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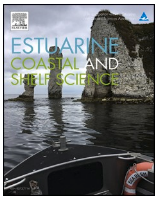

Fishing activities shape the flight behaviour of an opportunistic predator species

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ABSTRACT

Human activities provide opportunistic species with abundant and predictable feeding opportunities that may shape their ecology, including their movement patterns and behaviour. Investigating human-wildlife interactions in marine ecosystems is challenging because of the logistic constraints of surveying vast and remote geographical areas. Fortunately, miniaturized biologging devices now provide the possibility of assessing the influence of human activities on marine life, particularly in the case of large-sized predators. Here, we used GPS tracking data for Mediterranean endemic Audouin's gulls, *Ichthyaetus audouinii*, to quantitatively characterise gulls' foraging trips and evaluate individuals' foraging behaviour in relation with fisheries. By using ca. 38,090 space-time locations (i.e., 362 foraging trips), we calculated eight flight behaviour movement metrics to describe gull's flight behaviour within foraging trips. We used these movement metrics to analyse individuals' flight behaviour in contrasting fishing activity scenarios (i.e., presence/absence of fishing activity by trawlers and purse-seiners) and in response to spatial-temporal co-occurrence with fishing vessels operating in the area. Our results showed that Audouin's gulls adapted their flight behaviour in response to fisheries. When fishing vessels were active (particularly trawlers), gulls flew faster (particularly when co-ocurring with a fishing vessel) and more directly (i.e. lower directional changes), compared to non-fishing situations or when temporally co-occurring with purse seiners. This work enhances our understanding on seabird-fishery interactions, and may contribute to further evaluations on species responses to resource shortage scenarios, such as the collapse of local fish stocks and landing obligations. Beyond this ecological information, our results may also contribute to the use of seabirds for monitoring fisheries, and help fight Illegal, Unreported and Unregulated fishing (IUU) in areas where fishing vessels cannot be monitored by other means (e.g., through Vessel Monitoring Systems -VMS- or Automatic Monitoring Systems -AIS-).

1. Introduction

Planet Earth is holding a very large pressure derived from human activities, and there is no part of the global environment that humans have kept within its pristine state (Halpern et al., 2008). Among the Earth biomes, the ones within the marine environment are of particular concern as they include some of the most human-impacted ecosystems (Halpern et al., 2015; Ramírez et al., 2017). There is a range of human activities that can disturb marine wildlife, including tourism, petrol extraction, commercial shipping, offshore wind farms, pollution, biological invasions and fishing activity (Higham and Lück, 2008; Fraser, 2014; Pirotta et al., 2019; Dierschke et al., 2016; Garcia-Garín et al., 2020; Keith et al., 2016; Coll et al., 2019). In this sense, evaluating how marine life responds to this wide range of human pressures is a research priority for the conservation of ecosystem keystone species and the provision of science-based information to exploit and manage the oceans in a more sustainable way (Hays et al., 2016).

Fisheries are one of the main drivers of change in the global ocean

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(Cury and Pauly, 2020). Their impacts on wildlife range from habitat degradation to bycatch and depletion of fish biomass (Furness, 2007; Cury et al., 2011). Furthermore, fisheries can provide wildlife with new feeding opportunities or food subsidies that can largely influence the ecological dynamics of opportunistic species at many levels (Furness, 2003; Oro et al., 2013). Ultimately, an increase in food availability may propagate through marine trophic webs and alter the structure and functioning of marine ecosystems, as it may enhance ecological processes such as predation, competition or the transfer of nutrients between trophic levels (Oro et al., 1999; Arcos et al., 2001; Baumberger et al., 2012). From an ecological perspective, the importance of food subsidies of anthropogenic origin lays in the fact that they are usually predictable over space and time, which makes them readily exploitable by opportunistic species (Oro et al., 2013; Zeller et al., 2018). This can have direct implications on the species that use these resources, such as diet variations, distribution shifts and behavioural changes (Navarro et al., 2009; Chilvers et al., 2003; Collet et al., 2017; Corbeau et al., 2019), with subsequent energetic implications due to an increase of available calories in the environment (van Donk et al., 2019). However, human food subsidies may as well have drawbacks such as increased pollutant burdens or the surge of ecological traps when sudden shortages of particular food subsidies happen (Arcos and Oro, 2002; Schlaepfer et al., 2002).

From small invertebrates to large seabirds and marine mammals, an extensive list of marine taxa has been reported to use food subsidies originated in fishing activities, such as trawling (discard consumption: Ramsay et al., 1997; Bozzano and Sardà, 2002; Karris et al., 2018; Sherley et al., 2020), purse seining (surface predation; J Arcos and Oro, 2002) or pelagic longlining (bait/catch predation; Janc et al., 2018; Richard et al., 2020). In particular, seabirds are known to largely benefit from food subsidies generated by fisheries all around the globe (Sherley et al., 2020), especially from fishing discards, which are considered as the major food subsidy in the marine environment (Oro et al., 2013). In this sense, fishing discards consumption has been detected in the four seabird taxonomic orders (Procellariiformes, Sphenisciformes, Charadriiformes and Pelecaniformes; Cherel et al., 2000; Crawford et al., 2017; Calado et al., 2018; Jodice et al., 2011) and is a major feeding source for opportunistic seabird species, characterized by their high adaptability, and whose behavioural and trophic plasticity allows them to take advantage of such food subsidies shortly after they become available in the environment (Oro and Ruiz, 1997; Louzao et al., 2006; Ouled-Cheikh et al., 2020).

Besides direct dietary changes (e.g. consumption of prey species that would not be naturally available for a (sub-)surface predator; Arcos et al., 2008; Navarro et al., 2009), opportunistic seabird species are known to adapt their behavioural patterns to fishing schedules and activities in order to efficiently exploit associated food resources and feeding opportunities (Ouled-Cheikh et al., 2020; Parra-Torres et al., 2020). For instance, seabirds may redirect flight trajectories towards boats (Collet et al., 2015) or adopt different movement patterns in scenarios with and without fishing activity (Bartumeus et al., 2010; Bécares et al., 2015), showing characteristic opportunistic behaviours to take advantage of changing prey and environmental conditions. Assessing these behavioural shifts can be challenging, but the recent development and miniaturization of tracking devices has significantly improved the way we approach the movement and at sea behaviour of vagile species in response to both natural and human-induced environmental variability (Yoda, 2019).

Based on GPS continuous tracking data of a generalist species, the Audouin's gull, *Ichthyaetus audouinii,* we quantitatively characterised the individuals' foraging trips using various movement metrics that allowed us to investigate flight behaviour throughout contrasting fishing activity scenarios. The Audouin's gull is a Mediterranean-endemic opportunistic species that largely relies on discards (Oro et al., 1995, 1996, 1999; Arcos et al., 2001) and, hence, constitutes an ideal model species to evaluate the effects of contrasting fishing conditions on the behaviour of marine species. Previous research showed that Audouin's gulls are able to adjust their daily activity patterns to the operating schedules of different fishing fleets in the study area (Bécares et al., 2015; Ouled-Cheikh et al., 2020). However, flight behaviour has been overlooked in previous research efforts, so we aimed to fill this gap in the present study. We calculated eight movement metrics to describe gull's flight behaviour within foraging trips. We then used these movement metrics to analyse the daily patterns of flight behaviour in contrasting fishing activity scenarios. We hypothesized that gulls would adjust their flight behaviour (and hence their feeding behaviour and foraging strategy) to the co-occurring trawlers (diurnal) and purse-seiners (nocturnal). We discuss our results in the light of implications resource and energetic shortages associated to collapses of local fish stocks and ongoing policy changes, such as landing obligations. Beyond these ecological consequences, we also highlight the implications in using opportunistic seabird species for monitoring illegal activities, such as Illegal, Unreported and Unregulated fishing (IUU; see Navarro et al., 2016).

2. Material and methods

2.1. Study area and species

Our study area was defined from the movements of GPS-tracked Audouin's gulls breeding at La Punta de la Banya colony (40°40′N, 0°45′E) in 2011. La Punta de la Banya is a protected sandy peninsula with salt pans in the Ebro Delta Natural Park (NE Spain; Fig. 1), a wetland zone mostly covered by rice fields. The area comprised the NE Levantine coast of Spain and extended from the mainland coast over the continental shelf to the upper slope. There are numerous fishing ports scattered along the coast of the study area, which is one of the most important fishing grounds for clupeids and demersal resources in the Mediterranean due to the wide continental shelf and the nutrients supplied by the Ebro River (Fig. 1; Maynou et al., 2008). This supports two main fishing activities: trawling (diurnal activity 7:00 h to 17:00 h GMT+1) and purse seining (nocturnal activity, starting at 23:00 h and with no return limit; Ouled-Cheikh et al., 2020). The fishing activity of both fleets is concentrated on the weekdays (Monday to Friday), with no fishing activity at the weekend. Trawling is a non-selective fishing practice that produces large quantities of discards (Stithou et al., 2019). These discards are thrown back to the sea after every trawl casting and two to four castings can be carried out per day. In the Ebro Delta, trawling fishing vessels begin to produce discards around 11:00 h (Fishing Advisory Service, pers. comm.). However, it is at the end of the fishing day, between 16:00 h and 17:00 h, when all the fishing vessels discard simultaneously as they approach the fishing ports (Fishing Advisory Service, pers. comm.). This results in an abundant and highly predictable anthropogenic food subsidy for marine scavengers (Martínez-Abraín et al., 2002; Karris et al., 2018). A discard ban policy has been progressively implemented since 2015 in the waters of the EU under the EU Common Fisheries Policy, and applies to species exploited under Total Allowable Catches (TACs) or with a minimum landing size, leading to significant decreases of discard production. This ban was expected to be fully in place in 2019 (Stockhausen, 2019). However, in Spanish waters the implementation of the ban is still underway because of the lack of infrastructure to land all the bycatch in fishing ports, so since 2011 (when the tracking data was recorded) until the present-day, discarding is still a common practice in the study area (Fishing Advisory Service, pers. comm.).

Trawling activity contrasts with the nocturnal purse-seining activity, which produces few discards but can influence the foraging behaviour of scavengers through a process of resource facilitation, as it concentrates epipelagic fish close to the water surface (Arcos and Oro, 2002). Presence/absence of fishing activity has been shown to have an effect on habitat use of Audouin's gulls (Christel et al., 2012; Bécares et al., 2015), shifting from marine to terrestrial habitats when fishing vessels are not

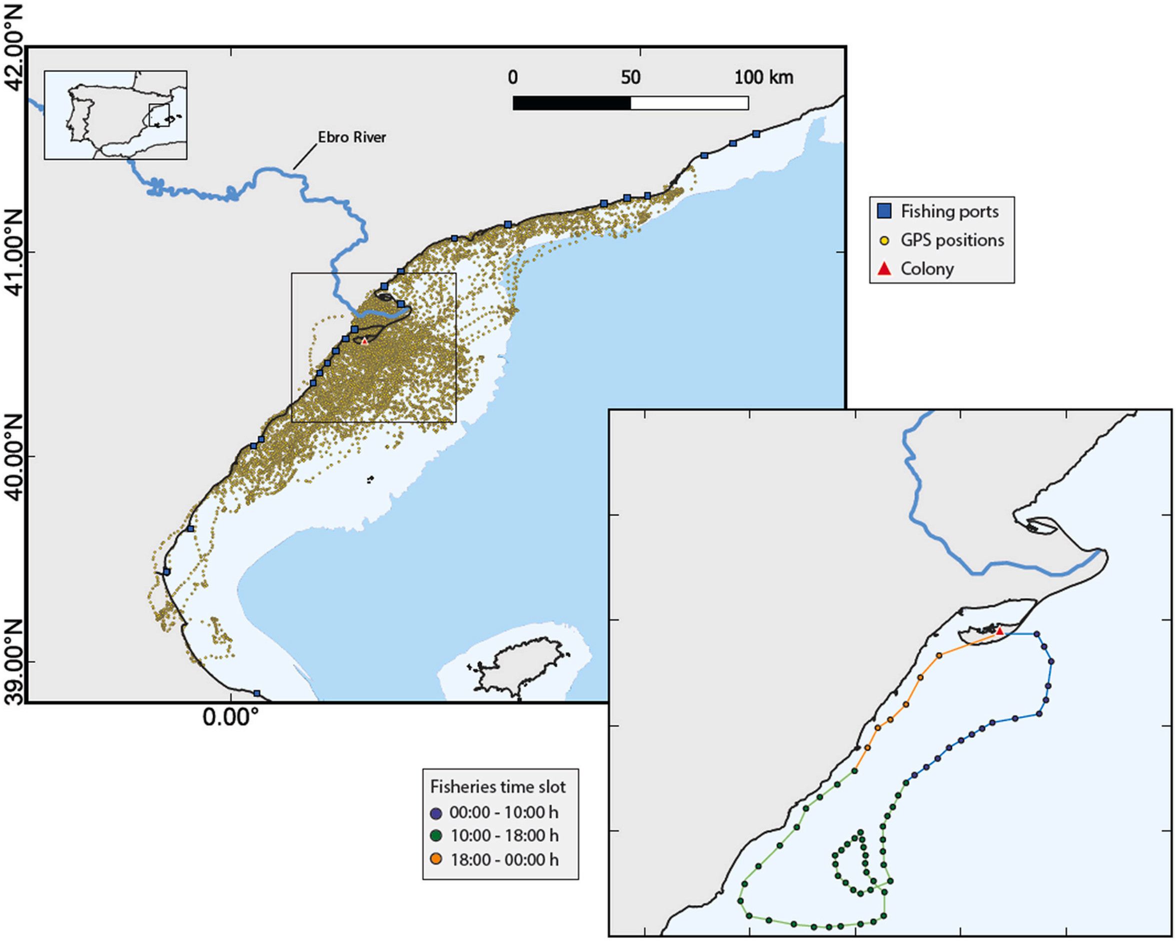

Fig. 1. Trajectories of the GPS-tracked Audouin's gulls at the NE Levantine coast of Spain. This area encompasses the most important fishing ground for clupeids and demersal resources in the Mediterranean. Yellow points indicate GPS locations recorded every 5 min during the 2011 breeding season (incubation). Inset map shows one foraging trip split by three segments, corresponding to each fisheries time slot. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

operating (i.e. during the weekends). Their use of terrestrial habitat is mainly concentrated on rice fields, where they feed on crustaceans molluscs and insects (Ruiz et al., 1996). In 2011, when the study was carried out there were 11,967 breeding pairs, representing ca. 60% of the global population (BirdLife International, 2020).

2.2. GPS tagging

Between the 8th and the May 26, 2011, during the incubation period of the species in the study site, 60 breeding gulls were captured in randomly chosen nests, with either box or tent-labelled traps (Bub, 1991), and equipped with CatTrack GPS loggers (Perthold, 2011). These loggers were programmed to record locations (10 m accuracy; Forin-Wiart et al., 2015) every 5 min. Devices were sealed using a shrink tube to make them waterproof, and attached to the back of the gulls using a Teflon adjustable harness (Bécares et al., 2010). The total weight of sealed devices (ca. 25 g) roughly represented the 3% of the bird's body mass, as it was recommended in Phillips et al. (2003). More recent works suggest a potential tag effect for thresholds lower than 3% (Bodey et al., 2018; Gillies et al., 2020). Nevertheless, as we aimed to compare behaviour of tracked birds among contrasting fishing conditions, we expected that any supposed tag effect would affect equally to the tracked birds, and thus quantitative characterization of gulls' foraging trips (hereafter flight behaviour) would be still valid and useful for comparisons. Thirty-six tagged birds were recaptured between one and two weeks after the deployment of GPS devices. Recorded data included GPS positions for these 36 individuals between May 8th and 26th (Fig. 2). No adverse weather conditions (e.g. rain or strong winds) that could potentially affect gulls' foraging behaviour occurred during the study period (based on the site-specific WANA model for winds: http://www.puertos.es/es-es/oceanografia/Paginas/portus.aspx wind speed for the study period mean ± SD: 3.55,190 ± 2.27 m/s).

2.3. Data analyses

2.3.1. Fishing scenarios and gull-vessel interactions

Based on the activity rhythms described in Ouled-Cheikh et al. (2020), 362 Audouin's gull foraging trips (i.e. locations since a bird leaves the colony until it returns; BirdLife International, 2005) were grouped in three categories (foraging trip segments hereafter) that combined information on fishing activity (presence vs. absence) per time slot (night-time vs. day-time; hereafter fisheries time slots; Table 1). These categories included 'no activity' (weekends plus workdays between 18:00 h and 00:00 h) when no fishing gear operates in the study area; 'diurnal activity' (workdays between 10:00 h and 18:00 h) when trawlers operate; and 'nocturnal activity' (workdays between 00:00 h and 10:00 h) when individuals may take advantage of feeding opportunities provided by purse-seiners. This three-level categorization responds to our main aim of evaluating behavioural responses by Audouin's gull to contrasting fishing activity scenarios: no fishing, trawlers operating (i.e., enhanced food availability through fishing discards) and purse-seiners operating (i.e., enhanced food availability

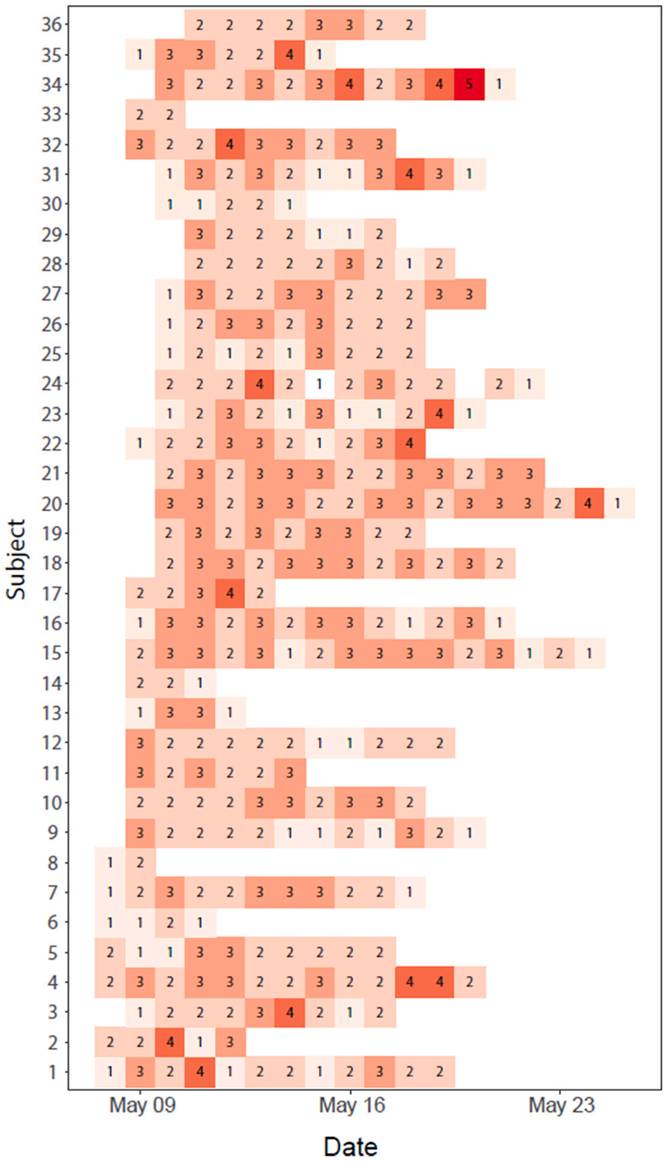

Fig. 2. Number of trips performed by each tagged individual split by day. Colour code represents the number of trips. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Summary of fisheries time slots considered in the study. We split Audouin's foraging trips in three categories, depending on the fishing scenario. Fisheries time slots are: no (no fishing activities), night (nocturnal fishing activity; purse seining) and day (diurnal fishing activity; trawling).

Fisheries time slot	Schedule	Co-occurring fleet	Discard production
Nocturnal activity	00:00–10:00 h (Weekdays)	Purse-seiners	Low
Diurnal activity	10:00–18:00 h (Weekdays)	Trawlers	High
No fishing activity	18:00–00:00 h (Weekdays + Weekends)	–	–

through resource facilitation). However, foraging at-sea did not necessarily imply interacting with fishing vessels as individuals may prey on marine resources naturally, even in the presence of fishing vessels operating (Bécares et al., 2015). Accordingly, we also considered a two-level factor informing on whether interactions with fishing vessels occurred for each fisheries time slot. To this aim, we followed Ouled-Cheikh et al. (2020) procedures and used a spatiotemporal buffer (500 m ± 10 min since the bird position was recorded) around Vessel Monitoring System (VMS) positions to evaluate co-occurrence between Audouin's gulls and fishing vessels (see details in Ouled-Cheikh et al., 2020). VMS positions are recorded every 2 h, thus preventing from a continuous recording of seabird-vessel interactions. The combination of fisheries time slots with the two-level factor informing on the presence/absence of co-occurrence was therefore selected as the most conservative approach.

2.3.2. *Flight behaviour movement metrics*

Foraging trips data were firstly pre-processed using the *trajr* R package (McLean and Skowron Volponi, 2018; R Core Team, 2021). The pre-processing steps were: 1) splitting foraging trips into trajectories (i.e. foraging trip segments) based on Cartesian coordinates and time (TrajFromCoords function in the *trajr* package) and 2) trajectory smoothing applying a Savitzky-Golay filter (TrajSmoothSG function in the *trajr* package; only for metrics related to speed and acceleration; McLean and Skowron Volponi, 2018). We then calculated eight movement metrics to describe gull's flight behaviour within each foraging trips' segments, which were temporally split according to fisheries time slots. **(1)** Duration: time between the beginning and the end of the foraging trip segment (time that a segment lasts within a fisheries time slot; hours). **(2)** Mean speed: average displacement per unit time ($km \cdot h^{-1}$). **(3)** Mean acceleration: average rate of change of speed with respect to time ($km \cdot h\text{-}^{2}$). **(4)** Mean directional change: average angular change (in degrees) between any two points in the trajectory, divided by the time difference between the two points. Directional change is measured as change in direction over time (Kitamura and Imafuku, 2015). It also incorporates the speed of change, indicating how frequently and how fast an animal changes its direction of movement. The mean and standard deviation of directional change have been previously used to quantify nonlinearity and irregularity in the trajectories of butterflies (Kitamura and Imafuku, 2015). **(5)** Mean sinuosity of a (constant step length) trajectory. Sinuosity can be defined as the total travelled distance/straight distance between the beginning and the end of a trajectory segment, and ranges between 0 (straight trajectory) and 1 (highly curved trajectory). This is a widely used movement metric to describe avian flight (e.g. Zavalaga et al., 2011; Tremblay et al., 2014; Corbeau et al., 2019). We calculated sinuosity following equation 8 in Benhamou (2004). We also considered **(6)** mean speed SD, **(7)** mean acceleration SD, and **(8)** mean directional change SD as measures on the variation of previous parameters within foraging trips' segments.

Mean speed and sinuosity were transformed for normalisation using a square root and log transformation respectively.

As an exploratory analysis and to provide a general overview of individuals' flight behaviour associated to the three former fisheries time slots ('no activity', 'diurnal activity', and 'nocturnal activity'), we first conducted a Principal Component Analysis (PCA) using *FactoMineR* R package (Lê et al., 2008). Next, linear mixed models were fitted on the movement metrics using the *nlme* R package (Pinheiro et al., 2020) to assess differences in average patterns in flight behaviour according to fisheries time slots. Besides fisheries time slots, flight duration, proportion of time over marine habitat and interaction with vessels were included as fixed effects in the model. Subjects were considered as a random effect. Also, as several foraging trip segments may come from a single foraging trip, we included trip ID as a random effect too. Moreover, the presence of autoregressive correlation was assessed by means of the ACF function implemented in the *nlme* package. In case of existence of significant autocorrelation an autoregressive effect of order 1 was included in the model. Additionally, quantile-quantile plots of residuals were used to check the normality assumption. The movement metrics differences among fisheries time slots were assessed by applying Wald's F-tests. In case of a significant result ($p\text{-value} < 0.05$) post-hoc comparisons were carried on using the Tukey's approach. We were not able to include other factors that may be have influenced gulls' behaviour, such as daily environmental conditions (e.g. winds, sea surface height). Nevertheless, in case of such effects really existed the consequence would be a larger random error in data making more difficult to find significant effects. Other factors that could influence our results but that were not included are age or sex. However, we argue that the fact that even not including these factors, we found significant behavioural differences, and relying on previous knowledge on the species, we can relate our findings to different fishing scenarios.

3. Results

We estimated eight quantitative movement metrics based on ca. 38,090 space-time locations from 362 gull foraging trips (Fig. 2). The results from the linear mixed models fitted on the movement metrics (Tables 2 and 3) showed contrasting flight behaviours among fisheries time slots. In particular, individuals flew faster in "diurnal activity" (mean of 14.73 km/h) than in "nocturnal activity" (mean of 11.88 km/h) or "no activity" (mean of 11.08 km/h) fisheries time slots, but no differences were found among the "nocturnal activity" and the "no activity" ones. A faster flight was particularly detected when they interacted with fishing vessels (likely trawlers) along the foraging trip segment (mean of 13.51 km/h; *vs* mean of 11.56 km/h; no interaction). A similar pattern arose from directional change, from which we can draw that gulls flew more directly (i.e. smaller mean directional change) in "diurnal activity" (mean of 5.70°) than in "nocturnal activity" (mean of 6.56°) or "no activity" (mean of 6.57°), which is consistent with the results on sinuosity. We also found that speed SD and acceleration SD were significantly larger in "diurnal activity" (mean of 12.80 km/h and 929.08 km/h^2) than in "nocturnal activity" (mean of 12.54 km/h and 796.49 km/h^2). In contrast, we found no differences among fisheries time slots in duration, but we found that birds that interacted with a fishing vessel along the foraging trip segment, had longer-lasting segments (in terms of time) than when they did not (Fig. 3, Tables 2 and 3, Figs. S5–S12).

These results were further confirmed by a PCA, in which we incorporated movement metrics (with PC1 and PC2 explaining 64.5% of the variation, Figs. S1–S3). Although it was an exploratory analysis, we observed some signal of differential gull flight behaviour associated to fishing activity, as shown by the centroids of the three fisheries time slots (diurnal activity, nocturnal activity and no activity; Fig. S4). According to the variables to which PCs were directly correlated, flights during the 'no activity' period were longer and more sinuous (PC1), but also slower (PC2). Foraging trips and all their parameters can be visualized in the R Shiny application hosted in the following link: https://jlcarrasco.shinyapps.io/Trajectories/.

4. Discussion

Understanding how marine species respond to the rapidly changing anthropized seascape is key to promote efficient management and

Table 2

Movement metrics estimates in the different fisheries time slots and in interaction/no interaction foraging trips. Results shown are: movement metric estimate, lower confidence interval (CI 95%), upper confidence interval (CI 95%) and p-value from the and p-value from the likely ratio test (LRT). Fisheries time slots are: no (no fishing activities), night (nocturnal fishing activity; purse seining) and day (diurnal fishing activity; trawling).

Movement metric	Fixed effect	Fisheries time slot	Estimate	Lower CI	Upper CI	p-value
Duration (hours)	Fisheries time slots	Nocturnal activity	3.20	2.63	3.88	
		Diurnal activity	3.27	2.84	3.76	0.66 (F = 0.42)
		No activity	3.42	2.89	4.03	
	Fishing vessel interaction	Interaction	4.57	3.96	5.27	<0.01 (F = 88.99)
		No interaction	2.37	2.07	2.72	
Speed mean (km/h)	Fisheries time slots	Nocturnal activity	11.88	11.15	12.63	
		Diurnal activity	14.73	13.59	15.92	<0.01 (F = 37.46)
		No activity	11.08	10.31	11.87	
	Fishing vessel interaction	Interaction	13.51	12.71	14.34	<0.01 (F = 115.14)
		No interaction	11.56	10.91	12.22	
Speed SD (km/h)	Fisheries time slots	Nocturnal activity	12.54	12.04	13.03	
		Diurnal activity	12.80	12.17	13.42	<0.01 (F = 10.86)
		No activity	11.20	10.57	11.83	
	Fishing vessel interaction	Interaction	12.75	12.22	13.29	<0.01 (F = 11.27)
		No interaction	11.60	11.12	12.08	
Acceleration mean (km/h^2)	Fisheries time slots	Nocturnal activity	1.30	−1.73	4.33	
		Diurnal activity	0.67	−1.55	2.88	0.93 (F = 0.07)
		No activity	0.56	−1.66	2.79	
	Fishing vessel interaction	Interaction	0.74	−1.31	2.79	0.87 (F = 0.03)
		No interaction	0.95	−0.88	2.78	
Acceleration SD (km/h^2)	Fisheries time slots	Nocturnal activity	796.49	760.11	832.87	
		Diurnal activity	929.08	868.23	989.92	<0.01 (F = 16.53)
		No activity	734.90	691.30	778.50	
	Fishing vessel interaction	Interaction	836.64	795.50	877.78	0.20 (F = 1.65)
		No interaction	803.67	766.62	840.72	
Sinuosity (dimensionless)	Fisheries time slots	Nocturnal activity	1.74	1.64	1.83	
		Diurnal activity	1.71	1.62	1.81	<0.01 (F = 4.70)
		No activity	1.85	1.75	1.95	
	Fishing vessel interaction	1.70	1.60	1.79	<0.01 (F = 8.80)	
		No interaction	1.84	1.75	1.93	
DC mean (°)	Fishing vessel interaction	Nocturnal activity	6.56	6.27	6.86	
		Diurnal activity	5.70	5.40	6.00	<0.01 (F = 14.54)
		No activity	6.57	6.32	6.83	
		Interaction	6.22	5.96	6.49	0.52
		No interaction	6.34	6.10	6.57	(F = 0.42)
DC SD (°)	Fishing vessel interaction	Nocturnal activity	183.89	169.27	198.52	
		Diurnal activity	149.76	135.49	164.04	<0.01 (F = 8.83)
		No activity	171.75	162.53	180.98	
		Interaction	168.95	157.24	180.65	0.89 (F = 0.02)
		No interaction	167.99	157.20	178.78	

Table 3
Movement metrics pairwise comparisons among fisheries time slots. Results shown are mean (0–1 scale), lower confidence interval (CI 95%), upper confidence interval (CI 95%) and p-value from the mean comparison test. Fisheries time slots are: no (no fishing activities), night (nocturnal fishing activity; purse seining) and day (diurnal fishing activity; trawling). Duration differences are log-transformed. Speed mean differences are square root transformed.

Movement metric	Fixed effect	Pairs	Estimate	Lower CI	Upper CI	p-value
Duration (hours)	Fisheries time slots	Night – No	0.07	−0.12	0.25	0.68 (t = 0.83)
		Day - No	0.04	−0.19	0.27	0.89 (t = 0.45)
		Day - Night	−0.02	−0.30	0.26	0.98 (t = −0.18)
	Fishing vessel interaction	Int. - No int.	0.65	0.52	0.79	<0.01 (t = 9.43)
		Night – No	−0.12	−0.30	0.07	0.29 (t = −1.51)
Speed mean (km/h)	Fisheries time slots	Day - No	−0.51	−0.72	−0.30	<0.01 (t = −5.63)
		Day - Night	−0.39	−0.62	−0.16	<0.01 (t = −4.01)
	Fishing vessel interaction	Int. - No int.	−0.28	0.13	0.42	<0.01 (t = 3.73)
		Night - No	−1.34	−2.30	−0.47	<0.01 (t = −3.40)
Speed SD (km/h)	Fisheries time slots	Day - No	−1.60	−2.50	−0.74	<0.01 (t = −4.38)
		Day - Night	−0.26	−1.17	0.69	0.79 (t = −0.65)
	Fishing vessel interaction	Int. - No int.	−1.15	0.49	1.85	<0.01 (t = −3.36)
		Night - No	−0.74	−4.06	4.38	0.92 (t = −0.38)
Acceleration mean (km/h^2)	Fisheries time slots	Day - No	−0.10	−2.97	4.79	0.99 (t = −0.07)
		Day - Night	0.63	−3.77	5.27	0.94 (t = 0.32)
	Fishing vessel interaction	Int. - No int.	0.21	2.75	3.18	0.87 (t = 0.16)
		Night - No	−61.60	−128.05	0.15	0.07 (t = −2.19)
Acceleration SD (km/h^2)	Fisheries time slots	Day - No	−194.20	−267.08	−112.55	<0.01 (t = −5.75)
		Day - Night	−132.60	−207.48	−44.25	<0.01 (t = −3.76)
	Fishing vessel interaction	Int. - No int.	33.00	−16.04	84.23	0.20 (t = 1.29)
		Night - No	0.12	0.00	0.22	<0.05 (t = 2.45)
Sinuosity (dimensionless)	Fishing vessel interaction	Day - No	0.14	0.02	0.26	<0.05 (t = 2.79)
		Day - Night	0.025	0.02	0.26	0.87 (t = 0.51)
		Int. - No int.	−0.15	−0.24	−0.05	<0.01 (t = 2.97)
		Night - No	0.01	−0.40	0.43	0.99 (t = 0.06)
DC mean (°)	Fishing vessel interaction	Day - No	0.88	0.45	1.30	<0.01 (t = 4.85)
		Day - Night	0.87	0.42	1.30	<0.01 (t = 4.60)
		Int. - No int.	−0.11	−0.45	0.22	0.52 (t = 0.65)
		Night – No	−12.10	−31.02	7.32	0.30 (t = −1.49)
DC SD (°)	Fishing vessel interaction	Day - No	22.00	3.93	40.35	<0.05 (t = 2.84)
		Day - Night	34.10	13.56	54.52	<0.01 (t = 4.09)
		Int. - No int.	0.95	−12.63	14.50	0.89 (t = −0.14)

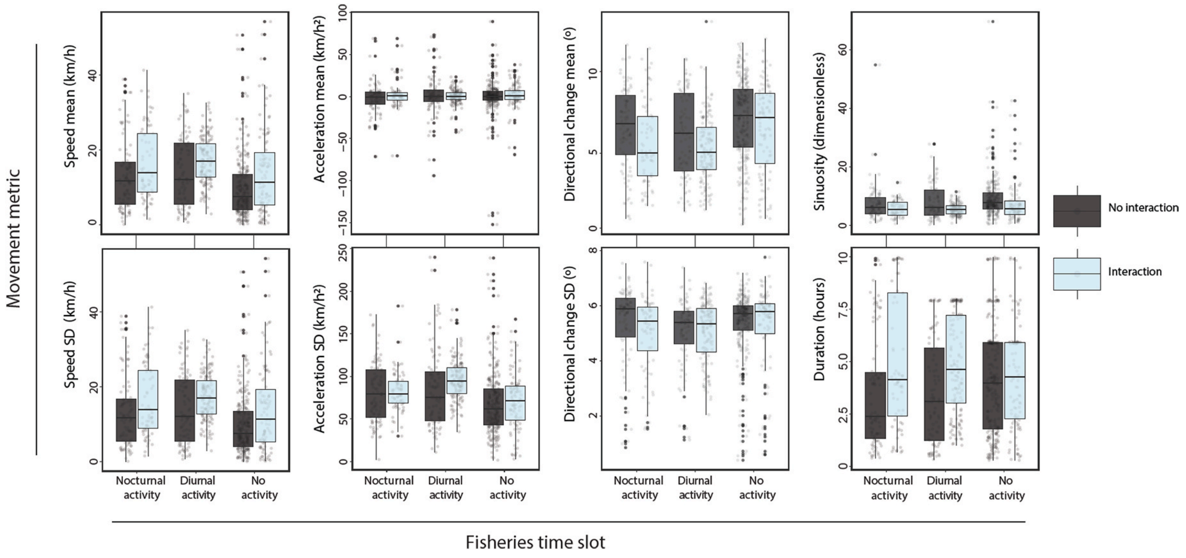

Fig. 3. Movement metrics split by fisheries time slot and grouped by whether gulls interacted with a fishing vessel within fisheries time slots (interaction) or not (no interaction).

conservation measures (Hays et al., 2016), but may also contribute to monitor human drivers of environmental change (Ramírez et al., 2015; Navarro et al., 2016). Previous research based on contrasting techniques (from biologging to boat-based surveys) has broadly shown that Audouin's gull are very plastic, and can modulate its habitat use and daily patterns of activity depending on the presence/absence of fishing activity (Oro, 1995; JM Arcos and Oro, 2002; Christel et al., 2012; Bécares et al., 2015; Ouled-Cheikh et al., 2020). However, we provide additional evidence on the role of human fisheries in shaping the flying behaviour of a paradigmatic opportunist species that efficiently exploits human associated food subsidies and feeding opportunities.

Fisheries have shaped seabirds' behavioural tactics (e.g., through previous experience) by providing the individuals with abundant, predictable and accessible food resources in the form of discards (both purse seiners and, mainly, trawlers: Hudson and Furness, 1988; Abelló et al., 2003; Petersen et al., 2009) and/or feeding opportunities (i.e., resource facilitation through fish concentrations near the surface or in the water column, as in the case of purse seiners or long-liners: Petersen et al., 2009). In our case, individuals flew faster and in a smoother manner (i.e. lower values of directional change) when there was fishing activity, and particularly when they were interacting with trawlers. This might be interpreted as a likely mechanism to optimize energy gain by increasing the intake of human food subsidies (by accessing earlier these food resources and feeding opportunities) while reducing foraging costs (i.e., costs of searching for food patches; Mullers et al., 2009). Furthermore, we found speed SD and acceleration SD differences when gulls temporally co-occurred with trawlers (higher) or with purse seiners (lower). This may respond to gear-specific fishing practices, as trawling occurs in movement and with variations in speed (lower speed during trawls than during transportation to fishing grounds), and purse-seining occurs in a static way. These patterns of differential behaviour in relation to intermittent fishing activity have been described in other seabird species, like in the case of the Balearic shearwater *Puffinus mauretanicus* and Cory's shearwater *Calonectris diomedea* (Bartumeus et al., 2010), or the white-capped albatross *Thalassarche steadi* (Torres et al., 2011).

Conversely, when predictable human food subsidies are not available (i.e., no fishing activity), individuals breeding in the Ebro Delta need to search for scattered prey patches in a highly heterogeneous marine landscape or in the surrounding rice fields. At sea, the Audouin's gull naturally feeds on small pelagic fish like European sardine (*Sardina pilchardus*) or European anchovy (*Engraulis encrasicolus*), taking advantage of their diel migrations (Blaxter and Hunter, 1982; Arcos and Oro, 2002). Small pelagic fish have been reported to preferentially occur within particular environmental conditions in our study area (Palomera et al., 2007; Pennino et al., 2020), which can provide their predators with certain predictability regarding the optimal locations and set ups to find them. However, even if the marine environment can be somehow predictable, the availability and accessibility of natural prey is still way less predictable than anthropogenic food subsidies provided by fishing activities (Weimerskirch, 2007). This could be a plausible reason for the higher directional change of the foraging trips we observed in Audouin's gulls when fishing vessels were absent.

Fisheries-induced behavioural changes may have important implications in individuals' energy balance (i.e., food intake vs. foraging costs), with potential impacts on fitness and performance. Moreover, prey quality may vary among fishing scenarios, as in the case of interaction with trawlers, when gulls obtain demersal, energy-poor prey ($4.07\ \text{kJ}\cdot\text{g}^{-1}$; Batchelor and Ross, 1984), contrasting with the interaction with purse seiners, in which gulls usually obtain small pelagic species (e.g. European sardine, European anchovy) which are considered higher quality prey ($8.59\ \text{kJ}\cdot\text{g}^{-1}$; Batchelor and Ross, 1984; Albo-Puigserver et al., 2017). Small pelagic fish are also the natural prey of Audouin's gulls, so when feeding at sea in a non-fishing scenario, they may search for these energy-rich species, but the overall energy budget may be lower due to the larger directional changes we reported in non-fishing scenarios, which may enhance energy consumption while foraging. Yet, we did not assess energetics in this study, which opens opportunities for future research.

5. Conclusions and perspectives

In this study, we showed that Audouin's gull is able to adapt its flight behaviour in relation to the presence/absence of fishing activity. Our research is in concurrence with other studies that conducted analysis on seabird-fisheries interactions, showing that the presence of fishing activities shapes flight behaviour in a similar manner across different seabird taxa (Bartumeus et al., 2010; Torres et al., 2011; Collet et al., 2015). Our study adds further evidence, showing that flight behaviour can vary not only in presence/absence of fishing activities, but also depending on the fishing activity that is conducted (trawling/purse seining in our case). In a broader context, the interaction of opportunistic seabird species with discard-providing fishing vessels can have benefits for seabird populations, as they constitute a predictable food source both in space and time. Even though, sudden shortage of these resources as a consequence of new legislations such as the discard ban policy (the so-called landing obligation: EU Common Fisheries Policy; Borges, 2015), or the collapse of commercial fish stocks, may increase the tendency to natural feeding of this species, and thus their energy expenditure on foraging, which in combination with the depletion of the stocks of its natural prey may have deleterious consequences such as a decreased breeding success, or the location change of current colonies (Oro et al., 1995; Arcos and Oro, 2002). Our results thus provide a basis that may serve in the future to compare flight behaviour of this species in a scenario with no food subsidies at all, which may allow to better understand future colony dynamics. Our results may also contribute to monitoring fishing activities using seabirds. This is particularly relevant for IUU fisheries and/or those areas where fishing activity is not properly monitored by other means (e.g., through VMS or AIS).

Ethics approval and consent to participate

All authors agree to participate in this paper.

All work was carried out with the necessary permits, awarded by both the Wildlife Service of the Catalan Government and the Ebro Delta Natural Park. A detailed description and justification of the fieldwork procedures was presented to these institutions, including the use of harnesses and timeliness of device removal, to get these permits. Handling time was minimized to reduce any inconvenience to the birds, not exceeding 10 min in any case. Birds were captured in daylight hours, avoiding periods when either low (dawn) or high temperatures (noon) could pose a problem for the eggs. Whenever a bird was reluctant to get captured, we left it. The tags represented 3–5% of the weight of the birds; about the recommended limit when the fieldwork was conducted.

Consent for publication

The authors consent the publication of this paper.

Foraging trips and all their parameters can be visualized in the R Shiny application hosted in the following link

https://jlcarrasco.shinyapps.io/Trajectories/.

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CRediT authorship contribution statement

Jazel Ouled-Cheikh: Writing – review & editing, Writing – original draft. **Francisco Ramírez:** Writing – review & editing, Writing – original draft, Conceptualization. **Moisès Sánchez-Fortún:** Conceptualization. **Augusto Cortejana:** Formal analysis. **Carola Sanpera:** Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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