



Changes in habitat use by a deep-diving predator in response to a coastal earthquake

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ARTICLE INFO

Keywords:

Earthquake
Foraging
Habitat use
Natural disturbance
Sperm whale
Submarine canyon

ABSTRACT

Earthquakes can significantly impact ecosystem function and survivability of marine organisms, however their effect on marine predators remains unknown. In November 2016, a 7.8 magnitude earthquake triggered a ‘canyon flushing’ event in the submarine canyon of Kaikōura (New Zealand), a year-round foraging ground for sperm whales (*Physeter macrocephalus*). Underwater landslips and turbidity currents caused significant changes to the seafloor and removed large quantities of benthic biomass from the canyon. To investigate the potential impact of the earthquake on habitat use by sperm whales, we used a multi-year dataset to quantify changes in their behaviour, foraging distribution and use of food resources before and after the earthquake. The diving locations and behaviour of individual whales were recorded during summer and winter from January 2014 to January 2018, and samples of sloughed skin were collected for bulk and amino acid specific stable isotope analyses. While blow rates remained unchanged, the mean surface interval between dives was 25% longer for about one year after the earthquake, potentially reflecting increased effort searching for prey. Stable isotope ratios of sperm whale skin provided no evidence for change in diet. However, significant changes in the distribution of core foraging areas indicated shifts in habitat use for at least one year, potentially driven by changes in the seafloor and prey availability following the canyon flushing. Overall, our observations suggested that the earthquake caused alterations in the foraging patterns of sperm whales over a period of at least 12 months. This was the first study to quantify the impact of an earthquake on a marine mammal population, providing new insights into how top predators react and adapt to large-scale events of natural disturbance.

1. Introduction

Extreme natural events, such as earthquakes, hurricanes and volcanic eruptions are rare, but can profoundly impact ecosystems through modifications to habitat and mortality of plants and animals (Bell and Hall, 1994; Fraile-Nuez et al., 2012; Kitahashi et al., 2014). Knowledge of how animal populations respond to such events is important for understanding the ecological impacts of large-scale disturbances and the risks they pose to population viability. The effects of earthquakes on marine species, especially mobile organisms, are poorly understood. With the exception of observations of a fin whale (*Balaenoptera physalus*) immediately following a 5.5 magnitude earthquake (Gallo-Reynoso et al., 2011), the effects on marine mammals are undocumented. Because earthquakes are infrequent and unpredictable, the

opportunities to assess their impact on marine mammal populations are extremely rare.

In November 2016, a 7.8 magnitude earthquake hit Kaikōura, New Zealand, and was described as one of the most complex crustal earthquakes ever recorded (Hamling et al., 2017). Strong ground shaking triggered widespread underwater mudslides in the submarine canyon off Kaikōura, causing a full flushing event and powerful turbidity currents, as well as changes in bathymetry of up to 50 m (Mountjoy et al., 2018). The Kaikōura Canyon is a highly productive deep-sea habitat (De Leo et al., 2010) and a foraging ground for male sperm whales (*Physeter macrocephalus*; Childerhouse et al., 1995), deep-diving predators that use echolocation to find their prey (Watkins et al., 1993; Madsen et al., 2002). Sperm whales have an important ecological role as top predators (Heithaus et al., 2008; Rosenblatt et al., 2013) and are a key natural

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<https://doi.org/10.1016/j.dsr.2020.103226>

Received 16 July 2019; Received in revised form 3 January 2020; Accepted 13 January 2020

Available online 17 January 2020

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asset for the local tourism industry, which is the main driver of Kaikōura's economy (Curtin, 2003). The abundance of sperm whales foraging in the area has almost halved over the last three decades (Sommerford, 2018), but the causes for the decline remain unknown. The decline makes the population particularly vulnerable to additional impacts, highlighting the importance of monitoring the whales' responses to disturbance events. The sperm whales of Kaikōura have been studied since 1990. Data on abundance (Childerhouse et al., 1995; Sommerford, 2018), behaviour (Jaquet et al., 2000, 2001; Miller et al., 2013; Guerra et al., 2017), distribution (Jaquet et al., 2000) and trophic ecology (Guerra, 2018) gathered prior to the earthquake provided a unique opportunity to assess the earthquake's impact on the population.

There are several ways in which earthquakes and subsequent aftershocks could affect sperm whales. In the short-term (hours to days), potential impacts include noise and re-suspension of sediment. Odonotocete cetaceans, including sperm whales, depend on sound for communication, detection of prey and navigation, and are also highly sensitive to noise (e.g. Richardson et al., 1995; Southall et al., 2007). Earthquakes produce among the loudest underwater sounds, characterised by low-frequency noise similar to anthropogenic explosions (Hildebrand, 2009). Demonstrated impacts of underwater noise on cetaceans include injury, hearing damage, displacement and behavioural modifications (Ketten et al., 1993; Richardson et al., 1995; Nowacek et al., 2007). Re-suspension of sediment has the potential to interfere with the whales' echolocation, as increased turbidity can impede propagation and processing of sound (Krahforst et al., 2012). Over longer periods (months to years), potential impacts include changes in distribution or foraging brought on by physical and biological alterations to deep-sea habitats. In the case of the Kaikōura earthquake, the large-scale erosion and sediment flow through the canyon had a dramatic impact on the seafloor structure and benthic ecosystem (Mountjoy et al., 2018). Of particular importance was the removal of benthic invertebrate communities which previously existed in the upper canyon (De Leo et al., 2010), with an estimated 39×10^6 kg of biomass removed due to sediment flushing (Mountjoy et al., 2018). Such impacts on benthos are likely to have significant consequences for the canyon food web, and thus may impact the top predators, including sperm whales, which forage on both demersal and pelagic prey (Miller et al., 2013; Guerra et al., 2017).

In the present study we aimed to identify the ecological impact of the Kaikōura earthquake on the sperm whale population by assessing pre- vs. post-earthquake patterns in diving behaviour, spatial distribution, and utilisation of food resources. Specifically, we quantified the temporal variability in: (1) ventilation and echolocation behaviour, including the time spent at the surface between dives, intervals between blows, and time taken to start echolocating after diving. These variables are related to metabolic rate and diving strategy (e.g., Richter et al., 2006; Fais et al., 2015), and can thus reflect changes in foraging efficiency; (2) spatial distribution, by examining the location of high-use areas; and (3) food resources utilised by sperm whales, using bulk and amino acid specific stable isotope analyses of sloughed whale skin. To address these questions, we analysed data gathered before and after the earthquake over a period of four years, and partitioned seasonal and annual variability.

2. Methods

2.1. Data collection

Data necessary for estimating sperm whale spatial distribution, behaviour and use of food resources were collected via boat-based surveys in a study site centred over the Kaikōura Canyon, New Zealand. Surveys were carried out during austral spring/summer (November–February, hereafter 'summer') and austral autumn/winter (May–July, hereafter 'winter') over a four-year period between January 2014 and January 2018, from a 6 m research boat, *RV Grampus*. Sperm

whales were tracked acoustically with a custom-built directional hydrophone (Dawson, 2000) until they were visually located at the surface (Childerhouse et al., 1995; Jaquet et al., 2000). Acoustic-visual surveys followed a standardised protocol so that in each field season, the study area was covered as uniformly as permitted by the prevailing weather conditions. Research was conducted during daylight hours, in sea states of up to Beaufort 3 and swell heights less than 2 m.

Data collected during each sperm whale encounter included: (1) observations of surface behaviour, including surface interval (time from first blow until fluke-up) and blow intervals (time between consecutive breaths, logged on a voice recorder); (2) photographs of the flukes for individual identification, taken at the time of diving ('fluke-up'), using a digital SLR camera (Nikon D750, D2H or D3, with a Nikkor 300 mm lens); (3) time and location of dive; (4) an acoustic recording of the whale's vocalisations for 10 min after fluke-up; and (5) samples of sloughed skin for stable isotope analyses, collected using a dip-net while following a whale at the surface, or from the "slick" after the whale had dived. Skin samples were kept on ice packs until the end of each field day and stored frozen until analysis.

The time from fluke-up to the first echolocation click was used to estimate the time taken for the whale to start searching for prey after diving (Jaquet et al., 2001), which is proportional to the depth at the start of echolocation (Fais et al., 2015). A custom-built stereo hydrophone array (Barlow et al., 2008) on a 50 m cable was deployed while the whale was at the surface and a 10 min high-resolution recording made with a Roland R44 digital recorder (sampling rate 96 kHz, 16 bit). Search effort and encounter data were recorded and stored on a GPS linked HP-200LX palmtop computer running custom-written software, or on a Samsung Galaxy Tab A tablet running Cybertracker software. The position of the research vessel was logged every 60 s.

High-quality photographs of sperm whale flukes were used to identify individuals by matching them to the Kaikōura photo-identification catalogue (Childerhouse et al., 1995), allowing behaviour data, locations and stable isotope values to be assigned to individual whales. In addition, photographs of sperm whale flukes taken by a local tour operator (Whale Watch Kaikōura) in November 2016 were used to determine the presence of sperm whales at Kaikōura in the weeks following the earthquake before our surveys could recommence. These photographs and locations were not used for analysis of spatial distribution due to methodological differences.

2.2. Stable isotope analysis of sperm whale skin

Stable isotope analyses are a useful tool to examine temporal patterns in foraging by cetacean top predators, including sperm whales (Marcoux et al., 2007; Ruiz-Cooley et al., 2014; Zupcic-Moore et al., 2017). Isotope ratios of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) change in predictable ways as a food source is assimilated into the tissues of a consumer, providing information on a predator's trophic level and utilisation of primary organic sources at the base of its food web, respectively (Peterson and Howarth, 1987; Fry, 2006). Isotopic measurements of individual amino acids (hereafter, AA) can increase the power of isotope analysis (McMahon and McCarthy, 2016). The $\delta^{15}\text{N}$ of 'trophic' AA changes substantially with trophic transfer, providing a robust indicator of a predator's trophic level, while in 'source' AA it changes marginally, reflecting the $\delta^{15}\text{N}$ value at the base of the food web (McClelland and Montoya, 2002; Popp et al., 2007; Ohkouchi et al., 2017; Zupcic-Moore et al., 2017). In this study, stable isotope analyses of whole skin tissue ('bulk-tissue SIA') and compound specific isotope analysis of individual amino acids ('CSIA-AA') were used to identify potential changes in the food resources utilised by sperm whales after the earthquake.

2.2.1. Bulk-tissue stable isotope analysis

Skin samples were rinsed with distilled deionised water, oven dried at 60 °C for 48 h and homogenised to a fine powder. Lipids were

extracted from skin samples (Ruiz-Cooley et al., 2004; Post et al., 2007) using accelerated solvent extraction (ASE, Bodin et al., 2009) carried out on a DIONEX 300 ASE system. We performed a triple extraction with dichloromethane at 70 °C and 1500 psi for a static hold time of 5 min, 60% flushing volume and a 60 s N₂ purge (Bodin et al., 2009). Samples were dried at 60 °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. Samples were analysed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ by Iso-Trace (University of Otago) on a Europa Scientific '20/20 Hydra' stable isotope ratio mass spectrometer (IRMS) interfaced to a Carlo Erba NC2500 elemental analyser in continuous flow mode. Isotope ratios were normalised by three-point calibration to the international scales using two IAEA (International Atomic Energy Agency) reference materials and an EDTA laboratory standard. Ratios are expressed per mil (‰) in the standard delta (δ) notation (Peterson and Fry, 1987), as natural abundance relative to an international standard: Vienna Pee Dee Belemnite (V-PDB) for $\delta^{13}\text{C}$, and atmospheric nitrogen for $\delta^{15}\text{N}$ (instrument precision: $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.2\text{‰}$ for $\delta^{15}\text{N}$).

2.2.2. Amino acid compound specific stable isotope analysis

AA were extracted by hydrolysing dry homogenised skin samples with 2 ml of 6 M HCl at 110 °C for 24 h. Solutes were then dried under a gentle flow of N₂ at 60 °C, and subsequently converted into N-Acetylisopropyl (NAIP) ester derivatives following the protocol described in Sabadel et al. (2016), modified from Styring et al. (2012). Values of $\delta^{15}\text{N}$ of AA in skin samples were measured on a Thermo Scientific Delta V Plus Isotopic Ratio Mass Spectrometer, interfaced to a Thermo Trace gas chromatograph at Iso-Trace. Isotope ratios are expressed per mil (‰) in the standard delta (δ) notation (Peterson and Fry, 1987, as above). $\delta^{15}\text{N}$ was measured in three source AA and seven trophic AA. Exploratory analyses indicated that temporal patterns in $\delta^{15}\text{N}$ varied little among source AA or among trophic AA. For simplicity, phenylalanine (Phe) was used as the model source AA, while glutamic acid (Glx) was used as the model trophic AA (McMahon and McCarthy, 2016; Ohkouchi et al., 2017).

2.3. Data analysis

2.3.1. Sperm whale behaviour and stable isotope ratios

Three response variables were used to estimate changes in sperm whale behaviour before vs after the earthquake: surface interval, average blow interval and time to first echolocation click. Due to seasonal differences in the diving behaviour of sperm whales at Kaikōura (Jaquet et al., 2000), changes in behaviour were investigated while allowing for the natural variability between summer and winter.

Four response variables were used to assess potential changes in diet and use of food resources before vs after the earthquake: $\delta^{15}\text{N}$ of bulk tissue ($\delta^{15}\text{N}_{\text{Bulk}}$) and the difference between Glx and Phe $\delta^{15}\text{N}$ values ($\Delta\delta^{15}\text{N}_{\text{Glx-Phe}}$) were used to detect changes in relative trophic level, while $\delta^{13}\text{C}$ of bulk tissue ($\delta^{13}\text{C}_{\text{Bulk}}$) and $\delta^{15}\text{N}$ of Phe ($\delta^{15}\text{N}_{\text{Phe}}$) were used to detect changes in the utilisation of primary organic sources at the base of the food web. The actual trophic level of sperm whales was not calculated to avoid assumptions of trophic discrimination values (McMahon and McCarthy, 2016), and because we were only interested in whether there had been changes in trophic level after the earthquake. The isotopic values for each whale were determined for each season in which it had been sampled. For individuals with more than one skin sample within a season, the average isotope ratios for that season were used for further analysis.

Sperm whales at Kaikōura have a wide range of sighting frequencies (Childerhouse et al., 1995), and the value of both $\delta^{13}\text{C}_{\text{Bulk}}$ and $\delta^{15}\text{N}_{\text{Bulk}}$ in an individual's skin is correlated with the extent to which it uses the Kaikōura Canyon for foraging (represented by its mean sighting frequency; Guerra, 2018). To account for this source of variability, sighting frequencies were assigned to each whale, based on encounter histories from the photo-identification data. Individual sighting frequencies for

each field season were calculated as the number of days in which a whale was encountered, standardised by the total number of effort days in that field season, and scaled by whale abundance to account for lower encounter rates per individual during seasons of higher abundances. Mean sighting frequencies were averaged across the duration of the study (summer 2013/14 to summer 2017/18). This proxy assumed that the more time whales spent foraging inside the study area, the more frequently they were encountered.

Changes in sperm whale behaviour and stable isotope ratios were assessed using an Information-Theoretic Approach (Burnham and Anderson, 2002). For each response variable, a suite of models was constructed to include all combinations of explanatory variables, and models were ranked using Akaike's Information Criterion (AIC_C). Temporal variability in behavioural variables was modelled using linear mixed models (LMM, Bolker et al., 2009; Zuur et al., 2009), with the factors 'year' and 'season' (summer, winter) as explanatory variables and whale identity as the random effect. Surface intervals and log-transformed blow intervals were thus modelled with a Gaussian distribution. The time to first echolocation click (number of seconds) was modelled with a Poisson distribution, using a generalised linear mixed model (GLMM, Bolker et al., 2009). The response of stable isotope ratios was modelled independently for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ using generalised additive mixed models (GAMM, Hastie and Tibshirani, 1990; Zuur et al., 2009), with 'year', 'season' and 'sighting frequency' as explanatory variables and whale identity as the random effect. GAMMs were used (rather than LMM) to account for the nonlinear relationship of isotope ratios with sighting frequencies (Guerra, 2018). 'Sighting frequency' was modelled as a smooth term, derived using thin-plate regression splines limited to a maximum of four degrees of freedom to reduce the risk of overfitting (Vaughan and Ormerod, 2005). Because the response variables were continuous data, the GAMMs used a Gaussian error structure and identity link function. Diagnostic plots were used to check the assumptions of normality (via histograms of residual distributions and normal Q-Q plots) and homogeneity of variance (via plots of residuals vs fitted values).

The time taken for the isotope values of sperm whales to reflect those of their prey (known as 'turnover time') is likely to be greater than two months (Ruiz-Cooley et al., 2004; Guerra, 2018). Thus, the samples collected in summer 2016/17 (within two months after the earthquake) were likely to reflect a diet assimilated before the earthquake. This was taken into account in the arrangement of the variable 'year', so that samples from summer 2016/17 were included in the pre-earthquake years.

Model interpretation involved two steps. Firstly, the best models were chosen based on the lowest AIC_C score (Burnham and Anderson, 2002). Akaike weights (calculated as the model likelihood relative to the sum of the likelihoods of all models in the set) were used to evaluate the support for the selected models. Secondly, if the best model included the variable 'year', this indicated that there was interannual variability in the response, potentially correlated with the earthquake. In this case, the modelled effects of the explanatory variables included in the best model were used to describe the magnitude of change between years (e.g., years before the earthquake vs years after the earthquake). Statistical analyses were carried out in RStudio v 1.1.3. (R Development Core Team, 2012).

2.3.2. Spatial distribution

Diving locations of sperm whales were used to assess changes in the spatial distribution of foraging before vs after the earthquake, based on changes in 'high-use' (or core) areas. To minimise autocorrelation, only the first location per day for each individual was used in the analysis. Because survey effort was not uniform throughout the study area, sightings were analysed using effort-weighted density maps for each field season (Horne et al., 2007; e.g., Rayment et al., 2009; Gill et al., 2011). Density maps were created via kernel density estimation (KDE, Worton, 1989; Fieberg, 2007). KDE analysis fits a probability density

function to weighted sightings, creating a map of isopleths according to the probability of sighting an animal at any location within the range of the population. The estimated area within which there was at least 50% probability of sighting a sperm whale (termed K_{50}), was used to define the location and size of the population's high-use areas. K_{50} is commonly used to define core foraging areas in wildlife distribution studies (Gill et al., 2011; Leung et al., 2012), and provides a standardised area for comparisons over time (e.g., Brough et al., 2019). K_{50} was estimated via KDE for each summer and winter, based on sperm whale sightings weighted for survey effort (see Methods S1 in supplement).

To investigate changes in the spatial distribution of sperm whales before vs after the earthquake, three methods were used. (1) The high-use areas of each field season were mapped for visual examination of changes in distribution after the earthquake. (2) The extent of the high-use areas was calculated as a measure of how dispersed the sperm whales were in each field season. (3) The overlap between the high-use areas for every combination of two field seasons was calculated as a measure of the year-to-year consistency in foraging distribution before and after the earthquake. The overlap between any two seasons was

calculated as:

$$overlap (\%) = \frac{area\ of\ AxB_{K50}}{area\ of\ A_{K50} + area\ of\ B_{K50} - area\ of\ AxB_{K50}}$$

where ' AxB_{K50} ' is the overlapping area between the 50% isopleths of field seasons A and B, ' A_{K50} ' is the area contained by the 50% isopleth in field season A, and ' B_{K50} ' is the area contained by the 50% isopleth in field season B. Potential changes in high-use areas were assessed independently for summers and winters, as sperm whales at Kaikōura have significant seasonal differences in distribution and habitat use (Jaquet et al., 2000). All spatial analyses were carried out in ArcMap 10.2.

3. Results

3.1. Sperm whale behaviour at kaikōura before and after the earthquake

A total of 678 encounters with 54 individual sperm whales were recorded in 149 days over nine field seasons from January 2014 to January 2018 (Table S1 in supplement). Of these, 486 were used for

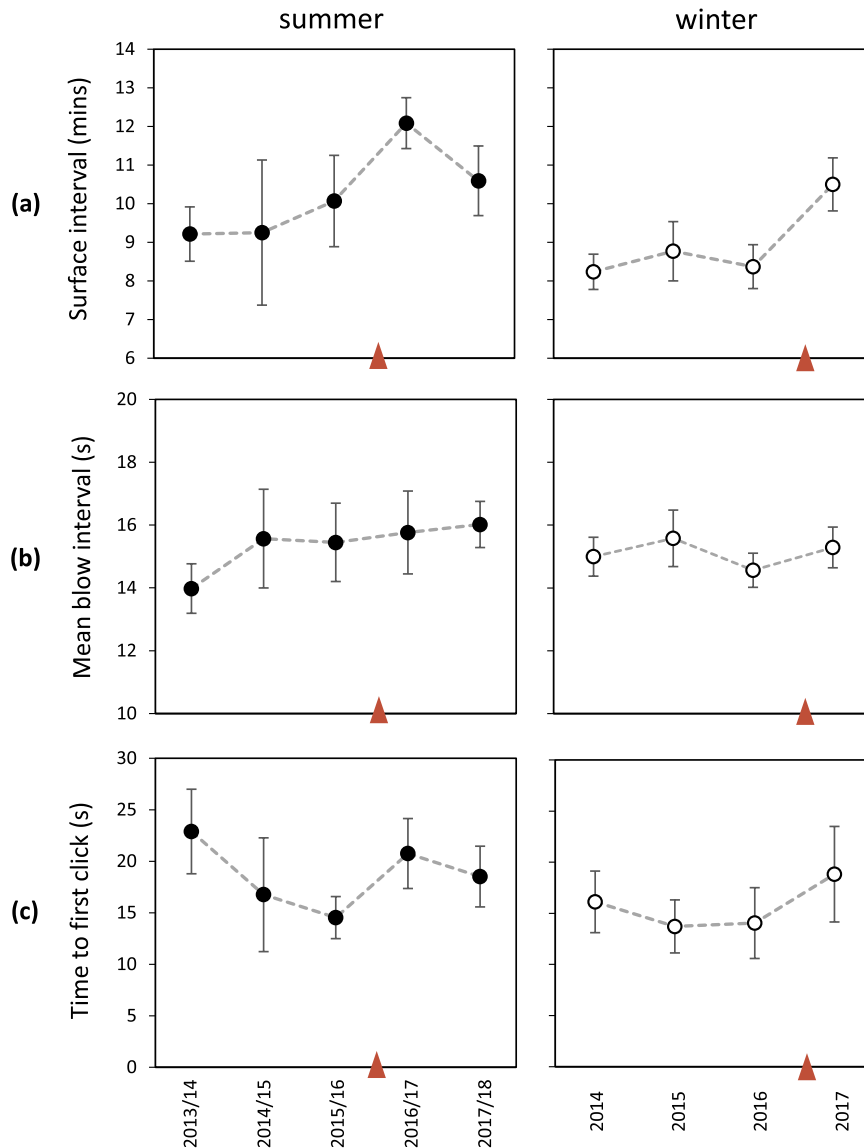


Fig. 1. Surface behaviour of sperm whales at Kaikōura in pre-earthquake and post-earthquake years. Circles represent the means of (a) surface interval, (b) mean blow interval and (c) time to start of foraging for each summer (black) and winter (white). Error bars are 95% confidence intervals. The triangle on the time-axis separates pre-earthquake from post-earthquake years.

further analyses after excluding repeated encounters with the same individual on the same day. Data from these sightings were used for the analysis of spatial distribution ($n = 486$) and behaviour ($n = 325$ surface intervals; $n = 237$ mean blow intervals; $n = 188$ times from fluke-up to first echolocation click).

Sperm whales spent longer times at the surface between foraging dives ('surface interval') in the year following the earthquake than in the three previous years, for both summer and winter (Fig. 1a). The LMM results showed 100% support for the model including the factors 'year' and 'season' (Table 1), with a significantly longer surface interval in the first post-earthquake year (Table 2). The mean difference in surface intervals between pre- and post-earthquake years was more than 2 min (increasing from 9.5 to 12.1 min in summer, and from 8.5 to 10.5 min in winter, Fig. 1a). Surface intervals in the second post-earthquake summer showed a return to pre-earthquake values. In contrast, there was no evidence for change in mean blow interval in years before vs after the earthquake (Fig. 1b), with full support for models excluding an effect of 'year' (Table 1). The time taken by sperm whales to start foraging at the start of a dive ('time to first click') showed considerable inter-year variation (Fig. 1c), with the best GLMM having 97% support and including the factors 'year' and 'season' (Table 1). The model indicated a significantly longer time to start foraging during the first post-earthquake year (Table 2), however this deviation fell within that of previous years, and the significantly shorter time to start foraging during one of the pre-earthquake years ('year 3') emphasised high inter-year variability. This result indicated no clear support for an earthquake-induced change in the time to start foraging. The time to start foraging in the second post-earthquake year was not significantly different from pre-earthquake years (Table 2).

3.2. Spatial distribution of sperm whales at kaikōura before and after the earthquake

Three boat-trips by local tour operators confirmed the presence of sperm whales at Kaikōura six, ten and 21 days after the main earthquake (November 14, 2016), indicating that sperm whales did not completely avoid the study area in the weeks following the earthquake. We were able to return to Kaikōura on the 9th Dec (25 days after the earthquake) to resume surveys. Based on photo-ID, we confirmed the presence of at least five different individuals in the study area over December and January.

The spatial distribution of sperm whales at Kaikōura changed noticeably after the earthquake, especially during summer. High-use areas (represented by the 50% kernel density isopleths, K_{50}) were consistently located in the mid- and upper-canyon during the three pre-earthquake summers (Fig. 2). In the two summers after the earthquake, however, the upper canyon was not included in the high-use areas, and sperm whales increased their use of areas in the lower canyon and areas further offshore. This change was reflected in a clear decrease in the overlap of high-use areas between pre- and post-earthquake summers (Fig. 3). During post-earthquake summers, sperm whales were slightly

Table 1

Highest-ranking linear mixed models used to explain temporal variability in sperm whale behaviour from summer 2013/14 to summer 2017/18, and metrics of model performance. (1|ID) = random effect of whale identity included in all models; df = degrees of freedom; W_i = Akaike weight; Adj. R^2 = variance explained by fixed effects only.

Response	Factors	df	W_i (%)	Adj. R^2 (%)
Surface interval ($n = 325$)	year + season + (1 ID)	8	100	17.4
Log (Mean blow interval) ($n = 237$)	(1 ID)	3	99.4	–
Time to first click ($n = 188$)	year + season + (1 ID)	7	97.2	9.9

Table 2

Effect of explanatory variables (year and season) on sperm whale behaviour, based on the estimate ($\pm 95\%$ confidence interval) from the model with most support. EQ = main earthquake. Statistically significant effects ($\alpha = 0.05$) are indicated in bold.

Variable	Surface interval	Log (Mean blow interval)	Time to first click
Intercept	9.70 (± 0.78)	1.17 (± 0.02)	2.90 (± 0.15)
year 2 (pre-EQ)	0.57 (± 0.76)	0.01 (± 0.02)	–0.09 (± 0.13)
year 3 (pre-EQ)	0.39 (± 0.71)	0.00 (± 0.02)	–0.20 (± 0.13)
year 4 (post-EQ)	2.28 (± 0.74)	0.00 (± 0.02)	0.16 (± 0.12)
year 5 (post-EQ)	0.70 (± 0.97)	0.02 (± 0.02)	0.01 (± 0.13)
winter	–1.32 (± 0.59)	0.00 (± 0.01)	–0.14 (± 0.09)

more dispersed than before the earthquake. This result was shown by the increase in the K_{50} area during the two post-earthquake summers (between 16 and 91% larger than the mean K_{50} of pre-earthquake summers, respectively).

In winter, the whales' high-use areas prior to the earthquake showed a consistent use of the head of the canyon and the Conway Trough (Fig. 2). In the winter following the earthquake the head of the canyon was used less, while the mid-canyon and areas further offshore were used slightly more. This shift was reflected in a decrease in the consistency of overlap between high-use areas from pre- to post-earthquake winters (Fig. 3). As in summer, sperm whales were more dispersed after the earthquake (between 27 and 54% increase in the size of K_{50}).

3.3. Isotope ratios of sperm whales at kaikōura before and after the earthquake

A total of 127 samples of sloughed skin from 38 individual sperm whales were collected between January 2014 and January 2018 and subsequently used for bulk-tissue SIA. Thirty of these were repeated samples from individual whales within the same field season and were therefore averaged for further analysis. The resulting 97 isotopic values (for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) across nine field seasons (Table S1) represented 70% of the whales identified over the study period. Of the 127 samples, 42 from 19 individual whales were used for CSIA-AA. Three of these were repeated samples from individuals within the same field season and were averaged for further analysis. This resulted in 39 $\delta^{15}\text{N}$ isotopic values for each AA, across eight field seasons, representing 35% of the whales identified over the study period. Fewer samples were available for CSIA-AA because these analyses were restricted to material left-over from previous analyses for bulk-tissue SIA.

There was low inter-year variability in the means of $\delta^{15}\text{N}_{\text{Bulk}}$ and $\delta^{13}\text{C}_{\text{Bulk}}$ (Fig. 4a and b), and GAMM results showed 99.7% and 100% support for models excluding the factor 'year' in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively (Table 3). The lack of a 'year' effect on $\delta^{15}\text{N}_{\text{Bulk}}$ and $\delta^{13}\text{C}_{\text{Bulk}}$ suggested no detectable change in the whales' trophic level and utilisation of carbon source pools, respectively. The GAMM analysis indicated some support for models including interannual variability in $\delta^{15}\text{N}$ of Phe and $\Delta\text{Glx-Phe}$ (<22% and <8%, respectively; Table 3). However, isotopic values in the year after the earthquake were clearly within the variability of previous years (Fig. 4c and d), and the partial effect of year on $\delta^{15}\text{N}$ modelled by the GAMMs was not statistically significant for either Phe or $\Delta\text{Glx-Phe}$. Overall, these results provide no evidence for an earthquake-related change in the food web base or in the trophic level of sperm whales.

4. Discussion

This study is the first to examine the impacts of a large earthquake on a population of marine mammals, and helps to advance our

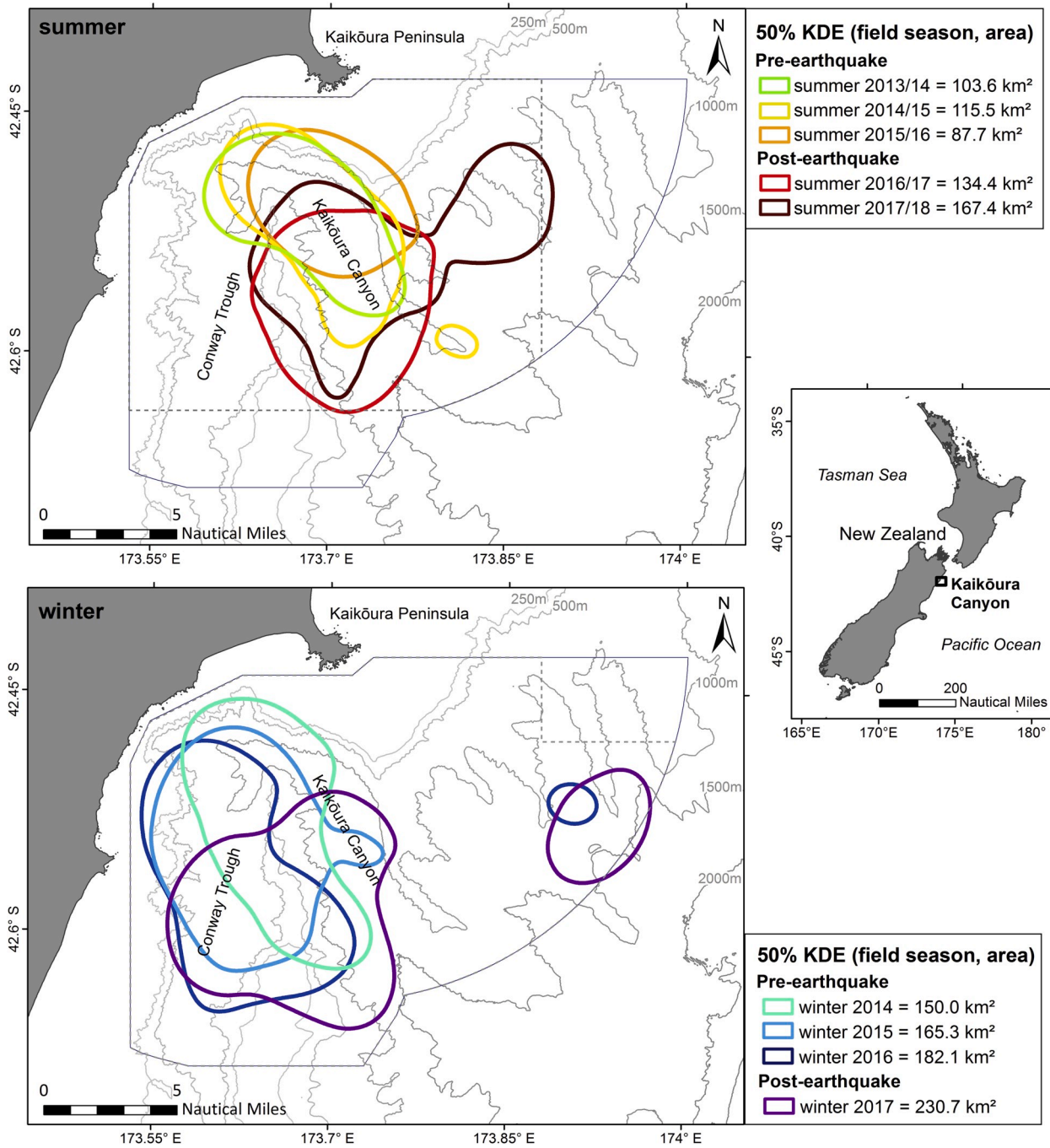


Fig. 2. Spatial distribution of sperm whales at Kaikōura during summer and winter in pre- and post-earthquake years. Coloured lines represent high-use areas, based on the 50% isopleth of kernel density estimates (KDE). The study area is represented by the blue line (offshore bounds are 12 nmi survey limits). The limits of the area used for the KDE analysis are represented by the dashed lines. Depth contours show 250, 500, 1000, 1500 and 2000 m isobaths. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

understanding of the ecological effects of natural disturbance events on marine ecosystems. We observed substantial changes in the whales' surface intervals between foraging dives and in the distribution of high-use areas, indicating shifts in habitat use for more than a year. These changes may reflect an increased search effort for prey and use of sub-optimal habitat, however the return of surface intervals to pre-earthquake levels after one year suggested some recovery of pre-earthquake foraging efficiency.

4.1. Effect of the earthquake on sperm whale behaviour

We detected clear changes in sperm whale behaviour in the year following the earthquake. Most noticeably, the time spent at the surface between dives was significantly longer during the first summer and first winter after the earthquake (i.e., up to 8 months later), compared to previous years. Whales showed a 25% increase in their average surface time (8.8–9.1 min, based on the present study and Jaquet et al., 2000, respectively). Sperm whales are deep divers (Watwood et al., 2006), at Kaikōura usually spending around 40 min foraging at depth between periods at the surface (e.g. Jaquet et al., 2000). The duration of surface

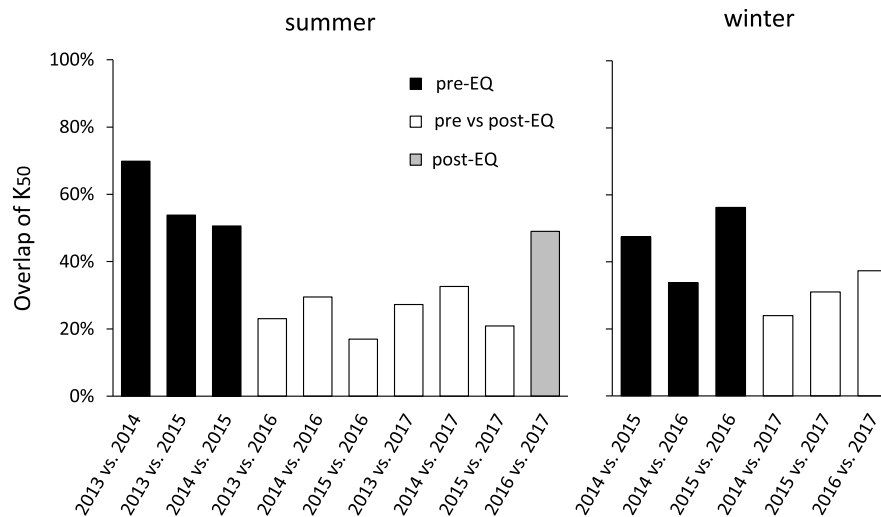


Fig. 3. Consistency in the spatial distribution of sperm whales at Kaikōura pre- and post-earthquake during summer and winter, expressed as the overlap between the high-use areas (contained by the 50% isopleth of kernel density estimates, K_{50}) for every two-year combination.

intervals is considered to be an energetic balance between two essential but mutually exclusive resources; air at the surface and food at depth (Kramer, 1988). Surface intervals of foraging sperm whales are remarkably consistent among populations around the globe (typically 8–10 min, see below). Increased surface intervals after the earthquake suggest that the whales' foraging efficiency was reduced. The average surface interval during the summer just after the earthquake (12.1 min, CV = 11%) was longer than that found by any previous studies at Kaikōura (9.0 min – Gordon et al., 1992; 9.1 min – Jaquet et al., 2000; 9.3 min – Richter et al., 2006) or elsewhere (8.0 min – Jaquet et al., 2003; 8.1, 9.3 and 9.9 min – Watwood et al., 2006; median of 8.3 min – Teloni et al., 2008; 8.0 min – Cosentino, 2016), suggesting a strong effect.

Ventilation patterns in marine mammals are related to metabolism and energy expenditure (Costa and Williams, 2000). Increased energy expenditure during foraging dives (e.g., by diving for longer or over larger distances) should result in an increased oxygen demand during subsequent surface intervals (Dolphin, 1987; Miller and Roos, 2017). Meeting this demand can be achieved by longer surface intervals (i.e., more breaths), higher ventilation rates, or a combination of the two. We found no evidence for higher ventilation rates after the earthquake, but substantially longer surface intervals suggest an increase in energy demand during foraging dives. We propose that the longer surface intervals reflected an increased search effort required to locate food resources. Although the proximal cause of the longer intervals is unknown, it could be mediated by longer or deeper dives, or by longer distances travelled per dive cycle (Jaquet et al., 2003). Changes in dive duration could not be directly examined because only the end time of each dive cycle was known, as acoustic tracking of each whale commenced while diving was already underway.

There are at least two mechanisms that could explain an increase in search effort. Firstly, the removal of benthic invertebrate communities by the canyon-flushing event (Mountjoy et al., 2018) may have reduced the availability of food resources used by higher trophic levels, resulting in sparser prey and reduced foraging opportunities for sperm whales. Secondly, the changes in underwater structure produced by sediment deposition and erosion (Mountjoy et al., 2018) may have required sperm whales to 're-familiarise' with a modified habitat, increasing the effort to navigate and to locate prey whose distribution may have changed. In any case, surface intervals returned to pre-earthquake levels in the second summer after the earthquake. It is possible that foraging opportunities increased as the ecosystem began to recover (as suggested by

the re-colonisation of benthic invertebrates; NIWA, 2017), or that sperm whales adapted to the modified habitat.

The time to the first echolocation click during a dive is directly related to the depth at which sperm whales start foraging, and can indicate changes in the prey layers targeted by the whales (Fais et al., 2015). We found no evidence to suggest that whales were targeting substantially different depth layers after the earthquake than in previous years. The drivers of the time to first click and mean blow interval, however, are still poorly understood, and it is possible that changes in foraging patterns occur without being reflected in these variables.

4.2. Effect of the earthquake on spatial distribution

The presence of sperm whales at Kaikōura within one week of the earthquake (and continued presence over the following months) showed that short-term impacts were not sufficiently strong to completely displace the whales from the area. This outcome suggests that the whales that remained at Kaikōura were relatively resilient to the short-term disturbance of the earthquake, and that sufficient foraging opportunities remained within the canyon area. Over a longer time-scale, mark-recapture analyses indicated that the estimated number of sperm whales in the three field seasons following the earthquake (Summer, 2016/17, Winter, 2017; Summer, 2017/18) were within previously observed variability (Sommerford, 2018), indicating no evidence for an impact of the earthquake on overall whale abundance.

While there was no evidence for displacement of the population away from Kaikōura, fine-scale analysis of whale sightings showed a clear shift in spatial distribution after the earthquake. The upper Kaikōura Canyon was a consistent core area of sperm whale habitat before the earthquake, but in the year after, this habitat was excluded from high-use areas. In contrast, there was an increase in the use of the lower canyon and areas further offshore, which previously comprised a smaller portion of the whales' core areas. Overall, these observations suggest a shift in habitat use by sperm whales due to earthquake-related changes.

The upper part of the canyon was the area most affected by the flushing event triggered by the earthquake, experiencing the strongest erosion levels (Mountjoy et al., 2018). Given that the decline in sperm whale density was most pronounced in that area, these changes are likely to be related. The large-scale removal of benthic biomass through erosion and turbidity currents at the head of the canyon (Mountjoy et al., 2018) probably resulted in a localised shortage of food resources

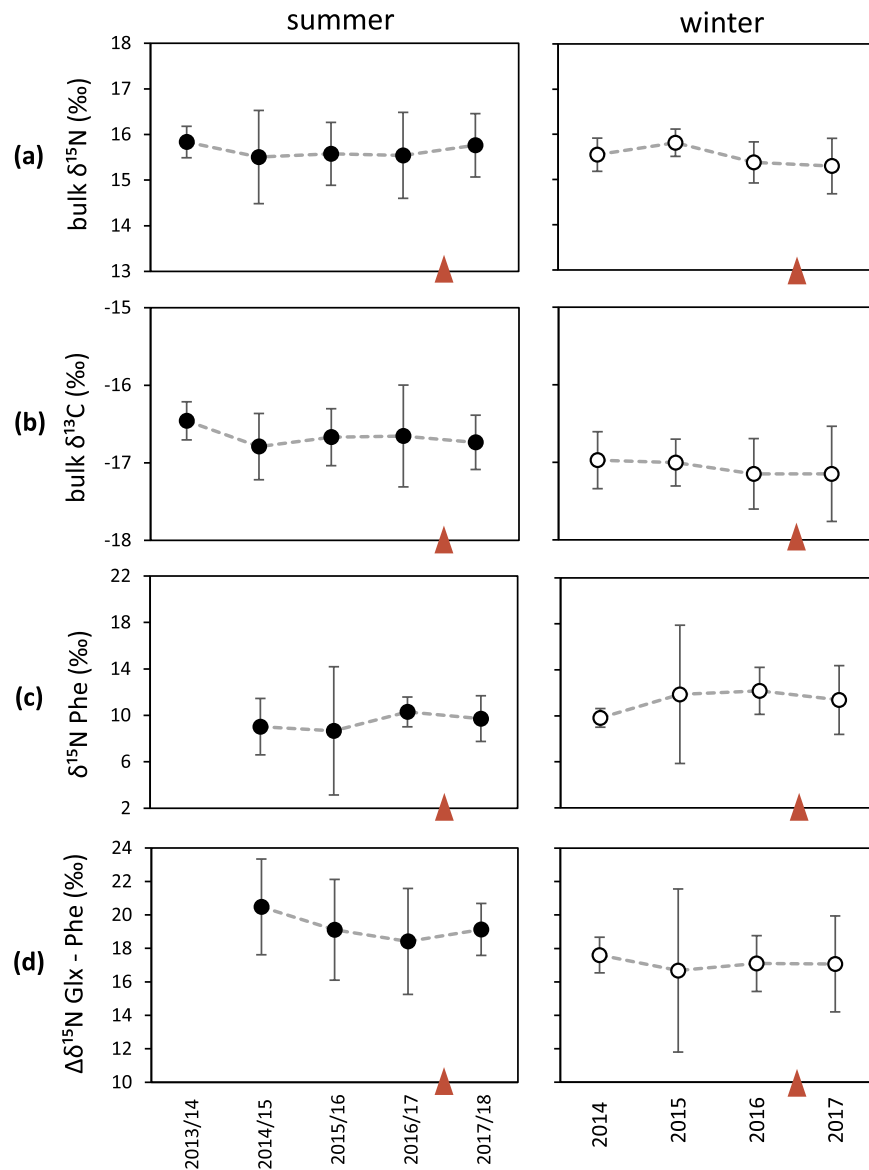


Fig. 4. Stable isotope ratios of sperm whales at Kaikōura in pre-earthquake and post-earthquake years. Circles represent means of (a) bulk-tissue $\delta^{15}\text{N}$, (b) bulk-tissue $\delta^{13}\text{C}$, (c) $\delta^{15}\text{N}$ of Phe (model source amino acid), (d) difference in $\delta^{15}\text{N}$ between Glx and Phe ($\delta^{15}\text{N}$ $\Delta\text{Glx-Phe}$, indicator of relative changes in trophic level) for each summer (black) and winter (white). Error bars are 95% confidence intervals. The triangle on the time-axis separates pre-earthquake from post-earthquake years.

available to benthic and demersal consumers, which may have relocated to other areas where food availability was higher. Although sperm whales in the upper canyon forage mostly on pelagic prey (Miller et al., 2013), they also target demersal layers in other parts of the canyon (Guerra et al., 2017), and demersal fish are an important part of their diet (Gaskin and Cawthorn, 1967). Thus, the whales' absence from the upper canyon could have been driven by a decline in food resources affecting the availability of sperm whale prey.

The post-earthquake shift in distribution towards areas which were previously outside their core habitat, suggested that whales might have been forced into lower-quality habitat, with less available prey. In addition, the more dispersed distribution of sperm whales after the earthquake, especially in summer, suggested wider search patterns during foraging. During periods of low prey abundance, sperm whales are more dispersed and increase their foraging effort by diving for longer, moving over larger distances and at higher average speeds (Jaquet et al., 2003). The increased surface times and wider distribution of sperm whales at Kaikōura after the earthquake are consistent with

these patterns, suggesting an increase in search effort during a period of reduced prey availability.

4.3. Effect of the earthquake on utilisation of food resources

Stable isotope analyses of sloughed skin detected no changes in the food web of sperm whales after the earthquake. The lack of significant change in $\delta^{15}\text{N}_{\text{Bulk}}$ and in $\Delta\delta^{15}\text{N}_{\text{Glx-Phe}}$ between pre- and post-earthquake years indicated that any potential changes in foraging did not involve feeding at a different trophic level. In addition, the lack of significant differences in $\delta^{13}\text{C}_{\text{Bulk}}$ and $\delta^{15}\text{N}_{\text{Phe}}$ suggested that the relative contribution of organic matter sources at the base of the food web utilised by sperm whales had not changed. Due to the spatial variability in isotope ratios of primary producers (Rau et al., 1982; Somes et al., 2010), changes in foraging region by top predators are often reflected in shifts of their baseline isotopic values (e.g., Zupcic-Moore et al., 2017). While we observed a post-earthquake shift in foraging areas by sperm whales, these occurred at a fine spatial scale, with no effect on the whales'

Table 3

Ranking of GAMMs used to explain the temporal variability in stable isotope ratios of sperm whale skin from summer 2013/14 to summer 2017/18, and metrics of model performance. For simplicity, only models with >5% support are shown. (1|ID) = random effect of whale identity included in all models; df = degrees of freedom; ΔAIC_C = difference in AIC_C values compared to model with most support; W_i = Akaike weight; Adj. R^2 = variance explained by fixed effects only.

Response	Model rank	Factors	df	ΔAIC_C	W_i (%)	Adj. R^2 (%)
$\delta^{15}N_{Bulk}$ (n = 97)	1	season + SF + (1 ID)	6	0	62.4	38.8
	2	SF + (1 ID)	5	1.0	37.3	36.9
$\delta^{13}C_{Bulk}$ (n = 97)	1	season + SF + (1 ID)	6	0	95.6	37.9
	2	season + SF + (1 ID)	6	0	95.6	37.9
$\delta^{15}N_{Phe}$ (n = 39)	1	season + SF + (1 ID)	6	0	33.4	25.5
	2	season + (1 ID)	4	0.6	24.4	11.5
	3	season + year + (1 ID)	7	0.9	21.6	11.4
	4	season + year + SF + (1 ID)	9	3.0	7.4	21.5
	5	SF + (1 ID)	5	3.6	5.4	14.9
$\Delta\delta^{15}N_{Glx-Phe}$ (n = 39)	1	season + SF + (1 ID)	6	0	71.7	41.9
	2	season + (1 ID)	4	3.1	15.5	20.7
	3	season + year + SF + (1 ID)	9	4.6	7.3	38.9

baseline isotopic values.

4.4. Conclusions

Sperm whales altered their fine-scale spatial distribution and diving behaviour in apparent response to the changes in the canyon system triggered by the Kaikōura earthquake. While such changes suggest an impact on habitat use, they also indicate a capacity for adaptation and some resilience to natural disturbance. Nevertheless, due to the ongoing decline in abundance at Kaikōura (Sommerford, 2018), the population may be particularly vulnerable to impacts on their habitat. As top predators, sperm whales are valuable indicators of ecosystem health and recovery. Their changes in habitat use may provide important insights into the re-distribution of food resources in the Kaikōura canyon over the next decade. Considering the economic importance of sperm whales to Kaikōura, continued study will be essential to assess the long-term impacts of the earthquake on the canyon as the ecosystem reaches a new equilibrium.

Our results support the finding that earthquakes and associated underwater slips affect the structure and function of deep-sea ecosystems, from benthic communities of small invertebrates (Kitahashi et al., 2014; Mountjoy et al., 2018) to large pelagic predators. This study highlights the importance of long-term monitoring studies for understanding the impact of disturbance on marine mammal populations.

Author contributions

MG, SD, AS, ES, TS, LW, RW and WR conceived the study ideas and designed methodology; MG, SD, TS, RW and WR collected the data; MG and AS carried out the chemical analyses; MG, AS and TS analysed the data; MG and WR led the writing of the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

Acknowledgements

This research was supported by the New Zealand Whale and Dolphin Trust, Whale Watch Kaikōura, the Ministry for Primary Industries and the University of Otago. This work was completed under Objectives 1–3 of Ministry for Primary Industries project KAI2016-06. We would like to thank all the volunteers who assisted with data collection in the field. We are grateful to Whale Watch Kaikōura for their overall support and for providing photographs of sperm whales outside the time of our surveys. We would also like to thank Kim Hageman, Rob van Hale, Dianne Clarke, and the Departments of Marine Science and Chemistry at the University of Otago, as well as Rich Ford and Darryl MacKenzie. Sloughed sperm whale skin was collected under permit 42960-MAR issued by the New Zealand Department of Conservation to Will Rayment, Steve Dawson and Marta Guerra.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2020.103226>.

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