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Human influence on gull non-breeding distribution: potential consequences of changes in fishing practices

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ABSTRACT: Interpopulation mixing of migratory species at particular stopover and wintering hotspots increases their vulnerability to anthropogenic impacts. Animal associations with human activities at this time of the annual cycle should, therefore, inform management policies. The Gulf of Cadiz, Spain is a key non-breeding area for the Near-Threatened Audouin's gull *Ichthyaetus audouinii* and the over-abundant lesser black-backed gull *Larus fuscus*, both of which heavily depend on human fisheries. Here, we used long-term (1990–2013) data on coastal censuses, along with spatially-explicit information on fish landings (2000–2014) and on-board surveys of fishing vessels (2012–2013), to unravel the association of these gulls with human fisheries and evaluate its role in shaping their distribution at this important non-breeding hotspot. Fishing discards from trawlers were extensively used by lesser black-backed gulls, whereas Audouin's gulls apparently benefited from fish aggregations that occurred where purse seines were retrieved. Fishing influence was identified as an important driver of the non-breeding distribution of these gulls, particularly for the lesser black-backed gull, which congregated near main fishing ports. Within this scenario, we speculate that changes in fishing practices, such as those proposed by the upcoming EU Reform of the Common Fisheries Policy that includes a ban on fishing discards, will almost certainly impact the lesser black-backed gull. In contrast, the impact on the Audouin's gull remains unclear and will likely depend on how the proposed ban is implemented.

KEY WORDS: Audouin's gull · Lesser black-backed gull · Non-breeding distribution · Human fisheries · European Union Common Fisheries Policy

INTRODUCTION

Population dynamics are highly dependent on the environmental conditions experienced by individuals throughout the species' distribution ranges, as well as over annual cycles (Oro et al. 2004, Bowler & Benton 2005, Klaassen et al. 2014). Our knowledge of the environmental drivers of demographic variations is generally restricted to the breeding period when animals are especially accessible as they are linked to nests or burrows (but see Clemens et al. 2014, Klaassen et al. 2014). However, challenging conditions faced by animals during the non-breeding season (e.g. food constraints or interactions with human activities) may also act as important drivers of individual survival (Harris & Wanless 1996, Klaassen et al. 2014) and breeding performance through long-term carry-over effects (Harrison et al. 2011), thus shaping population dynamics and growth rates (Barbraud & Weimerskirch 2003, Grosbois & Thompson 2005). An understanding of the non-breeding distribution of free-living animals, their associations with habitat features and their vulnerability to anthropogenic impacts is therefore necessary for a thor-

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ough comprehension of the environmental drivers underlying demographic variations, and may have important implications for the management and conservation of species and communities (Martin et al. 2007, De La Cruz et al. 2014).

Management applications are particularly challenging for migratory species, such as most seabirds. Their non-breeding distribution and ecology are poorly known (e.g. Frederiksen et al. 2012). Interpopulation mixing during non-breeding seasons at particular stopover or wintering hotspots increases their vulnerability to adverse conditions and human impacts (Esler 2000, González-Solís et al. 2007, Frederiksen et al. 2012). In turn, local management and conservation policies at these hotspots may simultaneously affect widely distributed breeding populations. Conservation efforts can therefore be targeted at these hotspots where individuals congregate (Hodgson et al. 2009, Frederiksen et al. 2012).

The complexity of conservation plans increases for inshore gulls that extensively rely on multiple natural and human-impacted coastal habitats. For these seabirds, environmental drivers of animal distribution and associations with human activities may change as individuals move among and within regions throughout their annual cycle. Management and conservation plans for these species therefore require a thorough understanding of the timing of their movements and associations with habitat features and human activities during all their life stages, particularly when and where species compete with human interests (Sol et al. 1995, De La Cruz et al. 2014). Management policies should also account for specific traits of different gull species which co-occur in space and time during the non-breeding season but contrast in their conservation requirements. For instance, most large gulls are considered worldwide as super-abundant and nuisance species (e.g. Vidal et al. 1998), likely as a result of their ability to exploit human-derived fishing discards or refuse tips (e.g. the lesser black-backed gull *Larus fuscus*) (Oro 1996, Schwemmer & Garthe 2005, Kim & Monaghan 2006). Conservation plans for these species are commonly directed to limiting the availability and accessibility of these trophic resources to gulls (e.g. the European Union [EU] Landfill Directive, and the EU Reform of the Common Fisheries Policy [CFP]). However, these management decisions may also negatively impact other threatened gull species that also rely extensively on the same human-derived food resources (e.g. the Audouin's gull *Ichthyaetus audouinii*) (Navarro et al. 2009, Bicknell et al. 2013).

Among the general flyways used by Eurasian migratory seabirds, the Gulf of Cadiz, Spain, has emerged as a key stopover and wintering hotspot (Arcos et al. 2009); this is likely the result of its high marine productivity (García Lafuente & Ruiz 2007) and its strategic location between the Eurasian and African continents. The Gulf of Cadiz is also one of the most human-impacted marine systems (Halpern et al. 2008) with its intense industrial fishing activity (Silva et al. 2002) and important shipping lanes (Halpern et al. 2008). Human density is high along the coast, particularly during the summer months when thousands of tourists flock to its beaches. Accordingly, the Gulf of Cadiz warrants conservation plans based on a proper comprehension of the human impact on seabirds and designed to complement wildlife conservation with socioeconomic activities inherent to this region.

Here, we present an investigation aimed at understanding the role of human activities in shaping the non-breeding distribution of 2 gull species, the Audouin's gull and lesser black-backed gull, in the Gulf of Cadiz. These 2 migratory gulls differ in their breeding distribution, ecology and conservation status (Burger & Gochfeld 1996, Olsen & Larsson 2004), but both strongly depend on human fisheries (Bicknell et al. 2013, and references therein). We used data from on-board surveys, long-term monthly censuses (1990–2013) and spatially explicit information on fish landing to examine the role of fishing activities in determining the spatial distribution of the 2 gulls at this important non-breeding hotspot. On the basis of observed results, we further speculate on the potential consequences for these species of management policies affecting socioeconomic practices, e.g. the CFP.

MATERIALS AND METHODS

Study area and species

The Gulf of Cadiz (southwest Iberian Peninsula) is greatly influenced by the exchange of water between the North Atlantic Ocean and the western Mediterranean Sea (i.e. the Alboran Basin) (Ruiz & García-Lafuente 2006). Its particular oceanographic conditions, along with the wide continental shelf and nutrient inflow through some important rivers, result in an enhanced marine productivity that commonly peaks during late winter rather than during the upwelling summer season, typical of the surrounding waters of the North Atlantic and the Eastern Canary Current (García Lafuente & Ruiz 2007). Consequently, the Gulf of Cadiz has emerged as a key non-breeding area for a number of seabirds (Arcos et al. 2009). Its coastline is characterized by a patchy landscape that alternates between highly anthropized estuarine areas and stretches of unaltered coastal habitats (e.g. Doñana National Park located in the central-western sector, Fig. 1).

The Audouin's gull is an endemic breeder of the western Mediterranean basin. In contrast, the lesser black-backed gull is a polytypic species whose breeding grounds are widely distributed along the North European coasts. Most breeding individuals of both species migrate following a southwesterly route from late-July to October, using many stopovers enroute, and reaching the Southwestern European and North African coasts for wintering (del Hoyo et al. 1996, Klaassen et al. 2012). They are both considered generalist omnivores (Bicknell et al. 2013), with a diet, distribution and demography strongly influenced by the availability of fishing discards (Oro et al. 2004, Schwemmer & Garthe 2005, Kim & Monaghan 2006, Bartumeus et al. 2010). The IUCN lists Audouin's gull as a Near-Threatened species since most individuals (ca. 85% of the worldwide population) congregate in just 2 breeding colonies (Pedrocchi et al. 2002), and as a result is particularly vulnerable to certain perturbations such as changes in fishing practices (Oro et al. 2004). In contrast, the lesser black-backed gull is listed as Least Concern, because of its high abundance and wide distribution. Indeed, it is commonly viewed as an over-abundant pest species, due to its negative impact on human interests (Furness & Monaghan 1987, Vidal et al. 1998, Oro & Martínez-Abraín 2007).

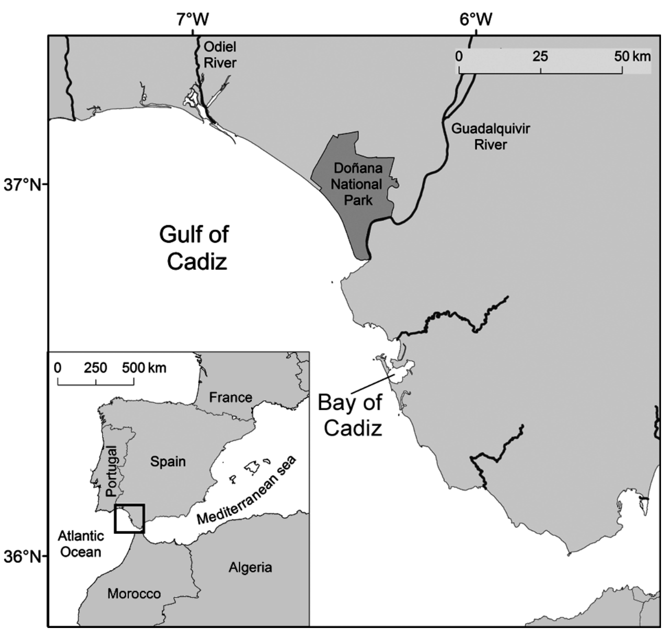

Fig. 1. Map of the study area

Gull phenology

Long-term (1990–2013) information on the abundance of Audouin's gulls and lesser black-backed gulls along the coastline of Doñana National Park was used to identify key time-windows likely related to the post-breeding, wintering and pre-breeding periods. Abundances were obtained on a monthly basis through terrestrial linear transects conducted by the monitoring team of the Doñana Biological Station and the Conservation Area of Doñana National Park. This protected area is nearly devoid of human disturbance, thus representing a suitable area for accurately depicting intra-annual trends in the abundance of gulls in the Gulf of Cadiz.

Spatio-temporal distribution of gulls along the coast

We investigated the distribution of both gull species during the previously defined post-breeding, wintering and pre-breeding periods (based on gull phenology in the Gulf of Cadiz) by using monthly terrestrial censuses carried out at 19 different locations along the Gulf of Cadiz coastline during the 2004–2013 period. Censuses were conducted by the Programa de Emergencias, Control Epidemiológico y Seguimiento de Fauna (Andalusia Government), and the monitoring team of the Doñana Biological Station and the Conservation Area of Doñana National Park. Censuses were consistently performed during the entire period, always during the morning and following the same procedure, so that the obtained abundance estimates are directly comparable. Annual abundances were estimated by averaging the maximum number of individuals counted for a given year, period (post-breeding, wintering and pre-breeding) and location (19 locations). Outside the breeding season, when individuals are no longer central-place foragers, they are expected to occur in areas where they can maximize energy intake with respect to foraging costs. Accordingly, proximity to food patches is considered among the key factors likely determining the non-breeding distribution of seabirds (Frederiksen et al. 2012). In our view, this argument validates the use of coastal censuses to ascertain the non-breeding distribution of these inshore gulls, as individuals resting along the coastline likely forage in the vicinity.

Fishing influence

The main fishing fleets in the Gulf of Cadiz (in terms of total landing) utilize purse seining and trawling gear (Silva et al. 2002). Here, we firstly evaluated the association of Audouin's gulls and lesser black-backed gulls with these fishing activities using a total of 15 on-board surveys (7 on purse seiners, 8 on trawlers); surveys were carried out by the same observer during the non-breeding season (late July to early April) of the 2012–2013 period. The total observation effort comprised 1967 km transect lines throughout which the observer focused on vessel-seagull interactions during fishing operations, including the retrieval of purse seines (n = 60) or fish discarding episodes from trawlers (n = 31). During these surveys, 259 Audouin's gulls and 9538 lesser black-backed gulls were observed interacting with fishing vessels. Most Audouin's gulls (ca. 80%) interacted with purse seiners, whereas most lesser black-backed gulls (90%) were associated with trawlers. Accordingly, we considered both fishing fleets separately when investigating the role of fishing activity in determining the spatiotemporal distribution of the 2 gull species. Remarkably, the fishing fleets differed in the amount of fishing discards produced; whilst trawlers discarded ca. 80% of captured biomass, purse seiners discarded only ca. 5%, but provided gulls with highly efficient feeding opportunities (Arcos & Oro 2002).

Spatial gradients in fishing activities were constructed through an index of fishing influence (rescaled to 0–1 values) based on a modified version of an isolation function (Hanski 1998, Afán et al. 2014): $F_i = \sum\exp(-d_{ij} \cdot B_j) \cdot P_j$, where d_{ij} was the distance from each grid cell i (cell size = 0.041667°) to the fishing port j, and P_j corresponded to fish landings (associated with purse seining and trawling) of harbour j for the post-breeding, wintering and pre-breeding periods identified for each gull species. B_j was the inverse of the minimum Euclidean distance from each fishing port to 200 m isobaths (delimiting the continental shelf), which determines the spatial influence threshold of fishing fleet operability. Monthly data on fish landings for the 2000–2014 period, grouped as purse seining and trawling, was sourced online from the Consejería de Agricultura, Pesca y Desarrollo Rural, Andalusia Government website at www.juntadeandalucia.es/agriculturaypesca (accessed on January 2014). The influence of fishing activities at a given census location was estimated by averaging data on fishing influence in what we considered a suitable foraging range for non-breeding gulls, i.e. a 30 km surrounding buffer. Information concerning the at-sea distribution of gulls is commonly restricted to the breeding period, when they tend to congregate in coastal waters within a ca. 50 km distance (Schwemmer & Garthe 2005, Christel et al. 2012). However, foraging ranges during the non-breeding period are expected to be constrained in order to maximize net energy intake (Frederiksen et al. 2012). Furthermore, 30 km was the average extent of the continental shelf where fishing vessels operate and where gulls likely forage.

Marine productivity patterns

Our research question focused on the role of human fisheries in shaping the spatial distribution of gulls in the Gulf of Cadiz. However, we also controlled for habitat suitability, in terms of the availability of natural food resources in the surrounding area. In particular, we averaged long-term (2002–2012) data on chlorophyll *a* (chl *a*) concentration (mg m^{-3}) to investigate spatial patterns of marine productivity in the Gulf of Cadiz, as this biological feature has been previously considered as a reliable proxy to prey availability for seabirds (Afán et al. 2014, Ramírez et al. 2014). Chl *a* data was sourced online from the Aqua MODIS database at http://oceancolor.gsfc.nasa.gov/ (accessed on January 2014) as Level 3 HDF seasonal composites (summer: June–September, autumn: September–December, and winter: December–March) at a spatial resolution of 0.041667°, and converted to raster images using the Marine Geospatial Ecology Tools (Roberts et al. 2010) for ArcGIS 10.1 (Esri). Natural food availability was subsequently approximated by averaging derived data on chl *a* within considered foraging ranges for gulls (30 km buffer areas from focal census points, see above).

Statistical analysis

We explored the role of human fisheries as a driver of the non-breeding distribution of Audouin's gulls and lesser black-backed gulls in the Gulf of Cadiz. Owing to the nature of the response variable (among-year averaged maximum number of individuals at 19 different locations along the coast of the Gulf of Cadiz during the post-breeding, wintering and pre-breeding period), this question was addressed through generalized linear models (GLM) with negative binomial error structure and log-link function to account for overdispersion. A set of competing models was built by considering the indices of fishing influence and marine productivity, and the interaction of the these variables with the studied non-breeding periods (post-breeding, wintering and pre-breeding). There was little correlation between these indices either for Audouin's gulls (Pearson's r = 0.02, p = 0.92, df = 27) or for lesser black-backed gulls (Pearson's r = 0.15, p = 0.32, df = 45), thus allowing their simultaneous inclusion in the model set. Additionally, we included a 2 level factor regarding the type of habitat at the census location (estuarine vs. beach). Model selection was accomplished using the Akaike information criteria corrected for small sample sizes (AIC_c) and the corresponding AIC_c increments (ΔAIC_c) and weights (AIC_c wt, Johnson & Omland 2004). Owing to the similar support observed for the top-ranked models, we averaged the models accumulating 90% of AIC_C wt. Input variables were previously standardized using Gelman (2008) approach (based on 2 SD), as this is essential for interpreting parameter estimates after model averaging (Grueber et al. 2011). Pseudo-R^2 values were based on an improvement from the null model (intercept only; *n*) to the fitted model (*f*), and calculated as: $R^2 = 1 - \exp(-2/n \cdot \text{logLik}(n) - \text{logLik}(f))$, where LogLik = log-likelihood function. GLMs were conducted in R version 3.0.2 (R Core Team 2013) with additional functions provided by the R packages MASS (function glm.nb; Venables & Ripley 2002) and MuMIn (functions dredge and model.avg; Bartoń 2013).

RESULTS

Gull phenology

Intra-annual trends in the abundance of Audouin's gulls and lesser black-backed gulls indicate the importance of the Gulf of Cadiz as stopover and wintering hotspot. These 2 gull species, breeding in the Mediterranean basin and Northwestern Europe respectively, pass through the Gulf of Cadiz during annual migrations to wintering quarters. The initial peak in the absolute abundance of gulls in Doñana National Park was therefore ascribed to the post-breeding migration. The time-window for this period varied according to the species considered. The Audouin's gull arrived earlier (August–September) than the lesser black-backed gull (September–October). However, the post-breeding peak was wider for Audouin's gulls, so that the studied wintering period occurred later in this species (December–January for Audouin's gull, and November–December for the lesser black-backed gull). Although most migratory gulls exclusively use the Gulf of Cadiz for stopover, the occurrence of individuals throughout the entire non-breeding season suggests that this area also acts as a wintering ground. The latter peak in the abundance of lesser black-backed gulls (January–February) was assigned to the pre-breeding period, when individuals wintering in the south use the Gulf of Cadiz for stopover during their annual migrations to breeding sites. No pre-breeding peak was observed for Audouin's gulls, thus suggesting they use alternative routes when moving from wintering quarters to breeding sites (Fig. 2).

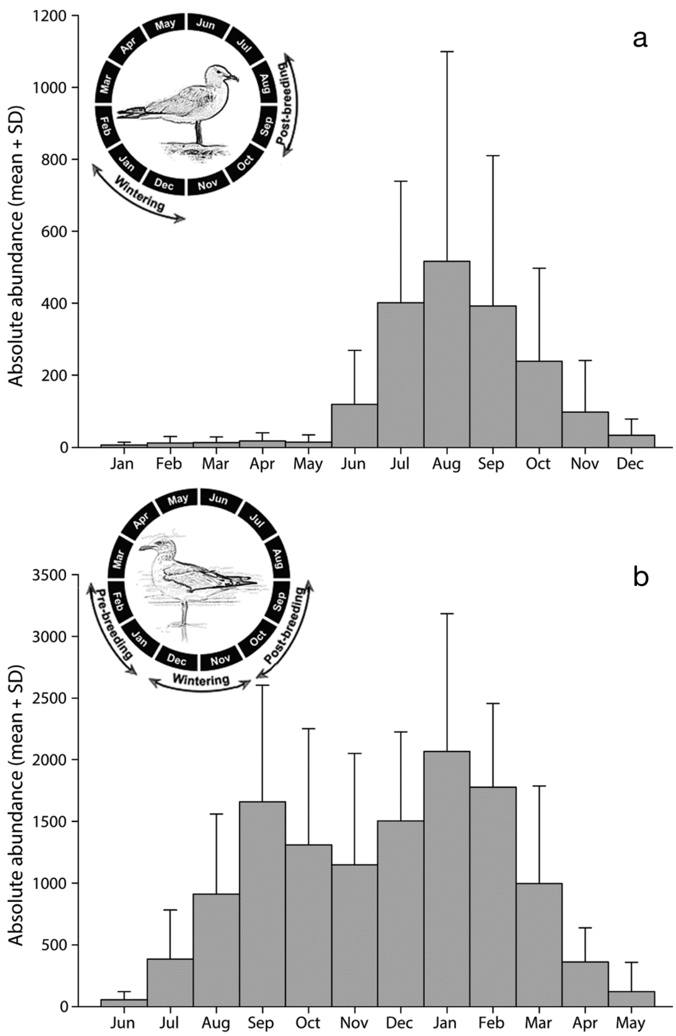

Fig. 2. Monthly information on the abundance (mean ± SD) of (a) Audouin's gulls and (b) lesser black-backed gulls along the coast of Doñana National Park; intra-annual trends concerning the abundance of these 2 gull species were obtained by averaging annual cycles from 1990 to 2013. Circular graphs represent identified key time-windows associated with post-breeding, wintering and pre-breeding periods

Human fisheries and marine productivity in the Gulf of Cadiz

The Gulf of Cadiz is characterized by a marked seasonality in the spatial distribution of human fisheries and marine productivity patches. Fishing activities mainly occurred in the central-eastern sector where a number of important fishing ports are located in a relatively small area between the mouth of the Guadalquivir River and the Bay of Cadiz. However, fishing activity of both purse seiners and trawlers was also important in the western sector close to the Odiel marshes (at the mouth of the Odiel River) during the studied post-breeding periods for the Audouin's gull and the lesser black-backed gull (Fig. 3). This seasonality also affected fish captures by both fishing fleets, which peaked during the gulls' post- and pre-breeding periods. In particular, average landing (2000–2014) for purse seiners reached ~115×10^3 kg during the Audouin's gull's post-breeding period, but only ~50×10^3 kg during the wintering period. Average landing for trawlers was ~69×10^3 kg, 47×10^3 kg and 52×10^3 kg for the lesser black-backed gull post-breeding, wintering and post-breeding periods, respectively. Marine productivity also showed a marked seasonality with max. chl *a* values occurring in winter. Furthermore, chl *a* patches primarily occurred over the continental shelf and in the central-western sector; however, the extent of these patches strongly varied throughout the annual cycle, with wider areas occurring during the winter and autumn seasons (Fig. 4).

Gull distribution along the coast of the Gulf of Cadiz

During the 2004–2013 period, experienced observers counted ~500 000 lesser black-backed gulls during the post-breeding (~135 000 ind.), wintering (~120 000 ind.) and pre-breeding (~215 000 ind.) periods. Total number of counted Audouin's gulls was lower (~35 000 ind.) and more heterogeneously distributed throughout the non-breeding season (~29 000 and 6000 ind. counted during the post-breeding and wintering periods, respectively). The spatial distribution of gulls (averaged maximum number of individuals at 19 different locations along the coast of the Gulf of Cadiz) differed between species and among studied time periods. The Audouin's gull congregated in the protected areas of Doñana National Park (central-western sector) and the vicinity of the Bay of Cadiz during the post-breeding period, but the species was distributed widely during the wintering period (Fig. 5). In contrast, the lesser black-backed gull was relatively abundant in the western sector (near Portugal) during the post-breeding and wintering periods, and occurred mainly in the Bay of Cadiz during the pre-breeding period (Fig. 5).

Human fishery was revealed as an important driver of the non-breeding distribution of these gulls (Tables 1 & 2). The 7 top-ranked models (i.e. those accumulating 90 % of AIC_c wt) for the Audouin's gull (Pseudo-R^2 = 0.39 to 0.51, Table 1) included habitat category, period, marine productivity, fishing influence and its interaction with period as explanatory

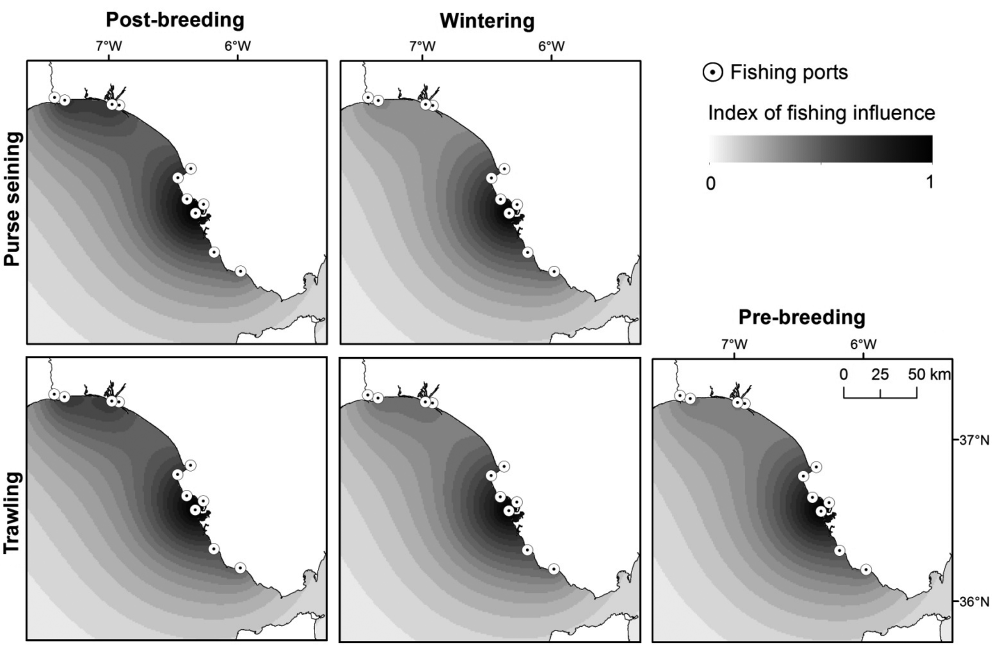

Fig. 3. Distribution of purse seining and trawling fishing activities, estimated through an index (rescaled to 0–1 values) based on an isolation function that considered average fish landing (monthly data for the 2004–2013 period) per fishing port and key time-windows for gull species: post-breeding, wintering and pre-breeding periods (see 'Materials and methods' and Afán et al. 2013). Audouin's gull and the lesser black-backed gull interact mostly with purse seiners and trawlers, respectively

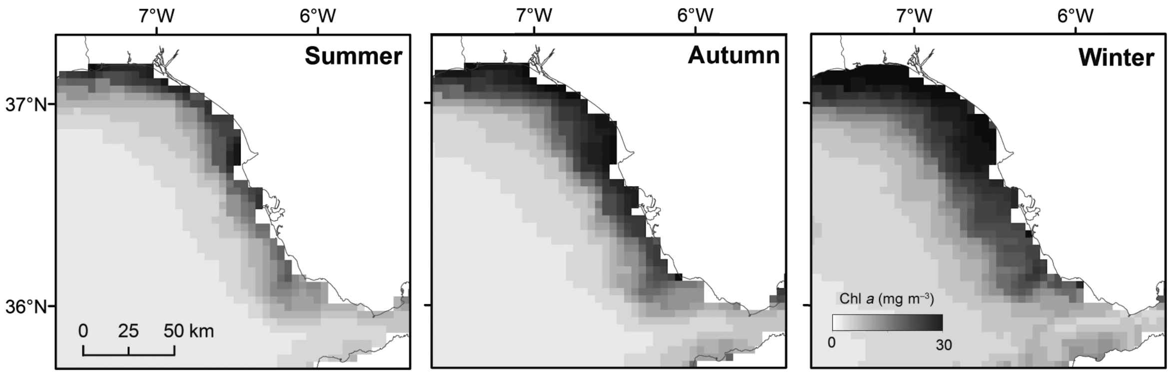

Fig. 4. Marine productivity patterns in the Gulf of Cadiz based on averaging long term (2002–2012) data on chl *a* concentrations (mg m^{-3}) from satellite imagery seasonal composites for summer (June–September), autumn (September–December), and winter (December–March) periods

variables (Table 1). Habitat and period apparently were the most relevant predictors in terms of relative importance (1 and 0.85, respectively), followed by the indices of fishing influence (0.65) and marine productivity (0.25) (Table 3). Standardized effect sizes pointed to sandy beaches as the preferred habitat type for Audouin's gulls. Fishing influence positively affected the abundance of individuals. Although the top ranked models also included the interaction term between period and fishing influence, the low relative importance of this parameter (0.09) along with its standardized effect size, with a 95% confidence interval that clearly included zero (−1.34 to 0.39) (Table 3), suggested that the influence of fishing practices was similar throughout the non-breeding season. Similarly, standardized effect size was relatively low for the index of marine productivity. Indeed, the 95% confidence interval for the parameter estimate clearly included zero (−0.81 to 0.26, Table 3), thus indicating the limited role of this predictor in explaining the non-breeding distribution of Audouin's gulls in the Gulf of Cadiz.

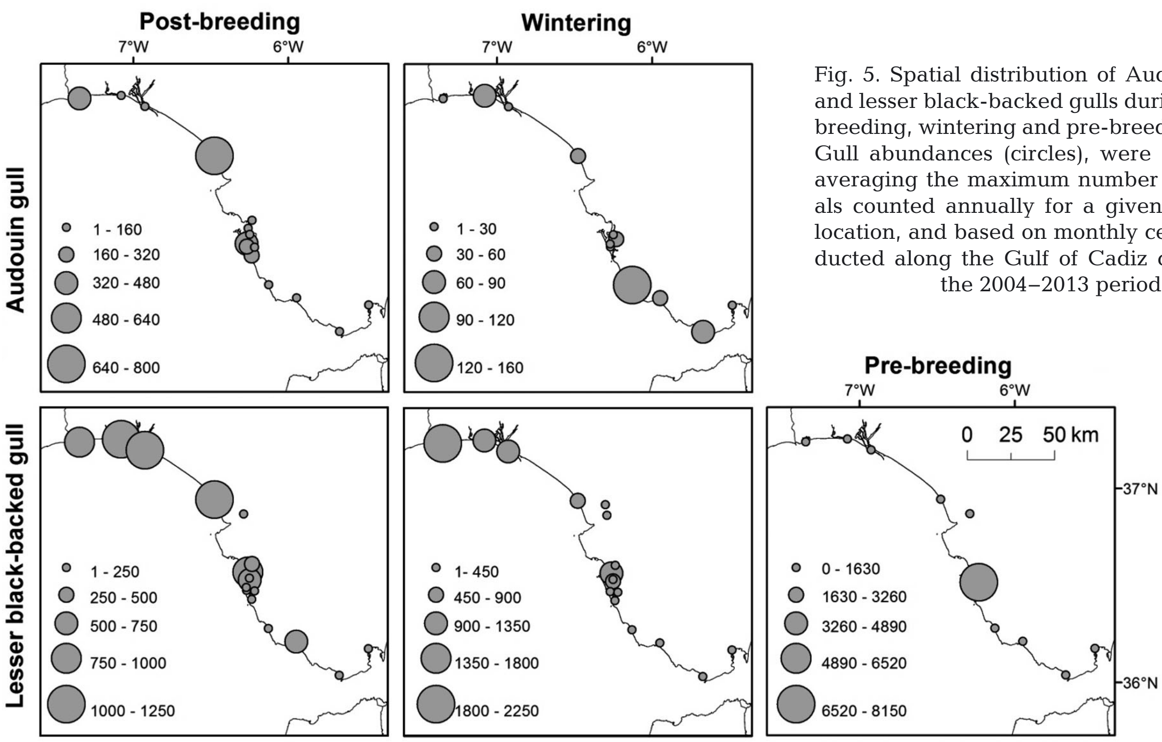

Fig. 5. Spatial distribution of Audouin's gulls and lesser black-backed gulls during the post-breeding, wintering and pre-breeding periods. Gull abundances (circles), were obtained by averaging the maximum number of individuals counted annually for a given period and location, and based on monthly censuses conducted along the Gulf of Cadiz coast during the 2004–2013 period

Table 1. Set of candidate models to assess the impact of human fisheries on the non-breeding spatial distribution of Audouin's gulls along the Spanish coast of the Gulf of Cadiz. Competing models included the effect of habitat (estuarine vs. beach), non-breeding period, indices of fishing influence and marine productivity (average chl *a* concentrations (mg m^{-3}), and the interaction of the latter 2 variables with studied non-breeding periods. k = number of parameters; AIC_c = corrected AIC, ΔAIC_c = AIC_c increments, AIC_c wt = AIC_c weights (for Pseudo-R^2, see 'Materials and methods: Statistical analysis'); the 7 top-ranked models (**bold**) accumulated 90% of AIC_c wt. Environmental predictors were z-transformed

Models for Audouin's gull	k	AIC_c	ΔAIC_c	AIC_c wt	Pseudo-R^2
Habitat + Period + Fishing influence	**5**	**308.9**	**0**	**0.26**	**0.494**
Habitat + Period	**4**	**309**	**0.16**	**0.24**	**0.437**
Habitat + Period + Chl *a* + Fishing influence	**6**	**310.9**	**2**	**0.095**	**0.514**
Habitat + Period + Fishing influence + Period:Fishing influence	**6**	**311.2**	**2.27**	**0.084**	**0.51**
Habitat + Fishing influence	**4**	**311.4**	**2.5**	**0.074**	**0.389**
Habitat + Period + Chl a	**5**	**311.6**	**2.69**	**0.068**	**0.445**
Habitat + Chl a + Fishing influence	**5**	**311.8**	**2.87**	**0.062**	**0.441**
Habitat + Period + Chl *a* + Fishing influence + Period:Chl *a*	7	313.2	4.36	0.029	
Habitat + Period + Chl *a* + Period:Chl *a*	6	313.5	4.61	0.026	
Habitat + Period + Chl *a* + Fishing influence + Period:Fishing influence	7	313.8	4.87	0.023	
Period	3	315.8	6.92	0.008	
Habitat	3	316	7.09	0.008	
Habitat + Period + Chl a + Fishing influence + Period:Chl a + Period:Fishing influence	8	316.5	7.62	0.006	
Habitat + Chl *a*	4	316.7	7.84	0.005	
Period + Fishing influence	4	318.1	9.17	0.003	
Period + Chl *a*	4	318.4	9.47	0.002	
Period + Chl *a* + Period:Chl *a*	5	318.4	9.55	0.002	
Fishing influence	3	319.5	10.65	0.001	
Period + Fishing influence + Period:Fishing influence	5	319.7	10.82	0.001	
Null	2	320.5	11.6	0.001	
Period + Chl *a* + Fishing influence	5	320.9	12.02	0.001	
Period + Chl *a* + Fishing influence + Period:Chl *a*	6	321.3	12.44	0.001	
Chl a + Fishing influence	4	322.2	13.32	0	
Period + Chl *a* + Fishing influence + Period:Fishing influence	6	322.8	13.92	0	
Chl a	3	323	14.1	0	
Period + Chl *a* + Fishing influence + Period: Chl *a* + Period:Fishing influence	7	324.1	15.21	0	

The 5 top-ranked models (i.e. those accumulating 90% of AIC_c wt) for the lesser black-backed gull (Pseudo-R^2 = 0.14 to 0.28, Table 2) included the habitat category, period, fishing influence and marine productivity as explanatory variables (Table 2). The interaction terms were excluded from the averaged model as they were not in the top model set. We interpreted this result as indicating that the influence of fishing activities and marine productivity was similar for all studied periods. Habitat and fishing influence were the most relevant predictors (relative importance = 1 and 0.92, respectively), followed by marine productivity (0.21) and period (0.15) (Table 3). Similarly to Audouin's gulls, standardized effect sizes identified sandy beaches as the preferred habitat type for lesser black-backed gull, which also congregated in areas with a higher fishing influence. Marine productivity was also a poor predictor of the non-breeding distribution of the lesser black-backed gull, with a 95% confidence interval for the standardized effect size ranging from −0.49 to 0.42 (Table 3).

DISCUSSION

Gull-fisheries associations

In this work we demonstrate that Audouin's gulls and lesser black-backed gulls are associated with human fisheries along the Spanish coast of the Gulf of Cadiz during the non-breeding season. Whilst Audouin's gulls may benefit from purse seiners, lesser black-blacked gulls rely on fishing discards from trawlers throughout the entire non-breeding season. Fishing activity apparently attracts individuals of both species, but its actual role in shaping the non-breeding distribution of these gulls varies according to the species considered.

Human fisheries have shaped many aspects of seabird foraging behavior, distribution and population dynamics by providing an abundant and predictable food resource (Oro et al. 2004, Bartumeus et al. 2010, Cury et al. 2011). During the breeding period, the Audouin's gull and the lesser black-backed gull behave as generalist omnivores largely relying on fishing discards (Oro 1996, Oro et al. 1996, Schwemmer & Garthe 2005, Navarro et al. 2010). Although the non-breeding diet of these species is unknown, results from our on-board surveys suggest that human fisheries might be also important for these gulls at this time of the annual cycle. We identified species-specific preferences for fishing gears. In particular, Audouin's gulls may benefit from fish aggregations which occur during the retrieval of purse seiners (Oro et al. 1996, Arcos et al. 2001, Arcos & Oro 2002). However, the moderate number of interactions with fishing vessels recorded for this seagull in the on-board surveys (n = 259), relative to its expected abundance in the Gulf of Cadiz (Fig. 2), suggests this species may largely rely on non-fisheries associated feeding during the non-breeding season. In contrast, lesser black-backed gulls apparently rely largely on fish discards from trawlers (~8600 recorded interactions with this fishing gear), suggesting they are more effective in competing for this plentiful subsidy (Oro 1996; see Arcos et al. [2001] for interactions between the Audouin's gull and the similar-sized yellow-legged gull *Larus michahellis*).

Few studies have accurately quantified the role of industrial fisheries in shaping the non-breeding distribution of gulls (Bicknell et al. 2013). We demonstrate that Audouin's gulls and lesser black-backed gulls tend to congregate close to main fishing ports in the Gulf of Cadiz, where interactions with fishing vessels are expected to be particularly frequent. Indeed, the index of fishing influence was a more important driver of gulls' non-breeding distribution than the spatial distribution of marine productivity patches. Accordingly, and as expected for these scavenger species, individuals apparently relies on fishing activity throughout the entire annual cycle, not only at breeding sites (Oro 1996, Schwemmer & Garthe 2005) but also at stopovers and wintering grounds.

Table 2. Set of candidate models to assess the impact of human fisheries on the non-breeding spatial distribution of lesser black-backed gulls along the Spanish coast of the Gulf of Cadiz. Competing models included the effect of habitat (estuarine vs. beach), non-breeding period, indices of fishing influence and marine productivity (average chl *a* concentrations, mg m^{-3}), and the interaction of the latter 2 variables with studied non-breeding periods. k = number of parameters; AIC_c = corrected AIC, ΔAIC_c = AIC_c increments, AIC_c wt = AIC_c weights (for Pseudo-R^2, see 'Materials and methods: Statistical analysis'); the 5 top-ranked models (**bold**) accumulated 90% of AIC_c wt. Environmental predictors were z-transformed

Models for lesser black-backed gull	k	AIC_c	ΔAIC_c	AIC_c wt	Pseudo-R^2
Habitat + Fishing influence	**4**	**647.4**	**0**	**0.532**	**0.246**
Habitat + Chl *a* + Fishing influence	**5**	**649.9**	**2.51**	**0.152**	**0.246**
Habitat + Period + Fishing influence	**6**	**650.7**	**3.33**	**0.101**	**0.275**
Habitat	**3**	**651.5**	**4.06**	**0.07**	**0.136**
Habitat + Period + Chl *a* + Fishing influence	**7**	**652.9**	**5.52**	**0.034**	**0.284**
Habitat + Chl *a*	4	653.3	5.91	0.028	
Chl *a*	3	653.4	5.97	0.027	
Chl *a* + Fishing influence	4	654.3	6.87	0.017	
Habitat + Period + Fishing influence + Period:Fishing influence	8	655.6	8.19	0.009	
Null	2	656	8.62	0.007	
Habitat + Period	5	656	8.64	0.007	
Period + Chl *a*	5	657.8	10.38	0.003	
Fishing influence	3	657.9	10.46	0.003	
Habitat + Period + Chl *a* + Fishing influence + Period:Fishing influence	9	658	10.6	0.003	
Habitat + Period + Chl *a*	6	658.3	10.87	0.002	
Habitat + Period + Chl *a* + Fishing influence + Period:Chl *a*	9	658.4	11.05	0.002	
Period + Chl *a* + Fishing influence	6	658.9	11.54	0.002	
Period	4	660.1	12.75	0.001	
Period + Fishing influence	5	661.5	14.07	0	
Period + Chl *a* + Period:Chl *a*	7	662.7	15.31	0	
Period + Chl *a* + Fishing influence + Period:Fishing influence	8	663.2	15.81	0	
Habitat + Period + Chl *a* + Period:Chl *a*	8	663.9	16.5	0	
Period + Chl *a* + Fishing influence + Period:Chl *a*	8	664.2	16.82	0	
Habitat + Period + Chl *a* + Fishing influence + Period:Chl *a* + Period:Fishing influence	11	664.3	16.93	0	
Period + Fishing influence + Period:Fishing influence	7	664.7	17.33	0	
Period + Chl *a* + Fishing influence + Period:Chl *a* + Period:Fishing influence	10	669.1	21.71	0	

Table 3. Summary results of the averaged models comprising those candidate models that accumulated 90% of AIC_c wt (see Tables 1 & 2); effect sizes (Estimate) were standardized using 2 SD following Gelman (2008)

	Relative importance	Estimate	Adjusted SE	Confidence interval Min	Max
Audouin's gull					
(Intercept)	–	3.83	0.43	2.96	4.69
Habitat	1	–	–	–	–
Estuarine	–		Reference category		
Beach	–	1.58	0.44	0.66	2.49
Period	0.85	–	–	–	–
Post–breeding	–		Reference category		
Wintering		−1.23	0.47	−2.18	−0.28
Fishing influence	0.65	0.59	0.25	0.08	1.1
Chl *a*	0.25	−0.27	0.26	−0.81	0.26
Period:Fishing influence	0.09	–	–	–	–
Post–breeding:Fishing influence	–		Reference category		
Wintering:Fishing influence	–	−0.48	0.42	−1.34	0.39
Lesser black–backed gull					
(Intercept)	–	5.22	0.32	4.58	5.86
Habitat	1	–	–	–	–
Estuarine	–		Reference category		
Beach	–	1.52	0.42	0.67	2.37
Period	0.15	–	–	–	–
Post–breeding	–		Reference category		
Wintering	–	0.44	0.43	−0.42	1.31
Pre–breeding	–	0.72	0.53	−0.35	1.8
Fishing influence	0.92	0.67	0.2	0.27	1.08
Chl *a*	0.21	−0.03	0.22	−0.49	0.42

Tourism may also play an important role in determining the non-breeding distribution of gulls, particularly during the post-breeding period when large numbers of tourists and gulls co-occur in coastal areas of the Gulf of Cadiz. The mere presence of humans disturbs gulls (Webb & Blumstein 2005, Martínez-Abraín et al. 2008), so that individuals may tend to congregate in areas with some degree of protection, i.e. where human activities are restricted. This was particularly the case for Audouin's gulls that occurred in large numbers in Doñana National Park, where human activities are restricted, during the summer season. Tourism may have contrasting impacts on wildlife by either disturbing wildlife populations (Anderson & Keith 1980) or supporting habitat conservation (e.g. Burger 2000, Kiss 2004). Natural protected areas may act as refuge systems, thus buffering the negative impacts of tourism on wildlife (Anderson & Keith 1980), while generating economic benefits from ecotourism. Delimitation of natural protected areas will benefit from information on species' distribution, whereas management of these areas should consider the particular requirements of the species for protection, along with the demands of tourism.

Based on long-term information, we provide here for the first time accurate quantification of the influence of an important economic activity in determining the non-breeding distribution of gulls at an important non-breeding hotspot. In particular, this work supports the importance of human fisheries for these species during the non-breeding season as well, while pointing to the relevance of natural protected areas for conservation and economic purposes. We argue that this information is crucial for evaluating, and even predicting, the impact on individuals of potential management actions or changes in socioeconomics practices. Given the potential wide distribution of breeding populations occurring in the Gulf of Cadiz during the non-breeding season (particularly in the case of the lesser black-backed gull), management actions implemented locally may have important conservation implications at a much larger scale. Furthermore, this approach could be extended to a large suite of seabirds occurring during the non-breeding season in the Gulf of Cadiz and other migratory hotspots, and may potentially contribute to the development of suitable management policies for seabird communities.

Conservation implications

A proper understanding of the relationship between fishing industry and seabirds is mandatory to provide rational assessments on the effects of EU regulation on discard banning. The upcoming EU Common Fisheries Policy, which includes a ban on fishing discards, will likely result in unforeseen knock-on consequences for the large number of scavenging seabirds that consume this plentiful subsidy. Predictions of the potential impacts of this discard reform for seabirds will clearly benefit from accurate information regarding seabird-human interactions outside the breeding season (Bicknell et al. 2013), when the potential effect of such policies on metapopulation dynamics may be exacerbated (Esler 2000, González-Solís et al. 2007, Frederiksen et al. 2012). In view of our obtained results, discard declines in the Gulf of Cadiz may contribute to reversing population trends for the over-abundant, nuisance populations of lesser black-backed gulls, thus potentially benefiting human interests. However, the impact on the Near-Threatened Audouin's gull remains unclear.

Due of the large reliance of Audouin's gull on fishing discards during the breeding season (Oro 1996, Oro et al. 1996, Navarro et al. 2010), a decline in discords will presumably negatively affect demographic parameters linked to breeding sites (e.g. reproductive performance) (Bicknell et al. 2013). In contrast, their reliance on non-fisheries associated feeding during the non-breeding season suggests that the expected increase in fish biomass in the Gulf of Cadiz following discard banning will affect positively those parameters linked to non-breeding grounds (e.g. individual survival).

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LITERATURE CITED

Afán I, Navarro J, Cardador L, Ramírez F and others (2014) Foraging movements and habitat niche of two closely related seabirds breeding in sympatry. Mar Biol 161: 657–668

Anderson DW, Keith JO (1980) The human influence on seabird nesting success: Conservation implications. Biol Conserv 18:65–80

Arcos J, Oro D (2002) Significance of nocturnal purse seine fisheries for seabirds: a case study off the Ebro Delta (NW Mediterranean). Mar Biol 141:277–286

Arcos J, 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

Arcos J, Bécares J, Rodríguez B, Ruiz A (2009) Áreas importantes para la conservación de las aves marinas en España, Sociedad Española de Ornitología. SEO/BirdLife, Madrid

Barbraud C, Weimerskirch H (2003) Climate and density shape population dynamics of a marine top predator. Proc R Soc Lond B Biol Sci 270:2111–2116

Bartoń K (2013) Model selection and model averaging based on information criteria (AICc and alike) (available at www.cran.r-project.org/web/packages/MuMIn/index.html)

Bartumeus F, Giuggioli L, Louzao M, Bretagnolle V, Oro D, Levin SA (2010) Fishery discards impact on seabird movement patterns at regional scales. Curr Biol 20:215–222

Bicknell AWJ, Oro D, Camphuysen KCJ, Votier SC (2013) Potential consequences of discard reform for seabird communities. J Appl Ecol 50:649–658

Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biol Rev Camb Philos Soc 80: 205–225

Burger J (2000) Landscapes, tourism, and conservation. Sci Total Environ 249:39–49

Burger J, Gochfeld M (1996) Family Laridae (Gulls). In: del Hoyo J, Elliott A, Sargatal J (eds) Handbook of the Birds of the World. Lynx Edicions, Barcelona, p 572–623

Christel I, Navarro J, del Castillo M, Cama A, Ferrer X (2012) Foraging movements of Audouin's gull (*Larus audouinii*) in the Ebro Delta, NW Mediterranean: a preliminary satellite-tracking study. Estuar Coast Shelf Sci 96:257–261

Clemens RS, Herrod A, Weston MA (2014) Lines in the mud; revisiting the boundaries of important shorebird areas. J Nat Conserv 22:59–67

Cury PM, Boyd IL, Bonhommeau S, Anker-Nilssen T and others (2011) Global seabird response to forage fish depletion — one-third for the birds. Science 334: 1703–1706

De La Cruz SEW, Eadie JM, Keith Miles A, Yee J, Spragens KA, Palm EC, Takekawa JY (2014) Resource selection and space use by sea ducks during the non-breeding season: implications for habitat conservation planning in urbanized estuaries. Biol Conserv 169:68–78

del Hoyo J, Elliott A, Sargatal J (1996) Handbook of the birds of the world. Vol 3, Hoatzin to auks. Lynx Edicions, Barcelona

Esler D (2000) Applying metapopulation theory to conservation of migratory birds. Conserv Biol 14:366–372

Frederiksen M, Moe B, Daunt F, Phillips RA and others (2012) Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. Divers Distrib 18:530–542

Furness RW, Monaghan P (1987) Seabird ecology. Blackie, Glasgow

García Lafuente J, Ruiz J (2007) The Gulf of Cádiz pelagic ecosystem: A review. Prog Oceanogr 74:228–251

Gelman A (2008) Scaling regression inputs by dividing by two standard deviations. Stat Med 27:2865–2873

González-Solís J, Croxall JP, Oro D, Ruiz X (2007) Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. Front Ecol Environ 5:297–301

Grosbois V, Thompson PM (2005) North Atlantic climate variation influences survival in adult fulmars. Oikos 109: 273–290

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. J Evol Biol 24:699–711

Halpern BS, Walbridge S, Selkoe KA, Kappel CV and others (2008) A global map of human impact on marine ecosystems. Science 319:948–952

Hanski I (1998) Metapopulation dynamics. Nature 396: 41–49

Harris MP, Wanless S (1996) Differential responses of guillemot *Uria aalge* and shag *Phalacrocorax aristotelis* to a late winter wreck. Bird Study 43:220–230

Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S (2011) Carry-over effects as drivers of fitness differences in animals. J Anim Ecol 80:4–18

Hodgson JA, Thomas CD, Wintle BA, Moilanen A (2009) Climate change, connectivity and conservation decision making: back to basics. J Appl Ecol 46:964–969

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:101–108

Kim SY, Monaghan P (2006) Interspecific differences in foraging preferences, breeding performance and demography in herring (*Larus argentatus*) and lesser black-backed gulls (*Larus fuscus*) at a mixed colony. J Zool (Lond) 270:664–671

Kiss A (2004) Is community-based ecotourism a good use of biodiversity conservation funds? Trends Ecol Evol 19: 232–237

Klaassen RHG, Ens BJ, Shamoun-Baranes J, Exo KM, Bairlein F (2012) Migration strategy of a flight generalist, the lesser black-backed gull *Larus fuscus.* Behav Ecol 23: 58–68

Klaassen RHG, Hake M, Strandberg R, Koks BJ and others (2014) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. J Anim Ecol 83:176–184

Martin TG, Chadès I, Arcese P, Marra PP, Possingham HP, Norris DR (2007) Optimal conservation of migratory species. PLoS ONE 2:e751

Martínez-Abraín A, Oro D, Conesa D, Jiménez J (2008) Compromise between seabird enjoyment and disturbance: the role of observed and observers. Environ Conserv 35:104–108

Navarro J, Louzao M, Igual JM, Oro D and others (2009) Seasonal changes in the diet of a critically endangered seabird and the importance of trawling discards. Mar Biol 156:2571–2578

Navarro J, Oro D, Bertolero A, Genovart M, Delgado A, Forero MG (2010) Age and sexual differences in the exploitation of two anthropogenic food resources for an opportunistic seabird. Mar Biol 157:2453–2459

Olsen KM, Larsson H (2004) Gulls of North America, Europe, and Asia. Princeton University Press, Princeton, NJ

Oro D (1996) Effects of trawler discard availability on egg laying and breeding success in the lesser black-backed gull *Larus fuscus* in the western Mediterranean. Mar Ecol Prog Ser 132:43–46

Oro D, Martínez-Abraín A (2007) Deconstructing myths on large gulls and their impact on threatened sympatric waterbirds. Anim Conserv 10:117–126

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, Cam E, Pradel R, Martínez-Abraín A (2004) Influence of food availability on demography and local population dynamics in a long-lived seabird. Proc R Soc Lond B Biol Sci 271:387–396

Pedrocchi V, Oro D, González-Solís J, Ruiz X, Jover L (2002) Diferencias en la dieta entre las dos mayores colonias del mundo de Gaviota de Audouin: efectos de las actividades pesqueras. Sci Mar 66:313–320

R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ramírez F, Afán I, Hobson KA, Bertellotti M, Blanco G, Forero MG (2014) Natural and anthropogenic factors affecting the feeding ecology of a top marine predator, the Magellanic penguin. Ecosphere 5:art38

Roberts JJ, Best BD, Dunn DC, Treml EA, Halpin PN (2010) Marine Geospatial Ecology Tools: An integrated framework for ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C++. Environ Model Softw 25: 1197–1207

Ruiz J, García-Lafuente J (2006) Topical studies in oceanography: The Gulf of Cádiz oceanography: A multidisciplinary view. Deep-Sea Res II 53:1141–1143

Schwemmer P, Garthe S (2005) At-sea distribution and behaviour of a surface-feeding seabird, the lesser black-backed gull *Larus fuscus*, and its association with different prey. Mar Ecol Prog Ser 285:245–258

Silva L, Gil J, Sobrino I (2002) Definition of fleet components in the Spanish artisanal fishery of the Gulf of Cádiz (SW Spain ICES division IXa). Fish Res 59:117–128

Sol D, Arcos J, Senar JC (1995) The influence of refuse tips on the winter distribution of yellow-legged gulls *Larus cachinnans.* Bird Study 42:216–221

Venables WN, Ripley BD (2002) Modern applied statistics with S. Springer-Verlag, New York, NY

Vidal E, Medail F, Tatoni T (1998) Is the yellow-legged gull a superabundant bird species in the Mediterranean? Impact on fauna and flora, conservation measures and research priorities. Biodivers Conserv 7:1013–1026

Webb NV, Blumstein DT (2005) Variation in human disturbance differentially affects predation risk assessment in Western gulls. Condor 107:178–181

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