Marine Mammal Science

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A Comparison of Diving Behavior of Goose-Beaked and Dense-Beaked Whales From Tagging Studies in Multiple Ocean Basins

Jay Barlow[1] | Robin W. Baird[2] | Janelle Badger[3] | Gregory S. Schorr[4] | Erin A. Falcone[4] | Shannon N. Coates[4] | Peter L. Tyack[5] | Andrew J. Read[6] | Leigh S. Hickmott[7] | John W. Durban[8] | Diane Claridge[9] | Natacha Aguilar de Soto[10] | Daniel Miranda Gonzalez[10] | Fleur Visser[11,12] | Machiel G. Oudejans[11] | Stacy DeRuiter[13] | David A. Sweeney[4,14] | Brenda K. Rone[4] | Stephanie L. Watwood[15]

[1]Cascadia Scientific Services, Olympia, Washington, USA | [2]Cascadia Research Collective, Olympia, Washington, USA | [3]Cetacean Research Program, Pacific Islands Fisheries Science Center, Honolulu, Hawai'i, USA | [4]Marine Ecology and Telemetry Research, Washington, USA | [5]School of Biology, University of St Andrews, St Andrews, UK | [6]Duke University Marine Laboratory, Beaufort, North Carolina, USA | [7]Open Ocean Consulting, Hampshire, UK | [8]Anderson Cabot Center for Ocean Life, New England Aquarium, Massachusetts, USA | [9]Bahamas Marine Mammal Research Organisation, Abaco, The Bahamas | [10]Oceanographic Centre of the Canary Islands (IEO/CSIC) and University of La Laguna, Tenerife, Canary Islands, Spain | [11]Kelp Marine Research, Hoorn, the Netherlands | [12]Royal Netherlands Institute for Sea Research, Texel, the Netherlands | [13]Department of Mathematics and Statistics, Calvin University, Grand Rapids, Michigan, USA | [14]Centre for Research Into Ecological and Environmental Modelling, University of St Andrews, St Andrews, UK | [15]Naval Undersea Warfare Center, Newport, Rhode Island, USA

Correspondence: Jay Barlow (jaybarlow33@yahoo.com)

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ABSTRACT

Studies of cetacean diving behavior in multiple locations in different ocean basins allow for an assessment of variability within and among populations. We examine foraging dive behaviors of goose-beaked whales (*Ziphius cavirostris*) and dense-beaked whales (*Mesoplodon densirostris*) using data from 132 tagged whales in seven locations in the Pacific and Atlantic Oceans and the Mediterranean Sea. Acoustic recording tags are used to identify foraging dives by the presence of echolocation. For other tag types, foraging dives are identified based on maximum dive depth. Five parameters are used to characterize foraging dives: maximum dive depth, foraging dive duration, dive cycle duration, and the mean and standard deviation of echolocation depths. We find that differences among dives within one tagged individual are typically larger than the differences among individuals or among locations, and that differences among individuals are typically similar in magnitude to differences among locations. Regression is used to estimate the mean and standard deviation of echolocation depths from maximum dive depth for dives without acoustic data. Composite values of foraging dive parameters (and standard deviations) are estimated as the average of all study locations.

1 | Introduction

Beaked whales are a distinct clade that diverged from other cetaceans in the early Miocene (~16–23 million years ago) (Lambert et al. 2015). Although early beaked whales appear to have included species that fed in epipelagic waters (Lambert et al. 2015), surviving beaked whale species are highly evolved for deep diving (Pabst et al. 2016). The goose-beaked whale (*Ziphius cavirostris*, also known as Cuvier's beaked whale) holds the record for the deepest (2992 m, Schorr et al. 2014) and longest (222 min, Quick et al. 2020) dives of any mammal. Although the deep foraging behavior of beaked whales was first inferred from the depth distribution of their prey (MacLeod et al. 2003), research on their diving behavior took a great leap forward with the recent development of depth recording tags that could be deployed on beaked whales (Tyack et al. 2006; Baird et al. 2006). Here we provide insights into the diving behavior of two beaked whale species based on a synthesis of tagging studies in multiple locations.

The diving behavior of goose-beaked whales and dense-beaked whales (*Mesoplodon densirostris*, also known as Blainville's beaked whale) is highly stereotypical. They perform dive cycles composed of a long, deep foraging dive followed by a series of shorter, shallower non-foraging dives with short periods at the surface between each dive (Tyack et al. 2006; Baird et al. 2006, 2008; Joyce et al. 2017; Arranz et al. 2011). Consistent periods of echolocation typically occur only during deeper portions of deep foraging dives, and both species are typically silent during the initial descent and most of the ascent from these dives (Johnson et al. 2004; Warren et al. 2017; Aguilar de Soto et al. 2020; Sweeney et al. 2022).

The preferred prey species for beaked whales are meso-pelagic squid, fish, and crustacean species that are found predominantly between 200 and 2000 m (MacLeod et al. 2003; New et al. 2013). Variation in foraging depths may be due to variation in prey availability. Off the Azores, the depth of prey capture attempts for goose-beaked whales (as inferred from foraging buzzes) showed either within-dive layer-restricted foraging around 1000 m or a wide target prey field between 800 m and the sea floor (up to 1700 m) (Visser et al. 2021). These two foraging modes were matched with a wide diversity of potential prey species across the foraging depth range. Acoustic biologging data from the Canary Islands show that dense-beaked whales forage both in mid-water depths, exploiting the deep scattering layer, and at deeper depths near the seafloor, and that they could switch between these foraging habitats even within the same dive (Arranz et al. 2011). Hence, beaked whale foraging habitat covers a wide meso- to bathypelagic range, with local dynamic prey fields driving dive-to-dive foraging decisions (Arranz et al. 2011; Visser et al. 2021). Goose-beaked whales frequently dive to the seafloor in the Azores and off the coast of Southern California (Visser et al. 2021; Coates et al. 2024). Hence, maximum dive depth for this species may be directly related to the seafloor depth, particularly in water depths of less than 2000 m (Schorr et al. 2014; Barlow et al. 2020). In deeper waters, however, goose-beaked whales spend very little time foraging within 500 m of the bottom, possibly because bottom-associated feeding becomes energetically less profitable (Barlow et al. 2020). Maximum dive depths are highly correlated with bottom depth for goose-beaked whales in The Bahamas (Joyce et al. 2017) and off Southern California (Coates et al. 2024) but that correlation was low for dense-beaked whales in The Bahamas (Joyce et al. 2017). In the Bahamas and Hawai'i, where both species are found in close proximity, foraging dive depths are typically greater for goose-beaked than for dense-beaked whales (Baird et al. 2008; Joyce et al. 2017).

Several approaches have been proposed for estimating beaked whale population density and abundance from acoustic detections (Moretti et al. 2006; Marques et al. 2009; Hildebrand et al. 2015; Arranz et al. 2023), and all of these methods rely on tagging data to quantify diving behavior. Barlow et al. (2021, 2022) developed a method to estimate the density and abundance of goose-beaked whales using acoustic detections of beaked whale echolocation pulses obtained from drifting acoustic recorders and population-level knowledge of their stereotypical diving and foraging behavior. That method requires the observed duration of nearly continuous bouts of echolocation and dive cycle durations (time from the end of one deep foraging dive to the end of the next). It uses estimates of acoustic availability and the distribution of downward detection angles together with the expected distribution of echolocation depths to quantify the effective distance at which beaked whale echolocation signals can be detected on a near-surface recorder. Barlow et al. (2021, 2022) used tagging data from prior studies to estimate three key parameters (mean dive cycle duration and the mean and standard deviation of echolocation depth) that were not directly estimated from acoustic surveys. If these key parameters were available for all locations, the use of this acoustic survey approach could be greatly expanded.

The density estimation for goose-beaked whales off the US West Coast (Barlow et al. 2022) was based, in part, on tagging studies of that species within the San Nicolas and Catalina Basins off southern California, USA (Schorr et al. 2014; Barlow et al. 2020). The lack of beaked whale tagging efforts across most beaked whale species' ranges may impede future studies of density and abundance using passive acoustic methods. However, if beaked whale diving behavior is similar among areas, it may be possible to estimate dive cycle duration and echolocation depth variables from studies in other areas and derive density estimates using acoustic methods. Here, we aim to extend the potential for density and abundance estimation of goose-beaked and dense-beaked whales to parts of their range where no or limited acoustic tag data exist. To that end, we quantify the differences in goose-beaked and dense-beaked whale diving behavior among tags from multiple locations in the Atlantic and Pacific Oceans and the Mediterranean Sea and estimate the expected error from extrapolating estimates among those locations. Results may be used to estimate the parameters needed for passive acoustic surveys in areas where tag data are not available.

2 | Methods

2.1 | Tagging Studies

Data on diving behavior of goose-beaked whales were collected from tagging studies in six locations: within the Hawaiian Islands (USA), off southern California (USA), off Cape Hatteras,

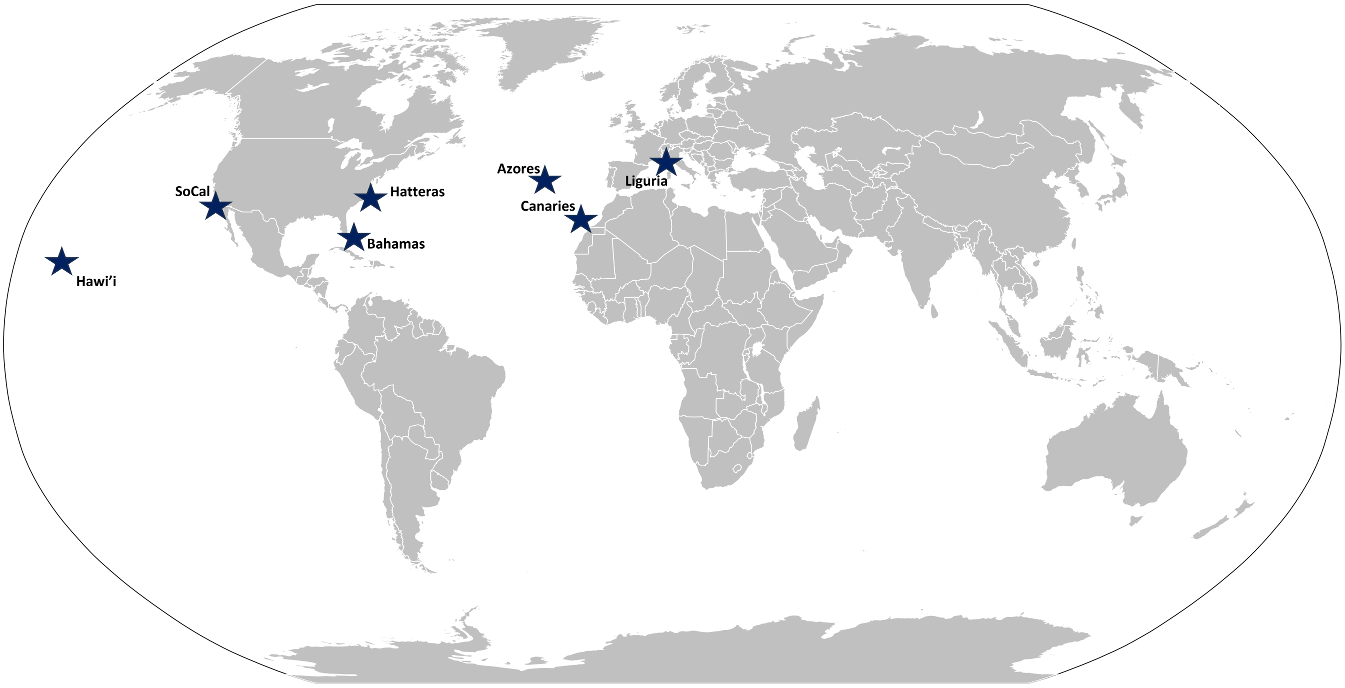

FIGURE 1 | World map showing tagging locations (as abbreviated in this publication). Public domain base map from Wikimedia Commons.

North Carolina (USA), within the Azores (Portugal), within The Bahamas, and in the northern Ligurian Sea (Italy) (henceforth referred to as Hawai'i, SoCal, Hatteras, Azores, Bahamas, and Liguria, Figure 1). Data on the diving behavior of dense-beaked whales were collected from tagging studies at three locations: Hawai'i, Bahamas, and the Canary Islands (Spain; henceforth referred to as Canaries).

A variety of tag types were used for these studies including shorter duration, suction-cup-attached tags (Mk8 and Mk9 time-depth recorders [TDR] from Wildlife Computers, Redmond, WA, USA) and DTAGs (Johnson and Tyack 2003); longer duration, dart-attached, satellite-transmitting tags (SPLASH10 from Wildlife Computers, Redmond, WA, USA), and dart-attached acoustic recording tags (Sound & Motion Recording & Telemetry [SMRT] tags from Wildlife Computers, Redmond, WA, USA). The DTAG, TDR, and SMRT tags were recovered to download stored data. SPLASH10 tags transmitted their data via an Argos satellite link, though in some cases, data from these tags were also obtained through land- or boat-based receivers (i.e., Motes from Wildlife Computers, Redmond, WA, USA or Argos goniometers from Xerius, Saint Jean, France). The recorded dive data include a time series of depth measurements (from TDR, DTAG, SMRT, and most SPLASH10 tags), a behavior log providing summary information on each dive and surface period (from all SPLASH10 tags), and compressed audio files (stereo for DTAGs and mono for SMRT tags). For the time series data, a sample interval of 1 s is used for the TDR, DTAG, and SMRT data; the time series data from SPLASH10 tags are not used here. The SPLASH10 behavior log includes start and end times of diving-related events (dives and surfacing periods) and maximum dive depth. The acoustic data from DTAGs and SMRT tags are particularly important in determining what constitutes a foraging dive, using the persistent presence of echolocation pulses.

Table 1 presents a summary of the tag deployments for each tagging site used in this paper. Details on deployment methods can be found in papers specific to each study, and details for each deployment are in Supporting Information (Table S1). Navy sonar has been linked to mass stranding of beaked whales in two of our study areas (Bahamas and Canaries), likely by affecting their dive behavior (Bernaldo de Quirós et al. 2019; Henderson 2023), and Navy sonar has been shown to affect beaked whale behavior in the SoCal (Falcone et al. 2017) and Bahamas (Tyack et al. 2011; Joyce et al. 2020) study areas. We exclude any tags that were deployed on animals that were deliberately exposed to Navy sonar or simulated sounds (e.g., sonar and killer whale vocalizations) as part of behavioral response studies using controlled exposure experiments. Beyond Navy sonar, other anthropogenic sound sources have been suggested to affect the foraging behavior of beaked whales (e.g., Aguilar de Soto et al. 2006; Cholewiak et al. 2017; Henderson 2023). However, sound exposures are not known for most of our tag data, which did not record sounds, and future study sites, which may use the results of this work, are likely to have anthropogenic impacts as well. Therefore, we present the behaviors recorded within each study area as characteristic of the behaviors within each study location given its typical soundscape.

2.2 | Parameter Estimation

We estimate means and standard deviations of five parameters that describe beaked whale behavior during foraging dives: maximum dive depth, foraging dive duration, dive cycle duration, and the mean and standard deviation of echolocation depth. Foraging dives are identified based on the presence of regular echolocation pulses for acoustic recording tags (DTAGs and SMRT tags) or on maximum dive depth for all

TABLE 1 | Summary of information on tagged beaked whales including the species (dense-beaked whales: Md and goose-beaked whales: Zc), location, type of tag, number of tags of that type deployed on that species in that location, study years used in this report, and total of all deployment durations (between the first and last dive).

Species	Region	Tag type	# Tags	Study years	Data duration (days)	Co-author source	Citations
Md	Bahamas	SPLASH10	13	2011–2015	149.0	a, b, d	9, 13
Md	Bahamas	DTag	17	2006–2017	8.5	c, d	5, 6
Md	Canaries	DTag	18	2003–2022	6.8	c, e, f	1, 2, 6
Md	Hawai‘i	TDR	9	2004–2008	9.9	g	3, 4, 6, 14
Md	Hawai‘i	SPLASH10	4	2013–2021	29.3	g	14
Zc	Azores	DTag	7	2015–2022	5.0	h, i	
Zc	Bahamas	SPLASH10	5	2011–2013	118.1	a, b	9
Zc	Hatteras	SPLASH10	18	2014–2017	526.7	g, j	10
Zc	Hawai‘i	TDR	2	2004–2006	1.7	g	3, 4, 6
Zc	Hawai‘i	SPLASH10	4	2010–2015	85.3	g	6, 14
Zc	Liguria	DTag	11	2003–2006	3.2	c	1, 2, 6
Zc	SoCal	SPLASH10	19	2010–2015	622.0	k, l	6, 7, 8, 11
Zc	SoCal	SMRT	5	2019	15.7	k, l, m, n, o, p, q	12

Note: Tag types include time-depth recorders (TDR), satellite-transmitting behavior recorders (SPLASH10), multi-sensor acoustic recorders (DTAG), and satellite-transmitting acoustic recorders (SMRT). Co-author sources are: (a) Durban, (b) Claridge, (c) Tyack, (d) Hickmott, (e) Aguilar de Soto, (f) Miranda Gonzalez, (g) Baird, (h) Visser, (i) Oudejans, (j) Read, (k) Schorr, (l) Falcone, (m) Coates, (n) Sweeney, (o) DeRuiter, (p) Rone, and (q) Watwood. Previous papers using the same data are: (1) Johnson et al. (2004), (2) Tyack et al. (2006), (3) Baird et al. (2006), (4) Baird et al. (2008), (5) Tyack et al. (2011), (6) Barlow et al. (2013), (7) Schorr et al. (2014), (8) Falcone et al. (2017), (9) Joyce et al. (2017), (10) Shearer et al. (2019), (11) Barlow et al. (2020), (12) Sweeney et al. (2022), (13) Joyce et al. (2020), and (14) Baird (2019).

other tags. Previous research has shown that maximum dive depth has a multi-modal distribution for goose-beaked and dense-beaked whales, with a shallower mode composed of non-foraging dives and one or more deeper modes composed of foraging dives (Tyack et al. 2006; Baird et al. 2008; Joyce et al. 2017). For non-acoustic tags (TDR and SPLASH10 tags), we use the distribution of the maximum dive depths to identify foraging dives. We infer that whales will be foraging and producing echolocation signals if their maximum dive depths are greater than the approximate mid-point of the gap between the shallow and deeper modes in maximum dive depth (see Results). We recognize that no single depth criterion can correctly distinguish between all foraging and non-foraging dives, but tags with acoustic data show that the vast majority can be correctly assigned (Warren et al. 2017; Sweeney et al. 2022).

Maximum dive depth is taken as the maximum observed depth during a dive from DTAG, TDR, and SMRT tags. SPLASH10 tags record depth in bins, and their behavior logs give two estimates of maximum depth for each dive (representing the upper and lower range of a given depth bin); we used the mean of these two values as our estimate of maximum dive depth. Deep foraging dive duration is measured from the time the whale leaves the surface until the time it returns to the surface. Dive cycle duration is measured from the end of one deep dive until the end of the next. Dive duration and dive cycle duration are based on behavior log data for SPLASH10 tags and time series data for all other tag types. Many suction cup tag deployments are not long enough to measure the longest foraging dives or dive cycles; so, mean estimates can be biased by including these short records. To avoid this censoring bias, we only include foraging dives and dive cycles if the dive record includes at least 2 and 5 h, respectively, prior to the end of a foraging dive. This approach also typically excludes the first foraging dive and the first dive cycle after tagging, which have been shown in some studies to be unusually long (Barlow et al. 2013). For each foraging dive with acoustic data, we calculate the mean and standard deviation of all depths recorded between the start and end of consistent echolocation pulses.

The means, standard deviations, and percentiles (5th, 10th, 25th, 50th, 75th, 90th, and 95th) of the five key parameters for goose-beaked and dense-beaked whale foraging dives (maximum dive depth, foraging dive duration, dive cycle duration, and the mean and standard deviation of echolocation depth) are calculated for each location. Location means are simple averages of the mean values of all tagged individuals in the given location. Composite means and standard errors for each species are averages of the location means.

2.3 | Statistical Analyses to Partition Sources of Variance

We fit linear mixed-effect models to determine factors influencing variation in maximum dive depth, foraging dive duration, dive cycle duration, mean echolocation depth, and standard deviation of echolocation depth of goose-beaked and dense-beaked whales. The two species are modeled separately. For acoustic recording tags, the mean and standard deviation of echolocation depth are calculated for each dive.

All variables are modeled as functions of location and tagging occasion (or "Deployment ID") as random effects, with Deployment ID nested within location. For dive i of Deployment ID j in location k, the simple random-effects models are as follows:

$$variate_{i,j,k} \sim \mu + \alpha_j + \beta_k + \varepsilon_{i,j,k}$$

To evaluate whether the mean and standard deviation of echolocation depth can be predicted from maximum dive depth (which is available for more locations than echolocation depth), we also fit linear mixed-effect models with the random effects of location and individual plus the linear fixed effect of maximum dive depth (*MaxDepth*) as follows:

$$variate_{i,j,k} \sim \mu + \alpha_j + \beta_k + \delta * MaxDepth_i + \varepsilon_{i,j,k}$$

In these models, μ represents the intercept, the random effects α_j and β_k are distributed as Normal $(0, \sigma_{ID})$, δ represents the slope of the relationship with maximum dive depth and ε values are normally distributed residuals.

All models are fit using the R package *lme4* (version 1.1–34, Bates et al. 2015) from which we extracted estimates of the variance explained by the random effects. For the mixed-effect models, we used the function *r.squaredGLMM* in the R package *MuMIn* (version 1.41.0, Bartoń 2023) to estimate the variance explained by the fixed effect *MaxDepth* using the method of Nakagawa et al. (2017).

3 | Results

3.1 | Identification of Foraging Dives

For dense-beaked whales, foraging dives can be identified using a simple criterion based on maximum dive depth. From DTAG data with audio recordings, all dives with a maximum depth greater than 500 m were accompanied by regular echolocation pulses, and none of the dives with a maximum depth of less than 470 m had regular echolocation pulses. The distributions of maximum depth for the much larger sample of dives that also includes SPLASH10 and TDR tags show minima at ~500 m (Figure 2). We use a maximum dive depth criterion of > 500 m to define foraging dives of dense-beaked whales.

For goose-beaked whales acoustic tag data, a single maximum depth criterion cannot separate all foraging and non-foraging dives. Using acoustic recording SMRT tags in SoCal, Sweeney et al. (2022) found several deep dives (> 800 m) of goose-beaked whales that did not have regular echolocation pulses and some shallower dives (650–800 m) that did. Baird et al. (2008), Barlow et al. (2020), and Shearer et al. (2019) used 800 m maximum depth as a criterion for defining deep foraging dives. Our distributions of maximum depth (Figure 2) show minima at ~800 m in all locations except Liguria, where the minimum is at ~650 m. Although no single maximum depth criterion can separate all foraging and non-foraging dives for goose-beaked whales without error, classification errors are small if we use these minima (maximum dive depths > 650 m for Liguria and > 800 m for all other locations) as our criteria to define foraging dives for this species.

3.2 | Maximum Foraging Dive Depth, Foraging Dive Duration, and Dive Cycle Duration

Maximum foraging dive depths (Figure 3) and durations (Figure 4) vary considerably between dives for the same tagged individual (Table S2). The differences among individuals of the same species in the same location are often greater than the differences among locations (Figures 3 and 4). In general, maximum dive depths are greater for goose-beaked whales than for dense-beaked whales (composite difference = 310 m, Table 2), and the same is consistently true for foraging dive duration (composite difference = 14.1 min, Table 2). Within goose-beaked whales, dive depths are shallowest and foraging dive durations shortest in samples from Liguria. Goose-beaked whales have the deepest dives (means greater than 1400 m) in Hatteras and SoCal and have the longest foraging dive durations (over 1 h) in the Azores, Bahamas, and SoCal. Within dense-beaked whales, maximum dive depths are deeper in the Bahamas than in Hawai‘i, and are shallowest in the Canaries, whereas mean foraging dive durations are remarkably similar in all three locations. For models of maximum dive depth for both species, residuals account for the largest share of variation (> 56%), indicating a large degree of variation between dives within an individual, and the variation due to location is slightly greater than that due to among-individual differences (Table 3). For models of foraging dive duration, residuals (including within-individual variation) also account for the largest share of variation (> 73%), but for this variable, the variation among locations is smaller than the variation among individuals (Table 3).

Dive cycle durations vary considerably within the same tagged individual (Figure 5), and residuals (including variation within individuals) are the greatest source of variation in models of dive cycle duration for both species (Table 3). However, within species, mean values are generally very similar for both species. Mean values are also very similar within and among locations for each species, albeit with some variability for goose-beaked whales. The dive cycles for this species in Liguria and SoCal are the shortest and longest, respectively. In models of dive cycle duration, location explains more of the variation than Deployment ID for goose-beaked whales, but the location effect is trivially small for dense-beaked whales (Table 3).

The dive cycles of goose-beaked whales in SoCal and Hatteras and dense-beaked whales in The Bahamas have several outliers with dive cycles longer than 6 h (the longest values seen in any of the other locations) (Figure 5). Some of these outliers may be attributed to the larger sample size in these areas. However, these locations are near naval training and testing areas where the use of mid-frequency active sonar is common. Although we excluded any tagged animals that were deliberately exposed to Navy sonar, at least some of our tagged whales were incidentally exposed to mid-frequency active sonar and exhibited behaviors that may be influenced by it (Falcone et al. 2017).

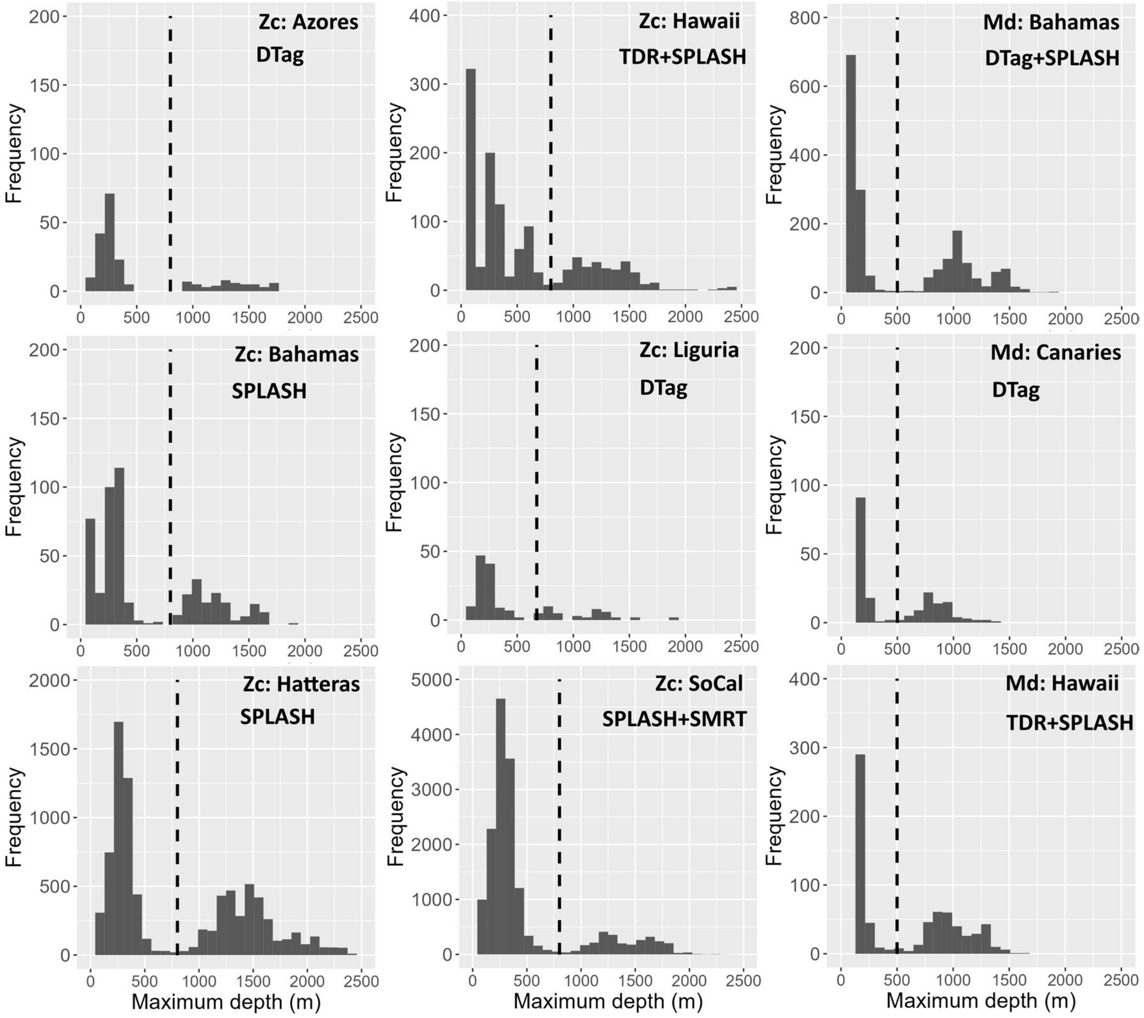

FIGURE 2 | Frequency distributions of maximum dive depths for goose-beaked whales (Zc) in six locations and for dense-beaked whales (Md) in three locations. Dashed lines indicate the depth used to identify deep foraging dives: 800 m for Zc (except 650 m in Liguria) and 500 m for Md. Data include all tag types (SPLASH10, DTAG, SMRT, and TDR). Note that dives to less than a minimum dive depth criterion (typically 50 m but up to 250 m for some SPLASH10 tags) are not counted as dives and are excluded from these frequency distributions.

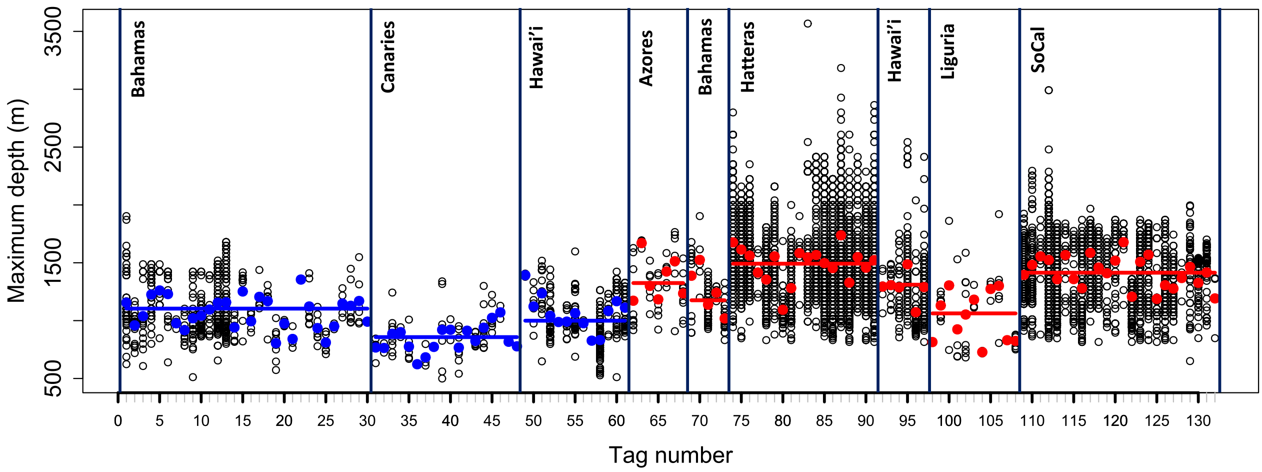

FIGURE 3 | Maximum foraging dive depths of individual dives (open circles) and mean values for each tagged whale (solid circles). Tag numbers are from Table S1. Horizontal lines represent mean values of all dives by species (blue for dense-beaked whale and red for goose-beaked whale) within the given location. Values are excluded for tags that did not record at least 2 h of continuous data prior to the end of at least one dive.

Percentiles of the observed distributions of maximum dive depth, dive duration, and dive cycle duration are given in Supporting Information (Tables S3–S5).

3.3 | Echolocation Depth

Observed echolocation depths are consistently deeper for goose-beaked than for dense-beaked whales (composite difference = 231 m, Table 4). Mean echolocation depth also varies considerably between dives for the same tagged individual (Figure 6). Individual variation within and between locations for the same species appears greater for echolocation depth (Figure 6) than the variation seen for maximum dive depth (Figure 3). The variance in echolocation depth explained by location is 22% for goose-beaked whales and 43% for dense-beaked whales (Table 3). For goose-beaked whales, mean echolocation depths are appreciably shallower in Liguria than off Azores or SoCal (Table 4, Figure 6). Mean echolocation depths from acoustic tags are strongly correlated to maximum dive depth (Figure 7), with correlation coefficients of 0.938 and 0.940 (respectively for goose-beaked and dense-beaked whales, $p < 0.0001$ for both). In the linear mixed-effect models, maximum dive depth explained 89% and 86% of the variance in mean echolocation depth for goose-beaked and dense-beaked whales, respectively (Table 3). With that covariate, location explains 0% of the remaining variation for goose-beaked whales and 4.1% for dense-beaked whales.

The standard deviation of echolocation depths for each dive is a measure of the spread in foraging depths. The standard deviation of echolocation depth is also related to maximum dive depth (Figure 7). In the random-effects models of the standard deviation of echolocation depth, the largest source of variation is the residual (including the variation within individuals), with the among-location variation being higher than the among-individual variation for one species and smaller for the other (Table 3). When maximum dive depth is included in this model as a fixed effect, this covariate explained the most variance: 81% for goose-beaked whales and 63% for dense-beaked whales (Table 3). Location explains very little of the variance seen in the standard deviation of echolocation depth for dense-beaked and goose-beaked whales (Table 3).

Percentiles of the observed distributions, the means and standard deviations of echolocation depth are given in Supporting Information (Tables S6, S7).

3.4 | Predicting the Mean and Standard Deviation of Echolocation Depths From Maximum Dive Depth

Because direct measures of the mean and standard deviation of echolocation depth are only available from acoustic recording tags in some areas, we are interested in predicting these values from maximum dive depth when direct measures are not available. Our mixed model shows that maximum dive depth explains most of the variation in echolocation depth variables. Location effects are very small when maximum dive depth is included in the model. Using the mixed-effect models (Table 5), predictions of the mean and standard deviations of echolocation depth are very close to the observed values (Table 4, Figure 8). For dense-beaked whales, the average absolute values of the prediction errors are only 24 and 18 m for the mean and standard deviation (respectively). For goose-beaked whales, these average prediction errors are only 6 and 15 m (respectively).

3.5 | Inter-Dependence in Dive Parameters

Bivariate plots of deep (presumed foraging) dive parameters are given in Figures 6 and 7. Mean echolocation depths are strongly positively correlated with maximum depth for deep foraging dives of both goose-beaked and dense-beaked whales; the relationships between the two are nearly linear. Foraging dive durations and dive cycle durations are less strongly correlated with maximum dive depth for both species. The relationship between foraging dive duration and maximum dive depth appears nonlinear, with a positive relationship for dives to less than 1000 m

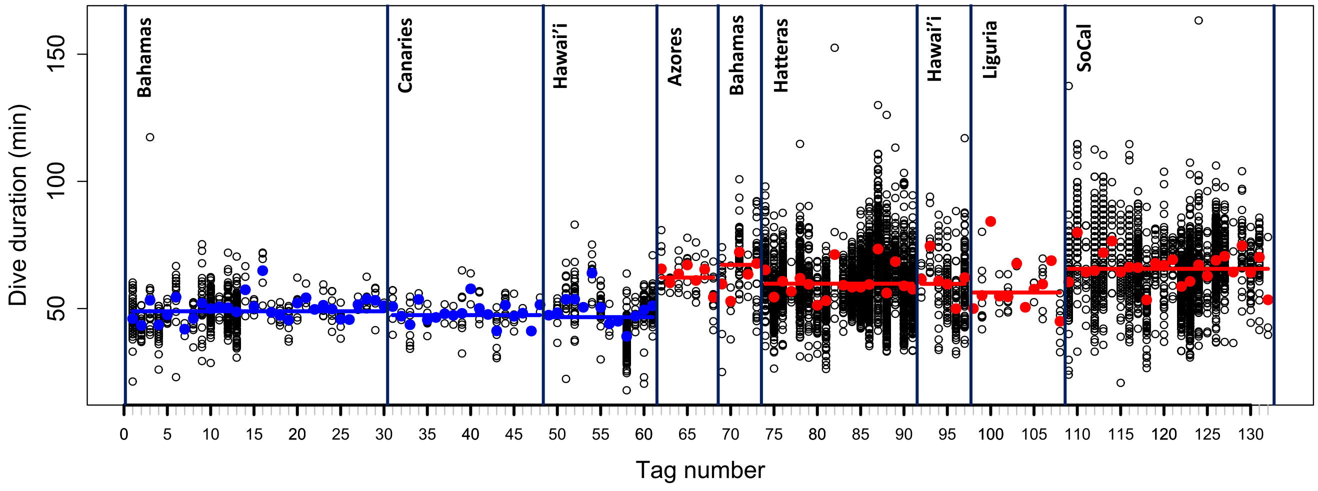

FIGURE 4 | Foraging dive durations of individual dives (open circles) and mean values for each tagged whale (solid circles). Tag numbers are from Table S1. Horizontal lines represent mean values of all dives by species (blue for dense-beaked whale and red for goose-beaked whale) within the given location. Values are excluded for tags that did not record at least 2 h of continuous data prior to the end of at least one dive.

TABLE 2 | Means and standard deviations (SD) of three diving parameters (maximum dive depth, duration, and dive cycle) summarized by species and location.

Species	Location	Foraging dives (n)	Mean maximum foraging dive depth (m)	SD maximum foraging dive depth (m)	Mean foraging dive duration (min)	SD foraging dive duration (min)	Dive cycles (n)	Mean dive cycle duration (hrs)	SD dive cycle duration (hrs)
Md	Bahamas	543	1104	223	48.9	7.7	389	2.45	1.11
Md	Canaries	79	857	170	47.4	6.8	61	2.44	0.84
Md	Hawai‘i	336	1000	213	46.6	9.5	283	2.42	1.00
Zc	Azores	52	1325	253	62.2	8.1	45	2.51	0.60
Zc	Bahamas	99	1176	216	67.2	12.8	38	2.51	0.58
Zc	Hatteras	3384	1492	334	59.8	11.1	3029	2.45	0.99
Zc	Hawai‘i	258	1311	328	59.7	12.3	176	2.29	0.94
Zc	Liguria	45	1063	311	56.3	11.3	34	1.94	0.76
Zc	SoCal	2556	1414	275	65.6	12.8	2066	3.08	1.23
Md	Composite	958					733		
	Mean		987	202	47.7	8.0		2.44	0.99
	SE		124	28	1.2	1.4		0.02	0.14
Zc	Composite	6394					5388		
	Mean		1297	286	61.8	11.4		2.46	0.85
	SE		157	47	4.1	1.8		0.37	0.25

Note: Means of all dives from each individual (Table S2) are used to calculate these means, and standard deviations represent the variation among individuals. Sample sizes are given separately for foraging dives and dive cycles. Composite means and standard errors (SE) are calculated for both species as the means and standard deviations of values for each location.

TABLE 3 | Estimates of the percentages of variance in modeled variables explained by tagging location, individual whale (Deployment ID), and (for mean and standard deviation (SD) of echolocation depth) maximum dive depth.

		Percentage variance explained by			
Species	**Modeled variable**	**Location (Loc)**	**Individual (deployment ID)**	**Maximum dive depth (MaxDepth)**	**Residual**
Zc	Maximum dive depth	17.1	15.8		67.1
Zc	Mean echolocation depth	22.2	14.8		63.0
Zc	Mean echolocation depth	0.0	2.4	88.9	8.7
Zc	SD echolocation depth	18.0	13.0		69.0
Zc	SD echolocation depth	2.7	3.6	81.0	12.7
Zc	Foraging dive duration	4.6	22.2		73.2
Zc	Dive cycle duration	9.8	5.3		84.9
Md	Maximum dive depth	24.6	18.7		56.7
Md	Mean echolocation depth	42.8	17.5		39.7
Md	Mean echolocation depth	4.1	1.4	85.9	8.6
Md	SD echolocation depth	8.1	16.6		75.3
Md	SD echolocation depth	2.7	5.4	62.9	28.9
Md	Foraging dive duration	0.0	26.7		73.3
Md	Dive cycle duration	0.0	10.1		89.9

Note: Estimates are made with linear mixed-effect models, with location and individual treated as random variables and maximum dive depth (if included) as a linear fixed effect. Species are modeled separately. Residuals represent sources of variation that were not explained by the model and include the variability of multiple dives within an individual. Zero values for the variance due to location represent singularities where the effect was so small that the model did not converge on a stable solution and likely do not represent a true value of zero.

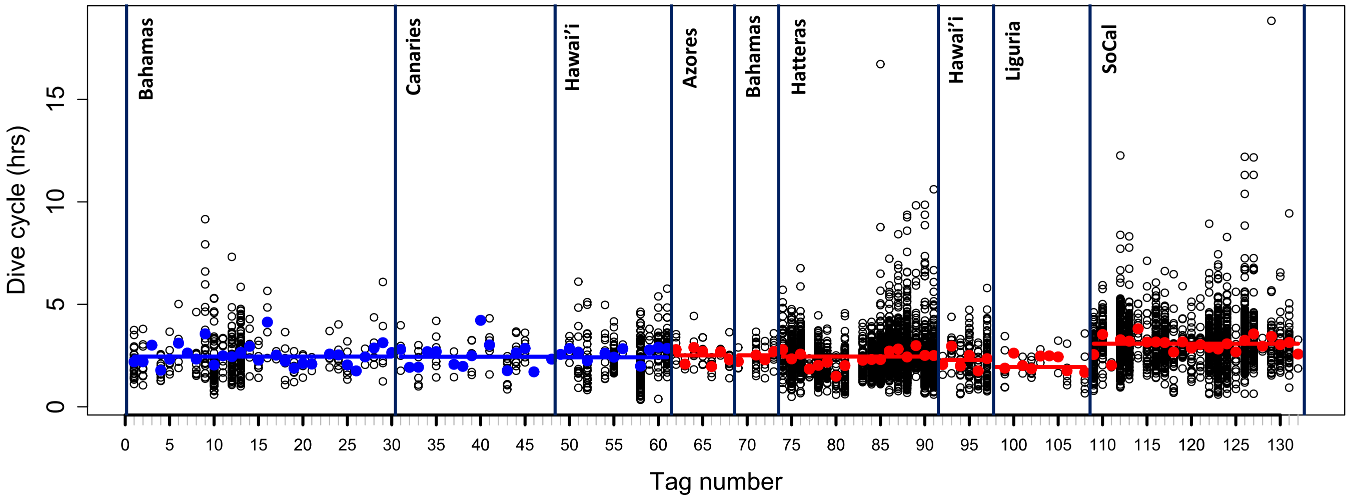

FIGURE 5 | Dive cycle durations of individual dives (open circles) and mean values for each tagged whale (solid circles). Tag numbers are from Table S1. Horizontal lines represent mean values of all dives by species (blue for dense-beaked whale and red for goose-beaked whale) within the given location. Values are excluded for tags that did not record at least 5 h of continuous data prior to the end of at least one dive.

and very little pattern for deeper dives (Figure 9). Inter-deep-dive intervals (IDDIs) are positively correlated with subsequent foraging dive duration ($r = 0.35$ and 0.36, respectively for dense-beaked and goose-beaked whales).

In our presentation, IDDIs are paired with the subsequent dive (as in Tyack et al. 2006) which contrasts with comparisons to the prior dive in more recent studies (Arranz et al. 2011; Barlow et al. 2013; Falcone et al. 2017). Although IDDI can be viewed as the recovery time from the previous dive, it can also be viewed as necessary preparation time for the next dive. This change in perspective results in some new insights. As has been noted by others (Schorr et al. 2014), goose-beaked whales can make two successive foraging dives with very little time between them (just one surfacing series). For this species, a recovery period appears to be optional. However, the bottom left panel in Figure 9

TABLE 4 | Observed and predicted mean values for the mean and standard deviations (SD) of echolocation depth of tagged goose-beaked and dense-beaked whales summarized by species and location.

			Mean observed		Mean predicted		Prediction error	
Species	**Location**	**Dives with acoustic tags (n)**	**Mean echolocation depth (m)**	**SD echolocation depth (m)**	**Mean echolocation depth (m)**	**SD echolocation depth (m)**	**Mean echolocation depth (m)**	**SD echolocation depth (m)**
Md	Bahamas	86	872	131	900	154	28.0	23.2
Md	Canaries	68	711	103	732	91	20.3	12.2
Md	Hawai‘i	0	NA	NA	828	127	NA	NA
Zc	Azores	46	1059	185	1066	209	6.9	23.6
Zc	Bahamas	0	NA	NA	964	164	NA	NA
Zc	Hatteras	0	NA	NA	1181	259	NA	NA
Zc	Hawai‘i	0	NA	NA	1056	205	NA	NA
Zc	Liguria	41	888	143	886	130	2.4	13.6
Zc	SoCal	122	1119	244	1128	236	8.9	7.7
Md	Composite	154						
	Mean		791	117	820	124.1	24.1	17.7
	SE		113	20	84	31.9	5.5	7.8
Zc	Composite	209						
	Mean		1022	191	1047	200.4	6.1	15.0
	SE		120	50	108	47.2	3.4	8.0

Note: Means of all dives from each individual (Table S2) are used to calculate these means, and standard deviations represent the variation among individuals. Observed values are from acoustic recording tags and are not available (NA) for locations without acoustic tags. Predicted values are calculated from the mean maximum dive depths in Table 2 and the regression coefficients in Table 5. Prediction errors are the absolute values of the difference between the predicted and observed values for the given location. Composite means and standard errors (SE) are calculated for both species as the means and standard deviations of values for each location.

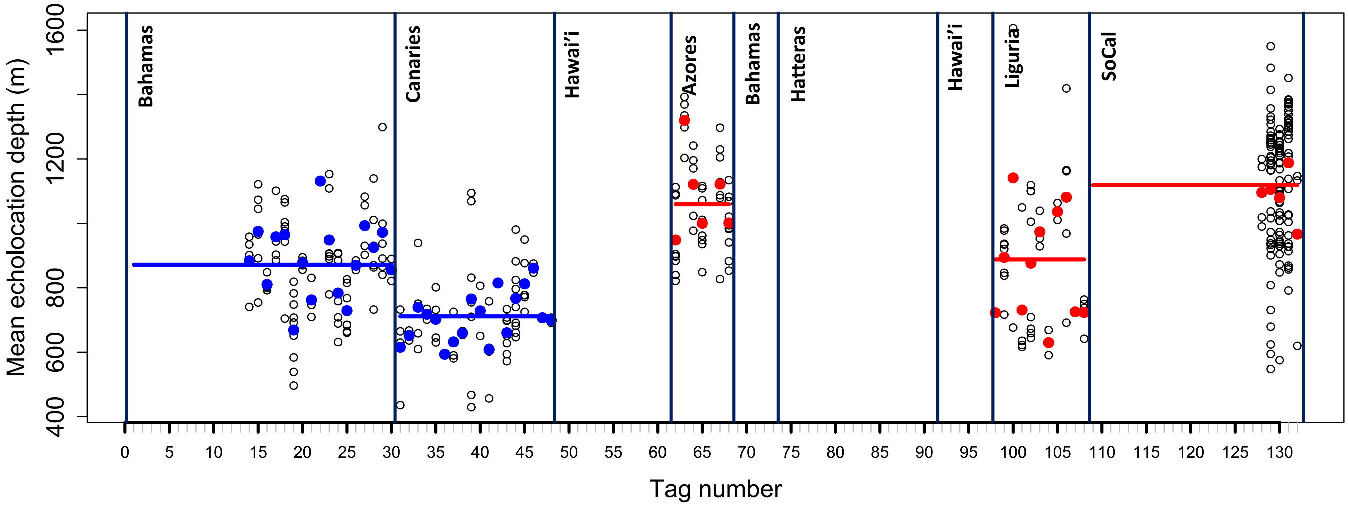

FIGURE 6 | Mean echolocation depths of individual dives (open circles) and for each whale (solid circles) with an acoustic recording tag. Tag numbers are from Table S1. Horizontal lines represent mean values of all dives by species (blue for dense-beaked whale and red for goose-beaked whale) within the given location. Values are excluded for tags that did not record at least 2 h of continuous data prior to the end of at least one dive and for tags that did not record acoustic data.

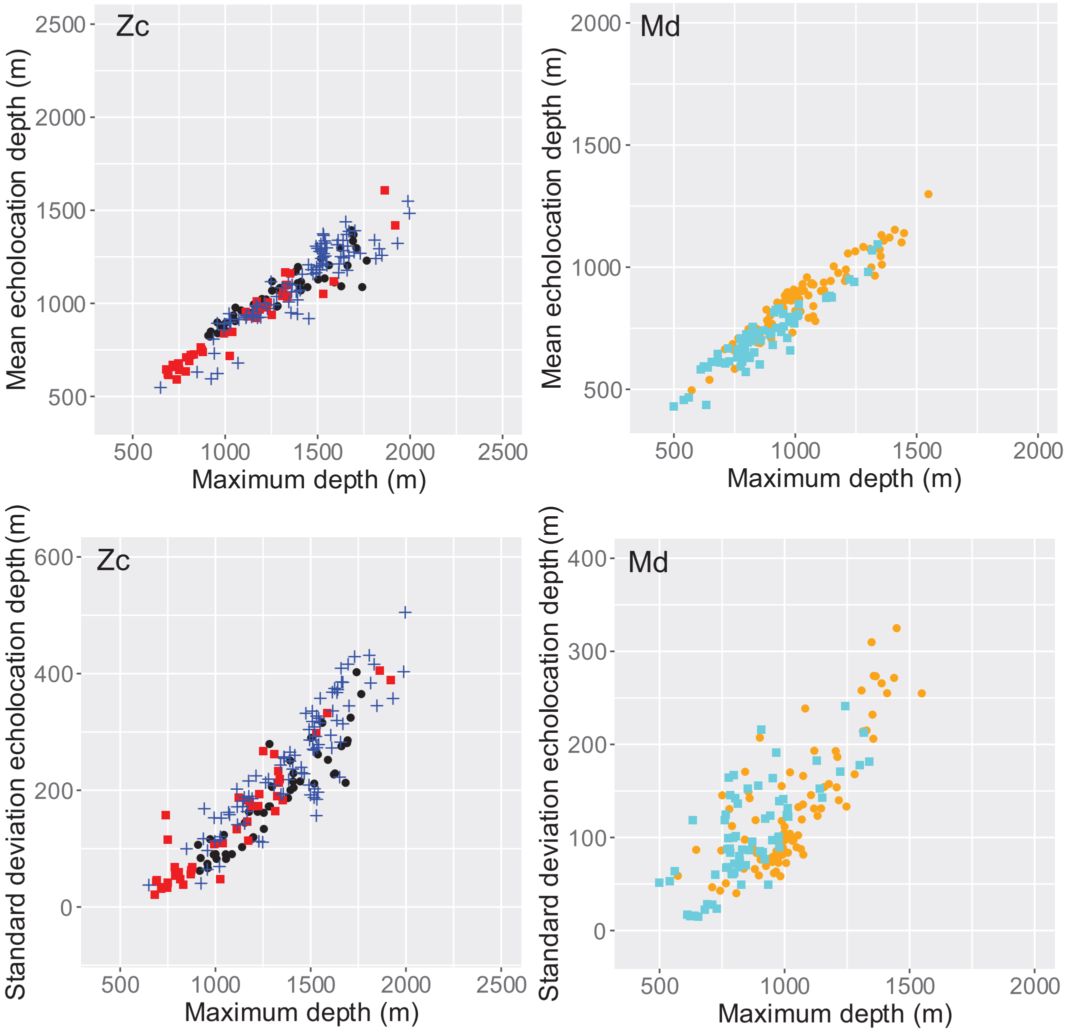

FIGURE 7 | Observed relationships between mean (top panels) and standard deviation (bottom panel) of echolocation depth and the maximum dive depth for deep foraging dives of goose-beaked whales (Zc, left panels) and dense-beaked whales (Md, right panels) based on acoustic recording tags (DTAGs and SMRT tags). Symbols colors indicate the tagging location: SoCal (Blue +), Liguria (red square), Azores (black circle), Bahamas (orange circle), and Canaries (cyan square).

TABLE 5 | Linear regression coefficients estimated by the linear mixed-effect models of the means and standard deviations (SD) of echolocation depth as a function of the maximum dive depth (as a fixed effect).

		Intercept		Slope	
Species	**Variable**	**Value (m)**	**SE**	**Value**	**SE**
Zc	Mean echolocation depth	154.2	22.9	0.688	0.017
Zc	SD echolocation depth	−190.6	16.2	0.302	0.010
Md	Mean echolocation depth	146.4	30.4	0.682	0.022
Md	SD echolocation depth	−130.1	18.8	0.258	0.017

Note: Species are modeled separately. Explained variances for these models (including random effects of location and tagged individual) are given in Table 3.

shows that dives of greater than 70 min almost always have a prior preparatory period. Successive deep dives with very short IDDIs are very rarely seen for dense-beaked whales (Figure 9, bottom right panel).

4 | Discussion

Our results show the importance of obtaining large sample sizes from multiple locations to quantify the foraging dive behavior of beaked whales, and likely other widely distributed cetacean species. Within individuals, we see considerable variation between dives for all dive parameters. The differences between dives within one tagged individual are typically much larger than the differences between individuals or between locations; Schorr et al. (2014) found a similar pattern. The differences between individuals are typically of similar magnitude to the differences between locations. Only by having a large sample of dives from each individual and a large sample of individuals from each location can we discern location-level differences in diving behavior with any certainty.

Although we have assembled the largest collection of beaked whale diving data ever analyzed, these tagging studies do have limitations. Most tagging studies have been in near-shore slope or basin habitats that are accessible by small vessels. A whale's diving behavior may change on longer time scales as it forages in different habitats. Many individual whales of both species exist in the vast abyssal areas of the world's oceans (MacLeod et al. 2006) where tagging studies are virtually absent. It is important to keep these limitations in mind when interpreting the results of our tagging studies.

We recognize that some recorded behaviors are likely to have been influenced by the presence of anthropogenic sounds, particularly those of animals tagged in areas where naval sonar is frequently used. We have noted the particularly long dive cycles (> 6 h) found in our Bahamas, Hatteras, and SoCal study areas. Longer dive cycles have been recorded in goose-beaked and dense-beaked whales that have been exposed to a variety of sound sources, including operational Navy sonar (Falcone et al. 2017) and sounds that mimic Navy sonar and killer whales (Tyack et al. 2011; DeRuiter et al. 2013). Unusually short dives and dive cycles have also been reported during exposure to shipping noise (Aguilar de Soto et al. 2006). Although we excluded tagged animals that were deliberately exposed to anthropogenic sound, we know that some of the included samples are likely affected by such exposures. Some of the tags from SoCal were in fact previously used to investigate behavioral changes associated with sonar use; sonar is used so frequently in the region that it is virtually impossible to collect extended behavioral records from goose-beaked whales there without its effect (Falcone et al. 2017; Barlow et al. 2020). We present our estimates as representations of behavior under the conditions where the whales were tagged, including the concurrent levels of anthropogenic sound sources in those areas, as these same effects are likely to be present in any acoustic detection data from these regions.

4.1 | Maximum Foraging Dive Depth and Mean Echolocation Depth

Maximum dive depth and mean echolocation depth are highly correlated for goose-beaked and dense-beaked whales, so, not surprisingly, the geographic variation in these parameters shows similar patterns. Dense-beaked whales foraged deepest in The Bahamas and the shallowest in the Canaries (Table 2). Goose-beaked whales foraged deepest off Hatteras and shallowest in Liguria (Table 2). With the exception of Liguria, the mean values of both parameters are greater for goose-beaked whales than for dense-beaked whales in all locations (Tables 3 and 5). As has been found in other studies using subsets of these data (Tyack et al. 2006; Baird et al. 2008; Joyce et al. 2017; Baird 2019), goose-beaked whales dive, on average, to deeper depths than dense-beaked whales; however, our data show considerable overlap between species for individual dives, and goose-beaked whale dives in Liguria are, on average, more similar to those of dense-beaked whales in other locations.

Our results are likely influenced by the bathymetric characteristics of the tagging locations. We did not include bottom depth in our analyses because our satellite localizations were primarily based on the Argos system and, consequently, our position fixes were not frequent enough or accurate enough to determine bottom depth for each dive in regions of highly variable depths. Previous studies in flat-bottomed basins (much of our SoCal and Bahamas study areas with maximum depths of 1800 and 2247 m, respectively) showed a correlation between maximum dive depth and bottom depth for goose-beaked whales using Argos locations that were smoothed with a tracking model (Joyce et al. 2017; Barlow et al. 2020). The Bahamas study did not show a strong correlation between maximum dive depth and bottom depth for dense-beaked whales (Joyce et al. 2017). The recently developed SMRT tags have Fastloc GPS technology (Dujon et al. 2014) that collect accurate

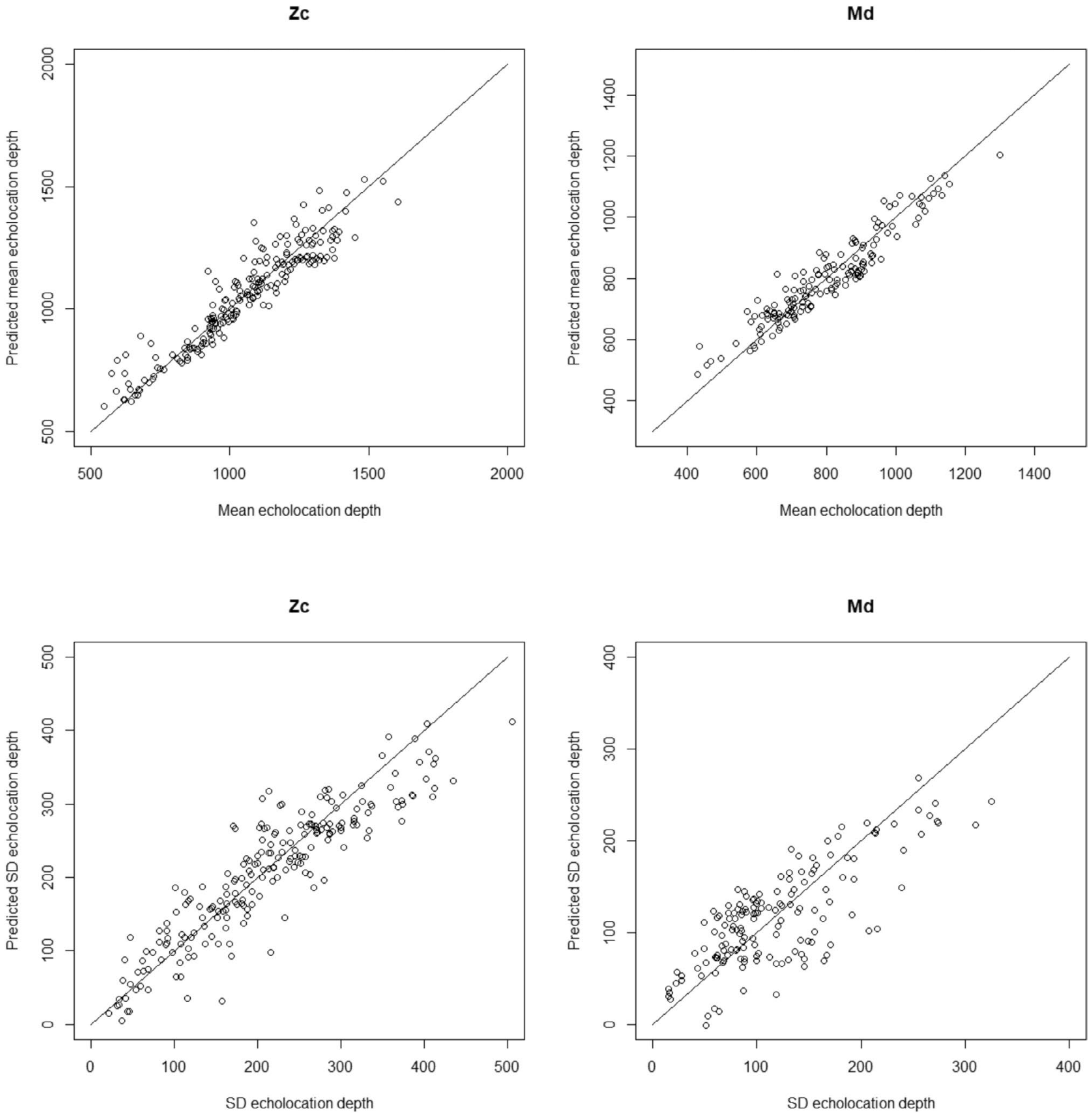

FIGURE 8 | Means and standard deviations of echolocation depths predicted by the linear mixed-effect models' fixed effect "maximum dive depth" plotted against observed values for goose-beaked whales (Zc) and dense-beaked whales (Md). Linear regression slope and intercept values are given in Table 5. Diagonal lines represent the 1:1 ratio.

positions for most surfacings, and an analysis of the resulting dive data showed a strong correlation between maximum foraging dive depth and bottom depths for goose-beaked whales in water depths of less than 2000 m (Coates et al. 2024). In the Azores, Liguria, and the Canaries, animals were tagged in waters less than 2000 m deep in regions with steep bathymetry (Tyack et al. 2006; Visser et al. 2021). In these areas, deeper dives can only be observed when animals move from the tagging location, which was uncommon. Off Hatteras, where tagging occurred in steep slope waters near very deep waters, goose-beaked whales are frequently recorded diving to greater than 2000 m (Figure 3). Short-duration suction-cup tags (TDR and DTAG types) are potentially more sensitive to fine-scale effects of tagging location than longer duration dart tags because there is less time available for animals to move to other locations. Most tagging studies are done from small vessels close to shore, which not only can affect the estimates of dive depths immediately after tagging, but also can select individual whales that have a preference for foraging at shallower depths. In our Hawai'i study area, photo-identification studies have shown that island-associated populations exist for both goose-beaked and dense-beaked whales and that most tags have been deployed on individuals from these populations (McSweeney et al. 2007; Baird et al. 2008, 2011; Baird 2019). Virtually no

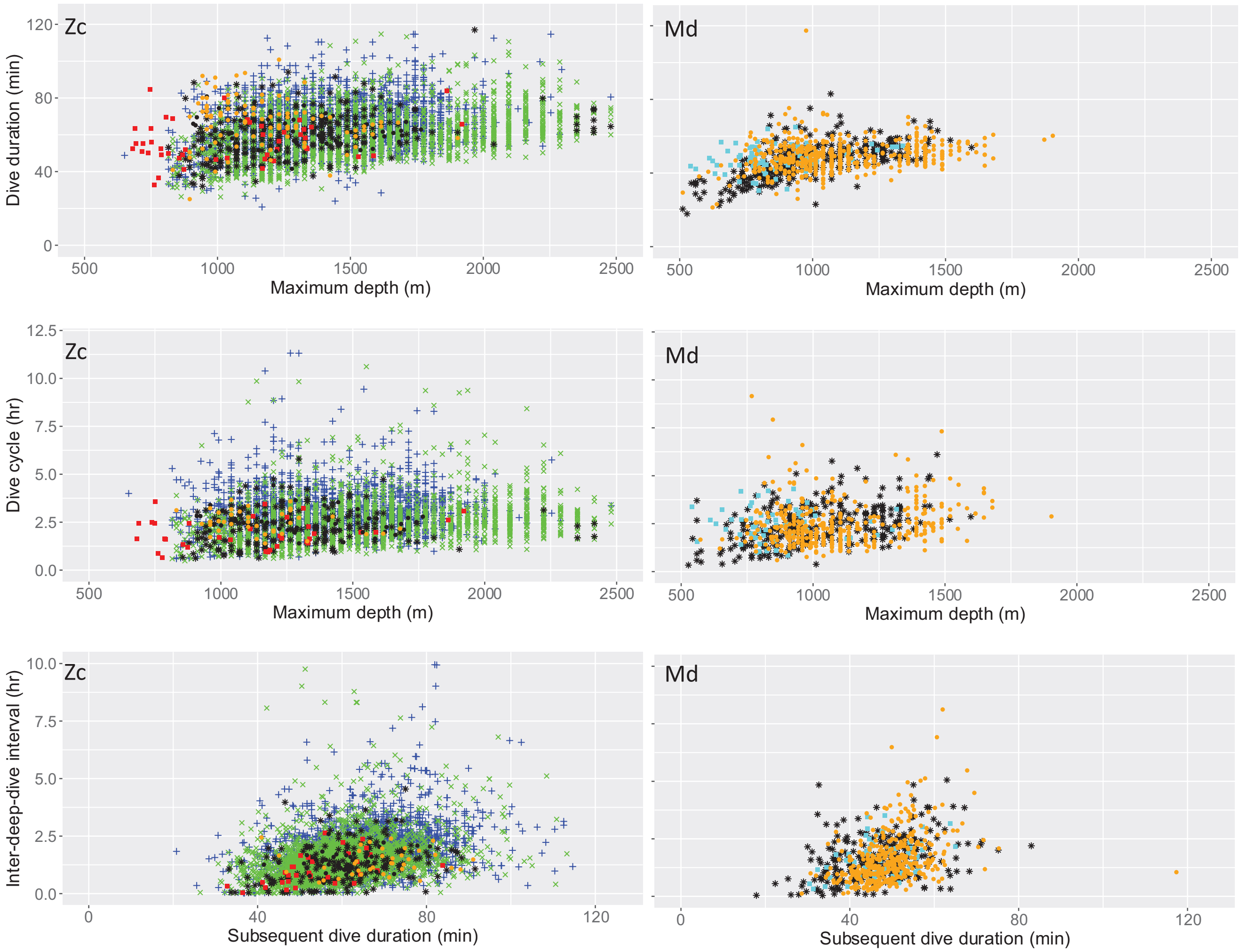

FIGURE 9 | Bivariate relationships between maximum foraging dive depth and foraging dive duration, maximum foraging dive depth and dive cycle duration, and foraging dive duration and the preceding inter-deep-dive interval for individual dives by goose-beaked whales (Zc, left panels) and dense-beaked whale (Md, right panels). Symbols indicate the tagging location: Hatteras (green x), SoCal (blue +), Hawai'i (black *), Liguria (red square), Azores (black circle), Bahamas (orange circle), and Canaries (cyan square). Note, a few extreme values are not shown to allow more detail for the remaining values.

beaked whale tagging has been in abyssal waters deeper than 3000 m water depth (Baird et al. 2011). Although our results should be representative of the areas studied, little is known about beaked whale diving depths in the ~75% of the ocean areas that are deeper than 3000 m (from figure 1 in de Lavergne et al. 2016).

4.2 | Foraging Dive Duration and Dive Cycle Duration

Inter-deep-dive intervals are positively correlated with the duration of subsequent deep foraging dives for both goose-beaked and dense-beaked whales. Tyack et al. (2006) found a similar correlation for goose-beaked whales based on a subset of the data used here. Because dive cycle is the sum of the IDDI and foraging dive duration, it will also be the case that longer dives are associated with longer dive cycles. This may occur because whales need longer periods to replenish their oxygen stores before a very long dive.

As has been found in previous studies using subsets of these data (Tyack et al. 2006; Baird et al. 2008; Joyce et al. 2017), goose-beaked whales dive, on average, for longer durations than dense-beaked whales, and this is true for all of our locations. Foraging dive durations are generally expected to increase with body mass (Joyce et al. 2017), which is consistent with this result. However, as noted by Joyce et al. (2017), the mean foraging dive durations of both species appear to exceed the aerobic dive limits that would be expected for their masses (but see Velten et al. 2013). The composite mean dive cycle durations are remarkably similar for both species (2.44–2.46 h); the lower extreme value is in Liguria (1.94 h) and the upper extreme is in SoCal (3.08 h) (Table 2).

4.3 | Extrapolating Estimates of Dive Parameters to Unstudied Areas

The major motivation for this comparative study of beaked whale diving is our desire to extrapolate the parameters that describe beaked whale diving behavior from well-studied areas to unstudied areas. There have been no tagging studies of beaked whales in the vast majority of the world's oceans, but recently developed methods to estimate beaked whale density and abundance from monitoring their echolocation signals require knowledge of their diving behavior. Although it would be optimal to conduct tagging studies in conjunction with any acoustic surveys of beaked whale abundance, this is often not feasible. Given that we lack estimates for many locations, we have attempted to quantify the degree to which beaked whale dive parameters differ between study locations. Here we concentrate on two parameters, mean echolocation depth and dive cycle duration, that are important in deriving acoustic estimates of beaked whale abundance (Barlow et al. 2022).

Our statistical analyses show that, despite the large variation between dives of a given individual and between individuals, location is an important explanatory variable in describing variation in echolocation depth for both species and dive cycle duration for goose-beaked whales (Tables 4 and 5). For dense-beaked whales, mean echolocation depth varies by 161 m between The Bahamas and the Canary Islands (Table 4), while mean dive cycle duration varies by only 0.03 h between the locations with the largest differences (Table 3). For goose-beaked whales, mean echolocation depth varies by 231 m (Table 4) and mean dive cycle duration varies by 1.1 h between the locations with the largest differences (Table 3). Although location does contribute to the overall variance in echolocation depth, its contribution is smaller than the sum of the variation seen between individuals and between dives within individuals (the residual variance) (Table 3). Consequently, a large sample size is needed to even discern these location effects.

Our composite estimates for dive parameters for a given species (Tables 3 and 5) may be reasonable estimates to use for extrapolating to unstudied areas. These composites weight each of our study areas equally and, thus, can be considered to be a sample of potential study areas. Of course, our study areas were selected for their potential to allow tagging of beaked whales in an area of interest. We cannot evaluate how this non-random selection of study areas might be biasing estimates of beaked whale dive parameters, or whether beaked whales primarily using abyssal areas may differ in their diving behavior from those that inhabit slopes or basins. Also, some regions are more affected by anthropogenic activities than others. In estimating dive parameters for an unstudied area, there may be compelling reasons for using a subset of our study areas for this extrapolation if that study area is more similar to one or more of our study areas. For example, in estimating mean echolocation depth for elsewhere in the Mediterranean Sea, it may make more sense to use our estimates for Liguria than to use our composite estimates.

In a case where the mean maximum dive depth is known for a location, for example, from non-acoustic tagging studies, it is possible to estimate the mean and standard deviation of echolocation depth from their relationship to maximum dive depth. Given their strong correlation with maximum depth (Figure 7), this approach is likely to give a more accurate estimate of echolocation depth (in an area where it has not been directly measured) than the composite estimate which includes locations with, potentially, very different dive depths.

5 | Future Research

The focus of this paper is on comparisons of dive parameters that have been used in past studies of beaked whale behavior and that have been useful in making acoustic-based estimates of beaked whale abundance. In doing so, we have concentrated on measures of central tendency (e.g., mean values) and have not examined in detail how parameter distributions may differ among study sites. We recognize that we have only explored a small fraction of the potential information in our rich set of tagging data. In this section, we highlight potential future studies that could aid in our further understanding of diving behavior for goose- and dense-beaked whales.

There is a need for studies of beaked whale diving behavior in a greater number of locations and including a greater number of species. Most of the behavioral tagging studies to date have been in near-shore locations and only included the two beaked whale species examined in this paper. There is a dearth of information on the diving behavior of beaked whales in deep abyssal waters where the majority of individuals in these species may live. There are 24 recognized species of beaked whales, and little is known about the diving behavior of most species.

Within the two species studied in this paper, we do not know why dive behavior differs among locations. A logical explanation is that their prey differs between sites, but prey composition and distributions are hard to directly measure at the extreme depths at which beaked whales feed (Southall et al. 2019). Several previous studies of tagging data have noted two apparent modes of feeding: mid-water and near-bottom (Visser et al. 2021; Coates et al. 2024) which may indicate different prey sources. Our data suggest the possibility of bimodal distributions of foraging depths for some species in some areas (Figure 2), and these modes may be related to these two foraging modes. Acoustic data from tags can be used to discern foraging success (Coates et al. 2024) and may help understand why some whales appear to prefer deeper or near-bottom foraging in some areas.

Anthropogenic sound, especially Navy SONAR, has been shown to affect beaked whale behavior, including foraging. A full exploration of the effect of such sounds on the beaked whale foraging is needed but is beyond the intended scope of this paper. A few studies have explored this for single species in single locations (Tyack et al. 2011; Falcone et al. 2017; Joyce et al. 2020), but there is a need for an integrated analysis of the effect of anthropogenic sounds on beaked whale foraging in multiple locations globally (Henderson 2023).

Author Contributions

Jay Barlow: conceptualization; data curation; formal analysis; funding acquisition; investigation; project administration; resources; writing – original draft; writing – review and editing. **Robin W. Baird:** conceptualization; data curation; funding acquisition; investigation; project administration; resources; writing – review and editing. **Janelle Badger:** conceptualization; formal analysis; investigation; resources; writing – original draft; writing – review and editing. **Gregory S. Schorr:** investigation; data curation; resources; writing – review and editing. **Erin A. Falcone:** investigation; resources; writing – review and editing. **Shannon N. Coates:** investigation; resources; writing – review and editing. **Peter L. Tyack:** investigation; data curation; resources; writing – review and editing. **Andrew J. Read:** investigation; resources; writing – review and editing. **Leigh S. Hickmott:** investigation; data curation; resources; writing – review and editing. **John W. Durban:** investigation; data curation; resources; writing – review and editing. **Diane Claridge:** investigation; resources; writing – review and editing. **Natacha Aguilar de Soto:** investigation; data curation; resources; writing – review and editing. **Daniel Miranda Gonzalez:** investigation; resources; writing – review and editing. **Fleur Visser:** investigation; data curation; resources; writing – review and editing. **Machiel G. Oudejans:** investigation; resources; writing – review and editing. **Stacy DeRuiter:** investigation; formal analysis; resources; writing – review and editing. **David A. Sweeney:** investigation; data curation; resources; writing – review and editing. **Brenda K. Rone:** investigation; resources; writing – review and editing. **Stephanie L. Watwood:** investigation; resources; writing – review and editing.

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Ethics Statement

Tagging in Hawai‘i and off Hatteras was approved by the Cascadia Research Collective Institutional Animal Care and Use Committee (IACUC) and authorized under NMFS Scientific Research Permits No 731-1509, 731-1774, 15330 and 20605. Tagging in Liguria was approved by the Woods Hole Oceanographic Institution IACUC and was conducted under US NMFS permits # 981-1578-02 and 981-1707-00. Tagging in The Bahamas was approved by the IACUCs of the Woods Hole Oceanographic Institution and The Bahamas Marine Mammal Research Organization, by the United States Department of the Navy Bureau of Medicine and Surgery (BUMED) Veterinary Affairs Office, and by the ethics committees of the University of St Andrews, Scotland. Tagging in The Bahamas was performed under Bahamas permit Nos. 01/09, 02/07, and 02/08, US National Marine Fisheries Service Research Permit Nos. 1121-1900, 981-1578-02 and 981-1707-00 and was authorized by Bahamas Marine Mammal Research Permit #12A issued by the Government of The Bahamas under the Bahamas Marine Mammal Protection Act of 2005. Tagging off the Azores was performed under Secretaria Regional do Mar e das Pescas, Direção Regional dos Assuntos do Mar (Azores) research permits 10/2015/DRA, 34/2017/DRA, LMAS-DRAM/2018/01, LMAS-DRAM/2019/01, and LMAS-DRAM/2022/02 and was approved by the KMR IACUC. Tagging in the Canary Islands was conducted under permit from the Ethical Committee for Animal Experimentation of the University of La Laguna and under permit from the Ministry of Ecological Transition of the Spanish Government. Tagging in SoCal was conducted under NMFS Scientific Permits 15330, 16111, 20465, and 21163, and approved by IACUC committees associated with the respective permit holders.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Supporting Information.