

# Movements and Dive Patterns of Pygmy Killer Whales (*Feresa attenuata*) Released in the Gulf of Mexico Following Rehabilitation

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## Abstract

The habits and habitats of pygmy killer whales (*Feresa attenuata*) in the Gulf of Mexico (GoM) are poorly known outside of strandings and line-transect surveys. Two adult male pygmy killer whales were found live-stranded in the state of Mississippi (USA) on 1 September 2015 and were subsequently rehabilitated and returned to the offshore waters of the GoM on 11 July 2016. To monitor the animals post-release, both were tagged with satellite-linked location and dive behavior tags. Tags were programmed to record and transmit dive duration and depth (when dives were  $\geq 30$  m deep for  $\geq 30$  s), duration of time spent above 30 m depth, and estimate locations using the Argos system. The tags transmitted for 15 and 88 days, respectively, providing a total of 1,027 filtered locations and 3,150 dive duration and maximum depth records. The animals began diving after two and four days, respectively, post-release. More than 96% of dives occurred at night. The longest recorded dive was more than 9 min in duration, and the deepest was to 368 m. More than 98% of the locations were over the GoM shelf break, spanning water 200 to 1,200 m deep. Diving patterns indicate that this species is most active at night in the GoM, suggesting its prey species are likely diel migrators that are below reachable depths during daylight hours. Near simultaneous location data from both animals confirmed that they stayed in close proximity but did not dive synchronously. Success of the rehabilitation and release was inconclusive for pygmy killer whale ID 30IMMS, whereas 31IMMS met the established criteria for success with  $\geq 6$  weeks of documented post-release survival. Follow-up

monitoring through satellite-linked telemetry provided not only important data for evaluating the success of the rehabilitation but also for documenting the activity and habitat use of these seldom-observed cetaceans.

**Key Words:** cetacean tag, dive behavior, pygmy killer whale, *Feresa attenuata*, marine mammal, post-release monitoring, satellite-linked telemetry

## Introduction

The pygmy killer whale (*Feresa attenuata* Gray, 1974) is a small species of pelagic delphinid found in tropical waters around the world. The margins of the species' range are poorly defined due to the infrequency of verified live observations. Nowhere are they considered to be common; however, they are observed frequently off Hawaii where deep water occurs close to shore, and cetacean research projects also encounter them (McSweeney et al., 2009; Baird et al., 2013; Baird, 2016). Also confounding our knowledge of the distribution and density of the species is its physical similarity to other species, creating uncertain identification at times (Mullin et al., 2004; Baird, 2010). In addition, pygmy killer whale behavior may decrease the chance of being sighted compared to other similar-sized delphinids that occur more often in larger groups and are more active or acrobatic during daylight hours when surveys occur (McSweeney et al., 2009; Roberts et al., 2016). Among Hawaiian cetacean species observed by Baird et al. (2013) where the mean distance to sighting was provided, pygmy killer whales had the lowest mean distance at first sighting and were considered fairly cryptic in their surfacing profile and behavior.

Pygmy killer whales are rarely seen in the Gulf of Mexico (GoM). More than 313,000 km of cetacean sighting surveys, by ship and plane, have resulted in only 27 positively identified groups of pygmy killer whales (summarized by Roberts et al., 2016). Stock Assessment Reports produced by the National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service (NMFS) provide abundance estimates for this species in the GoM U.S. Exclusive Economic Zone of 152 (CV = 1.02) to 518 (CV = 0.81) individuals (Waring et al., 2013). More recent density estimates, including all positive identifications of pygmy killer whales from NOAA ship and aerial surveys and reclassification of some groups previously identified as "*Feresa attenuata* or *Peponocephala electra*" to pygmy killer whales, suggest 2,126 (CV = 0.30) inhabit the U.S. portion of the GoM (Roberts et al., 2016). That model, using only depth as a covariate, predicted an *F. attenuata* density increasing from the edge of the shelf to the 1,000 m isobath that remained constant in deeper waters.

The *F. attenuata* is a generalist feeder, preying on fishes and squids using a combination of raptorial and suction feeding (Werth, 2000). Pygmy killer whales observed by McSweeney et al. (2009) off Hawaii were not documented feeding during daylight hours and were usually engaged in low energy behaviors such as milling, resting, and logging. Stomach content analyses from stranded individuals found fishes and squids that display diel vertical migration, which indicates that pygmy killer whales forage during low-light periods (Zerbini & Santos, 1997; Mignucci-Giannoni et al., 1999; Rodriguez-Lopez & Mignucci-Giannoni, 1999).

When offshore delphinids strand alive, responders either push them back out to sea or admit them to a rehabilitation facility where they are treated and released as deemed appropriate. Post-release monitoring via telemetry provides the only metric able to assess the success of those cases as direct visual observation of the released individuals is unlikely in deep offshore habitats. Satellite-linked tags are often attached to rehabilitated animals to assess the success of the release and obtain behavioral data (Wells et al., 1999, 2013a, 2013b; Nawojchik et al., 2003; Gales et al., 2012).

Most reported observations of pygmy killer whales are from Hawaii where the relief from island to open ocean allows access to their habitat, and the species is encountered during activities directed for general or other cetacean species (McSweeney et al., 2009). From long-term photographic identification studies of odontocetes, pygmy killer whales were incidentally observed ( $n = 72$  sightings) most often in waters deeper than 500 m, and there were no observations of feeding or pursuing prey (McSweeney et al.,

2009). Baird et al. (2011) attached satellite-linked tags to two pygmy killer whales for a combined total of 32 d and found that they stayed close to the island of Hawaii in waters of about 1,000 m depth. It is generally assumed that pygmy killer whales forage nocturnally on organisms that move higher in the water column at night (McSweeney et al., 2009; Baird et al., 2011), similar to behavior observed for Hawaiian spinner dolphins (*Stenella longirostris*; Norris et al., 1994), common bottlenose dolphins (*Tursiops truncatus*) off the island of Bermuda (Klatsky et al., 2007), and melon-headed whales (*Peponocephala electra*) off the Bahamas (Joyce et al., 2017).

## Methods

On the morning of 1 September 2015, two stranded pygmy killer whales were reported by an angler near Ansley, Mississippi, to the Institute for Marine Mammal Studies (IMMS), a marine mammal stranding and rehabilitation organization. The stranding occurred on the northern marsh shoreline of Mississippi Sound, a large estuary in the northern GoM near the mouth of the Pearl River. The animals, both males, were designated 30IMMS and 31IMMS. The stranding occurred in a marsh dominated by *Spartina* spp.; 30IMMS was in shallow water, and 31IMMS was above the water level in the marsh itself. Based on local tides, the animals likely stranded late afternoon of 31 August or possibly 30 August. The animals were transported to IMMS in Gulfport, Mississippi, where they were rehabilitated until deemed releasable by NOAA NMFS.

On 11 July 2016, both pygmy killer whales were transported aboard the U.S. Coast Guard cutter *Cypress* to about 145 km SSE of Gulfport, Mississippi, 45 km east of the East Pass of the Mississippi River mouth, where they were released (Figure 1). On the day of release, the animals were weighed and measured (straight line rostrum to tail notch).

Suitable release sites were determined to be greater than 200 m depth and in the vicinity of known sightings of the species during marine mammal surveys. Upon reaching a suitable release site at 1600 h local time, both animals were fitted with SPLASH10-268D Finmount tags (Wildlife Computers, Redmond, WA, USA) following methods described in Wells et al. (2013b, 2017). Final veterinary assessments were completed by 1701 h, and the tagged animals were released at 1703 h.

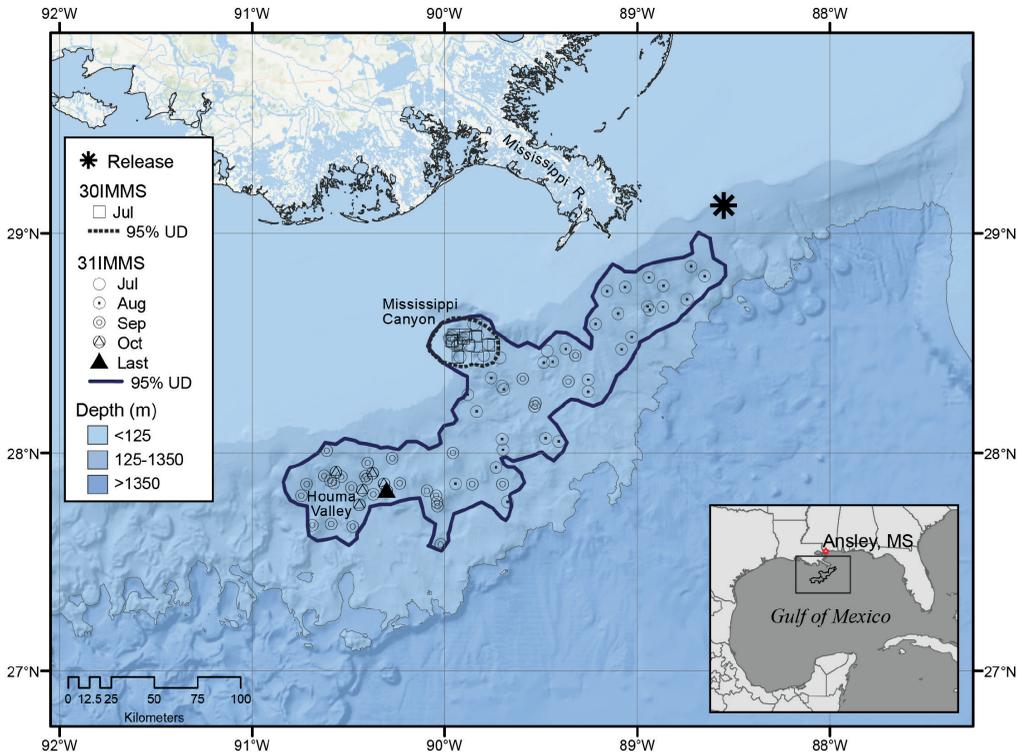
Both tags were programed for 400 transmissions per day. The duty cycle was set to acquire locations throughout the day while also optimizing communications with satellites based on predictions when satellites would pass over the GoM > 20° above

the horizon for more than 3 min. Data transmission intervals were set as UTC 2300 to 0059 h (local time is UTC-5 hours), 0200 to 0359 h, 1100 to 1259 h, 1500 to 1559 h, and 1900 to 2059 h. *Behavior message generation* was enabled. Dive data programming was set with the goal of obtaining at least 42 d of data, allowing for the assessment of release success as described by Wells et al. (2013a). Dives shorter than 30 s and less than 30 m in depth were ignored. Dive depth determining the start and end of a dive was 2 m to capture surfacing events where the tag may not fully clear the water. The selected dive histogram data sampling interval was 1 s, and 24 h of data were binned into each histogram reporting period. All other data transmit settings were disabled.

Tag transmissions were received and processed by Service Argos (CLS System, France), locations were estimated with the Kalman algorithm, and data were acquired monthly from CLS on CD-ROM. Implausible locations were excluded using the Douglas Argos Filter (Douglas et al., 2012), which judged movement rates, distances, turning angles, and location quality. Standard quality location classes (LCs 1, 2, or 3) were retained unconditionally.

Auxiliary locations (LCs 0, A, and 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  $< 5.6 \text{ m}\cdot\text{s}^{-1}$ , and the internal angles ( $\alpha$ , 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  $\beta = 25$ ). We derived a kernel utilization distribution (UD) for each animal on a 5-km resolution grid with the Dynamic Brownian Bridge movement model (Kranstauber et al., 2012) in the *R* statistical software (R Core Team, 2017) package ‘move,’ using the filtered Argos locations and estimated LC errors from Douglas et al. (2012). We then extracted the 95% UD contours for mapping. To examine habitat use, only locations from 31IMMS were used due to its longer tracking record and its persistent close proximity to 30IMMS.

Rates of travel (km/h) and distance from deployment were calculated along great circle paths that connected daily locations obtained during 1900 to 2059 h GMT (1400 to 1559 h local time). If more than one location was obtained during the daily 2-h period, the highest-quality Argos LC



**Figure 1.** Map showing locations of two pygmy killer whales (*Feresa attenuata*) that were tagged with satellite-linked tracking tags and released 11 July until 6 October 2016. Inset shows stranding location near Ansley, Mississippi, USA.

was used. In the case of a tie, the earlier location was used. The time period was chosen based on the observations of McSweeney et al. (2009) who observed that this species is generally engaged in low energy activities during the day. For distance from deployment when a location from a day was missing (30IMMS,  $n = 1$ ; 31IMMS,  $n = 4$ ), that point was skipped. For rates of travel when one or more days were missed, the distance between obtained locations was divided by the number of intervening decimal days to calculate the  $\text{km}\cdot\text{d}^{-1}$ .

Water depth at each location was obtained from NOAA (Amante & Eakins, 2009). Due to the close spatiotemporal proximity of the two animals, water depths were only presented for 31IMMS and were not reported before 31IMMS commenced meeting the minimum deep diving criteria exceeding 30 m and 30 s on 14 July 2016.

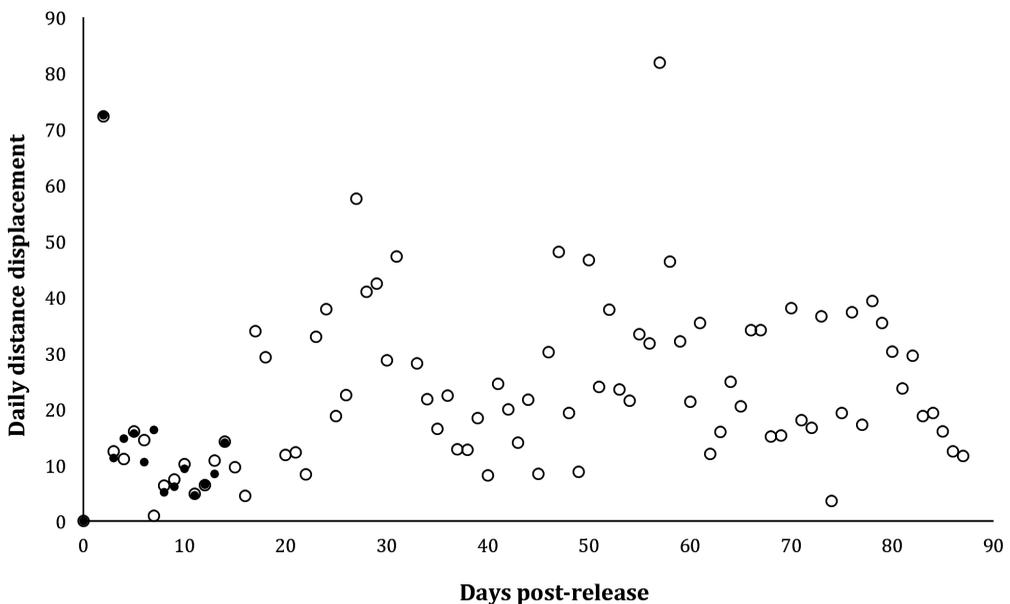
Behavior log records were assigned a sun altitude value using the *R* package 'oce' (Kelley & Richards, 2016). Nautical twilight, sunrise, and sunset times were obtained from the U.S. Naval Observatory (<http://aa.usno.navy.mil>). For comparison of dive times, dive depths, and subsequent surface duration, dives in the behavior data time series were used when they were accompanied by a subsequent "surface" period (above 30 m) that was not confounded by overlapping or missing data. The paired dive and surface durations were binned

into groups based on 10-m dive depth increments, and the median dive duration and surface duration across bins were analyzed with linear regression.

To estimate distance between the two animals, we followed the method of Wells et al. (2013b), with the exception that we retained points from the two animals that were obtained up to 15 min apart; if one animal's location was book-ended by the other animal's locations (within 15 min), then the early pair was retained. Only Argos standard LCs (1, 2, and 3) were used in this analysis. Calculated distances between the two animals of less than 1.5 km were considered indicative of close spatial affiliation given Argos location accuracy (Douglas et al., 2012). Dive depth and durations were considered synchronous when both animals started a dive within 1 min of each other.

## Results

Following release, location estimates from both animals were obtained within about 12 km of the release location on 11 and 12 July. About 27 h post-release, at the outset of nightfall, both animals commenced directed movement to the SSW (Figure 1), generally paralleling the shelf break (200 to 300 m) until reaching the Mississippi Canyon roughly 19 h later ( $\sim 6.8 \text{ km h}^{-1}$ ). 30IMMS remained in the Mississippi Canyon until 27 July



**Figure 2.** Daily travel  $\text{km}\cdot\text{d}^{-1}$  for two pygmy killer whales. Distance displacement from previous day's location. Only locations from the 1400 to 1559 h transmission window were used. Day 0 is the release day 11 July 2016. 30IMMS is represented by filled circles, and 31IMMS is represented by open circles.

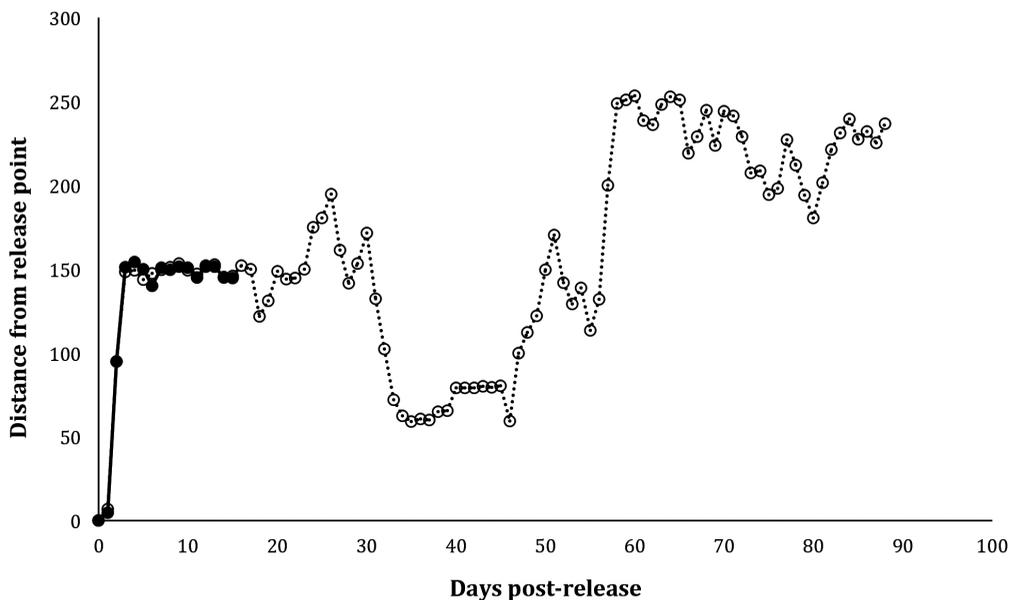
when its transmissions ceased. 31IMMS occupied the Mississippi Canyon area until 3 August after which it moved SSW for a week, and then moved NE and spent 13 to 28 August south of the Mississippi River Delta. From 29 August to 7 September, 31IMMS traveled SW to the Houma Valley, roughly 70 km SW of the Mississippi Canyon, and remained in that area until transmissions ceased 30 d later on 7 October. While transmitting, the mean daily movement for 30IMMS was 15.1 km 24 h<sup>-1</sup> and median of 10.5 km 24 h<sup>-1</sup> ( $n = 13$ ; range: 4.6 to 72.4; SD = 17.0). 31IMMS's mean daily movement was 23.7 km 24h<sup>-1</sup> and median of 20.2 km 24 h<sup>-1</sup> ( $n = 84$ ; range: 0.9 to 81.8; SD = 14.7) (Figure 2). The farthest distance from deployment was for 31IMMS during the second week of September when the animal was at the Houma Valley (Figures 1 & 3).

Fifteen pairs of locations were obtained where both animals had an LC of 1, 2, or 3 within a 15-min period. The last pair of near-simultaneous locations was on 25 July 2016. The farthest estimated distance between location pairs was 1.6 km, and 13 of the pairs were within 0.7 km or less, which is within the estimated error of the locations and, hence, consistent with the hypothesis that the two animals were traveling together.

The first dive to meet minimum requirements was not obtained until 13 July 2016 for

31IMMS, and not until 15 July 2016 for 30IMMS (Figure 3). Subsequently, 30IMMS spent 25.8% and 31IMMS 27.7% of the recorded time meeting the minimum requirements for the tag to recognize the event as a deep dive (i.e.,  $\geq 30$  s and  $\geq 30$  m). Behavioral data were transmitted over 9.70 d for 30IMMS and 82.02 d for 31IMMS; and during that time, 30IMMS successfully transmitted the behavior data for 3.85 cumulative days and 31IMMS for 46.59 d. The behavioral data log for each animal had 60.3 and 46.0% of time missing for 30IMMS and 31IMMS, respectively (Table 1).

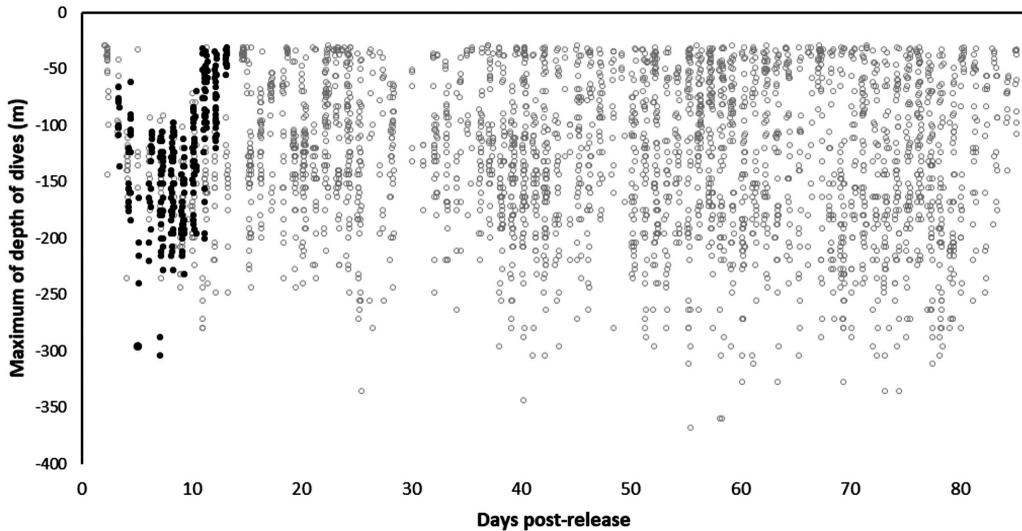
30IMMS had 11 d during which dives were recorded, with a maximum of 40 dives d<sup>-1</sup> and a mean and median of 24.5 (SD = 11.9) and 28.0, respectively. 31IMMS had 83 d where dives were recorded, with a maximum of 73 dives d<sup>-1</sup> and a mean and median of 34.2 (SD = 18.4) and 35.0, respectively (Figure 4). 30IMMS recorded 270 dives, with only nine (3.3%) occurring when the sun was above the horizon. Dives that commenced when the sun was above the horizon had a mean depth of 121 m (SD = 54 m) and median at 144 m. For the 261 night dives, the mean depth reached was 127 m (SD = 53 m) and median 124 m. The maximum depth reached for the day and the night was 196 and 304 m, respectively. 31IMMS recorded 2,880 dives, with 102 (3.5%) occurring during the day. Dive depth for daylight dives had a mean of



**Figure 3.** Distance displacement from the release location for two pygmy killer whales. Only locations from the 1400 to 1559 h transmission window were used. Day 0 is the release day 11 July 2016. 30IMMS is represented by filled circles and a solid line, and 31IMMS is represented by open circles and a dotted line.

**Table 1.** Summary information for the two male pygmy killer whales (*Feresa attenuata*) tagged and released on 11 July 2016

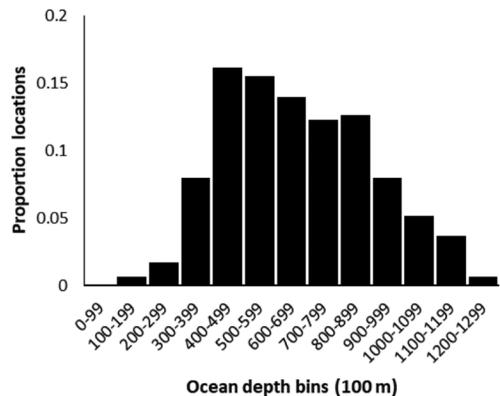
Animal ID	Body length (cm)	Weight (kg)	Days tracked	Last behavioral	Time of events recorded (h)	Missing time (h)	Percent not transmitted	Total locations	Number of filtered locations
30IMMS	218	153	15	24 July	92.40	145.42	61.57	136	129
31IMMS	223	133	88	4 October	1,118.04	930.26	45.42	990	947

**Figure 4.** Time series of maximum dive depths attained during individual dives by two male pygmy killer whales following post-rehabilitation release. Only dives deeper than 30 m for longer than 30 s were recorded. 30IMMS filled circles; 31IMMS open circles.

73 m (SD = 73 m) with a median of 38 m. For the 2,778 night dives, the average depth reached was 130 m (SD = 65 m) and median 128 m. The maximum depth reached for the day and the night was 280 and 364 m, respectively (Table 2). Of all the daytime deep dives, 28 occurred prior to 25 July 2016, and all but five exceeded 100 m. Of the 83 deep daytime dives recorded after 26 July 2016, only one exceeded 100 m.

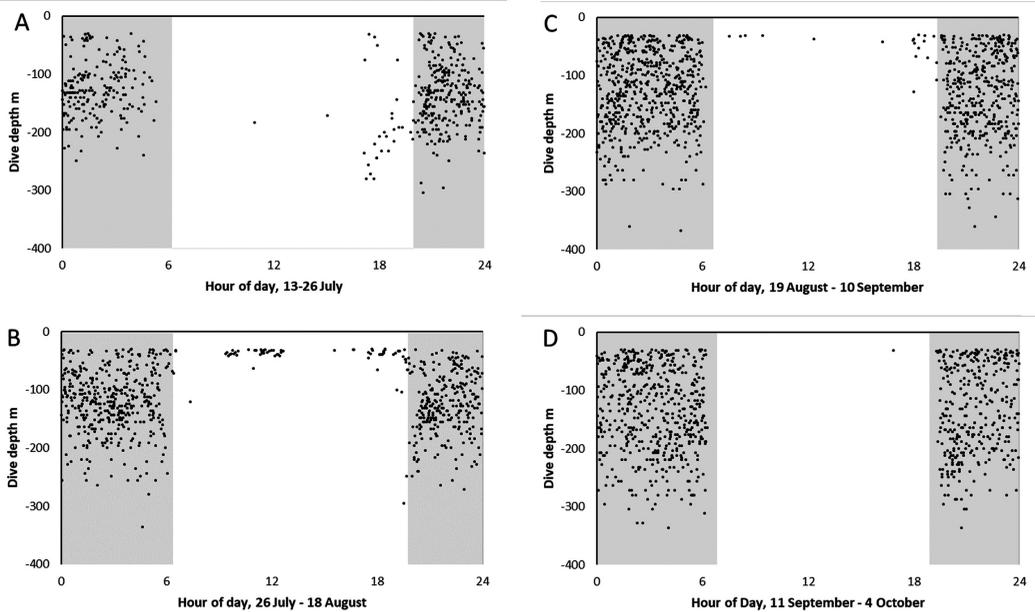
Location estimates received while 30IMMS was diving indicate that the mean water depth utilized was 402 m (SD = 112 m) with a range of 73 to 606 m; 95% of locations were between 86 to 560 m. Ocean depth for locations obtained while 31IMMS was diving averaged 671 m (SD = 233 m) with a range of 73 to 1,274 m; 95% of locations were between 297 to 1,134 m (Figure 5).

There were 43 periods without diving to at least 30 m that exceeded 10 h: three (0.31/d) for 30IMMS and 40 (0.49/d) for 31IMMS (excluding

**Figure 5.** Proportion of locations over 100-m ocean depth (bathymetry) bins for 31IMMS. Only those locations after 31IMMS began transmitting dive data are included.

**Table 2.** Summary of deep dives and time spent above 30 m for two satellite-tagged pygmy killer whales

Animal ID	Event	<i>n</i>	Depth			Duration			Max. (min)	Day ( <i>n</i> )	Depth average (m)	Duration average (min)	Night ( <i>n</i> )	Depth average (m)	Duration average (min)
			average (m)	Median (m)	SD (m)	average (min)	SD (min)								
30IMMS	Dive	270	127	124	54	4.2	0.8	5.8	9	121	4.0	261	127	4.2	
	Surface	271				16.3	102.3	1,181.0	9		21.6	262		16.1	
31IMMS	Dive	2,880	128	124	66	4.7	1.3	9.0	102	73	4.2	2,778	130	4.7	
	Surface	2,879				18.5	113.7	3,285.0	99		47.2	2,780		16.3	

**Figure 6.** Diel dive patterns for pygmy killer whales tagged in this study. Time presented as hour of the day, local time (central daylight time). Shaded areas denote the sunrise and sunset time for Grand Isle, Louisiana, USA (obtained from <http://aa.usno.navy.mil>): (A) time and depth of dives for 30IMMS and 31IMMS, and sun data for 19 July 2016; (B) 31IMMS, sun data for 7 August 2016; (C) 31IMMS, sun data for 30 August 2016; and (D) 31IMMS, sun data for 23 September 2016.

the 2 d preceding the first dive). Long, near surface bouts for 30IMMS were 12.5, 15.8, and 19.5 h, commencing between 0036 and 0444 h local time on 22, 23, and 24 July, with diving resuming between 1712 and 2030 h. Surface bouts exceeding 10 h for 31IMMS occurred from 20 July to 2 October 2016 and averaged 13.5 h (range: 10.1 to 19.6 h). On average, the extended surface periods by 31IMMS began at 0546 h local time (range: 0036 to 0726 h). Diving resumed during the evening at an average of 1936 h local time (range: 1615 to 0123 h) (Figure 6).

Over the range of dives collected for the two animals, dive duration and subsequent surface duration were linearly related to dive depth. For

pairs of dives and subsequent surface periods, binned by 10-m dive depth intervals, median dive duration =  $0.0098 * \text{midpoint of depth bin} + 3.4884$  ( $r^2 = 0.9465$ ). In contrast, median duration of the surface period immediately following a dive was not related to dive depth: surface duration =  $0.0006 * \text{midpoint of depth bin} + 2.6249$  ( $r^2 = 0.0258$ ) (Figure 7).

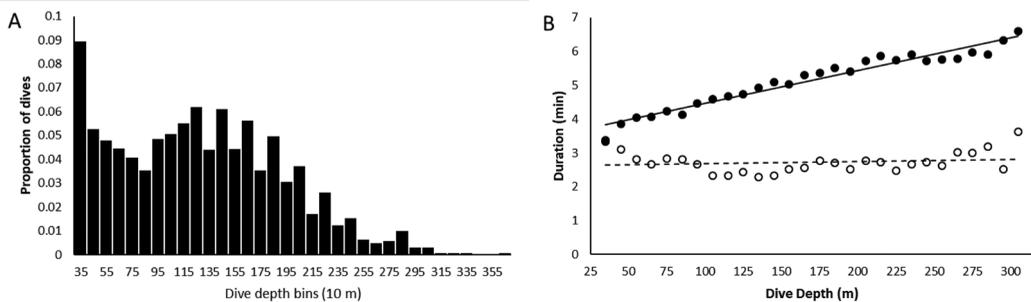
The average dive depths for 31IMMS during the periods spent near the Mississippi Canyon, Mississippi River Mouth, and Houma Valley were 123 m ( $n = 567$ ;  $SD = 54$  m), 128 m ( $n = 600$ ;  $SD = 61$  m), and 134 m ( $n = 1,022$ ;  $SD = 74$  m), respectively, compared to 122 m ( $n = 223$ ;  $SD = 61$  m) and 123 m ( $n = 469$ ;  $SD = 68$  m) for the periods

when the animal was moving between these locations. Sixty-four pairs of dives were commenced by the two animals within 1 min of each other. For these paired dives, there was no correlation between the depths each animal reached ( $r^2 = 0.00$ ) and a weak correlation between the duration of the dives ( $r^2 = 0.44$ ) (Figure 8).

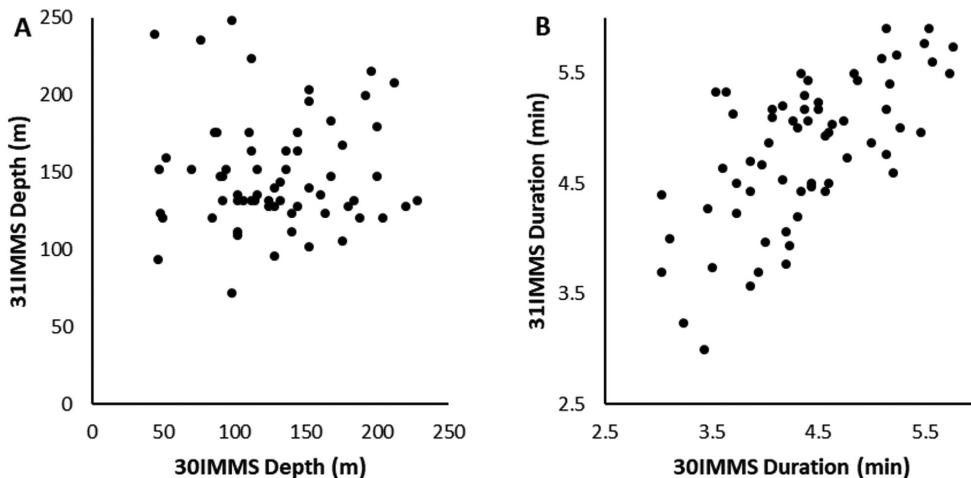
The 95% UD for 31IMMS spanned a length of about 250 km along the continental shelf break in the northern GoM south of the Mississippi River Delta (Figure 1) and was largely confined to an area between the 200 and 1,000 m isobaths. The area occupied by 30IMMS overlapped in the Mississippi Canyon (Figure 1).

The last behavioral log event received from 30IMMS was a 3 min, 10 s long surface bout that ended at 2247 h local time 24 July 2016, and the

final location transmission was almost 24 h later at 2228 h on 25 July 2016. The evening of 24 July 2016, 30IMMS ended an almost 20 h surface bout at 2017 h local time with a 3 min, 54 s dive to 41 m. In the last 2 h that behavioral data were obtained, 30IMMS made 12 dives, with the deepest and longest to 55 m and 4 min, 10 s in duration. On the evening of 24 July 2016, 31IMMS ended a 23 h, 47 min period of missing data at 2154 h local time and made five dives from 94 to 144 m, lasting up to 4 min, 26 s. Following the end of 30IMMS's dive record, 31IMMS made 10 more dives that evening from 136 to 249 m. On 25 July, nine pairs of locations between the two animals were obtained within 3 min, 15 s of each other, with distances between them of 0.6 to 3.0 km (average 1.4 km). However, some of



**Figure 7.** (A) Proportion of deep dives to depth across 10 m depth bins, with midpoint of bin labeled on x-axis; and (B) median duration of dives (filled circles) and surface duration following a dive to depth [open circles] as a function of dive depth in 10 m intervals (Dive duration =  $0.0098 * \text{Dive Depth} + 3.4884$  [solid line];  $r^2 = 0.9465$ ) (Surface duration =  $0.0006 * \text{Dive Depth} + 2.6249$  [dashed line];  $r^2 = 0.0258$ ); A and B include data from both 30IMMS and 31IMMS.



**Figure 8.** Dive depth (A) and duration (B) for 64 dives by 30IMMS and 31IMMS that commenced within 1 min of each other

these location pairs included lower LC qualities (A and B) for which errors are likely to be greater, so inferring spatial coincidence of the two animals has greater uncertainty. Following the last location from 30IMMS, 31IMMS spent about 8 d more in the Mississippi Canyon area.

During the 48 h prior to the final behavioral data from 30IMMS, the only missing behavior data time was a 1 h, 12 min period. 31IMMS's last behavioral data transmission was a 2 min, 4 s surface bout at 0251 h on 5 October 2016 and the last location was at 1923 h on 6 October 2016. The night of 4 October, 31IMMS made 20 dives, from 33 to 140 m, before behavioral transmissions ceased. During the 48 h prior to the final behavioral data from 31IMMS, there were 42 h, 5 min of missing data.

### Discussion

In the GoM, pygmy killer whales are seldom observed nor often definitively identified (Mullin et al., 1994, 2004; Maze-Foley & Mullin, 2006; Roberts et al., 2016). Therefore, general behavior and habitat use for this species are lacking in the GoM. Following the rehabilitation of these two animals, as recommended, the animals were monitored remotely to assess the success of the release (Whaley & Borkowski, 2009). Using satellite-linked tags that provided both locations and dive data, we obtained data for a combined total of 103 d from a little known species.

During the time the tags on the two animals were recording and transmitting data, they stayed in close proximity to each other, although, for near synchronous dives, the lack of correlation in depth between the two animals suggested they foraged individually. Because the two animals were consistently in close proximity, we considered them to be a single unit for location while both tags were transmitting. Once 31IMMS began diving, about 70% of the locations obtained were in waters of 400 to 900 m depth. By comparison, records from the OBIS Seamap (<http://seamap.env.duke.edu>) show 11 observations of pygmy killer whales in the GoM, and only one was located in waters less than 1,000 m deep. The methods used by Roberts et al. (2016) to estimate density incorporated both aerial and ship-based transect data and attempted to reconcile ambiguous sightings that were not definitively classified to species in the *Peponocephala/Feresa* category. Their results indicated that the sightings of smaller groups were more likely to be *F. attenuata* than *P. electra* and that ambiguous sightings in the GoM south of Louisiana and Mississippi (where the two animals tracked here remained) were more likely to be *P. electra* rather than *F. attenuata*.

The pygmy killer whales tracked in this study were generally found in shallower waters than had been reported for other surveys and observations, but this study tracked animals in late summer whereas most of the surveys and observations were in April and May (<http://seamap.env.duke.edu>). Generally, the northern GoM is cooler and windier in spring (Müller-Karger et al., 2015), whereas sea surface temperatures peak and the mixed layer depth is at its minimum in August (Müller-Karger et al., 1991), and this variation may influence seasonal habitat selection patterns by pygmy killer whales and their prey species. Nevertheless, the bathymetric relief of the shelf break where the two pygmy killer whales were tracked when combined with nutrients from the Mississippi River, eddies, and upwellings, likely provides a productive environment for delphinid prey species regardless of season (Vukovich & Maul, 1985; Zavala-Hidalgo et al., 2006; D'Sa, 2014). In the GoM, offshore large delphinids have the highest predicted abundance on or near the shelf break (Roberts et al., 2016), much like the pygmy killer whales observed here, which suggests the area is sufficiently productive to support those populations.

31IMMS used a 250-km-long span of the northern GoM shelf break for 88 d after release. The distances from the release (or tagging) location and travel rates may not be particularly useful for judging the condition of an individual of this species. Our results here agree with those of McSweeney et al. (2009) and Baird et al. (2011) that pygmy killer whales appear not to be as prone to long distance movements as species such as Risso's dolphin (*Grampus griseus*; Wells et al., 2009) or short-finned pilot whales (*Globicephala macrorhynchus*; Wells et al., 2013b). The two pygmy killer whales tracked exhibited similarities in habitat use to Baird et al.'s (2011) Hawaiian animals, suggesting that pygmy killer whales use specific relief features of their habitat and remain faithful to those areas, at least seasonally.

The diving ability of marine mammals is limited by their oxygen stores (e.g., body size, blood volume, and muscle myoglobin content) and metabolic rate, with some species extending their submerged time by using anaerobic respiration to increase the duration and frequency of dives (Kooyman et al., 1980; Noren & Williams, 2000; Costa et al., 2001). The pygmy killer whales did not show an increase in the median recovery time following a dive until dives were nearly 6 min in duration. The depth of dives reached and the duration of the dives were shallower and shorter than *P. electra* tagged off the Bahamas, with similar dive-to-recovery ratios. The Bahamian *P. electra* made over 50% of their dives to 300 m or deeper, whereas the

pygmy killer whales made less than 1% of dives to 300 m or beyond (Joyce et al., 2017). Of the subfamily Globicephalinae, pygmy killer whales are the smallest species, and the dive data collected herein support the expectation that they have less diving capability to very deep depths relative to other subfamily members. The ability of the larger globicephalin species to exploit deeper depths than pygmy killer whales may explain their more regular documented use of the open ocean away from the shelf (Baird et al., 2010, 2013; Woodworth et al., 2012; Wells et al., 2013b). Data for the two pygmy killer whales reported herein were collected only during late summer and, therefore, may not be comparable to other seasons or areas of the GoM.

Dive data obtained from the tagged pygmy killer whales were consistent with nocturnal feeding patterns. In necropsied individuals that had stranded on the British Virgin Islands and Puerto Rico, stomach contents included unidentified squid beaks and fish otoliths (Mignucci-Giannoni et al., 1999; Rodriguez-Lopez & Mignucci-Giannoni, 1999). Zerbini & Santos (1997) were able to identify some squid beaks obtained from a female pygmy killer whale stranded off Brazil as *Illex argentinus*, *Loligo plei*, *Ornithoteuthis volatilis*, and one unidentified Ommastrephidae. The fishes eaten by pygmy killer whales have not been identified to species level; however, their diving profiles suggest that their diet is largely composed of species that spend the daylight hours deeper than 350 m and move up in the water column at night (D'Elia et al., 2016), suggesting the two pygmy killer whales tagged in this study may not have had the ability to reach their prey until the prey ascended during low light periods. The diving profiles obtained here do not entirely rule out daytime foraging, but the ratio of recorded day to night deep dives (1:27) indicates that if they are occurring, daytime feeding dives exceeding 30 m for > 30 s are uncommon.

Feeding patterns of pygmy killer whales in the GoM may be similar to those of other odontocetes based on habitat use and parasite occurrence. The habitat used by the tagged pygmy killer whales is very similar to that of the squid specialist *G. griseus*, with the majority of sightings on the upper continental slope (~200 to 1,000 m). This slope habitat accounts for only 12% of the GoM, and the slopes are steeper than average for the GoM in the area used by the two tagged pygmy killer whales (Baumgartner, 1997). The deepest dives recorded for these animals did not exceed 370 m, while water depths were less than 400 m for only ~11% of their locations. We, therefore, conclude that they conducted the majority of their foraging within the water column rather than on the sea floor.

Although we suspect that the animals were foraging on these deep water dives, this cannot be confirmed directly. Thus, we are left to examine clues from discovered carcasses and likely prey species. Specifically, we expect that pygmy killer whales prey on fishes and squids in common with other sympatric pelagic dolphins such as *G. griseus*, pantropical spotted dolphin (*Stenella attenuata*), and rough-toothed dolphin (*Steno bredanensis*), which share some of the same trophically transmitted cestodes and trematodes in the GoM (reviewed by Jensen, 2009; Overstreet et al., 2009). Although the hosts for the infective intermediate stages are unknown for these parasites (Hoberg, 1994; Gibson, 2005; Fraija-Fernández et al., 2016), trophically transmitted parasites' life cycles and host diversity are needed to better understand trophic interactions among pelagic cetaceans, their prey species, and parasites (Thompson et al., 2005; Blasco-Costa & Poulin, 2017). For example, Andres et al. (2016) found a larval specimen of *Bolbosoma* sp. (Acanthocephala: Polymorphidae) from a *Mauroliticus weitzmani* (Sternoptychidae, hatchetfish), trawled from northern GoM, which is known from Blainville's beaked whale (*Mesoplodon densirostris*) in the GoM (Salgado-Maldonado & Amin, 2009) and from several species of odontocetes, including pygmy killer whales, in the adjacent Caribbean (Mignucci-Giannoni et al., 1999). This additional information confirms that pygmy killer whales do forage at these depths.

Collective success of the rehabilitation/release of the two pygmy killer whales is difficult to assess and, at minimum, mixed. 31IMMS was tracked for more than double the length of time suggested by Wells et al. (2013a) as a threshold for defining success. Given that 31IMMS survived for at least 88 d, it seems reasonable to conclude that for most of the tracking period, the animal was engaged in normal behaviors used by members of the species for day-to-day survival. However, whether the animal succumbed at the end of the 88 d tracking period is not clearly dismissible. Beginning on about 1 October, 31IMMS's deep dive pattern declined steadily through the final transmission on 7 October. Dives decreased in maximum depth each night, and the number of dives each day also declined. There were no deep dives on 6 or 7 October, although location data were received in the Houma Valley. Battery strength was still at a good level in the final status report obtained from 31IMMS's tag. Alternatively, there were other periods when 31IMMS had shown a similar decrease in diving activity (nights of 26 July, 10-11 August, and 29 August). Had cessation of transmissions followed those periods, we may have been tempted to incorrectly presume the animal had died. It is also possible that signal cessation resulted

from the tag being shed; however, the single pin attachment method has been shown to be preferable to other attachment methods, and tag loss should not have been an issue for the less than 90 d observed here (Balmer et al., 2010, 2011, 2014).

After 15 d of tracking in July, there was an abrupt decline in maximum dive depths and durations immediately prior to cessation of transmissions for 30IMMS, with no indications of tag failure in the diagnostics transmitted from the tag. Changes in the behavior of 31IMMS coinciding with the changes for 30IMMS, including a lack of deep dives during the final day of dive data from 30IMMS, followed by a return the next night to “normal” diving patterns by 31IMMS and possible movement out of the region where they had remained together for many days, might suggest the death of 30IMMS. The pair of animals’ data are very similar to those from two *G. macrorhynchus* released from a mass stranding in the Florida Keys, as reported by Wells et al. (2013a), where one of the animals showed a perceived decline in condition and cessation of transmission about 2 wks post-release, and it was concluded that the outcome was potentially negative. While the fate of an animal can only be definitively assessed when the animal is observed alive or dead, we consider that the rehabilitation and release of 31IMMS was a success, and the results for 30IMMS are inconclusive, possibly negative.

Post-release monitoring through satellite-linked telemetry provided the means to assess the response of stranded pygmy killer whales to rehabilitation and release, and to learn about the behavior of a small pelagic cetacean species that has been little-studied in the wild. Tracking data indicated an apparent acclimation period of several days before the pygmy killer whales began to engage in presumed normal diving behavior after release. Following the acclimation period, similarities in diving and ranging patterns between the two released individuals, and with those studied elsewhere, suggested that they engaged in behaviors typical of the species for much of each individual’s tracking period.

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