

Evaluating the dependence of opportunistic Yellow-legged Gulls (*Larus michahellis*) on marine habitat and fishing discards

NERE ZORROZUA,*^{1,2}  IGOR GRANADO,³  JOSE A. FERNANDES-SALVADOR,⁴ MAITE LOUZAO,³ MIKEL BASTERRETxea⁴ & JUAN ARIZAGA² 

¹Department of Zoology and Animal Cell Biology, University of The Basque Country UPV/EHU, Sarriena z/g, Leioa, E48940, Spain

²Department of Ornithology, Aranzadi Sciences Society, Zorroagaina 11, Donostia, E20014, Spain

³AZTI, Marine Research, Basque Research and Technology Alliance (BRTA), Herrera Kaia, Portualdea z/g, Pasaia (Gipuzkoa), E20110, Spain

⁴AZTI, Marine Research, Basque Research and Technology Alliance (BRTA), Txatxarramendi Ugarteia z/g, Sukarrieta (Bizkaia), E48395, Spain

Several bird species benefit from anthropogenic food subsidies, such as landfills and fishing discards, that are being reduced owing to introduced legislation. For instance, since 2019, Europe has passed legislation to reduce dramatically the amount of fisheries discards through the Landing Obligation (LO), which states that all fish species under Total Allowable Catch (TAC) should not be discarded at sea. This European discard ban is expected to impact some gulls, as several gull populations have been observed to be heavily reliant on this resource. In this work, GPS tracking data from adult Yellow-legged Gulls *Larus michahellis* and Vessel Monitoring System (VMS) data (i.e. detailed data of the spatial distribution of fishing vessels) are used to determine the utilization of the marine habitat and the level of interaction of gulls with fishing activity offshore and discards in the south-eastern part of the Bay of Biscay. We found that these gulls had a low use of the marine habitat (ca. 15%) compared with terrestrial habitats, in contrast to the ca. 40% of the diet of this population which comprises marine prey. Furthermore, we detected that most of the gull tracking positions at sea did not interact with the fishing vessels (an overlap of 21.5% between gulls and VMS data). Conversely, other gull populations of the Iberian Peninsula were found to depend much more strongly on fishing activity. Therefore, the Yellow-legged Gull population of the SE Bay of Biscay did not obtain most of its fish prey from interactions with offshore fishing activity but most possibly by taking fish remains in harbours and by feeding themselves. Consequently, we expect a minimal effect of the European policies oriented to ban fishing discards offshore on this population, which would be more affected by policies directed towards the reduction of food availability in landfills or fish landing management in harbours.

Keywords: EU policies, fishing vessels, foraging activity, GPS, habitat use, VMS.

Food subsidies of anthropogenic origin, also known as predictable anthropogenic food subsidies (PAFS; Oro *et al.* 2013), are provided either in marine (e.g. fishing discards) or terrestrial environments (e.g. organic refuse available in landfills). These

food subsidies have direct implications at ecosystem, community, animal population and individual levels (Hidalgo-Mihart *et al.* 2004, Olea & Baglione 2008, Weiser & Powell 2010, Oro *et al.* 2013, Steigerwald *et al.* 2015, Gilbert *et al.* 2016). Landfills, for instance, can have a large impact on movement ecology and territory use, trophic ecology, and demographic or

*Corresponding author.

Email: ner.zorrozua@ehu.es

toxicological aspects for several opportunistic species, such as vultures, storks and gulls (Auman *et al.* 2008, de la Casa-Resino *et al.* 2014, Arizaga *et al.* 2017, Shaffer *et al.* 2017, Ackerman *et al.* 2018, Arizaga *et al.* 2018, Plaza & Lambertucci 2018, Langley *et al.* 2021). Dependence on these PAFS can stimulate sedentary strategies or decrease dispersal distances (Gilbert *et al.* 2016), improve survival and reproduction, and, overall, promote population growth (Duhem *et al.* 2008, Weiser & Powell 2010). However, these effects depend on the alternative resources available within the foraging range. For example, in gulls, a higher fish consumption has been related to a better reproductive performance compared with a diet focused on refuse (Annett & Pierotti 1999). For marine PAFS, fishing discards are usually produced due to fishing quotas, low economic value of target species and/or small sizes of individual fish caught. Resources such as discards or waste from fisheries have been also well documented to modulate many life history aspects of scavenging species. For instance, movements of fishing vessels significantly affect some seabird foraging patterns and habitat use (Bartumeus *et al.* 2010, Bodey *et al.* 2014) and the exploitation of such fishing discards can modify diet and breeding success (Oro *et al.* 1996, Arcos & Oro 2002, Matos *et al.* 2018). In the North Sea, seabird numbers of those species which were supported by fishing discards declined by 39% after a reduction in discards (Sherley *et al.* 2020).

Many gull species, particularly large gulls, have a generalist feeding ecology and typically use a broad range of habitats, from marine to terrestrial (Arizaga *et al.* 2013, Washburn *et al.* 2013, Corman *et al.* 2016, Isaksson *et al.* 2016, Shaffer *et al.* 2017, Zorroza *et al.* 2020a). However, these generalist populations often conceal a broad spectrum of individual strategies ranging from generalist to specialist foragers (Ceia & Ramos 2015, Navarro *et al.* 2017, Maynard & Ronconi 2018). Likewise, the trophic ecology can also vary seasonally and between sex and age classes (Moreno *et al.* 2010, Navarro *et al.* 2010, Ramos *et al.* 2011, Alonso *et al.* 2015, Camphuysen *et al.* 2015, Calado *et al.* 2020a, Zorroza *et al.* 2020a). The high availability of PAFS, together with the increasing protection of gulls since the end of the 20th century, has supported growth in the populations of several gull species worldwide (Coulson 1963, Duhem

et al. 2008, Coulson & Coulson 2009). These demographic changes may have undesirable ecological or social consequences (García *et al.* 2002, Rock 2005, Calladine *et al.* 2006, Araújo *et al.* 2014), such as nuisance in cities.

In Europe, on 1 January 2015, the Landing Obligation (LO) was put into force and began with the prohibition of discarding certain fish species, while in 2019 all species subject to TAC (Total Allowable Catches; European Commission 2008) had to be kept on board and landed at the port of destination. In the Bay of Biscay, application of the new ban started on 1 January 2015 for small and large pelagic fisheries. These include purse-seine fisheries, pelagic trawl fisheries and fisheries that target the following species: Mackerel *Scomber scombrus*, Herring *Clupea harengus*, Horse Mackerel *Trachurus* spp., Blue Whiting *Micromesistius poutassou*, Boarfish *Capros aper*, Anchovy *Engraulis encrasicolus*, Greater Argentine *Argentina silus*, Sardine *Sardina pilchardus* and Sprat *Sprattus sprattus*. On 1 January 2016, the ban was applied to the fisheries of demersal species subject to TAC, including the bottom trawl fisheries and longline that operate in the Bay of Biscay with Hake *Merluccius merluccius* as target species. In 2017, fisheries with a main species subject to TAC were obliged to land the total catch corresponding to that species. Finally, on 1 January 2019, this was applied to all species subject to TAC. Horse Mackerel, Mackerel, Blue Whiting, Boarfish, Hake, Monkfish *Lophius* spp. and Megrin *Lepidorhombus* spp. are among the species most discarded by the trawl fleet operating in the Bay of Biscay (Rochet *et al.* 2014).

Studies of the Yellow-legged Gull *Larus michahellis* on the Iberian coast and the Mediterranean region show that fish prey can constitute one of the main feeding sources for some populations, and high availability of fishing discards allows a very fast population growth (Arizaga *et al.* 2009, 2011, Real *et al.* 2017, Calado *et al.* 2020b, 2021a). Thus, breeding success declines of up to 46% have been observed when these resources dramatically decrease or disappear (Oro *et al.* 1995), as well as strong population declines (Payo-Payo *et al.* 2015). Fish prey can be obtained as subsidies either from vessels at sea or in harbours, where gulls also forage on eviscerated fish remains (Martínez-Abraín *et al.* 2002, Whittington *et al.* 2006, Cama *et al.* 2012, Alonso *et al.* 2015, Karris *et al.* 2018).

The Yellow-legged Gull is the most abundant gull species in the Iberian Peninsula, with a population of *ca.* 125 000 adult breeding pairs in 2007–2009 in Spain (Molina & Bermejo 2009). The population increased significantly between the 1980s and 2000s (Olsen & Larson 2004), mainly due to the large amount of food available from human food subsidies, including fisheries waste (Duhem *et al.* 2008, Arizaga *et al.* 2009). Within the south-eastern Bay of Biscay, marine prey, mostly fish presumably related to fishing activity (Arizaga *et al.* 2013), comprise a large proportion of the diet composition (*ca.* 40%; Zorrozua *et al.* 2020a, see Supporting Information Fig. S1). Previous studies carried out in the Bay of Biscay found that large gulls were highly attracted to fishing vessels (Depestele *et al.* 2016, Louzao *et al.* 2020, Ruiz *et al.* 2021). These gulls, however, could comprise flocks of birds with several different origins, as well as other species apart from the Yellow-legged Gull.

Thus, it remains unknown whether the resident Yellow-legged Gull population from the south-eastern Bay of Biscay obtain fish prey from fishing vessels within their foraging range, as reported in other marine areas (Arcos *et al.* 2001, Valeiras 2003), or from the activity at harbours (e.g. fish remains, vessel cleaning). Using data from GPS-tracked adult Yellow-legged Gulls from the south-eastern Bay of Biscay, we aimed to quantify the potential use of fishing discards by this population and evaluate their dependence on this resource. With that goal, we first described the overall habitat use by two of the main colonies of Yellow-legged Gull of the Bay of Biscay, exploring sex and seasonal variation. Secondly, we assessed the overlap between marine trips by gulls and the presence of fishing vessels within the marine area potentially exploitable by breeding adults. Thirdly, we compiled information on the foraging ecology of the gull population (testing for sex and seasonal differences), fishing gear types and discards, in order better to understand the relationship between the fishing activity and the movement pattern and habitat use of this gull population and to determine whether the gulls' potential overlap with fishing vessels could be related to the trophic ecology of the population. Based on previous studies on the foraging ecology of this population (Arizaga *et al.* 2013, Zorrozua *et al.* 2020a) and seabird observations from fishing vessels in the Bay of Biscay (Depestele *et al.* 2016, Louzao

et al. 2020, Ruiz *et al.* 2021), we expected a high use of marine habitats with important interaction with offshore fishing activity, in addition to a significant impact of the discard ban on gulls' foraging ecology. Understanding the dependence of gull populations of the Bay of Biscay on the marine environment and fishing discards produced offshore will help us to determine the impact of European policies on this population of Yellow-legged Gulls.

METHODS

Fieldwork was carried out in two Yellow-legged Gull colonies in Gipuzkoa (northern Iberian Peninsula): Getaria and Ulia (Fig. 1). Diet estimation made for gulls of these colonies showed that *ca.* 40% of their prey was of marine origin (Fig. S1; Zorrozua *et al.* 2020a). Getaria's breeding population is estimated at 165 adult breeding pairs (in 2017) and it has a positive growth rate (Arizaga *et al.* 2014, Zorrozua *et al.* 2020b). Ulia's population comprises 660 breeding pairs (in 2017) and is the largest colony in Gipuzkoa. Its population trend remains unclear due to the lack of an adequate long-term sampling protocol.

Overall, 22 adults were captured while incubating, using spring traps during the breeding period of 2017 and 2018. In all, 18 individuals were captured in Ulia and four in Getaria; the distance between the two colonies is *ca.* 20 km (Table S1). Once caught, each individual bird was ringed with both an official metallic ring (Aranzadi ringing scheme) on one tarsus and a Darvic ring (can be read from a distance) on the other tarsus. The first inner primary feather (P1) was taken and was used to sex the bird by DNA analysis at the University of Navarra (Griffiths *et al.* 1998). Of the 22 birds captured, 11 were males and 11 females (Table S1). A GPS device (model: Wimbi SF; manufacturer: Wimbitek) was attached in the mantle region of each individual with a hand-made Teflon body harness. The study period comprised the time between GPS deployments (from mid-May to June) up to 31 August (Table S1). This period was subdivided into three phenological units: (1) breeding period (BP), from deployment to 30 June; (2) transition period (TP), July; and (3) post-breeding period (PP), August. The BP comprises a season where adult birds are in the colony (incubation, parental care to chicks). The TP is a month where some adult birds are still in

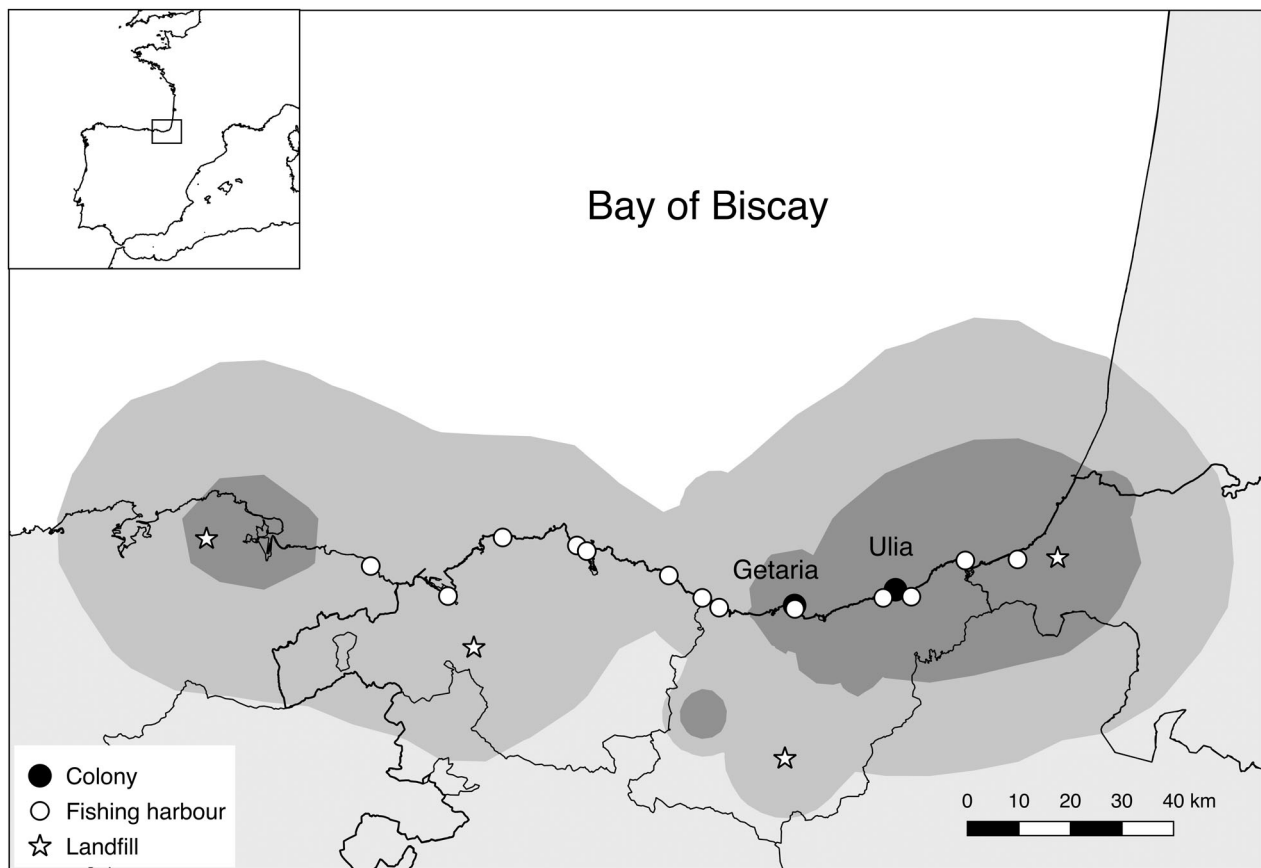


Figure 1. Foraging patterns of Yellow-legged Gulls breeding in the SE Bay of Biscay. The 95% (light grey) and 50% (dark grey) kernel density estimates (without considering positions in the colony) estimated from the GPS tracking data are shown. The black dots represent the location of the two breeding colonies, Getaria and Ulia. The main fishing harbours and landfills of the area are also indicated (white dots and white stars, respectively).

the colony but others may have started to leave the colony as their offspring fledge. Finally, the PP is a season when breeding has finished and when all adults are not conditioned by chick-rearing, no longer being constrained to return to the colony regularly. The devices were equipped with a solar panel and reported the position of the gull at least every 30 min (66% of the positions were reported at least every 30 min and 81% of the positions at least every hour). The proportion of the positions reported at least every 30 min (breeding 63%, transition 67%, post-breeding 66%) and every hour (breeding 80%, transition 80%, post-breeding 82%) were very similar among periods. The mass of the device and the harness was *ca.* 25 g (2.8% of gulls' average weight; Table S1), whereas the mass of the Darvic and metal rings was negligible (\ll 1% of the bird mass).

Analysis of bird tracks

As gulls usually make short movements near to the colony, we defined a virtual radius of 500 m from the colonies to determine when a bird was inside (< 500 m) and outside (> 500 m) the colony. This distance has already been used in previous research on habitat use (Furst *et al.* 2018, Romero *et al.* 2019). The same was applied to the existing landfills and harbours, which are known to be used by gulls of our two colonies (Egunez *et al.* 2018): any location within 500 m of a landfill site and a harbour was counted as present at them. Apart from this, we used the Corine Land Cover (CLC 2012; <https://land.copernicus.eu/pan-european/corine-land-cover/clc-2012>) in QGIS (QGIS Development Team 2009) to determine the land use of all the GPS locations. Overall,

taking into account the highest habitat use by gulls, we considered seven 'habitat' types: colony, landfill, fishing harbour, marine (Sea), pastures (non-irrigated arable land; pastures; complex cultivation; land principally occupied by agriculture, with significant areas of natural vegetation; natural grassland; moors and heathland), urban (continuous urban fabric; discontinuous urban fabric; industrial or commercial units; road and rail networks; airports; mineral extraction sites; construction sites; green urban areas; sport and leisure facilities) and 'other'. The category 'other' constituted less than 10% of all the obtained GPS locations.

GPS data were segmented in foraging trips using a spreadsheet. Each trip was defined as the locations of a particular bird from the time it left the colony, up to the time it returned, considering the first and the last positions of each trip to be placed within the 500-m buffer around the colony. For each trip, we determined whether it comprised (1) only marine (only habitat at the 'open' sea was included here), terrestrial or mixed habitat types (terrestrial habitats comprised all non-purely marine habitats, including urban areas, meadows, landfills and others, but also fishing harbours were considered as terrestrial locations, as we wanted to separate the use of the open sea from the exploitation of fishing discards at harbours); (2) total distance travelled during a trip (km); (3) maximum distance reached from the colony (km) and (4) the total duration of the trip (h). The total distance was assessed as the sum of the linear segments existing between successive temporal GPS locations.

To determine the exploited areas by gulls, we calculated the Utilization Distribution (UD) using fixed Kernel polygons (KDEs) calculated with the 'href' reference bandwidth of the 'adehabitatHR' package (Calenge 2006) in R 3.5.1 (R Development Core Team 2011). The 50% KDEs (km²) were used to estimate core foraging areas, and the 95% KDEs (km²) to estimate overall home-ranges (Avalos *et al.* 2017, Schirmer *et al.* 2019). Both 50% and 95% KDEs were determined for each individual bird and period (BP, TP, PP). Additionally, as we were particularly interested in the marine habitat use, the proportion of the 95% KDE consisting of marine habitat was calculated using the QGIS Geographical Information System (QGIS Development Team 2009).

Analysis of fishing vessel tracks

To test for the possible overlap between fishing activity and gull at-sea movement, Vessel Monitoring System (VMS) data were used. As VMS data were available with a maximum frequency of 2 h (i.e. a vessel location at least every 2 h), we re-calculated (interpolated) the position of each vessel for a new time-framework based on every 10-min position. A linear interpolation method was used with the assumption that the vessel followed a linear trajectory between each pair of known positions. Fishing vessel trajectories were obtained from VMS data collected by the Spanish Secretary of Fisheries for the Spanish vessels operating within the study area during 2017–2018. VMS data reported the vessel position, identifier, velocity, heading, date and time for vessels over 12 m in length (Fernandes *et al.* 2019). The use of VMS is not mandatory for vessels between 12 and 15 m in length, which make up only a small proportion of fishing vessels, when they only fish in national waters or the fishing trips are shorter than 24 h (EC No. 1224/2009). VMS data usually contain erroneous registers due to malfunctions that need to be removed ('VMStools' R package; Hintzen *et al.* 2012). These common errors are incomplete or duplicated registers, headings outside a compass range, points on land or unlikely speed (> 20 knots). Furthermore, the pseudo-duplicated records (i.e. entries with a time interval between pings < 5 min) were removed. This data processing allowed us to identify the temporal and spatial presence of Spanish fishing vessels within the study area. Then, for each gull position at sea that was from marine trips that went further than 1 km from the colony, we defined a spatial grid of 5 × 5 km (the centroid was the gull position; Sommerfeld *et al.* 2016), and then checked whether, within a temporal window of ± 1 h, there was any vessel within that cell. Using this approach, we were able to model the presence/absence of fishing vessels for each gull GPS location.

For the positions where gulls and vessels overlapped, we analysed the fishing gear to evaluate the relative importance of each fishing gear in the trophic and spatial ecology of the gulls. The fishing gears considered in this study were trawlers (TB), purse seiners (PS), surface longline (LLD), bottom

longline (LLS), live bait (LHP), minor arts (MIS), trollers (LTL), machined vertical lines (LHM) and gillnets (GNS).

Fishing discards data

To better understand the relationship between foraging ecology and fishing discards, we gathered information on rates of fish discarded by the Basque fleets in the years 2017 and 2018 in the Bay of Biscay. These data come from routine sampling carried out for the collection of fishery data (Data Collection Framework Council Regulation (EC) No. 199/2008, and Regulation (EU) 2017/1004), funded in part by the Basque Government through the 'Acuerdo Marco'. The Basque fleets with a higher discard rate (i.e. trawling fleet, cod and freezer tuna vessels) have traditionally been the target of this monitoring programme carried out by AZTI (a Basque non-profit research institution). More recently, discards from purse-seine fishery targeting small pelagic species and small-scale fisheries have been also monitored. As a consequence, the trawl fleet has been the one within the region with the longest and most representative historical data set and is also the one accounting for the majority of discards. Therefore, the trawl fleet has been considered in this work as the one best representing the amount and yearly variation of fishing discards produced in the southeastern part of the Bay of Biscay. The methodology for the data collection follows the standards established in the different ICES working groups in which AZTI has participated annually since samplings began and that are adapted to the particularities of each fleet.

Stomach content data

To have a better understanding of the trophic ecology of the investigated Yellow-Legged Gull population we compiled data available from analyses of regurgitations (data taken from Arizaga *et al.* 2013; J. Arizaga pers. comm.). However, these regurgitations collected in Uliá, Getaria and a third colony not studied here (Santa Clara) were from different chick individuals and years to those from which the tracking data were obtained, giving only a general indication of the diet of the studied colonies/populations.

Statistical analyses

In this work we combined data from the two colonies and considered all the positions, such as flight, foraging or resting. However, colony data were excluded from the analyses (i.e. locations within 500 m from the colony), as these could potentially mask the use of other habitat types and foraging patterns outside the colony. First, chi-square tests were conducted to compare habitat use among periods and between sexes. To analyse the possible effect of period and sex on habitat use based on Kernel polygons, trip duration and travel distance, we conducted separate General Linear Mixed Models (GLMMs) on the log-transformed 50% KDE in km², log-transformed 95% KDE proportion of marine area in km², log-transformed trip duration, total distance travelled per trip or maximum distance reached per trip as the response variable with period, sex and year as fixed factors, with a linear-link function with Gaussian (normal) distribution errors. The period–sex interaction was also included, and individual was added as a random factor. For trip duration and travel distance we also included trip type (marine/terrestrial/mixed) with its interaction with period and sex.

To test for the existence of a spatio-temporal overlap between the fishing vessels and the gulls at sea we conducted a GLMM on this overlap (yes/no) as a binary response variable with a logit-link function with binomial error distribution, and year, period, sex and distance to colony as explanatory variables, and individual and foraging trip identity nested within individual identity as random factors.

For all models, all the possible factor combinations starting from the full (saturated) model were run and then ranked based on Akaike Information Criterion values corrected for small sample size (AICc; Akaike 2011). Models differing by less than 2 AICc values were considered to fit the data equally well (Akaike 2011) and were averaged to obtain 'averaged' parameter estimates. The 'dredge' and 'model.avg' functions from the 'MuMIn' package (Barton 2018) were used for this purpose. All statistical analyses were conducted in R 3.5.1 (R Development Core Team 2011).

RESULTS

We obtained a total of 45 217 locations, of which 42% corresponded to the breeding period, 36% to

the transition period and 22% to the post-breeding period. Regarding habitat use, less than 10% of all the GPS locations of tracked gulls were in the marine environment and gulls spent more time in the colony during breeding than during transition and post-breeding periods (*ca.* 50% more in the breeding period than the post-breeding period; Supporting Information Table S2). When removing colony data which might mask other potentially interesting differences in habitat use, the importance of marine habitats for foraging gulls was revealed. For instance, marine habitat was the most important (*ca.* 30%) habitat for breeding males (Fig. 2). This use, however, varied among periods ($\chi^2 = 388.0$, $df = 2$, $P < 0.001$) and between sex classes ($\chi^2 = 106.4$, $df = 1$, $P < 0.001$). The proportion of locations around landfills and urban areas was higher in the post-breeding period than in the other two periods (Fig. 2), and males spent more time at sea compared with females (in the breeding period the difference was *ca.* 20%), whereas females used

landfills more (up to *ca.* 50% more than males in the breeding period) (Fig. 2).

We calculated a mean core range of 236 km² across individuals, which remained relatively similar between periods (Tables 1 and 2; see Supporting Information Table S3 for averaged models and Table S4 for model values for the Uliia colony only). The mean home-range area was 1392 km² and the mean proportion of marine habitat within that area was 34.8% (Table 1), proportions that varied seasonally (Tables 2 and S3). Gulls in this study were found to use a higher proportion of marine habitat during the breeding period than in the two subsequent phenological periods (*ca.* 30% more, Table 1). Gulls made trips with a total mean distance of 19.2 km; the maximum distance reached in the trips was on average 8.5 km from the colony and overall trips were found to last 4.4 h (Table 1). Distances and duration varied significantly in relation to several factors – distances: period, type of trip, sex and year, including some interactions; duration: period, type of trip and sex;

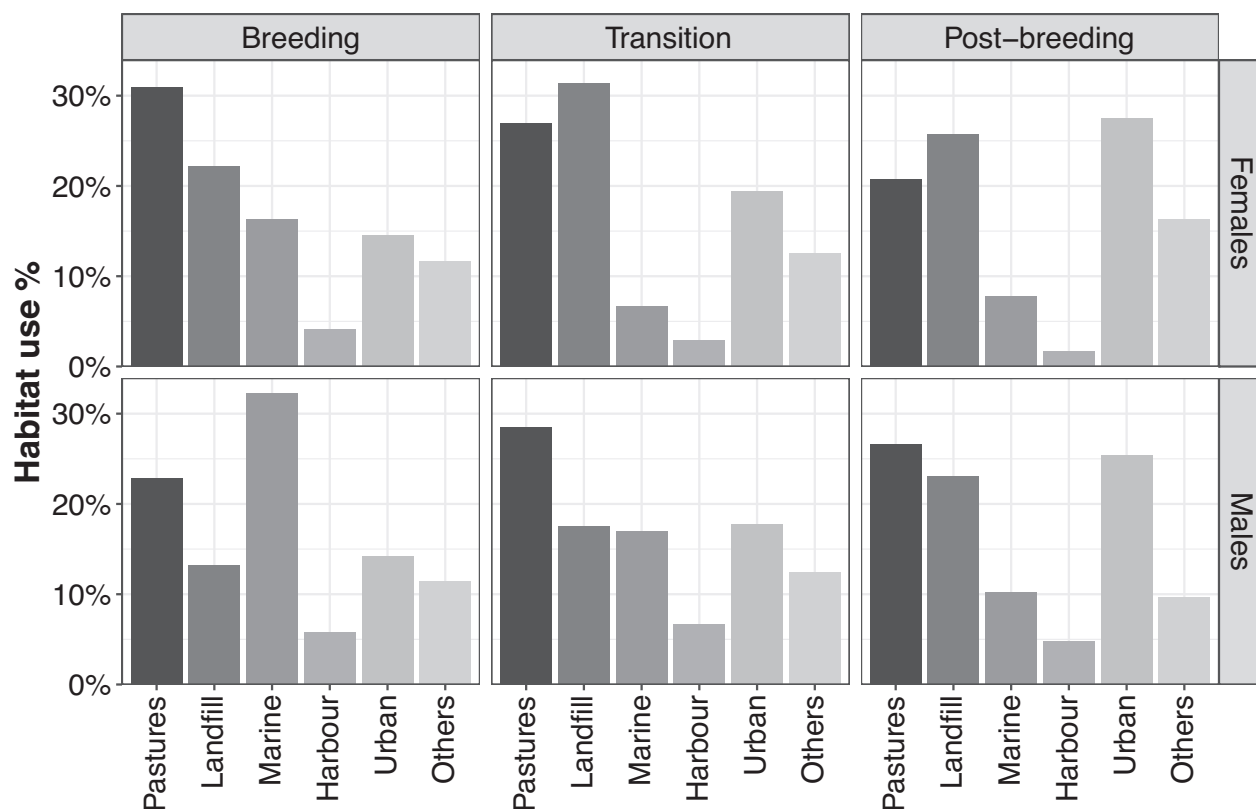


Figure 2. Habitat use by GPS-tracked adult Yellow-legged Gulls in three different study periods: breeding (up to the end of June), transition (July) and post-breeding (August). Positions in the colony have been removed.

Table 1. Summary table showing estimated mean and 95% CI values for core range area (50% kernel) (CORE), home-range area (95% kernel) (HOME), proportion of marine habitat within home-range area (PMAR), total distance of trip (TDIS), maximum distance of trip (MDIS) and trip duration (TDUR). Values are indicated for different periods, colonies and sexes.

	CORE (km ²)	HOME (km ²)	PMAR (%)	TDIS (km)	MDIS (km)	TDUR (h)
Overall	235.7 (182.5–304.4)	1391.7 (1121.2–1727.3)	34.8 (31.6–38.2)	19.2 (18.2–20.2)	8.5 (8.0–8.9)	4.4 (4.2–4.6)
Breeding	267.4 (205.9–347.3)	1565.2 (1305.1–1877.1)	44.1 (37.8–51.4)	17.7 (16.4–19.0)	7.9 (7.4–8.5)	3.7 (3.5–4.0)
Transition	227.4 (148.6–347.9)	1325.9 (911.1–1929.4)	30.4 (26.4–34.9)	19.7 (18.1–21.4)	8.7 (8.0–9.5)	4.3 (4.0–4.7)
Post-breeding	208.9 (100.6–433.7)	1265.4 (677.4–2363.6)	30.0 (25.6–35.2)	24.6 (21.0–28.9)	10.1 (8.7–11.7)	8.2 (7.2–9.4)
Male	276.8 (187.9–407.7)	1594.4 (1129.0–2251.6)	38.6 (34.6–42.9)	17.7 (16.6–18.9)	7.8 (2.3–8.3)	3.9 (3.7–4.1)
Female	192.2 (139.5–265.0)	1171.0 (929.7–1475.0)	30.5 (26.0–35.8)	21.7 (20.0–23.6)	9.6 (8.9–10.4)	5.2 (4.8–5.5)

Tables 2 and S3. Thus, travelled distances and duration were longer in the post-breeding period for terrestrial and mixed trips, but not marine trips, where the birds travelled longer distances in the breeding period (Table 2, Supporting Information Table S3 and Fig. S2). Females made longer trips and distances than males in the post-breeding period and when the trip was terrestrial (Tables 2 and S3, Fig. S2). Individuals from Getaria made a higher proportion of trips to the sea (*ca.* 35% vs. 25%, Table S1; $\chi^2 = 87.2$, $df = 1$, $P < 0.001$). Males were found to make proportionally more marine trips than females ($\chi^2 = 11.4$, $df = 1$, $P < 0.001$; Table S1).

All except one individual showed at least one marine trip, but the spatio-temporal overlap between vessels and gulls was observed to vary between individuals from 0% to 52% (Table 3). The averaged model was based on seven models that fitted the data equally well (Tables 2 and S3), revealing a higher overlap with an increasing distance from colonies, and in the breeding period as compared with the transition period (Tables 2 and S3). Additionally, females were found to overlap more with fishing vessels than were males (Tables 2 and S3). When gull positions overlapped with fishing vessels, gulls were found to follow mainly purse seiners and trawlers (Table 4).

Regarding the fish species found in regurgitations from previous years ($n = 70$, Arizaga *et al.* 2011), only genus, family or order of the items were identified: Belonidae, Clupeidae, Gadiformes *Merluccius* sp., Carangidae, Sparidae *Boops* sp., Trachinidae, Mullidae *Mullus* sp. With respect to fishing discards, the main families discarded were Gadidae and Carangidae: in the years 2017 and 2018 on average 56% of the discards were of the family Gadidae, 42% Carangidae, 1%

Clupeidae and 1% Trachinidae. Among the Gadiformes the majority were Hake, while for the Carangidae they were Horse Mackerel. Therefore, the species with highest discard rates were also observed in the gulls' diet.

DISCUSSION

In this work we have described the habitat use of the Yellow-legged Gull population in the south-eastern Bay of Biscay and we have analysed the overlap between gulls and fishing vessels. We found that habitat use varied among periods and sexes, males in the breeding period being those that used more the marine habitat. Moreover, females' positions overlapped more with fishing vessels compared with males, and gulls followed mainly purse seiners and trawlers.

Using data on GPS-tracked adult Yellow-legged Gulls, we detected a relatively small use of the marine habitat compared to other habitat types, including landfills, urban areas and meadows. Although it varied with period and sex, on average, 19% of the foraging trips were marine (range: 0% to *ca.* 50%) in the SE Bay of Biscay colonies, in contrast with other Yellow-legged Gull populations such as Portuguese (in the breeding period ranging between *ca.* 60% to nearly 100%; Mendes *et al.* 2018). Such differences between populations presumably represent the high adaptability of this species to exploit locally abundant resources (Ramos *et al.* 2009, Romero *et al.* 2019). Interestingly, our Yellow-legged Gull population showed a relatively high use of marine prey (roughly 40% of adults' diet; Fig. S1; Zorrozua *et al.* 2020a), a considerable percentage taking into account their low proportion of marine trips. When looking at the habitat use results, we obtained a relatively higher

Table 2. Ranking of the best GLMMs ($\Delta\text{AICc} < 2$), together with the global and null models, according to their small-sample size-corrected Akaike Information Criterion (AICc) values.

Models	AICc	ΔAICc	df	Dev	r^2
<i>Kernel 50</i>					
1. Null	164.5	0.00	3	158.1	0.099
2. Sex	165.7	1.21	4	157.0	0.116
3. Year	166.8	2.29	4	158.1	0.100
4. Sex + year	168.1	3.54	5	156.9	0.117
5. Period	168.3	3.78	5	157.2	0.113
Global: period + sex + year + period \times sex	176.9	12.4	9	155.2	0.142
<i>Marine proportion in kernel 95</i>					
1. Period + sex	14.2	0.00	6	0.6	0.548
2. Period	16.8	2.58	5	5.7	0.507
3. Period + sex + year	16.8	2.58	7	0.6	0.548
4. Period + sex + period \times sex	18.4	4.20	8	-0.4	0.556
5. Period + year	19.2	5.00	6	5.6	0.508
Global: period + sex + year + period \times sex	21.2	7.0	9	-0.4	0.556
Null	48.9	34.7	3	42.5	0.081
<i>Cumulative distance</i>					
1. Global: trip + period + sex + year + trip \times period + trip \times sex + period \times sex	7296.6	0.00	17	7262	0.334
2. Trip + period + sex + year + trip \times period + period \times sex	7297.5	0.88	15	7267	0.332
3. Trip + period + year + trip \times period	7298.3	1.67	12	7274	0.330
4. Trip + period + sex + year + trip \times period + trip \times sex	7299.4	2.73	15	7269	0.332
5. Trip + period + sex + year + trip \times period	7299.8	3.17	13	7274	0.331
Null	7986.8	690.16	3	7981	0.105
<i>Maximum distance</i>					
1. Global: trip + period + sex + year + trip \times period + trip \times sex + period \times sex	7166.3	0.00	17	7132	0.314
2. Trip + period + sex + year + trip \times period + period \times sex	7168.2	1.92	15	7138	0.312
3. Trip + period + year + trip \times period	7170.9	4.64	12	7147	0.310
4. Trip + period + sex + year + trip \times period + trip \times sex	7171.0	4.72	15	7141	0.312
5. Trip + period + sex + year + trip \times period	7172.5	6.19	13	7146	0.310
Null	7757.3	591.07	3	7751	0.116
<i>Trip duration</i>					
1. Trip + period + sex + trip \times period + trip \times sex + period \times sex	6312.9	0.00	16	6281	0.380
2. Trip + period + sex + trip \times period + trip \times sex	6313.2	0.31	14	6285	0.379
3. Global: trip + period + sex + year + trip \times period + trip \times sex + period \times sex	6314.9	2.01	17	6281	0.380
4. Trip + period + sex + year + trip \times period + trip \times sex	6315.2	2.32	15	6285	0.379
5. Trip + period + sex + trip \times period + period \times sex	6320.4	7.50	14	6292	0.377
Null	7133.7	820.82	3	7128	0.122
<i>Overlap vessels – gulls</i>					
1. Dist.colony + sex	942.4	0.00	5	421.8	0.283
2. Dist.colony	942.6	0.27	4	420.9	0.282
3. Dist.colony + sex + year	942.8	0.45	6	422.4	0.284
4. Dist.colony + period	943.6	1.25	6	421.2	0.284
5. Dist.colony + year	943.8	1.41	5	421.4	0.283
6. Dist.colony + period + sex	943.8	1.41	7	424.0	0.285
7. Global: Dist.colony + period + sex + year	943.9	1.59	8	424.9	0.286
Null	1129.5	187.20	3	543.7	0.163

AICc, small sample size-corrected Akaike values; ΔAICc , difference in AICc values in relation to the first model; df, degrees of freedom; Dev, deviance; r^2 , likelihood-ratio based F^2 . The global model included all the possible factors and the null one corresponds to a constant model.

number of locations at sea than in harbours, which might be tentatively linked to a higher consumption of fishing discards offshore. Furthermore, note

that the use of harbours was defined with a 500 m buffer, so some gulls could have foraged out at sea or urban environment adjacent to the harbour

Table 3. Percentage of gulls positions in marine habitat that overlap with vessels' position in a spatio-temporal window of 5 × 5 km and ± 1 h through the breeding cycle.

Individual	Overlap (%)			Overall
	Breeding	Transition	Post-breeding	
17-02	33.33	16.00	12.00	23.16
17-06	0.00	-	-	0.00
17-08	No marine trips			
17-09	0.00	0.00	-	0.00
17-11	11.76	0.00	0.00	5.56
17-12	26.67	-	-	26.67
17-13	16.22	5.67	0.00	12.29
17-14	35.29	13.64	25.00	23.73
17-15	23.91	0.00	-	23.16
18-01	36.13	0.00	-	35.90
18-03	39.29	0.00	-	31.43
18-04	20.00	0.00	0.00	12.50
18-06	40.43	0.00	100.00	36.36
18-07	59.10	0.00	-	52.00
18-08	33.33	-	-	33.33
18-09	12.82	0.00	0.00	10.00
18-10	33.33	0.00	-	27.78
18-11	25.00	-	-	25.00
18-12	39.10	26.23	0.00	32.78
18-13	22.22	0.00	0.00	18.18
18-14	-	0.00	-	0.00
18-16	0.00	-	-	0.00

proper, overestimating the use of harbours. However, it remains unknown in which habitat types (offshore vs. harbours) gulls might be more efficient at foraging (in terms of food intake rate by foraging time invested in a habitat). Therefore, we cannot make a direct link between habitat use and the contribution of a given type of prey in the diet.

This is the first study aiming to test the spatial overlap between the fishing activity and the foraging patterns of a resident, breeding seabird species within the Bay of Biscay. In contrast to other gull populations from the Mediterranean or oceanic islands (Arcos *et al.* 2001, Martínez-Abraín *et al.* 2002, Louzao *et al.* 2011, Bécares *et al.* 2015, Romero *et al.* 2019), that have shown a relatively high overlap with vessels, the Yellow-legged Gull breeding in the SE Bay of Biscay showed a low spatial overlap with fishing vessels. However, the methodologies used in other studies were different (e.g. visual census), and thus the comparisons are not always easy. For instance, Romero *et al.* (2019) used a 500 m radius from a fishing vessel to state a positive overlap with a gull,

obtaining high interaction, while in our work the spatial window used was larger and yet the overlap was less. This suggests that the population breeding in the SE Bay of Biscay does not depend strongly on scavenging for discards at sea, and hence they would obtain the fish they eat either by active fishing at sea or by exploiting the discards and eviscerates at harbours (N. Zorrozueta pers. obs.). Energetic and nutritional quality of fishing discards at sea (probably whole fish) could also be different to that of the discards in harbours (proportionally more eviscerates). Therefore, it would be interesting to address this aspect in the future to evaluate the relative importance and trade-offs of alternative feeding resources.

It could be argued that the overlap analyses could be modified by changing the spatial grid (5 × 5 km) and the temporal window (± 1 h) used, as well as the recording frequency of the GPS (30 min). As far as a larger grid and temporal window are used, a higher overlap should be expected, but it would probably be misleading and overestimated (Amoroso *et al.* 2018). Overall, therefore, we consider that our approach was a good compromise because it covered reasonably wide geographic/temporal ranges (but see Sugishita *et al.* 2015). In this framework, overall, the percentage of marine trips was small, although we note the high variability among individual birds (range: 0% to ca. 50%). Furthermore, the relatively low overlap between vessels and gulls during spring/summer may suggest that European fishery policies would probably have a negligible effect on the Yellow-legged Gull population of the south-eastern Bay of Biscay during the breeding season, although the foraging efficiency by gulls at vessels should be studied. Additionally, this issue should be further studied for the autumn/winter period which could not be covered with the gulls' GPS-tracking data.

We also detected a differential use of the habitat between the sexes: males spent more time in the colony and foraged more at sea compared to females, which was also previously observed for this population (Zorrozueta *et al.* 2020c). Previous studies on the trophic ecology of Basque Yellow-legged Gulls did not show sex-related differences in the diet (Zorrozueta *et al.* 2020a). However, this study suggested a certain degree of spatial segregation between sexes in their foraging range. While males spent more time at sea, females showed a higher overlap with fishing vessels than males. In

Table 4. Proportion of different fishing gears in the positions where gulls overlapped with vessels, by individuals and periods.

Individual	Period	Overlap (%) per gear									
		TB	LLD	LLS	LHP	PS	MIS	LTL	LHM	GNS	NOGEAR
17-02	Breed	20.0	0.0	0.0	0.0	93.3	0.0	0.0	0.0	0.0	33.3
	Trans	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
	Post	33.3	0.0	0.0	0.0	33.3	33.3	0.0	0.0	0.0	0.0
17-11	Breed	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
	Trans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
17-12	Breed	75.0	0.0	0.0	0.0	25.0	0.0	0.0	0.0	0.0	12.5
	Trans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
17-13	Breed	40.0	10.0	0.0	0.0	46.7	0.0	0.0	0.0	0.0	6.7
	Trans	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
17-14	Breed	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
	Trans	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
17-15	Breed	40.9	0.0	0.0	0.0	59.1	0.0	0.0	0.0	0.0	18.2
	Trans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18-01	Breed	89.3	1.8	0.0	0.0	8.9	0.0	1.8	0.0	0.0	0.0
	Trans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18-03	Breed	81.8	0.0	0.0	9.1	0.0	0.0	0.0	0.0	0.0	9.1
	Trans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18-04	Breed	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Trans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18-06	Breed	84.2	0.0	0.0	0.0	10.5	0.0	0.0	5.3	0.0	10.5
	Trans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0
18-07	Breed	92.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	7.7	0.0
	Trans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18-08	Breed	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Trans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18-09	Breed	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Trans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18-10	Breed	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Trans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18-11	Breed	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Trans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18-12	Breed	83.7	0.0	0.0	2.3	14.0	0.0	0.0	0.0	0.0	9.3
	Trans	81.3	0.0	0.0	18.8	0.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18-13	Breed	100.0	0.0	0.0	0.0	0.0	0.0	50.0	0.0	0.0	0.0
	Trans	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Post	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

The sum of the percentages of the different fishing gears can be >100%, as in some cases gulls overlapped at the same time with more than one fishing vessel. Fishing gear codes: TB, trawler; LLD, surface longline; LLS, bottom longline; LHP, live bait; PS, purse seiners; MIS, minor arts; LTL, hunt or trolley; LHM, machined vertical lines; GNS, gillnets; NOGEAR, no data for gear identification. Breed: Breeding period; Trans: Transition period; Post: Post-breeding period. Individuals with no overlap with fishing vessels are not shown in the table.

contrast, other populations of Yellow-legged Gulls located on the western Iberian coast showed sexual segregation in their trophic ecology: males foraged more in association with fisheries (Calado *et al.* 2020a). The authors of that study proposed that sexual size dimorphism plays an important role in this segregation, although the same sexual size dimorphism is also present in our population but did not seem to have the same effect. A higher use of marine habitat and fisheries discards by males has also been reported in other gull species (Camphuysen *et al.* 2015, Baert *et al.* 2021). In contrast to this result, evidence from other seabird species shows that sexual segregation in foraging patterns is common with females often making longer foraging trips than males (Cleasby *et al.* 2015, Paiva *et al.* 2017, Kazama *et al.* 2018, but see Pinet *et al.* 2012). Due to the long interval between fixes in our data set, a possible bias in the results cannot be rejected. For instance, short foraging trips might be missed and then the duration and distance of the tracks may have been overestimated, although the bias might also go in the opposite direction, with potentially more frequent gaps in GPS positions at longer trips, reducing the duration and maximum distances of these trips. Regardless, we consider that these gaps should have a marginal, negligible impact on the direction and magnitude of the effect of the independent variables on our response variable. The proportion of gaps in the data set were similar between years (2017: 85%; 2018: 95%), sexes (females: 94%; males: 89%) and periods (breeding: 91%; transition, 90%; post-breeding: 95%), so the effect of period for instance on trip duration or distance should be detected independently of the potential influence of gaps on the estimation of this duration or distance.

We observed that habitat use varied seasonally. Gulls spent more time in the colony when they were breeding, as observed in other studies especially for females (e.g. Baert *et al.* 2021), and increasing their presence in the landfills and urban areas after this period. This change could be linked to the end of the breeding duties (e.g. incubation, chick attendance; Gaston 2004) at the end of the breeding period. Then, gulls do not need to invest more time in the colony, and they can exploit feeding sources over a wider geographical range (Ackerman *et al.* 2018), as revealed by the higher home-range area used in the post-breeding period of this study. In addition, we detected a higher use

of the marine habitat during the breeding period and a higher overlap with fishing vessels. This could be partly due to the fact that purse seiners and trawlers have a higher activity in May and June compared to July and August. Marine prey may favour faster chick growth (Annett & Pierotti 1999), although differences in trophic ecology between adults and chicks have not been observed previously in the studied colonies (Zorrozua *et al.* 2020a).

Purse seiners' target species are mostly from the families Engraulidae and Carangidae, whereas trawlers' target species belong to the Gadidae and Merlucciidae. However, main discarded species (mainly from trawlers) are from the families Gadidae and Carangidae. These were two of the main fish families also found in gulls' regurgitations, which could be related to the higher attendance of gulls to these vessels. Trawlers are the vessels that produce more amount of fishing discards, so it may be more worthwhile for gulls to attend these vessels. However, we cannot reject the possibility that it is the quality of the discarded species rather than the quantity of the discard that attracts the gulls, although this issue should be further studied. Furthermore, we should keep in mind that we do not have GPS data from all the vessels (e.g. smallest ones), and it would be interesting to obtain more detailed information for these fleets, which are widely distributed along all of the coast. Regardless, the amount of vessel discards is very small (less than 2%, M. Basterretxea pers. comm.) in comparison with the rest of the vessels. In Portuguese coastal waters, purse seiners had the highest seabird–fishery interactions (Calado *et al.* 2021b). Oceanographic conditions and chicks' dietary requirements have also been suggested as factors influencing seasonal patterns of habitat use (Thaxter *et al.* 2015). However, previous studies carried out in the area revealed a higher consumption of marine prey in winter than in spring/summer (Zorrozua *et al.* 2020a); moreover, the percentage of fish in the diet did not vary between chicks and adults (Arizaga *et al.* 2013, Zorrozua *et al.* 2020a), unlike in other populations, where chicks are fed with a different proportion of fish compared with adults (Alonso *et al.* 2015, Pais de Faria *et al.* 2021). Therefore, we have no evidence supporting that a higher use of the marine habitat during the breeding may be associated with a higher consumption of marine prey in this period. Perhaps the need to feed

themselves and their chicks may force adults to invest more time in the sea as compared with other seasons, which would be in accordance with studies that found higher fishery interactions during spring for Yellow-legged Gulls (Calado *et al.* 2021b); this is a question that would need further investigation. Furthermore, in the breeding period, marine trips were the shortest, which could suggest that parents may minimize time away from the nest in order to ensure more effective brood guarding. Moreover, previous studies have found that seabirds consume more discards offshore in winter (Depestele *et al.* 2016). It would therefore be interesting to study the overlap of this population with fishing activity in that season.

In conclusion, we found that a Yellow-legged Gull population breeding in the SE Bay of Biscay showed little spatial overlap with fishing vessels, possibly suggesting a relatively low dependence on fishing discards produced offshore, although potential high foraging efficiency by gulls at vessels should be studied. Specifically, gulls were found to follow mainly trawlers and purse seiners. Our study suggests that the impact of reducing fishing discards will have a negligible impact on this population during summer, which would probably be more affected by management actions focused on other food subsidies such as landfills. However, the impact of different prey on reproductive output should be taken into account, as fish has been described as high-quality food for chicks and thus a small change in the proportion of high-quality prey can still have a large effect on the population. An open question would be whether Yellow-legged Gulls exploit fish remains in harbours and the impact of future environmental management policies of treating fisheries remains on gulls. Three anonymous referees and the Editor (R. Nager) and Associate Editor (C. Horswill) provided very valuable comments that helped us improve an earlier version of the manuscript.

AUTHOR CONTRIBUTIONS

Nere Zorrozua: Conceptualization; data curation; formal analysis; methodology; writing – original draft; writing – review and editing. **Igor Granado:** Data curation; formal analysis; writing – review and editing. **Jose A. Fernandes:** Methodology; writing – review and editing. **Maite Louzao:** Methodology; writing – review and editing. **Mikel**

Basterretxea: Methodology; writing – review and editing. **Juan Arizaga:** Conceptualization; data curation; methodology; writing – original draft; writing – review and editing.

FUNDING

This research was partly funded by the Basque Government and the Gipuzkoa Administration. This last entity also authorized the captures and GPS-tracking of gulls. The research was partly funded by the European Union's Horizon 2020 research and innovation programme under the FutureMARES project (Grant Agreement No. 869300), in addition to the PETFISH project funded by the Department of Economic Development and Competitiveness of the Basque Government, and the European Commission Data Collection Framework. N.Z. benefited from a predoctoral fellowship from the Basque Government. I.G.'s work was funded by an IKERTALENT grant from the Department of Economic Development and Infrastructures of the Basque Government. M.L. was funded by a Ramón y Cajal (RYC-2012-09897) postdoctoral contract of the Spanish Ministry of Economy, Industry and Competitiveness.

ETHICAL NOTE

None.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

REFERENCES

- Ackerman, J.T., Peterson, S.H., Tsao, D.C. & Takekawa, J.Y.** 2018. California Gull (*Larus californicus*) space use and timing of movements in relation to landfills and breeding colonies. *Waterbirds* **41**: 384–400.
- Akaike, H.** 2011. Akaike's information criterion. In *International Encyclopedia of Statistical Science*. 25. Berlin, Heidelberg: Springer.
- Alonso, H., Almeida, A., Granadeiro, J.P. & Catry, P.** 2015. Temporal and age-related dietary variations in a large population of yellow-legged gulls *Larus michahellis*:

- Implications for management and conservation. *Eur. J. Wildl. Res.* **61**: 819–829.
- Amoroso, R.O., Parma, A.M., Pitcher, C.R., McConnaughey, R.A. & Jennings, S.** 2018. Comment on “tracking the global footprint of fisheries”. *Science* **361**: eaat6713.
- Annett, C.A. & Pierotti, R.** 1999. Long-term reproductive output in western gulls: Consequences of alternate tactics in diet choice. *Ecology* **80**: 288–297.
- Araújo, S., Henriques, I.S., Leandro, S.M., Alves, A., Pereira, A. & Correia, A.** 2014. Gulls identified as major source of fecal pollution in coastal waters: A microbial source tracking study. *Sci. Total Environ.* **471**: 84–91.
- Arcos, J.M. & Oro, D.** 2002. Significance of fisheries discards for a threatened Mediterranean seabird, the Balearic shearwater *Puffinus mauretanicus*. *Mar. Ecol. Prog. Ser.* **239**: 209–220.
- Arcos, J.M., Oro, D. & Sol, D.** 2001. Competition between the yellow-legged Gull *Larus cachinnans* and Audouin's Gull *Larus audouinii* associated with commercial fishing vessels: The influence of season and fishing fleet. *Mar. Biol.* **139**: 807–816.
- Arizaga, J., Galarza, A., Herrero, A., Hidalgo, J. & Aldalur, A.** 2009. Distribución y tamaño de la población de la Gaviota Patiamarilla *Larus michahellis lusitanicus* en el País Vasco: tres décadas de estudio. *Rev. Catalana d'Ornitol.* **25**: 32–42.
- Arizaga, J., Aldalur, A., Herrero, A., Cuadrado, J.F., Mendiburu, A. & Sanpera, C.** 2011. High importance of fish prey in diet of yellow-legged Gull *Larus michahellis* chicks from the Southeast Bay of Biscay. *Seabird* **23**: 1–6.
- Arizaga, J., Jover, L., Aldalur, A., Cuadrado, J.F., Herrero, A. & Sanpera, C.** 2013. Trophic ecology of a resident yellow-legged Gull (*Larus michahellis*) population in the Bay of Biscay. *Mar. Environ. Res.* **87–88**: 19–25.
- Arizaga, J., Aldalur, A. & Herrero, A.** 2014. Tendencia poblacional en tres colonias de gaviota patiamarilla *Larus michahellis* Naumann, 1840 en Gipuzkoa: 2000–2013. *Munibe* **62**: 61–69.
- Arizaga, J., Laso, M., Zorrozua, N., Delgado, S., Aldalur, A. & Herrero, A.** 2017. Uso del espacio por adultos de gaviota patiamarilla *Larus michahellis* Naumann, 1840 durante el período reproductor: resultados preliminares en relación al uso de vertederos. *Munibe* **65**: 67–80.
- Arizaga, J., Resano-Mayor, J., Villanúa, D., Alonso, D., Barbarin, J.M., Herrero, A., Lekuona, J.M. & Rodríguez, R.** 2018. Importance of artificial stopover sites through avian migration flyways: A landfill-based assessment with the white stork *Ciconia ciconia*. *Ibis* **160**: 542–553.
- Auman, H.J., Meathrel, C.E. & Richardson, A.** 2008. Supersize me: Does anthropogenic food change the body size of silver gulls? A comparison between urbanized and remote, non-urbanized areas. *Waterbirds* **31**: 122–126.
- Avalos, M.R., Ramos, J.A., Soares, M., Ceia, F.R., Fagundes, A.I., Gouveia, C., Menezes, D. & Paiva, V.H.** 2017. Comparing the foraging strategies of a seabird predator when recovering from a drastic climatic event. *Mar. Biol.* **164**: 48.
- Baert, J.M., Stienen, E.W.M., Verbruggen, F., Van de Weghe, N., Lens, L. & Müller, W.** 2021. Context-dependent specialisation drives temporal dynamics in intra- and inter-individual variation in foraging behaviour within a generalist bird population. *Oikos* **130**: 1272–1283.
- Barton, K.** 2018. *MuMIn: Multi-model inference*. R package version 1.42.1 Available at: <https://CRAN.R-project.org/package=MuMIn> (accessed 15 October 2019).
- Bartumeus, F., Giuggioli, L., Louzao, M., Bretagnolle, V., Oro, D. & Levin, S.A.** 2010. Fishery discards impact on seabird movement patterns at regional scales. *Curr. Biol.* **20**: 215–222.
- Bécares, J., García-Tarrasón, M., Villero, D., Bateman, S., Jover, L., García-Matarranz, V., Sanpera, C. & Arcos, J.M.** 2015. Modelling terrestrial and marine foraging habitats in breeding Audouin's gulls *Larus audouinii*: Timing matters. *PLoS One* **10**: e0120799.
- Bodey, T.W., Jessopp, M.J., Votier, A.C., Gerritsen, H.D., Cleasby, I.R., Hamer, K.C., Patrick, S.C., Wakefield, E.D. & Bearhop, S.** 2014. Seabird movement reveals the ecological footprint of fishing vessels. *Curr. Biol.* **24**: R514–R515.
- Calado, J.G., Paiva, V.H., Ceia, F.R., Gomes, P., Ramos, J.A. & Velando, A.** 2020a. Stable isotopes reveal year-round sexual trophic segregation in four yellow-legged gull colonies. *Mar. Biol.* **167**: 65.
- Calado, J.G., Paiva, V.H., Ramos, J.A., Velando, A. & Munilla, I.** 2020b. Anthropogenic food resources, sardine decline and environmental conditions have triggered a dietary shift of an opportunistic seabird over the last 30 years on the northwest coast of Spain. *Reg. Environ. Change* **20**: 10.
- Calado, J.G., Verissimo, S.N., Paiva, V.H., Ramos, R., Vaz, P.T., Matos, D., Pereira, J., Lopes, C., Oliveira, N., Quaresma, A., Ceia, F.R., Velando, A. & Ramos, J.A.** 2021a. Influence of fisheries on the spatio-temporal feeding ecology of gulls along the western Iberian coast. *Mar. Ecol. Prog. Ser.* **661**: 187–201.
- Calado, J.G., Ramos, J.A., Almeida, A., Oliveira, N. & Paiva, V.H.** 2021b. Seabird-fishery interactions and bycatch at multiple gears in the Atlantic Iberian coast. *Ocean Coast. Manag.* **200**: 105306.
- Calenge, C.** 2006. The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. *Ecol. Model.* **197**: 516–519.
- Calladine, J., Park, J.R., Thompson, K.J. & Wernham, C.V.** 2006. *Review of Urban Gulls and their Management in Scotland: A Report to the Scottish Executive*. Edinburgh: Scottish Executive.
- Cama, A., Abellana, R., Christel, I., Ferrer, X. & Vieites, D.** 2012. Living on predictability: Modelling the density distribution of efficient foraging seabirds. *Ecography* **35**: 912–921.
- Camphuysen, K.C.J., Shamoun-Baranes, J., van Loon, E.E. & Bouten, W.** 2015. Sexually distinct foraging strategies in an omnivorous seabird. *Mar. Biol.* **162**: 1417–1428.
- de la Casa-Resino, I., Hernandez-Moreno, D., Castellano, A., Perez-Lopez, M. & Soler, F.** 2014. Breeding near a landfill may influence blood metals (Cd, Pb, Hg, Fe, Zn) and metalloids (Se, As) in white stork (*Ciconia ciconia*) nestlings. *Ecotoxicology* **23**: 1377–1386.
- Ceia, F.R. & Ramos, J.A.** 2015. Individual specialization in the foraging and feeding strategies of seabirds: A review. *Mar. Biol.* **162**: 1923–1938.

- Cleasby, I.R., Wakefield, E.D., Bodey, T.W., Davies, R.D., Patrick, S.C., Newton, J., Votier, S.C., Bearhop, S. & Hamer, K.C. 2015. Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Mar. Ecol. Prog. Ser.* **518**: 1–12.
- Corman, A.M., Mendel, B., Voigt, C.C. & Garthe, S. 2016. Varying foraging patterns in response to competition? A multicolony approach in a generalist seabird. *Ecol. Evol.* **6**: 974–986.
- Coulson, J.C. 1963. The status of the kittiwake in the British Isles. *Bird Study* **10**: 147–179.
- Coulson, J.C. & Coulson, B.A. 2009. Ecology and colonial structure of large gulls in an urban colony: Investigations and management at Dumfries, SW Scotland. *Waterbirds* **32**: 1–15.
- Depestele, J., Rochet, M.-J., Dorémus, G., Laffargue, P. & Stienen, E.W.M. 2016. Favorites and leftovers on the menu of scavenging seabirds: Modelling spatiotemporal variation in discard consumption. *Can. J. Fish. Aquat. Sci.* **73**: 1446–1459.
- Duhem, C., Roche, P., Vidal, E. & Taton, T. 2008. Effects of anthropogenic food resources on yellow-legged gull colony size on Mediterranean islands. *Popul. Ecol.* **50**: 91–100.
- Egunez, A., Zorrozuza, N., Aldalur, A., Herrero, A. & Arizaga, A. 2018. Local use of landfills by a yellow-legged gull population suggests distance-dependent resource exploitation. *J. Avian Biol.* **49**: jav-01455.
- European Commission. 2008. *Directive 2008/56/EC of the European Parliament and of the council. Establishing a Framework for Community Action in the Field of Marine Environmental Policy (Marine Strategy Framework Directive)*. Brussels: EC.
- Fernandes, J.A., Granado, I., Murua, H., Arrizabalaga, H., Zarauz, L., Mugerza, E., Arregi, L., Galparsoro, I., Murua, J., Iriondo, A., Merino, G., Basurko, O.C., Quincoces, I., Santiago, J. & Irigoien, X. 2019. Bay of Biscay VMS/logbook comparison (FAO subarea 27.8). In Taconet, M., Kroodsma, D. & Fernandes, J.A. (eds) *Global Atlas of AIS-Based Fishing Activity: Challenges and Opportunities*. Rome: FAO ISBN: 978-92-5-131964-2.
- Fuirst, M., Veit, R.R., Hahn, M., Dheilily, N. & Thorne, L.H. 2018. Effects of urbanization on the foraging ecology and microbiota of the generalist seabird *Larus argentatus*. *PLoS One* **13**: e0209200.
- García, L.V., Marañón, T., Ojeda, F., Clemente, L. & Redondo, R. 2002. Seagull influence on soil properties, chenopod shrub distribution, and leaf nutrient status in semi-arid Mediterranean islands. *Oikos* **98**: 75–86.
- Gaston, A. 2004. *Seabirds. A Natural History*. London: T & AD Poyser.
- Gilbert, N.I., Correia, R.A., Silva, J.P., Pacheco, C., Catry, I., Atkinson, P.W., Gill, J.A. & Franco, A.M.A. 2016. Are white storks addicted to junk food? Impacts of landfill use on the movement and behaviour of resident white storks (*Ciconia ciconia*) from a partially migratory population. *Mov. Ecol.* **4**: 7.
- Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. 1998. A DNA test to sex most birds. *Mol. Ecol.* **7**: 1071–1075.
- Hidalgo-Mihart, M.G., Cantú-Salazar, L., López-González, C.A., Fernandez, E.C. & González-Romero, A. 2004. Effect of a landfill on the home range and group size of coyotes (*Canis latrans*) in a tropical deciduous forest. *J. Zool.* **263**: 55–63.
- Hintzen, N.T., Bastardie, F., Beare, D., Piet, G.J., Ulrich, C., Deporte, N., Egekvist, J. & Degel, H. 2012. VMStools: Open-source software for the processing, analysis and visualisation of fisheries logbook and VMS data. *Fish. Res.* **115–116**: 31–43.
- Isaksson, N., Evans, T.J., Shamoun-Baranes, J. & Åkesson, S. 2016. Land or sea? Foraging area choice during breeding by an omnivorous gull. *Mov. Ecol.* **4**: 11.
- Karris, G., Ketsilis-Rinis, V., Kalogeropoulou, A., Xirouchakis, S., Machias, A., Maina, I. & Kavadas, S. 2018. The use of demersal trawling discards as a food source for two scavenging seabird species: A case study of an eastern Mediterranean oligotrophic marine ecosystem. *Avian Res.* **9**: 26.
- Kazama, K., Nishizawa, B., Tsukamoto, S., Gonzalez, J.E., Kazama, M.T. & Watanuki, Y. 2018. Male and female black-tailed gulls *Larus crassirostris* feed on the same prey species but use different feeding habitats. *J. Ornithol.* **159**: 923–934.
- Langley, L.P., Bearhop, S., Burton, N.H.K., Banks, A.N., Frayling, T., Thaxter, C.B., Clewley, G.D., Scragg, E. & Votier, S.C. 2021. GPS tracking reveals landfill closures induce higher foraging effort and habitat switching in gulls. *Mov. Ecol.* **9**: 56.
- Louzao, M., Arcos, J.M., Guijarro, B., Valis, M. & Oro, D. 2011. Seabird-trawling interactions: Factors affecting species-specific to regional community utilisation of fisheries waste. *Fish. Oceanogr.* **20**: 263–277.
- Louzao, M., Ruiz, J., Oyarzabal, I., Basterretxea, M., Pedrajas, A., Mugerza, A., Krug, I., Cotano, U., Mugerza, E., Zarauz, L. & Santurtun, M. 2020. Including ecosystem descriptors in current fishery data collection programmes to advance towards a holistic monitoring: Seabird abundance attending demersal trawlers. *Mar. Environ. Res.* **160**: 105043.
- Martínez-Abraín, A., Maestre, R. & Oro, D. 2002. Demersal trawling waste as a food source for Western Mediterranean seabirds during the summer. *ICES J. Mar. Sci.* **59**: 529–537.
- Matos, D.M., Ramos, J.A., Calado, J.G., Ceia, F.R., Hey, J. & Paiva, V.H. 2018. How fishing intensity affects the spatial and trophic ecology of two gull species breeding in sympatry. *ICES J. Mar. Sci.* **75**: 1949–1964.
- Maynard, L.D. & Ronconi, R.A. 2018. Foraging behaviour of great black-backed gulls *Larus marinus* near an urban Centre in Atlantic Canada: Evidence of individual specialization from gps tracking. *Mar. Ornithol.* **46**: 27–32.
- Mendes, R.F., Ramos, J.A., Paiva, V.H., Calado, J.G., Matos, D.M. & Ceia, F.R. 2018. Foraging strategies of a generalist seabird species, the yellow-legged gull, from GPS tracking and stable isotope analyses. *Mar. Biol.* **165**: 168.
- Molina, B. & Bermejo, A. 2009. La gaviota patiamarilla. In Molina, B. (ed) *Gaviotas reidora, sombría y patiamarilla en España*. Población en 2007-2009 y método de censo: 50–111. Madrid: SEO/BirdLife.
- Moreno, R., Jover, L., Munilla, I., Velando, A. & Sanpera, C. 2010. A three-isotope approach to disentangling the diet of a generalist consumer: The yellow-legged Gull in Northwest Spain. *Mar. Biol.* **157**: 545–553.
- Navarro, J., Oro, D., Bertolero, A., Genovart, M., Delgado, A. & Forero, M.G. 2010. Age and sexual differences in the

- exploitation of two anthropogenic food resources for an opportunistic seabird. *Mar. Biol.* **157**: 2453–2459.
- Navarro, J., Grémillet, D., Ramirez, F.J., Afán, I., Bouten, W. & Forero, M.G. 2017. Shifting individual habitat specialization of a successful predator living in anthropogenic landscapes. *Mar. Ecol. Prog. Ser.* **578**: 243–251.
- Olea, P.P. & Baglione, V. 2008. Population trends of rooks *Corvus frugilegus* in Spain and the importance of refuse tips. *Ibis* **150**: 98–109.
- Olsen, K.M. & Larson, H. 2004. *Gulls of Europe, Asia and North America*. London: Christopher Helm.
- Oro, D., Bosch, M. & Ruiz, X. 1995. Effects of a trawling moratorium on the breeding success of the yellow-legged Gull *Larus cachinnans*. *Ibis* **137**: 547–549.
- Oro, D., Jover, L. & Ruiz, X. 1996. Influence of trawling activity on the breeding ecology of a threatened seabird, Audouin's gull *Larus audouinii*. *Mar. Ecol. Prog. Ser.* **139**: 19–29.
- Oro, D., Genovart, M., Tavecchia, G., Fowler, M.S. & Martínez-Abraín, A. 2013. Ecological and evolutionary implications of food subsidies from humans. *Ecol. Lett.* **16**: 1501–1514.
- Pais de Faria, J., Vaz, P.T., Lopes, C.S., Calado, J.G., Pereira, J.M., Veríssimo, S.N., Paiva, V.H., Gonçalves, A.M.M. & Ramos, J.A. 2021. The importance of marine resources in the diet of urban gulls. *Mar. Ecol. Prog. Ser.* **660**: 189–201.
- Paiva, V.H., Pereira, J., Ceia, F.R. & Ramos, J.A. 2017. Environmentally driven sexual segregation in a marine top predator. *Sci. Rep.* **7**: 2590.
- Payo-Payo, A., Oro, D., Igual, J.M., Jover, L., Sanpera, C. & Tavecchia, G. 2015. Population control of an overabundant species achieved through consecutive anthropogenic perturbations. *Ecol. Appl.* **25**: 2228–2239.
- Pinet, P., Jaquet, S., Phillips, R.A. & Le Corre, M. 2012. Sex-specific foraging strategies throughout the breeding season in a tropical, sexually monomorphic small petrel. *Anim. Behav.* **83**: 979–989.
- Plaza, J.I. & Lambertucci, S.A. 2018. More massive but potentially less healthy: Black vultures feeding in rubbish dumps differed in clinical and biochemical parameters with wild feeding birds. *PeerJ* **6**: e4645.
- QGIS Development Team 2009. *QGIS Geographic Information System*. Beaverton: Open Source Geospatial Foundation <http://qgis.osgeo.org>
- R Development Core Team 2011. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Ramos, R., Ramirez, F., Sanpera, C., Jover, L. & Ruiz, X. 2009. Diet of yellow-legged Gull (*Larus michahellis*) chicks along the Spanish Western Mediterranean coast: The relevance of refuse dumps. *J. Ornithol.* **150**: 265–272.
- Ramos, R., Ramirez, F., Carrasco, J.L. & Jover, L. 2011. Insights into the spatiotemporal component of feeding ecology: An isotopic approach for conservation management sciences. *Divers. Distrib.* **17**: 338–349.
- Real, E., Oro, D., Martínez-Abraín, A., Igual, J.M., Bertolero, A., Bosch, M. & Tavecchia, G. 2017. Predictable anthropogenic food subsidies, density-dependence and socio-economic factors influence breeding investment in a generalist seabird. *J. Avian Biol.* **48**: 1462–1470.
- Rochet, M.-J., Arregi, L., Fonseca, T., Pereira, J., Pérez, N., Ruiz, J. & Valeiras, J. 2014. *Demersal Discard Atlas for the South Western Waters*. Technical Report: 121 pp.
- Rock, P. 2005. Urban gulls: Problems and solutions. *Br. Birds* **98**: 338–355.
- Romero, J., Catry, P., Menezes, D., Coelho, N., Silva, J.P. & Granadeiro, J.P. 2019. A gull that scarcely ventures on the ocean: Yellow-legged gulls *Larus michahellis atlantis* on the oceanic Island of Madeira. *Ardeola* **66**: 101–112.
- Ruiz, J., Louzao, M., Oyarzabal, I., Arregi, L., Mugerza, E. & Uriarte, A. 2021. The Spanish purse-seine fishery targeting small pelagic species in the Bay of Biscay: Landings, discards and interactions with protected species. *Fish. Res.* **239**: 105951.
- Schirmer, A., Herde, A., Eccard, J.A. & Dammhahn, M. 2019. Individuals in space: Personality-dependent space use, movement and microhabitat use facilitate individual spatial niche specialization. *Oecologia* **189**: 647–660.
- Shaffer, S.A., Cockerham, S., Warzybok, P., Bradley, R.W., Jahnle, J., Clatterbuck, C.A., Lucia, M., Jelincic, J.A., Cassell, A.L., Kelsey, E.C. & Adams, J. 2017. Population-level plasticity in foraging behavior of western gulls (*Larus occidentalis*). *Mov. Ecol.* **5**: 27.
- Sherley, R.B., Ladd-Jones, H., Garthe, S., Stevenson, O. & Votier, S.C. 2020. Scavenger communities and fisheries waste: North Sea discards support 3 million seabirds, 2 million fewer than in 1990. *Fish Fish.* **21**: 132–145.
- Sommerfeld, J., Mendel, B., Fock, H.O. & Garthe, S. 2016. Combining bird-borne tracking and vessel monitoring system data to assess discard use by a scavenging marine predator, the lesser black-backed gull *Larus fuscus*. *Mar. Biol.* **163**: 116.
- Steigerwald, E.C., Igual, J.-M., Payo-Payo, A. & Tavecchia, G. 2015. Effects of decreased anthropogenic food availability on an opportunistic gull: Evidence for a size-mediated response in breeding females. *Ibis* **157**: 439–448.
- Sugishita, J., Torres, L.G. & Seddon, P.J. 2015. A new approach to study of seabird-fishery overlap: Connecting chick feeding with parental foraging and overlap with fishing vessels. *Glob. Ecol. Conserv.* **4**: 632–644.
- Thaxter, C.B., Ross-Smith, V.H., Bouten, W., Clark, N.A., Conway, G.J., Rehfish, M.M. & Burton, N.H.K. 2015. Seabird-wind farm interactions during the breeding season vary within and between years: A case study of lesser black-backed gull *Larus fuscus* in the UK. *Biol. Conserv.* **186**: 347–358.
- Valeiras, J. 2003. Attendance of scavenging seabirds at trawler discards off Galicia, Spain. *Sci. Mar.* **67**(S2): 77–82.
- Washburn, B.E., Bernhardt, G.E., Kutschbach-Brohl, L., Chipman, R.B. & Francoeur, L.C. 2013. Foraging ecology of four Gull species at a coastal-urban Interface. *Condor* **115**: 67–76.
- Weiser, E.L. & Powell, A.N. 2010. Does garbage in the diet improve reproductive output of glaucous gulls? *Condor* **112**: 530–538.
- Whittington, P.A., Martin, A.P. & Klages, N.T.W. 2006. Status, distribution and conservation implications of the kelp Gull (*Larus dominicanus vetula*) within the eastern cape region of South Africa. *Emu – Aust. Ornithol.* **106**: 127–139.
- Zorrozua, N., Aldalur, A., Herrero, A., Diaz, B., Delgado, S., Sanpera, C., Jover, L. & Arizaga, J. 2020a. Breeding

yellow-legged gulls increase consumption of terrestrial prey after landfill closure. *Ibis* **162**: 50–62.

Zorrozua, N., Egunez, A., Aldalur, A., Galarza, A., Diaz, B., Hidalgo, J., Jover, L., Sanpera, C., Castège, I. & Arizaga, J. 2020b. Evaluating the effect of distance to different food subsidies on the trophic ecology of an opportunistic seabird species. *J. Zool.* **311**: 45–55.

Zorrozua, N., Delgado, S., Aldalur, A. & Arizaga, J. 2020c. Adverse weather reduces the spatial use of an opportunistic gull. *Behaviour* **157**: 667–681.

Received 7 March 2022;

Revision 27 March 2023;

revision accepted 17 April 2023.

Associate Editor: Cat Horswill.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Diet estimation (95%, 75% and 50% credible intervals) showing the contribution of different sources to the diet of adult Yellow-legged Gulls in 2016 in Getaria and Ulia (modified from Zorrozua *et al.* 2020a).

Fig. S2 Boxplots representing the total and the maximum distance, as well as the trip duration in relation to period and habitats. Mixed trips are those in which some GPS locations were observed in the sea and others on the mainland (terrestrial) habitats.

Fig. S3 Examples of gulls' marine trips and vessels' positions in the same temporal window (± 1 h).

Table S1 Information on different individuals tagged with a GPS: Id (Individual), Year, Colony, Sex, First data, Last data (maximum 31 August),

N (Number of positions), % Mar (% Marine trips), % Ter (% Terrestrial trips) and % Mix (% Mixed trips). Additionally, estimated mean and 95% CI values for total distance of the trips (TDIS), maximum distance (MDIS) of trips and trip duration (TDUR) are indicated.

Table S2 Information on habitat use of different individuals tagged with a GPS: Id (Individual), Year, Sex, % Col (% Colony), % Mea (% Meadow), % Lan (% Landfill), % Mar (% Marine), % Por (% Port), % Urb (% Urban), % Oth (% Others).

Table S3 Beta-parameter estimates and 95% confidence intervals of the best GLMM (averaged models; see Table 2 for more details) predicting effects of several external factors on the territory use of adult Yellow-legged Gulls. Reference beta-parameter values ($\beta = 0$): Period—Breeding, Sex—Female, Trip—Marine, Year—2017. K50—kernel 50, K95mar—marine proportion of the kernel 95, TDIS—total distance, MDIS—maximum distance, TDUR—trip duration, OVER—overlap between vessels and gulls.

Table S4 Beta-parameter estimates and 95% confidence intervals of the best GLMM (averaged models) predicting effects of several external factors on the territory use of adult Yellow-legged Gulls from the colony of Ulia. Reference beta-parameter values ($\beta = 0$): Period—breeding, Sex—female, Trip—marine, Year—2017. K50—kernel 50, K95mar—marine proportion of the kernel 95, TDIS—total distance, MDIS—maximum distance, TDUR—trip duration, OVER—overlap between vessels and gulls.