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FEATURE ARTICLE

Short-finned pilot whales exhibit behavioral plasticity in foraging strategies mediated by their environment

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ABSTRACT: Predators adapt their foraging behavior to exploit a variety of prey in a range of environments. Short-finned pilot whales are wide-ranging predators in tropical and sub-tropical oceans, but most previous studies of their foraging ecology have been conducted near oceanic islands. We deployed sound- and movement-recording tags on 43 short-finned pilot whales off Cape Hatteras, North Carolina, USA, to measure their foraging behavior in a continental shelf-break ecosystem and investigate how variation in the environment shapes their behavior. Overall, the foraging behavior of pilot whales off Cape Hatteras was similar to that of their counterparts from island-associated habitats. Off Cape Hatteras, pilot whales made foraging dives as deep as 1077 m (mean: 445 m), lasting up to 23 min (mean: 12.8 min), with sprints (pursuit at speeds over 3 m s⁻¹ and up to 6.9 m s⁻¹) in more than half of foraging dives. However, tagged whales off Cape Hatteras produced higher buzz rates (11.3 buzzes dive⁻¹), foraged more extensively in daytime hours, and engaged in more frequent benthic foraging than island-associated ecotypes. By parsing the echoic scene generated by the animal's own echolocation clicks, we show that pilot whales off Cape Hatteras frequently exploit bathymetric features for foraging, with benthic dives resulting in higher prey capture



Short-finned pilot whale tagged with a suction-cup attached digital acoustic tag near the Cape Hatteras shelf break.

Photo: Danielle Waples

attempts than pelagic dives. The ability of these predators to strategically adapt foraging strategies to local habitat features likely contributes to their ecological success and may allow them to adjust to shifts in prey distributions in a rapidly changing Anthropocene ocean.

KEY WORDS: Short-finned pilot whale · Foraging strategy · Behavioral plasticity · Habitat

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1. INTRODUCTION

Toothed whales (Odontoceti) are a diverse clade of marine predators that use echolocation to detect and capture prey. By emitting intense echolocation clicks and listening for returning echoes, odontocetes can detect objects at distances of 10s to 100s of meters (Jensen et al. 2018, Tønnesen et al. 2020) and assess the size, quality, and movement of their prey (Fenton et al. 2014, Wisniewska et al. 2016). Combined with adaptations that allow for increased diving capabilities, echolocation allows toothed whales to exploit deep, light-limited habitats that hold abundant prey (Benoit-Bird et al. 2016, Goldbogen et al. 2019). Toothed whales exhibit varying levels of foraging plasticity, from ecotypes with narrow dietary niches, such as southern resident killer whales *Orcinus orca* (Hanson et al. 2021) to bottlenose dolphins *Tursiops truncatus*, which exhibit individual differences in diet and prey capture strategies, resulting in considerable foraging plasticity at the population level (e.g. Mann et al. 2008, Nowacek 2002, Methion & Díaz López 2020).

Pilot whales *Globicephala* spp. are medium-sized odontocetes that are distributed across open oceans and continental shelf ecosystems. Two species are recognized: the long-finned pilot whale *G. melas*, distributed anti-tropically in temperate and sub-polar ecosystems, and the short-finned pilot whale *G. macrorhynchus*, found in tropical and subtropical regions (Olson 2009). Studies of stomach contents from stranded and bycaught animals indicate that both species have a relatively diverse diet (Hernández-García & Martín 1994, Gannon et al. 1997a,b, Mintzer et al. 2008, Fernández et al. 2009, Mansilla et al. 2012, Santos et al. 2014). Both species forage on a variety of mesopelagic (Spitz et al. 2011, Mèndez-Fernandez et al. 2012), benthic neritic (Spitz et al. 2011, Mèndez-Fernandez et al. 2012), and epipelagic prey (Aguilar de Soto 2006), sometimes following fishing vessels (Gannon et al. 1997a) and depredating bait and catch (Hamer et al. 2012).

Short-finned pilot whales occupy diverse habitats; however their foraging behavior has been studied primarily near volcanic islands (Hawaii, North Pacific: Abecassis et al. 2015, Baird et al. 2003, Owen et al. 2019; Canary Islands, North Atlantic: Aguilar Soto et al. 2008). Marine ecosystems surrounding volcanic islands are characterized by steep bathymetry, providing whales with access to deep-water prey relatively close to shore. Whales tagged in these environments make deep foraging

dives (>1000 m and lasting up to 20 min), with distinct diurnal diving patterns involving long periods of surface resting with occasional deep dives during the day (Baird et al. 2003, Aguilar Soto et al. 2008, Owen et al. 2019). In the Canary Islands, daytime foraging dives typically contain high-speed 'sprints' over 3 m s^{-1} culminating in a single foraging buzz, presumably as the whales are chasing large, highly mobile prey (Aguilar Soto et al. 2008). However, most foraging in the Canary Islands occurs at night, with many buzzes in both shallow and deep (>500 m) dives but few sprints. In Hawaii, in addition to a higher number of moderately deep dives at night, pilot whales also move into shallower inshore waters following horizontal diel prey movements (Abecassis et al. 2015). A small sample of daytime deployments in Madeira in the North Atlantic also showed extended daytime surface behavior with few foraging dives (Alves et al. 2013).

In the western North Atlantic, short-finned pilot whales are frequently found near the continental shelf break in areas of steep slope, with an apparent preference for submarine canyons (Thorne et al. 2017, NOAA 2020). Off Cape Hatteras, North Carolina, the cold, southward-flowing Labrador Current collides with the warm Gulf Stream over the shelf break, creating a productive system that supports a diverse suite of oceanic predators (Gawarkiewicz et al. 1992, 1996, Lohrenz et al. 2002). Pilot whales here are strongly associated with the shelf break, although some travel offshore into pelagic waters in association with Gulf Stream frontal eddies (Thorne et al. 2017). Despite their extensive ranges, most foraging effort documented to date is focused along the shelf break (Thorne et al. 2017). Little information exists about their diet in this region; a single study of stranded animal stomach contents indicated a varied diet of small-bodied fish and squid, including neritic, bathypelagic, and mesopelagic species (Mintzer et al. 2008).

In this paper, we quantified foraging behavior of short-finned pilot whales along the Cape Hatteras shelf break, where the seafloor is within reach of these deep divers, to understand how habitat shapes foraging behavior in these broadly distributed upper trophic level predators and how such adaptations may influence their susceptibility to disturbance or environmental changes. In particular, we tested whether pilot whales are able to forage at or near the sea floor off Cape Hatteras and whether this affects diurnal variations in their diving behavior.

2. MATERIALS AND METHODS

2.1. Data collection

We tagged short-finned pilot whales approximately 60–90 km north and east of Cape Hatteras, North Carolina, USA, during May through September 2008–2016. We tagged whales near the shelf break in water depths from 100–1600 m. We deployed version 2 (2008–2014, 2016) and version 3 (2015) digital acoustic tags (DTAGs; Johnson & Tyack 2003) using a carbon-fiber pole from a 6 or 9 m rigid-hulled inflatable boat. Field and focal follow protocols varied, but in general, we targeted animals with distinct dorsal fins and avoided groups with neonates. We used the VHF radio transmitter in the tag to track the focal group and recorded information on movements and behavior throughout each deployment. During some years, animals were tracked overnight from a larger support vessel. Tags were programmed to detach at pre-determined times and located using the VHF transmitter.

2.2. Data processing

We used DTAGs to collect high-resolution acoustic (2 hydrophones sampling at 96, 192, or 240 kHz, depending on year) and movement data. Pressure sensors and tri-axial accelerometers and magnetometers sampled movement at 50 Hz (version 2) or 250 Hz (version 3), decimated to 25 Hz for analysis. All data were processed and calibrated in MATLAB 2016b (MathWorks) using the DTAG toolbox (www.animaltags.org) and custom-written scripts (Johnson & Tyack 2003). We computed the animal's pitch, roll, and heading from calibrated data using the expected orientation of the animal during surfacings (Johnson 2011), adjusted to account for shifts in tag placement during deployment. We truncated data to remove incomplete dives and dives without audio from the end of the tag records. We did not exclude dives following biopsy sampling given the transitory reactions displayed by sampled whales (Crain et al. 2014). Some deployments included playbacks of conspecific calls, killer whale calls, humpback whale calls, or pseudo random noise; we truncated tag records to exclude periods following exposure to killer whale calls, as we found no response to other sound types (Bowers et al. 2018).

2.2.1. Dive behavior

We defined a dive as any submergence greater than 20 m, following Aguilar Soto et al. (2008) and Quick et al. (2017). We identified descent, bottom, and ascent phases using a threshold of the first and last time the animal crossed 85% of the dive's maximum depth. Definitions for terms used to describe dives and buzzes (see Section 2.2.2) are given in Table 1.

2.2.2. Echolocation behavior

We identified timestamps of all echolocation clicks using semi-automatic click detectors (dynamic thresholds ranging from -46 to -20 dB re: $1 \mu\text{Pa}$ of the clip value, blanking time 15 ms for regular clicking and 1 ms for buzz clicks, and frequency band 5–20 kHz). Clicks were manually inspected for missed detections with a supervised graphic user interface (GUI). Focal animal clicks were distinguished from those of conspecifics by the distorted waveforms and low-frequency components of tagged animal clicks (Johnson et al. 2009). Prey capture attempts were defined by the presence of buzzes, in which whales switch from regular clicking to faster, lower amplitude buzz clicks near prey items (Johnson et al. 2004). We defined foraging buzzes as click sequences with an inter-click interval (ICI) less than 0.05 s (Madsen et al. 2013) (Video S1 at www.int-res.com/articles/suppl/m695p001_supp/). Each foraging buzz represents a prey capture attempt but is not indicative of capture success (Johnson et al. 2004, Madsen et al. 2005, Wisniewska et al. 2016). Pilot whales occasionally use short-duration, low-ICI click sequences (rasps) for communication (Pérez et al. 2017), so we set a threshold of 50 clicks for an event to be considered a buzz (Table S1 in the Supplement at www.int-res.com/articles/suppl/m695p001_supp/).

Table 1. Definitions of short-finned pilot whale dive and buzz characteristics

Term	Description
Dive	≥ 20 m
Foraging dive	Dive states 2 and 3 (hidden Markov model)
Altitude	Distance (m) above seafloor
Benthic (dive/buzz)	Minimum altitude within 40 m of seafloor
Pelagic (dive)	Minimum altitude > 40 m or seafloor depth is not known
Pelagic (buzz)	Any buzz in a pelagic dive
Benthic-pelagic (buzz)	Dive is benthic but buzz occurs > 40 m altitude
Sprint	Speed $\geq 3 \text{ m s}^{-1}$ (over 6 s intervals)

2.3. Analysis

2.3.1. Velocity

The flow noise of water past the tag correlates with the velocity of the tagged animal (Goldbogen et al. 2006), but the relationship between measured flow noise and animal velocity needs to be calibrated against known speeds. For diving animals, the change in depth over time corrected by the pitch angle of the animal can be used to estimate velocity for periods where the average pitch is relatively steep ($>60^\circ$). To estimate velocity across the entire dive, we calculated a regression between velocity (pitch-corrected depth change) and measured flow noise (1/3 octave band centered at 100 Hz) in 6 s overlapping increments from all time periods with high pitch angles ($>60^\circ$) (Text S1). We fit a linear model to the flow noise estimate and the natural log of the velocity estimate and applied this regression to the entire dive, producing a velocity estimate at 1 s intervals:

$$v[m/s] = a \times I_F + b \quad (1)$$

where I_F is the sound intensity associated with flow noise (in dB), and a and b represent the slope and intercept of a linear fit.

Flow noise at a given speed depends on tag placement, so we combined correlation data from all of an individual's dives with the same tag placement and orientation, applying the regression to the same subset of dives, for an initial total of 92 correlations over 39 tags (multiple regressions per tag, updated every time the tag moved or rotated during the deployment). We used velocity estimates only if the R^2 of the correlation model was greater than 0.8, resulting in estimates for 295 dives from 30 tags.

2.3.2. Seafloor echoes

We constructed echograms (e.g. Johnson et al. 2008, Arranz et al. 2011, Guerra et al. 2017) to visualize seafloor echoes and understand if tagged whales interacted with the ocean bottom and canyon walls. An echogram is a stack plot of envelopes of filtered sound around each click, rotated 90° to synchronize the outgoing clicks, with color representing the instantaneous level of the signal in dB (see Fig. 1F). The width of each envelope in the stack plot is equal to the ICI. This produces a visualization with time on the x-axis and time delay corresponding to the 2-way travel time (TWTT) of returning echoes on the y-axis.

This data can be converted to distance by multiplying half of the TWTT by the average speed of sound in the ocean.

We plotted echograms and tracked seafloor and canyon wall echoes with an interactive GUI which interpolates energy peaks between user-defined start and end points of an echo trace. Seafloor echoes are large, semi-continuous reverberant echoes that show slow variations in TWTT (Teloni et al. 2008, Arranz et al. 2011, Fais et al. 2015, Guerra et al. 2017). We made no attempt to differentiate between echoes from the sea floor and echoes from canyon walls, although 3-D track reconstruction could be integrated to help differentiate these bathymetric features. The distance from the animal to the seafloor (altitude) was added to the animal's depth to calculate the absolute depth of the seafloor. Seafloor echoes were not continuous, so we used a piecewise cubic Hermite interpolating polynomial (p-chip) interpolation (to preserve shape and avoid overshoots) with a 4 s moving average to interpolate across measured seafloor depths. The interpolation was constrained to values deeper than the animal's depth to produce a continuous seafloor depth estimate from the first to last echo trace in a dive (see Fig. 2B).

2.4. Statistical methods

Following Quick et al. (2017), we categorized dives using a multivariate hidden Markov model (HMM) with the 'momentuHMM' package (McClintock & Michelot 2018) in R version 4.0.5. All input parameters followed Quick et al. (2017): depth (gamma distribution), duration (gamma distribution), and number of buzzes per dive (Poisson distribution). The HMM included a single transition probability matrix for all individuals with no random effects (to make population-level inferences), the observed data depended only on the dive state with no covariates, and the probability of being in the current dive state depended only on the previous state. We computed both 3- and 4-state models, but we selected a 3-state model as the most parsimonious, given that the 4-state model had high levels of overlap between States 2–4 and appeared to split deep foraging dives (States 3 and 4) into multiple states with no clear biological significance.

We modeled the effect of dive category (benthic or pelagic) and time of day (day or night, defined by local sunset/sunrise) on dive depth and buzz rate (square root) using linear mixed effect models

with the ‘nlme’ package in R (Pinheiro et al. 2021). Individual whale ID was modeled as the random effect. To avoid heteroscedasticity, we took the square root of the buzz rate. We used residual plots (autocorrelation function plots, histograms, $Q-Q$ plots, and standardized residuals vs. fitted values) to check model assumptions of normality, independence, and constant variance (Fig. S1). Given moderate amounts of autocorrelation, we added a correlation argument to the models, with a time covariate of dive number and a grouping factor of tag ID. We assessed pair-wise differences in dive types using Tukey’s method (R package ‘emmeans’; Lenth 2018).

Finally, we modeled whether seafloor echo presence in a dive was affected by time of day using a generalized linear mixed effect model (GLME) with a binomial distribution, a logit link function, and individual ID as the random effect using the ‘lme4’ package in R (Bates et al. 2015). This model had less autocorrelation, so we felt justified in

using the GLME rather than a generalized estimating equation (GEE).

3. RESULTS

3.1. Summary of data

We deployed 43 tags on short-finned pilot whales between 2008 and 2016, which produced 193 h of data after truncation (mean: 4.5 h deployment duration; range: 0.6–17.3 h; Fig. 1, Table S2). Whales made 410 dives to depths greater than 20 m, with a maximum dive depth of 1077 m. Six tag records extended into the night, which we defined as any period after local sunset. We identified 3237 buzzes from 38 deployments, with a maximum of 562 buzzes on a single tag record. The average number of buzzes per dive ranged from 0.6–25.8 per whale, with a maximum of 54 buzzes in a single dive. We observed sprints of more than 3 m s^{-1} in 157 dives from 29 tag records.

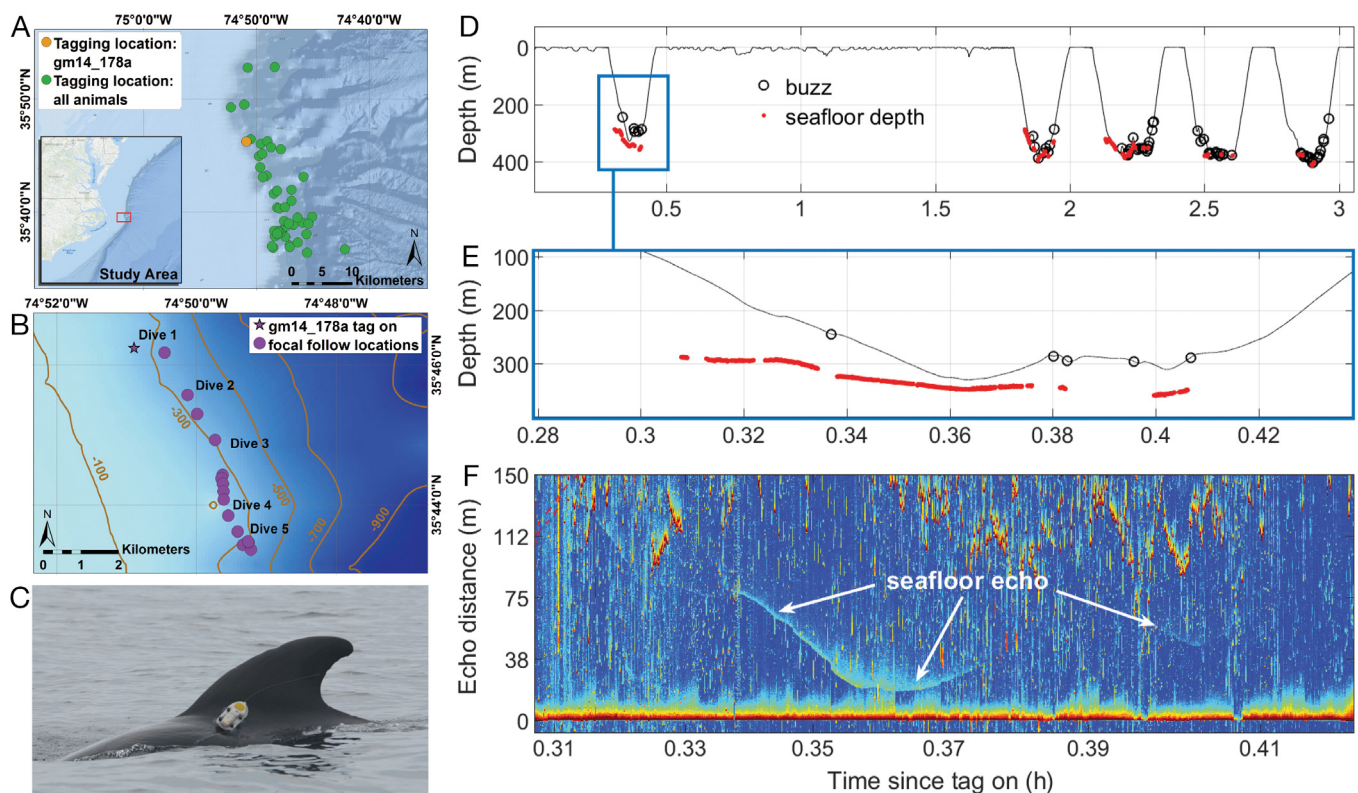


Fig. 1. (A) Study area off Cape Hatteras, North Carolina, showing tagging locations of all short-finned pilot whales. (B–F) Tagged whale gm14_178a, showing (B) focal follow locations and bathymetry contour lines at 200 m intervals and (C) placement of the digital acoustic tag. (D) Dive profile of the 5 dives shown in (B). Black circles: buzzes; red broken lines: seafloor depth from echo analysis. (E) Dive 1, showing buzzes and seafloor depths. (F) Echogram showing the seafloor echo which generated the depths in (E); y-axis represents the distance from the tagged animal to the echo. Buzz clicks were removed from the echogram; the x-axis is not spaced equally in time due to buzzes and other gaps being removed. See Section 2.3.2 for a complete description of echogram calculation

3.2. Dive classification using HMMs

The HMM separated dives into states primarily based on buzz count, with more overlap in dive depth and duration between states. State 1 dives contained very few buzzes (123 dives, total of 6 buzzes) and were shallow (mean: 44 m) and of short duration (mean: 4 min). State 2 dives were deeper than State 1 dives, but were shallower, shorter, and had fewer buzzes (mean: 331 m, 11.2 min, 4.6 buzzes) than State 3 dives (mean: 650 m, 15.8 min, 23 buzzes). States 2 and 3 had considerable overlap in depth and duration and mainly differed in number of buzzes. Given the very low number of buzzes in State 1, we considered only States 2 and 3 to be foraging dives and removed State 1 dives from the remainder of the analysis. All subsequent models and statistics use only dives from the foraging dives data set (38 animals, 287 dives).

3.3. Foraging behavior

3.3.1. Seafloor echoes

We observed seafloor echoes in 114 of 287 foraging dives from 31 animals (43% of dives >100 m) (Fig. 2, Table 2). In 104 dives (91% of the dives with visible echoes), tagged whales dove to within 40 m of the seafloor (Table S3). The average minimum altitude (animal height above seafloor) in dives with seafloor echoes was 13.4 m, ranging from 1.2–72 m across animals. The seafloor was detected in a broad range of dive depths, from 213–1077 m.

3.3.2. Benthic and pelagic dives

We separated foraging dives into benthic dives, in which the animal's minimum altitude was less than

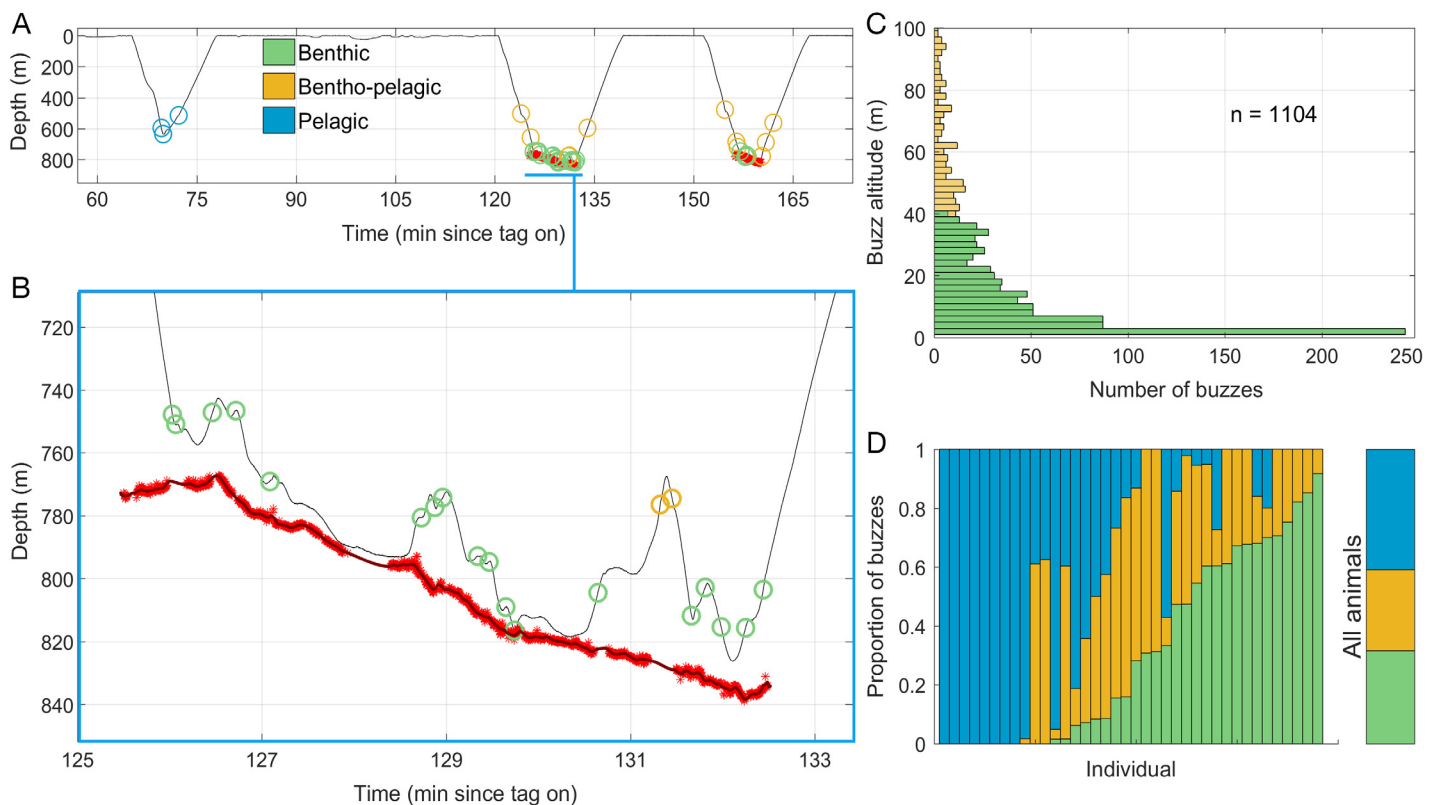


Fig. 2. (A) Dive profile for gm16_181a, showing 3 types of buzzes. (B) Graphic illustration of the seafloor interpolation methodology using the second dive. Black line: dive profile; red stars: seafloor depths obtained from echoes on the tag; dark red line: interpolation between the red stars. Circles on the dive profile are buzzes; green circles: less than 40 m altitude (considered 'benthic'); orange circles: above 40 m ('benthic-pelagic'). (C) Buzz altitudes above seafloor for all animals combined ($n = 1153$ buzzes for which altitude is available). Histogram is cutoff at 100 m for readability; 49 more buzzes were made above 100 m and not plotted, and a further 2084 buzzes occurred outside of interpolated times or in dives without echoes. (D) Proportion of benthic, benthic-pelagic, or pelagic buzzes by animal (sorted in ascending order based on number of benthic buzzes). Each vertical bar represents a single animal. Overall average for all animals is presented in the far-right panel

Table 2. Summary of seafloor echo and sprint characteristics for short-finned pilot whales. Velocity was only calculated for dives in which $R^2 > 0.8$ in the regression model, resulting in velocity calculations for 230 foraging dives

Seafloor echoes						
No. of tags	No. of dives	Mean minimum altitude (m)	Absolute seafloor depth (range; m)	Mean no. of benthic buzzes dive ⁻¹	Benthic buzz ratio (per benthic dive; %)	Benthic buzz ratio (all dives; %)
31	114	13.4	270–1082	8.0	47	28
Sprints						
No. of tags	No. of dives	Mean no. of sprints dive ⁻¹	Max. velocity (m s ⁻¹)	Mean no. of sprint-associated buzzes dive ⁻¹	Sprint buzz ratio (per sprinting dive; %)	Sprint buzz ratio (all dives; %)
29	157	4.6	6.9	4.5	44	22

40 m, and pelagic dives, which included all others. We selected 40 m altitude as a cutoff for benthic classification based on a minimum point in the distribution of dive minimum altitudes for all dives (Fig. S2). There were 183 pelagic dives from 28 animals (64% of foraging dives) and 104 benthic dives from 30 animals (36% of foraging dives) (Table 3); 20 animals made both benthic and pelagic dives.

We classified 915 buzzes as benthic, where buzzes were produced at an altitude of <40 m. In dives with seafloor echoes, whales produced an average of 8 benthic buzzes dive⁻¹, accounting for 47% of all buzzes in those dives. For animals that produced benthic buzzes, benthic buzzes ranged between 2 and 92% of foraging attempts (Table S3). For all animals combined, benthic buzzes comprised 28.3% of all foraging attempts, benthic-pelagic (above 40 m in a benthic dive) made up 29.3%, and pelagic buzzes (buzzes in a pelagic dive) constituted 42.2% (Fig. 2).

3.3.3. Sprints

We observed sprints in 157 foraging dives (55% of foraging dives, 68% of foraging dives for which velocity was calculated) (Table 2). The mean number of sprints per dive in which they occurred was 4.6, with a maximum of 14 sprints dive⁻¹. Sprint depths ranged from 43–1053 m. Sprint speeds averaged 3.3 m s⁻¹, but 15 animals had speeds above 4 m s⁻¹, and the maximum speed was 6.9 m s⁻¹. On average, 3.9 buzzes dive⁻¹ were associated with sprints, which represents 36% of all buzzes in sprinting dives. In total, 708 buzzes were associated with sprints, representing 21.9% of all buzzes (Table S3).

A total of 25 tag records included both sprints and seafloor echoes. Of those, there were 76 occurrences of both a sprint and a seafloor echo in the same dive (Fig. 3), and 60 dives contained both a sprint-associated buzz and a benthic buzz.

Table 3. Short-finned pilot whale benthic and pelagic foraging dive parameters (means, with maximum values or ranges in parentheses). Buzz rate: number of buzzes per minute of dive duration; foraging period duration: the first buzz to the last buzz in a dive; sprint buzz ratio: number of sprint-associated buzzes divided by the total number of buzzes in that dive, averaged across all dives

	Depth (m)	Duration (min)	Max. velocity (m s ⁻¹)	No. of buzzes dive ⁻¹	Buzz rate (no. min ⁻¹)	Foraging period duration (min)	No. of sprint-associated buzzes	Sprint buzz ratio dive ⁻¹ (%)	Sprinting duration dive ⁻¹ (min)
Benthic (n = 104)	543 (1077)	14.1 (22.5)	3.88 (5.39)	17.9 (2–54)	1.24 (3.58)	6.5 (0.15–11.9)	5.5 (0–19)	35	1.39 (0.13–3.98)
Pelagic (n = 183)	389 (959)	12.1 (21.4)	4.27 (6.90)	7.5 (0–44)	0.56 (2.61)	4.7 (0–13.1)	3.7 (0–16)	52	1.49 (0.13–4.68)

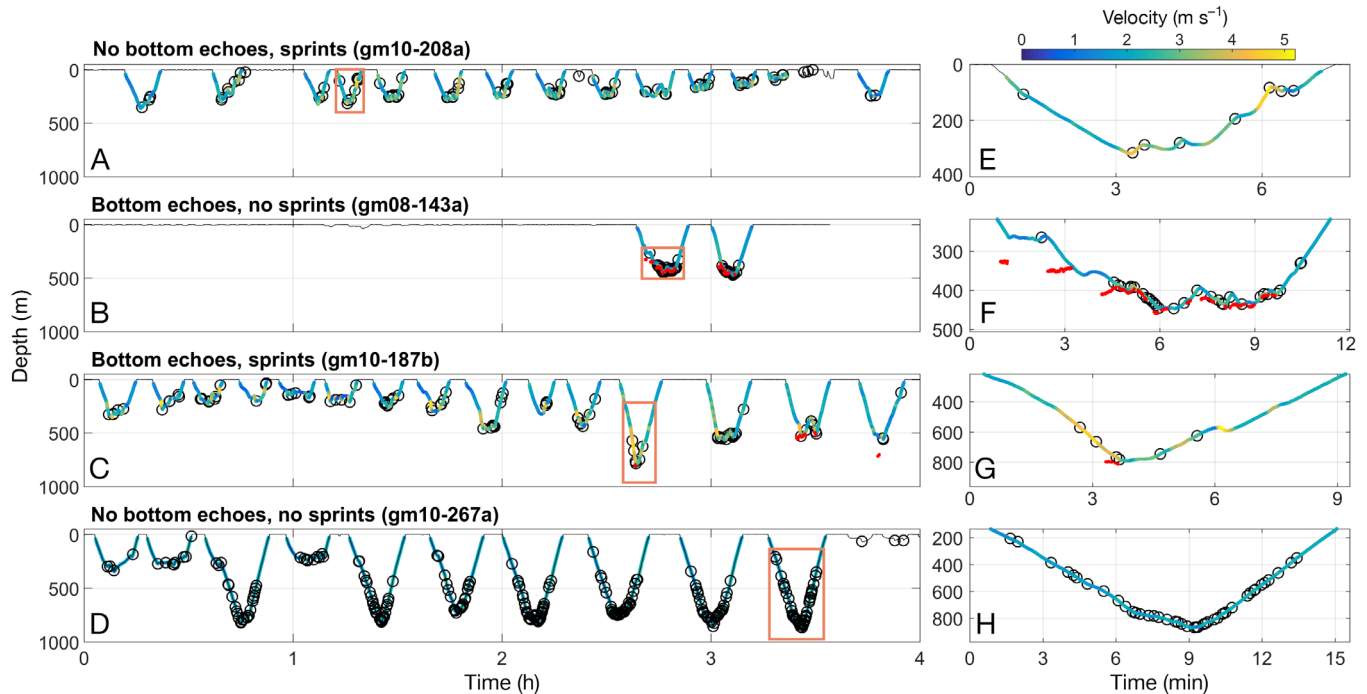


Fig. 3. Foraging strategies of pilot whales showing (A–D) 4 h of dive profiles from 4 different animals. (E–H) Bottom portion of a single dive from each animal (brown boxes in A–D) showing dives with (E) sprints but no bottom echoes, (F) bottom echoes but no sprints, (G) both sprints and bottom echoes, and (H) neither sprints nor bottom echoes. Colors of the dive profile represent the velocity; all dives are on the same color scale. Red marks below dive profiles: absolute seafloor depth as determined from bottom echoes; black circles: buzzes

3.3.4. Diel patterns and category differences using mixed effects models

Benthic dives contained over twice as many buzzes as pelagic dives (17.9 vs. 7.5) and longer foraging durations (time between first and last buzz in the dive: 6.5 vs. 4.7 min) (Table 3). Benthic buzzes comprised 47% of all the buzzes in benthic dives and 28% of all buzzes. Benthic dives also had more buzzes associated with sprints per dive than pelagic dives (5.5 vs. 3.7), but sprint buzzes comprised a higher proportion of buzzes in pelagic dives than benthic (52 vs. 35%) due to overall lower number of buzzes in pelagic dives. Pelagic dives had a higher average maximum velocity (4.27 vs. 3.88 m s^{-1}) than benthic dives. The median inter-buzz interval for benthic buzzes was 18.8 s, compared to 25.6 s for pelagic buzzes.

We validated the LME models by dropping the interaction term and comparing the models with ANOVA; there was no significant difference in the buzz rate models, and the dive depth model showed a significant improvement from the interaction. Therefore, we kept the interaction term in only the dive depth model and dropped it from the buzz rate model (Table S4). To account for potential group

effects, we ran an additional set of models using groupID as the random effect; those model results did not differ from those using tagID, so we kept tagID as the random effect.

Benthic dives had significantly higher buzz rates than pelagic dives (Fig. 4, Tables 4 & S5). Night-time dives had significantly lower buzz rates compared to daytime dives (Table S5). In the depth model, benthic dives were significantly deeper than pelagic dives (Fig. 4, Tables 4 & S5). There were no diel differences in depth for benthic dives, but pelagic dives were significantly shallower at night than during the day (Tables 4 & S5). Daytime foraging dives had roughly equal proportions of benthic and pelagic dives (48 and 52%, respectively), but nighttime foraging dives had a lower proportion of benthic dives (13%). In the daytime, 53% of dives had echoes present ($n = 100$) compared to 14% of nighttime dives ($n = 14$), but this relationship was not significant in the GLME model (Tables 4 & S6), possibly due to the small number of animals with both day and night echoes ($n = 3$). However, in a GLM with all animals pooled (without an individual random effect), we found significantly fewer dives with echoes present at night ($p < 0.001$).

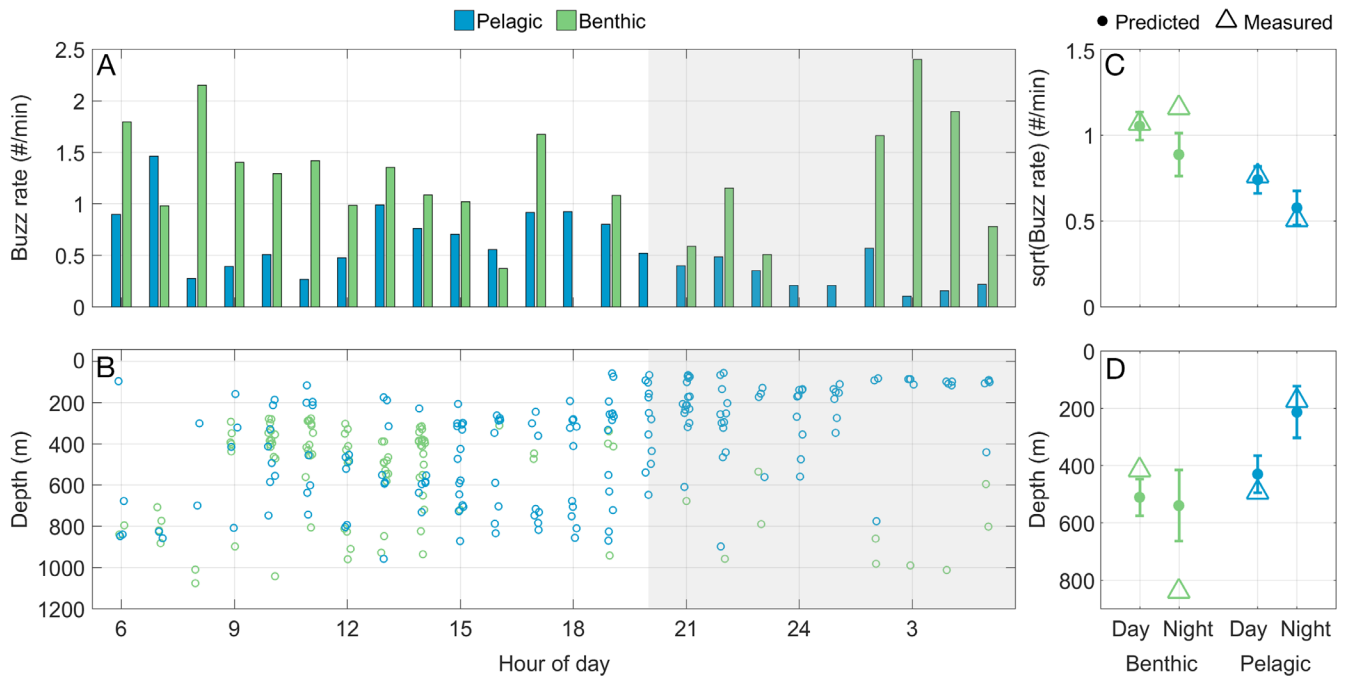


Fig. 4. Short-finned pilot whale (A) buzz rates and (B) maximum dive depths from all foraging dives, by hour of day (local time). Dives are grouped into 24 h bins based on the hour in which the dive started. Points are jittered for clarity. Model results for (C) square root buzz rate model and (D) dive depth model, showing model estimates and confidence intervals along with measured values (median) for all categories

Table 4. Model results for short-finned pilot whale foraging dives. For all models, a random effect of individual (tag ID) on intercept was included. *p < 0.05

LME Model 1: sqrtBuzzRate ~ Category + DayNight						
Random Effects: ~1 tagID						
Correlation structure: ARMA(1,0) ~DiveNum tagID						
Autocorrelation coefficient: 0.467						
Response	Predictor(s)	Coefficients	t	p	Lower 95 % CI	Upper 95 % CI
sqrt(BuzzRate)	Intercept (benthic day)	1.0507	26.01	<0.0001*	0.9711	1.1302
	Category	-0.3126	-7.04	<0.0001*	-0.4000	-0.2251
	DayNight	-0.1636	-2.77	0.006*	-0.2800	-0.0472
LME Model 2: Depth ~ Category * DayNight						
Random Effects: ~1 tagID						
Correlation structure: ARMA(1,0) ~DiveNum tagID						
Autocorrelation coefficient: 0.479						
Response	Predictor(s)	Coefficients	t	p	Lower 95 % CI	Upper 95 % CI
Depth	Intercept (benthic day)	511.75	16.04	<0.0001*	448.92	574.57
	Category	-81.55	-2.93	0.0037*	-136.36	-26.75
	DayNight	28.69	0.48	0.6331	-89.54	146.92
	Category:DayNight	-245.1455	-4.37	<0.0001*	-355.72	-134.57
GLME Model 3: Echo Presence ~ DayNight						
Random effects: ~1 tagID						
Response	Predictor(s)	Coefficients	z	p	Lower 95 % CI	Upper 95 % CI
Echo presence	Intercept (day)	0.5095	1.079	0.281	-0.4163	1.4354
	Night	-0.6346	-1.178	0.239	-1.6902	0.4210

During the day, 59% of dives ($n = 113$) contained sprints compared with 45% ($n = 44$) of dives at night (Table S6). The number of sprints per dive was similar at 2.6 per daytime dive and 2.3 per nighttime dive. Daytime sprint dives had a maximum velocity of 5.9 m s^{-1} while nighttime dives had a maximum velocity of 6.9 m s^{-1} . Sprint-associated buzzes were 22% of all daytime buzzes and 22% of all nighttime buzzes. Benthic buzzes comprised 32% of daytime buzzes and 15% of all nighttime buzzes.

3.3.5. Dive phases

Animals foraged in all dive phases, with buzzes occurring during the ascent ($n = 551$) and descent ($n = 440$) in addition to the bottom period ($n = 2240$) (Fig. S3). A total of 69% of buzzes occurred during the bottom phase of all dives combined, but this was slightly higher (77%) for benthic dives than pelagic dives (60%). Benthic dives had higher mean numbers of buzzes in the bottom phase of the dive (13.7) compared to pelagic dives (4.4).

4. DISCUSSION

4.1. Extensive benthic foraging

Along the continental shelf break, where the seafloor is available to these predators, short-finned pilot whales rely heavily on benthic foraging, a tactic previously only inferred from dietary studies. Benthic dives comprised over one-third of all foraging dives, with benthic buzzes accounting for 28% of all foraging attempts. Longer foraging periods and shorter inter-buzz intervals contributed to the significantly higher buzz rates in benthic compared to pelagic dives. The single study of pilot whale stomachs in this area showed that a bathypelagic fish *Scopelogadus beanii* represented 25% of prey items found in pilot whale stomachs (Mintzer et al. 2008). In addition, the squid species found in these stomachs inhabit a range of habitats, including the bathypelagic realm. The otoliths and beaks were small, and Mintzer et al. (2008) suggested that pilot whales would need to eat large numbers of these prey items; this was confirmed by the high buzz rates in our study. We conclude that whales engaging in benthic dives likely target prey that are relatively easy to capture, given their high foraging rates, short inter-buzz intervals, and presumed small prey sizes. To our knowledge, this is the first time that the importance

of benthic foraging has been quantified for short-finned pilot whales, although it has been described for long-finned pilot whales in Norway (Isojunno et al. 2017).

4.2. Frequent, short sprints

Sprints occurred in both benthic and pelagic dives, but pelagic sprints were, on average, slightly longer and faster, and a higher proportion of buzzes were associated with sprints in pelagic dives than in benthic dives. This sprinting behavior in pilot whales off Cape Hatteras differs from that reported from the Canary Islands, with whales in our study exhibiting lower average (3.3 vs. 4 m s^{-1}) and maximum speeds (6.9 vs. 9 m s^{-1}) (Aguilar Soto et al. 2008). We calculated sprints in slightly different ways (flow noise correlation vs. vertical depth changes in the Canary Islands), precluding a more direct comparison. Our method produced a higher number of sprints because it allows for sprints in a horizontal orientation. Despite these caveats, our average number of sprints per dive (in which they occurred) was 4.6, compared to 1–2 in the Canary Islands (Aguilar Soto et al. 2008). Our sprint duration was also slightly shorter, with an average of 19 vs. 23 s (Aguilar Soto et al. 2008). It is likely that the prevalence, patterns, and speed of sprints are dictated by individual prey behavior. In the Canary Islands, pilot whales use single, long sprints to capture large prey items. Off Cape Hatteras, pilot whales make a larger number of slightly shorter sprints, appearing to forage on smaller prey rather than pursue the higher-risk, higher-reward strategy employed by whales in the Canary Islands.

4.3. Diel differences: daytime dives deeper with higher buzz rates

Significant diel differences in dive depth occurred only in pelagic dives; benthic dives showed little variation with time of day. However, care should be taken when interpreting these results, as the data were unbalanced, with few benthic dives at night and many of the deep benthic night dives coming from a single animal (Fig. S4). Pelagic dives were shallower at night, a pattern which suggests that whales were foraging on vertically migrating organisms associated with the deep scattering layer (DSL), as is common with other pelagic marine mammals (Aoki et al. 2007, Arranz et al. 2011). Lower buzz

rates at night could reflect either less dense distributions of prey, predation on larger items that require greater handling time, or that whales are selective about how often to engage in high-energy prey capture attempts. We hypothesize that these dive patterns, and the higher proportion of benthic dives during the day, reflect a tradeoff in which whales forage during the day on reliably located and densely aggregated but relatively small benthic organisms on the shelf. At night, they feed on vertically migrating prey that are closer to the surface. Lower feeding rates indicate longer search or handling times, but these prey items may be of higher energetic value or else the whales would not switch from benthic foraging (assuming no changes in the distribution or availability of benthic prey). However, we had only a small number of deployments that extended into the night, so these findings should be considered preliminary, emphasizing the need for more deployments during nighttime hours.

We observed diel patterns in depths and buzz rates, but we did not observe extended-duration surface resting patterns interspersed with occasional deep dives described for both Hawaii and the Canary Islands (Baird et al. 2003, Aguilar Soto et al. 2008, Owen et al. 2019). Pilot whales off Cape Hatteras foraged at higher rates during both day and night than whales in the Canary Islands (day: 13.2, confidence interval [CI] = 11.7–14.7 buzzes dive^{-1} vs. 0.6–1.5 buzzes dive^{-1} ; night: 7.5, CI = 5.3–9.7 buzzes dive^{-1} vs. 4.8–5 buzzes dive^{-1} , respectively). In Cape Hatteras, more foraging effort occurred during the day, with higher buzz rates in predominately benthic foraging. In contrast, in the Canary Islands, foraging effort was concentrated at night and likely driven by vertical migration of the DSL. The substantial contribution of bathypelagic prey off Cape Hatteras may explain the lack of distinct diel patterns found here.

4.4. Importance of studying species in different environments

Flexible foraging strategies occur in a variety of marine top predators. Male sperm whales forage both benthically and pelagically in high-latitude feeding grounds, but with different strategies depending on location (Teloni et al. 2008, Guerra et al. 2017, Isojunno & Miller 2018). Sperm whales in Norway forage at high rates with short-duration, low-energy buzzes on benthic prey, while mid-water buzzes are longer with higher energy maneuvers (Teloni et al. 2008, Isojunno & Miller 2018). The op-

posite is true in New Zealand, with short pelagic buzzes and long, low-rate benthic buzzes (Guerra et al. 2017). Likewise, northern elephant seals *Mirovunga angustirostris* show sex-specific differences in foraging behavior, with males foraging benthically near the coast on higher value prey and females foraging pelagically on small fish at high rates (Le Boeuf et al. 2000, Adachi et al. 2021).

The pilot whales we tagged spent most of their time along the shelf break but made occasional forays to abyssal waters, where they forage along fronts and eddies associated with the Gulf Stream (Thorne et al. 2017). In these pelagic waters, where the sea floor is not within reach, we predict that they will behave more like island-associated animals, targeting the DSL and exhibiting diel variations in foraging behavior. The deployment of digital acoustic tags farther offshore would offer insights into how animals from the same population can switch foraging strategies in different habitats.

4.5. Advantages of behavioral plasticity in a rapidly changing ocean

Behavioral flexibility allows predators to exploit a greater variety of prey items. In turn, increased dietary flexibility allows generalist predators to utilize more habitats and buffers them from environmental perturbations which may alter prey resources on various time scales. This could include ephemeral changes associated with environmental or anthropogenic disturbance or longer-term shifts in prey distribution associated with climate change. Here, we demonstrate that short-finned pilot whales adapt their foraging behavior to take advantage of variation in local environments. Such plasticity may also help generalist predators adapt to changing prey distributions in an Anthropocene ocean (Wong & Candolin 2015, Beever et al. 2017, Karkarey et al. 2017, Evans & Moustakas 2018). Generalist species are favored when environments change rapidly (Holland et al. 2020), and dietary breadth is a predictor of extinction risk (Gallagher et al. 2015). Among odontocetes, the positive conservation status (reflected by broad distributions in multiple environments and large population sizes) of generalist pilot whales (e.g. Aguilar Soto et al. 2008, this study) and bottlenose dolphins (e.g. Nowacek 2002, Sargeant et al. 2005, Mann et al. 2008, Powell & Wells 2011) stands in stark contrast to some endangered specialists, such as endangered southern resident killer whales (Hanson et al. 2021). While other factors play a role in

population status, the ability to forage in multiple habitats on a variety of prey species should help to buffer populations from shifts in prey distribution and availability driven by climate change or other anthropogenic factors on variable time scales. We have shown that pilot whales adapt their foraging behavior to their specific location and habitat features, demonstrating behavioral flexibility in foraging strategies and illustrating the role of the local environment in shaping the foraging strategies of marine generalist predators.

Data availability. Data used in this analysis are available on Dryad at <https://doi.org/10.5061/dryad.xsj3tx9h7>.

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