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Variation in dive behavior of Cuvier's beaked whales with seafloor depth, time-of-day, and lunar illumination

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ABSTRACT: Depth distributions were analyzed from a study of 19 Cuvier's beaked whales *Ziphius cavirostris* that were tagged with satellite transmitting instruments off southern California, USA. Over 113 000 depth measurements were made over the equivalent of ~200 sampling days. The mean foraging depth was 1182 m (SD = 305 m), and the mean of the maximum depth of all foraging dives was 1427 m (SD = 298 m). Mean foraging depths increased with seafloor depths up to a maximum of ~1300 m at a seafloor depth of 1900 m, but decreased slightly to a mean of ~1200 m at seafloor depths of 2000–4000 m. Near-bottom habitat appears to be important for foraging; whales spent ~30 % of their foraging time within 200 m of the bottom at seafloor depths of 1000–2000 m. However, little foraging time was spent near the bottom at seafloor depths greater than 2000 m. The percentage of time spent at near-surface depths (<50 m) was more than twice as high at night (25 %) than during the day (12 %). Lunar light also appears to affect diving, with 28 % of dark nights and only 17 % of brightly moonlit nights spent at these near-surface depths. The apparent avoidance of surface waters during daytime and on brightly moonlit nights is consistent with avoidance of visual predators. A considerably greater fraction of time was spent foraging at night (24.8 %) than during the day (15.7 %), possibly due to energetic constraints imposed by predator avoidance during the day.

KEY WORDS: Cuvier's beaked whale · *Ziphius cavirostris* · Diving · Foraging · Tagging · Satellite telemetry · Depth profile · Diel patterns · Lunar patterns

1. INTRODUCTION

The recent development of methods to place electronic recording tags on Cuvier's beaked whales *Ziphius cavirostris* has greatly increased our understanding of the diving and foraging behavior of this otherwise hard-to-study species (Johnson et al. 2004, Tyack et al. 2006, Baird et al. 2008, DeRuiter et al. 2013, Schorr et al. 2014, Joyce et al. 2017, Shearer et al. 2019). Acoustic localization and tracking studies have provided additional insights (Gassmann et al. 2015, DeAngelis et al. 2017, Barlow et al. 2018). Echolocation and presumed foraging by Cuvier's beaked whales commonly occur only during deep foraging dives (Tyack et al. 2006). Maximum recorded depths of deep foraging dives for tagged individuals have ranged from a minimum of ~750 m (Tyack et al. 2006) to a maximum of ~3000 m (Schorr et al. 2014). The mean of maximum foraging dive depths from all tagged individuals range from 1070 m in the Ligurian Sea (Tyack et al. 2006) to 1492 m off Cape Hatteras (Shearer et al. 2019). In a meta-analysis of the tagging studies, Barlow et al. (2013) found that Cuvier's beaked whales spend ~47 % of their time in long, deep foraging dives and only ~28 % of their time actively foraging. Non-foraging time is spent in surfacing bouts (a series of several surfacings within 1.5–2.5 min), in shorter, shallower dives

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to less than 600 m depth, and in transit to and from their preferred foraging depths (Tyack et al. 2006, Baird et al. 2008, Schorr et al. 2014).

Although the accumulation of information on diving and foraging of Cuvier's beaked whale has been rapid, one remaining gap is in understanding the relationship between foraging depths and seafloor depth. Cuvier's beaked whales are found in slope waters along continental margins (MacLeod & Mitchell 2006, Shearer et al. 2019), in 1000–2000 m deep basins (Schorr et al. 2014), and in abyssal waters of the great ocean basins (Ferguson et al. 2006, MacLeod et al. 2006). Three studies have reported gouge marks in the seafloor postulated to result from benthic prey capture attempts by beaked whales at depths up to 4200 m (Woodside et al. 2006, Auster & Watling 2009, Marsh et al. 2018). Tyack et al. (2006) showed that echolocation buzzes (associated with prey capture attempts) were only common deeper than ~600 m and at a mean depth (863 m) that is considerably less than the maximum dive depth. Acoustic tracking studies show that, although some beaked whales forage near the bottom at depths of ~1300 m, the majority of their echolocation (and, presumably, foraging) occurs several hundred meters above the seafloor (Gassmann et al. 2015, Barlow et al. 2018). The mean depths of Cuvier's beaked whales when deeper than 800 m and presumed to be foraging were 1282 m (SD = 113 m) off Hawaii, USA (Baird et al. 2008; an average of day and night measurements) and 1180 m (SD = 225 m) off the Bahamas (T. Joyce pers. comm., based on Joyce et al. 2017). From acoustic localizations, mean depths of echolocation are 1158 m off the US Atlantic coast (De Angelis et al. 2017) and 967 m in the Catalina Basin off California (Barlow et al. 2018). These observations and others suggest that there may be biologically important differences in foraging depths among study areas (Schorr et al. 2014, Shearer et al. 2019). Those differences are likely to be related to seafloor depth and primary prey species, but prior studies do not provide analyses of the association between seafloor depth and beaked whale foraging depth.

Another knowledge gap is in understanding day/night difference in the diving behavior of beaked whales. A study in Hawaii examined diel differences in detail (Baird et al. 2008). That study included 6 Blainville's beaked whales *Mesoplodon densirostris* and 2 Cuvier's beaked whales and found that, at night, both species spent a greater proportion of their time in near-surface waters (<50 m depth) and below 500 m, and much less time in mid-water depths between 50 and 500 m. The authors attributed the greater proportion of time in near-surface waters to a reduced vulnerability to visual predators at night. A similar diel pattern was described for Cuvier's beaked whales tagged off Southern California (Schorr et al. 2014; based on analyses of a subset of the data presented here). Schorr et al. (2014) found maximum dive depths were slightly deeper at night in California, and Baird et al. (2008) found maximum depths were slightly deeper during the day in Hawaii. Both these studies found that deep-dive durations were longer during the day than during the night (Baird et al. 2008, Schorr et al. 2014). Previous studies did not examine the effect of lunar illumination on beaked whale diving behavior, but Henderson et al. (2016) found an interaction effect between lunar illumination and time-of-day on the acoustic activity of Blainville's beaked whales in Hawaii.

Here we analyze tagging data that were collected with satellite-linked dive recorders to examine depth distributions, foraging depths and the relationship between seafloor depth and presumed foraging depth for Cuvier's beaked whales. These tags provide geolocation information, which is used with bathymetric data to estimate seafloor depth. The tags were applied with a dart attachment system and had attachment times of up to 90 d, which provide greater sample sizes in a greater diversity of habitats, often far from the original tagging location, and more nighttime observations for diel comparisons. We examine variations in depth distributions among different tagged individuals and among regions, with emphasis on the relationship between the distribution of presumed foraging depths and seafloor depth, and on diel and lunar changes in depth distributions. Because Navy use of mid-frequency active sonar (MFAS) has been shown to affect beaked whale diving behavior (Falcone et al. 2017), we use a subset of our data for which sonar use has been documented to evaluate the degree to which our measures of depth distributions and other dive parameters may be biased by sonar use in our study area.

2. MATERIALS AND METHODS

2.1. Tagging

SPLASH10-292 Argos-linked dive recorders (Wildlife Computers) were deployed on 19 individual Cuvier's beaked whales *Ziphius cavirostris* in the San Nicolas and Catalina Basins off southern California, USA, in 2010–2015 (Table 1, Fig. 1). The Low Impact Minimally Percutaneous External-electronics Trans-

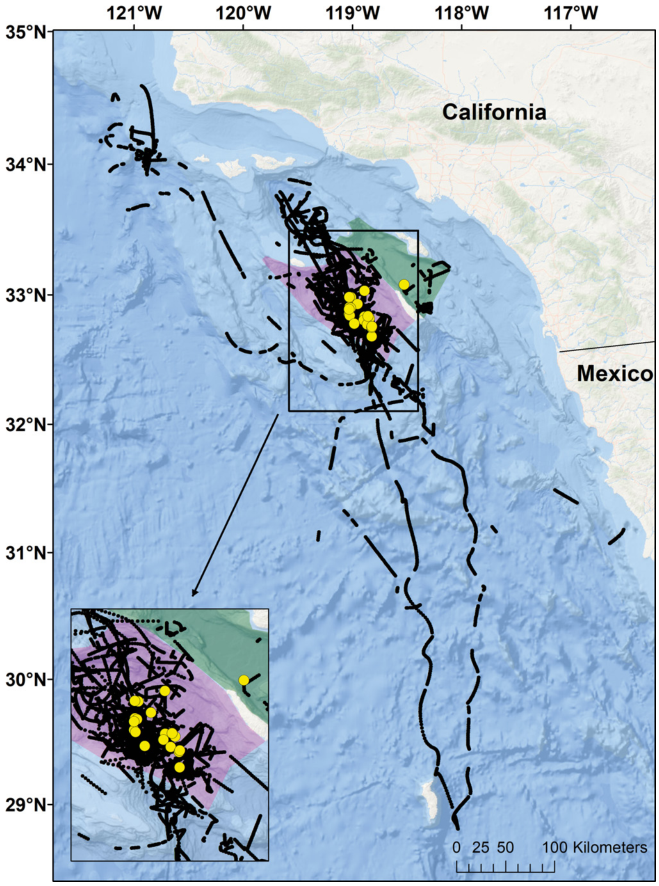

Fig. 1. Estimated movement tracks of 19 tagged Cuvier's beaked whales (thin black lines). Tagging locations are indicated with yellow circles and correspond to locations in the San Nicolas Basin (purple polygon) (n = 18) and the Catalina Basin (green polygon) (n = 1). Inset shows additional details in those basins

mitter (LIMPET) package (Andrews et al. 2008) was applied on or near the dorsal fin. Two medical-grade, gas-sterilized titanium darts attached the tag to the whale. Data from 8 tag deployments in this study were also in an earlier study by Schorr et al. (2014), and data from 15 deployments were used previously by Falcone et al. (2017).

2.2. Tag data

Table 1. Summary of satellite tag deployments by individual Cuvier's beaked whales *Ziphius cavirostris* (Zc)

Whale tag ID	Deployment date	Tag duration (d)
Zc10	29 Jun 2010	54
Zc11	29 Jun 2010	90
Zc14	6 Jan 2011	23
Zc15	6 Jan 2011	71
Zc16	6 Jan 2011	89
Zc17	23 Jul 2011	10
Zc19	15 Jan 2012	12
Zc20	15 Jan 2012	26
Zc21	29 Mar 2013	47
Zc22	30 Mar 2013	28
Zc23	30 Mar 2013	7
Zc24	4 Jan 2014	12
Zc26	7 Jan 2014	47
Zc28	11 Jan 2014	49
Zc32	5 Oct 2014	44
Zc34	3 Jan 2015	16
Zc35	7 Jan 2015	14
Zc36	9 Jan 2015	43
Zc37	9 Jan 2015	14

Detailed dive data were recorded on the tag and a subset was transmitted using the Argos satellite network. Due to the limited bandwidth of Argos transmissions, 2 data reduction schemes were applied to depth data before transmission, creating 2 types of record: behavior log dive data (BL data) and time series data. Not all time series data have associated BL data. BL data included precise start times, end times, and maximum depths of dives deeper than 50 m and longer than 30 s. Time series data included depth measurements at fixed time intervals. Here we use the time series of depths sampled at 2.5 min intervals as a random representation of the depth distribution of the whales. Transmitted depth samples were binned in variable depth intervals to decrease the number of data bits and thereby increase the number of observations that could be included in each transmission. Depth bin widths varied based on depth range within a reporting period but were, on average, ~10% of depth measurements. Tags Zc10–20 were programmed to transmit data continuously for 28 d and on alternating days afterwards to maximize the effective battery life. Tags Zc21–37 transmitted time series data for a duty cycle of 1 d every 5 d from the start.

Argos location estimates were initially filtered for plausibility with the Douglas Argos filter (Douglas et al. 2012) using the same parameters as Schorr et al. (2014). A continuous-time correlated random walk model (Johnson et al. 2008) at 30 min intervals was fit to the time series of locations (Argos-derived estimates of location and location errors) for each tag in the R (R Core Team 2018) package *crawl* (Johnson 2013).

2.3. Bathymetric data

Seafloor depth data are from the ETOPO1 1-arc-minute global relief model (Amante & Eakins 2009).

Each tag location estimate was associated with the seafloor depth at the closest point in the gridded data, which results in a maximum horizontal mismatch of about 1 km, much smaller than the median localization error (SE = 6 km) from the Argos tracking model. Recognizing that localization error can introduce considerable error in estimates of seafloor depths, analyses that include seafloor depth were limited to measurements when the estimated localization error is less than that median value (SE < 6 km), and seafloor depth was defined as the maximum seafloor depth within 6 km of an estimated location. To further limit the effect of location uncertainty on estimates of seafloor depth, we also limited our sample to regions where the seafloor was relatively flat (less than 300 m variation within 6 km of the tag location).

2.4. Analyses of depth distributions

Whale depth distributions were based on the depth-binned 2.5 min time series samples transmitted to an Argos receiver. Foraging dives were identified based on maximum depth and dive duration. If both variables were available from BL data, foraging and non-foraging dives were classified using *K*-means clustering (with $K = 2$; Schorr et al. 2014). Intermediate values in the tails of the distributions for depth or duration were examined in detail, and a few dives were re-classified based on the whales' behavior during adjacent time periods (per methods detailed by Schorr et al. 2014). If only maximum depth was available, as was the case for approximately 41% of time series samples, foraging dives were identified by having a maximum dive depth deeper than a critical threshold (800 m). This threshold was determined as the value that gave approximately equal misclassification errors in the *K*-means clustering (a non-foraging dive being classified as a foraging dive, and vice versa).

Because these tags did not directly measure echolocation or other indicators of foraging activity (e.g. accelerometry), likely foraging times within a foraging dive were inferred from other studies that used acoustic recording D-tags to record echolocation clicks that were, in-turn, used as a proxy for foraging. Seven Cuvier's beaked whales in the Ligurian Sea began echolocation at a mean depth of 457 m on descent and ended echolocation at a mean depth of 856 m on ascent (Tyack et al. 2006). Two Cuvier's beaked whales in our Southern California study area began echolocation at a mean depth of 478 m on descent and ended echolocation at a mean depth of 967 m on ascent (digitized from Figs. 1 & 2 in DeRuiter et al. 2013 using WebPlotDigitizer, excluding 2 dives with controlled exposure to simulated Navy sonar). Therefore, we assumed foraging occurred at depths deeper than 462 m on descent and deeper than 881 m on ascent of foraging dives, the average values from these 2 studies weighted by the number of whales sampled. For brevity, we use the term 'foraging' to refer to time spent at these foraging depths, but we remind the reader that this is based on an assumption from other studies.

For studies of diel patterns in diving, each depth record was classified as being either daytime or nighttime based on the estimated sun altitude at the start of the dive. Daytime was defined as having a sun altitude greater than −6° (the solar declination of civil dusk and dawn). Sun altitude was calculated from time and location using the function *getSunlightPosition* in the R package *suncalc* (Agafonkin 2018). The same 3 depth ranges (<50, 50–500, and >500 m) reported by Baird et al. (2008) were used to facilitate diel comparisons with Hawaii. Analyses of effect of lunar illumination on dive depths were limited to nighttime samples. Dark nights were defined as times when the moon was less than half illuminated by the sun or when the moon was below the horizon. Moonlit nights were defined as times when the moon was above the horizon and more than half illuminated. Moon altitude and illumination are calculated from time and location using the functions *getMoonPosition* and *getMoonIllumination* in the R package *suncalc* (Agafonkin 2018). Ascent and descent rates were calculated from the changes in depth of the time series samples during the non-echolocating periods of deep foraging dives (above 462 m on descent and above 881 m on ascent).

Median deep dive durations (DDD) and inter-deep dive intervals (IDDI) were calculated for each individual from the BL data, and individual medians were averaged for overall mean DDD and IDDI values. Dive rates (expressed in units of dives h^{-1}) were calculated for each individual as the number of deep dives divided by the total number of hours in the BL data, and individual values were averaged for an overall mean (Schorr et al. 2014). The deep dive period (i.e. the period between the start times of successive deep dives) was calculated by 2 methods: (1) the sum of DDD and IDDI and (2) the inverse of the dive rate (as calculated above). Again, values were calculated for each individual and then averaged.

Because multiple factors might be simultaneously influencing depth distributions, multivariate generalized additive models (GAMs) were used to help discern the shape and magnitudes of individual factors. Spline-smoothed models were used to predict mean depth when foraging, the fraction of time spent at a depth less than 50 m, and the fraction of time individuals were predicted to be foraging. Mean depth was modeled with a Gaussian distribution and an identity link function. The latter 2 dependent variables were modeled with a binomial distribution and a logit link function. All were modeled with the function *gam* in the R package *mgcv* with the parameter *gamma* set to 1.4 to avoid over-fitting (Wood 2006). Potential predictor variables included sun altitude, Julian day (day of the year), seafloor depth (maximum depth within 6 km), and individual tagged animal as a factor. Julian day was treated as a cyclic variable to force continuity between the end of December and the beginning of January (specified as *bs* = 'cc' in the *gam* function within *mgcv*).

To avoid undue influence of individual differences between tagged animals on our statistical inferences, individuals were used as the unit for statistical comparisons. For diel and lunar differences in depth distributions, individuals were considered as replicates in paired *t*-tests to examine differences. For multivariate analyses, tagged individuals were treated as a random effect (specified as *bs* = 're' in the function *gam* within *mgcv*).

In the present study, we follow recent statistical recommendations and avoid using arbitrary critical values (α-levels) to determine statistical significance (Wasserstein & Lazar 2016). We report p-values as an aid in evaluating the compatibility between our observations and a null hypothesis and strive to show the magnitude (or effect size) of the patterns that we observe.

2.5. Effects of Navy sonar

To evaluate the effect of Navy MFAS on our results, we estimated depth distribution metrics and other dive metrics for a subset of our data for which MFAS use data were available. We used the same sonar exposure data as a previous study that documented sonar effects on many of the same tagged individuals (see Falcone et al. 2017 for methods), limiting the sample to periods when the tagged whale was on the Southern California Anti-Submarine Warfare Range (SOAR; Fig. 1 in Falcone et al. 2017), and hydrophone archives were available so that sonar absence could be confirmed. Sonar was considered 'present' if detected by the seafloor hydrophones inside SOAR or reported in the Navy's internal sonar use database outside SOAR, and localized to within 100 km of a tagged whale at onset for 'high-power' MFAS or 50 km for 'mid-power' MFAS. Tagged animals were considered exposed if sonar was present at any time during either the IDDI or the preceding deep dive that a given sample was a part of (as was done by Falcone et al. 2017).

3. RESULTS

3.1. Overall depth distributions

The total number of depth estimates at 2.5 min intervals was 113 707 for the 19 tag deployments (Table 1). At this sample rate, this is equivalent to a total of 4738 h or 197 d of sampling. All tags were deployed in the San Nicolas Basin (n = 18) and the Catalina Basin (n = 1, tag Zc26) (Fig. 1). The distribution of depths had modes at 0–50, 200–250, and 900–1300 m (Fig. 2A) which, based on previous

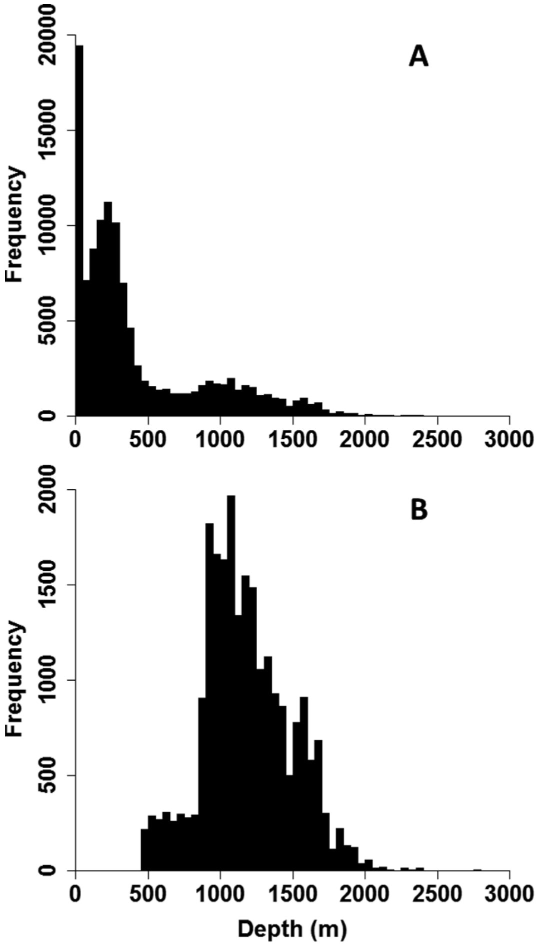

Fig. 2. Depth frequency distribution (A) for all depth measurements and (B) for times when the whales are predicted to be producing echolocation pulses (see Section 2)

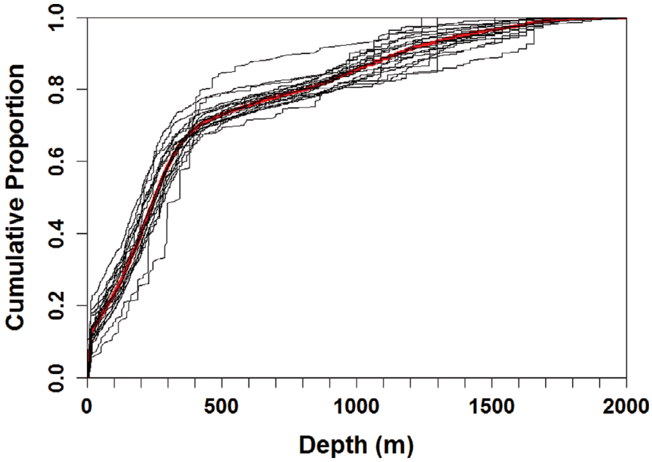

Fig. 3. Cumulative distribution of the proportion of measurements below the specified depth for the 19 tagged whales (black lines). The overall cumulative distribution of all whales is shown in red. Values above 2000 m are indistinguishable from 1.0 on this scale

studies of this species, represent time spent in surfacing bouts, in short non-foraging dives, and in long foraging dives, respectively (Tyack et al. 2006, Baird et al. 2008). The depth distribution for whales that were predicted to have been actively foraging (see Section 2) showed additional detail in the depth distributions (Fig. 2B). The cumulative depth distributions of tagged whales showed little variation among most individuals (Fig. 3).

3.2. Relationship between depth distributions and seafloor depths

All whales were tagged in basins that were 1000–2000 m deep and spent most of their time in those deep basins (Fig. 1). The maximum depths of those basins constrained the maximum dive depths to ~1300 m in the Catalina Basin and ~1800 m in the San Nicolas Basin. A bivariate plot of the estimated whale and seafloor depths for each depth measurement in our time series indicates a clear relationship between maximum whale depths and seafloor depths of less than 2000 m (Fig. 4), but at seafloor depths greater than 2000 m there appears to be little relationship between maximum whale depths and seafloor depths. A typical depth profile for one tagged whale shows that presumed foraging dives (long, deep dives) frequently, but not always, reach the seafloor (Fig. 5).

In our filtered sample with more precise locations (i.e. where the estimated tag location SE < 6 km) and a relatively flat seafloor, the seafloor depth distribution shows distinct modes at 1250–1300 and 1600–1750 m (Fig. 6). Based on these modes, we stratified depth distributions with seafloor depths of 1000–1400, 1400–2000, and greater than 2000 m (Fig. 6). As expected in these 3 subsamples, the maximum foraging depth was deeper where the seafloor is deeper (Fig. 7). However, the mean foraging depth (1217 m, SD = 354 m), where the seafloor was deeper than 2000 m, was very similar to mean foraging depth (1191 m, SD = 296 m), where seafloor depths are 1400–2000 m (Table 2). The distributions of distances from the seafloor show that whales spent a propor-

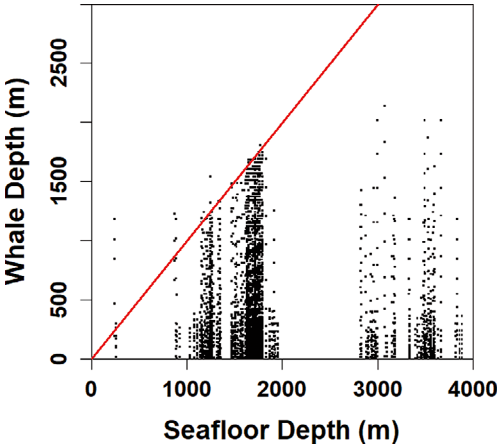

Fig. 4. Whale depths measured at 2.5 min intervals and seafloor depths (maximum depth within 6 km of the estimated whale locations) for a filtered subset with better than median localization errors (SE < 6 km) and a relatively flat seafloor. Despite the filtering, some impossible whale depths are evident (points above the red line), likely due to localization errors in regions of steep bathymetry

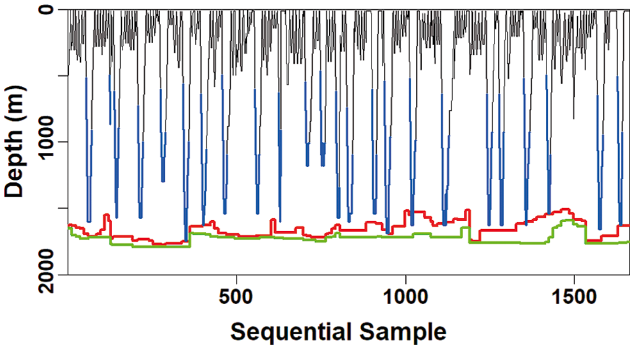

Fig. 5. Sequential depth measurements for a single tagged whale (Zc28) after filtering to remove times when location accuracy was poor. Whale depths indicate that dives during presumed periods of foraging (blue lines) frequently reached or nearly reached the estimated seafloor (red and green lines) in water depths of 1500–1750 m. Red line represents the seafloor depth at the animal's estimated position; green line represents the maximum seafloor depth within 6 km of that position. Note, some dives are not represented in their entirety due to instrument duty cycles

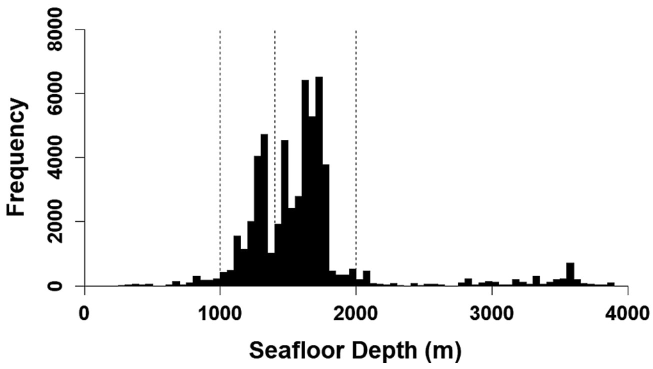

Fig. 6. Distribution of maximum seafloor depth (within 6 km of whale locations) after filtering to remove times when whale location accuracy was poor. Vertical dashed lines delimit ranges of seafloor depths used in subsequent analyses (1000–1400, 1400–2000, and greater than 2000 m)

tion of their foraging time within 200 m of the seafloor at depths less than 2000 m, but not at greater depths (Fig. 8). During presumed foraging activity, the estimated percentages of whale depth samples within 200 m of the seafloor were 32.2, 29.4 and 0.0% for seafloor depth ranges of 1000–1400, 1400–2000, and greater than 2000 m, respectively.

3.3. Diel patterns

Cuvier's beaked whales in our study spent roughly twice as much time at near-surface depths (<50 m) at night as during the day (Fig. 9, Table 3). At night, less

Table 2. Mean and SD (in parentheses) of dive depth statistics by individual and by seafloor depth strata. Maximum depth is the greatest depth recorded on each foraging dive. Foraging depths include periods when echolocation is likely (see Section 2.4). Seafloor depth strata exclude samples when location accuracy was poor. SDs represent the variation seen in individual measurements taken at 2.5 min intervals

Tag ID/ Depth strata	Depth (m)	Maximum depth (m)	Foraging depth (m)
Zc10	422 (436)	1373 (266)	1136 (310)
Zc11	461 (481)	1478 (295)	1257 (290)
Zc14	431 (427)	1315 (283)	1154 (270)
Zc15	415 (459)	1541 (349)	1222 (357)
Zc16	416 (404)	1337 (237)	1122 (252)
Zc17	370 (484)	1664 (159)	1346 (325)
Zc19	394 (443)	1404 (282)	1158 (310)
Zc20	373 (403)	1281 (280)	1110 (272)
Zc21	423 (480)	1568 (223)	1239 (295)
Zc22	411 (446)	1455 (188)	1209 (285)
Zc23	442 (482)	1400 (142)	1217 (251)
Zc24	456 (423)	1392 (n/a)	1225 (150)
Zc26	345 (368)	1214 (120)	1024 (173)
Zc28	443 (464)	1501 (254)	1184 (298)
Zc32	471 (491)	1478 (229)	1274 (318)
Zc34	462 (542)	1727 (64)	1374 (330)
Zc35	381 (324)	1488 (217)	1169 (289)
Zc36	400 (385)	1318 (177)	1090 (211)
Zc37	379 (367)	1301 (239)	1077 (229)
All whales	419 (443)	1427 (298)	1182 (305)
1000–1400 m seafloor	381 (382)	1241 (151)	1056 (199)
1400–2000 m seafloor	426 (450)	1482 (245)	1191 (296)
>2000 m seafloor	386 (446)	1615 (398)	1217 (354)

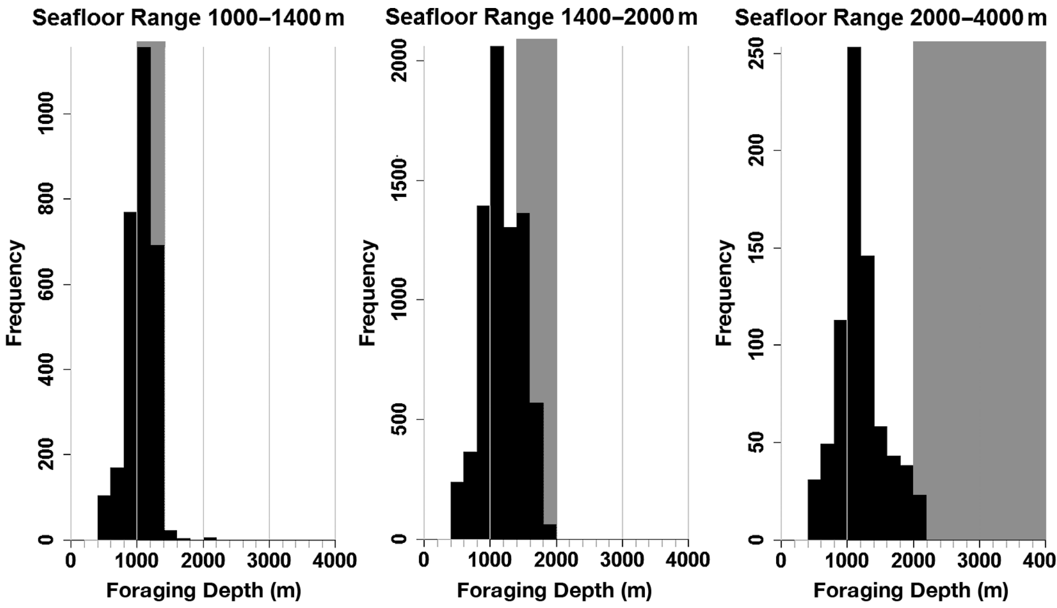

Fig. 7. Distributions of depths for foraging whales (estimated to be producing echolocation pulses) for 3 ranges of seafloor depths (gray area in each plot), after filtering to remove times when whale location accuracy was poor. Note, *y*-axis scales vary among panels

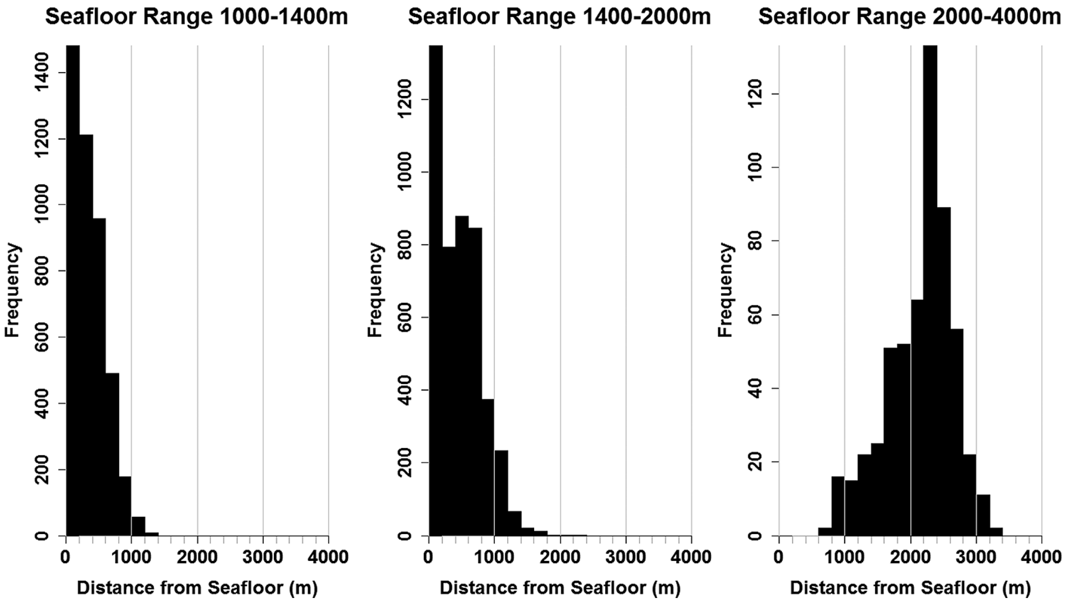

Fig. 8. Distribution of distances from the seafloor for foraging whales within 3 ranges of seafloor depths, after filtering to remove times when whale location accuracy was poor

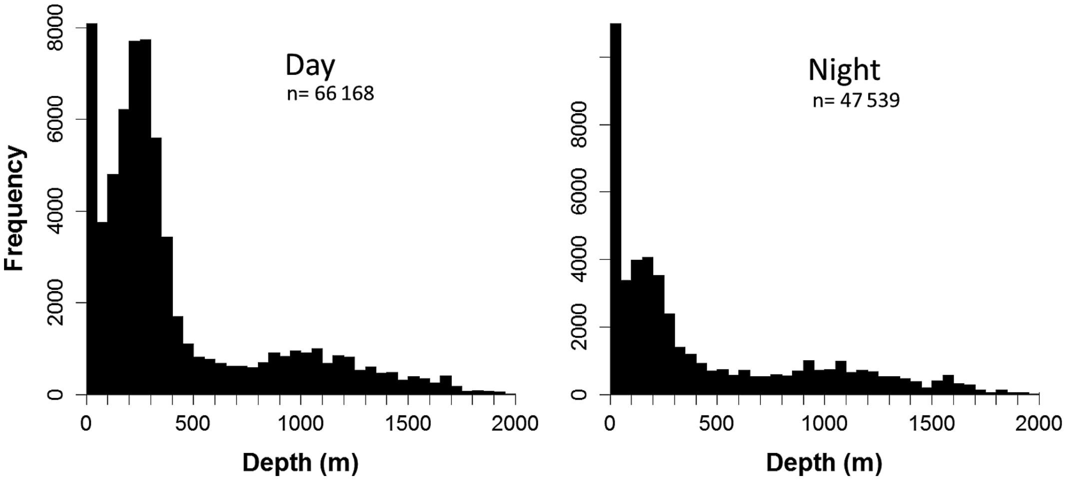

Fig. 9. Distributions of depth estimates for Cuvier's beaked whales during the day and night. The daytime sample is larger because it is defined by a sun declination angle (> −6°) rather than by sunset

time was spent at mid-water depths (50–500 m) and more time was spent at foraging depths (greater than 500 m) (Table 3). None of these 3 differences can be attributed to random chance (paired *t*-tests, $p < 0.0004$ for all). The fraction of time spent foraging (inferred from diving behavior) was also greater at night than during the day (Table 3) (paired *t*-test, $p = 0.0003$). Mean foraging depths were, on average, slightly greater at night (1207 m) than during the day (1167 m), but this difference was small and not consistently different among individuals (paired *t*-test, $p = 0.05$). Perhaps related to that, the percentage of time within 200 m of the seafloor was greater at night (Table 3) (paired *t*-test, $p = 0.013$). DDDs were slightly shorter (~6%) at night (Table 3), a difference that was consistent among individuals (paired *t*-test, $p < 0.00001$), and IDDIs were ~22% shorter at night (paired *t*-test, $p < 0.00001$). As a net effect of slightly shorter DDD at night and much shorter IDDI at night, dive rates were about 20% higher at night (paired *t*-test, $p = 0.00002$). Mean ascent rates were ~33% greater at night than during the day (Table 3) (paired *t*-test, $p < 0.00001$). Mean descent rates were similar for day and night (Table 3) (paired *t*-test, $p = 0.61$). Deep dive periods were ~12% shorter when estimated as the sum of DDD and IDDI than when estimated as the inverse of the dive rate (Table 3), possibly from a bias in the way that IDDI was estimated (see Section 4).

Table 3. Diel variation in dive statistics for Cuvier's beaked whales. All values are averages (SDs in parentheses) of the median or percentage value for each tagged whale. Percentages of time are given for 3 depth ranges, when foraging, and when close to (<200 m) the seafloor. Deep dive periods are estimated by 2 methods (see Section 2.4). Descent and ascent rates are the rates of change in depth and not speeds through the water. DDD: deep dive durations; IDDI: inter-deep dive intervals

Dive statistic	Day	Night	Overall
% time < 50 m deep	11.6 (2.3)	24.9 (9.4)	17.1 (4.7)
% time 50–500 m deep	67.4 (8.6)	43.2 (11.2)	57.0 (6.4)
% time >500 m deep	20.9 (7.3)	31.9 (5.6)	26.0 (3.6)
% time foraging	15.7 (5.7)	24.8 (4.2)	19.9 (3.1)
% time <200 m from seafloor	5.3 (3.0)	8.6 (3.3)	6.5 (2.6)
Mean foraging depth	1167 (115)	1207 (95)	1188 (89)
DDD (min)	67.9 (6.9)	63.5 (5.7)	65.5 (6.4)
IDDI (min)	113.0 (23.8)	94.7 (23.4)	103.1 (23.1)
Dive rate (dives h^{-1})	0.289 (0.046)	0.351 (0.050)	0.319 (0.041)
Deep dive period (min) DDD+IDDI	180.8 (28.6)	158.2 (27.2)	168.6 (27.7)
Deep dive period (min) 1/(dive rate)	213.0 (35.6)	174.4 (28.5)	191.4 (28.2)
Descent rate (m s^{-1})	1.45 (0.20)	1.46 (0.11)	1.45 (0.14)
Ascent rate (m s^{-1})	0.59 (0.13)	0.79 (0.15)	0.70 (0.13)

3.4. Lunar patterns

Limiting our data to nighttime, we found that the percentage of time spent at near-surface depths (<50 m) was greater on dark nights (28.1%) than on nights with a bright moon (17.2%). Cumulative distribution plots (Fig. 10) show that this lunar effect was only apparent above 250 m depth. This pattern of higher values on dark nights was consistent for all 14 tagged individuals which had data in both dark and bright moon-lit conditions, and this result was unlikely to be attributable to random chance (paired *t*-test, $p < 0.0001$).

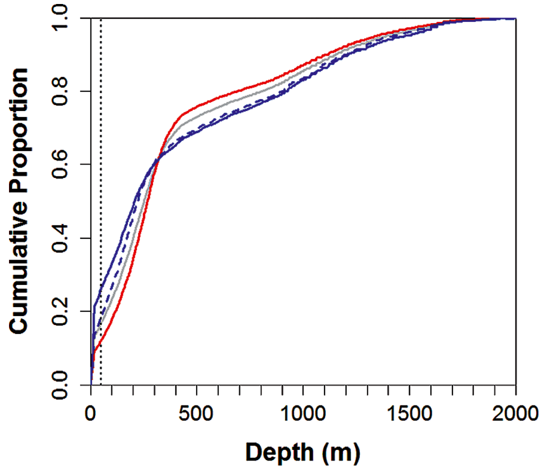

Fig. 10. Cumulative distributions of the proportion of measurements below the specified depth for the 19 tagged whales during the daytime (solid red line), on dark nights (solid blue line), on moonlit nights (dashed blue line) and for all measurements pooled (gray line). Vertical dotted line indicates 50 m depth. Values above 2000 m are indistinguishable from 1.0 on this scale

3.5. Multivariate comparisons

The multivariate model of the proportion of time spent at shallow depths (<50 m) (Fig. 11) illustrates the diel pattern with sun angle. The spline smooth shows that the best sun angle to describe the transition from daytime to nighttime patterns is closer to −6° (civil dawn, or the middle of nautical twilight) rather than 0° (sunrise and sunset) or −12° (nautical dawn and dusk). Little pattern can be seen in this proportion of time in shallow water with Julian day or seafloor depth. There was considerable variability between individual whales (tag number). The effects of the tag number, Julian day and seafloor depth variables may be confounded because tagging periods were short compared to the entire year and only a few whales were represented at deeper seafloor depths. The corrected Akaike's information criterion (AIC_c) values for models without each of the 4 explanatory variables were lower than for the full model, indicating that all the variables appear to contribute explanatory power (but see the consideration of non-independent measurements in Section 4).

The multivariate model of the proportion of time spent foraging (Fig. 12) shows the same pattern of more foraging time at night, as was seen in the univariate data, but also shows temporal variation within this general pattern. Foraging was estimated to be particularly low at sunrise and sunset, and higher at sun angles of −20° to −25° (just after sunset or before dawn). Although the sample of tagged animals was small (only 2 individuals), the time spent foraging was estimated to increase dramatically between Days 250 and 300 (early September to late October). The variation among tagged individuals in the proportion of time spent foraging was smaller than the individual variation seen in the proportion of time in shallow waters. Based on AIC_c values, all the variables appear to contribute explanatory power.

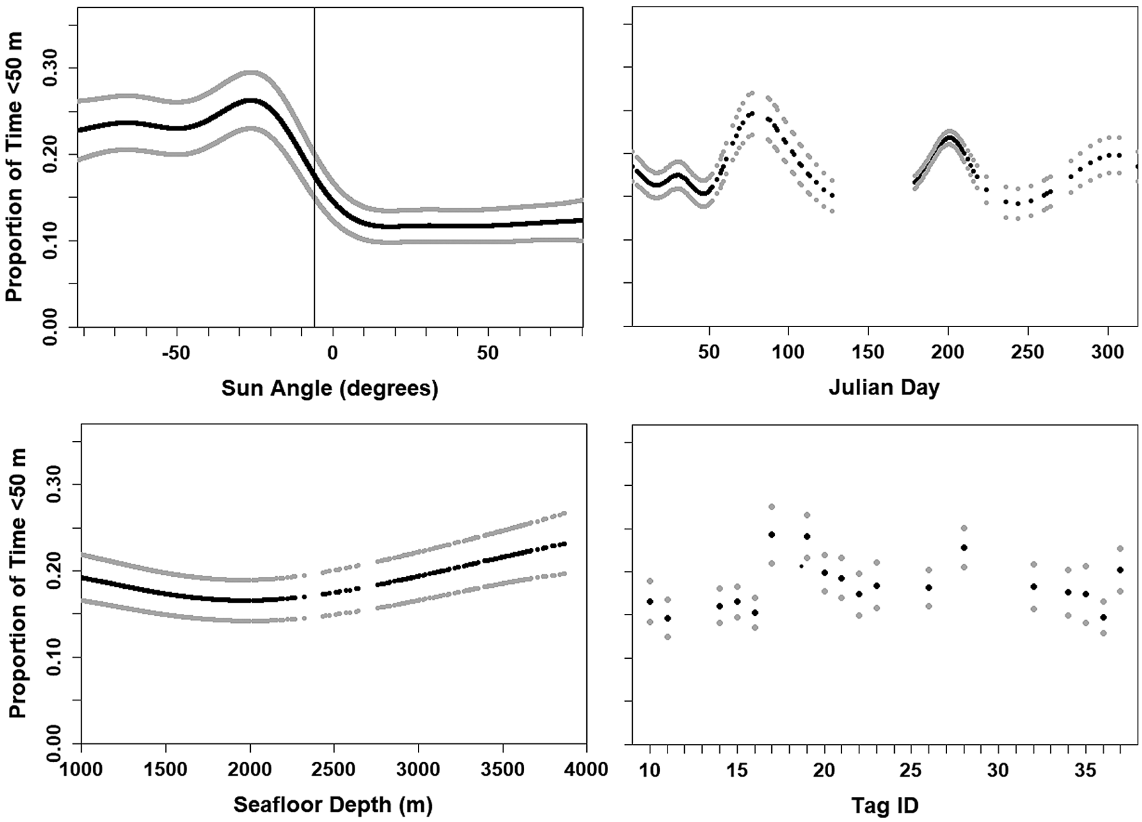

Fig. 11. Generalized additive model predictions of the proportion of time in shallow depths (<50 m) for a multivariate model which includes spline fits to sun angle, Julian day, and seafloor depth and a random effect (tag number). Marginal mean values (black) and confidence intervals (means ±1 SE, gray) are given for each predictor variable. Vertical line at a sun angle of −6° represents civil dusk and dawn which is used to define day and night times in other analyses. Gaps in the predicted values indicate a lack of data for that variable

For seafloor depths that are less than approximately 1900 m, the multivariate model of mean foraging depth showed the expected relationship between foraging depth and seafloor depth (Fig. 13). Data were sparse at seafloor depths of more than 2000 m, so little can be said about the apparent patterns at those depths given the variation that was also seen among individuals. There was no overall pattern of increasing foraging depth with seafloor depth of 2000–4000 m. As was seen in the univariate analyses, foraging appears to be slightly deeper at night, but this effect was small compared with the seafloor depth effect. $\mathrm{AIC_c}$ values indicate that all the variables contribute explanatory power.

3.6. Effects of Navy sonar

Navy MFAS was present during 10.4% of the time whales were on SOAR and archives of sonar use were available. The effect of sonar on most of our dive metrics was small (Table 4). The effect size (the difference in estimates with and without sonar) was less than 4% of the overall values for all the metrics except IDDI. Paired *t*-tests with individual values as replicates showed that observed differences could have occurred by chance ($p > 0.2$) for all metrics except IDDI. The effect of MFAS on IDDI was large, and this difference is not likely to have occurred by chance ($p = 0.01$ in a paired *t*-test). Because the effect sizes were small and because sonar was only present ~10% of the time, estimates of the same metrics for the overall sample were very similar to estimates made in the absence of Navy sonar. Even for IDDI, which had the largest effect size, the overall value differed from the value without sonar by only 3%.

4. DISCUSSION

Most previous studies of the diving behavior of Cuvier's beaked whales *Ziphius cavirostris* have focused on maximum dive depths (Tyack et al. 2006, Schorr et al. 2014, Shearer et al. 2019) and provide

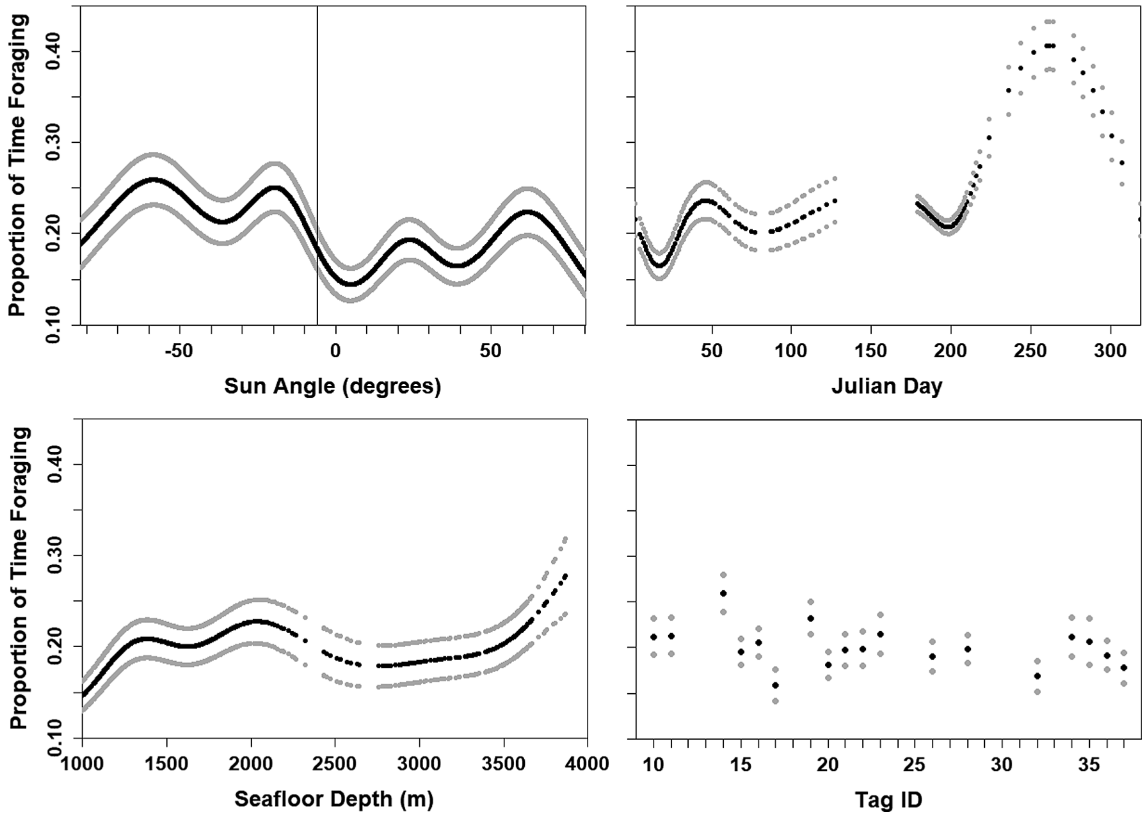

Fig. 12. Generalized additive model predictions of the proportion of time foraging for a multivariate model which includes spline fits to sun angle, Julian day, and seafloor depth and a random effect (tag number). Marginal mean values (black) and confidence intervals (means ±1 SE, gray) are given for each predictor variable. Vertical line at a sun angle of −6° represents civil dusk and dawn which is used to define day and night times in other analyses. Gaps in the predicted values indicate a lack of data for that variable

little information on the percentage of time spent as a function of depth for foraging and non-foraging dives. Only the study by Baird et al. (2008) showed the cumulative distribution of depths. Geolocation tags were used on Cuvier's beaked whales in 2 published studies. A study off Cape Hatteras, North Carolina, USA, did not examine seafloor depth effects because the slope bathymetry in that area was too steep to estimate depth given the precision of their localizations (Shearer et al. 2019). In the Bahamas, Joyce et al. (2017) found that ~74% of tag localizations were at seafloor depths of 800–1900 m, which they considered to be within the effective dive range of Cuvier's beaked whales.

In our study, available data spanned a wide range of depths. We examined the distributions of dive and presumed foraging depths of Cuvier's beaked whales from a very large sample that includes tagging locations in the San Nicolas and Catalina Basins in Southern California as well as excursions of up to 500 km from those locations (Fig. 1). Because our tags allowed locations to be estimated, we were also able to estimate bottom depths during dives. We show that foraging dives often extend to the bottom in water depths up to 2000 m and occasionally do so in water depths of almost 3000 m. Mean foraging depths increase with seafloor depths up to a maximum of ~1300 m at a seafloor depth of 2000 m (Fig. 13). Joyce et al. (2017) also found that Cuvier's beaked whale maximum dive depth was correlated with seafloor depth over the range of 850–2250 m seafloor depth.

Approximately 30% of foraging time is spent within 200 m of the seafloor at depths of 1000–2000 m. Near-bottom habitat appears to be favored foraging habitat, likely because of higher prey densities, or perhaps because of the ability to use the bottom to facilitate prey handling (Woodside et al. 2006, Auster & Watling, 2009). However, very little foraging time is spent near the bottom at depths greater than 2000 m, suggesting that the importance of near-seafloor foraging depends on water depth. This reduced importance of seafloor foraging at greater depths is likely a result of diminishing returns given

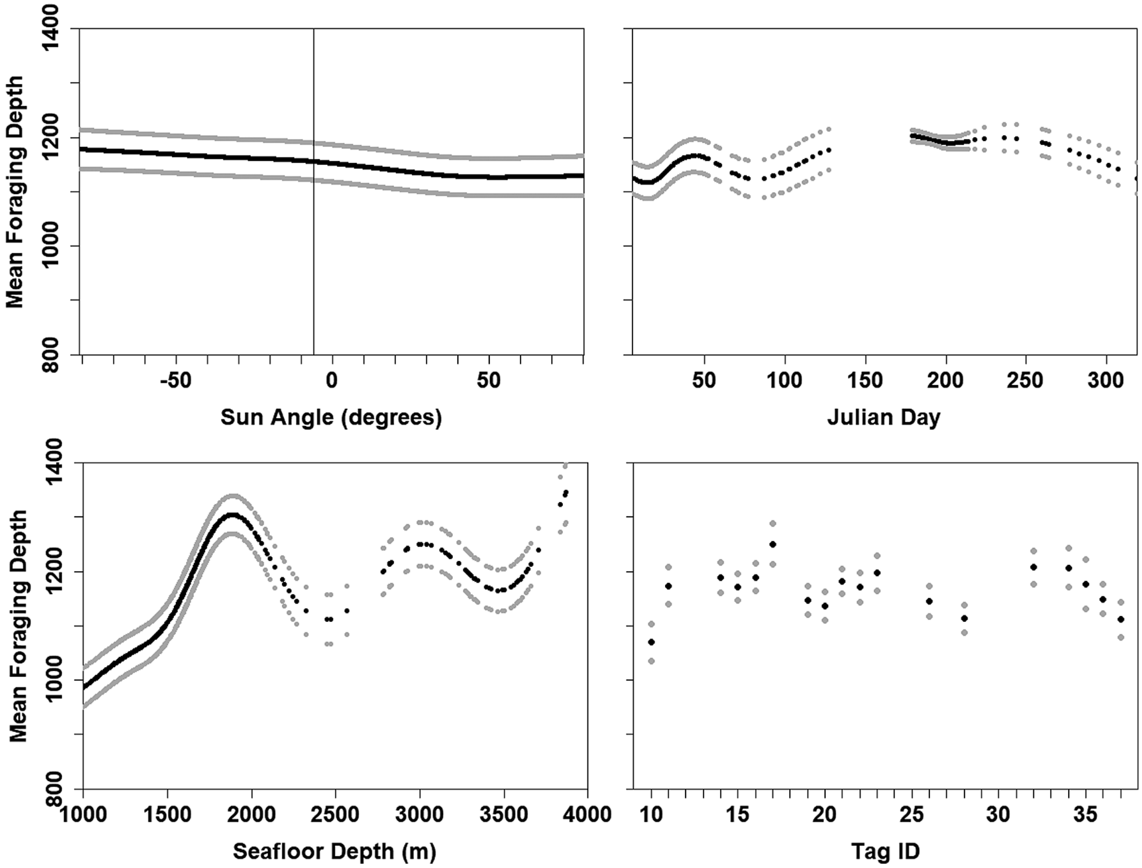

Fig. 13. Generalized additive model predictions of the mean foraging depth for a multivariate model which includes spline fits to sun angle, Julian day, and seafloor depth and a random effect (tag number). Marginal mean values (black) and confidence intervals (means ±1 SE, gray) are given for each predictor variable. Vertical line at a sun angle of −6° represents civil dusk and dawn which is used to define day and night times in other analyses. Gaps in the predicted values indicate a lack of data for that variable

the longer transit times but may also be related to changes in the density or availability of bottom-associated prey in deeper waters. Ultimately, foraging depth is likely to depend on the depth and availability of prey, which is affected by many factors other than seafloor depth.

Table 4. Variation in dive statistics for Cuvier's beaked whales with and without the presence of Navy mid-frequency active sonar, and in the overall dataset. All values are averages (SD in parentheses) of the median or percentage value for each tagged whale. Percentages of time are given for 3 depth ranges and when foraging. Samples were limited to whales within the bounds of SOAR during periods when data from bottom-mounted hydrophones were available to verify sonar absence when sonar was neither detected on range hydrophones nor reported in the Navy's internal sonar use database within specified distances. For inter-deep dive intervals (IDDI), sonar was present if it occurred during the IDDI or during the preceding deep dive. DDD: deep dive durations

Dive statistic	With sonar	Without sonar	Overall
% time < 50 m deep	16.9 (12.1)	17.0 (4.2)	17.3 (3.6)
% time 50–500 m deep	59.3 (27.7)	56.6 (6.8)	56.4 (6.9)
% time >500 m deep	23.7 (19.5)	26.3 (3.5)	26.3 (4.2)
% time foraging	17.2 (17.9)	20.2 (3.1)	20.2 (3.4)
Mean foraging depth (m)	1223 (178)	1177 (78)	1187 (86)
DDD (min)	65.6 (14.2)	63.1 (5.1)	63.6 (5.1)
IDDI (min)	177.5 (87.7)	92.6 (26.6)	95.6 (28.0)
Dive rate (dives h^{-1})	0.338 (0.168)	0.341 (0.039)	0.340 (0.044)

Importantly, our sample is limited to whales that were tagged in relatively flat-bottomed basins that are 1000–2000 m deep. Our inferences are limited to this subset of whales which may have adapted specialized feeding behavior that is effective in these areas. Prior study of these whales has shown a high degree of residency in these habitats (Falcone & Schorr 2014). Although several whales in our sample moved into deeper areas outside these basins, whales that are normally resident in the basins may still not be behaving in the same way as individuals whose typical habitat is over deep abyssal waters.

Deep basins have some of the highest densities of beaked whales that have been estimated for any habitat (Moretti et al. 2006, 2010, Marques et al. 2009). The apparent preference for near-bottom feeding at seafloor depths less than 2000 m may help explain their preference for deep basin habitat. Comprehensive beaked whale prey studies are needed to better understand prey distributions in these basins. Results from this study may help in the design of future prey mapping studies in the region, e.g. focusing on near-bottom habitat. However, in one study of potential beaked whale prey density in the San Nicolas Basin (where much of our study took place), acoustic backscatter was similar between depths of 900–1200 m and depths within 50 m of the bottom (Southall et al. 2019); however, that study was not able to measure near-bottom acoustic backscatter in the deeper parts of the basin where most beaked whales are found.

Although the density of Cuvier's beaked whales may be greater in slope and basin waters, the total area of available habitat is much greater in abyssal waters, and most individuals of this species likely live in areas that are greater than 3000 m deep (Keating et al. 2018). Clearly there is a need to conduct studies of beaked whale diving and foraging depths in this very different environment. Although feeding on seafloor-associated prey is uncommon at depths greater than 2000 m in our data, others have attributed seafloor gouge marks at depths up to 4200 m to beaked whales (Woodside et al. 2006, Auster & Watling 2009, Marsh et al. 2018).

The diel differences in dive depths of Cuvier's beaked whales are similar to those that have been documented off Hawaii (Baird et al. 2008) and Southern California (Schorr et al. 2014, based on different analyses of a subset of the data presented here). Non-foraging dives are much shallower at night, and animals spend much more time in near-surface waters (<50 m) at night. The percentage of time in near-surface waters at night was greater in Hawaii (35 and 51% for 2 tagged individuals in Baird et al. 2008) than in our California sample (mean = 25%); however, one of our tagged individuals spent 43% of its time in near-surface waters at night, which is within the range observed for the 2 Hawaii animals. The mean percentage of time spent at depths greater than 500 m was also greater at night than during the day in our study (32 vs. 21%) and in Hawaii (43 vs. 36%, Baird et al. 2008). Since most dives greater than 500 m are likely to be foraging dives, whales in Hawaii appear to be spending more time foraging than whales in California, consistent with the observations from Schorr et al. (2014).

Using inferred foraging behavior from our tag data, we also found that animals spent a greater fraction of time foraging at night than during the day (25 vs. 16%). As was noted by Schorr et al. (2014) and is reenforced with our larger sample size, DDDs are slightly longer during the day, which might be expected to result in a reduced amount of foraging at night. However, we found that mean IDDIs are ~25 min longer during the daytime, and ascent rates are considerably slower during the daytime (an ascent from 900 m would take approximately 6.4 min longer than at night). The net effect of all these diel differences is a reduced fraction of time feeding and a reduced dive rate during the day.

A reduced ascent rate during the day was also reported by Baird et al. (2008). The slower ascent than descent for Cuvier's and Blainville's beaked whales is hypothesized as a mechanism to avoid visual predators (e.g. killer whales *Orcinus orca*) (Aguilar de Soto et al. 2018). Ascending slowly at a shallow pitch angle (typically 35° above horizontal) may help maximize the distance between the location of their last echolocation click and the location of their surfacing and may thereby reduce the likelihood that a killer whale could find a beaked whale (Aguilar de Soto et al. 2018). Given that killer whales are likely to be a greater threat to beaked whales during the daytime, our observation of slower ascents during the day is consistent with this hypothesis.

We also found that Cuvier's beaked whales spend less time in near-surface waters during nights with strong moonlight. Baird et al. (2008) interpreted the avoidance of near-surface waters during the daytime as a strategy to avoid visual predators. Previous studies show that beaked whales rarely produce echolocation clicks above 500 m depth (Tyack et al. 2006), so this change is unlikely to be related to foraging. It may be that beaked whales also avoid surface waters on moonlit nights for the same reason, i.e. avoidance of killer whales, although the pattern is not as strong as the day/night difference. Delphinid foraging has also been found to depend on lunar illumination (Simonis et al. 2017), but in that case, the effect is thought to be related to the greater availability of vertically migrating species on dark nights. Blainville's beaked whales appear to forage more at night when lunar illumination is strongest (Henderson et al. 2016).

The greater proportion of time foraging at night is harder to explain. Beaked whales typically feed at depths of perennial darkness on deep-water species of squid and fish that are not believed to migrate vertically on a diel rhythm. Assuming that feeding is equally efficient during the day and night, their daytime predator avoidance strategy may affect their foraging by reducing the time or the energy available for foraging. However, even small diel changes in the behavior of their prey could affect the efficiency of feeding and the relative benefits of nocturnal feeding. Beaked whale prey are too deep and have target strengths that are too small to be reliably detected with shipboard scientific echosounders. Future studies of their prey with echosounders mounted on the seafloor or in deep submersible vehicles may help explain their diel foraging patterns.

The results of our multivariate analyses generally support our univariate results but allow the simultaneous consideration of multiple interacting and nonlinear effects. Both approaches show additional insights and details that might be testable with future data collections. Although AIC scores show that all tested variables contributed to the explanatory power of our multivariate models, that metric assumes that each data point is independent. This assumption is violated with our time-series measurements that are only 2.5 min apart. Therefore, we are cautious in not interpreting every bump and dip in the resulting smoothed effects of individual variables.

The *gam* smooth shows that the transition between the day/night difference in the proportion of time in near-surface waters might be best described by a sun angle of –6°, which we recommend for future studies. That analysis also shows considerable individual variation in the proportion of time spent in shallow waters, which is helpful in interpreting differences between other studies. The large change in the proportion of time spent foraging in September and October may be related to changes in prey availability in this area which could also be tested in future studies. The *gam* smooth of mean foraging depth with seafloor depth shows that a maximum in foraging depth is reached with a seafloor depth of ~1900 m. This may be a good measure of the depth of transition at which bottom-associated feeding is no longer energetically advantageous.

The foraging depth distributions we present are potentially of value in estimating beaked whale density and abundance. The use of distance-sampling methods to estimate animal density requires knowledge of the distributions of ranges at which whales can be detected (Barlow et al. 2013). Barlow & Griffiths (2017) proposed a method of estimating this distribution of acoustic detection ranges for estimating beaked whale density in acoustic point-transect surveys. If the distribution of declination angles to acoustically detected beaked whales can be measured from near-surface or bottom-mounted hydrophone recorders, this information can be combined with information on the distribution of echolocation depths to estimate the distribution of acoustic detection range.

Compared with most previous studies, the tag and tagging method we use has the distinct advantages of providing location information, albeit coarse, and a long tag duration. However, the lack of acoustic recording capability of these tags is clearly a shortcoming. We were required to use prior studies with acoustic recording D-Tags to estimate the depths of echolocation (and hence foraging). Although the depths at which echolocation starts and ends during a foraging dive appear to be very consistent between the Ligurian Sea and Southern California, the California sample included only 2 individuals. Although echolocation onset depth may indicate where animals start to search for prey, the depth distribution of successful foraging would be much more informative. Echolocation buzzes are believed to be associated with finding prey, and buzzes followed by a pause are believed to indicate successful prey capture. Prey chases and captures are also often represented in accelerometer data from tags equipped with these sensors. Tags that combine acoustic, accelerometer data, improved location accuracy via GPS sensors, and the ability to collect these data for extended periods are under development and testing now. These tags will add considerable precision to our understanding of the fine-scale foraging ecology of beaked whales.

All of our tags were deployed, and most of our observations were made, within the US Navy's Southern California Offshore Range (SCORE), an area with relatively frequent use of military MFAS from high-power systems on Navy ships and mid-power dipping systems from helicopters (Falcone et al. 2017, which included a large subset of the data presented here). That study found a variety of changes in diving behavior associated with proximity to MFAS use, which could affect some of our results relative to the same area without sonar use. In particular, that study noted a strong, distance-mediated increase in IDDI, and correspondingly reduced deep dive rate, with decreasing exposure distances up to 100 km of a MFAS source (Falcone et al. 2017). The effect of sonar on our general results appears very small, likely because the effect size was relatively small for most metrics and because sonar activity was relatively infrequent across the subset of data we assessed for sonar effects. Further, exposed data were pooled across the full range of exposure distances, the more distant of which likely elicited very weak responses. Thus, we conclude that the presence of sonar use within the overall data is not unduly influencing our key findings.

Our results confirm the earlier observation by Schorr et al. (2014) that the period between deep dive starts is longer when estimated as the inverse of the dive period than when estimated as the sum of IDDI plus DDD. We believe that this difference is likely caused by a bias in the estimation of IDDI from BL data. We only estimate IDDI when there is a complete record of surfacings and short/shallow (presumed non-foraging) dives between 2 deep foraging dives. Because of satellite data limitations, not all short/shallow dives were successfully transmitted. Longer IDDIs are therefore more likely to be underrepresented in our data because they are more likely to be excluded due to failed data transmission. This leads to a biased underestimation of IDDI and of dive period using the IDDI + DDD method. Therefore, we recommend estimating dive periods as the inverse of the dive rate. If unbiased estimates of IDDI are required from similar tagging data, they might be better estimated as this dive period minus the DDD.

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