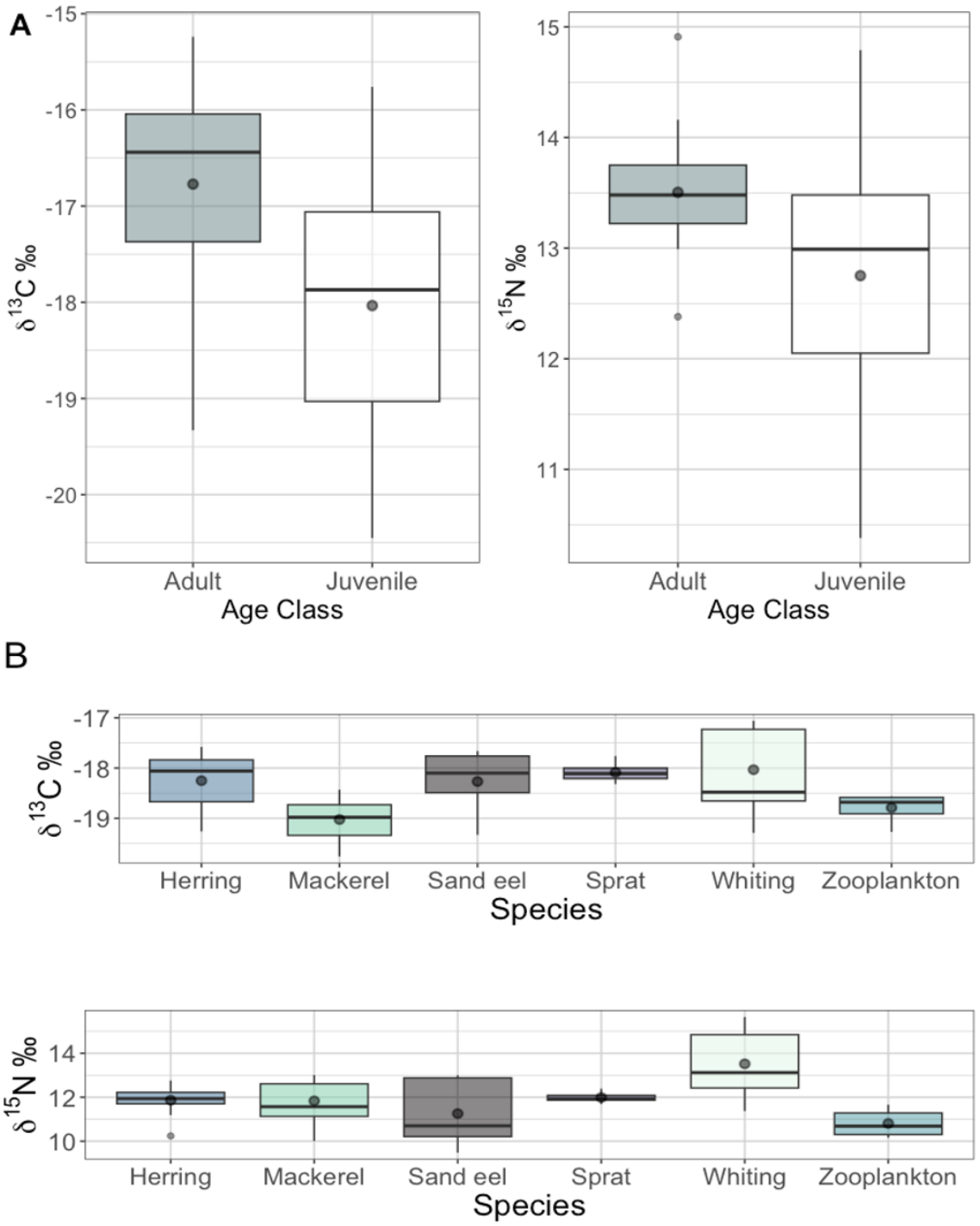


Figure 2.3. A) $\delta^{13}C$ and $\delta^{15}N$ variation between adult and juvenile whales; **B)** isotope variation in the sampled putative prey species. A fish source TDF ($\Delta^{13}C$ = 1.0 ± 0.5 ‰, $\Delta^{15}N$ = 2.7 ± 1.0 ‰) and krill TDF ($\Delta^{13}C$ = 1.3 ± 0.4 ‰, $\Delta^{15}N$ = 2.8 ± 0.3 ‰) have been applied. Means and medians are denoted by the dark circles and lines, respectively. Outer box edges represent the 25th and 75th percentiles, whilst whiskers and dots show data extremes and outliers, respectively.

Mixing model dietary estimates

Some ontogenetic variation was observed in the relative dietary proportions of some prey sources. Sand eel made the largest contribution to the diet of adult (0.34, 0.03 - 0.68), and juvenile minke whales (0.36, 0.03 - 0.74). Krill followed as the next largest contributor to the juvenile diet (0.29, 0.06 - 0.55), whereas in adults, the respective proportion of krill was half (0.14, 0.02 - 0.38). Clupeidae was the second largest contributing source in the adult diet (0.27, 0.07 - 0.54), whereas in juveniles, it was less important (0.16, 0.04 - 0.40). The proportional difference of secondary consumers in the diets of both age classes was slightly different: 0.15, 0.04 - 0.33 and 0.10, 0.03 - 0.26 of the respective adult and juvenile diets. Capelin was the least important source for both adults (0.06, 0.01 - 0.23) and juveniles (0.05, 0.01 - 0.17) (Figure 2.4).

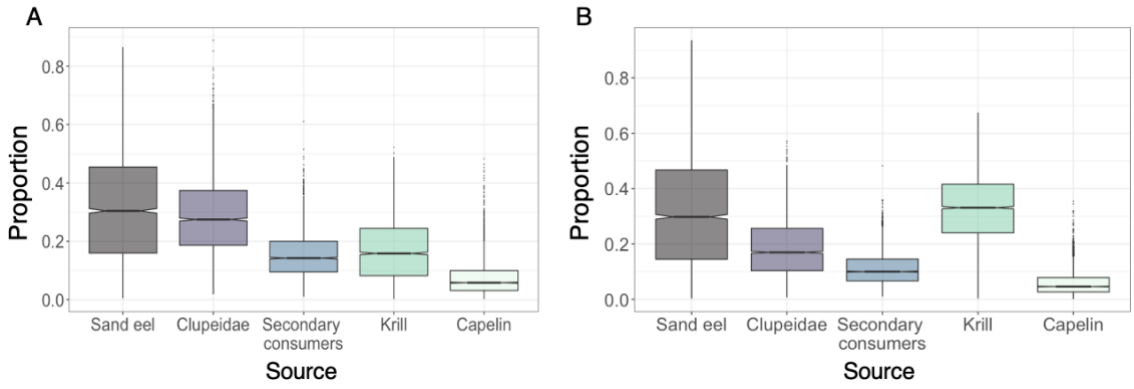


Figure 2.4. Results of BSIMMs showing the proportions of putative prey to the diet of (A) adult whales, and (B) juvenile whales. Median is denoted by the black bar, and coloured boxes show the interquartile range with outer box edges representing the 25th and 75th percentiles.

Site-specific analysis of the Moray Firth minke whale diet were largely consistent with results from across the Northeast Atlantic. Sand eel was the dominant dietary source (0.53, 0.07 - 0.78) whilst Clupeidae contributed about a third (0.30, 0.08 - 0.77). The secondary consumer group contributed the remaining 0.16, 0.04 - 0.41 proportion. Within grouped sources, herring was 59% more likely to have a larger contribution than that of sprat, whilst mackerel was 57% more likely to contribute more than whiting (Figure 2.5).

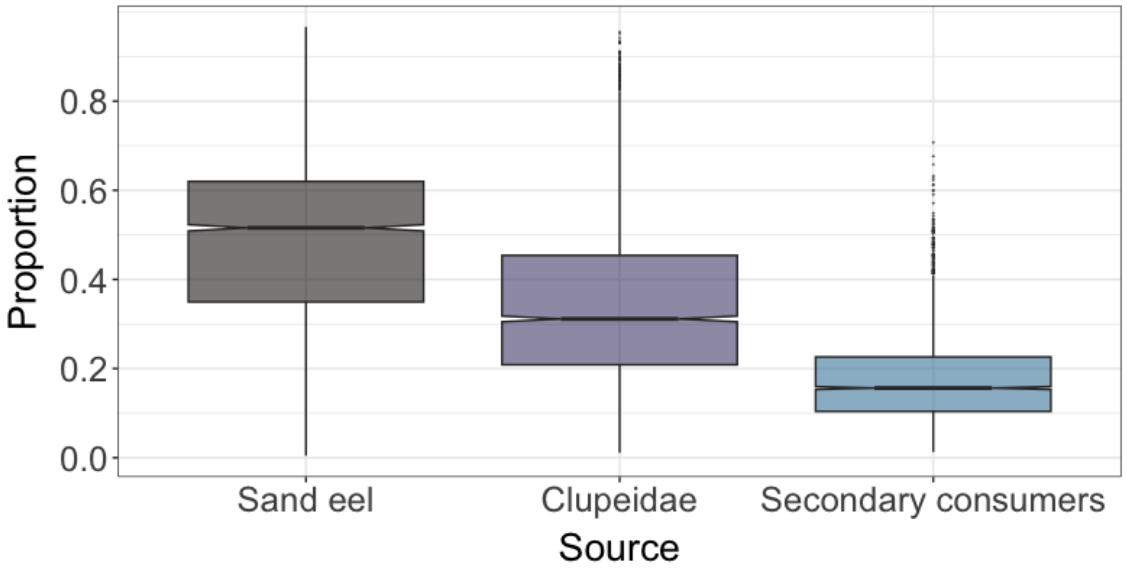


Figure 2.5. Relative proportions of grouped putative prey to the diet of minke whales in the Moray Firth. Median is denoted by the black bar, and coloured boxes show the interquartile range with outer box edges representing the 25th and 75th percentiles.

Sensitivity analysis

Four additional models were run, with each altering the TDFs of each isotope by ±1SD. Sensitivity analysis revealed that, upon alteration, the posterior distributions changed extensively (Appendix 2.6; Supplementary material), indicating that the models were sensitive to changes in the TDF. Increasing $\Delta^{13}C$ by 1SD caused the median contribution of sand eel to drop from 0.65 to 0.10, while krill rose to 0.44. Conversely, decreasing the $\Delta^{13}C$ by 1SD inflated sand eel contribution to 0.79, while it substantially reducing the proportions of the other sources. Changes to $\Delta^{15}N$ also had marked effects: increasing it by 1SD reduced sand eel to 0.39 and increased krill to 0.44, while decreasing it by 1SD further reduced sand eel 0.23 and increased the relative importance of Clupea (0.34) and secondary consumers (0.19).

Trophic position

Using a Bayesian framework and two different mathematical models, minke whale trophic position was estimated using zooplankton isotope data from the Moray Firth as a trophic baseline with respect to whale bulk skin isotope data. Adult whales were found to occupy the higher trophic position (mean ± SD) with the Bayesian model estimating a value of 3.05 ± 0.19 while Equations 4 (Germain

et al., 2013) and 5 (Post, 2002) estimated 3.01 and 3.02, respectively . Juveniles were estimated to have the lowest trophic positions by all three methods (Figure 2.6). The Bayesian model estimated 2.76 ± 0.19, whilst Equations 4 and 5 provided estimates of 2.79 and 2.73, respectively (Appendix 7 Supplementary material).

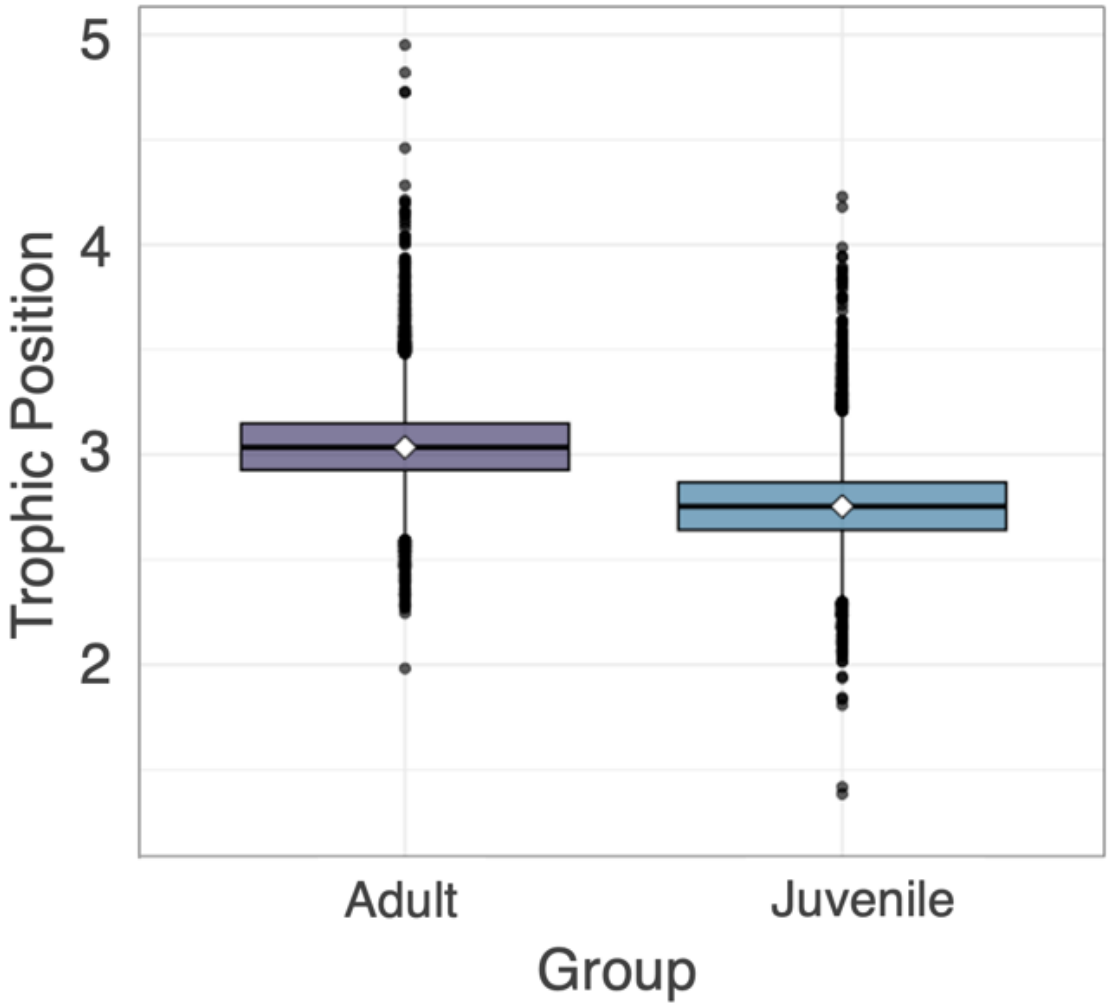


Figure 2.6. Trophic positions of adult and juvenile minke whales as inferred from the Bayesian methods in tRophic Position. The white diamond and black bar denote the mean and median, respectively. Coloured boxes show the interquartile range with outer box edges representing the 25th and 75th percentiles.

Discussion

This study demonstrates the first application of Bayesian isotopic mixing models to infer minke whale foraging ecology in Scottish waters. Assessing isotopic variation, distinct dietary differences were observed between adult and juvenile minke whales in Northeast Scotland. These differences were highlighted further

by the disparity in trophic position between adult and juvenile whales, reaffirming variable dietary preferences.

Dietary estimates

This study used stable isotope analysis (SIA) and Bayesian mixing models to provide new insights into the diet and trophic ecology of minke whales in Northeast Scotland. Results revealed the significance of sand eel and clupeids consistent with previous studies across the North Atlantic but also showed age-related variation in prey composition. Adults consumed more clupeid fish such as sprat and herring, while juveniles assimilated greater proportions of krill. These findings suggest that both prey availability and prey quality shape foraging behaviour, with potential implications for energy balance, reproductive success, and population resilience.

The significance of sand eel aligns with earlier work from UK waters, where the arrival of minke whales in spring coincides with the emergence of sand eels (Macleod *et al.*, 2004; Robinson *et al.*, 2009; De Boer, 2010). Comparable mixing model studies in the Gulf of St Lawrence (Gavrilchuk *et al.*, 2014), and Iceland (García-Vernet *et al.*, 2021) estimated sand eel contributions of 0.57 and 0.54, respectively. Stomach contents studies from the North Sea similarly report sand eels as comprising 0.62 - 0.87 of the diet (Olsen and Holst, 2001; Pierce *et al.*, 2004). These consistent patterns confirm the central role of sand eels as an energy conduit between lower trophic levels and marine predators (Van Deurs *et al.*, 2013).

Clupeid fish (sprat and herring) were proportionally more important for adults (0.27, 0.07 - 0.54) than juveniles (0.16, 0.04 - 0.40) and were also significant in the diet of whales sampled in the Moray Firth (0.30, 0.08 – 0.77). Spatial variation in clupeid use is consistent with patterns seen across the North Atlantic; herring and capelin contribute <0.10 in Icelandic waters (García-Vernet *et al.*, 2021) but more than 0.20 in the Northwest Atlantic (Gavrilchuk *et al.*, 2014). Local observations and eDNA data from the Moray Firth have indicated that clupeids become more important later in the season (Robinson *et al.*, 2023; Boyse *et al.*, 2024), suggesting a seasonal prey shift driven by changing availability. Short- and long-term fluctuations in clupeid stocks (Haug *et al.*, 1996; Víkingsson *et al.*,

2013) likely explain much of this spatial and temporal variability in diet composition.

Such fluctuations have management relevance because forage fish such as sand eel, sprat, and herring underpin marine food webs and are major components of Northeast Atlantic fisheries (Engelhard et al., 2014; Clausen et al., 2018). Recent declines in North Sea sand eel and clupeid recruitment have led to reduced quotas and temporary fishery closures (DEFRA, 2023; ICES, 2024). Depletion of these prey sources could intensify competition between minke whales and commercial fisheries, and whilst minke whales are generalists capable of switching to alternative prey such as gadids (Haug *et al.*, 2002), prey switching may not fully compensate for the energetic loss of lipid-rich forage fish. In this study, secondary consumers (mackerel and whiting) made up only a small proportion of both adult (0.15, 0.04 – 0.33) and juvenile (0.10, 0.03 - 0.26) diets implying that preferred prey remained relatively abundant during sampling. High-latitude prey species showed contrasting importance. Krill and capelin differed markedly in their importance to the minke whale diet. Krill contributed 0.29, 0.06 – 0.55 to the juvenile diet – double the amount estimated for adults (0.14, 0.02 - 0.38), whilst the relative proportion of capelin was negligible in both age-classes (<0.10). Krill are key prey for baleen whales in Arctic and sub-Arctic waters (Haug *et al.*, 1996, 2002), but their decline in the North Sea 63% over the last six decades (Beaugrand et al., 2008; Edwards et al., 2021), could explain the minor contribution observed in the adult diet. Juvenile whales, however, assimilated almost twice as much krill as adults, suggesting broader foraging or seasonal latitudinal movement to higher productivity zones. Although not yet documented for minke whales in the Northeast Atlantic, comparable seasonal movements have been observed in humpback whales (*Megaptera novaeangliae*) (Stevick *et al.*, 2006; Ramm, 2020). These geographic shifts would reduce interspecific competition and may reflect age-related differences in experience or energetic need.

Model Performance and Limitations

Bayesian mixing models are powerful for inferring dietary contributions but are sensitive to assumptions about TDFs and isotopic variation among sources (Phillips *et al.*, 2014), and cannot account for individual species life history. Given the absence of age and species-specific TDFs for baleen whales, this study

conducted sensitivity analysis to assess robustness. Shifting $\Delta^{13}C$ or $\Delta^{15}N$ by ± 1SD substantially altered estimated source proportions—particularly between sand eel and krill—indicating model sensitivity to small changes in input values. This highlights the need for improved empirical TDFs for mysticetes, potentially inferred from consistent meta-analytical scaling.

Temporal variability in prey isotope values may also introduce uncertainty. Prey samples were collected at different times of year (January and August), moreover baseline isotopic values can vary seasonally due to fluctuations in temperature and primary productivity (Cloern and Jassby, 2008). Consequently, isotopic mismatch between prey and consumer samples could partly explain the wide credible intervals. Uncertainty was likely further introduced by prey source omission within the model. Models with absent sources will favour/discriminate other included sources resulting in inflated and diffuse estimates (Parnell *et al.*, 2013). Despite this, the consistently low contribution and sharply peaked posterior distributions of capelin reinforce its limited dietary importance (Appendix 2.5; Supplementary material).

Varying baseline isotope values, tissue turnover rates and life history can make interpreting isotopic data from capital breeding species challenging. Given the latitudinal and oceanographic differences in $\delta^{13}C$ (Newsome *et al.*, 2007), combined with skin tissue turnover rates of up to approximately three months (Teixeira *et al.*, 2022), isotopic signals in recently migrated minke whales may reflect previous foraging locations rather than local foraging, and can therefore be misinterpreted as seasonal dietary or habitat shifts. However, analysis of other diagnostic markers such as $\delta^{34}S$ (Sulphur), would help differentiate migratory signals from true habitat shifts.

Trophic Position

Trophic position estimates from Bayesian and arithmetic approaches were highly consistent, validating the use of the tRophicPosition framework for mysticetes. Adults occupied a higher trophic level (3.1 ± 0.2) than juveniles (2.8 ± 0.2), reflecting their greater reliance on higher-trophic-level prey such as clupeids and secondary consumers. Comparable studies in the North Atlantic have reported minke whale trophic positions between 3.1 and 4.3 (Born et al., 2003; Haug et al., 2017), indicating that values in this study are on the lower end of that range.

The relatively low trophic position for fish-eating individuals may reflect the integration of earlier feeding on zooplanktonic prey, given that isotopic turnover in cetacean skin integrates diet over several months (Giménez et al., 2016; Busquets-Vass et al., 2017). Thus, whales sampled in summer may still carry isotopic signatures from earlier spring feeding on lower-trophic prey.

Alternatively, the lower trophic estimates could reflect genuine ecological differences. Minke whales in Northeast Scotland may exploit prey webs with compressed trophic spacing relative to Arctic ecosystems, where there are more abundant lower trophic level sources like krill. Given ongoing shifts in North Sea food webs driven by warming and altered plankton regimes (Djeghri *et al.*, 2023), such regional variation in trophic position could indicate broad-scale ecological change.

Future considerations

This study represents the first use of SIA to estimate prey contributions to minke whale diets in Scottish waters, but whilst results provide valuable baseline data, several limitations remain. Firstly, acquiring a sufficient sample size should be a central requirement of future studies, particularly those assessing consumer covariables such as age-class or sex. This study subset minke whale samples into adults and juveniles, reducing the sample size of each group and therefore the robustness of the model posterior distributions.

Secondly, Bayesian mixing models depend heavily on accurate isotopic characterisation of prey and appropriate TDFs. It is possible that some prey sources may have been omitted, and potential sources are likely to have high $\delta^{13}C$ and relatively low $\delta^{15}N$ ratios (Figure 2.2). Future work should aim for more comprehensive prey sampling across seasons and habitats so that the full isotopic breadth is represented, including prey with distinct isotopic signatures such as demersal fish which could help strengthen model resolution. Furthermore, the temporal mismatch between consumer and prey sampling limits inference of seasonal diet shifts. Collecting both whale and prey samples within defined seasonal windows would allow for testing intra-annual variation in prey use and trophic position. Similarly, isotopic baselines (e.g., zooplankton $\delta^{13}C$ and $\delta^{15}N$) should be monitored throughout the year to capture seasonal and spatial variability in primary production (Kürten *et al.*, 2011; Giering *et al.*, 2019).

Establishing such baselines would not only refine mixing model accuracy but also contribute to broader understanding of ecosystem isotopic dynamics in the North Sea.

Finally, linking stable isotope data from multiple elements with movement data from tagging or telemetry would greatly improve ecological interpretation. Combining isotopically derived diet reconstruction with spatial foraging data could test whether isotopic differences between adults and juveniles correspond to habitat partitioning, latitudinal shifts, or differential prey targeting.

Conclusion

This study provides new insights into the dietary composition and trophic position of minke whales in the Northeast Atlantic. Sand eels remain a principal prey species across age classes underscoring their critical ecological role and the vulnerability of minke whales to fluctuations in sand eel populations. Ongoing declines in sand eel and other forage fish stocks highlight the need for precautionary, ecosystem-based fisheries management that maintains sufficient prey availability for top predators.

Clupeid fish were important, especially for adults and in local hotspots such as the Moray Firth, suggesting that regional conservation and management strategies must account for spatiotemporal prey dynamics. While minke whales can switch prey, the energetic and reproductive consequences of such shifts remain poorly understood. Integrating nutritional ecology into conservation planning could help assess the broader ecosystem impacts of prey depletion.

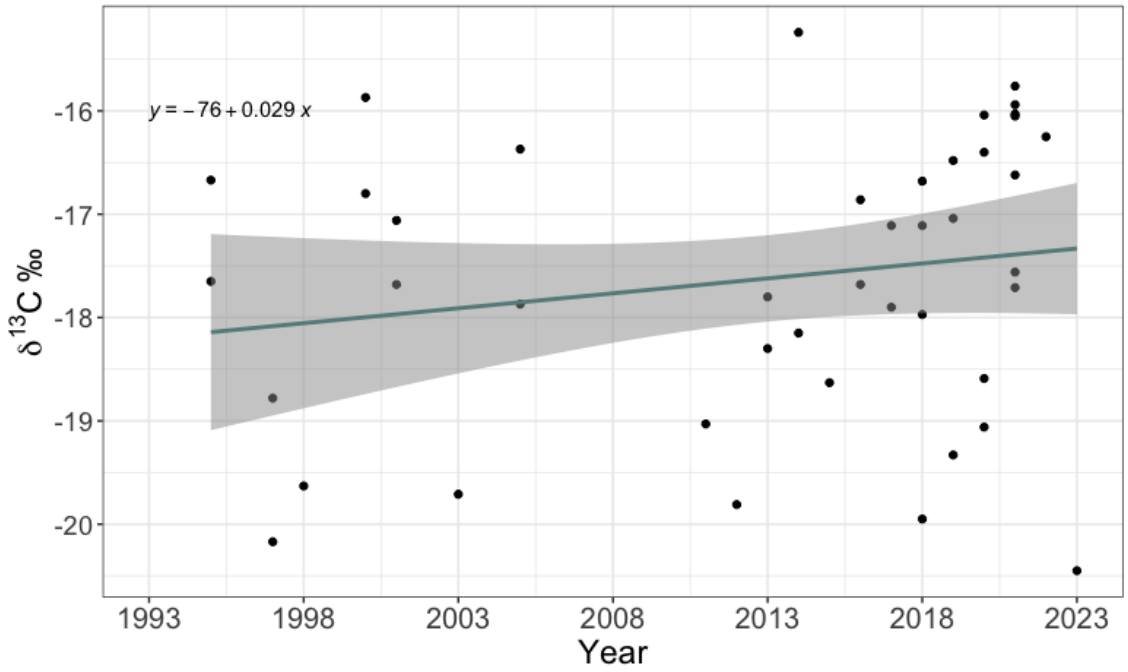
The elevated krill contribution in juveniles suggests partial dietary segregation and possible northward latitudinal movement during summer months, consistent with flexible foraging strategies observed in other baleen whales. However, rapid ocean warming and declining krill abundance may restrict access to these high-latitude resources in future, increasing competition and energetic stress. Age based dietary partitioning corresponded to distinct trophic positions, but temporal resolution was limited. Future isotopic monitoring across seasons as well as including other data sources would enable more precise assessments of foraging dynamics and ecological plasticity.

Overall, this study demonstrates the value of stable isotope analysis for understanding the foraging ecology of elusive marine predators and highlights

the need to align fisheries and MPA planning and management with the prey requirements of minke whales. Protecting key prey populations such as sand eel and clupeids is essential to sustaining both the ecological function and long-term resilience of minke whales in the Northeast Atlantic.

Appendices

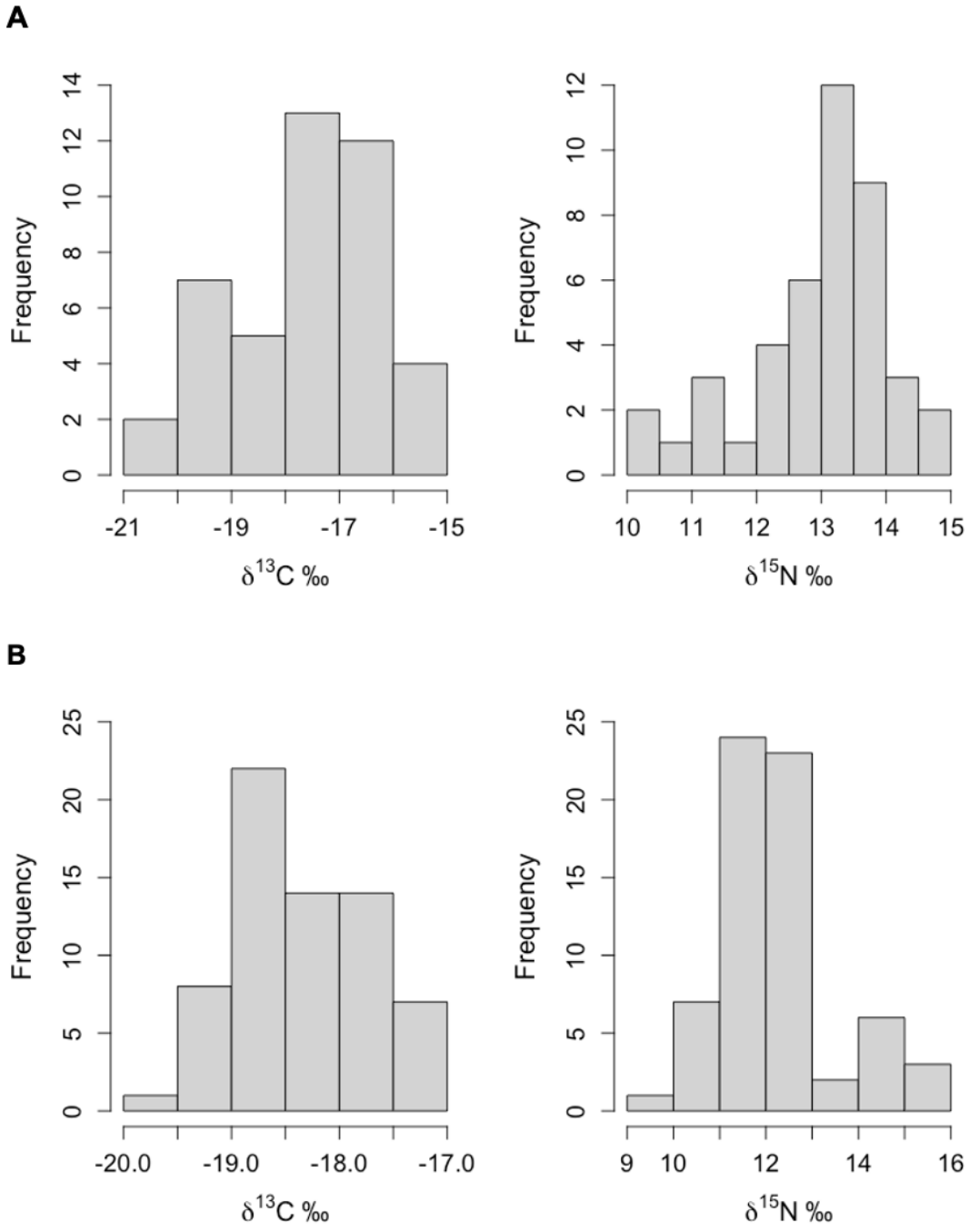
Appendix 2.1. Linear model describing variation of minke whale bulk skin $\delta^{13}C$ ratios over time, possibly due to the Suess effect.



Appendix 2.2. Mean $\delta^{13}C$ and $\delta^{15}N$ and ranges of the minke whale skin tissue samples.

	Mean ± SD (Range)	
	$\delta^{13}C$	**$\delta^{15}N$**
All (*n* = 43)	-17.6 ± 1.4	13.0 ± 1.1
	-20.5 – -15.2	10.4 – 14.9
Adult (n = 14)	-16.8 ± 1.3	13.5 ± 1.1
	-19.3 – -15.2	12.4 – 14.9
Juvenile (n = 29)	-18.0 ± 1.4	12.8 ± 1.1
	-20.5 – -15.8	10.4 – 14.8

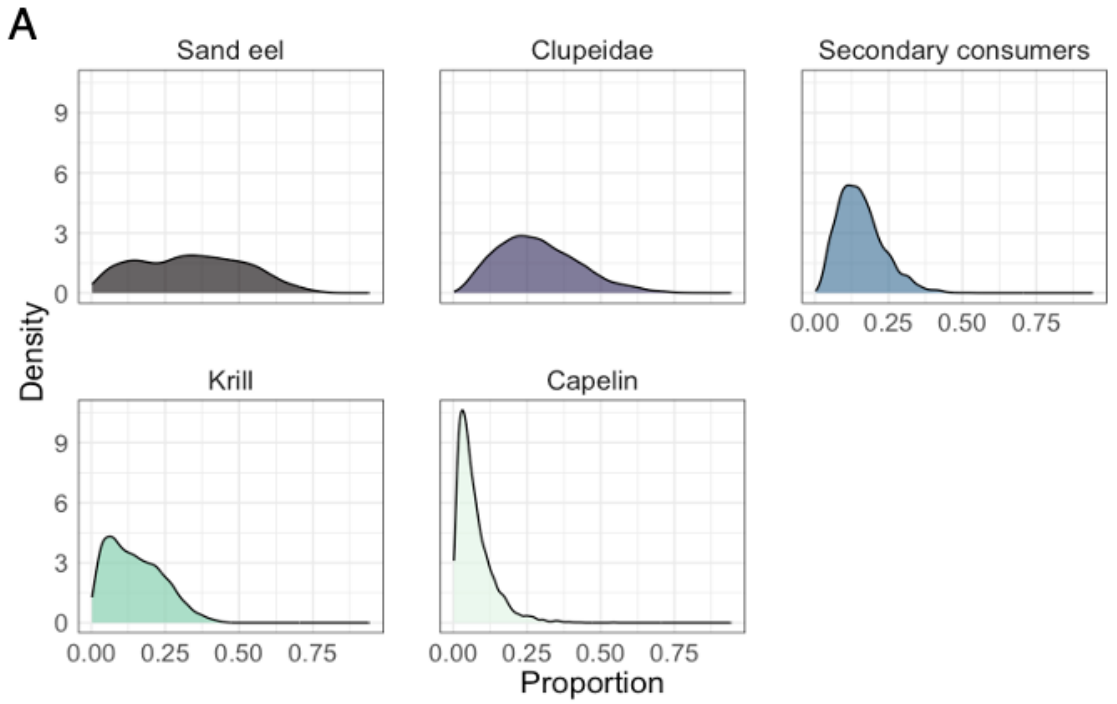
Appendix 2.3. Distribution of $\delta^{13}C$ and $\delta^{15}N$ isotope ratios in (A) minke whale skin tissue and (B) prey muscle tissue.

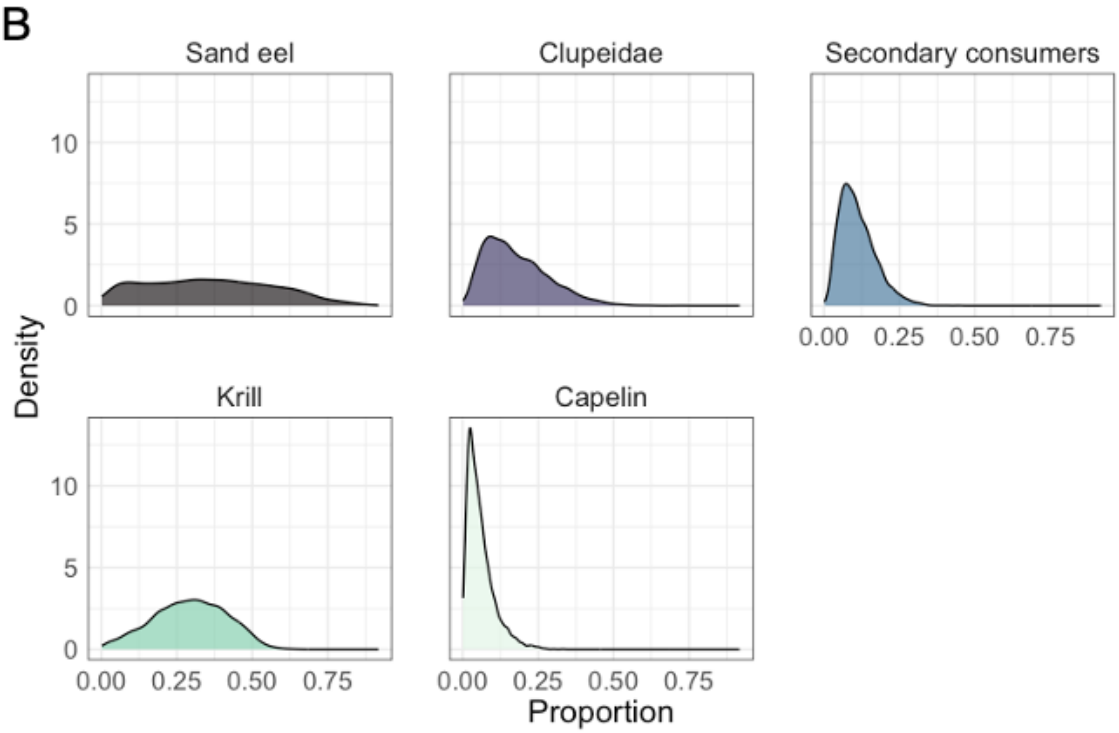


Appendix 2.4. Results of pairwise comparisons of $\delta^{13}C$ and $\delta^{15}N$ ratios in prey sources. A Bonferroni correction was applied to produce adjusted p-values. Significant differences (p = < 0.5) are denoted by "*".

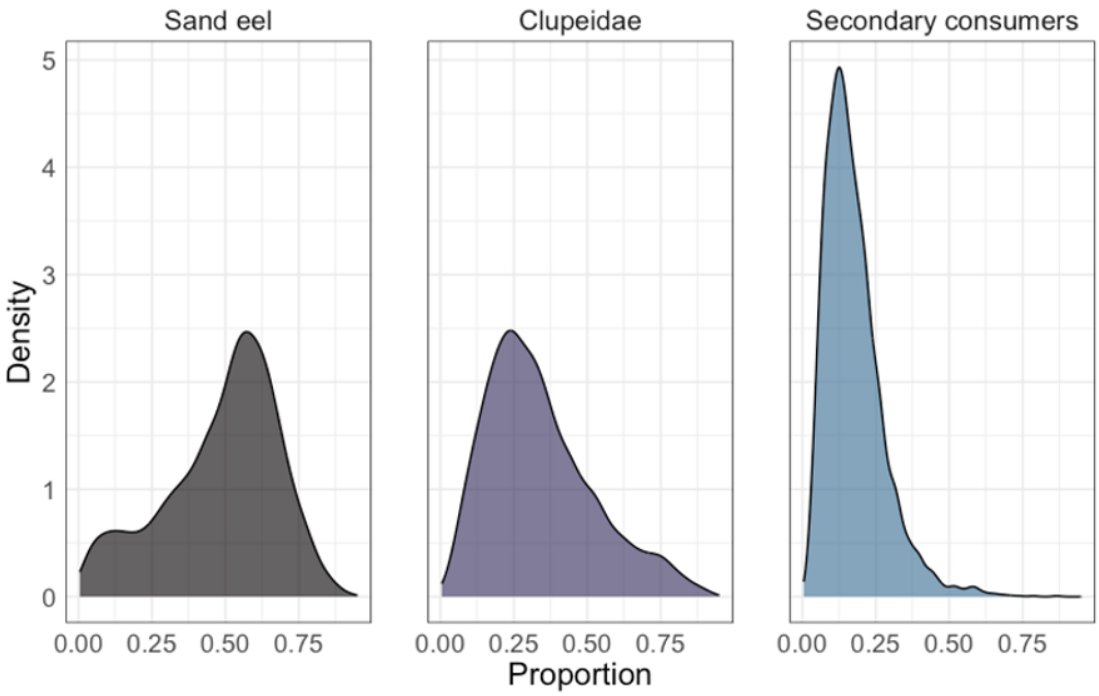
Source pairs	Df	SumsOfSqs	F.Model	R2	p.value	p.adjusted	sig
Sand eel vs sprat	1	1.663	1.320	0.117	0.267	1	
Sand eel vs herring	1	1.494	1.451	0.059	0.23	1	
Sand eel vs mackerel	1	2.918	1.598	0.117	0.223	1	
Sand eel vs whiting	1	20.517	7.887	0.264	0.003	0.045	*
Sand eel vs zooplankton	1	1.280	0.797	0.081	0.424	1	
Sprat vs herring	1	0.217	0.448	0.018	0.661	1	
Sprat vs mackerel	1	3.552	4.793	0.255	0.024	0.36	
Sprat vs whiting	1	12.010	6.309	0.208	0.018	0.27	
Sprat vs zooplankton	1	6.078	22.894	0.675	0.002	0.03	*
Herring vs mackerel	1	3.714	4.674	0.148	0.02	0.3	
Herring vs whiting	1	27.106	17.667	0.323	0.001	0.015	*
Herring vs zooplankton	1	6.483	11.112	0.316	0.001	0.015	*
Mackerel vs whiting	1	23.355	11.040	0.298	0.003	0.045	*
Mackerel vs zooplankton	1	3.983	4.231	0.246	0.043	0.645	
Whiting vs zooplankton	1	36.099	17.461	0.4312	0.002	0.03	*

Appendix 2.5. Density plots of grouped source posterior distributions for (A) adult whales (B) juvenile whales and (C) CRRU samples.





C


Sand eel
Clupeidae
Secondary consumers
Density
0
1
2
3
4
5
0.00
0.25
0.50
0.75
Proportion

Appendix 2.6. Posterior proportion estimates (mean ± SD, (median)) of grouped sources of the main model, and the four additional models performed for sensitivity analysis.

Source	Main model	$\Delta^{13}C$ +1 SD	$\Delta^{13}C$ -1 SD	$\Delta^{15}N$ +1 SD	$\Delta^{15}N$ -1 SD
Sand eel	0.62 ± 0.18, (0.65)	0.13 ± 0.10, (0.10)	0.77 ± 0.10, (0.79)	0.38 ± 0.17, (0.39)	0.24 ± 0.15, (0.23)
Clupeidae	0.13 ± 0.09, (0.10)	0.18 ± 0.08, (0.17)	0.10 ± 0.06, (0.08)	0.10 ± 0.06, (0.08)	0.34 ± 0.15, (0.34)
Secondary consumer	0.08 ± 0.04, (0.7)	0.15 ± 0.07, (0.14)	0.06 ± 0.03, (0.05)	0.06 ± 0.03 (0.05)	0.20 ± 0.09, (0.19)
Krill	0.14 ± 0.10, (0.12)	0.49 ± 0.09, (0.44)	0.05 ± 0.05, (0.04)	0.44 ± 0.13, (0.44)	0.13 ± 0.07, (0.12)
Capelin	0.04 ± 0.03, (0.03)	0.11 ± 0.08, (0.09)	0.03 ± 0.02, (0.02)	0.03 ± 0.02, (0.02)	0.09 ± 0.06, (0.07)

Appendix 2.7. Minke whale trophic position estimates derived from Bayesian model 'tRophic Position' and two different mathematical equations from (Germain *et al*., 2013) (equation 1) and (Post 2002) (equation 2). Each method used the prey-consumer nitrogen TDF generated for application in the mixing models (2.65 ± 1.0‰). Equation 1 also applied a TDF constant of 3.4‰.

Groups	**'tRophic Position'**	(Germain *et al.*, 2013)	(Post, 2002)
ADULTS (n = 14)			
Mean ± SD	3.05 ± 0.19	3.01	3.02
Lower 95%	2.71	-	-
Median	3.04	-	-
Upper 95%	3.44	-	-
JUVENILES (n = 29)			
Mean ± SD	2.76 ± 0.19	2.79	2.73
Lower 95%	2.42	-	-
Median	2.75	-	-
Upper 95%	3.14	-	-

Appendix 2.8. Minke whale samples data (n = 47).

	Specimen ID	Date	Length (cm)	Age class	Sex	Collection region	Institution	Condition code
1.	M2035/93	02/09/1993	814	Adult	M	Highland	SMASS	2a
2.	M1333/95	18/07/1995	585	Juvenile	M	Grampian	SMASS	4
3.	M1723/95	31/08/1995	363	Juvenile	M	Highland	SMASS	4
4.	M1606/97	15/07/1997	460	Juvenile	F	Shetland	SMASS	2a
5.	M2655/9	19/11/1997	248	Juvenile	M	Grampian	SMASS	4
6.	M803/98	09/04/1998	450	Juvenile	F	Highland	SMASS	4
7.	M53/00	20/03/2000	770	Adult	F	Highland	SMASS	3-4
8.	M70/00	30/04/2000	700	Adult	F	Highland	SMASS	4
9.	M42/01	14/04/2001	490	Juvenile	F	Fife	SMASS	3
10.	M153/01	12/11/2001	470	Juvenile	F	Highland	SMASS	4
11.	M86/02	19/06/2002	755	Adult	F	Lothian	SMASS	2b
12.	M288/03	19/10/2003	475	Juvenile	M	Orkney	SMASS	2a
13.	M275/05	19/10/2005	700	Adult	U	Grampian	SMASS	4
14.	M311/05	11/12/2005	553	Juvenile	F	Orkney	SMASS	2b
15.	M67/11	01/04/2011	466	Juvenile	F	Orkney	SMASS	2b
16.	M98/12	03/04/2012	445	Juvenile	M	Lothian	SMASS	2a
17.	M226/13	09/07/2013	655	Adult	F	Highland	SMASS	3

18.	M292/13	06/09/2013	487	Juvenile	F	Fife	SMASS	2a
19.	M251/14	07/09/2014	830	Adult	F	Grampian	SMASS	2a
20.	M297/14	07/10/2014	483	Juvenile	M	Fife	SMASS	2b
21.	M319/15	10/10/2015	355	Juvenile	M	Grampian	SMASS	2b
22.	M411/15	06/12/2015	530	Juvenile	U	Orkney	SMASS	3
23.	M251/16	01/06/2016	635	Juvenile	M	Fife	SMASS	3
24.	M466/16	03/11/2016	379	Juvenile	M	Fife	SMASS	3
25.	M200/17	05/05/2017	590	Juvenile	F	Fife	SMASS	2a
26.	M447/17	09/10/2017	396	Juvenile	F	Fife	SMASS	2a
27.	M317/18	10/06/2018	383	Juvenile	M	Fife	SMASS	3
28.	M586/18	18/09/2018	644	Juvenile	F	Highland	SMASS	2a
29.	M592/18	25/09/2018	417	Juvenile	F	Highland	SMASS	3
30.	M366/19	16/07/2019	875	Adult	F	Grampian	SMASS	4
31.	M450/19	27/08/2019	545	Juvenile	F	Shetland	SMASS	4
32.	M509/19	28/09/2019	804	Adult	F	Orkney	SMASS	2a-2b
33.	M157/20	15/03/2020	NA	Juvenile	F	Fife	SMASS	2a
34.	M239/20	11/05/2020	422	Juvenile	F	Highland	SMASS	2b
35.	M377/21	03/07/2021	762	Adult	M	Grampian	SMASS	2b
36.	M270/23	07/05/2023	457	Juvenile	F	Highland	SMASS	3-4
37.	MW01_17	13/06/2017	-	Adult	-	Moray	CRRU	Biopsy

38.	MW01_18	10/08/2018	-	Adult	-	Moray	CRRU	Biopsy
39.	MW01_20	14/09/2020	-	Juvenile	-	Moray	CRRU	Biopsy
40.	MW02_20	18/09/2020	-	Juvenile	-	Moray	CRRU	Biopsy
41.	MW01_21	23/06/2021	-	Adult	-	Moray	CRRU	Biopsy
42.	MW02_21	28/06/2021	-	Juvenile	-	Moray	CRRU	Biopsy
43.	MW04_21	14/07/2021	-	Juvenile	-	Moray	CRRU	Biopsy
44.	MW05_21	06/09/2021	-	Adult	-	Moray	CRRU	Biopsy
45.	MW06_21	06/09/2021	-	Adult	-	Moray	CRRU	Biopsy
46.	MW07_21	15/09/2021	-	Adult	-	Moray	CRRU	Biopsy
47.	MW01_22	02/07/2022	-	Adult	-	Moray	CRRU	Biopsy

Chapter 3: Niche partitioning between adult and juvenile minke whales (*Balaenoptera acutorostrata*) in Northeast Scottish waters using bulk skin stable isotopes.

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Abstract

The seas of Northeast Scotland experience heightened primary productivity in spring and summer, driving increased abundance of lower trophic level prey and intensified activity across the food web. This seasonal dynamic is particularly evident amongst the higher trophic-level cetaceans, many of which are seasonal visitors. Understanding resource use and the trophic dynamics of these long-distance migrants is vital to assessing their intermittent ecological roles in this region. Here, we analysed the stable isotope ratios of bulk skin tissue from both live and stranded minke whales (*Balaenoptera acutorostrata*) sampled in Northeast Scotland. Using a Bayesian statistical framework, we calculated the isotopic niche metrics - total area (TA), standard ellipse area (SEA), sample size corrected SEA (SEA_C) and Bayesian inferred SEA (SEA_B) to assess differences between adults and juveniles across spring and summer. Using the strandings samples, the isotopic niche of males and females was also modelled to assess differences in sex, which could suggest migratory strategies as a contributing factor to their isotopic profiles. No notable partitioning was observed between sexes, however, females occupied a niche (SEA_B ‰^{2}, 95% CI) roughly double that of males (males: 3.25, 1.66 – 7.21; females: 6.41; 3.25 – 12.22). Regardless of season, juveniles consistently exhibited a larger isotopic niche than adults (juveniles: 1.89, 1.08 – 3.29; adults: 4.66, 3.28 – 6.95). Niche overlap (SEA_C) between age classes was greatest in spring (51%) but completely partitioned by summer. From spring to summer, the adult niche contracted markedly, whereas the juvenile niche expanded slightly. Both age groups shifted niches seasonally with minimal overlaps across these periods (adults: 2% and juveniles: 10%). Our findings demonstrate temporal differences in the isotopic niches between adult and juvenile minke whales indicating flexible foraging strategies in Northeast Scotland. This study fills key knowledge gaps in regional minke whale foraging ecology and supports previously observed behaviour patterns and provides a foundation for adaptive marine protected area (MPA) management. As prey populations are threatened by exploitive fishing practices and climate change reshapes prey distributions and seasonal productivity, such insights will be critical for anticipating shifts in foraging dynamics within protected areas.

Key words: Niche partitioning, minke whale, Northeast Scotland, stable isotope, trophic level

Introduction

Coexisting communities often exhibit niche partitioning to reduce competition and avoid competitive exclusion (Gauze, 1934; Hutchinson, 1957). Niche occupation is expressed through resource and habitat use (Bolnick *et al.*, 2003), and has traditionally been defined in terms of Grinnellian and Eltonian niches. The Grinnellian niche describes how a species is influenced by their surrounding environmental conditions (Grinnell, 1917), and is commonly represented in species distribution and habitat modelling (Devictor *et al.*, 2010). In contrast, the Eltonian niche describes how a species influences its environment and interacts with others (Elton, 1927). Advances in stable isotope analysis (SIA) over the last few decades, have provided a powerful tool for measuring Eltonian niches, giving rise to the concept of the isotopic niche (Newsome *et al.*, 2007; Giménez *et al.*, 2018). Together, these dimensions define the biotic and abiotic space within which populations persist (Hutchinson, 1957; Devictor *et al.*, 2010). However, these frameworks rarely account for the influence of anthropogenic activities.

SIA examines the ratios of stable isotopes such as $\delta^{13}C$ and $\delta^{15}N$, in biological tissues to infer trophic ecology (Newsome *et al.*, 2007). It has been widely applied to cetaceans to study trophic level (Bury *et al.*, 2024; Rita *et al.*, 2024), diet (Ryan *et al.*, 2014; García-Vernet *et al.*, 2021; Jackson *et al.*, 2025) and migration (Smith *et al.*, 2024). Variation in stable isotope values also allows niche width to be quantified (Bearhop *et al.*, 2004), whilst the calculated standard ellipse area (SEA) can be applied to assess niche overlap among groups (Layman *et al.*, 2007; Jackson *et al.*, 2011).

Cetaceans have broad geographic ranges and are particularly sensitive to human driven environmental change. For example, balaenopterids undertake long migrations between low latitude breeding and high latitude feeding grounds, relying on the latter to replenish energy reserves lost during the winter (Bannister, 2009). These feeding opportunities are increasingly threatened by habitat degradation, shifting prey distributions, and climate change. Because prey abundance and availability vary seasonally, the energetic potential of feeding grounds also fluctuates. Understanding how cetacean isotopic niche varies is therefore central to conservation and fisheries management, including the design of moratoria and quota systems.

The common minke whale *(Balaenoptera acutorostrata)*, the smallest member of the *Balaenopteridae* family, is the most abundant rorqual in the North Atlantic (Moller *et al.*, 2003). Its trophic ecology has been studied in Canada (Gavrilchuk *et al.*, 2014), Iceland (García-Vernet *et al.*, 2021), and Ireland (Ryan *et al.*, 2013). However, most of this research has focussed on interspecific competition among sympatric rorquals, rather than intraspecific variation. Conspecifics are often assumed to be ecological equivalents (Hutchinson, 1957; Abrams, 1980; Bolnick *et al.*, 2003), yet intraspecific competition, age differences, seasonal shifts, and individual foraging preferences can all drive variation and expand the niche of a species (Valen, 1965). This is particularly relevant for baleen whales, which play key roles in ecosystem functioning as nutrient cyclers and carbon transporters (Durfort *et al.*, 2022; Herr *et al.*, 2022; Freitas *et al.*, 2023).

Northeast Scotland is an important seasonal foraging area for minke whales (Robinson *et al.*, 2009; Paxton *et al.*, 2014; Hague *et al.*, 2020). The region from the Moray Firth to the Humber Estuary has been recognised as an Important Marine Mammal Area (IMMA) (IUCN-MMPATF, 2024). Furthermore, in 2020 the Southern Trench in the Moray Firth was designated a marine protected area (MPA), with the minke whale listed as the protected biological feature, due to its reliance on the area for feeding. Despite this protection, little is known about how foraging efforts vary temporally or between age groups, or how prey availability and preference shape their isotopic niches.

In this study, we analysed bulk skin $\delta^{13}C$ and $\delta^{15}N$ values from adult and juvenile minke whales sampled in the Moray Firth and from strandings across Northeast Scotland. We quantified isotopic niches using SEA to examine demographic and seasonal variation in niche width and overlap across spring and summer. In addition, isotopic mixing models were constructed using prey isotope data grouped by wet mass energy density (kJ/g WM) thresholds (Spitz *et al.*, 2010) to investigate demographic and temporal differences in prey use.

Materials and Methods

Samples from Stranded Animals

Skin samples from stranded minke whales (n = 36) were collected by the Scottish Marine Animal Stranding Scheme (SMASS) between 1993 and 2023 from sites spanning Firth of Forth to the Shetland Isles (Figure 3.1; Appendix 3.4;

Supplementary material). Individuals ranged from 2.48 m – 8.30 m in length. Tissue samples were collected during post-mortem examinations and stored at -20 °C, as per standard procedure (Kuiken and Hartmann, 1991; Ijsseldijk *et al.*, 2019). Age class (adult or juvenile) was determined from a combination of body length and reproductive organ assessment using standardised criteria (Kuiken and Hartmann, 1991; Ijsseldijk *et al.*, 2019). Samples were collected across decomposition codes 2a “Freshly dead. Died on beach” to code 4 “Advanced decomposition”, as previous studies have shown that the stage of decomposition had minimal effects on $\delta^{13}C$ and $\delta^{15}N$ values (Payo-Payo *et al.*, 2013; Burrows *et al.*, 2014; Cloyed *et al.*, 2023) and so all samples were retained for analysis (Table 3.1).

Table 3.1. Number of stranded samples of each condition code (n = 36).

Condition code	**Number of skin tissue samples**
2a (Freshly dead)	10 (2 adults, 8 juveniles)
2b (Slight decomposition)	8 (3 adults, 5 juveniles)
3 (Moderate decomposition)	7 (1 adults, 6 juveniles)
4 (Advanced decomposition)	11 (4 adults, 7 juveniles)

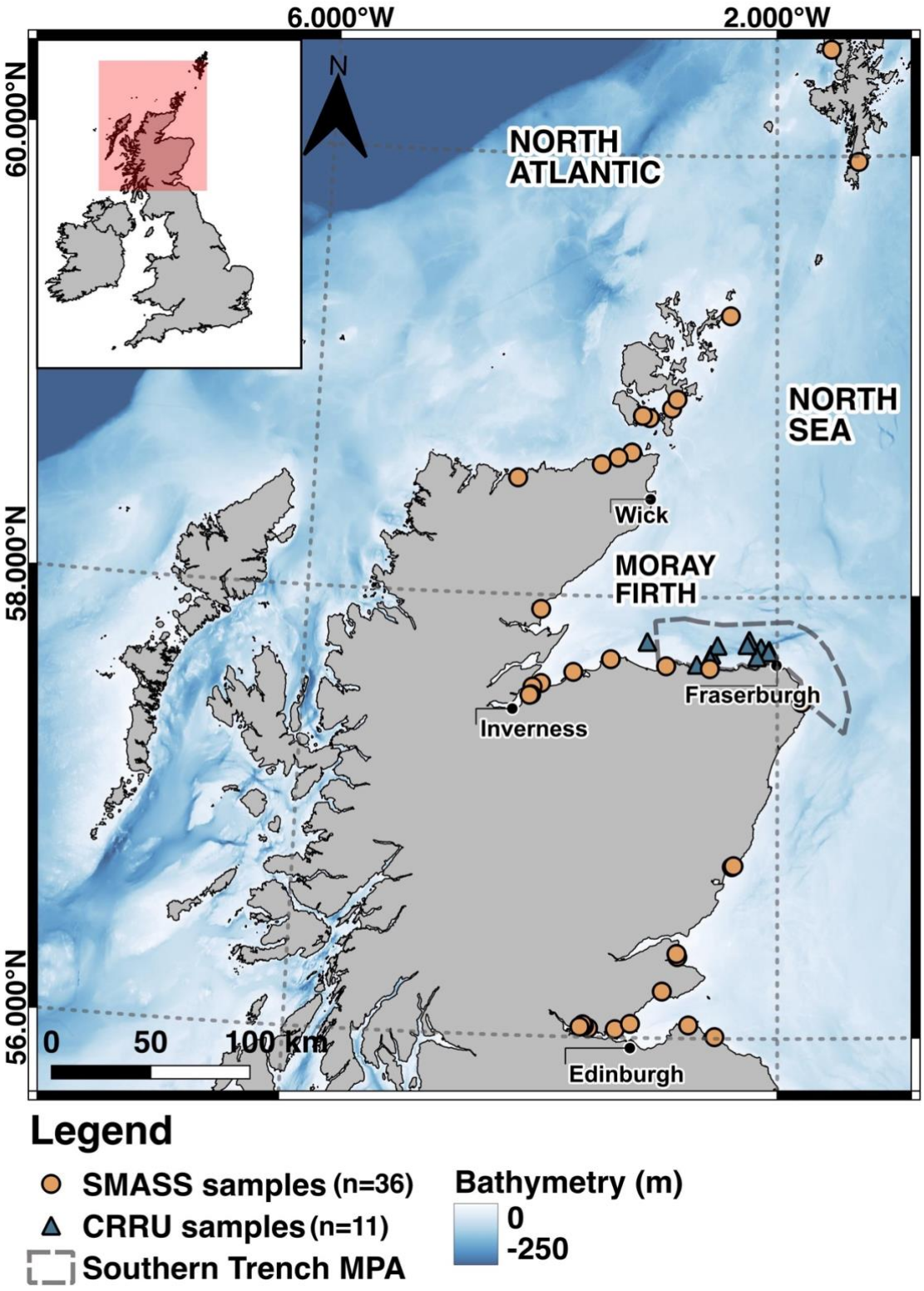


Figure 3.3. Northeast Scotland study area and locations of minke whale samples n = 47 (Live animals CRRU n=11; Stranded animals SMASS n=36). Map projection: OSGB36 / British National Grid (EPSG: 27700). Units: kilometres. Data sources: British Iles polygon was sourced from ESRI. Bathymetry was sourced from Geospatial Data Abstraction Library (GDAL).

Live biopsy samples

Skin tissue was also collected from free ranging minke whales (n = 11) between June and September from 2017 - 2022, under license (License number 211818) (Table 3.2, Appendix 3.4; Supplementary material). Sampling was conducted by the Cetacean Research and Rescue Unit (CRRU) using the crossbow and dart method (Noren and Mocklin, 2012). Custom bolts (CETA-DART®, Finn Larsen) fitted with 6 mm x 40 mm stainless steel tips and foam back-stops were shot from a 150 lbs *Jandao* recurve crossbow. The full sampling methodology can be found in Chapter 2. Standard protocols were followed to minimise risk and animal stress. Individuals were photo-identified in advance to avoid resampling. Age class of individuals was determined by their observed length in relation to the survey vessel, as well as their colouration (Mitchell and Kozicki, 1975). Attempts were aborted if whales showed signs of avoidance, poor body condition or active feeding behaviour. From 2021 onwards, a drone was used to track individuals during dives and assist vessel positioning during sampling.

Biopsies were targeted to the area behind the dorsal fin along the peduncle (upper) flank. Upon retrieval, the dart tip (with sample) was placed in a sterile container and placed on ice. Skin and blubber were separated using a sterile scalpel, with skin stored in 20% dimethyl sulfoxide (DMSO), saturated with 5 mol/L sodium chloride (NaCl), while blubber was wrapped in sterilized foil and frozen at -20 °C (Gavrilchuk *et al.*, 2014; Durante *et al.*, 2021).

Table 3.2. Number of free ranging minke whale samples taken in each year (n = 11).

Year	Number of samples
2017	1 (1 adult)
2018	1 (1 juvenile)
2020	2 (2 adults)
2021	6 (4 adults, 2 juveniles)
2022	1 (1 juvenile)

Lipid extraction

All samples were prepared at the Lyell Centre for Earth and Marine Sciences, Heriot-Watt University, Edinburgh, UK. Lipids, which are depleted in ^{13}C can bias $\delta^{13}C$ values (DeNiro and Epstein, 1977; Post *et al.*, 2007; Newsome *et al.*, 2018). To address this issue, each of the 47 minke whale samples were split: one subsample underwent lipid extraction for $\delta^{13}C$ analysis, while the untreated portion was used for $\delta^{15}N$ analysis.

Lipids were removed using an Accelerated Solvent Extractor (Dionex ASE 350), with a 9:1 dichloromethane-methanol solution (DCM:MeOH), under the following conditions: three 5-minute cycles at 100°C (10.3 MPa), with a 75% rinse volume (Magill *et al.*, 2015). Lipid-free tissues were dried under a fume hood for ~12 hours, and all samples (lipid-extracted and non-extracted) were freeze dried for 24 h, and then ground to a fine powder. Subsamples of 0.5 – 0.7 mg were weighed into tin capsules for analysis. The grinding and weighing of samples were conducted at the University of Exeter's Environment and Sustainability Institute (ESI), Penryn, UK.

Lipid normalisation

Although $\delta^{13}C$ values can be normalised using C:N ratios (McConnaughey and McRoy, 1979; Post *et al.*, 2007), this approach has proven unreliable for balaenopterid skin (Ryan *et al.*, 2012). We therefore excluded samples with C:N >4 (n=3) instead of applying corrections.

Stable isotope analysis

Isotopic measurements were conducted at the University of Exeter's Environment and Sustainability Institute (ESI) stable isotope facility, using a Sercon Integra 2 continuous-flow stable isotope analyser. Samples were calibrated against in house reference material (bovine liver; δ13C -28.6‰, δ15N +6.3‰ and Alanine; δ13C -19.6‰, δ15N -1.9‰). These were used to correct for instrument drift and to determine sample $\delta^{13}C$ and $\delta^{15}N$ content. The beam area relative to the bovine liver standard (%C 47.2, %N 9.3) was used to determine the elemental % (%C and %N). The values of in-house reference material had been previously determined by running alongside the following certified reference material: IAEA-N-1, IAEA-N-2, IAEA-LSVEC, IAEA-CH-6 and B2155 (protein standard, elemental microanalysis). Instrument precision was +0.12‰ (C) and +0.23‰ (N)

based on 2σ of repeated standards. All ratios were expressed in the standard delta notation (δ) using the equation:

Equation 3.

$$\delta X = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 10^3$$

where *X* is the stable isotope, *R* represents the ratio of the heavy isotope to the lighter.

Statistical analysis

All analyses were performed in R v4.2.2 (R Core Team, 2023). Normality was assessed with the rstatix package (Kassambara, 2023) and differences in isotope values were tested with a two-way ANOVA using age class and season with an interaction. Isotopic niches were quantified using the SIBER package (Jackson *et al.*, 2011; R Core Team, 2023), which estimates niche metrics using Bayesian Ellipse methods. We calculated Standard Ellipse Area (SEA), sample size corrected SEA (SEA_C), Bayesian SEA (SEA_B), and Total Area (TA). Where the TA refers to the convex hull of the data and is used to describe niche width, the SEA, a bivariate equivalent of standard deviation (SD), can be used to assess overlap between groups. Seasonal comparisons were made with care due to isotopic turnover of cetacean skin ($\delta^{15}N$: 3 – 8 months; $\delta^{13}C$: 2 – 3 months (Giménez *et al.*, 2016; Busquets-Vass *et al.*, 2017). Individuals sampled between June and August were grouped as ’spring' reflecting earlier isotopic incorporation, whilst those sampled between September and November were grouped as ’summer’.

To assess prey contributions, we constructed isotopic mixing models using the same minke whale data included in the SIBER niche analysis (see chapter 2 for more details). Prey samples were plotted (Figure 3.2) and grouped by energy density (kJ/g WM) into low, medium and high-quality categories derived from a previous study (Spitz *et al.*, 2010) (Table 3.3). Models were run to test demographic and seasonal differences, although age × season comparisons were precluded by limited sample size.

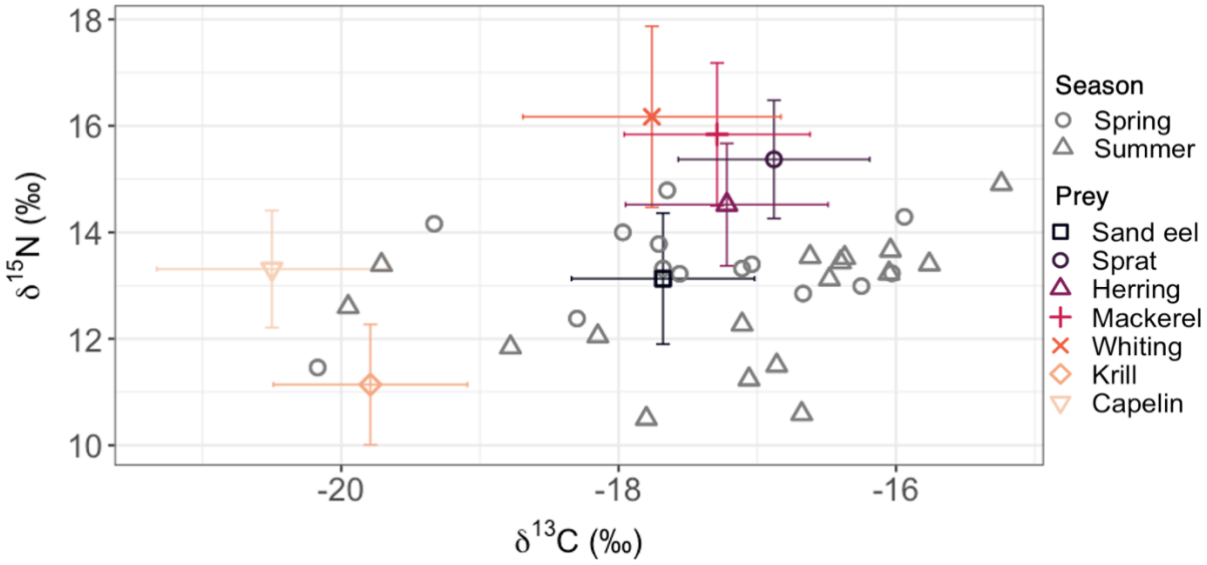


Figure 3.4. Mean ± 1SD $\delta^{13}C$ and $\delta^{15}N$ ratios modelled prey sources, and individual $\delta^{13}C$ and $\delta^{15}N$ isotope ratios of minke whales by season with grey circles and triangles denoting spring and summer individuals, respectively.

Table 3.3. The energetic quality, based on energy density (kJ/g WM) of each source (Spitz et al., 2010). Low quality (<4 kJ/g), medium quality (4 - 6 kJ/g), and high quality (>6 kJ/g).

Source	Quality	Study
Sand eel	Medium	(Spitz *et al.*, 2010)
Sprat	High	(Spitz *et al.*, 2010)
Herring	High	(Spitz *et al.*, 2010)
Mackerel	High	(Spitz *et al.*, 2010)
Whiting	Low	(Spitz *et al.*, 2010)
Capelin	Medium	(Hedeholm *et al.*, 2011)
Krill	Low	(Spitz *et al.*, 2010)

Results

Variability between seasons

A total of 43 skin samples (14 adults, 29 juveniles), were retained for SIBER analyses after excluding duplicates, anomalies and samples with C:N >4. Seasonal subsampling reduced this to 12 adults (5 spring, 7 summer) and 19 juveniles (9 spring, 10 summer). Across all samples, adult $\delta^{13}C$ ranged from -

19.3 ‰ to -15.2 ‰, and juvenile $\delta^{13}C$ ranged from -20.2 ‰ to -15.8 ‰. Adult $\delta^{15}N$ ranged from 12.4 ‰ to 14.9 ‰, compared with 10.5 ‰ to 14.8 ‰, in juveniles (Appendix 3.1 Supplementary material).

Using a Shapiro-Wilk test, the data were tested for normality. $\delta^{13}C$ values were normally distributed ($\delta^{13}C$ $W = 0.96$, $p = 0.13$), whilst $\delta^{15}N$ values were not ($\delta^{15}N$ $W = 0.94$, $p = 0.02$). Juveniles had significantly lower $\delta^{13}C$ and $\delta^{15}N$ values than adults (ANOVA: $\delta^{13}C$ $F_{1,41} = 9.74$, $p = 0.003$; Welch's ANOVA: $\delta^{15}N$ $F_{1,28} = 7.34$, $p = 0.01$). Significant interactions were observed for both isotopes between age class and season (ANOVA: $\delta^{13}C$ $F_{1,27} = 5.48$, $p = 0.03$; $\delta^{15}N$ $F_{1,27} = 6.98$, $p = 0.01$). There were also significant main effects of age class and season in $\delta^{15}N$ (ANOVA: $\delta^{15}N$ $F_{1,27} = 7.70$, $p = 0.01$; $\delta^{15}N$ $F_{1,27} = 6.20$, $p = 0.02$). Adult isotope values were typically higher than juvenile values except for $\delta^{15}N$ in spring, where juveniles exhibited greater values (Figure 3.3B; Appendix 3.1 Supplementary material).

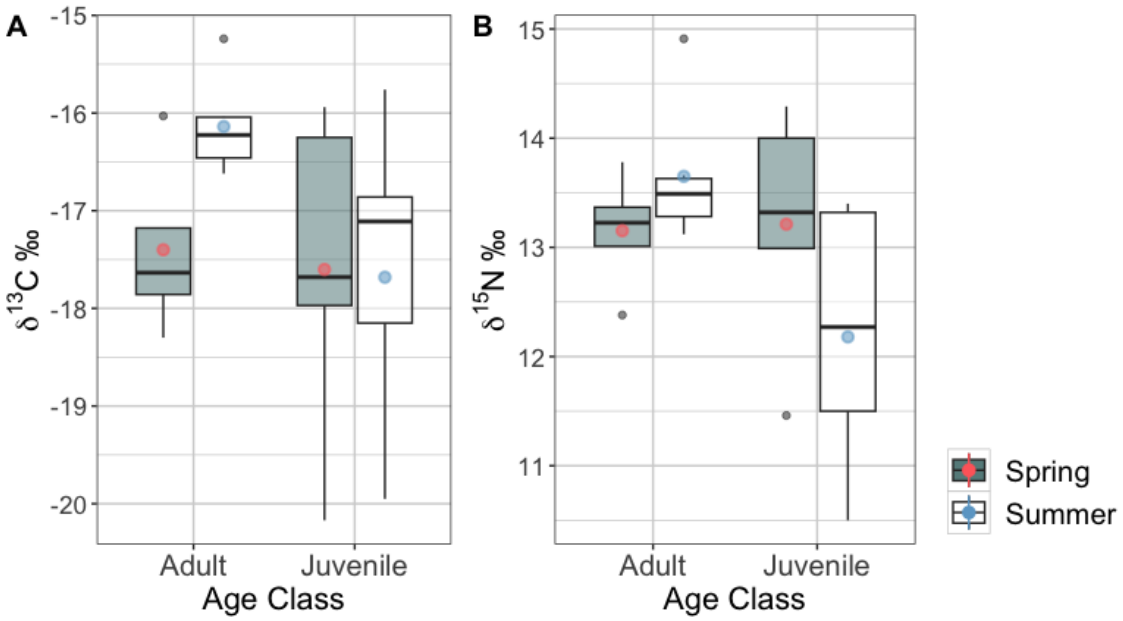


Figure 3.3. A) $\delta^{13}C$ and **B)** $\delta^{15}N$ variation in adult and juvenile minke whale skin between spring and summer seasons. Means and medians are denoted by the coloured circles and black lines, respectively. Outer box edges represent the 25th and 75th percentiles, whilst whiskers and dots show data extremes and outliers, respectively.

Isotopic niche space

When data were combined across seasons, adult and juvenile isotopic niches overlapped by only 11% (Figure 3.4A). Juveniles occupied a much larger TA (15.11 ‰^{2}) that was three times larger than adults (5.60 ‰^{2}) (Appendix 3.2 Supplementary material). Within seasons, adult TA contracted sharply from spring (2.58 ‰^{2}) to summer (0.70 ‰^{2}), whereas juveniles expanded from 5.79 ‰^{2} to 8.35 ‰^{2} (Appendix 3.2 Supplementary material). Within age groups, seasonal overlap was low (SEA_C 2% in adults, 10% in juveniles; Figure 3.4B). Between age classes, core niche overlap was 51% in spring but completely partitioned by summer (Figure 3.4C). Between sexes, females had larger values across all metrics (Appendix 3.2 Supplementary material). Male TA (7.32 ‰^{2}) was almost half that of the females (14.20 ‰^{2}).

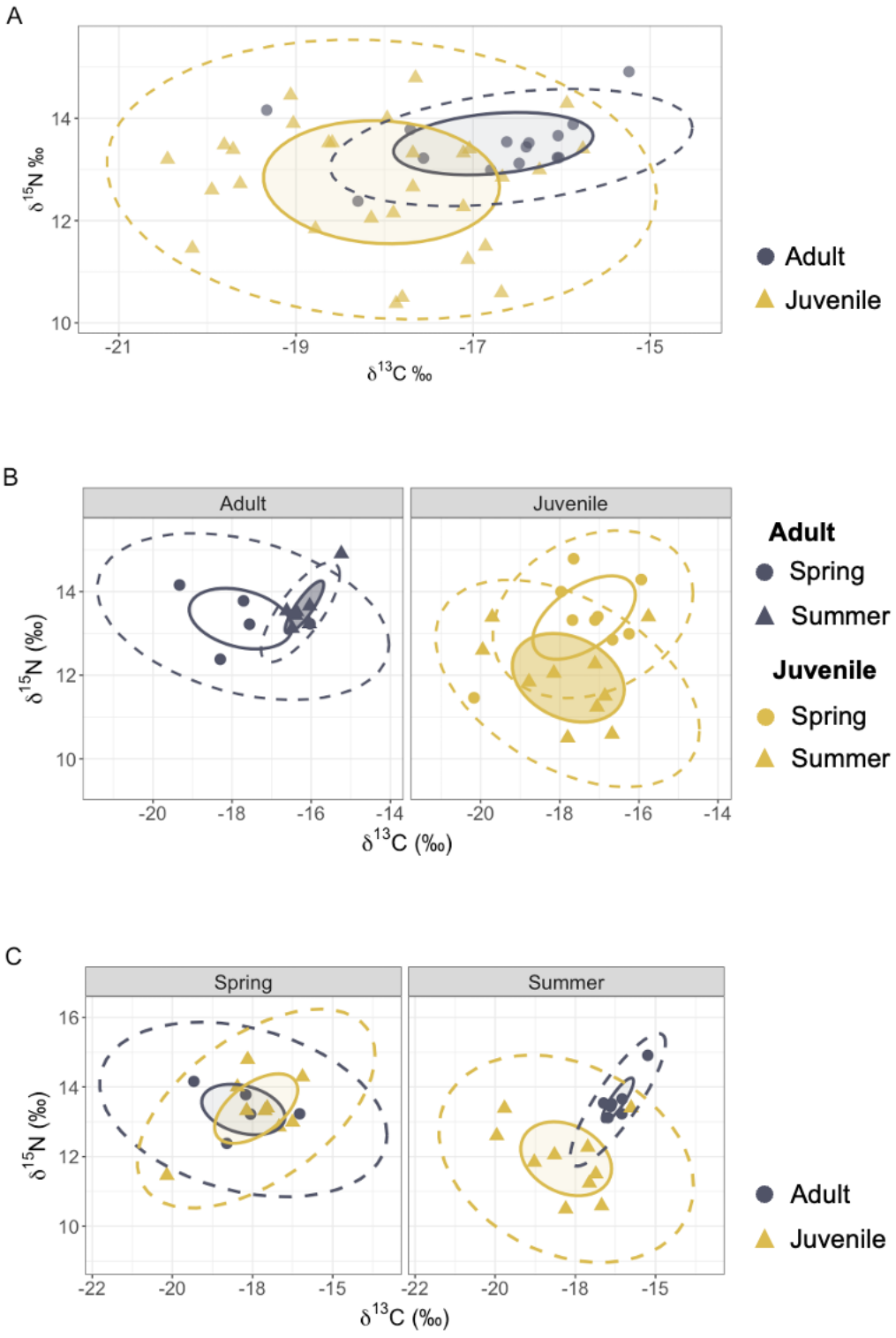


Figure 3.4. SIBER analysis showing the core 40% data (solid line) niche and 95% data ellipse (dashed line) of (A) all analysed adult and juvenile whale samples, (B) adult and juvenile niche shifts from spring to summer, and (C) the comparison of seasonal niches for both age classes.

Standard ellipse area

Juveniles consistently exhibited larger SEA_C and SEA_B values (5.01 ‰^{2} and 4.66 ‰^{2}, respectively) than adults (2.14 ‰^{2} and 1.89 ‰^{2}; Figure 3.5A; Appendix 3.2 Supplementary material). Bayesian comparisons indicated a 67% and 100% probability that juveniles had a larger SEA_B than adults in spring and summer, respectively (Figure3.5B; Appendix 3.2 Supplementary material). Adults showed a marked decrease in niche size between spring and summer (92% probability of contraction), while juveniles showed a slight expansion in niche size with a 48% probability of the spring niche being larger than summer (Figure 3.5B; Appendix 3.2 Supplementary material). When corrected for samples size, females remained having a notably SEA_C than the males (4.27 ‰^{2} and 7.51 ‰^{2}, respectively) (Appendix 3.2, 3.3 Supplementary material). Bayesian analysis similarly revealed that the female ellipse area as almost double the size of the male area (Appendix 3.2, 3.3 Supplementary material). When compared, the probability of females having a larger SEA_B than the males was 90%.

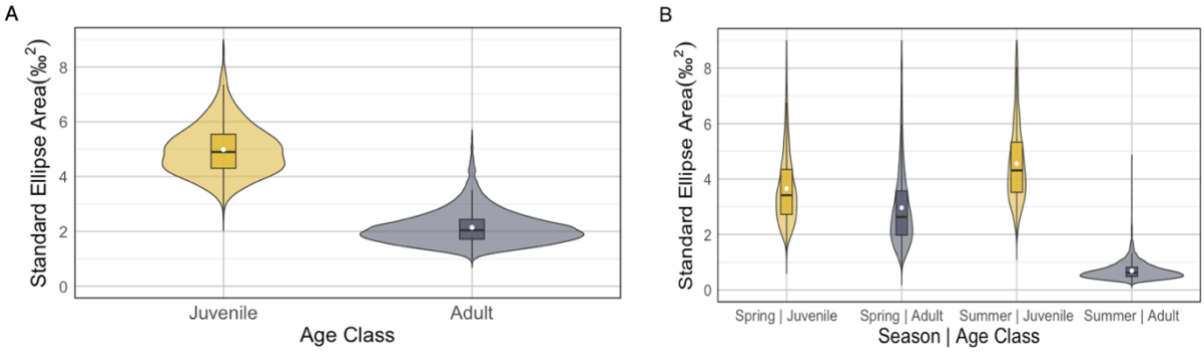


Figure 3.5. Bayesian standard ellipse areas (SEA_B) calculated from the posterior distributions indicated by the density curves. (A) shows the SEA_B for collective adults and juveniles, regardless of season and (B) shows the SEA_B of both age classes over the spring and summer seasons. Median SEA_B and the interquartile range are represented by the black bar and outer box lines, respectively. SEA_C is shown by the white dot. Range of the data is shown by whiskers.

Mixing models

The mixing models, where prey were grouped by wet mass energy density, suggested that the minke whale diet contributions (median, 95% credible interval (CI)) were dominated by medium-energy prey in both seasons (spring: 0.40, 0.07 – 0.77; summer: 0.48, 0.07 - 0.87; Figure 3.5). High-energy prey contributed more during spring (0.34, 0.12 – 0.64) than in summer (0.25, 0.06 – 0.63), whereas

low-energy prey contributed similarly across seasons (spring: 0.24, 0.06 – 0.52; summer: 0.22, 0.03 – 0.62).

Age-class comparisons revealed stronger contrasting differences. Adults relied equally on medium- and high-energy prey (0.38, 0.09 - 0.74; 0.37, 0.14 - 0.66, respectively), with relatively little low-energy prey (0.24, 0.05 - 0.46). Juveniles, by contrast consumed similar proportions of low- and medium-energy prey (0.38, 0.09 - 0.59; 0.37, 0.08 - 0.80, respectively), with lower reliance on high-energy prey (0.23, 0.07 -0.47).

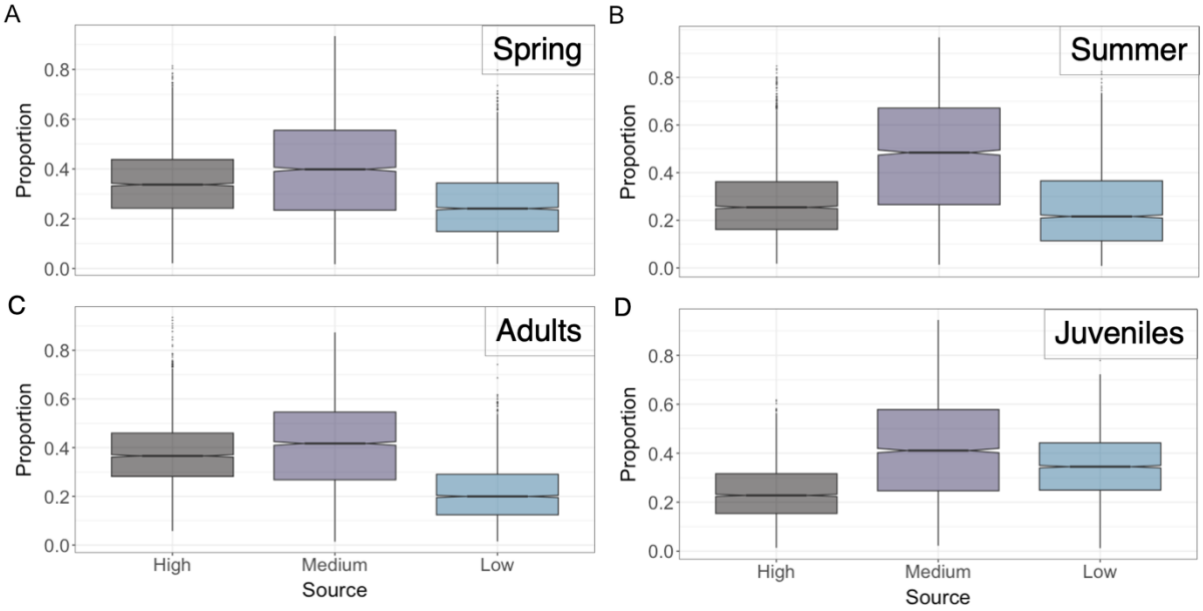


Figure 3.6. Dietary proportions of sources grouped by energy density (kJ/g WM): sprat, herring and mackerel (high), sand eel and capelin (medium), and krill and whiting (low) for (A) spring whales, (B) summer whales, (C) adult whales, and (D) juvenile whales. Median is denoted by the black bar, and coloured boxes show the interquartile range with outer box edges representing the 25th and 75th percentiles. Whiskers reflect the range of the data.

Discussion

This study provides the first detailed characterisation of the isotopic niche of minke whales in Northeast Scottish waters, highlighting both ontogenetic and seasonal variation in resource use. Analysis of bulk skin $\delta^{13}C$ and $\delta^{15}N$ values revealed clear differences between adults and juveniles, both in isotope ratios and in the breadth of their isotopic niches. Adults exhibited higher $\delta^{13}C$ and $\delta^{15}N$ values, consistent with foraging on higher trophic level prey, potentially inshore habitats, whereas juveniles displayed lower values and a broader isotopic niche,

indicative of more generalist feeding at lower trophic levels (Newsome *et al.*, 2007). Seasonal analysis further revealed that niche overlap between adults and juveniles was highest in spring (51%), reflecting shared use of abundant spring prey, but completely partitioned by summer, illustrating divergence in foraging strategies as seasonal prey distributions shift. Although differences in niche size were observed between males and females, no partitioning was reported. Mixing model outputs reinforced ontogenetic differences in prey selection: adults primarily targeted medium- and high-energy prey, such as clupeids, whereas juveniles relied more on low- and medium-energy sources. These patterns collectively indicate that both age and season are key drivers of isotopic niche width and structure in minke whale foraging ecology in this region and improve our understanding of the species' resource use – important information in the adaptive management of the Scottish MPA network.

Variation in isotope ratios and niche width

The high $\delta^{13}C$ and $\delta^{15}N$ in adults likely reflects consumption of higher trophic level prey, including sprat, herring and secondary consumers, across inshore and coastal habitats. In contrast, the lower $\delta^{13}C$ and $\delta^{15}N$ values observed in juveniles suggest feeding on lower trophic level prey such as sand eel or small pelagic fish further offshore. This ontogenetic segregation is consistent with the broader ecological principle that juvenile balaenopterids often exhibit generalist feeding habits to compensate for inexperience, smaller body size, or lower prey capture efficiency (Haro *et al.*, 2021; Robinson *et al.*, 2023; Bird *et al.*, 2024).

However, given the variation in $\delta^{13}C$ throughout latitudinal ranges (Newsome *et al.*, 2007), the respective $\delta^{13}C$ values may also be residual signals carried over from other Northeast Atlantic foraging grounds or from lower latitudes. Furthermore, skin tissue will integrate up to roughly three months of dietary sourced $\delta^{13}C$, complicating the interpretation of isotopic data from a migratory species. Considering this, it is possible that the higher $\delta^{13}C$ values of adults reflect feeding events at lower latitude stop over grounds during their migration, a behaviour often exhibited by baleen whales (Silva *et al.*, 2019).

Since no individuals were resampled from spring to summer, it is difficult confirm that the observed variation is solely explained by habitat or dietary shifts. Male and female niche areas were therefore modelled to help determine if the higher

$\delta^{13}C$ could suggest signal carry-over from breeding whales arriving later in the foraging season. If so, this could suggest that the lower values were from non-breeding individuals or individuals that departed their breeding grounds early. Either way, it could imply a staggered migration. However, the analysis between sexes showed no isotopic niche separation, as has been found in studies on humpback whales in their foraging grounds (Witteveen *et al.*, 2011; Gavrilchuk *et al.*, 2014). Although, in the Southern Ocean, male humpback whales potentially occupy a different isotopic niche to females (Bury et al., 2024), in this case suggesting partitioning over large spatial scales, between foraging grounds. Furthermore, complete isotopic segregation has been reported between male and female sperm whales (*Physeter Macrocephalus*) (Pirotta *et al.*, 2020), the males of which are known to make long distance migrations in bachelor groups, whilst the females remain local to their nursing grounds. Nevertheless, the observed partitioning between age classes in this study indicates potential habitat shifts that may mask differences in timing of latitudinal movements.

The larger isotopic niche of juveniles indicates a more exploratory behaviour, allowing them to exploit a wider range of prey types and foraging habitats. This flexibility may confer an adaptive advantage in environments where prey availability is patchy or unpredictable as described for minke whales in northern Norway (Haug *et al.*, 2010). Juveniles also targeted a mix of low- and medium-energy prey, including sand eel and krill, consistent with a generalist strategy that maximizes prey encounter rates while minimizing energy expenditure. Similar observations have been made of juvenile humpback whales in Southern Chile (Haro *et al.*, 2021). Adults, by contrast, displayed narrower niche metrics, consistent with a foraging strategy that optimizes energetic returns from high-quality prey. Furthermore, the mixing models suggested that adults predominantly targeted medium- and high-energy prey, reflecting a focus on clupeids that provide high caloric returns. Such specific targeting of highly evasive prey (Sharpe and Dill, 2011) is likely a result of foraging experience and physiological efficiency, aligning with patterns observed in Irish minke whales, where adults demonstrated a smaller Standard Ellipse Area (SEA_C) relative to sympatric fin and humpback whales (Ryan *et al.*, 2013) and may be essential for supporting reproductive energy demands and maintaining body condition.

Comparisons with studies from Japanese waters provide additional context. Endo *et al*. (2021) reported higher $\delta^{15}N$ in calves than mature individuals, reflecting maternal milk intake (Carroll *et al.*, 2022), but among mature individuals $\delta^{13}C$ decreased with body length while $\delta^{15}N$ remained stable, suggesting offshore foraging with age but minimal trophic level change. In the present study, the opposite trend is observed: adults have higher $\delta^{13}C$ than juveniles, potentially indicating greater inshore habitat use and more selective foraging on high-trophic-level prey. This demonstrates that ontogenetic partitioning in minke whales may manifest differently across ocean basins, reflecting local prey availability, habitat structure, and population density.

Seasonal variation and temporal niche shifts

Seasonal changes in isotopic values revealed dynamic foraging behaviour within both age classes. Adult $\delta^{13}C$ increased markedly from spring to summer while their isotopic niche contracted, potentially highlighting a shift toward inshore habitats and high-trophic-level prey such as clupeids. Whilst eDNA studies have shown peaks in clupeid abundance in September – October (Boyse *et al.*, 2024, 2025), supporting the idea that prey availability drives adult habitat selection and dietary preferences, visual surveys in the Moray Firth have documented adults foraging inshore in early summer before moving further offshore later in the season (Robinson *et al.*, 2023). These contradicting observations underscore the limitations of assigning age class from only visual cues and crucially emphasises the challenge of differentiating latitudinal $\delta^{13}C$ signals from local scale habitat shifts.

Juvenile $\delta^{15}N$ decreased from spring to summer while their isotopic niche expanded slightly, suggesting that juveniles maintain a generalist strategy by continuing to consume sand eel and other low- and medium-trophic-level prey, while opportunistically incorporating clupeids as they become available (Skern-Mauritzen *et al.*, 2011). The seasonal expansion of the juvenile niche may also reflect adaptive responses to competition with adults; by exploiting a broader range of prey types and habitats, juveniles can reduce direct resource competition with older, more efficient conspecifics. A behaviour more commonly associated with sympatric species (Gavrilchuk *et al.*, 2014; García-Vernet *et al.*, 2021). Notably, the models showed no strong seasonal shifts in prey quality

selection, indicating that temporal niche shifts are likely driven more by prey distribution and habitat use than by changes in diet preference.

The high degree of niche overlap in spring (51%) likely reflects the synchronous emergence of sand eel in coastal waters and the spring phytoplankton bloom, which collectively increase prey density and accessibility (van der Kooij *et al.*, 2008; OSPAR, 2017; Henriksen *et al.*, 2021). This resource pulse enables both age classes to exploit the same prey without intense competition. By summer, prey abundance and distribution shifts push adults to target energetically profitable clupeids, while juveniles continue a more opportunistic foraging strategy, resulting in complete niche partitioning. These temporal shifts demonstrate how seasonal variation in prey availability shapes both trophic ecology and intra-specific competition in balaenopterids (Robinson *et al.*, 2023; MacDougall and Robinson, 2025). The present study provides evidence that such ontogenetic partitioning is a key mechanism in reducing competition within minke whale populations in Northeast Scotland.

Comparison with Northeast Atlantic foraging grounds and management implications

When compared with other Northeast Atlantic (NEA) foraging grounds, Scottish minke whales displayed relatively high $\delta^{15}N$ values, reflecting a stronger reliance on shoaling fish such as sand eel, sprat, and herring, rather than the krill-dominated diets observed off Norway, Svalbard, or Jan Mayen (Born *et al.*, 2003; Eerkes-Medrano *et al.*, 2021; Haug *et al.*, 2024). Interpretation of $\delta^{13}C$ values is complicated by confounding factors including latitude, inshore–offshore gradients, and baseline isotopic variation (Hobson *et al.*, 1994; Cherel and Hobson, 2007; Trueman and St John Glew, 2019). This indicates that Scottish minke whales exploit a distinctive foraging niche within the NEA, shaped by the availability of high-trophic-level prey in coastal and nearshore habitats.

Ontogenetic and seasonal niche partitioning observed in this study has clear ecological consequences. By targeting different prey and habitats, adults and juveniles reduce inter-age-class competition, potentially to better exploit temporally and spatially variable resources. These patterns are significant because many of the prey species consumed by both age classes—particularly clupeids and sand eel—are also commercially exploited (Dickey-Collas *et al.*,

2010; Vitale *et al.*, 2015; Dickey-Collas, 2016). Consequently, minke whale foraging dynamics are intrinsically linked to fishery management, and any shifts in prey abundance or availability can have cascading effects on whale populations higher up the trophic web, as shown in central and western North Atlantic (Víkingsson *et al.*, 2013; Gavrilchuk *et al.*, 2014; García-Vernet *et al.*, 2021).

Disruption of these seasonal prey patterns—whether through overfishing, climate-induced shifts in abundance or distribution, or habitat degradation—could alter the balance between generalist and specialist feeding strategies, potentially increasing competition, reducing foraging efficiency, and impacting reproductive success. Therefore, these findings highlight the need for an integrated approach that considers both age-specific dietary requirements and the seasonal ecology of prey species. Effective conservation strategies for minke whales in Northeast Scotland, including MPAs such as the Southern Trench in the Moray Firth, must account for temporal and ontogenetic variation in resource use. Likewise, fisheries management measures—such as quota setting and seasonal protections—must recognize that exploitation of commercially important prey species can have wider ecological consequences beyond target stocks, influencing whale foraging success across multiple age classes and even across broader Northeast Atlantic regions.

Moreover, climate change may exacerbate these pressures by altering the phenology, abundance, and distribution of key prey species. Juvenile whales, which are less capable of capturing evasive clupeids, may be particularly vulnerable, while adults relying on high-energy prey may be forced to expand their foraging range or shift diet composition, potentially increasing interactions with fisheries. Long-term monitoring of isotopic niches can therefore provide an essential tool to assess consumer responses to changes in prey availability and to anticipate ecological consequences for both whale populations and fisheries management.

Limitations and future considerations

This study is the first to provide novel insights into the isotopic niche of minke whales in Northeast Scotland. However, several caveats should be acknowledged. In exploring niche variation, small samples sizes were used,

particularly once individuals were subdivided by age class and season, potentially limiting the statistical power of some comparisons and leaving outputs open to overinterpretation. Second, isotope data were derived from a combination of samples collected from both live and dead individuals. Using tissue samples from a combination of free ranging and stranded animals may introduce subtle differences in sampling procedures or collection context that cannot be fully excluded. Third, assigning individuals to the spring and summer seasons was achieved using best available estimates of tissue incorporation rates (Busquets-Vass *et al.*, 2017). While this allowed us to capture important temporal patterns, the variability of tissue incorporation times mean that our results should be interpreted as indicative of general coarse patterns rather than definitive quantifications of foraging behaviour. Furthermore, isotopic differences over notable latitudinal scales as well as the annual migrations made by minke whales emphasises that isotope data must be carefully interpreted, especially that of mature individuals who may carry signals from other locations. Future work building on the foundations laid in this study would benefit greatly from using larger samples sizes that could explore isotopic differences between sex over the full extent of the foraging season. This would strengthen the patterns reported here and allow for a more nuanced understanding of minke whale foraging ecology.

Conclusion

This study provides the first assessment of isotopic niche dynamics in minke whales from Northeast Scottish waters, highlighting how age-class and season shape patterns of resource use. In combining stable isotope ratios, isotopic niche metrics, and mixing model outputs, we show marked differences in the isotopic niche and diet of adult and juvenile minke whales, with important consequences for understanding intra-specific competition and ecosystem interactions.

Adults displayed selective foraging strategies and efficient exploitation of high-quality prey, such as clupeids, likely driven by the energetic demands of reproduction and maintenance of body condition. In contrast, juveniles showed greater dietary plasticity reflective of generalist feeding on lower-trophic-level or pelagic prey. Seasonal analyses further revealed that while resource overlap between age classes was high in spring, complete niche partitioning occurred by summer. This course of events, likely driven by synchronous exploitation of sand

eel and other abundant prey in spring, followed by a divergence of feeding behaviours in summer clearly reduces intra-specific competition. These findings highlight the dependence of both age classes on prey species that are commercially exploited, particularly clupeids and sand eel. This intersection of ecological and economic value underscores the need for management approaches that integrate minke whale foraging ecology into broader fisheries and ecosystem-based frameworks.

Appendices

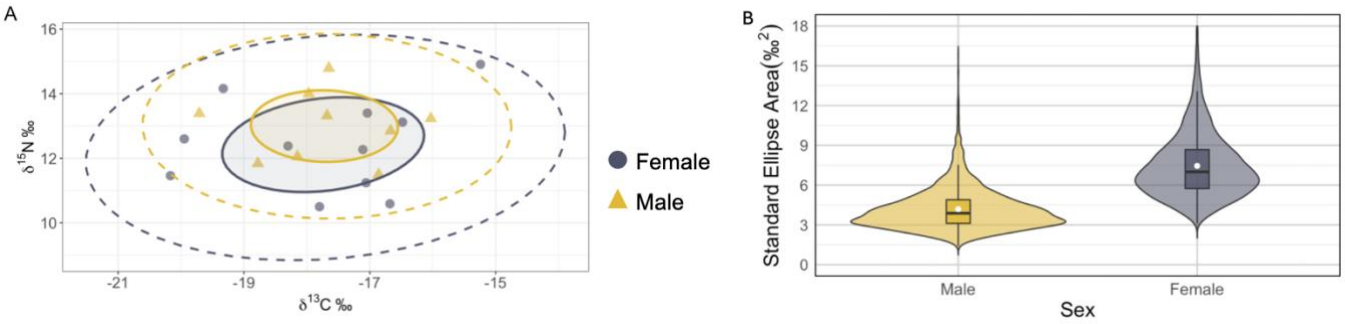
Appendix 3.1. Means and ranges of $\delta^{13}C$ and $\delta^{15}N$ in the modelled minke whale skin tissue samples.

	Mean (Range)	
	$\delta^{13}C$	**$\delta^{15}N$**
Adult (n = 14)	-16.77	13.50
	(-19.33 – -15.24)	(12.38 – 14.91)
Spring (n = 5)	-17.40	13.15
	(-18.30 – -16.03)	(12.38 – 13.78)
Summer (n = 7)	-16.13	13.65
	(-16.62 – -15.24)	(13.12 – 14.91)
Juvenile (n = 29)	-18.03	12.75
	(-20.45 – -15.76)	(10.38 – 14.79)
Spring (n = 9)	-17.60	13.21
	(-20.17 – -15.94)	(11.46 – 14.29)
Summer (n = 10)	-17.68	12.18
	(-19.95 – -15.76)	(10.50 – 13.40)

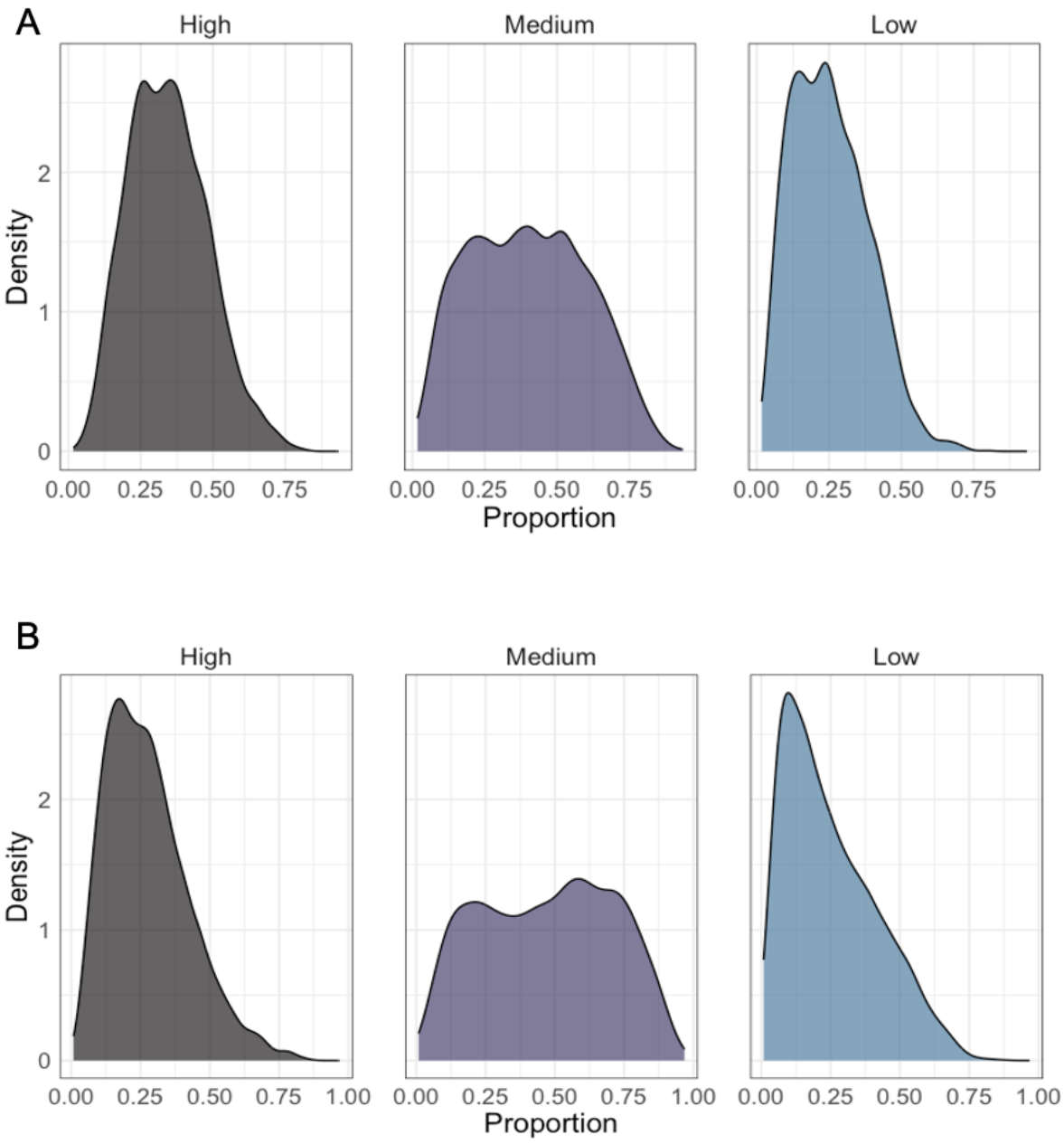
Appendix 3.2. Niche metrics from SIBER for male, female, adult and juvenile minke whales, as well as each age class for spring and summer. TA reflects the convex hull (100% of the data), SEA is the standard ellipse area (40% of the data), SEA_C refers to the standard ellipse area, corrected for sample size, and finally SEA_B which denotes the Bayesian SEA. All metrics are reported in ‰^{2}.

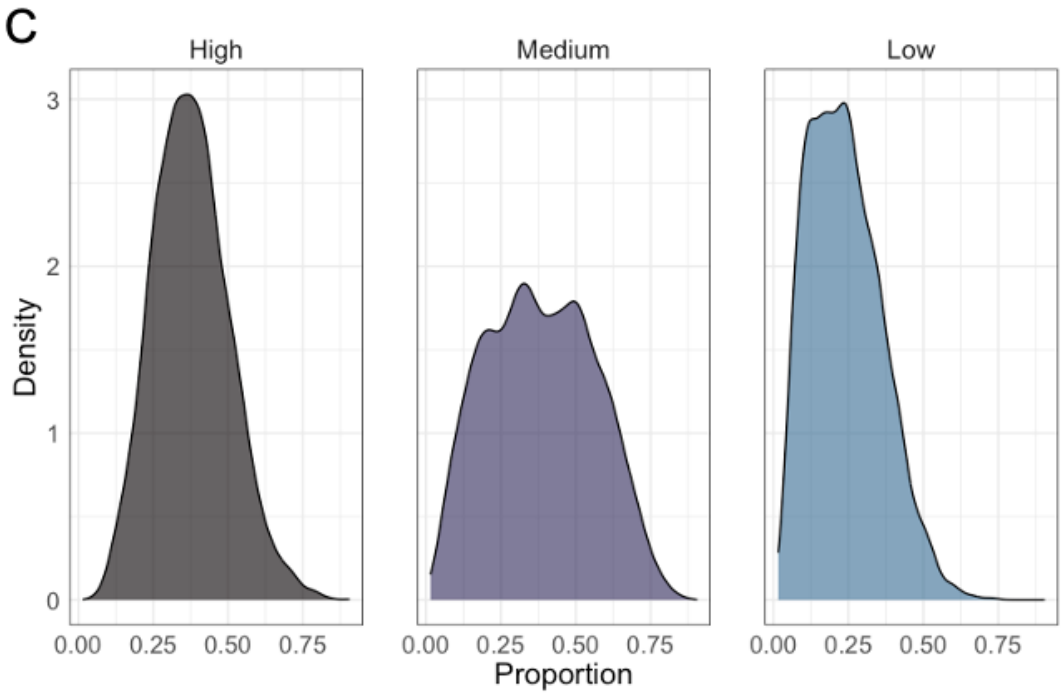
	TA (‰^{2})	**SEA (‰^{2})**	**SEA_C (‰^{2})**	**SEA_B (‰^{2}) (95% CI)**
Male (n = 9)	7.32	3.74	4.27	3.25 (1.66 – 7.21)
Female (n = 11)	14.20	6.76	7.51	6.41 (3.25 – 12.22)
Adult (n = 14)	5.60	1.97	2.14	1.89 (1.08 – 3.29)
Spring (n = 5)	1.34	1.64	2.46	1.39 (0.44 – 5.01)
Summer (n = 7)	0.70	0.52	0.65	0.58 (0.26 – 1.66)
Juvenile (n = 29)	15.11	4.83	5.01	4.66 (3.28 – 6.95)
Spring (n = 9)	4.57	3.79	5.05	3.91 (1.53 – 11.76)
Summer (n = 10)	8.35	4.88	5.57	4.57 (2.17 – 9.52)

Appendix 3.3. (A) SIBER analysis showing the core 40% data (solid line) niche and 95% data ellipse (dashed line) of male and female minke whales; (B) Bayesian standard ellipse areas (SEA_B) for males and females calculated from the posterior distributions indicated by the density curves. Median SEA_B and the interquartile range are represented by the black bar and outer box lines, respectively. SEA_C is shown by the white dot. Range of the data is shown by whiskers.



Appendix 3.4. Density plots of grouped source quality posterior distributions for (A) spring whales (B) summer whales (C) adult whales and (D) juvenile whales.

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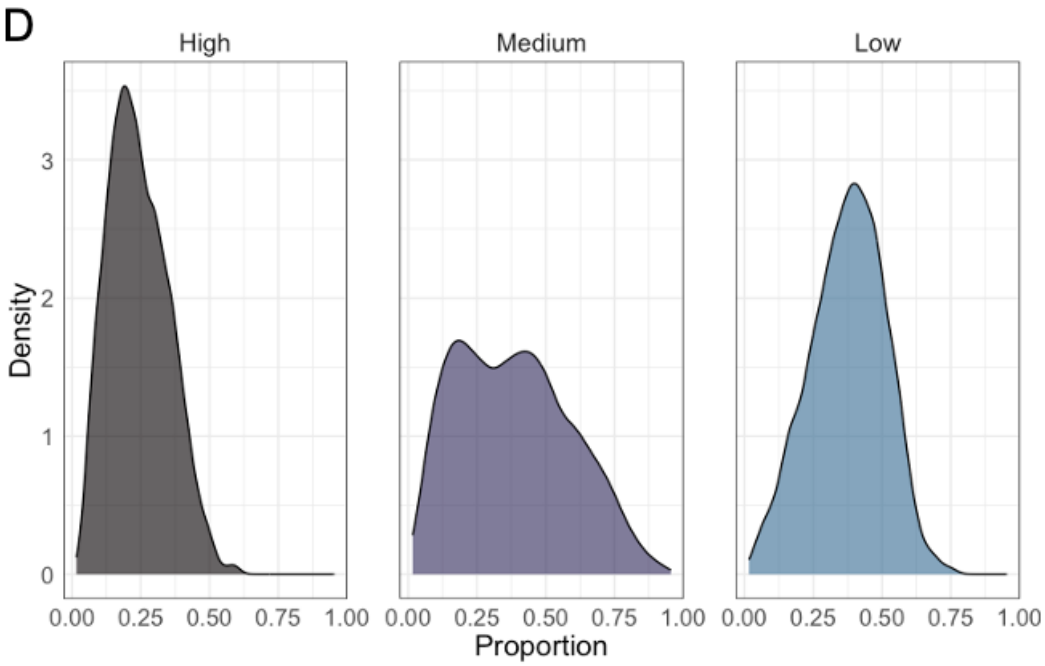
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Appendix 3.5. Minke whale sample data (n = 47).

	Specimen ID	Date	Length (cm)	Age class	Sex	Collection region	Institution	Condition code
1.	M2035/93	02/09/1993	814	Adult	M	Highland	SMASS	2a
2.	M1333/95	18/07/1995	585	Juvenile	M	Grampian	SMASS	4
3.	M1723/95	31/08/1995	363	Juvenile	M	Highland	SMASS	4
4.	M1606/97	15/07/1997	460	Juvenile	F	Shetland	SMASS	2a
5.	M2655/97	19/11/1997	248	Juvenile	M	Grampian	SMASS	4
6.	M803/98	09/04/1998	450	Juvenile	F	Highland	SMASS	4
7.	M53/00	20/03/2000	770	Adult	F	Highland	SMASS	3-4
8.	M70/00	30/04/2000	700	Adult	F	Highland	SMASS	4
9.	M42/01	14/04/2001	490	Juvenile	F	Fife	SMASS	3
10.	M153/01	12/11/2001	470	Juvenile	F	Highland	SMASS	4
11.	M86/02	19/06/2002	755	Adult	F	Lothian	SMASS	2b
12.	M288/03	19/10/2003	475	Juvenile	M	Orkney	SMASS	2a
13.	M275/05	19/10/2005	700	Adult	U	Grampian	SMASS	4
14.	M311/05	11/12/2005	553	Juvenile	F	Orkney	SMASS	2b
15.	M67/11	01/04/2011	466	Juvenile	F	Orkney	SMASS	2b
16.	M98/12	03/04/2012	445	Juvenile	M	Lothian	SMASS	2a

17.	M226/13	09/07/2013	655	Adult	F	Highland	SMASS	3
18.	M292/13	06/09/2013	487	Juvenile	F	Fife	SMASS	2a
19.	M251/14	07/09/2014	830	Adult	F	Grampian	SMASS	2a
20.	M297/14	07/10/2014	483	Juvenile	M	Fife	SMASS	2b
21.	M319/15	10/10/2015	355	Juvenile	M	Grampian	SMASS	2b
22.	M411/15	06/12/2015	530	Juvenile	U	Orkney	SMASS	3
23.	M251/16	01/06/2016	635	Juvenile	M	Fife	SMASS	3
24.	M466/16	03/11/2016	379	Juvenile	M	Fife	SMASS	3
25.	M200/17	05/05/2017	590	Juvenile	F	Fife	SMASS	2a
26.	M447/17	09/10/2017	396	Juvenile	F	Fife	SMASS	2a
27.	M317/18	10/06/2018	383	Juvenile	M	Fife	SMASS	3
28.	M586/18	18/09/2018	644	Juvenile	F	Highland	SMASS	2a
29.	M592/18	25/09/2018	417	Juvenile	F	Highland	SMASS	3
30.	M366/19	16/07/2019	875	Adult	F	Grampian	SMASS	4
31.	M450/19	27/08/2019	545	Juvenile	F	Shetland	SMASS	4
32.	M509/19	28/09/2019	804	Adult	F	Orkney	SMASS	2a-2b
33.	M157/20	15/03/2020	NA	Juvenile	F	Fife	SMASS	2a
34.	M239/20	11/05/2020	422	Juvenile	F	Highland	SMASS	2b
35.	M377/21	03/07/2021	762	Adult	M	Grampian	SMASS	2b

36.	M270/23	07/05/2023	457	Juvenile	F	Highland	SMASS	3-4
37.	MW01_17	13/06/2017	-	Adult	-	Moray	CRRU	Biopsy
38.	MW01_18	10/08/2018	-	Adult	-	Moray	CRRU	Biopsy
39.	MW01_20	14/09/2020	-	Juvenile	-	Moray	CRRU	Biopsy
40.	MW02_20	18/09/2020	-	Juvenile	-	Moray	CRRU	Biopsy
41.	MW01_21	23/06/2021	-	Adult	-	Moray	CRRU	Biopsy
42.	MW02_21	28/06/2021	-	Juvenile	-	Moray	CRRU	Biopsy
43.	MW04_21	14/07/2021	-	Juvenile	-	Moray	CRRU	Biopsy
44.	MW05_21	06/09/2021	-	Adult	-	Moray	CRRU	Biopsy
45.	MW06_21	06/09/2021	-	Adult	-	Moray	CRRU	Biopsy
46.	MW07_21	15/09/2021	-	Adult	-	Moray	CRRU	Biopsy
47.	MW01_22	02/07/2022	-	Adult	-	Moray	CRRU	Biopsy

Chapter 4: General Discussion

Summary

Despite being the most abundant baleen whale in UK waters, the minke whale (*Balaenoptera acutorostrata*) remains one of the least studied. Their small size, rapid surfacing and cryptic behaviour make them difficult to observe compared with larger and more conspicuous balaenopterids such the fin and humpback whale (Gedamke *et al.*, 2001; Risch *et al.*, 2019). As a result, key aspects of their life history, habitat use, and trophic ecology remain poorly understood. In a period of accelerating environmental change, these knowledge gaps hinder the development of effective conservation and management strategies, leaving the species vulnerable to direct and indirect anthropogenic pressures.

This thesis set out to address these gaps by investigating the foraging ecology of minke whales in Northeast Scottish waters using complementary stable isotope analyses (SIA). Chapter two examined the trophic position and quantified the contribution of known prey species to the diet of minke whales through SIA of stranded and biopsied individuals. Chapter three established the isotopic niche and its associated seasonal and age-class differences. Together, these studies provide the first insight into the ecological niche of minke whales in British waters and contribute new insights into their resource use and habitat dependence. The results presented in this thesis contribute new evidence to support adaptive management of Scottish MPAs, particularly those that list the minke whale as a protected feature. By identifying key prey resources, seasonal shifts in resource use, and ontogenetic niche partitioning, the findings highlight the need for conservation strategies that explicitly protect prey stocks and foraging habitats. Such information is critical for mitigating the impacts of unsustainable fishing and habitat degradation that continue to threaten this species within designated MPA boundaries.

Addressing research questions

The analyses reaffirms that sand eel represents the principal prey of minke whales in Scottish waters, consistent with earlier observations from stomach content and opportunistic feeding studies (Pierce *et al.*, 2004; Robinson *et al.*, 2023). However, this work also refines our understanding of other dietary components, including clupeids (sprat and herring) and, in juveniles, krill. The

presence of both pelagic fish and zooplankton prey supports the classification of the minke whale as a generalist predator capable of exploiting a range of trophic resources depending on availability and energetic requirements.

Contrary to expectations, the isotopically derived trophic position of minke whales in this study was not elevated relative to conspecifics feeding mostly on lower trophic level krill at higher latitudes. This outcome suggests that trophic enrichment alone does not fully capture the complexity of prey use within Scottish waters, and that the isotopic signatures of local prey species likely overlap more than anticipated. Nevertheless, the combination of diet composition and isotopic data supports a flexible foraging strategy. Seasonal and ontogenetic variation in both $\delta^{13}C$ and $\delta^{15}N$ values revealed clear age-class differences: adults exhibited higher isotope values and narrower isotopic niches, indicating selective feeding at higher trophic levels, while juveniles displayed wider niches and lower isotopic values, consistent with exploratory foraging behaviours or reduced access to preferred prey (Skern-Mauritzen *et al*., 2011; Eerkes-Medrano *et al*., 2021). The significant seasonal and age-class interactions observed in isotope ratios further suggest temporal shifts in prey use and possible intraspecific competition. In spring, isotopic overlap between adults and juveniles was considerable, whereas by summer, the two groups occupied distinct isotopic niches. This divergence likely reflects spatial or behavioural segregation in foraging grounds as the feeding season progresses, possibly to minimise competition for shared prey resources. Collectively, these results provide new evidence of fine-scale ecological partitioning among minke whales in Scottish waters, with important implications for conservation management that must account for temporal and demographic variation in habitat use.

Linking isotopic evidence to MPA management

Obtaining tissue samples from live cetaceans remains costly and logistically challenging (Mathews *et al.*, 1988). Strandings therefore offer an invaluable, low-cost source of ecological information allowing retrospective analysis of diet, trophic position and health (Gulland *et al.*, 2025; Lennon *et al.*, 2025). Access to different tissue types from stranded individuals enable reconstruction of diet over different temporal scales, which is of utility when monitoring mobile and wide-ranging species such as minke whales. While caveats exist, particularly the potential for bias introduced by sampling individuals that strand after illness, injury

or altered behaviour (Cloyed *et al.*, 2023), the urgent requirement for ecological data in a rapidly changing marine environment underscores the importance of using strandings as a tool to inform and guide management decisions.

Climate change is exerting increasing pressure on marine ecosystems worldwide (Jaureguiberry et al., 2022; Ortega-Cisneros et al., 2025). In Scottish waters, MPAs are designated areas that are intended to safeguard ecologically valuable and vulnerable habitats, yet current frameworks do not adequately account for dynamic environmental change (Hopkins *et al.*, 2016). Whilst management guidelines acknowledge the need to enhance ecosystem resilience, few mechanisms exist to address the spatial or temporal shifts in species distributions that climate change induces (Hopkins *et al.*, 2018). As of 2023, 38% of UK seas fall within MPAs, surpassing international area-based targets outlined in the Kunming-Montreal Global Biodiversity Framework that calls for 30% protection by 2030 (30 x 30 agenda) (JNCC, 2023). However, protection does not necessarily equate to effective conservation outcomes (Hopkins *et al*., 2020). Many MPAs remain open to damaging activities, particularly bottom-trawling (Dureuil *et al.*, 2018; Shankar-Balakrishnan, 2025; Victorero *et al.*, 2025) thereby undermining the ability of MPAs to protect trophic linkages and prey resources.

This issue is particularly relevant to the Southern Trench MPA in Northeast Scotland, an area recognised for its importance to minke whales and other migratory cetaceans (Robinson *et al.*, 2009). The persistence of industrial fishing within and adjacent to the MPA continues to threaten the abundance of prey species such as sand eel, sprat and herring (Chapter two). This contradicts the MPA network's guiding principle of ensuring connectivity through the protection of prey species critical to mobile predators (OSPAR Commission, 2003, 2006). Effective management must therefore include explicit protection measures of prey populations and their habitats. Without such measures, MPAs risk failing to meet their indented conservation outcomes of protecting their vulnerable selected features (Jentoft *et al.*, 2011; Yates *et al.*, 2019).

Stable isotopes as a tool for adaptive management

Adaptive management relies on consistent, high-quality monitoring to guide evidence-based adjustments to policy (Hopkins *et al.*, 2020). In Scotland, this has involved integrating acoustic (Boswarva et al., 2018; van Ge((Boyse et al., 2024, 2025), and genetic (Boyse *et al.*, 2024, 2025) monitoring approaches to assess

cetacean distribution and population structure. However, SIA remains underutilised despite its capacity to provide information on diet and habitat use. The present study demonstrates the potential of SIA to complement existing monitoring tools and inform adaptive management for species listed as protected features within MPAs.

Stable isotopes offer several advantages for management: (1) they can be obtained from tissues collected opportunistically, including strandings; (2) they integrate foraging information over weeks, months, or years providing a dietary record that is not biased by short-term feeding events; and (3) they can reveal trophic and spatial relationships that are otherwise difficult to observe directly. Previous studies have successfully utilised SIA to delineate resource use and habitat preferences of cetaceans (Hooker *et al.*, 2002; Becker *et al.*, 2021; Ogilvy *et al.*, 2022). The integration of SIA with acoustic and genetic data would enable a more holistic understanding of minke whale ecology, linking trophic behaviour with movement patterns and population structure. Such a multi-faceted approach would substantially enhance the evidence base for adaptive management.

Future directions

The combined findings from this thesis provide two key insights. First, minke whales in Northeast Scotland target sand eel as a principal prey resource. Second, clear isotopic partitioning between adult and juvenile whales demonstrate differences in resource use and foraging habitat. Continued monitoring of these aspects of their foraging ecology is essential to ensure that MPA management remains responsive to environmental change and is grounded in robust, long-term evidenced based data.

Dietary analysis (Chapter two) revealed sand eel and clupeids as dominant prey, while krill also contributed to the diet of juvenile minke whales. The occurrence of krill, a typically high-latitude prey species in the diet of juveniles may suggest some degree of seasonal or latitudinal movement between foraging grounds, though further evidence is required. Applying satellite telemetry to track individual movement would help clarify whether Scottish minke whales exhibit seasonal migrations between regional feeding grounds and could strengthen the interpretation of isotopic data.

Chapter three demonstrated clear age-class and seasonal differences in isotopic niche and overlap of minke whales. However, the resolution of these patterns is constricted by small samples sizes and the lack of spatially and temporally resolved baseline isotope data. Understanding the spatial and temporal variation of $\delta^{13}C$ and $\delta^{15}N$ at the base of the food web is essential for interpreting consumer values accurately (Graham *et al.*, 2009; Kurle and McWhorter, 2017). The development of zooplankton isoscapes – maps of baseline isotopic variation – have proven highly effective in identifying the foraging grounds of highly mobile marine predators (Troina *et al.*, 2020; Bury *et al.*, 2024). Developing similar temporal isoscapes for Scottish waters would enable stronger inferences of movements and resource use by different demographic groups to be made. Coupling isotopic, telemetry and oceanographic data would therefore represent a powerful framework for linking prey dynamics, whale movements and decision making.

Conclusion

Minke whales in Northeast Scotland exhibit complex and dynamic foraging strategies with clear dietary partitioning between adults and juveniles and pronounced seasonal shifts in isotopic niches. These findings suggest that intraspecific competition is reduced through spatial and trophic segregation, allowing both age groups to exploit different foraging habitats and available resources efficiently within Scottish waters. However, despite their designation as a protected feature within the Scottish MPA network, minke whales remain exposed to anthropogenic threats including depletion of prey stocks and habitat degradation within MPA boundaries. Stable isotope analysis represents a robust and cost-effective method for monitoring the foraging ecology of minke whales. When integrated with existing and well-established acoustic and genetic monitoring approaches, SIA can provide a powerful evidence base to support more effective adaptive management, enabling MPAs to function as dynamic and responsive conservation tools. In the context of accelerating marine environmental change, such integrative and data driven approaches are essential to ensure the long-term resilience of both minke whales and the ecosystems upon which they depend.

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