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Quantifying deep-sea predator–prey dynamics: Implications of biological heterogeneity for beaked whale conservation

Brandon L. Southall[1,2] | Kelly J. Benoit-Bird[3,4] | Mark A. Moline[5] | David Moretti[6]

[1]Southall Environmental Associates, Inc., Aptos, California; [2]Long Marine Laboratory, University of California, Santa Cruz, Santa Cruz, California; [3]College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, Oregon; [4]Monterey Bay Aquarium Research Institute, Moss Landing, California; [5]College of Earth, Ocean, and Environment, University of Delaware, Lewes, Delaware and [6]Naval Undersea Warfare Center, Newport, Rhode Island

Correspondence
Brandon L. Southall
Email: brandon.Southall@sea-inc.net

Abstract

1. Prey distribution and density drive predator habitat usage and foraging behaviour. Understanding ecological relationships is necessary for effective management in any environment but can be challenging in certain contexts. While there has been substantial effort to quantify human disturbance for some protected, deep-diving marine mammals, there are virtually no direct measurements of deep-sea predator–prey dynamics.

2. We used recently developed techniques to measure deep-water squid abundance, size and distribution within foraging habitat areas of deep-diving Cuvier's beaked whales (*Ziphius cavirostris*) on and around a Navy training range where sonar is often used. Beaked whales are a management priority as both mortal strandings and sublethal disturbance have occurred in association with Navy mid-frequency sonar.

3. We found large differences in prey (squid) abundance over small horizontal distances. Highest squid densities occurred within a commonly utilized foraging area on the range. Much lower prey abundance was measured in adjacent, bathymetrically similar areas less commonly used for foraging.

4. By combining prey densities with available behavioural and energetic data, we generate relativistic energetic assessments of foraging habitat quality. This provides a simple, yet quantitative means of evaluating fitness implications of spatial prey heterogeneity and associated consequences of disturbance.

5. *Synthesis and applications*. Given the challenges deep-diving predators face with limited foraging time in extreme environments, small-scale prey heterogeneity can have substantial implications for foraging success. Our results provide fine-scale data within neighbouring beaked whale foraging habitat areas commonly disturbed by sonars. These results have direct management implications and inform population-level models of disturbance consequences with empirical data on the foraging ecology of these protected species. These issues have been at the heart of recent debate and litigation over spatial management and proposed sonar exclusion zones, which have previously been based entirely on indirect assumptions regarding

habitat quality. While limited in temporal and spatial scope, our novel results provide the first direct ecological data to inform such applied decisions. They also highlight broader regulatory implications of different disturbance consequences in nearby areas and demonstrate the value of empirical, biologically based approaches to spatial management of marine ecosystems generally.

1 | INTRODUCTION

The deep sea is a mostly unexplored area that represents >90% of the ocean's total volume (Robison, 2004) and contains vast, dynamic and biologically rich ecosystems. There are extreme challenges in studying the biology and ecosystem dynamics of these harsh, inaccessible environments and little is consequently known about even basic aspects of marine life beneath the photic zone (Martin & Reeves, 2009). The potential impacts and sustainability of some deep-sea and pelagic fisheries have been considered (e.g. Koslow et al., 2000; Roberts, 2002), but most deep-water management decisions have focused on the sea floor (Januchowski-Hartley, Selkoe, Gallo, Bird, & Hogan, 2017; Robison, 2004).

Since Lindeman (1942) introduced the idea that energy flow mediated by trophic interactions could control communities, simple bioenergetics models have been used to address basic and applied ecological questions (Brown, Gillooly, Allen, Savage, & West, 2004; Nisbet, Muller, Lika, & Kooijman, 2000). In aquatic and shallow water marine ecosystems, bioenergetics models have played key roles in informing management decisions. For example, they have been used to predict invasion pathways and novel species dynamics in pristine and eutrophied habitats (Schneider, 1992), evaluate mortality in endangered species (Chasco et al., 2017) and assess population declines (Winship, Trites, & Rosen, 2002). Similar bioenergetics methods of quantifying deep-sea predator–prey dynamics, while challenging to obtain, are needed to better understand ecosystem functions and improve decisions for these vast and vital habitats.

Beaked whales are deep-diving predators that have evolved remarkable physiological and behavioural characteristics to forage at depths exceeding 1,000 m while enduring radical changes in hydrostatic pressure, temperature and light (Tyack, Johnson, Soto, Sturlese, & Madsen, 2006). Although knowledge of basic biology is limited for some species within this diverse group, beaked whales are generally believed to be primarily income breeders (New, Moretti, Hooker, Costa, & Simmons, 2013), feeding day and night (Baird, Webster, Schorr, McSweeney, & Barlow, 2008). Regular access to prey is likely a key factor influencing short-term behaviour, individual fitness and, consequently, long-term demographic trends (e.g. New et al., 2013).

Mortal stranding events involving several beaked whale species (primarily including Cuvier's beaked whales [*Ziphius cavirostris*; hereafter *Ziphius*]) have been documented in association with Navy mid-frequency

(1–10 kHz) active sonar (MFAS; D'Amico et al., 2009). These events have fuelled substantial public interest, management actions, litigation and research over the past several decades, particularly regarding military sonar systems. However, mass strandings of beaked whales, or other marine mammals, do not occur during most sonar operations. Rather, some beaked whales have been observed avoiding MFAS operations by abandoning known foraging areas on U.S. Navy undersea ranges, returning once disturbances abate. Interestingly, these observations are largely the result of studies that have successfully utilized the listening capabilities of the Navy ranges themselves to monitor the behaviour and behavioural changes of beaked whales during potential disturbance events (McCarthy et al., 2011; Moretti, Thomas, Marques, Harwood, & Diley, 2014; Tyack et al., 2011). Energetic modelling approaches have been applied in designing marine protected areas related to beaked whale conservation (Hooker, Whitehead, & Gowans, 2002) and are currently being used to better evaluate potential population consequences of disturbances (Costa, 2012; New et al., 2013). These kinds of population models for beaked whales are strongly influenced by assumptions regarding prey 'quality' and distribution, which affects interpretations of potential disturbance. However, there are essentially no direct measures available with which to quantify the differential biological value of foraging habitats and thus inform these population models with empirical data. Such results are needed to better parameterize emerging population models and inform applied management decisions for these protected species (e.g. from MFAS operations). Specifically, direct measurements of prey characteristics are needed to quantify the biological importance of known foraging areas to which beaked whales continue to return despite repeated disturbance as well as the relative energetic implications of foraging in alternative habitat (New et al., 2013).

We designed this study to provide such data for *Ziphius*, extreme deep-diving cetaceans thought to feed primarily on squid (Santos et al., 2001), in a unique setting on and near a military training range. The U.S. Navy's Southern California Anti-Submarine Warfare Range (SOAR) includes an array of nearly 200 bottom-mounted hydrophones covering >1,000 km^2 west of San Clemente Island in the San Nicolas Basin. Areas on and around SOAR have been the focus of studies considering the effects of sonar on cetaceans, with particular interest in *Ziphius* (DeRuiter et al., 2013; Falcone et al., 2009, 2017; Schorr, Falcone, Moretti, & Andrews, 2014). These areas have also been the subject of ongoing regulatory and legal debates regarding sonar use and *Ziphius* habitat foraging quality (Mollway, 2015). Historical data

on *Ziphius* distribution and behaviour suggest differential use of areas on and around SOAR (Falcone et al., 2009; Schorr et al., 2014). These results and extensive unpublished records of *Ziphius* habitat use from monitoring on SOAR (D. Moretti, unpubl. data) were used to guide an initial study of deep-water squid (Benoit-Bird, Southall, & Moline, 2016a). This provided an important foundation for the current study by quantifying distinct prey metrics (abundance, local density, prey size) that differed among potential *Ziphius* foraging habitat.

Our goal was to integrate direct measurements of deep-water prey distribution over fine-scale geographic ranges to derive a quantitative metric of *Ziphius* foraging habitat quality within biologically important areas frequently disturbed by MFAS. We used an integrated energetic and behavioural framework to evaluate foraging opportunities for animals in different habitats and the associated potential consequences of disturbance. There are considerable data limitations regarding relevant input variables, particularly *Ziphius* energetic parameters. This approach is consequently deliberately simple, examining relative differences in foraging habitat quality using biologically informed assumptions. Such biologically relevant, sub-mesoscale evaluation of spatial habitat heterogeneity has previously been unavailable but is directly applicable to effective beaked whale management decisions. Our results also highlight the general need for such approaches to spatial management of marine ecosystems, including the deep sea.

2 | MATERIALS AND METHODS

2.1 | Field data collection

An autonomous echosounder system (38 and 120 kHz) integrated into a 600-m depth-capable AUV was introduced by Moline,

Benoit-Bird, O'Gorman, and Robbins (2015) and used here to measure squid distribution and density. We utilized methods and selected squid metrics from Benoit-Bird et al. (2016a), including an integrated biomass proxy; the number of separable individuals; estimates of individual size; and distribution heterogeneity at depths of 900–1,200. Neighbouring, bathymetrically similar areas of known beaked whale feeding habitat were sampled, including two adjacent portions of the northern half of the SOAR sonar training range ('western' and 'eastern') and a third ('off-range') area north of SOAR (Figure 1). All areas are regularly exposed to MFAS to some degree, with use more concentrated within SOAR given the application of range hydrophones in testing and training. The 'western' range area has relatively higher use by foraging *Ziphius* than 'eastern' SOAR based on extensive historical spatial distribution and foraging dives derived from both satellite tag tracks and passive acoustic monitoring (D. Moretti, unpubl. data; Falcone et al., 2009; Schorr et al., 2014). The off-range area north of SOAR enabled us to evaluate relative prey quality in a nearby, readily accessible deep-water area that is known to be used as foraging habitat by some tagged whales (Schorr et al., 2014). While not the only, or necessarily most preferred, alternate foraging area for animals outside SOAR, its proximity to high-use sonar areas provides one of the lowest transit distance and least costly options for reaching presumably less-impacted foraging habitat.

2.2 | Depth effects on prey

An important question in understanding beaked whale foraging behaviour is determining how available ecological data relate to the depths at which they forage. Previous measurements in this region demonstrate that neither the distribution and density of potential prey
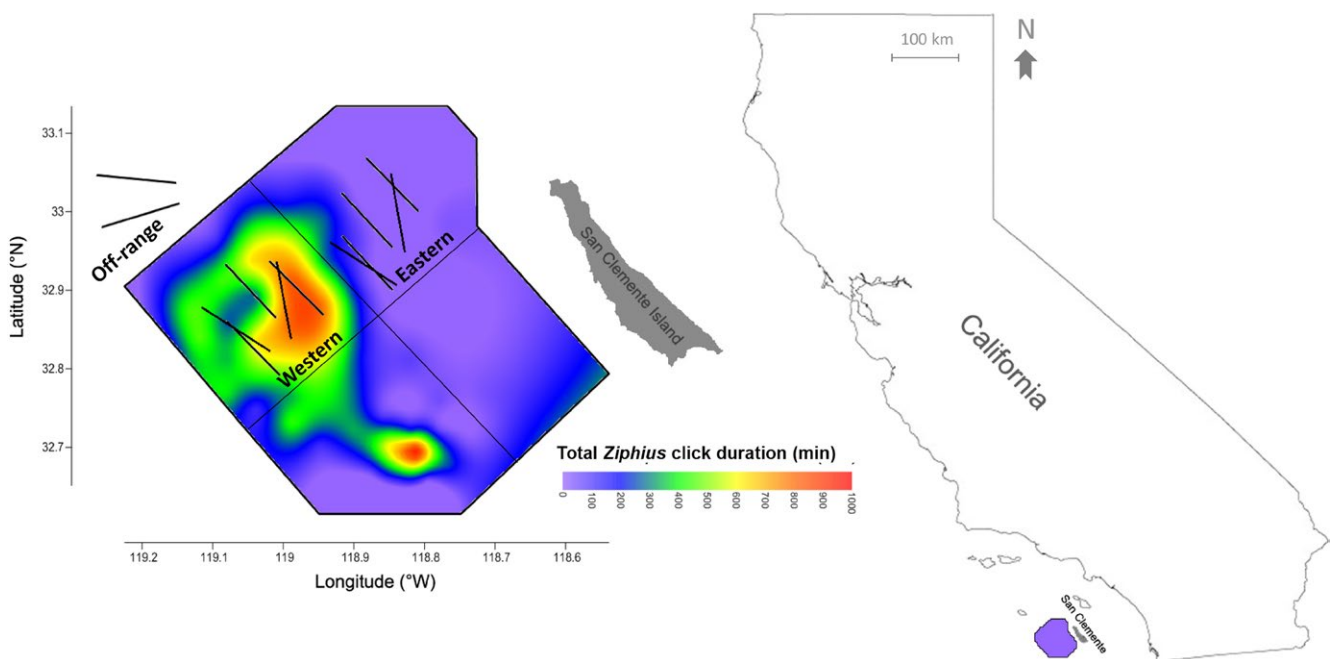

FIGURE 1 Total duration of *Ziphius* clicks (colour) detected by hydrophones on the U.S. Navy's SOAR range off Southern California. 'Eastern' and 'western' areas on the northern half of SOAR are delineated. An 'off-range' area to the north is a physically similar nearby habitat that can be used by animals when range activities displace them. Prey data were collected along 10-km long transects (black lines)

in the upper water column nor surface measures of temperature, chlorophyll or other proxies are good predictors of biota at depth (Benoit-Bird et al., 2016a). Previous studies have suggested *Ziphius* foraging depths in the Mediterranean of ~900–1,200 m (Tyack et al., 2006). However, others studying *Ziphius* off southern California (DeRuiter et al., 2013; Schorr et al., 2014) have measured diving (and presumably feeding) at much greater depths. Some evidence suggests that they may forage close to the seafloor and maximum recorded dive depths may thus be limited by water depth (Schorr et al., 2014). A subset of available metrics (acoustic backscatter data, but not individual target identification) from 1,200 m to the sea floor was evaluated to determine if the results from 900 to 1,200 m reasonably reflected the full-depth range for *Ziphius* foraging off southern California. We used an Analysis of Variance to examine the effects of depth range and sampling zone on measures of integrated backscatter. We conducted post hoc Dunnett's C tests to explore observed differences.

2.3 | Beaked whale distribution and behaviour

To investigate whether historical *Ziphius* spatial distributions based on satellite tag and acoustic monitoring were similar to the survey period, SOAR hydrophones were monitored for echolocation signals during September 2013 when prey sampling was conducted. SOAR consists of a widely spaced (2–4 nm), bottom-mounted array of ~180 hydrophones arranged in offset rows. Based on the hydrophone characteristics and *Ziphius* signals, any echolocating *Ziphius* will most likely be detected on at least one hydrophone. A custom support vector machine classifier was used to detect and classify *Ziphius* echolocation clicks (Jarvis, Morrissey, Moretti, & Shaffer, 2014). Click detection reports were archived before, during and after prey mapping periods and post-processed. Click detections were aggregated into click trains and used to identify *Ziphius* group vocal periods (GVPs). For each dive, the hydrophone with the largest number of clicks was designated the central hydrophone for the group and the total number of times a hydrophone occurred as a group centre was tallied. Additionally, the GVP (defined as the detection time from the first click to the last for each group) was determined and summed for all groups centred on each hydrophone over the month to quantify total GVP duration (as in Moretti et al., 2010). Spatial distribution patterns were very similar for total number of groups and total click duration, which is arguably a better proxy for foraging rather than simple searching and which is thus shown in relation to the survey lines along which prey data were collected (Figure 1).

This study was not explicitly designed to measure *Ziphius* behavioural responses to prey sampling. It did not include a controlled exposure design and high-resolution animal-borne tag measurements to study individual behaviour and potential responses to sonar signals from prey mapping survey used, which would likely have been audible to nearby beaked whales. However, we did evaluate potential responses to survey operations in a general sense. The SOAR hydrophones support a broad assessment of *Ziphius* distribution on SOAR and they were consequently used to evaluate total GVP duration in the vicinity of surveys on SOAR during the survey and during non-survey periods in September 2013.

2.4 | Predator–prey data synthesis

To examine the relative implications of observed differences in prey fields for *Ziphius* foraging in each identified area, we integrated prey data with published dive metrics from tagged whales and basic energetic assumptions. The complications of observing beaked whales in situ limit our knowledge of vital rates (New et al., 2013). Given the large uncertainty in key variables, the intent was to develop a comparative framework to evaluate relative habitat quality. Relative assessments are made using a biologically meaningful metric that integrates key prey and species-typical behavioural parameters using simplifying assumptions, as shown in Table 1 with additional methodological details provided in footnotes. To assess fine-scale prey structure, we compared the effects of both mean inter-prey spacing, affected only by prey abundance, and mode spacing, which incorporates the effects of both prey abundance and distribution. Beaked whales have been observed to make 30 prey capture attempts on average per dive during approximately 30 min of effective foraging (Tyack et al., 2006). Using this information, we estimated the distance a beaked whale would have to cover to capture 30 prey under each scenario (inter-prey spacing × 30 prey per dive) and the swimming velocity required to cover that distance in 30 min (distance to capture 30 prey/30 min per dive).

We also employed an energetic approach to assess relative potential foraging outcomes between areas, incorporating observed differences in prey size (from Benoit-Bird et al., 2016a). First, we estimated the number of prey encountered per dive using a range of feasible predator velocities from 1 to an extreme of 8 m/s (1/inter-prey spacing × whale swimming velocity × 30 min per dive). Based on tagging studies (Johnson, Madsen, Zimmer, De Soto, & Tyack, 2004) and surface observations of free-ranging *Ziphius* and other beaked whales during field studies, 3 m/s was chosen as a reasonable value.

We used two approaches to convert median prey target strengths to calories. While no measures relating target strength of these presumed squid to length, biomass or caloric content are available, conversions are available for related species. Target strength was initially converted directly to caloric content using data for mid-water squid species (Benoit-Bird & Au, 2002). A second, more indirect approach converted target strength to length using relationships established for other squid species (Benoit-Bird & Au, 2001; Benoit-Bird, Gilly, Au, & Mate, 2008). Length was then converted to mass using relationships measured for squid of similar sizes (Hoving et al., 2013; Merella, Quetglas, Alemany, & Carbonell, 1997) and then mass to calories using energy density measures from mid-water squid species (Abitia-Cardenas, Galvan-Magaña, & Rodriguez-Romero, 1997; Benoit-Bird, 2004; Cherel & Ridoux, 1992; Cox, Gaglione, Prowten, & Noonan, 1996). Twenty-one predictions of individual prey caloric content were made. Direct acoustic scattering to caloric conversion was within 50 calories of the median of all other calculated values and was applied as the most likely value.

To calculate foraging dives needed per day (see Table 1), we estimated the baseline daily metabolic needs for a 2,400 kg adult *Ziphius*, based on a metabolic rate of 50 kCal kg^{-1} day^{-1}, which is

TABLE 1 Measured differences (Benoit-Bird et al., 2016a) between three regions categorized by their historic use by beaked whales (see Figure 1) were combined with measurements from previous tagging studies and energetic requirements to predict differences in foraging benefits of the three regions. The most likely predictions are shown followed by the full range in parentheses

Inter-prey spacing metric	Low use		High use		Alternate	
	Mean	Mode	Mean	Mode	Mean	Mode
Inter-prey spacing (m)	3,300	3,200	230	57	1,000	875
Distance to capture 30 prey[a] (km)	99	96	7	2	30	26
Average velocity required to capture 30 prey (m/s)	55	53	4	1	17	15
Prey encountered/dive at typical swimming speed[b] (#)	3 (2–5)	3 (2–6)	24 (9–64)	96 (33–254)	6 (3–15)	7 (3–17)
Prey median length[c] (cm)	16		22		22	
Predicted kCal/prey[d]	475 (100–850)		850 (400–1,350)		850 (400–1,350)	
Dives needed/day[e] (#)	96 (26–776)	94 (26–768)	6 (1.4–34)	1.5 (0.4–9)	22 (6–107)	20 (6–98)

[a]Tagged individuals average 30 prey capture attempts/dive (Tyack et al., 2006). [b]Observed swimming speeds: 1–8 m/s, 3 m/s sustained (Johnson et al., 2004). [c]No measures relating the target strength of squid to length, biomass or caloric content are available for deepwater squid. Relationships for several shallow water species were used to estimate length (Benoit-Bird & Au, 2001; Benoit-Bird et al., 2008). The consistent slope of these relationships suggests that relative length differences can be reliably assessed (McClatchie, Macaulay, & Coombs, 2003). [d]Median target strength was converted directly to calories using measurements for mid-water squid species (Benoit-Bird & Au, 2002) and indirectly by converting length to mass (Hoving et al., 2013; Merella et al., 1997), then mass to calories (Abitia-Cardenas et al., 1997; Benoit-Bird, 2004; Cherel & Ridoux, 1992; Cox et al., 1996). The direct conversion was in both cases within 50 calories of the median of all other calculated values (N = 21) and was used as the most likely value. [e]Baseline daily metabolic requirement of a 2,400 kg individual, adult *Ziphius* with a metabolic rate of 50 kCal/kg/day (Benoit-Bird, 2004; Kastelein et al., 2003), was divided by the calorie content per prey times the number of prey encountered.

commonly used as a feeding rate for a number of captive cetacean species (Benoit-Bird, 2004; Kastelein, Hagedoorn, Au, & De Haan, 2003). This value was divided by the caloric content per prey times the number of prey encountered per dive. Calculations were replicated using the most likely predictions and extreme values of each variable to examine the respective sensitivity of metrics.

3 | RESULTS

3.1 | Beaked whale distribution and behaviour

Passive acoustic monitoring on SOAR during September 2013 revealed similar patterns of *Ziphius* distribution as in earlier observations of habitat use. Substantially higher foraging rates (quantified as total duration of echolocation clicks) occurred in western versus eastern SOAR range areas (Figure 1). In evaluating potential behavioural responses to active sonar during the survey, it is noteworthy that the general distribution of vocalizing whales was not different between survey and non-survey periods. For all hydrophones within 5 km of any portion of any track line conducted on the range, total click duration for 26 non-survey days in the same month (September) was 11,762 total min (452 min/day) whereas total GVP duration for four survey days on identical hydrophones was 2,477 total min (619 min/day). This does not necessarily indicate that beaked whales do not respond individually to active acoustic sources at shorter time-scales and smaller spatial scales than would be detectable with this kind of broad measure, such as those observed by Cholewiak, DeAngelis, Palka, Corkeron, and van Parijs (2017). However, it

suggests that beaked whales generally remained in similar areas and continued to forage in similar ways during periods of active acoustic surveys used here.

3.2 | Prey metrics

There was a significant effect ($p \ll 0.05$ for all comparisons) of sampling zone on every measure of potential *Ziphius* prey between 900 and 1,200 m (see Figures 2 and 3), including a proxy for total biomass, number of individual scattering targets, number of squid, distribution of squid length and the spatial distribution of squid (also see Benoit-Bird et al., 2016a). This pattern was similar for depths greater than 1,200 m (for those variables that could be measured—see below), but not shallower than 600 m (Figures 2 and 3), much like the decoupling of shallow and deep prey layers identified by Benoit-Bird et al. (2016a). There was no effect on similar measures for fish targets. We were unable to identify individual targets at depths >1,200 m, although acoustic backscatter could be measured to the seafloor for all transects. Expanding the analysis of integrated backscatter to include depths greater than 1200 m, there was a significant effect of depth range ($df = 5,54$; $F = 28.7$; $p < 0.05$) and sampling zone ($df = 2,54$; $F = 25.2$; $p < 0.02$) as well as an interaction between these two variables ($df = 10,54$; $F = 59.2$; $p < 0.01$) on 38 kHz acoustic scattering (Figure 3). Post hoc results showed no significant differences between the 900–1,200 m, 1,200 m bottom and the 50 m above the seafloor ($p > 0.3$ for all comparisons). The integrated scattering below 1,200 m closely mirrored both the levels and the habitat difference patterns observed between 900 and 1,200 m and at depths within 50 m of the seafloor.

Empirical prey metrics from each habitat area were combined with simplified behavioural and energetic parameters to describe relative features of foraging habitat (Table 1). Within the low use area, mean inter-prey spacing (3,300 m) greatly exceeded that observed in the alternate (1,000 m) and high use area (230 m). This translates to a much greater distance and average velocity required to capture 30 prey items in the low use area (99 km; 55 m/s) as opposed to the alternate (30 km; 17 m/s) and high use areas (7 km; 4 m/s). Based on these predictions and additional prey energetic parameters (Table 1), *Ziphius* in the low use area would require 96 dives per day to meet their energetic needs, while whales in the alternate habitat area would require 22, and individuals in the high use area on the western side of the range were found to require only six.
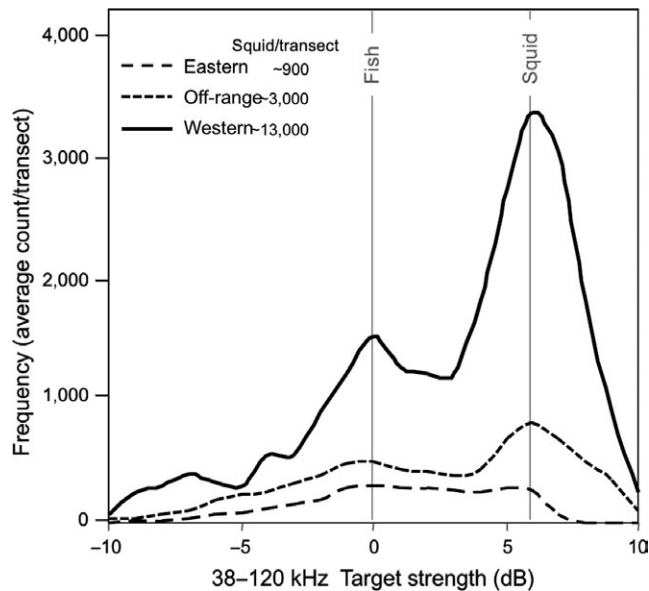

FIGURE 2 Average number of targets per transect shown as function of their acoustic frequency response for each *Ziphius* habitat area. The expected frequency response for fish and squid is highlighted

4 | DISCUSSION

Quantifying variability in prey distribution patterns is critical to understanding foraging habitat quality for predators (Benoit-Bird et al., 2013) and to predicting the consequences of disturbance of foraging behaviour in different foraging areas. These needs may be particularly salient for deep diving, air-breathing predators that face challenges in accessing food and are limited in foraging time. Energy is the currency of survival for all free-ranging animals. As a result, approaches to understand the flow of energy in an individual, population and ecosystem are key tools in both understanding ecosystem function and developing effective management. As beaked whale interactions with human activities have become increasingly recognized and debated, compliance with protective regulations (e.g. the U.S. Marine Mammal Protection Act of 1973, which mandates protection at the stock or population level) has necessitated the use of energetic models to link behaviour with demographic outcomes. Not surprisingly, these models have identified energy intake as a key limiting factor (New et al., 2013). However, this factor is typically evaluated qualitatively as 'habitat quality' and rarely linked with direct environmental or prey measurements. Our data provide the first direct, quantitative assessments of prey resources for *Ziphius* (or any beaked whales) at depths where they feed. The correlation between the 900 and 1,200 m depth interval and greater depths for prey metrics that could be quantified and compared suggests that the 900–1,200 m data are representative of deeper water prey fields in this region for *Ziphius*, particularly regarding relative conclusions between the three foraging zones. Our approach provides a quantitative framework for incorporating a large number of prey metrics into an integrated measure related directly to predator behavioural and energetic characteristics. These resulting metrics provide boundaries, variance estimates and scalars for habitat quality factors used in existing and emerging population consequences of disturbance models (see McHuron, Schwarz, Costa, & Mangel, 2018; Pirotta et al., 2018).

We used recently developed empirical methods of obtaining key missing data to evaluate deep-sea foraging habitat quality for a
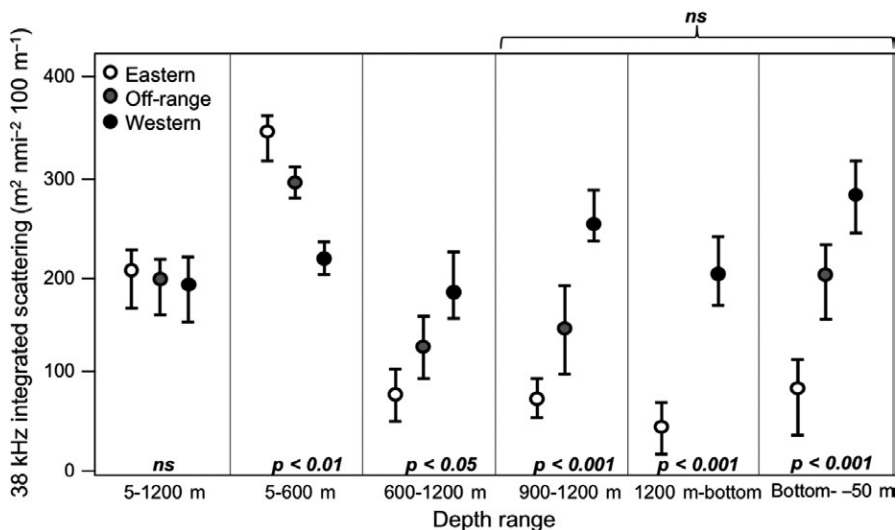

FIGURE 3 Acoustic scattering integrated over each transect is shown as a function of depth range and *Ziphius* habitat area. Error bars show the total range of values for transects in that category. Significance levels for post hoc analysis of the effects of habitat type are given

protected marine mammal species with known sensitivity to military MFAS. These analyses provide a direct means of evaluating the relative consequences of animals leaving preferred habitat during disturbance events known to occur regularly. Our results demonstrate considerable spatial heterogeneity in the primary prey resource of deep-diving beaked whales for this survey period on and around a Navy training range over horizontal distances that are small relative to the swimming capabilities of beaked whales. Neighbouring habitats offered profoundly different prey quality, meaning that the potential energetic consequences of disturbance and/or avoidance of different habitat areas also vary substantially. The results have applied implications for ongoing debates, regulatory decisions and federal litigation over spatial management and 'sonar-free zones' in nearby areas that have previously been based on indirect assumptions about habitat quality.

Beaked whales in the eastern SOAR and off-range areas would not have been able to encounter 30 prey in 30 min during the survey period, even assuming an extreme maximum *Ziphius* swimming velocity of 8 m/s measured during a strong reaction to an experimental MFAS signal (DeRuiter et al., 2013). Using simplifying assumptions necessitated by data limitations, the relativistic energetic analysis we used incorporates prey size differences to evaluate differences in foraging conditions between these areas. *Ziphius* typically conduct between 7 and 12 foraging dives/day (Schorr et al., 2014; Tyack et al., 2006). Under no conditions during our study could a beaked whale encounter, let alone capture, enough prey to meet its needs in eastern SOAR using only 12 dives. Conversely, in the western SOAR area, when accounting for prey distribution, there are no conditions under which a *Ziphius* would need more than 12 dives to meet its daily needs. Despite the remarkably low number of successful dives that would be required in higher use habitats in western SOAR, foraging gains are unlikely to be unlimited; physiological constraints and prey suitability cannot be accounted for by this analysis. We note that if we had assumed a homogenous prey distribution, as implied by the use of mean density values, the higher use habitat would not appear nearly as valuable. Our results demonstrate substantial spatial heterogeneity over small spatial scales and calculated mean densities may thus be unlikely to actually occur.

While the energetic calculations presented are deliberately simplistic given the lack of data for key energetic parameters (New et al., 2013), they clearly demonstrate large relative differences in foraging conditions over small horizontal distances. The potential alternate 'off-range' *Ziphius* foraging habitat area north of SOARs was intermediate to the two range areas in all squid metrics. These findings have important practical and timely implications for *Ziphius* management in this region. First, western areas of the range had relatively higher concentrations of aggregations of large deep-water squid during the sampling period than adjacent regions both on and off SOAR. This is consistent with and likely primarily why these animals continue to return to high sonar use areas despite repeated disturbances to which some beaked whales appear not to habituate (e.g. McCarthy et al., 2011). Relatively

lower abundance and more diffusely distributed, smaller squid in the nearby off-range area does not necessarily reflect all available foraging options to *Ziphius* displaced from the range. However, it does indicate that at least some of the closest comparable habitat is notably inferior in terms of available prey resources to preferred areas within SOAR. These results suggest that beaked whales leaving preferred habitat on SOAR due to disturbance may face not only the energetic costs of moving but also substantially poorer foraging options in alternative areas. Given the very large differences in prey quality measured between these areas, it may prove challenging for individuals to meet basic energetic requirements in some areas. This may help explain the rapid repatriation observed in disturbed individuals within these and other beaked whale habitat areas on some training ranges (e.g. McCarthy et al., 2011).

In 2015, facing legal challenges to requests for authorized disturbance of federally protected marine mammals in several areas during regular MFAS training operations, the U.S. Navy agreed to establish several sonar-free areas outside the primary sonar use areas on SOAR but in the same general area off California (see Mollway, 2015). One of these areas was specific to *Ziphius* and extends to the east and south of San Nicholas Island, within less than 10 km of the alternative, off-range foraging area evaluated here. However, the establishment of this sonar exclusion area was based entirely on indirect assumptions about habitat quality and use, with no direct information about beaked whale prey availability. While our surveys did not directly overlap this sonar exclusion area, nearby habitat (our intermediate use area) appears to be markedly inferior to some areas on the range (high use area) while superior to other range areas. This remains a timely and contentious debate, with specific recent discussions of habitat quality of proposed sonar-free areas at a hearing on 6 June 2018 for the U.S. Navy's request for a federal consistency determination (California Coastal Commission, 2018). Our direct measurements of prey in the off-range alternative habitat provide the best available information with which to assess habitat quality for the proposed sonar exclusion area. These results suggest that this area is markedly inferior to preferred feeding habitat areas on the range, although the spatial heterogeneity in foraging habitat observed over small horizontal distances suggests that careful direct evaluation immediately within the proposed sonar exclusion area is needed. Until additional data are collected, our directly obtained results should be used as measures of habitat quality for models estimating the consequences of disturbance, both for animals within preferred feeding habitat and those who avoid these areas and forage within the proposed sonar exclusion area.

Ziphius appear to have much to gain in the northwestern sector of the SOAR range. However, it may be practically infeasible to suggest establishing a sonar-free area in this area given the presence of the expensive, extensive range facility. Furthermore, animals in this area appear to have, to some degree at least, acclimated to continued sonar disturbance. Concentrating sonar use in other areas where it is uncommon could well result in greater overall negative impact to beaked whales and other species and those effects might

be more difficult to quantify and interpret in less well-studied regions. However, potential mitigation actions that are consistent with our results would be to concentrate MFAS operations on the eastern (low use) side of the northern SOAR area rather than the western (high use) side in order to reduce the potential consequences of disturbance, at least for those occurring at higher sonar intensities. Future considerations of sonar exclusion areas should be based on direct measurements of prey distribution and assessed habitat quality.

Our results also provide empirical data to parameterize new and emerging models evaluating the population consequences of disturbance from Navy MFAS. Explicit comparisons among sites made here, when combined with versions of these models currently being designed to incorporate such data, could enable comparative evaluation of relative energetic consequences of various disturbance scenarios. For example, more empirically informed models of disturbance consequences should consider the energetic implications of disturbance associated with variable sonar use when activity is concentrated into a fewer, more intense training periods (with potentially less frequent, but longer disturbance of foraging) as opposed to being more evenly spaced (where disturbance may be more common but individually briefer). Understanding the potential energetic implications of such scenarios using models of the consequences of disturbance requires critical biological parameters that should be measured in future studies. Population energy management has been viewed as a practical approach, one that may be particularly suitable for pelagic ecosystems that vary considerably over space and time and are used by highly mobile predators. However, for these models to achieve their objectives, they need to incorporate real measurements of available prey resources; something published models for beaked whale populations have not yet been designed to do.

We focus here on measuring the prey environment and evaluating relative foraging quality of habitat areas for *Ziphius*. However, the comparative, ecologically based evaluative methods applied here provide a generalizable approach for quantifying habitat quality and evaluating the consequences of disturbance that is more broadly applicable for beaked whales and other top predators. As human interference in the deep sea increases through resource exploitation (fishing, mining and hydrocarbon extraction) and larger scale influences including climate change, ocean acidification and acute and chronic noise pollution, human interference in the deep sea could outpace our basic understanding of how it functions (Taylor & Roterman, 2017). Deep-sea management efforts have largely focused on protecting the seafloor or habitats associated with geological features (reviewed in Davies, Roberts, & Hall-Spencer, 2007; see also Januchowski-Hartley et al., 2017), including in one case, the presence of a submarine canyon providing important habitat for several deep-diving cetaceans (Hooker, Whitehead, & Gowans, 1999). Our results indicate that management of the deep sea should also consider water column features that may be persistent, as indicated by long-term beaked whale habitat preferences, but associated with neither clear geological or epipelagic features. Recent and ongoing

management decisions within the Gulf of Mexico and off the U.S. Atlantic coast regarding potential disturbance from seismic surveys associated with offshore energy exploration have considered spatial management schemes based on presumed habitat quality in shelf and pelagic 'hotspot' areas. These areas are believed to be biologically important based on the presence of marine mammals and other top predators or surface measures of productivity. However, virtually none of these areas have been studied in terms of the prey environment where many intermediate or deep-diving protected species actually feed. Surface measures are not good indicators of deep sea resources and may even be inversely related to prey availability for beaked whales (Benoit-Bird et al., 2016a). The kinds of empirical data obtained here applied within even similarly simplistic relative characterization of habitat quality can substantially inform assessments of the potential for disturbance and aid regulatory decision makers in spatial management decisions.

These findings of spatial heterogeneity in prey availability and associated predator habitat preference provide unique, generalizable insight into deep-sea ecological interactions. They highlight additional research needed to directly quantify spatial and temporal aspects of habitat quality and spatial usage by predators and the needed application of such data within effective management and mitigation strategies for potential disturbance that move beyond simple presumptions of environmental quality. While physical and chemical properties of the deep sea are generally thought to be relatively similar in the horizontal plane over the scales we sampled, our data clearly demonstrate that biological properties directly affecting animal behaviour and fitness are not. These results demonstrate the need for biologically and spatially explicit means of understanding and managing marine ecosystems that begin to address predator–prey dynamics. They highlight the fact that such relationships must be considered, and at relatively fine scales, to begin to understand deep-sea ecological interactions and address key issues, including predator–prey dynamics, ecosystem linkages and informed and effective resource management of these important habitat areas.

AUTHORS' CONTRIBUTIONS

B.L.S., K.J.B-.B. and M.A.M. participated in experimental design and fieldwork; K.B.B. provided statistical analysis of prey data; D.M. provided beaked whale detection data; B.L.S. and K.J.B-.B. drafted the

manuscript. All authors revised the manuscript and gave final approval for publication.

ORCID

Brandon L. Southall iD https://orcid.org/0000-0002-3863-2068

REFERENCES

Abitia-Cardenas, L. A., Galvan-Magaña, F., & Rodriguez-Romero, J. (1997). Food habits and energy values of prey of striped marlin, *Tetrapturus audax*, off the coast of Mexico. *Fishery Bulletin*, *95*, 360–368.

Baird, R. W., Webster, D. L., Schorr, G. S., McSweeney, D. J., & Barlow, J. (2008). Diel variation in beaked whale diving behavior. *Marine Mammal Science*, *24*(3), 630–642. https://doi.org/10.1111/j.1748-7692.2008.00211.x

Benoit-Bird, K. J. (2004). Prey caloric value and predator energy needs: Foraging predictions for wild spinner dolphins. *Marine Biology*, *145*, 435–444.

Benoit-Bird, K. J., & Au, W. W. L. (2001). Target strength measurements of animals from the Hawaiian mesopelagic boundary community. *Journal of the Acoustical Society of America*, *110*, 812–819. https://doi.org/10.1121/1.1382620

Benoit-Bird, K. J., & Au, W. W. L. (2002). Energy: Converting from acoustic to biological resource units. *Journal of the Acoustical Society of America*, *111*, 2070–2075. https://doi.org/10.1121/1.1470505

Benoit-Bird, K. J., Battaile, B. C., Heppell, S. A., Hoover, B., Irons, D., Jones, N., … Trites, A. W. (2013). Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. *PLoS ONE*, *8*, e53348. https://doi.org/10.1371/journal.pone.0053348

Benoit-Bird, K. J., Gilly, W. F., Au, W. W. L., & Mate, B. R. (2008). Controlled and *in situ* target strengths of the jumbo squid *Dosidicus gigas* and identification of potential acoustic scattering sources. *Journal of the Acoustical Society of America*, *123*, 1318–1328. https://doi.org/10.1121/1.2832327

Benoit-Bird, K. J., Southall, B. L., & Moline, M. A. (2016a). Predator-guided sampling reveals biotic structure in the bathypelagic. *Proceedings of the Royal Society, B: Biological Sciences*, *283*, 20152457. https://doi.org/10.1098/rspb.2015.2457

Benoit-Bird, K. J., Southall, B. L., & Moline, M. A. (2016b). Data from: Predator-guided sampling reveals biotic structure in the bathypelagic. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.g8g20

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*, 1771–1789. https://doi.org/10.1890/03-9000

California Coastal Commission. (2018). June meeting, agenda item 14, topic CD-0001-18 (US Navy, Southern California). Retrieved from https://www.coastal.ca.gov/meetings/agenda/#/2018/6

Chasco, B., Kaplan, I. C., Thomas, A., Acevedo-Gutiérrez, A., Noren, D., Ford, M. J., … Pearson, S. (2017). Estimates of Chinook salmon consumption in Washington State inland waters by four marine mammal predators from 1970 to 2015. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*, 1173–1194.

Cherel, Y., & Ridoux, V. (1992). Prey species and nutritive value of food fed during summer to king penguin *Aptenodytes patagonica* chicks at Possession Island, Crozet Archipelago. *IBIS*, *134*, 118–127.

Cholewiak, D., DeAngelis, A. I., Palka, D., Corkeron, P. J., & van Parijs, S. M. (2017). Beaked whales demonstrate a marked acoustic response to the use of shipboard echosounders. *Royal Society Open Science*, *4*(12), 170940. https://doi.org/10.1098/rsos.170940

Costa, D. P. (2012). A bioenergetics approach to developing a population consequences of acoustic disturbance model. In A. N. Popper & A. Hawkins (Ed.), *The effects of noise on aquatic life* (pp. 423–426). New York: Springer-Verlag.

Cox, M., Gaglione, E., Prowten, P., & Noonan, M. (1996). Food preferences communicated via symbol discrimination by a California sea lion (*Zalophus californianus*). *Aquatic Mammals*, *22*, 3–10.

D'Amico, A., Gisiner, R. C., Ketten, D. R., Hammock, J. A., Johnson, C., Tyack, P. L., & Mead, J. (2009). Beaked whale strandings and naval exercises. *Aquatic Mammals*, *35*, 452–472. https://doi.org/10.1578/AM.35.4.2009.452

Davies, A. J., Roberts, J. M., & Hall-Spencer, J. (2007). Preserving deep-sea natural heritage: Emerging issues in offshore conservation and management. *Biological Conservation*, *138*, 299–312. https://doi.org/10.1016/j.biocon.2007.05.011

DeRuiter, S. L., Southall, B. L., Calambokidis, J., Zimmer, W. M., Sadykova, D., Falcone, E. A., … Schorr, G. S. (2013). First direct measurements of behavioural responses by Cuvier's beaked whales to mid-frequency active sonar. *Biology Letters*, *9*, 20130223. https://doi.org/10.1098/rsbl.2013.0223

Falcone, E. A., Schorr, G. S., Douglas, A. B., Calambokidis, J., Henderson, E., McKenna, M. F., … Moretti, D. (2009). Sighting characteristics and photo-identification of Cuvier's beaked whales (*Ziphius cavirostris*) near San Clemente Island, California: A key area for beaked whales and the military? *Marine Biology*, *156*, 2631–2640. https://doi.org/10.1007/s00227-009-1289-8

Falcone, E. A., Schorr, G. S., Watwood, S. L., DeRuiter, S. L., Zerbini, A. N., Andrews, R. D., … Moretti, D. J. (2017). Diving behaviour of Cuvier's beaked whales exposed to two types of military sonar. *Royal Society Open Science*, *4*(8), 170629. https://doi.org/10.1098/rsos.170629

Hooker, S. K., Whitehead, H., & Gowans, S. (1999). Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. *Conservation Biology*, *13*, 592–602. https://doi.org/10.1046/j.1523-1739.1999.98099.x

Hooker, S. K., Whitehead, H., & Gowans, S. (2002). Ecosystem consideration in conservation planning: Energy demand of foraging bottlenose whales (*Hyperoodon ampullatus*) in a marine protected area. *Biological Conservation*, *104*, 51–58. https://doi.org/10.1016/S0006-3207(01)00153-7

Hoving, H.-J., Gilly, W. F., Markaida, U., Benoit-Bird, K. J., Brown, Z. W., & Daniel, P., … Campos, B. (2013). Extreme plasticity in life-history strategy allows a migratory predator (jumbo squid) to cope with a changing climate. *Global Change Biology*, *19*, 2089–2103 https://doi.org/10.1111/gcb.12198

Januchowski-Hartley, S. R., Selkoe, K. A., Gallo, N. D., Bird, C. E., & Hogan, J. D. (2017). Knowledge sharing about deep-sea ecosystems to inform conservation and research decisions. *FACETS*, *2*, 984–997. https://doi.org/10.1139/facets-2017-0037

Jarvis, S. M., Morrissey, R. P., Moretti, D. J., & Shaffer, J. A. (2014). Detection, localization, and monitoring of marine mammals in open ocean environments using fields of spaced bottom mounted hydrophones. *Marine Technology Society Journal*, *48*, 5–20. https://doi.org/10.4031/MTSJ.48.1.1

Johnson, M., Madsen, P., Zimmer, W., De Soto, N., & Tyack, P. (2004). Beaked whales echolocate on prey. *Proceedings of the Royal Society B: Biological Sciences*, *271*, 383–386.

Kastelein, R. A., Hagedoorn, M., Au, W. W. L., & De Haan, D. (2003). Audiogram of a striped dolphin (*Stenella coeruleoalba*). *Journal of the Acoustical Society of America*, *113*, 1130–1137. https://doi.org/10.1121/1.1532310

Koslow, J., Boehlert, G. W., Gordon, J. D. M., Haedrich, R. L., Lorance, P., & Parin, N. (2000). Continental slope and deep-sea fisheries:

Implications for a fragile ecosystem. *ICES Journal of Marine Science*, *57*(3), 548–557. https://doi.org/10.1006/jmsc.2000.0722

Lindeman, R. L. (1942). The trophic-dynamic aspect of ecology. *Ecology*, *23*, 399–417. https://doi.org/10.2307/1930126

Martin, A. R., & Reeves, R. R. (2009). Diversity and zoogeography. In A. R. Hoelzel (Ed.), *Marine mammal biology – An evolutionary approach.* Oxford, UK: Blackwell Publishing.

McCarthy, E., Moretti, D., Thomas, L., DiMarzio, N., Morrissey, R., Jarvis, A., ... Dilley, A. (2011). Changes in spatial and temporal distribution and vocal behavior of Blainville's beaked whales (*Mesoplodon densirostris*) during multiship exercises with mid-frequency sonar. *Marine Mammal Science*, *27*, E206–E226. https://doi.org/10.1111/j.1748-7692.2010.00457.x

McClatchie, S., Macaulay, G., & Coombs, R. F. (2003). A requiem for the use of 20log length for acoustic target strength with special reference to deep-sea fishes. *ICES Journal of Marine Science*, *60*, 419–428. https://doi.org/10.1016/S1054-3139(03)00004-3

McHuron, E. A., Schwarz, L. K., Costa, D. P., & Mangel, M. (2018). A state-dependent model for assessing the population consequences of disturbance on income-breeding mammals. *Ecological Modeling*, *385*, 133–144. https://doi.org/10.1016/j.ecolmodel.2018.07.016

Merella, P., Quetglas, A., Alemany, F., & Carbonell, A. (1997). Length-weight relationship of fishes and cephalopods from the Balearic Islands (western Mediterranean). *Naga, The ICLARM Quarterly*, *20*, 66–68.

Moline, M. A., Benoit-Bird, K. J., O'Gorman, D., & Robbins, I. C. (2015). Integration of scientific echosounders with an adaptable autonomous platform to extend our understanding of animals from the surface to the bathypelagic. *Journal of Oceanic and Atmospheric Technology*, *32*, 2173–2186. https://doi.org/10.1175/JTECH-D-15-0035.1

Mollway, S. (2015). Ruling of the U.S. District Court for the District of Hawaii in the case of Conservation Council for Hawaii and Natural Resources Defense Council (NRDC) vs. National Marine Fisheries Service (NMFS). Case 1:13-cv-00684-SOM-RLP Document 117. Filed 14 September 2015.

Moretti, D., Marques, T. A., Thomas, L., DiMarzio, N., Dilley, A., Morrissey, R., ... Jarvis, S. (2010). A dive counting density estimation method for Blainville's beaked whale (*Mesoplodon densirostris*) using a bottom-mounted hydrophone field as applied to a Mid-Frequency Active (MFA) sonar operation. *Applied Acoustics*, *71*, 1036–1042. https://doi.org/10.1016/j.apacoust.2010.04.011

Moretti, D., Thomas, L., Marques, T., Harwood, J., & Diley, A. (2014). A risk function for behavioral disruption of Blainville's beaked whales (*Mesoplodon densirostris*) from mid-frequency active sonar. *PLoS ONE*, *9*, e85064. https://doi.org/85010.81371/journal.pone.0085064

New, L. F., Moretti, D. J., Hooker, S. K., Costa, D. P., & Simmons, S. E. (2013). Using energetic models to investigate the survival and reproduction of beaked whales (family Ziphiidae). *PLoS ONE*, *8*, e68725. https://doi.org/10.1371/journal.pone.0068725

Nisbet, R., Muller, E., Lika, K., & Kooijman, S. (2000). From molecules to ecosystems through dynamic energy budget models. *Journal of Animal Ecology*, *69*, 913–926. https://doi.org/10.1046/j.1365-2656.2000.00448.x

Pirotta, E., Mangel, M., Costa, D. P., Mate, B., Goldbogen, J. A., Palacios, D. M., ... New, L. (2018). A dynamic state model of migratory behavior and physiology to assess the consequences of environmental variation and anthropogenic disturbance on marine vertebrates. *The American Naturalist*, *191*, E40–E56. https://doi.org/10.1086/695135

Roberts, C. M. (2002). Deep impact: The rising toll of fishing in the deep sea. *Trends in Ecology & Evolution*, *17*(5), 242–245. https://doi.org/10.1016/S0169-5347(02)02492-8

Robison, B. H. (2004). Deep pelagic biology. *Journal of Experimental Marine Biology and Ecology*, *300*, 253–272. https://doi.org/10.1016/j.jembe.2004.01.012

Santos, M., Pierce, G., Herman, J., Lopez, A., Guerra, A., Mente, E., & Clarke, M. (2001). Feeding ecology of Cuvier's beaked whale (*Ziphius cavirostris*): A review with new information on the diet of this species. *Journal of the Marine Biological Association of the UK*, *81*, 687–694. https://doi.org/10.1017/S0025315401004386

Schneider, D. W. (1992). A bioenergetics model of zebra mussel, *Dreissena polymorpha*, growth in the Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*, 1406–1416. https://doi.org/10.1139/f92-156

Schorr, G. S., Falcone, E. A., Moretti, D. J., & Andrews, R. D. (2014). First long-term behavioral records from Cuvier's beaked whales (*Ziphius cavirostris*) reveal record-breaking dives. *PLoS ONE*, *9*, e92633. https://doi.org/10.1371/journal.pone.0092633

Taylor, M., & Roterman, C. (2017). Invertebrate population genetics across Earth's largest habitat: The deep-sea floor. *Molecular Ecology*, *26*, 4872–4896. https://doi.org/10.1111/mec.14237

Tyack, P., Johnson, M., Soto, N., Sturlese, A., & Madsen, P. (2006). Extreme diving of beaked whales. *Journal of Experimental Biology*, *209*, 4238. https://doi.org/10.1242/jeb.02505

Tyack, P. L., Zimmer, W. M., Moretti, D., Southall, B. L., Claridge, D. E., Durban, J. W., ... Jarvis, S. (2011). Beaked whales respond to simulated and actual navy sonar. *PLoS ONE*, *6*, e17009. https://doi.org/10.1371/journal.pone.0017009

Winship, A. J., Trites, A. W., & Rosen, D. A. (2002). A bioenergetic model for estimating the food requirements of Steller sea lions (*Eumetopias jubatus*) in Alaska, USA. *Marine Ecology Progress Series*, *229*, 291–312. https://doi.org/10.3354/meps229291

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