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LETTER

Selective foraging behavior of seabirds in small-scale slicks**Lilian Lieber** ^{1*}, **Cynthia Füchtencordsjürgen**², **Rebecca L. Hilder**², **Paula J. Revering**², **Ina Siekmann**², **Roland Langrock**²,
W. Alex M. Nimmo-Smith³¹School of Ocean Sciences, Bangor University, Wales, UK; ²Department of Business Administration and Economics, Bielefeld University, Bielefeld, Germany; ³School of Biological and Marine Sciences, University of Plymouth, Plymouth, UK**Scientific Significance Statement**

Slicks are common ocean features resembling meandering lines that can accumulate floating debris and marine organisms (e.g., plankton and small fish). Seabirds are often observed around conspicuous slicks, yet their interactions have rarely been quantified. We used low-cost aerial drones to track terns foraging over evolving slicks at scales of meters and seconds. Our high-resolution drone imagery captures how terns directly plunge-dive into slicks. Furthermore, our analysis shows that terns are more likely to switch into foraging behaviors when flying over slicks compared to adjacent water. Our findings demonstrate that terns select slicks for foraging, thereby shedding new light on fine-scale foraging associations between seabirds and dynamic ocean features. Our approach also lends itself to ecological interaction studies with pollutants, plumes, and fronts.

Abstract

Marine predator foraging opportunities are often driven by dynamic physical processes enhancing prey accessibility. Surface slicks are ubiquitous yet ephemeral ocean features where convergent flows accumulate flotsam, concentrating marine organisms and pollutants. Slicks can manifest on the sea surface as meandering lines and seabirds often associate with slicks. Yet, how slicks may influence the fine-scale foraging behavior of seabirds is only coarsely resolved. Here we show that seabirds selectively forage in small-scale slicks. We used aerial drone technology to track surface-foraging terns (*Sternae*, 107 tracks) over evolving slicks advected by the mean flow and reshaped by localized turbulence at scales of meters and seconds. Terns were more likely to switch into high-tortuosity foraging behavior when over slicks, with plunge-dive events occurring significantly more often within slicks. As we demonstrate that terns select dynamic slicks for foraging, our approach will also lend itself to interaction studies with pollutants, plumes, and fronts.

*Correspondence: l.lieber@bangor.ac.uk**Associate editor:** Rana El-Sabaawi**Author Contribution Statement:** LL and ANS conceived the ideas and LL collected the data. All authors performed analyses and interpreted the results. LL drafted the initial manuscript. All authors contributed to writing and editing the final manuscript and gave the final approval for publication.**Disclaimer:** The views and opinions expressed in this paper do not necessarily reflect those of the European Commission or the Special EU Programmes Body (SEUPB).**Data Availability Statement:** The data and metadata are available in the Figshare repository at <https://doi.org/10.6084/m9.figshare.20496957.v1>. This includes the metadata, the processed input dataset (.csv), including the tern tracking data and the associated slick variables, and the R code (.txt) supporting this article's results.

Additional Supporting Information may be found in the online version of this article.

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Marine predator foraging locations are strongly driven by underlying physical processes that enhance prey density or accessibility (Cox et al. 2018). On broad scales, more persistent physical features such as meso- or sub-mesoscale eddies and fronts are important drivers of predator foraging habitat in the open ocean (Tew Kai et al. 2009; Scales et al. 2014; Abrahms et al. 2018). However, in coastal environments, there are a variety of highly dynamic physical processes operating at much finer scales which can directly influence organism distribution (Wolanski and Hamner 1988; Franks 1992). In tidal seas, strong currents interacting with complex bathymetry can generate smaller-scale physical features ranging from island wakes and shear lines, to localized regions of divergence (upwelling) and convergence (downwelling). Such tidally driven hydrodynamics can physically enhance prey availability and there is increasing evidence on their ecological importance as predictable marine predator foraging locations (Hunt and Schneider 1987; Johnston and Read 2007; Thorne and Read 2013; Waggitt et al. 2016; Lieber et al. 2019).

Hydrodynamic features that can aggregate and upwell small prey items are of particular importance to surface foraging seabirds, such as gulls and terns (Hunt and Schneider 1987). Tern (*Sternidae*) coastal foraging patterns are strongly influenced by tidal dynamics (Pearson 1968; Becker et al. 1993). Here, terns often forage in areas of bathymetry-generated turbulence that give rise to near-surface regions of vorticity, upwelling, and downwelling (Schwemmer et al. 2009; Urmy and Warren 2018; Lieber et al. 2019, 2021). Surface convergence will lead to the aggregation of buoyant material, and in the presence of abundant flotsam, such as foam or seaweed, slicks can manifest on the sea surface as conspicuous meandering lines. Slicks present ubiquitous ocean features and their formation can result from varying physical processes, including internal waves, Langmuir cells, and other surface flow convergences (La Fond 1959; Shanks 1983; Weller et al. 1985; Smith et al. 2021). Therefore, while slicks can be conspicuous, especially in the presence of abundant flotsam, they are ephemeral with their occurrence and persistence influenced by dynamic physical processes, including wind.

Apart from accumulating flotsam, slicks have been shown to host higher concentrations of zooplankton, meroplankton, and small fish compared to ambient water (Shanks 1983; Kingsford and Choat 1986; Gade et al. 2013; Weidberg et al. 2014; Whitney et al. 2021). There is also growing evidence that slicks concentrate plastics (Gove et al. 2019; Gallardo et al. 2021), raising concerns about plastic ingestion (direct or indirect) by seabirds foraging within slicks (Young and Adams 2010).

Seabirds are often associated with visual slicks. For instance, a study in the Aleutian Passes found fulmars foraging in tight flocks over converging slicks (Ladd et al. 2005). Furthermore, physical sampling of surface slicks over a small offshore bank in the Gulf of Maine found high concentrations of calanoid copepods in association with near-surface seabird (e.g., storm-petrels) foraging (Stevick et al. 2008). Seabird associations were

also found where convergence leads to patches of floating seaweeds (Haney 1986), with surface-foraging seabirds benefiting from the seaweed and their associated ichthyofauna (Vandriessche et al. 2007). Despite these documented coarse-scale observations, how slicks influence the fine-scale foraging behavior of seabirds is less well resolved.

With mounting evidence on slicks as hotspots of both potential prey and plastics, it is timely to conduct more focused studies on seabird associations with slicks to identify underlying mechanisms and prevalence. Here, we use aerial drone surveys to investigate the fine-scale interactions of surface-foraging seabirds (tern species, *Sternidae*) with meandering slicks in a tidal channel at scales of meters and seconds. Terns are highly mobile and can rapidly respond to foraging cues which often leads to localized foraging flocks (Goyert 2014; Urmy and Warren 2018; Lieber et al. 2019). The high-resolution drone imagery allowed us to reliably identify and track individual terns, while the auxiliary extraction of evolving slicks was used to quantify tern-slick interactions. We tested the hypotheses that in the presence of visible slicks, terns selectively forage within slicks and that slicks directly shape their fine-scale foraging movements. We predicted that terns exploit ephemeral slicks as profitable foraging opportunities given their propensity to concentrate material.

Methods

Study site

The study was performed in the Narrows tidal channel, Strangford Lough, Northern Ireland, UK (Fig. 1). Strangford Lough supports various tern (*Sterna sandvicensis*, *Sterna hirundo*, *Sterna paradisaea*) breeding colonies and this study was motivated by several observations in mid-July 2021 of tern feeding flocks over visual signatures of flotsam deemed to be slicks, prompting dedicated aerial drone observations. Slicks tend to manifest in the study area (Fig. 1c) during the flooding tide when underlying conditions are favorable (e.g., abundant flotsam, low wind, and associated sea states). This video (<https://youtu.be/3T1bXIWrzV4>) shows the scale of the slick manifestations at the site, where random slicks were chosen to focus on with the drone.

Aerial drone surveys

Aerial drone (uncrewed aerial vehicle [UAV]) surveys were conducted on 02 August 2021 during flood tide and low wind speeds (2.1 m s^{-1}) to capture terns foraging over slicks. UAV hovers (holding station with a vertically downward-facing camera) at 120 m altitude were performed using a DJI Mini2 recording 4 K video at 30 Hz, translating into a footprint of $170.02 \times 95.09 \text{ m}$ at 4.41 cm per pixel ground resolution (Fig. 1d). The UAV was flown manually using the DJI Fly application, with the major axis of the field of view oriented with the mean advection direction of underlying slicks. Missions included two separate hovers ($h_1 = 83 \text{ s}$; $h_2 = 273 \text{ s}$) at different locations (Fig. 1c) completed within a 7.5 min

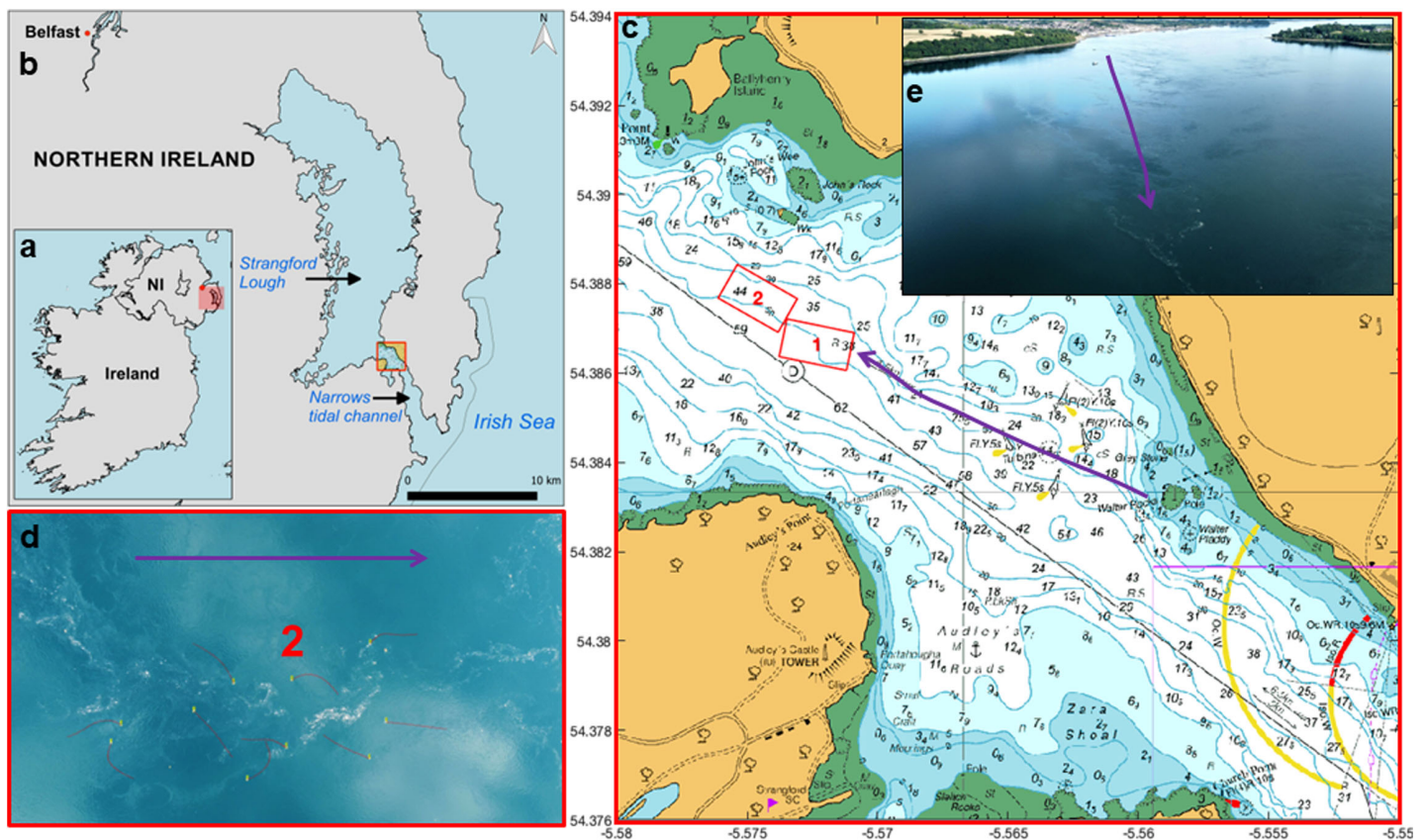


Fig. 1. Location of aerial drone observations of surface-foraging terns over small-scale slicks in a tidal channel. (a) Overview map of Ireland showing the study area within the Narrows tidal channel, Strangford Lough, Northern Ireland (NI), UK, highlighted by a red box. (b) Location of drone hovers in the tidal channel highlighted by a red box. (c) Bathymetric chart showing the exact locations of the two drone hovers (red rectangles labeled 1&2). (d) Aerial shot of drone hover 2 ($t = 2$ s), showing the beginning of tern tracks (red lines, yellow markers indicate most recent position) over slick line manifestations. (e) Oblique drone shot looking upstream (southeast) toward the island wake with the onset of slick formation visible closer to the observer. (c–e) Purple arrows indicate mean flow direction. OSNI data were reproduced from Land and Property Services data with the permission of the Controller of Her Majesty's Stationery Office, ©Crown Copyright and Database Rights MOU203. Bathymetry: ©Crown Copyright/SeaZone Solutions Limited (2022). All Rights Reserved. Not to be used for navigation.

period, resulting in a total sampling time of 356 s. Missions were completed following local regulations by the same qualified (UK Civil Aviation Authority) pilot. The UAV camera was calibrated using a checkerboard target in the MATLAB Camera Calibrator App and video sequences post-processed in MATLAB (R2021b; Mathworks).

Seabird tracking and slick extraction

Tern tracking followed Lieber et al. (2021) with some minor modifications detailed in the Supporting Information. Slicks were visualized and extracted using computer vision techniques to reduce transient artifacts from ambient lighting and moving terns (Fig. 2). Stepping at 0.25 s intervals through the raw video, five adjacent frames were extracted, processed, and combined using the following steps to produce the time sequence of labeled slick distributions. For each frame, the difference between the red and green channel was calculated, which increases the contrast between pale flotsam and green

coastal waters. Large-scale intensity variations due to clouds were reduced by high-pass filtering using a 128×128 pixel kernel. The resulting intensity distribution was binarized using a fixed threshold (0.05). Sun glint speckles < 50 adjacent pixels in size were removed and continuous slick regions were coalesced using dilation (48-pixel radius disk structuring element) and triple erosion (8-pixel radius disk structuring element). Remaining small patches $< 12,500$ pixels in size, that included isolated terns, were also removed (Fig. 2b). The final labeled slick distribution at each timestep was then established in those pixel locations where slicks appeared in all five frames. The resulting array thus had binary regions labeled as slicks (Fig. 2c). Slick positions were extracted for each instantaneous position along each tern track using three-dimensional interpolation in space and time. The slick parameter was matched to tern tracks into a .csv file where every track position had a binary variable (“slick = 1” or “no slick = 0”), along with an associated continuous variable “time-to-slick” (in seconds, hereafter *slick proximity*),

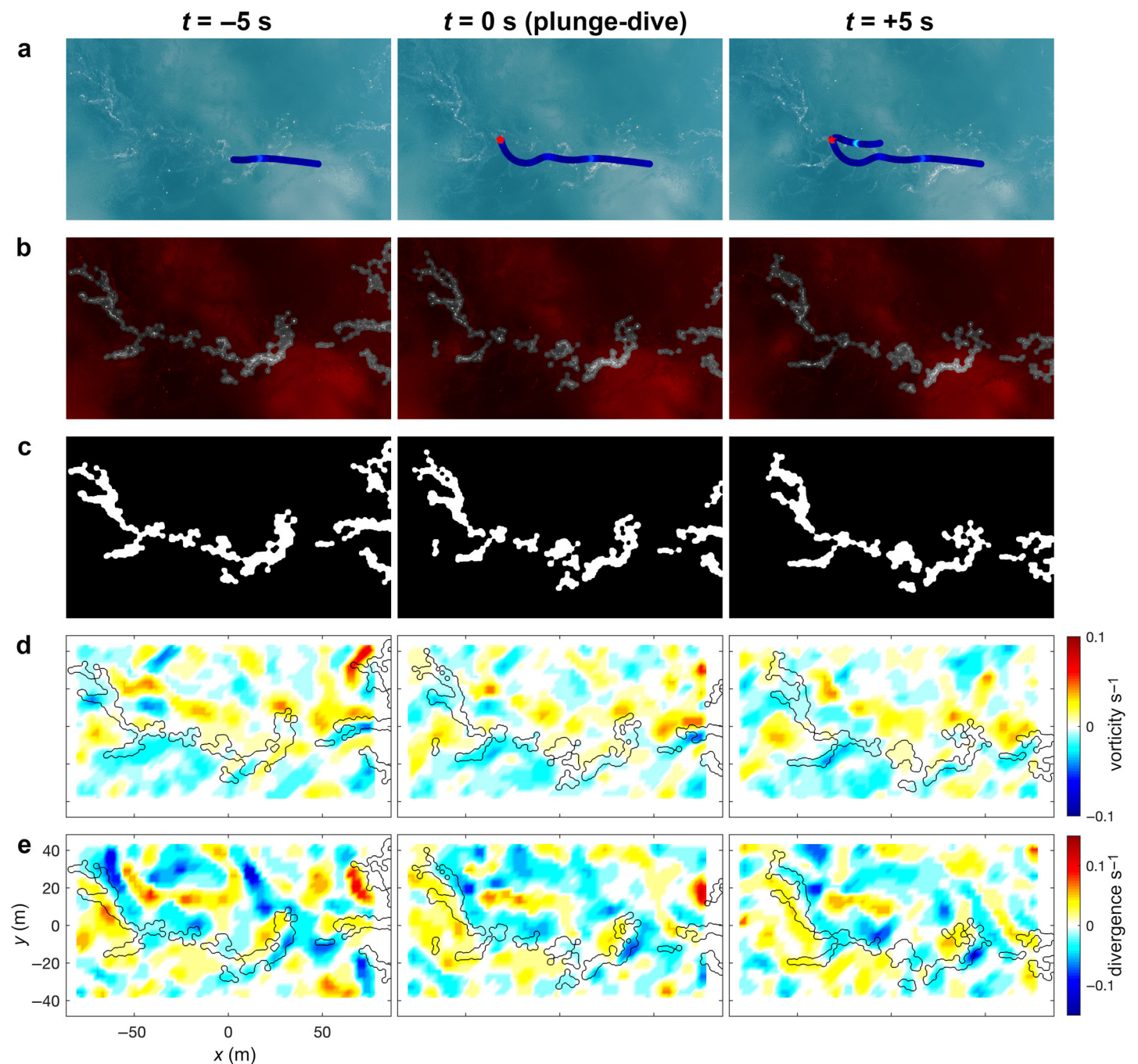


Fig. 2. Slick extraction and mapping of physical flow features. Time series at indicated intervals of (a) raw video footage overlaid with a tern track (colored by tortuosity) where red star indicates a foraging event (plunge-dive). (b) Slick extraction processing (red = removed, e.g., clouds). (c) Final extracted slick used as binary covariate in HMM modeling (white = slick). Regions of (d) vorticity and (e) divergence (positive = upwelling) and convergence (negative = downwelling) shown with contour line of slick for context.

calculated from the timestep a tern was spatially over a slick until it next encountered a slick. For the assessment of plunge-dive events, an output video was created for each individually tracked tern (highlighting one bird at a time) with the evolving slick line visualized to manually quantify

plunge-dives in relation to slicks using two independent video observers (Supporting Information Fig. S1). Finally, we used particle image velocimetry techniques to characterize the flow features around the slicks (Fig. 2d-e) following Lieber et al. (2021).

Statistical analysis: Hidden Markov models

To quantify tern foraging associations with underlying slicks, we applied covariate-dependent hidden Markov models (HMMs) to the data. HMMs can help classify behavioral states such as “searching” or “travelling” and can quantify state-switching probabilities as a function of covariates, thereby relating movement behaviors to underlying environmental factors (Van Beest et al. 2019; McClintock et al. 2020). Specifically, we modelled the terns’ log(tortuosity) values as an outcome of a gamma distribution, with the mean and standard deviation depending on the model state currently active. Tortuosity is a measure of the curvature of an animal’s path or how much the animal is turning (see Supporting Information Section S1). The three states we considered could be related to displacement, searching, and foraging behavior. To assess how tern state-switching and steady-state probabilities were influenced by the slicks, we used the extracted binary slick variable, indicating if a tern was associated with an underlying slick or not (an alternative model using *slick proximity* was deemed inferior by model selection criteria, and hence was not further investigated). The evolution of the three states over time, as governed by a three-state Markov chain, was investigated by relating the state transition probabilities to the binary slick covariate, resulting in two different state transition probability matrices, denoted Γ_0 (when “slick = 0”) and Γ_1 (when “slick = 1”). Model selection involved a likelihood-ratio test of significance of the slick covariate and, for additional guidance, the consideration of the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC) values for the model with and without the slick covariate, respectively. Model checking was conducted via simulation and a pseudo-residual analysis (Supporting Information Section S2). The HMM was fitted in R (R Core Team, 2020) and the input data and associated code can be found in Lieber et al. (2022).

Results

Slick line manifestations

Although various gull species and a seal associated with the slicks, terns were the most common (see video link: <https://youtu.be/3T1bXIWrzV4>). The frequent manifestation of a slick line (broken into discontinuous slicks) in this area may be primarily driven by a small island (Walter’s Rock) approximately 1 km upstream of the survey site during the flooding tide. It generates a typical island wake effect (Neill and Elliott 2004; Johnston and Read 2007), characterized by vortex shedding in the lee of the island (flow separation) and a visible shear line extending into the main flow of the channel (Fig. 1e). The shear line demarcates the faster flows within the main channel, characterized by strongly erupting boils (regions of upwelling) and transient vortices, from the flows circulating more slowly within the embayment (Ballyhenry Bay) to the north of the main channel. The shear line acts as a region of convergence accumulating flotsam at the surface forming the visible slicks. In combination with low wind speeds and the presence of

biological material, the slick lines were particularly conspicuous during the sampling period. The slicks were advected with the mean flow (0.94–1.02 m s⁻¹) and evolved with time as they were reshaped by turbulent boils and vortices that acted to concentrate and locally reorganize the accumulation of material near the sea surface (Fig. 2d–e).

Tern track summaries and foraging events

Following removal of very short tracks (< 5 s), there were 107 tracks in the analyzed data set and track duration ranged from 5.04 to 149.82 s with a mean duration of 20.63 s (SE = 1.66). Fifty-four of the tracks did not contain a foraging event (plunge-dive), while the remaining 53 tracks had a minimum of one plunge-dive per track (range: 1–4). However, even tracks without plunge-dives are ecologically meaningful in the investigation of flight behavior as a function of slick presence, and hence were not excluded from the analysis. Altogether, there were 67 individual plunge-dive events among the tracks, 56 of which occurred within visible slicks, corresponding to 84%. Taking into account the proportion of time terns spent above slicks (35%), this proportion is significantly higher than expected by chance (binomial test, $p < 0.001$).

Matching state-dependent distributions to behaviors

Log(tortuosity) was used as an observed variable in the HMM to decompose the tracking data into three states. Based on the fitted state-dependent distributions of log(tortuosity), the three states could be interpreted as (1) displacement, (2) searching, and (3) foraging behaviors, respectively (Fig. 3). “Displacement” was associated with more directional movements and observed tortuosity near zero (mean log [tortuosity] = 0.0028 ± 0.0018 s.d.), “searching” was indicative of more tortuous movements (mean log [tortuosity] = 0.0124 ± 0.0051 s.d.), while “foraging” included highly erratic movements with spikes in tortuosity indicating hovering, swooping and plunge-dive events (mean log [tortuosity] = 0.0771 ± 0.0717 s.d.). Indeed, the majority of the observed high spikes (> 0.3) could be related to observed dive events in the corresponding video data.

Significance of underlying slicks

The likelihood ratio test of the simpler model with homogeneous state-switching probabilities (without an effect of underlying slicks) against the model including the binary slick variable rejected the simpler model ($p < 0.001$). This was further corroborated by both the AIC ($\Delta\text{AIC} = 151.6$) and the BIC ($\Delta\text{BIC} = 97.1$) clearly favoring the model including the slick covariate. Model checking implied an adequate model fit and all model selection and checking results can be found in the Supporting Information.

State probabilities depending on underlying slicks

The transition probability matrix provides information on the probabilities of a tern remaining in or switching to another state given the state a tern is currently in:

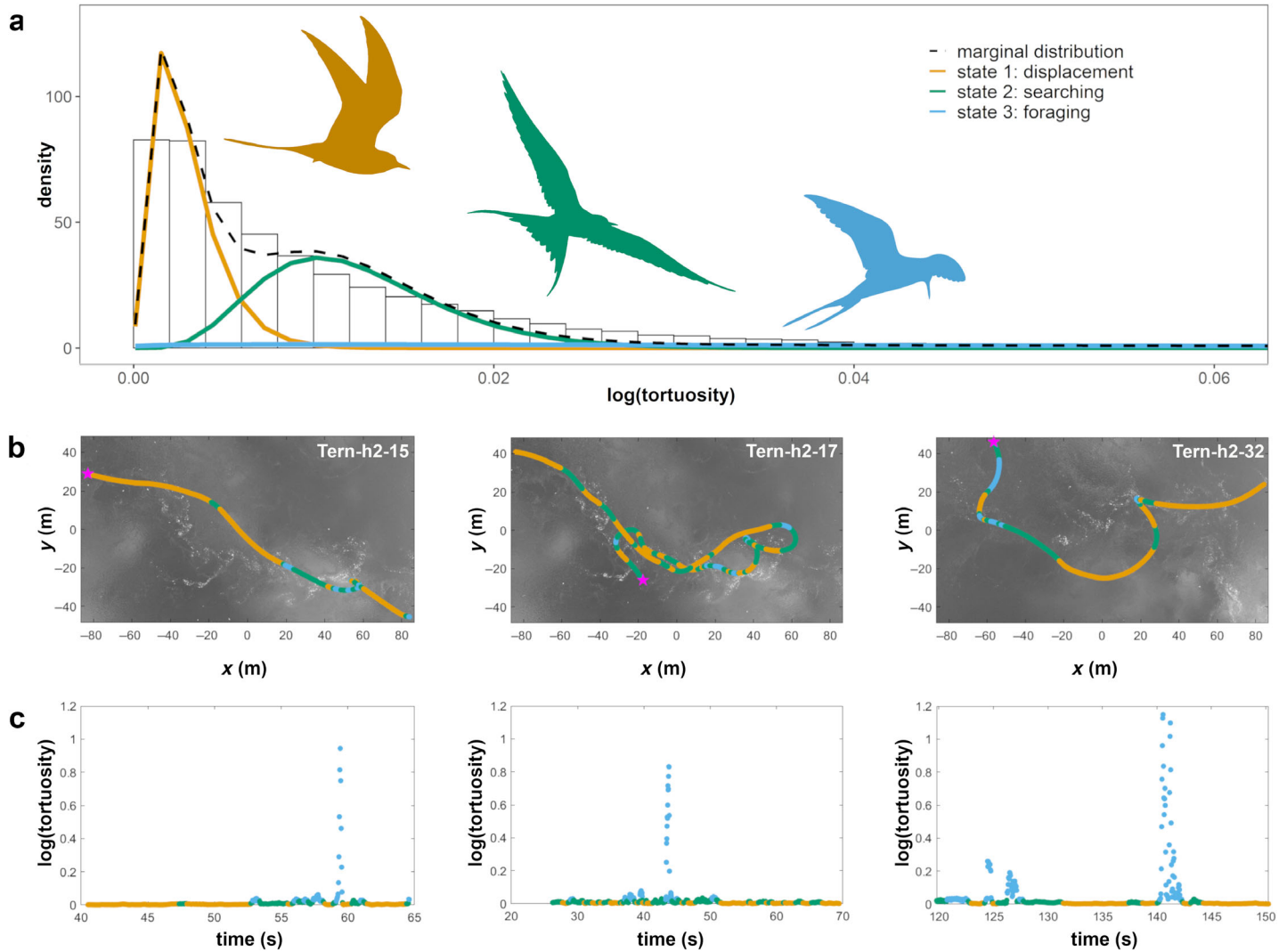


Fig. 3. HMM fitted to $\log(\text{tortuosity})$ data. **(a)** Histogram shows the observed $\log(\text{tortuosity})$ overlaid with the color-coded state-dependent distributions as estimated by the HMM, weighted according to the proportion of time the corresponding state is active. This was used to identify the three states, displacement (state 1 = orange), searching (state 2 = green), and foraging behavior (state 3 = blue). State 1 was associated with more directional movements and very low tortuosity, state 2 was indicative of more tortuous movements during searches and state 3 included highly erratic movements with spikes in tortuosity indicating hovering, swooping, and plunge dive events. Plunge dives were later identified in the corresponding video sequences and > 80% of all plunge-dives occurred within slicks. **(b)** Example movement tracks (star symbol demarks the starting location) overlaid onto a gray-scale image of the slick extracted mid-way through the track and **(c)** time series along the same track and variation in $\log(\text{tortuosity})$, color-coded by the predicted behavioral state where spikes (> 0.5) indicate confirmed plunge-dive foraging events. Tern silhouettes downloaded from [PhyloPic.org](https://www.phylopic.org/) (orange and green tern by Mathieu Pélissié, used under CC BY-NC-SA 3.0/colorized).

$$\Gamma = \begin{pmatrix} \Pr(1 \rightarrow 1) & \Pr(1 \rightarrow 2) & \Pr(1 \rightarrow 3) \\ \Pr(2 \rightarrow 1) & \Pr(2 \rightarrow 2) & \Pr(2 \rightarrow 3) \\ \Pr(3 \rightarrow 1) & \Pr(3 \rightarrow 2) & \Pr(3 \rightarrow 3) \end{pmatrix},$$

$$\Gamma_0 = \begin{pmatrix} 0.979 & 0.020 & 0.000 \\ 0.024 & 0.966 & 0.011 \\ 0.000 & 0.039 & 0.961 \end{pmatrix}$$

and

$$\Gamma_1 = \begin{pmatrix} 0.959 & 0.040 & 0.001 \\ 0.034 & 0.942 & 0.024 \\ 0.002 & 0.053 & 0.945 \end{pmatrix}$$

where $\Pr(i \rightarrow j)$ is the probability to switch from state i to state j , and states 1, 2, and 3 indicate displacement, searching, and foraging behaviors, respectively. Depending on the binary slick covariate, the matrices were estimated as:

for situations without or with slick association, respectively. The lower diagonal entries in Γ_1 imply an increased frequency of switches between behavioral modes in the presence of slicks. The steady-state probabilities—effectively the average proportions of time spent in the different states—implied by these transition probability matrices are

$$\Delta_0 = (0.470, 0.412, 0.118)$$

and

$$\Delta_1 = (0.369, 0.435, 0.196),$$

indicating a much-increased probability of the terns exhibiting foraging behavior (state 3) when associated with underlying slicks. This was further confirmed by a simple logistic regression analysis—neglecting temporal correlation for simplicity—where we related the response variable “foraging” (with value 1 if the HMM allocated an observation to state 3, and 0 otherwise) to the binary slick covariate (odds ratio = 1.8, $p < 0.001$).

Discussion

The fine-scale foraging behavior of terns was strongly influenced by the presence of small-scale meandering slicks generated and redistributed by turbulent tidal flow features. Tern foraging events (plunge-dives) occurred significantly more often inside than outside of slicks, supporting our hypothesis that terns selectively forage within slicks. Furthermore, terns were more likely to switch into high-tortuosity behavioral states when over slicks, indicative of search behavior. Together, our results clearly demonstrate the ecological importance of ephemeral slick occurrences.

Seabird foraging behavior is highly complex and sensory cues that may trigger search or foraging behaviors range from visual inputs, for example, from conspecifics (social cues) and near-surface signatures (environmental cues), to memory effects and olfactory cues (Nevitt et al. 1995; Goyert 2015; Urmey and Warren 2018; Lieber et al. 2021). While unexplored, we cannot disregard that slicks accumulating flotsam as observed here may thus provide an array of scale-dependent foraging cues for the terns. For example, social cues may be dominant at a distance, whereas near-surface physical cues may be more important at smaller scales. Here, the slicks were formed at the boundaries of evolving physical features that acted to concentrate and locally reorganize the accumulation of material near the sea surface (Fig. 2d–e). Vortices generated along regions of persistent horizontal shear aggregate buoyant materials at their centers, while erupting boils accumulate materials at their peripheries before dissipating into smaller vortical structures (Nimmo-Smith et al. 1999; Mulligan et al. 2018). Although we do not know how prey was distributed in these local water masses, slicks have been shown to promote fish and invertebrate aggregation and transport (Shanks 1983; Kingsford and Choat 1986;

Whitney et al. 2021). We have previously shown that terns in the tidal channel associate with wakes at peak flows (Lieber et al. 2019), while the slick associations occurred after peak flows when upstream wake features were less dominant. Therefore, ephemeral slicks here provide a further foraging opportunity in the absence of tidally predictable features.

Our results provide unambiguous evidence that an aerial predator tracks slicks for foraging. Over 80% of all plunge-dive foraging events occurred within slicks and the presence of underlying slicks increased the probability of terns exhibiting foraging behavior (state 3). State 3 was associated with highly tortuous or erratic movements, including hovering, swooping, and plunge-diving, indicative of finding or foraging for near-surface prey (Fig. 3). With numerous observations of marine predators associating with slick convergences (Haney 1987; Sims and Quayle 1998; Ladd et al. 2005; Vandendriessche et al. 2007; Dewar et al. 2008; Brischoux and Lillywhite 2011; Thorne and Read 2013), our fine-scale observational approach lends itself to other marine settings, such as foraging associations with small-scale thermal fronts (Sims and Quayle 1998) or river plumes (Zamon et al. 2014). Furthermore, it could assess how seabirds interact with slicks in areas exposed to pollutants. The accumulation of plastic debris in pelagic surface waters is pronounced in areas of convergence (Cózar et al. 2014) and seabird ingestion of floating plastic is an increasing, global concern (Wilcox et al. 2015). Many seabirds are opportunistic foragers and surface- or shallow-diving species may be at greatest risk of direct ingestion of prey-sized plastics in slicks (Young and Adams 2010). Foraging strategy impacts plastic ingestion risk in seabirds (Caldwell et al. 2020) and for terns foraging for single prey items, secondary plastic ingestion may be more likely. In summary, while we show that slicks provide seabird foraging opportunities, their propensity to accumulate plastics warrants further investigation.

We used a quiet, white-colored micro drone (249 g) at its maximum permitted altitude (120 m), thereby minimizing potential impacts or bias in observations during surveys (Kuhlmann et al. 2022). UAVs provide a bird’s eye, rather than oblique, view on seabird movement and underlying flows (Lieber et al. 2021) and thus provide a suitable tool to quantify slick interactions. Satellite remote sensing can now capture near-surface oceanographic features of length-scales ranging from kilometers to several meters (Marmorino 2022), such as slick lines (Gade et al. 2013), but cannot track seabird movements. Therefore, UAVs are a bio-physical remote sensing tool which can address these blind spots, providing on-demand, high-resolution data at relatively low costs (Gray et al. 2022). Our tracking of distinct water masses can also be applied in understanding the dispersion and advection of small-scale tidal fronts, plumes, wakes, or oil spills.

In conclusion, our results support our prediction that terns select slicks for foraging. Future studies evaluating the prevalence, benefits, and risks associated with marine predator foraging within slicks would also benefit from concurrent *in situ* sampling as done elsewhere (Stevick et al. 2008; Young and Adams 2010; Gove et al. 2019; Gallardo et al. 2021; Whitney et al. 2021). This

integration of remote sensing approaches and statistical analyses of high-resolution tracking data in combination with in situ sampling will improve our understanding of marine species interactions with small-scale dynamic features, allowing better predictions of species' responses to a changing ocean.

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Conflict of interest

The authors have no conflict of interest to declare.

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