Diel vertical movements of short-finned pilot whales in the Gulf of Mexico from time-at-temperature data

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ABSTRACT

We analysed 180 time-at-temperature (TAT) histograms from satellite-linked LIMPET-SPOT5 tags deployed in April 2018 on seven short-finned pilot whales (*Globicephala macrorhynchus*) in the southwestern Gulf of Mexico to investigate diel patterns in vertical movements as a proxy of their diving behaviour. TAT data were transformed into time-at-depth (TAD) data using satellite-Gravest Empirical Mode (satGEM) projections. TAD data were classified into four behavioural states: State 1 (surface movements < 20 m), State 2 (non-foraging dives 20–45 m), State 3 (shallow foraging dives > 45–300 m), and State 4 (deep foraging dives > 300 m). A Bayesian ANOVA test was used to analyse the time budget between early morning, daytime and nighttime. Overall, pilot whales spent ~50% of their time in the surface strata (< 45 m) engaged in activities other than foraging, 38.3% performing shallow-foraging dives, and only 11.2% in deep dives. The Bayesian ANOVA was inconclusive for States 1–2 but showed differences for shallow and deep foraging dives (States 3–4) across time periods. *Post hoc* comparisons showed that pilot whales spent less time in shallow-foraging dives (State 3) during daylight hours compared to both early morning and night. Still, they spent more time in deep-foraging dives (State 4) during the daytime and early morning than at night, a pattern consistent with the diel vertical migration of their main prey (squid). Despite the small number of tagged animals, our results are the first description of the vertical habitat use of deep-diving cetaceans in the Gulf of Mexico, an essential component for understanding the ecological role of these large predators.

KEYWORDS: BEHAVIOUR; DIVING; MOVEMENTS; SATELLITE TAGGING

INTRODUCTION

Ecological studies of free-ranging marine vertebrates have always been challenging due to their high movement capacity. However, in recent decades, the use of satellite telemetry, complemented by environmental and physiological data, has made it possible to characterise foraging strategies, migratory patterns, habitat use and diving behaviour for a wide variety of fish, birds, reptiles and marine mammals (Crossin *et al*., 2014). Smart Position Only Tags (SPOT; Wildlife Computers Inc., WA) are small tags that, in addition to providing the location of the animals (latitude, longitude), can also transmit periodic records of the amount of time (in percentage) that an animal spends within user-defined temperature bins. These records are summarised in the form of

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time-at-temperature (TAT) histograms. This type of data has been widely used to analyse the distribution of various species of marine vertebrates, such as sharks (e.g., Tyminski *et al*., 2015; Skomal *et al*., 2017) and turtles (e.g., Dodge *et al*., 2014; Wildermann *et al*., 2019) in the thermal strata of the water column. In contrast, TAT histograms have been limited in cetacean studies, although they can be used as a proxy for diving behavior (Joyce *et al*., 2016).

Short-finned pilot whales (*Globicephala macrorhynchus*) are deep-diving odontocetes (i.e., toothed cetaceans) that are distributed in tropical and warm waters worldwide, including semi-enclosed seas (Olson, 2007). Although oxygen minimum zones (OMZs) could influence predator-prey interactions because they can act as vertical barriers, short-finned pilot whales are not limited by the OMZ because they do not depend on dissolved oxygen in the water but rather on their physiological adaptations for deep diving (Aoki *et al*., 2017; Goldbogen *et al*., 2019), which allows them to exploit prey that reside in or move through these low-oxygen layers. They feed mainly on squids, as well as on mesopelagic fish (Mintzer *et al.*, 2008; Luna *et al*., 2024), but their foraging strategies differ between localities, likely reflecting not only the spatial and temporal distribution of prey under different environmental conditions, but also physiological constraints and socially mediated diving behaviors (Blawas *et al*., 2024).

In some areas, short-finned pilot whales exhibit diel patterns in their diving behaviour, with differences in both the frequency and depth of the dives between day and night, depending on the activity patterns of their prey (Aguilar Soto *et al*., 2008; Wells *et al*., 2013; Hill *et al*., 2019). In the Hawaiian Islands (Baird *et al*., 2003), the Canary Islands (Aguilar Soto *et al*., 2008), and the Bahamas (Joyce *et al*., 2017), short-finned pilot whales make few but deep dives during the day, while during the night, the dives are more frequent but shallow. In contrast, in the northwestern Atlantic Ocean, diel patterns in diving behaviour are inconsistent. Bowers (2015) found no differences in dive frequency or depth between day and night, while Shearer *et al*. (2022) reported diel variation in pelagic dives but not in benthic dives.

Short-finned pilot whales inhabit the Gulf of Mexico year-round (Würsig, 2017), where, recently, a satellite telemetry study using SPOT tags was conducted to analyse their horizontal movements (García-Aguilar *et al*., 2021). The data suggest that short-finned pilot whales in this semi-enclosed sea do not perform long-distance movements and use the southwestern continental shelf-break extensively, mainly between the 500 and 800 m isobaths. This restricted-movement pattern is suggestive of a degree of residency to the southwestern Gulf of Mexico, although year-round site fidelity has not yet been confirmed with longer-term tracking. However, until now, there was no information on their diving behaviour and/or foraging strategy in this area. Therefore, our objective was to identify diel activity patterns in vertical movements as a proxy for their foraging strategy. To do that, we first transformed the TAT histograms recorded by the SPOT tags into time-at-depth (TAD) histograms using the Gravest Empirical Mode (GEM) technique, and then we analysed their time budget.

MATERIALS & METHODS

Tagging and study area

On 24 April 2018, seven short-finned pilot whale adults were tagged in the southwestern Gulf of Mexico (18°59'N and 95°19'W; Fig. 1) with LIMPET-SPOT5 satellite transmitters (Wildlife Computers, WA). Tagging was carried out under an official permit issued by the Secretaría de Medio Ambiente y Recursos Naturales, Government of Mexico (SGPA/DGVS/08053/17).

Tags were programed to operate with a continuous transmission rate during the first day (transmitting every time the animal surfaced and a satellite was available, with no daily limit), followed by a fixed quota of 250 transmissions per day from day 2 to 99, and 100 transmissions per day for the tag's remaining life, in 8 h cycles per day. Satellite-linked locations were received by the Argos Data Collection and Location System[4] and were processed with the Douglas Argos-Filter (Douglas *et al*., 2012). For more details on both tags' deployment, programing, and data processing, see García-Aguilar *et al*. (2021). The transmission period spanned from late April to mid-July 2018 (Table 1; ranging from 14 to 87 days of transmission per individual), and after filtering, all

[4] *http://www.argos-system.org*

Table 1
Tracking effort and number of time-temperature (TAT) histograms recorded from the seven adult short-finned pilot whales tagged in the southwestern Gulf of Mexico on 24 April 2018.

Tag ID	Sex	Last transmission day	Transmission period (d)	TAT histograms
171903	Unknown	12/05/2018	19	24
171909	Male	12/05/2018	19	21
171910	Male	07/05/2018	14	25
171914	Unknown	20/06/2018	58	38
171915	Unknown	19/07/2018	87	28
171919	Unknown	31/05/2018	29[a]	3
171920	Unknown	11/06/2018	49	41

[a]No data from May 7 to 14 2018.

locations were southward of 24°N and westward of 93°W. Hence, the study area was delimited on the southwestern Gulf of Mexico (Fig. 1).

Tags were also programed with 11 temperature bins to calculate TATs: < 4°C, 4–7°C, 7–10°C, 10–13°C, 13–16°C, 16–19°C, 19–22°C, 22–25°C, 25–28°C, 28–30°C and 30–33°C, based on the average vertical structure of temperature in the western Gulf of Mexico (e.g., Portela *et al*., 2018). By default, records begin after midnight UTC and over a 24 h cycle. An 8 h summary period was selected to generate three TAT histograms per day: (1) from 00:00 to 07:59h UTC; (2) from 08:00 to 15:59h UTC; and (3) from 16:00 to 23:59h UTC. Considering the local time zone (Central Standard Time, CST), and the time of sunrise and sunset in the study area during the transmission period, these summary periods were classified as early morning (from 02:00 to 09:59h CST), daytime (from 10:00 to 17:59h CST), and nighttime (18:00 to 01:59h CST).

Transformation from time-at-temperature data to time-at-depth data

The satellite-Gravest Empirical Mode technique (satGEM: Swart *et al*., 2010; Meijers *et al*., 2011; Meunier *et al*., 2022) was used to transform the temperature bins into depth strata. Since observations of the temperature structure within the ocean are scarce, the satGEM allows for the combination of sparse hydrographic profiles available in a given region with the sea surface height obtained from satellite altimetry data, which provide data frequently and with large spatial coverage. The principle is that most of the variability in the thermohaline field in a stratified sea is due to the passage of mesoscale structures such as cold (cyclonic) and warm (anticyclonic) eddies. Thus, the presence of cyclonic eddies decreases the depth of the isotherms (and decreases the sea surface height), while anticyclonic eddies increase isotherm depth resulting in high sea surface height (e.g., Meijers *et al*., 2011; Meunier *et al*., 2022). Projecting the hydrographic profiles into geostrophic stream-function space (in this case sea surface height) removes most of the variability in the isotherm depths, since the projection preserves the frontal attributes of these baroclinic structures (e.g., Sun & Watts, 2001). The satGEM technique has shown good results in reproducing the thermal structure of the anticyclonic Loop Current Eddies in the Gulf of Mexico (Meunier *et al*., 2022).

We used 36 temperature and pressure profiles from three Argo free-drifting profiling floats (4902350, 4902915 and 4902916), which are part of the Global Ocean Observing System (GOOS) and were in the study area during the tags' transmission period (Fig. 1). These data are freely accessible by ARGO International Project[5] via Mercator Coriolis Mission Group (GMMC).[6] The floats were released during the Deep-Water Dispersion Experiment cruises DWDE-2 and DWDE-3 (Meunier *et al*., 2021), carried out onboard the oceanographic vessel *R/V Pelican* from the Louisiana Universities Marine Consortium (USA), as part of the Woods Hole Oceanographic Institution Argo programme.[7]

The sea surface height data were obtained from the gridded AVISO Absolute Dynamic Topography product (10-day composites objectively mapped on a 0.25° daily regular grid)[8] The sea surface height associated with

[5] *http://www.argo.net*
[6] *https://www.mercator-ocean.fr*
[7] *https://www2.whoi.edu/site/argo/*
[8] *https://www.aviso.altimetry.fr* (last accessed in June 2020)

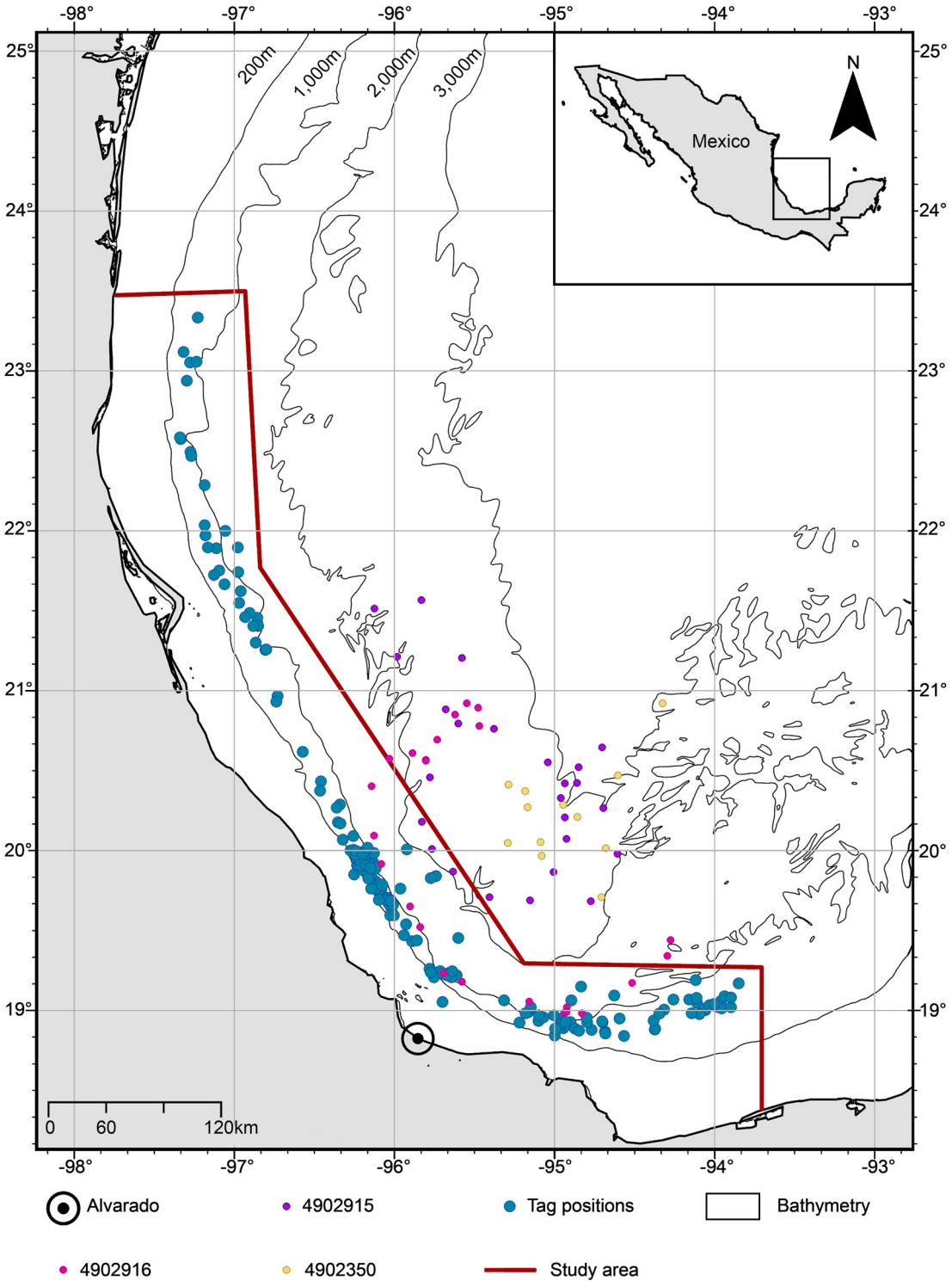

Figure 1. Study area in the southwestern Gulf of Mexico (outlined in red), delineated using the filtered locations of seven short-finned pilot whales (blue dots) tagged on 24 April 2018. Buoys used for GEM analysis are shown (purple, pink, and yellow dots). The town of Alvarado is marked as a coastal reference point near the tagging location, to orient the reader; it has no analytical role in the study.

each hydrographic profile was obtained by linearly interpolating the AVISO field to the position and time at which the profile was taken.

The satGEM temperature fields were constructed by fitting cubic splines to the temperature as a function of sea level (ψ) for each depth (z) recorded by the Argo hydrographic profiles, using all available data regardless of the date and position where they were recorded ($T_{GEM}(\psi,z)$; Figs. 2a, b). The root mean squared error of the

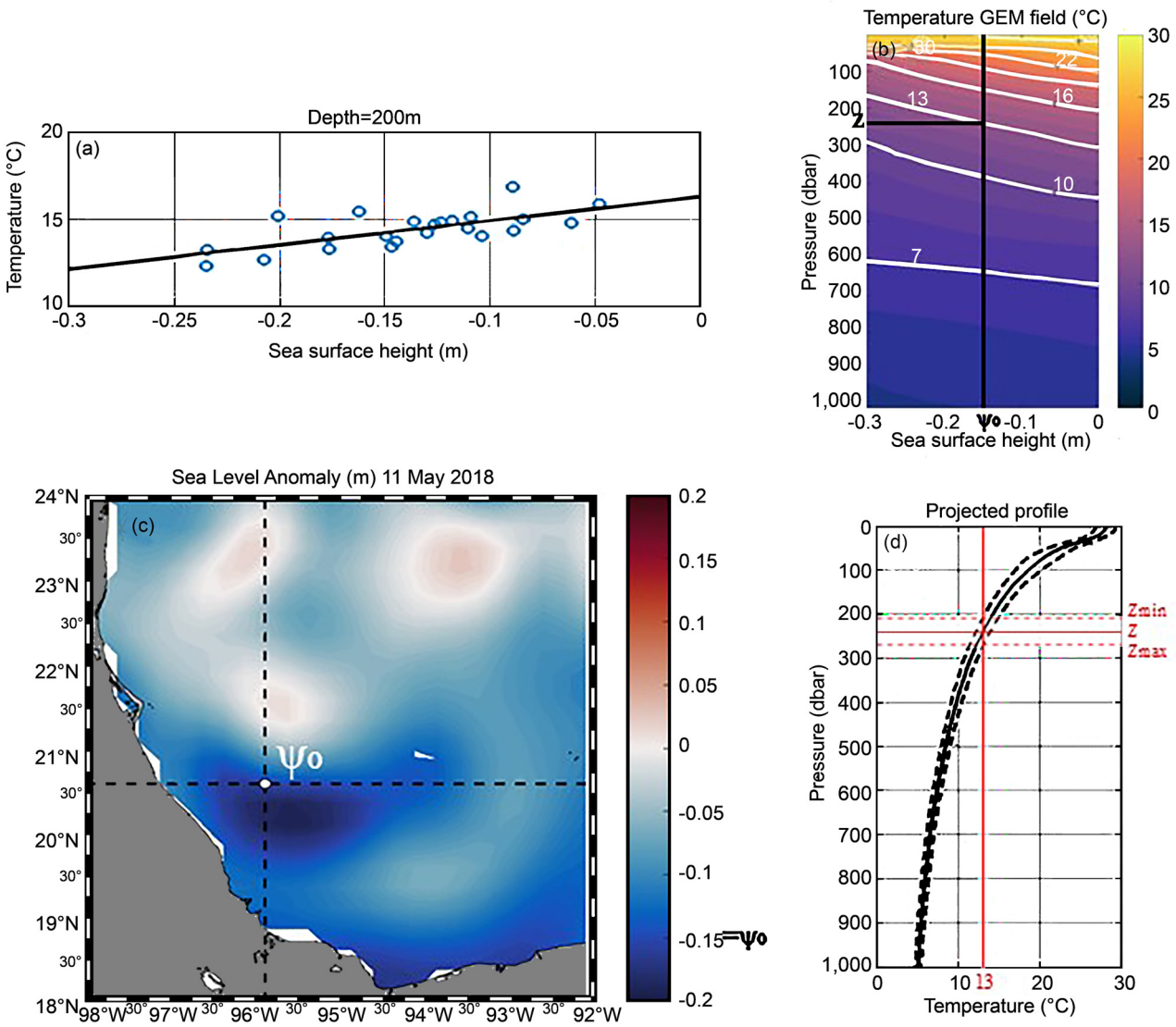

Figure 2. satGEM methodology to estimating isotherm depth corresponding to a pilot whale dive. (a) Temperature (°C) at 200 m depth as a function of sea surface height (SSH). Circles represent Argo float measurements; each paired with the SSH at the float's location and time. The black line shows the cubic spline fit. (b) The TGEM(ψ,z) field constructed from cubic spline fits at all depths. White contours indicate isotherms used to define histogram bin limits. The black vertical line marks the temperature profile associated with the sea surface height ψ_o, corresponding to the location and time indicated by the white circle in panel (c). The black horizontal line denotes the depth Z of 13°C isotherm. (c) SSH field for a selected date. The white circle marks the location and time for one pilot whale's dive, defining the corresponding ψ_o. (d) Projected temperature profile for the example dive (black line), with associated uncertainty bounds (black dashed lines). The vertical red line intersects the 13°C isotherm at depth Z, with the red dashed lines indicating the estimated depth uncertainty interval [Zmin Zmax].

satGEM (ΔT (z)), which is obtained from the difference in the projected temperature profile and the one observed, is associated with small-scale processes not captured by the satGEM projection, as can be seen in Figure 2a. The procedure by which the satGEM field is used to transform the time-at-temperature data into time-at-depth data for each TAT histogram was performed with MATLAB (The MathWorks, Inc., 2019, version 9.6) and follows these steps:

The sea surface height (ψ_o) associated to the TAT histogram was obtained by interpolating the gridded altimetry field to the position (latitude, longitude) and date associated to corresponding pilot whale's dive (Fig. 2b).

The satGEM is then used as a 'look-up table,' finding the temperature profile (and its error) associated to that sea surface height value ($T_{GEM}(\psi_o,z) \pm \Delta T(z)$; Figs. 2c and d).

This profile was then used to obtain the depth (Z) for each of the isotherms delimiting the bins of the histogram, resulting in an interval of depths associated to each isotherm ([Zmin, Z, Zmax]; Fig. 2d).

Time budget

The time-at-depth data obtained using the satGEM technique were grouped into four behavioral states, based on both previous descriptions of short-finned pilot whale diving behavior (e.g., Aguilar Soto *et al*., 2008; Quick *et al*., 2017; Joyce *et al*., 2017) and the characteristics of our dataset. State 1 represents surface movements (< 20 m depth; Aguilar Soto *et al*., 2008). State 2 includes dives between 20 and 45 m, typically associated with non-foraging activities (Quick *et al*., 2017). Dives deeper than 45 m were considered foraging dives and were further classified into two categories. State 3 includes shallow foraging dives (> 45–300 m) and state 4 deep foraging dives (> 300 m). The cutoff between shallow and deep foraging dives was determined based on the patterns observed in the data (see below).

We used Bayesian one-way ANOVA tests with fixed effects to compare the proportion of time pilot whales spent in each behavioural state across different schedules (i.e., early morning, daytime and nighttime). These tests were computed based on Kery (2010). In all tests, the data were assumed to be independent and drawn from normal distributions. The posterior distributions of the means for early morning, daytime and nighttime (m_1, m_2 and m_3 respectively) and the residual standard deviation (σ_{res}), as well as the posterior distribution of the difference between effects, $\Delta = (m_2 - m_1) - (m_3 - m_1)$, were estimated using Monte Carlo Markov Chains simulation implemented in the R2WinBUGS package (version 2.1; Sturtz *et al*., 2005) in R (version 3.6; R Core Team, 2019). In all models, we used non-informative priors, and 250,000 iterations were run in three independent chains, with a 10% warm-up phase, and retaining the tenth value. The performance of the MCMC simulation was evaluated using the statistic (Gelman & Rubin, 1992) and the effective sample size (neff; Gelman *et al*., 2013).

The HDI+ROPE decision rule (Kruschke, 2015; Kruschke & Liddell 2018) was used to determine whether the null value was among the most credible values of the parameter Δ, and was computed using the BayesPostEst package (Scogin *et al*., 2019) in R. Briefly, the null value of Δ is credible (i.e., $\mu 1$, $\mu 2$ and $\mu 3$ are practically equivalent) when the percentage of the 95% highest density interval (95%HDI) within a region of practical equivalence (ROPE, defined here as ± 0.1 SD of the aggregate data) exceeds 95%; the null value is rejected when this percentage is below 5%; intermediate values are inconclusive.

RESULTS

Overall, the tags performed well, yielding 180 TAT histograms (Table 1, with individual transmission periods ranging from 14 to 87 days), representing 1,440 hours of data from seven pilot whales. Of these, 59 histograms were recorded during the early morning (472 hours), 64 during the daytime (512 hours), and 57 during the nighttime (456 hours).

Transformation from time-at-temperature data to time-at-depth data

The satGEM field of temperature is shown in Figure 2b. The resulting mean, minimum and maximum depth for each TAT histogram bin are shown in Figure 3, and, as expected, these values were highly variable. For example, the depth of isotherm 28°C ranged from 0 to 46 m. The 4°C, 30°C and 33°C isotherms were excluded from the GEM field projections because they were not observed in the SPOT tag data or the profiling float records. Since the depth interval corresponding to the 7–10°C temperature bin ranged from ~350 m to ~750 m (Fig. 3), the cutoff between shallow and deep dives was established at 300 m depth.

Time budget

All TAT histograms were successfully converted into TAD histograms (Fig. 4). Across the 1,440 hours of recorded data, pilot whales spent most of their time in shallow-foraging dives (State 3: mean = 38.3%; 95% credible interval [95%CrI]: 36.9–39.8%), followed by non-foraging dives (State 2: 29.4%; 95%CrI: 28.1–30.7%), surface movements (State 1: 21.0%; 95%CrI: 19.8–22.2%), and finally deep-foraging dives (State 4: 11.2%; 95%CrI: 9.9–12.6%) (Fig. 5).

There was insufficient evidence to conclude whether the time pilot whales spent in surface movements and non-foraging dives (State 1 and 2) was equivalent across early morning, daytime and nighttime, since the PrWROPE was greater than 5% but less than 95% in both tests (Table 2; Fig. 6). In contrast, the results for shallow-

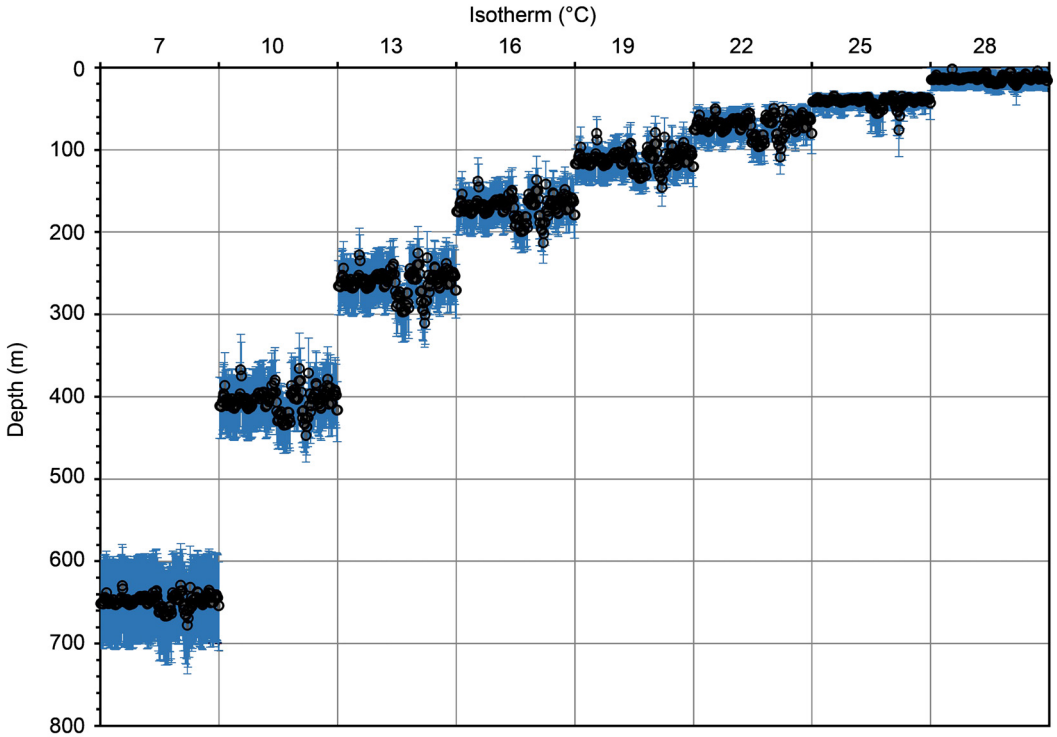

Figure 3. Depth of the isotherms estimated for each time-at-temperature (TAT) histogram (n = 180). Black dots represent the average depth and blue lines the range (minimum and maximum).

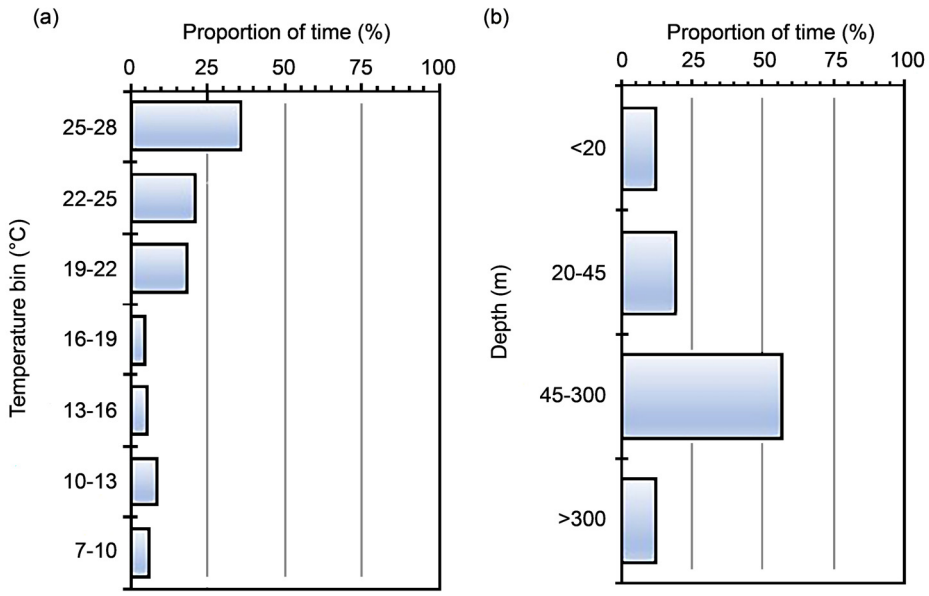

Figure 4. Example of the transformation from time-at-temperature (TAT) histogram (A) to time-at-depth (TAD) histogram (B). TAT data corresponds to tag 171903 and was recorded on 25 April 2018 between 00:00 and 7:59 h UTC at 19.2338°N and 95.6639°W.

and deep-foraging dives (State 3 and 4) indicated non-equivalence among them, with a PrWROPE of 0% in both cases (Table 2; Fig. 6).

Post hoc pairwise comparison tests showed that the time pilot whales spent in in shallow-foraging dives (State 3) during the daytime was lower than, and therefore not equivalent to, the time spent during both early morning and nighttime, with a PrWROPE of $\delta = 0\%$ in both cases (Table 3) (see Supplementary Material for full results). Similarly, the time spent in deep-foraging dives (State 4) at night was lower than, and therefore not equivalent to, the time spent during the early morning and daytime (PrWROPE = 0% for both tests; Table 3).

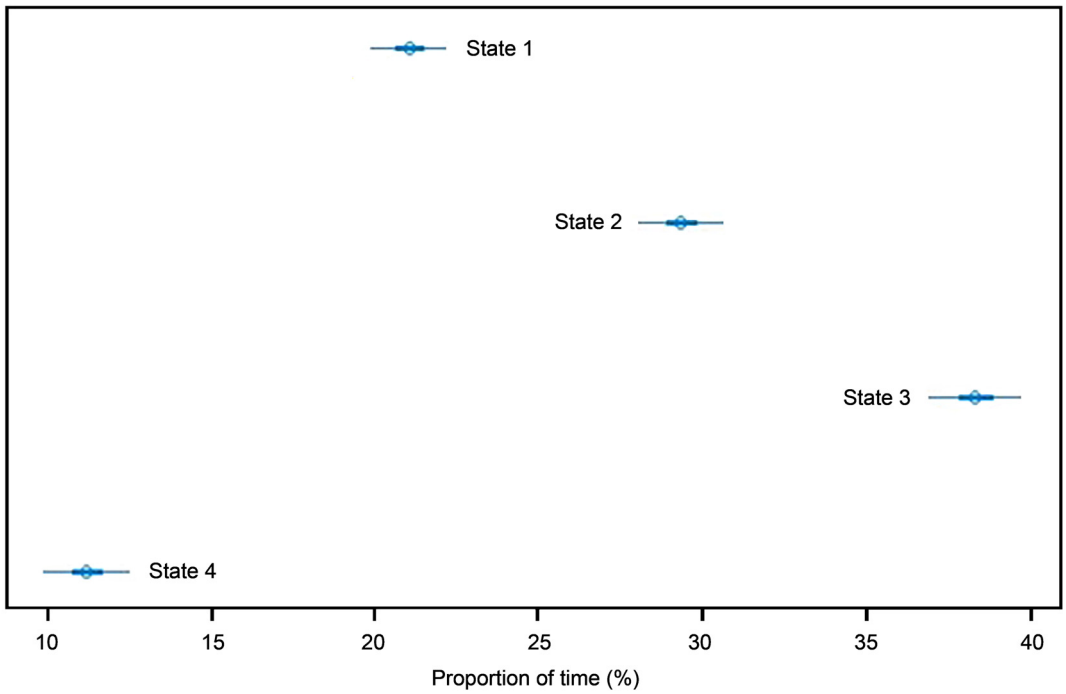

Figure 5. Caterpillar plot of the proportion of time that pilot whales spent in each state during the tags' transmission period, showing the median (dot) and the 50% (thick line) and 95% (thin line) credible intervals. State1 = surface movements (< 20 m depth), State 2 = non-foraging dives (20–45 m depth), State 3 = shallow-foraging dives (> 45–300 m depth), State 4 = deep-foraging dives (> 300 m depth).

Table 2

Summary of the Bayesian one-way ANOVA tests.

μ_i = mean of the proportion of time that pilot whales spent in each state during early morning, daytime, and nighttime (μ_1, μ_2 and μ_3, respectively), σ_{res} = residual standard deviation, $\Delta = (\mu_2 - \mu_1) - (\mu_3 - \mu_1)$. SD = standard deviation, 95%HDI = 95% high density interval, $\hat{R}$ = Gelman-Rubin statistics, neff = effective sample size, PrWROPE = percentage of the 95%HDI within the region of practical equivalence (ROPE). State1 = surface movements (< 20m depth), State 2 = non-foraging dives (20–45m depth), State 3 = shallow-foraging dives (> 45–300m depth), State 4 = deep-foraging dives (> 300m depth).

					95%HDI				
State	Parameter	Mean	SD	Median	Lower	Upper	$\hat{R}$	neff	PrWROPE
1	μ_1	19.00	1.03	19.00	17.01	21.06	1.00	42,000	
	μ_2	22.94	1.04	22.93	20.92	24.99	1.00	68,000	
	μ_3	21.27	1.06	21.27	19.17	23.31	1.00	68,000	
	σ_{res}	7.96	0.43	7.94	7.14	8.81	1.00	68,000	
	Δ	1.67	1.48	1.67	–1.25	4.56	1.00	68,000	27.2%
	Deviance	1,220.93	2.89	1,220.00	1,217.00	1,228.00	1.00	68,000	
2	μ_1	27.13	1.18	27.13	24.76	29.40	1.00	68,000	
	μ_2	30.21	1.18	30.21	27.87	32.48	1.00	68,000	
	μ_3	30.86	1.20	30.86	28.53	33.23	1.00	68,000	
	σ_{res}	9.03	0.49	9.01	8.10	10.01	1.00	68,000	
	Δ	–0.65	1.68	–0.65	–3.99	2.63	1.00	68,000	29.3%
	Deviance	1,265.33	2.90	1,265.00	1,262.00	1,273.00	1.00	58,000	
3	μ_1	40.82	1.85	40.82	37.18	44.4	1.00	68,000	
	μ_2	31.63	1.84	31.63	28.12	35.32	1.00	68,000	
	μ_3	41.47	1.88	41.47	37.85	45.19	1.00	68,000	
	σ_{res}	14.19	0.77	14.16	12.67	15.68	1.00	68,000	
	Δ	–9.84	2.64	–9.84	–15.11	–4.708	1.00	68,000	0.0%
	Deviance	1,423.42	2.91	1,423.00	1,420.00	1,430.00	1.00	31,000	
4	μ_1	12.82	1.10	12.82	10.61	14.95	1.00	32,000	
	μ_2	15.00	1.11	15.01	12.81	17.15	1.00	68,000	
	μ_3	6.18	1.13	6.18	3.965	8.399	1.00	68,000	
	σ_{res}	8.49	0.46	8.47	7.607	9.401	1.00	68,000	
	Δ	8.83	1.58	8.82	5.692	11.89	1.00	68,000	0.0%
	Deviance	1,243.72	2.89	1,243	1,240.00	1,245.00	1.00	65,000	

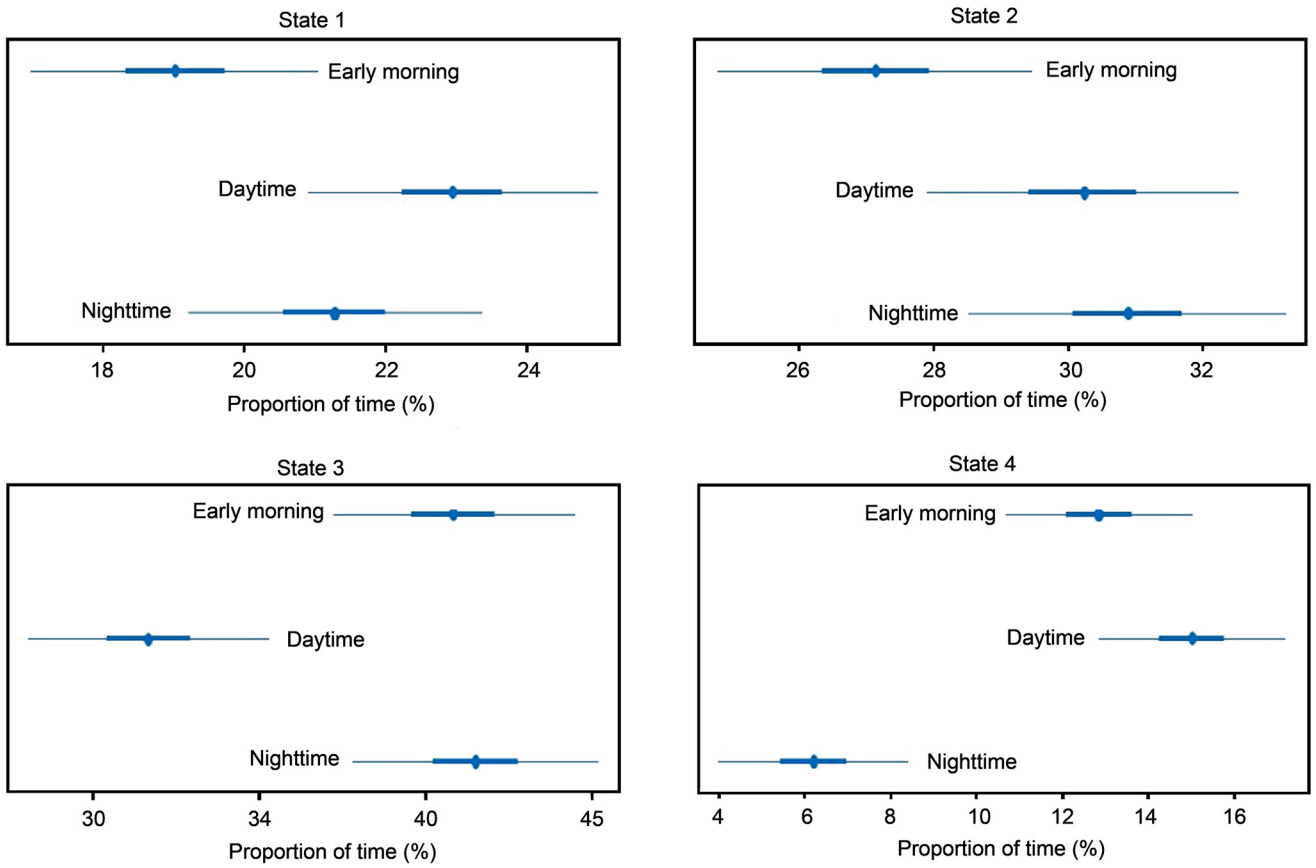

Figure 6. Caterpillar plots of the proportion of time that pilot whales spent in each state during early morning (02:00–09:59 CST), daytime (10:00–17:59 h CST) and nighttime (18:00–01:59 h CST), showing the median (dot) and the 50% (thick line) and 95% (thin line) credible intervals. State 1 = surface movements (< 20 m depth), State 2 = non-foraging dives (20–45 m depth), State 3 = shallow-foraging dives (> 45–300 m depth), State 4 = deep-foraging dives (> 300 m depth).

Table 3

Summary of the posterior distribution of the difference (d) between the means of the proportion of time that pilot whales spent in states 3 (> 45–300m depth) and 4 (> 300m depth) during the early morning, daytime, and nighttime (m_1, m_2 and m_3, respectively). $d_{2,1} = m_2 - m_1$, $d_{3,1} = m_3 - m_1$, $d_{3,2} = m_3 - m_2$. SD = standard deviation, 95%HDI = 95% high-density interval, PrWROPE = percentage of 95%HDI within the region of practical equivalence (ROPE).

				95%HDI		
State	Parameter	Mean	SD	Lower	Upper	PrWROPE
3	$d_{2,1}$	–9.75	2.19	–14.00	–5.42	0.0%
	$d_{3,1}$	2.59	2.80	–2.88	8.15	66.3%
	$d_{3,2}$	12.35	2.77	6.91	17.79	0.0%
4	$d_{2,1}$	2.35	1.64	–0.85	5.58	26.4%
	$d_{3,1}$	–7.74	1.36	–10.39	5.06	0.0%
	$d_{3,2}$	–10.10	1.46	–13.03	–7.27	0.0%

These results suggest that, during the study period, pilot whales spent less time in shallow dives (State 3) during daylight hours compared to early morning and night. In contrast, they spent more time in deep dives (State 4) during the day and early morning than at night.

DISCUSSION

Understanding how large marine predators use the water column and what drives their diving behaviour is essential for interpreting their ecological role and how they are physiologically adapted to it. In this study, we

used satellite tracking and time-based data at different temperature strata of the water column to analyse the diving behaviour of a deep-diving marine mammal, the short-finned pilot whale. Our findings provide novel insights into the vertical habitat use of this species in the southwestern Gulf of Mexico, marking the first description of this behaviour in the region.

The satGEM technique offers a valuable approach for analysing the diving behaviour of deep-diving mammals when diving profiles are unavailable but high-resolution temperature data are. SatGEM fields have been mainly used to measure the variability of the thermohaline structure of ocean currents and calculate the geostrophic flows (e.g., Watts *et al*., 2001; Pérez-Brunius *et al*., 2004; Stendardo *et al*., 2021; Meunier *et al*., 2023). However, it is also a valuable tool for the thermal gradient of the water column (Swart *et al.*, 2010, Swart & Speich, 2010). One of the main advantages of the satGEM technique is that it includes a significant fraction of the temporal variability and transitory events that are present within short data series (Swart *et al*., 2010), as is the case in our study, and that the calculated results are vertically consistent (Sun & Watts, 2001). Furthermore, below the seasonal thermocline, the thermal structure of the water column is comparatively stable over short time scales, which reduces the influence of high-frequency variability not captured by the satGEM projection and lends additional confidence to the depth estimates for the deeper isotherms used to define State 3 and State 4 in this study. Still, there is also the disadvantage that the satGEM technique can present some inconsistencies in near-surface strata (Nardelli & Santoleri, 2005). For this reason, satGEM projections of thermal strata to depth are only suitable for studying organisms that frequent deep strata (e.g., pilot whales, sperm whales, beaked whales and elephant seals).

The calculated isotherm depths reflect the specific oceanographic conditions in the study area for April–July 2018. The obtained values concur with those reported in the center and southwest of the Gulf of Mexico (Rivas *et al*., 2005; Sheinbaum *et al*., 2007) when the Campeche cyclonic gyre is present (Pérez-Brunius *et al*., 2013) and there is a marked thermal stratification gradient in the water column (Zavala-Hidalgo *et al*., 2003). The 4, 30, and 33°C isotherms were not recorded in the SPOT tags or the profiling floats during the study period. However, some authors mention that the surface temperature in the Gulf of Mexico is > 29°C during the months of July–September and the 4°C isotherm is located at > 1,000 m of depth (de la Lanza Espino & Gómez Rojas, 2004; Rivas *et al*., 2005).

Our findings indicate that, during the study period, short-finned pilot whales in the southwestern Gulf of Mexico spent approximately half of their time in the upper strata of the water column (< 45 m) engaged in non-foraging activities, such as socialising, resting or traveling. Time spent at the surface is also physiologically important, allowing animals to replenish oxygen stores from the atmosphere, eliminate accumulated CO_2, and reoxygenate tissues to repay the oxygen debt associated with anaerobic metabolism during long, deep dives (Mori, 2002; Isojunno *et al*., 2018). Regarding foraging dives, shallow dives (45–300 m) were more than three times more frequent than deep dives (> 300 m), suggesting that shallow foraging plays a key role in the pilot whales' behavioural budget. This result is consistent with previous studies on *Globicephala* spp. in other regions, such as the Canary Islands (Aguilar Soto *et al*., 2008) and the Ligurian Sea (Aoki *et al*., 2017).

The 300 m cutoff we used to distinguish shallow from deep-foraging dives was derived from the depth distribution of our own TAD data (see Results) rather than adopted from previous studies. Other regional studies have used broadly comparable, although not identical, depth thresholds to separate foraging dive classes. For example, both the hidden Markov model states used to describe shallower and deeper foraging modes of pilot whales off the western North Atlantic (Quick *et al*., 2017), and the multi-state dive classifications in the Bahamas (Joyce *et al*., 2017), show that a two-level, i.e., shallow/deep, foraging framework similar to the one applied here is appropriate throughout the distribution of this species, although the exact depth at which the transition occurs depend on local prey distributions and water-column structure.

Non-foraging dives remained relatively stable throughout the day, while patterns of foraging dives varied. Shallow foraging was notably more frequent during the early morning and nighttime than during the daytime. In contrast, deep foraging was most common during daylight hours, decreasing during the early morning and becoming rare at night. This pattern aligns with the diel vertical migration of cephalopods (primary prey of pilot whales) and other mesopelagic organisms, which descend to deep, cold layers during the day and ascend at

night (Watanabe *et al*., 2006; Judkins *et al*., 2009; Judkins & Vecchione, 2020). Similar diel foraging partitioning has been observed in other deep-diving odontocetes, such as beaked whales (*Ziphiidae*; Baird *et al*., 2008) and sperm whales (*Physeter macrocephalus*; Watwood *et al.*, 2006), where dives strongly correspond to the vertical movements of prey.

The diet of the pilot whale in the Gulf of Mexico is unknown. However, at least two cephalopod species identified as important prey, *Stigmatoteuthis arcturi* and *Taonius pavo* (Mintzer *et al*., 2008), inhabit the region (Judkins *et al*., 2019). These species undertake daily vertical migrations, moving between 200 and 600 m deep during the day and ascending to depths < 200 m at night (Judkins *et al*., 2009; Judkins & Vecchione, 2020). It is worth noting that this characterisation of the species as primarily teutophagous is based on stomach content analysis, where the chitinous beaks of cephalopods are usually well preserved and easily recovered, whereas otoliths and/or soft tissues of fish or other organisms can be lost during digestion. Consequently, cephalopods may be overrepresented. This is why biogeochemical approaches, such as stable isotope analysis (Hinton *et al*., 2022) or fatty acid profiles (Íñiguez *et al*., 2025), as well as molecular approaches, such as DNA analysis in feces (Claver *et al*., 2025), are increasingly used to identify other potential prey (e.g., mesopelagic fish) and better understand the trophic ecology of deep-diving cetaceans. However, regardless of the relative contribution of each prey type (i.e., cephalopods and fish) to the diet of pilot whales in the southwestern Gulf of Mexico, our results indicate a diel pattern in vertical movements that is consistent with and presumably driven by the vertical migration of their prey.

Demographic and/or physiological factors can also influence differences in diving behaviour. Larger individuals, such as adult males, make longer and deeper dives due to greater oxygen stores and lower mass-specific metabolic rates (Mori, 2002; Isojunno *et al*., 2018). The observed diel pattern could be influenced by some degree of habitat segregation based on sex or age, as reported for other sexually dimorphic deep-diving marine mammals, including elephant seals (*Mirounga spp.*; McIntyre *et al*., 2010) and sperm whales (Mori, 2002). However, our sample size (7 animals) prevents us from testing this idea.

'Island-associated' pilot whale populations tend to exhibit strong and consistent diel vertical migration in their foraging dives (e.g., Hawaii, Baird *et al*., 2003; the Canary Islands, Aguilar Soto *et al*., 2008; the Bahamas, Joyce *et al*., 2017), whereas, in populations along continental shelf-break habitats, such as those in the northwestern Atlantic, diel patterns are weak or inconsistent (Bowers, 2015; Shearer *et al*., 2022). The pilot whales tagged for this study moved exclusively on the southwestern Gulf of Mexico continental shelf-break during the transmission period. However, our findings show a pronounced and statistically well-supported diel pattern similar to that associated with islands. This suggests that habitat type (shelf-break vs. island-associated) alone does not determine whether a population exhibits diel vertical movements, but rather that prey ecology and local oceanographic characteristics appear to be more important factors than geomorphology alone in establishing diving patterns.

Overall, this study provides novel insights into short-finned pilot whales' vertical habitat use and foraging ecology in the Gulf of Mexico. By applying the satGEM technique to time-at-temperature data derived from SPOT tags, we were able to characterise the diel pattern in diving behaviour and use it as a proxy for the pilot whales' foraging dynamics. As human activities continue to expand into the deep waters of the Gulf of Mexico, a clearer understanding of how deep-diving species use this habitat will be essential for guiding conservation and management efforts. Future work incorporating a larger sample size and trophic ecology analysis will be key to our understanding of these sociable whales' ecological roles and vulnerabilities.

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Supplementary Material

POST HOC PAIRWISE COMPARISON TESTS SHALLOW-FORAGING DIVES (STATE 3)

A. Posterior distribution of the difference (δ) between the means of the proportion of time that pilot whales spent in state 3 during the early morning (μ_1) and daytime (μ_2).

				95%HDI			
Parameter	**Mean**	**SD**	**Median**	**Lower**	**Upper**	$\hat{R}$	**n.eff**
μ_1	40.86	1.57	40.87	37.77	43.96	1.00	68000
μ_2	31.12	1.54	31.12	28.1	34.15	1.00	68000
δ	–9.75	2.19	–9.75	–14.04	–5.44	1.00	68000
σ_1	12.02	1.15	11.93	10.03	14.51	1.00	68000
σ_2	12.20	1.12	12.12	10.25	14.63	1.00	18000
deviance	959.56	2.94	958.90	955.90	967.00	1.00	68000

B. Posterior distribution of the difference (δ) between the means of the proportion of time that pilot whales spent in state 3 during the early morning (μ_1) and nighttime (μ_3).

				95%HDI			
Parameter	**Mean**	**SD**	**Median**	**Lower**	**Upper**	$\hat{R}$	**n.eff**
μ_1	40.87	1.58	40.88	37.77	43.99	1.00	68000
μ_3	43.46	2.31	43.46	38.93	48.04	1.00	68000
δ	2.59	2.80	2.58	–2.90	8.12	1.00	64000
σ_1	12.01	1.15	11.93	10.03	14.51	1.00	68000
σ_3	17.42	1.7	17.28	14.49	21.14	1.00	68000
deviance	945.21	2.95	944.50	941.60	952.60	1.00	53000

C. Posterior distribution of the difference (δ) between the means of the proportion of time that pilot whales spent in state 3 during the daytime (μ_2) and nighttime (μ_3).

				95%HDI			
Parameter	**Mean**	**SD**	**Median**	**Lower**	**Upper**	$\hat{R}$	**n.eff**
μ_2	31.12	1.53	31.12	28.10	34.11	1.00	32000
μ_3	43.47	2.32	43.47	38.90	48.02	1.00	45000
δ	12.35	2.77	12.35	6.88	17.77	1.00	68000
σ_2	12.20	1.12	12.11	10.25	14.64	1.00	68000
σ_3	17.40	1.69	17.27	14.48	21.09	1.00	68000
deviance	986.14	2.94	985.50	982.50	993.60	1.00	20000

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D. Posterior distribution of the difference (δ) between the means of the proportion of time that pilot whales spent in state 4 during the early morning (μ_1) and daytime (μ_2).

				95%HDI			
Parameter	**Mean**	**SD**	**Median**	**Lower**	**Upper**	$\hat{R}$	**n.eff**
μ_1	12.83	1.09	12.83	10.67	15.00	1.00	68000
μ_2	15.17	1.23	15.17	12.77	17.58	1.00	68000
δ	2.35	1.64	2.36	–0.87	5.56	1.00	68000
σ_1	8.35	0.80	8.29	6.96	10.08	1.00	68000
σ_2	9.76	0.89	9.69	8.20	11.68	1.00	54000
deviance	888.00	2.94	887.30	884.40	895.45	1.00	36000

E. Posterior distribution of the difference (δ) between the means of the proportion of time that pilot whales spent in state 4 during the early morning (μ_1) and nighttime (μ_3).

				95%HDI			
Parameter	**Mean**	**SD**	**Median**	**Lower**	**Upper**	$\hat{R}$	**n.eff**
μ_1	12.82	1.09	12.81	10.67	14.95	1.00	21000
μ_3	5.07	0.81	5.07	3.47	6.67	1.00	68000
δ	–7.74	1.36	–7.75	–10.41	–5.07	1.00	21000
σ_1	8.34	0.80	8.28	6.96	10.08	1.00	32000
σ_3	6.09	0.59	6.05	5.07	7.39	1.00	68000
deviance	782.49	2.94	781.80	778.80	789.90	1.00	68000

F. Posterior distribution of the difference (δ) between the means of the proportion of time that pilot whales spent in state 4 during the daytime (μ_2) and nighttime (μ_3).

				95%HDI			
Parameter	**Mean**	**SD**	**Median**	**Lower**	**Upper**	$\hat{R}$	**n.eff**
μ_2	15.18	1.23	15.17	12.78	17.60	1.00	46000
μ_3	5.08	0.81	5.07	3.47	6.68	1.00	68000
δ	–10.10	1.46	–10.10	–12.98	–7.21	1.00	49000
σ_2	9.77	0.89	9.70	8.21	11.70	1.00	68000
σ_3	6.09	0.59	6.05	5.07	7.40	1.00	61000
deviance	838.00	2.94	837.30	834.30	845.50	1.00	68000