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Stable isotope analyses reveal seasonal and inter-individual variation in the foraging ecology of sperm whales

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ABSTRACT: Studying inter-individual variation in foraging by top predators is key for understanding the ecology of their populations, while knowledge of seasonal variability in foraging helps explain temporal changes in habitat use and ecological role. We investigated the inter-individual and seasonal differences in stable isotope ratios of sperm whales *Physeter macrocephalus* in the temperate foraging ground of the Kaikōura Canyon, New Zealand. Isotope ratios of carbon and nitrogen were measured in 107 samples of sloughed skin from 37 individual males with a wide range of residency patterns and body lengths, sampled over 4 summers and 3 winters. Variability in individual isotope ratios was analysed with generalised additive mixed models. The whales' residency patterns, but not body size, accounted for most heterogeneity of $\delta^{13}C$ and $\delta^{15}N$. Specifically, whales that visited Kaikōura occasionally had more diverse and lower isotope ratios than more frequent visitors (by ca. −1‰ $\delta^{13}C$ and −2‰ $\delta^{15}N$), likely reflecting a range of foraging habitats further offshore and/or south of Kaikōura Canyon. We suggest that these patterns reflect differences in large-scale foraging patterns within the population. In addition, whales sampled in winter had significantly lower values of $\delta^{13}C$ than whales sampled in summer (by ca. −0.5‰), indicating seasonal differences in the use of food resources. Our results provide new insights into foraging patterns of sperm whales, and highlight the value of accounting for individual differences in the ecology of top predators.

KEY WORDS: Marine top predator · Diet · *Physeter macrocephalus* · Cetaceans · Kaikōura · Submarine canyon

1. INTRODUCTION

Food resources in the marine environment are often patchy and temporally variable (Steele 1976, Levin & Dayton 2009). This influences how marine predators use their habitat, shaping their distribution, movements and diet to optimise foraging (Sims et al. 2006, Womble et al. 2009, Benoit-Bird et al. 2013). Much of the variation in resource use by wild populations occurs at the population level, in response to fluctuations in their environment. Notably, the feeding habits of many marine predators vary seasonally with the availability of food resources (Hall-Aspland et al. 2005, O'Toole et al. 2015). Knowledge of such variability is useful for understanding seasonal changes in predator distribution, their ecological role, and their overlap with anthropogenic impacts (Matich & Heithaus 2014, Samarra et al. 2017). An additional source of intra-population variation in resource use emerges as individuals sharing an environment target different habitats or prey (Matich et al. 2011, Kernaléguen et al. 2015, Samarra et al. 2017). Such diversity in foraging strategies among conspecifics can shape ecological communities, as well as influence population stability and social interactions (Bolnick et al. 2003, 2011). Investigating individual variation in foraging ecology, and the traits that drive it, can therefore be

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helpful for understanding the population dynamics of marine top predators and their food webs (Schreiber et al. 2011).

Studying variability in foraging is particularly challenging for oceanic, deep-diving mammals, such as the sperm whale *Physeter macrocephalus*. Sperm whales are globally distributed top predators, with extremely large ranges (Whitehead 2003), specialised in hunting deep-water squid and fish (Gaskin & Cawthorn 1967, Martin & Clarke 1986). Limited analyses of stomach contents suggest that certain prey are preferentially targeted at different times of the year (Gaskin & Cawthorn 1967), but very little is known about the seasonality of their foraging ecology, or of what drives differences in foraging among individuals.

The Kaikōura Canyon (South Island, New Zealand) is a highly productive deep-sea habitat (De Leo et al. 2010) and a foraging ground for male sperm whales (Childerhouse et al. 1995, Guerra et al. 2017). The abundance of whales feeding in the area during summer has almost halved over the last 3 decades, for reasons that are unknown (Somerford 2018). Knowledge of the foraging ecology of the population is needed to help identify resource requirements and how they vary seasonally. The whales' spatial distribution and diving behaviour differ between summer and winter; in summer, whales are more concentrated in the deeper waters of the canyon, diving for longer and travelling further per dive than in winter (Jaquet et al. 2000). It has been proposed that these differences are driven by fluctuations in prey (Jaquet et al. 2000), but seasonal variation in utilised food resources has not yet been directly addressed at Kaikōura.

Sperm whales visiting Kaikōura show a wide range of residency patterns. Some individuals are seen once or twice over a season, while others spend months foraging in the area (Jaquet et al. 2000). At a longer timescale, some whales have been seen only once over the duration of a 28 yr photo-identification study, while others have been re-sighted consistently for up to 25 yr (Childerhouse et al. 1995, Somerford 2018). These patterns indicate individual variability in the use of the canyon, which may include heterogeneity in the whales' diet. There is also wide variation in body sizes among sperm whales at Kaikōura, with total length varying by up to 30% among individuals (Growcott et al. 2011). If body size plays a role in competition for foraging habitat, or if larger individuals can target larger or deeper prey, size variation might influence differences in diet among whales (e.g. Nifong et al. 2015).

Stable isotope analyses have been commonly used to address a wide range of ecological questions, including diet and movement patterns of top predators (Newsome et al. 2009, Matich & Heithaus 2014, Kernaléguen et al. 2015). Isotope ratios of carbon (^{13}C:^{12}C, denoted $\delta^{13}C$) and nitrogen (^{15}N:^{14}N, or $\delta^{15}N$) transform in a predictable way as a food source is assimilated into the tissues of a predator (DeNiro & Epstein 1978, 1981). Values of $\delta^{13}C$ change little (0.5–1‰) with each trophic step, providing a way to identify which primary producers support a food web (Peterson & Howarth 1987). Values of $\delta^{15}N$ change more substantially with each step (2–4‰; although this change may be smaller at high trophic levels; Hussey et al. 2014, Giménez et al. 2016), and are useful for estimating the trophic level of a consumer (DeNiro & Epstein 1978, 1981). Importantly for marine food webs, the baseline isotope ratios in autotrophic sources (such as pelagic phytoplankton) show strong variation with latitude and within ocean basins (Rau et al. 1982, Somes et al. 2010, Magozzi et al. 2017). Thus, the isotope ratios of predators with large home ranges will not only be influenced by their trophic level and the sources supporting their diet, but also by the region where they forage (Cherel & Hobson 2007, Díaz-Gamboa et al. 2017).

Variation in isotopic ratios in cetacean skin can be used to differentiate foraging patterns among conspecifics and over time (e.g. Marcoux et al. 2007, Samarra et al. 2017); however, seasonal variability in foraging by sperm whales has never been addressed using stable isotopes. Sperm whales slough skin naturally and continuously, providing a reliable source of tissue that can be obtained non-invasively for use in dietary studies (Whitehead et al. 1990, Ruiz-Cooley et al. 2004). Elsewhere, stable isotope analyses have been used to identify variation in the diet of sperm whales among populations and geographical areas (Mendes et al. 2007a, Ruiz-Cooley et al. 2012, Zupcic-Moore et al. 2017), as well as between sexes (Ruiz-Cooley et al. 2004) and in relation to ontogenetic movements (Mendes et al. 2007b). Differences in isotope ratios among sympatric social groups in the tropics (Marcoux et al. 2007) suggest that diversity in foraging may occur within the same area. Individual variation in foraging by sperm whales has never been addressed in temperate regions or among adult males, and is key to understanding how the population at Kaikōura utilises the productive canyon ecosystem.

In this study, we investigated the variability in stable isotope ratios of male sperm whales found in and

around the Kaikōura Canyon, to identify seasonal patterns and differences in foraging among individuals. Values of $\delta^{13}C$ and $\delta^{15}N$ were used as proxies for food web baselines and trophic level, respectively, as well as for diversity in foraging region. To investigate the drivers of inter-individual differences in foraging, isotope ratios of uniquely identified whales were modelled in relation to individual traits, including sighting frequency and body size.

2. MATERIALS AND METHODS

2.1. Sample and data collection

Samples of sloughed sperm whale skin were collected from the Kaikōura Canyon and surrounding areas (Fig. 1) between January 2014 and January 2017. This period included sampling over 4 spring/summers (November–February; hereinafter summer) and 3 autumn/winters (May–July; hereinafter winter). Surveys were conducted aboard a 6 m outboard-powered boat, RV 'Grampus', within a research area of ca. 40 × 30 km. A standardised survey protocol was followed to maximise the chances of evenly sampling all individuals present at Kaikōura at any given time. Sperm whales were tracked acoustically with a custom-built directional hydrophone (Dawson 1990) until they were visually located at the surface. Data collected during a sperm whale encounter included (1) a photograph of the tail fluke for individual identification, taken at the time of diving, using a digital SLR camera (Nikon D750, D2H or D3, with a Nikkor 300 mm f4 lens), (2) sloughed skin for stable isotope analysis, and (3) an acoustic recording to estimate body size from the inter-pulse intervals of echolocation clicks (Growcott et al. 2011). Search effort and encounter data were logged via a custom written

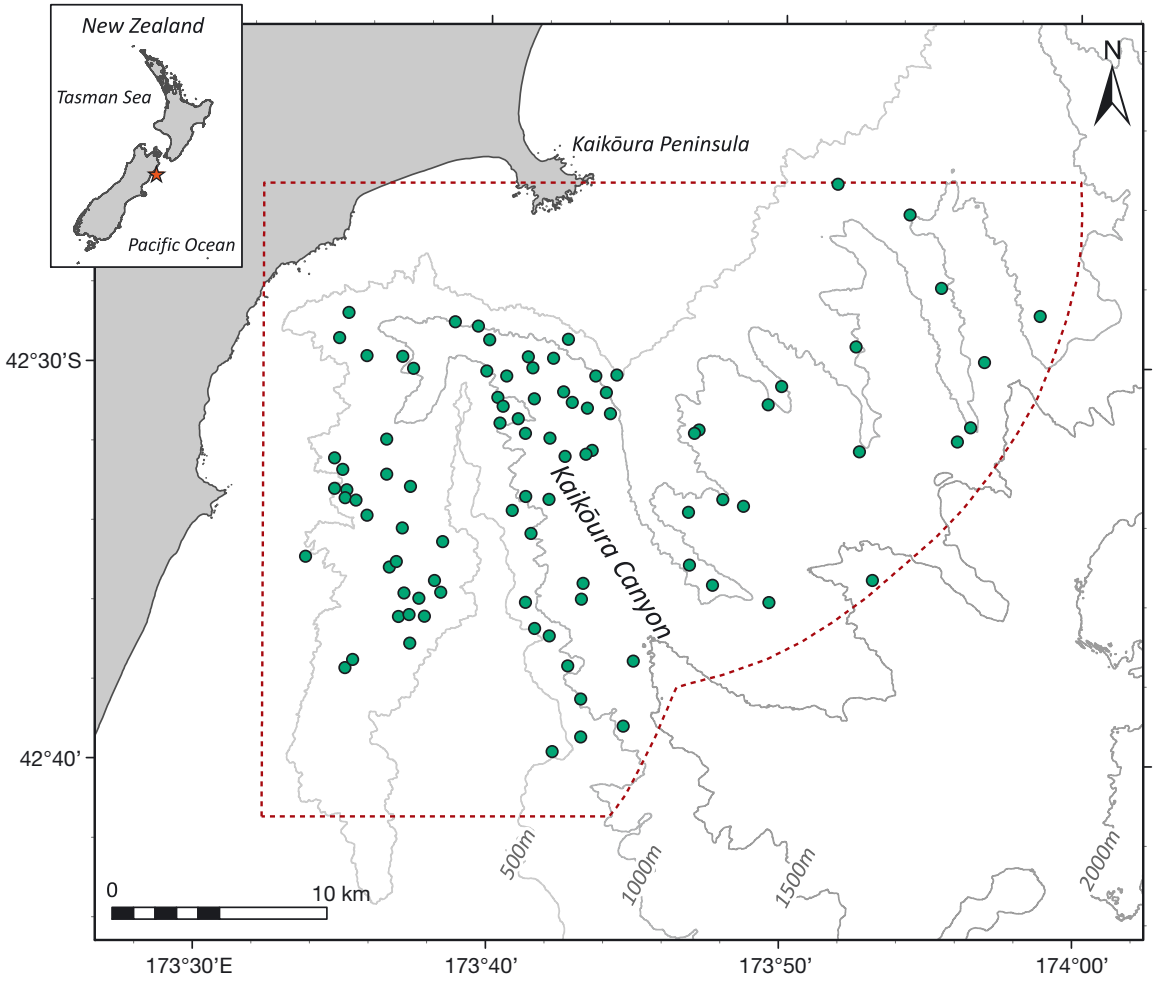

Fig. 1. Locations of sperm whale skin collection at Kaikōura Canyon (inset: New Zealand, with red star indicating study area). Study area is bounded by the dashed line (offshore bounds are 12 nautical mile survey limits). Only the locations of collected samples that were subsequently analysed are included (green dots)

program running on a palmtop computer (HP 200LX) interfaced with a GPS, or on a tablet (Samsung Galaxy Tab A) running Cybertracker software.

Individual whales were identified via photography of the nicks and notches in the trailing edge of the tail flukes (Childerhouse et al. 1995), and matched to the existing Kaikōura photo-ID catalogue held by the University of Otago Marine Mammal Research Group. Samples of sloughed skin (Fig. 2) were collected using a dip-net while following a whale at the surface, or by entering the 'slick' after the whale had fluked, and stored frozen at −20°C until analysis. Skin samples were unequivocally assigned to the whale being followed, as whales were typically spaced at least 1 nautical mile apart. Skin type was classified as type 1 (sheet-like, with a robust structure; Fig. 2b) or type 2 (strands lacking a robust structure, presumed less fresh than type 1 skin; Fig. 2c), with the 2 types being clearly distinguishable. This classification was done to account for potential differences in $\delta^{15}N$ and $\delta^{13}C$ due to skin quality. While skin degradation does not alter stable isotope ratios in some dolphin species (Payo-Payo et al. 2013), it is not known if this is also the case for sperm whales.

The body length of each whale was estimated from the structure of echolocation clicks, using acoustic recordings obtained after the whale dived. Recordings were made with a custom-built stereo hydrophone array (Barlow et al. 2008) on a 50 m cable, deployed while the whale was at the surface and recovered 10 min after fluke-up. Details of the recording process and equipment are included in Methods S1 in the Supplement at www.int-res.com/articles/suppl/m638p207_supp.pdf. Sightings of female sperm whales are extremely rare at Kaikōura (Childerhouse et al. 1995), and no females (body length <12 m) were encountered during this time. Our study included males only, with all whales being longer than 12.8 m.

2.2. Stable isotope analysis of skin

Skin samples were rinsed with distilled deionised water, oven-dried at 60°C for 48 h, and homogenised to a fine powder using a mortar and pestle. Lipids were extracted from skin to avoid confounding interpretation of $\delta^{13}C$ results (Ruiz-Cooley et al. 2004, 2012, Post et al. 2007). Lipid extraction was performed using accelerated solvent extraction (ASE; Richter et al. 1996, Bodin et al. 2009). Samples were individually packaged in pre-combusted GF/F filters and transferred to 34 ml ASE cells. Lipid extraction was carried out on a DIONEX 300 ASE system (Department of Chemistry, University of Otago, New Zealand), using a triple extraction with dichloromethane at 70°C and 1500 psi (~10 300 kPa) for a static hold time of 5 min, 60% flushing volume and a 60 s N_2 purge (Bodin et al. 2009). Samples were dried at 50°C for 12 h to evaporate any traces of solvent. Aliquots of 1 mg (±0.1 mg) of lipid-free skin powder were packed into individual tin capsules for isotope ratio mass spectrometry (IRMS) analysis. Samples were analysed for $\delta^{13}C$ and $\delta^{15}N$ by Iso-Trace (University of Otago) on a Europa Scientific 20/20 Hydra stable isotope mass spectrometer interfaced to a Carlo Erba NC2500 elemental analyser in continuous flow mode. Isotope ratios were normalised by 3-point calibration to the international scales using 2 International Atomic Energy Agency (IAEA) reference materials and an EDTA laboratory standard. Results are expressed per mille (‰) in the standard notation (Peterson & Fry 1987), as $\delta X = ([R_{sample}/R_{standard}] - 1) \times 1000$, where X = the element in question and R = the ratio of the heavy over the light isotope (i.e. $^{13}C/^{12}C$ or $^{15}N/^{14}N$). Vienna Pee Dee Belemnite (VPDB) and atmospheric N_2 were used as standard for ^{13}C and ^{15}N, respectively (precision: ±0.1‰ for $\delta^{13}C$ and ±0.2‰ for $\delta^{15}N$).

Ideally $\delta^{15}N$ is measured in untreated samples (Post et al. 2007, Ryan et al. 2012), but this was not possible

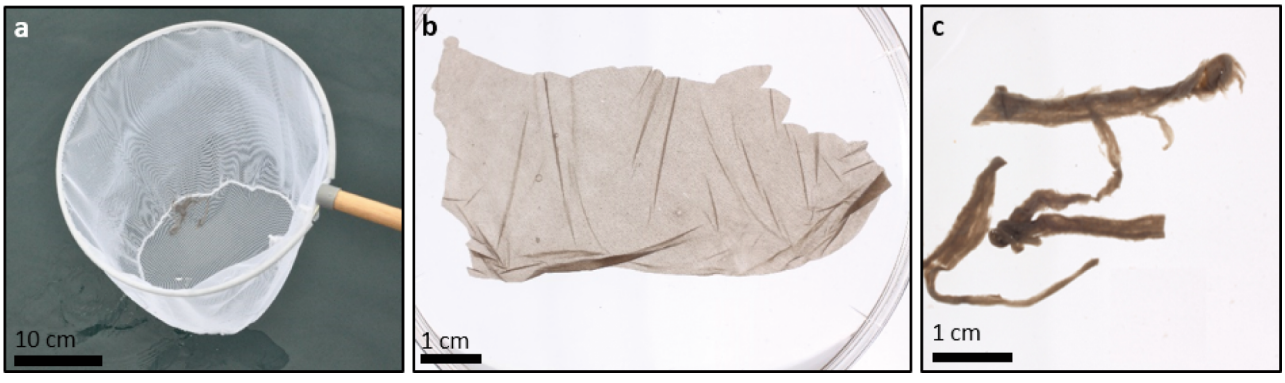

Fig. 2. Sloughed sperm whale skin. (a) Collection from the sea surface; (b) skin type 1; (c) skin type 2

because skin samples were often too small to allow subsampling. We quantified the error in $\delta^{15}N$ caused by lipid extraction using a subset of skin samples that were large enough to measure $\delta^{15}N$ in both untreated and lipid-free skin. The mean change in $\delta^{15}N$ of whale skin after lipid extraction was 0.16‰ (SD: 0.14, n = 34), which was within the analytical error of IRMS (±0.20‰). Therefore, whale $\delta^{15}N$ values from lipid-extracted samples were used for further analysis. The C:N ratios of the samples that were not in the tested subset were within the range of C:N ratios of those tested (range: 3.8–4.5), suggesting that samples with higher lipid content were unlikely. The mean C:N mol ratio of untreated samples was 4.5 (SD: 0.2, n = 34), changing on average by −0.3 (SD: 0.1, n = 34) after lipid extraction. It was not possible to know where on the whales' bodies each piece of skin originated from. Studies of small-bodied cetacean species have found isotopic homogeneity throughout the skin on the whole body (Arregui et al. 2017), but it is not known if similar homogeneity applies to large cetaceans. To quantify the variability associated with the isotope ratios of an individual whale, we measured the differences in $\delta^{13}C$ and $\delta^{15}N$ among pairs of samples collected from the same individual on the same day.

2.3. Individual traits

2.3.1. Body length estimation

The body lengths of sperm whales were estimated acoustically from the inter-pulse intervals (IPI) within their echolocation clicks, following the approach of Growcott et al. (2011) and Miller et al. (2013). Details on the analysis to estimate length are included in Methods S2 in the Supplement.

2.3.2. Individual residency patterns

Sighting frequencies of individual sperm whales were based on encounter histories from photo-identification data, and used as a proxy for how much they utilised Kaikōura as a foraging ground. The proxy of sighting frequency was based on the assumption that the more time whales spend foraging inside the study area, the more frequently they would be encountered. Seasonal sighting frequencies were calculated as the number of days on which a whale was photographed in a season (summer or winter), standardised by the total number of effort days in that season. Because whale abundance varied among seasons, sighting frequencies were scaled by the number of whales sighted in each season relative to the maximum number of whales sighted in any season during the study. This way, individual sighting frequencies would not be biased high in seasons of low abundance, when each whale was likely to be encountered more often.

The time taken for the isotope ratios of sperm whale skin to reflect the ratios of their prey (turnover time) is not known. In bottlenose dolphin skin, near-complete turnover times are thought to take ca. 3.5 and 6 mo for $\delta^{13}C$ and $\delta^{15}N$, respectively (Giménez et al. 2016). These times are likely to be longer in large cetaceans, as turnover rates increase with body mass (Vander Zanden et al. 2015). There are no published data on turnover times for $\delta^{13}C$ in whale skin, while it has been estimated to be ca. 3–9 mo for $\delta^{15}N$ in blue whales (Busquets-Vass et al. 2017). Therefore, it was not known if a particular skin sample would be better represented by an individual's sighting frequency in the field season in which the skin was collected, in the previous season (i.e. 5–6 mo before), or over some other time period. Based on this range of temporal scales, 4 covariates were considered for further analysis. These included the sighting frequency in the season of sampling, the sighting frequency in the previous season, the average of those 2 frequencies, and a global mean across the duration of the study (i.e. 3 yr). The global mean was considered for 2 reasons: (1) potential variability in the turnover times among whales or among samples (e.g. Giménez et al. 2016) may have prevented any of the other 3 time-lags from accurately representing the turnover time in the population, and (2) although the global mean sighting frequency was not expected to reflect a particular turnover time, its larger sample size (7 seasons) may provide a better representation of the typical residency pattern of each whale. The selection of the covariate of sighting frequency to be used in the final model is described below (Section 2.4).

2.4. Statistical analysis

The variability in stable isotope ratios among samples of sperm whale skin was investigated using generalised additive mixed models (GAMMs; Hastie & Tibshirani 1990, Zuur et al. 2009), a data-driven approach that enables fitting smoothed non-linear curves and includes random effects, in addition to fixed effects. Whale identity was included as the random effect in all GAMMs to account for the

dependency among measurements from the same individual (Zuur et al. 2009). GAMMs were used to model the whales' isotope ratios as a function of month, year, sighting frequency, total body length and skin type. The variable 'year' was included to quantify potential inter-annual variation in foraging. The variable 'month' was included to account for temporal variation in isotope ratios and explore their seasonal variability. 'Month' was preferred over 'season' (summer vs. winter) to account for potential within-season variability, because gradual changes in isotope ratios are more likely to be detected at a monthly resolution, and because generalisations from monthly to seasonal trends could then be inferred after analysis. Samples from the same individual collected in the same month and of the same skin type were averaged for further analysis to avoid autocorrelation. 'Skin type' was included as a factor in the models to account for potential variability in isotope ratios associated with using skin of 2 different qualities. The variable 'sighting frequency' was used to quantify the correlation between residency patterns and isotope ratios. Prior to modelling, we selected the timescale of sighting frequency that would best help explain variability in isotope ratios. To achieve this, each of the 4 covariates was fitted independently to univariate GAMMs for the response in $\delta^{13}C$ and $\delta^{15}N$, with whale identity as a random effect. The covariate with the highest explained variance and lowest Akaike's information criterion (corrected for small sample sizes, AIC_c; Symonds & Moussalli 2011) was selected for subsequent use in the full model.

Correlation among pairs of explanatory variables (including global sighting frequency and total body length) was investigated using concurvity tests (Wood 2006). A threshold index of 0.3 (with 0 indicating no correlation and 1 indicating 100% correlation) was used to identify concurvity (He et al. 2006). Concurvity was not an issue, so no variables were excluded from further analysis.

The suite of GAMMs used to model variability in $\delta^{13}C$ and $\delta^{15}N$ included all combinations of independent explanatory variables. We modelled the effect of the predictor variables on $\delta^{13}C$ and $\delta^{15}N$ independently because they reflect different aspects of foraging ecology. Models were ranked according to AIC_c (Burnham & Anderson 2002). Akaike weights (model probabilities) for each model were calculated as the model likelihood relative to the sum of the likelihoods of all models in the set. The response in $\delta^{13}C$ and $\delta^{15}N$ were modelled using a Gaussian distribution with an identity link function. The predictor variables 'year' and 'skin type' were modelled as categorical factors. The variables 'month', 'sighting frequency' and 'body length' were modelled as smoothed terms, derived using thin-plate regression splines, except 'month', which was modelled with a cyclic regression spline. All smooths were limited to a maximum of 4 degrees of freedom to reduce the risk of overfitting (Zuur et al. 2009). Statistical analyses were run in R (R Core Team 2012), using the packages 'mgcv' and 'gamm4' (Wood 2006, 2016, Wood & Scheipl 2017). Interaction terms were not included to facilitate interpretation of the fitted functions, and because there was no compelling biological reason to include them. Diagnostic plots (histograms of residual distributions and normal Q-Q plots) were used to verify assumptions of normality. Plots of residuals vs. fitted values were used to verify homogeneity of variance.

3. RESULTS

A total of 107 samples of sloughed sperm whale skin were collected over 7 field seasons between January 2014 and January 2017 and subsequently analysed for stable isotope ratios. This resulted in 90 non-duplicate samples from 37 different whales, representing 80% of the 46 individuals that were identified during the study period. The number of whales sampled per field season ranged between 6 and 16 (mean: 11), while the number of seasons in which individual whales were sampled ranged between 1 and 5 (mean: 2). Overall, values of $\delta^{13}C$ in sperm whale skin ranged between −18.1 and −15.7‰ (mean ± SD: −16.9 ± 0.5‰, n = 90), and $\delta^{15}N$ values ranged between 12.1 and 17.1‰ (mean ± SD: 15.6 ± 0.9‰, n = 90) (Fig. 3).

The mean isotopic differences between skin samples from the same individual collected within 1 mo of each other (mean difference ± SD: $\delta^{13}C$: 0.2 ± 0.1; $\delta^{15}N$: 0.3 ± 0.2; n = 20) were of similar magnitude to laboratory error. These results indicated consistency in isotope ratios among samples obtained from the same animal over short timescales. This provided reassurance that isotope ratios in sloughed skin were a suitable approach to examine variability in foraging among individuals and over seasonal and inter-annual timescales.

Estimates of total body length varied between 12.9 and 15.9 m (mean ± SD: 14.4 ± 0.7 m, n = 77), representing a large proportion of the size range in the male population (12.6–16.1 m; Growcott et al. 2011, Miller et al. 2013).

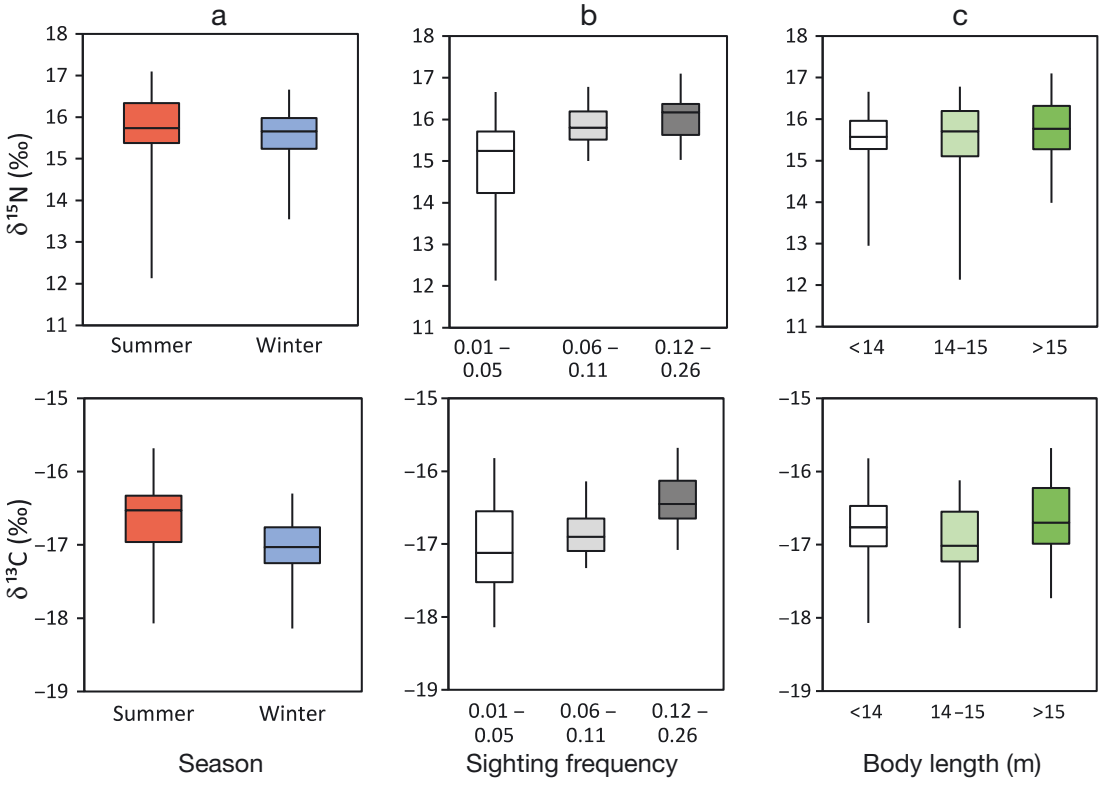

Fig. 3. Variation in stable isotope ratios (upper row: $\delta^{15}N$; lower row: $\delta^{13}C$) in sperm whale skin with (a) season, (b) global mean sighting frequency, and (c) body length. Sample size = 90. For visual clarity, sighting frequency and body length are divided into categories according to approx. 1/3rd of samples, and summer and winter months are grouped per season. Box: 25th – 75th percentile; line: median; whiskers: min. – max.

3.1. Temporal scale of sighting frequencies

Of the 4 covariates used to describe the whales' sighting frequencies at Kaikōura, the global mean sighting frequency was selected for further analysis in the GAMMs. This covariate had the most power to predict the variability of both $\delta^{13}C$ and $\delta^{15}N$ in sperm whale skin, with Akaike weights of 47 and 89%, respectively, and an explained variance of 29 and 36%, respectively (Table 1). In the case of $\delta^{13}C$ values, the whales' sighting frequency in the season previous to data collection (i.e. 5–6 mo before) also had high support (45%), explaining 28% of $\delta^{13}C$ variance.

Table 1. Correlation between isotope ratios in the skin of sperm whales and sighting frequencies (SF) at different temporal scales. Model parameters show the performance of univariate GAMMs using 4 alternative covariates of whales' SF to model the response of isotope ratios. SF global mean: mean SF for all seasons; SF season: SF from the season of sample collection; SF previous: SF from the previous season; SF ssn+prev: average SF of the season of sample collection and the previous season; ΔAIC_c: Akaike's information criterion corrected for small sample sizes, relative to the best model; w_i: Akaike weight (probability of model being the best in the set); Adj. R^2: proportion of variance explained by each model (by fixed effects only)

SF descriptor	$\delta^{13}C$			$\delta^{15}N$		
	ΔAIC_c	w_i (%)	Adj. R^2	ΔAIC_c	w_i (%)	Adj. R^2
SF global mean	0.0	0.47	0.29	0.0	0.89	0.36
SF previous	0.1	0.45	0.28	6.7	0.03	0.10
SF ssn+prev	10.3	0.00	0.09	4.8	0.08	0.17
SF season	3.7	0.07	0.14	12.3	0.00	0.01

3.2. Intra-population variability in isotope ratios

For explaining variability in $\delta^{13}C$ of sperm whale skin, the model with most support (Akaike weight: 64%; variance explained: 41%) included month and mean sighting frequency as significant variables (Table S1a in the Supplement). Seasonal effects on $\delta^{13}C$ variation were explained by a cyclic function over 1 yr: whales sampled in winter months (May–July) had lower $\delta^{13}C$ (by ca. 0.5‰) than those sam-

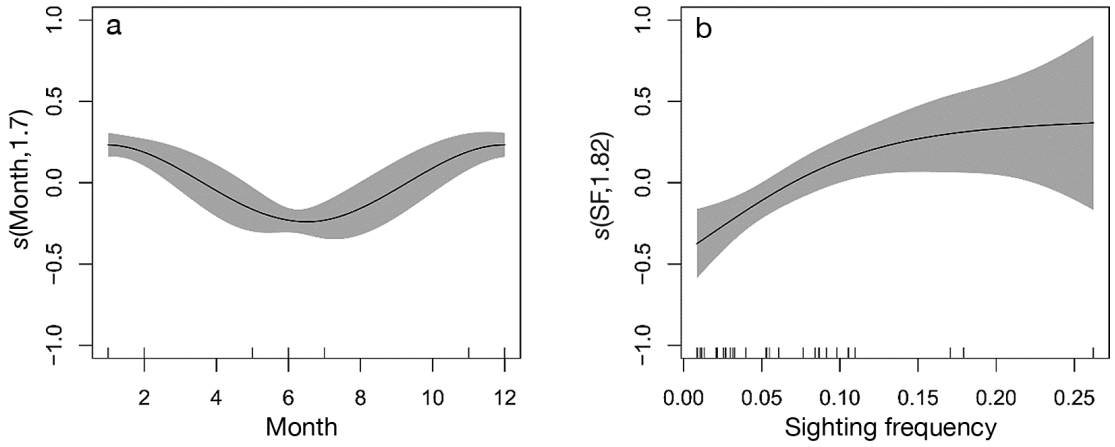

Fig. 4. GAMM smoother functions for the variability in $\delta^{13}C$ of sperm whale skin. The *y*-axes show the smooth function of each variable that was retained in the best model, with the estimated degrees of freedom in brackets. Shaded area: 95% confidence interval of the response. Response of $\delta^{13}C$ shown as a function of (a) month and (b) global mean sighting frequency. Note that May–July (months 5–7) are part of austral winter, while November–February (months 11–2) are part of austral summer

pled in spring and summer (November–February) (Figs. 3a & 4a). The seasonal difference in $\delta^{13}C$ was statistically significant, as indicated by the GAMM smoother (Fig. 4a), while differences between consecutive months were small. Whales with higher sighting frequencies (i.e. that spent more time at Kaikōura) had higher $\delta^{13}C$ values than whales that were sighted less frequently (Figs. 3b & 4b). The modelled difference in $\delta^{13}C$ between whales with the lowest and highest sighting frequencies was up to ca. 1‰ and statistically significant (Fig. 4b, Table S1b). There was very little support for models including a correlation between $\delta^{13}C$ and skin type or body length (Akaike weight: 5%), and no support for models including inter-annual variability.

For explaining $\delta^{15}N$ variability among sperm whales, the best model (Akaike weight: 62%, explained variance: 39%) included sighting frequency only (Table S2a in the Supplement). The non-linear relationship between $\delta^{15}N$ and sighting frequency was statistically significant (Table S2) and indicated that whales with sighting frequencies above ca. 0.06 (i.e. equivalent of being sighted on average at least twice in a season) had similar $\delta^{15}N$ values (Figs. 3b & 5). In addition, whales with sighting frequencies above 0.06 had a narrower range in $\delta^{15}N$ values (15–17‰), while individuals with lower sighting frequencies ranged from 12 to 17‰ (Fig. 3b). The modelled difference in $\delta^{15}N$ between whales with the lowest and highest sighting frequencies was up to ca. 2‰ (Figs. 3b & 5). There was little support for a correlation of $\delta^{15}N$ with month, skin type or body length, given the low Akaike weights of models including these variables, and their p-values indicating no statistical significance (Table S2b). There was no support for models including inter-annual variation.

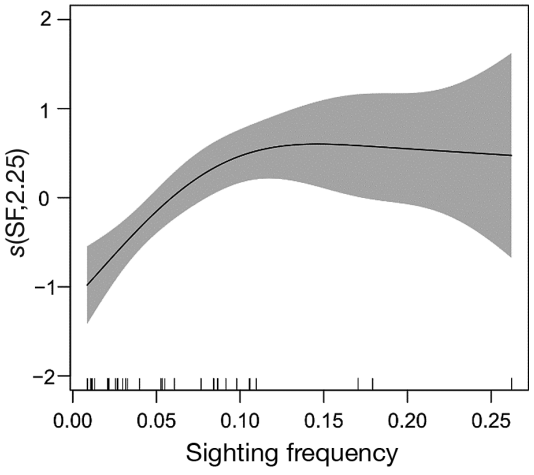

Fig. 5. GAMM smoother functions for the variability in $\delta^{15}N$ of sperm whale skin. The *y*-axis shows the smooth function of the variable that was retained in the best model, with the estimated degrees of freedom in brackets. Shaded area: 95% confidence interval of the response. Response of $\delta^{15}N$ shown as a function of mean sighting frequency

4. DISCUSSION

Stable isotope ratios of carbon and nitrogen in skin from male sperm whales off Kaikōura were used to identify intra-population differences in foraging. Isotope ratios varied seasonally and according to differences in residency among individuals, while there was no apparent correlation with body size. Applied

for the first time to a population of sperm whales in a temperate region, bulk stable isotope analyses proved a valuable method to investigate the foraging ecology of sperm whales. Skin samples produced relatively consistent isotopic values from individual whales within a short period of time (ca. 1 mo), allowing for comparisons among conspecifics. Furthermore, temporal variability in stable isotope ratios was small within a field season and among years, but was significantly different between seasons (i.e. summer and winter), allowing for the identification of lagged seasonal patterns in foraging.

4.1. Inter-individual variation in foraging in relation to sighting frequency

We found a wide diversity in carbon and nitrogen isotope ratios among individuals foraging at Kaikōura, especially considering the small spatial scale of the study region. A large proportion of isotopic variability was correlated with the whales' residency times, implying that individuals foraging in the same location are not ecologically equivalent: they utilise the food resources of the Kaikōura foraging ground to different extents. While this was suspected based on sighting histories, stable isotope data provide the dietary evidence necessary to understand the ecological implications. Sperm whales are highly mobile, and it is likely to take months for their skin to integrate the isotope ratios of their prey. Whales may therefore 'carry' the isotopic values of a food web from a foraging area to a different location where they are sampled. Whales with high sighting frequencies (which we can refer to as 'frequent visitors') use Kaikōura extensively for foraging, likely incorporating the isotope ratios of locally sourced prey. In contrast, whales with low sighting frequencies ('occasional visitors') had different isotopic values, probably reflecting the integrated diet from where they had been foraging prior to being sampled at Kaikōura. Occasional visitors had particularly diverse isotopic values, suggesting the use of not one, but a range of foraging grounds with different trophic characteristics to Kaikōura.

Because the isotopic values of occasional visitors likely reflect a different food web than that of frequent visitors, direct comparisons of primary organic sources or trophic level are not possible. However, isotope ratios can provide information about foraging areas at a larger spatial scale (Ruiz-Cooley et al. 2004, Cherel & Hobson 2007, Mendes et al. 2007a), because latitudinal and regional gradients in the isotope baselines of marine primary producers are reflected in organisms at higher trophic levels (Marcoux et al. 2007, Popp et al. 2007). An interpretation of isotope ratios in this context is valuable, because, to date, it remains unknown where sperm whales from this population go when they are not at Kaikōura. Values of $\delta^{13}C$ and $\delta^{15}N$ in pelagic phytoplankton typically decrease at higher latitudes within an ocean basin, on a scale of up to 5‰ over 5–10° of latitude (Rau et al. 1982, Wada & Hattori 1991, Lourey et al. 2003). In addition, pelagic and offshore food webs are typically more depleted in $\delta^{13}C$ than benthic and inshore food webs (France 1995, Cherel & Hobson 2007, Díaz-Gamboa et al. 2017), and tend to be shorter, resulting in lower $\delta^{15}N$ at high trophic levels (Iken et al. 2005). Sperm whales that were occasional visitors to Kaikōura had lower isotopic values than frequent visitors, by ~1‰ in $\delta^{13}C$ and ~2‰ in $\delta^{15}N$ (equivalent in magnitude to the isotopic change of 1 trophic level). The observed trend in isotopic values is consistent with occasional visitors coming from foraging grounds further to the south and further offshore, but within New Zealand latitudes. Isoscape maps of baseline isotope ratios and cetacean top predators around New Zealand currently do not exist, but would be valuable for narrowing down the whales' likely foraging regions.

Overall, our results show that male sperm whales that are sympatric at a small regional scale vary in their large-scale foraging patterns according to their residency rate at Kaikōura. Males are generally solitary, but there is evidence for long-term preferred associations between pairs of individuals at Kaikōura (Somerford 2018). Further study on social and genetic structure of whales at Kaikōura may shed light on whether differences in foraging are linked to whales originating from different social groups or populations. Alternatively, competition among conspecifics may act to limit the time spent foraging at Kaikōura by some individuals, driving the diversity in foraging patterns of sperm whales that visit Kaikōura. The isotope ratios of male sperm whales off Kaikōura were not correlated with body size, suggesting that larger whales did not have isotopically distinct diets, at least within the sampled population of mature and sub-adult males. It is still possible that segregation in foraging habitat is influenced by size, but that a better habitat reflects higher prey densities or easier access to prey rather than differences in prey types. Therefore, habitat segregation among sperm whales according to body size (if it does occur) might be better assessed through individual patterns in spatial distribution.

4.2. Timescale of sighting frequencies: insights into turnover times

The time taken for the isotope ratios of cetacean skin to reflect the ratios of assimilated prey (turnover time) has only been estimated for dolphins in captivity ($\delta^{13}C$ and $\delta^{15}N$; Browning et al. 2014, Giménez et al. 2016) and blue whales ($\delta^{15}N$ only; Busquets-Vass et al. 2017). Knowledge of turnover times is necessary to interpret temporal variability in foraging ecology, but acquiring this knowledge is very challenging, particularly in the case of highly mobile and large-bodied cetaceans. Our assessment of the relationship between the whales' sighting frequencies and their isotopic values at different timescales provided some indirect insight into turnover times in sperm whales. In the case of $\delta^{13}C$, individual isotope values were much more correlated with the sighting frequency from the season prior to sampling than from the season of sampling. While other factors might influence this correlation, this suggests that, for sperm whales at Kaikōura, $\delta^{13}C$ turnover time in skin is more likely to approximate 5–6 mo than 1–2 mo. However, because the time or extent of the shift in diet was not known, this assumption is subject to uncertainty. More research is required to obtain reliable estimates of turnover rates for isotopes in the skin of free-ranging cetaceans.

4.3. Seasonal variability in foraging

The $\delta^{13}C$ values of sperm whales varied between seasons, with samples collected during summer months being ca. 0.5‰ more enriched than those collected during winter. This variability is most likely to indicate seasonal differences in the use of food resources, suggesting that the variation in spatial distribution and diving behaviour between summer and winter (Jaquet et al. 2000) is driven by changes in prey or foraging habitat. Specifically, seasonal differences in $\delta^{13}C$ may be caused by consumption of prey with different isotopic values (e.g. as in other marine top predators; Hall-Aspland et al. 2005), a change in the carbon source supporting the food web (e.g. as in other deep-sea systems; Papiol et al. 2013), and/or temporal variability in baseline isotope values (Magozzi et al. 2017). Given that $\delta^{13}C$ turnover time in sperm whale skin was more likely to approximate 5–6 mo than 1–2 mo, $\delta^{13}C$ values in whales sampled in summer are more likely to reflect the diet that was integrated over winter, and vice versa. These results establish a framework to study the seasonal dynamics in the whales' trophic ecology in the context of the Kaikōura Canyon food web. An ecological interpretation of the seasonal patterns in isotope ratios will require data on the isotopic values of potential prey and organic sources at the base of the food web, which are currently lacking for the Kaikōura Canyon system. The seasonal cycle in $\delta^{13}C$ values helps our understanding of patterns in habitat use, and demonstrates that stable isotope analyses can be a valuable tool to track seasonal fluctuations in the trophic ecology of male sperm whales in temperate regions.

We found no changes in the whales' $\delta^{15}N$ between winter and summer. $\delta^{15}N$ in sperm whales may turn over too slowly to be a useful tool to discern seasonal variability in diet and trophic level, or there may be no differences in the mean trophic level of the summer and winter diets. In general, seasonal changes in $\delta^{15}N$ values of odontocetes are more challenging to detect than those in $\delta^{13}C$, due to longer turnover times potentially swamping the isotope ratios specific to each season (Newsome et al. 2010, Giménez et al. 2016).

4.4. Strengths and limitations

The use of stable isotope analyses for studying the ecology of marine animals has some limitations. Perhaps the most important caveat is that, for highly mobile predators, bulk-tissue stable isotope ratios cannot easily discriminate between differences in diet, foraging region and type of organic source pool at the base of the food web. More specific biochemical tools, such as amino-acid-specific isotope analysis (Popp et al. 2007, Zupcic-Moore et al. 2017), would help to determine if the isotopic differences among individuals reflect a different food web baseline and/or different prey. The lack of information on turnover rates in whale skin is also an important caveat, as it prevents robust interpretations of temporal variability in foraging ecology. Compared to more traditional approaches, such as examination of stomach contents from stranded individuals (Santos et al. 1999), isotope analyses cannot always identify particular prey species included in their diet, unless these have distinct isotope values. However, bulk stable isotope analyses of skin offer some key advantages to study the foraging ecology of cetaceans, especially for studying a large subset of a population within its natural environment, and providing information on feeding patterns over larger timescales (i.e. months vs. hours/days). In this study, isotope analyses allowed detection of trophic differences among individuals, despite them foraging in the same location. Sampling known

individuals over multiple years could allow investigation of individual vs. population niche specialisation (Bolnick et al. 2003, Matich et al. 2011). While repeat samples per individual were available in the current study, sample sizes were not large enough to examine individual specialisation. The use of skin with 2 different structural forms (with potentially different properties) resulted in marginal variability in isotope ratios, providing further assurance for the use of sloughed skin in isotopic studies to investigate trophic dynamics of cetaceans in a non-invasive way.

This study is the first to show variability in stable isotope ratios of sperm whales with season and in relation to individual characteristics, providing new insights into the foraging ecology of the species. Our study highlights the importance of considering individual variation in foraging by roving marine predators. While sperm whales aggregate in feeding grounds and share common ecological traits, there are clearly important differences in how conspecifics use their habitat. Discerning the level of ecological structuring and specialisation within populations of top predators is essential if we are to understand their role in marine ecosystems, the formation of ecotypes, and the population's resilience to environmental change.

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