A R T I C L E

Marine Mammal Science

Overwintering humpback whales adapt foraging strategies to shallow water environments at the mouth of the Chesapeake Bay, Virginia, USA

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Abstract

Some humpback whales from the Northwestern Atlantic population forgo migration to the Caribbean, spending winter months feeding along the U.S. mid-Atlantic coast. We studied the foraging behavior of these whales at the mouth of the Chesapeake Bay, Virginia during winter from 2017 to 2022. While shipping channels here reach depths of up to 30 m, most of the area is 11–15 m deep. This shallow-water environment poses physical constraints on classical humpback whale feeding modes. We deployed 20 digital acoustic tags (DTAGs) on humpback whales and identified foraging lunges from accelerometer data, detecting 788 lunges from 10 animals. Tagged whales averaged a single lunge per dive, lunging primarily in a horizontal orientation, with limited maneuvering compared to other study sites. Our results indicate that some elements of humpback whale foraging behavior are conserved across environments, but that the shallow depths in our study area constrain how animals are able to feed. The relatively high lunge rates we observed suggest this area is an important foraging ground. However, foraging in shipping channels increases the risk of ship strikes, which frequently occur in this area.

KEYWORDS
foraging kinematics, foraging strategy, habitat, humpback whale, lunge-feeding, *Megaptera novaeangliae*

1 | INTRODUCTION

Although researchers typically use behavioral observations to gain insight into how animals find and capture food, in the marine environment foraging behavior is often hidden from observers at the surface. We can address this knowledge gap by employing high-resolution biologging tags to understand the kinematics of foraging when animals feed at depth. Here we study the foraging behavior of presumed juvenile humpback whales (*Megaptera novaeangliae*) in a near-shore, shallow water environment. Humpback whales are generalist predators and consume a wide variety of prey species, including krill (order Euphausiacea), herring (*Clupea harengus*), capelin (*Mallotus villosus*), sand lance (*Ammodytes* spp.), and juvenile salmon (family Salmonidae) (Burrows et al., 2016; Chenoweth et al., 2017; Friedlaender et al., 2006; Hain et al., 1982; Hazen et al., 2009; Johnson & Davoren, 2021; Jurasz & Jurasz, 1979; Nowacek et al., 2011). Along the U.S. mid-Atlantic coast humpback whales have also been documented feeding on drum (*Larimus fasciatus*), croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), and weakfish (*Cynoscion* spp.; Laerm et al., 1997).

Humpback whales demonstrate considerable behavioral plasticity and exhibit some of the most complex foraging behaviors recorded in baleen whales. Humpback whales are rorqual whales, so typically feed by lunging, in which they accelerate rapidly, open their mouths at speed, engulf large volumes of water and prey, which causes a rapid deceleration, and then close their mouths to filter out water through baleen and trap prey items (Goldbogen et al., 2017; Jurasz & Jurasz, 1979; Pivorunas, 1979; Simon et al., 2012). Lunges may occur near the surface or at depth, and can occur at relatively steep pitch angles (Simon et al., 2012; Ware et al., 2011). While lunging, humpback whales may or may not roll, depending on the depth and type of prey (Cade et al., 2016; Jurasz & Jurasz, 1979; Simon et al., 2012; Ware et al., 2011). Humpback whale lunges can occur in conjunction with a variety of other behaviors, one of the most striking of which is the use of a bubble net. In bubble net feeding, whales create rings of bubbles by expelling air from their blowholes, which serve to concentrate prey prior to lunging (Hain et al., 1982; Jurasz & Jurasz, 1979; Wiley et al., 2011). Bubble nets may be used by individual whales or in cooperating groups.

Humpback whales also utilize a variety of other feeding tactics, including lobtailing (Hazen et al., 2009; Weinrich et al., 1992) and flick feeding (Jurasz & Jurasz, 1979), which involve striking the surface of the water with the tail flukes prior to lunging. In the Northwest Atlantic, humpback whales forage benthically by rolling on their sides as they engulf prey at or near the sea floor (Friedlaender et al., 2009; Ware et al., 2014), often leaving abrasions on their rostra (Hain et al., 1995) and creating sediment plumes (Swingle et al., 1993). Novel foraging behaviors continue to be discovered, including "trap feeding," in which whales remain stationary at the surface with their mouths open for an extended period (McMillan et al., 2019). They have also recently been discovered to feed opportunistically on captive-bred salmon as they are released from hatcheries (Chenoweth et al., 2017), sometimes using their pectoral fins to herd and further concentrate the salmon (Kosma et al., 2019). Many of these foraging behaviors show evidence of lateral bias, with animals tending toward right-sided rolls and clockwise spirals (Canning et al., 2011), and with significantly more animals exhibiting abrasions on their right jaw (Clapham et al., 1995).

In general, humpback whales appear to tailor their foraging strategy to the type of prey and the environment in which they are feeding. As predicted by optimal foraging theory, whales tend to make more lunges per dive when foraging at depth (Ware et al., 2011), which helps to maximize the energetic return on each long breath-hold dive. Shallow dives tend to be short, often with a single lunge per dive (Ware et al., 2011). These shorter dives facilitate oxygen intake when the animals are feeding in shallow water and the cost of returning to the surface is low (Tyson et al., 2016). Although there is debate about the energetic costs of lunge feeding (e.g., Goldbogen et al., 2008; Videsen et al., 2023), humpback whales appear to switch foraging tactics depending on prey density, preferring to forage in areas of high density even if this results in longer travel times from the surface to the prey patch (Burrows et al., 2016). Individual whales may move between patches of mobile prey to target patches of high prey density, rather than remaining on a dispersed patch (Kirchner et al., 2018). They may switch from lunging to less costly trap feeding when prey density is low (McMillan et al., 2019). Humpback whales also exhibit strong diel patterns that track the movements of prey. In the Antarctic, for example, humpback whales closely track the daily vertical

migration of krill, feeding more often at night when krill are at shallower depths, especially during autumn when krill densities are high (Friedlaender et al., 2013; Ware et al., 2011). In the Gulf of Maine, humpback whales follow diel changes in the behavior of sand lance, feeding at the surface during the day and benthically at night (Friedlaender et al., 2009).

Humpback whales are capital breeders and they separate foraging and breeding in space and time. Most foraging occurs on high latitude feeding grounds during summer, but some instances of feeding during migration or on the breeding grounds have been documented. For example, subadult whales have been documented feeding in winter in Caribbean breeding grounds (Baraff et al., 1991). And off the east coast of Australia, humpback whales feed during their migration to Antarctic feeding grounds (Owen et al., 2015). In the western North Atlantic, adult humpback whales typically travel from Caribbean breeding grounds to summer feeding grounds ranging from the Gulf of Maine (USA and Canada) to Norway (Katona & Beard, 1990; Stevick et al., 1999, 2003, 2006). However, some individuals remain on midlatitude feeding grounds during winter (Christensen et al., 1992; Whitehead, 1987).

At the mouth of the Chesapeake Bay, Virginia Beach, Virginia, primarily juvenile humpback whales have been documented feeding during winter since the early 1990s (Barco et al., 2003; Swingle et al., 1993, 2017; Wiley et al., 1995). Individual whales remain in the area for weeks to months and have been resighted in multiple years (Aschettino et al., 2018; Barco et al., 2003). In this area, the distribution of these whales overlaps significantly with shipping lanes leading to the busy ports of Norfolk and Baltimore (Aschettino et al., 2020). The whales have been observed lunge feeding and defecating, and satellite telemetry shows evidence of area restricted search behavior (Aschettino et al., 2020), but accelerometry tags have not previously been deployed in this area. Examination of the stomach contents of stranded whales shows evidence of feeding on Atlantic menhaden (A. Costidis, personal communication, March 2019), Atlantic croaker, and spot (Laerm et al., 1997). To date there have been no formal descriptions of the behavior of humpback whales feeding on these prey species. This area is extremely shallow, typically varying from 11 to 15 m in depth, with the shipping lanes dredged up to 30 m (Aschettino et al., 2020). Here we investigate the effects of this unique shallow water environment and prey types on the foraging behavior of predominately juvenile humpback whales in a winter, mid-latitude feeding ground.

2 | METHODS

2.1 | Data collection

We tagged humpback whales in the coastal waters off Virginia Beach, Virginia, <20 km from shore. The area is characterized by two shipping lanes which converge in a turning basin just east of the Chesapeake Bay Bridge-Tunnel. We tagged whales in or near the shipping lanes from Duke University Marine Laboratory's 9-m research vessel, the R/V *Richard T. Barber*, from January through March 2017–2022 (Figure 1). We deployed digital acoustic tags (DTAGs; Johnson & Tyack, 2003) using a carbon-fiber pole and obtained images of dorsal fins and flukes for photo-identification. We conducted focal follows of whale behavior and recorded animal's distance and bearing in relation to the research vessel to recreate each animal's track. During focal follows the research vessel remained on average 185 m from the whale, and was typically between 50 and 300 m. The VHF radio transmitter on the tag facilitated focal follows and allowed us to locate each tag after it released from the whale.

2.2 | Data processing

We deployed version 4 DTAGs in 2017 and version 3 DTAGs in all other years. DTAGs recorded high-resolution acoustic (two hydrophones sampling at 120 kHz (version 3) and 192 kHz (version 4)) and kinematic (tri-axial accelerometers and magnetometers) data. Version 3 kinematic sensors sampled movement and pressure (depth) at 250 Hz,
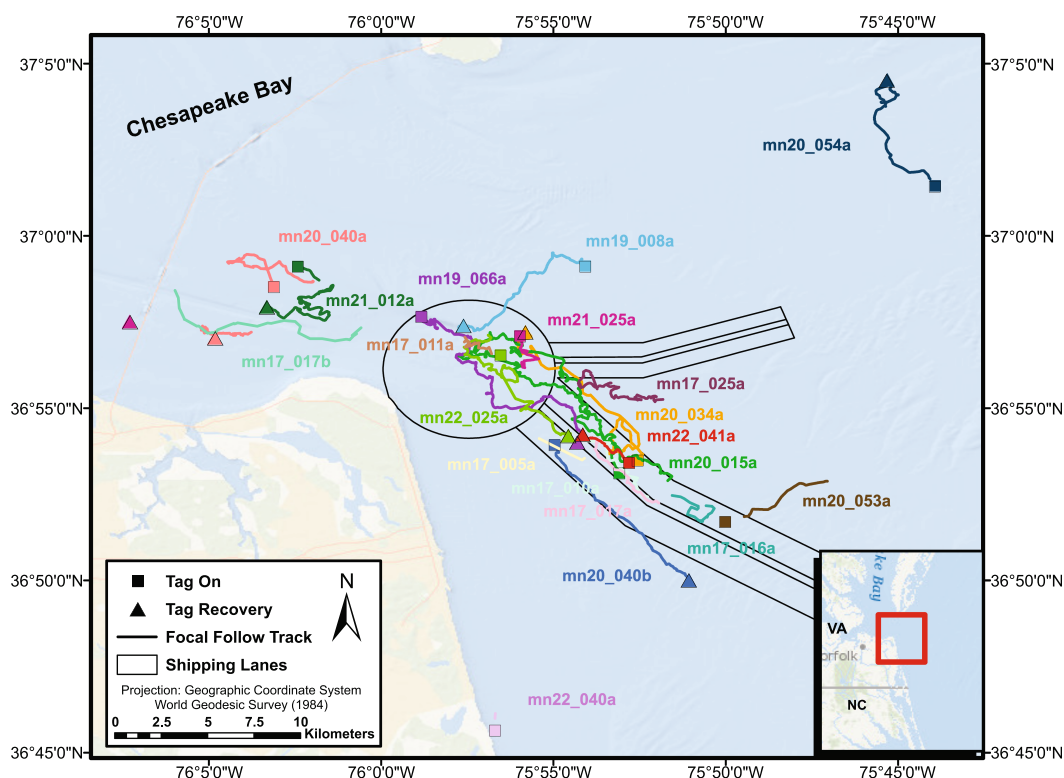
FIGURE 1   Map of study area and tagging locations of all whales. Focal follows from the R/V *Richard T. Barber* during deployments are shown as colored lines corresponding to each individual whale. Tag recovery locations for mn20_054a to mn20_053a are omitted for map clarity. Shipping lanes and the turning basin are shown in black. Average water depths outside of the shipping lanes are 11–15 m, while the shipping channels are dredged up to 30 m.

while version 4 tags sampled acceleration at 1,000 Hz and pressure and magnetometry at 50 Hz. We decimated all sensor data to 25 Hz for analysis, and processed all data in MATLAB 2016b (MathWorks, Inc.) using the DTAG toolbox (https://animaltags.org; https://soundtags.wp.st-andrews.ac.uk) and custom-written scripts. We computed the animal's pitch, roll, and heading from calibrated data using the expected orientation of the animal during surfacings (i.e., flat, horizontal surfacings; (Johnson, 2011)), adjusted to account for shifts in tag position during deployment.

2.3 | Dive definition

We defined a dive as any submergence deeper than 2 m. Although this is shallower than typical thresholds used for this species (e.g., Goldbogen et al., 2008), some animals only dove to a maximum of 8–10 m, so we had to set a low threshold to describe foraging behavior in this shallow habitat.

2.4 | Lunge definition

We audited tags using adaptations of tools from the DTAG toolbox (available at https://soundtags.wp.st-andrews.ac.uk). We conducted audits using 120-s windows with 10-s overlap, with the display showing the animal's

dive profile, pitch and roll, fluking, norm jerk, speed, and a spectrogram of the acoustic recording (Figure 2). We calculated these data streams from the calibrated movement data as follows: fluking was visualized as the differential of the smoothed pitch signal (smoothed in a half-second moving average). Norm jerk was calculated by taking the differential of the 2-norm (square root of the sum of the squares of each axis) of the acceleration data and measured quick events (Ydesen et al., 2014). We set a jerk threshold by filtering out all surface periods (<1 m depth) to reduce noise and taking the mean plus two standard deviations of the jerk signal. Jerk is sensitive to tag placement, so we updated the jerk threshold after every tag slide. DTAGs do not have a dedicated speed sensor, so speed must be calculated from other movement metrics. Typically, a correlation is drawn between speed from orientation-corrected depth change and either flow noise or tag jiggle (Cade et al., 2018; Goldbogen et al., 2006; Shearer et al., 2022). In our study area, tagged whales did not dive steeply enough to accurately calculate orientation-corrected depth change, and flow noise could not be used because of high levels of masking from ship noise. Therefore, we calculated tag jiggle for the entire tag record following (Cade et al., 2018). We used a calibrated tow-tank to define a relationship between known speeds and tag jiggle with version 3 DTAGs. Results from this calibration were used to define velocity using an exponential equation:

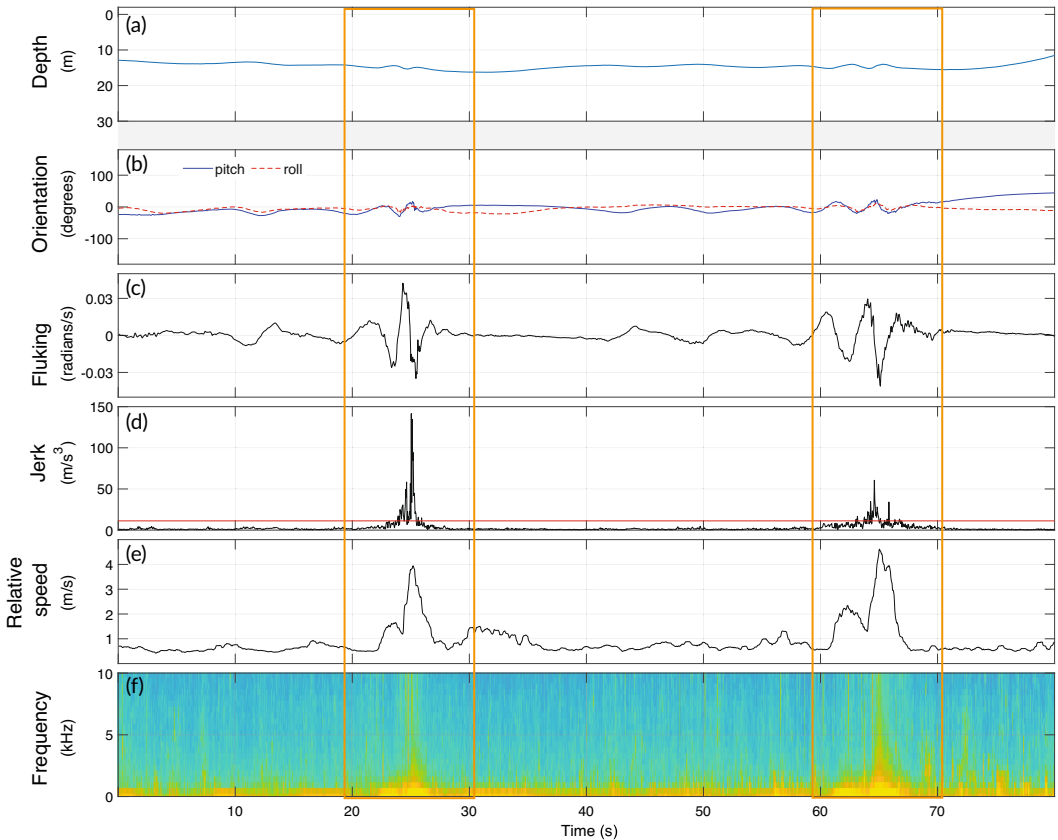$$Velocity = 12.86 * \exp(0.05992 * tagJiggle).$$

FIGURE 2 Audit window showing two lunges (orange boxes) from mn20_040a. (a) Dive profile of the tagged whale. (b) Pitch (blue) and roll (red). (c) Fluking, the derivative of the smoothed pitch signal, in radians per second. (d) Jerk, with the threshold of 2 standard deviations over the mean for that tag placement indicated by the red horizontal line. (e) Relative speed as calculated from the tag jiggle correlation. (f) Spectrogram of the acoustic recording (Hamming window, NFFT 512).

The vibration patterns of the tow plate are different from that of the animal, so we cannot estimate exact speed with this method, but we can evaluate relative changes in speed. Therefore, we do not report the speed of the animal during lunges, but instead use relative speed to detect lunges from the rise and fall in velocity.

We marked audits for the presence of both lunges and rolling events. Lunges were marked if there was evidence of fluke strokes, a jerk signal greater than the threshold, and a rise and quick fall in speed. We also marked rolling events, which occurred when the animal rolled more than 50°. In 2017, tags were used as part of a startle response experiment and the tagged whales were exposed to startle tones. Very few responses were noted (Janik et al., 2019), so we retained these tags in the analysis, and only censored the data to remove the 2 min following each startle playback.

2.5 | Acceleration parameters

Definitions for acceleration parameters are found in Table 1. We manually marked the timing of lunges by eye during audits, but for the acceleration analyses, we set the time of the lunge to the peak in the associated jerk signal. For all acceleration parameters, we used a time window of 3 s before and after this peak. We calculated the interlunge interval as the time difference between lunge midpoints (jerk peaks) in the same dive. We calculated the pitch as the median absolute value of the pitch signal, and roll as the median and maximum absolute value, in degrees. Because the exact magnitude of the jerk signal is not comparable among animals or tag placements, we normalized the jerk using a baseline period, which we calculated as the mean jerk during that tag placement (i.e., updated baseline period for every tag slide), excluding surface periods <1 m. We then calculated the jerk during the lunge as the median root mean squared (RMS) jerk over 1-s time windows. We normalized the jerk in the lunge by dividing by the corresponding baseline jerk. We normalized the overall dynamic body acceleration (ODBA) in the same way, calculating a baseline ODBA from the mean ODBA during that tag placement, excluding surface periods <1 m. To obtain the mean ODBA during the lunge, we calculated the 2-norm ODBA over the whole tag record, then took the mean of the ODBA values during the lunge period. We then normalized the lunge ODBA by dividing by the baseline ODBA. Therefore, both jerk and ODBA are presented as relative measures compared to the animal's baseline. Finally, we calculated tortuosity, which is a measure of the maneuvering of the animal, using an index of stretched out track length (STL) compared to distance made good (DMG; the distance between start and end point) as $(STL - DMG)/STL$. Values of this parameter close to 0 indicate straight line movement, while values close to 1 are more circular. Tortuosity estimation requires a 2-dimensional track, which is not measured by the tag; to compute the animal's positions we used a dead-reckoned track calculated from the accelerometer and magnetometer data. We estimated tortuosity, the dead-reckoned track, and ODBA using tools available from https://animaltags.org.

TABLE 1 Definitions and calculations of kinematic variables.

Lunge variables	Units	Calculation
interlunge interval	seconds	time difference between lunge mid-points in a single dive
pitch	degrees	absolute value of the median pitch during the lunge
roll	degrees	absolute value of the median or max roll during the lunge
jerk	normalized units	differential of tri-axial acceleration, normalized against baseline movement
ODBA	normalized units	2-norm of high-pass filtered tri-axial acceleration (high-pass filter cut-on frequency 0.125 Hz), normalized against baseline movement
tortuosity	[0 1]	index comparing stretched out track length (STL) to distance made good (DMG; distance between start and end point) $(STL - DMG)/STL$

2.6 | Diel patterns in foraging

We used a linear model to test for diel patterns in lunge rates, for animals that executed at least one lunge. We divided each tag record as follows: dawn (sunrise ±1 hr), day (1 hr after sunrise −1 hr before sunset), dusk (sunset ±1 hr), and night (1 hr after sunset −1 hr before sunrise). We obtained sunrise and sunset values from a sun calculator available from https://www.timeanddate.com. Because tags differed in the number of hours of data in each time bin, we calculated lunges per hour as the number of lunges in that time bin divided by the number of hours of data recorded in that time bin for each individual. We included one value per time-of-day period, per whale. If the data for one whale spanned two different days, these were combined into one row (total lunges in that time category/total hours in that category). Individual differences in foraging rates likely exist, but we had only two deployments with data in all time bins, so we could not use random effects in a mixed model structure. Instead, we used a linear model to test differences in lunges per hour in different time periods using the "stats" package in R (R Core Team, 2021). To check model assumptions of normality, independence, and constant variance, we plotted model residuals. We compared the time-of-day model with the null model using an analysis of variance test (ANOVA, R "stats" package). We used a Tukey post hoc test to test for pair-wise differences between time periods using the "emmeans" package (Lenth, 2018).

3 | RESULTS

We tagged 20 likely juvenile humpback whales between 2017 and 2022 and obtained 122 hr of tag data (Table 2). Tagged whales dove to a maximum depth of 28 m, but most animals did not dive deeper than 20 m. We recorded 788 lunges from 10 animals, with a maximum of 409 lunges on a single tag deployment.

3.1 | Few lunges per dive and short interlunge intervals

Lunges were at shallow depths, occurring at a median depth of 10.3 m (Table 3). Only one animal had an average lunge depth > 14 m. In general, tagged whales made few lunges on each dive, with a median of one lunge per foraging dive (dive containing at least a single lunge), and a maximum of five lunges per dive (Table 3). For dives with more than one lunge, interlunge intervals were short, with a median interlunge interval of 33 s (Table 3). The minimum interlunge interval was 11.4 s. The amount of foraging varied between animals, ranging from 1.4 to 33.8 lunges per hour of tag recording (Table 3).

3.2 | Kinematic patterns show little maneuvering during lunges

Tagged humpback whales typically lunged in a horizontal, flat orientation. The average pitch during the lunge was 6.0 degrees, and the average roll was 7.6° (Table S1, Figure 3). The maximum roll during a lunge was on average only 23.7° (Table S1). Lunges illustrated the large jerk peak typical of baleen whales, with jerk peaks on average 4.7 times higher than the baseline (Table S1). ODBA was 3.1 times higher than the baseline (Table S1). Tortuosity was very low, indicating that lunges occurred primarily in a straight line, with a median tortuosity index of just 0.035.

3.3 | Some evidence of diel patterns, though models are inconclusive

Foraging occurred at almost all hours of the day and night, but a high number of lunges occurred at dawn in both tags that were deployed over 24 hr. Whales foraging at dawn had almost seven times as many lunges at dawn than

TABLE 2 Summary of humpback whale tag deployments. Animal length measurements via UAV photogrammetry are available for four whales in 2020 and 2022 which were measured independently by Aschettino et al. (2022). All animals tagged in 2017 were less than 10 m in length based on comparisons with the 9-m tagging boat when animals were close to the boat during tagging operations.

Tag ID	Date tagged	Length (m)	Deployment duration (hr)	# dives (>2 m)	Maximum depth (m)	# lunges
mn17_005a	01/05/2017	<10	2.23	32	13.3	0
mn17_010a	01/10/2017	<10	2.23	28	15.5	0
mn17_011a	01/11/2017	<10	1.95	43	25.3	66[a]
mn17_016a	01/16/2017	<10	1.53	85	14.8	0
mn17_017a	01/17/2017	<10	2.27	59	14.6	0
mn17_017b	01/17/2017	<10	2.23	77	19.5	0
mn17_025a	01/25/2017	<10	2.23	152	10.7	55[b]
mn19_008a	01/08/2019		2.20	77	10.1	0
mn19_066a	03/07/2019		6.32	171	24.8	9
mn20_015a	01/15/2020		7.62	200	19.8	15
mn20_034a	02/03/2020	9.0	4.60	186	14.0	7
mn20_040a	02/09/2020	7.6	25.53	766	28.0	148
mn20_040b	02/09/2020		2.08	41	11.5	0
mn20_053a	02/22/2020	9.6	7.60	182	20.7	0
mn20_054a	02/23/2020		3.07	137	12.6	0
mn21_012a	01/12/2021		25.92	932	24.8	409
mn21_025a	01/25/2021		6.18	415	18.0	49
mn22_025a	01/25/2022		3.65	105	18.2	21
mn22_040a	02/09/2022	7.0	11.67	242	8.01	0
mn22_041a	02/10/2022		0.95	41	15.3	9
Total			122.06	3930	28.0	788

[a]Ten lunges were removed because they occurred within 2 min of startle tones.
[b]Two lunges were removed because they occurred within 2 min of startle tones.

during day or night (Table 4, Figure 4). However, there was not a significant difference between the linear model with time of day included and the null model, although the p value from the ANOVA test was .056. While post hoc Tukey tests did not show significant differences between lunge rates at different times of day, lunge rates at dawn were much higher than during day ($p = .05$) or night ($p = 0.06$; Table 5).

3.4 | Nonlunge rolling events near the seafloor

In addition to regular lunges, we observed rolling events that did not include a lunge, although sometimes they followed typical lunges. We detected 119 such rolling events with a maximum roll over 50° in 13 tag deployments (Table S2, Figures 5 and S1). The average maximum roll reached during these rolling events was 133 degrees, though some rolls were to at least 180° (upside down), and some whales completed an entire 360° roll (Table S2, Figures 5 and S1). The pitch during rolling was somewhat steeper than during regular lunges, but was still relatively horizontal, with an average of 17.1° (Table S2). On average, rolls lasted for 18.8 s and occurred at 8 m (Table S2). However, some rolls, regardless of depth, occurred at the seafloor, as the sound

TABLE 3 Characteristics of foraging for tag deployments that included at least one lunge. The median number of lunges per dive includes only dives with at least one lunge. Interlunge interval is the time difference between lunge peaks.

| Tag ID	# lunges	Lunges/hr recording	Lunge depth (m), median	Lunges/dive, median (maximum)	Interlunge interval (s), median (range)
mn17_011a	66	33.8	23.5	3.5 (5)	30.5 (14.4–90.8)
mn17_025a	55	24.7	9.0	1 (3)	21.0 (14.9–32.7)
mn19_066a	9	1.4	11.6	1 (2)	94.4
mn20_015a	15	2.0	6.3	1 (2)	32.6
mn20_034a	7	1.5	10.0	1 (2)	46.7 (27.7–65.7)
mn20_040a	148	5.8	13.1	1 (4)	38.4 (18.0–70.0)
mn21_012a	409	15.8	10.1	1 (4)	34.8 (11.4–85.8)
mn21_025a	49	7.9	5.3	1 (2)	26.1 (21.9–43.1)
mn22_025a	21	5.8	10.1	1 (3)	32.2 (14.1–43.8)
mn22_041a	9	9.5	13.2	1 (1)	n/a
Total	788		10.3	1 (5)	33.2 (11.4–94.4)
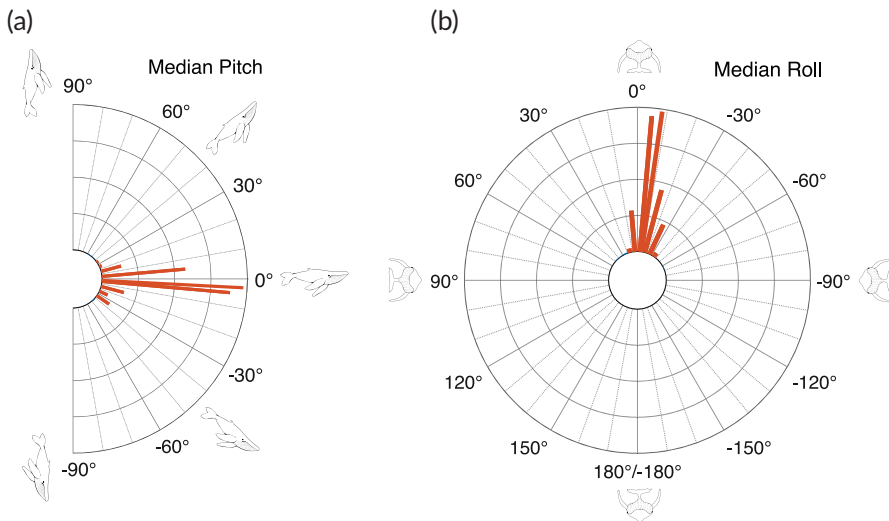
FIGURE 3 Polar plots showing the distribution of pitch (a) and roll (b) during lunges. Circular grid lines are at intervals of 100 lunges.

of the tag scraping the substrate was audible on acoustic recordings. Eighteen rolls from five animals had audible seafloor scraping sounds, at depths ranging from 5 to 17 m. There was little evidence of strong fluking, and jerk and ODBA were both low (Table S2).

Animals rolled in both directions, although there was a slight but significant preference for rolling to the right (55%, binomial test, $p = .036$). Three animals had more than 10 rolling events, and these showed a stronger preference for rolling in a certain direction (Table S3). These preferences were in different directions, with two preferring right-hand rolls (62%, $p = .16$; 85%, $p = .001$) and one preferring left-hand rolls (65%, $p = 0.003$) (Table S3).

TABLE 4 Number of lunges and hours of data at different times of day.

| Time period	# lunges	# hours data	Lunges/hour	Lunge depth median
Day	395	77.175	5.1	12.6
Night	161	29.092	5.5	7.9
Dusk	94	11.514	8.2	5.3
Dawn	138	4	34.5	12.5
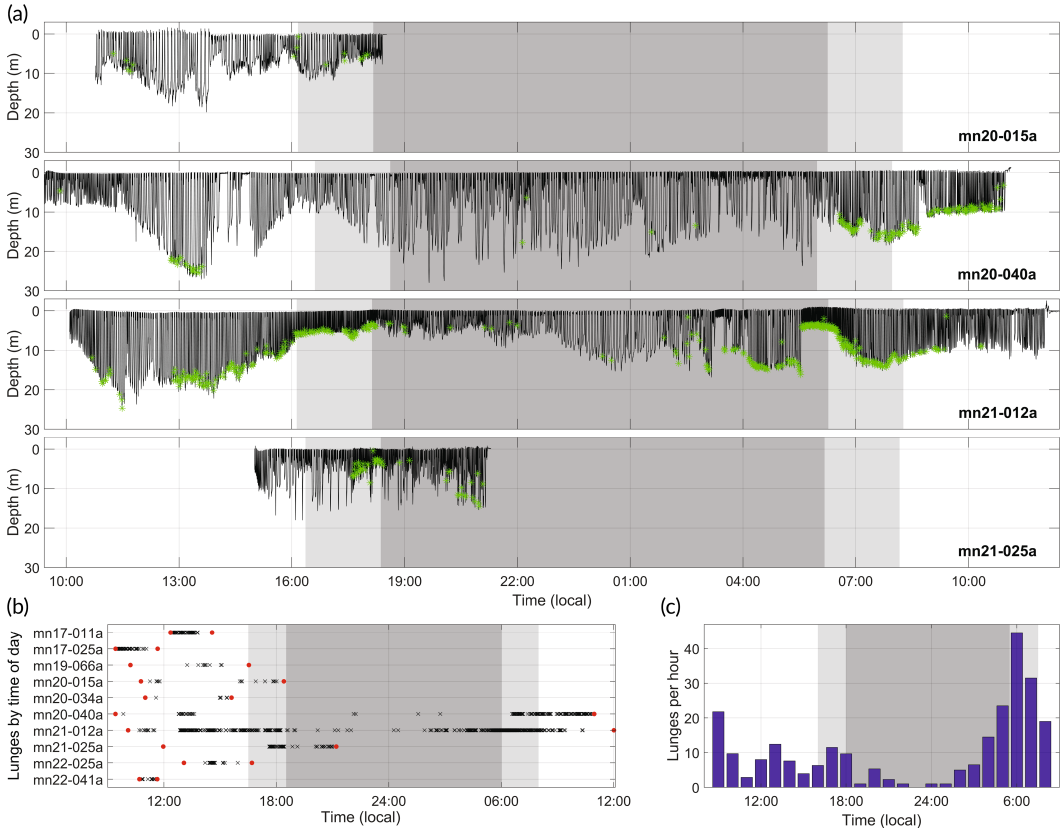
FIGURE 4 (a) Dive profiles for four tag deployments that include nighttime hours. Lunges are indicated by green stars. (b) Lunge times by time of day, for all animals that lunged. Lunges are denoted by X markings; red circles indicate the tag on and tag off times. (c) Number of lunges per hour in each time bin, for all whales that lunged.

4 | DISCUSSION

Foraging in very shallow water substantially constrains the ways in which humpback whales can feed. While individuals maintained many traits characteristic of typical lunging behavior, such as high levels of jerk and quick drops in speed, they foraged in a horizontal orientation, with very low pitch angles. In many other places where foraging humpback whales have been studied, they typically forage at steep pitch angles, often oriented toward the surface (Simon et al., 2012; Ware et al., 2011). In our study area, the water was simply not deep enough for humpback whales to lunge upward towards their prey. This horizontal orientation during lunging also meant that lunges did not

TABLE 5 Tukey post hoc comparison of linear model results. Significance level α = 0.05.

Lunges per hour ∼ time period				
Comparisons	Estimate	SE	t	p
Dawn–day	24.81	8.61	2.881	.0501
Dawn–dusk	22.75	9.63	2.363	.1278
Dawn–night	28.18	10.15	2.776	.0609
Day–dusk	−2.06	6.58	−0.313	.9889
Day–night	3.37	7.32	0.460	.9666
Dusk–night	5.43	8.49	0.639	.9177
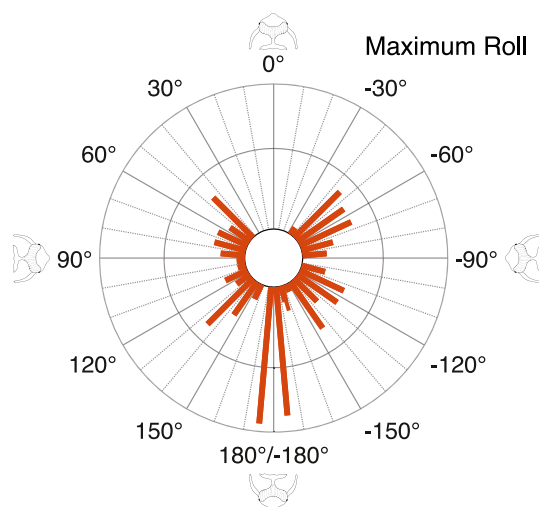
FIGURE 5 Polar plot of maximum roll values reached during the rolling event. Circular grid lines are at intervals of 10 lunges.

result in stereotypical depth excursions, which have been used to help identify lunging behavior in other areas (e.g., Simon et al., 2012). Tagged whales also demonstrated limited rolling during lunges, which is similar to behavior observed at other study sites (Cade et al., 2016; Simon et al., 2012). The tortuosity index during foraging was very low, indicating that feeding whales were moving in a straight line, rather than in a circular pattern. Because over half of lunges recorded in this study came from a single animal (mn21_012a), we tested whether data from this individual could be influencing the results by dropping this animal from the dataset and recalculating kinematic variables. All kinematic parameters were similar in the reduced data set, indicating that this animal is not skewing these results. Taken as a whole, these metrics indicate that feeding humpback whales at the mouth of Chesapeake Bay employed very little maneuvering and simple kinematics. Startle playbacks in 2017 did not seem to affect the whales' foraging behavior as animals resumed feeding shortly after exposures and only one whale showed a startle reaction. Dive and foraging characteristics of these whales did not differ from those in later years, further indicating that these exposures did not influence their foraging behavior. This is perhaps not surprising given the high background noise in the environment caused by a high level of vessel traffic.

The presence of the seafloor in this shallow environment limits the number of directions in which humpback whales can lunge, but it may also act as a barrier that whales can exploit while feeding. Whales in our study were often solitary and, unsurprisingly given the depth of the water column, we did not observe any bubble nets. Instead,

we hypothesize that whales foraged near the seafloor to restrict the number of escape routes for their mobile prey. It is also possible that they trapped prey along the sides of the shipping channels, as whales worked their way up and down the margins of these deeper channels. Six whales were also equipped with satellite-linked dive recorders, and future work will combine these data streams to determine how often whales are lunging within the shipping channels, if their foraging behavior is concentrated on the edges of the channel, and how far above the seafloor they are foraging.

Unsurprisingly in such a shallow habitat, our tagged humpback whales averaged only a single lunge per dive. This is consistent with animals foraging at relatively shallow depths in other areas (Ware et al., 2011). Because there is very little cost of returning to the surface to breathe between foraging events, whales maximized their oxygen intake by employing short dives (Tyson et al., 2016). This results in fewer lunges per dive than in other deeper areas, where humpbacks can average 3–8 lunges per dive (Burrows et al., 2016; Goldbogen et al., 2008; Simon et al., 2012). Nevertheless, humpbacks in this area achieved hourly lunge rates that were comparable with those from other areas, because of the minimal amount of time spent on ascent and descent (Friedlaender et al., 2009, 2013). With such short transit distances, whales do not appear to sacrifice foraging efficiency by returning to the surface more often to breathe.

When whales executed more than a single lunge per dive, interlunge intervals were low. There have been a wide range of interlunge intervals reported for humpback whales from other areas, ranging from 13–25 s (Goldbogen et al., 2008, 2012) to 40–60 s (Simon et al., 2012; Ware et al., 2011). Values in our study were toward the lower end of this range, with a minimum of 11 s (median 33 s). Some of these differences may reflect how inter-lunge intervals are calculated. We calculated intervals from lunge mid-point to lunge mid-point, but some other studies have used the end of mouth closing (using camera tags) to the start of the next lunge, resulting in lower time intervals. Quantitative body length measurements were available for only a few animals in our study, but both directly measured and estimated animals were small, <10 m (Aschettino et al., 2022). Humpback whale size at sexual maturity is estimated to be around 12 m, indicating that most whales in this study were juveniles or subadults (Barco et al., 2003; Clapham & Mead, 1999). The time required to filter prey after each lunge scales with body size, so the smaller humpbacks in our study should have relatively low prey handling times, more like those of minke whales ($M = 9$ s) than adult humpback whales ($M = 17$ s; Kahane-Rapport et al., 2020).

Only two tags recorded through a full 24-hr period, and post hoc tests showed no significant differences between lunge rates and time of day. There was some suggestion of higher foraging rates in early morning hours; however, with only two deployments recording through an entire diel cycle, results should be cautiously interpreted, and it is possible that these two animals are not representative. Both overnight tag deployments occurred in the same area, to the northwest of the turning basin, and these animals exhibited more circuitous behavior during the focal follow, rather than following the edges of the shipping channels. These two whales also exhibited the most rolling behavior, indicating that differences in bathymetry over a small spatial scale may be playing a role in the patterns of behavior seen here. More tag deployments that exceed 24 hr are needed to test the hypothesis of diel variation in foraging rate. Because some animals in our study were also equipped with satellite-linked dive recorders, future work will compare these data streams to investigate whether foraging signatures are visible in satellite tag records. If foraging signatures can be detected, these longer-duration tags may provide more clues about diel patterns. There is some evidence that croaker exhibit diel vertical movements (Hale & Targett, 2018), but in situ prey mapping using active acoustics is needed to provide a direct measure of diel vertical movement by potential prey targets.

In addition to regular lunges, we observed presumed foraging events that did not share the characteristic jerk peaks and speed changes of lunge feeding but consisted of high rolls. Several of these rolling events occurred at the bottom of dives, sometimes at the seafloor as the sound of the tag scraping the substrate was audible in 15% of rolling events. While there may be alternate explanations for rolling during dive ascents and descents, we suggest that these rolling events at the bottom of dives may represent bottom side-roll foraging, as has been described in the Gulf of Maine (Ware et al., 2014). The average duration, pitch, and roll angles we detected during rolling events

were similar to those reported by Ware et al. (2014). In the Gulf of Maine, bottom side rolls occurred within 5–10 m of the bottom. We do not know the water depth for each dive in our study, but a similar behavior is certainly possible given the shallow nature of the study area and the depths at which rolling events occurred. Bottom side rolls in the Gulf of Maine appear to target sand lance, which burrow in the substrate at night (Friedlaender et al., 2009). At the mouth of Chesapeake Bay, rolling events could be used to target croaker, which are a benthic species. There was some limited evidence for laterality in rolling events, with a slight but significant preference for rolling to the right. The two animals with the most data showed stronger preferences, but in opposite directions. Humpback whales foraging in other areas exhibit some evidence of laterality, both in the direction of spirals and rolls (Canning et al., 2011), and in abrasions on the jaw (Clapham et al., 1995; Hain et al., 1995). Small numbers of rolls per animal do not allow for definitive conclusions about laterality here, and more data would be needed to determine if there is a similar right-hand bias, as has been observed elsewhere. In addition, to confirm that these rolling events are indeed bottom side roll feeding, rather than some other behavior (such as exfoliation on the sandy substrate, e.g., Meynecke et al. 2023), camera tag deployments would be required.

Some animals in our study foraged at extremely high rates, with up to 47 lunges per hour. Most of our tagged whales were likely juveniles, given field observations, UAV measurements, and historical stranding data, and with little motivation to travel to Caribbean breeding grounds, these animals gain an advantage by continuing to feed and grow over winter months. However, this energetic advantage comes at a potential high cost, as the whales are feeding in one of the busiest shipping lanes on the U.S. East Coast (e.g., fig. 2 in Aschettino et al. 2020). North Atlantic humpback whales are currently experiencing an unusual mortality event, with 227 whales stranded from January 2016 through July 2024, with many stranded whales showing evidence of ship strikes (NOAA, 2024). In the Virginia Beach area, humpback whales have been sighted with ship strike injuries or have stranded as a result of collisions with large vessels (Aschettino et al., 2018). The high spatial overlap between these animals and busy shipping lanes puts them at increased risk of ship strikes. In this area, drafts of large freighters and tankers can be up to 10–15 m, and three-quarters of humpback whale lunges occurred at depths <15 m. There is a tradeoff between foraging efficiency and vigilance (Brown, 1999), and the high rates of foraging seen here may indicate that animals are sacrificing some level of vigilance to maximize energetic intake, which may put them at the risk of a collision, particularly given the overlap between foraging depths and ship drafts. Conversely, if these whales are juveniles, they may not have yet learned the necessary vigilance skills required to avoid collisions.

4.1 | Conclusions

We studied the foraging behavior of presumed juvenile humpback whales feeding on a likely novel prey assemblage on a winter, mid-latitude feeding ground, in a very shallow environment. Foraging in such shallow water constrains their kinematics, with lunges showing low levels of pitch, roll, and tortuosity. Whales make few foraging attempts per dive but maintain foraging rates per hour that are similar to those reported from other areas. The whales showed relatively low interlunge intervals, but prey handling times were consistent with expectations for relatively small juvenile animals. The whales we studied foraged at high rates to take advantage of this off-cycle food resource. Our results strengthen the observation that humpback whales demonstrate considerable foraging plasticity, can adapt to a variety of environments, and modify foraging strategies to their habitat and the behavior of their prey.

AUTHOR CONTRIBUTIONS

Jeanne M. Shearer: Conceptualization; data curation; formal analysis; funding acquisition; investigation; visualization; writing – original draft. **Heather J. Foley:** Investigation; project administration. **Zachary T. Swaim:** Investigation; project administration. **Vincent M. Janik:** Funding acquisition; investigation. **Andrew J. Read:** Conceptualization; funding acquisition; investigation; supervision.

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REFERENCES

Aschettino, J. M., Engelhaupt, D., Engelhaupt, A., Richlen, M., & Cotter, M. (2022). *Mid-Atlantic Baleen Whale Monitoring, Virginia Beach, Virginia: 2020/21 Annual Progress Report*. Prepared for U.S. Fleet Forces Command. Submitted to Naval Facilities Engineering Systems Command Atlantic, Norfolk, Virginia, under Contract N62470-20-0016.

Aschettino, J. M., Engelhaupt, D., Engelhaupt, A., Richlen, M., & DiMatteo, A. (2018). *Mid-Atlantic Humpback Whale Monitoring, Virginia Beach, Virginia*: 2017/18 *Annual Progress Report*. Prepared for U.S. Fleet Forces Command. Submitted to Naval Facilities Engineering Command Atlantic, Norfolk, Virginia, under Contract N62470-15-8006, Task Order 17F4013, Issued to HDR, Inc., Virginia Beach, Virginia.

Aschettino, J. M., Engelhaupt, D. T., Engelhaupt, A. G., DiMatteo, A., Pusser, T., Richlen, M. F., & Bell, J. T. (2020). Satellite telemetry reveals spatial overlap between vessel high-traffic areas and humpback whales (*Megaptera novaeangliae*) near the mouth of the Chesapeake Bay. *Frontiers in Marine Science*, 7, 1–16. https://doi.org/10.3389/fmars.2020.00121

Baraff, L. S., Clapham, P. J., Mattila, D. K., & Bowman, R. S. (1991). Feeding behavior of a humpback whale in low-latitude waters. *Marine Mammal Science*, 7(2), 197–202. https://doi.org/10.1111/j.1748-7692.1991.tb00567.x

Barco, S. G., McLellan, W. A., Allen, J. M., Asmutis-Silvia, R., A., Mallon-Day, R., Meagher, E. M., Pabst, D. A., Robbins, J., Seton, R. E., Swingle, W. M., Weinrich, M. T., & Clapham, P. J. (2003). Population identity of humpback whales (*Megaptera novaeangliae*) in the waters of the US mid-Atlantic states. *Journal of Cetacean Research Management*, 4(2), 135–141. https://doi.org/10.47536/jcrm.v4i2.849

Brown, J. S. (1999). Vigilance, patch use and habitat selection: Foraging under predation risk. *Evolutionary Ecology Research*, 1(1), 49–71.

Burrows, J. A., Johnston, D. W., Straley, J. M., Chenoweth, E. M., Ware, C., Curtice, C., De Ruiter, S. L., & Friedlaender, A. S. (2016). Prey density and depth affect the fine-scale foraging behavior of humpback whales *Megaptera novaeangliae* in Sitka Sound, Alaska, USA. *Marine Ecology Progress Series*, 561, 245–260. https://doi.org/10.3354/meps11906

Cade, D. E., Barr, K. R., Calambokidis, J., Friedlaender, A. S., & Goldbogen, J. A. (2018). Determining forward speed from accelerometer jiggle in aquatic environments. *Journal of Experimental Biology*, 221, jeb.170449. https://doi.org/10.1242/jeb.170449

Cade, D. E., Friedlaender, A. S., Calambokidis, J., & Goldbogen, J. A. (2016). Kinematic diversity in rorqual whale feeding mechanisms. *Current Biology*, 26(19), 2617–2624. https://doi.org/10.1016/j.cub.2016.07.037

Canning, C., Crain, D., Eaton, T. S., Nuessly, K., Friedlaender, A., Hurst, T., Parks, S., Ware, C., Wiley, D., & Weinrich, M. (2011). Population-level lateralized feeding behaviour in North Atlantic humpback whales, *Megaptera novaeangliae*. *Animal Behaviour*, 82, 901–909. https://doi.org/10.1016/j.anbehav.2011.07.031

Chenoweth, E. M., Straley, J. M., McPhee, M. V., Atkinson, S., & Reifenstuhl, S. (2017). Humpback whales feed on hatchery-released juvenile salmon. *Royal Society Open Science*, 4(7), Article 170180. https://doi.org/10.1098/rsos.170180

Christensen, I., Haug, T., & Oien, N. (1992). Seasonal distribution, exploitation and present abundance of stocks of large baleen whales (Mysticeti) and sperm whales (*Physeter macrocephalus*) in Norwegian and adjacent waters. *ICES Journal of Marine Science*, 49, 341–355.

Clapham, P. J., Leimkuhler, E., Gray, B. K., & Mattila, D. K. (1995). Do humpback whales exhibit lateralized behaviour? *Animal Behaviour*, *50*(1), 73–82. https://doi.org/10.1006/anbe.1995.0222

Clapham, P. J., & Mead, J. G. (1999). Megaptera novaeangliae. *Mammalian Species*, *604*, 1–9. https://doi.org/10.2307/3504352

Friedlaender, A. S., Halpin, P. N., Qian, S. S., Lawson, G. L., Wiebe, P. H., Thiele, D., & Read, A. J. (2006). Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. *Marine Ecology Progress Series*, *317*, 297–310. https://doi.org/10.3354/meps317297

Friedlaender, A. S., Hazen, E. L., Nowacek, D. P., Halpin, P. N., Ware, C., Weinrich, M. T., Hurst, T., & Wiley, D. (2009). Diel changes in humpback whale *Megaptera novaeangliae* feeding behavior in response to sand lance *Ammodytes* spp. behavior and distribution. *Marine Ecology Progress Series*, *395*, 91–100. https://doi.org/10.3354/meps08003

Friedlaender, A. S., Tyson, R. B., Stimpert, A. K., Read, A. J., & Nowacek, D. P. (2013). Extreme diel variation in the feeding behavior of humpback whales along the western Antarctic Peninsula during autumn. *Marine Ecology Progress Series*, *494*, 281–289. https://doi.org/10.3354/meps10541

Goldbogen, J. A., Cade, D. E., Calambokidis, J., Friedlaender, A. S., Potvin, J., Segre, P. S., & Werth, A. J. (2017). How baleen whales feed: The biomechanics of engulfment and filtration. *Annual Review of Marine Science*, *9*(1), 367–386. https://doi.org/10.1146/annurev-marine-122414-033905

Goldbogen, J. A., Calambokidis, J., Croll, D. A., Harvey, J. T., Newton, K. M., Oleson, E. M., Schorr, G., & Shadwick, R. E. (2008). Foraging behavior of humpback whales: kinematic and respiratory patterns suggest a high cost for a lunge. *Journal of Experimental Biology*, *211*(23), 3712–3719. https://doi.org/10.1242/jeb.023366

Goldbogen, J. A., Calambokidis, J., Croll, D. A., McKenna, M. F., Oleson, E., Potvin, J., Pyenson, N. D., Schorr, G., Shadwick, R. E., & Tershy, B. R. (2012). Scaling of lunge-feeding performance in rorqual whales: Mass-specific energy expenditure increases with body size and progressively limits diving capacity. *Functional Ecology*, *26*(1), 216–226. https://doi.org/10.1111/j.1365-2435.2011.01905.x

Goldbogen, J. A., Calambokidis, J., Shadwick, R. E., Oleson, E. M., McDonald, M. A., & Hildebrand, J. A. (2006). Kinematics of foraging dives and lunge-feeding in fin whales. *Journal of Experimental Biology*, *209*(7), 1231–1244. https://doi.org/10.1242/jeb.02135

Hain, J. H. W., Carter, G. R., Kraus, S. D., Mayo, C. A., & Winn, H. E. (1982). Feeding behavior of the humpback whale, *Megaptera novaeangliae*, in the western North Atlantic. *Fishery Bulletin*, *80*(2), 259–268.

Hain, J. H. W., Ellis, S. L., Kenney, R. D., Clapham, P. J., Gray, B. K., Weinrich, M. T., & Babb, I. G. (1995). Apparent bottom feeding by humpback whales on Stellwagen Bank. *Marine Mammal Science*, *11*(4), 464–479. https://doi.org/10.1111/j.1748-7692.1995.tb00670.x

Hale, E. A., & Targett, T. E. (2018). Vertical distribution of larval Atlantic menhaden (*Brevoortia tyrannus*) and Atlantic croaker (*Micropogonias undulatus*): Implications for vertical migratory behaviour and transport. *Fisheries Oceanography*, *27*(3), 222–231. https://doi.org/10.1111/fog.12247

Hazen, E. L., Friedlaender, A. S., Thompson, M. A., Ware, C. R., Weinrich, M. T., Halpin, P. N., & Wiley, D. N. (2009). Fine-scale prey aggregations and foraging ecology of humpback whales *Megaptera novaeangliae*. *Marine Ecology Progress Series*, *395*, 75–89. https://doi.org/10.3354/meps08108

Janik, V. M., Gotz, T., Oswald, J. N., Martin Lopez, L. M., Read, A. J., & Nowacek, D. P. (2019). *Acoustic startle responses as aversive reactions and hearing indicators in cetaceans* [Technical report]. ONR Marine Mammal and Biology Program Review. https://www.nre.navy.mil/media/document/onr-marine-mammal-biology-program-review-23-26-april-2019

Johnson, K. F., & Davoren, G. K. (2021). Stable isotope analysis reveals that humpback whales (*Megaptera novaeangliae*) primarily consume capelin (*Mallotus villosus*) in coastal Newfoundland, Canada. *Canadian Journal of Zoology*, *99*(7), 564–572. https://doi.org/10.1139/cjz-2020-0257

Johnson, M. (2011, March). Measuring the orientation and movement of marine animals using inertial and magnetic sensors - a tutorial. *Fine-Scale Animal Movement Workshop*, Hobart.

Johnson, M. P., & Tyack, P. L. (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering*, *28*(1), 3–12. https://doi.org/10.1109/JOE.2002.808212

Jurasz, C. M., & Jurasz, V. P. (1979). Feeding modes of the humpback whale, *Megaptera novaeangliae*, in southeast Alaska. *Scientific Reports of the Whales Research Institute, Tokyo*, *31*, 69–83.

Kahane-Rapport, S. R., Savoca, M. S., Cade, D. E., Segre, P. S., Bierlich, K. C., Calambokidis, J., Dale, J., Fahlbusch, J. A., Friedlaender, A. S., Johnston, D. W., Werth, A. J., & Goldbogen, J. A. (2020). Lunge filter feeding biomechanics constrain rorqual foraging ecology across scale. *Journal of Experimental Biology*, *223*(20), jeb.224196. https://doi.org/10.1242/jeb.224196

Katona, S. K., & Beard, J. A. (1990). Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. *Reports of the International Whaling Commission, Special Issue 12*, 295–305.

Kirchner, T., Wiley, D. N., Hazen, E. L., Parks, S. E., Torres, L. G., & Friedlaender, A. S. (2018). Hierarchical foraging movement of humpback whales relative to the structure of their prey. *Marine Ecology Progress Series*, *607*, 237–250. https://doi.org/10.3354/meps12789

Kosma, M. M., Werth, A. J., Szabo, A. R., & Straley, J. M. (2019). Pectoral herding: An innovative tactic for humpback whale foraging. *Royal Society Open Science*, 6(10), Article 1911104. https://doi.org/10.1098/rsos.191104

Laerm, J., Wenzel, F., Craddock, J. E., Weinand, D., McGurk, J., Harris, M. J., Early, G. A., Mead, J. G., Potter, C. W., & Barros, N. B. (1997). New prey species for northwestern Atlantic humpback whales. *Marine Mammal Science*, 13(4), 705–711. https://doi.org/10.1111/j.1748-7692.1997.tb00094.x

Lenth, R. (2018). *Emmeans: Estimated marginal means, aka least-squares means* (R package version 1.3.0) [Computer software]. https://cran.r-project.org/package=emmeans

McMillan, C. J., Towers, J. R., & Hildering, J. (2019). The innovation and diffusion of "trap-feeding," a novel humpback whale foraging strategy. *Marine Mammal Science*, 35(3), 779–796. https://doi.org/10.1111/mms.12557

Meynecke, J., Gustafon, J., & Cade, D. E. (2023). Exfoliating whales–sandy bottom contact behaviour of humpback whales. *Journal of Marine Science and Engineering*, 11, Article 600. https://doi.org/10.3390/jmse11030600

NOAA. (2024). *2016–2024 humpback whale Unusual Mortality Event along the Atlantic coast*. https://www.fisheries.noaa.gov/national/marine-life-distress/2016-2024-humpback-whale-unusual-mortality-event-along-atlantic-coast

Nowacek, D. P., Friedlaender, A. S., Halpin, P. N., Hazen, E. L., Johnston, D. W., Read, A. J., Espinasse, B., Zhou, M., & Zhu, Y. (2011). Super-aggregations of krill and humpback whales in Wilhelmina Bay, Antarctic Peninsula. *PLoS ONE*, 6(4), e19173. https://doi.org/10.1371/journal.pone.0019173

Owen, K., Warren, J. D., Noad, M. J., Donnelly, D., Goldizen, A. W., & Dunlop, R. A. (2015). Effect of prey type on the fine-scale feeding behaviour of migrating east Australian humpback whales. *Marine Ecology Progress Series*, 541, 231–244. https://doi.org/10.3354/meps11551

Pivorunas, A. (1979). The feeding mechanisms of baleen whales. *American Scientist*, 67(4), 432–440.

R Core Team (2021). *R: A language and environment for statistical computing* (Version 4.0.5) [Computer software]. R Foundation for Statistical Computing.

Shearer, J. M., Jensen, F. H., Quick, N. J., Friedlaender, A., Southall, B., Nowacek, D. P., Bowers, M., Foley, H. J., Swaim, Z. T., Waples, D. M., & Read, A. J. (2022). Short-finned pilot whales exhibit behavioral plasticity in foraging strategies mediated by their environment. *Marine Ecology Progress Series*, 695, 1–14. https://doi.org/10.3354/meps14132

Simon, M., Johnson, M., & Madsen, P. T. (2012). Keeping momentum with a mouthful of water: behavior and kinematics of humpback whale lunge feeding. *Journal of Experimental Biology*, 215(21), 3786–3798. https://doi.org/10.1242/jeb.071092

Stevick, P. T., Allen, J., Bérubé, M., Clapham, P. J., Katona, S. K., Larsen, F., Lien, J., Mattila, D. K., Palsbøll, P. J., Robbins, J., Sigurjónsson, J., Smith, T. D., Øien, N., & Hammond, P. S. (2003). Segregation of migration by feeding ground origin in North Atlantic humpback whales (*Megaptera novaeangliae*). *Journal of Zoology*, 259(3), 231–237. https://doi.org/10.1017/S0952836902003151

Stevick, P. T., Allen, J., Clapham, P. J., Katona, S. K., Larsen, F., Lien, J., Mattila, D. K., Palsbøll, P. J., Sears, R., Sigurjónsson, J., Smith, T. D., Vikingsson, G., Øien, N., & Hammond, P. S. (2006). Population spatial structuring on the feeding grounds in North Atlantic humpback whales (*Megaptera novaeangliae*). *Journal of Zoology*, 270(2), 244–255. https://doi.org/10.1111/j.1469-7998.2006.00128.x

Stevick, P. T., Oien, N., & Mattila, D. K. (1999). Migratory destinations of humpback whales from Norwegian and adjacent waters: evidence for stock identity. *Journal of Cetacean Research and Management*, 1(2), 147–152. https://doi.org/10.47536/jcrm.v1i2.461

Swingle, W. M., Barco, S. G., Costidis, A. M., Bates, E. B., Mallette, S. D., Phillips, K. M., Rose, S. A., & Williams, K. M. (2017). *Virginia Sea Turtle and Marine Mammal Stranding Network 2016 Grant Report*. A Final Report to the Virginia Coastal Zone Management Program Department of Environmental Quality, Commonwealth of Virginia, NOAA Grant #NA15NOS4190164, Task #49. http://www.seaturtle.org/PDF/SwingleWM_2014_VAQFTechReport.pdf

Swingle, W. M., Barco, S. G., Pitchford, T. D., McLellan, W. A., & Pabst, A. (1993). Appearance of juvenile humpback whales feeding in the nearshore waters of Virginia. *Marine Mammal Science*, 9(3), 309–315. https://doi.org/10.1111/j.1748-7692.1993.tb00458.x

Tyson, R. B., Friedlaender, A. S., & Nowacek, D. P. (2016). Does optimal foraging theory predict the foraging performance of a large air-breathing marine predator? *Animal Behaviour*, 116, 223–235. https://doi.org/10.1016/j.anbehav.2016.03.034

Videsen, S. K. A., Simon, M., Christiansen, F., Friedlaender, A., Goldbogen, J., Malte, H., Segre, P., Wang, Tobias., Johnson, M., & Madsen, P. T. (2023). Cheap gulp foraging of a giga-predator enables efficient exploitation of sparse prey. *Science Advances*, 9(25), eade3889. https://doi.org/10.1126/sciadv.ade3889

Ware, C., Friedlaender, A. S., & Nowacek, D. P. (2011). Shallow and deep lunge feeding of humpback whales in fjords of the West Antarctic Peninsula. *Marine Mammal Science*, 27(3), 587–605. https://doi.org/10.1111/j.1748-7692.2010.00427.x

Ware, C., Wiley, D. N., Friedlaender, A. S., Weinrich, M., Hazen, E. L., Bocconcelli, A., Parks, S. E., Stimpert, A. K., Thompson, M. A., & Abernathy, K. (2014). Bottom side-roll feeding by humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine, U.S.A. *Marine Mammal Science*, 30(2), 494–511. https://doi.org/10.1111/mms.12053

Weinrich, M. T., Schilling, M. R., & Belt, C. R. (1992). Evidence for acquisition of a novel feeding behaviour: lobtail feeding in humpback whales, *Megaptera novaeangliae*. *Animal Behaviour*, *44*(6), 1059–1072. https://doi.org/10.1016/S0003-3472(05)80318-5

Whitehead, H. (1987). Updated status of the humpback whale, *Megaptera novaeangliae*, in Canada. *Canadian Field-Naturalist*, *101*(2), 284–294.

Wiley, D. N., Asmutis, R. A., Pitchford, T. D., & Gannon, D. P. (1995). Stranding and mortality of humpback whales, *Megaptera novaeangliae*, in the mid-Atlantic and southeast United States, 1985-1992. *Fishery Bulletin*, *93*(1), 196–205.

Wiley, D. N., Thompson, M., Pace, R. M., & Levenson, J. (2011). Modeling speed restrictions to mitigate lethal collisions between ships and whales in the Stellwagen Bank National Marine Sanctuary, USA. *Biological Conservation*, *144*(9), 2377–2381. https://doi.org/10.1016/j.biocon.2011.05.007

Ydesen, K. S., Wisniewska, D. M., Hansen, J. D., Beedholm, K., Johnson, M., & Madsen, P. T. (2014). What a jerk: prey engulfment revealed by high-rate, super-cranial accelerometry on a harbour seal (*Phoca vitulina*). *Journal of Experimental Biology*, *217*(13), 2239–2243. https://doi.org/10.1242/jeb.100016

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.