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Diverse foraging strategies by a marine top predator: Sperm whales exploit pelagic and demersal habitats in the Kaikōura submarine canyon

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ABSTRACT

The submarine canyon off Kaikōura (New Zealand) is an extremely productive deep-sea habitat, and an important foraging ground for male sperm whales (*Physeter macrocephalus*). We used high-resolution archival tags to study the diving behaviour of sperm whales, and used the echoes from their echolocation sounds to estimate their distance from the seafloor. Diving depths and distance above the seafloor were obtained for 28 dives from six individuals. Whales foraged at depths between 284 and 1433 m, targeting mesopelagic and demersal prey layers. The majority of foraging buzzes occurred within one of three vertical strata: within 50 m of the seafloor, mid-water at depths of 700–900 m, and mid-water at depths of 400–600 m. Sperm whales sampled during this study performed more demersal foraging than that reported in any previous studies – including at Kaikōura in further inshore waters. This suggests that the extreme benthic productivity of the Kaikōura Canyon is reflected in the trophic preferences of these massive top predators. We found some evidence for circadian patterns in the foraging behaviour of sperm whales, which might be related to vertical movements of their prey following the deep scattering layer. We explored the ecological implications of the whales' foraging preferences on their habitat use, highlighting the need for further research on how submarine canyons facilitate top predator hot-spots.

1. Introduction

Submarine canyons are complex topographic features that cross continental margins all over the globe, connecting the shallow continental shelves to deep ocean basins (Shepard and Dill, 1966). They are extremely productive, serving as hotspots of benthic and pelagic biomass and diversity (De Leo et al., 2010; Vetter et al., 2010; van Oevelen et al., 2011), and are key habitats for top predators, including deep-diving cetaceans (Yen et al., 2004; Moors-Murphy, 2014). Despite being globally numerous, submarine canyons are poorly studied, and the drivers behind their exceptional productivity are not well understood (De Leo et al., 2010; Moors-Murphy, 2014).

The Kaikōura Canyon, off the east coast of New Zealand (Fig. 1), has been described as the most productive non-chemosynthetic habitat recorded to date in the deep sea (De Leo et al., 2010). It harbours exceptional biomass of infaunal and epifaunal invertebrates, including nematodes, and also benthic-feeding fish (De Leo et al., 2010; Leduc

et al., 2012). Furthermore, the presence of many top-predators targeting mesopelagic prey (e.g., Benoit-Bird et al., 2004; Boren et al., 2006) suggests that the area hosts a highly productive pelagic system.

The Kaikōura Canyon is also an important year-round foraging ground for male sperm whales (*Physeter macrocephalus*) (Childerhouse et al., 1995; Jaquet et al., 2000), deep-diving predators (Papastavrou et al., 1989; Watkins et al., 1993) that use echolocation to detect and locate prey (Møhl et al., 2000; Madsen et al., 2002). Although squid are their primary food source (Okutani and Nemoto, 1964; Rice, 1989; Santos et al., 1999), demersal fish appear to be an important component of their diet in some regions (Martin and Clarke, 1986), including the Kaikōura/Cook Strait region of New Zealand (Gaskin and Cawthorn, 1967).

Deep-diving predators exploit specialist niches below the photic zone, where most biomass is concentrated in two vertical bands: the deep scattering layer (DSL, Johnson, 1948) and the benthic boundary layer (BBL, Marshall, 1965). The DSL is typically between 200 and

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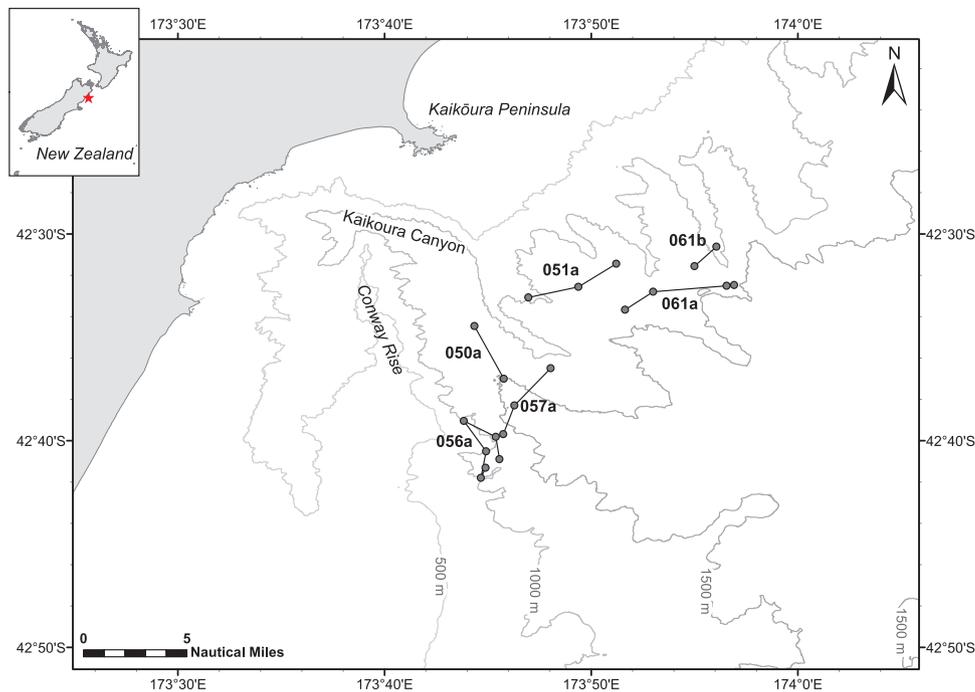


Fig. 1. The Kaikōura submarine canyon, New Zealand. The known surface positions of tagged whales are shown (black circles) together with the tag ID. Note that whales could not always be followed and therefore some of their positions were unknown. Depth contours show 500, 1000 and 1500 m isobaths.

600 m deep, and is composed of mesopelagic organisms, dominated by micronektonic fish (Barham, 1966; Hays, 2003), while the BBL comprises benthopelagic organisms that move freely on and just above the sea bed (Angel and Boxshall, 1990). Studies of diving and acoustic behaviour can reveal which types of prey are targeted by deep-diving odontocetes (Teloni et al., 2008; Arranz et al., 2011; Miller et al., 2013). The underwater behaviour of sperm whales has been investigated using a variety of methods including implanted transponders (Watkins et al., 1993), archival tags attached via suction cups (Johnson and Tyack, 2003; Watwood et al., 2006; Fais et al., 2015), tags attached with darts or barbs (Davis et al., 2007; Mate et al., 2016), and passive acoustics (Thode et al., 2002; Wahlberg et al., 2001; Wahlberg, 2002; Miller et al., 2013).

Foraging ecology of sperm whales at Kaikōura was first studied in 2007 using a three-dimensional (3-D) passive acoustic array (Miller and Dawson, 2009; Miller et al., 2013). The study revealed that whales foraged throughout the water column, with the majority of foraging buzzes occurring in mid-water at depths of 400–550 m. The Miller et al. (2013) dataset included 78 recordings of full or partial dive cycles, with whale identity known for 42 recordings (12 whales). These data were gathered over one year in the upper portion of the Kaikōura Canyon and around the Conway Rise (see Fig. 1). The foraging behaviour of sperm whales in the deeper parts of the canyon, and areas further offshore, has remained unstudied.

The abundance of sperm whales feeding at Kaikōura has suffered a recent decline, from nearly 100 individuals in 1991 to half that number in 2007 (van der Linde, 2009). With no evidence for direct impacts on survival, it is possible that the decline has been driven by a change in distribution away from Kaikōura, potentially reflecting underlying ecological changes that affect the availability or distribution of their prey. It is therefore essential to better understand what sustains the diet of sperm whales and the environmental features which drive their distribution. Given the extreme benthic biomass of the Kaikōura Canyon (De Leo et al., 2010; Leduc et al., 2012), and that demersal fish are known to constitute an important part of the diet of sperm whales in the region (Gaskin and Cawthorn, 1967), we hypothesise that sperm whales at Kaikōura are likely to forage extensively near the seafloor.

To address this hypothesis, we attached acoustic multi-sensor tags ('Dtags', Johnson and Tyack, 2003) to sperm whales at Kaikōura. Our

main objective was to investigate which prey layers are targeted by sperm whales in the Kaikōura Canyon system. We also aimed to identify circadian patterns in their foraging behaviour, and compare foraging preferences with other populations and previous observations at Kaikōura. We use the findings from this study to better understand how sperm whales use the different vertical strata in their habitat in order to meet their high energy requirements.

2. Methods

2.1. Field site and data collection

Field work took place off the Kaikōura coast, New Zealand (42.5°S, 173.8°E; Fig. 1), from February 19 to March 3, 2013 (austral late summer). The study area covered water depths of 800–1600 m extending over the main canyon (ca. 20 km from the canyon head) and adjacent secondary canyons (Fig. 1).

Adult male sperm whales were tagged with high-resolution digital archival tags (DTag2) to collect acoustic, depth and movement data. Whales were tracked acoustically while underwater using a hand-held directional hydrophone (Dawson, 1990), then after surfacing approached slowly from behind using a 6 m rigid-hulled inflatable boat. The tag was attached with four suction cups to the dorsal surface of the whale using an 8 m handheld pole. The tags included a hydrophone, a depth sensor and three-axis accelerometers and magnetometers (Johnson and Tyack, 2003). Depth and orientation of the whales was sampled at 50 Hz, decimated to 5 Hz for analysis, and sounds were sampled at 96 kHz. When possible, tagged whales were followed visually from the 56 m M/V (motor vessel) *Alucia* or from the 10 m RHIB (rigid-hull inflatable boat) *Northwind* (tender to *Alucia*). Whales were identified prior to tagging via photos of the unique marks (nicks and notches) along the trailing edge of their flukes, and matched to a photo-identification catalogue of sperm whales sighted at Kaikōura since 1990. This was done to ensure that the same animal was not tagged more than once. The tags released after a pre-programmed duration and floated to the surface where they were located by VHF radio tracking. All tag data were analysed with custom scripts (M. Johnson, <<https://www.soundtags.org/dtags/dtag-toolbox/>>) in Matlab R2013a (MathWorks).

To assess the behavioural reactions of sperm whales to tagging attempts, we recorded whether whales exhibited a startle response (e.g., a swipe of the flukes), performed a shallow dive (i.e., not lifting flukes), displayed evasive behaviour by turning and swimming away from the tagging boat, or performed an early dive. A dive was considered to be ‘early’ if the whale’s time at the surface was < 4.5 min, which is half of the mean surface time recorded for sperm whales at Kaikōura (Douglas et al. 2005).

2.2. Dive cycle and foraging activity

While diving, sperm whales regularly produce loud broadband echolocation clicks (known as ‘usual clicks’) to search for prey (Weilgart and Whitehead, 1988), as well as buzzes (or ‘creaks’) which are assumed to indicate prey capture attempts (Miller et al., 2004; Fais et al., 2015). Acoustic recordings were examined acoustically and visually using spectrograms (512 point FFT, Hanning window, 50% overlap) to locate the start and end of the clicking phase of each dive, and to identify buzzes. Buzzes were defined as a series of clicks with inter-click intervals shorter than 0.22 s (Teloni et al., 2008; Fais et al., 2015). An automatic click finder in Matlab (“findallclicks” by M. Johnson, <<https://www.soundtags.org/dtags/dtag-toolbox/>>) was used to detect individual clicks for posterior echo analysis.

To facilitate the interpretation of the whales’ foraging behaviour, we divided each dive cycle into distinct phases (Fig. 2), based on the dive profiles and foraging vocalisations (Watwood et al., 2006; Miller et al., 2013; Fais et al., 2015). The ‘descent’ phase started when the whale fluked up, and ended with the first decrease in whale depth; this phase is therefore characterised by a continuous downwards orientation. The ‘bottom’ phase of the dive followed immediately after the descent phase and continued until the time when the whale was last oriented downwards. The ‘ascent’ phase was characterised by a continuous upwards orientation, starting immediately after the end of the bottom phase, and finishing at the time of surfacing. The ‘search’ phase comprised the part of the dive when the whale was producing usual echolocation clicks. The ‘foraging’ phase of the dive was defined as the period from the first to last buzz, representing the time when sperm whales were actively encountering prey. For the specific purpose of comparing foraging behaviour to that of sperm whales tracked

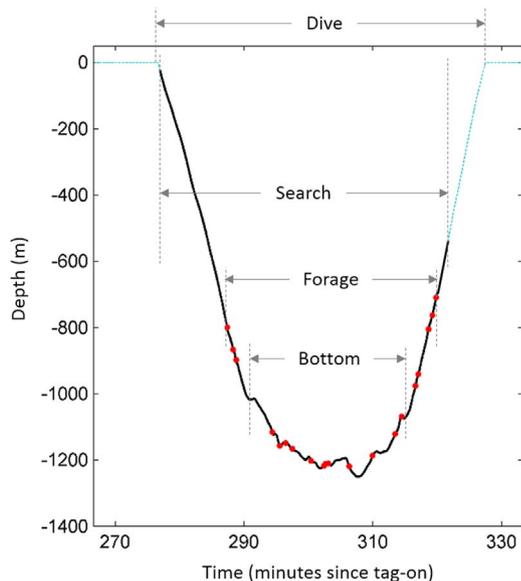


Fig. 2. Phases of an example foraging dive. The time-depth profile is shown by a blue line while the whale is silent and a black line while it is producing echolocation clicks. Buzzes (assumed prey capture attempts) are marked by red dots. Vertical dashed lines define the start and end of each phase. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

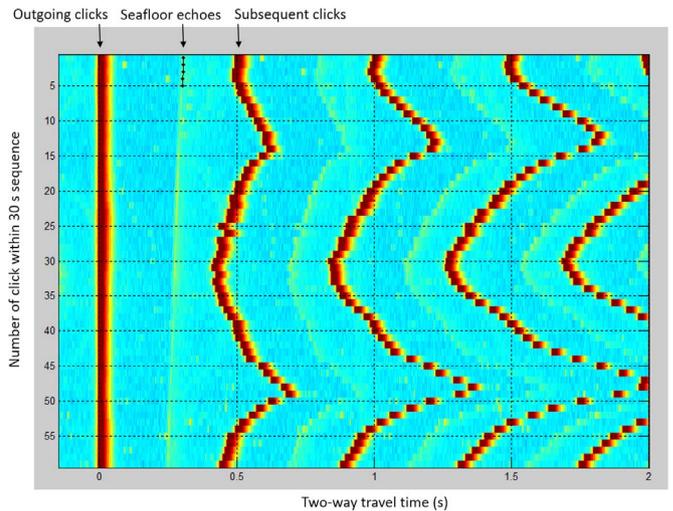


Fig. 3. Echogram showing sperm whale clicks and echoes reflected from the seafloor. Each row represents the 2 s envelope of a single outgoing click, with colour representing sound pressure level. Echolocation clicks appear as well-defined dark red blocks, while the seafloor echoes appear as thinner yellow segments. The manual selection of the first five seafloor echoes is indicated by small black circles. In this example the whale is approaching the seafloor, with its distance above it decreasing from about 200–180 m within this 30 s interval. The saw-tooth pattern of subsequent clicks reflects a dynamic inter-click interval as the whale searches for prey at varying ranges. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

acoustically at Kaikōura in near-shore waters, we also used an alternative definition of ‘bottom’ phase which continued until the whale became silent on ascent, following Miller et al. (2013).

2.3. Seafloor echoes and distance above the seafloor

Dtags record the sounds emitted by sperm whales, but also any echoes returning from the sea surface, seafloor or organisms in the water (Thode et al., 2002; Arranz et al., 2011; Fais et al., 2015). The distance of a sperm whale above the seafloor (also known as ‘whale altitude’, Arranz et al., 2011; Fais et al., 2015) was thus obtained from the echoes generated by the whale’s clicks as they reflected from the sea bed (Thode et al., 2002; Arranz et al., 2011; Fais et al., 2015). In essence, this method taps into the whales’ sonic perception of their surroundings, eavesdropping on their bio-sonar to collect information that the whales themselves receive from their physical environment.

Click echoes were automatically identified using a supervised click and echo detector in Matlab (“d3echotool” by M. Johnson, <<https://www.soundtags.org/dtags/dtag-toolbox/>>), and echoes from the seafloor were then manually selected using echograms (Fig. 3). Echograms were constructed by stacking the envelopes of high-pass filtered 2 s duration sound segments synchronised to each produced click (Johnson et al., 2004; Arranz et al., 2011; Fais et al., 2015). The high-pass filter was used to remove flow noise, with a cut-off frequency set to 2 kHz. These segments enabled detection of seafloor echoes at ranges up to 1490 m from the whale, covering the entire water column within the research area. Reflections from the seafloor appeared on the echograms as sequences of echoes with well-defined onset times and slowly varying delay times from the outgoing click. The two way travel time (TWT) of each echo from the whale to the closest seafloor surface and back to the DTag was estimated using a supervised edge detector (resolution < 500 μ s). Whale distance above the seafloor was calculated as half the TWT multiplied by the speed of sound underwater. An average speed of sound of 1490 m s^{-1} was assumed based on the sound speed profile measured with a CTD to a depth of 550 m in the same area. The seafloor depth was estimated by adding the whale’s distance above the seafloor to the whale’s depth.

Seafloor echoes were rarely detected during buzzes due to the low sound pressure level and high repetition rate of clicks obscuring returning echoes. Whale distance above the seafloor during buzzes was thus estimated by using a value of seafloor depth obtained via linear interpolation between the previous and following estimates, as long as these had been acquired within 120 s of the buzz. With this method we could not account for the occurrence of irregularities in the seafloor during the time of interpolation, inevitably adding some uncertainty around the estimates of whales' distance above the seafloor during buzzes.

To evaluate the accuracy of echo-derived distances we compared the whale's depth (as recorded by the tag's pressure sensor) with the distance from the whale to the surface derived from the TWT of surface echoes. Whale depths were obtained by both these methods at 40 random times (including all tags), covering depths between 30 and 1130 m. The error in whale depth derived from surface echoes increased with distance to the surface, varying between 1 and 23 m (mean = 10.8 m) over distances between 30 and 1135 m (mean = 547). In relative terms, the error varied by between 1.0% and 9.1% of the whale's depth (mean = 2.3%). For the purpose of this study, we consider this error to be acceptable.

2.4. Data analysis

Data from all tagged whales were pooled for analysis. Our analysis focused on foraging dives only, thus excluding shallow dives in which no usual clicks or buzzes were detected. The depth and duration of each dive phase was calculated. We also recorded the duration of each buzz and the inter-buzz interval (IBI, measured as the time between the last click of a buzz and the first click of the following one) to compare foraging behaviour at different depths and distances from the seafloor.

To explore circadian differences in foraging behaviour we compared the characteristics of the buzzes that took place before and after sunset. Due to the small sample size of recorded night dives, we used this analysis to identify knowledge gaps and guide research questions rather than test diel differences empirically.

Due to the low number of dives obtained in this study and its limited spatial and temporal scope, we limited statistical testing to only a few relevant comparisons to assess the rates and durations of buzzes. For these cases we chose a simple confidence-interval approach (Di Stefano, 2004; Foody, 2009), whereby differences in means and 95% confidence intervals (CI) were used as the measure of magnitude and uncertainty of each comparison (Di Stefano, 2004). Diagnostic plots (histograms of residual distributions and normal Q-Q plots) were used to verify assumptions of normality in buzz patterns.

3. Results

3.1. General foraging behaviour

A total of 33.6 h of combined acoustic and movement data were collected from six successful tag deployments on six different mature male sperm whales, including 24 complete foraging dive cycles (descent-bottom-ascent) and another four incomplete dives (i.e., in which

Table 2

Summary of data derived from 28 foraging dives by six tagged sperm whales at Kaikōura. Sample size (N) varies because the tag detached part way through four of the dives. All depths are in metres.

	N	Mean (SD)	Median (range)
Search-start depth	28	48 (38)	35 (18–162)
Search-end depth	24	595 (215)	573 (303–1272)
Min depth of bottom phase	24	701 (260)	729 (222–1076)
Max depth of bottom phase	24	1074 (261)	1130 (535–1439)
Mean depth of bottom phase	24	924 (232)	978 (462–1226)
Start depth of bottom phase	28	806 (286)	888 (248–1387)
End depth of bottom phase	24	885 (296)	1000 (474–1396)
<i>Sensu Miller et al. (2013)*:</i>			
Min depth of bottom phase	24	560 (194)	511 (222–1061)
Mean depth of bottom phase	24	903 (220)	958 (452–1204)
End depth of bottom phase	24	595 (215)	573 (303–1272)

* Note: The definitions of start and maximum depths of the bottom phased used in this study are the same as those in Miller et al. (2013).

the tag came off before the end of the dive) (Table 1). The tag-on-animal times varied between 2.3 and 8.1 h (mean = 5.6). Tagged whales performed foraging dives with a mean duration of 50 min (range 33–66 min) and a mean bottom-phase depth of 924 m (462–1226 m) (Table 2). The maximum depth recorded was 1439 m. Whales started echolocating at a mean depth of 48 m (18–162 m) after a silent descent lasting on average 34 s (15–109 s). At the end of the dive, whales stopped clicking at a mean depth of 595 m (303–1272 m), followed by a silent ascent of 7 min on average (5–14 min). The search phase of the dive lasted for 42 min on average (27–55 min) while the foraging phase lasted 33 min (13–48 min).

Between consecutive foraging dives, whales spent on average 15 min at the surface (median 12 min, range 6–41 min). On two occasions, two different whales spent 4.2 and 1.5 h travelling silently, alternating between swimming at the surface and at depths of 10–20 m.

Echoes from the seafloor were detected for a total of 20,911 echolocation clicks, with the estimated whale distance from the seafloor varying from 6 to 1418 m. Two general foraging modes were observed, which we defined as pelagic and demersal (Figs. 4 and 5). Pelagic dives (n = 8) had a relatively narrow bottom phase at average depths of either ca. 500 m or 850 m, and at least 50 m from the seafloor (but typically > 200 m). Demersal dives (n = 12) had a bottom phase at or near (< 50 m) the seafloor (mean distance from the seafloor = 23 m, 9–44), with variable depth as the whales roughly followed the contours of the sea bed. In a few dives (n = 4) we observed a combination of both modes, with part of the bottom phase in mid-water before and/or after foraging on the seafloor. Both types of foraging were recorded for all the tagged whales. Regardless of the foraging mode, dives were bracketed by steep descents and ascents typical of sperm whale dives (Watkins et al., 1993; Watwood et al., 2006). Whales often foraged opportunistically in the descents and ascents to/from the bottom phases of demersal dives, as shown by occasional buzzes during these periods (e.g., Fig. 4b). Across the 24 complete dives, 57% of the total time of active foraging was spent within 50 m of the seafloor.

There was a positive and significant correlation between the depth

Table 1

Summary of tag deployments. Only foraging dives are included here, defined by the presence of usual clicks.

Tag ID	Date of deployment	Start time	Programmed tag-on time (h)	Tag-on time (h)	N dives	N complete dives
050a	19-Feb-13	12:09 p.m.	3.0	2.3	3	2
051a	20-Feb-13	11:43 a.m.	3.0	3.7	4	3
056a	25-Feb-13	12:36 p.m.	6.0	8.1	7	7
057a	26-Feb-13	1:00 p.m.	6.0	6.3	2	2
061a	2-Mar-13	4:24 p.m.	6.0	6.8	7	6
061b	2-Mar-13	5:09 p.m.	6.0	6.4	5	4
TOTAL				33.6	28	24

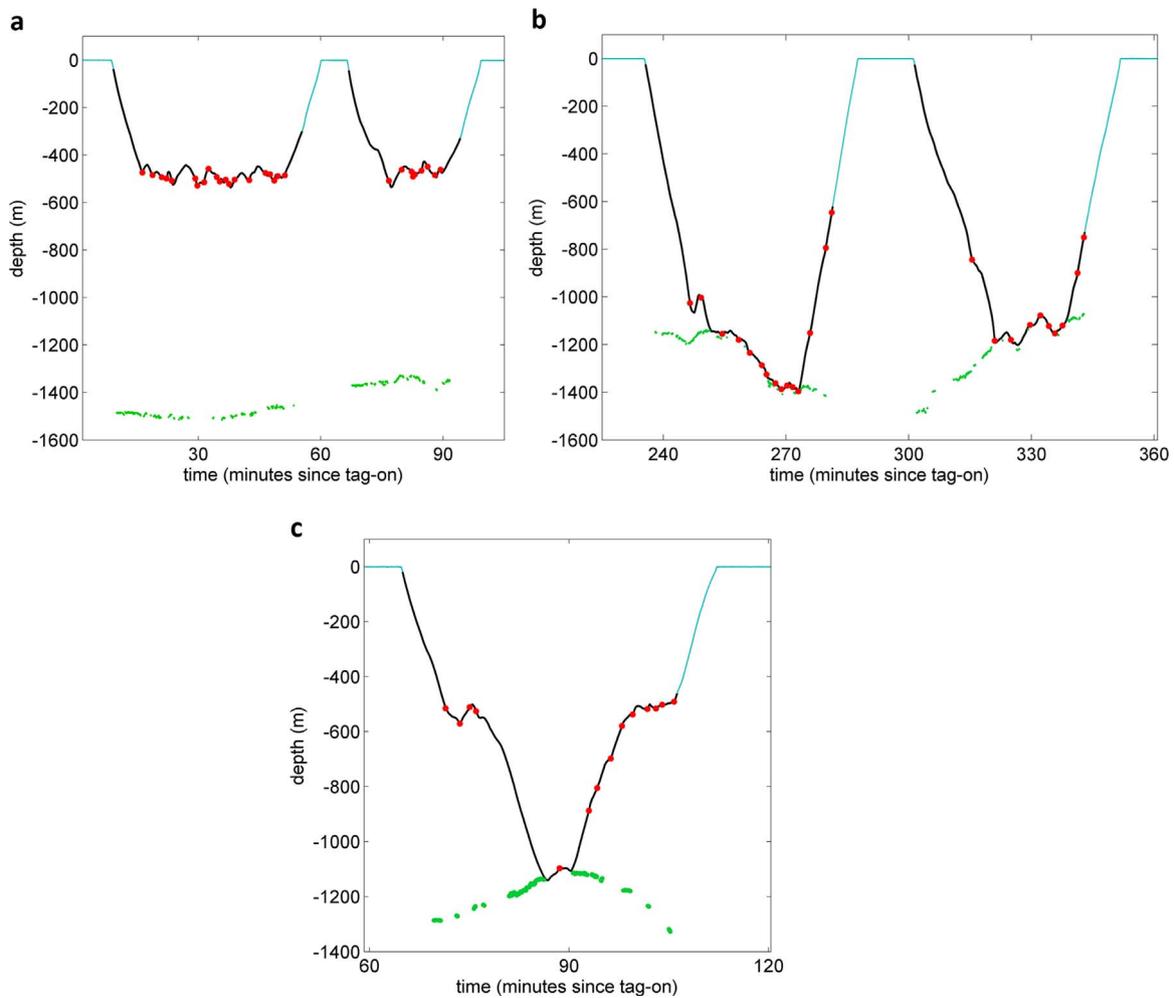


Fig. 4. Foraging activity of sperm whales in relation to the seafloor. Time-depth profiles of whales during example pelagic (a), demersal (b), and combined (c) dives. Black lines represent the portion of the dive when the whale was echolocating, red dots represent buzzes and green dots represent seafloor depths estimated from echo reflections. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

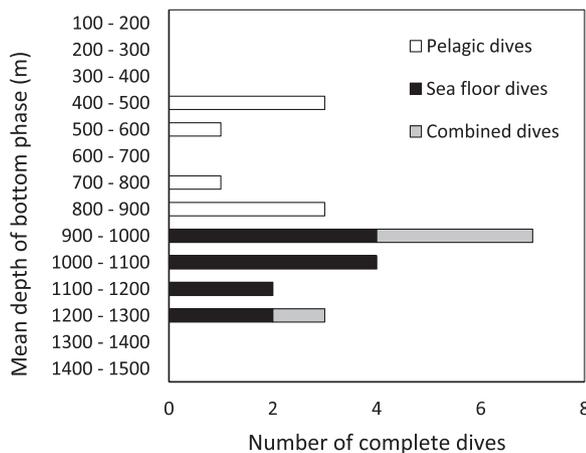


Fig. 5. Types of foraging dives performed by tagged sperm whales. A histogram of the mean bottom phase depths for all complete foraging dives ($n = 24$), distinguishing between dive types.

at the end of the search phase (marked by the last echolocation click during a dive) and the time taken by the whale to resurface from this depth ($r^2 = 0.86$, $p < 0.001$, $n = 24$). Although this relationship is based on a small sample size, it has the potential to be used as a useful proxy of foraging depth when the time from the last click to surfacing is

known. The correlation between this time interval and the mean buzz depth during a dive was also positive and significant, but with a much lower predictive power ($r^2 = 0.33$, $p = 0.003$, $n = 24$), and therefore has less potential as a biologically meaningful proxy.

3.2. Vertical distribution of buzzes

A total of 438 buzzes were detected in 28 foraging phases. The number of buzzes per dive ranged from 9 to 38, with a mean of 17 (Table 3). Buzz duration had a normal distribution with a mode at 6–8 s, varying from 2 to 50 s. The mean buzz depth per dive was 869 m (475–1205 m), and whales emitted buzzes at depths between 284 and

Table 3
Summary of buzz depths and distance from the seafloor produced by six tagged sperm whales at Kaikōura. All depths are in metres.

	N	Mean (SD)	Median (range)
No. of buzzes per dive	24	17 (7)	15 (9–38)
Depth of first buzz	27	611 (208)	511 (284–1033)
Depth of last buzz	24	663 (193)	633 (421–1261)
Min buzz depth	24	549 (156)	496 (284–949)
Max buzz depth	24	1056 (261)	1099 (508–1433)
Mean buzz depth	24	869 (208)	891 (475–1205)
Min buzz distance from the seafloor	24	182 (315)	17 (6–953)
Max buzz distance from the seafloor	24	623 (273)	601 (116–1052)
Mean buzz distance from the seafloor	24	319 (299)	164 (23–997)

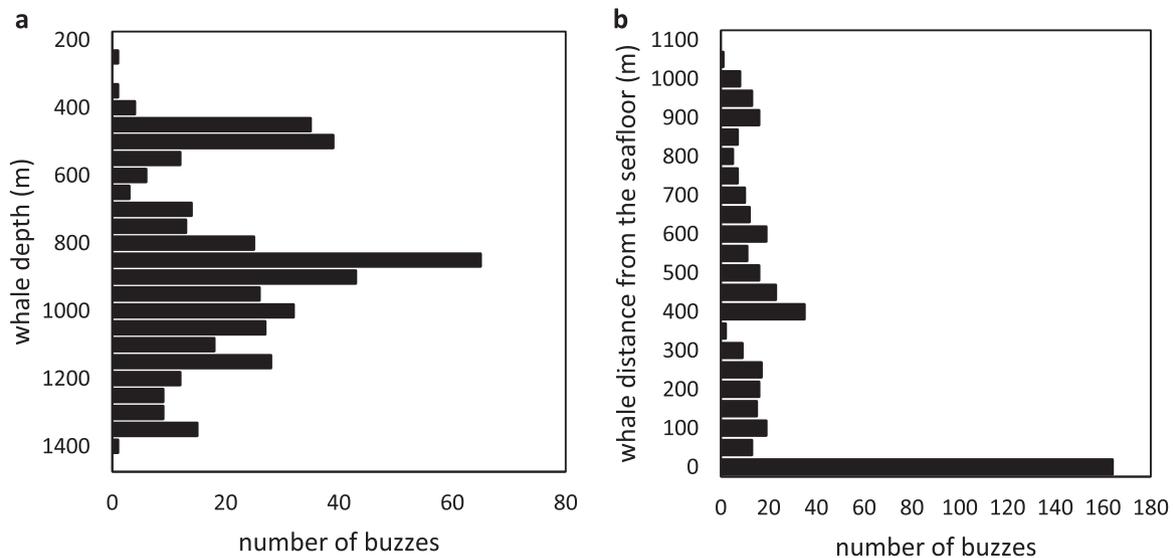


Fig. 6. Vertical distribution of sperm whale buzzes. Histograms of depth (a) and distance from the seafloor (b) of buzzes recorded during foraging phases. Depths are the lower bounds of 50 m bins.

1433 m (Table 3). On average, the first buzz in a dive was made 8.4 min after fluking up (range 4.7–14.4 min).

Buzz depth had a clear bimodal distribution (Fig. 6a), with one mode at 850–950 m (accounting for 25% of all buzzes) and a second mode at 450–550 m (17% of all buzzes). The majority of the buzzes (71%) occurred at depths greater than 800 m.

Estimates of whale distance from the seafloor were possible via linear interpolation for 354 out of a total of 438 recorded buzzes. The remaining 84 buzzes were recorded while the whale was foraging near the seafloor during times in which seafloor echoes were not detected within 120 s either side of the buzz. Because whale departures from the seafloor were always obvious in the echograms and there was no indication of such departures before any of these 84 buzzes, we assumed that they were performed within 50 m of the seafloor.

Sperm whale buzzes took place at distances from the seafloor varying from 6 to 1052 m. The distribution of buzz distance from the seafloor had one clear mode within 50 m of the seafloor (Fig. 6b). The rest of the buzzes ($n = 274$) were fairly evenly distributed across distances between 50 and 1000 m from the seafloor, with perhaps a second mode at 400–450 m from the seafloor. Following the definition of the benthic boundary layer (BBL) as extending from the seafloor to 200 m above it (Angel and Boxshall, 1990), 48% ($n = 211$) of buzzes occurred within this layer, indicating a substantial amount of benthopelagic foraging.

To identify vertical patterns in foraging behaviour more clearly, we assessed the distribution of buzzes simultaneously across whale depth and distance from the seafloor. The majority of buzzes fell within one of three clusters: 37% of all buzzes were produced within 50 m of the seafloor (depths of 800–1400 m), 35% were in mid-water at depths of 700–1000 m, and 21% were in mid-water at depths of 400–600 m (see Fig. 7a).

Distance from the seafloor appeared to influence buzz patterns. Buzzes emitted at or near the seafloor (distance < 50 m) were longer (mean buzz duration = 15.9 s, range = 2.0–49.7 s, $n = 164$) than buzzes emitted at distances > 50 m (mean = 9.0 s, range = 3.2–27.1 s, $n = 274$). The rate of buzzes was also different between pelagic and demersal prey, with longer inter-buzz intervals at the seafloor (mean IBI = 149.0 s, range = 2–976, $n = 164$) than in the water column (mean IBI = 90.5 s, range = 4–471, $n = 246$). This effect was statistically significant for both buzz duration and IBI (95% CI of the difference between means = 5.2–8.6 s and 26.0–90.9 s, respectively). To reduce the influence of within-individual autocorrelation, we analysed the

patterns in buzz duration and inter-buzz intervals separately for each whale. There was high inter-individual variability, especially in inter-buzz intervals. Consistent with the overall trend, five out of the six tagged whales produced longer buzzes near the seafloor than at distances > 50 m (Fig. 7a), and four whales produced longer inter-buzz intervals at the seafloor than in the water column (Fig. 7b).

No surface feeding was observed or recorded during this study. The minimum buzz depth was 284 m, indicating that no foraging occurred at or near the surface.

3.3. Day/night patterns in foraging behaviour

Data on foraging behaviour after sunset were available for three of the tagged whales, comprising seven hours of nocturnal data from nine dives, with 142 recorded buzzes. Due to the small number of dives recorded at night, diel patterns in foraging behaviour were only investigated by comparing depth and distance from the seafloor of buzzes.

There was some evidence for diel differences in the vertical distribution of buzzes (Fig. 8a–c). The mode in buzz depth at 450–550 m was almost exclusively (97%) composed of day-time buzzes, while the mode at 850–950 m was most evident for night-time buzzes. This diel variation was most evident in the depths of pelagic buzzes (Fig. 8b,c). Of the 175 pelagic buzzes recorded during day-time, a large proportion (41%) were made at depths of 450–550 m, with a smaller proportion (22%) at 850–950 m (Fig. 8b). In contrast, of the 99 pelagic buzzes recorded at night, only 2% were made at 450–550 m deep, while the vast majority (63%) were produced at 850–950 m (Fig. 8c). The mode in buzz distance from the seafloor at less than 50 m was apparent for both day-time and night-time buzzes.

3.4. Reaction to tagging attempts and tag deployment

We made 27 close approaches (< 200 m) to sperm whales to attempt a tag deployment, with 8 successful tag attachments. One tag was never recovered, and another malfunctioned. Behavioural reactions to the tagging attempt included startles ($n = 3$), evasive behaviours such as swimming away from the boat ($n = 9$), shallow diving ($n = 15$), and early diving ($n = 8$). After shallow diving, whales often resurfaced within a few minutes. Note that whales could exhibit multiple reactions during the same tagging attempt. No reaction to a tagging attempt was recorded on five occasions.

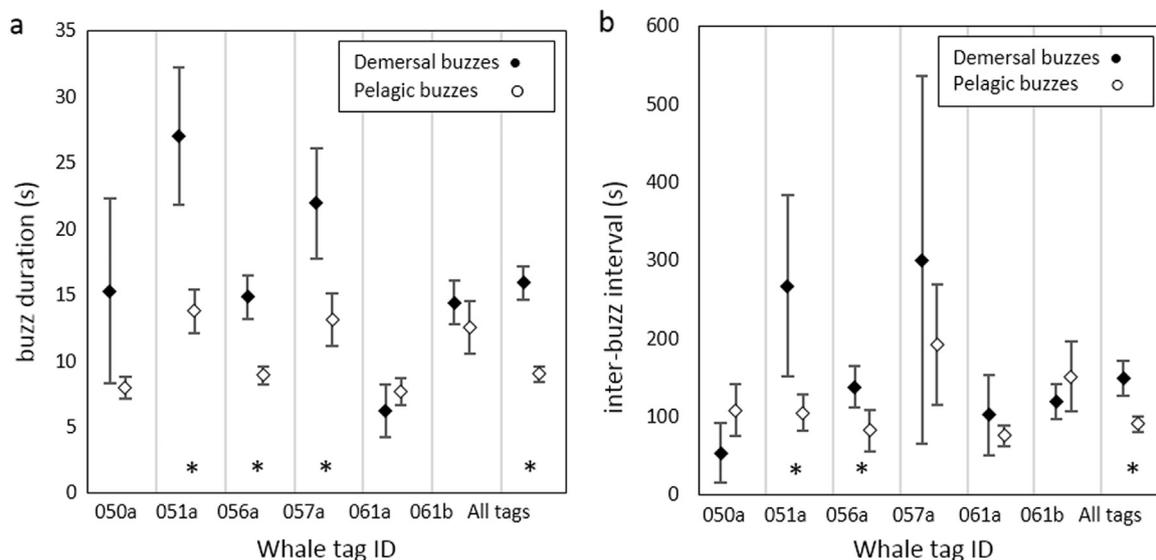


Fig. 7. Individual patterns of sperm whale buzzes. Mean buzz duration (a) and inter-buzz interval (b) of buzzes recorded during foraging phases. Demersal buzzes (black) include those produced within 50 m of the seafloor, while pelagic buzzes (white) include those produced above 50 m of the seafloor. Error bars represent 95% confidence intervals (CI), with the * symbol indicating lack of overlap in the CI of demersal and pelagic buzzes.

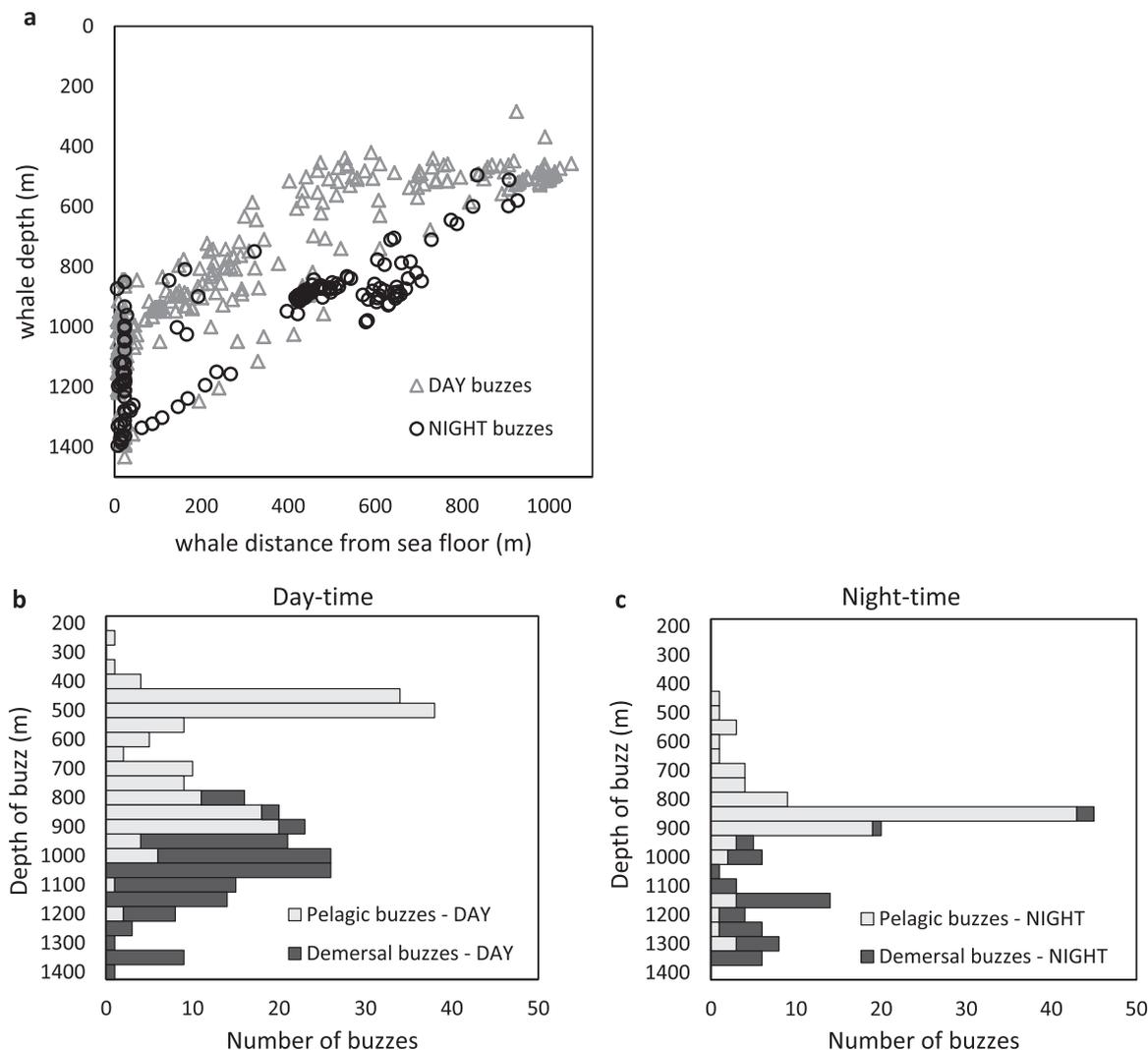


Fig. 8. Diel patterns in foraging behaviour of sperm whales at Kaikōura. (a) Buzz depth vs distance from the seafloor, with day buzzes represented by grey triangles and night buzzes by black circles. (b, c) Histogram of buzz depths recorded during the day (b) and at night (c) for pelagic (light grey, > 50 m from the seafloor) and demersal buzzes (dark grey, < 50 m from the seafloor). Depths in (b) and (c) are the lower bounds of 50 m bins.

4. Discussion

This study investigated the foraging behaviour of male sperm whales over the Kaikōura submarine canyon. While the data are from a limited period and from only six whales, they provide novel insights into the use of the water column by sperm whales at Kaikōura. Assumed prey capture attempts, indicated by buzzes, occurred at all depths below the epipelagic zone, from ca. 300–1430 m. Depth sensor data and echoes from the seafloor indicated that sperm whales searched for prey within three main vertical strata. Demersal prey were targeted when whales foraged within 50 m of the seafloor (and as close as 6 m) at depths of 900–1300 m, while mesopelagic prey were hunted in mid-water at depths of around 500 m and around 850 m. The wide and multimodal distribution of diving depths by sperm whales is consistent with previous studies (Teloni et al., 2008; Miller et al., 2013; Fais et al., 2015). It reflects the flexibility of their long-range sampling strategies to detect patchy food resources (Fais et al., 2015), and adaptability to track them down over vast volumes of water.

Average diving and foraging depths in our study were much deeper (ca. 200–500 m more) than those previously reported for male sperm whales in Kaikōura (Miller et al., 2013) and northern Norway (Teloni et al., 2008), and slightly deeper (ca. 100–200 m more) than those in the Atlantic Ocean, Gulf of Mexico and Ligurian Sea (Watwood et al., 2006). The drivers of these differences remain unknown, but the deeper foraging tendencies observed in this study appear to be mostly driven by the high incidence of foraging at or near the seafloor. Moreover, the water depths in the areas studied by Teloni et al. (2008) and Watwood et al. (2006) were generally deeper than those in our research area, suggesting that the shallower foraging depths recorded in their studies were not driven by demersal foraging at shallower bathymetries. The average number of buzzes per dive was almost double those previously recorded in Norway (Teloni et al., 2008), and similar to those reported by Watwood et al. (2006), suggesting relatively high prey densities at Kaikōura.

4.1. Demersal foraging by pelagic predators

The sperm whales tagged in our study spent more than half of their active foraging time within 50 m of the seabed. Compared to pelagic foraging, the prevalence of benthic or demersal foraging is generally reported to be infrequent (Watwood et al., 2006; Miller et al., 2013). Male sperm whales in the Andøya Canyon (Norway) performed a few dives to the seafloor, but pelagic foraging was dominant (Teloni et al., 2008; Fais et al., 2015). The high proportion of demersal foraging found in the present study suggests that the extreme benthic productivity of the Kaikōura Canyon (De Leo et al., 2010) plays an important role in sustaining the diet of these deep-diving predators.

Intriguingly, the high incidence of demersal foraging found in our study contrasts with the mostly pelagic hunting by sperm whales recorded at Kaikōura in a previous study (Miller et al., 2013), in which only one out of 28 full dives had a bottom phase foraging on the seafloor. The whales sampled by Miller et al. (2013) were tracked further inshore (but only by a few km) and in generally shallower waters than the whales tagged in the present study. Given the differences in bathymetry, seasonality, methodology and individual whales sampled, the study by Miller et al. (2013) and the present one are not directly comparable. The observed difference, however, raises the question of why the exploitation of benthic biomass was rare in Miller et al., 2013 (which covered a period of one year), yet so commonplace in the present one.

Submarine canyons have complex patterns of topography and hydrography, creating heterogenous habitats with strong gradients in biomass distribution and community structure (McClain and Barry, 2010; Ramirez-Llodra et al., 2010). It is possible that the organisms that support the demersal component of the sperm whales' diet are found mostly in the deeper and lower parts of the canyon, resulting in the

observed inshore-offshore differences in habitat use. On the other hand, the dominance of pelagic foraging by sperm whales in the upper canyon might simply reflect a particularly high pelagic productivity there. Steep slopes – which are more prevalent in the upper Kaikōura canyon – have been shown to increase the biomass of faunal assemblages by truncating the vertical distribution of pelagic organisms (Mauchline and Gordon, 1991; Sutton et al., 2008). Canyon heads and upper slopes are also known to facilitate aggregations of pelagic zooplankton (Macquart-Moulin and Patriti, 1996). If pelagic prey are more abundant, or if prey energy density is higher, shallower pelagic dives might be more economical than deep dives to the seafloor. Further research on the drivers of habitat use by sperm whales at Kaikōura, with simultaneous sampling of prey, is necessary to clarify the observed differences.

4.2. Sperm whale prey

The average inter-buzz interval (IBI), and duration of sperm whale buzzes were generally different when whales were foraging in mid-water vs near the seafloor, suggesting that whales might be targeting different prey types in these two habitats. Although there was some individual variation, typically longer intervals between buzzes while foraging within 50 m of the seafloor suggests that prey are more widely spread in this habitat than in the water column. Longer buzzes for prey found close to the seafloor might reflect longer chases, perhaps of faster or more motile prey. Interestingly, previous findings at Kaikōura from Miller et al. (2013) showed that buzzes near the seafloor had fewer sharp turns than pelagic ones. It was suggested that whales might line up slow-moving or unsuspecting prey from a distance. The combined findings highlight the fact that much of the foraging ecology of sperm whales remains unknown, but indicate that they have the flexibility to adjust their hunting tactics to efficiently target a variety of prey types. The fact that they forage on different prey types is also likely to be reflected in the multimodal nature of their preferred diving depths. Further research would be necessary to clarify the energetic balance of the different prey layers, but it appears that prey at the seafloor are sparser and require longer (i.e., more energy) to catch, in addition to being found at greater depths. Perhaps they have a higher caloric value compared to pelagic prey, outweighing the increased energetic costs to obtain them.

Although the trophic pathway from the productive benthos to the prey targeted by sperm whales at the seafloor is unknown, benthopelagic fish are a likely candidate to mediate this link. Ling (*Genypterus blacodes*) and hāpuku (*Polyprion oxygeneios*, also known as grouper) are two fish species common at Kaikōura (Francis, 1979) which are frequent prey for New Zealand sperm whales (Gaskin and Cawthorn, 1967). Ling is a demersal species which feeds primarily on benthic prey, including macrourid fishes (Clark, 1985), which are extremely abundant in the Kaikōura Canyon (De Leo et al., 2010). Hāpuku have a more flexible vertical distribution, foraging on demersal and mesopelagic squid and fish (Nguyen et al., 2015; Tromp et al., 2016). Further studies are necessary to better understand prey preferences and the relative contribution of benthic vs pelagic energy sources to the diet of sperm whales. As sperm whales rarely strand at Kaikōura, precluding stomach contents analysis, stable isotope analyses (Ruiz-Cooley et al., 2004; Newsome et al., 2010) might provide useful insights into their trophic ecology.

The great majority of the available pelagic biomass in deep-sea systems below the photic zone is found within the DSL, composed of mesopelagic organisms (Johnson, 1948; Hays, 2003). Many of these mesopelagic animals undergo a diel vertical migration (Gjøsaeter and Kawaguchi, 1980) from their day-time depths below the twilight zone (typically 400–800 m) up to the productive surface waters where they feed at night in the shelter of darkness. However, some mesopelagic organisms do not undergo a diel migration and remain in the deeper parts of the DSL during the night (Childress, 1995; Kaartvedt et al., 2009). The foraging by tagged sperm whales in Kaikōura at depths of

400–600 m fall within the typical boundaries of the lower parts of DSLs reported globally (O'Driscoll et al., 2009; Netburn and Koslow 2015; Klevjer et al., 2012, 2016). Although simultaneous sampling of sperm whale behaviour and prey distribution has not yet been attempted at Kaikōura, at least a fraction of the mesopelagic prey targeted by sperm whales is likely to be associated with the lower boundaries of the DSL.

Based on stomach contents analysis, the primary prey item of New Zealand sperm whales are Onychoteuthid squid, and predominantly the warty squid *Onykia ingens* (formerly known as *Moroteuthis ingens*) (Gaskin and Cawthorn, 1967). Warty squid undergo a gradual ontogenetic migration from epipelagic waters into deeper demersal habitats as they mature (Jackson, 1997), with depth ranges of 300–1400 m (Jackson et al., 2000). Adults are demersal at night but appear to migrate vertically into pelagic waters during the day, where they feed on mesopelagic myctophids associated with the DSL (Jackson et al., 1998, 2000). We found some evidence in this study for circadian shifts in the foraging depths of sperm whales, and a likely association of pelagic prey captures with depths typical of lower-DSL boundaries (i.e., ca. 500 m). Warty squid are found at Kaikōura, and mature specimens have been found floating at the surface with marks consistent with sperm whale teeth (Guerra, pers. obs.) It seems very plausible that sperm whales are targeting warty squid during their dives to 400–600 m in mid-water during the day, and possibly during demersal foraging at night. Strong associations with the DSL have been shown for many deep-diving top predators including pilot whales (Abecassis et al., 2015), elephant seals (Saijo et al., 2016) and Blainville's beaked whales (Arranz et al., 2011), for which circadian changes in foraging behaviour have been associated with changes in the vertical distribution of their prey.

4.3. Use of Dtags to study sperm whale behaviour

Dtags can provide useful insights into the foraging behaviour of deep-diving mammals in relation to the seafloor, in addition to providing night-time behaviour information. They can also offer useful information on the density of organisms in the water column, by quantifying the backscatter from animals that are ensonified by the whales (Arranz et al., 2011). However, they have some limitations – such as not being able to provide accurate georeferenced locations – which prevent relating the whales' foraging behaviour to other relevant physical characteristics of their habitat. For example, we were not able to address if demersal foraging was more or less prevalent over particular topographic features such as canyon slopes. Passive acoustic studies using three-dimensional arrays (e.g., Wahlberg, 2002; Miller and Dawson, 2009; Miller et al., 2013) are an alternative research tool, with the advantage of providing high-resolution georeferenced 3D locations for relating whale movement and behaviour to their physical environment.

We found a strong correlation between a whale's depth at the end of the search phase and the time taken to resurface, revealing a potential proxy for foraging depth when the underwater track of a whale is unknown. The duration of this silent ascent is an easy metric to record while acoustically tracking a whale. The application of this variable is however limited to sperm whales foraging individually and it only provides an estimate of depth for the final phase of a dive. In spite of these caveats, it could be useful for investigating temporal and spatial differences in foraging depth between seasons, or for assessing anthropogenic impacts on behaviour.

Our observations of sperm whale behaviour during tagging attempts revealed behavioural reactions to close vessel approaches and tagging. Tendencies to reduce time at the surface, for example, correspond to changes expected under a stress response (Richter et al., 2006; Lusseau, 2003). The rate of shallow diving (55% of all approaches) was substantially higher than the average rate recorded for Kaikōura sperm whales (6% of 677 approaches, Otago University Marine Mammal Research Group, unpublished data). The fact that sperm whales often

resurfaced within a few minutes after shallow diving suggested that this was used as an evasive manoeuvre. Although the physiological costs to the animals are unknown, they are unlikely to be long-lasting. However, this evidence suggests that sperm whales may experience some stress from tagging attempts, and that foraging behaviour measured via attached tags may be modified (Miller et al., 2005, 2009). Passive acoustic studies (Wahlberg, 2002; Miller et al., 2013) can be used to study foraging behaviour in detail, with minimal influence on the target animals. This should be considered when choosing the most appropriate method to study diving and foraging behaviour.

4.4. Ecological implications of the observed foraging behaviour

The present study has provided useful data for understanding which strata might be important for foraging sperm whales at Kaikōura. Oceanographic characteristics of mid-water depths at ca. 500 and 900 m (e.g., temperature, salinity and dissolved oxygen), in addition to physical aspects of the seafloor (e.g., slope, aspect and sediment type) would be useful additions to the candidate set of environmental variables used to investigate the habitat preferences of sperm whales. The apparent differences in foraging behaviour between inshore and offshore habitats at Kaikōura (Miller et al., 2013, present study) provide a useful framework for future research aimed at understanding intra-population variability in the spatial distribution of sperm whales.

By feeding at depth and releasing fecal plumes close to the surface (Kooyman et al., 1981; Whitehead, 1996), whales play an important role in ecosystem connectivity and enhancing productivity (Lavery et al., 2010; Roman and McCarthy, 2010; Sutton, 2013). They act as an 'upward whale pump', recycling organic carbon and nutrients from the deep by bringing them to the photic zone, where they become available to phytoplankton (Roman and McCarthy, 2010; Roman et al., 2014). The vertical flux of nutrients is particularly great in the case of sperm whales (Roman et al., 2014), due to their extreme foraging depths and their uptake of food sources across the entire water column. In Kaikōura, where the density of sperm whales has been historically high (Childerhouse et al., 1995), their contribution to the biological pump could be an important driver of the canyon's high productivity. The fact that abundance of sperm whales at Kaikōura appears to be declining (van der Linde, 2009), raises questions about whether this productivity will be sustained. Unexpected responses of coastal ecosystems to anthropogenic stressors arise from insufficient knowledge about complex food web interactions and feedback loops (Doak et al., 2008). It is therefore essential to better understand food web structures, mechanisms and functions. Elucidating the processes that result in the extraordinary biological assemblages associated with submarine canyons is key to their long-term protection.

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