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Stable isotope ecology and interspecific dietary overlap among dolphins in the Northeast Atlantic

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Dolphins are mobile apex marine predators. Over the past three decades, warm-water adapted dolphin species (short-beaked common and striped) have expanded their ranges northward and become increasingly abundant in British waters. Meanwhile, cold-water adapted dolphins (white-beaked and Atlantic white-sided) abundance trends are decreasing, with evidence of the distribution of white-beaked dolphins shifting from southern to northern British waters. These trends are particularly evident in Scottish waters and ocean warming may be a contributing factor. This mobility increases the likelihood of interspecific dietary overlap for prey among dolphin species previously separated by latitude and thermal gradients. Foraging success is critical to both individual animal health and overall population resilience. However, the degree of dietary overlap and plasticity among these species in the Northeast Atlantic is unknown. Here, we characterise recent (2015-2021) interspecific isotopic niche and niche overlap among six small and medium-sized delphinid species co-occurring in Scottish waters, using skin stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$), combined with stomach content records and prey $\delta^{13}C$ and $\delta^{15}N$ compiled from the literature. Cold-water adapted white-beaked dolphin have a smaller core isotopic niche and lower dietary plasticity than the generalist short-beaked common dolphin. Striped dolphin isotopic niche displayed no interspecific overlap, however short-beaked common dolphin isotopic niche overlapped with white-beaked dolphin by 30% and Atlantic white-sided dolphin by 7%. Increasing abundance of short-beaked common dolphin in British waters could create competition for cold-water adapted dolphin species as a significant portion of their diets comprise the same size Gadiformes and high energy density pelagic schooling fish. These priority prey species are also a valuable component of the local and global fishing industry. Competition for prey from both ecological and anthropogenic sources should be considered when assessing cumulative stressors acting on cold-water adapted dolphin populations with projected decline in available habitat as ocean temperatures continue to rise.

KEYWORDS

dolphin, stable isotope, Scotland, Northeast Atlantic, niche, dietary overlap

1 Introduction

As apex predators, cetaceans (whales, porpoises, and dolphins) are considered valuable indicators of marine ecosystem health (Bossart, 2011; Williamson et al., 2021; Williams et al., 2023). Their ecology and conservation are currently topics of global concern (Burgener et al., 2012; Penniman et al., 2018). Limited baseline information on these charismatic mammals means that novel monitoring tools and long-term data are crucial to assess cetacean population conservation status and inform marine management decisions. Among a multitude of other anthropogenic stressors (e.g., by-catch, noise pollution, persistent organic pollutants), climate change poses an active threat to cetacean populations in the Northeast Atlantic (Jepson et al., 2016; Erbe et al., 2018; Gordon, 2018; Albouy et al., 2020; Evans and Waggitt, 2020). Warming ocean temperatures since ~1980 are altering marine species distribution around Britain and impact cetacean population health through changes in habitat availability, pathogen exposure, and prey abundance (Robinson et al., 2010; Heath et al., 2012; Evans and Bjørge, 2013; Lambert et al., 2014; Hammond et al., 2017; Simmonds, 2017; IJsseldijk et al., 2018; Evans and Waggitt, 2020). Globally, warming sea surface temperatures actively shrink available habitat of cold-water adapted cetaceans and their prey, while warm-water adapted species can shift their ranges towards the poles (Higdon and Ferguson, 2009; Kovacs et al., 2011; Kerosky et al., 2012; Hastings et al., 2020; Chaudhary et al., 2021). This can result in range overlap and competition among marine species (including cetaceans and their prey) previously separated by habitat or latitude (Milazzo et al., 2013; Albouy et al., 2020; Evans and Waggitt, 2020).

Dolphins are highly mobile and are theoretically able to relocate to pursue preferred prey or seek more favourable habitat and water temperatures (Silva et al., 2008; Pinsky et al., 2020). Their mobility, abundance in British waters, and relevant ecologies (differing thermal tolerances and feeding specialisations) render them excellent "sentinels" for changing marine environmental conditions (Williamson et al., 2021). However, this adaptability has also resulted in increased geographical range overlap among dolphin species previously separated by latitude and thermal gradients (Sunday et al., 2012; Williamson et al., 2021).

Historical stranding and sighting data since ~1800 show that Atlantic white-sided and white-beaked dolphins (*Leucopleurus acutus* and *Lagenorhynchus albirostris*) are two of the most common cetaceans in British waters, whereas striped dolphins (*Stenella coeruleoalba*) were rarely recorded in British waters prior to the 1980s (Reid et al., 1993; Sheldrick et al., 1994; Coombs et al., 2019). short-beaked common dolphin (*Delphinus delphis*) are historically present in British waters, with evidence of a west-to-east and northward shift in population distribution during the early to mid-twentieth century (Murphy et al., 2013). There is a clear increase over the past three decades (1980 to 2020) in the frequency of both short-beaked common and striped dolphin sighting and stranding events in British waters (Paxton and Thomas, 2010; Evans and Waggitt, 2020; Williamson et al., 2021). This trend is particularly notable in northern regions such as Scotland (Waggitt et al., 2020; Williamson et al., 2021). Meanwhile, white-beaked dolphin abundance in the North Atlantic has decreased over the past three decades, and Atlantic white-sided dolphin abundance has decreased since the early 2000s (Evans and Waggitt, 2020). Future ocean warming predicts severe decline in available habitat and white-beaked dolphin abundance over the next century (Lambert et al., 2014).

In British waters, recent and increasing degrees of range overlap between sentinel cold-water adapted dolphins (Atlantic white-sided and white-beaked) and warm-water adapted dolphins (short-beaked common and striped) increases the likelihood of interspecific dietary overlap and the potential for competition. Foraging success is critical to animal health and fecundity (IJsseldijk et al., 2021). As such, foraging pressure introduced from new sources of dietary overlap may have a negative impact on already stressed populations. Stomach content records from these four sentinel dolphin species indicate overlap in preferred prey (Couperus, 1997; Lahaye et al., 2005; Spitz et al., 2006; Canning et al., 2008; Santos et al., 2008; Brophy et al., 2009; Jansen et al., 2010). However, the degree of dietary overlap and plasticity of these species in the Northeast Atlantic is unknown. In addition, these sentinel dolphin species overlap geographically with two other cosmopolitan medium-sized delphinids, Risso's and bottlenose dolphins (*Grampus griseus* and *Tursiops truncatus*) that potentially utilise the same resources (Clarke and Pascoe, 1985; Santos et al., 2001; Spitz et al., 2011).

Carbon and nitrogen stable isotopes (δ^{13}C and δ^{15}N) are used as a proxy for dietary niche in elusive and highly mobile marine mammals. In an isotopic sense, "you are what/where you eat", with predictable enrichment factors in both δ^{13}C and δ^{15}N associated with trophic level increase (DeNiro and Epstein, 1978; DeNiro and Epstein, 1981). The spatial distribution of marine habitats (latitude and water depth) also has a strong influence on primary producer δ^{13}C, the effects of which are carried up the food chain by consumers (Magozzi et al., 2017; Espinasse et al., 2022). Carbon and nitrogen stable isotope compositions of consumer proteinaceous tissues (such as skin) are directly correlated with diet, providing proxy evidence of nutrient flow within a marine ecosystem as well as trophic position (Madgett et al., 2019; Parzanini et al., 2019; MacKenzie et al., 2022). The trophic enrichment factor between diet (prey muscle) and dolphin skin is approximately 1 ‰ for δ^{13}C and 1.5 ‰ for δ^{15}N (Browning et al., 2014; Giménez et al., 2016). Cetacean skin is a metabolically active tissue, with a half-life of approximately 24.2 (SD ± 8.2) days for carbon and 47.6 (SD ± 19.0) days for nitrogen as documented in captive bottlenose dolphins fed a controlled diet over a one-year period (Giménez et al., 2016). As in similar odontocete studies (e.g., Samarra et al., 2017; Louis et al., 2018), we assume a similar tissue turn-over rate among all six dolphin species, where skin δ^{13}C and δ^{15}N are representative of the diet assimilated during the last 4 to 6 weeks of life. However, the age of the animal and diet lipid-content also have a significant effect on isotopic turn-over rate in dolphin skin (Browning et al., 2014). In contrast with skin stable isotope composition, stomach content analysis is heavily biased towards the final meal of the animal which may not be wholly representative of the species in by-caught or stranded animals (Barros and Odell, 1990; Gibbs et al., 2011). Stomach content analysis is typically limited to prey species that possess distinguishable hard parts (e.g., otoliths, squid beaks), leading to an underrepresentation of soft-bodied or small prey. Pairing cetacean stomach content records with skin stable isotope data therefore provides a more complete picture of cetacean diet (McCluskey et al., 2021).

This study characterises and visualises current interspecific isotopic overlap among six small and medium-sized delphinid species co-occurring in Northeast Atlantic waters. To do so, we combined dolphin skin stable isotope (δ^{13}C and δ^{15}N) data from stranding events (2015-2021) along the Scottish coastline with published stomach content records of individuals fromthe Northeast Atlantic. Dolphin skin δ^{13}C and δ^{15}N allow us to identify isotopic niche size and position, as well as dietary plasticity and potential sources of overlap (Newsome et al., 2007). Based on current stomach content records, we hypothesise that there will be significant isotopic overlap between the striped and the Atlantic white-sided dolphin, and between the short-beaked common and the white-beaked dolphin. This exploratory work on interspecific isotopic niche overlap will improve our understanding of the ecology, interactions, and conservation requirements of sentinel cetacean species in Scottish waters. Specific calls for further research pertaining to diet composition, threats to current populations, lack of data, and likely impact of projected climate change on cold-water dolphin species in British waters highlight the timeliness of this work (Lambert et al., 2014; Evans, 2018; IJsseldijk et al., 2018; Kiszka and Braulik, 2018).

2 Materials and methods

2.1 Sample collection and preparation

Skin samples were collected from six species of stranded dead dolphins (Atlantic white-sided; white-beaked; short-beaked common; striped; Risso's; and bottlenose) found on the Scottish coastline between 2015 and 2021. Bottlenose dolphins were assigned a "local" or "non-local" classification based on their presence in photo identification databases for Great Britain and Ireland. Associated stranding event data are reported in Table 1. Skin samples are routinely collected during post-mortem examinations conducted by the Scottish Marine Animal Stranding Scheme (IJsseldijk et al., 2019; Davison and ten Doeschate, 2020) and stored at −20°C in dedicated SMASS and National Museums Scotland (NMS) tissue archives until preparation for analysis. Calves and very young animals primarily reliant on nursing for nutrition were excluded from the analysis based on their body length measurements (Jefferson et al., 1993; Kinze et al., 1997; Kastelein et al., 2003; Jefferson et al., 2008; Meissner et al., 2012; Peters et al., 2020) (Supplementary Material Table 1). Therefore, the animals included in this study are a combination of both adults and nutritionally independent juveniles. Stranding events were selected from the north, east, and west coasts of Scotland, including the Orkney and Shetland Isles. To control for degradation effects, specimens were selected based on carcass condition at time of tissue collection. The majority of samples were classified as 2a to 2b: "freshly dead" to "slight decomposition" (Table 1) (Kuiken, 1991; Payo-Payo et al., 2013; IJsseldijk et al., 2019).

2.2 Lipid extraction and lipid correction for skin δ^{13}C

Lipids have a strong influence on tissue δ^{13}C (DeNiro and Epstein, 1977; Post et al., 2007). Lipids are ^{13}C-depleted relative to protein and should be removed to reduce variability caused by differing lipid content among individuals and species (McConnaughey and McRoy, 1979; Post et al., 2007). While dual analysis of samples is recommended, this can be labour intensive and cost-prohibitive with large sample sets. One aliquot of each sample ($n = 57$) underwent no lipid extraction to avoid the deleterious effect of chemical extraction on collagen amino acids and its impact onresultant δ^{15}N (Smith et al., 2020). A subset of dolphin skin samples ($n = 37$) was separated into two aliquots, where one aliquot was chemically lipid extracted to accurately calculate skin lipid content and account for its impact on the proteinaceous component of the remaining non-lipid extracted samples (McConnaughey and McRoy, 1979; Post et al., 2007). Following a modified Bligh and Dyer (1959) method, the lipid extracted aliquot underwent three rinses of 30 minutes each in 10 mL of 2:1 chloroform:methanol, prior to drying at 60°C. Dolphin skin samples were desiccated at 60°C, powdered, and weighed into pressed-tin capsules.

TABLE 1 Northeast Atlantic dolphin $\delta^{13}C$ (lipid-corrected), $\delta^{15}N$, and stranding event data (n = 57).

Specimen no.	Common name	Year	Stranding month	Sex	Length (cm)	Region (Scotland)	Latitude WGS84	Longitude WGS84	Necropsy status	PM code	$\delta^{13}C$ ‰ (VPDB)	$\delta^{15}N$ ‰ (AIR)
M434/15	White-beaked dolphin	2015	12	M	275	Fife	56.25305939	-2.631024361	sampled	2b	−16.9	+13.9
M497/15	White-beaked dolphin	2015	12	F	209	Western Isles	58.19838333	-6.208683491	necropsied	2b	−17.5	+13.2
M267/16	White-beaked dolphin	2016	6	M	264	Highland	58.60824203	-3.351047516	necropsied	2b	−16.7	+14.1
M385/16	White-beaked dolphin	2016	9	M	238	Highland	57.586336	-6.3755252	necropsied	2a	−17.1	+12.7
M350.1/17	White-beaked dolphin	2017	8	M	215	Orkney	58.89316559	-2.921369314	necropsied	2b	−17.8	+12.3
M496/17	White-beaked dolphin	2017	10	M	264	Grampian	57.68124771	-2.952453136	necropsied	2a	−17.6	+12.7
M495/18	White-beaked dolphin	2018	7	F	264	Lothian	55.981884	-3.298130274	sampled	2a	−17.5	+13.4
M299/16	Atlantic white-sided dolphin	2016	6	M	246	Highland	58.59825897	-3.360981941	necropsied	2b	−19.4	+11.1
M276/17	Atlantic white-sided dolphin	2017	7	M	275	Borders	55.93165207	-2.3344841	sampled	3	−18.1	+11.7
M298/17	Atlantic white-sided dolphin	2017	7	M	173	Shetland	60.14886856	-1.1156919	necropsied	2b	−19.0	+11.9
M129/18	Atlantic white-sided dolphin	2018	7	F	223	Orkney	58.91575241	-3.319611788	necropsied	2a	−18.2	+11.1
M379/19	Atlantic white-sided dolphin	2019	7	M	170	Shetland	60.13583333	-1.161944444	sampled	2b	−18.8	+12.1
M33/15	Striped dolphin	2015	1	F	189	Western Isles	57.24046326	-7.451052189	necropsied	2b	−17.9	+10.4
M101/15	Striped dolphin	2015	3	M	175	Highland	57.20108032	-6.288246155	necropsied	2b	−18.2	+10.8
M338/15	Striped dolphin	2015	10	M	154	Orkney	59.13132095	-3.31917119	necropsied	2b	−18.2	+10.8
M40/16	Striped dolphin	2016	1	M	212	Shetland	60.15354538	-1.142580748	necropsied	2b	−18.3	+11.0
M449/17	Striped dolphin	2017	10	F	185	Western Isles	57.99418259	-7.094299793	necropsied	2a	−18.1	+10.3
M531/17	Striped dolphin	2017	11	M	188	Western Isles	57.16648865	-7.413619518	sampled	2b	−18.3	+10.4
M94/18	Striped dolphin	2018	2	M	148	Highland	57.9602623	-3.990828753	necropsied	2a	−17.6	+11.1
M553/18	Striped dolphin	2018	9	F	175	Strathclyde	56.49323654	-5.421152592	necropsied	2a	−17.6	+10.6
M86/19	Striped dolphin	2019	1	F	177	Orkney	58.82333333	-2.9975	necropsied	3	−17.7	+11.0
M185/19	Striped dolphin	2019	3	M	165	Highland	58.15472222	-5.239444444	necropsied	2a	−18.3	+10.9
M32.1/15	Short-beaked common dolphin	2015	1	F	194	Western Isles	57.48439407	-7.238466263	necropsied	2b	−17.4	+12.6
M58/15	Short-beaked common dolphin	2015	1	M	182	Western Isles	58.47645569	-6.310609341	necropsied	2b	−18.1	+12.6
M134/15	Short-beaked common dolphin	2015	4	F	171	Western Isles	58.26371384	-6.325642109	necropsied	2b	−18.0	+11.5
M267.2/15	Short-beaked common dolphin	2015	8	F	167	Fife	56.06364059	-3.210935354	necropsied	2b	−17.1	+13.1
M409/16	Short-beaked common dolphin	2016	9	F	188	Western Isles	58.19682312	-6.739969254	necropsied	2b	−18.0	+12.5

(Continued)

TABLE 1 Continued

Specimen no.	Common name	Year	Stranding month	Sex	Length (cm)	Region (Scotland)	Latitude WGS84	Longitude WGS84	Necropsy status	PM code	δ^{13}C ‰ (VPDB)	δ^{15}N ‰ (AIR)
M31.1/17	Short-beaked common dolphin	2017	1	M	162	Highland	57.66284561	-4.103600979	necropsied	2a	−18.4	+12.6
M37/17	Short-beaked common dolphin	2017	1	F	203	Highland	57.72995758	-4.010083675	necropsied	2b	−17.0	+13.2
M57/17	Short-beaked common dolphin	2017	1	M	200	Orkney	58.9270134	-2.828470469	Sampled	2a	−17.5	+13.0
M146/17	Short-beaked common dolphin	2017	3	M	153.5	Strathclyde	56.21400452	-5.659215927	necropsied	2b	−17.6	+13.4
M189/17	Short-beaked common dolphin	2017	4	M	151	Western Isles	57.67196655	-7.250453472	Sampled	2a	−17.8	+11.4
M537/17	Short-beaked common dolphin	2017	11	M	165	Highland	58.33271027	-8.460983276	necropsied	2b	−18.5	+12.3
M548/17	Short-beaked common dolphin	2017	11	M	216	Western Isles	57.15582657	-7.410402298	sampled	2b	−18.3	+11.0
M563/17	Short-beaked common dolphin	2017	11	M	156	Grampian	57.66950226	-3.512102127	necropsied	2a	−18.3	+11.5
M251.1/18	Short-beaked common dolphin	2018	4	F	152	Western Isles	57.39875031	-7.327902317	sampled	2a	−18.1	+12.8
M251.2/18	Short-beaked common dolphin	2018	4	M	167	Western Isles	57.39875031	-7.327902317	necropsied	2b	−18.2	+12.3
M571/18	Short-beaked common dolphin	2018	9	F	190	Highland	57.44032669	-5.812624454	necropsied	2b	−18.0	+11.9
M773/18	Short-beaked common dolphin	2018	12	M	162	Strathclyde	55.52267838	-4.640683174	necropsied	2b	−17.1	+13.9
M195/19	Short-beaked common dolphin	2019	3	F	200	Shetland	59.89916667	-1.335555556	necropsied	2b	−17.8	+11.0
M112/20	Short-beaked common dolphin	2020	2	M	213	Western Isles	57.30916667	-7.401388889	necropsied	2a	−17.6	+12.4
M659/20	Short-beaked common dolphin	2020	11	M	173	Highland	57.57805556	-4.113055556	necropsied	2a	−18.2	+12.2
M432/20	Bottlenose dolphin	2020	8	M	318	Tayside	56.45694444	-2.9625	necropsied	3	−17.0	+14.5
M639.1/20	Bottlenose dolphin	2020	11	F	251	Western Isles	57.49388889	-7.2725	necropsied	2b	−17.3	+12.6
M639.2/20	Bottlenose dolphin	2020	11	M	301	Western Isles	57.4925	-7.268611111	necropsied	2b	−17.1	+13.3
M639.3/20	Bottlenose dolphin	2020	11	F	296	Western Isles	57.49388889	-7.2725	necropsied	2b	−16.7	+13.4
M455.1/21	Bottlenose dolphin	2021	8	M	219	Highland	57.69277778	-4.016944444	necropsied	2a	−18.1	+11.8
M455.2/21	Bottlenose dolphin	2021	8	F	280	Highland	57.71388889	-4.025833333	necropsied	2a	−18.5	+12.4
M455.3/21	Bottlenose dolphin	2021	8	M	310	Highland	57.68333333	-4.034166667	necropsied	2b	−18.5	+12.7
M455.4/21	Bottlenose dolphin	2021	8	F	307	Highland	57.71388889	-4.025833333	necropsied	2b	−18.1	+12.5
M456/21	Bottlenose dolphin	2021	8	F	293	Grampian	57.66333333	-3.623055556	necropsied	2b	−18.3	+12.4
M457/21	Bottlenose dolphin	2021	8	M	310	Grampian	57.66555556	-3.524166667	necropsied	3	−18.1	+12.3

(Continued)

TABLE 1 Continued

Specimen no.	Common name	Year	Stranding month	Sex	Length (cm)	Region (Scotland)	Latitude WGS84	Longitude WGS84	Necropsy status	PM code	δ^{13}C ‰ (VPDB)	δ^{15}N ‰ (AIR)
M458/21	Bottlenose dolphin	2021	8	M	317	Grampian	57.6775	-3.499722222	necropsied	3	−18.3	+12.5
M60/15	Risso's dolphin	2015	1	U	213	Western Isles	57.36122513	-7.405709267	sampled	2b	−18.0	+11.4
M64/15	Risso's dolphin	2015	2	M	292	Highland	57.95162201	-4.081609249	necropsied	2a	−16.8	+12.9
M155/17	Risso's dolphin	2017	3	F	264	Western Isles	57.53614426	-7.39817524	necropsied	2b	−17.8	+11.7
M459/17	Risso's dolphin	2017	10	M	256	Western Isles	57.40404129	-7.330330372	necropsied	2a	−16.8	+12.3

Skin samples were collected from animals stranded on Scottish coastlines between 2015-2021. PM (post-mortem) code refers to decomposition status of the animal at time of sampling, where 2a is freshly dead and 3 is mild to moderate decomposition.

The following equation, adapted to this dataset and following Post et al. (2007), was used to correct the remaining non-lipid extracted (NLE) dolphin δ^{13}C values (Figure 1 and Supplementary Material Table 2):

$$\delta^{13}C_{Normalized} = \delta^{13}C_{NLE} + \alpha + (\beta \times C/N)$$

where α is the intercept of regression between $\Delta^{13}C_{LE\text{-}NLE}$ and $C{:}N_{NLE}$, and β is the slope (Supplementary Material Table 2):

$$\delta^{13}C_{Normalized} = \delta^{13}C_{NLE} + (-3.47 + 1.18 \times C/N)$$

2.3 Stable isotope analysis

The carbon and nitrogen stable isotope compositions (δ^{13}C and δ^{15}N) of dolphin skin (n = 50) were measured using an Elementar Pyrocube elemental analyser (EA), coupled to a ThermoScientific^{TM} Delta Plus XP isotope mass spectrometer *via* a ConFlo IV system, using helium as the carrier gas at the National Environmental Isotope Facility (NIEF) isotope ecology laboratory. Additional (n = 7) bottlenose dolphin samples were analysed using a Costech elemental analyser coupled to a ThermoScientific^{TM} Delta V

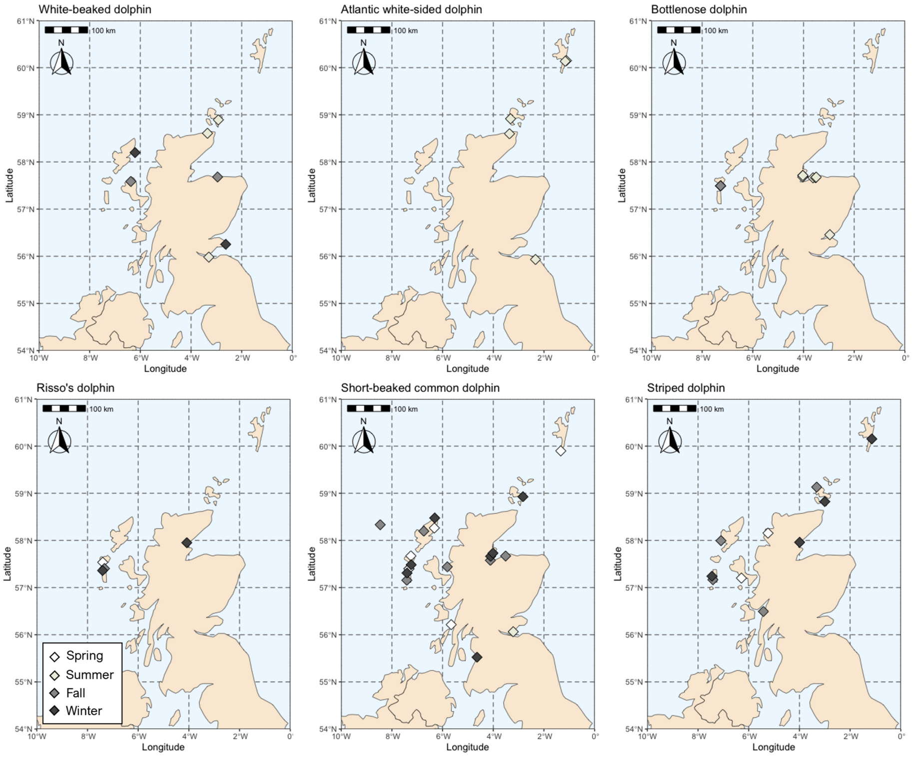

FIGURE 1
Stranding locations (Scottish coastline) of each dolphin species. Stranding season is also indicated (Spring [March-May], Summer [June-August], Fall [September-November], and Winter [December-February).

isotope ratio mass spectrometer *via* a ConFlo IV system, using helium as the carrier gas at the Laboratory for Stable Isotope Science (LSIS) at the University of Western Ontario. Sample duplicates were included for every ten samples. All isotope results are reported in δ-notation in per mil (‰) relative to international standards calibrated to VPDB and AIR, respectively.

At the NEIF laboratory, carbon and nitrogen stable isotope compositions were calibrated using Fluka gel (porcine gelatine; n = 29; 1σ standard deviation [SD] measured δ^{13}C = 0.15 ‰, accepted δ^{13}C = –20.10 ‰ and 1σ SD δ^{15}N = 0.14 ‰, accepted δ^{15}N = +5.73 ‰) and USGS40 (L-glutamic acid; n = 4; 1σ SD δ^{13}C = 0.2 ‰, accepted δ^{13}C = –26.39 ± 0.04 ‰ and 1σ SD δ^{15}N = 0.2 ‰, accepted δ^{15}N = –4.52 ± 0.06 ‰). Fluka gel, Alagel (alanine and gelatine; n = 11; 1σ SD δ^{13}C = 0.09 ‰, accepted δ^{13}C = – 8.98 ‰ and 1σ SD δ^{15}N = 0.12 ‰, accepted δ^{15}N = +2.29 ‰), and Glygel (glycine and gelatine; n = 11; 1σ SD δ^{13}C = 0.07 ‰, accepted δ^{13}C = –38.47 ‰ and 1σ SD δ^{15}N = 0.11 ‰, accepted δ^{15}N = +23.12 ‰) were used to monitor instrument accuracy, precision, and drift. Fluka gel of different weights were used to monitor instrument linearity. Standards were repeated every ten samples. Analytical error was <0.2 ‰ for both δ^{13}C and δ^{15}N.

At LSIS, standards were analysed at the start and end of each analytical session and after every five samples; no instrumental drift was detected in the analytical sessions. The carbon and nitrogen stable isotope compositions were calibrated using USGS40 (L-glutamic acid; n = 4; 1σ SD δ^{13}C = 0.04 ‰, accepted δ^{13}C = –26.39 ± 0.04 ‰; 1σ SD δ^{15}N = 0.04 ‰, accepted δ^{15}N = –4.52 ± 0.06 ‰) and USGS41a (L-glutamic acid; n = 5; 1σ SD δ^{13}C = 0.04 ‰, accepted δ^{13}C = +36.55 ± 0.08 ‰; 1σ SD δ^{15}N = 0.22 ‰, accepted δ^{15}N = +47.55 ± 0.15 ‰). The accuracy of the calibration curve was tested using the LSIS internal standard (keratin, MP Biomedicals Inc., Cat No. 90211, Lot No. 9966H; n = 20) (measured δ^{13}C = –24.09 ± 0.05 ‰ [1σ SD]; measured δ^{15}N = +6.45 ± 0.13 ‰ [1σ SD]; n = 20 for both), which compared well with its accepted values (δ^{13}C = –24.05 ‰; δ^{15}N = +6.40 ‰; n = 1999 for both). Accuracy was also assessed using P. Szpak's SRM-14 (polar bear bone collagen; measured δ^{13}C = –13.75 ± 0.03 ‰; measured δ^{15}N = +21.65 ± 0.06 ‰; n = 2 for both), which compared well with its accepted values (δ^{13}C = –13.63 ± 0.09 ‰; accepted δ^{15}N = +21.62 ± 0.28 ‰; n = 794 for both). Sample duplicate analyses differed by an average of 0.08 ‰ for δ^{13}C and 0.20 ‰ for δ^{15}N (n = 7 for both).

2.4 Data analysis

Data analyses were performed using R version 4.2.1 (R Core Team, 2022). Dolphin data distribution was assessed using a Shapiro-Wilk normality test. A PERMANOVA was used to identify differences in mean δ^{13}C and δ^{15}N among species. A *post hoc* pair-wise comparison (with Bonferroni correction to produce adjusted significance levels) was used to identify which species differed. Welch's Two Sample *t*-test (assuming unequal variance) was used to assess intraspecific differences between local and non-local bottlenose dolphins. Dolphin isotopic niches, as represented by skin carbon and nitrogen stable isotope compositions (lipid-corrected δ^{13}C and δ^{15}N), were evaluated using the package SIBER (Stable Isotope Bayesian Ellipses in R [Jackson et al., 2011]). SIBER creates isotopic niche models of consumers using Bayesian multivariate normal distributions, calculating core (ellipses constraining 40% of data per species - Standard Ellipse Area corrected for small sample size [SEAc] and Bayesian Standard Ellipse Area [SEA_B]) and total (convex hull containing 100% of data per species - Total Area [TA]) isotopic niches, in addition to interspecific core niche overlap.

2.5 Dietary comparison of prey δ^{13}C and δ^{15}N

Northeast Atlantic fish, cephalopod, and crustacean muscle δ^{13}C and δ^{15}N (n = 1964 specimens) were compiled to provide additional context for interpreting dolphin diet (Das et al., 2003; Schaal et al., 2010; Chouvelon et al., 2012; Varela et al., 2013; Jennings and Cogan, 2015; Louzao et al., 2017; Madgett et al., 2019;

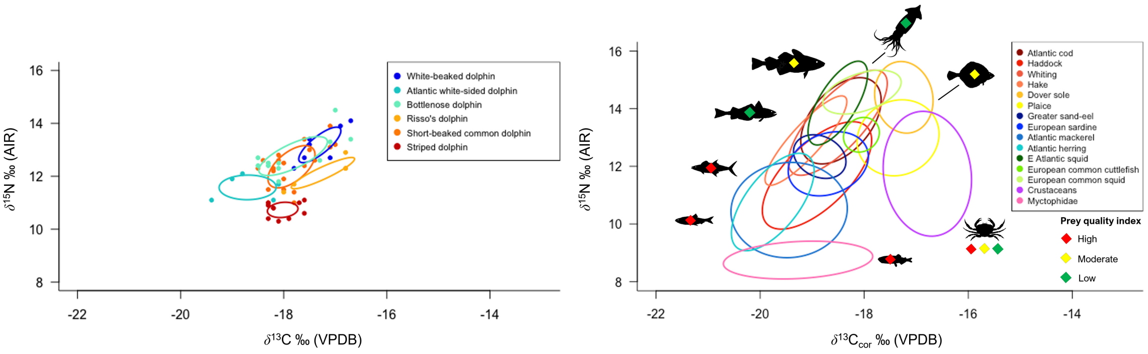

FIGURE 2
Left: Core isotopic feeding niches (as represented by Standard Ellipse Area containing 40% of the data per species, corrected for small sample size [SEAc, ‰^{2}]) of co-occurring dolphin species stranded on Scottish coastlines. *Right:* Distribution of Northeast Atlantic dolphin prey species $\delta^{13}C_{cor}$ and δ^{15}N. Prey quality (energy density in kJ/g^{-1}) is also indicated. Fish, cephalopod, and crustacean muscle tissue $\delta^{13}C_{cor}$ has been normalised for lipid content following Post et al. (2007) and Suess Effect-corrected to 2021. The trophic enrichment factor between diet (prey muscle) and dolphin skin is approximately 1 ‰ for δ^{13}C and 1.5 ‰ for δ^{15}N.

TABLE 2 Prey muscle $\delta^{13}C_{cor}$ and $\delta^{15}N$ mean and standard deviation (SD).

Common name	Species	$\delta^{13}C_{cor}$ ‰ (VDPB) mean ± SD	$\delta^{15}N$ ‰ (AIR) mean ± SD	Prey quality	Energy density (kJ/g^{-1})	Energy density source	Stable isotope source
Atlantic cod	*Gadus morhua*	−18.4 ± 0.8	+13.6 ± 1.5	Moderate	4.2	Lawson et al., 1998	Jennings and Cogan, 2015
Haddock	*Melanogrammus aeglefinus*	−18.9 ± 1.0	+11.7 ± 1.8	Moderate	4.4	Pedersen and Hislop, 2001	Jennings and Cogan, 2015
Whiting	*Merlangius merlangus*	−18.5 ± 0.9	+13.5 ± 1.8	Low	3.9	Spitz et al., 2010a	Jennings and Cogan, 2015
Hake	*Merluccius merluccius*	−19.1 ± 0.8	+12.9 ± 1.5	Low	3.7	Spitz et al., 2010a	Jennings and Cogan, 2015
Dover sole	*Solea solea*	−17.2 ± 0.6	+14.4 ± 1.2	Moderate	5	Spitz et al., 2010a	Jennings and Cogan, 2015
Plaice	*Pleuronectes platessa*	−17.3 ± 0.8	+13.0 ± 1.3	Moderate	5.8	Spitz et al., 2010a	Jennings and Cogan, 2015
Greater sand-eel	*Hyperoplus immaculatus*	−18.9 ± 0.5	+12.3 ± 0.8	Moderate	4.8	Spitz et al., 2010a	Jennings and Cogan, 2015
European sardine	*Sardina pilchardus*	−18.6 ± 0.8	+12.1 ± 1.1	High	8.7	Spitz et al., 2010a	Jennings and Cogan, 2015
Atlantic mackerel	*Scomber scombrus*	−19.4 ± 1.1	+10.5 ± 1.6	High	7.9	Spitz et al., 2010a	Jennings and Cogan, 2015
Atlantic herring	*Clupea harengus*	−19.8 ± 0.8	+10.8 ± 1.7	High	10.2	Spitz et al., 2010a	Jennings and Cogan, 2015
Eastern Atlantic squid	*Loligo forbesii*	−18.5 ± 0.6	+14.2 ± 1.4	Moderate	4.6	Spitz et al., 2010a	Jennings and Cogan, 2015
European common cuttlefish	*Sepia officinalis*	−18.1 ± 0.3	+13.1 ± 0.6	Low	3.8	Spitz et al., 2010a	Jennings and Cogan, 2015
European common squid	*Alloteuthis subulata*	−18.0 ± 0.7	+14.6 ± 0.8	Low	3.9	Spitz et al., 2010a	Jennings and Cogan, 2015
Crustaceans	(Compilation of sp.; see Table 3 in Sup. Mat.)	−18.1 ± 0.0 to −15.5 ± 0.4	+8.0 ± 0.4 to +17.3 ± 0.2	Low to High	(3.4 - 6.9)	Andersen, 1999; Spitz et al., 2010a	Das et al., 2003; Schaal et al., 2010; Chouvelon et al., 2012; Baltadakis et al., 2020; Madgett et al., 2019
Myctophidae	(Compilation of sp.; see Table 3 in Sup. Mat.)	−21.1 ± 0.8 to −16.3 ± 0.3	+7.4 ± 0.7 to +10.1 ± 0.4	High	6.6	Spitz et al., 2010a	Louzao et al., 2017; Olivar et al., 2019; Varela et al., 2013

Prey $\delta^{13}C_{cor}$ are lipid-extracted/lipid-corrected and Suess Effect-corrected to 2021. Northeast Atlantic prey quality index, where quality is defined by Spitz et al. (2010a) based on average energy density in kJ/g^{-1}: Low quality (<4 kJ/g^{-1}), moderate quality (4 - 6 kJ/g^{-1}), and high quality (>6 kJ/g^{-1}).

Olivar et al., 2019; Baltadakis et al., 2020) (Figure 2, Table 2; Figure S2 and Supplementary Material Table 3). Prey muscle $\delta^{13}C_{cor}$ has been normalised for lipid content following Post et al. (2007), and Suess Effect-corrected (0.015 ‰ per year) to 2021 (Keeling, 1979; Sonnerup et al., 1999). Information on prey quality (determined by energy density in kJ/g^{-1}) are also presented (Table 2) (Lawson et al., 1998; Andersen, 1999; Pedersen and Hislop, 2001; Spitz et al., 2010a).

3 Results

3.1 Dolphin skin stable isotopes

Collectively, dolphin skin $\delta^{13}C$ ranged from −19.4 to −16.7 ‰ and $\delta^{15}N$ ranged from +10.3 to +14.5 ‰ (Tables 1, 3). White-beaked dolphin (n = 7) had the highest measured $\delta^{13}C$ and $\delta^{15}N$, with a mean of −17.3 ± 0.4 ‰ and +13.4 ± 0.8 ‰, respectively.

TABLE 3 Northeast Atlantic dolphin skin $\delta^{13}C$ (lipid-corrected) and $\delta^{15}N$ mean and standard deviation (SD).

Dolphin species	*n*	$\delta^{13}C$ ‰ (VPDB) mean ± SD	$\delta^{15}N$ ‰ (AIR) mean ± SD	TA (‰^{2})	SEA (‰^{2})	SEAc (‰^{2})	SEA$_B$ (‰^{2}) (95% CI)
White-beaked	7	−17.3 ± 0.4	+13.4 ± 0.8	0.75	0.51	0.61	0.53 (0.25-1.32)
Short-beaked common	20	−17.9 ± 0.5	+12.4 ± 0.8	2.31	0.92	0.97	0.92 (0.56-1.42)
Striped	10	−18.0 ± 0.3	+10.7 ± 0.3	0.45	0.26	0.29	0.24 (0.12-0.48)
Atlantic white-sided	5	−18.7 ± 0.5	+11.6 ± 0.5	0.87	0.79	1.06	0.71 (0.21-2.05)
Bottlenose	11	−17.8 ± 0.7	+12.8 ± 0.7	2.19	1.03	1.14	1.02 (0.57-2.00)
Risso's	4	−17.4 ± 0.6	+12.1 ± 0.7	0.39	0.47	0.63	0.65 (0.25-1.87)

Skin samples were collected from animals stranded on Scottish coastlines between 2015-2021. SIBER niche metrics are provided per dolphin species, where TA is Convex Hull Total Area (100% of isotopic data per species), SEA is Standard Ellipse Area (encompassing 40% of isotopic data per species), SEAc is Standard Ellipse Area (encompassing 40% of isotopic data per species) with correction for small sample size, and SEA$_B$ is Bayesian Standard Ellipse Area (encompassing 40% of isotopic data per species) calculated based on posterior distribution of the covariance matrix per species. All SIBER niche metric are reported in ‰^{2}.

Atlantic white-sided dolphin (*n* = 5) had the lowest measured $\delta^{13}C$ with a mean of –18.7 ± 0.5 ‰, whereas striped dolphin (*n* = 10) had the lowest $\delta^{15}N$, with a mean of +10.7 ± 0.3 ‰. The data were checked for normality with a Shapiro-Wilk test ($\delta^{13}C$ $W = 0.96242$, $p = 0.07395$; $\delta^{15}N$ $W = 0.97528$, $p = 0.2922$). Interspecific variation was identified among dolphin species (PERMANOVA: $F = 97.005$, $p = 0.001$) (Supplementary Material Table 4). Pair-wise comparison results with Bonferroni correction are reported in Supplementary Material Table 5. Mean $\delta^{13}C$ and $\delta^{15}N$ of warm-water adapted species (short-beaked common and striped dolphin) were significantly different from one another (adjusted *p*-value = 0.015). Likewise, mean $\delta^{13}C$ and $\delta^{15}N$ of cold-water adapted species (white-beaked and Atlantic white-sided dolphin) were also significantly different (adjusted *p*-value = 0.03). Striped dolphin mean $\delta^{13}C$ and $\delta^{15}N$ was significantly different from both white-beaked and Atlantic white-sided dolphin (adjusted *p*-value = 0.015), whereas common dolphin was not significantly different from either cold-water adapted species due to isotopic overlap.

3.2 Intraspecific isotopic variation

Intraspecific isotopic variation is driven by a number of factors. Within this strandings dataset, there was a higher proportion of male animals for all species. Stranding season also varied by species, where Atlantic white-sided, white-beaked, and bottlenose dolphins stranded most during the summer and autumn months (peak July-September), while striped, short-beaked common, and Risso's dolphins stranded primarily during the fall and winter months (peak November-March) (Figure 1, Table 1).

Within this dataset, no significant differences (Welch's Two Sample *t*-test, short-beaked common dolphin: $\delta^{13}C$ $t = 1.45$, df = 15, $p = 0.167$, $\delta^{15}N$ $t = -0.16$, df = 16, $p = 0.875$; bottlenose dolphin: $\delta^{13}C$ $t = 0.16$, df = 8, $p = 0.873$, $\delta^{15}N$ $t = -0.44$, df = 7, $p = 0.671$) were found between the $\delta^{13}C$ and $\delta^{15}N$ of male and female animals for species where *n* >10. No significant difference (Welch's Two Sample *t*-test; $t = -0.28$, df = 16, $p = 0.783$; $t = -0.65$, df = 16, $p = 0.522$) was observed between $\delta^{13}C$ and $\delta^{15}N$ of short-beaked common dolphin stranded in the Spring-Summer versus the Fall-Winter periods.

3.3 Isotopic niches and % overlap

Northeast Atlantic dolphin species stranded in Scottish waters possessed distinct isotopic niches (Figure 2; Supplementary Material Figure 3). Short-beaked common dolphin had the largest total isotopic niche (TA), followed by bottlenose dolphin. Risso's dolphin had the smallest TA, followed by striped dolphin. Bottlenose dolphin had the largest core isotopic niche (SEA$_C$ and SEA$_B$), while striped dolphin had the smallest. Non-local bottlenose dolphins had significantly lower $\delta^{13}C$ than known local animals (Welch's Two Sample *t*-test; $t = 9.68$, df = 5.07, $p < 0.001$) (Figure 3). Five dolphin species displayed some degree of interspecific core niche (SEAc) overlap (Table 4, Figure 2). Short-beaked common dolphin SEAc overlapped with every species, except striped dolphin. Short-beaked common SEAc overlapped with bottlenose dolphin by 51%, with white-beaked dolphin by 30%, and with Atlantic white-sided dolphin by 7%. Striped dolphin was the only species with no interspecific core niche overlap.

4 Discussion

4.1 Isotopic niche of dolphins in the Northeast Atlantic

4.1.1 Cold-water adapted species

Of the six Northeast Atlantic dolphin species examined in this study, the white-beaked dolphin occupies the highest isotopic niche. Stomach content records indicate that white-beaked dolphin are

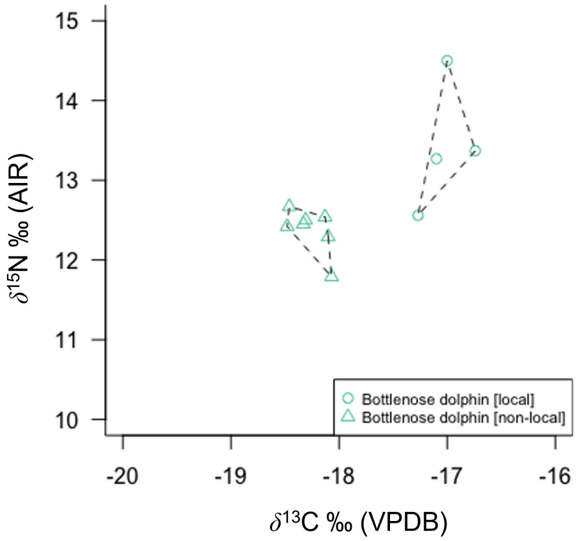

FIGURE 3
Bottlenose dolphin skin δ^{13}C and δ^{15}N from three different stranding events in Scotland show clear regional differences in isotopic composition. Isotopic differentiation is primarily driven by inshore (local pods: Tayside and Western Isles) versus offshore (non-local pod) habitat use.

food specialists that consume high trophic level fish, although priority prey species vary by region (whiting and cod in the southern North Sea, versus haddock and whiting in northeast Scottish waters). White-beaked dolphin isotopic niche concurs with stomach content records that its diet is dominated by medium to large bodied (20 - 60 cm) pelagic and demersal Gadiformes (e.g., cod, hake, whiting, and haddock) (Kinze et al., 1997; Reeves et al., 1999; Canning et al., 2008; Jansen et al., 2010). Gadiformes are low to moderate quality prey based on energy density (<4 – 6 kJ/g^{-1}) (Table 2) (Spitz et al., 2010a). Squid and high quality (>6 kJ/g^{-1}) pelagic schooling fish (e.g., herring and mackerel) are important secondary prey depending on the region (Reeves et al., 1999; Canning et al., 2008).

The Atlantic white-sided dolphin occupies a lower isotopic niche than the white-beaked dolphin. Their lack of isotopic overlap indicates spatial and trophic segregation of resources. Atlantic white-sided dolphin stomach content records from Irish waters found that medium to small (~30 cm or less) Gadiformes (poor cod, pouting, blue whiting) are priority prey. High quality species like mackerel and mesopelagic fish (Myctophidae and silver pout) also contribute significantly to their overall diet (Hernandez-Milian et al., 2015). Although the Atlantic white-sided dolphin feeds at a lower trophic level and consumes smaller mesopelagic and pelagic prey, it appears to target higher quality prey species than the white-beaked dolphin in Scottish waters (Spitz et al., 2010a).

4.1.2 Warm-water adapted species

The striped dolphin occupies the lowest isotopic niche of all six Northeast Atlantic species. Striped dolphin isotopic niche in Scottish waters suggest that low trophic level, high quality mesopelagic (e.g., Myctophidae) and pelagic schooling fish (e.g., herring and mackerel) are priority prey. Stomach content records from the Bay of Biscay indicate a similar pattern of low trophic level small-bodied (~10-30 cm) prey, where small schooling fish (e.g., blue whiting, whiting, sand smelt) and vertically migrating cephalopods were primarily consumed (Meissner et al., 2012; Spitz et al., 2006).

The short-beaked common dolphin occupies a higher trophic niche than the striped dolphin. It possesses the largest total isotopic niche (TA) of all six studied dolphin species. A large isotopic niche is indicative of opportunistic foraging at various trophic levels and in a variety of spatially distinct habitats. In Scottish waters, their isotopic niche suggests a diet of Gadiformes, pelagic schooling fish, and cephalopods. The intraspecific isotopic variation may be the

TABLE 4 Total (‰^{2}) and per species % overlap of core isotopic niche, as represented by Standard Ellipse Area corrected for small sample size (SEAc).

Species 1	Species 2	SEAc total overlap (‰^{2})	% Overlap Species 1	% Overlap Species 2
White-beaked	Short-beaked common	0.18	30.0	19.1
White-beaked	Bottlenose	0.37	61.0	32.9
Short-beaked common	Atlantic white-sided	0.07	7.2	6.6
Short-beaked common	Bottlenose	0.58	59.7	50.7
Short-beaked common	Risso's	0.01	1.2	1.8

result of either individual dolphins with specialised diets, or a generalist population. Regardless of foraging strategy, stomach content records indicate that low trophic level high-fat (high quality) schooling fish (e.g., Myctophidae, sardine, anchovy, sprat, and horse mackerel) are critical to its overall energy intake (Pusineri et al., 2007; Meynier et al., 2008; Spitz et al., 2010b).

4.1.3 Cosmopolitan species

Risso's dolphin occupies a broad isotopic niche of primarily ^{13}C-enriched prey, corresponding with deep-diving foraging behaviour and a diet predominantly composed of squid and octopus from slope and deep-ocean waters (Clarke and Pascoe, 1985; Fabbri et al., 1992; Cañadas et al., 2002; Pereira, 2008; Jefferson et al., 2013; Benoit-Bird et al., 2019; Luna et al., 2022). However, the isotopic niche of Risso's dolphin suggest that benthic flatfish and high quality schooling pelagic fish may contribute more significantly to their diet than previously reported from stomach contents.

Bottlenose dolphins' high mean δ^{13}C and δ^{15}N (Figures 2, 3) combined with large TA and SEAc concur with stomach content records of a variable and high trophic level diet. Large-bodied Gadiformes (e.g., cod, whiting, haddock) and Atlantic salmon are known priority prey, in addition to squid and schooling pelagic fish (e.g., herring and sand-eel) (Santos et al., 2001). A wide range of bottlenose skin δ^{13}C concurs with an opportunistic diet and variable habitat use (Walker et al., 1999; Santos et al., 2001; Fernández et al., 2011; Louis et al., 2014). This is particularly evident in the difference between samples from known individuals (based on photo identification databases) belonging to local Scottish coastal pods and a non-local pod (Figure 3). Non-local animals have significantly lower δ^{13}C than local animals, consistent with feeding in an off-shore environment. Opportunistic feeding and habitat segregation have been documented in sympatric Galician bottlenose dolphin populations, where animals foraging in offshore habitat were characterised by lower δ^{13}C than their coastal inlet counterparts (Fernández et al., 2011). In addition, this study identifies potential specialist feeding behaviour in an old (30+ years) male bottlenose dolphin resident to the Tayside region of Eastern Scotland. The animal (M432/20) exhibited very high δ^{15}N (+14.5 ‰) and stomach contents during post mortem examination revealed extensive salmonoid feeding. Combined, this supports the interpretation of an animal that specialised in feeding on high trophic level fish, potentially targeting seasonally available ^{15}N-enriched salmon returning to spawn annually in rivers along the Eastern coastline of mainland Scotland (Sear et al., 2022). Prey specialisation in individuals or local groups have been identified in other bottlenose dolphin populations (Sargeant et al., 2005; McCabe et al., 2010; Allen et al., 2011; McCluskey et al., 2021).

4.2 Interspecific niche interactions and dietary plasticity

Dolphin species isotopic niche confers information about dietary niche, relative trophic level, and habitat use (Figure 2). The two cold-water adapted species (Atlantic white-sided and white-beaked dolphin) have non-overlapping TA and SEAc (Figure 2, Table 3; Supplementary Material Figure 3). White-beaked dolphins target moderate quality, high trophic level prey, while Atlantic white-sided dolphins target high quality, low trophic level prey. Additionally, there is minimal overlap between TA and no overlap among SEAc of warm-water adapted short-beaked common and striped dolphins.

Short-beaked common and striped dolphin core isotopic niches do not overlap in the Northeast Atlantic (Mèndez-Fernandez et al., 2012; this study). The overlap in δ^{13}C, but separation in δ^{15}N in Scottish waters may indicate that they target similar habitat and species, but feed at different trophic levels. Common dolphins may be feeding on many of the same high quality prey species (e.g., Myctophidae, herring, mackerel) as striped dolphins, but simply targeting larger individuals. In contrast, short-beaked common and striped dolphin populations in the north- and southwest Mediterranean Sea exhibit a high degree of isotopic overlap (Giménez et al., 2017; Borrell et al., 2021). However, spatial segregation (deep water versus coastal water use) was observed between the two species, which allowed them to co-exist while exploiting adjacent habitats to avoid competition for prey (Giménez et al., 2017). This spatial and trophic partitioning presumably decreases competition between cetacean species evolved to occupy similar thermal ranges (see also MacKenzie et al., 2022).

Dolphin isotopic niche size and range are correlated with species foraging strategy. Large TA and SEAc typically indicate a consumer with a generalist diet and a high degree of dietary plasticity, whereas small TA and SEAc indicates specialist feeding with minimal plasticity. Striped, white-beaked, and Risso's dolphins possess the smallest SEAc, indicating low dietary plasticity. Risso's dolphins' small SEAc and lack of interspecific isotopic overlap (Table 3) highlight how their specialisation in cephalopod prey help them avoid competition with the other predominantly piscivorous dolphin species (Pusineri et al., 2007; Meynier et al., 2008; Luna et al., 2022). Likewise, striped dolphin SEAc does not overlap with any other species, indicating their specialisation in small, low trophic level (yet high energy density) mesopelagic and pelagic prey. Short-beaked common dolphins are generalists, and their extensive SEAc overlap with bottlenose, white-beaked, and Atlantic white-sided dolphin is likely driven by interspecific consumption of Gadiformes and high energy density pelagic schooling fish. The range and abundance of prey species (notably pelagic schooling fish and cod) in the North Atlantic are highly reactive to ocean warming and nutrient availability (Rose, 2005; van der Kooij et al., 2016; Olafsdottir et al., 2019), with knockdown effects on predator distribution. The high degree of dietary plasticity and increasing abundance of warm-water adapted short-beaked common dolphins in Scottish waters could create future competition for prey among cold-water adapted white-beaked and Atlantic white-sided dolphins. The white-beaked dolphin is considered a food specialist (Jansen et al., 2010), where increasing dietary overlap may pose future challenges as it faces contracting and displaced habitat.

4.3 Competition with fisheries

Based on combined isotopic niche and stomach content records, medium sized Gadiformes and shoaling pelagic fish are the most highly consumed resources among the six Northeast Atlantic dolphin species, eliciting the highest degree of potential interspecific dietary overlap. White-beaked and Atlantic white-sided dolphin preferred prey are also economically important species to United Kingdom fisheries, where pelagic fish (e.g., herring and mackerel) followed by demersal fish (e.g., Gadidae species such as cod and haddock) are the most frequently landed species by UK fisheries (2008-2018) (Elliott and Holden, 2018). There is heavy commercial fishing in Scotland, with a strong impact on regional prey stocks (sometimes resulting in stock crashes), where the highest takes come from areas with the highest observed abundance of white-beaked and Atlantic white-sided dolphins (west of Scotland and the northern North Sea) (Elliott and Holden, 2018). As such, competition for prey from both ecological and anthropogenic sources should be considered when assessing cumulative stressors acting on cold-water adapted dolphin populations.

4.4 Data source considerations

Isotopic variation exists within the data of each analysed dolphin species. This expected variation is driven by a variety of regional, behavioural, and ontogenetic factors. While no significant difference in $\delta^{13}C$ and $\delta^{15}N$ was observed based on sex or stranding season for short-beaked common and bottlenose dolphins (where n >10), the small sample size of this exploratory study limits further in-depth analyses of other dolphin species. Strandings in cold-water and warm-water adapted dolphin species peaked during the warmer and colder months, respectively (Figure 1). Water temperature significantly impacts dolphin stress response (Houser et al., 2011). The interaction between dolphin thermal preference and thermal stress may play a role in their overall health, prey choice, and stranding incidence in Scottish waters. Future work with an expanded sample set is required to address intraspecific differences and the impact of sex, age class, stranding season, and prey quality in regional populations.

Most intraspecific isotopic variation is likely due to seasonal differences between cetacean stranding events and seasonal changes in diet or prey $\delta^{13}C$ and $\delta^{15}N$ (for example, Troina et al., 2020a; Troina et al., 2020b). Dolphin habitat choice and foraging patterns can vary with seasonal changes in prey abundance, body size, and quality (McCluskey et al., 2016). Male-female pod segregation and sex-specific caloric requirements and movement patterns during mating and calving seasons may also produce different diets (Canning et al., 2008). Species that experience large-scale seasonal mobility (as documented in Atlantic white-sided dolphins) or a high degree of dietary plasticity (for example, short-beaked common and bottlenose dolphins) consume a wider variety of prey with differing isotopic compositions (Northridge et al., 1997; Santos et al., 2001; Pusineri et al., 2007; Meynier et al., 2008). Adult and juvenile animals of the same species (e.g., white-beaked dolphin) can also consume different prey (Ringelstein et al., 2006; Hernandez-Milian et al., 2015), or prey size may be correlated with body length (as seen in bottlenose dolphins) resulting in clear ontogenetic shifts in diet (Knoff et al., 2008).

Use of tissue samples obtained from stranded animals is a low-cost and opportunistic way to monitor wild cetacean populations. We acknowledge the caveats associated with utilising these samples and their associated data, where cetacean health frequently plays a role in stranding events (Arbelo et al., 2013). The reporting of stranding cases can be biased by a variety of physical and social factors (for example: coastal geography, direction of ocean currents, human population density in coastal area, ease of reporting) (ten Doeschate et al., 2018). In addition, we assume carcass decomposition has not altered the original skin isotopic composition. Payo-Payo et al. (2013) reported no significant change in dolphin skin $\delta^{13}C$ and $\delta^{15}N$ after 62 days of non-submerged decomposition, applicable to carcass condition code 4 and above. The pressing demand for cetacean ecological information, however, coupled with the extensive challenges associated with collecting live biopsy samples (or tissue from by-caught animals) highlight the continual utility and importance of opportunistic samples taken from stranded animals.

5 Conclusions

This exploratory stable isotope analysis of stranded animals is a highly effective tool to identify and visualise isotopic niche and interspecific dietary overlap among complex cetacean communities. Dolphin species with defined thermal tolerances are useful indicator species for climate change. Over the past three decades, warm-water adapted dolphin species (short-beaked common and striped) have expanded their ranges northward and are increasingly abundant in British waters. Striped dolphin isotopic niche did not overlap with any other species in Scottish waters. However, short-beaked common dolphin isotopic niche overlapped with both cold-water adapted dolphin species. Increasing abundance of short-beaked common dolphin in Scottish waters could create further dietary overlap and potential competition for both white-beaked and Atlantic white-sided dolphins, where a significant portion of their diets comprise the same Gadiformes and high energy density pelagic schooling fish. These priority prey species are also important takes for UK fishery industries.

Dietary overlap with species experiencing northward range expansion should be considered when assessing stressors acting on Atlantic white-sided and white-beaked dolphin populations facing projected decline in available habitat.

From a marine ecosystem and resource monitoring perspective, the combined Atlantic white-sided, short-beaked common, and striped dolphin isotopic niches provide a proxy for mesopelagic, pelagic, and continental shelf habitats. White-beaked and Risso's dolphin isotopic niches are a proxy for pelagic and deep-water habitats. Local bottlenose dolphin isotopic niche is a proxy for regionally specific inshore coastal habitat. Cetacean monitoring programs would benefit from routine carbon and nitrogen stable isotope analysis of stranded dolphins to track long-term niche utilisation and evolving interspecific dietary overlap. Ideally, these analyses should be paired with contemporary stomach content analysis of by-caught or stranded individuals.

Combining isotopic niche data with evolving species distribution data and *in situ* observations of dolphin behaviour in British waters would be a valuable exercise. Not only would it inform if instances of isotopic overlap directly translate to dietary overlap or competition, but also patterns of seasonal resource portioning or new behavioural changes intended to minimise interspecific dietary overlap (Shipley and Matich, 2020).

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Ethics statement

Samples were acquired from dead stranded animals. No ethics approval required.

Author contributions

TP: Conceptualisation, Formal Analysis, Investigation, Writing – Original Draft. MtD: Conceptualisation, Sample Provision, Data Curation, Writing - Review and Editing. AB: Sample Provision, Writing - Review and Editing. ND: Sample Provision, Writing - Review and Editing. GH: Sample Provision, Writing - Review and Editing. AK: Sample Provision, Writing - Review and Editing. FL: Sample Analysis, Writing - Review and Editing. RM: Sample Analysis, Writing - Review and Editing. CS-N: Software, Writing - Review and Editing. CM: Supervision, Writing - Review and Editing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1111295/full#supplementary-material

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