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| Title | Beyond dive shape: the identification of fine-scale vertical movements reveal within-dive behavioural structure in a pursuit-diving seabird |
| Authors | Dedieu, Astrid;Jessopp, Mark;Cox, Sam L. |
| Publication date | 2026-06-22 |
| Original Citation | Dedieu, A, Jessopp, M & Cox, S L 2026, 'Beyond dive shape: the identification of fine-scale vertical movements reveal within-dive behavioural structure in a pursuit-diving seabird', Marine Biology, vol. 173, no. 8, 126, pp. 1-9. https://doi.org/10.1007/s00227-026-04878-7 |
| Type of publication | Article (peer-reviewed) |
| Link to publisher's version | https://www.scopus.com/pages/publications/105042427781 - 10.1007/s00227-026-04878-7 |
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| Item downloaded from | https://hdl.handle.net/10468/19088 |




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Marine Biology (2026) 173:126
https://doi.org/10.1007/s00227-026-04878-7

ORIGINAL PAPER

# Beyond dive shape: the identification of fine-scale vertical movements reveal within-dive behavioural structure in a pursuit-diving seabird

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Received: 13 January 2026 / Accepted: 27 April 2026 / Published online: 22 June 2026
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## Abstract

Understanding how diving predators exploit prey in dynamic marine environments provides insight into their foraging strategies, energetic trade-offs, and capacity to adapt to changing conditions. While traditional classifications of dive shape have provided valuable albeit coarse insights, fine-scale behaviours embedded within dives, such as prey encounter/capture attempts, can be overlooked. We used time-depth recorders (TDR) deployed on Atlantic puffins (*Fratercula arctica*) between 2021 and 2025 on Skellig Michael, County Kerry, Ireland (51.7707°N, 10.5405°W) to detect fine-scale vertical undulations ("wiggles") in dives as proxies for prey-capture attempts. We used a broken-stick model to divide dives into segments and built a custom function to identify wiggles within segments. Wiggle occurrence differed significantly among dive phases ($p < 0.001$). Wiggles were most frequent during the ascent and bottom phases. Less than 10% of wiggles occurred during descent phases, despite descent making up 30.3% of the time spent diving. Our findings indicate that puffins, like other pursuit-diving predators, forage not only during the bottom phase but extensively while surfacing. More broadly, the integration of broken-stick segmentation with wiggle detection provides a simple, transferable framework for quantifying prey-capture attempts across pursuit-diving predators. This approach enhances inference from TDR data and contributes to a comparative understanding of how diving predators partition foraging effort within dives.

**Keywords** Atlantic puffin · Seabird · Auk · Wiggles · TDR · Dive patterns · Foraging

## Introduction

To meet their metabolic demands, marine predators must locate and capture enough prey within vast and often unpredictable environments. This challenge is amplified for species that must also provision offspring, requiring efficient foraging strategies to balance self-maintenance with parental care (Trillmich 1990; Wischnewski et al. 2019). Among these predators, seabirds face particularly demanding trade-offs as they search for prey in highly dynamic marine systems while returning regularly to breeding colonies to provision chicks (Burke and Montevecchi 2009). Diving behaviour provides one of the clearest behavioural windows into at-sea foraging ecology of diving predators, with dive shape and fine-scale movement patterns offering insight into how predators exploit prey patches, adjust search effort, and maximise energy intake (Chimienti et al. 2017; Heerah et al. 2019). For air-breathing marine predators, such as seabirds and marine mammals, these behaviours are further shaped by the need to regularly return to the surface to breathe, creating a trade-off between time spent foraging at depth and the physiological limits of oxygen storage.

Dive profiles, reconstructed from time-depth recorders (TDRs) or accelerometers, are typically described by their overall shape, which reflects the allocation of time to different phases of the dive. Three general dive types are most often recognised among pursuit diving predators: complex W-shaped dives, V-shaped dives involving rapid descents and ascents with minimal time spent at depth, and U-shaped dives, which include a distinct bottom phase at or near maximum depth (Heerah et al. 2014). Typically, V-shaped dives are interpreted as exploratory or targeted foraging dives

Responsible Editor: Ulrich Sommer.

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and W-/U- shaped dives are considered foraging dives, as this is where time is spent searching for or handling prey (Schreer et al. 2001; Elliott et al. 2008; Shoji et al. 2015; Cox et al. 2016). While this dichotomy has proven useful in distinguishing between exploratory and foraging dives, any dive can involve prey encounters, and coarse classification does not capture the full behavioural complexity that occurs within dives (Godard et al. 2020).

To address this limitation, there has been an increasing focus on fine-scale behaviours embedded within dive profiles (Heerah et al. 2014). Among these, vertical undulations known as "wiggles" have emerged as promising proxies for prey capture attempts (Bost et al. 2007; Halsey et al. 2007). Wiggles represent rapid, small-scale reversals in vertical direction, which are thought to correspond to pursuit or handling of individual prey items. In marine mammals, wiggles show strong correlations with independently verified feeding events and have been used to infer foraging success (Heerah et al. 2014; Carter et al. 2016). Similarly, in penguins, wiggles have been linked to prey encounters, as individuals adjust their trajectories to chase or capture prey (Carroll et al. 2014; Del Caño et al. 2021). Beak opening events and oesophageal temperature drops in King penguins (*Aptenodytes patagonicus*; (Hanuise et al. 2010; Brisson-Curadeau et al. 2021)) and Adelie penguins (*Pygoscelis adeliae*; (Bost et al. 2007)) have also been used to verify prey capture. Wiggle occurrence is considered a more reliable proxy of prey capture in fish-eating species, such as Magellanic penguins (*Spheniscus magellanicus*), than in krill-eating species such as Chinstrap penguins (*Pygoscelis antarctica*) (Takahashi et al. 2004; Heerah et al. 2014; Oosthuizen et al. 2025), suggesting its universality in inferring successful prey capture may be limited. However, depending on prey type, it still likely represents prey capture attempts.

Despite their potential, the use of wiggles as behavioural indicators in pursuit-diving seabirds remains relatively underexplored compared to marine mammals with most work concentrating on flightless seabirds (i.e. penguins). Integrating wiggle detection with dive shape analysis could provide a much more nuanced picture of foraging effort, distinguishing exploratory dives, prey-search phases, and active capture attempts. This would be especially valuable for both a range of far/free ranging species alongside small-bodied animals (e.g. auks), for which direct observation at sea is challenging and accelerometry data are often unavailable due to limitations in data transmission and tag size.

Atlantic puffins (*Fratercula arctica*) are small, deep pursuit-diving seabirds that forage primarily on small schooling fish, such as sandeels (*Ammodytes marinus)* and sprat (*Sprattus sprattus*) (Piatt and Nettleship 1985). As visual predators targeting discrete, mobile prey items, their foraging behaviour involves active pursuit and capture of prey at fine spatial scales (Shoji et al. 2015). In other seabirds as well as other pursuit diving predators, wiggle occurrence has been shown to be a reliable proxy of prey capture attempts particularly for fish-eating species (Takahashi et al. 2004; Oosthuizen et al. 2025). Given similarities in prey type and foraging mode, wiggles are therefore likely to provide a meaningful indicator of prey pursuit or capture attempts in puffins.

In this study, we develop a tailored algorithm to identify wiggles in Atlantic puffin dives, separating fine-scale reversals from the broader oscillations that define dive shape. By detecting not only the occurrence but also the position of wiggles within dives (descent, bottom or ascent), our method provides a framework for inferring foraging strategies and associated energetic trade-offs. We additionally tested for potential diel variation in wiggle occurrence by incorporating time of day into our analysis, as prey availability and visual conditions may change over the course of the day. This approach offers new insight into the fine-scale foraging ecology of puffins and other pursuit-diving seabirds.

## Methods

### Data collection

A total of 38 Atlantic puffins were equipped with tags on Skellig Michael, County Kerry, Ireland (51.7707°N, 10.5405°W) across four field seasons: 10 individuals in July 2021, 10 in June 2023, 8 in July 2024 and 10 in June 2025. Birds were fitted with combined GPS-time-depth recorders (TDR) devices (geoFIX, PathTrack), each weighing 3.5 g (< 1.5% of mean puffin body mass of 386 g (335 – 425 g)). Capture and recapture were conducted during the chick-rearing period by hand-extracting adults ('grubbing') from their burrows, and in some cases the use of hand nets outside burrows. Individuals were weighed to the nearest 5 g using a spring balance, and devices were attached to the lower back feathers using tesa® 4651 tape. TDRs sampled depth every 2 s when submerged below 1 m.

Deployment duration differed across years: tags were left on for 24–48 h in 2021, 2023 and 2025, and for 4–6 days in 2024. Of the 38 puffins tagged with TDRs, 10, 8, 7 and 5 were successfully recovered in 2021, 2023, 2024 and 2025 respectively (four recovered TDRs failed to record dive data in 2025, leaving 1 working tag). All data processing and analysis were conducted using R version 4.4.0.

## Data processing and analysis

### Dive data processing

Individual dives were separated based on a minimum surface interval of 5 s. Dives containing fewer than 4 data points or with a maximum depth of less than 2 m were omitted from analyses to exclude cleaning behaviour and potential recording errors near the surface (Bennison et al. 2019; Petalas et al. 2024).

### Wiggle identification function and application

To split dives into segments with overall consistent movements patterns (e.g. descent, ascent, w-sections, etc.) within which small vertical fluctuations ('wiggles') could be identified, we applied a broken stick model (BSM) to dive profiles (Photopoulou et al. 2015). Dives with fewer than 10 data points were excluded prior to analysis to aid model fitting. For each dive, we applied an automated broken-stick segmentation approach (Photopoulou et al. 2015) using the *optBrokenstick* function (Le Bras, 2017), which implements an iterative optimisation process to approximate the shape of a dive profile using a series of straight-line segments. The algorithm begins with a minimum of three points (*npmin* = 3) and sequentially adds breakpoints to minimize the residual distance between the observed profile and its piecewise-linear fit. Model improvement is evaluated using a cost function (*max_dist_cost*), which quantifies the maximum deviation between the segmented model and the observed trajectory. To constrain model complexity so that the small vertical movements attributed to wiggles do not wrongly trigger the addition of breakpoints, we defined a maximum number of allowed breakpoints (*npmax* = 6) and a stopping threshold (*threshold* = 9), such that additional breakpoints were only included if they produced a meaningful reduction in model error. The algorithm terminated when these criteria were met or when further additions no longer improved the fit, as confirmed by visual inspection. The BSM identified turning points in depth–time space, partitioning each dive into distinct linear segments. This approach effectively captured the major structural phases of each dive; descent, bottom phase, and ascent while avoiding overfitting of small-scale variability that is of interest in wiggle identification. BSM segments containing fewer than four data points were excluded from wiggle identification as a minimum number of 4 points per BSM segment is required to establish baseline direction of the segment and changes in trajectory associated with wiggles.

We developed a custom R function to detect wiggles, as small reversals in vertical movement within individual broken-stick segments. For each segment, the function calculated depth differences between successive time points to identify local turning points in the vertical trajectory. Depending on whether the segment represented a descent or ascent, different criteria were applied to define a wiggle. A wiggle was recorded when a local change in slope direction (e.g., from descending to ascending or vice-versa) exceeded a threshold of 0.25 m, and the bird subsequently returned to its initial direction of movement within the BSM segment, ensuring that only complete reversals were classified as wiggles. This threshold was chosen following an iterative process, examining the trade-off between wiggle identification and the recording frequency of the TDRs used. Dive profiles were plotted with BSM segmentation and detected wiggles highlighted, allowing visual assessment of whether identified wiggles corresponded to clear, discrete reversals in trajectory. Wiggles defined as a change and return to the initial trajectory of the segment were consistently visible in these plots at the chosen threshold. Lower thresholds resulted in detection of minor fluctuations likely driven by measurement noise or the 2 s sampling interval of the TDRs, whereas higher thresholds omitted visually distinct reversals. We therefore selected 0.25 m as the smallest threshold that reliably captured meaningful vertical reversals while remaining appropriate for the resolution of this data.

The start and end times of each wiggle were recorded, alongside total duration, total depth change, and the dive phase in which the wiggle occurred (i.e. descent, bottom, or ascent; see classification of dives phases below).

### Dive phase and wiggle allocation

Descent, bottom and ascent phase were identified for all dives. The bottom phase was identified as 80–100% of the maximum depth (Kuroki et al. 2003; Karnovsky et al. 2025), "descent" was allocated to any point that came before the bottom, and "ascent" assigned to points following the bottom phase. Dives were standardised as percentage of dive duration (start = 0% and end = 100%) and percentage of maximum depth (surface is 0% and max depth 100%) to visualize where wiggles occurred throughout the dives. Each pre-identified wiggle was allocated a dive phase based on when it occurred during the dive.

## Generalized mixed linear model

We used generalized linear mixed models (*glmmTMB* package in R) to test whether wiggle occurrence differed among dive phases (descent, bottom, ascent) and with time of day. Wiggle presence (0/1) within each phase was modelled as a binomial response, with dive ID nested within bird ID as random intercepts. The logarithm of phase duration was included as an offset. A null model was compared to models

**Table 1** Summary of all dive data

| Year | n° of birds | n° of dives | Mean max depth and range (in m) | Mean duration and range (in s) |
|---|---|---|---|---|
| 2021 | 10 | 4,131 | 26.8 (2.07–59.6) | 69.6 (6–141) |
| 2023 | 8 | 4,649 | 13.2 (2.02–39.8) | 36 (5–125) |
| 2024 | 7 | 7,724 | 13.3 (2–40.3) | 43.5 (5–135) |
| 2025 | 1 | 155 | 20.4 (2.1–34,4) | 62.5 (6–110) |

including dive phase and subsenquently, dive phase plus time of day (scaled hour), using Akaike's Information Criterion (AIC) and likelihood ratio test. Model fit was assessed by inspecting residual patterns and testing for overdispersion, and the variance of random effects was examined to confirm appropriate model structure.

## Results

Dives were only recorded between 4 am and 10 pm and puffins did not dive during hours of darkness. A total of 16,659 dives were recorded by 26 TDRs, with 13,975 retained for further analysis following data cleaning and processing (Table 1). 30.3%±0.07% of dive time was spent in the descent phase, 38.2%±0.08% in bottom phase and 31.5%±0.07% in ascent phase (Fig. 1).

Dives were split into 28,939 broken stick segments (Fig. 2b) suitable for wiggle detection, with 10,239 wiggles identified across 7,130 dives (51% of analysed dives; Fig. 3). Within these dives, the number of wiggles per dive ranged from 1 to 7, and an average of 1.45 wiggles per dive (median = 1).

Probability of wiggle occurrence differed significantly among dive phases (GLMM, binomial logit; dive_phaseB: $z = -12.95$, $P < 0.001$; dive_phaseD: $z = -42.53$, $P < 0.001$; Table 2, Fig. 4). Wiggles were more likely during a dive's ascent, with 53.7% of wiggles recorded during this phase (Fig. 1). A concentration of wiggles was evident near the surface, at the end of the dive (Fig. 3). 37.1% of wiggles were recorded during bottom phases. Wiggles were least likely during the descent, with only 9.2% of wiggles occurring during this phase (Fig. 1, 2c).

Including time of day (scaled hour) did not improve model fit relative to the dive phase model ($\Delta AIC = 0.6$), indicating no strong evidence for a diel effect on wiggle occurrence after accounting for dive phase. Although fewer wiggles were observed during early morning and late night hours, this pattern largely reflected reduced diving activity during these periods rather than a change in behaviour (Fig. 4).

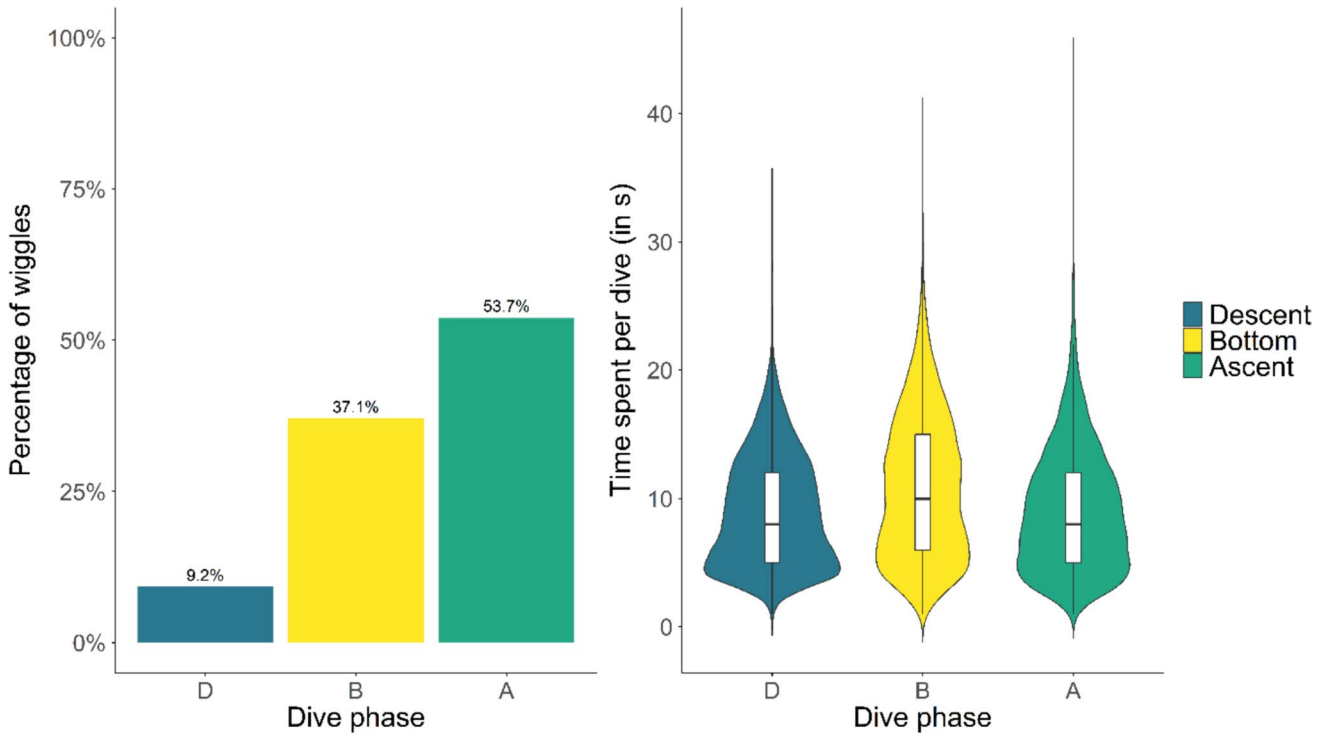



**Fig. 1** Barplot and violin plot showing the percentage of wiggles occurring across different dive phases (left) and the mean time spent in each phase across all dives (right) respectively. In both plots, colours correspond to phases; descent is blue, bottom is yellow and ascent is green

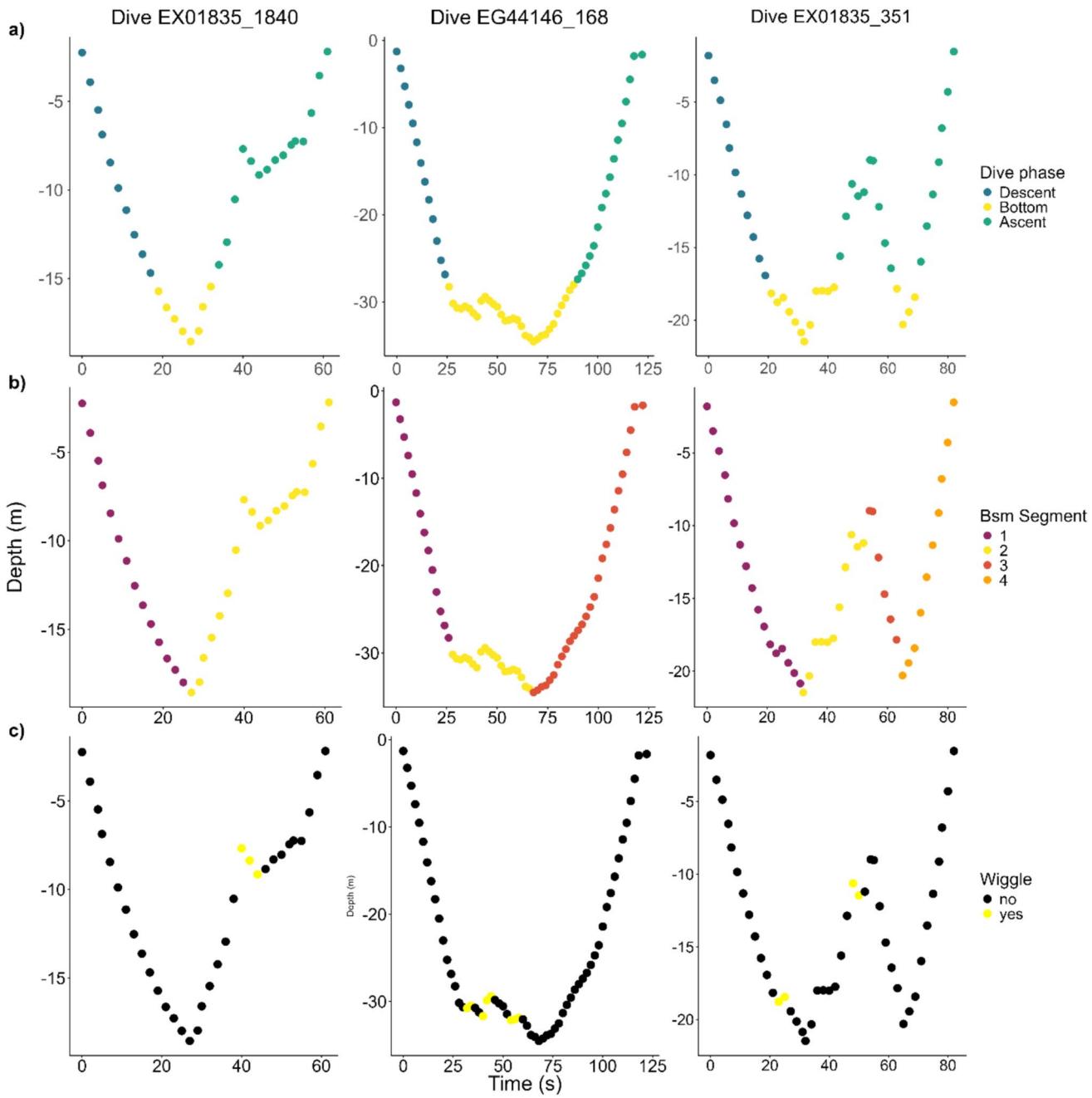



**Fig. 2** Dive profile plots of three example dives. Row **a**) shows phase classification with an 80% bottom phase. Row **b**) shows broken-stick segmentation and row **c**) highlights where wiggles were recorded in the dives

## Discussion

By developing a customised framework to identify fine-scale vertical undulations or "wiggles" as proxies for prey capture attempts, we show that while active foraging by a pursuit-diving predator occurs in all three dive phases, it is disproportionately concentrated during ascent and, to a lesser extent, bottom phases. This allocation is dependent on a coarse dive phase classification and may introduce ambiguity in W-shaped dives, where portions of the third (descending) segment could be misclassified as ascent. However, W-shaped dives were relatively rare (n = 47), and only 10 wiggles (out of 10,239) were potentially affected by this misclassification, suggesting minimal impact on the overall results. Over half of all wiggles (53.7%) were recorded on the ascent, compared to 37.1% in the bottom phase and only 9.2% during descent. The predominance of wiggles during ascents suggests puffins frequently forage

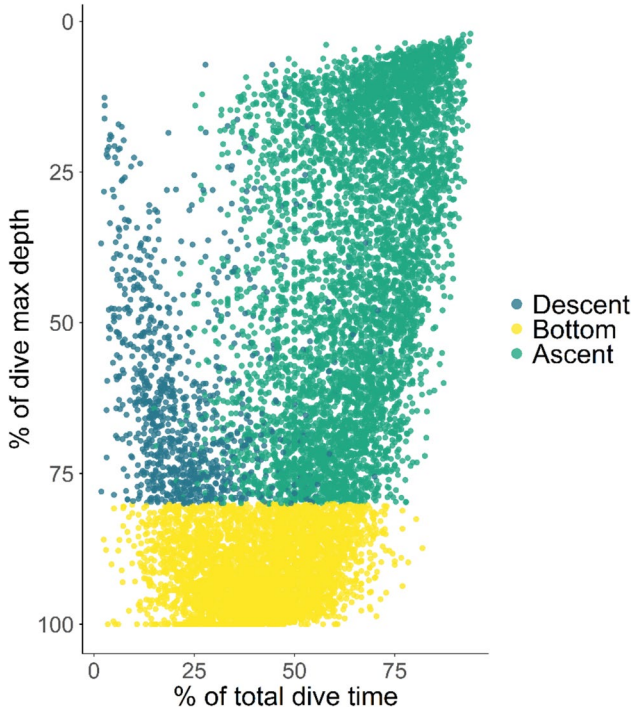



**Fig. 3** Standardised visualization of wiggle occurrence throughout dives with percentage of maximum depth and percentage of total dive duration. Wiggles occurring in; the descent are blue, the bottom are yellow and the ascent are green

**Table 2** Results from GLMM of wiggle presence with dive phase and hour of the day

| | Estimate | Std. error | ΔAIC | p-value |
|---|---|---|---|---|
| Dive phase | - | - | 2195.2 | <0.001 |
| *Ascent (intercept)* | -3.647 | 0.0226 | | |
| *Bottom* | -0.380 | 0.0291 | | |
| *Descent* | -1.569 | 0.0371 | | |
| Time of day (scaled hour) | | | | |
| *Hour (z)* | -0.017 | 0.0147 | 0.6 | 0.24 |

From left to right: estimate and standard errors from GLMM summary table, change in AIC relative to the null model (for the dive phase model) and relative to the dive phase model (for the model including time of day), p-value from likelihood ratio test against the null model(for the dive phase model) and relative to the dive phase model (for the model including time of day)

while returning to the surface, rather than concentrating prey pursuit within descent phases. This pattern is consistent with findings from other diving seabirds: African penguins (*Spheniscus dermersus*) often herd fish schools upwards and capture prey on the ascent (McInnes et al. 2017), while Razorbills (*Alca torda*) and Guillemots (*Uria aalge*) also exhibit prey capture attempts late in dives, including during ascent dive phases (Chimienti et al. 2017). Several mechanisms may explain why the ascent is an important foraging window for puffins. First, prey items flushed upwards from the bottom may remain accessible as the bird ascends and escapees break off from their schools (McInnes et al. 2017). Second, increasing light levels closer to the surface may enhance prey contrast (i.e. downwelling light creating a silhouette), improving detectability (Darby et al. 2022). Atlantic puffins, like many other pursuit-diving seabirds, are efficient visual predators whose foraging behaviour is constrained to daylight hours, which is supported by the foraging patterns observed in our data and elsewhere (Croll et al. 1992; Shoji et al. 2015). Third, ascent-foraging may represent an energy-efficient strategy, combining the locomotion required for surfacing with buoyancy to aid prey pursuit (Lovvorn et al. 2004; Wilson et al. 2011).

Wiggles recorded in the bottom phase likely correspond to active prey search or handling within discrete prey patches, potentially at or near the benthos. The relatively low frequency of wiggles on descent aligns with this expectation, as puffins are likely prioritizing efficient travel to depth rather than engaging in prey capture (Hanuise et al. 2013). Many wiggles were observed near the surface at the end of dives, suggesting that puffins may exploit prey layers or trapped individuals against the surface (Chimienti et al. 2017; McInnes and Pistorius 2019) immediately before re-emerging or as a strategy to avoid predators or minimise interactions with other birds sitting on the water. The presence of dives with no detected wiggles indicates potential exploratory dives or that puffins may employ alternative foraging strategies, such as targeting benthic prey patches without frequent reversals or capturing prey during smoother trajectories. Overall, these patterns highlight the importance of considering ascent behaviour as a key component of the foraging ecology of visual, pursuit-diving seabirds such as the Atlantic puffin.

Beyond puffins, our approach demonstrates the use of combining broken stick segmentation with wiggle detection for studying fine-scale foraging behaviour across a wide range of diving seabirds and marine predators. Many air-breathing pursuit divers share the constraint of limited oxygen stores and must balance travel efficiency with prey capture (Green et al. 2005). Applying a standardised framework for identifying wiggles allows for comparisons across taxa, study systems, and environments. However, while wiggles provide a potentially useful proxy for prey-capture attempts, a lack of accelerometer data prevents us from identifying finer-scale 'jerks' (change of acceleration over time in m.s), which can be indicative of prey capture attempts (Viviant et al. 2014; Ydesen et al. 2014; Oosthuizen et al. 2025). Additionally, the inference of prey capture attempt through wiggles as proxies provide conservative estimates compared to accelerometer-derived approached (Brisson-Curadeau et al. 2021) which identified 10–77% more capture per unit time in a study on Magellanic penguins (Del Caño et al. 2021). Owing to stringent tag-weight constraints in puffins, the deployment of cameras or

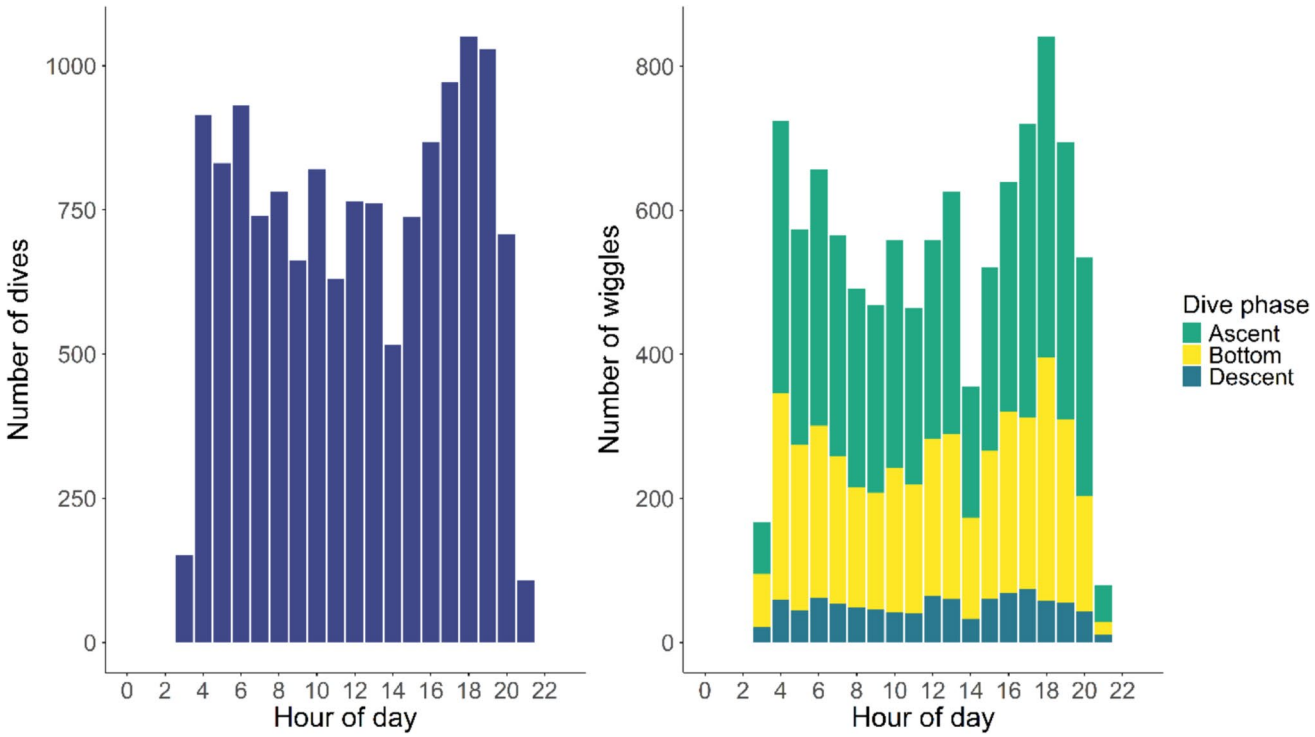



**Fig. 4** Diel patterns in diving behaviour of puffins. (**a**) Number of dives per hour. (**b**) Number of wiggles per hour, shown by dive phase (descent—blue, bottom—yellow, ascent—green)

additional high-resolution sensors was not possible. While the interpretation of wiggles as prey-capture attempts is supported by studies in other pursuit-diving seabirds and marine predators, we cannot directly confirm these detections in the absence of on-animal validation. The 2-s sampling interval of the TDR's used here, although relatively fine, may also underestimate the frequency of short-duration events. Increasing the resolution of data recording to 0.5–1 s would likely capture more subtle undulations. Nonetheless, the wiggle framework presented here provides a valuable tool for quantifying how diving predators partition foraging effort across dive phases and how these strategies vary with prey type, distribution, or depth. Combined with GPS data, wiggle detection within dives can improve the identification of prey patches and core foraging areas, while also enabling inference of fine-scale energetic strategies through behavioural modelling approaches such as hidden Markov models. More broadly, applying this approach to extensive existing TDR datasets can enhance comparative analyses across diving species and improve understanding of the energetic and ecological drivers of underwater foraging. This framework should therefore be adapted on a case-by-case basis to the resolution of the dataset and species-specific diving behaviour, with wiggle thresholds defined as the smallest vertically resolvable and visually verifiable reversal in dive trajectory.

## Conclusion

Our study demonstrates the value of combining dive shape classification with fine-scale wiggle detection to investigate the foraging ecology of Atlantic puffins. Puffins performed wiggles disproportionately during bottom and, especially, ascent phases, which likely reflects adaptive strategies to balance prey capture and oxygen constraints. Wiggle identification offers a straightforward proxy for prey-capture attempts, complementing conventional dive-shape metrics. Future work integrating accelerometry, higher-resolution sensors, and prey field data will refine wiggle-based proxies and further elucidate links between diving behaviour, foraging success, and ecological context.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s00227-026-04878-7.

**Acknowledgements** This research is funded by the Sustainable Energy Authority of Ireland under the SEAI Research, Development & Demonstration Funding Programme 2021 (Grant number 21/RDD/670) and is publication #5 of the SEAI-funded CETUS Project. SL Cox was funded through the European Union's Horizon 2020 research and innovation programme (101029802—SEAFICS). We would like to thank the Office of Public Works for facilitating the fieldwork and all those who helped collect the data, particularly Jamie Darby, Manon Clairbaux and Emma Murphy. Additionally, we would like to thank the two anynomous reviewres for providing comments and feedback on earlier versions of this manuscript.

**Author contribution** Dr Mark Jessopp purchased the equipment. Astrid Dedieu and Dr Mark Jessopp collected the data. Astrid Dedieu and Dr Sam L Cox conceived the methodological approach and analysed the data. Astrid Dedieu led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

**Funding** Open Access funding provided by the IReL Consortium. Sustainable Energy Authority of Ireland, 21/RDD/670, Mark Jessopp, HORIZON EUROPE Marie Sklodowska-Curie Actions, 101029802, Sam L Cox.

**Data availability** Both the data and the code are uploaded as separate supplementary material with the following names: data—"puffin_dives_labelled.csv"; code—"wiggles_code.txt" and "functions_for_wigglescode.txt". Code for this can also be found at the following DOI: 10.5281/zenodo.20309196. Additionally, the data is already available upon request on the seabird tracking database (https://data.seabirdtracking.org/dataset/2244). Dataset ID 2244. The code and data used for this project will be made freely available upon publication.

## Declarations

**Conflicts of interests** The authors have no relevant financial or non-financial interests to disclose.

**Ethics approval** The procedures were reviewed and approved by the University College Cork animal ethics committee (application #2019–001) and the British Trust for Ornithology Special Methods Committee prior to being undertaken under permits from the BTO (C/6143, C/7158) and National Parks & Wildlife Service (C145/2024, 044/2024, C114/2023, 020/2023, C155/2021, 54/2021).

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