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Post-Release Monitoring of a Stranded and Rehabilitated Short-Finned Pilot Whale (*Globicephala macrorhynchus*) Reveals Current-Assisted Travel

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Abstract

A subadult female short-finned pilot whale (*Globicephala macrorhynchus*), which stranded on the northeastern Gulf of Mexico coast of Florida in June 2017, was rehabilitated for 38 days and then monitored with a satellite-linked, time-depth recording tag for 32 days after being released off the West Florida Shelf. The individual, "Gale," appeared to regularly use ocean currents to facilitate a southeastward movement around Florida, and then a northward movement along the continental shelf break to the waters off Cape Hatteras, North Carolina. Indeed, 57% of her travel along the coast of Florida was at speeds consistent with the surface speed and direction of the Gulf Stream. Overall, current-assisted travel contributed to a 19% increase in distance traveled (4,152 km) and to an average rate of travel (130 km/d) that was higher than previously reported for *Globicephala* spp. Gale's dive behavior was typical of other short-finned pilot whale observations, with average dive depths (243 ± 136 m; max = 712 m) and durations (7.9 ± 2.2 min; max = 16.0 min) within the range of reported values for *Globicephala* spp. Gale also occupied habitats known to be used by pilot whales, and her movements and behaviors were consistent with those observed in other short-finned pilot whales in the Gulf of Mexico and the northwestern Atlantic Ocean. The information presented herein contributes to a better understanding of short-finned pilot whales and to the assessment of rehabilitation and release protocols.

Key Words: post-release monitoring, tagging, tracking, dive behavior, current-assisted travel, Gulf Stream, pilot whale, *Globicephala macrorhynchus*

Introduction

Short-finned pilot whales (*Globicephala macrorhynchus*) are pelagic, deep diving, social odontocetes typically found along or near the continental shelf break, slope, and areas of high relief habitat in tropical, subtropical, and warm temperate waters (Leatherwood & Reeves, 1983; Bernard & Reilly, 1999; Olson, 2009). These animals use habitats over large spatial and temporal scales (e.g., Lewison et al., 2004; Moore, 2008; Thorne et al., 2017), historically limiting systematic studies of their distribution to shipboard and aerial surveys. While opportunistic studies of whales released from mass strandings (e.g., Fehring & Wells, 1976; Irvine et al., 1979) provided much of the early information about short-finned pilot whale movements, recent advances in tagging technology have enabled detailed studies of the movements and diving behaviors of some individuals. These efforts, however, have been limited to a few areas and populations as field studies are expensive and logistically challenging to carry out (e.g., The Bahamas: Sayigh et al., 2012; Hawai'i: Baird et al., 2003, Andrews et al., 2011, Abecassis et al., 2015; the Mariana Archipelago: Hill et al., 2019; the Mid-Atlantic Bight: Bowers, 2016, Quick et al., 2017, Thorne et al., 2017, Bowers et al., 2018; and Tenerife: Jensen et al., 2011, Aguilar Soto et al., 2018).

In the southeastern United States, short-finned pilot whales are among the most common cetaceans to engage in mass stranding events (Geraci & Lounsbury, 2005). These stranding events offer unique opportunities to increase our understanding of short-finned pilot whales and other pelagic species, particularly when they involve individuals suitable for release (Moore et al., 2007).

Released animals can be monitored with satellite-linked tracking instruments for several months post-release, providing data about an individual's movements and behaviors, such as habitat use, travel rates, and dive patterns, as well as movement among stocks. For example, post-release monitoring of a stranded and rehabilitated long-finned pilot whale (*Globicephala melas*) using satellite-linked time-depth recorders in the northwest Atlantic revealed horizontal movements of at least 3,144 km with overall minimum travel speeds of 1.4 km/h (Mate et al., 2005). Similar monitoring of two stranded and rehabilitated long-finned pilot whales released in the northwest Atlantic revealed diurnal variation in diving behavior presumably related to diurnal vertical migrations of their prey, as well as synchronous horizontal movements (Nawojchik et al., 2003). Synchronous movements were also observed in two short-finned pilot whales tagged and released after a mass standing event in May 2011 in the Florida Keys as the whales travelled together into the Atlantic as far north as South Carolina (Wells et al., 2013b).

While post-release monitoring of stranded individuals increases the sample size and geographic distribution for behavioral studies of pilot whales, the efforts are also important for evaluating treatment and release protocols (Mate et al., 2005; Zagzebski et al., 2006; Wells et al., 2013a). Wells et al. (2013a) examined 69 cases of released cetaceans following human intervention and concluded that if an animal survived at least 6 wks post-release, it was likely to continue to live and, thus, the release could be deemed successful. Given the expense and challenges of rescuing and rehabilitating stranded cetaceans, assessing the success of such efforts through post-release monitoring can help guide decisions about best practices when treating future stranding cases (Nawojchik et al., 2003). Herein, we report on the post-release monitoring of a short-finned pilot whale that stranded with nine others along the northeastern Gulf of Mexico coast of Florida and was rehabilitated for 38 d. Our findings contribute to a better understanding of the distribution and behavior of short-finned pilot whales in the southeastern U.S. and to a growing dataset that can be used for evaluating the post-release outcome of stranded cetaceans and guiding future release efforts of stranded pilot whales.

Methods

Rescue and Rehabilitation

On 30 June 2017, a 310-cm-long, 334-kg subadult female short-finned pilot whale stranded between Dixie and Taylor Counties on the west coast of Florida (29.5911° N, -83.4110° W) along with nine conspecifics over a 36-h period. The pilot whale was assigned the identifier GM-1701B and was referred to as "Gale." Rescue teams from Clearwater Marine Aquarium and the University of Florida College of Veterinary Medicine stabilized Gale and administered injectable Vitamin E/Se and 2.5 mg/kg prednisolone sodium succinate before transporting her to SeaWorld Orlando's cetacean rehabilitation facility on 1 July 2017. The other conspecifics either spontaneously expired or were humanely euthanized because of poor prognosis.

During the veterinary assessment upon admission to the rehabilitation facility, Gale was found to be lethargic but in moderate to good body condition. She was able to support herself upright in the water column but exhibited minimal active swimming and was inappetent. A small superficial circular lesion, presumed to be a cookie-cutter shark bite, was present on her left ventral peduncle. Some rust-colored fluid was expelled from her blowhole upon admission. Heart rate, respiratory rate, respiratory quality, and mucous membranes were within normal limits. The findings of an ultrasonographic exam were unremarkable, although mild pleural irregularities were noted within caudal lung fields bilaterally that were interpreted as being within the normal range of variation for a free-ranging cetacean. Hematology at the time of admission revealed a mild leukocytosis (7,970 WBC/mm^3) with lymphopenia, slight monocytosis, and eosinophilia (6, 8, and 19%, respectively). Serum chemistries indicated there was moderate hyperglycemia (160 mg/dL), moderately low alkaline phosphatase (101 IU/L), mildly elevated aspartate aminotransferase (331 IU/L), and moderate to marked elevations in creatinine kinase (228 IU/L) and lactate dehydrogenase (1,009 IU/L). Cytology of exhalate showed abundant debris and rare squamous epithelial cells, but no white blood cells. Fecal cytology showed abundant heterogeneous bacteria, few epithelial cells, and no white blood cells. Gastric fluid cytology revealed moderate presence of epithelial cells and few heterogeneous bacteria. Based on these findings, antibiotics ceftiofur (6.6 mg/kg, one time) and danofloxacin (8 mg/kg, one time) were administered. Gale was rehydrated by administering 2.5 to 3.0 l of balanced electrolyte solution via an orogastric tube three times daily.

Approximately 24 h following admission, assisted feeding of frozen/thawed squid (*Illex illecebrosus*) was initiated. At this time, antibacterial treatment was changed to amoxicillin/clavulanate (7.5 mg/kg twice daily) combined with levofloxacin (6.7 mg/kg once daily) and other supportive medications orally. About 48 h following admission, Gale started independently ingesting squid when offered, and she maintained an appetite for the remainder of her rehabilitation. All hematological and serum chemical parameters gradually normalized, and all medications were discontinued by 12 July 2017. The findings of all subsequent physical examinations, cytologic analyses, and microbial cultures remained unremarkable. The results of molecular and serologic tests for presence of, or exposure to, *Brucella* spp. and cetacean morbilliviruses, performed twice on whole blood, blowhole swabs, and feces, were negative. Gale was progressively swimming more, navigating away from pool walls, responding to visual and auditory stimuli, diving (the pool was 2.1 m deep), and actively foraging (up to 15.5 kg squid per day). Based on clinical progression, activity level, active foraging, and the above diagnostic results, Gale was deemed healthy and free of diseases of concern for wild pilot whales. Gale was recommended for release by the National Oceanic Atmospheric Administration (NOAA) to avoid developing physical (scoliosis) or behavioral complications associated with housing an unhabituated individual of an otherwise highly social species alone in a hospital pool.

Tagging and Release

On 7 August 2017, after 38 d in rehabilitation, Gale was transported via truck in a wet transport container to the U.S. Coast Guard base in St. Petersburg, Florida, for tagging and release. Just prior to loading onto the vessel, experienced personnel (RSW) fitted Gale with a SPLASH10-268D Finmount tag (Wildlife Computers, Redmond, WA, USA) following methods described in Wells et al. (2013b) (Figure 1) and approved by Mote Marine Laboratory's Institutional Animal Care and Use Committee. This tag provides data about an animal's location as well as dive depth, duration, and shape. The tag was positioned at the highest point on the dorsal fin possible while still maintaining a normal vertical orientation of the antenna. The tag was attached with a single 24-mm-long, 5/16" diameter cored delrin pin, secured with 3/8" Tri-P 10-14 zinc-plated steel thread-forming screws for plastic through stainless steel washers.

Upon arrival in St. Petersburg, Gale was transferred in a wet transport container to the U.S. Coast Guard Cutter *Joshua Appleby* for transit to the release site. The release site was chosen at the edge of the West Florida Shelf, at the location closest to the stranding site and Coast Guard dock where there were previously confirmed sightings of short-finned pilot whales. At 1205 h UTC on 8 August 2017, Gale was released at 26.7552º N, -85.0729º W (Figure 2). Water depth at the release site was approximately 3,050 m.

Tracking

The tag was programmed for a maximum 500 transmissions per day during 0000 to 0359 h, 0800 to 1659 h, and 2000 to 2359 h UTC. Dives shorter than 30 s and shallower than 50 m were ignored to focus data collection on deeper dives, which likely represent foraging dives, and to extend the battery life of the tag (Quick et al., 2017). The tag was also programmed to collect individual dive behavior data, including maximum depths, dive shapes, and the start/end times of dives and surfacings. All other data collection options were disabled. These

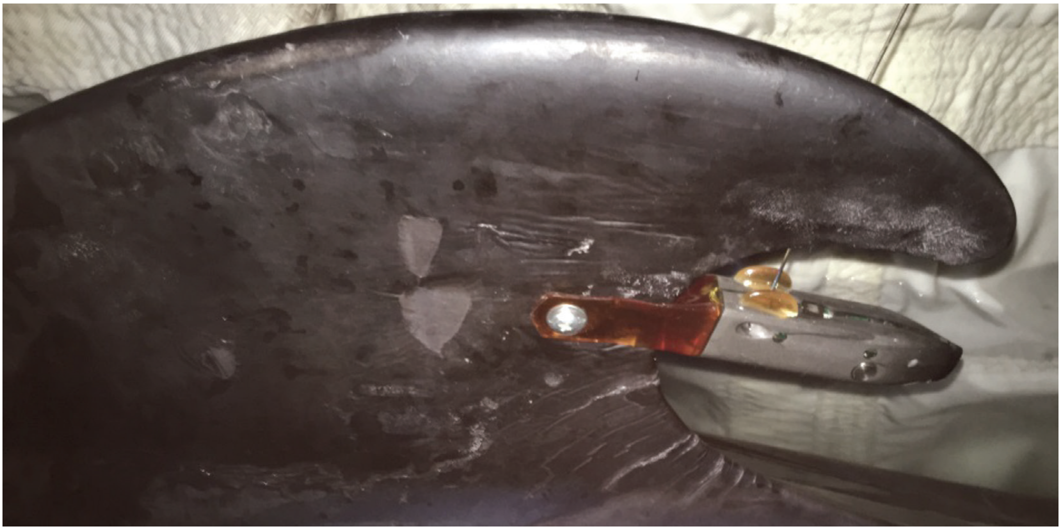

Figure 1. SPLASH10-268D Finmount tag on short-finned pilot whale (*Globicephala macrorhynchus*), Gale, in transport container

settings were chosen to balance the goal of obtaining at least 6 wks of data, allowing for the assessment of release success (Wells et al., 2013a), with the optimal number and timing of transmissions based on predicted satellite passes. Tracking data will be archived at the Animal Telemetry Network (https://ioos.noaa.gov/project/atn).

Tag Data Analyses

Location and dive data were obtained from Service Argos (aka CLS America of Lanham, MD, USA; www.argos-system.org) by ordering their retrospective reprocessing service which applies a multiple-model smoothing technique to improve location accuracy (Lopez et al., 2015). The raw reprocessed dataset contained 531 locations. We applied two

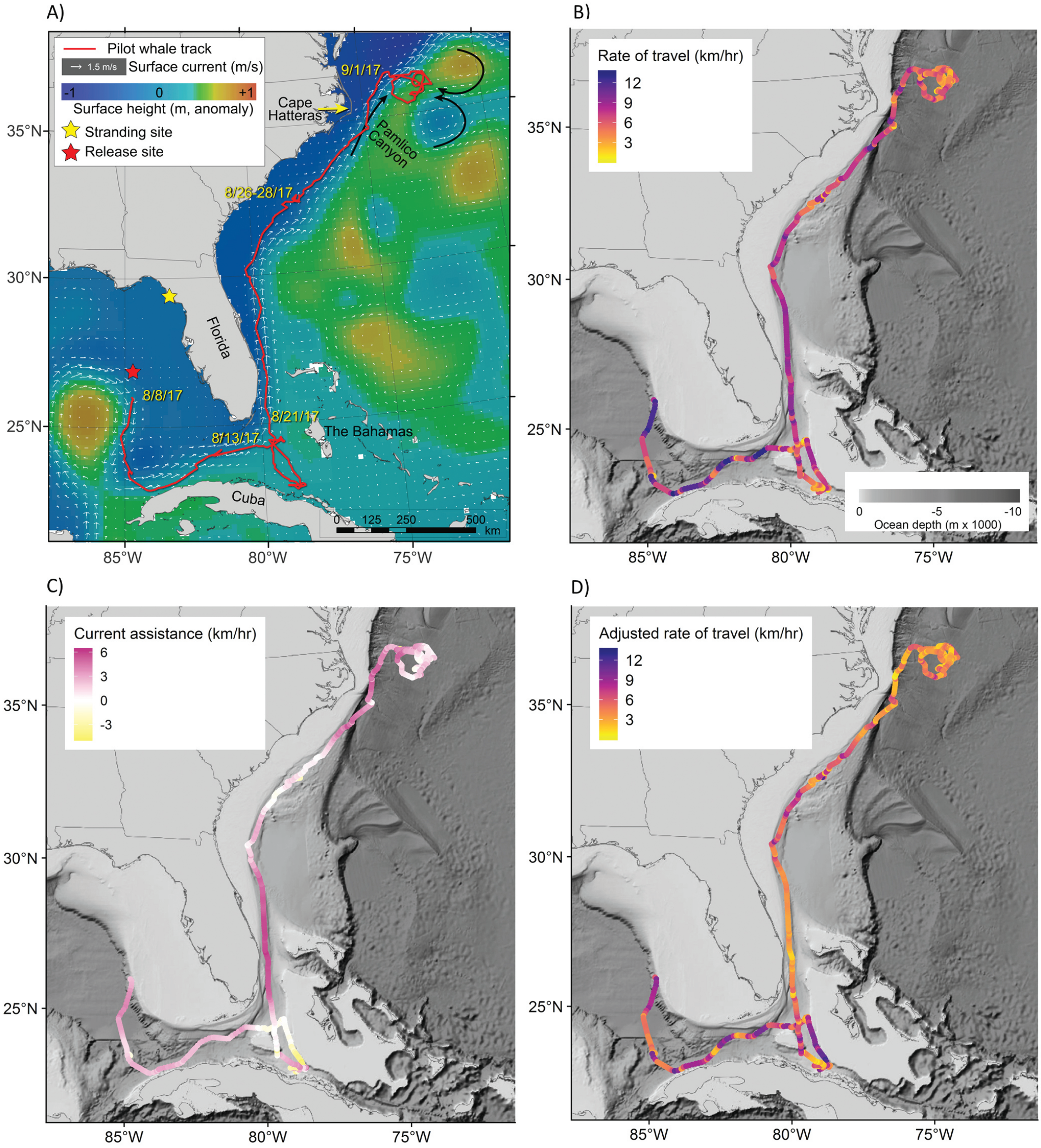

Figure 2. Estimated hourly locations of short-finned pilot whale, Gale, with (A) August 2017 mean surface currents and sea surface height, (B) estimated hourly rates of travel, (C) hourly estimates of current assistance (i.e., length of the hourly surface current vector in the direction of the hourly tracking vector), and (D) adjusted rate of travel after accounting for current effects

strategies to exclude implausible locations. First, we attributed each location with ocean depth from ETOPO1 (Amante & Eakins, 2009) using the EnvData tool (Dodge et al., 2013) at Movebank (www.movebank.org) with nearest neighbor sampling and then examined locations for which concurrent dive depth data (within 2 h) exceeded the ocean depth by > 150 m. Sixteen locations were identified; the mean (± SD) depth disparity was 258 ± 61 m, and the mean difference between location time and dive time was 12.9 ± 21.1 min. All 16 locations were excluded after further inspection. We excluded two other implausible locations based on manual inspection, as well as all Argos LC Z locations. Second, we used the Douglas Argos Filter (Douglas et al., 2012) to assess plausibility of the remaining 513 locations by judging movement rates, distances, turning angles, and location quality. Standard quality location classes (LC: 1, 2, or 3), which have 1-sigma errors in radius ranging from ~250 to 1,500 m, were retained unconditionally. Auxiliary LCs (0, A & B) within 5 km of a preceding or subsequent location were retained by virtue of spatial redundancy. Remaining auxiliary locations were included only if the resultant movement rates were < 15 km/h (4.17 m/s), and the internal angles (α, in degrees) formed by preceding and subsequent vectors (of lengths d1 and d2 km) were not suspiciously acute ($\alpha > -25 + \beta \times \ln[\text{minimum}(d1, d2)]$, where $\beta = 25$). The final dataset used for subsequent analyses included 455 filtered locations.

We fit a continuous-time correlated random walk model to the filtered locations using the *crawl* package, Version 2.0.1 (Johnson et al., 2008), of *R*, Version 3.4.1 (R Core Team, 2017), then applied the model to estimate locations at hourly intervals and at the mid-times of all dives. Argos LC errors used for the *crawl* modeling were taken from Douglas et al. (2012), specifically 0.4, 1.0, 2.5, 5.1, 2.9, and 4.3 km for LCs 3, 2, 1, 0, A, and B, respectively. We attributed each *crawl*-estimated dive location with ocean depth from ETOPO1 (Amante & Eakins, 2009) as described above. We assessed the influence of ocean surface currents (Gaspar et al., 2006; Fossette et al., 2012) on Gale's movements by matching the hourly tracking vectors to coincident hourly current estimates from the *GLOBAL ANALYSIS FORECAST PHY 001 024* dataset (accessed 8 November 2018) distributed by the Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu). We calculated current assistance (C_a) as the length of the ocean current vector that was in the direction (α, in degrees) of the whale's movement vector (Safi et al., 2013):

$$C_a = (u^2 + v^2)^{1/2} * \cos(((\mathrm{atan2}(u,v)*(180/\pi))-\alpha)*(\pi/180)),$$

where u and v were the ocean current vector components in the east-west and north-south directions, respectively. Positive values represent assistance, and negative values represent resistance. Distances between *crawl*-estimated hourly locations were calculated using the 'pointDistance' function from the *raster* package in *R*, Version 3.5.2 (R Core Team, 2018; Hijmans, 2019). We calculated Gale's total (tracking) rate of travel (km/h; which includes current drift) as well as her independent rate of travel (movement independent of currents) between each *crawl*-estimated hourly location. Tracking rates were calculated using the great-circle distances between each hourly *crawl*-estimated location. An estimate of Gale's independent movement vector (Chapman et al., 2011) was calculated by subtracting the surface current vector from the tracking vector. Turning angles between estimated hourly locations were calculated using the 'turnAngleGc' function from the *move* package in *R* (Kranstauber et al., 2018; R Core Team, 2018). Plots and maps were made in *R* using the following packages: *ggplot2* (Wickham, 2016), *rgdal* (Bivand et al., 2018), *RStoolbox* (Leutner et al., 2019), and *viridis* (Garnier, 2018).

Behavioral dive data (i.e., individual dive depths, durations, shapes, and intervening surface periods) were first examined for anomalies (e.g., dive times with inconsistent post-dive surfacing times and implausible dive depths). Two records had end times that were 60 s later than the start of the subsequent record and were corrected by setting the start times of these records to be equivalent to the end times of the previous records. This is within the range of error of these tags and an issue not uncommon with these tags due to the way they encode temporal data (Wildlife Computers, 2019). Dive depths, durations, and post-dive surface durations for all remaining records were taken as the midpoint of the reported minimum and maximum depth and time values which spanned the instrument's uncertainty (typically ~2% in depth and 2 s in timing). Only complete dives (records that paired a dive and a subsequent post-dive surfacing interval and had a temporal gap ≤ 60 s between records) were used for comparing dive duration and depth with post-dive surface duration and for calculating the percentage of time spent diving (equal to dive duration/[dive duration + post-dive surface duration] * 100). Dive shapes were reported as square ($B > 50\%\ T$), V ($B \leq 20\%\ T$), or U ($20\%\ T < B \leq 50\%\ T$), where T is the duration of the dive and B is the time between the first and last bottom reading of the dive, assuming the bottom is any depth reading ≥ 80% the maximum dive depth (Wildlife Computers, 2019). Diurnal dive patterns were examined using sunrise and sunset times obtained from the U.S. Naval Observatory (http://aa.usno.navy.mil) on the release date and the last date of tag transmissions. All times are reported in local (EDT) time (EDT = UTC minus 4 h).

Results

The tag reported Gale's location and diving behavior for 32 d, from 8 August 2017 through 9 September 2017 (Figures 2 & 3). The final filtered dataset for analysis included 455 locations (Table 1), 636 dives, and 633 surfacings, which included 612 pairs of dives with post-dive surfacings. High-quality Argos locations (LC 1, 2 & 3) comprised 25.71% (*n* = 117) of the filtered total. Temporal gaps in the location data occurred primarily due to interactions between the tag's transmission schedule, the satellite overpass schedule, and the animal's surfacing behavior. Mean, median [max] ± SD time between filtered locations was

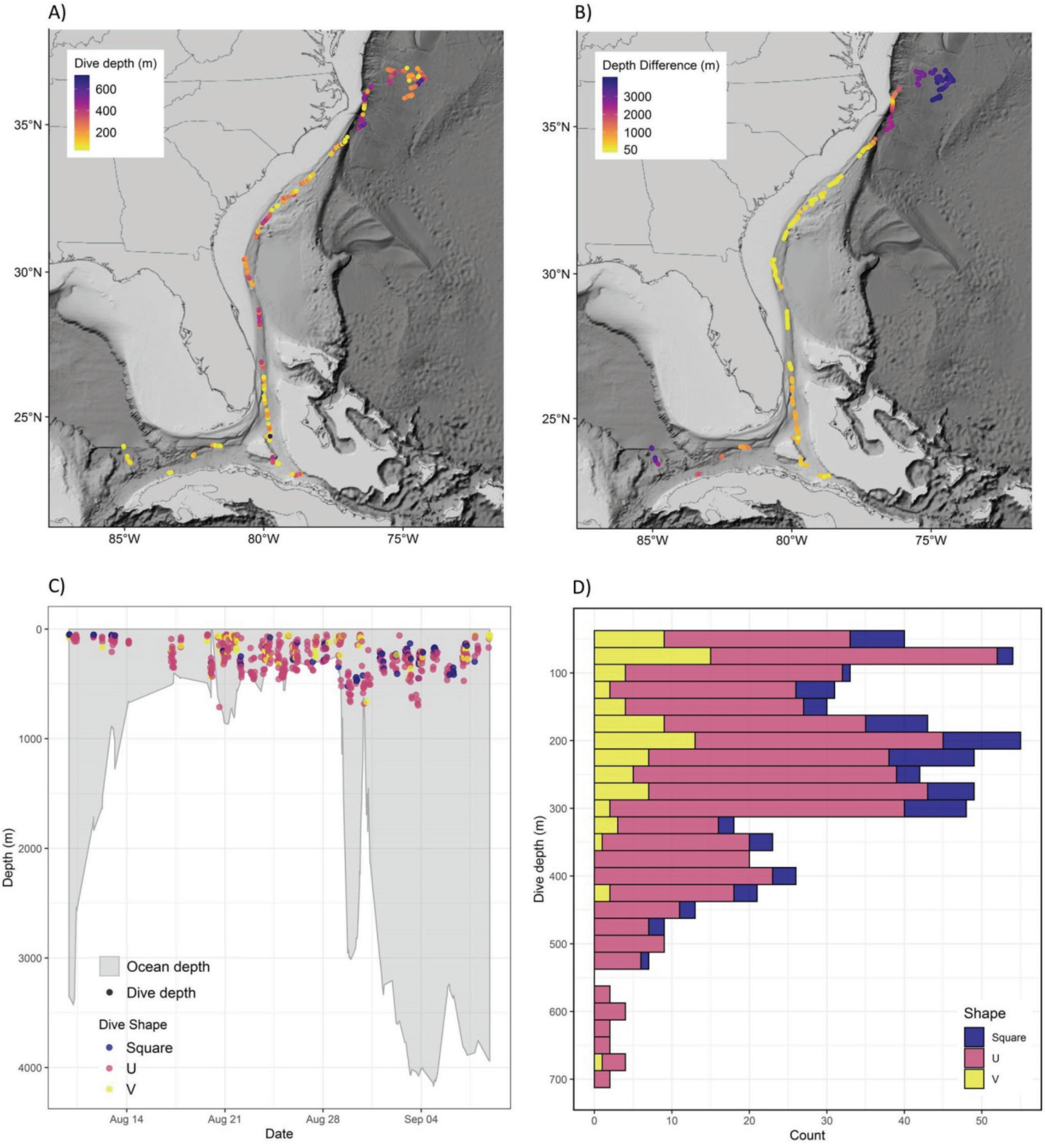

Figure 3. Estimated locations of short-finned pilot whale, Gale, at the times of individual recorded dives shown as (A) dive depth, (B) the difference between dive depth and ocean depth, (C) dive depth relative to ocean depth colored by dive shape, and (D) dive shape depth distribution

Table 1. Number of Argos locations by location class (LC) obtained from the SPLASH10-268D Finmount tag attached to short-finned pilot whale (*Globicephala macrorhynchus*), Gale, during a 32-d tracking period (8 August to 9 September 2017), before and after filtering

LC	Estimated error*	Raw	Filtered
3	< 100 m	18	18
2	250 m << 500 m	42	42
1	500 m << 1,500 m	57	57
0	> 1,500 m	64	44
A	No accuracy estimation	95	77
B	No accuracy estimation	248	217
Z	Invalid location	7	0
Total		531	455

*Section 3.4 in www.argos-system.org/manual. **Note:** For Kalman filtered data (as is the case for Gale), LCA and LCB are defined as "unbounded accuracy."

1.7, 0.9 [17.0] ± 2.6 h. Temporal gaps in the behavior data could be related to these factors or to Gale's behavior resulting in a lack of recorded dives due to how the dives were defined (i.e., dives shorter than 30 s and shallower than 50 m were not recorded). Gaps in dive behavior data (*n* = 81) had mean, median [max] ± SD durations of 5.12, 1.03 [71.88] ± 10.65 h and cumulatively represented 57.5% of the total tag deployment period.

Overall, Gale used the Loop Current and then the Gulf Stream to facilitate a southeastward movement around Florida, and then traveled north along the U.S. coast to the waters off Cape Hatteras, North Carolina (Figure 2). The total cumulative track distance was 4,152 km, and the current-adjusted animal movement distance was 3,354 km. Similarly, the overall mean, median [max] ± SD rate of travel was 5.5, 5.7 [13.5] ± 3.0 km/h (or 130, 120 [221] ± 50 km/d), while the current adjusted mean, median [max] ± SD rate of travel was 4.4, 4.0 [13.5] ± 2.5 km/h (or 105, 100 [237] ± 42 km/d). These differences indicate that passive drift afforded by the ocean surface current may have contributed to as much as 19.2% of Gale's total movement.

After release on 8 August 2017, Gale travelled rapidly away from the release site (mean, median [max] ± SD rate of travel from the release site to 13 August 2017 1800 EDT = 7.4, 6.9 [13.5] ± 3.7 km/h; Figure 2) and stayed in the upper water column (mean, median [max] ± SD dive depths = 85, 81 [208] ± 30 m; Figure 3) until reaching southeast Florida where she spent several days between Cuba and The Bahamas (Figure 2). During this time (13 August, 1900 EDT, to 21 August, 0400 EDT), Gale's turning angles became more variable (ranging 317º), and she executed deeper dives (mean, median [max] ± SD dive depths = 211, 200 [712] ± 127 m), including the deepest dive recorded during the tag deployment to 712 m (Figure 3). On 21 August, Gale reentered the Gulf Stream and commenced northward travel along the shelf break (Figure 2).

As Gale moved past Florida (25.0º to 30.0º N during 21 to 24 August), she experienced notable assistance from the Gulf Stream. The surface currents during this period were congruent with 57.2% (322 km) of Gale's total 563-km travel distance (Figure 2). While transiting north, Gale often dove along the shelf break and close to the seafloor (Figure 3B & C): 28.36% (*n* = 57) of dives executed between 26.5º to 33.5º N from 22 to 28 August were within 50 m of the ocean floor (mean, median [max] ± SD dive depths = 248, 256 [456] ± 106 m; Figure 3). During this period, she spent an estimated 24.9% of her time diving. On 29 August, Gale left the shelf break and traveled toward Pamlico Canyon, where she executed deeper dives (mean, median [max] ± SD dive depths = 513, 501 [664] ± 81 m), albeit at least 2,330 m shallower than the ocean depth (Figure 3). Gale continued to move with the Gulf Stream along the shelf break for another day before turning east on 31 August 2018 off Cape Hatteras. Gale remained 200 to 300 km east/northeast of Cape Hatteras for 9 d (until transmission ended on 9 September), travelling in a clockwise pattern where currents from the Gulf Stream and two mesoscale eddies converged (Figure 2A). During these last 10 d of transmissions, Gale spent 32.9% of her time diving to mean, median [max] ± SD depths of 278, 256 [696] ± 115 m in waters several thousands of meters deep (Figure 3).

The mean, median [max] ± SD dive depths recorded by the tag for the entire tag deployment

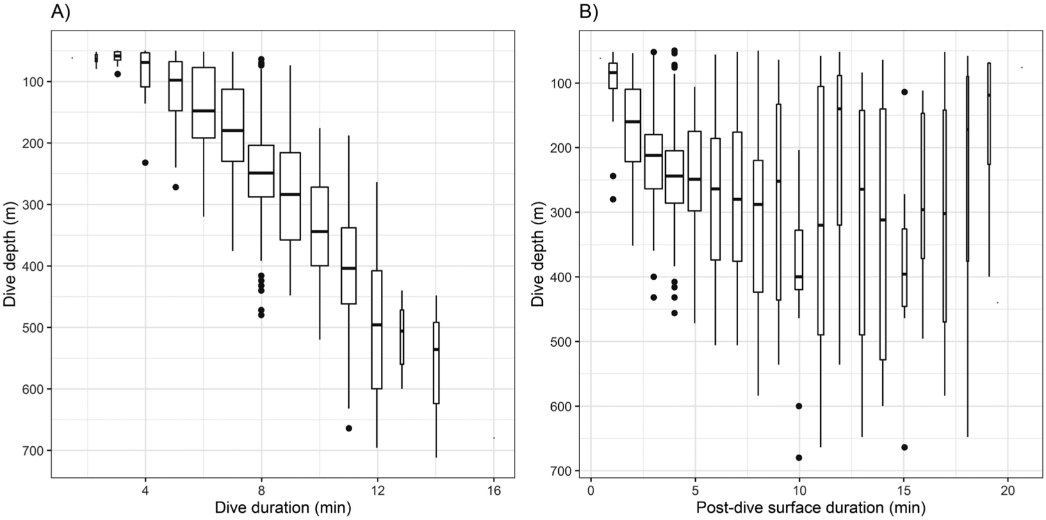

Figure 4. Recorded dive depths of short-finned pilot whale, Gale, relative to (A) dive duration and (B) post-dive surface duration. Data in B are from records with a paired dive and post-dive surfacing event, with post-dive surface durations > 20.7 min excluded. Boxes span the inter-quartile range, and box widths are proportional to the square root of *n*. Thick horizontal lines show medians, and box whiskers extend no greater or less than 1.5 × the inter-quartile range. Outliers are shown as points.

period were 243, 228 [712] ± 135 m (Figure 3). Most dives (71.70%, *n* = 456) were ≤ 300 m, while only 4.56% (*n* = 29) were deep dives (> 500 m; Aguilar-Soto et al., 2008; Figure 3). Sixty three of these dives (9.91%) were to depths within 50 m of the estimated depth of the ocean floor. Dive durations increased with dive depth ($y = -146.9 + 49.3 \times 1$ m depth, $R^2 = 0.65$, $p < 0.001$; Figure 4A), with mean, median [max] ± SD dive durations of 7.9, 7.8 [16.0] ± 2.2 min. Post-dive surface durations ranged from 0.4 to 791.0 min (mean, median [max] ± SD = 21.1, 4.7 [791.0] ± 71.5 min; Figure 4B) but included all contiguous time spent shallower than 50 m and, thus, may include periods of repeated shallow diving in addition to discrete post-dive surfacing events. When post-dive surface durations ≥ 20.7 min are removed (durations that are greater than 1.5 * the 75th percentile; McHill et al., 1978), post-dive surface durations increased with increasing dive depth ($y = 184.1 + 10.3$ min $\times 1$ m depth, $R^2 = 0.1$, $p < 0.001$; Figure 4B).

Most dive shapes were U (74.2%, *n* = 455), while 12.6% were square (*n* = 80) and 13.2% were V (*n* = 84) (Figure 3C & D). V dives were statistically shallower and shorter than U and square dives; U and square dive depths and durations were statistically similar (mean, median [max] ± SD dive depths were V = 181, 184 [664] ± 107 m, U = 256, 244 [712] ± 140 m, and square = 235, 220 [520] ± 111 m, respectively; and mean, median [max] ± SD dive durations were V = 6.4, 6.4 [11.5] ± 2.1 min, U = 8.1, 8.0 [16.0] ± 2.1 min, and square = 8.6, 8.4 [14.0] ± 2.3 min, respectively; Table 2). Post-dive surface durations for all dive types of complete dives were statistically similar (mean, median [max] ± SD post-dive surface durations: V = 30.7, 4.4 [752.0] ± 95.8 min, U = 19.0, 4.8 [653.0] ± 62.7 min, and square = 7.0, 4.6 [38.5] ± 6.8 min, respectively; Table 2).

Gale adhered to a strong diurnal dive pattern (Figure 5), diving deep at sunset (mean, median [max] ± SD dive depths between 1932 and 2023 EDT = 341, 320 [696] ± 173 m), then slightly more shallow at night (mean, median [max] ± SD dive depths between 2024 and 0628 EDT = 251, 236 [680] ± 122 m), and then slightly deeper again at dawn (mean, median [max] ± SD dive depths between 0629 and 0959 EDT = 272, 288 [632] ± 149 m). During the day, Gale dove less frequently and shallower: mean, median [max] ± SD dive depths between 1000 and 1931 EDT = 161, 90 [712] ± 57 m. Dive depths were significantly different between day, night, and sunrise/sunset (ANOVA: *df* = 2, F = 20.41, $p < 0.001$).

Table 2. Results of Wilcoxon rank sum test for all pairwise comparisons of dive shapes and dive depth, duration, and post-dive surface duration. * indicates significant differences of the pairwise comparisons at the 0.5 level.

	U, Square	U, V	Square, V
Dive depth	W = 17,000, $p = 0.5$	W = 13,000, $p < 0.01$*	W = 300, $p < 0.01$*
Dive duration	W = 20,000, $p = 0.5$	W = 11,000, $p < 0.01$*	W = 470, $p < 0.01$*
Post-dive surface duration	W = 17,000, $p = 0.5$	W = 18,000, $p = 0.6$	W = 3,100, $p = 1.0$

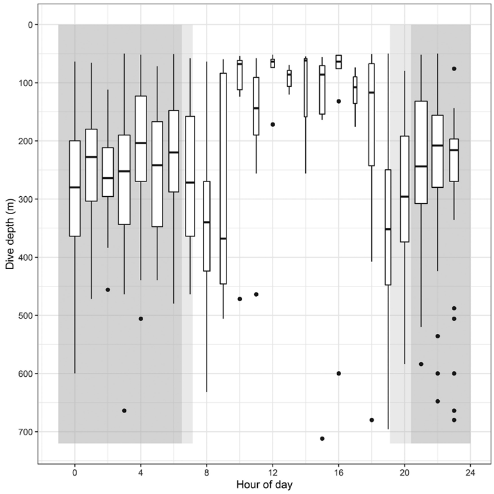

Figure 5. Box and whisker plot of Gale's dive depths during each hour of the day (local time). Gray shading denotes night time, and light-gray shading spans the range of sunrise and sunset times during the 32-d tracking period. Box and whisker definitions as in Figure 4.

Discussion

Location and dive data obtained from Gale, a stranded and rehabilitated subadult female short-finned pilot whale, documented 32 d of wide-ranging movements and repeated deep diving after she was released in the northeastern Gulf of Mexico. Wells et al. (2013a) suggested that releases of small cetaceans can be deemed successful if the animal is monitored for at least 6 wks because animals that have survived at least this long are likely to continue to live. While the tracking duration for Gale was less than the accepted approximate success threshold of 6 wks, there were no behavioral changes suggesting that the whale would not have survived beyond the 32 documented days, unlike patterns demonstrated by a rehabilitated/released pygmy killer whale (*Feresa attenuata*; Pulis et al., 2018) and short-finned pilot whale (Wells et al., 2013b). As of 6 September 2017, the tag's battery voltage was adequate for continued transmissions. While cause of the tag's abrupt and premature end remains unknown (e.g., animal death, tag failure, antenna damage, and/or attachment failure; Hays et al., 2007), there were no extreme oceanographic or atmospheric events that may have impacted Gale or the tag, and there were no obvious changes in Gale's behavior to suggest her health was compromised. During the last 10 d of the tag's transmission, Gale was in a region of typically high productivity that was historically occupied by *Globicephala* spp. (Gannon et al., 1997; Bowers, 2016; Quick et al., 2017; Thorne et al., 2017), and she appeared to be behaving in ways characteristic of free-ranging short-finned pilot whales (e.g., Wells et al., 2013b; Quick et al., 2017; Thorne et al., 2017). These observations, therefore, provide evidence that the loss of transmissions was likely due to tag or tag attachment failure rather than failing animal health.

Gale's recorded dive depths and durations were within the range of reported values for short-finned pilot whales (e.g., Baird et al., 2003; Nawojchik et al., 2003; Aguilar Soto et al., 2008; Andrews et al., 2011; Wells et al., 2013b; Claridge et al., 2015; Hill et al., 2019; Figures 3 & 4). Deep dives (> 500 m; Aguilar Soto et al., 2008) accounted for only 4.6% ($n = 29$) of Gale's dives, despite 63.8% ($n = 406$) occurring in waters > 500 m deep. This is consistent with other studies that similarly observed few deep dives by tagged short-finned pilot whales: only 1.6% of dives reported by Aguilar Soto et al. (2008) were > 500 m, and only four dives reported by both Aguilar Soto et al. (2008) and Wells et al. (2013b) were > 900 m deep. Rather, Gale's dives were focused primarily in the upper water column, with 71.7% ($n = 456$) < 300 m. Quick et al. (2017) also found dives of intermediate depth were the most common among 20 short-finned pilot whales tagged with digital acoustic recording tags (DTAGs; Johnson & Tyack, 2003) off Cape Hatteras and that the diving behavior of these animals is more complex than a simple dichotomy of shallow and deep dives.

Interestingly, 9.91% of Gale's dives ($n = 63$) were within 50 m of the estimated depth of the ocean floor, with most ($n = 57$) occurring when Gale was transiting the continental shelf break along the east coast of Florida (Figure 3). This finding is consistent with observations by Nawojchik et al. (2003) and Bowers (2016) who reported *Globicephala* spp. diving close to the seafloor, particularly along the continental shelf break. Shelf break habitats often provide good foraging opportunities for cetaceans as the steep slopes interact with ocean currents influencing biological productivity and aggregations of lower- and mid-tropic level prey species (Munk et al., 1995; Genin, 2004; Yen et al., 2004; He et al., 2011). While the diet of pilot whales is largely unknown, stomach contents of 27 mass-stranded pilot whales near Cape Hatteras in 2005 contained a diverse assemblage of small-bodied meso- and bathypelagic cephalopods (Mintzer et al., 2008), providing evidence that they may have been foraging in both the water column as well as near the seafloor. While we have no direct information about prey captures or attempts, we think that at least some (if not most) dives executed by Gale were foraging dives given their depth, duration, and location (Quick et al., 2017).

Dive shapes have been used as a proxy for defining foraging dives in other pelagic odontocetes (e.g., sperm whales [*Physeter macrocephalus*]: Irvine et al, 2017; harbor porpoises [*Phocoena phocoena*]: Wright et al., 2017); however, they appear to be poor predictors of foraging behavior in short-finned pilot whales (Bowers et al., 2016), perhaps due to the complexity of their diving behaviors (Quick et al., 2017) or to improper classification schemes for this species (Bowers et al., 2016). Instead, dive duration and maximum dive depth appear to be the two most important predictors of foraging behavior for this species (Bowers et al., 2016), with dives shallower than 87 m and shorter than 5.7 min typically lacking echolocation buzzes (Quick et al., 2017). Given Gale's mean dive depth and duration were 243 m and 7.9 min, respectively, and the finding that few dives were transmitted (i.e., most dives were shorter/shallower than our dive definition) during periods of fast travel (e.g., after Gale's release and while transiting along the coast of Florida; Figures 2 & 3), we believe Gale was likely foraging throughout much of the tag deployment record despite her periods of rapid horizontal travel. Future comparisons of dive shapes in pilot whales with more fine-scale data that incorporate sensors such as accelerometers and hydrophones to measure prey capture attempts may reveal insights into the relationships between dive shapes and foraging success.

Gale showed a clear diurnal pattern in her diving behavior, with deeper diving at dusk, night, and dawn, and less-frequent shallower diving during the day (Figure 5). Similar diurnal diving patterns in other populations of *Globicephala* spp. (e.g., Baird et al., 2002, 2003; Nawojchik et al., 2003; Mate et al., 2005; Aguilar Soto et al., 2008; Andrews et al., 2011; Wells et al., 2013b; Abecassis et al., 2015; Claridge et al., 2015; Hill et al., 2019) are thought to be indicative of individuals capitalizing on the vertical migration of the deep scattering layer, presumably meeting the rising layer at night for feeding (Olson, 2009). While the majority of Gale's deeper dives occurred between 1800 and 0900 EDT, Gale occasionally dove deep during the day, including her deepest recorded dive to 712 m. Other pilot whale studies, such as Baird et al. (2003), Aguilar Soto et al. (2008), Andrews et al. (2011), and Claridge et al. (2015), documented similar diurnal diving patterns as well as some deep, presumably feeding, dives during daylight hours.

By combining data on ocean currents with satellite-linked tracking data (Gaspar et al., 2006; Chapman et al., 2011; Fossette et al., 2012), we determined that Gale often received net positive assistance from the ocean currents during the tag deployment (Figure 2C). This was particularly true when Gale was east of Florida where over half of her total movement could be explained by the Gulf Stream. The use of currents to assist in long-distance movements and migrations has been observed in many animals such as sea turtles, fish, and marine mammals (Hays et al., 2014), including pilot whales. For example, 12 short-finned pilot whales tagged with satellite-linked transmitters in the Mid-Atlantic Bight were associated with offshore Gulf Stream waters for portions of their tracks (Thorne et al., 2017). Wells et al. (2013b) and Claridge et al. (2015) similarly observed live-stranded and released short-finned pilot whales move from the Florida Keys and the Great Bahama Canyon, respectively, into the Gulf Stream near Florida, and then travel north with the prevailing current.

Globicephala spp. are not known to migrate, but they are known to range widely (e.g., Lewison et al., 2004; Moore, 2008; Thorne et al., 2017), with reported tracking distances ranging up to 3,790 km over 77 d in long-finned pilot whales (Nawojchik et al., 2003) and 900 km over 16 d in a short-finned pilot whale (Wells et al., 2013b). Herein, Gale travelled 4,152 km during 32 d of tracking (Figure 2). While her movements may be related to seasonal changes in the ecosystem (Payne & Heinemann, 1993), they also provide additional evidence of spatial connectivity between the recognized stocks of *Globicephala* spp. in the Gulf of Mexico and Western North Atlantic Ocean. The stock structure definitions of short-finned pilot whales in this region are complicated by limited observations and genetic samples, overlapping population ranges, and difficulties differentiating long-finned pilot whales (Marina et al., 2018; Hayes et al., 2019; Van Cise et al., 2019). Pending further analysis of stock structure for this species, populations occupying the Western North Atlantic, the Northern Gulf of Mexico, and Caribbean waters are currently considered separate stocks; however, representative movement patterns between these regions are unknown (Hayes et al., 2019). Gale demonstrated movements between these stock jurisdictions, specifically the Northern Gulf of Mexico stock where she stranded and the Western North Atlantic stock where her tag stopped transmitting.

Similar observations of movements across stock boundaries in pilot whales have been reported. For example, two short-finned pilot whales tagged and released after a mass standing event in May 2011 in the Florida Keys were thought to be members of the Northern Gulf of Mexico stock based on their stranding location (Hayes et al., 2019), but they travelled into the Atlantic as far north as South Carolina, with one individual additionally moving into waters between Cuba and Haiti (Wells et al., 2013b). Other movements between stock jurisdictions were observed among five short-finned pilot whales that were tagged near the northern Bahamas and tracked into the Gulf Stream near Florida, with one individual travelling as far north as South Carolina (Claridge et al., 2015). Similarly, two short-finned pilot whales from a stranding of five individuals at Redington Beach, Florida, in July 2019 were tagged with satellite-linked transmitters and released over the West Florida Shelf; they followed a path similar to that of Gale into the Atlantic Ocean (R. S. Wells, unpub. data). The growing evidence of movements among the currently recognized stocks highlights the importance of reassessing stock boundaries using all biological markers available, including genetic markers, and the need to examine site fidelity and seasonal distributions in relation to individual long-range movements observed in this species where possible (e.g., Mahaffy et al., 2015; Van Cise et al., 2016; Hill et al., 2019).

Gale's movements during the 32 d of post-release monitoring were, to our knowledge, more extensive than previously reported for *Globicephala* spp. Her average rate of travel (5.5 km/h or 130 km/d; Figure 2B) was much higher than ranges previously reported for short-finned (e.g., 2 to 7 km/h; Wells et al., 2013b) or long-finned (e.g., 23 to 65.6 km/d: Nawojchik et al., 2003; 1.0 to 1.4 km/h: Mate et al., 2005) pilot whales. While Gale's travel rates were often assisted by the Gulf Stream, an unknown pathophysiological abnormality (Moore et al., 2007) and/or a release response, perhaps related to the absence of conspecifics, may have also contributed to her overall high rate of movement. Indeed, her highest rate of travel was during the first 5 d following her release when she reached travel speeds up to 13.5 km/h (Figure 2B). During this time, no dives were transmitted, suggesting she spent much of her time shallower than 50 m. A similar response was documented by Nawojchik et al. (2003) who observed the fastest rate of travel for two live-stranded and rehabilitated long-finned pilot whales during the first 16 d after release. Rapid travel rates and a dearth of transmitted dives were also recorded when Gale traveled at high rates in the Gulf Stream (Figures 2 & 3), although our estimate of current assistance is positively biased because it does not account for slower current speeds at depth when Gale was diving. Even after we remove the estimated current assistance, we find Gale's average independent rate of movement remains high (4.4 km/h or 1,055 km/d; Figure 2D).

Given that Gale appeared to be in good health prior to her release, we believe that her movements and behaviors post-release may be considered representative of a healthy individual and comparable to observations of other short-finned pilot whales. Indeed, during her 32 d of monitoring, she appeared to use habitats thought to represent good foraging opportunities for cetaceans, including the shelf break (Mintzer et al., 2008; Bowers, 2016; Thorne et al., 2017), a submarine canyon (Schoenherr, 1991; De Leo et al., 2010; Moors-Murphy, 2014; Thorne et al., 2017), and the productive waters off of Cape Hatteras (Gannon et al., 1997; Bowers, 2016; Quick et al., 2017; Thorne et al., 2017), where she increased her time spent diving (33%). Thus, while her distance and rate of travel are higher than those previously reported, her habitat use and dive behaviors appeared characteristic of a foraging pilot whale. In addition, while we do not have any information regarding whether Gale joined conspecifics during the tracking period, pilot whales are known to be highly social odontocetes (Heimlich-Boran, 1993) and to demonstrate synchronous behaviors (e.g., Nawojchik et al., 2003; Mate et al., 2005), suggesting Gale's movements and behaviors may have been influenced by the movements and behaviors of conspecifics and/or searching for conspecifics.

Gale did not begin to make deep dives until several days post-release. A similar multi-day lag period before beginning deep dives was reported for members of a similar species, pygmy killer whales, tracked after rehabilitation and release in the northern Gulf of Mexico (Pulis et al., 2018). Combined, these observations suggest that a period of post-release acclimation can be expected before rehabilitated deep-diving cetaceans regain or reengage their full diving capabilities. This response may be related to the stress the animal experienced from stranding and rehabilitation as well as individuals being released in an unfamiliar region or habitat and/or in disrupted social groups. Like Gale, we recommend that rehabilitations of pilot whales and other cetaceans be kept as short as possible to minimize any negative effects accumulated during time under human care that could affect an individual's release success.

Gale's post-release monitoring contributes to the growing body of evidence that oceanographic and bathymetric features such as the Gulf Stream, the continental shelf, submarine canyons, and the waters off Cape Hatteras are important habitat for short-finned pilot whales and that the broad regional movements of these animals may be more complex than previously thought. Even though the long-term success of Gale's release is uncertain (Wells et al., 2013a), the information obtained from her showcases the benefit of carrying out tracking studies of rehabilitated cetaceans. Although Gale was only monitored for 32 d, her recorded behaviors and movements provide useful information about *Globicephala* spp. ecology in the Gulf of Mexico and Western North Atlantic Ocean.

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