

# Evaluating the effect of distance to different food subsidies on the trophic ecology of an opportunistic seabird species

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#### Keywords

anthropogenic food source; diet; fish discards; management implications; refuse tips; seabird; stable isotopes mixing models; *Larus michahellis*.

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#### Abstract

The availability of food subsidies of anthropogenic origin has strong consequences on the trophic ecology and population dynamics of several opportunistic species. However, evidence suggests that the use of certain feeding sources is very local, and hence, potentially important food subsidies may have a relatively small area of influence, resulting in only limited impact from the large geographic-scale perspective. In the south-eastern part of the Bay of Biscay, the Yellow-legged Gull Larus michahellis population is distributed across several colonies, which are located close to each other but have variable dependence on the landfills and fishing harbours in the area. This population is therefore a good model to test the influence of anthropogenic food subsidies on the trophic ecology of an opportunistic species at the local scale. Distance to the nearest fishing harbour showed a stronger effect on the diet of Yellow-legged Gull chicks than distance to the nearest landfill site. Gulls notably reduced their consumption of marine prey (mostly comprised of fishing discards) in relation to decreasing distance of their colony to the nearest fishing harbour. This result has direct implications from a management standpoint, since fish discards were also found to have only a limited effect on diet at regional scales, but a very high impact at the local scale. Moreover, those colonies that consumed a higher proportion of marine prey showed better population trends. In line with European Union policies, a reduction in the availability of fish discards, together with the closure of landfill sites, will occur in the coming years, probably leading to a change in the trophic ecology and dynamics of Yellow-legged Gull populations.

## Introduction

The availability of food subsidies is one of the main factors driving the biology of animal species, including their spatial and trophic ecology (Blanco & Marchamalo, 1999; Massemin-Challet *et al.*, 2006; Kruszyk & Ciach, 2010) and population dynamics (Duhem *et al.*, 2008; Olea & Baglione, 2008; Weiser & Powell, 2010; Oro *et al.*, 2013). Food subsidies frequently have a predictable geographic distribution, are abundant and promote the sedentarization of populations (Carrete *et al.*, 2006). Thus, a decrease in dispersal distances and even the adoption of resident strategies is a well-known phenomenon in those species or populations that establish a strong dependence on certain feeding resources of human origin, such as landfills (Gilbert *et al.*, 2016). Understanding to what extent these

sources influence the life-history traits of populations and the geographic area of influence on the populations are key aspects of population ecology.

Many gull species have successfully adapted to forage on food subsidies such as fish discards or garbage from landfills (Belant *et al.*, 1998; Bertellotti *et al.*, 2001; Arizaga *et al.*, 2013a; Isaksson *et al.*, 2016). The consequence of such opportunistic trophic ecology results, in most cases, in rapid population growth (via increased survival and/or reproductive output) (Hatch, 1996; Rock, 2005; Duhem *et al.*, 2008), as well as the creation of new colonies and the extension of a species' distribution range (Olsen & Larson, 2004). Such demographic changes can produce undesired effects of an ecological (García *et al.*, 2002; Finney *et al.*, 2003; Oro & Martínez-Abraín, 2007), economic (Rock, 2005; DeVault *et al.*, 2018), social

(Calladine et al., 2006) or sanitary (Benton et al., 1983; Hatch, 1996; Araújo et al., 2014) nature.

Studies based on ring-recovery data, and more recently from satellite-tracking devices, have demonstrated that distance to a particular food resource determines the extent to which it will be used by individuals from nearby gull colonies, even at relatively small scales (e.g. tens of kilometres; Egunez *et al.*, 2018). In other words, even though gulls are efficient flyers and are able to cover long distances to find food (Isaksson *et al.*, 2016; Kazama *et al.*, 2018), there is evidence that the use of certain feeding sources can be very local. Consequently, potentially important food subsidies may have a relatively small area of influence, which would result in only a limited impact from the large geographic-scale perspective. In such a scenario, it might be expected that the differential exploitation of trophic resources by physically close colonies would be reflected in the average diet at the colony level (Zorrozua *et al.*, 2019).

In some species that breed in colonies, such as gannets, lesser kestrels or certain gull species, recent GPS studies have identified that colonies that are close together show spatial segregation in foraging patterns in order to avoid intraspecific competition (Gremillet et al., 2004; Wakefield *et al.*, 2013; Corman *et al.*, 2016; Enners *et al.*, 2018; Cecere *et al.*, 2018). However, this is only possible in areas where the food resource is large enough to sustain all the nearby colonies. To date, there are no data available to quantify the area of influence of a given food subsidy that can be presumed to have a high impact on population dynamics, an aspect that potentially has valuable applications for environmental managers and public administrations.

The Yellow-legged Gull is an opportunistic species that is known to forage on anthropogenic food subsidies (Duhem et al., 2005; Neves et al., 2006; Moreno et al., 2010; Arizaga et al., 2013a; but also see Ramos et al., 2009a). Previous studies dealing with dietary variation among Yellow-legged Gull colonies have often covered large geographic ranges (hundreds of kilometres) and in some cases have considered colonies situated in very different environments: remote offshore islets to continental colonies in or near urban areas (Ramos et al., 2006; Ramos et al., 2009a; Moreno et al., 2010). In contrast, little is yet known about how diet can vary across small geographic areas or what the main food subsidies are that might account for such potential variation. In the south-eastern part of the Bay of Biscay, the Yellow-legged Gull population is distributed in several colonies located close to each other, with a considerable degree of variance in each colony's dependence on the landfills and fishing harbours within the region. This population is therefore a good model to test at the local scale the effect that distance to important food subsidies has on the trophic ecology of an opportunistic species.

In this work, we aimed to (1) determine trophic variation among colonies close to each other, especially in relation to main food subsidies such as landfills or fishing harbours, and (2) quantify the effect of the distance to main food subsidies on the trophic ecology. At the same time, we explored whether the trophic profiles of the colonies were correlated with their population trend, since this could provide an insight into the role of

given feeding sources on population dynamics. For this, we used data from feathers collected from chicks and stable isotope mixing models. The main prediction is that those colonies situated closer to a main source of food subsidies (either a landfill site or a fishing harbour) will present a higher proportion of this resource in their diet. As compared to landfill sites, where the food has a stable distribution over time (food is deposited on a daily basis, indeed, often several times a day, and then remains available for a relatively long period: Burger & Gochfeld, 1983: Castège et al., 2016; Gilbert et al., 2016; Arizaga et al., 2018), the dynamic in fishing harbours is different - food is provided as fish discards from fishing vessels that come into harbour and is therefore only available for both a short period of time and during a narrow window of time during the day. In this scenario, it might be expected that harbours will be used more preferably by those birds that live in the vicinity, since those living further away run the risk of arriving at the harbour when there is no food available. If this is true, the decreasing effect of distance to a main food subside on the trophic ecology may be much stronger for the harbours as compared to landfills.

## **Materials and methods**

#### Study area and data collection

The study was carried out in 10 Yellow-legged Gull colonies situated on marine cliffs along the coast, or in small islets close to the coast, in the south-eastern part of the Bay of Biscay (Fig. 1). In a straight line, the two most distant colonies were 135 km apart. The overall estimated population size was 1851 breeding pairs (Table 1), with the smallest of the colonies having 27 pairs (Cas; Castro Urdiales) and the largest having 660 pairs (Uli; Ulia). Currently, between them these colonies host ca. 70% of the total number of breeding pairs along the coastline where this study was carried out.

In recent years, various censuses have been carried out in the different colonies included in this work, although only the most recent census used in this work (2017) considered all the colonies simultaneously (Table 1). Censuses, during which the minimum number of nesting pairs was counted, were carried out during the incubation period, before the hatching, and each site was preferably visited more than once (first visit: 15–30 April; second: 01–15 May).

#### **Sample collection**

During the breeding period in 2016 and in 2017 (June–July), 10 chicks per colony were captured by hand at the age of ca. 20 days. They were ringed (in order to avoid pseudo-replications in possible subsequent visits to the colonies where we were not able to take all the samples in 1 day), and 4-6 mantle feathers were taken from each chick for the stable isotope analysis ( $\delta^{15}$ N and  $\delta^{13}$ C). Previous studies carried out in three of these colonies reported no differences between adults' and chicks' diet in the breeding period (Zorrozua *et al.*, 2019), suggesting that the diet of the chicks may be also used to infer adults' foraging ecology.



Figure 1 Location of the ten colonies studied in this work, together with the harbours and landfill sites situated at a distance <75 km from at least one colony. Only harbours with a fishery landing of more than 500 t per year have been included (abbreviations as in Table 1).

 Table 1
 Population size (adult breeding pairs) and trend for the period 2010–2017 for the ten Yellow-legged Gull colonies studied in this work.

 Colony name (abbreviated) as in Fig. 1

	Size (pairs)								
Colony	2010	2011	2012	2013	2014	2015	2016	2017	Trend (% change/year)
Biarritz (Bia)	36	39	32	39	42	41	41	62	+5.97
Jaizkibel (Jai)							41	45	+9.76
Ulia (Uli)								660	-
Santa Clara (San)				52	87			100	+13.28
Getaria (Get)	156			130			190	165	+2.50
Lekeitio (Lek)				451				287	-10.68
Izaro (Iza)				795				409	-15.31
Billano (Bil)				28				32	+3.39
Punta Lucero (Pun)				102				69	-9.31
Castro (Cas)			45	41	36	46	47	27	-4.54

Significant trends (P < 0.05) shown in bold.

The trend in Ulia was not possible to ascertain due to insufficient data.

#### Stable isotope analysis and mixing models

As compared to other methods based on the direct analysis of prey consumption (such as regurgitates or pellets), one of the advantages of the analysis of isotopes is that they contain information for the whole period within which a given tissue was growing, and therefore, they potentially allow the estimation of a bird's diet over long periods (e.g. during the period of feather growth; Hobson *et al.*, 1994). It must be noted, however, that stable isotope analyses involve the assumption of a degree of uncertainty, since categorization of prey cannot be very specific, and quite general prey-type classifications need to be used (Ramos *et al.*, 2009b).

Firstly, feathers were cleaned in a 1M NaOH solution and oven-dried at 60°C to constant mass. Then, samples were placed in a cryogenic impactor mill (Freezer/mill 6750-Spex Certiprep) with liquid nitrogen in order to be homogenized into fine powder for the isotopic analysis. Subsamples of this powder (c. 0.3 mg) were placed in Sn capsules for combustion, and isotopic analysis was performed using an elemental analysis-isotope ratio mass spectrometry (EA-IRMS) with a Thermo Finnigan Flash 1112 coupled to a Delta isotope ratio mass spectrometer via a ConFlo III interface. Stable isotope values were calculated as  $\Delta x = [(R_{sample}/R_{standard}) - 1] \times 1000$ , where X is either <sup>13</sup>C or <sup>15</sup>N, and R is the corresponding ratio  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}.$  Atmospheric nitrogen  $(N_2)$  was the standard for the  $\delta^{15}$ N and Vienna PeeDee Belemnite (VPDB) calcium carbonate for the  $\delta^{13}$ C. To calibrate the system, international standards (ammonium sulphate, glutamic acid and potassium nitrate for  $\delta^{15}$ N and glutamic acid, polyethylene and sucrose for  $\delta^{13}$ C) were introduced every 12 samples. All analyses were carried out at the Centres Científics I Tècnics (CCiT), University of Barcelona.

To estimate diet, we used Bayesian multi-source stable isotope mixing models, which allowed us to assess the relative contribution of each main prey resource category. More particularly, and on the basis of work done previously in this same geographic area, we considered three main food resource categories: marine (mostly fish prey belonging to the families Carangidae, Clupeidae, Sparidae, Trachinidae and Gadidae, but may also contain other types of marine prey such as crabs or molluscs), landfill (mostly pork, beef or chicken) or terrestrial (earthworms, slugs; Arizaga et al., 2011; Arizaga et al., 2013a). All prey samples were collected from pellets freshly regurgitated by chicks in the colonies of Getaria, Santa Clara and Ulia during the breeding period in the years 2007-2010. The mean  $\delta^{15}N$  and  $\delta^{13}C$  signatures of several prey items from each category were used to obtain reference values for the mixing models (Arizaga et al., 2013a). The MixSIAR package in R (Stock & Semmens, 2016) was then used to estimate the relative contribution of each prey type within each colony. The default values used in these models were as follows: uninformative prior (alpha.prior = 1), chainLength =  $100\ 000$ , burn = 50 000, thin = 50, chains = 3. Isotopic discrimination values for  $\delta^{15}$ N and  $\delta^{13}$ C were, respectively: landfill + 5.0 and + 2.2%; terrestrial + 4.0 and + 2.7%; marine + 3.0and + 0.9% (Peterson et al., 1985; Hobson & Clark, 1992; Bearhop et al., 2002; Hobson & Bairlein, 2003; Ramos et al., 2009a), with sp = 0.1. Overall, we obtained the mean  $\pm$  50, 75 and 95% credible interval for each prey type and colony.

#### **Statistical analyses**

Dispersal analyses have previously revealed that adult Yellowlegged Gulls in the study area are very sedentary, moving no further than 75 km away from their natal site (Arizaga *et al.*, 2013b). Therefore, in calculating distance to main foraging sites of human origin, we only considered those landfill sites or fishing harbours situated less than 75 km away from at least one colony. Moreover, for the harbours, only those with an annual fishery landing higher than 500 t were considered (source: Basque Government, www.euskadi.eus). This resulted in three landfill sites (from east to west: Zuluaga, Jata and Meruelo) and nine harbours being considered in the study (for details, see Fig. 1).

To test for the effect of proximity to a main source of artificial food subsidies on trophic ecology, we used general linear mixed models (GLMMs) with a linear-link function and normal distribution errors on  $\delta^{13}$ C and  $\delta^{15}$ N as response variables, with distance to the nearest fishing harbour (harb) or landfill (land) as covariates and colony (colo) and sampling year (year) as random factors [R notation:  $\delta^{13}C \sim harb + land +$ (1|colo)+ (1|year), and the same for  $\delta^{15}N$ ]. In addition to this linear approach, we also tested for both a log and an exponential relationship between *land* and *harb* on  $\delta^{13}$ C and  $\delta^{15}$ N signatures. We used  $\delta^{13}$ C and  $\delta^{15}$ N values for individual birds rather than the percentage of each prey category consumed. When calculating the Akaike values (AIC; Akaike, 2011) for these three models, the linear and exponential models were found to fit the data better (i.e. had lower AIC values) than the log model for both  $\delta^{13}$ C (AIC, linear: 380.99; log: 384.00; exp: 380.06) and  $\delta^{15}$ N (AIC, linear: 439.72; log: 443.28; exp: 439.44). The difference in AIC for the linear and the exp approach was, however, less than 2 AIC units, indicating that the latter approach did not differ substantially from the former (Burnham & Anderson, 1998). As a result, we decided to work with linear models in order to more deeply investigate the effect of *harb* and *land* on  $\delta^{13}$ C and  $\delta^{15}$ N signatures. Starting from a saturated model, all the possible factor combinations were run and the best-ranked model(s), according to the small sample size-corrected Akaike values (AICc), were averaged in order to obtain parameter estimates. The relative importance of each variable when constructing the average model was referred as R.I. Model selection was made with the 'dredge' function in the MuMIn package (Barton, 2018). To look in even greater depth at these effects, we then conducted a second linear model using, in this case, the prey proportion (i.e. one value per colony) as a dependent variable and harb and land as covariates.

Additionally, we also tested for the relationship between the trophic ecology based on stable isotopes and the population trends of each colony. Trends were calculated with the TRIM software (log-linear models; Pannekoek & Van Strien, 2005) with census data for the period 2010–2017 and by performing the Wald significance tests. In the case of Ulia colony (Uli), this was, unfortunately, not possible since a census was only taken in this colony in 2017, meaning that we used only nine colonies for this analysis. That said, it should be noted that the scant amount of data for some of the colonies may have given rise to an underestimation of standard errors, which needs to be taken into account when looking at the results. Based on the Wald test, a given trend was considered to be 'certain' by TRIM if the slope was significant, but 'uncertain' if the slope was non-significant. We used a GLM with trend as a response

variable,  $\delta^{13}$ C and  $\delta^{15}$ N as a covariate and colony size as an additional factor. Interactions were not included due to the small sample size. As with the models used to test the distance effect, from all the possible factor combinations an average model was built using those models with  $\Delta$ AICc <2.

All the statistical analyses were carried out in TRIM (Pannekoek & Van Strien, 2005) and R 3.4.3 (R Development Core Team 2011).

#### Results

Overall, and as could be deduced from the lack of overlap of the 95% credible interval for some prey and colonies, the Mix-SIAR mixing models revealed that prey consumption differed between colonies (Fig. 2). Those situated to the east had a higher consumption of marine prey, while those situated to the west consumed less. The highest mean values were detected at Biarritz and Lekeitio (Bia and Lek; Table 1), where *c*. 60% of prey consumed was marine prey, while the lowest mean value recorded was at Punta Lucero (Pun; Table 1) marine prey accounted for <20% of consumption.

The mean  $\delta^{13}$ C and  $\delta^{15}$ N values were highly correlated with the estimated proportion of marine and landfill prey in the diet, but not with terrestrial prey ( $\delta^{13}$ C, marine: r = 0.98, P < 0.001, 95% CI: 0.91, 1.00; terrestrial: r = -0.18, P = 0.627, 95% CI: -0.73, 0.51; landfill: r = -0.84, P = 0.002, 95% CI: -0.96, -0.45;  $\delta^{15}$ N, marine: r = 0.99, P < 0.001, 95% CI: 0.95, 1.00; terrestrial: r = 0.16, P = 0.656, 95% CI: -0.52, 0.72; landfill: r = -0.97, P < 0.001, 95% CI: -0.99, -0.88).



**Figure 2** MixSIAR results ( $\pm$  95, 75 and 50% credible interval) for the three prey categories consumed by the chicks in different colonies (abbreviations as in Table 1).

For  $\delta^{13}$ C, we obtained two models, one which included distance to the nearest fishing harbour and nearest landfill, the other only the former, that fitted to the data equally well (Table 2), although only distance to the nearest fishing harbour proved to be statistically significant: harb:  $\beta \pm s_{\rm E} =$  $-0.04 \pm 0.02$ , P = 0.019, R.I.: 1.00, 95% CI: -0.08, -0.01; *land*:  $\beta \pm s_{\text{E}} = -0.01 \pm 0.01$ , P = 0.333, R.I.: 0.35, 95% CI: -0.03, 0.01 (Fig. 3). For  $\delta^{15}$ N, however, only one model was detected that fitted the data better than the rest (Table 2), and it only incorporated the variable distance to the nearest fishing harbour on  $\delta^{15}$ N: harb:  $\beta \pm s_{\rm E} = -0.06 \pm 0.02$ , P = 0.014, 95% CI: -0.11, -0.02 (Fig. 3). At the same time, we also observed a significant effect of distance to the nearest fishing harbour on consumption of marine or landfill prey (marine: *harb*:  $\beta + s_E = -0.01 + 0.00$ , P = 0.038, 95% CI: -0.02. -0.00; landfill: *harb*:  $\beta \pm se = 0.01 \pm 0.00$ , P = 0.019, 95% CI: 0.00, 0.02; Fig. 4). According to these models, the consumption of marine prey tended to decrease at a rate of ca. 10%/10 km. In addition, distance to the nearest landfill had a significant effect on consumption of terrestrial prey (terrestrial: *land*:  $\beta \pm s_{\text{E}} = -0.00 \pm 0.00$ , P = 0.024, 95% CI: 0.00, 0.00; Fig. 4), although terrestrial prey was not found to correlate with isotopic signatures.

The population trend for five of the nine colonies studied was positive, though for some of the colonies the values involved were not statistically significant (Fig. 5). These trends were correlated with the  $\delta^{13}$ C and  $\delta^{15}$ N and were also influenced by colony size ( $\delta^{13}$ C: $\beta \pm s_{\rm E} = -0.045 \pm 0.016$ , P = 0.005,95% CI: -0.08, -0.01;  $\delta^{15}$ N:  $\beta \pm s_{\rm E} = 0.054 \pm 0.012$ , P < 0.001, 95% CI: 0.03, 0.08; size:  $-0.0005 \pm 0.0000$ , P < 0.001, 95% CI: -0.00, -0.00; Table 3), suggesting that those colonies that depended less on landfills showed better (i.e. increasing) population trends, albeit that these colonies were those which were smaller.

## Discussion

This, as far as we are aware, is one of the few studies dealing with the quantification of the impact of main resources of food subsidies on the trophic ecology of a gull population at a very small geographic range, hence allowing us to determine the distance effect of given feeding sources (see also: Sol et al., 1995; Duhem et al., 2003; Duhem et al., 2008; Enners et al., 2018). Because of the degree of uncertainty assumed when using stable isotope analysis, the possibility cannot be rejected that a part of those 'landfill resources' assessed by the Mix-SIAR models could in fact be accounted for by the gulls scavenging in built-up areas, since food items taken from such zones would be very likely to show isotopic signatures similar to those found in food from landfills (Navarro et al., 2017). However, preliminary data from GPS-tracked birds have shown only marginal use of built-up areas (<20%, with> 90% of these being in terms of roosting places, such as roofs of industrial unit, river banks known to be used to rest, etc). Arizaga et al. (2017) and more unpublished data). It is therefore likely that prey consumption from built-up areas was small in this study and hence that the percentage of prey estimated to originate in 'landfill' was correct. The present work has been

Table 2         Ranking of the best models (	$\Delta$ AlCc < 2) c	obtained for trophic	ecology, t	together with	the global	and null n	nodels, a	iccording to	their	small
sample size-corrected Akaike (AICc) va	alues									

Models	AICc	ΔAICc	d.f.	Dev	r <sup>2</sup>
δ <sup>13</sup> C					
1. Harb	380.3	0.0	5	369.9	0.227
2. Harb + land	381.6	1.3	6	369.0	0.232
Global	381.6	1.3	5	369.0	0.232
Null	382.4	2.1	4	374.1	0.206
$\delta^{15}$ N					
1. Harb	438.2	0.0	5	427.8	0.333
Global	440.3	2.1	6	427.7	0.333
Null	442.4	4.2	4	434.1	0.305
Marine					
1. Harb	-9.9	0.0	3	0.080	0.427
2. (Null)	-8.7	1.3	2	0.139	0.000
Global	-4.2	5.8	4	0.078	0.441
Null	-8.7	1.3	2	0.139	0.000
Landfill					
1. Harb	-10.1	0.0	3	0.078	0.520
Global	-4.4	5.7	4	0.076	0.534
Null	-7.0	3.1	2	0.164	0.000
Terrestrial					
1. Land	-29.9	0.0	3	0.011	0.490
Global	-23.9	6.0	4	0.011	0.491
Null	-27.5	2.4	2	0.021	0.000

Abbreviations: AICc, small sample size-corrected Akaike values;  $\Delta$ AICc, difference in AICc values in relation to the first model; Dev, deviance; d.f., degrees of freedom;  $r^2$ , likelihood-ratio based  $R^2$ .

The global model included all the possible factors, and the null model corresponds to a constant model (all  $\delta^{13}$ C and  $\delta^{15}$ N models include random terms).

carried out under the premise that potential prey items taken by Yellow-legged Gulls and their baseline isotopic value have remained constant along the study period. Our experience based on field observations suggests that the main foraging sites and types of prey consumed did not vary substantially, but it would be important to go deeper about these issues and test for the existence of potential variations, both regarding other potential new feeding sources and variations across colonies even for the same type of prey.

Our analyses revealed some degree of variation in prey consumed in the 10 colonies, even though they all were situated along only 135 km of the same coastline. The mean consumption of marine prey per colony ranged from c. 20% to 60%, of landfill prey from c. 25% to 65% and of terrestrial prey from 15% to 25%. Such geographic variations have been also reported in other areas - for the Yellow-legged Gull in particular (Duhem et al., 2005; for larger geographic scales: Ramos et al., 2009a; Moreno et al., 2010) and for other gulls (Schmutz & Hobson, 1998; O'Hanlon et al., 2017; Enners et al., 2018) - and reflect the high levels of trophic plasticity between gull colonies, which is heavily influenced by given local resource availability. Most of these previous works, however, have failed to, or simply did not aim to, estimate the distance effect of such key food subsidies, one of the aspects specifically targeted in this work. According to our models, distance to the nearest fishing harbour showed a stronger effect

on the diet of the Yellow-legged Gull than distance to the nearest landfill site. This was the case for each of the models tested in this work, and although the transformation used to best fit the model could be disputed, the effect was evident. This means that these gulls notably reduced their consumption of marine prey (mostly comprised of fish, much of this being fish discards; Arizaga et al., 2011) when their colony is situated far from a fishing harbour, even when the distance is only a matter of tens of kilometres. This raises direct implications from a management standpoint, since fish discards have previously been found to have only limited effects on the diet of Yellow-legged Gull chicks at regional scales, but a very high impact at the local scale. Our study included only one colony situated further than 20 km (Pun) from a fishing harbour, which was responsible for the steep decline in marine resource consumption in our models. Consequently, colonies from areas situated further from these food sources should be included in future works, which would probably facilitate the selection of the most suitable transformation to fit the data to the model and thus provide more robust information on how distance to different food subsidies affects diet. As compared to other resources, including waste from landfills, fish discards are less predictable, only occurring in a very narrow time window when boats come into harbour to unload their catch. Fish discards, both at sea and in fishing harbours, as well as in the vicinity of fish/seafood processing plants, are thus the object of



**Figure 3**  $\delta^{13}$ C and  $\delta^{15}$ N values in relation to distance to nearest harbour, considering models that fitted a linear relationship of distance with isotopic values. We show both observed (dots) and predicted values (line) with 95% confidence intervals.

scramble competition between gulls, who generally consume this food source very quickly (N. Zorrozua, per. obs.). Therefore, once a vessel enters a harbour, only those gulls present at that time in the harbour and/or those following the vessel will have a chance to feed on this resource (Navarro et al., 2017). In contrast, those gulls from colonies even only short distances from the harbour and tied to the colony by breeding obligations will be unable to arrive at the harbour in time to compete effectively on this prey source. Clearly, once the breeding season has ended, the gulls' obligations at the colony become less, and thus, they could be expected to exploit these sources independently of their colony location. The effect of this would be to extend the 'trophic' impact of harbours at larger geographic scales, which would also have demographic consequences (e.g. increasing survival prospect). In support of this rationale, GPS-tracking data have revealed that breeding adult gulls from two of the colonies considered in this work (San and Uli in Fig. 1) did not use the fishing harbour of Ondarroa at 34-38 km from the colonies (unpublished data), although they did use Getaria (16-20 km from the two colonies), even though the former has considerably more fishing vessels. Thus,



Figure 4 Linear relationship ( $\pm$ 95% confidence interval) of consumption of either (a) marine or (b) landfill prey in each colony (dots) in relation to distance to a nearest harbour and(c) consumption of terrestrial prey category in relation to distance to the nearest landfill.

it would seem that even this relatively small difference in distance from colony has an impact on gull foraging behaviour.

Studies on breeding performance indicate that fish discards have a higher impact on Yellow-legged Gulls' breeding investment than landfills, and this has been attributed to the fact that organic waste is of a lower nutritional quality than fish, which is important not only for egg formation (Real *et al.*, 2017), but also for chick development, resulting in a higher reproductive



**Figure 5** Colony size trends with 95% CI for the period 2010-2017 for each colony, except Ulia, for which there were not enough data. In addition, some colonies did not have enough data to estimate trends with a high degree of certainty (grey dots).

**Table 3** Ranking of the best models ( $\Delta$ AICc < 2) obtained for trend, together with the global and null models, according to their small sample size-corrected Akaike (AICc) values

Models	AICc	ΔAICc	d.f.	Dev	r <sup>2</sup>
Trend					
1. $\delta^{13}C + \delta^{15}N +$	-330.8	0.0	5	0.615	0.526
Colony size					
Global	-330.8	0.0	5	0.615	0.526
Null	-237.3	93.5	2	1.295	0.000

Abbreviations: AICc, small sample size-corrected Akaike values;  $\Delta$ AICc, difference in AICc values in relation to the first model; Dev, deviance; d.f., degrees of freedom;  $r^2$ , likelihood-ratio based  $R^2$ .

The global model included all the possible factors, and the null model corresponds to a constant model.

output (Annett & Pierotti, 1999). Interestingly, in this work we observed that colonies with a higher consumption of marine and terrestrial prey showed increasing/more positive demographic trends than those which depended more on landfills or terrestrial prey. By way of example, the colony of Getaria (Get in Fig. 1), one of the colonies consuming most marine prey, only came into existence during the 2000s, when the activity at the fishing harbour at the same locality increased.

The positive effects of small colony size (which may be linked to density-dependent effects; Newton, 2013) and consumption of marine prey (which impacts positively on reproductive output) on the population trend found here seem to be additive and most likely independent. Our results may explain why the existence of several important fishing harbours within the region is insufficient to maintain, let alone increase, population size for all the Yellow-legged Gull colonies within the region. However, the population trends identified in this study should be treated with a degree of caution as for some of the colonies the number of censuses on which the analysis was based was low. Collecting more information on the size of colonies in the future will provide more certain and accurate trend estimations and hence better models.

The recent closure of several landfills within the region has resulted in a decrease in the consumption of landfill prey, which has been found to be replaced in the breeding season by an increase in consumption of prey of terrestrial origin, but not of marine origin (Zorrozua *et al.*, 2019). Our results suggest that harbours may not be suitable as a main alternative source of food for those colonies situated at a considerable distance from them, while at the same time, they are compatible with an increasing exploitation of terrestrial habitats during the summer. In winter, however, these gulls would be more likely to substitute the lack of landfill food by increasing the amount of marine prey they consume (Ramos *et al.*, 2011; Zorrozua *et al.*, 2019) since in the non-breeding period, they are able to remain for longer periods in the vicinity of the harbours and thus compete more effectively for fish discards.

In the coming years, European policies will oblige Member States to reduce or prohibit the dumping of fish discards (European Union 2013). Accordingly, this is expected to have a strong impact on the trophic ecology and population dynamics of those colonies that are highly dependent on this resource (Bicknell et al., 2013), especially during the breeding period, as well as on individuals from other colonies that might depend on this resource during the non-breeding period. The scenario is further complicated by the fact that the remaining landfill sites in the region must be closed by 2020 (European Union 1999). Given these changes, a decrease not only in reproductive output, but also in the non-breeding survival prospect of first-year and older birds can be expected. It is known that some colonies/gulls feed on terrestrial prey (mostly earthworms), though it has strong seasonal fluctuations (i.e. scarcer in winter), and may well have considerable geographic variation (Moreno et al., 2010). As such, it cannot be considered a plausible food resource to replace the closure of landfill sites and the expected decrease in fish discards. Other feeding sources such as food taken from urban areas are an alternative, but the quantity available is almost certainly insufficient to maintain a population of almost 2000 adult breeding pairs, together with probably several thousand immature individuals. More likely, this presumed widespread food diminution will be accompanied by a demographic adjustment, which might result in lower survival rates, increasing dispersal and/or smaller reproductive outputs (Newton, 1998, 2013). Predictions from a trophic ecology standpoint are not easy to make, meaning that the future scenario remains totally unknown.

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## **Authors' contributions**

NZ and JA conceived the ideas and designed the methodology; NZ, AE, AA, AG, BD, JH and IC collected the data; NZ, LJ, CS and JA analysed the data; NZ and JA led the writing of the paper and the supplementary material (Table S1, Table S2, Figure S1). All authors contributed critically to the drafts and gave final approval for publication.

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# **Supporting Information**

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

**Table S1.** Isotopic signatures of  $\delta^{13}$ C and  $\delta^{15}$ N (mean  $\pm$  SD) of chicks in relation to the colony of origin and year.

 Table S2.
 Amount (Tones) of fish discharged in the main harbours of the southeastern part of the Bay of Biscay.

**Figure S1.** Isotopic signatures of  $\delta^{13}$ C and  $\delta^{15}$ N of chicks from the ten colonies and of the three types of prey source categories (mean  $\pm$  SD) after applying the trophic discrimination factors to prey sources.