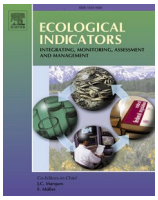
Ecological Indicators 129 (2021) 107943

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Foraging in the Anthropocene: Feeding plasticity of an opportunistic predator revealed by long term monitoring

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ARTICLE INFO

Keywords:
Dietary assessments
Longitudinal studies
Larus michahellis
Stable isotope analysis
Trophic plasticity
Yellow-legged gull

ABSTRACT

For centuries, human activities have altered the population dynamics of wildlife. New anthropogenic food sources provide a predictable and abundant food supply that often induces very significant changes in the size, distribution, and behaviour of many populations, with ultimate consequences on the structure and functioning of natural ecosystems. Here, we combine historical and contemporary feather samples of a population of a superabundant, opportunistic predator, the yellow-legged gull *Larus michahellis*, to assess its trophic ecology and relate it to human activities in the long term. Dietary assessments were based on stable isotope analysis of carbon, nitrogen, and sulphur ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$), and were conducted through three end-point (marine prey, waste from landfills-slaughterhouses, and terrestrial invertebrates) Bayesian mixing models. Our results suggest that gulls' diet showed a progressive decrease in the consumption of marine prey throughout the most recent period (late 20th century onwards), linked to an increase in the consumption of meat waste and small terrestrial invertebrates. Reported dietary changes over the sampling period correlated positively with the availability of marine resources around the breeding area. We provide evidence suggesting that the ability of gulls to exploit efficiently diverse anthropogenic food subsidies likely resulted in the exponential demographic increase of this population throughout the 20th century. In addition, current regulations affecting the availability of these food resources (e.g., fishing discards and landfill waste) likely reversed this trend over the last decade. Long-term evidence of population trophic plasticity, like the one we present here, is essential to implement and support management and conservation actions that limit the availability of anthropogenic resources, especially when it comes to superabundant, problematic species.

1. Introduction

Human activities are relevant drivers of wildlife population dynamics in many aspects. For instance, wildlife exploitation of anthropogenic food subsidies (i.e., food generated by human activities that becomes available for wildlife) is one of the main factors driving the current ecology and population dynamics of a wide range of opportunistic species worldwide (Rose and Polis, 1998; Kuijper et al., 2016; Table 1). A common trait among opportunistic species is trophic plasticity (i.e., the ability of organisms to modify their diet in response to fluctuating environmental resources; Zhang et al., 2019; Duclos et al., 2020), which facilitates the exploitation of anthropogenic food subsidies shortly after they become available in the environment. Opportunistic species efficiently exploit these resources because most of them are predictable over space and time, (e.g., landfill waste, fishing discards, meat industry waste, crop residues, bird feeders, etc.; Table 1). Furthermore, anthropogenic food subsidies may have seemingly positive effects on wildlife linked to reduced foraging energetic costs, such as improvements in physiology, breeding performance, and survival (Newsome et al., 2014; Petroelje et al., 2019, but see Pichegru et al., 2007) that can ultimately lead to demographic increases (Newsome and Van Eeden, 2017; Plaza and Lambertucci, 2017). However, the

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https://doi.org/10.1016/j.ecolind.2021.107943
Received 23 April 2021; Received in revised form 28 June 2021; Accepted 29 June 2021
Available online 8 July 2021

Table 1
A selection of studies that reported opportunistic usage of anthropogenic food subsidies by diverse wildlife worldwide.

Organism	Species	Anthropogenic food	Location	Reference
Terrestrial birds	Rook *Corvus frugilegus*	Landfill waste	Spain	Olea and Baglione, 2008
	Cinereous vulture *Aegypius monachus*	Livestock carrion	Spain	Costillo et al., 2007
	California condor *Gymnogyps californianus*	Livestock	USA	Chamberlain et al., 2005
	Ring-necked pheasants *Phasianus colchicus*	Feeding stations	UK	Draycott et al., 2005
	Lesser snow goose *Chen caerulescens*	Crops	Canada	Jefferies, 2004
	Griffon vulture *Gyps fulvus*	Livestock carrion	Spain	Parra and Tellería, 2004
Seabirds	Yellow-legged gull *Larus michahellis*	Fishing discards	Spain	Méndez et al., 2020
	Herring gull *Larus argentatus*	Food waste	Canada	Laurich et al., 2019
	Double-crested cormorant *Phalacrocorax auritus*	Aquaculture	USA	Hebert et al., 2008
	Cape gannet *Morus capensis*	Fishing discards	South Africa	Grémillet et al., 2008
	Black browed albatross *Thalassarche melanophrys*	Fishing discards	Argentina	González-Zevallos and Yorio, 2006
	White-chinned petrel *Procellaria aequinoctialis*	Fishing discards	Argentina	González-Zevallos and Yorio, 2006
	Kelp gull *Larus dominicanus*	Fishing discards	Argentina	González-Zevallos and Yorio, 2006
	Mediterranean shearwater *Puffinus mauretanicus*	Fishing discards	Spain	Arcos and Oro, 2002
	Audouin's gull *Ichthyaetus audouinii*	Fishing discards	Spain	Oro et al., 1996
	Cory's shearwater *Calonectris diomedea*	Fishing discards	Spain	Oro and Ruiz, 1997
Terrestrial mammal	Striped hyena *Hyaena hyaena*	Livestock	Nepal	Bhandari et al., 2020
	Rhesus macaque *Macaca mulatta*	Bread, fries, chips	India	Ganguly and Chauhan, 2018
	Wild boar *Sus scrofa*	Maize	Hungary	Katona and Heltai, 2018
	Wolf *Canis lupus*	Garbage, crop residues	Israel	Barocas et al., 2018
	Brown bear *Ursus arctos*	Corn	Canada	Coogan et al., 2018
	Dingo *Canis lupus dingo*	Pasta, bread, bones	Australia	Behrendorff et al., 2016
	Eurasian otter *Lutra lutra*	Fish farms	Portugal	Sales-Luís et al., 2011
	Baboon *Papio ursinus*	Fruit, sugar, eggs	South Africa	Kaplan et al., 2011
		Feeding stations	USA	
	Mule deer *Odocoileus hemionus*			Peterson and Messmer, 2011
	Jaguar *Panthera onca*	Livestock	Brazil	Michalski et al., 2006
	Cougar *Puma concolor*	Livestock	Brazil	Michalski et al., 2006
Marine mammal	Sperm whale *Physeter macrocephalus*	Toothfish fisheries	Kerguelen Is.	Richard et al., 2020
	Killer whale *Orcinus orca*	Toothfish fisheries	Kerguelen Is.	Richard et al., 2020

continued use and dependence on these resources may also contribute to an ecological trap (Schlaepfer et al., 2002). Other negative consequences of the dependence on anthropogenic food sources include higher exposure and susceptibility to pathogens and pollutants (Leat et al., 2011; Lawson et al., 2012; Streicker et al., 2012).

At a global scale, anthropogenic food subsidies are available for wildlife in specific regions with high human density and high per capita food waste (e.g. Europe, South East Asia, and North America; Oro et al., 2013). The three main anthropogenic food subsidies in terms of availability and global distribution are fishing discards, landfill waste, and crop residues (Parfitt et al., 2010; Foley et al., 2011; Bicknell et al., 2013; Table 1). Due to human population growth and industrialization of food production, the availability of these anthropogenic food subsidies has significantly increased over the last century (Hoornweg et al., 2013; Oro et al., 2013). At sea, fishing discards represent 10 to 20% of current worldwide catches (Zeller et al., 2018). On land, waste production has risen tenfold since 1900s, and it is expected to double again by 2025 (Hoornweg et al., 2013). In addition, the expansion and growth of agriculture has increased cultivated land up to ~11% of the total world land surface (Foley et al., 2011). All of these resources represent a superabundant and highly predictable food supply for opportunistic consumers, and consequently, these species have altered their population dynamics and behaviour for decades. Several official restrictions have limited the availability of these anthropogenic food subsidies worldwide (e.g., the Landfill Directive; European Commission, 1999 and the European Landing Obligation; European Commission, 2015); however, management authorities are increasingly concerned about how opportunistic species will respond to these resource restrictions (Bicknell et al., 2013; Bino et al., 2010; Oro et al., 2013).

Long-term dietary reconstructions of wildlife allow us to investigate the ability of consumers to adapt their feeding behaviour and strategies to the availability of anthropogenic food subsidies (Chamberlain et al., 2005). Particularly, stable isotope analysis in keratinous tissues, such as feathers, can provide a low-effort, non-invasive method to obtain dietary estimates for individuals, populations, and species (Dalerum and Angerbjörn, 2005; Ramos and González-Solís, 2012). In this study, we aimed to evaluate the trophic plasticity of a paradigmatic example of superabundant and opportunistic consumer, the yellow-legged gull *Larus michahellis*. To this aim, we used isotopic approaches to reconstruct the diet of a yellow-legged gull population breeding in the north eastern Iberian Peninsula over the last 20 years. We also considered dietary reconstructions of four museum specimens collected during the 20th century. We related feeding habits of this population to the availability of anthropogenic food subsidies around the study area and during the study period, and discuss these findings in relation to past, present and future population dynamics.

2. Material and methods

2.1. Species and population

Many studies have defined the yellow-legged gull as a generalist predator, with a very diverse diet adapted to the availability of resources (Méndez et al., 2020; Ramírez et al., 2020). In addition, these gulls exploit a wide range of resources and habitats closely linked to human activities, which makes them a suitable model species to investigate effects of the changes in anthropogenic food subsidies on wildlife. However, most previous dietary assessments have used either conventional methods (Calado et al., 2020) or integrated short periods of time (Arizaga et al., 2013), thus providing a snapshot of the diet of yellow-legged gulls or other similar species. Ultimately, this may hamper our ability to assess species trophic plasticity in relation to changes in the availability of anthropogenic food subsidies.

In addition, yellow-legged gull is considered a nuisance in several places because of its negative interactions with protected species (Oro and Martínez-Vilalta, 1994; Arcos et al., 2001; Skórka and Wójcik, 2005), disturbances caused in urban areas, and its potential role in pathogen dispersal (Al-Yasiri et al., 2016; Antilles et al., 2021). For this reason, population control measures have been implemented at several breeding sites (Paracuellos and Nevado, 2010; Bosch et al., 2019a, 2019b). Other management practices for this species include the regulation of their accessibility to food sources, particularly when they are linked to human activities (e.g. covered landfills; Belant, 1997). Thus, any robust contribution to understand yellow-legged gull trophic ecology is key for environmental and conservation sciences.

The study population is located on the Medes Islands (42°03′00″N 03°13′15″E), in the Western Mediterranean. These islands consist of seven calcareous rocks with an area of 20 ha that are 0.9 km off the coast, near intensely urbanised areas in the northeast of the Iberian Peninsula. In the last few decades, this population has undergone various fluctuations (Fig. 1). Specifically, during the 20th century, this population increased exponentially, likely due to their opportunistic feeding behaviour and the increase in the availability of anthropogenic food subsidies (with an intense growth from 6000 in 1974 to a peak of 14,000 pairs in 1991). After this peak, the population was culled from 1992 until 1996 to control its growth. Current regulations affecting the availability of anthropogenic food subsidies (e.g. landfill waste reduction) may have driven its demographic decrease over the most recent years (Fig. 1).

2.2. Fieldwork procedure

At the colony, we collected 4–6 breast feathers from gull fledglings (one per brood to avoid pseudoreplication) in 2004, 2005, 2009, 2010, 2011, 2014, 2015, 2016, 2017 and 2018. In addition, we also collected breast feather samples from four juvenile specimens stored in museums (*Museu de Ciències Naturals de Barcelona*, Barcelona, and *Museu Darder*, Banyoles, Spain), which had hatched in the study colony, to use as indicators of the base-line diet before the generalised abundance of anthropogenic food subsidies (early and late 20th century). In particular, we sampled a few breast feathers from one individual that hatched and died in 1916, and three individuals from the 1990s. Finally, we also collected spontaneous regurgitations occurring while handling the birds during the fieldwork conducted in 2004, 2005, 2017 and 2018.

To complement the breast feather and regurgitate samplings, we captured five breeding adults from the Medes Islands colony during the incubation period of 2018 using tent spring traps, and we equipped them with solar-powered GPS loggers (WIMBISF-25 from Wimbitek SL; see Table S1 for specifications about deployments). We programmed the loggers (that represented ~2% of the bird's body mass), to record locations every 30 min and attached them to the back of the gulls using a wing harness fixed with a reef knot in the tracheal pit, which is an attachment method recommended for large gulls (Thaxter et al., 2014). We then used the area covered by these five gulls as a proxy for the range where the gulls could find their main food sources during the chick-rearing season (May-June).

2.3. Laboratory and stable isotope analyses

We weighed every spontaneous regurgitation and identified its contents. Prey items within regurgitates were categorized as marine

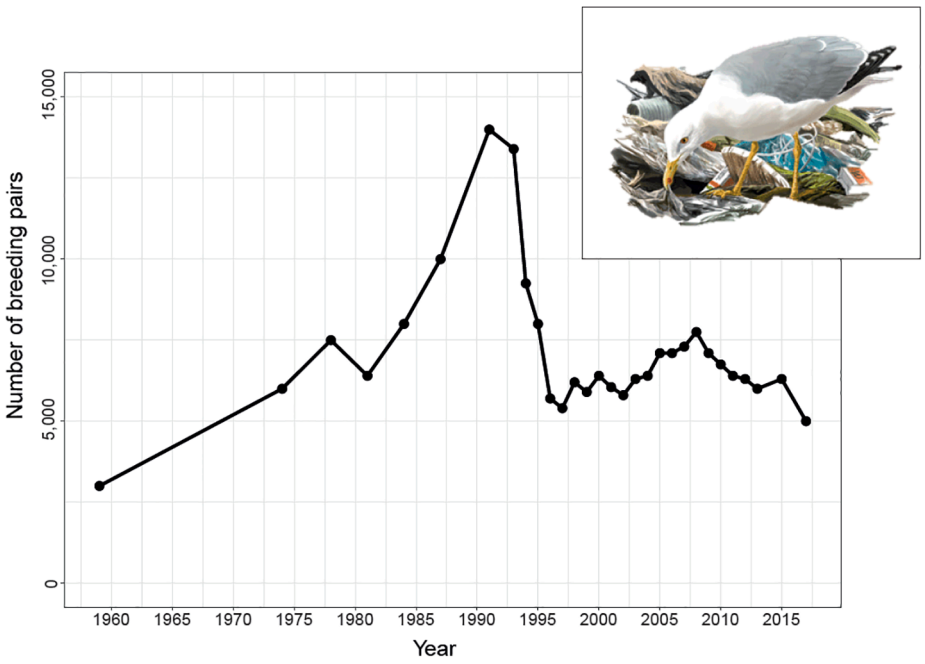

Fig. 1. Demographic trend (in number of breeding pairs) of yellow-legged gulls *Larus michahellis* in the colony of Medes Islands (northeast of the Iberian Peninsula; Western Mediterranean) from 1960 until 2017. Data gathered from Bosch et al., (2015), Bosch et al. (2017), Bosch et al. (2019a) and Bosch et al. (2019b). Image by Toni Llobet ©. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

prey (mostly marine fish), waste from landfills-slaughterhouses (chicken and pork meat), and terrestrial invertebrates (hereafter, marine, refuse and terrestrial, respectively). The best-preserved samples were selected and stored frozen at −20 °C. After that, we grounded them to a fine powder in a freezer mill (Spex Certiprep 6750; Spex Industries Inc., Metuchen, New Jersey, USA) operating at the temperature of liquid nitrogen. To reduce variability due to isotopically lighter lipids, which may have a particular influence on the stable isotope values of carbon (Attwood and Peterson 1989, Hobson and Welch 1992), we removed lipids through several chloroform–methanol (2:1) rinses before the stable isotope analysis (Folch et al., 1957).

Feathers were washed in a 0.25 M sodium hydroxide solution, dried to a constant mass, and ground to powder. As feathers are keratinous tissues with low lipid content, we did not perform lipid extraction before continuing with the process (Post et al., 2007). We weighed a subsample of 0.4 mg of feather powder to the nearest μg for carbon and nitrogen stable isotope values determinations and about 1.5 mg for sulphur isotope measurements, placed each sample in a tin capsule and crimped it for combustion. Stable isotope values are expressed as δ values in parts per mil (‰), related to the international standard measurements. See stable isotope standards and material used in the supporting information (M1).

2.4. Statistical analyses

Prior to the dietary assessments, we evaluated the inter-annual variability in δ^{13}C, δ^{15}N, and δ^{34}S values of the three prey categories (marine, refuse and terrestrial). To do so, we performed one-way ANOVAs with year as a fixed factor and the stable isotope values of each food source and element as response variables (Table S2). Moreover, we performed a cluster analysis using the Euclidean distance and a dendrogram using Ward's method (Ward, 1963) to visualize sample grouping according to their stable isotope values. We also performed a one-way ANOVA with element, food category and year as fixed factors and stable isotope values as a response variable. Then, we performed a Tukey pairwise comparisons test to evaluate if, globally, there were significant differences among the stable isotope values of the three elements, the three food categories and among years. The p-value of the Tukey pairwise comparison tests were subsequently corrected using a Bonferroni correction (Table S3).

To assess the relative contributions of different resources to the diet of yellow-legged gulls, we implemented a three element (δ^{13}C, δ^{15}N, and δ^{34}S), three end-point (marine, refuse, and terrestrial contributions) Bayesian stable isotope mixing model using the MixSIAR package (Stock et al., 2018) in R (R Core Team, 2008). These models allow for uncertainty associated with isotopic values and diet-to-tissue discrimination factors. We fitted a MixSIAR model with diet-to-tissue discrimination factors extracted from Bearhop et al. 2002, (for δ^{13}C and δ^{15}N), and Peterson et al. 1985 (for δ^{34}S). We ran the Markov Chain Monte Carlo (MCMC) model with three chains of 100,000 iterations, thinned by 50 and with a 50,000-iteration burn-in which produced a posterior distribution of 3000 draws. We then assessed model convergence through diagnostic plots and the Gelman-Rubin and Geweke diagnostics.

We gathered annual availability data for the main food resources of gulls around the study area (a 50 km buffer around the colony, inferred from the maximum range covered by the GPS-tracked gulls; Fig. 2) from several sources of information, including yearly fish landings in the harbours of the study area, yearly tonnes of landfill waste production, yearly tonnes of meat production, and arable land surface (Table 2). We explored the relationship between yearly dietary estimates and resource availability around the study area using Pearson's correlation tests for each of the three sources.

3. Results

Based on the analyses of inter-annual variability of the prey categories, we found significant differences in element-specific stable isotope values between years in three cases; marine δ^{13}C, marine δ^{34}S, and refuse δ^{34}S (Fig. S1, Table S2). However, we also found that, overall, there were no significant differences among years when pooling all of the stable isotope values but instead, there were among elements and food categories (Tables S3 and S4), showing that the differences found

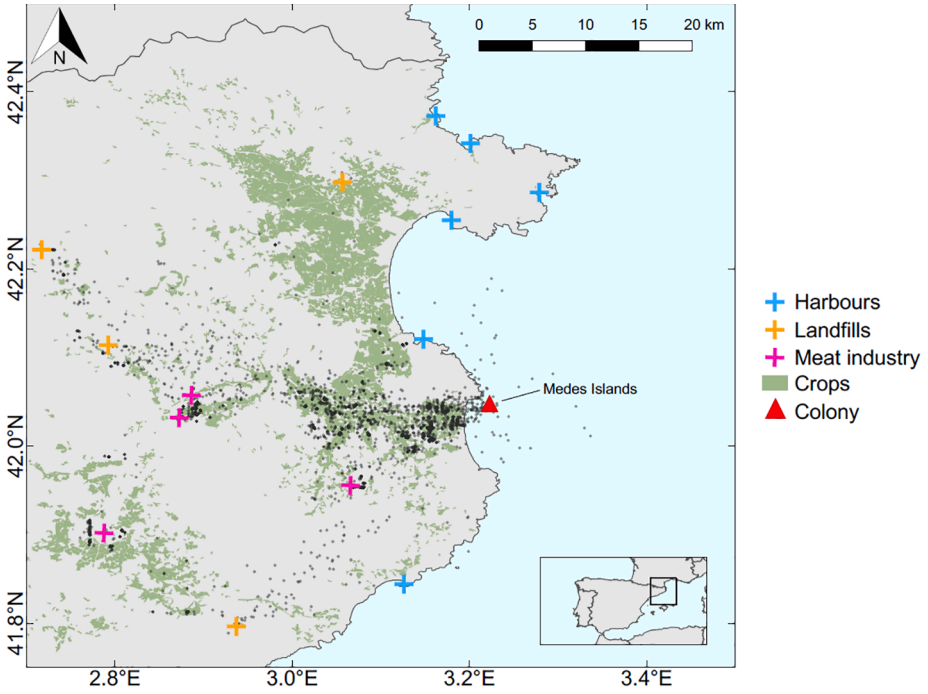

Fig. 2. Map of the study area with positions of GPS-tracked gulls (filled grey circles), main anthropogenic food sources (coloured crosses and green area) and the sampled colony of Medes Islands (red triangle). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Proxies for resource availability of potential food sources, our interpretation of it, time interval of each dataset and the data source. Landfill tonnage added with meat production tonnage constitutes the waste production proxy.

Proxy	Food source	Variable	Time period	Source
Landings in harbours (t)	Marine	Marine prey availability	2000–2019	*Direcció General de Pesca i Afers Marítims*
Landfill tonnage (t)	Refuse	Landfill food availability	1992–2018	Banyoles: *Consell Comarcal del Pla de l'Estany*
–	–	–	–	Beuda: *consorci SIGMA*
–	–	–	–	Pedret i Marzà: *Consell Comarcal de l'Alt Empordà*
–	–	–	–	Solius: *dipòsit controlat de Solius*
Meat production (t)	Refuse	Meat industry residues availability	2004–2018	*Ministerio de Agricultura, Pesca y Alimentación*
Arable land (ha)	Terrestrial	Terrestrial invertebrate availability	1999–2019	*Institut d'Estadística de Catalunya* (Idescat)

between years in individual elements were much smaller than between prey categories or elements, and that therefore they were not relevant to our analysis (Fig. S2, Table 3).

Regarding the dietary assessments, we found that yellow-legged gulls from the Medes Islands changed their diet repeatedly throughout the study period (Fig. 3, Table 4). Specifically, our results based on the dietary assessment of the museum specimens suggested that the proportion of marine prey in the diet of yellow-legged gulls was much higher at the beginning of the 20th century (~70%) compared to the one in the 1990s (~40%) and the 2004–2018 period (~50% and ~35%, respectively). Concurrently with this decrease in marine prey consumption during the study period, we also found an increase in the consumption of refuse. Our assessments of the individual from the beginning of the 20th century revealed the lowest refuse dietary proportion values (~20%), in contrast to those from the 1990s (30%) and from 2004 to 2018, when the consumption of refuse stabilized (41–52%). Similar to that of refuse, the consumption of terrestrial prey was low at the beginning of the 20th century (~15%) and larger in the 1990s (30%); however, this contribution dropped to ~0% in 2004 and then increased in a stepwise manner until 2018 (~20%).

To relate these findings to the availability of anthropogenic food subsidies, we gathered data on their availability in the study zone (Fig. 2), which revealed that landings in harbours (our proxy for the availability of marine prey) decreased from over 700 tonnes/year in the year 2000 down to 100 tonnes/year in 2018 (Fig. S3A). Landfill waste (one of our proxies for the availability of refuse items), decreased from 200,000 tonnes/year in the year 1992 down to 300 tonnes/year in 2018 (Fig. S3B). In contrast, meat production (the other proxy for the availability of refuse items) increased from 500,000 tonnes/year to 800,000 tonnes/year from 2004 until 2018 (Fig. S3C). Finally, arable land surface (our proxy for the availability of terrestrial invertebrates), remained fairly steady (around 80,000 ha) in the 1999–2019 period (Fig. S3D).

When linking our dietary assessments with anthropogenic food subsidies availability, we found that marine prey consumption was highly correlated with the tonnes of fish landings in harbours of the study area ($p = 0.003$; $r^2 = 0.720$; Fig. 4A and S3). However, we did not find relationships with refuse tonnage (landfill and meat wastes; $p = 0.730$; $r^2 = 0.014$; Fig. 4B) or arable land surface ($p = 0.730$; $r^2 = 0.016$; Fig. 4C).

Table 3
Carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulphur ($\delta^{34}S$) isotope values (mean ± SD) of main prey extracted from regurgitates, and categorized amongst marine (marine fish), refuse (chicken and pork meat) and terrestrial (terrestrial invertebrates). Discrimination factors were taken from Bearhop et al., 2002 ($\delta^{13}C$ and $\delta^{15}N$) and Peterson et al., 1985 ($\delta^{34}S$).

Source	n	$\delta^{13}C$	Discr. factor	$\delta^{15}N$	Discr. factor	$\delta^{34}S$	Discr. factor
Marine	47	−18.58 ± 0.45	3.60 ± 0.50	8.90 ± 0.87	5.30 ± 0.80	17.36 ± 0.31	−0.10 ± 0.50
Refuse	42	−21.55 ± 1.38	2.20 ± 0.50	4.71 ± 1.65	5.00 ± 0.50	5.21 ± 1.69	−0.10 ± 0.50
Terrestrial	12	−23.02 ± 1.07	1.94 ± 0.50	8.81 ± 0.96	4.00 ± 0.50	7.42 ± 1.35	−0.10 ± 0.50

4. Discussion

Our analyses provide long-term estimates regarding the diet of an opportunistic species inhabiting a highly human-modified landscape. We showed that yellow-legged gulls repeatedly adapted their diet to the anthropogenic food subsidies available around the study area, thus showing a very high trophic plasticity. This plasticity may have been an important driver in making this gull very successful, often at the expense of other species (Bosch, 1996; but see Oro and Martínez-Abraín, 2007), as shown by its trends in colony size. Therefore, our results point to the adaptable nature of this opportunistic species. Many other animal species worldwide have also experienced dietary changes related to human activities and the exploitation of anthropogenic food subsidies, but large gulls are especially plastic. Accordingly, they show a variety of location-specific strategies, including an extensive use of the terrestrial environment (lesser black-backed gull *Larus fuscus*; Spelt et al., 2019, herring gull *Larus argentatus*; Pennycott et al., 2020), a conservation of their traditional marine habits (kelp gull *Larus dominicanus*; Silva-Costa and Bugoni, 2013, great black-backed gull *Larus marinus*; Maynard and Davoren, 2018) or a mixture of strategies (Audouin's gull *Ichthyaetus audouinii*; Bécares et al., 2015; lesser black-backed gull; Isaksson et al., 2016).

In our study, yellow-legged gulls showed several dietary shifts throughout the study period, likely driven by changes in the availability of anthropogenic food subsidies in the study area. First, marine contribution to diet of this population showed a decrease throughout the period 2004–2018. It has been shown that in some colonies, the habitat use of yellow-legged gulls is not constant throughout the breeding cycle, with an increase in marine environment use during the breeding season (Ramos et al., 2011; Ramírez et al., 2020), suggesting that marine prey consumption may be even lower during the non-breeding period. Large gulls are known to have a dietary preference for marine fish (e.g. sardine *Sardina pilchardus*; Calado et al., 2020), as it can provide essential amino acids that cannot be synthesized by birds (e.g. leucine and valine) and that are key for processes such as egg formation (Hebert et al., 2002). Nowadays, most of the yellow-legged gull diet in colonies that are found in remote locations, far from human settlements (e.g. Columbretes Islands in the Western Mediterranean; Morera-Pujol et al., 2018), is still largely marine-based (either from fishing discards or naturally caught fish), as was the case for our sample in 1916. Our study population breeds very close to several fishing harbours where discarding operations are conducted, particularly by trawling and purse-seining fishing boats, which supply a predictable and abundant food source for the gulls (Oro et al., 1996; Karris et al., 2018). Indeed, we found a strong positive correlation between the proportion of marine prey in the yellow-legged gull diet and the tonnes of landed fish in the nearby harbours. This could indicate a plastic response of this species in face of the decrease in the availability of marine prey in the study area, mainly due to the stock collapse of some forage fish species (Demirel et al., 2020; Pennino et al., 2020). This stock collapse has led to a decrease in the fish catches in the

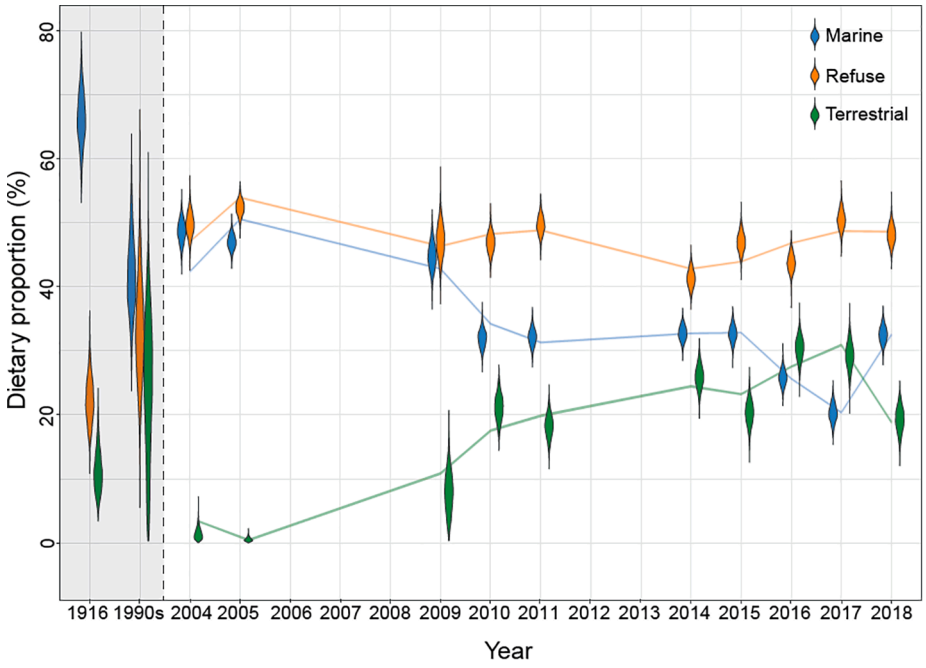

Fig. 3. Dietary contributions (in %) of the main food sources inferred from stable isotope analysis of feather samples during the sampled period. Grey-shaded area shows results from museum specimens (20th century). Coloured violins represent the density of the posterior distribution for each year and food source (marine: marine fish; refuse: chicken and pork meat and terrestrial: terrestrial invertebrates). Continuous, coloured lines linking yearly estimates are plotted only for better visualization purposes.

Table 4
Carbon (δ^{13}C), nitrogen (δ^{15}N), and sulphur (δ^{34}S) stable isotope values for each sampled year. Mean (±SD [minimum: maximum]).

Year	n	δ^{13}C	δ^{15}N	δ^{34}S
1916	1	−17.69	14.76	15.85
1990s	3	−18.94 ± 0.04 [−19.03: −18.90]	11.20 ± 0.25 [10.81:11.57]	11.87 ± 1.44 [10.00:12.71]
2004	22	−18.37 ± 0.49 [−19.31: −17.53]	9.93 ± 0.47 [9.09:11.06]	13.67 ± 1.77 [10.58:17.11]
2005	96	−18.24 ± 0.50 [−20.04: −17.05]	9.70 ± 0.44 [8.83:10.85]	12.05 ± 1.49 [7.63:15.39]
2009	16	−18.81 ± 0.46 [−19.69: −17.99]	10.37 ± 0.55 [8.83:11.24]	12.87 ± 1.29 [10.79:15.22]
2010	50	−19.45 ± 0.64 [−20.77: −18.01]	10.36 ± 0.40 [9.52:11.29]	10.77 ± 1.43 [7.88:13.43]
2011	71	−19.46 ± 0.51 [−20.89: −18.51]	10.17 ± 0.47 [9.07:11.45]	10.88 ± 1.55 [8.05:14.35]
2014	59	−19.29 ± 0.53 [−20.87: −18.42]	10.66 ± 0.46 [9.76:11.80]	10.16 ± 1.53 [6.24:13.16]
2015	60	−19.42 ± 0.56 [−21.87: −18.49]	10.35 ± 0.42 [9.35:11.16]	10.95 ± 1.61 [7.5:14.18]
2016	59	−19.70 ± 0.44 [−20.54: −18.68]	10.50 ± 0.49 [8.93:12.31]	9.32 ± 1.62 [6.10:13.82]
2017	56	−20.11 ± 0.59 [−21.34: −18.89]	10.18 ± 0.69 [10.81:11.57]	8.98 ± 1.64 [5.42:12.40]
2018	62	−19.55 ± 0.46 [−20.90: −18.70]	10.34 ± 0.56 [9.40:12.40]	11.61 ± 1.89 [6.90:16.00]

study area (from ~800 t/year to ~300 t/year) that may reflect the scarcity of natural prey availability, that has ultimately led to a decrease in the production of fishing discards which, in turn, may have affected the gulls' diet. We predict that the decreasing trend of marine prey consumption will be augmented in the near future, as the predictable anthropogenic food subsidy provided by fishing discards is influenced by the Landing Obligation that is currently being implemented in the EU (European Commission, 2015; Ramos et al., 2009; Karris et al., 2018).

The recorded decrease in the availability of marine prey can ultimately be compensated in caloric terms by the use of other anthropogenic food subsidies, such as refuse items and terrestrial invertebrates. Accordingly, our results suggest that there is an inverse relationship between the consumption of marine prey and refuse items. This may have nutritional downsides as marine prey (mostly fish) is rich in highly unsaturated fatty acids, key for growth and development in birds (Surai and Speake, 2008), contrasting with refuse, that has been shown to be inadequate for normal chick development (Pierotti and Annett, 2001). Refuse contributed to a low proportion of gull diet in the sample of 1916 (~20%), had a larger contribution in the 1990s (~30%), became a stable in the 2004–2018 period (ranging 41–52%), and is now the largest contributor to the yellow-legged gull diet. The main sources of refuse items for wildlife are landfills (i.e. organic leftovers from human food consumption; Ramos et al., 2009; Pedro et al., 2013), meat processing industries, and slaughterhouses. However, recent legislations have limited the amount and availability of landfill waste (European Commission, 1999) and, as a consequence, the landfills of our study area have significantly decreased their waste from a yearly peak of over 200,000 t of waste (late 1990s) to ~100,000 t (2018). Meanwhile, meat production has increased, which has potentially generated more availability of meat waste. This may compensate for the reduced availability of landfill waste, resulting in little change in refuse consumption during the 2004–2018 period. These results are of particular importance, as we provide explicit evidence to suggest that yellow-legged gulls may be feeding from meat industry waste (as inferred from the GPS data), which could be masking a decrease in landfill attendance (Zorrozua et al., 2020). The refuse items consumed by gulls in landfills and meat industries are often composed primarily of chicken, pork, or beef scraps (Ramos et al., 2009) because they can supply high values of energy per meal with a low energetic cost of foraging (Pierotti and Annett, 1991). Consequently, this can result in an increase in individual fitness that may reflect a better breeding performance and, ultimately, a demographic increase at a population level (Duhem et al., 2007; Plaza and Lambertucci, 2017). This could be the case for our study population, where the number of breeding pairs grew from 6000 to 14,000 in the 1974–1991 period, coinciding with the industrial and touristic development of the study area (Mundet, 2000). This demographic explosion, coupled with the fish stock collapse and the decrease in fishing activity, may have led to a lower availability of marine prey in the study area, which may explain the relatively large refuse and terrestrial prey consumption in the 1990s (combined proportion of 60%).

The low terrestrial prey consumption in 2004 (~0%) may be explained by the low number of breeding pairs in the colony due to culling procedures between 1992 and 1996. This may have reduced competition and increased the availability of refuse items and marine

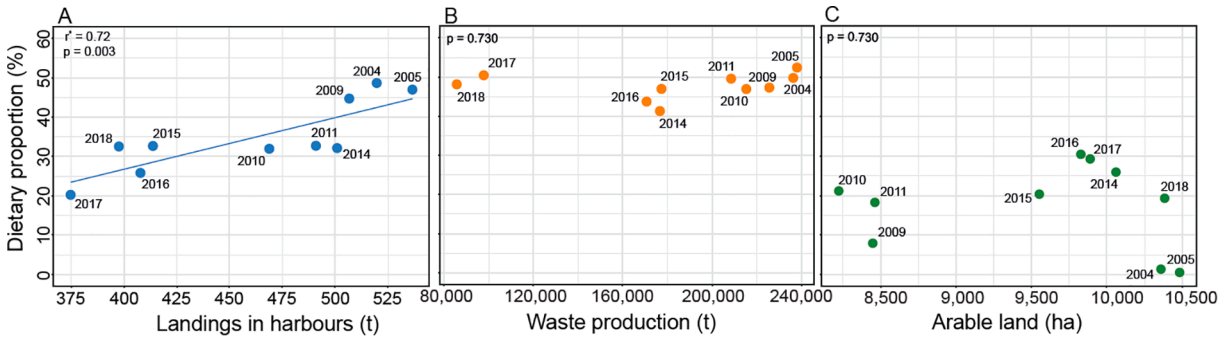

Fig. 4. Correlation between yearly dietary estimates of yellow-legged gull and anthropogenic food subsidies available along the study area; A) marine dietary proportion vs. landings in harbours; B) refuse dietary proportion vs. waste production (landfill tonnage added with meat production tonnage); C) terrestrial dietary proportion vs. arable land surface. Notice that 20th century samples from museum specimens are not considered due to the lack of estimations of anthropogenic food subsidies. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

prey for all individuals. Additionally, there is a consistent increase in the consumption of terrestrial prey (i.e. terrestrial invertebrates; Moreno et al., 2010; Arizaga et al., 2013) from 2004 to 2018 (from nearly 0% up to 35%), which coincides with the decrease in marine prey consumption. As in the case of refuse, the increase in consumption of terrestrial invertebrates seems to be linked to the continued decline of fishing discards availability at the nearby harbours throughout our study period. A decrease in fishing discards may be compensated by exploiting other resources, such as terrestrial invertebrates found in crops, which is similar to what may have happened in the 1990s during the demographic explosion. However, terrestrial invertebrates are less energetically rich than fish (~70 kcal/100 g vs. ~340 kcal/100 g; Finke, 2002; Oruwari et al., 1999), which could potentially lead to a decrease in individual fitness. This may explain the decrease in breeding pairs in the colony in the last 10 years of sampling (2008–2018; 7700–5000 pairs). Therefore, all of our results point to a reduction in energetically and nutritionally profitable prey (due to the Landing Obligation, forage fish stock collapse, Landfill Directive) that may lead to a sustained population decrease in the near future (Robertson et al., 2013).

4.1. Concluding remarks

In this study, we provide insights into the dietary changes of an opportunistic species, and we show that it repeatedly adapted its diet to the availability of anthropogenic food subsidies in the study area, with a gradient from high to low energetically profitable prey, particularly regarding the increase of terrestrial invertebrate consumption. These results highlight the high trophic plasticity of yellow-legged gulls, and predict future dietary changes in scenarios with anthropogenic food subsidy restrictions. Moreover, in the current situation of a rapidly changing environment due to global change, the behavioural and dietary plasticity shown here by yellow-legged gulls should provide a survival advantage, in comparison to specialist and less plastic species. However, the use of less energetically dense prey may have demographic consequences for yellow-legged gulls as well. This trophic plasticity may also have effects on interactions between wildlife and humans, especially when implemented restrictions reduce the availability of anthropogenic food subsidies and certain species are forced to change their foraging habits. For example, certain species may stop feeding in specific places (e.g. landfills or fishing harbours), but instead be forced to spread to other areas, including urban spaces, to meet their feeding requirements. This phenomenon already occurs in large gull populations across their distribution ranges, where it is rather common to observe these species colonising urban areas and foraging in the streets (Ramírez et al., 2020, Méndez et al., 2020, Coccon and Fano, 2020). This may also have undesired consequences, such as an increased transmission of pathogens (Navarro et al., 2019). Thus, it is essential to monitor opportunistic species that are in contact with humans, to be able to implement suitable management and conservation actions that limit the availability or accessibility of anthropogenic food sources, especially when it comes to superabundant species, such as large gulls.

CRediT authorship contribution statement

Jazel Ouled-Cheikh: Data curation, Formal analysis, Writing - original draft. **Virginia Morera-Pujol:** Formal analysis, Writing - review & editing. **Álvaro Bahillo:** Methodology. **Francisco Ramírez:** Conceptualization, Writing - review & editing. **Marta Cerdá-Cuéllar:** Funding acquisition, Writing - review & editing. **Raül Ramos:** Funding acquisition, Conceptualization, Writing - review & editing, Supervision, Project administration.

Declaration of Competing Interest

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

Acknowledgements

We dedicate this contribution to the memory of Lluís Jover, who passed away unexpectedly on the 30th October 2018; we will always be indebted to him for his extensive experience in ecological research with intrinsic biomarkers, his brilliant suggestions that improved our manuscripts, and his general encouragement. We also want to thank Jacob González-Solís, Carola Sanpera, Marc Bosch, Josep Simó, Natàlia Vilas, Agustí Bosch, David Parron, Martina Cubí, Albert Palà, Ricard Gutiérrez and Pilar Todó for facilitating data, Néstor Pérez-Méndez, and many students who contributed to fieldwork and laboratory analyses, Georgina Gratacós and Javier Quesada for providing museum samples, the rangers and managers of the Medes Islands Marine Reserve for boat journeys, and Sydney Hope for the English corrections. This work was supported by FAU2008-00012-C02-01 from INIA (*Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria*, Spain), CGL2009-11278/BOS from *Ministerio de Ciencia e Innovación* from the Spanish Government, Fondos FEDER, 2017/2349 of the PLEAMAR programme with the collaboration of the *Fundación Biodiversidad*, from the *Ministerio para la Transición Ecológica* (Spain), cofounded by the EMFF (European Union), and REN2003-07050 *Aplicación de biomarcadores a la gestión de una especie problemática* (*Larus cachinnans*). CERCA Programme from *Generalitat de Catalunya* is also acknowledged. RR was supported by a postdoctoral *Ramón y Cajal* contract (RYC-2017-22055) and VMP was supported by a pre-doctoral contract BES-2014-068025 both from the Spanish *Ministerio de Economía, Industria y Competitividad*.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107943.

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