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Original Article

Spatiotemporal analyses of tracking data reveal fine-scale, daily cycles in seabird–fisheries interactions

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Human fisheries provide scavengers with abundant and predictable feeding opportunities that may schedule their behavioural patterns. Using miniaturized global positioning system (GPS) tracking technology, we evaluated how Audouin's gull (*Ichthyaetus audouinii*), a Mediterranean endemic seabird that makes extensive use of feeding opportunities provided by fisheries, co-occurred (i.e. presumably interacted) with the most important fishing fleets operating off the NE Iberian Peninsula (i.e. diurnal trawlers and nocturnal purse seiners), both in space and time. Results showed that individuals were able to adapt their distribution and activity patterns to the scheduled routines of these fisheries. Waveform analyses based on co-occurring positions revealed that most interactions with trawlers occurred during the afternoon (16:00 h GMT + 1) when discarding occurs as vessels return to port. In contrast, gull-purse seiner interactions largely occurred at night (between 02:00 and 04:00 h) coinciding with the setting and hauling of the nets. Moreover, we found an individual component in seabird–fishery interactions, showing that there may be differential use of fisheries by individuals within the population. In addition to implications for our understanding of the behavioural ecology of this species, these results may have important management implications, particularly under the current European Union Common Fisheries Policy scenario of largely restricting discards.

Keywords: discards, fisheries, gulls, interaction, Mediterranean

Introduction

The marine environment is likely one of the most impacted biomes on Earth (Halpern *et al.*, 2015; Ramírez *et al.*, 2017). In addition to human-driven climate impacts, pollution and habitat degradation, marine resource overexploitation is causing severe changes to marine ecosystems and biodiversity (Cury *et al.*, 2011). For instance, fishing activities have resulted in the complete exploitation of 60% of fish stocks worldwide, whereas 33% are overexploited and 7% are depleted (FAO, 2018). Changes in fish abundances caused by fisheries may have further implications within the marine food webs (Pauly *et al.*, 1998; Essington *et al.*, 2006) with ultimate, often exacerbated, impacts on top predators through bottom-up trophic cascades (Frederiksen *et al.*, 2006; Lynam *et al.*, 2017). Concurrently, human fisheries may also impact these marine predators through direct mortality (i.e. bycatch, Lewison *et al.*, 2014), food depletion (through marine resource overexploitation), or by providing resources that would not be naturallyavailable otherwise (Hudson and Furness, 1988). These new feeding opportunities are largely driven by fisheries' discards,which is the part of the catch returned to the sea (Damalas, 2015).

Fishing discards represent ca. 10–20% of the global worldwide catch (Zeller *et al.*, 2018). Discarding occurs at specific times and locations, thus resulting in one of the most important and predictable anthropogenic food subsidies in the marine ecosystems worldwide (Oro *et al.*, 2013). Many species take advantage of this food subsidy and have adapted their distribution and activity patterns to the scheduled routines of human fisheries (Oro *et al.*, 2013). This is the case for some seabirds, whose foraging behaviour, habitat use, and movement patterns are highly affected by the presence/absence of fishing activity and, thus, of discards (Bartumeus *et al.*, 2010; Bodey *et al.*, 2014; Tyson *et al.*, 2015). This can have an influence on species habits with ultimate consequences on life history traits, population dynamics, biotic interactions and community structure (Oro, 1999; Votier *et al.*, 2004; Votier *et al.*, 2008; Laneri *et al.*, 2010; Soriano-Redondo *et al.*, 2016; Calado *et al.*, 2018; Sherley *et al.*, 2020). Opportunistic species with high adaptability can take particular advantage of this resource (Oro *et al.*, 2013), since discards can lead to highly competitive feeding interactions (Arcos *et al.* 2001; Calado *et al.*, 2018). The favoured species make up the communities of scavengers that feed on discards. These communities can vary greatly across different geographic locations in terms of species (Weimerskirch *et al.*, 2000; Louzao *et al.*, 2011; Tyson *et al.* 2015). In the Western Mediterranean, these communities are typically dominated by yellow-legged gulls (*Larus michahellis*), Balearic shearwaters (*Puffinus mauretanicus*), Audouin's gulls (*Ichthyaetus audouinii*), and Cory's shearwaters (*Calonectris diomedea*) (Arcos, 2001; Abelló *et al.*, 2003; Louzao *et al.*, 2011).

Scavenging seabird communities will likely be impacted by shortages in discards such as the one currently underway in the European Union (EU). A discard ban policy (the so-called landing obligation) has been progressively implemented since 2015 under the current EU Common Fisheries Policy (Borges, 2015) and was expected to be fully in place in 2019. However, in Spanish waters, progress towards this implementation has been weak, and to date the policy is not properly in place largely due to the lack of infrastructure needed to take all of the caught fish to the harbours (Fishing Advisory Service, pers. comm.). Thus, the food shortage faced by scavenging seabirds within the Spanish EEZ is a concern of the near future.

Reliable assessments on seabird–fishery interactions are key to providing reliable insights on how communities will respond when discards are no longer available (or severely reduced, Oro *et al.*, 2013). Many of the previous assessments on the interaction between seabirds and fisheries have considered either the temporal (Tyson *et al.* 2015) or the spatial dimension, with special attention to the latter (Yorio *et al.*, 2010; Cama *et al.*, 2012; Cama *et al.*, 2013; Bécares *et al.* 2015). Others have addressed this issue by integrating both dimensions simultaneously (Votier *et al.*, 2010; Granadeiro *et al.*, 2014). However, to the best of our knowledge, no previous works have addressed this issue using a spatio-temporal approach to assess daily patterns of interactions throughout periods of contrasting fishing activity. This approach can provide further insights into these interactions and can be key to assessing or predicting possible responses or consequences for seabirds as changes in discard availability occur.

Based on GPS tracking data for Audouin's gulls and fishing vessels [through miniaturized data loggers and the vessel monitoring system (VMS), respectively], we evaluated gull-fishery co-occurrences in both space and time throughout daily cycles on workdays (with fishing activity) and weekends (without fishing activity). This allowed us to investigate at a finer scale how the Audouin's gull interacts with the fishing fleet of the NE Iberian Peninsula in a *pre-ban* scenario (2011). The Audouin's gull largely relies on discards (Oro *et al.*, 1999; Arcos *et al.*, 2001) and, hence, constitutes an ideal model species to evaluate potential impacts of changes in fisheries dynamics. We predicted that gulls would adjust their feeding strategies to fleet-specific activity patterns by co-occurring with trawlers (diurnal) and purse seiners (nocturnal). In other words, we predicted that the interactions would occur at those times and locations at which the fishing boats provide the best feeding opportunities. On the other hand, based on the existence of individual and distinguishable strategies within the opportunistic/generalist species populations (e.g. Navarro *et al.*, 2010), we predicted a heterogeneous use of this trophic resource between individuals of this population. The information provided could be useful in making comparisons to *post-ban scenarios*, and to assessing other future changes in the interaction of birds and fisheries, especially when human food subsidies such as discards are involved in the interaction.

Material and methods

Study area and species

The study area was defined from the movements of the GPS-tracked Audouin's gulls breeding at the Punta de la Banya colony (40°40′N 0°45′E), a protected sandy peninsula with salt pans in the Ebro Delta Natural Park (NE Spain) (Figure 1). The area comprised the NE Levantine coast of Spain and extended from the coast over the continental shelf to the upper slope. There are numerous fishing ports scattered along the coast of the study area, which is the most important fishing ground for clupeids and demersal resources in the Mediterranean due to the wide continental shelf and the nutrients contributed by the Ebro River (Maynou *et al.*, 2008). This supports two main fishing activities: trawling (diurnal activity 07:00–17:00 h GMT + 1, Figure 2a and b) and purse seining (nocturnal activity, starting at 23:00 h and with no return limit, Figure 2a and c). The fishing activity of both fleets is concentrated on the weekdays (Monday–Friday), with no fishing activity on 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, and two to four trawls can be carried out per day. In the Ebro Delta, the trawling fishing vessels begin to produce discards around 11:00 h. However, it is at the end of the fishing day, between 16:00 and 17:00 h, when all the fishing vessels discard simultaneously as they approach the fishing ports. This results in an abundant and highly predictable food resource for marine scavengers (Martínez-Abraín *et al.*, 2002; Karris *et al.*, 2018). This

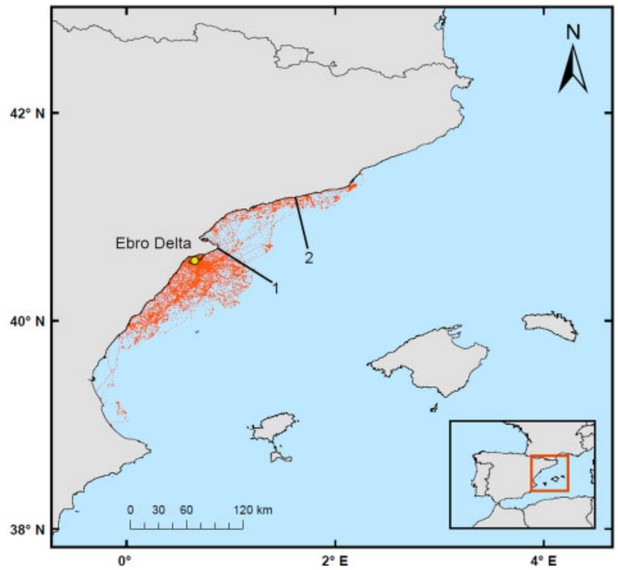

Figure 1. Spatial distribution of GPS-tracked Audouin's gulls at the NE Levantine coast of Spain. This area encompasses the most important fishing ground for clupeids and demersal resources in the Mediterranean. Orange dots indicate at-sea locations for tracked gulls recorded every 5 min during the 2011 breeding season. The area between 1 and 2 was under a trawling moratorium during the study period.

contrasts with nocturnal purse-seining activity, which produces few discards but can affect the foraging behaviour of scavengers through a process of resource facilitation, as it concentrates epipelagic fish close to the surface (Arcos and Oro, 2002). The study period coincided with a trawling moratorium established north of the Ebro River (Figure 1).

The Ebro Delta holds one of the most important colonies of Audouin's gull in the world, with up to two-third of the global population in the past, though it has experienced important fluctuations in numbers through time (BirdLife International, 2020a, b). Before the 1980s, the Audouin's gull was a scarce species in the Mediterranean, but during the 1980s and the 1990s, the studied colony in the Ebro Delta grew exponentially coinciding with the development of the fishing activity in the study area (Oro and Martínez-Vilalta, 1992). This exponential growth was likely due to the exploitation of the highly available human subsidies, particularly of discards (Oro and Martínez-Vilalta, 1992). In 2011, when the study was carried out, there were 11.967 breeding pairs, representing ca. 60% of the global population (Ebro Delta Natural Park, pers. comm.). The Audouin's gulls breeding at the Ebro Delta typically share their foraging distribution between terrestrial (mainly rice fields) and marine areas close to the colony (Christel *et al.*,2012; Bécares *et al.* 2015), where they often interact with fishing vessels (Oro *et al.*, 1996).

Fieldwork procedure

Between 8 May 2011 and 26 May 2011 (the incubation period), 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, Perthold, 2011) every 5 min. Devices were sealed using a rubber 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 3–5% of the bird's body mass. This threshold was below the accepted limit for deleterious effects on individual birds when the tagging was conducted (Wilson *et al.*, 2002; Phillips *et al.*, 2003). However, recent works suggest a potential tag effect for thresholds >1% (Bodey *et al.*, 2018). Although a tag effect on these individuals cannot be ruled out completely, we argue that this potential effect will homogeneously impact tracking gulls throughout daily cycles, so that our analyses on daily activity patterns are still valid. Thirty-six tagged birds were recaptured between 1 and 2 weeks after the deployment of GPS devices. Recorded data included GPS positions for these 36 individuals between 8 May and 26 May. 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 ; last accessed in October 2018) wind speed for the study period was mean ± *SD*: 3.55 ± 2.27 m s^{-1}].

Data analyses

Habitat use

We compared the differential use of the sea by the gulls on weekdays (Monday–Friday; period with fishing activity) and weekends (Saturday and Sunday; period without fishing activity) using the proportion of time spent at sea or inland (mainly in rice fields). A foraging trip was defined to include the locations from when a bird left the colony (500 m radius around it) until it returned (BirdLife International, 2005). For each study day, all the foraging trips were taken into account. The proportion of time spent at sea on each foraging trip in terms of the trip total duration was calculated, thus obtaining the daily use of the sea by the gulls. A linear mixed model was fitted, with the logit transformation of the proportion of time spent in each habitat as the dependent variable and the type of day (i.e. weekday and weekend) as the explanatory variable and individual as the random effect.

Activity rhythms and gull–fisheries interaction

We performed a waveform analysis on the daily use of the sea of both the fishing vessels and the gulls, to determine their daily temporal patterns of activity (Figure 2a). GPS locations for gulls were grouped into 2-h intervals, following the temporal resolution for VMS data. A total number of bird or boat positions per time interval were subsequently averaged to obtain a representative 24 h profile (the waveform) of the 17 days of sampling. The phase, defined as the significant increase in sea use by gulls and fisheries, was determined for each waveform by calculating the midline estimating statistic of rhythm (MESOR; Aguzzi *et al.*, 2015). The MESOR was computed by re-averaging all waveform values and was plotted as a threshold in the waveform plot. Waveform values above the MESOR indicated a significant use of the sea in a cyclic way, i.e. the phase.

We combined spatiotemporal information on the distribution of gulls and fishing vessels to assess gull–fishery interaction. To do so, we first retained bird positions within a 500 m and 20 min (i.e. ±10 min) buffer around fishing vessel positions (based on VMS positions at 2-h intervals). We selected this spatial threshold after a sensitivity analysis revealing that the number of individuals interacting within a given spatial buffer increased between 0 and

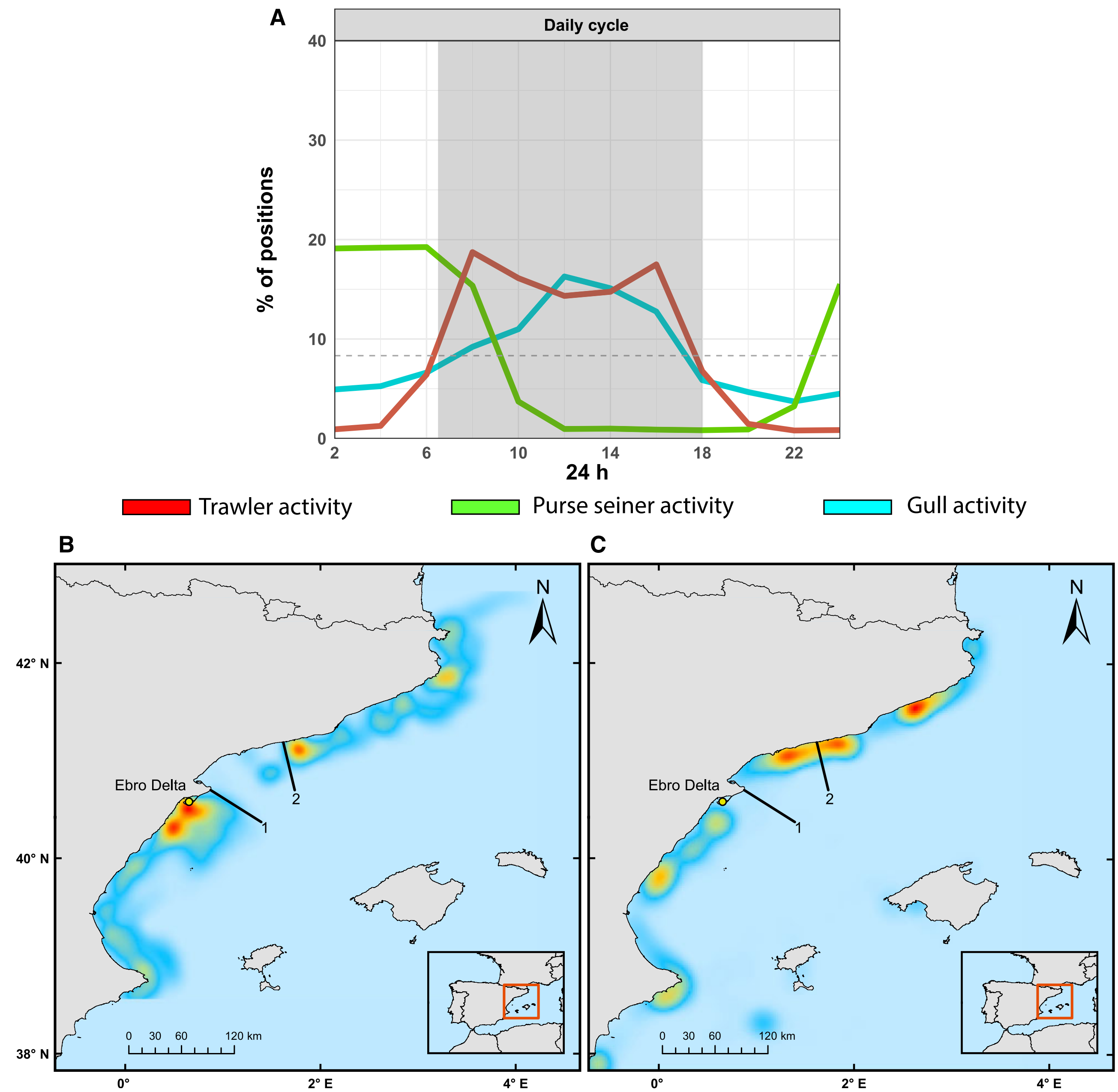

Figure 2. Daily activity rhythms for fishing gear (trawlers and purse seiners) and Audouin's gulls (a). The shaded area in (a) shows the period above theMESOR (phase of the cycle) defined as the significant increase in sea use by gulls and represented by the dashed line. Values in the *x*-axis represent time intervals within a 24 h cycle (e.g. 2 = period between 00:00 and 02:00 h; alike for all the other time intervals). The spatial distribution of trawlers (b) and purse seiners (c) is represented using a kernel density plot. The area between 1 and 2 in (b) and (c) was under a trawling moratorium during the study period.

200 m, but that it stabilized between 300 and 500 m. Thus, we selected the 500 m buffer for a more conservative approach. Filtered positions were subsequently included in a waveform analysis to test when the interactions occurred, and to estimate the number of bird positions within our spatiotemporal buffer in a specific time interval (as a proxy for the interaction magnitude). Finally, we carried out a kernel analysis of density for the interacting positions to visualize where the interactions were produced using the Kernel function of ArcMap (version 10.6, ESRI, United States).

The individual component of seabird–fishery interactions

We assessed the repeatability in the individual feeding strategies to evaluate whether there were different strategies within the population regarding the interaction (co-occurrence) with fishing vessels (likely driven by fishing discard exploitation). For every gull trip, we calculated a minimum, dimensionless distance between gulls and fishing boats that accounted for both the temporal and the spatial dimensions and was standardized to the above-defined spatiotemporal buffer. This minimum distance can be interpreted as the number of spatiotemporal buffers (i.e. 500 m and ±10 min) between a fishing vessel and a gull for a specific trip. We used these distances as an indicator of the degree of gull–fishery interaction to assess the repeatability in feeding strategies. These strategies can range from a high degree of interaction (consistently small distances) to a low degree of interaction (consistently large distances), with some intermediate strategies. The repeatability was evaluated by estimating the intraclass correlation coefficient (ICC) using a linear mixed model. ICC values range from 0 to 1, with higher ICC values indicating high intra-individual repeatability in feeding strategies, while lower ICC values denote individuals behaving randomly. R Statistical Software was used to compute the spatiotemporal buffers, compositional analysis and ICC (nlme package, version 3.1-142, R Development Core Team, 2008).

Results

Based on 36.251 recorded positions outside the colony, Audouin's gulls preferentially used the terrestrial environment (58% of positions) with less contribution by the marine environment (42% of positions) to overall habitat use by gulls. However, the relative contributions to habitat use differed between weekdays and weekends, with the proportion of time spent at sea during weekdays (0.36, *CI* 95% 2.61–1.85–4.84; $p < 0.001$) three times greater than weekends.

Gulls' daily activity patterns also differed between weekdays and weekends. On weekdays, the temporal patterns of sea use by gulls largely matched those of trawling boats, i.e. from 07:00 to 17:00 h, thus both being diurnal (Figure 2a). In the case of the purse seiners, the phase of the activity pattern was from 22:00 to 08:00 h (Figure 2a) and thus coincided less with that of the gulls. However, there was an overlap of 2 h, from 06:00 to 08:00 h, when both fleets and the gulls were at sea. On weekends, when there is no fishing activity, the temporal pattern of sea usage by the gulls changed noticeably, with significant sea use from 23:00 to 06:00 h, and thus being mainly nocturnal (Figure 3b).

On weekdays, we detected a stepwise increase in the magnitude of gull interaction with trawlers from 09:00 to 16:00 h, with a maximum at 16:00 h (38.8%). The magnitude of birds' interactions with trawlers sharply decreased after 16:00 h, reaching 8.3% by 18:00 h. Regarding interactions with purse seiners, there was a marked increase in the magnitude of the interactions from 02:00 to 04:00 h, during which interactions peaked (33.1%). From 04:00 h on, there was a clear decrease in the magnitude of the interaction, reaching 8.3% just before 10:00 h (Figure 3a). Averages and standard deviations for every analysis are provided in Table 1.

Regarding the geographic location of seabird–fishery interactions, our results showed that the interactions were concentrated within the 30 km south of the colony, near the main fishing ports of the area (Figure 3c).

Using the minimum distances as an indicator of gull–fishery interaction, we estimated that 47.6% of the trips at sea entered the spatiotemporal buffer (500 m, ±10 min) of distance around fishing vessels. However, we also detected a large heterogeneity among individuals showing minimum distances that ranged from 0.02 to 19.3 buffers of distance, thus indicating a degree of structuring in the foraging strategies within the population (Figure 4). We observed a repeatability of 34% (ICC 0.34, 95% *CI* 0.1963–0.4765, $p < 0.001$), a value rated as "fair" on the scale provided in Landis and Koch (1977).

Discussion

It is well known that fishing activity provides substantial food for opportunistic seabirds (Tasker *et al.*, 2000; Bécares *et al.*, 2015). However, to the best of our knowledge, no previous works have addressed seabird–fisheries interactions at a fine enough scale to investigate daily patterns as a likely response to the scheduled routines of human fisheries. Based on our new spatiotemporal approach, we show that Audouin's gulls scheduled their behaviour to that of fishing vessels, presumably to benefit from the feeding opportunities provided by the vessels, in the form of discards (both purse seiners and, mainly, trawlers) and/or fish congregating near the surface (purse seiners) (Arcos and Oro 2002). However, these feeding strategies were not homogeneous within the population, with different tracked individuals showing differential usage of these anthropogenic feeding opportunities (as predicted for opportunistic species, Navarro *et al.*, 2010; Ceia *et al.*, 2014). These results provide further insights into the dependence of scavenger seabird communities on human food subsidies but may also have implications for the management and conservation of these species, particularly within the current context of changes in fishing policies.

Opportunistic scavenger species can shape their schedules and their use of habitat depending on human activities (Tyson *et al.*, 2015; Parra-Torres *et al.*, 2020). Accordingly, Audouin's gulls showed a differential use of the sea depending on whether it was a weekday or a weekend, presumably/most likely driven by fishing activity schedules at our study area, as vessels only operate from Monday–Friday (Bécares *et al.*, 2015). The daily pattern of sea-use by gulls matched that of the trawlers and purse seiners on weekdays, providing some additional evidence regarding gull–fishery interactions (Bécares *et al.*, 2015). However, accurate assessments on seabird–fishery interactions require a detailed spatiotemporal approach as the one provided in the current study, and based on co-occurrences between tracked seabirds and fishing vessels within spatiotemporal buffers around fishing vessel positions.

Based on our spatiotemporal approach, we observed a higher degree of co-occurrences (and likely interactions) between seabirds and trawlers. This can be explained by the large amounts of discards usually provided by this type of fishing gear (Stithou *et al.*, 2019). The magnitude of the interaction increased gradually from the start of the fishing day (07:00 h) until 16:00 h, when it reached its maximum. This peak of interaction coincides with the time at which trawlers are returning to port and are thus more concentrated and closer to the coast and the colony, as they continue sorting out their catch and discarding.

Purse seiners operate nocturnally and usually produce few discards (Arcos and Oro, 2002). There was a sharp increase in the magnitude of interaction between seabirds and purse seiners from 02:00 to 04:00 h (i.e. half of the working day for purse seiners). At that time, the nets are usually pulled out of the water and there is a large concentration of available fish at the surface (Arcos and Oro, 2002). Purse seiners also use a large lamp to attract fish, improving visibility for birds and thus making it easier to catch the fish (Arcos and Oro, 2002). This can be considered a process of resource facilitation (Daleo *et al.*, 2005), as it allows the gulls to easily pick fish from the surface by dipping (Gaston, 2004). This is somewhat similar to the natural feeding strategy of the Audouin's gull feeding on epipelagic fish (Blaxter and Hunter, 1982; Arcos and Oro, 2002) or interacting with tuna

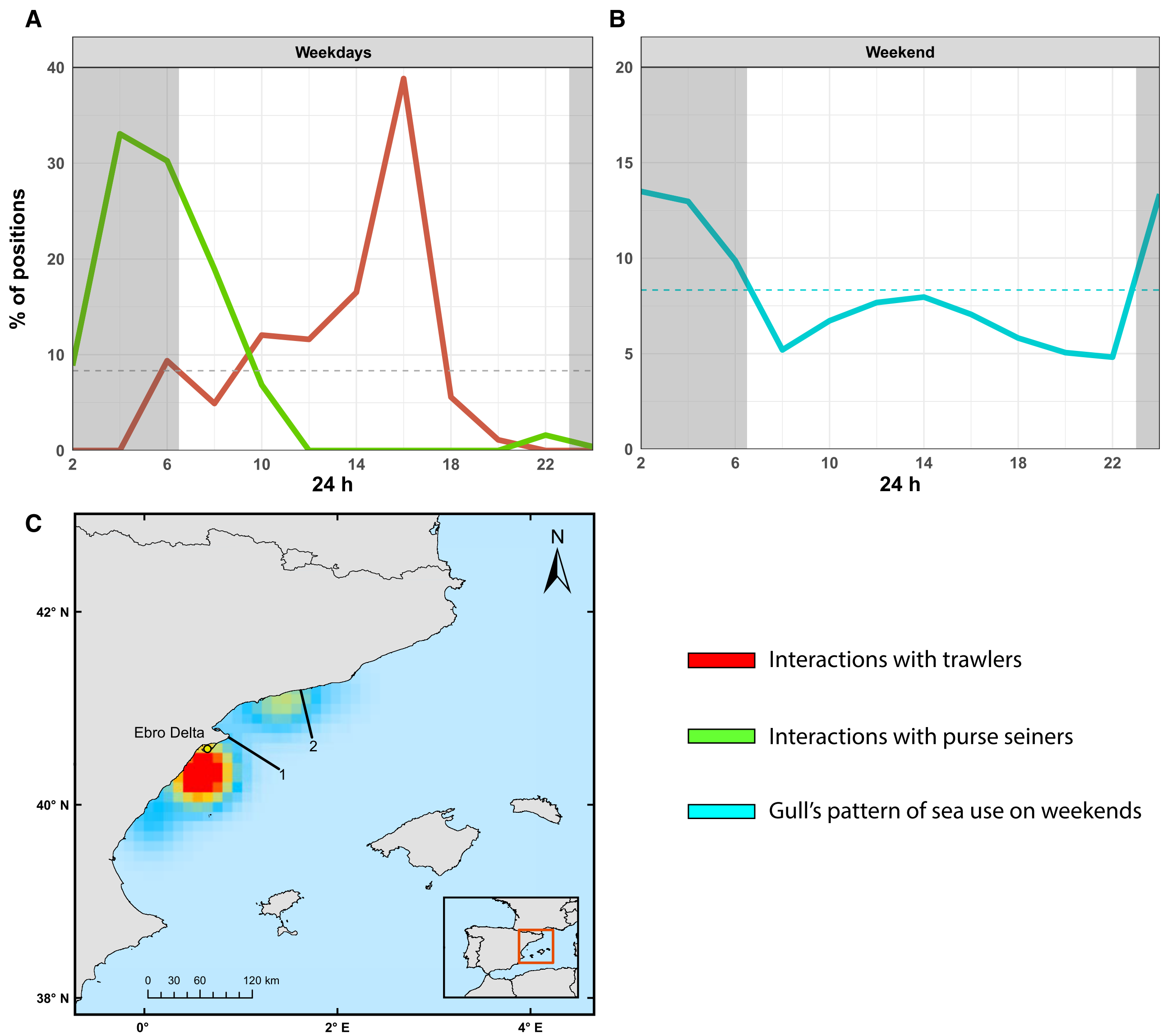

Figure 3. Daily rhythms of interaction between Audouin's gulls and fishing boats (i.e. trawlers and purse seiners) (a). (b) Daily activity rhythm of gulls during the weekend, when no fishing gears operate in the area. Shaded areas in (a) and (b) represent the areas above the MESOR (phase of the cycle) defined as the significant increase in sea use by gulls and represented by the dashed line. Values in the *x*-axis represent time intervals within a 24-h cycle (e.g. 2 = period between 00:00 and 02:00 h; alike for all the other time intervals). The spatial distribution of gull–fisheries interactions (c) is represented through a kernel density visualization of co-occurring locations. The area between 1 and 2 in (c) was under a trawling moratorium.

schools (Oro, 1995). In regard to the nocturnal activity, this could be explained by individual specialization or some sort of competitive exclusion (Hardin, 1960), as discarding (produced by the diurnal activity of trawlers) generates highly competitive interactions (Arcos *et al.*, 2001; Calado *et al.*, 2018).

Seabird–fisheries interactions largely occurred within an area located ca. 30 km south of the colony for both types of fishing gear. The fishing activity is carried out all along the Levantine Iberian coast (Figure 2b and c), with some hotspots in particular locations. During the study period, a trawling moratorium was implemented north of the colony, thus preventing interactions in that area. On the other hand, the proximity of the interaction hotspot to the colony can also be explained by the breeding stage and central-place foraging, as during the breeding season, the birds are energetically constrained and do not search far from the colony to find their prey (Orians and Pearson, 1979).

Our spatiotemporal approach revealed that gulls interacted with fishing vessels (i.e. entered the spatiotemporal buffer) during ca. 50% of their trips to sea. However, these values might be underestimated, as the VMS data were collected every 2 h, thus limiting the evaluation of interactions to 2-h intervals. Despite this constraint, we were able to detect an individual component (i.e. specialization) in seabird–fishery interactions, with differing degrees of interaction with both trawlers and purse seiners. Individual specialization is known to be widespread across a diverse set of taxa (Bolnick *et al.*, 2003), and particularly among generalist predators (Woo *et al.*, 2008, Tyson *et al.*, 2015, Navarro *et al.*, 2017), like the Audouin's gull (Christel *et al.*, 2012). The

Table 1. Mean values and standard deviation for both the number of GPS positions of tracked Audouin's gulls within the spatiotemporal buffers (i.e. 500 m and ±10 min) around fishing vessels that we have used in the waveform analysis shown in Figure 3.

Hour interval	Mean trawling interaction (% positions)	SD trawling interaction (% positions)	Mean purse seining interaction (% positions)	SD purse seining interaction (% positions)	Mean gulls (% positions weekend)	SD gulls (% positions weekend)
0–2	0	0	8.87	3.25	13.5	67.95
2–4	0	0	33.06	12.11	13	56.4
4–6	9.38	5.24	30.24	8.50	9.87	31.04
6–8	4.91	2.34	18.95	5.82	5.2	9.97
8–10	12.05	4.40	6.85	2.63	6.72	33.71
10–12	11.61	3.88	0	0	7.68	43.35
12–14	16.52	6.96	0	0	7.96	28.87
14–16	38.84	7.80	0	0	7.06	39.90
16–18	5.58	3.6	0	0	5.82	34.21
18–20	1.12	1.58	0	0	5.05	32.86
20–22	0	0	1.61	0.75	4.82	31.49
22–24	0	0	0.40	0.28	13.4	77.82

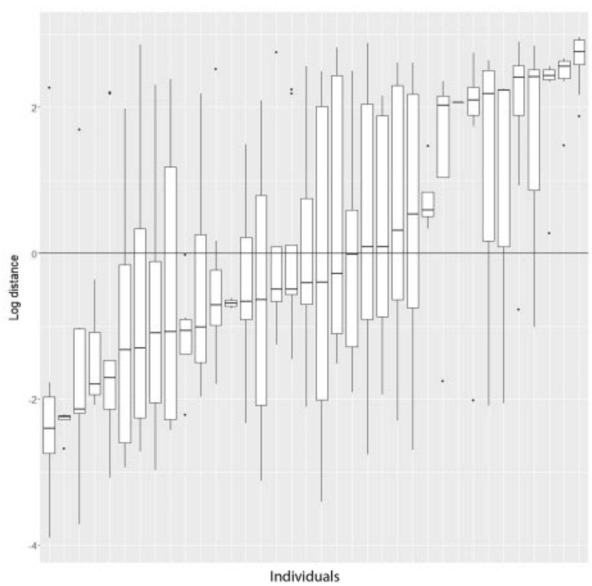

Figure 4. Boxplot showing the minimum, dimensionless, spatiotemporal distance (natural logarithm scale) between gulls and fishing vessels per individual. Spatiotemporal distances can be interpreted as the number of spatiotemporal buffers (i.e. 500 m and ±10 min) between a fishing vessel and a gull for a specific trip. Individuals have been ordered by median value.

reasons for the individual specialization in our study case could be related to the stage of the annual cycle of the gulls (i.e. the breeding season). All seabirds are central-place foragers during the breeding season (Rayner *et al.*, 2010), and therefore the availability of resources is constrained by the location of their colony. Similar results were presented in Patrick *et al.* (2015), as they found differences among individuals in the extent of fisheries overlap, as well as consistent strategies in scavenger behaviours.

The fact that some individuals tend to interact more often with fisheries than others is important in terms of conservation of the Audouin's gull colony in a *post-ban* scenario. These birds could be more affected by a depletion in discards suggesting that the effects of the discard ban will not be homogeneous across the Audouin's gull population. In contrast, the presence of individuals that make little or no use of discards would be key to the population overcoming the discard ban, as these individuals would be able to feed more easily in the absence of this food subsidy.

Conclusions and perspectives

In this study, we showed the fine-scale spatiotemporal co-occurrence, a proxy to interaction, between the Audouin's gull and the main fishing fleets operating near the Ebro Delta. The interactions were not constant throughout the day and showed some variability depending on the fishing fleet and the time of the day, with a larger magnitude of interaction during either discarding or hauling of the nets. Furthermore, differences between individuals regarding the feeding strategy were found, indicating a lack of homogeneity within the population.

Human fisheries have altered the dynamics of this and other scavenger species for decades, with cascading effects across communities and trophic levels (Oro *et al.* 2013). For instance, the studied population has experienced some fluctuations in the last 40 years (García-Tarrasón, 2014), with a demographic explosion coinciding with an increase in fishing activity in the area (Oro and Martínez-Vilalta, 1992). This indicates the importance of the fishing activity, and particularly trawling, for this population. Now that humans have started to restrict the availability of these food subsidies (e.g. EU landing obligation), we must consider how populations and communities will respond when these resources are no longer available or largely restricted (Pons 1992; Oro *et al.* 2013). Since 2009, our Audouin's gull population has declined to about 2000 pairs in 2019 (Ebro Delta Natural Park, pers. comm.). Fishing activity has not changed significantly in the study area, and discards are still produced. The decline in the gull population should be attributed, therefore, to other factors, such as predation episodes. However, feeding opportunities provided by human fisheries could be key to conserving the remaining population. Changes in the discarding policies may impact this and other species in the EU and Mediterranean scavenger community. A discard ban could imply a food shortage for this species (Bicknell *et al.* 2013), as an important portion of their energy is obtained from discarded fish, especially in the breeding season (Arcos, 2001; Arcos and Oro, 2002). For this reason, the discard-dependent individuals could contribute to a decline in the population when discards are no longer available (Bicknell *et al*, 2013).

Continuous monitoring of scavenger species through high-resolution tracking data that allows comparison with specific local food subsidies would be desirable to identify, and potentially prevent, unwanted impacts on natural communities and human interests (Oro *et al.*, 2013).

Data availability statement

Data was generated within the frame of LIFE+ Project INDEMARES. Data are available at the following address: http://seabirdtracking.org/mapper/?dataset_id=874. Please contact specifically J. M. Arcos. SEO/BirdLife (jmarcos@seo.org).

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