Universidade do Minho
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Joana Filipa Gomes Calado

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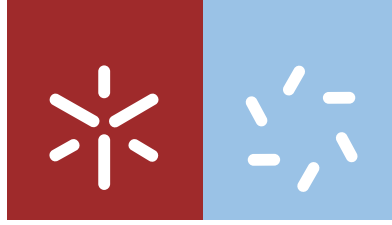
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# The role of fisheries in gulls' trophic and foraging ecology at different spatial and temporal scales

Ph.D. Thesis in Biology
Specialty in Sustainable Use of Marine Ressources

Work Supervised by
**Professor Pedro Gomes**
and
**Professor Alberto Velando**

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# STATEMENT OF INTEGRITY

I hereby declare having conducted this academic work with integrity. I confirm that I have not used plagiarism or any form of undue use of information or falsification of results along the process leading to its elaboration.

I further declare that I have fully acknowledged the Code of Ethical Conduct of the University of Minho.

**RESUMO**

**O papel da pesca na ecologia trófica e de procura de alimento de gaivotas em diferentes escalas espaciais e temporais**

As gaivotas são aves marinhas oportunistas com estratégias de procura de alimento plásticas que se podem alimentar em associação com atividades de pesca. Várias espécies exploram rejeições de pesca, o que tem sido associado ao aumento da população de gaivotas em todo o mundo. Nesta tese, duas espécies de gaivota, gaivota de patas-amarelas *Larus michahellis* e gaivota de Audouin *Larus audouinii*, foram usadas para investigar a influência da pesca na sua ecologia trófica e de procura de alimento e a sua variabilidade espaço-temporal em quatro ilhas ao longo da costa oeste da Península Ibérica. Várias técnicas foram realizadas, como análises de egagrópilas, de isótopos estáveis e bioquímicas, bem como observações a bordo para examinar a ecologia alimentar das gaivotas ao nível da comunidade, da população e do indivíduo. Os principais resultados foram: (1) ambas as gaivotas de patas-amarelas e de Audouin alimentaram-se de espécies de peixe demersais e pelágicos comerciais, mas as gaivotas de patas-amarelas pareceram tirar mais proveito da pesca do que as gaivotas de Audouin; (2) em todas as quatro ilhas de estudo, os machos de gaivota de patas-amarelas exibiram valores de isótopos estáveis de $\delta^{13}C$ e $\delta^{15}N$ mais altos do que as fêmeas, o que sugere uma maior proporção de machos a alimentar-se em associação com atividades de pesca; (3) de entre as aves marinhas que interagiram com os barcos da frota pesqueira de Peniche, a gaivota de patas-amarelas foi a espécie mais abundante, especialmente com as cercadoras; (4) nas quatro ilhas de estudo, houve uma associação entre as espécies de peixe consumidas pelas gaivotas e os desembarques locais de peixe; e (5) alterações nas práticas de pesca, juntamente com mudanças na gestão de lixo e condições ambientais, levaram a um declínio acentuado de peixe e lixo, acompanhado por um aumento de crustáceos, na dieta de gaivotas de patas-amarelas na costa noroeste da Espanha ao longo dos últimos 30 anos. Os resultados desta tese contribuem para uma melhor compreensão da ecologia trófica e de procura de alimento das gaivotas de patas-amarelas e de Audouin, e para a avaliação dos possíveis impactos ecológicos da política de proibição de rejeições da União Europeia.

**Palavras-chave**: Dieta; Gaivota de Audouin; Gaivota de patas-amarelas; Isótopos estáveis; Rejeições de pesca

# ABSTRACT

## The role of fisheries in gulls' trophic and foraging ecology at different spatial and temporal scales

Gulls are opportunistic seabirds with plastic foraging strategies that can feed in association with fishing activities. Several species exploit fishery discards, which has been associated with the increase of gull populations worldwide. In this thesis, two gull species, yellow-legged gull *Larus michahellis* and Audouin's gull *Larus audouinii*, were used to investigate the influence of fisheries in their trophic and foraging ecology and its spatio-temporal variability on four islands along the western Iberian coast. Several techniques were performed such as pellet, stable isotope, and biochemical analyses as well as onboard observations to examine the feeding ecology of gulls at the community, population, and individual levels. The main results were: (1) both yellow-legged and Audouin's gulls fed on demersal and commercial pelagic fish species, but yellow-legged gulls seemed to take more advantage of fisheries than Audouin's gulls; (2) on all four study islands, yellow-legged gull males exhibited higher $\delta^{13}C$ and $\delta^{15}N$ stable isotope values than females, which suggests a higher proportion of males feeding in association with fishing activities; (3) of all the seabird species that interacted with boats from the Peniche fishing fleet, the yellow-legged gull was the most abundant species, especially with purse-seiners; (4) on all four study islands, there was an association between the fish species consumed by gulls and local fish landings; and (5) alterations in fishing practices, along with changes in refuse management and environmental conditions, led to a sharp decline of fish and refuse accompanied by an increase of crustaceans in the diet of yellow-legged gulls on the northwest coast of Spain over the last 30 years. The results of this thesis contribute to the better understanding of the trophic and foraging ecology of yellow-legged and Audouin's gulls and to the evaluation of the possible ecological impacts of the European Union discard ban policy.


**Keywords**: Audouin's gull; diet; fishery discards; stable isotopes; yellow-legged gull

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**GENERAL INTRODUCTION**

## 1. Fisheries in marine ecosystems

Commercial fisheries have caused extensive changes in marine ecosystems worldwide (Pauly et al. 2005). The industrialization of fishing in the last century increased fishing power and effort due to the improved ability of boats to search vast pelagic areas for fishery resources (Anticamara et al. 2011). However, despite the technological advances and fishing expansion throughout the world, the catch per unit effort is decreasing, reflecting overexploitation of marine resources and fish depletion (Thurstan et al. 2010, Rousseau et al. 2019). Such unsustainable fishery practices have cascading trophic level effects across marine food webs. Indeed, intense fishing pressure not only devastates fishery stocks but also causes profound damages to ecosystem structure and functioning (Williams 1998, McCauley et al. 2015).

Marine coastal areas are among the most threatened ecosystems by fisheries (Guiet et al. 2019). These systems are characterized by high productivity and biodiversity (Suchanek 1994) and are heavily exploited by a wide range of fishing gears (Guiet et al. 2019), from artisanal (small-scale) to industrial (large-scale) fishing fleets (Stewart et al. 2010). Within these areas, overfishing is the most significant direct impact of fisheries (Jackson 2001). The recent collapse of coastal fish stocks raises serious concerns since they provide a large part the world's fishery yields (Pauly and Christensen 1995). Many coastal shelves and upwelling regions in temperate regions have a "wasp-waist" food web structure, with small pelagic fish as dominant species at intermediate trophic levels and high species diversity at the bottom and top of the food chain (Bakun 2006). These dominant species exert top-down control on lower trophic level prey and bottom-up control on top predators (Cury et al. 2000). Therefore, the worldwide overexploitation of such species has large impacts on other organisms such as plankton, predatory fish, cetaceans, and seabirds (Smith et al. 2011).

## 2. Seabirds and fisheries

Seabirds are a polyphyletic group that spends some of their lifetime at-sea and depend on the marine realm to obtain their food (Schreiber and Burger 2002a). Some species depend entirely on marine food resources (Shealer 2002), while others exhibit great feeding plasticity, using both terrestrial and marine food resources (Gotmark 1984). They can have wide-ranging distributions during the non-breeding season, but all species go to land and are central-place foragers during the breeding season, commuting between foraging areas and the nest (Coulson 2002). Seabirds are top predators that respond to natural and Human-related changes in their environment (Hazen et al. 2019). Due to their life-history traits, such

as long lifespan, deferred maturity, and high adult survival rates, they are particularly vulnerable to such changes (Heithaus et al. 2008). Diet and foraging behaviour are readily measured parameters, providing information about the food web structure and the abundance of different prey across various spatial and temporal scales (Velarde et al. 2019). However, seabird response may vary according to their life-history characteristics. For instance, in conditions of low food availability, generalist species are expected to switch to alternative prey and new foraging areas (including terrestrial environments), whereas specialist species may increase foraging effort (Furness and Camphuysen 1997).

Fisheries have long shaped many aspects of seabird ecology, including diet, foraging behaviour (Corbeau et al. 2019), activity patterns (Oro et al. 1997), distribution (Cama et al. 2013), and overall community structure (Votier et al. 2004). Influences of fisheries on seabirds prevail in seabird-fishery interactions, and these can be both direct or indirect and either positive or negative (Montevecchi, 2002; Table 1). However, fishermen also use seabird aggregations to identify fish schools in artisanal and industrial fisheries. Indeed, industrial purse-seines targeting tuna schools use bird radars to detect seabird distribution and behaviour (Hall and Roman 2013). On the other hand, seabirds can have negative effects on fisheries causing economic losses (Table 1).

**Table 1**. Effects of seabird-fishery interactions (based on Montevecchi, 2002)).

|  |  | **Positive** | **Negative** |
|---|---|---|---|
| **Effects of fisheries on seabirds** | **Direct** | Facilitate foraging | Compete with seabirds |
|  |  | Provide food (discards, offal, and bait) | Cause seabird injury and mortality |
|  | **Indirect** | Reduce seabird competitors | Deplete fish |
|  |  |  | Affect seabird communities |
| **Effects of seabirds on fisheries** |  | Signal fish schools | Cause gear damages |
|  |  |  | Steal bait |
|  |  |  | Reduce catch amounts |
|  |  |  | Time loss removing bycaught animals |

Feeding in association with fisheries can lead to highly competitive interactions between seabirds due to the relatively high number of individuals attending fishing boats (e.g. Arcos et al. 2001). Interference competition, including kleptoparasitism (i.e. stealing food caught by other individuals;

Rothschild and Clay, 1952), occurs between species (inter-specific competition) and within species (intra-specific competition) due to different foraging abilities between species, sexes, and age classes (Connell 1983). Body size and foraging experience may be relevant drivers of competitive exclusion (Gause 1934, Hardin 1960). However, immature birds could feed more in association with fishing activities due to their higher opportunistic foraging behaviour compared to adults (Pettex et al. 2019). Additionally, the attendance of different age classes, sexes, species composition, and the overall size of seabird aggregations at fishing boats can change throughout the annual cycle (Louzao et al. 2011). Indeed, several factors can influence seabird-fishery dynamics, such as breeding constraints, migration, and different levels of competition experienced at each stage of the annual cycle (Arcos et al. 2001). However, our understanding of the year-round foraging ecology of seabirds is often hampered by their dispersed distribution during the non-breeding season, making them inaccessible during this period (Ramírez et al. 2015). In this context, new techniques have helped to unravel seabird ecology outside the breeding season in the past years such as stable isotope analysis (Ramos and González-Solís 2012).

## 3. Modern techniques to study seabird-fishery interactions

Seabird-fishery interactions can be investigated by changes in diet and foraging behaviour. Fisheries provide new prey items not normally available to surface-feeders and shallow-divers seabirds, such as bathypelagic and demersal species through fishery discards (Mariano-Jelicich et al. 2014). In other seabirds, their diet may experience a shift from mesopelagic prey to commercially targeted species in response to opportunistic feeding in association with fisheries (Xavier et al. 2011). Additionally, fishing activities may change foraging distribution of seabirds as they may become more attracted to fishing boats than to the open sea due to facilitated foraging opportunities (Cama et al. 2013). For pelagic specialist species, fisheries may decrease their foraging range and shift their distribution to more coastal or within colony surrounding waters (Arcos and Oro 1996). For generalist species, fisheries may increase marine fish consumption and decrease terrestrial foraging (Tyson et al. 2015). Additionally, fisheries may change seabird non-breeding foraging grounds (Ramírez et al. 2015).

Diet and foraging habitats (e.g. offshore, coastal, freshwater, terrestrial) of seabirds have been traditionally studied through prey identification from pellets and regurgitates (Barrett et al. 2007). These conventional methods provide great taxonomic detail of diet composition but suffer from some limitations. They reflect ingested prey over short timescales, thus requiring intensive sampling and identification procedures. Additionally, due to different digestibility of food, these analyses are biased towards the larger

and more conspicuous prey, underestimating soft-bodied taxa (González-Solís et al. 1997a). More recently, the use of intrinsic markers such as stable isotopes have become increasingly used to study the trophic choices and foraging habitats of marine top predators as they overcome most of the limitations associated with traditional dietary methods (Inger and Bearhop 2008). This technique provides a time integrated view on the assimilated diet at the individual and population levels and is based on the fact that stable isotope ratios in consumer tissues reflect those in prey in a predictable manner, called isotopic discrimination (i.e. the difference between consumer and prey isotopic values; Caut *et al.*, 2009). Nitrogen ($^{15}N/^{14}N$, expressed as $\delta^{15}N$) and carbon ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) stable isotopes are the most used in marine studies. Regarding $\delta^{15}N$, during digestion and assimilation of prey, isotopic concentrations change mainly due to a selective retention of the heavy isotope ($^{15}N$) and excretion of the light ($^{14}N$) in metabolic reactions (Peterson and Fry 1987). Thus, consumer tissues exhibit a stepwise enrichment in $^{15}N$ at each trophic level, and $\delta^{15}N$ measurements can be used as indicators of trophic position (Hobson 1993). In contrast, $\delta^{13}C$ values vary little along the food chain, reflecting the different photosynthetic pathways used by primary producers (Farquhar et al. 1989). Within the marine environment, $\delta^{13}C$ values may present horizontal and vertical gradients due to $^{13}C$ enrichment in inshore plants and in particulate organic matter (Graham et al. 2010). Therefore, $\delta^{13}C$ measurements can be used as indicators of food types and foraging areas (e.g. inshore *vs*. offshore, benthic *vs*. pelagic). However, for generalist seabirds that also feed on terrestrial resources, carbon isotope ratios may not be sufficient to identify their foraging habitats, as both offshore pelagic areas and terrestrial environments exhibit lower $\delta^{13}C$ values than inshore marine areas (Kelly 2000). In this regard, sulphur stable isotope ratios ($^{34}S/^{32}S$, expressed as $\delta^{34}S$) provide extra discriminatory power to distinguish foraging habitats (e.g. marine, freshwater, terrestrial; Moreno *et al.*, 2010). The period of dietary integration reflected by stable isotope values depends on the metabolic activity of the tissue sampled. Tissues that have high turnover rates, like blood plasma and liver, reflect dietary information of the past few days, while tissues with lower growth and renewal rates, such as blood cells and muscle, encompass isotopic records over several weeks (Boecklen et al. 2011). Moreover, keratinous tissues such as feathers are metabolically inert after formation, thus maintain isotopic ratios of the time of their synthesis (Hobson 1999). Hence, by sampling different tissues in one colony visit during the breeding season, it is possible to investigate the trophic and foraging ecology of seabirds during different periods of their annual cycle (Hobson and Bond 2012). The use of stable isotope analysis is thus a powerful tool to investigate seabird-fishery interactions throughout the annual cycle and has the potential to help fill some major gaps in seabird ecology such as intra-specific seabird attendance to fishing boats (Navarro et al. 2010). For instance, demersal fish species made available by fisheries tend to have higher

$\delta^{15}$N and $\delta^{13}$C and lower $\delta^{34}$S values compared to natural pelagic prey of seabirds, and fish offal is usually $^{15}$N enriched, which can be traced in seabird tissues (Navarro et al. 2009a).

## 4. The use of fishery discards by seabirds

Fishery discards are defined as the portion of the catch which is not retained on board during commercial fishing operations and is returned to the sea, often dead or dying (Kelleher 2005). They do not include post-harvest waste, such as offal, but include slipped fish, i.e. fish caught in a net and released deliberately into the sea without being brought aboard (Kelleher 2005). Slipping is typically performed in purse-seine fisheries, where total catches might be released (Borges et al. 2001), and often cause physical damage and behavioural impairments to fish (Marçalo et al. 2013). Fishermen can discard both target and non-target (i.e. bycatch) species mainly due to economic and regulatory reasons (Table 2).

**Table 2.** Main motives for discarding (based on Kelleher, 2005; Fernandes *et al.*, 2015; Gilman *et al.*, 2017).

| Categories | Motives |
|---|---|
| **Economic** | Little or no market for species/sizes/sex |
| | Highgrading (i.e. discarding lower-value catch) |
| | Damaged catch |
| | Species that can damage the rest of the catch |
| | Poisonous/spoiled |
| **Regulatory** | Exceeded quotas |
| | Minimum landing size |
| | Limits on catch composition (percentages by species) |
| | Bycatch limits |
| | Protected and unmarketable species/sexes (including seasonal bans) |
| **Other** | Insufficient space to retain all catch |

Seabirds are the most conspicuous scavengers feeding on fishery discards (Furness et al. 2007). In accordance with the "optimal foraging theory" (MacArthur and Pianka 1966, Pyke et al. 1977), opportunistic species can decrease the time and energy spent foraging by feeding on easily accessible and abundant food resources provided by fisheries (Emlen 1966). These resources can be beneficial

during the breeding season, allowing greater nest attendance and chick food provisioning, thereby increasing breeding success (Oro et al. 1995, Oro 1996a). Additionally, these resources may be important during the non-breeding season, leading to higher body condition and survival of individuals through all life-stages, i.e. adults, immatures, and juveniles (Berón et al. 2013). Indeed, increases of scavenger populations worldwide have been attributed to the exploitation of fishery discards (Sherley et al. 2020). However, in areas where discards are mainly composed of demersal fish species, they can represent lower-quality food resources for seabirds and may not compensate the depletion of natural prey (i.e. small pelagic fish) (Le Bot et al. 2019). This "junk-food hypothesis" (i.e. negative effects due to the dietary shift from high-lipid to low-lipid prey, initially suggested for sea lions Alverson, 1992) has been proposed for seabirds in several regions of the world (e.g. Grémillet *et al.*, 2008) and supported by evidences from controlled conditions in captivity (Romano et al. 2006). Additionally, different digestive efficiencies among species (e.g. generalists *vs*. piscivorous; Hilton *et al.*, 2000) could explain some inter-specific differences on the beneficial or detrimental effects of discards (Bicknell et al. 2013). Seabirds can take advantage not only of discards but also of fish offal, bait, escapes, depredation (Le Bot et al. 2018), and facilitated foraging opportunities during hauling operations (Arcos and Oro 2002a). However, during these opportunistic behaviours, seabirds can collide with fishing gears, be entangled in nets, and caught by hooks (Le Bot et al. 2018). In this context, some legislations have been applied to reduce the collateral effects of fisheries in the overall ecosystem.

**5. The discard ban policy**

To promote sustainable fisheries, the European Union (EU) implemented the Common Fishery Policy (CFP). This policy was originally created in 1970 and went through successive updates, with the most recent in 2014 (European Union 2013, 2015). The new reform of the CFP includes a landing obligation (i.e. discard ban) for all catches of species under quotas, and in the Mediterranean also to those subject to minimum size limits, which became fully implemented in 2019 (Uhlmann et al. 2019). There are a few exceptions, such as prohibited species, species with high survival rates, catches falling under *de minimis* exemptions, and organisms damaged by predators (Uhlmann et al. 2019). This policy is expected to have negative ecological consequences on scavenger seabird populations that rely on this anthropogenic food resource (Table 3). Indeed, global discard production is decreasing due to increased retention of catches and gear selectivity (Gilman et al. 2017, Zeller et al. 2018), and this has already been suggested to impact seabird populations (Sherley et al. 2020). Additionally, trawling moratoriums

have been linked to decreased breeding success (Oro et al. 1995, Oro 1996a) and to increased longline attendance and bycatch (Laneri et al. 2010, Soriano-Redondo et al. 2016). Therefore, under this discard reduction scenario, knowledge on the current dependence of seabirds on fisheries is imperative for seabird ecology, conservation, and management.

**Table 3.** Possible impacts of the European Union Landing Obligation under the new Common Fisheries Policy (based on Bicknell *et al.*, 2013).

| Categories | Possible impacts |
|---|---|
| **Negative** | Food shortage |
| | Increase of kleptoparasitism and seabird predation |
| | Increase of foraging time and energy expenditure |
| **Positive** | Reduction of bycatch (except in longline) |
| | Reduction of overabundant scavenger populations |

## 6. Case study: Gulls on the western Iberian coast

### 6.1. Study area: The western Iberian coast

The western Iberian coast is the northern limit of the Canary Current Upwelling System (Arístegui et al. 2009), one of the world's four major Eastern Boundary Currents (Canary, Benguela, California, and Humboldt). This area is characterised by strong seasonal upwelling. During spring and summer, the cost is under persistent northerly along-shore winds that produce surface Ekman transport offshore (DeCastro et al. 2008). This offshore movement is compensated by upwelling from subsurface layers that brings deep, cold, and nutrient-rich waters into the to the surface (DeCastro et al. 2008). The upwelling movements control phytoplankton (primary) production that supports this rich coastal system and important fisheries (Arístegui et al. 2009). During autumn and winter, southerly and westerly winds prevail, and poleward slope currents carrying warm and salty waters and buoyant plumes from river discharges are the main oceanographic features (Santos et al. 2007).

Sardine *Sardina pilchardus* is the dominant small pelagic fish on the western Iberian coast (Veiga-Malta et al. 2019). This species is abundant in shallow nearshore waters until depths of approximately 120 m (Gomes et al. 2001). Beyond that depth, fish assemblages shift to a higher abundance of

bathypelagic and demersal species, such as blue whiting *Micromesistius poutassou* (Fariña et al. 1997a, Gomes et al. 2001). Other species such as horse mackerel *Trachurus trachurus*, chub mackerel *Scomber colias*, and hake *Merluccius merluccius* have ubiquitous distributions, with smaller individuals in shallower waters and larger individuals in deeper waters (Sousa et al. 2005). Sardines constitute an important prey for marine predators and are a major target of pelagic fisheries, namely purse-seines (Wise et al. 2019). However, in line with other ecosystems across the globe (Cury et al. 2011), the sardine stock is declining. Sardine stock biomass decline started in the 1980s (Silva et al. 2015), but a sharp decrease occurred since 2006, now reaching less than 25% of the biomass compared to that year (ICES 2018). The sardine decline was accompanied by increases of other small pelagic fish such as horse mackerel (ICES 2018) and especially of chub mackerel (Martins et al. 2013). These changes in fish assemblages seem to be associated with climate conditions (Santos et al. 2005), species interactions (Garrido et al. 2015), and fishing pressure (Rosa et al. 2010). The ecosystem changes induced by environmental variability and anthropogenic activities have not only impacted fish stocks but also marine top predators that depend on such resources (Paiva et al. 2013a). In fact, the western Iberian coast seems to be controlled by bottom-up forces, with low trophic level groups altering the food supply for predators such as seabirds, thus affecting their population dynamics (Veiga-Malta et al. 2019).

Fishing activities and practices vary along the western Iberian coast according to site-specific species assemblages, market demand, and fishing fleet Gross Tonnage (GT) (Sousa et al. 2005, Feijó et al. 2018). Overall, Portuguese and Galician fishing fleets widely differ. The Portuguese fleet is dominated by artisanal polyvalent (67% of boats and 46% of landings) and small- to medium-scale purse-seine (14% of boats and 42% of landings) boats (INE 2019). Fishing activities are mainly coastal, and 90% of boats have less than 12 m (INE 2019). Sardines used to dominate (i.e. > 40% of landings) mainland Portuguese fishery catches (INE 2001). However, their landings have been declining in the past years due to their lower abundance and limited quotas, comprising less than 12% in 2018 (INE 2019). Chub (33%) and horse mackerels (16%) are now the most landed species in national harbours (INE 2019). The Galician fleet represents important fishing activities at the European level and is the biggest fishing fleet in Spain (Iribarren et al. 2010). Fishing boats are also mainly artisanal (89%), but most landings come from industrial boats (4%), which are mostly longlines followed by trawlers (ARDAN 2018). Additional, coastal boats (7%) are dominated by purse-seiners (50%), but they are only responsible for 22% of GT, meaning that most landings from coastal fisheries are made by trawlers (42% GT) and longliners (31% GT; ARDAN, 2018). In accordance with its higher fishing gear diversity, the Galician fleet also shows higher diversity in their most landed species compared to the Portuguese fleet. Horse mackerel (18%), hake (16%), chub

mackerel (13%), and blue whiting (11%) comprised the majority of fishery catches in 2018 (https://www.pescadegalicia.gal/). Interestingly, sardines were only approximately 1% of the total landed species. Besides spatial, intra- and inter-annual variability also occurs in fishery catches composition and quantities in response to environmental conditions and fishing quotas (Surís-Regueiro and Santiago 2014).

On the western Iberian coast seabird-fishery interactions are poorly known (but see Valeiras, 2003; Oliveira *et al.*, 2015), despite the importance of this area as a foraging ground for several breeding and non-breeding seabird species. Yellow-legged gull *Larus michahellis* and Cory's shearwater *Calonectris borealis* breed in relatively high numbers at Berlenga archipelago and are especially abundant in western Iberian waters during the breeding season, while Northern gannet *Morus bassanus* and Balearic shearwater *Puffinus mauretanicus* are among the most common non-breeding seabird species foraging in this area (Meirinho et al. 2014). Additionally, the Audouin's gull *Larus audouinii* is especially abundant in south Portuguese waters (Mendes et al. 2018).

## 6.2. Study species: yellow-legged and Audouin's gulls

Gulls are among the seabird species with greater opportunistic foraging behaviour (Méndez et al. 2020). They can forage on both marine and terrestrial environments (Garthe et al. 2016), although fish is considered their main natural prey due to its high energy content (Elliott and Gaston 2008). Gulls are surface feeders and do not have diving capabilities (Gwiazda 2004). Thus, natural foraging in the marine environment involves preying on epipelagic prey or associations with sub-surface predators (Oro 1995). By having generalist feeding strategies, at least at the populational level, their diet reflects the availability of local food resources (Duhem et al. 2003). Gulls can feed on a wide range of prey, including anthropogenic food resources such as fishery discards from fisheries and refuse from landfills (Gotmark 1984). Indeed, most species exploit fishery discards, and this has been associated with gull population increases worldwide (Sherley et al. 2020).

The yellow-legged gull, whose breeding range extends from the Azores to the western Black Sea (BirdLife International 2020a), is the most abundant breeding seabird in western Iberian coastal waters, breeding in several locations along the coast (Meirinho et al. 2014). Most of the population is resident, although some individuals might disperse to northern Atlantic coastal waters or to the northwestern African coast during the winter (Meirinho et al. 2014). Similarly to other large gull species, its global

population growth over the last century is associated with the exploitation of anthropogenic food resources (Real et al. 2017). In the Mediterranean, yellow-legged gulls at Spanish colonies feed extensively on fishery waste produced by the intense trawling activity in that area (Oro et al. 1995). However, in the French Mediterranean area, due to the large number of landfills and limited fishing activities, refuse is their main food resource (Duhem et al. 2007). On the Atlantic Iberian coast, yellow-legged gulls feed mainly at sea (Munilla 1997, Moreno et al. 2010, Arizaga et al. 2011, Ceia et al. 2014, Mendes et al. 2018) and likely in association with fisheries (Alonso et al. 2015, Matos et al. 2018). Additionally, their diet composition and diversity show spatial and temporal variability according to the availability of their main prey and the presence of alternative food resources (Ramos et al. 2009b).

The Audouin's gull is endemic to the Mediterranean region (BirdLife International 2020b). Most individuals migrate to the northwestern African coast; however, some might remain close to breeding colonies during the winter (De Juana et al. 1987, Oro and Martinez 1994, Bécares et al. 2016). During the 1970s it was one of most endangered seabird species in the world, with less than 1,000 breeding pairs (Witt 1977). However, in the 2000s new colonies were established (Payo-Payo et al. 2017) and now the population is estimated over 23,000 breeding pairs (ICES 2008). Its population growth is attributed to the use of fishery discards, likely increasing their breeding success (Oro et al. 2014). In south Portugal, a colony establishment by a few individuals was first recorded in the early 2000s (Leal and Lecoq 2006, Gutiérrez and Guinart 2008), reaching more than 2,900 breeding pairs in 2018 (personal observation). Although specialized in marine fish, their diet can also contain crustaceans and insects in small proportions. However, in the Ebro Delta, Spain, the abundant and invasive American crayfish *Procambarus clarkii* from rice fields can be important in the diet of Audouin's gull (Navarro et al. 2010), especially in periods of lower discard availability (Bécares et al. 2015, García-Tarrasón et al. 2015).

Although several studies on the diet of both gull species have been conducted in the Mediterranean (e.g. Witt *et al.*, 1981; González-Solís *et al.*, 1997b), dietary studies on the Atlantic Iberian coast are scarce, only with some information on yellow-legged gulls breeding at Berlenga Island (Ceia et al. 2014, Alonso et al. 2015) and at Galicia (Munilla 1997, Moreno et al. 2010). Recently, during the course of this thesis, two more studies were published on this thematic regarding yellow-legged gulls breeding at Berlenga Island (Mendes et al. 2018) and both gull species breeding at Deserta Island (Matos et al. 2018). However, most studies were limited to the breeding season and restricted to single colonies, disregarding the fact that gull feeding strategies can vary spatially and temporally in response to local fishing activities, environmental conditions, and different levels of competition. Overall, previous studies

were based mainly on traditional methods such as prey identification from hard remains on pellets and chick regurgitates (e.g. González-Solís *et al.*, 1997a; López *et al.*, 2016). The attendance of yellow-legged gulls at fishing vessels were previously recorded in the Mediterranean (Oro and Ruiz 1997) and in the Atlantic Iberian coast (Oliveira et al. 2015). Regarding Audouin's gull, this behaviour was also registered in the Mediterranean (Oro and Ruiz 1997). Recently, Matos *et al.*, (2018) recorded an influence of fishing activities in diet composition and foraging behaviour of both gull species at Deserta Island. Yellow legged gulls increased terrestrial foraging and Audouin's gulls increased pelagic fish consumption (Matos et al. 2018). However, differences in foraging and competitive abilities between sexes and age classes are likely to lead to intra-specific differences in feeding behaviour, including discard-feeding behaviour (García-Tarrasón et al. 2015), and should be investigated in the western Iberian coast. In view of the new EU discard ban scenario, understanding the importance of fish in gull diet and the possible association of foraging gulls with fisheries at large spatio-temporal scales is crucial to assess its ecological implications at both population and individual levels.

**Thesis Outline and Objectives**

The main goal of this thesis was to assess the importance of fisheries in the trophic and foraging ecology of gulls on the western Iberian coast. By using several techniques such as diet identification, stable isotope analysis, biochemical parameters, and onboard observations this work provides an integrative approach to examine the opportunistic feeding behaviour of gulls in association with fisheries across several spatio-temporal scales and at both inter- and intra-population levels. The results of this thesis contribute to the better understanding of the feeding ecology and behaviour of yellow-legged and Audouin's gulls and to the evaluation of the possible ecological impacts of the EU discard ban policy. Thus, this work can help conservation and management strategies to apply adequate ecosystem-based measures.

To achieve the proposed main goal, the following specific objectives were pursued:

**1.** Compare the year-round feeding ecology (using dietary and stable isotope analyses) between yellow-legged and Audouin's gulls breeding in sympatry during two consecutive years and their use of fishery discards. (Chapter 1. Seasonal and annual differences in the foraging ecology of two gull species breeding in sympatry and their use of fishery discards)

**2.** Investigate the year-round sex-specific feeding ecology (using stable isotope analysis) of yellow-legged gulls on four islands along the western Iberian coast. (Chapter 2. Stable isotopes reveal year-round sexual trophic segregation in four yellow-legged gull colonies)

**3.** Use the Peniche fishing fleet as a case study to compare gear-specific seabird- and particularly gull- fishery interactions and bycatch during three consecutive years. (Chapter 3. Seabird-fishery interactions and bycatch at multiple gears in the Atlantic Iberian coast)

**4.** Investigate the consumption of fish by gulls across multiple colonies (for yellow-legged gull), years, and seasons (for yellow-legged and Audouin's gulls) and the influence of fisheries on their feeding ecology (using dietary, stable isotope, and biochemical analyses). (Chapter 4. Influence of fisheries on the spatio-temporal feeding ecology of gulls along the western Iberian coast)

**5.** Assess the effect of long-term changes in fishery landings and environmental conditions on the diet of the yellow-legged gull on the northwest Iberian coast, over the last 30 years (1987–2017). (Chapter 5. Anthropogenic food resources, sardine decline and environmental conditions have triggered a dietary shift of an opportunistic seabird over the last 30 years on the northwest coast of Spain)

These objectives were developed in five chapters and presented as independent scientific articles with its own introduction, methods, results, and discussion.

**CHAPTER 1.**

JG Calado, DM Matos, JA Ramos, F Moniz, FR Ceia, JP Granadeiro, VH Paiva. Seasonal and annual differences in the foraging ecology of two gull species breeding in sympatry and their use of fishery discards. Journal of Avian Biology, 49: 1-12.

**Seasonal and annual differences in the foraging ecology of two gull species breeding in sympatry and their use of fishery discards**

**Abstract.** Niche segregation between similar species will result from an avoidance of competition but also from environmental variability, including nowadays anthropogenic activities. Gulls are among the seabirds with greater behavioural plasticity, being highly opportunistic and feeding on a wide range of prey, mostly from anthropogenic origin. Here, we analysed blood and feather stable isotopes combined with pellet analysis to investigate niche partitioning between Audouin's gull *Larus audouinii* and yellow-legged gull *Larus michahellis* breeding in sympatry at Deserta Island, southern Portugal, during 2014 and 2015. During the breeding season there was considerable overlap in the adults' diet, as their stable isotope values of blood and primary feather (P1) did not differ, and their pellets were comprised mainly by marine fish species. However, Audouin's gulls presented higher occurrences of pelagic fish, while yellow-legged gulls fed more on demersal fish, insects, and refuse. SIAR mixing models also estimated a higher proportion of demersal fish in the diet of yellow-legged gulls. We also found differences between the two gull species in chicks' feathers, suggesting that Audouin's gull adults selected prey with lower carbon isotope values to feed their young. Secondary feather (S8) of Audouin's gull presented higher isotope values compared to yellow-legged gulls, indicating different foraging areas ($\delta^{13}$C) and/ or trophic levels ($\delta^{15}$N) between the two species in the non-breeding season. During both the all-year and non-breeding periods the yellow-legged gull showed a broader isotopic niche width than Audouin's gull in 2013, and in 2014 the two gull species exhibited different isotopic niche spaces. Our study suggests that both gull species foraged in association with fisheries during the breeding season. In this sense, a discard ban implemented under the new European Union Common Fisheries Policy may lead to a food shortage, therefore future research should closely monitor the population dynamics of Audouin's and yellow-legged gulls.

**Keywords:** niche partitioning; isotopic ecology; diet composition; fishery discards; *Larus michahellis*; *Larus audouinii*.

# 1. Introduction

Competition can be one of the major processes structuring avian communities, in particular among sympatric seabird species (Schreiber and Burger 2002b, Oro et al. 2009, Moreno et al. 2016). The degree of segregation among species may change seasonally due to the different constraints

experienced throughout the annual cycle (Navarro et al. 2009b, Azorit et al. 2012). However, most studies have focussed on the breeding season, when seabirds are present in discrete colonies and, therefore, easily accessible (e.g. Navarro et al. 2013, Afán et al. 2014). Comparatively less is known about their feeding ecology during the non-breeding period, when they can exploit different foraging areas and trophic resources. Therefore, studies focusing the entire annual cycle of seabirds are needed. Moreover, studies on seabirds feeding in association with anthropogenic activities are particularly important because such resources may be superabundant and predictable both in time and space (Ramos et al. 2009a, Kai et al. 2013), as well as lead to highly competitive feeding interactions (Martínez-Abraín et al. 2002, Sotillo et al. 2014). Nonetheless, a lack of partitioning and competition may arise from a superabundance of resources, allowing a large overlap in trophic niches between species (Vieira and Port 2007, Mancini and Bugoni 2014).

Gull diets have been studied mainly through analysis of pellets and regurgitates, which provide great taxonomic detail of prey items (González-Solís et al. 1997a). However, these traditional methods suffer from several limitations, namely the short time-scale of dietary integration, are usually restricted to the breeding season, and biased towards the larger and more conspicuous prey (Votier et al. 2003, Barrett et al. 2007). More recently, stable isotopes have been used to study the feeding ecology of marine top predators, providing an integrative view on assimilated diets (Forero and Hobson 2003, Ramos and González-Solís 2012). They can also be used to examine the diet of chicks with minimal detrimental effects (Ramos et al. 2009b, Cherel et al. 2014). In marine environments, consumers' tissues exhibit a stepwise enrichment of +2.0 – +5.0 ‰ in $^{15}$N at each trophic level. Thus, stable isotope of nitrogen can be used as a proxy of trophic position (Hobson et al. 1994, Hodum and Hobson 2000). Carbon stable isotope values ($\delta^{13}$C) change less than +1.0 ‰ per trophic level (Kelly 2000, Inger and Bearhop 2008), reflecting the source of carbon at the base of the food web. Therefore, carbon stable isotope values can be used to identify foraging habitats (Paiva et al. 2010, Ramírez et al. 2012). The period of dietary integration depends on the metabolic activity of the tissue sampled (Hobson 1999). Hence, by sampling tissues with different turnover rates, it is possible to assess the feeding ecology of consumers during different periods of their annual cycle (Cherel et al. 2008, Ceia et al. 2014). Furthermore, stable isotopes can be used to investigate niche segregation between species, using the isotopic variation of the animal tissues to calculate their isotopic niche width and overlap (Newsome et al. 2007). Overall, stable isotope analysis (SIA) is a powerful tool to unravel niche partitioning among sympatric taxa (Bocher et al. 2000, Barger et al. 2016, Delord et al. 2016), particularly when combined with traditional dietary techniques (Mancini and Bugoni 2014, Ronconi et al. 2014).

Here, we analysed blood and feather stable isotopes combined with traditional pellet analysis to investigate niche partitioning between Audouin's gull *Larus audouinii* and yellow-legged gull *Larus michahellis* breeding in sympatry at Deserta Island in Ria Formosa lacunar system, southern Portugal, during two consecutive years (2014 – 2015). Both populations were established recently, probably as the result of recruitment from nearby colonies and abundance of fishery discards. The yellow-legged gull is a large-sized (average body mass, 800 – 1200 g) and generalist species with a plastic foraging behaviour (Moreno et al. 2010, Arizaga et al. 2014). This species feeds opportunistically on fishery discards and refuse tips from anthropogenic activities (Duhem et al. 2008, Cama et al. 2012). The Audouin's gull is a medium-sized gull (500 – 700 g) endemic to the Mediterranean region (BirdLife International 2020b), regarded as specialist on epipelagic fish (Pedrocchi et al. 1996, Arcos and Oro 2002a). Nevertheless, their recent population increase has been attributed to the use of fishery discards (Oro and Ruxton 2001, Mañosa et al. 2004, Christel et al. 2012). Although these two gull species breed sympatrically in several Mediterranean colonies, very few studies investigated their trophic segregation (but see González-Solís *et al.*, 1997b; González-Solís, 2003). These species are of special interest to investigate niche segregation because they are closely related taxa, natural competitors, belong to the same trophic guild, have shown a great dependence on anthropogenic activities (i.e. fisheries), and both populations are increasing in numbers and expanding their geographical ranges. Specifically, we assessed and compared the diet composition of the two species, their trophic level ($\delta^{15}N$), foraging habitats ($\delta^{13}C$) and isotopic niche space. Given the presence of intense fishing activities near the colonies, fish was expected to be the main prey for both gull species, however, we predict Audouin's gulls to feed more on natural epipelagic fish. On the other hand, we expect yellow-legged gulls to have a more opportunistic and generalist diet, feeding on locally abundant and easily caught prey, such as demersal fish discarded from local fisheries and some tips from refuse dumps. Concerning trophic ecology, Audouin's gull was predicted to feed on prey at lower trophic levels (i.e. epipelagic fish), compared to yellow-legged gull, which was expected to feed more on demersal fish from fishery discards that typically occupy higher trophic levels (Navarro et al. 2010). Regarding foraging habitat, Audouin's gull was predicted to forage more in the marine environment and more offshore than yellow-legged gull, which was expected to forage in coastal areas and also inland, especially during the non-breeding season (Ramos et al. 2011). Consequently, we expect a broader isotopic niche for yellow-legged gulls. Overall, we expect a higher niche overlap between the two species during the breeding season, when breeding adults become central-place foragers.

## 2. Methods

### 2.1. Study area

The study was carried out in southern Portugal, at Deserta Island (36° 98′ N, 7° 54′ W; Figure 1.1), during the breeding seasons (April – June) of 2014 and 2015. The island has about 7 km long and lies about 5.5 km from mainland, hosting an estimate of 1200 and 900 breeding pairs of Audouin's and yellow-legged gulls, respectively, with both populations increasing on average ca. 300 pairs per year since 2014 (author's unpubl. data). It belongs to Ria Formosa Natural Park and it is one of the five barrier islands (and two peninsulas) that form a narrow strip of dunes that separates the lagoon from the Atlantic Ocean (Ceia et al. 2010). This area is characterized by high fishing activity (INE 2015), and the inlet separating Deserta and Culatra Islands was artificially stabilized to ensure the navigability of the fishing boats to the main local fishing harbour (Olhão).
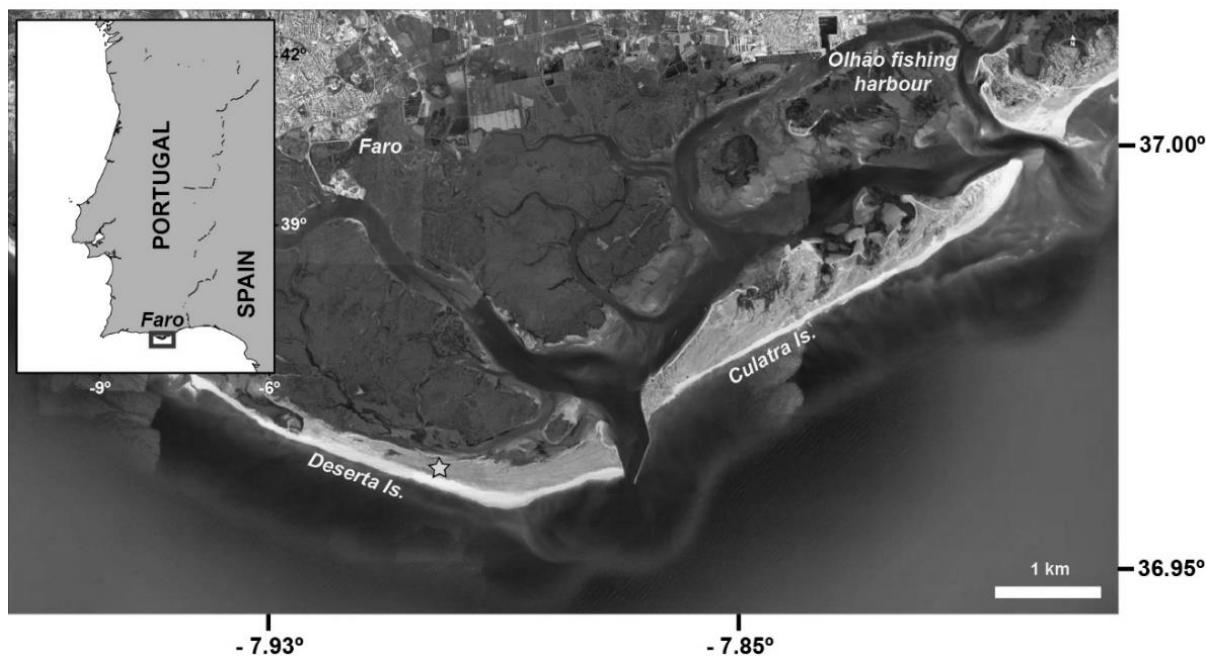


**Figure 1.1.** Southern Portugal, indicating the breeding colony (star), the inlet separating Deserta and Culatra Islands, and the Olhão fishing harbour.

### 2.2. Sample collection

A total of 525 pellets were collected weekly around the nests during the breeding seasons of 2014 (Audouin's gull: n = 186, yellow-legged gull: n = 128) and 2015 (Audouin's gull: n = 107, yellow-

legged gull: n = 104). Regurgitates were also collected in 2014 from birds that regurgitated spontaneously when handled, and the best preserved prey samples were used to create stable isotope mixing models (see Stable isotope analysis). The samples were placed in plastic bags and stored frozen until laboratory analysis.

Breeding adults were caught during late incubation (early May) with nest traps (Audouin's gull: n = 12, yellow-legged gull: n = 9 in 2014; and Audouin's gull: n = 15, yellow-legged gull: n = 12 in 2015). Blood samples (0.5 – 1.0 ml) were collected from the tarsal vein using 27-G needles and centrifuged within 3 – 5 hours to separate red blood cells (RBC) from plasma. RBC comprises dietary information from the previous 3 – 4 weeks until sampling (Bearhop et al. 2006), while plasma has a much faster turnover rate (about 7 days; Cherel et al. 2005a). Thus, these tissues represent the dietary input during the laying and incubation periods, respectively. Samples were then frozen until stable isotope analysis. We also collected feathers, which are metabolic inert after formation, therefore integrate isotope ratios during the time of synthesis and maintain the isotopic record almost indefinitely (Hobson 1999, Blight et al. 2014). We sampled four breast feathers (Br), the tips of the innermost primary (i.e. first primary, P1) and eighth secondary (S8) feathers from adults, which were stored in labelled sealed plastic bags. Since breast feathers are moulted more or less continuously throughout the year, we assumed they represent the year-round diet of birds (Dwight 1901, Pedro et al. 2013). On the other hand, moulting patterns of wing feathers are constant and predictable: P1 is replaced in the end of the breeding season and S8 in the middle of the non-breeding period, therefore isotope values of P1 and S8 represent dietary inputs during the previous breeding and non-breeding periods, respectively (Ramos et al. 2011). During the chick-rearing period we also collected 3 – 4 growing mantle feathers from chicks (Audouin's gull: n = 17, yellow-legged gull: n = 16 in 2014; and Audouin's gull: n = 15, yellow-legged gull: n = 15 in 2015).


**2.3. Diet analysis**

Pellets were examined using a stereomicroscope and prey items were identified to the lowest possible taxonomic level. Fish prey were identified using a reference collection of vertebrae and otoliths, and a published otolith guide (Tuset et al. 2008). Prey items from regurgitates were also identified and the best preserved were selected and prepared for SIA.

## 2.4. Stable isotope analysis (SIA)

In the laboratory, plasma and prey samples (fish muscle) were thawed and lipids were extracted with successive rinses of a 2 chloroform: 1 methanol solution (Cherel et al. 2005b). The C/N mass ratio for fish was $3.05 \pm 0.08$, indicating that the lipid extraction was efficient. The C/N mass ratio for Audouin's gull plasma collected in 2014 and 2015 was $3.36 \pm 0.21$ and for yellow-legged gull plasma was $3.31 \pm 0.16$. The lipid content of RBC is low (C/N ratio less than 3.5) and therefore does not require lipid extraction (Cherel et al. 2005a). Feathers were cleaned of surface lipids and contaminants also using a 2 chloroform: 1 methanol solution, and cut with stainless steel scissors into small fragments. All tissue samples were dried in an oven for at least 48 h at 50 °C to a constant mass and homogenized. Sub-samples of approximately 0.35 mg were weighed in a microbalance, placed in a tin cup, and crimped for combustion. Isotopic ratios of carbon and nitrogen were determined by continuous-flow isotope ratio mass spectrometry (CF-IRMS). Results are expressed in the usual $\delta$ notation as parts per thousand (‰) deviation from the international standards Vienna-PeeDee Belemnite (V-PDB) for $\delta^{13}C$ and atmospheric nitrogen ($N_2$) for $\delta^{15}N$, according to the following equation: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/ R_{standard}) - 1]$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate precision < 0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$. Stable isotope ratios are reported according to Bond and Hobson (2012).

## 2.5. Data analysis

We calculated numeric percentage (NP) as percentage of the number of individuals of each prey type in relation to the total number of individuals, and percentage of occurrence (PO) as the percentage of pellets with a certain prey type (Alonso et al. 2013), for each gull species in each year. To compare the occurrence of pelagic fish, demersal fish, refuse, and gulls' main prey (PO > 5%: *Diplodus* spp., *Micromesistius poutassou*, *Sardina pilchardus*, *Scomber* sp., *Scomberesox saurus*, *Trachurus* sp., and insects) between the two gull species, years, and their interaction, we performed generalised linear models (GLM) with a binomial distribution.

To analyse $\delta^{13}C$ and $\delta^{15}N$ values, GLM were run for each tissue type: feathers (P1 and S8) and blood (RBC and plasma), with isotope values as the dependent variable and gull species, year, and period as factors. Breast feathers were not used in the GLM because they represent both the breeding and non-breeding seasons; however they were kept in the SIBER (Stable Isotope Bayesian Ellipses in R; Jackson

et al. 2011) analysis to compare their annual isotopic niche space. The same was done for chick feathers, using gull species and year as factors. We used year as factor, and test for the significance of the interaction species*year because both fishery landings (Table S1.1) and environmental conditions (reflected in the extended winter North Atlantic Oscillation index; 2013: -1.97; 2014: +3.10), showed inter-annual variations.

We adopted the Bayesian stable isotope mixing model SIAR (Stable Isotope Analysis in R; Parnell et al. 2010) to estimate the relative proportions of each prey group (i.e. sources) in the diet of each gull species. Using the samples regurgitated by gulls, we created two dietary sources: pelagic fish ($\delta^{15}$N: +10.26 ± 0.58, $\delta^{13}$C: −18.20 ± 0.80, n = 26; *Ammodytes* sp., *Belone belone*, *Sardina pilchardus*, *Scomber* sp., *Trachurus* sp.) and demersal fish ($\delta^{15}$N: +11.06 ± 0.56, $\delta^{13}$C: −17.29 ± 0.34, n = 8; *Boops boops*, *Conger conger*, and *Diplodus* spp.; see average values of each fish species in Table S1.2), by grouping ecologically similar species and removing the outliers (mean ± 1.5 SD; pelagic: $\delta^{15}$N: +7.22, +8.36, +8.53; $\delta^{13}$C: −20.9, −20.49, −20.44, −20.42, −16.79; demersal: $\delta^{15}$N: +13.09; $\delta^{13}$C: −18.29, −16.17). Outliers were evident in boxplots while performing data exploration and corresponded to those values out of the range set by mean ±1.5 SD. Thus, we obtained two different ecological prey groups that also differed statistically in their isotope values (MANOVA, Wilk's lambda, $F_{1,32}$ = 7.32, $P$ = 0.002), both in $\delta^{15}$N (one-way ANOVA, $F_{1,32}$ = 11.72, $P$ = 0.002) and $\delta^{13}$C ($F_{1,32}$ = 9.70, $P$ = 0.004), as recommended by Phillips et al. (2005, 2014). Moreover, this method allowed us to estimate the consumption of demersal fish, which can only be accessible to gulls through fishery discards. The discrimination factors applied in the model were +2.85 and +0.30 ‰ for $\delta^{15}$N and $\delta^{13}$C, respectively. These are average values of whole blood obtained from controlled experiments with four seabird species available in literature (Hobson and Clark 1992, Bearhop et al. 2002, Cherel et al. 2005b), which were previously used in isotopic mixing models with yellow-legged gulls (Ceia et al. 2014) and are similar to the values obtained for "birds" from a meta-analysis (Caut et al. 2009). We used a standard deviation of ±1.0 ‰ to account for potential differences in discrimination factors among species and tissues.

To compare isotopic niches between the two gull species, we applied the isotope values of each tissue in SIBER analysis. We calculated the area of the standard ellipse corrected for sample size (SEA$_c$) for each species (which represent their isotopic niche width), the niches overlap, and a Bayesian estimate of the standard ellipse area (SEA$_B$) to test for differences in niche widths.

All analyses were performed with R software v. 3.2.0 (R Core Team 2019) with a significance level of $P$ < 0.05.

# 3. Results

## 3.1. Diet during breeding: pellets and SIAR mixing models

We identified a total of 1758 items in gull pellets. Fish was the main prey type for both gull species, and we identified a total of 36 fish species (Table 1.1). However, the two gull species differed in fish consumption, with 100% of occurrence in Audouin's gull pellets in both years and 88.3% in 2014 and 74.0% in 2015 for yellow-legged gull. This difference was even more marked in their numeric percentages (Audouin's gull: n = 92.0%, yellow-legged gull: n = 56.0% in 2014; and Audouin's gull: n = 87.0%, yellow-legged gull: n = 55.6% in 2015).

The GLM revealed that the yellow-legged gull consumed significantly more *Micromesistius poutassou*, *Trachurus* sp., insects and refuse, whereas Audouin's gull showed a significantly higher occurrence of *Scomberosox saurus* and pelagic fish ($F_{1,524} > 4.44$, $P < 0.04$; Table S1.3). We also found higher occurrences of *M. poutassou*, insects and refuse in 2015 compared to 2014 ($F_{1,524} > 7.51$, $P < 0.01$). There was also significantly lower occurrence of *M. poutassou* in the pellets of Audouin's gull collected in 2014 compared to all other samples ($F_{1,524} = 4.45$, $P = 0.03$).

SIAR mixing models estimated a higher proportion of demersal fish in the diet of yellow-legged gulls compared to Audouin's gulls, in both 2014 (modal values: yellow-legged gull = 44.2%, Audouin's gull = 19.7%) and 2015 (yellow-legged gull = 43.2%, Audouin's gull = 15.2%; Figure 1.2).

**Table 1.1.** Percentage of occurrence (PO, %) and numeric percentage (NP, %) of all items found in Audouin's (AG; *Larus audouinii*) and yellow-legged (YLG; *L. michahellis*) gull pellets collected in 2014 and 2015 breeding seasons.

| | PO | | | | NP | | | |
|---|---|---|---|---|---|---|---|---|
| | 2014 | | 2015 | | 2014 | | 2015 | |
| Prey | AG (n=186) | YLG (n=128) | AG (n=107) | YLG (n=104) | AG (n=449) | YLG (n=441) | AG (n=415) | YLG (n=453) |
| Pelagic fish | 86.6 | 68.0 | 87.9 | 57.1 | 67.7 | 32.0 | 58.3 | 33.1 |
| *Atherina* sp. | 0.5 | | | | 0.2 | | | |
| *Belone belone* | 7.5 | 0.8 | 6.5 | 1.9 | 3.3 | 0.2 | 1.9 | 0.4 |
| *Engraulis encrasicolus* | 0.5 | | 1.9 | 1.0 | 0.2 | | 0.5 | 0.2 |
| *Gadiculus argenteus* | 2.2 | 0.8 | 9.3 | 3.8 | 1.1 | 0.2 | 3.4 | 0.9 |
| *Liza aurata* | | 0.8 | | | | 0.2 | | |
| *Micromesistius poutassou* | 7.5 | 18.0 | 23.4 | 23.1 | 4.0 | 6.6 | 9.9 | 11.5 |
| *Myctophum* sp. | 8.6 | 1.6 | 2.8 | 2.9 | 7.6 | 0.5 | 0.7 | 2.4 |
| *Sardina pilchardus* | 24.7 | 25.8 | 21.5 | 18.3 | 12.7 | 9.5 | 7.2 | 7.5 |
| *Scomber* sp. | 16.1 | 19.5 | 13.1 | 20.2 | 7.1 | 5.9 | 3.4 | 4.9 |
| *Scomberesox saurus* | 51.1 | 7.0 | 45.8 | 5.8 | 29.0 | 2.3 | 28.9 | 2.9 |
| *Trachurus* sp. | 5.9 | 18.0 | 9.3 | 10.6 | 2.4 | 6.3 | 2.4 | 2.4 |
| Demersal fish | 31.7 | 41.4 | 45.8 | 41.0 | 17.6 | 16.3 | 19.5 | 14.6 |
| *Argyrosomus regius* | | 0.8 | | | | 0.2 | | |
| *Arnoglossus laterna* | | | | 1.9 | | | | 0.7 |
| *Boops boops* | 4.3 | 9.4 | 6.5 | 2.9 | 2.0 | 2.9 | 1.7 | 0.7 |
| *Capros aper* | | 1.6 | 1.9 | | | 0.5 | 0.5 | |
| *Cepola macrophthalma* | | 1.6 | 0.9 | | | 0.5 | 0.2 | |
| *Citharus linguatula* | | | | 1.9 | | | | 0.4 |
| *Chelon labrosus* | | 1.6 | | 2.9 | | 0.5 | | 0.7 |
| *Coelorinchus caelorinchus* | 4.3 | 2.3 | 4.7 | 2.9 | 3.8 | 0.9 | 4.1 | 0.9 |
| *Conger conger* | 0.5 | 3.1 | 5.6 | 1.0 | 0.2 | 0.9 | 1.4 | 0.2 |
| *Dicentrarchus labrax* | | | | 1.0 | | | | 0.2 |
| *Diplodus* sp. | 19.9 | 14.1 | 19.6 | 18.3 | 8.7 | 4.1 | 5.5 | 4.4 |
| *Echiichtys vipera* | | | | 1.9 | | | | 0.7 |
| *Gobius* sp. | | | 3.7 | 1.9 | | | 1.0 | 0.4 |
| *Halobatrachus didactylus* | | 0.8 | 0.9 | | | 0.2 | 0.2 | |
| *Lithognathus mormyrus* | | 0.8 | 1.9 | 2.9 | | 0.2 | 0.5 | 0.7 |
| *Macroramphosus scolopax* | | 2.3 | | 1.0 | | 1.4 | | 0.2 |
| *Merluccius merluccius* | 2.7 | 7.0 | 2.8 | 6.7 | 1.3 | 2.3 | 0.7 | 1.8 |
| *Microchirus variegatus* | 0.5 | 1.6 | | | 0.2 | 0.5 | | |
| *Mullus surmuletus* | | | | 1.0 | | | | 0.2 |
| *Pagrus* sp. | 0.5 | | | 1.9 | 0.2 | | | 0.4 |
| *Phycis blennoides* | | | | 2.9 | | | | 0.7 |
| *Pomatoschistus* sp. | | 0.8 | | | | 0.2 | | |
| *Scorpaena* sp. | | 1.6 | | | | 0.5 | | |
| *Serranus* sp. | 2.7 | 2.3 | 13.1 | 4.8 | 1.1 | 0.9 | 3.6 | 1.3 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Zeus faber* | | | | 1.9 | | | | 0.4 |
| Unidentified fish | 16.1 | 25.0 | 33.6 | 30.8 | 6.7 | 7.7 | 8.7 | 7.1 |
| Total fish | 100.0 | 88.3 | 100.0 | 74.0 | 92.0 | 56.2 | 87.0 | 55.6 |
| Others | | | | | | | | |
|   Birds | | 0.8 | | 6.7 | | 0.2 | | 1.5 |
|   Brachyura | 3.8 | 9.4 | 5.6 | 1.9 | 1.8 | 4.3 | 1.7 | 0.4 |
|   Cephalopoda | 3.8 | 4.7 | 0.9 | 1.0 | 1.6 | 2.0 | 0.2 | 0.2 |
|   Insects | 8.1 | 10.9 | 21.5 | 35.6 | 4.2 | 23.8 | 9.2 | 29.6 |
|   Mollusca | | 2.3 | 0.9 | 9.6 | | 0.7 | 0.2 | 2.2 |
|   *Rattus rattus* | | 1.6 | | | | 0.5 | | |
|   Refuse | 0.5 | 15.6 | 1.9 | 29.8 | 0.2 | 8.4 | 0.5 | 6.8 |
|   Vegetal remains | | 11.7 | | 12.5 | | 3.6 | | 2.9 |
|   Unidentified | 0.5 | 1.6 | 4.7 | 2.9 | 0.2 | 0.5 | 1.2 | 0.7 |
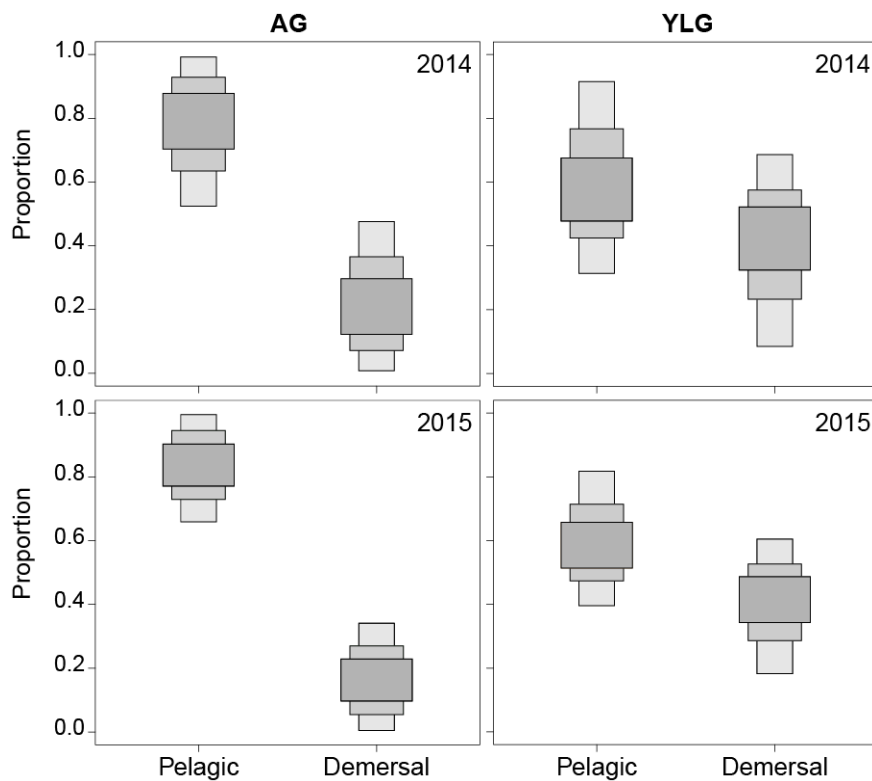


**Figure 1.2.** Estimated proportions of the two main prey groups (pelagic and demersal fish) in the diet of Audouin's (AG; *Larus audouinii*) and yellow-legged (YLG; *L. michahellis*) gulls in 2014 (AG: n = 12, YLG: n = 9) and 2015 (AG: n = 15, YLG: n = 12), based on $\delta^{13}$C and $\delta^{15}$N values of plasma. Decreasing bar widths represent 50, 75 and 95% Bayesian credibility intervals computed by SIAR (Stable Isotope Analysis in R; Parnell et al. 2010)

## 3.2. Isotope values and niche width

Stable isotope analysis revealed differences between the two gull species (Table 1.2). Blood isotope values revealed that yellow-legged gulls presented significant higher carbon and nitrogen isotope values in plasma, reflecting the incubation period, compared to RBC (laying period) and to Audouin's gulls in both periods (Table 1.3). Overall, both species presented higher carbon isotope values during the laying and incubation periods in 2014 than 2015, while both species showed higher nitrogen isotope values during incubation compared to the laying period. Adults also differed in their feather carbon and nitrogen isotope ratios, with significantly higher values in Audouin's gull eight secondary feathers (S8), which reflect the non-breeding season, compared to first primary feathers (P1) that reflect the breeding season, and to yellow-legged gulls during both seasons.

Chicks also differed in their carbon and nitrogen isotopes, with lower carbon isotope values in Audouin's gulls compared to yellow-legged gulls, and lower carbon and nitrogen isotope values in 2014 compared to 2015. There was also a significant effect of the interaction species*year, with Audouin's gull chicks having lower carbon and nitrogen isotope values in 2014 (Table 1.3).

SIBER analysis (Figure 1.3, Table S1.4) revealed differences in the isotopic niche between the two gull species during both the all-year (reflected in Br feathers) and non-breeding (reflected in S8 feathers) periods: in 2013, Audouin's gulls had significantly smaller isotopic niche widths compared to yellow-legged gulls (SEA$_B$, $P < 0.004$), and in 2014 the two species exhibited different isotopic niches (Figure 1.3, Table S1.5). Regarding the isotope values of chick feathers, SIBER revealed that in 2014 the Audouin's gull isotopic niche space differed from the other groups.

**Table 1.2.** Stable isotope ratios of carbon ($\delta^{13}$C, ‰) and nitrogen ($\delta^{15}$N, ‰) in breast (Br), first primary (P1), eight secondary (S8) feathers, red blood cells (RBC), and plasma of adults, and in chick feathers of Audouin's (AG; *Larus audouinii*) and yellow-legged (YLG; *L. michahellis*) gulls sampled in 2014 and 2015 breeding seasons. Adult feathers reflect dietary inputs from the year previous to the sampling. Values are mean ± SD, with sample size in parenthesis.

| | | $\delta^{13}$C | | | | | | $\delta^{15}$N | | | | | |
| | | 2013 | | 2014 | | 2015 | | 2013 | | 2014 | | 2015 | |
| Tissue | Period | AG | YLG | AG | YLG | AG | YLG | AG | YLG | AG | YLG | AG | YLG |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Br | All-year | −16.0 ± 0.5 (12) | −17.0 ± 1.7 (9) | −15.3 ± 1.0 (15) | −17.1 ± 0.7 (12) | | | +13.8 ± 0.7 (12) | +14.7 ± 1.9 (9) | +14.0 ± 0.7 (15) | +13.8 ± 0.8 (12) | | |
| P1 | Breeding | −16.6 ± 0.5 (12) | −16.1 ± 0.4 (9) | −16.8 ± 1.0 (15) | −16.1 ± 0.4 (12) | | | +13.3 ± 0.6 (12) | +13.8 ± 0.5 (9) | +13.7 ± 0.5 (15) | +14.1 ± 0.7 (12) | | |
| S8 | Non-breeding | −15.9 ± 0.2 (12) | −16.4 ± 0.8 (9) | −15.8 ± 0.6 (15) | −16.9 ± 0.6 (12) | | | +14.2 ± 0.5 (12) | +13.8 ± 1.1 (9) | +14.1 ± 1.0 (15) | +13.7 ± 1.0 (12) | | |
| RBC | Laying | | | −18.0 ± 0.5 (12) | −18.3 ± 0.5 (9) | −18.2 ± 0.3 (15) | −18.2 ± 0.5 (12) | | | +12.2 ± 0.8 (12) | +11.9 ± 0.8 (9) | +12.4 ± 0.3 (15) | +12.3 ± 0.7 (12) |
| Plasma | Incubation | | | −17.9 ± 0.8 (12) | −17.8 ± 0.5 (9) | −18.6 ± 0.4 (15) | −18.0 ± 0.5 (12) | | | +12.5 ± 0.6 (12) | +13.1 ± 1.1 (9) | +12.8 ± 0.5 (15) | +13.2 ± 0.5 (12) |
| Chick feathers | Chick-rearing | | | −17.3 ± 0.2 (17) | −16.7 ± 0.2 (16) | −16.8 ± 0.3 (15) | −16.7 ± 0.3 (15) | | | +12.3 ± 0.4 (17) | +12.9 ± 0.7 (16) | +13.0 ± 0.4 (15) | +12.8 ± 0.6 (15) |

**Table 1.3.** Results of the generalised linear models (GLM) showing the different comparisons of $\delta^{13}$C (‰) and $\delta^{15}$N (‰) values of blood (RBC and plasma) and feathers (P1 and S8) of adults, and chick feathers of Audouin's (AG) and yellow-legged (YLG) gulls sampled in 2014 and 2015 breeding seasons, as shown in Table 1.2. Significant effects are shown in bold.

| | $\delta^{13}$C | | | $\delta^{15}$N | | |
|---|---|---|---|---|---|---|
| | *F* | *P* | Main effect | *F* | *P* | Main effect |
| **Blood: 2014 and 2015 (RBC = laying, plasma = incubation)** | | | | | | |
| Species | $F_{1,94} = 1.55$ | 0.220 | - | $F_{1,94} = 0.88$ | 0.350 | - |
| Year | $F_{1,94} = 5.20$ | **0.025** | 2014 > 2015 | $F_{1,94} = 3.52$ | 0.064 | - |
| Period | $F_{1,94} = 0.25$ | 0.620 | - | $F_{1,94} = 21.04$ | **<0.001** | incubation > laying |
| Species*Year | $F_{1,92} = 3.64$ | 0.060 | - | $F_{1,92} = 0.08$ | 0.780 | - |
| Species*Period | $F_{1,92} = 5.09$ | **0.027** | YLG incubation > others | $F_{1,92} = 5.79$ | **0.018** | YLG incubation > others |
| Year*Period | $F_{1,92} = 3.85$ | 0.053 | - | $F_{1,92} = 0.08$ | 0.780 | - |
| Species*Year*Period | $F_{1,88} = 0.54$ | 0.460 | - | $F_{1,88} = 0.76$ | 0.390 | - |
| | | | | | | |
| **Feathers: 2013 and 2014 (P1 = breeding season, S8 = non-breeding)** | | | | | | |
| Species | $F_{1,94} = 0.98$ | 0.325 | - | $F_{1,94} = 0.07$ | 0.789 | - |
| Year | $F_{1,94} = 1.33$ | 0.251 | - | $F_{1,94} = 0.41$ | 0.523 | - |
| Period | $F_{1,94} = 3.56$ | 0.062 | - | $F_{1,94} = 2.83$ | 0.096 | - |
| Species*Year | $F_{1,92} = 1.04$ | 0.310 | - | $F_{1,92} = 0.001$ | 0.974 | - |
| Species*Period | $F_{1,92} = 30.73$ | **<0.001** | AG non-breeding > others | $F_{1,92} = 7.42$ | **0.008** | AG non-breeding > others |
| Year*Period | $F_{1,92} = 0.02$ | 0.089 | - | $F_{1,92} = 2.69$ | 0.104 | - |
| Species*Year*Period | $F_{1,88} = 2.62$ | 0.109 | - | $F_{1,88} = 0.004$ | 0.952 | - |
| | | | | | | |
| **Chick feathers: 2014 and 2015 (chick-rearing)** | | | | | | |
| | | | | | | |
| Species | $F_{1,61} = 32.70$ | **<0.001** | AG < YLG | $F_{1,61} = 2.56$ | 0.115 | - |
| Year | $F_{1,61} = 16.22$ | **<0.001** | 2014 < 2015 | $F_{1,61} = 5.17$ | **0.027** | 2014 < 2015 |
| Species*Year | $F_{1,59} = 8.83$ | **0.004** | AG 2014 < others | $F_{1,59} = 8.33$ | **0.005** | AG 2014 < others |
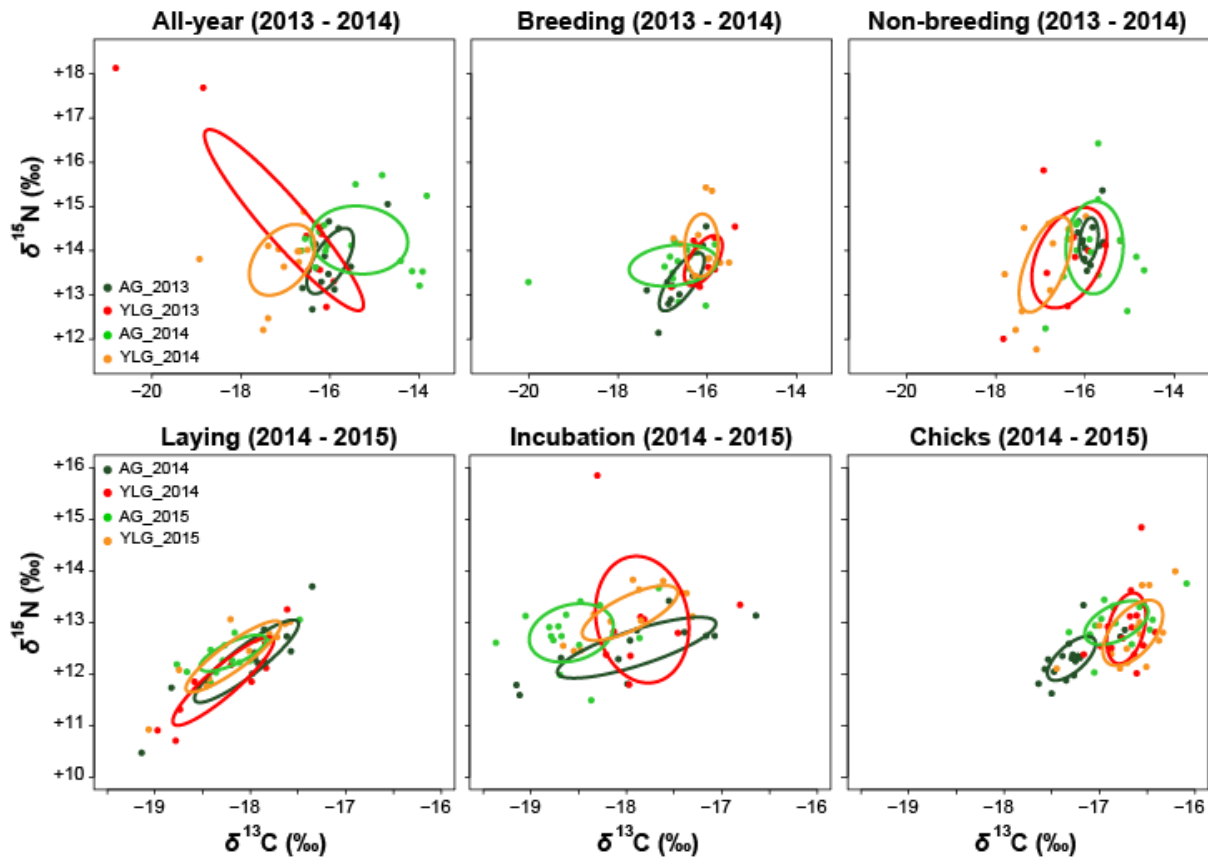
**Figure 1.3.** Isotopic niche space based on carbon and nitrogen isotope ratios ($\delta^{13}$C and $\delta^{15}$N) of Audouin's (AG; *Larus audouinii*) and yellow-legged (YLG; *L. michahellis*) gulls sampled in the breeding season of 2014 (AG: n = 12, YLG: n = 9) and 2015 (AG: n = 15, YLG: n = 12), during all-year (Br; breast feathers), breeding (P1; first primary feathers), non-breeding (S8; eighth secondary feathers), laying (RBC; red blood cells), and incubation (plasma) periods of adults and chicks (feathers; AG: n = 17, YLG: n = 16 in 2014; and AG: n = 15, YLG: n = 15 in 2015). Solid lines represent the standard ellipses areas corrected for small sample size (SEA$_c$) calculated in SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011). Please note that adult feathers reflect dietary inputs from the year previous to the sampling and have different scale axes from blood tissues and chick feathers.

## 4. Discussion

### 4.1. Resource use during the breeding season

During the breeding season, adults did not differ in their isotope values (i.e. RBC, plasma and P1), and there was also a considerable overlap in their diet composition, as found at Chafarinas Islands in the Mediterranean (González-Solís et al. 1997b), where the two species feed opportunistically on abundant discards provided by local fisheries (González-Solís 2003). As predicted, fish was the main prey in the pellets of both gull species. However there were some differences in gull diets. We found that Audouin's gulls breeding in southern Portugal were marine specialists, feeding mainly on the epipelagic *Scomberesox saurus*. *S. saurus* is probably caught naturally by the gulls, since this species is not targeted by local fisheries (Table S1.1) neither commonly discarded in the study area (Borges et al. 2001, Erzini et al. 2002). In contrast the isotopic mixing models of plasma indicated that yellow-legged gull fed more on demersal fish species than Audouin's gull during the laying period. Demersal species are made available to surface feeders, such as gulls, through fishery discards (Navarro et al. 2009a). *Sardina pilchardus* and *Scomber* sp. were the two fish species with the highest occurrences in yellow-legged gull pellets (Table 1.1), which were also the most captured (Table S1.1) and discarded species in the area (Borges et al. 2001, Erzini et al. 2002). Yellow-legged gulls are more likely to feed on discards than Audouin's gulls due to their more opportunistic feeding strategies and aggressive and competitive foraging skills at fishing vessels (Arcos et al. 2001). In the study area *Scomber* sp. is often discarded but we found that this species did not increase in the diet of both gull species during 2015, when their landings increased substantially in relation to 2014, suggesting that gulls may not be strongly dependent on *Scomber* sp. as discards.

Stable isotope analysis also revealed different isotope values in chick feathers between the two gull species, suggesting that Audouin's gulls selected prey with lower carbon isotope values to feed their chicks than yellow-legged gulls, in agreement with pellet analysis. In 2014, the low carbon isotope values in Audouin's gull chicks might be explained by the less favourable foraging conditions in that year (see fishery landings in Table S1.1). In fact, the extended winter (December to March) North Atlantic Oscillation (NAO) index was much lower in 2013 (-1.97) when compared to 2014 (+3.10), and Paiva et al. (2013) has showed that such conditions are usually associated with lower marine prey abundance. Thus, the lower $\delta^{13}C$ values suggest that Audouin's gull adults might have increased foraging effort into more offshore areas, typically depleted in $^{13}C$ compared to coastal environments (Graham et al. 2010), to find suitable prey for their chicks, in response to the lower prey availability, as found by Gonzalez-Solis et al.

(1997c) and Cama et al. (2013). This effect was not detected in yellow-legged gull, which might be related with their lowest dependency on pelagic prey.

## 4.2. Isotopic niche segregation in the non-breeding season

Stable isotope analysis revealed niche segregation between the two gull species during the non-breeding season, as expected because yellow-legged gull is resident species and Audouin's gull migrates after breeding. The higher isotope values of both carbon and nitrogen in Audouin's gull secondary feathers compared to yellow-legged gull suggested that Audouin's gulls foraged in a more productive area (Farquhar et al. 1989), probably related to the highly productive upwelling area in the northwest African coast (Arístegui et al. 2009). This area is an important non-breeding ground for several seabird species (Ramírez et al. 2013, Ramos et al. 2013), including Audouin's gulls (Oro and Martinez 1994, Bécares et al. 2016). Isotopic differences between the two gull species can also be related with the selection of different prey types during the non-breeding season; yellow-legged gulls might have fed on lower trophic level prey compared to Audouin's gulls. However, we cannot infer about diet composition due to the different baseline isotope values between the breeding and non-breeding, and detailed knowledge on geographic gradients in stable isotopes (i.e. isoscapes) is only reported on a broader scale for the Audouin's gull non-breeding area (McMahon et al. 2013).

Additionally, the Audouin's gull revealed a more specialist feeding ecology during the 2013 non-breeding and all-year periods compared to the yellow-legged gull, which showed a broader isotopic niche, suggesting that yellow-legged gulls exploited a wider range of food sources, as found by Ramos et al. (2011) in Mediterranean colonies. In 2014, there was an evidence indicating isotopic niche segregation between the two species, revealing exploitation of isotopically distinct resources. The different isotopic niche space between the two years could be related with the less favourable environmental conditions during the 2013 non-breeding season (reflected in the 2014 NAO index). In fact, the resident yellow-legged gull broaden their isotopic niche (Table S1.4) during this period, as expected for generalist species in conditions of low food availability, and as found by González-Solís *et al.*, (1997c).

## 4.3. On the use of fisheries subsidies

Throughout their breeding range, these two gull species have shown opportunistic behaviour, feeding in association with fisheries (Oro and Ruiz 1997, Arcos et al. 2001, González-Solís 2003, Cama

et al. 2012, 2013), as found in several seabird species (e.g. Garthe et al. 1996, Osterblom et al. 2008, Kai et al. 2013, Tyson et al. 2015). As expected, yellow-legged gulls fed on a wider range of prey than Audouin's gulls during the breeding season, including more items from anthropogenic activities (i.e. fishery discards) in their diet, determined by pellet analysis and isotopic mixing models. Fishing activities have led to a global population increase for both Audouin's and yellow-legged gulls (Oro et al. 2013). One major goal of the Common Fisheries Policy of the European Union is a discard ban, which will be fully implemented in 2020. The degree of both immediate and long-term consequences of such policy for scavenging seabirds is still poorly understood and long-term seabird monitoring is needed, especially for gull species that show a great dependence on discards (Bicknell et al. 2013, Bécares et al. 2015). Although Audouin's and yellow-legged gulls breeding populations in southern Portugal are recent (first breeding attempts of Audouin's gulls in 2000; Cabral et al. 2005) and currently of relatively small size (ca. 1200 and 900 breeding pairs of Audouin's and yellow-legged gulls, respectively), their numbers are increasing exponentially (ca. 300 breeding pairs per year; unpublished data), most likely due to the presence of intense fishing activities in the colony surroundings and abundance of fishery discards. Therefore, future research should closely monitor the impact of the discard ban policy on Audouin's and yellow-legged gulls' population dynamics.

**CHAPTER 2.**

JG Calado, VH Paiva, FR Ceia, P Gomes, JA Ramos, A Velando. Stable isotopes reveal year-round sexual trophic segregation in four yellow-legged gull colonies. Marine Biology, 167: 1-11.

# Stable isotopes reveal year-round sexual trophic segregation in four yellow-legged gull colonies

**Abstract.** Sexual segregation in trophic ecology is widespread among sexually dimorphic marine vertebrates. The degree of such segregation can change throughout the annual cycle, however, year-round data on seabird inter-sexual differences is scarce. Here we investigated sexual trophic segregation in yellow-legged gulls *Larus michahellis* evaluating two hypothetical drivers of such segregation: the different nutritional requirements hypothesis and the sexual size dimorphism hypothesis. We used stable isotope analyses of blood and feathers to estimate year-round gull trophic ecology in four colonies along the western Iberian coast. $\delta^{15}$N and $\delta^{13}$C values were consistently higher in males than in females throughout the year and in all four study colonies, suggesting consistent sexual differences in trophic level prey as well as in foraging habitats. Significantly wider isotopic niches of females in the innermost primary and eight secondary feathers suggest that they are more generalists than males during most of the annual cycle. In accordance, isotopic mixing models estimated a higher proportion of marine invertebrates in female diet, while males consumed a higher proportion of fish, which could indicate that males forage more in association with fisheries, having major implications in view of the newly implemented discard ban policy. Overall, our results revealed a clear pattern of sexual trophic segregation in yellow-legged gulls that was maintained throughout the year in four colonies along the western Iberian coast, arguing against the different nutritional requirements hypothesis and suggesting that sexual size dimorphism plays an important role in driving sexual segregation in trophic niches.

**Keywords:** sexual size dimorphism; *Larus michahellis*; western Iberian coast; isotopic niche; fisheries.

## 1. Introduction

Sexual differences in foraging behaviour are a widespread phenomenon in the animal kingdom influencing population dynamics (Ruckstuhl and Neuhaus 2005, Wearmouth and Sims 2008). Inter-sexual differences in trophic ecology may emerge through foraging in distinct areas and/or by selecting different prey within the same area (Phillips et al. 2017). Sexual segregation in trophic niche can lead to reduced intra-specific competition for food resources and therefore increase individual fitness and population health (Slatkin 1984, Patrick and Weimerskirch 2014). Moreover, the degree of sexual segregation may change throughout the annual cycle due to different constraints such as breeding duties

(Burke et al. 2015, Catry et al. 2016) and different levels of between-sex competition, although these variations still remain poorly studied across taxa.

Seabirds are monogamous species that often display sexual segregation in foraging strategies (Schreiber and Burger 2002b). These inter-sexual differences can have important implications for seabird conservation and management since diverse environmental conditions and anthropogenic threats can affect each sex differently. For instance, sex-specific responses to climate change (Barros et al. 2013, Gianuca et al. 2019, Kiat et al. 2019) and sex-biased mortality associated with anthropogenic activities (Gianuca et al. 2017, 2019, Oro et al. 2018) have been previously reported in seabirds and could be directly linked to foraging ecology. Additionally, during the breeding period when seabirds are central-place foragers, sexual segregation might be relieved due to increased niche overlap between sexes (Barrionuevo et al. 2019) or accentuated due to a higher competition for food resources (Stauss et al. 2012). However, our understanding of year-round sexual segregation in seabirds is often hampered by their dispersed distribution during the non-breeding season, making them often inaccessible during that period of the annual cycle (Phillips et al. 2011). Studies have typically been performed on a single colony (but see Forero et al. 2002), but segregation could vary among sites as the result of differences in food availability, environmental conditions, and density-dependent competition. Therefore, most of our knowledge on sexual segregation is colony-specific and biased towards the breeding season. This limits our comprehension of how this segregation in trophic niches operates across colonies and might drive their year-round ecology. In addition, inter-sexual differences have been mostly studied on wide-ranging pelagic species, such as Procellariiformes, focussing on sex-specific foraging distributions, and comparatively less is known about sex-specific dietary differences in coastal seabirds (see reviews in Lewis et al. 2002; Phillips et al. 2011, 2017; and references therein).

Two main hypotheses have been proposed to explain sex-specific trophic segregation in dimorphic seabirds. The different nutritional requirements hypothesis states that specific nutrients are required differently by females and males as the result of differential breeding investment (Ludynia et al. 2013). Breeding females may require specific nutrients for egg formation (e.g. calcium; Ramírez et al. 2013) and therefore select different prey types. The sexual size dimorphism hypothesis states that size-related differences are responsible for year-round resource partitioning through competitive exclusion or niche specialization due to different foraging abilities (Shaffer et al. 2001, Phillips et al. 2004, Lewis et al. 2005). However, due to complex interactions between factors during the breeding season (e.g. central-place foraging, niche overlap, competition), it is difficult to identify the main driver of sexual segregation

in seabirds. Thus, inter-sexual trophic differences should be investigated throughout the various stages of the annual cycle.

Stable isotope analysis has become a powerful tool to unravel year-round sexual trophic segregation, providing integrative views on assimilated diets (Boecklen et al. 2011). Despite the increasing use of stable isotopes in seabird studies, inter-sexual foraging differences remain one of the main gaps of knowledge in seabird ecology (Lewison et al. 2012) as most studies are population- and not individual-level focussed. Stable isotope analysis can contribute to filling this knowledge gap by focussing on sex-specific differences and revealing important insights into the trophic choices and foraging distributions of each sex during both the breeding and the non-breeding seasons (Phillips et al. 2011). The period of dietary integration reflected by stable isotopes depends on the metabolic activity of the tissue sampled (Hobson and Clark 1992b, Inger and Bearhop 2008). Hence, by sampling multiple tissues with different turnover rates, we can assess seabird trophic ecology during different periods of the annual cycle (Bond et al. 2016). Feathers integrate isotope values during their synthesis and are metabolically inert after formation, making it possible to investigate diet during the non-breeding season by sampling feathers that were synthetized during that period (Hobson 1999). Furthermore, stable isotopes can be used to examine isotopic niche segregation and niche width differences between sexes (Newsome et al. 2007, Jackson et al. 2011). Stable nitrogen isotope values ($\delta^{15}$N) can be used as a proxy of trophic position, while stable carbon isotope values ($\delta^{13}$C) reflect the food web carbon source (i.e. foraging areas; Kelly 2000).

We investigated the year-round sexual trophic segregation in a dimorphic coastal seabird, the yellow-legged gull *Larus michahellis*, in four colonies along the western Iberian coast. We used stable isotope analyses of blood and feathers to evaluate two hypothetical drivers of such segregation: the different nutritional requirements hypothesis and the sexual size dimorphism hypothesis. If sex differences in the trophic ecology of gulls are mediated by different nutritional requirements, sexual segregation should be more evident in the breeding season and disappear during the non-breeding period. On the other hand, if sex differences are mediated by sexual size dimorphism, sexual segregation should persist throughout the annual cycle. Additionally, our results provide new insights regarding the possible sex-specific impacts of the new European Union discard ban policy (European Union 2015) in the yellow-legged gull.

## 2. Methods

### 2.1. Study species

The yellow-legged gull is a sexually size dimorphic species, with males being larger than females, despite some overlap (Bosch 1996, Arizaga et al. 2008, Galarza et al. 2008). There is some evidence of sex-specific feeding differences during the breeding season based on conventional analyses (Steigerwald et al. 2015) and stable isotope analyses (Payo-Payo et al. 2015). This species is one of the most abundant gulls in the southwestern Paleartic (Olsen and Larsson 2004). They display a highly opportunistic foraging behaviour, feeding on a wide range of prey, including anthropogenic food subsidies (Duhem et al. 2005, Ramos et al. 2009b). In the western Iberian coast, yellow-legged gulls feed mostly on marine resources (Moreno et al. 2010, Calado et al. 2018, Mendes et al. 2018), with fish being most likely caught in association with fisheries (Matos et al. 2018). The pelagic crab *Polybius henslowii* is also an important prey in the diet of gulls in this area (Munilla 1997, Ceia et al. 2014), which can be caught naturally at the sea surface (Munilla 1997).

### 2.2. Study areas

This study was carried out in four yellow-legged gull colonies along the western Iberian coast (Figure 2.1): Deserta Island (36° 57′ N, 7° 53′ W), Pessegueiro Island (37°49' N, 8°47' W), Berlenga Island (39° 24′ N, 9° 30′ W), and Sálvora Island (42° 28′ N, 9° 00′ W). The islands differ in several abiotic and biotic factors, such as climate, gull population size, and anthropogenic food availability (see Table S2.1).

### 2.3. Sample collection

Breeding adults were captured during late incubation with nest traps in 2017 (Sálvora N = 10) and in 2018 (Deserta N = 9; Pessegueiro N = 11; Berlenga N = 13). We measured body mass and wing length of birds, and blood samples (0.5–1.0 ml) were collected from the tarsal vein using 27-G needles and centrifuged within 3–5 h to separate red blood cells (RBC) from plasma for stable isotope analyses. An aliquout (~2μl) of blood cells were separated for sex determination. All samples were stored frozen at -20° C. We sampled the tip of the innermost primary (P1) and eighth secondary (S8) feathers, which were stored in labelled sealed plastic bags for stable isotope analyses.
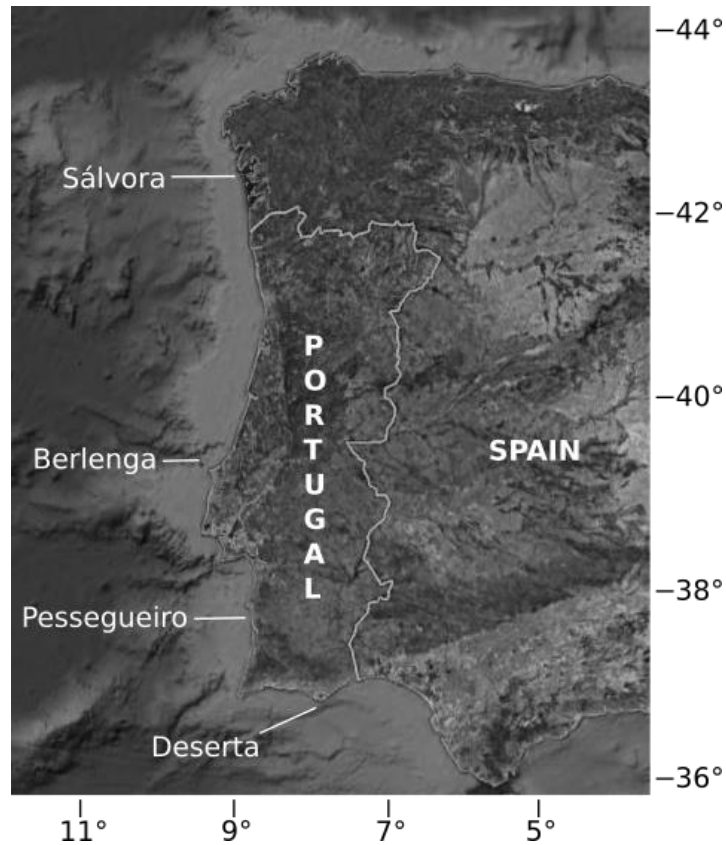
**Figure 2.1.** Western Iberian Peninsula (southwest Europe), indicating the colonies of yellow-legged gull *Larus michahellis* included in the study.


## 2.4. Sex determination

DNA extraction was performed by heating blood in 100mM NaOH for 10 minutes at 96°C. Polymerase Chain Reaction (PCR) protocols were modified from Fridolfsson and Ellegren (Fridolfsson and Ellegren 1999), using the primers 2550F and 2718R to amplify CHD1Z and CHD1W genes (Griffiths et al. 1998). PCR fragments were separated by electrophoresis on a 2% agarose gel stained with ethidium bromide. A single band of DNA on the gel indicated males (corresponding to CHD1Z gene), while two bands indicated females (corresponding to both CHD1Z and CHD1W genes). We identified a total of 21 males (Deserta N = 5; Pessegueiro N = 6; Berlenga N = 6; Sálvora N = 4) and 22 females (Deserta N = 4; Pessegueiro N = 5; Berlenga N = 7; Sálvora N = 6).

## 2.5. Stable isotope analysis

We measured stable isotope ratios ($\delta^{15}$N and $\delta^{13}$C) in blood and feathers of yellow-legged gulls. Plasma retains information on diet over few days prior to sampling, i.e. half-life of ~3 days, reflecting recent meals during the late incubation period. RBC have a longer time-integration period, reflecting diet over at least the previous 4 weeks, i.e. half-life of ~30 days (Hobson and Clark 1993). Thus, RBC reflect diet since the late pre-laying period. Feathers are metabolically inert after formation, retaining isotopic records from the time of their synthesis (Hobson 1999). P1 is replaced during late breeding and S8 during non-breeding, therefore, isotope values of P1 and S8 represent dietary inputs during the previous late breeding and non-breeding periods, respectively (Ramos et al. 2011).

Successive rinses of a 2 chloroform: 1 methanol solution were used to extract lipids from plasma samples and to clean feathers from surface lipids and contaminants (Cherel et al. 2005a, Kojadinovic et al. 2008). Feathers were cut with stainless steel scissors into small fragments. All tissue samples were dried in an oven for at least 48 h at 50°C to a constant mass and homogenized. Sub-samples of approximately 0.35 mg were weighed in a microbalance, placed in a tin cup, and crimped for combustion. Isotopic ratios were determined by continuous-flow isotope ratio mass spectrometry (CF-IRMS). Results are expressed in the usual $\delta$ notation as parts per thousand (‰) deviation from the international standards atmospheric nitrogen ($N_2$) for $\delta^{15}$N and Vienna-PeeDee Belemnite (V-PDB) for $\delta^{13}$C, according to the following equation: $\delta^{15}$N or $\delta^{13}$C = [(Rsample /Rstandard) − 1], where R = $^{15}$N/$^{14}$N or $^{13}$C/$^{12}$C, respectively. Replicate measurements of internal laboratory standards indicate precision < 0.2 ‰ for the two stable isotope ratios.

## 2.6. Statistical analyses

Linear models (LMs) were performed to investigate the effect of (1) sex and (2) colony (Sálvora, Berlenga, Pessegueiro, and Deserta) on gull body mass and wing length.

Linear mixed models (LMMs) were used to test the effect of (1) sex, (2) period (late breeding – P1 feathers, non-breeding – S8 feathers, pre-laying – RBC, and incubation – Plasma), and (3) colony on $\delta^{15}$N and $\delta^{13}$C values. Bird identity was included as a random effect to account for the non-independence of repeated measures (i.e. several tissues) from the same individual. Mean $\delta^{15}$N and $\delta^{13}$C values are predictably higher in feathers than blood of the same individual due to tissue-specific isotopic discrimination factors (Cherel et al. 2014). Thus, we applied correction factors (-0.6 ‰ for $\delta^{15}$N and -1.8

‰ for $\delta^{13}C$) on stable isotopic values of feathers, according to previous measurements in yellow-legged gulls (Calado 2015) to enable the investigation of differences in the trophic ecology between periods. Interactions between sex and the other two independent variables (i.e. period and colony) were tested in all models, starting with the full model and dropping interactions using backward stepwise selection. However, no interactions were significant and therefore not included in any of the final models. Post-hoc analyses were performed using Estimated Marginal Means (EMM) and Tukey's p-value adjustment under the *emmeans* R package (Lenth 2019).

Normality and homogeneity were verified by visual inspection of residuals. All analyses were performed with R software ver. 3.5.2 (R Core Team, 2018), and significance was set at alpha = 0.05.

## 2.7. Mixing models and isotopic niche

SIBER (Stable Isotope Bayesian Ellipses in R; package SIBER; Jackson et al. 2011) was used separately for each tissue to compare isotopic niches between sexes throughout the annual cycle. Only gulls from Berlenga, Pessegueiro, and Deserta islands were used in this modelling because gulls from Sálvora Island exhibited significantly higher nitrogen values than gulls from Pessegueiro and Deserta (see Table S2.2), and the higher differences among colonies (EMM: Sálvora - Pessegueiro = 0.96; Sálvora - Deserta = 1.0) than between sex (EMM: Males - Females = 0.66) would lead to erroneous results. We calculated the area of the standard ellipse corrected for small sample size that contains approximately 40% of the data (SEA$_c$) for each sex (i.e. niche width), which was used to calculate niche overlap between sexes. Bayesian standard ellipse areas (SEA$_B$) were calculated from 10,000 iterations of Markov-chain Monte Carlo (MCMC) simulation using the *rjags* R package (Plummer 2018) to test for differences in niche widths between sexes (i.e. the proportion of draws of the posterior distribution of the SEA$_B$ in which the area of females was smaller than that of males).

Bayesian stable isotope mixing models (SIAR; Parnell et al. 2010) were used to compare the estimated relative proportion of the different dietary sources between sexes in plasma isotope values of gulls from Berlenga, Pessegueiro, and Deserta islands. We used prey isotope values reported by Ceia et al. (2014) from regurgitates of incubating yellow-legged gulls on Berlenga Island: fish (*Trachurus trachurus* $\delta^{15}N$: 11.9 ‰ ± 0.6, $\delta^{13}C$: -18.6 ‰ ± 0.6, n = 5), pelagic crab (*Polybius henslowii* $\delta^{15}N$: 6.2 ‰ ± 0.2, $\delta^{13}C$: -17.8 ‰ ± 0.6, n = 4), and terrestrial resources ($\delta^{15}N$: 10.6 ‰ ± 4.4, $\delta^{13}C$: -20.0 ‰ ± 3.5, n = 9). Terrestrial resources comprised refuse (meat scraps) and terrestrial invertebrates, which were

pooled *a posteriori* into one food source to avoid uncertainties in source proportions (i.e. high correlation among sources) following Phillips et al. (2014). The discrimination factors applied in the model were 2.85 and 0.30 ‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively. These are average values of whole blood obtained from controlled experiments with four seabird species available in literature (Hobson and Clark 1992a, Bearhop et al. 2002, Cherel et al. 2005a), which were previously used in the yellow-legged gulls from the studied populations (Ceia et al. 2014, Calado et al. 2018) and are similar to the values obtained for 'birds' from a meta-analysis (Caut et al. 2009). We used a standard deviation of ± 1.0 ‰ to account for potential differences among discrimination factors driven by species, tissues, or prey types. To evaluate isotopic mixing models, we constructed a mixing polygon simulation using metrics provided by Smith et al. (2013). All consumers were within the 95% mixing region (see Figure S2.1), validating our isotopic mixing models.

## 3. Results

Yellow-legged gull males exhibited significantly higher values of body mass ($F_{1,41}$ = 57.5, P < 0.001) and wing length ($F_{1,41}$ = 52.3, P < 0.001) than females (see body measurements in Table 2.1). We also found significant differences between colonies, with lower values in Sálvora compared to Deserta in both body mass ($F_{3,39}$ = 4.4, p = 0.01) and wing length ($F_{3,39}$ = 3.2, p = 0.04).

**Table 2.1.** Mean (±SD) body measurements of male and female yellow-legged gulls in each colony. Sample size (N) is also shown.

| Sex | Colony | N | Body mass (g) | Wing length (mm) |
|-----|--------|---|---------------|------------------|
| Male | Sálvora | 4 | 918 ± 41.9 | 438 ± 5.1 |
| Female | Sálvora | 6 | 774 ± 41.8 | 414 ± 9.3 |
| Male | Berlenga | 6 | 983 ± 88.9 | 441 ± 8.7 |
| Female | Berlenga | 7 | 784 ± 77.1 | 420 ± 8.1 |
| Male | Pessegueiro | 6 | 1,007 ± 63.5 | 443 ± 10.2 |
| Female | Pessegueiro | 5 | 870 ± 90.3 | 426 ± 13.4 |
| Male | Deserta | 5 | 1,088 ± 104.9 | 451 ± 14.0 |
| Female | Deserta | 4 | 851 ± 131.3 | 428 ± 11.7 |

Both $\delta^{15}N$ and $\delta^{13}C$ values were higher in males than in females (Table 2.2, see isotope values in Table S2.2). $\delta^{15}N$ values varied significantly among periods, with higher values during late breeding and non-breeding periods compared to both incubation and prey-laying periods, with the latter presenting the lowest values among all periods. $\delta^{15}N$ values also differed among colonies, with higher values in Sálvora compared to both Pessegueiro and Deserta colonies. Estimated marginal means and post hoc comparisons revealed that differences between sexes were constant throughout tissues and colonies (Figure 2.2), suggesting that the sexual segregation in trophic level is maintained throughout the annual cycle and across the four colonies. In contrast, $\delta^{13}C$ values did not vary significantly among periods nor colonies (Table 2.2 and Figure 2.3).

SIBER analysis revealed different isotopic niche spaces for each sex (Figure 2.4). Isotopic niche widths of males were significantly smaller than those of females in late breeding and non-breeding periods (reflected by P1 and S8 feathers, Table 2.3). We detected some degree of niche segregation between sexes throughout the annual cycle (Table 2.3 and Figure 2.4), however, a complete niche segregation in SEA$_c$ (i.e. no overlap) was only detected during the non-breeding period.

SIAR mixing models revealed that during incubation males consumed mainly fish (52%), followed by pelagic crabs (36%), while females consumed mainly pelagic crabs (50%), followed by fish (37%; Figure 2.5). Terrestrial resources presented similar proportions in both sexes (Figure 2.5).
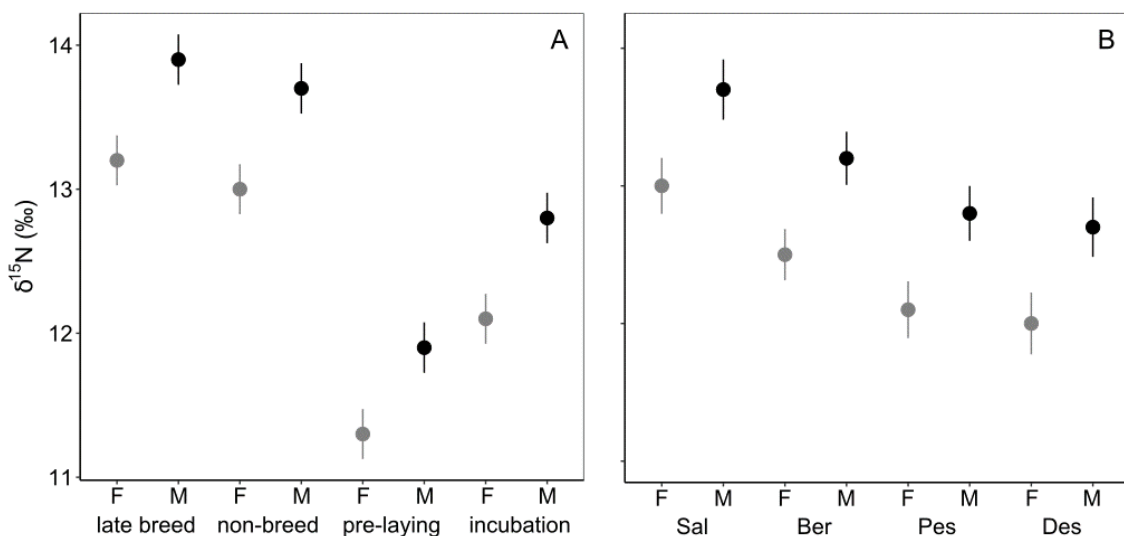


**Figure 2.2.** Estimated marginal means and standard error of $\delta^{15}N$ values of female (F; grey) and male (M; black) yellow-legged gulls in: (A) each period of the annual cycle: late breeding (innermost primary feathers – P1), non-breeding (eighth secondary feathers – S8), pre-laying (red blood cells – RBC), and incubation (Plasma); and (B) each colony: Sálvora (Sal), Berlenga (Ber), Pessegueiro (Pes), and Deserta (Des).

**Table 2.2.** Results of the linear mixed models (LMMs) testing the effect of sex (Males – M and Females – F), period (late breeding – P1 feathers, non-breeding – S8 feathers, pre-laying – RBC, and incubation – Plasma), and colony (Sálvora – Sal, Berlenga – Ber, Pessegueiro – Pes, Deserta – Des) on yellow-legged gull $\delta^{15}$N and $\delta^{13}$C values. Significant P values are shown in bold. Correction factors (-0.6 ‰ for $\delta^{15}$N and -1.8 ‰ for $\delta^{13}$C) were applied on stable isotope values of feathers to allow direct comparisons between periods (see Cherel et al. 2014). Bird identity was included as a random factor to account for non-independence of repeated measures (i.e. several tissues) from the same individual.

| Response | Sex | | | Period | | | Colony | | |
|---|---|---|---|---|---|---|---|---|---|
| | F | P | Effects | F | P | Effects | F | P | Effects |
| $\delta^{15}$N | $F_{1,170} = 13.0$ | **< 0.001** | M > F | $F_{3,168} = 45.6$ | **< 0.001** | late breed = non-breed > incubation > pre-laying | $F_{3,168} = 6.0$ | **0.002** | Sal > Pes = Des; Ber = others |
| $\delta^{13}$C | $F_{1,170} = 5.2$ | **0.028** | M > F | $F_{3,168} = 0.1$ | 0.95 | - | $F_{3,168} = 0.4$ | 0.79 | - |
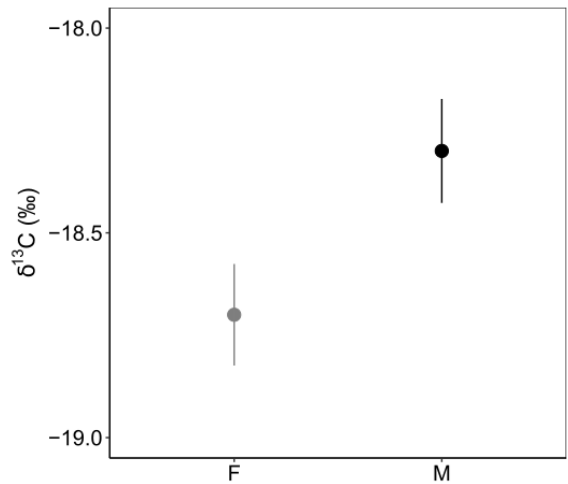
**Figure 2.3.** Estimated marginal means and standard error of $\delta^{13}C$ values of female (F; grey) and male (M; black) of yellow-legged gulls.
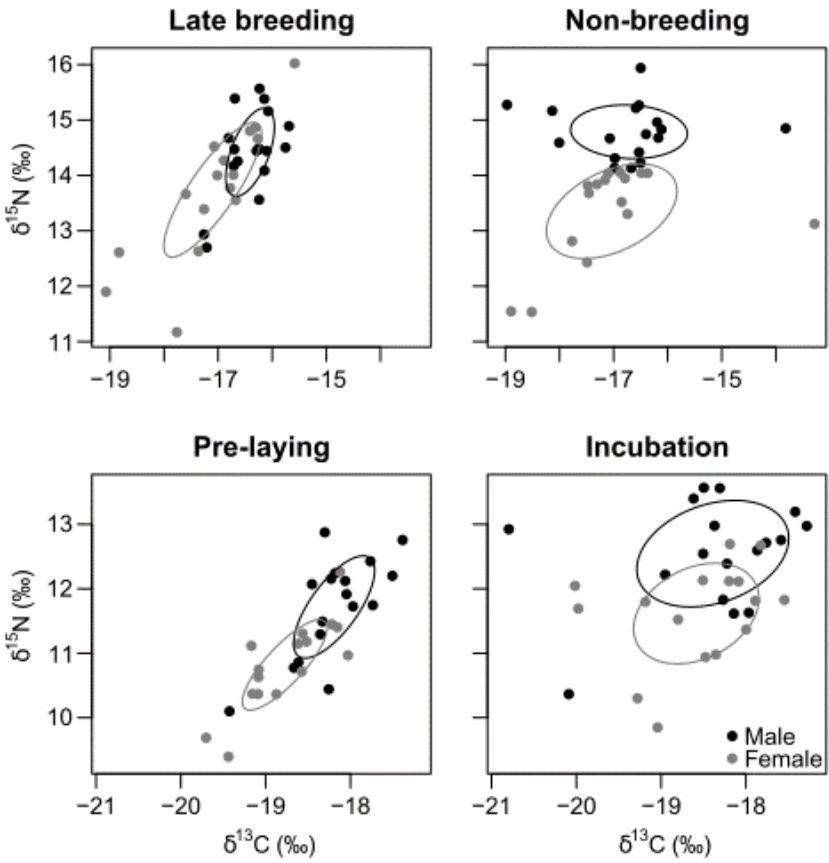


**Figure 2.4.** Isotopic niche space based on $\delta^{13}C$ and $\delta^{15}N$ values of female (F; grey) and male (M; black) yellow-legged gulls from Berlenga, Pessegueiro, and Deserta islands during late breeding (innermost primary feathers – P1), non-breeding (eighth secondary feathers – S8), pre-laying (red blood cells – RBC), and incubation (Plasma). Solid lines represent the standard ellipses areas corrected for small sample size (SEA$_c$).

**Table 2.3.** Isotopic niche metrics calculated in late breeding (innermost primary feathers – P1), non-breeding (eighth secondary feathers – S8), pre-laying (red blood cells – RBC), and incubation (Plasma) of male and female yellow-legged gulls from Berlenga, Pessegueiro, and Deserta islands. $SEA_c$ (standard ellipse area corrected for small sample size) was used to calculate male and female ellipse areas (‰$^2$) as well as their overlap (%). Mode values of $SEA_B$ (Bayesian standard ellipse area) and their 95% credible intervals (CI) are also shown. P values were calculated based on $SEA_B$ and represent the probability of females presenting smaller ellipse areas than males (see Jackson et al. 2011 for more details). P values lower than 0.05 are shown in bold.

| Period | $SEA_c$ | | | $SEA_B$ | | |
| --- | --- | --- | --- | --- | --- | --- |
| | Male | Female | Overlap (%) | Male (CI) | Female (CI) | P |
| Non-breeding | 1.8 | 3.2 | 0 | 1.5 (1.0-2.6) | 2.8 (1.7-4.8) | **0.04** |
| Post-breeding | 1.0 | 2.1 | 61 | 0.9 (0.6-1.5) | 2.1 (1.2-3.5) | **0.01** |
| Pre-laying | 0.9 | 0.7 | 31 | 0.8 (0.5-1.4) | 0.6 (0.4-1.1) | 0.7 |
| Incubation | 2.4 | 1.9 | 37 | 2.2 (1.3-3.6) | 1.7 (1.0-2.8) | 0.8 |
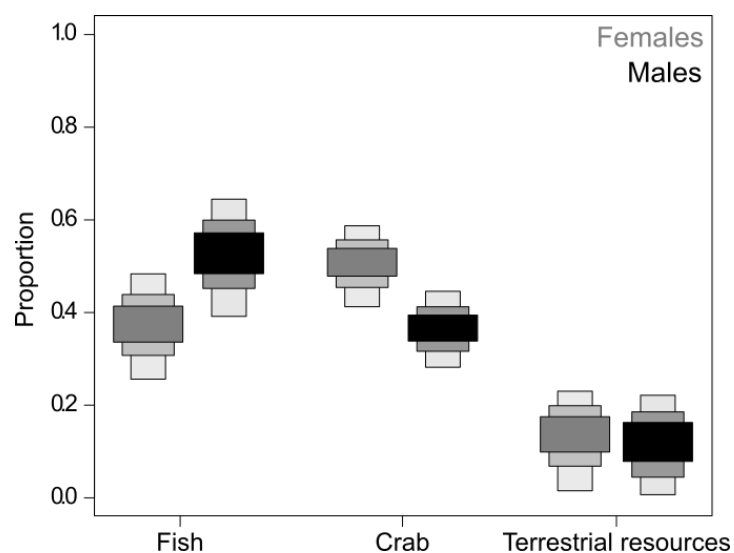


**Figure 2.5.** Estimated proportions of the 3 main prey groups in the diet of female (grey) and male (black) yellow-legged gulls from Berlenga, Pessegueiro, and Deserta islands based on $\delta^{13}C$ and $\delta^{15}N$ values in plasma. Decreasing bar widths represent 50, 75, and 95% Bayesian credibility intervals.

## 4. Discussion

Both body mass and wing length were significantly larger in male than in female yellow-legged gulls, despite wing length being one of the least dimorphic traits in the species (Bosch 1996; Galarza et al. 2008; but see Arizaga et al. 2008). Interestingly, our results suggest a latitudinal geographical gradient in body measurements. Gulls breeding at lower latitudes (Deserta) showed larger body mass and wing length than those breeding at the most northern colony (Sálvora). These patterns contradict the Bergmann's rule (Bergmann 1847), which posits that body mass increase in northern (colder) environments, but agree with the Allen's rule (Allen 1877), which states that the lengths of the extremities of endotherms are positively associated with temperature. Given our small sample sizes, these colony differences should be viewed with caution, and future studies should examine these patterns. Importantly, colony differences were not affected by sex, suggesting similar sexual dimorphism among the study colonies.

$\delta^{15}N$ and $\delta^{13}C$ values were consistently higher in males than in females throughout the annual cycle and across the four study colonies. Higher nitrogen values of males indicate the consumption of higher trophic level prey, which might be related with the selection of different prey types by each sex, as suggested by our isotopic mixing models. These models estimated a higher proportion of fish in male diet and of marine invertebrates in female diet during incubation. Other studies investigating sexual trophic segregation on dimorphic species also found that males consume more fish than females (Forero et al. 2002, Kazama et al. 2018, Colominas-Ciuró et al. 2018). Additionally, some studies detected that males feed more on demersal fish than females (e.g. Navarro et al. 2009a), including in the closely related Audouin's gull (Navarro et al. 2010). In our study, we were not able to discriminate different fish prey and different terrestrial resources in the diet of gulls. Indeed, one limitation of stable isotopes is that they do not provide taxonomic detail, and different prey may have similar isotope values, precluding their incorporation in isotopic mixing models (Phillips et al. 2014). Additionally, we did not account for spatio-temporal variability in isotopic baseline values, which could lead to slightly different estimates of gull dietary proportions. However, differences between prey groups are higher than the variability in baseline values (see Velando et al. 2010; Moreno et al. 2010; Ceia et al. 2014; Calado et al. 2018), thus allowing the interpretation that there were trophic differences between sexes regarding two major prey groups (i.e. fish and marine invertebrates).

Carbon ratios suggested different foraging areas between sexes. Higher carbon values of males might indicate that they foraged more in the marine environment (Kelly 2000) and might have fed more

on demersal fish species (Navarro et al. 2009a, Calado et al. 2018) compared to females. However, we were not able to assess foraging distributions of each sex in detail due to limited knowledge on marine isoscapes and low isotopic variation at regional scales in the North Atlantic (McMahon et al. 2013). Nevertheless, a recent study found a strong inshore to offshore pattern in carbon ratios in this area (Ceia et al. 2018). Thus, the higher carbon values of males could indicate a more inshore foraging distribution compared to females. Interestingly, we did not detect seasonal nor spatial differences in carbon isotope values of gulls. Isotopic similarities across colonies agree with the overall weak effect of latitude in shaping $\delta^{13}C$ isoscapes in the western Portuguese coast (Ceia et al. 2018). Seasonal similarities in yellow-gull carbon isotope values suggest identical and consistent foraging distributions of each sex of this resident species throughout the annual cycle (Ceia et al. 2014). Additionally, Payo-Payo et al. (2015) also reported slightly higher, but not significant, nitrogen and carbon isotope values in male than in female yellow-legged gulls during the breeding season in the Mediterranean. However, there were significant differences in sulphur isotope values, indicating different foraging habitats between sexes (Payo-Payo et al. 2015).

Isotopic niche spaces also differed between sexes. Females exhibited larger isotopic niches than males in late breeding (reflected by P1 feathers) and non-breeding (reflected by S8 feathers) periods, suggesting that they are more generalists than males during most of the annual cycle, consuming a wider range of prey at the population-level. This is in accordance with isotopic mixing model results, suggesting that, besides fish, females also include a considerable amount of marine invertebrates in their diet year-round. Similar results were found in the closely related lesser black-backed gull (Camphuysen et al. 2015, Thaxter et al. 2015), including outside the breeding season (Baert et al. 2018). During the peak of the breeding season, sexes presented more similar isotopic niche widths, which could be related to gull breeding constraints. Pre-laying (reflected by RBC) and incubation (reflected by plasma) periods are highly demanding for both male and female yellow-legged gulls (Ramírez et al. 2010), and during this period they are more constrained in their foraging time and ranges (Mendes et al. 2018). We highlight that, although there is some temporal overlap in the synthesis of RBC and plasma (Hobson and Clark 1993), these tissues reflect different and consecutive periods during the breeding season (Votier et al. 2010, Ceia et al. 2014). Furthermore, isotopic niche overlap was low in all periods, except in late breeding, when sexes might increase overlap to restore body condition, and a complete isotopic niche segregation between sexes was found in the non-breeding period, when birds are no longer constrained by breeding. Importantly, during egg formation, female gulls are mainly income breeders, i.e. females allocate exogenous nutrients obtained by diet to egg (Hobson 2006). Thus, sexual segregation during the non-breeding season cannot be attributed to female specific storage of resources for egg formation.

Our findings indicate that sexual trophic segregation extends beyond different nutritional requirements during breeding, as suggested by the sexual size dimorphism hypothesis. Studies have shown that in seabirds, foraging differences between sexes are not limited to the breeding season (see reviews in Phillips et al. 2011, 2017). In gulls, dietary and foraging differences between sexes were previously reported during the breeding season (Watanuki 1992, Pons 1994, García-Tarrasón et al. 2015), and foraging (Bosman et al. 2012, Camphuysen and Gronert 2012, Baert et al. 2018) and trophic (Hobson and Bond 2012) sexual segregation during the non-breeding season were also detected. Although we cannot exclude the possibility that there are sex-specific nutritional requirements during the breeding season, the fact that sexual trophic segregation occurred throughout the annual cycle argues against the different nutritional requirements hypothesis as the main driver of sexual differences in trophic niches. Moreover, sexual differences occurred across very distinct islands along the western Iberian coast (see Table S2.1), which might indicate that segregation occurred independently of environmental variability, prey availability, and density-dependent competition. Additionally, our results revealed that sexual segregation occurred in two sampling years (i.e. 2017 in Sálvora Island and 2018 in Berlenga, Pessegueiro, and Deserta islands). Because feathers reflect dietary information from the year preceding the sampling (i.e. 2016 and 2017), while blood tissues reflect diet from the sampling year (i.e. 2017 and 2018), our results suggest that sexual segregation persist across years, even though we did not analyse the same period in different years. Yet, future studies with larger sample sizes and encompassing multiple years should better disentangle the drivers of the reported sexual trophic segregation in yellow-legged gulls.

Our results revealed that males consumed more fish than females, which may indicate that males foraged more in association with fisheries. Yellow-legged gulls are well known for opportunistic feeding at fishing boats (Oro and Ruiz 1997, Karris et al. 2018), including in the study area (Valeiras 2003, Oliveira et al. 2015, Matos et al. 2018). Fisheries may provide larger prey and demersal species that would otherwise be inaccessible to surface-feeders such as gulls (Tasker et al. 2000). These types of prey tend to have higher isotopic values compared to smaller (Cherel et al. 2010) and pelagic (Navarro et al. 2009a, Calado et al. 2018) species, which is in accordance with the higher isotopic values in male tissues. Feeding in association with fisheries can be highly competitive, where larger individuals may exclude smaller ones (Arcos et al. 2001). Sex-biased attendance to fishing boats was also found in other seabird species (e.g. Votier et al. 2013; Cortés et al. 2018), including gulls (García-Tarrasón et al. 2015, Tyson et al. 2015), and a review showed that global patterns of seabird bycatch are male-biased (Gianuca et al. 2017). The European Union applied a discard ban policy

(https://ec.europa.eu/fisheries/cfp/fishing_rules/discards/) to promote sustainable fisheries, which became fully implemented in 2019. However, the new implemented measures may have direct negative impacts on seabird populations (Bicknell et al. 2013). Our results suggest that such impacts are expected to be higher in male than in female yellow-legged gulls. However, future studies are needed to confirm the male-biased ratio of yellow-legged gulls attending fisheries and to understand the impacts of the discard ban on scavenger populations.

In conclusion, we found consistently higher nitrogen and carbon stable isotope values in males than in females throughout the year and in all four study colonies along the western Iberian coast, and isotope niche segregation between sexes was higher during the non-breeding period. These results argue against the different nutritional requirements hypothesis and suggest that sexual size dimorphism plays an important role in driving sexual trophic segregation in the yellow-legged gull. Additionally, isotope mixing models estimated a higher consumption of marine invertebrates by females and of fish by males, which may indicate a higher association with fisheries by male yellow-legged gulls. In view of the newly implemented discard ban policy, this sex-specific foraging behaviour may have major implications for yellow-legged gull populations, and potentially other sexually dimorphic seabird species. Our study highlights the need for close monitoring of sex-specific foraging behaviour in scavenger seabird populations.

**CHAPTER 3.**

JG Calado, JA Ramos; A Almeida, N Oliveira, VH Paiva. Seabird-fishery interactions and bycatch at multiple gears in the Atlantic Iberian coast. Ocean & Coastal Management, in press.

# Seabird-fishery interactions and bycatch at multiple gears in the Atlantic Iberian coast

**Abstract.** Seabirds are marine predators known to forage in association with fisheries, however detailed knowledge on seabird-fishery interactions remains scarce in several regions of the world. We quantified seabird-fishery interactions and bycatch in central Portuguese coastal waters (NE Atlantic) between 2016 and 2018 in four gears: purse-seines, longlines, gillnets and fishing traps. We mapped gear-specific fishing effort and seabird bycatch events and characterized fishery catches. Specific objectives were to determine separately for seabird-fishery interactions and bycatch (i) the gear with the highest rates, (ii) the most abundant species, and (iii) to assess the main drivers (i.e. year, season, gear, and fishery catch) of seabird-fishery interactions. Purse-seines had the highest seabird-fishery interactions, and the most abundant species were Yellow-legged and Lesser black-backed gulls, Northern gannet, and Cory's shearwater. Total seabird-fishery interactions varied inter-annually but not seasonally, indicating high total seabird numbers at fishing boats year-round. In contrast, higher fishery interactions were found during spring for Yellow-legged gulls. Age classes of individuals varied according to species, and fishery catches had a positive effect on seabird-fishery interactions. Seabird bycatch occurred mostly in longlines and within the 'Ilhas Berlengas' Special Protection Area. Northern gannet and Cory's shearwater were the most bycaught species, and species ecological traits seemed important in determining gear-specific bycatch. Our results suggest a strong influence of purse-seine and artisanal fisheries on seabirds in the NE Atlantic coast, and future studies should investigate the effects of these fisheries on seabird populations in other regions of the world.

**Keywords:** purse-seines; longlines; Yellow-legged gull; Northern gannet; Cory's shearwater.

## 1. Introduction

Seabird-fishery interactions have been documented in a wide range of seabird species (Tasker et al. 2000), however their quantification remains elusive in most parts of the world. Multiple fisheries management can have different effects on seabird populations (Arcos et al. 2001, Laneri et al. 2010), however most studies investigated only one gear type (e.g. (Valeiras 2003, Louzao et al. 2011, Cortés et al. 2017). Additionally, several studies evaluated interactions during restricted time periods (e.g. (Arcos and Oro 2002b, Paz et al. 2018) but seasonal and inter-annual variations are very likely to occur due to different intra-annual stages of seabirds (e.g. breeding and migration) and environmental variability (Lewison and Crowder 2003). Current knowledge is based on industrial longlines (Anderson et al. 2011)

and gillnets (Žydelis et al. 2013), while seabirds interacting with other fishery types such as purse-seines and artisanal fisheries remain largely undocumented (Pott and Wiedenfeld 2017). Moreover, seabird bycatch is the most studied seabird-fishery interaction, however several species forage in association with fisheries, which can influence their population dynamics (Votier et al. 2004, Foster et al. 2017). Additionally, the new European Union discard ban policy, which became fully implemented in 2019 under the Common Fisheries Policy (European Union 2015), is expected to reduce food availability to scavenger species and thus affect seabird-fishery interactions (Bicknell et al. 2013). Therefore, adequate and detailed knowledge on both seabird-fishery interactions and bycatch are key to fully understand seabird ecology and apply appropriate management and conservation measures.

Commercial fisheries use a diverse array of fishing gears that affect seabirds differently (Wagner and Boersma 2011). Purse-seines enables the active catch of fish near the sea surface while the net is still in the water during hauling operations (Arcos and Oro 2002b). Additionally, slipping (i.e. deliberate release of part of the catch over the floating line; (Stratoudakis and Marçalo 2002) also provides facilitated foraging opportunities for seabirds that can easily catch slipped fish, which suffer from physical damage and behavioural impairments (Marçalo et al. 2013). In Portugal, purse-seines were identified as a threat to the critically endangered Balearic shearwater *Puffinus mauretanicus* (Lowe, 1921) (Oliveira et al. 2015), which uses Portuguese waters during the non-breeding period (Pérez-Roda et al. 2017). Longlines use baited hooks, thus providing additional food for seabirds (Sánchez and Belda 2003). This fishery type was previously recorded as the most dangerous for seabirds in Portuguese waters (Oliveira et al. 2015). Gillnets use vertical mesh nets to capture fish (He 2006). In the northeastern Atlantic, gillnets were associated with the collapse of the Common guillemot *Uria aalge* (Pontoppidan, 1763) population in Iberia (Munilla et al. 2007) and decreased adult survival of the European shag *Gulosus aristotelis* (Linnaeus, 1761) in Galicia, Spain (Velando and Freire 2002).

In the Atlantic Iberian coast seabird-fishery interactions are poorly known (see reviews in (Žydelis et al. 2013, Gianuca et al. 2017, Pott and Wiedenfeld 2017); but see (Valeiras 2003, Oliveira et al. 2015) despite the importance of this area as a valuable foraging ground for several breeding species and as a key migratory corridor for non-breeding species (Pereira et al. 2018). This coast is characterized by high productivity and intense seasonal upwelling, targeted by both seabirds and fisheries (Veiga-Malta et al. 2019). Portuguese fisheries are dominated by two fishing fleets, the polyvalent fleet (67% of boats and 46% of landings) and the purse-seine fleet (14% of boats and 42% of landings; (INE 2019). Overall, fisheries that operate in Portuguese waters are mainly coastal, and 90% of boats have less than 12 m

(INE 2019). Polyvalent (or multi-gear) boats can use longlines, gillnets, and fishing traps, but do not discriminate each activity, leading to unknown gear-specific fishing effort and seabird bycatch rates.

In this study, onboard observers monitored purse-seines, longlines, gillnets, and fishing traps from 2016 to 2018 to quantify gear-specific seabird-fishery interactions in central Portuguese coastal waters. This is the first multi-gear study investigating simultaneously seabird-fishery interactions and bycatch in Atlantic Iberian waters, with special focus on the events occurring within the 'Ilhas Berlengas' Special Protection Area (SPA). We mapped gear-specific fishing effort and bycatch events and characterized fishery catch species composition and amounts. Specific objectives were to determine separately for seabird-fishery interactions and bycatch (i) the gear with the highest rates, (ii) the most abundant species, and (iii) to assess the main drivers (i.e. year, season, gear, and fishery catch) of total seabird interactions as well as species-specific fishery interactions (for the three most abundant species). Given the higher catches of purse-seines (INE 2019), we expected this gear to attract more seabirds. Yellow-legged gull *Larus michahellis* (Naumann, 1840) and Northern gannet *Morus bassanus* (Linnaeus, 1758) should be the most common species interacting with fishing boats due to their high abundance (Meirinho et al. 2014) and scavenging behaviour (Valeiras 2003). Inter-annual and seasonal variability in seabird-fishery interactions were expected due to environmental conditions and the presence of different seabird species in Portuguese waters throughout the year. Yellow-legged gull, which is a resident species, should interact more with fishing boats during breeding (i.e. spring and summer), while Northern gannet, a non-breeding species, should interact more during winter (Meirinho et al. 2014). Fishery catches were expected to positively influence seabird numbers as the result of higher prey availability, including discards (Oro and Ruiz 1997). Seabird bycatch rates should be higher at longlines and for Northern gannet and Balearic shearwater (Oliveira et al. 2015).

## 2. Methods

## 2.1. Study area

The study was performed in the northeastern Atlantic, covering one of the main fishing harbours in Portugal (i.e. Peniche; (INE 2019) and the Berlengas archipelago; Figure 3.1). Their surrounding waters were identified as a marine Important Bird and Biodiversity Area (IBA) and designated as a Specially Protected Area (SPA). Berlenga archipelago holds several seabird colonies, including the largest Portuguese colony of Yellow-legged gull (Morais et al. 1998), important populations of Cory's shearwater

*Calonectris borealis* (Cory, 1881) (Lecoq et al. 2011), the only colony of Band-rumped storm-petrel *Hydrobates castro* (Harcourt, 1851) in continental Portugal (Carreiro et al. 2020), the main Portuguese colony of European shag (Lecoq et al. 2012), and small numbers of Lesser black-backed gulls *Larus fuscus* (Linnaeus, 1758) (Meirinho et al. 2014). The study area also serves as an important foraging ground for several non-breeding species. The most common include the Northern gannet and the Balearic shearwater (Elmberg et al. 2013).
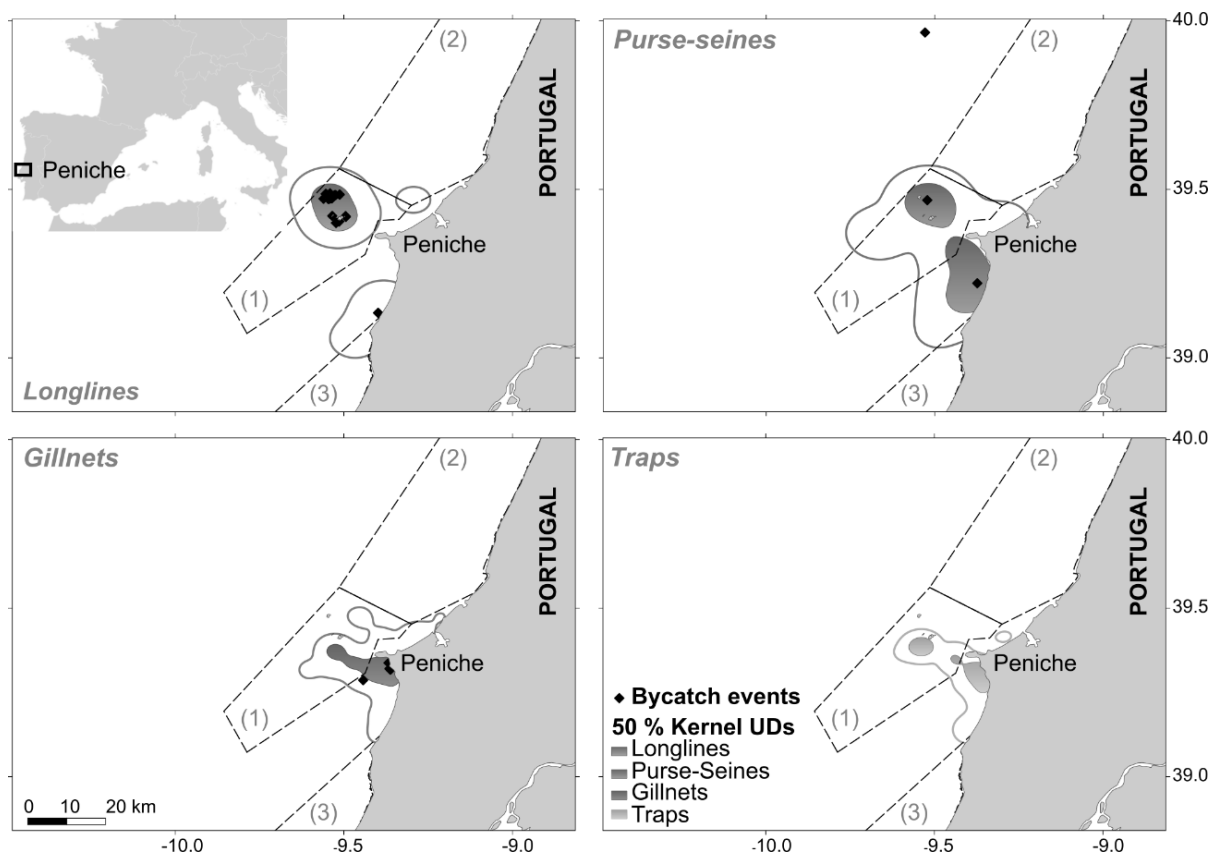


**Figure 3.1.** Study area showing gear-specific fishing effort (95% - solid line contours, and 50% - areas, kernel Utilization Distributions) and seabird bycatch events (black symbols). The locations of Special Protection Areas (1- Ilhas Berlengas SPA, 2 – Ria Aveiro-Nazaré SPA, and 3 – Cabo Raso SPA) and the Peniche fishing harbour are also indicated in dashed lines.

## 2.2. Data collection

Data was obtained from 17 fishing boats, 313 daily trips, and 3901 sets. Trained observers monitored fishing activities during 3 consecutive years (from January 2016 to December 2018), covering

four types of gear: purse-seines (N = 103 trips), demersal longlines (N = 85 trips), bottom gillnets (including single, double, and triple (i.e. trammel) nets; N = 106 trips), and traps (i.e. cage and shelter traps; N = 95 trips). Longlines, gillnets, and traps are used in polyvalent boats that are usually licenced to operate multiple gears, which means they can use more than one gear type during a single trip. Fishing sets were defined as the setting or the hauling separately due to the possibility of consecutive settings, except for purse-seines, where fishing set was defined from moment the net was set in the water until the last fish was taken aboard. Seabirds were counted every 15 minutes, focussing on the area of the fishing gear. Age class (adult *vs* immature) was also registered when possible. Directional flights and distances >100 m were removed from the analysis in order to only account for seabirds that were interacting with fishing boats during active fishing sets. Seabird counts were not performed during night settings due to poor visibility. However, observers recorded seabird bycatch and fishery catch species and quantities during all monitored fishing sets. To calculate seabird bycatch rates, we only considered hauling because no bycatch was recorded during setting or hauling of longlines or gillnets, meaning that birds were entangled during the time the gear was passively fishing. Fishing traps trips and sets were also removed because no seabird bycatch was recorded in this gear. Fishery catch was divided into retained (if retained on board) and discarded (if returned to the sea after being hauled aboard). The GPS location of fishing sets and seabird bycatch was also recorded. For visualization purposes, 95% and 50% kernel Utilization Distributions were built under *adehabitatHR* (Calenge 2006) for each gear type (i.e. longlines, purse-seines, gillnets, and traps) operating in the area.

## 2.3. Data analysis

Seabird-fishery interactions were recorded in 252 trips and 773 sets. Hurdle models assuming a binomial distribution for presence–absence data and a negative binomial distribution for count data were performed to describe interactions, using the R package *glmmTMB* (Brooks et al. 2017). Analyses were performed considering all seabird species and the three most common species at fishing boats (i.e. Yellow-legged gull, Northern gannet, and Cory's shearwater). All models included year, season, gear type, and fishery catch (log transformed units) as predictors, except for Cory's shearwater. This species was not observed during winter, therefore, this season was not included in the analysis, and neither season nor year were included as predictors in the model. Interactions between predictors were also tested and dropped if not significant, starting with a full model and dropping interactions using backward stepwise selection. Fishing trip was included in all models as a random effect to account for the non-independence

of sets within the same trip. *DHARMa* package (Hartig 2019) was used for model validation, and post-hoc analyses were performed using estimated marginal means and Tukey's p-value adjustment within the *emmeans* package (Lenth 2019). Age was recorded for 83.4% and 99.6% of Yellow-legged gulls and Northern gannet, respectively, and chi-squared tests were used to compare the number of adults and immatures interacting with fishing boats. Fisher's exact test (efficient with low expected values) was used to evaluate bycatch susceptibility (i.e. compare the number of seabird bycatch with the number of seabird interactions) of the species bycaught and of each gear type. All analyses were performed with R software ver. 3.6.1 (R Core Team 2019), and significance was set at alpha = 0.05.

## 3. Results

### 3.1. Fishery catches

Sardine *Sardina pilchardus* (Walbaum, 1792) was the most caught species in the monitored fisheries from the Peniche fishing fleet (Table 3.1). This species was also the most discarded, followed by Bogue *Boops boops* (Linnaeus, 1758) and Chub mackerel *Scomber colias* (Gmelin, 1789). The latter was also commercially important, being the second most caught species. Other mackerels (i.e. Blue jack mackerel *Trachurus picturatus* (Bowdich, 1825), Horse mackerel *T. trachurus* (Linnaeus, 1758)*,* and Atlantic mackerel *Scomber scombrus* (Linnaeus, 1758)) were also commercially important species, as well as European anchovy *Engraulis encrasicolus* (Linnaeus, 1758) and Black seabream *Spondyliosoma cantharus* (Linnaeus, 1758). Common octopus *Octopus vulgaris* (Cuvier, 1797) was the most important commercial non-fish species, caught mainly by traps. Garfish *Belone belone* (Linnaeus, 1760) and Henslow's swimming crab *Polybius henslowii* (Leach 1820) were relatively abundant in fishery catches, however the majority of individuals were discarded (see Table 3.1).

### 3.2. Seabird-fishery interactions

Seabirds were present in 93% of trips and 88% of sets. The total number of individuals recorded was 26,515 from at least 17 species (Table 3.2). The most common were Yellow-legged/Lesser black-backed gulls, followed by Yellow-legged gulls, Northern gannets, and Cory's shearwater. Overall, *Larus* spp. accounted for 91% of the total species interacting with fishing boats. The age of seabirds interacting with fishing boats differed according to species. Yellow-legged gulls were mainly adults (78%; $\chi^2 = 1562.8$, $P < 0.001$), while Northern gannets were mainly immatures (81%; $\chi^2 = 613.4$, $P < 0.001$; Figure 3.2).

**Table 3.1.** Main fishery catch species in the monitored fisheries from Peniche fishing fleet (N = 252 trips, N = 773 sets). Percentages were calculated by catch type and by species. Species are order by decreasing total catch.

| Species | Percentages by catch (%) | | | Percentages by species (%) | |
|---|---|---|---|---|---|
| | Total | Retained | Discarded | Retained | Discarded |
| *Sardina pilchardus* (Walbaum, 1792) | 51.0 | 49.8 | 64.9 | 89.1 | 10.9 |
| *Scomber colias* (Gmelin, 1789) | 25.4 | 26.9 | 9.5 | 96.8 | 3.2 |
| *Trachurus picturatus* (Bowdich, 1825) | 11.2 | 12.2 | 0.7 | 99.5 | 0.5 |
| *Trachurus trachurus* (Linnaeus, 1758) | 5.6 | 6.1 | 0.01 | 100.0 | 0.01 |
| *Boops boops* (Linnaeus, 1758) | 1.9 | 0.1 | 21.5 | 4.8 | 95.2 |
| *Trachurus mediterraneus* (Steindachner, 1869) | 1.9 | 2.1 | - | 100.0 | - |
| *Engraulis encrasicolus* (Linnaeus, 1758) | 1.6 | 1.8 | - | 100.0 | - |
| *Scomber scombrus* (Linnaeus, 1758) | 0.5 | 0.5 | 0.7 | 87.0 | 13.0 |
| *Belone belone* (Linnaeus, 1760) | 0.2 | 0.1 | 1.5 | 27.6 | 72.4 |
| *Spondyliosoma cantharus* (Linnaeus, 1758) | 0.1 | 0.1 | 0.01 | 99.2 | 0.8 |
| *Trachurus* sp. (Rafinesque, 1810) | 0.1 | 0.1 | - | 100.0 | - |
| *Octopus vulgaris* (Cuvier, 1797) | 0.1 | 0.1 | 0.02 | 98.3 | 1.7 |
| *Polybius henslowii* (Leach 1820) | 0.1 | 0.001 | 0.8 | 1.8 | 98.2 |

**Table 3.2.** Seabird species diversity at fishing boats. Number (N), percentage (%), and average birds/trip (N = 252 trips) of each species and total seabirds are shown.

| Species | N | % | Birds/trip |
|---|---|---|---|
| *Larus michahellis/fuscus* | 17319 | 65.3 | 68.7 |
| *Larus michahellis* (Naumann, 1840) | 6039 | 22.8 | 24.0 |
| *Morus bassanus* (Linnaeus, 1758) | 1578 | 6.0 | 6.3 |
| *Calonectris borealis* (Cory, 1881) | 495 | 1.9 | 2.0 |
| *Larus* sp. (Linnaeus, 1758) | 452 | 1.7 | 1.8 |
| *Larus fuscus* (Linnaeus, 1758) | 315 | 1.2 | 1.3 |
| *Puffinus mauretanicus* (Lowe, 1921) | 94 | 0.4 | 0.4 |
| *Catharacta skua* (Brünnich, 1764) | 70 | 0.3 | 0.3 |
| *Hydrobates pelagicus* (Linnaeus, 1758) | 57 | 0.2 | 0.2 |
| *Alca torda* (Linnaeus, 1758) | 23 | 0.1 | 0.1 |
| *Gulosus aristotelis* (Linnaeus, 1761) | 18 | 0.1 | 0.1 |
| *Thalasseus sandvicensis* (Latham, 1787) | 16 | 0.1 | 0.1 |
| *Ardenna gravis* (O'Reilly, 1818) | 12 | 0.05 | 0.05 |
| *Larus melanocephalus* (Temminck, 1820) | 7 | 0.03 | 0.03 |
| *Phalacrocorax carbo* (Linnaeus, 1758) | 5 | 0.02 | 0.02 |
| *Larus argentatus* (Pontoppidan, 1763) | 4 | 0.02 | 0.02 |
| *Chlidonias niger* (Linnaeus, 1758) | 3 | 0.01 | 0.01 |
| *Hydrobates* sp. (Boie, 1822) | 3 | 0.01 | 0.01 |
| *Larus ridibundus* (Linnaeus, 1766) | 3 | 0.01 | 0.01 |
| *Stercorarius pomarinus* (Temminck, 1815) | 2 | 0.01 | 0.01 |
| Total | 26515 | 100.0 | 105.2 |

### 3.3. Factors influencing seabird-fishery interactions

Models revealed that total seabird-fishery interactions were influenced by year ($\chi^2$ = 16.9, P < 0.001), gear type ($\chi^2$ = 96.6, P < 0.001), and fishery catch ($\chi^2$ = 8, P = 0.005), but not season. The number of birds was higher in 2016, in purse-seines, and positively associated with fishery catch (Table 3.3). Tukey´s post-hoc tests showed that significantly higher values were found in 2016 compared to both 2017 and 2018 and in purse-seines compared to all other gear types.

Yellow-legged gull interactions were influenced by year ($\chi^2$ = 9.3, P < 0.001), season ($\chi^2$ = 11.5, P = 0.009), and gear type ($\chi^2$ = 72.1, P < 0.001). Fishery catch was not significant in explaining Yellow-legged gull numbers, however the interactions gear*catch ($\chi^2$ = 16.4, P < 0.001) and season*catch ($\chi^2$ = 10.7, P = 0.01) were significant. The number of gulls was higher in 2016, during spring, in purse-seines, and positively associated with fishery catch during autumn and in longlines (Table 3.3). Tukey´s post-hoc tests showed that significantly higher values were found in 2016 and 2017 compared to 2018, but no difference was found between 2016 and 2017. Post-hoc tests also showed significantly higher values in spring than in winter and autumn, but statistically similar to summer. Purse-seines presented significantly higher values compared to all other gear types.

Regarding Northern gannets, we only detected the influence of gear type ($\chi^2$ = 9.5, P = 0.02) and of the interaction year*catch ($\chi^2$ = 6.1, P = 0.05) in explaining gannet interactions. The number of gannets was higher in purse-seines and longlines and was slightly negatively associated with fishery catch in 2016 (Table 3.3). Tukey´s post-hoc tests revealed that longlines presented significantly higher values compared to traps.

Concerning Cory's shearwater, both gear type ($\chi^2$ = 32.2, P < 0.001) and fishery catch ($\chi^2$ = 4.4, P = 0.04) were significant in explaining the interactions with fishing boats. The number of Cory's shearwater was higher in longlines and positively associated with fishery catch (Table 3.3). Tukey´s post-hoc tests revealed that longlines presented significantly higher values than all other gear types.

Interestingly, in all models, fishery catch was significant in explaining the number of seabirds at fishing boats but not their presence, except for Northern gannet, where catch was significant in both (Table 3.3).

**Table 3.3.** Coefficients (±SD) of each variable included in hurdle models, considering all seabird species, the three most common species at fishing boats (i.e. Yellow-legged gull *Larus michahellis,* Northern gannet *Morus bassanus*, and Cory's shearwater *Calonectris borealis*). Coefficients of categorical factors (i.e. all except "Catch") were calculated relative to their reference categories (whose coefficients are zero): 2016 (Year), autumn (Season), and longlines (Gear). Abundance corresponds to the count part and presence corresponds to the zero part of hurdle models. Fishing trip was included in all models as a random effect. Values significantly different from the reference categories are highlighted in bold.

| Variables | Categories | All species | | *Larus michahellis* | | *Morus bassanus* | | *Calonectris borealis* | |
|---|---|---|---|---|---|---|---|---|---|
| | | Abundance | Presence | Abundance | Presence | Abundance | Presence | Abundance | Presence |
| Year | 2017 | **-1.00 ± 0.29** | -1.46 ± 0.85 | -0.21 ± 0.24 | **-0.90 ± 0.31** | **-2.77 ± 1.14** | **1.39 ± 0.41** | - | - |
| | 2018 | **-1.14 ± 0.36** | -0.90 ± 1.10 | **-0.85 ± 0.30** | 0.02 ± 0.39 | **-3.98 ± 1.52** | 0.53 ± 0.51 | - | - |
| Season | Spring | 0.16 ± 0.29 | 1.91 ± 0.98 | **1.34 ± 0.32** | **-1.09 ± 0.40** | -1.09 ± 0.91 | **0.98 ± 0.36** | - | - |
| | Summer | -0.42 ± 0.27 | 1.13 ± 0.92 | 0.58 ± 0.30 | **-0.77 ± 0.38** | -1.70 ± 0.88 | **1.22 ± 0.36** | - | - |
| | Winter | -0.16 ± 0.30 | 1.96 ± 1.02 | 0.43 ± 0.35 | -0.71 ± 0.44 | 0.67 ± 0.81 | 0.67 ± 0.35 | - | - |
| Gear | Purse-seines | **2.01 ± 0.33** | **-3.19 ± 1.24** | **2.00 ± 0.40** | **-1.43 ± 0.52** | 0.65 ± 1.02 | 0.20 ± 0.47 | **-5.57 ± 1.26** | 0.76 ± 0.71 |
| | Gillnets | -0.31 ± 0.31 | **-3.20 ± 0.99** | **0.92 ± 0.40** | **-2.08 ± 0.47** | -1.27 ± 0.95 | 0.57 ± 0.37 | **-3.94 ± 0.97** | **2.29 ± 0.77** |
| | Traps | **-1.24 ± 0.29** | **-2.63 ± 0.84** | **-0.76 ± 0.37** | **-1.49 ± 0.43** | **-2.72 ± 1.00** | **1.73 ± 0.38** | **-3.04 ± 0.93** | **2.51 ± 0.74** |
| Catch | | **0.19 ± 0.07** | -0.27 ± 0.27 | **1.21 ± 0.34** | -0.43 ± 0.41 | **-1.55 ± 0.57** | **0.54 ± 0.26** | **0.72 ± 0.34** | 0.12 ± 0.18 |
| Gear*Catch | Purse-seines:Catch | - | - | **-0.97 ± 0.35** | 0.09 ± 0.41 | - | - | - | - |
| | Gillnets:Catch | - | - | **-1.28 ± 0.38** | -0.25 ± 0.47 | - | - | - | - |
| | Traps:Catch | - | - | -0.48 ± 0.39 | -0.42 ± 0.49 | - | - | - | - |
| Season*Catch | Spring:Catch | - | - | **-0.47 ± 0.15** | 0.39 ± 0.22 | - | - | - | - |
| | Summer:Catch | - | - | **-0.26 ± 0.12** | 0.25 ± 0.20 | - | - | - | - |
| | Winter:Catch | - | - | -0.24 ± 0.26 | 0.43 ± 0.41 | - | - | - | - |
| Year*Catch | 2017:Catch | - | - | - | - | **1.37 ± 0.66** | **-0.66 ± 0.30** | - | - |
| | 2018:Catch | - | - | - | - | **1.75 ± 0.71** | -0.37 ± 0.32 | - | - |
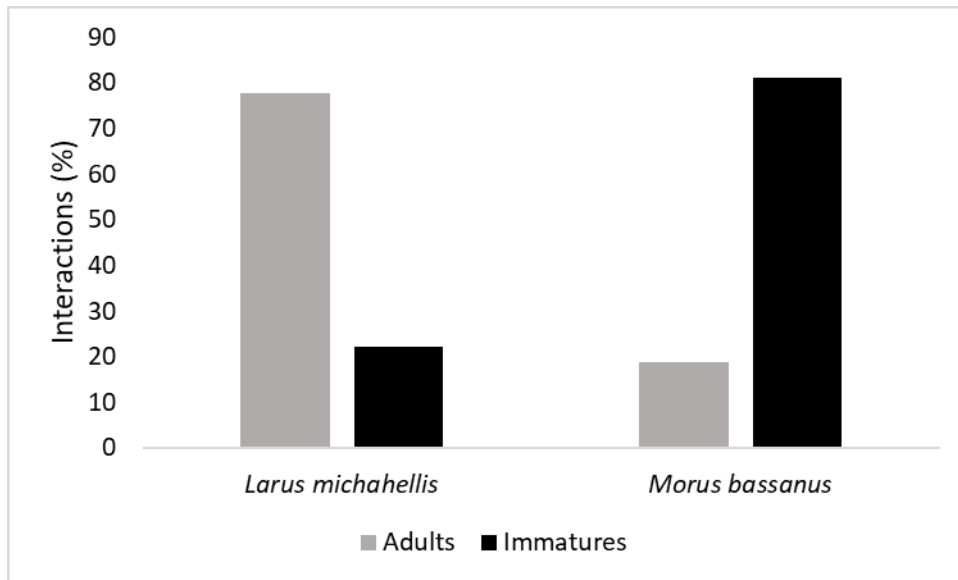
**Figure 3.2.** Age classes (%) of Yellow-legged gulls *Larus michahellis* and Northern gannets *Morus bassanus* interacting with fishing boats.

## 3.4. Seabird bycatch

Bycatch occurred in 8% of trips and 0.02% of sets, accounting for 67 seabirds of at least 6 species (Figure 3.3). Overall, bycatch was 0.24 birds/trip and 0.04 birds/set. Longlines had the highest bycatch rate (88%; 0.69 birds/trip; 0.07 birds/set), while purse-seines and gillnets had much lower bycatch rates (both 6%; 0.04 birds/trip; 0.01 birds/set; Figure 3.4). No seabird bycatch was recorded in fishing traps. Northern gannet was the most bycaught species (N = 51, 75%), with just 1 individual caught by gillnets, while all others were caught by longlines. All bycaught individuals were immatures. For this species, bycatch occurred in 15% of all longline trips (0.59 birds/trip) and 3% of all longline sets (0.06 birds/set). Cory's shearwater was exclusively caught by longlines (N = 8), while Great cormorant *Phalacrocorax carbo* (Linnaeus, 1758) (N = 1), and European shag (N = 2) were exclusively caught by gillnets. Gulls were caught by purse-seines (N = 3) and longlines (N = 1). Great shearwater *Ardenna gravis* (O'Reilly, 1818) was caught by purse-seines (N = 1). Bycatch in longlines occurred more offshore and mostly inside the 'Ilhas Berlengas' SPA, while in gillnets bycatch occurred mainly along the coast (Figure 3.1).

Bycatch susceptibility differed among species (Fisher's exact test, P < 0.001). All species bycaught, except gulls, were more frequently caught than expected based on their interactions (Figure 3.3). Gulls showed the opposite effect (i.e. less frequently caught than expected). Bycatch susceptibility was also higher in some gear types (Fisher's exact test, P < 0.001); Longlines caught more birds than

expected based on the number of seabirds interacting with this fishery, while purse-seines and gillnets showed the opposite effect (Figure 3.4).
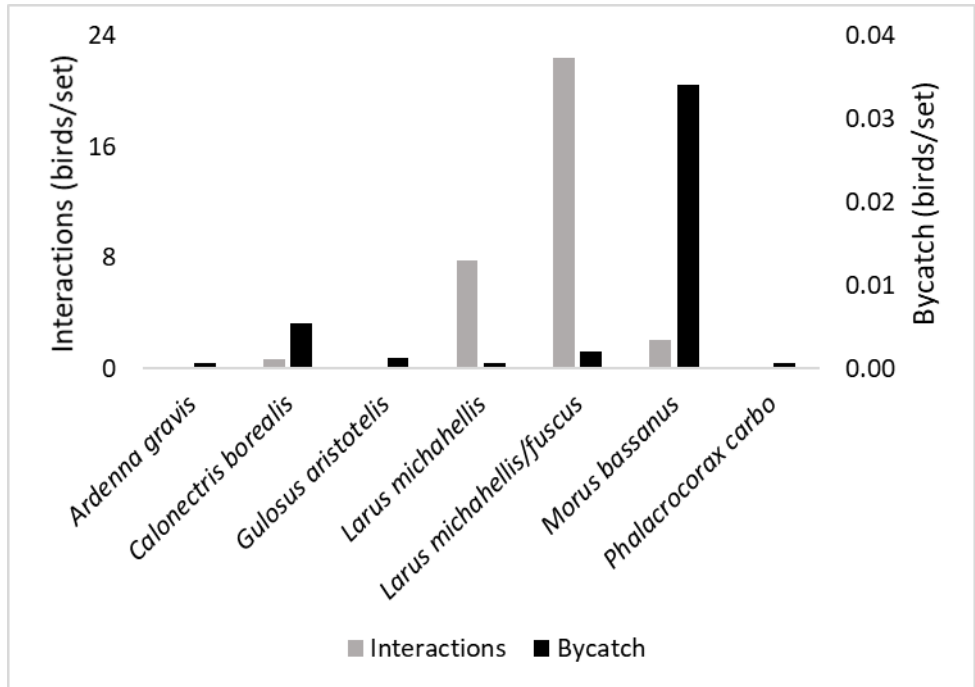


**Figure 3.3.** Average seabird-fishery interactions (grey) and bycatch (black) for each species.
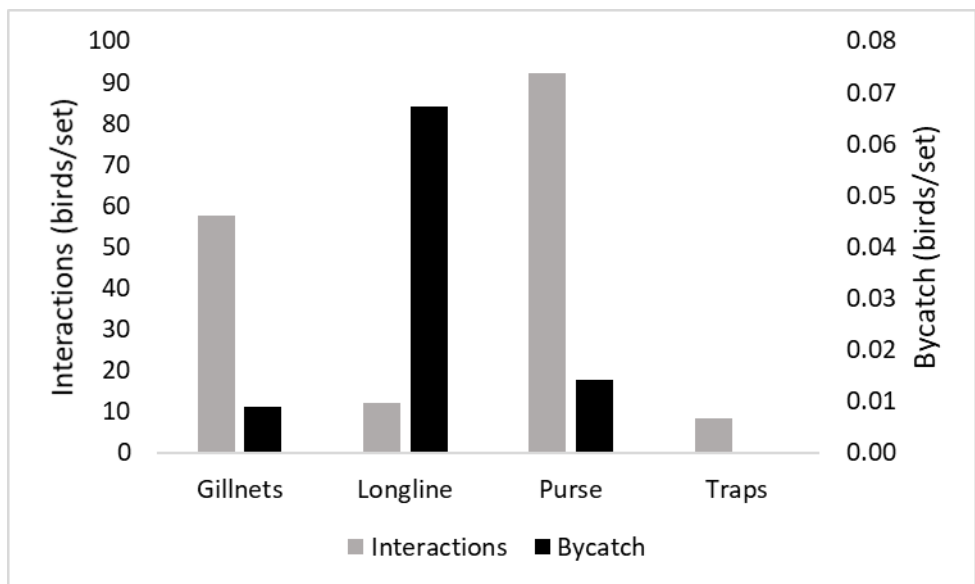


**Figure 3.4.** Average seabird-fishery interactions (grey) and bycatch (black) in each gear type.

## 4. Discussion

This study showed high seabird-fishery interactions for the Peniche fishing fleet, in the central Portuguese coast. Most common species interacting with fisheries were Yellow-legged and Lesser black-backed gulls, Northern gannet, and Cory's shearwater. Excluding gulls, the critically endangered Balearic shearwater was the third most abundant species interacting with fishing boats, yet no bycatch was recorded for this species. Northern gannet and Cory's shearwater were the most bycaught seabirds. Purse-seine was the gear with higher seabird-fishery interactions, while longline had the highest bycatch rate. A positive association was detected between seabird numbers at fishing boats and fishery catch quantities. Two small pelagic fish species, Sardine and Chub mackerel, comprised the majority of the catches.

### 4.1. Ecological drivers of seabird-fishery interactions

Marked inter-annual variability in seabird-fishery interactions was found, with higher numbers of seabirds at fishing boats in 2016. Fishery landings at Peniche fishing harbour were lower in 2016 compared to both 2017 (18% less) and 2018 (10% less; see Table S3.1). The landings of Sardine and Chub mackerel, which are both targeted by fisheries and consumed by seabirds (Wise et al. 2019), were also lower in 2016: 55% less Sardine than in 2017, and 46% less Chub mackerel than in 2018. The lower fishery landings in 2016 suggest lower marine prey availability, which may have led seabirds to increase foraging in association with fisheries, similarly to previous studies (Arcos and Oro 2002b, Paiva et al. 2017).

Models revealed that season was not significant in explaining total seabird-fishery interactions, indicating high seabird numbers at fishing boats all year-round. Unexpectedly, season was also not significant in explaining Northern gannet interactions. This might be explained by the higher number of immatures at fishing boats, which can remain in Portuguese waters all year-round (Veron and Lawlor 2009). In contrast, the number of Yellow-legged gulls interacting with fishing boats was higher in spring, which coincides with the early breeding season of this species at Berlenga (Mendes et al. 2018). During chick-rearing, breeding adults are constrained in their foraging ranges and daily activity patterns (Phillips et al. 2017), which might have led to slightly less interactions with fishing boats in summer when compared to spring. Autumn and winter correspond to the non-breeding season, when gulls can disperse and exploit different food resources (e.g. from landfills; (Egunez et al. 2018), explaining their lower

interactions with fishing boats at this time of the year. The higher number of adults interacting with fisheries compared to immatures might be related with competitive exclusion (Gause 1934), whereby larger and more experienced individuals such as adults may displace smaller and inexperienced immatures (Hudson and Furness 1989). Overall, these results indicate that total seabird numbers at fishing boats were similar throughout the year, however species composition differed seasonally, and age classes of individuals also varied according to species.

Purse-seines attracted higher total seabird numbers compared to all other gear types, which could be related with boat sizes, fishery catch quantities, and targeted species. Purse-seines are usually larger and catch greater amounts of fish per set than polyvalent boats (INE 2019). Target species of purse-seines are small pelagic fish, mostly Sardine and Chub mackerel, which are also the main prey for seabirds (Wise et al. 2019), whereas longlines and gillnets target both pelagic and demersal fish, and octopus was the main caught species in traps. Additionally, purse-seines facilitate active foraging by seabirds during hauling operations (Arcos and Oro 2002b) and slipping (Stratoudakis and Marçalo 2002). Gillnets had highly variable seabird-fishery interactions, with high numbers on few fishing trips. Indeed, 3 fishing sets from different trips on the same boat in the autumn and winter of 2016 comprised 50% of all seabird numbers at gillnets. Yellow-legged gulls interacted more with purse-seines, whereas Cory's shearwaters interacted more with longlines. Northern gannets interacted with both purse-seines and longlines, although slightly more with longlines. This species is well known for feeding in association with industrial fisheries (e.g. (Valeiras 2003, Le Bot et al. 2019), but their presence in artisanal fisheries was not previously recorded in the North Atlantic (Votier et al. 2013). Species-specific attendance at each fishing gear could be related with foraging behaviour and diving capabilities. Gulls are surface-feeders (Schwemmer and Garthe 2005), whereas gannets can plunge and dive (Ropert-Coudert et al. 2009) and thus reach sank baited hooks of longlines. Cory's shearwater can perform shallow dives and reach hooks near the surface in artisanal longlines (Cortés et al. 2017). Also, the greater use of longlines by this species could be related with increased inter-specific competition with gulls at purse-seines (Arcos et al. 2001).

Fishery catch had a positive effect on total seabird interactions with fishing boats regardless of gear type. Interestingly, the amount of catch was not significant in explaining Yellow-legged gull interactions, except in longlines and in autumn (i.e. the season with lower interactions), which indicates that gull numbers were relatively high regardless of the amount of catches. Purse-seines attract and concentrate fish near the sea surface (Arcos and Oro 2002b), therefore gulls can forage actively in

association with purse-seines and obtain fish even with low catches. On the other hand, gulls might rely more on fishery discards in longlines. Additionally, longlines and traps had the lowest catch per set, which could make them less attractive to surface-feeders such as gulls unless high amounts of discards are produced. Cory's shearwater numbers were also positively associated with fishery catch, suggesting the usage of fishery discards/ offal, in accordance in previous studies in the Mediterranean and Atlantic Ocean (Valeiras 2003, Louzao et al. 2011). Regarding Northern gannets we detected a slightly negative association with fishery catches in 2016. This was the year with higher seabird-fishery interactions. Since Yellow-legged gull numbers were higher in longlines with higher fishery catches, Northern gannets would be greatly outnumbered and thus could have higher feeding success at fishing boats with slightly less catches (Gause 1934). Nevertheless, catch was positively associated with gannet presence (i.e. 0/1 data), suggesting the use of fishery discards, in accordance with previous studies (e.g. (Patrick et al. 2015).

## 4.2. Seabird bycatch patterns

Contrary to seabird-fishery interactions, seabird bycatch was higher at longlines and affected mostly Northern gannets and Cory's shearwaters. Surprisingly, no bycatch of Balearic shearwaters was detected, contrasting with previous data for mainland Portugal, where multiple individuals were caught in few purse-seine sets (Oliveira et al. 2015). This could be related to the spatial distribution of the species that mainly uses northern Portuguese waters (Oppel et al. 2012, Araújo et al. 2017), or to limited coverage of the observer program. Indeed, large mortality events are difficult to detect in small-scale fisheries due to the large number of small boats (Genovart et al. 2017). Therefore, future studies should examine further the impact of Portuguese fisheries in the critically endangered Balearic shearwater.

Species ecological traits seemed important in determining gear-specific bycatch, as reviewed by (Zhou et al. 2019). Longlines affected mainly plunge diving and scavenging species, i.e. Northern gannet and Cory's shearwater, while gillnets affected mainly deep-diving and non-scavenging seabirds, i.e. Great cormorant and European shag As expected due to their surface-feeding and scavenging behaviour, gulls were mostly caught by purse-seines. Overall, longlines had the highest bycatch rate and species diversity and occurred mainly within the 'Ilhas Berlengas' SPA, which raises serious conservation and management concerns. Our results agree with a previous study on bycatch in mainland Portugal (Oliveira et al. 2015) and suggest that longlines can have significant impacts on breeding (e.g. Cory´s shearwater) and non-breeding (e.g. Northern gannet) species. In the Mediterranean, previous studies reported increased

seabird bycatch at longlines with diminished discard availability (Laneri et al. 2010, Soriano-Redondo et al. 2016). Therefore, seabird-fishery interactions in the Atlantic Iberian coast should be closely monitored to investigate the impacts of the newly implemented EU discard ban policy (European Union 2015).

# CHAPTER 4.

JG Calado, SN Veríssimo, VH Paiva, R Ramos, PT Vaz, D Matos, J Pereira, C Lopes, N Oliveira, A Quaresma, FR Ceia, A Velando, JA Ramos. Influence of fisheries on the spatio-temporal feeding ecology of gulls along the western Iberian coast. Marine Ecology Progress Series, in press.

# Influence of fisheries on the spatio-temporal feeding ecology of gulls along the western Iberian coast

**Abstract.** Gulls are highly opportunistic seabirds, and the exploitation of fishery discards led to many population increases worldwide. We investigated the importance of fish in the diet of yellow-legged and Audouin's gulls and assessed the influence of fishery discards in their feeding ecology. We collected pellets in four islands along the western Iberian coast during pre-breeding, breeding, and post-breeding seasons and from 2014 to 2018. Stable isotopes (adult blood and chick and adult feathers) were used to investigate spatial, seasonal, and inter-annual differences in their feeding ecology. We used pellet, stable isotope ($\delta^{15}$N, $\delta^{13}$C, and $\delta^{34}$S), and biochemical (triglycerides, uric acid, total protein, and carotenoids in adult plasma) analyses to investigate their relationships with fish landings across the annual cycle. Results revealed that the fish species consumed by gulls matched those landed by local fisheries in all study islands, and there was a positive association of pelagic and demersal fish diets with fish landing quantities in two islands. $\delta^{34}$S values suggest different self-feeding and chick provisioning strategies in relation to fisheries. $\delta^{15}$N values exhibited strong negative correlations with fish landings, and triglycerides were positively correlated with pelagic but not with demersal fish landing quantities, suggesting that gulls fed more on lower trophic level and higher energetic content pelagic fish than on demersal fish. Overall, our results based on several techniques suggest that gull feeding ecology was linked to fishery discards, which in view of the new landing obligation may have major implications for both gull populations across Europe.

**Keywords:** *Larus michahellis*; *Larus audouinii*; pellets; stable isotopes; plasma biochemistry; fishery discards.

## 1. Introduction

Fishing activities have major impacts on marine ecosystems (Pauly et al. 2005), especially in coastal areas which are characterized by high biodiversity and intense fishing pressure (Halpern et al. 2015). Commercial fisheries capture large amounts of non-target organisms, and the discarding of these unwanted catches has become a matter of global concern (Bellido et al. 2011). This non-selective fishing and subsequent discarding not only have negative effects on fishery stocks but also have community and ecosystem level consequences (Catchpole et al. 2005). For example, fishery discards represent an important anthropogenic food subsidy for scavenger species (Kaiser and Hiddink 2007, Sherley et al.

2020). To promote a sustainable fishery management, the European Union (EU) implemented a landing obligation under the new Common Fisheries Policy (CFP) that became fully effective in 2019 (European Union 2015). Although some exceptions exist, this measure will reduce discards substantially, which might have negative consequences on scavenger populations that use this anthropogenic food resource, including vulnerable species of marine top predators (Votier et al. 2004, Bicknell et al. 2013).

Seabirds are the most conspicuous animals exploiting fishery discards, with some scavenger populations greatly benefitting from this feeding behaviour (Bicknell et al. 2013). However, the degree of dependence of seabirds on fishery discards at different spatio-temporal scales is not clear yet because most research is performed either on single colonies (but see Duhem et al. 2008, Votier et al. 2008, Morera-Pujol et al. 2018) or restricted to the isolated breeding season (but see López et al. 2016, Calado et al. 2018). Thus, studies investigating the feeding ecology of seabirds simultaneously at multiple colonies under different fishing intensities and during different phases of the annual cycle are needed as several factors may affect their relationship with fisheries through space and time. Indeed, density-dependent competition (Real et al. 2017), breeding constraints, and migration (Arcos et al. 2001) are likely to influence this relationship. Overall, understanding the importance of food subsidies provided by fisheries for seabirds is a key issue in seabird ecology and conservation, especially when assessing the possible impacts of the food shortage created by the new EU landing obligation.

Seabird diets can be studied through the analysis of pellets that provide a high taxonomic detail of prey items (Barrett et al. 2007). However, pellets suffer from some limitations, namely short time-scale integration and overestimation of larger and conspicuous prey (Moreno et al. 2010). Additionally, Stable Isotope Analysis (SIA) has become a powerful tool to unravel assimilated diets of consumers (Kelly 2000). In the marine environment, stable isotope ratios of nitrogen ($\delta^{15}$N) are used as a proxy of trophic position, as consumer tissues exhibit a stepwise enrichment in $^{15}$N at each trophic level (Hobson 1993). Stable isotope ratios of carbon ($\delta^{13}$C) change less than $\delta^{15}$N throughout the food chain and are mostly used as a reflection of the source of carbon at the base of the food web, allowing to detect a marine to terrestrial gradient in carbon ratios (Kelly 2000). Thus, $\delta^{13}$C values of consumers can be used to identify their food types and foraging habitats (Hobson 1999). Sulphur isotope ratios ($\delta^{34}$S) are increasingly used to study the diet of generalist consumers, providing extra discriminatory power to distinguish between and within marine and terrestrial foraging habitats (Moreno et al. 2010). The period of dietary integration reflected by stable isotope values depends on the tissue metabolic activity (Hobson and Clark 1992b, Inger and Bearhop 2008). Hence, by sampling tissues with different turnover rates, it is possible to assess seabird

feeding ecology during different periods of the annual cycle (Bond et al. 2016). Diet can be also traced by plasma nutrients (Navarro et al. 2007). High total protein levels along with high uric acid (which reflects protein catabolism) indicate high protein consumption. Fat, which is usually higher in pelagic than in demersal fish (Spitz et al. 2010), can be traced by triglyceride levels (Alonso-Alvarez et al. 2002). Additionally, carotenoids, which are only obtained from diet, could indicate a higher intake of pelagic planktivorous fish than of demersal fish (Czeczuga 1976).

Gulls display highly opportunistic foraging behaviours, feeding on the most locally abundant prey (Duhem et al. 2003, Ramos et al. 2009b, Schwemmer et al. 2013), in accordance with the optimal foraging theory (MacArthur and Pianka 1966). Most species exploit fishery discards, which have led to population increases worldwide (Tasker et al. 2000). The yellow-legged gull *Larus michahellis* is one of the most common and widespread seabirds in the southwestern Palearctic (Olsen and Larsson 2004). This species shows variable foraging strategies, feeding on a wide range of prey from marine to terrestrial habitats (Bosch et al. 1994, Ramos et al. 2009a). Previous studies on the species in the Mediterranean showed that its diet varies spatially according to local prey availability and anthropogenic activities (Ramos et al. 2009a, b). Indeed, their global population growth over the last decades is attributed to the exploitation of anthropogenic food subsidies (Real et al. 2017). In the Atlantic Iberian coast, yellow-legged gulls feed mainly at sea (Moreno et al. 2010, Calado et al. 2018, Mendes et al. 2018), most likely in association with fisheries (Matos et al. 2018, Calado et al. 2020). In contrast, the Audouin's gull *Larus audouinii* is endemic to the Mediterranean region and exhibits more specialist foraging strategies, feeding mainly on small pelagic fish (Pedrocchi et al. 2002, Calado et al. 2018). However, in the Ebro Delta, the American crayfish *Procambarus clarkii* is also important in its diet (Navarro et al. 2010). Its recent global population increase was partly related with feeding in association with fisheries and the use of fishery discards (Oro et al. 2014).

We used dietary (pellets), stable isotope ($\delta^{15}$N and $\delta^{13}$C of blood and feathers and $\delta^{34}$S of feathers), and biochemical (total protein, uric acid, triglycerides, and carotenoid levels in plasma) analyses of yellow-legged gulls in four islands in the western Iberian coast (Sálvora, Spain, and Berlenga, Pessegueiro, and Deserta, Portugal) and of Audouin's gulls in one of these islands (Deserta). The main aim of this study was to investigate the importance of fish in the diet of yellow-legged and Audouin's gulls and assess the influence of fishery discards in their overall feeding ecology and its spatio-temporal variations. Fishery discards are highly correlated with the amount of fish captured and landed afterwards (Oro and Ruiz 1997). Indeed, commercial species targeted by fisheries, i.e. pelagic fish, are also the most discarded

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species in both Portugal (Borges et al. 2001, Erzini et al. 2002) and Galicia, Spain (Vázquez-Rowe et al. 2011). Thus, we used fish landings as a proxy of the discards available to gulls, similarly to previous studies (e.g. Oro et al. 2014, Foster et al. 2017). To investigate the influence of fishery discards in gull feeding ecology, we investigated the relationships between (1) the most consumed species by gulls *vs.* their landed percentages in nearby harbours; (2) pelagic and demersal fish in diet *vs* pelagic and demersal fish landing quantities; and (3) adult and chick stable isotope values and adult nutrients *vs* pelagic and demersal fish landing quantities. We expected spatial and temporal differences in fish consumption by gulls related with discard availability, breeding constraints, and environmental variability (Ramos et al. 2009b, Ceia et al. 2014, López et al. 2016). Overall, we expected an association between gull feeding ecology (diet, stable isotope values, and nutrients) and fish landings. The results of this study will help to assess the role of the newly implemented landing obligation policy in reducing the availability of food subsidies to gulls.

## 2. Materials and Methods

### 2.1. Study area

The study was performed in four islands along the western Iberian coast (from north to south; Figure 4.1): Sálvora Island (42° 28′ N, 9° 00′ W), Berlenga Island (39° 24′ N, 9° 30′ W), Pessegueiro Island (37°49' N, 8°47' W), and Deserta Island (36° 57′ N, 7° 53′ W). The islands differ in several abiotic and biotic factors, such as gull population size and food availability (see Table 4.1). Fishing activities in colony surroundings also differ among islands, being higher in Sálvora and lower in Pessegueiro (see fish landings for each colony in Figure 4.2).
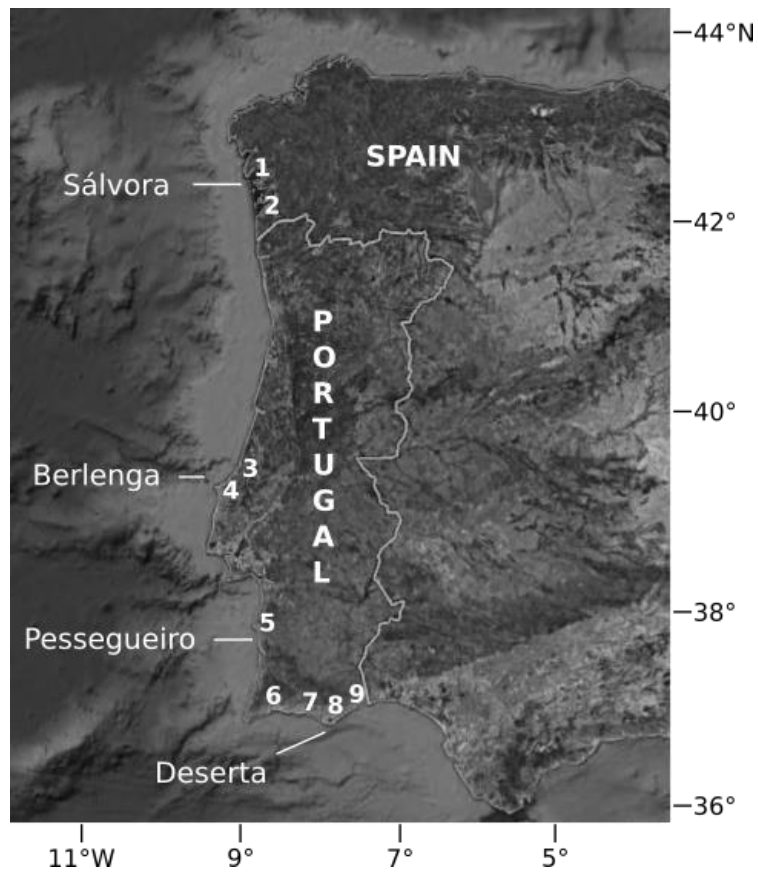
**Figure 4.1.** Geographical location of yellow-legged gull (Sálvora, Berlenga, Pessegueiro and Deserta islands) and Audouin's gull (Deserta Island) colonies. Numbers indicate fishing harbours in the colonies' surroundings: 1 – Ribeira, 2 – Vigo, 3 – Nazaré, 4 – Peniche, 5 – Sines, 6 – Portimão, 7- Quarteira, 8 – Olhão, and 9 – Vila Real de Santo António.

**Table 4.1.** Informative parameters of gull colonies. For more information on fishing activity near each colony see Figure 4.2.

| Island | Size (km long and ha) | Dist. to land | Gull species | Breeding pairs | Population trend | Fishing activity | Alternative foraging habitats |
|---|---|---|---|---|---|---|---|
| Sálvora | 2.0 km (190 ha) | 3.0 km | Yellow-legged gull | 3,800 | Decreasing | High | Rías* |
| Berlenga | 1.5 km (78.8 ha) | 11.0 km | Yellow-legged gull | 8,500 | Decreasing (annual egg culling) | Moderate | Refuse dumps |
| Pessegueiro | 0.4 km (7.8 ha) | 0.3 km | Yellow-legged gull | 500 | Unknown | Low | Terrestrial |
| Deserta | 7.0 km (200 ha) | 5.5 km | Yellow-legged gull | 1,400 | Increasing | Moderate - Low | Lagoon |
| | | | Audouin's gull | 2,900 | Increasing | | |

*Rías are coastal embayments under ocean influence.
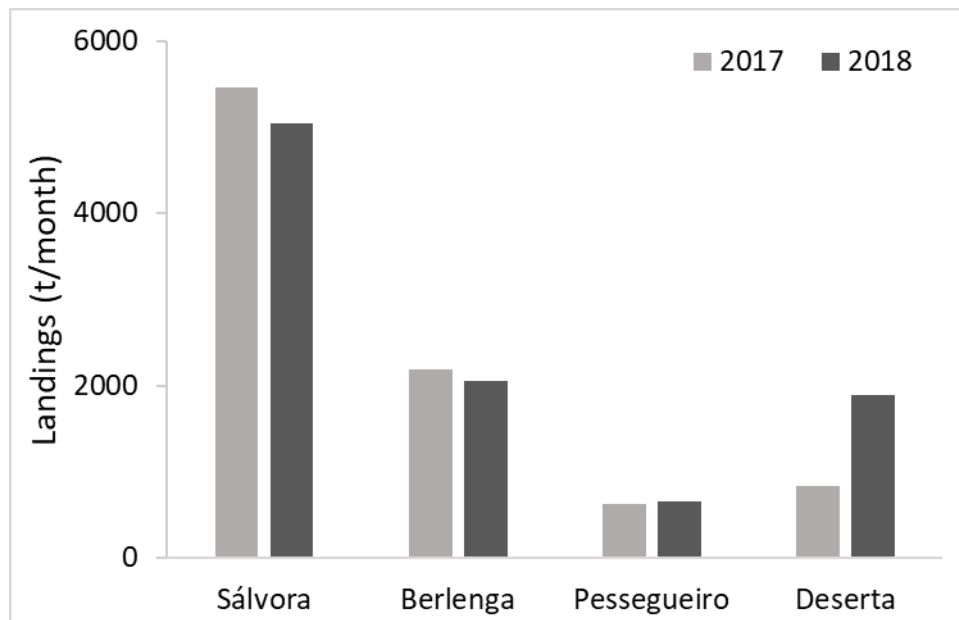
**Figure 4.2.** Total fish landings (tonnes/month) during the breeding seasons of 2017 and 2018 at each gull colony.

## 2.2. Diet sample collection and identification

To investigate spatial differences in gull diet, pellets were collected in 5 gull colonies (yellow-legged gull: Sálvora, Berlenga, Pessegueiro, and Deserta; Audouin's gull: Deserta) in the breeding seasons of 2017 and 2018. To investigate inter-annual differences in gull diet, pellets were also collected for both gull species in Deserta Island during the breeding seasons of 2014 to 2016. To investigate seasonal differences in gull diet, pellets were collected during pre-breeding (i.e. pre-laying period, mostly February - March), breeding (i.e. chick-rearing period, mostly May), and post-breeding (i.e. after fledging, mostly September - October) seasons in Berlenga and Deserta islands from 2016 to 2018. Additionally, pellets of yellow-legged gulls from Sálvora and Pessegueiro and of Audouin's gulls were collected in some seasons/years (Figure 4.3), which were used to investigate relationships with fish landings. Overall, we collected a total of 4,583 pellets. For detailed information on sample size and sampling months see Tables S4.1-S4.13.

Pellets were sorted under a steromicroscope, and prey items were identified to the lowest possible taxon based on hard remains (e.g. bones and exoskeleton). Fish was identified using our own reference collection and identification guides (Assis 2004, Tuset et al. 2008). Diet contents were classified according to the following categories: fish, marine invertebrates, refuse, vegetable matter, and others (i.e.

insects, small mammals, eggshells, and fishing hooks). We further separated pelagic and demersal fish species, following previous studies (Matos et al. 2018, Calado et al. 2018). We assessed the presence or absence of each category in gull pellets and calculated its percentage of occurrence (PO), defined as the percentage of pellets with a certain prey category.

## 2.3. Gull sampling and stable isotope analyses

Breeding adults were captured during late incubation with nest traps. In 2017, yellow-legged gulls were captured in Sálvora (N = 9), Berlenga (N = 16), Pessegueiro (N = 7), and Deserta (N = 10), and Audouin's gulls were captured in Deserta (N = 12). In 2018, yellow-legged gulls were captured in Berlenga (N = 16), Pessegueiro (N = 11), and Deserta (N = 8), and Audouin's gulls were captured in Deserta (N = 14). Blood samples (0.5–1.0 mL) were collected from the tarsal vein using 27-G needles and centrifuged within 3–5 h to separate Red Blood Cells (RBC) from plasma. All samples were stored frozen. Plasma retains information on diet over a few days prior to sampling (Cherel et al. 2005a), reflecting recent meals during the late incubation period. RBC has a longer time-integration period of at least 4 weeks (Hobson and Clark 1992b, Bearhop et al. 2002), reflecting diet since the late pre-laying period. We also sampled 3 breast feathers and the tips of the first primary (P1) and eighth secondary (S8) feathers, which were stored in labelled sealed plastic bags. Feathers are metabolically inert after formation, therefore maintain isotopic ratios of the time of their synthesis (Hobson 1999). P1 is moulted during late breeding and S8 during non-breeding, therefore, isotope values of P1 and S8 reflect diet during the previous late breeding and non-breeding seasons, respectively (Ramos et al. 2011). Breast feathers are moulted continuously throughout the year (Dwight, 1901), therefore reflect the year-round diet of gulls (Pedro et al. 2013).

During chick-rearing, 3 mantle feathers of chicks were also sampled in 2017 (yellow-legged gulls: Sálvora N = 15, Berlenga N = 10, Pessegueiro N = 13, and Deserta N = 14; Audouin's gull: Deserta N = 15) and 2018 (yellow-legged gulls: Berlenga N = 10, Pessegueiro N = 10, Deserta N = 10; Audouin's gull: Deserta N = 11), reflecting their diet during the chick-rearing period (Cherel et al. 2014).

We measured $\delta^{15}$N and $\delta^{13}$C values in blood and P1, S8, and chick feathers of yellow-legged and Audouin's gulls and in adult breast feathers of yellow-legged gulls. Additionally, adult breast and chick feathers of yellow-legged gulls were used for $\delta^{34}$S analysis. For specifications on SIA laboratory procedures, see Text A4.1.

## 2.4. Biochemical analyses

We measured the uric acid and triglycerides levels in plasma samples (10 μL) with commercially available kits (Biosystems, Spain; COD 11521 and COD 11528). The kits were based on the uricase/peroxidase method and the glycerol phosphate oxidase/peroxidase method, respectively. The concentrations of uric acid and triglycerides were estimated from the sample absorbance at 520 and 500 nm, respectively, using an ELISA (Enzyme-Linked Immunosorbent Assay) spectrophotometer (Biotek Instruments, USA). Total protein was determined with Pierce BCA Protein Assay Kit (23225; Thermo Scientific, USA). The absorbance of the resulting complex was measured at 562 nm. For carotenoid measurements, plasma samples (15 μL) were diluted in 135 mL of absolute ethanol. The solution was mixed in a vortex and subsequently centrifuged at 1,500 g for 10 min. The absorbance of the supernatant was measured at 440 nm. Carotenoid concentration was determined from a standard curve of lutein. All samples were assessed in duplicate, and mean values were used.

## 2.5. Fish landings

Fish landings were provided by Docapesca - Portos e Lotas, S.A. (http://www.docapesca.pt/) for Portuguese harbours and sourced online from the Pesca de Galicia - Plataforma tecnolóxica da pesca website at https://www.pescadegalicia.gal/ for Galician harbours. Nearby fishing harbours, whose boats operate in the colonies' surrounding waters, were Ribeira (~ 10 km from the colony) and Vigo (~ 34 km) for Sálvora Island, Nazaré (~ 41 km) and Peniche (~ 13 km) for Berlenga Island, Sines (~ 14 km) for Pessegueiro Island, and Portimão (~ 59 km), Quarteira (~ 22 km), Olhão (~ 8 km), and Vila Real de Santo António (~ 48 km) for Deserta Island (see Figure 4.1).

Daily fish landings were summed according to sampling date to match gull feeding ecology in the same period. For pellets, it corresponded to the months when pellets were collected (see Tables S4.1-S4.13). For feathers, landings corresponded to the moulting period, which for breast feathers corresponded to the entire year before sampling, and for chick feathers, landings were summed over the sampling month (June; see Table S4.14). For plasma, landings were summed up to the 15 days prior to sample collection (see Table S4.15). RBC was not used because it encompasses the period reflected by plasma, and the same applies to P1 and S8 feathers, which are reflected by breast feathers. Thus, regarding adult stable isotope values, the relationships between fish landings and gull feeding ecology

was only tested in breast feathers (reflecting the year-round) and in plasma (reflecting the breeding period).

## 2.6. Statistical analysis

Gull diet from the pellets collected during the 2017 and 2018 breeding seasons was plotted in an ordination via Non-Metric Multidimensional Scaling (NMDS) to visualize the importance of each prey group in each colony using the *vegan* R package (Oksanen et al. 2019).

Three different Generalised Linear Models (GLM) with a binomial distribution were performed to analyse the diet of gulls, with total fish, pelagic fish, and demersal fish as response variables. (1) To investigate spatial differences in yellow-legged gull diet, we tested the effect of colony (Sálvora, Berlenga, Pessegueiro, and Deserta) during the breeding seasons of 2017 and 2018. (2) To investigate seasonal differences, we tested the effect of season (pre-breeding, breeding, and post-breeding) at Berlenga and Deserta yellow-legged gull colonies from 2016 to 2018. (3) To investigate inter-annual differences in gull diet during breeding at Deserta Island, we tested the effect of year (2014-2018) in both gull species (yellow-legged and Audouin's gulls). P values were adjusted using the Bonferroni method because multiple tests were performed with the same data (Jafari and Ansari-Pour 2019).

Two separate Linear Mixed Models (LMM) were performed to examine differences in gull $\delta^{15}$N and $\delta^{13}$C values using *lme4* (Bates et al. 2015) and *lmerTest* (Kuznetsova et al. 2017) R packages. We tested the effect of year (2017, 2018), colony (yellow-legged gulls from Berlenga, Pessegueiro, and Deserta, Audouin's gulls), and tissue (P1 feathers – late breeding, S8 feathers – non-breeding, RBC – breeding, chick feathers). Bird identity was included as a random effect in all models to control for pseudo-replication issues (i.e. several tissues sampled from the same individual). Corrections on the stable isotopic values (yellow-legged gull: -0.6‰ for $\delta^{15}$N and -1.8‰ for $\delta^{13}$C; Audouin's gull: -0.4‰ for $\delta^{15}$N and -1.6‰ for $\delta^{13}$C) were applied to feathers to allow direct comparisons between tissues (i.e. blood and feathers; Cherel et al. 2014), according to previous measurements in both study species (Calado 2015). Additionally, we restricted this analysis to 2017 and included gulls from Sálvora to further investigate spatial differences.

A Linear Model (LM) was used to test the effect of year (2017, 2018), colony (Berlenga, Pessegueiro, Deserta), and tissue (adult breast feathers, chick feathers) on yellow-legged gull $\delta^{34}$S values.

Post-hoc pairwise comparisons in all models (i.e. GLM, LMM, and LM) were performed using estimated marginal means and Tukey's p-value adjustment, under the *emmeans* R package (Lenth 2019).

LMM was also used to investigate the relationship between the most consumed fish species by gulls (PO > 5% in pellets; see Tables S4.1-S4.13) and their landed percentages (also arcsine-transformed) in nearby harbours. Each date (season and year) and colony were grouped and included as a random effect to control for pseudo-replication of using several fish species from the same date/location. To investigate the relationships between pelagic and demersal fish in diet (PO arcsine-transformed) and monthly averages of pelagic and demersal fish landing quantities (tonnes log-transformed), Pearson's correlation coefficients were used. Spearman's correlation coefficients were used to investigate the relationships between (1) gull's feeding ecology ($\delta^{15}$N, $\delta^{13}$C, and $\delta^{34}$S values of adult breast and chick feathers of yellow-legged gulls) and pelagic and demersal fish landing quantities; (2) Principal Component Analysis (PCA) scores (based on $\delta^{15}$N and $\delta^{13}$C values, triglycerides, uric acid, total protein, and carotenoids from adult plasma of yellow-legged and Audouin's gulls) and pelagic and demersal fish landing quantities.

Normality and homogeneity were verified by visual inspection of data and residuals. Two-way interactions between independent variables were tested in all models and dropped if not significant, using backward stepwise selection. All analyses were performed with R software ver. 3.6.1 (R Core Team 2019), and significance was set at alpha = 0.05.

## 3. Results

### 3.1. Spatio-temporal differences in diet

Based on pellet samples, gulls from Sálvora and Berlenga colonies consumed mainly marine invertebrates, mostly Henslow's swimming crab *Polybius henslowii*, while gulls from the other two colonies (Pessegueiro and Deserta) consumed mainly fish (Figure 4.3). Other food resources were also important for yellow-legged gulls but only in certain colonies/years: vegetable matter, mostly Portuguese crowberry *Corema album,* had a high occurrence in Pessegueiro in the 2018 breeding season, and refuse had a higher occurrence in Deserta in the 2017 breeding season. Audouin's gulls consumed mostly the epipelagic fish Atlantic saury *Scomberosox saurus*. The NMDS revealed similarities in the diet of yellow-legged gulls between Berlenga and Sálvora islands and between Deserta and Pessegueiro islands, as well as the separation of Audouin's gulls (Figure 4.4).

|  | Pre-breeding | Breeding | Post-breeding |
|---|---|---|---|
| Sálvora | N=65 | N=152 | |
| Berlenga | N=270 | N=466 | N=332 |
| Pessegueiro | N=55 | N=112 | N=126 |
| Deserta | N=500 | N=801 | N=270 |
| Audouin's gull | N=170 | N=1,039 | N=108 |

Legend: ■ Pelagic fish ■ Demersal fish ■ Marine invertebrates ■ Vegetable matter ■ Refuse ■ Others
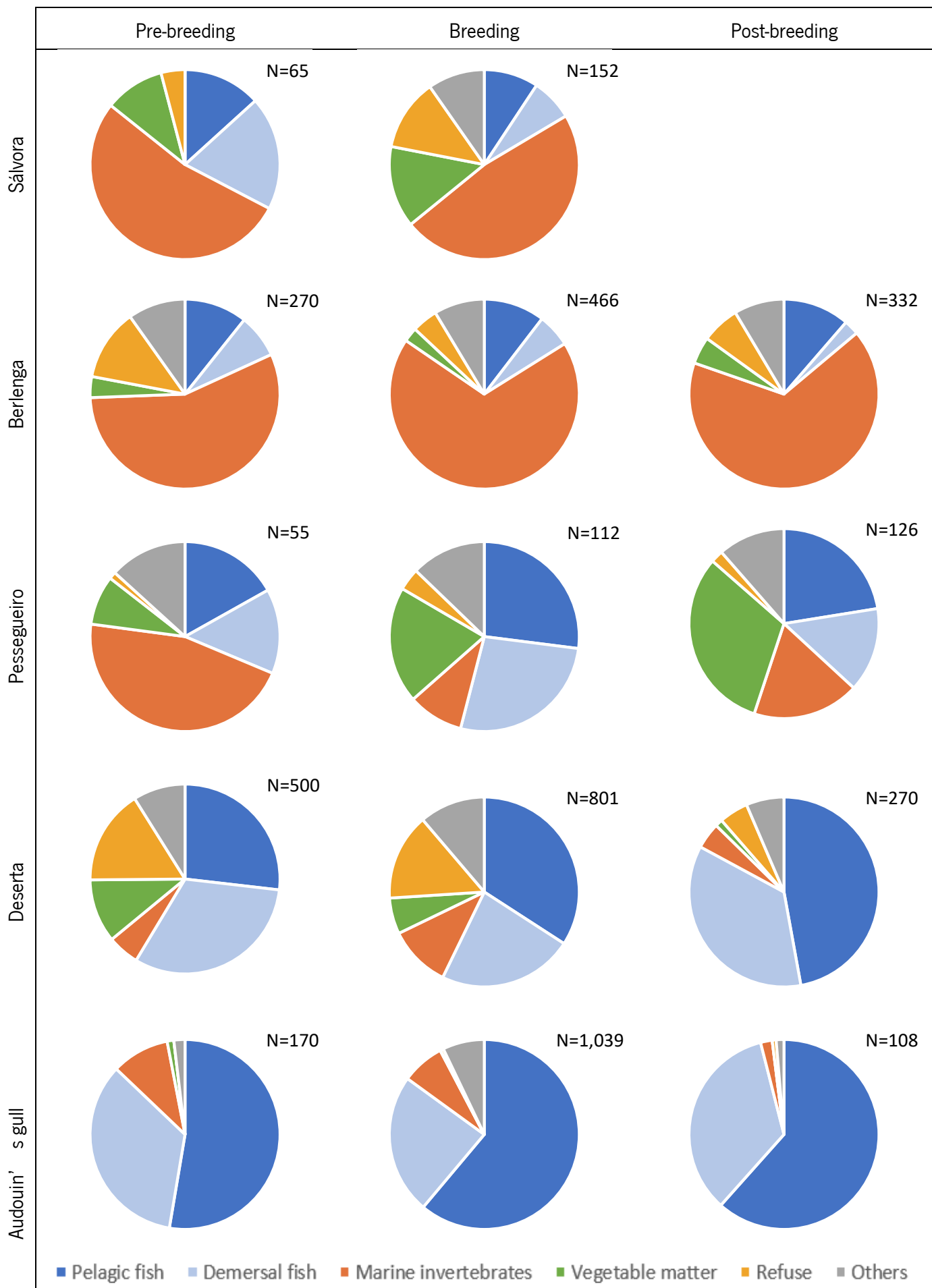
**Figure 4.3.** Diet composition of yellow-legged gulls from Sálvora, Berlenga, Pessegueiro, and Deserta islands and of Audouin's gulls during the pre-breeding, breeding, and non-breeding seasons based on pellets. Data is based on percentages of occurrences summed and transformed to a scale of 100%. All years were pooled for visualization purposes. Detailed percentages of occurrences in each year are shown in Tables S4.1-S4.13.
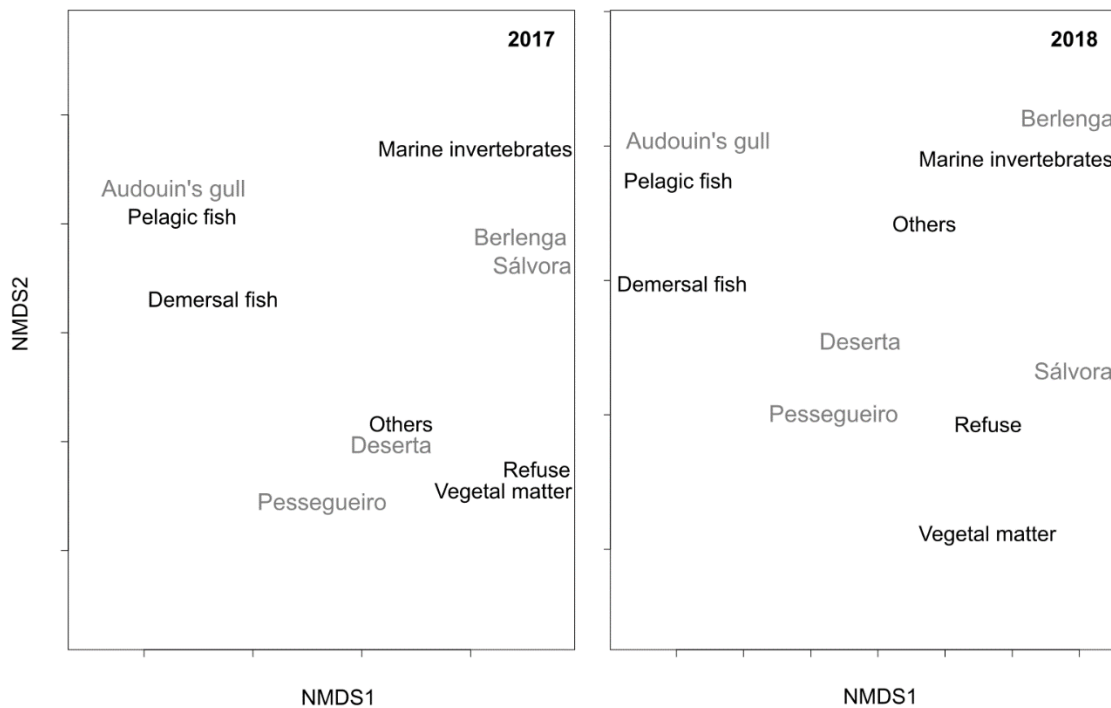


**Figure 4.4.** Two-dimensional Non-Metric Multidimensional Scaling (NMDS) ordination showing dietary differences among colonies (in grey) of yellow-legged gulls from Sálvora, Berlenga, Pessegueiro, and Deserta islands and of Audouin's gulls during the breeding seasons of 2017 and 2018, based on six main prey categories (in black): pelagic fish, demersal fish, marine invertebrates, refuse, vegetable matter, and others (i.e. insects, small mammals, eggshells, and fishing hooks).

In the 2017 and 2018 breeding seasons, all three fish categories (pelagic, demersal, and total fish) in the diet of yellow-legged gulls differed significantly among colonies ($\chi^2 > 982.0$, $P < 0.01$) but did not vary between years ($\chi^2 < 1434.9$, $P > 0.204$). Gulls from Deserta and Pessegueiro consumed more pelagic and total fish than those from Berlenga and Sálvora, and gulls from Pessegueiro consumed more demersal fish than those from Deserta.

Regarding seasonal differences in gull diets at Berlenga and Deserta colonies from 2016 to 2018, all three fish categories differed among years and seasons and between the two colonies (Table 4.2a). Gulls consumed more fish in Deserta and in 2017, and the consumption of pelagic and total fish was higher during the post-breeding period. The interaction year*season revealed that gulls consumed more demersal fish during the 2018 post-breeding and 2017 pre-breeding seasons. The interaction year*colony revealed inter-annual differences only for gulls from Deserta regarding pelagic fish diet and only for gulls from Berlenga regarding demersal and total fish diets. The significant interaction season*colony indicates stronger seasonal differences in Deserta.

Data from 2014 to 2018 revealed that at Deserta Island the consumption of both pelagic and total fish differed significantly between the two gull species (higher for Audouin's gull, $\chi^2 > 985.4$, $P < 0.01$), but the consumption of demersal fish was similar between species ($\chi^2 = 2404.3$, $P = 0.432$). The consumption of these three fish categories varied across the study years ($\chi^2 > 971.1$, $P < 0.018$): 2016 had the highest and the lowest consumption of pelagic and demersal fish, respectively, and the consumption of total fish was higher in 2014. The significant interaction gull*year ($\chi^2 = 2348.0$, $P < 0.01$) revealed that Audouin's gulls consumed less demersal fish in 2016 compared to all other groups, except their own diet in 2014.

### 3.2. Spatio-temporal differences in stable isotope values

$\delta^{15}N$ values differed between years and among tissues, while $\delta^{13}C$ values differed among colonies and tissues (Table 4.2b). Plus, for both stable isotopes, all interactions between variables were significant. $\delta^{15}N$ was higher in 2017, indicating the consumption of higher trophic level prey, and pairwise comparisons revealed the lowest $\delta^{15}N$ values in adults during the breeding season (RBC) compared to both the late breeding (P1) and non-breeding (S8) seasons. The highest $\delta^{13}C$ values were found during the non-breeding season and the lowest values occurred at Berlenga. The significant interaction colony*tissue indicates that during the breeding season gulls from Pessegueiro had higher $\delta^{15}N$ values than yellow-legged gulls from Deserta, and the highest $\delta^{13}C$ were found in Audouin's gulls during the non-breeding season. The interaction year*colony revealed that gulls from Berlenga had similar $\delta^{15}N$ values between years and the lowest $\delta^{13}C$ values in 2017. The interaction year*tissue revealed inter-annual differences in $\delta^{13}C$ values during the non-breeding season (higher in 2017).

**Table 4.2.** Models investigating inter-annual, colony, seasonal, and age class differences in gull feeding ecology. a) Generalised Linear Models (GLM) with a binomial distribution testing the effect of year (2016-2018), colony (Berlenga, Deserta), and season (pre-breeding, breeding, post-breeding) on the occurrence of pelagic fish, demersal fish, and total fish in yellow-legged gull pellets. P values were adjusted using the Bonferroni method. b) Linear Mixed Models (LMM) testing the effect of year (2017-2018), colony (yellow-legged gulls from Berlenga, Pessegueiro, and Deserta islands and Audouin's gulls), and tissue (P1 feathers – late breeding, S8 feathers – non-breeding, RBC – breeding, chick feathers) on the $\delta^{15}N$ and $\delta^{13}C$ values of gulls, with bird identity as a random effect. c) Linear Model (LM) testing the effect of year (2017-2018), colony (yellow-legged gulls from Berlenga, Deserta, and Pessegueiro), and tissue (adult breast feathers, chick feathers) on the $\delta^{34}S$ values of gulls. Correction factors were applied on stable isotope values of feathers to allow direct comparisons between tissues (see Methods). Significant P values are shown in bold.

| a) GLM | Year | | Colony | | Season | | Year*Colony | | Year*Season | | Colony*Season | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $\chi^2$ | P | $\chi^2$ | P | $\chi^2$ | P | $\chi^2$ | P | $\chi^2$ | P | $\chi^2$ | P |
| Pelagic fish | 3055.3 | **< 0.01** | 2645 | **< 0.01** | 3038.6 | **< 0.01** | 2578.3 | **< 0.01** | 2617.9 | **< 0.01** | – | – |
| Demersal fish | 2801.6 | **< 0.01** | 2319.5 | **< 0.01** | 2747.8 | **< 0.01** | 2247.1 | **< 0.01** | 2279.9 | **< 0.01** | 2229.5 | **< 0.01** |
| Total fish | 3093 | **< 0.01** | 2155.9 | **< 0.01** | 3068 | **< 0.01** | 2068.6 | **< 0.01** | 2096.6 | **< 0.01** | 2045.5 | **< 0.01** |

| b) LMM | Year | | Colony | | Tissue | | Year*Colony | | Year*Tissue | | Colony*Tissue | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | P | F | P | F | P | F | P | F | P | F | P |
| | | | | | | | | < | | | | |
| $\delta^{15}N$ | 46.1 | **< 0.001** | 1.2 | 0.307 | 100.2 | **< 0.001** | 9.7 | **0.001** | 15.4 | **< 0.001** | 3.6 | **< 0.001** |
| $\delta^{13}C$ | 1.4 | 0.235 | 14.0 | **< 0.001** | 8.9 | **< 0.001** | 3.2 | **0.026** | 8.3 | **< 0.001** | 12.8 | **< 0.001** |

| c) LM | Year | | Colony | | Tissue | | Year*Colony | | Year*Tissue | | Colony*Tissue | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | P | F | P | F | P | – | – | F | P | F | P |
| $\delta^{34}S$ | 2.2 | 0.142 | 9.6 | **< 0.001** | 8.1 | **0.005** | – | – | 10.1 | **0.002** | 4.9 | **0.009** |

Additionally, when restricting this analysis to 2017, to include gulls from Sálvora, colony and tissue differences were found in both $\delta^{15}N$ and $\delta^{13}C$ (Table A4.1), with lower values at Berlenga followed by Sálvora.

$\delta^{34}S$ differed among colonies and between tissues (Table 4.2c), with higher values in adults breast feathers than in chick feathers and in Pessegueiro and Berlenga than in Deserta. The significant interactions colony*tissue and year*tissue indicate that only adults differed among colonies and between years (i.e. higher in 2017), respectively.

### 3.3. Relationships of gull diet with fish landings

When analysing species-specific consumption of fish by gulls, all colonies exhibited a significant positive association with fish landings ($F_{1,1159.5}$ = 304.4, P < 0.001), indicating that the fish species found in gulls' pellets matched those landed at nearby harbours (Figure 4.5). When analysing the relationships of both pelagic and demersal fish in gull diet with fish landings, neither were significantly correlated with pelagic fish landings, but they were negatively correlated with demersal fish landings (d.f. = 38; pelagic fish: $r$ = -0.4, P = 0.020 and demersal fish: $r$ = -0.4, P = 0.011). These results indicate that in the colonies with higher demersal fish landings (i.e. Sálvora and Berlenga), gulls consumed less fish. However, when excluding these colonies from the analysis, there was a positive association of both pelagic and demersal fish diets with demersal fish landings (d.f. = 26; $r$ = 0.6, P < 0.001 and $r$ = 0.4, P = 0.028, respectively), and of pelagic fish diet with pelagic fish landings (d.f. = 26, $r$ = 0.5, P = 0.006).

### 3.4. Relationships of gull stable isotopes and nutrients with fish landings

From the correlations between stable isotope values ($\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$) in adult breast feathers (n = 68), reflecting their year-round feeding ecology, with both pelagic and demersal fish landings, only $\delta^{34}S$ was significantly correlated with pelagic and demersal fish landings ($r_s$ = 0.3, P = 0.012 and $r_s$ = 0.4, P = 0.003, respectively). Regarding chick feathers (n = 67), $\delta^{15}N$ and $\delta^{34}S$ were negatively correlated with both pelagic ($\delta^{15}N$: $r_s$ = -0.6, P < 0.001 and $\delta^{34}S$: $r_s$ = -0.4, P = 0.004) and demersal fish landings ($\delta^{15}N$: $r_s$ = -0.5, P < 0.001 and $\delta^{34}S$: $r_s$ = -0.5, P < 0.001), and $\delta^{13}C$ was negatively correlated with demersal fish landings ($r_s$ = -0.3, P = 0.026).
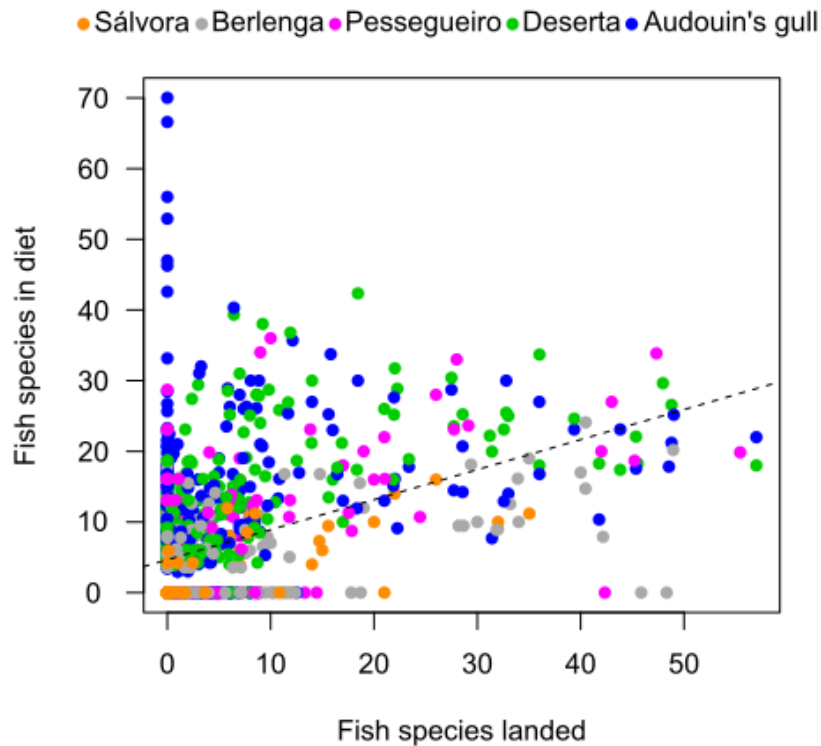
**Figure 4.5.** Positive relationship between the fish species (percentage of occurrence) in gull pellets (yellow-legged gulls from Sálvora, Berlenga, Pessegueiro, and Deserta islands and Audouin's gulls) and their percentage landed in local harbours. Both percentages were arcsine-transformed. The dashed line is based on a linear mixed model (see Methods).

In relation to the parameters reflecting adult feeding ecology during the breeding season, the PCA based on plasma parameters generated three principal components explaining respectively 28.8, 23.1, and 19.0% of the total variance. Variables contributing more to PC1 were uric acid (0.64), total protein (0.62), and carotenoids (-0.35). PC2 was negatively associated with $\delta^{13}C$ (-0.69) and positively with $\delta^{15}N$ (0.68). PC3 was highly associated with triglycerides (0.86). PC2 showed significant negative correlations (all n = 94) with both pelagic and demersal fish landings ($r_s$ = -0.4, P < 0.001 and $r_s$ = -0.3, P = 0.008, respectively; Figure 4.6). Additionally, PC3 was positively correlated with pelagic fish landings ($r_s$ = 0.3, P = 0.001). PC1 was not correlated with either pelagic or demersal fish landings. These results indicate that $\delta^{15}N$ and $\delta^{13}C$ values in adult blood were negatively and positively associated with both pelagic and demersal fish landings, respectively, and that triglycerides were positively associated with pelagic fish landings.
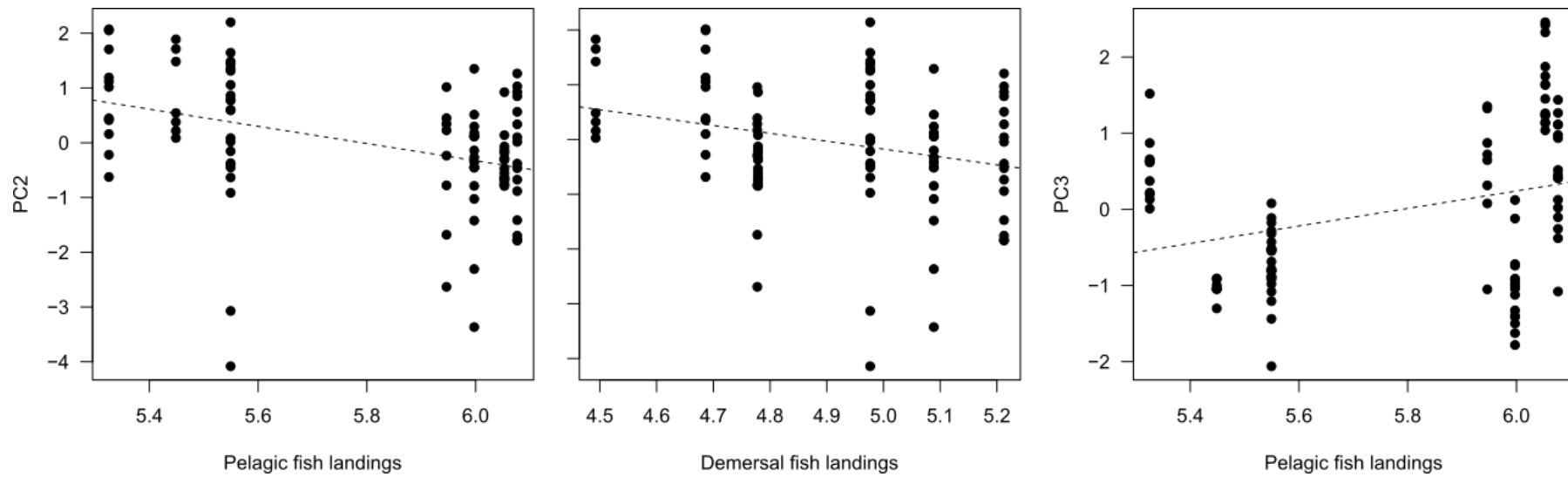
**Figure 4.6.** Significant relationships (using Spearman's correlation coefficients) of Principal Component Analysis (PCA) scores based on $\delta^{15}N$ and $\delta^{13}C$ values, triglycerides, uric acid, total protein, and carotenoids from adult plasma of yellow-legged gulls from Berlenga, Pessegueiro, and Deserta islands and of Audouin's gulls with pelagic and demersal fish landings (tonnes log-transformed).

**4. Discussion**

**4.1. Spatio-temporal differences in gull feeding ecology**

In this study we used multiple techniques to investigate gull feeding ecology across the annual cycle during consecutive years in four colonies along the western Iberian coast. Gulls from Pessegueiro and Deserta islands consumed mainly fish, while gulls from Sálvora and Berlenga consumed mainly marine invertebrates. The Henslow's swimming crab was previously recorded as one of the main prey of yellow-legged gulls at Sálvora (Munilla 1997, Moreno et al. 2010) and Berlenga (Ceia et al. 2014, Alonso et al. 2015) islands. They can attain very high densities, gathering in large shoals close to the sea surface (Signa et al. 2008), and are especially abundant in northern Portuguese (Sousa et al. 2005) and Galician (González-Gurriarán et al. 1993) waters. Thus, according to the optimal foraging theory, gulls can feed on this easily caught and locally abundant alternative prey (MacArthur and Pianka 1966), explaining its higher consumption at these islands. Although there were no colony differences in gull $\delta^{15}N$ values considering both 2017 and 2018, when restricting the analysis to 2017, we detected a significant effect of colony (see Table A4.1), with gulls from Berlenga exhibiting the lowest $\delta^{15}N$ values, indicating the consumption of lower trophic level prey. The lower $\delta^{13}C$ and higher $\delta^{34}S$ values also reflect the higher consumption of marine invertebrates at Berlenga Island (Moreno et al. 2010, Velando et al. 2010). The presence of sporadically important alternative food resources such as vegetable matter and refuse in Pessegueiro and Deserta, respectively, could be related to local environmental conditions affecting the availability of their main prey (i.e. fish; Howells et al. 2017). As expected, Audouin's gulls fed almost exclusively on fish, mostly pelagic, confirming its specialization on fish at Deserta Island (Matos et al. 2018, Calado et al. 2018), even outside the breeding season.

Pellet analysis revealed a higher fish consumption during the post-breeding season. Both López et al. (2016) and Arizaga et al. (2013) also recorded the highest occurrence of fish in yellow-legged gull pellets outside the breeding season, which could be related with gull breeding constraints. During the breeding period, gulls are central-place foragers (Patenaude-Monette et al. 2014) and thus constrained by their breeding duties in their foraging ranges and time spent at sea, which might hamper their capability to capture fish. Greater consumption of fish during post-breeding season could also be related with the need of adults to restore body condition (Gilg et al. 2010) with high energy prey after the energetically demanding breeding season (Ramírez et al. 2010). In agreement with pellet analysis, $\delta^{15}N$ values were lower, indicating foraging at a lower trophic level, during the breeding season compared to the late breeding and non-breeding seasons. Additionally, Audouin's gulls exhibited distinctly higher $\delta^{13}C$ values

during the non-breeding season compared to all other seasons and to yellow-legged gulls, most likely reflecting their wintering grounds at the northwest African Atlantic coast (Sanpera et al. 2007, Calado et al. 2018).

Our results suggest a slight decrease of fish consumption over the study years (2014-2018 at Deserta, 2016-2018 at Berlenga, and 2017-2018 at Pessegueiro and Sálvora islands). Global tendencies show decreasing fish consumption by several gull species (Ronconi et al. 2014, Blight et al. 2015, Hobson et al. 2015, Bond 2016), including yellow-legged gulls (Pedro et al. 2013, Calado et al. 2020), which could be linked to increased gear selectivity producing smaller discard ratios and greater discard retention (Zeller et al. 2018). Our study seems to suggest this tendency across the Atlantic Iberian coast, based on pellet analysis. Additionally, both $\delta^{15}N$ and $\delta^{34}S$ values of adults were higher in 2017 than in 2018, and this difference was also detected in $\delta^{13}C$ values during the non-breeding season, which could indicate a higher fish consumption in 2017, in agreement with pellet analysis.

## 4.2. Relationships of gull diet with fish landings

Our results revealed that in all colonies, the fish species consumed by gulls matched those landed in local harbours across the annual cycle. Additionally, in two of the four study islands (Pessegueiro and Deserta) there was a strong association between gull diet (pelagic and demersal fish) and fish landing quantities. Indeed, the most consumed fish at Sálvora Island was blue whiting *Micromesistius poutassou*, which was also one of the most landed species in Galicia (see Tables S4.5 and S4.19). This bathypelagic species lives far from the sea surface (Gomes et al. 2001), thus it is most likely caught in association with fisheries. In Portuguese colonies, the most consumed fish by yellow-legged gulls also matched the most landed species, i.e. chub mackerel *Scomber colias*, horse/jack mackerel *Trachurus* sp., and sardine *Sardina pilchardus*. Although they are pelagic species, they are most likely consumed by gulls in association with fisheries (Alonso et al. 2015). Interestingly, Audouin's gulls also exhibited a positive association with fish landings despite their main prey, i.e. Atlantic saury, presenting zero catches in commercial fish landings. The high occurrence of this species suggests natural foraging by Audouin's gulls. However, association with purse-seines and fishery discards could also facilitate the capture of this species (Arcos and Oro 2002a). Indeed, we did not account for the discarded portion of the catch nor facilitated foraging (e.g. during net encirclement or slipping), which leads to an underestimation of the associations found between gull diet and fisheries. Additionally, Audouin's gulls also consumed highly landed and discarded pelagic fish species (i.e. sardine and chub mackerel) as well as fish living at deeper

depths (i.e. blue whiting and seabreams *Diplodus* spp.) that should be made available to gulls by fisheries. Overall, these results suggest that gulls foraged in association with fisheries, feeding on fishery discards of both pelagic and demersal fish provided by fisheries. Previous studies also revealed the importance of local fishing activities (using fish landings as proxy of food availability provided by fisheries) in shaping seabird populations (Martín et al. 2019), including gulls (Oro et al. 2014, Ramírez et al. 2015, Foster et al. 2017).

$\delta^{34}$S values of adults and chicks of yellow-legged gulls were differently associated with fish landings; adults were positively associated while chicks were negatively associated. These opposite relationships suggest different foraging strategies of adults in relation to fisheries for self-feeding and chick provisioning (Calado et al. 2018), which could be related with less marine prey consumption by chicks (Pedrocchi et al. 1996). However, considerable differences exist in the period reflected by these tissues, adult breast feathers should reflect their year-round feeding ecology, while chick feathers reflect their chick-rearing. Additionally, we collected three breast feathers randomly, and it is not possible to know exactly when these particular feathers were moulted, and these reasons could be the causes for the opposite relationships found with fishing landings. On the other hand, both adult and chick $\delta^{15}$N values were strongly negatively correlated with fish landings, suggesting that gulls foraging in association with fisheries fed on lower trophic level prey, such as small pelagic fish (Navarro et al. 2009a, Calado et al. 2018). Indeed, pelagic fish landings are more abundant (see Tables S4.1-S4.15) and match gull natural prey (Alonso et al. 2015). Additionally, the higher lipid and energetic content of small pelagic fish compared to demersal fish (Spitz et al. 2010) might represent higher-quality prey for gulls and therefore lead to higher triglycerides levels in plasma, as observed in this study. Thus, the relationship found between gull feeding ecology and fish landings over a large spatial and temporal scale in the western Iberian coast suggest that the increase of gull populations worldwide could be linked to the availability of anthropogenic food subsidies such as fishery discards (Oro et al. 2013). However, multiple factors are likely to interplay in this relationship such as the presence of alternative food resources (e.g. Henslow's swimming crab), density-dependent competition, discard production, and breeding constraints, as found in the Mediterranean (Arcos et al. 2001, Ramos et al. 2009b, Real et al. 2017). Additionally, the new EU landing obligation, which became fully implemented in 2019 under the CFP (European Union 2015), is expected to further reduce fish availability to scavenger species (Bicknell et al. 2013) and thus affect the feeding ecology of both yellow-legged and Audouin's gulls, highlighting the need of their continuous monitoring.

# CHAPTER 5.

JG Calado, VH Paiva, JA Ramos, A Velando, I Munilla. Anthropogenic food resources, sardine decline and environmental conditions have triggered a dietary shift of an opportunistic seabird over the last 30 years on the northwest coast of Spain. Regional Environmental Change, 20: 10.

# Anthropogenic food resources, sardine decline and environmental conditions have triggered a dietary shift of an opportunistic seabird over the last 30 years on the northwest coast of Spain

**Abstract.** Human activities and changing environmental conditions are the main drivers of ecosystem change. One major change near the western Iberian coast has been the collapse of the Atlanto-Iberian sardine *Sardina pilchardus* stock, with important cascading effects on marine top predators. We investigated the effect of long-term changes in fishery landings, sardine availability, and environmental conditions on the diet of the yellow-legged gull *Larus michahellis* in the northwest coast of Spain, over the last 30 years (1987-2017). Dietary trends of gulls were investigated through the analysis of 5010 pellets that revealed a sharp decline of fish and refuse and a shift to a crustacean-based diet. General additive mixed models showed that both total fish and sardine occurrences in gull pellets were negatively associated with total fishery landings and positively associated with sardine landings, suggesting fish depletion and higher fishing efficiency (i.e. reduced discards) during the study period. The winter North Atlantic Oscillation (NAO) index was also positively related with sardine occurrence in gull pellets, possibly due to low sardine abundance and rough conditions in years with very low NAO values. The refuse decline was most probably caused by the closure of open-air landfills, implemented under the European Union Landfill Directive. Our results suggest that changes in fishing practices and waste disposal were the main factors responsible for the sharp decline of fish and refuse in yellow-legged gull diet.

**Keywords:** yellow-legged gull; fisheries; landfills; North Atlantic Oscillation; S*ardina pilchardus*; *Larus michahellis*.

## 1. Introduction

Climate change and human activities have major impacts on marine ecosystems, affecting all trophic levels (Halpern et al. 2008, Sydeman et al. 2015). Cumulative impacts of these stressors increased world-wide, especially in coastal areas where human occupation and activities are particularly intense (Harley et al. 2006, Maxwell et al. 2013). Commercial fisheries are one of the most significant pressures in coastal areas, being responsible for the depletion of fish stocks, habitat destruction, and changes in food web structure (Pauly et al. 1998, Hussey et al. 2014, Kroodsma et al. 2018). By altering the composition and quantities of both commercially exploited marine species (i.e. landings) and bycatch species (i.e. discards), fisheries can have severe long-lasting consequences for marine top predators,

such as seabirds, that use these resources (Bodey et al. 2014, Grémillet et al. 2018). However, fishing activities can also be advantageous for seabird species that rely on fishery offal and discards, and on other facilitated foraging opportunities during fishing operations (e.g. Votier et al. 2008; Patrick et al. 2015; Matos et al. 2018).

Seabirds are long-lived species, with high adult survival rates and deferred maturity, making them particularly vulnerable to changes in their environment (Cairns 1988, Furness and Camphuysen 1997). Seabirds forage on productive marine areas such as upwelling zones and oceanic fronts (Grecian et al. 2016), being highly sensitive to fluctuations in pelagic fish abundances (Cury et al. 2011, Gulka et al. 2017). Generalist species may respond to changes in profitable prey availability by diversifying their diet (MacArthur and Pianka 1966). Previous studies reported dietary shifts of seabirds in response to environmental change (Montevecchi and Myers 1996, Wu et al. 2017), which may influence body condition, reproductive success, and survival of individuals (Grémillet et al. 2008, Oro et al. 2014, Kowalczyk et al. 2014, van Donk et al. 2017). Recently, temperature and the frequency and severity of extreme climatic events increased in many areas of the world (IPCC 2014), with negative consequences for marine top predators (Cubaynes et al. 2011, Pardo et al. 2017). Along the western Iberian coast, environmental changes imply shifts in the North Atlantic Oscillation (NAO) index and in sea surface temperature (Santos et al. 2005), affecting both pelagic fish and their predators (Santos et al. 2012, Barros et al. 2013). The NAO index refers to a north−south alternation in atmospheric mass between the subtropical Atlantic and the Arctic (Hurrell et al. 2003). The NAO reflects westerly winds and storms across the North Atlantic (Hurrell et al. 2003), which can affect the abundance of small pelagic fish such as sardine *Sardina pilchardus* (Borges et al. 2003, Santos et al. 2007), with probable consequences on their marine predators such as seabirds (Paiva et al. 2013b, Barros et al. 2013).

One of the major ecosystem changes along the western Iberian coast in recent years has been the collapse of the Atlanto-Iberian sardine stock (Silva et al. 2009, Veiga-Malta et al. 2019). Sardines play a central role in the food web dynamics in these waters due to their high abundance, high energy content (Rosa et al. 2010), and high number of trophic connections (Veiga-Malta et al. 2019), being an important prey for several marine predators (e.g. Mouriño et al. 2003, Begoña et al. 2014). Moreover, sardines support important commercial fisheries (Feijó et al. 2018, Santos et al. 2018). One of the main sardine recruitment areas is located in northwest Iberia, particularly off southern Galicia (northwest Spain) and northern Portugal (Carrera and Porteiro 2003, Silva et al. 2009). In 2012, Spain and Portugal, the two main countries targeting sardines, implemented a management plan to protect the Atlanto-Iberian sardine

stock (Silva et al. 2015). The management plan was not successful in reversing the sardine decline, leading to the International Council for the Exploration of the Seas (ICES) advising for zero catches of sardines (ICES 2017). The stock collapse has led to major changes in the ecosystem structure (Veiga-Malta et al. 2019), affecting the diet of marine top predators (Paiva et al. 2013a, Marçalo et al. 2018).

Small pelagic fish, such as sardine, are very important food resources for yellow-legged gulls *Larus michahellis* (Alonso et al. 2015, Calado et al. 2018). The yellow-legged gull is an opportunistic species that displays great behavioural plasticity, feeding on a wide range of prey, including natural species of marine and terrestrial origin and human food resources such as fishery discards and refuse (Duhem et al. 2003, Ramos et al. 2009b). Their diet responds to fluctuations in prey availability and environmental conditions (Pedro et al. 2013, Alonso et al. 2015). While several studies have described the diet of this species (e.g. Munilla 1997; Neves et al. 2006; López et al. 2016), long-term observations on diet are scarce and inter-annual dietary changes of this highly plastic species and their underlying drivers remain poorly understood. The Galician coast hosts one of the largest populations of yellow-legged gulls in the world, and is characterized by high marine primary productivity, standing as one of the most important fishing areas in Europe (Tenore et al. 1995, Arístegui et al. 2009). Regular breeding censuses of this species in the Atlantic Islands of Galicia National Park have been performed since 1976, revealing that numbers of yellow-legged gulls were increasing until 2006, reaching over 31500 breeding pairs (Arcea 2007). Since 2006, the population size has decreased by ca. 65% for unclear reasons, with 10795 breeding pairs in 2015 (Barros 2015). Annual monitoring suggests that the breeding population crash continues (-35% since 2015; see [mardeaves.org](mardeaves.org)). The European Union Landfill Directive (European Commission 1999) promoting the closure of open-air landfills, implemented in the early 2000s, has reduced the availability of human food resources to scavenger species such as the yellow-legged gull, and the recent full implementation of the European ban on fishery discards (European Union 2013, European Union 2015) in January 2019 has further reduced the availability of these food resources (Bicknell et al. 2013). These European policies, in combination with the depletion of fish stocks and environmental change, might lead to dietary shifts with significant population-level consequences for the yellow-legged gull population.

We investigated the effect of long-term changes in fishery landings and environmental conditions on the diet of the yellow-legged gull in the northwest coast of Spain, over the last 30 years (1987-1994 & 2004-2017) to understand how environmental change and anthropogenic activities affect gull diet in this region. We characterized diet composition and identified main dietary trends of the yellow-legged gull

population, focussing mainly on the importance of fish in their diet over the study period. We also assessed the main drivers of such dietary changes, particularly changes in the availability of fish food resources and environmental conditions. Previous studies in the northwest coast of Spain suggest that yellow-legged gulls may have consumed less fish and refuse in 2004 compared to 1987-1993 (Munilla 1997, Moreno et al. 2010), which is in accordance with other gull studies across the globe (Pedro et al. 2013, Ronconi et al. 2014, Blight et al. 2015, Bond 2016). Thus, we expected a decrease in fish occurrence in gull pellets throughout the study period. On the other hand, we expected a negative relationship between fish consumption by gulls and fishery landings, if fisheries caused fish depletion (Cury et al. 2011), but a positive relationship is expected if fisheries provide food resources (i.e. discards; Ramírez et al. 2015; Foster et al. 2017) or served as a proxy of prey abundance (Bennett et al. 2017). NAO index is expected to be positively associated with fish in gull diet, if very low NAO values can lead to lower abundance of marine prey (Santos et al. 2007, Paiva et al. 2013a), while sea surface temperature (SST) is expected to be negatively related with fish consumption, because high SST values are usually associated with lower marine productivity, and consequently lower fish abundance (Garrido et al. 2017).

## 2. Methods

### 2.1. Diet identification

Pellets (N = 5010) were collected at 14 yellow-legged gull colonies along the northwest coast of Spain, from Cíes (42° 10' N, 8° 54' W) to Pantorgas (43° 33' N, 6° 59' W; Figure 5.1), in 1987-1994 and 2004-2017, during the breeding period (March-August). Efforts were made to visit the same colonies, however, not all were sampled in all years (see Table S5.1). Diet samples were examined in a stereomicroscope, and prey items were identified to the lowest taxonomic level possible based on hard prey remains (i.e. exoskeleton and bones). Fish prey were identified using a reference collection (i.e. otoliths, vertebrae, and other fish bones) and identification keys. Refuse remains included chicken, beef, and pork bones, cooked fish bones, and manufactured materials, such as plastic, paper, or glass. We assessed the presence or absence of each prey type in gull pellets and calculated its percentage of occurrence (PO), defined as the percentage of pellets with a certain prey type, calculated for each sampling year. Prey items were grouped according to taxonomic categories (see Table 5.1) to investigate major temporal trends in the diet of gulls over the last 30 years.
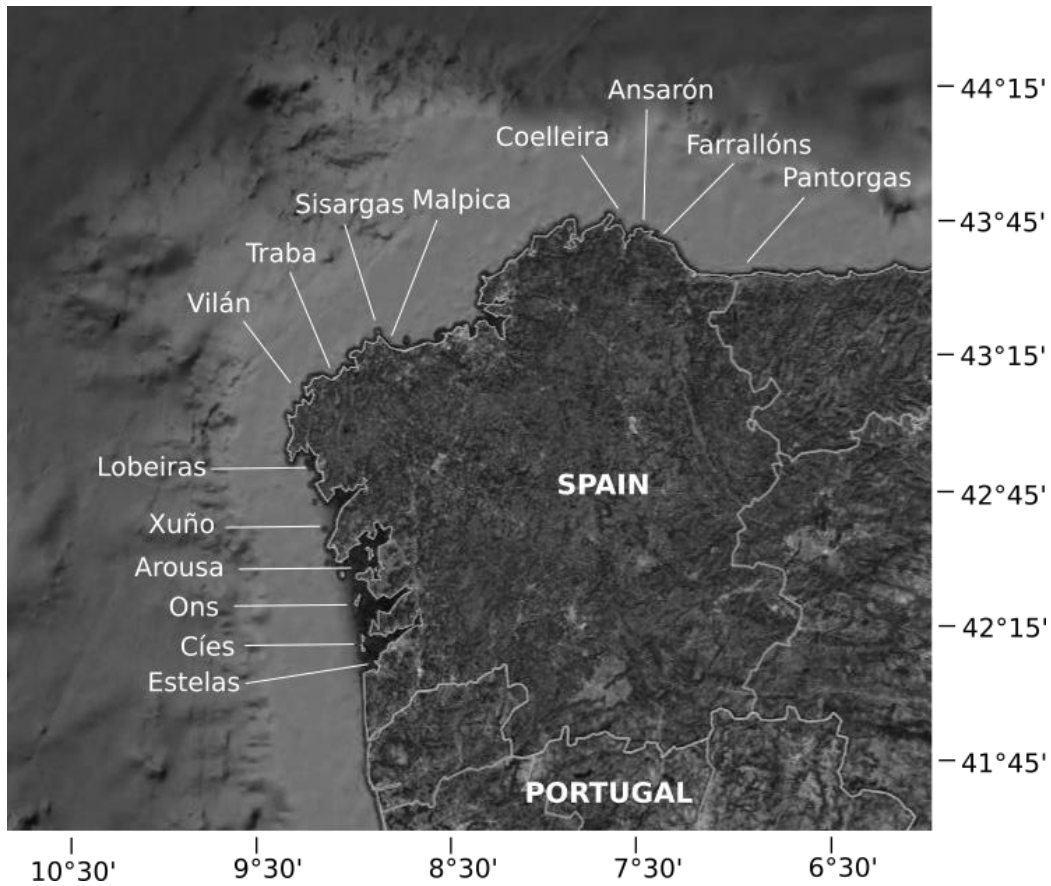
**Figure 5.1.** Sampled locations of yellow-legged gull *Larus michahellis* pellets.

## 2.2. Fishery data

Total fishery landings (hereafter "fishery landings") and sardine landings data were downloaded from the ICES database (http://www.ices.dk) for the Cantabrian Sea and Atlantic Iberian waters (ICES area 27 subareas VIIIc and IXa). Fishery landings data were only available until 2016, and for the first two study years (i.e. 1987 and 1988) there were no data from Spain, which underestimated substantially the landings in those years. Therefore, to perform general additive mixed models (GAMMs; see statistical analysis), we tested imputation in which any missing value contributed zero to the linear predictor from its smooth but had its own random effect. However, best supported models (ΔAICc < 2) did not include this imputation, meaning that data series averaged values performed better in models (see Tables S5.2 and S5.3).

## 2.3. Environmental variables

The North Atlantic Oscillation (NAO) index is a large-scale integrative index and is the main climate influence at mid and high latitudes of the North Atlantic Ocean, inducing variations in upwelling patterns and changes across various marine trophic levels, including small pelagic fish and marine top predators such as seabirds (Hurrell et al. 2003, Stenseth et al. 2003). Sardines are the main small pelagic fish species in western Iberian waters and were reported to be highly influenced by NAO (Guisande et al. 2001, 2004, Santos et al. 2007) and sea surface temperature (SST; Santos et al. 2005, 2012; Leitão et al. 2014; Garrido et al. 2017) The NAO is one of the oldest and best known world climatic patterns (Stenseth 2002, Hurrell et al. 2003), and SST is one of the most used oceanographic variables in seabird ecology (Tremblay et al. 2009), therefore, their usage provides comparable results with previous studies. We used the extended winter (December–March) NAO index, as a proxy of climatic conditions, extracted from (https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based; Hurrell 1995), and the annual average of sea surface temperature anomaly (SSTa), as a proxy of oceanographic conditions, extracted from IGOSS (Integrated Global Ocean Services Systems; Reynolds et al. 2002) between 40.5-44.5° N and 6.5-9.5° W. IGOSS platform provides both SST and SSTa data. We tested univariate models with SST or SSTa, and models with 1-year lagged variables (SST-1 and SSTa-1), and selected SSTa based on AIC values.

## 2.4. Statistical analysis

General additive mixed models (GAMMs) following a normal distribution were performed to test the influence of fisheries and environmental conditions on the percentages of occurrence (PO) of sardine and total fish (arcsine square root transformed) in yellow-legged gull pellets between 1987 and 2016. GAMMs are especially suitable to model multisite-time series data, allowing linear and non-linear relationships between continuous explanatory variables and the response variable. We included colony as a random factor to account for differences between colonies, including the differences caused by sporadic sampling of some colonies (Zuur et al. 2009), and a temporal autocorrelation was integrated in the model after visual inspection of model-validation plots (i.e. ACF and PACF plots). Models were weighted by annual sample size to account for variation in sampling effort. Multi-collinearity between explanatory variables was examined by the variation inflation factor (VIF; Zuur et al. 2007) using the *vif.gam* R function, and *concurvity* was also used to check collinearity between smoothed terms (Morlini 2006). Additionally, we also calculated Pearson correlation coefficients to check correlation among

explanatory variables. Multivariate GAMMs were carried out since VIF values were below 1.6, concurvity was below 0.4, and Pearson correlation coefficients were also low (< 0.5; see Table S5.4). We used the R package 'mgcv' (Wood 2017) and limited thin plate regression splines to a maximum of 3 knots to avoid overfitting. Models were constructed for all possible combinations of explanatory variables and the missing values imputation using the *dredge* function in the R package 'MuMIn' (Barton 2018). Model selection was performed using Akaike's Information Criterion corrected for small sample sizes (AICc), and models with ΔAICc (the difference in AICc between a given model and the model with the smallest AICc) below 2 were considered the best supported models (Burnham and Anderson 2002). We performed the same analyses considering only Cíes, the colony with more sampled years (Table S5.1). Similar patterns were found in both analyses (Figure S5.1), suggesting that similar conditions affected yellow-legged gulls on both local and regional scales.

Pearson correlation coefficients were calculated to investigate temporal trends in fishery data and environmental variables and in the yellow-legged gull main prey (i.e. sardine, total fish, crustaceans, and refuse; all arcsine square root transformed). All analyses were performed with R software ver. 3.5.2 (R Core Team 2019), and significance was set at alpha = 0.05.

## 3. Results

### 3.1. Dietary trends

The diet of yellow-legged gulls varied widely through time and comprised a great variety of prey taxa, including fish, crustaceans, molluscs, echinoderms, insects, small vertebrates, vegetable matter, and refuse items (Table 5.1). Fish were mostly sardine *Sardina pilchardus*, horse mackerel *Trachurus* sp., pout *Trisopterus* sp., and blue whiting *Micromesistius poutassou*. Crustaceans consisted mostly of Henslow's swimming crabs *Polybius henslowii* and goose barnacles *Pollicipes cornucopia*. Mussels *Mytilus galloprovincialis* comprised the majority of molluscs.

**Table 5.1.** Percentage of occurrence (PO %) of prey items found in yellow-legged gull pellets between 1987-1994 and 2004-2017. Sample size is shown in parenthesis.

| Prey | 1987 (590) | 1988 (176) | 1989 (393) | 1990 (208) | 1991 (479) | 1992 (50) | 1993 (463) | 1994 (10) | 2004 (859) | 2005 (199) | 2006 (65) | 2007 (129) | 2008 (94) | 2009 (98) | 2010 (8) | 2011 (262) | 2012 (18) | 2013 (138) | 2014 (73) | 2015 (359) | 2016 (154) | 2017 (185) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total fish | 37 | 24 | 34 | 23 | 27 | 18 | 42 | 30 | 18 | 22 | 12 | 15 | 5 | 13 | 0 | 2 | 33 | 6 | 8 | 3 | 10 | 5 |
| *Sardina pilchardus* | 12 | 9 | 9 | 9 | 4 | 4 | 10 | 10 | 2 | 2 | 3 | 0 | 0 | 5 | 0 | 0 | 6 | 0 | 0 | 0 | 1 | 0 |
| *Trachurus* sp. | 6 | 5 | 13 | 4 | 8 | 4 | 10 | 20 | 7 | 12 | 0 | 10 | 0 | 2 | 0 | 1 | 6 | 4 | 4 | 1 | 6 | 2 |
| *Trisopterus* sp. | 2 | 1 | 4 | 3 | 4 | 2 | 4 | 0 | 1 | 4 | 0 | 0 | 2 | 1 | 0 | 0 | 17 | 1 | 1 | 0 | 0 | 1 |
| *Micromesistius poutassou* | 13 | 4 | 8 | 4 | 7 | 8 | 17 | 0 | 4 | 3 | 9 | 4 | 1 | 4 | 0 | 0 | 0 | 1 | 3 | 0 | 3 | 2 |
| Other fish | 12 | 12 | 10 | 7 | 8 | 8 | 16 | 0 | 5 | 4 | 0 | 2 | 2 | 1 | 0 | 2 | 11 | 1 | 0 | 2 | 1 | 0 |
| Total crustaceans | 39 | 28 | 39 | 52 | 47 | 42 | 30 | 10 | 54 | 13 | 12 | 57 | 61 | 67 | 38 | 80 | 56 | 55 | 42 | 67 | 60 | 65 |
| *Pollicipes cornucopia* | 1 | 1 | 1 | 2 | 3 | 2 | 6 | 0 | 5 | 6 | 12 | 22 | 20 | 3 | 25 | 11 | 6 | 30 | 32 | 9 | 12 | 17 |
| *Polybius henslowii* | 32 | 23 | 36 | 47 | 43 | 40 | 22 | 0 | 47 | 5 | 0 | 35 | 41 | 64 | 13 | 70 | 50 | 25 | 12 | 58 | 49 | 47 |
| Other crustaceans | 8 | 6 | 3 | 7 | 4 | 0 | 6 | 10 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Total bivalves | 18 | 11 | 7 | 13 | 10 | 10 | 8 | 0 | 7 | 1 | 28 | 6 | 14 | 7 | 0 | 2 | 0 | 26 | 22 | 12 | 12 | 6 |
| *Mytillus galloprovincialis* | 18 | 11 | 7 | 13 | 9 | 10 | 8 | 0 | 7 | 1 | 28 | 6 | 14 | 7 | 0 | 2 | 0 | 26 | 22 | 12 | 12 | 6 |
| Other bivalves | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Cephalopods | 1 | 5 | 2 | 5 | 2 | 0 | 5 | 0 | 2 | 3 | 8 | 2 | 2 | 4 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 |
| Echinoderms | 3 | 3 | 2 | 0 | 2 | 2 | 1 | 0 | 1 | 2 | 0 | 1 | 2 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 2 | 1 |
| Polyplacophora | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Gastropods | 5 | 4 | 2 | 1 | 2 | 0 | 6 | 0 | 0 | 2 | 0 | 2 | 3 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 3 |
| Vegetable matter | 4 | 5 | 5 | 8 | 3 | 0 | 5 | 0 | 15 | 8 | 20 | 11 | 6 | 4 | 0 | 3 | 11 | 7 | 11 | 6 | 5 | 8 |
| Insects | 3 | 2 | 4 | 2 | 2 | 0 | 3 | 0 | 4 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| Terrestrial vertebrates[1] | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 2 |
| Refuse | 39 | 61 | 36 | 40 | 39 | 50 | 50 | 90 | 11 | 56 | 42 | 17 | 12 | 6 | 63 | 12 | 11 | 9 | 21 | 13 | 16 | 15 |

[1]Terrestrial vertebrates are amphibians, birds, and small mammals.
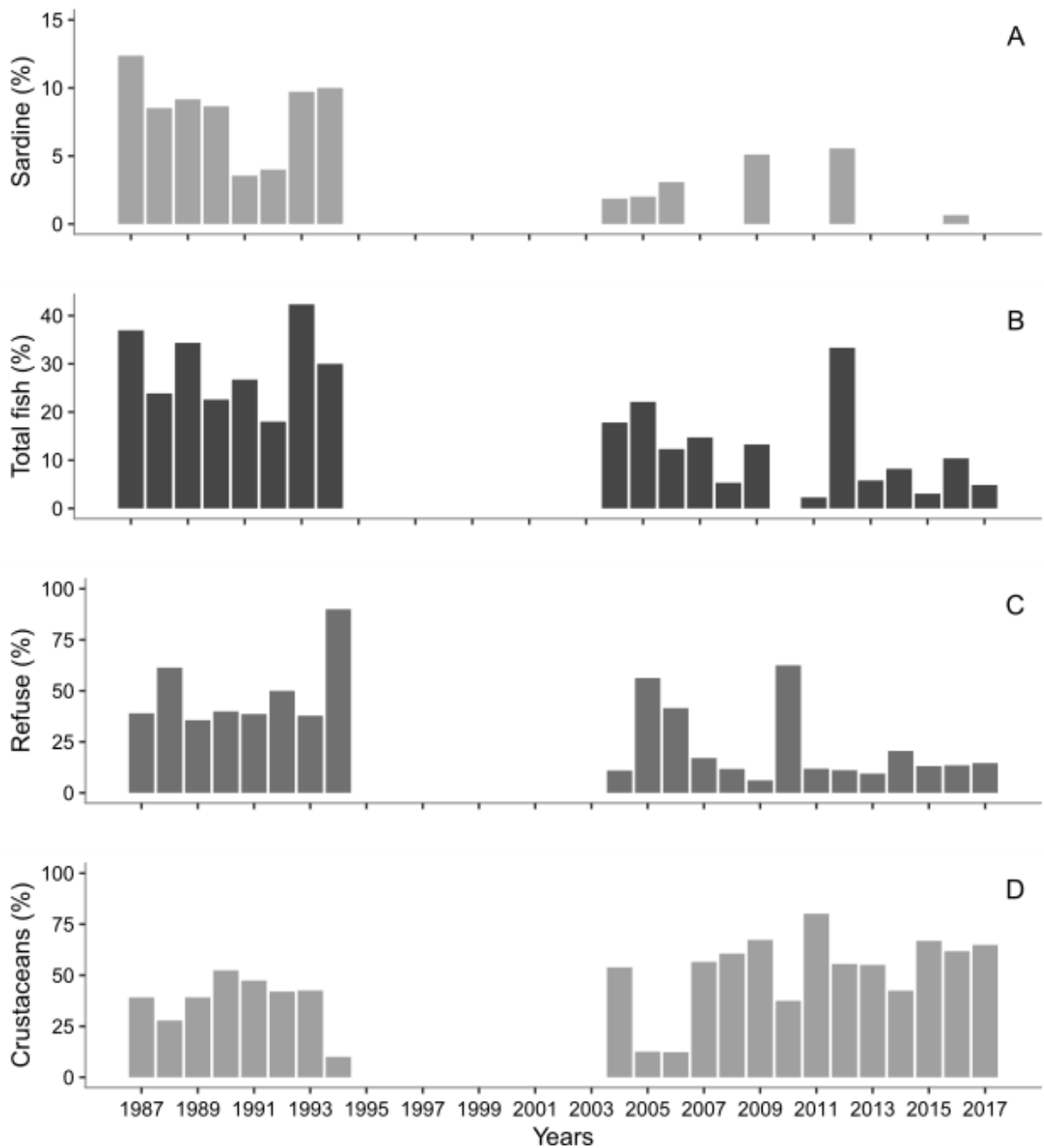
**Figure 5.2.** Interannual variation in the percentage of occurrence of yellow-legged gull main prey (A - sardine; B - total fish; C - refuse and D - crustaceans) based on pellets collected between 1987-1994 and 2004-2017.

Total fish occurrence showed a significant negative trend in gull pellets from 1987 to 2017 (r = -0.73, P < 0.001), with an occurrence of 37% in 1987 and 5% in 2017 (Figure 5.2). Sardine occurrence showed a more pronounced trend, decreasing from 12% to 0% over the study period. In fact, sardines became practically non-existent in gull pellets from 2004 onwards (i.e. PO < 6%, Figure 5.2), and had the

sharpest decline among all fish species between 1987 to 2017 (sardine: r = -0.82, P < 0.001; horse mackerel: r = -0.47, P = 0.03; pout: r = -0.21, P = 0.2; blue whiting: r = -0.58, P = 0.005; other fish: r = -0.67, P < 0.001).

Refuse and crustacean occurrences had inverse temporal patterns (Figure 5.2). While refuse decreased in gull pellets between 1987 and 2017 from 39% to 15% (r = -0.63, P = 0.002), crustaceans increased from 39% in 1987 to 65% in 2017 (r = 0.46, P = 0.03).

### 3.2. Influence of fisheries and environmental conditions

Both fishery data and environmental conditions showed inter-annual variability (Figure 5.3). Fishery landings increased from 228,509 (tonnes) in 1989 to 345,790 in 2016 (r = 0.68, P < 0.001). On the contrary, sardine landings decreased from 177,696 (tonnes) in 1987 to 22,704 in 2016 (r = -0.93, P < 0.001). Environmental variables did not present statistically significant temporal trends, however, exhibited high inter-annual variability over 1987-2017. NAO index ranged from 5.08 in 1989 to -4.64 in 2010, and SSTa varied between -0.21 in 1991 and 0.97 in 1997.
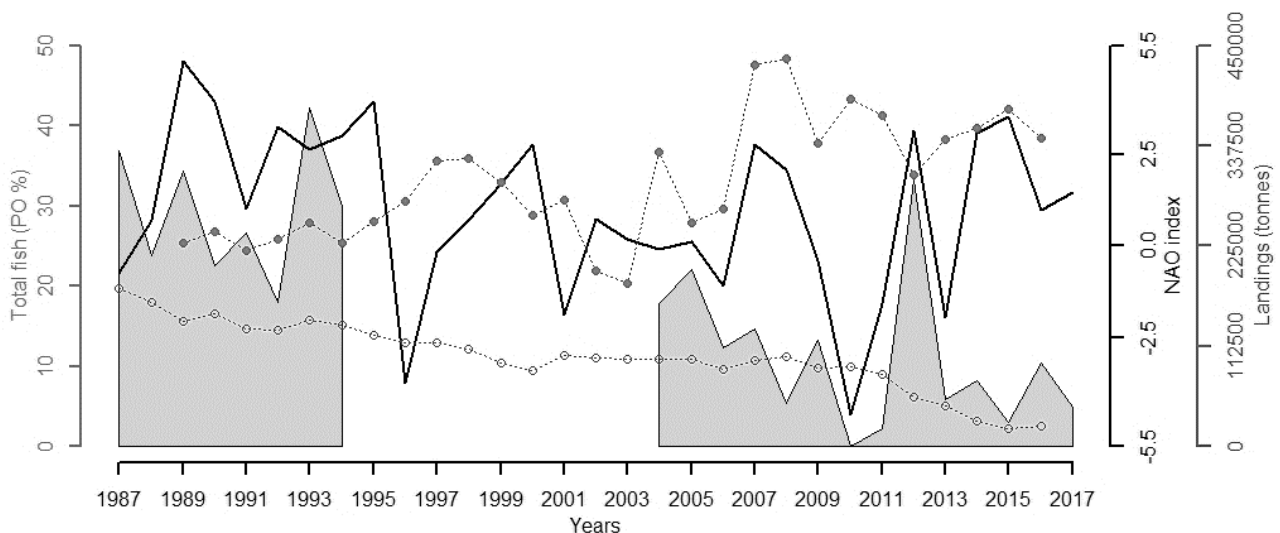


**Figure 5.3.** Temporal trends of total fish percentage of occurrence (PO %) in yellow-legged gull pellets (grey shaded area represented in the left y-axis), the North Atlantic Oscillation (NAO) index (solid black line represented in the first right y-axis), and landings (fishery landings indicated by filled grey points and sardine landings indicated by open grey points, represented in the second right y-axis).

Models with sardine landings and fishery landings as explanatory variables were the best supported models for total fish occurrence in yellow-legged gull pellets (Table 5.2). Considering sardine occurrence in yellow-legged gull pellets, best supported models included sardine landings, fishery landings, and NAO index as explanatory variables (Table 5.2). Both sardine and total fish occurrences in gull pellets were positively associated with sardine landings (Figures 5.4A and 5.4B) and negatively associated with fishery landings (Figures 5.4C and 5.4D). Higher NAO values were also positively associated with sardine occurrence in yellow-legged gull pellets (Figure 5.4E). SSTa was not significant in none of the final models (see model selection in Tables S5.2 and S5.3).

**Table 5.2.** Final general additive mixed models (GAMMs), within ΔAICc < 2, explaining the occurrence of A) sardine and B) total fish in yellow-legged gull pellets. Models are ordered by increasing Akaike Information Criterion corrected for small sample sizes (AICc). Explanatory variables tested were sardine landings, fishery landings, North Atlantic Oscillation index (NAO), and Sea Surface Temperature anomaly (SSTa). Number of estimated parameters (df) and Akaike weight (Wi) are also shown. All models include colony as a random effect.

| Models | df | AICc | ΔAICc | Wi |
|---|---|---|---|---|
| **A) Sardine** | | | | |
| Sardine ~ sardine landings + fishery landings | 8 | 545.0 | 0.0 | 0.34 |
| Sardine ~ sardine landings + fishery landings + NAO index | 10 | 546.1 | 1.1 | 0.20 |
| Sardine ~ sardine landings | 6 | 546.9 | 1.9 | 0.13 |
| **B) Total fish** | | | | |
| Total fish ~ sardine landings + fishery landings | 8 | 622.6 | 0.0 | 0.36 |
| Total fish ~ sardine landings | 6 | 623.7 | 1.1 | 0.21 |
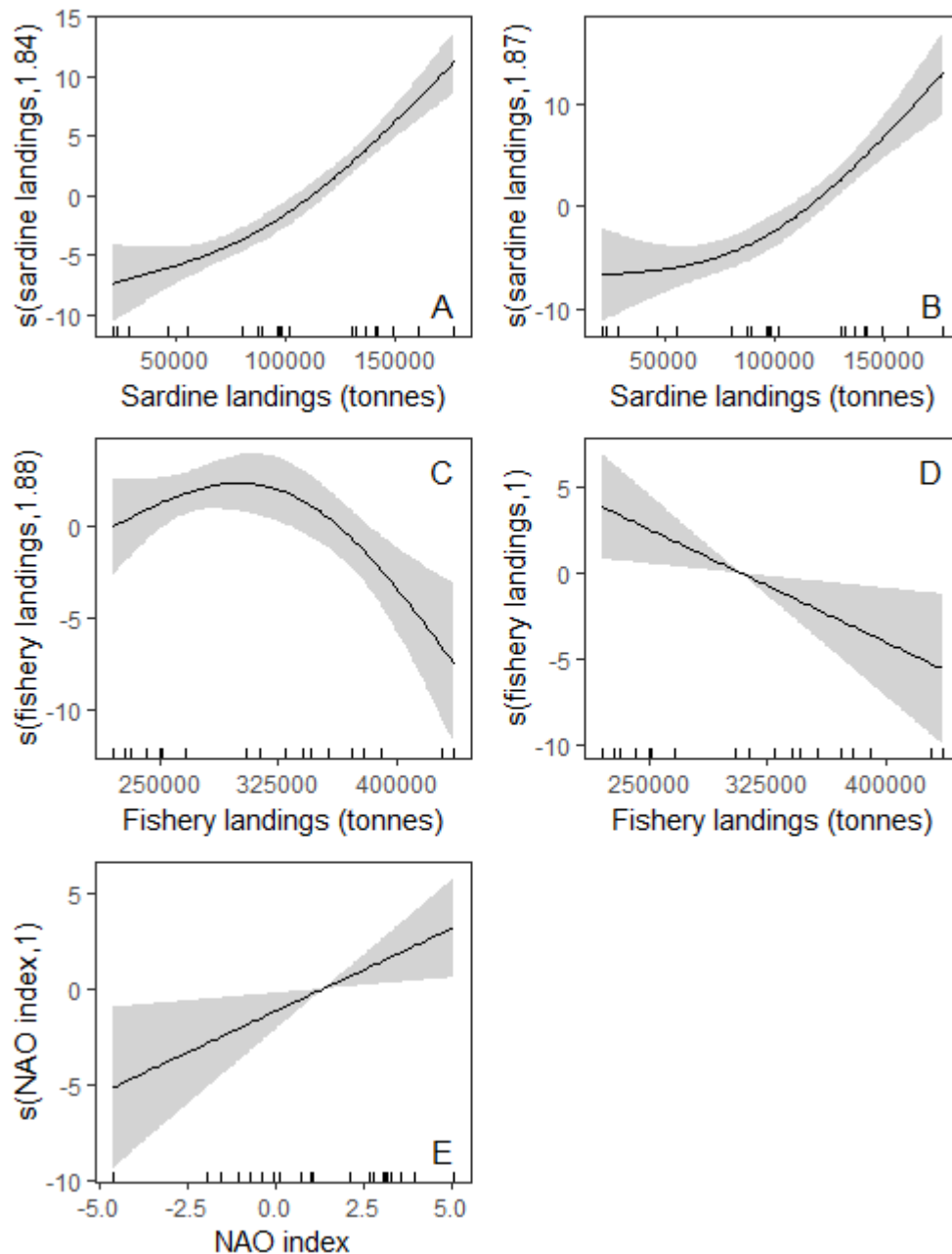
**Figure 5.4.** Response curves of the variables explaining the temporal trends of fish prey (percentage of occurrence (PO %), arcsine square root transformed) of yellow-legged gulls based on general additive mixed models (GAMMs) outputs. Plots show the predicted curve (black solid lines), 95% confidence intervals (grey shaded areas). A - Sardine landings effect on sardine occurrence, B - Sardine landings effect on total fish occurrence, C - Fishery landings effect on sardine occurrence, D - Fishery landings effect on total fish occurrence, E - North Atlantic Oscillation (NAO) index effect on sardine occurrence.

**4. Discussion**

**4.1. Dietary trends of yellow-legged gulls**

The results revealed a major dietary change of yellow-legged gulls over the last 30 years in northwest Spain. There was a sharp decline of fish and refuse in gull pellets and a shift to a crustacean-based diet related to increased fishery landings, decreased sardine availability, and low NAO values. The decline of refuse in yellow-legged gull pellets was most probably caused by the closure of open-air landfills that began in 1999, implemented under the European Union (EU) Landfill Directive (European Commission 1999), which decreased refuse availability to scavenger species. Indeed, in Galicia most landfills were closed in 2002 (Pérez et al. 2012). Previous work in Galician colonies revealed a high dependency of yellow-legged gulls on fish and refuse from 1987 to 1993, with an occurrence of 32% of fish in gull pellets (Munilla 1997). A later study reported a significant decline of fish in 2004, with an occurrence of less than 3% in five colonies in the northwest coast of Spain (Moreno et al. 2010). Our study confirms these trends in a longer time period. A yellow-legged gull study in the Azores archipelago, Portugal, also found a decrease in the occurrence of fish and an increase in crustaceans (i.e. goose barnacles) from the 1990s to the 2000s (Pedro et al. 2013), in accordance with our results. Our study suggests that gulls changed their foraging locations through the study period. The decreased consumption of fish may indicate that gulls used less offshore marine areas, and the decreased occurrence of refuse probably indicates less terrestrial foraging (i.e. in landfills). On the other hand, the increased occurrence of crustaceans in their diet suggests an increased usage of coastal environments by gulls. This agrees with a previous GPS-tracking study on the yellow-legged gull in the western Iberian coast, which revealed a change in foraging locations when gulls increased the consumption of Henslow's swimming crabs and reduced the consumption of refuse and fish (Ceia et al. 2014). Even though we have no data on the abundance and availability of crustaceans, their increasing trend in yellow-legged gull pellets is most likely associated with their high abundance and accessibility, associated with lower fish and refuse availability. Indeed, the Henslow's swimming crab is the most abundant decapod species over the continental shelf of northwest Spain (Fariña et al. 1997b), gathering in large shoals close to the sea surface (Signa et al. 2008), and therefore easily accessible to yellow-legged gulls. Similar changes have been reported in other large gull species, e.g., herring gull, (Bond 2016), glaucous-winged gulls (Blight et al. 2015), great black-blacked gull (Ronconi et al. 2014), associated with less fish consumption. However, these studies did not analyse possible causes for such dietary shifts.

Recent studies reported long-term shifts in seabird diets related with increases in the consumption of alternative fish species (Howells et al. 2018, Peterson et al. 2018, Riordan and Birkhead 2018, Vihtakari et al. 2018). Contrastingly, in this study all fish species in the diet of yellow-legged gulls showed negative trends over the study period. In western Iberian waters, the sharp decline of the sardine stock was followed by increases of other pelagic species, such as horse mackerel and chub mackerel, which are natural competitors of sardines (Martins et al. 2013, Garrido et al. 2015). However, gull diet did not reflect these increases. Yellow-legged gulls are surface feeders and do not have diving capabilities (Gwiazda 2004), therefore, may not have the ability to compensate the sardine stock decline and increase the consumption of other fish species, as was also found in the Mediterranean (Cardona et al. 2015). Additionally, yellow-legged gull is a coastal species and do not often venture to offshore marine areas (i.e. < 100 km from the colony; Mendes et al. 2018; Matos et al. 2018). Indeed, both horse and chub mackerels occupy larger geographical ranges, also occurring in deeper and more offshore waters compared to sardines (Gomes et al. 2001, Sousa et al. 2005), which may hamper predation by gulls.

## 4.2. Influence of fisheries

The two landing categories had opposite effects on gull diet; while high values of total fishery landings were associated with lower fish consumption, sardine landings were positively associated with fish occurrence in yellow-legged gull pellets. Demersal species, such as pout and blue whiting, are made available to surface feeders, such as gulls, through fishery discards (Garthe et al. 1996, Wagner and Boersma 2011). However, gulls can capture pelagic species, such as sardine and mackerels, by themselves or in association with fisheries. Opportunistic feeding behaviour of yellow-legged gulls in association with fishing activities is well described throughout their breeding range (Oro and Ruiz 1997, Matos et al. 2018), including in the northwest coast of Spain (Valeiras 2003). Sardines are mostly caught by purse-seiners (Tenore et al. 1995, Silva et al. 2015), which can facilitate fish caught by gulls during encirclement of fish, slipping (i.e. catch release while the net is in the water; Stratoudakis and Marçalo 2002), and discarding process (Arcos and Oro 2002a). The decrease in sardine consumption was accompanied by the negative trend of sardine landings, indicating lower sardine availability to gulls, most likely through resource depletion. Total fishery landings increased substantially in tonnes during the study period, suggesting an increased fishing effort. However, this was contemporaneous to less fish consumption by yellow-legged gulls. This suggests that fisheries are depleting stocks, and therefore decreasing fish abundance/ availability to predators such as gulls, and that fisheries are becoming more

efficient, decreasing the amount of fishery discards available to scavenger species. Global tendencies show that commercial fisheries are responsible for collapses of pelagic fish stocks with negative consequences for seabird populations (Furness and Tasker 2000, Cury et al. 2011, Guillemette et al. 2018), and that fishing fleets are becoming more efficient, reducing both the total and relative amount of discards (Zeller et al. 2018). Indeed, fishing practices are changing in European waters, and one implementation of the new reform of the EU Common Fisheries Policy (European Union 2013, 2015) is a discard ban policy ([http://ec.europa.eu/fisheries/cfp/fishing_rules/discards/index_en.htm](http://ec.europa.eu/fisheries/cfp/fishing_rules/discards/index_en.htm)), which became fully implemented in 2019. This policy might further reduce fish availability to scavenger species, such as yellow-legged gulls, and lead to overall population declines (Bicknell et al. 2013).

## 4.3. Influence of environmental conditions

Environmental variability also affected the diet of gulls, namely, higher NAO values were positively associated with sardine occurrence in yellow-legged gull pellets. Higher NAO values are also associated with higher juvenile survival of Audouin's gull in West Africa (Payo-Payo et al. 2016) and with higher abundance of seabird species in Bay of Biscay (North Spain; Louzão et al. 2015). In our study area, both lower and higher than usual NAO values affect negatively sardine recruitment, which could be related with high turbulence that limited primary production (Guisande et al. 2004). Additionally, Paiva et al. (2013a) revealed that very low NAO values represent extreme oceanic conditions, which later in the year lead to lower marine prey abundance and, consequently, lower availability to top predators such as gulls. In fact, in 2010 the NAO index was one of the lowest ever recorded (Osborn 2011), and the climatic event depicted by such value may have been responsible for the non-occurrence of fish, decrease of crustaceans, and increase of refuse in gull pellets that year. Despite low sample size in 2010, several studies reported similar negative effects in several seabird species in the northeast Atlantic (Paiva et al. 2013b, Ramos et al. 2015, Fagundes et al. 2016). Stronger southerly winds in years with extremely low NAO values could have caused low recruitment of sardines during spring and summer due to the mortality of eggs and larvae caused by high turbulence during winter (Guisande et al. 2004). Environmental conditions may have short- and mid-term ecological effects, however, the mechanisms of how environmental changes affect top predators are complex and still poorly understood. For instance, we failed to detect the influence of SSTa on dietary trends of yellow-legged gulls, despite warming trends in SST being found to influence seabird diets (Montevecchi and Myers 1997, Howells et al. 2017) with long-term consequences on their population dynamics (Luczak et al. 2012, Pardo et al. 2017, Goyert et al.

2018). Our results suggest that yellow-legged gulls are more influenced by anthropogenic activities and climate than oceanographic conditions, as expected due to their highly opportunistic and coastal foraging behaviour (Real et al. 2017, Matos et al. 2018).

## 5. Conclusions

Our results suggest that changes in fishing practices and waste disposal were the main factors responsible for the dietary shift of the yellow-legged gull in the northwest coast of Spain, and that environmental conditions mediated the human impacts on gull diet. Moreover, gulls seem to be more influenced by large scale climatic phenomena (i.e. NAO) than local oceanographic conditions (i.e. SST). Yellow-legged gulls decreased sardine consumption over the last 30 years, reflecting the overall decline of the Atlanto-Iberian sardine stock.

**GENERAL DISCUSSION**

This thesis contributes to the understanding of the influence of fisheries on gull trophic and foraging ecology, and its spatio-temporal variability on the western Iberian coast. Several methods were used to examine gull feeding behaviour at the community, population, and individual levels. The results of this thesis revealed gull opportunistic feeding in association with fisheries throughout the Atlantic Iberian coast. Specifically, the main findings were: (Chapter 1) both yellow-legged and Audouin's gulls fed on demersal and commercial pelagic fish species, but yellow-legged gulls seemed to take more advantage of fisheries than Audouin's gulls; (Chapter 2) on all four study islands along the western Iberian coast, yellow-legged gull males exhibited higher $\delta^{13}$C and $\delta^{15}$N stable isotope values than females, which suggests a male-biased ratio at fisheries; (Chapter 3) yellow-legged gulls were the most abundant species interacting with boats from the Peniche fishing fleet, especially with purse-seines; (Chapter 4) on all four study islands, there was an association between the fish species consumed by gulls and local fish landings; and (Chapter 5) alterations in fishing practices, along with changes in refuse management and environmental conditions, led to a sharp decline of fish and refuse accompanied by an increase of crustaceans in the diet of yellow-legged gulls on the northwest coast of Spain over the last 30 years.

## 1. Spatio-temporal patterns of gull feeding ecology

This study provides an integrative and comprehensive view of yellow-legged and Audouin's gulls feeding ecology across multiple seasons, years, and colonies (for yellow-legged gulls only). Spatial and temporal variability in the trophic ecology of yellow-legged gull and Audouin's gull chicks (Ramos et al. 2009a, b, Morera-Pujol et al. 2018) and adults (Pedrocchi et al. 2002, Ramos et al. 2011) were previously found in the Mediterranean. The results from this thesis reveal these patterns in detail for the Atlantic Iberian coast, while also addressing the influence of age class and sex separately. Additionally, this thesis provides important insights into the less-known ecology of both gull species during the non-breeding period.

The seasonal differences found in the stable isotope values of yellow-legged gulls (Chapters 1 and 2) are likely a reflection of a broader dietary range during the non-breeding period compared to the breeding period, however, in Audouin's gulls (Chapter 1) these differences are also likely to reflect their wintering grounds at the northwest African Atlantic coast (Sanpera et al. 2007). The main pattern was a higher consumption of fish outside the breeding phase, characterized by a higher consumption of demersal fish species, which was also the case for Audouin's gulls (Chapter 4). These dietary changes could be related with constraints experienced by breeding adults (Schreiber and Burger 2002b). Indeed,

seasonal differences were also detected at onboard observations within the Berlenga Special Protection Area (Chapter 3), which suggest the use of different foraging grounds by yellow-legged gulls throughout their annual cycle. However, seasonal differences in diet composition were more evident in some colonies/ years likely in response to shifts in prey availability (Piatt et al. 2007).

Inter-annual changes in seabird trophic and foraging ecology are expected in response to fluctuations in prey abundance and environmental conditions (Goyert et al. 2018). Indeed, there was marked inter-annual variability in gull stable isotope values, isotopic niche, diet composition (Chapters 1 and 4), and foraging behaviour (Chapter 3). Long-term data revealed a decreasing trend of fish in the diet of yellow-legged gulls on the northwest coast of Spain over the last 30 years (Chapter 5), and this tendency seems to occur across the Atlantic Iberian coast (Chapter 4), in accordance with other gull populations throughout the world (Pedro et al. 2013, Ronconi et al. 2014, Blight et al. 2015, Hobson et al. 2015, Bond 2016).

Spatial differences were found in the diet and stable isotope values of yellow-legged gull (Chapters 2 and 4). Gulls from northern colonies (Sálvora and Berlenga islands) consumed mostly marine invertebrates (i.e. Henslow's swimming crab *Polybius henslowii*) while gulls from southern colonies (Pesegueiro and Deserta islands) consumed mainly fish. The Henslow's swimming crab was previously recorded as one of the main prey of yellow-legged gulls at Sálvora (Munilla 1997, Moreno et al. 2010) and Berlenga (Ceia et al. 2014, Alonso et al. 2015) islands, where this species can attain very high densities in shallow coastal waters (González-Gurriarán et al. 1993, Sousa et al. 2005). Thus, the main spatial pattern in yellow-legged gull diet reflects Henslow's swimming crab local availability. Supporting this idea, on Pesegueiro and Deserta islands, when there was a decreased consumption of fish, gulls increased the consumption of vegetable matter and refuse, respectively. Moreover, the majority of the marine invertebrates found in the diet of gulls from Pesegueiro Island were goose barnacles *Pollicipes cornucopia*, suggesting that Henslow's swimming crab was not as available to gulls in southern Iberian waters. Additionally, this crab species seems to be consumed more by yellow-legged gull females than males (Chapter 2).

Stable isotope values revealed higher inter-annual and spatial dietary consistency in chicks than in adults, which suggest distinct feeding strategies of adults for self-feeding and for chick provisioning (Chapters 1 and 4). Parent-offspring dietary segregation was previously found in Audouin's (Pedrocchi et al. 1996, Navarro et al. 2010) and yellow-legged (Soldatini *et al.*, 2005; Moreno *et al.*, 2010; Romero *et al.*, 2019; but see Arizaga *et al.*, 2013; Zorrozua *et al.*, 2018) gulls and linked to their different food

requirements. Consistency was also found in the dietary differences between male and female yellow-legged gulls, reflected in their stable isotope values, which could be linked to sexual size dimorphism dictating differential access to fishery-related prey/ remains (Chapter 2), as found in other seabird species (see reviews in Phillips *et al.*, 2011, 2017). Nevertheless, future studies should further explore the inter- and intra- population spatio-temporal patterns found in this study to better understand the main drivers of such patterns and examine its consistency in shaping gull foraging strategies.

## 2. Influence of fisheries on gull feeding ecology

The results of this thesis revealed that both gull species consumed demersal (e.g. sea breams *Diplodus* sp.), bathypelagic (e.g. blue whiting *Micromesistius poutassou*), and commercial pelagic species (e.g. sardine *Sardina pilchardus* and mackerels *Scomber* sp. and *Trachurus* sp.), suggesting feeding in association with fishing activities, as found by Alonso *et al.*, (2015) (Chapters 1, 4, and 5). Demersal and bathypelagic species are most likely made available to surface-feeders such as gulls through fishery discards (Wagner and Boersma 2011). On the other hand, pelagic species can be caught by gulls naturally, through facilitated foraging opportunities during fishing operations, or as fishery discards (Arcos and Oro 2002a). Atlantic Iberian fisheries target mainly pelagic fish species, which are also the most discarded species due to high grading and minimum landing size restrictions (Borges et al. 2001, Vázquez-Rowe et al. 2011). Thus, discard composition in the western Atlantic is different from that of the western Mediterranean, where the fishing fleet is dominated by trawlers (Arcos et al. 2001) targeting demersal species (Arcos and Oro 2002b), which is reflected in the diet of gulls (Oro et al. 1996, Pedrocchi et al. 2002, González-Solís 2003).

Yellow-legged gull males presented consistently higher stable isotope values and narrower isotopic niche than females throughout the year and in all four study colonies, suggesting consistent sex-specific segregation in foraging strategies (Chapter 2). Isotopic mixing models estimated a higher proportion of fish in male diet, while females consumed a higher proportion of marine invertebrates. These results support the idea of a male-biased ratio at fisheries, in accordance with other gull populations (Navarro et al. 2010, Camphuysen et al. 2015). Indeed, fishery discards tend to have higher stable isotope values than natural prey (i.e. smaller pelagic fish), and a review showed that global patterns of seabird bycatch are adult- and male-biased (Gianuca et al. 2017). However, in northern Iberia, this species exhibited isotopically similar $\delta^{13}C$ and $\delta^{15}N$ values between sexes (Zorrozua et al. 2018), which does not necessarily mean similar foraging strategies (Inger and Bearhop 2008). In fact, in the

Mediterranean both species seem to present sexual differences in foraging behaviour, including in response to fishing activities, which may have ecological and conservation implications (Payo-Payo et al. 2015, García-Tarrasón et al. 2015).

In the monitored fisheries from the Peniche fishing fleet, yellow-legged gulls were the most abundant species interacting with fishing boats, especially with purse-seiners (Chapter 3). Most individuals were adults, following global patterns (Gianuca et al. 2017). In this fishery type, gull numbers were high regardless of fishery catch quantities, which suggests that gulls forage actively in association with purse-seiners through facilitated foraging opportunities (Arcos and Oro 2002a, González-Solís 2003). However, in the Ebro Delta (Mediterranean Sea), yellow-legged gulls interact more with trawlers than purse-seiners, likely due to the higher number of boats and discard availability (Arcos et al. 2001). In Portugal, trawling activity is limited, and yellow-legged gulls breeding at an oceanic Atlantic island (i.e. Madeira Island), where the trawling activity is absence, also interacted more with purse-seiners (Romero et al. 2019). Dietary analyses indicate that the most consumed fish species by yellow-legged gulls across all four study colonies match those most landed by local fisheries (i.e. pelagic fish; Chapters 1 and 4), suggesting a strong association between gull diet and fishing activities. Additionally, fish landings, namely pelagic fish landings, seemed to affect gull stable isotope values and blood biochemical parameters, suggesting trophic and nutritional effects. However, the results of this thesis indicate a decreasing trend in fish consumption over the study years in the western Iberian coast, despite an increasing trend in fishery landings, which is probably related with increased fishing effort (Chapters 4 and 5). This could indicate that fisheries are depleting fish stocks and thus decreasing fish abundance to predators such as gulls, or that fisheries are becoming more efficient (i.e. producing less discards), or likely a combination of both (Zeller et al. 2018). These results are in accordance with other gull studies across the globe (Pedro et al. 2013, Ronconi et al. 2014, Blight et al. 2015, Hobson et al. 2015, Bond 2016). Indeed, global patterns indicate that fisheries are collapsing pelagic fish stocks, which may have strong negative consequences for seabird populations (Furness and Tasker 2000, Cury et al. 2011, Guillemette et al. 2018). In the western Iberian coast, the decrease in fish consumption was accompanied by an increase in the consumption of crustaceans, which have lower energetic content compared to fish (Spitz et al. 2010). Hence, gulls may experience fitness and energetic costs in a dietary switch from a fish- to a crustacean-based diet (van Donk et al. 2019).

### 3. Effects of the discard ban policy

The newly implemented discard ban policy is expected to further reduce fish availability to gulls. Fishery discards have altered many aspects of gull biology including foraging behaviour, body condition, and demography (Bicknell et al. 2013). During the breeding season, by feeding on locally abundant and easily accessible discards, breeding adults improve individual fitness and have more time to feed and guard their chicks, thereby increasing breeding success (Oro 1996b). During the non-breeding season, feeding on discards may increase juvenile survival and adult body condition, which may enhance overall population recruitment (Ramírez et al. 2015). Thus, a ban on discarding is expected to lead to gull population declines. However, in long-lived species, lower food availability affects fecundity before survival (Oro et al. 1999), therefore population declines are only expected in the long-term.

Generalist species such as the yellow-legged gull may increase the consumption of alternative prey species and the use of alternative habitats such as terrestrial and urban environments (Bicknell et al. 2013). The results from this thesis indicate that dietary and foraging habitat shifts in yellow-legged gulls might be site-dependent according to local prey availability. In conditions of lower fish availability, gulls from Sálvora and Berlenga islands are expected to increase the consumption of marine invertebrates, mainly the pelagic crab *Polybius henslowii*, while gulls from Pesegueiro may increase the consumption of other marine invertebrates, i.e. goose barnacles *Pollicipes cornucopia* and vegetable matter, i.e. *Corema album*, and yellow-legged gulls from Deserta may increase the consumption of refuse. In contrast, Audouin's gulls, given their more piscivorous habits, may increase marine foraging effort (i.e. foraging time and ranges) and change their at-sea distribution (González-Solís et al. 1997b, Bécares et al. 2015). Dietary changes can also occur, namely a decreased consumption of demersal fish while increasing epipelagic fish and pelagic crab in their diet. Additionally, other foraging habitats may be more explored, such as terrestrial and freshwater (De Juana et al. 1979, Oro et al. 1997, Navarro et al. 2010), however in southern Portugal the adequacy of such habitats to compensate for lower fish availability under a discard ban scenario for this species requires further exploration (Matos et al. 2018). Additionally, agonistic interactions are expected in response to food shortage for both gull species. Increased intra-specific kleptoparasitism is mainly expected for Audouin's gull, while for yellow-legged gulls both intra- and inter-specific kleptoparasitism as well as predation on other seabird species are likely to occur (Arcos et al. 2001, Martínez-Abraín et al. 2003). This raises concerns regarding seabird community dynamics. Within the study area, disturbance of yellow-legged gulls on other seabird species are of particular concern at Berlenga archipelago, where Cory's shearwater *Calonectris borealis*, band-rumped storm-petrel

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*Hydrobates castro*, European shag *Gulosus aristotelis* and small numbers of lesser black-backed gulls *Larus fuscus* also breed, and at Deserta Island, a breeding site for little tern *Sternula albifrons* and Audouin's gull (Meirinho et al. 2014).

Individual responses to lower discard availability are also expected within gull populations due to individual specialization, different competitive skills, and/or nutritional requirements among distinct age classes and between breeding *vs* non-breeding (e.g. immatures) birds (Bicknell et al. 2013). Individual specialization was found in yellow-legged gulls (Sanz-Aguilar et al. 2009, Ceia et al. 2014), and age and sexual differences were also found in both gull species (Navarro et al. 2010, Alonso et al. 2015, Payo-Payo et al. 2015, García-Tarrasón et al. 2015). The results from this thesis suggest that the impact of the discard ban might be higher for yellow-legged gull adults than for immatures (Chapter 3) and for males than for females (Chapter 2). Age and sex-specific foraging differences in Audouin's gull should also be evaluated to compare with the patterns found in the Mediterranean, where males fed more on fishery discards (Navarro et al. 2010) and each sex foraged differently in the absence of fisheries (García-Tarrasón et al. 2015).

Nevertheless, in the Iberian Peninsula the impacts of the discard ban policy might be less significant when compared to other locations in Europe due to the types of fishing activities operating in its surrounding waters. Purse seiners produce less discards than other fisheries, namely trawling, and most discards are comprised by pelagic fish species (Borges et al. 2001). This contrasts with the North Sea, where trawlers dominate the fishing fleet and demersal species are the main target species (Greenstreet et al. 1999). Most commercial demersal species are subject to catch limits (i.e. Total Allowable Catches, TACs) and thus included in the landing obligation (Uhlmann et al. 2019). Contrastingly, two of the most landed and discarded species in Portuguese fisheries, sardine and chub mackerel (small pelagics), can still be discarded as they are not subject to TACs. The southern Atlantic sardine stock is managed by Portugal and Spain, but species under national regulations (e.g. minimum landing size, quotas) are not included in the landing obligation (Damalas 2015). Additionally, there are a number of exemptions to the discard ban besides species not covered by catch limits, such as forbidden capture, high survivability (especially allowed for small pelagics through slipping, e.g. horse mackerel *Trachurus* spp., anchovy *Engraulis encrasicolus* and mackerel *Scomber scombrus* in Portugal), and the "*de minimis*" exemption, where a certain percentage of discarding is allowed (Uhlmann et al. 2019).

To conclude, in the western Iberian coast gulls face climate- and fisheries-mediated declines in fish availability, which will have direct and immediate effects on their diet and foraging behaviour. The

magnitude of these effects is site-dependent considering local fishing activities (e.g. types of fisheries and intensity), the presence of alternative food resources, and intra and inter-specific competition. The correct management of anthropogenic activities and implementation of environmental policies are key to control populations of overabundant species and for the conservation of threatened species.

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**APPENDICES**

**Table S1.1.** Fishery landings (tonnes) of the ten most important species in the two local harbours (Olhão and Quarteira), during May and June of 2014 and 2015.

| Species | 2014 | 2015 | Total |
|---|---|---|---|
| *Scomber* sp. | 822 | 1576 | 2398 |
| *Trachurus* sp. | 329 | 237 | 566 |
| *Sardina pilchardus* | 319 | 197 | 515 |
| *Octopus vulgaris* | 85 | 97 | 182 |
| *Sarda sarda* | 3 | 80 | 83 |
| *Diplodus* sp. | 33 | 29 | 62 |
| *Sepia officinalis* | 25 | 23 | 49 |
| *Merluccius merluccius* | 16 | 21 | 37 |
| *Sarpa salpa* | 18 | 10 | 28 |
| *Lophius piscatorius* | 10 | 12 | 22 |
| Sum | 1660 | 2281 | 3941 |

**Table S1.2.** Stable isotope ratios of carbon ($\delta^{13}$C, ‰), nitrogen ($\delta^{15}$N, ‰) and C/N mass ratios of fish species regurgitated by Audouin's (*Larus audouinii*) and yellow-legged (*L. michahellis*) gulls in 2014. Group type for each species (P pelagic, D demersal) is indicated following FishBase (http://www.fishbase.org). For sample size N > 1, values are mean ± SD.

| Fish species | Group | $\delta^{15}$N | $\delta^{13}$C | C/N | N |
|---|---|---|---|---|---|
| *Ammodytes* sp. | P | +11.01 | −18.70 | 3.09 | 1 |
| *Belone belone* | P | +9.50 | −19.71 | 2.91 | 1 |
| *Sardina pilchardus* | P | +10.05 ± 0.35 | −17.55 ± 0.57 | 3.03 ± 0.05 | 4 |
| *Scomber* sp. | P | +10.27 ± 0.60 | −18.10 ± 0.58 | 3.05 ± 0.09 | 10 |
| *Trachurus* sp. | P | +10.34 ± 0.63 | −18.36 ± 0.90 | 3.07 ± 0.10 | 10 |
| *Boops boops* | D | +11.03 ± 0.46 | −17.40 ± 0.27 | 3.01 ± 0.04 | 6 |
| *Conger conger* | D | +10.44 | −16.65 | 3.05 | 1 |
| *Diplodus* sp. | D | +11.90 | −17.28 | 3.07 | 1 |

**Table S1.3.** Numeric percentage (NP, %), percentage of occurrence (PO, %) and generalised linear model (GLM) results investigating the differences in the occurrence of pelagic, demersal fish, refuse and the main prey (PO > 5%) identified in Audouin's (AG; *Larus audouinii*) and yellow-legged (YLG; *L. michahellis*) gull pellets collected in 2014 and 2015 breeding seasons, with sample size in parenthesis. Significant effects are shown in bold.

| Prey | NP 2014 AG (n=449) | NP 2014 YLG (n=441) | NP 2015 AG (n=415) | NP 2015 YLG (n=453) | PO 2014 AG (n=186) | PO 2014 YLG (n=128) | PO 2015 AG (n=107) | PO 2015 YLG (n=104) | Species $F_{1,524}$ | Species $P$ | Species Main effect | Year $F_{1,524}$ | Year $P$ | Year Main effect | Species*Year $F_{1,524}$ | Species*Year $P$ | Species*Year Main effect |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Pelagic | 67.7 | 32.0 | 58.3 | 33.1 | 86.6 | 68.0 | 87.9 | 57.1 | 40.15 | **<0.001** | AG > YLG | 1.68 | 0.19 | - | 1.22 | 0.27 | - |
| Demersal | 17.6 | 16.3 | 19.5 | 14.6 | 31.7 | 41.4 | 45.8 | 41.0 | 1.03 | 0.31 | - | 2.89 | 0.09 | - | 2.84 | 0.09 | - |
| *Diplodus sp.* | 8.7 | 4.1 | 5.5 | 4.4 | 19.9 | 14.1 | 19.6 | 18.3 | 1.14 | 0.29 | - | 0.34 | 0.56 | - | 0.36 | 0.55 | - |
| *Micromesistius poutassou* | 4.0 | 6.6 | 9.9 | 11.5 | 7.5 | 18.0 | 23.4 | 23.1 | 4.44 | **0.04** | AG < YLG | 10.58 | **<0.01** | 2014 < 2015 | 4.45 | **0.03** | AG 2014 < others |
| *Sardina pilchardus* | 12.7 | 9.5 | 7.2 | 7.5 | 24.7 | 25.8 | 21.5 | 18.3 | 0.11 | 0.74 | - | 2.00 | 0.16 | - | 0.39 | 0.53 | - |
| *Scomber sp.* | 7.1 | 5.9 | 3.4 | 4.9 | 16.1 | 19.5 | 13.1 | 20.2 | 2.03 | 0.15 | - | 0.18 | 0.67 | - | 0.33 | 0.57 | - |
| *Scomberesox saurus* | 29.0 | 2.3 | 28.9 | 2.9 | 51.1 | 7.0 | 45.8 | 5.8 | 125.65 | **<0.001** | AG > YLG | 0.78 | 0.38 | - | 0.00 | 0.96 | - |
| *Trachurus sp.* | 2.4 | 6.3 | 2.4 | 2.4 | 5.9 | 18.0 | 9.3 | 10.6 | 7.60 | **<0.01** | AG < YLG | 0.34 | 0.56 | - | 3.49 | 0.06 | - |
| Insects | 4.2 | 23.8 | 9.2 | 29.6 | 8.1 | 10.9 | 21.5 | 35.6 | 7.30 | **<0.01** | AG < YLG | 30.16 | **<0.001** | 2014 < 2015 | 0.49 | 0.48 | - |
| Refuse | 0.2 | 8.4 | 0.5 | 6.8 | 0.5 | 15.6 | 1.9 | 29.8 | 69.76 | **<0.001** | AG < YLG | 7.51 | **<0.01** | 2014 < 2015 | 0.13 | 0.72 | - |

**Table S1.4.** Area of the standard ellipse (SEA$_c$) of Audouin's (AG; *Larus audouinii*) and yellow-legged (YLG, *L. michahellis*) gulls sampled in the breeding season of 2014 (AG: n = 12, YLG: n = 9) and 2015 (AG: n = 15, YLG: n = 12), during all-year (Br; breast feathers), breeding (P1; first primary feathers), non-breeding (S8; eighth secondary feathers), laying (RBC; red blood cells), and incubation (plasma) periods of adults and chicks (feathers; AG: n = 17, YLG: n = 16 in 2014; and AG: n = 15, YLG: n = 15 in 2015), calculated in SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011). Adult feathers reflect dietary inputs from the year previous to the sampling.

| Tissue | Period | 2013 | | 2014 | | 2015 | |
|--------|--------|------|------|------|------|------|------|
| | | AG | YLG | AG | YLG | AG | YLG |
| Br | All-year | 0.93 | 4.05 | 2.63 | 1.70 | | |
| P1 | Breeding | 0.69 | 0.61 | 1.42 | 0.83 | | |
| S8 | Non-breeding | 0.33 | 2.78 | 2.11 | 1.61 | | |
| RBC | Laying | | | 0.60 | 0.61 | 0.26 | 0.50 |
| Plasma | Incubation | | | 0.94 | 1.87 | 0.77 | 0.57 |
| Chicks | Chick-rearing | | | 0.25 | 0.38 | 0.41 | 0.52 |

**Table S1.5.** Ellipse area overlap between Audouin's (AG; *Larus audouinii*) and yellow-legged (YLG, *L. michahellis*) gulls sampled in the breeding season of 2014 (AG: n = 12, YLG: n = 9) and 2015 (AG: n = 15, YLG: n = 12), during all-year (Br; breast feathers), breeding (P1; first primary feathers), non-breeding (S8; eighth secondary feathers), laying (RBC; red blood cells), and incubation (plasma) periods of adults and chicks (feathers; AG: n = 17, YLG: n = 16 in 2014; and AG: n = 15, YLG: n = 15 in 2015), calculated in SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011). Adult feathers reflect dietary inputs from the year previous to the sampling.

| Tissue | Species/ Year | YLG 2013 | AG 2014 | YLG 2014 |
|--------|---------------|----------|---------|----------|
| Br | AG 2013 | 60.2 | 55.9 | 0.0 |
| Br | YLG 2013 | - | 21.8 | 38.8 |
| Br | AG 2014 | - | - | 1.2 |
| P1 | AG 2013 | 39.3 | 55.1 | 21.7 |
| P1 | YLG 2013 | - | 67.2 | 70.5 |
| P1 | AG 2014 | - | - | 44.6 |
| S8 | AG 2013 | 100.0 | 100.0 | 0.0 |
| S8 | YLG 2013 | - | 61.1 | 69.6 |
| S8 | AG 2014 | - | - | 4.3 |
|  |  | YLG 2014 | AG 2015 | YLG 2015 |
| RBC | AG 2014 | 71.7 | 46.2 | 52.0 |
| RBC | YLG 2014 | - | 38.5 | 44.0 |
| RBC | AG 2015 | - | - | 92.3 |
| Plasma | AG 2014 | 60.6 | 7.8 | 0.5 |
| Plasma | YLG 2014 | - | 12.7 | 89.5 |
| Plasma | AG 2015 | - | - | 24.6 |
| Chicks | AG 2014 | 0.0 | 3.8 | 0.0 |
| Chicks | YLG 2014 | - | 63.2 | 86.8 |
| Chicks | AG 2015 | - | - | 46.3 |

**Table S2.1.** Informative parameters of the four study colonies of yellow-legged gulls.

| Colony | Breeding pairs | Fishing activity | Alternative foraging locations |
|---|---|---|---|
| Sálvora | 3,800 | High | Ría |
| Berlenga | 8,500 | Moderate | Refuse dumps |
| Pessegueiro | 500 | Low | Terrestrial |
| Deserta | 1,400 | Moderate - Low | Lagoon |

**Table S2.2.** Mean (±SD) $\delta^{15}$N and $\delta^{13}$C values (‰) during late breeding (innermost primary feathers – P1), non-breeding (eighth secondary feathers – S8), pre-laying (red blood cells – RBC), and incubation (Plasma) of male and female yellow-legged gulls in each colony. Values are original stable isotope ratios (i.e. without corrections).

| Sex | Colony | Late breeding (P1) | | Non-breeding (S8) | | Pre-laying (RBC) | | Incubation (Plasma) | |
|-----|--------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|
| | | $\delta^{15}$N | $\delta^{13}$C | $\delta^{15}$N | $\delta^{13}$C | $\delta^{15}$N | $\delta^{13}$C | $\delta^{15}$N | $\delta^{13}$C |
| Male | Sálvora | 14.6 ± 0.8 | -16.0 ± 0.8 | 14.2 ± 1.0 | -15.7 ± 0.3 | 13.2 ± 0.5 | -18.1 ± 0.6 | 14.0 ± 0.3 | -18.1 ± 0.5 |
| Female | Sálvora | 14.4 ± 0.8 | -16.8 ± 0.7 | 13.2 ± 1.3 | -16.3 ± 1.7 | 12.4 ± 0.7 | -19.2 ± 0.8 | 13.4 ± 1.4 | -19.2 ± 0.8 |
| Male | Berlenga | 14.9 ± 0.4 | -16.5 ± 0.3 | 15.1 ± 0.5 | -16.7 ± 0.7 | 11.8 ± 0.8 | -18.3 ± 0.1 | 12.8 ± 0.9 | -18.3 ± 0.2 |
| Female | Berlenga | 14.2 ± 0.6 | -16.9 ± 0.5 | 14.3 ± 0.6 | -17.4 ± 0.9 | 11.0 ± 0.7 | -18.7 ± 0.4 | 11.1 ± 0.8 | -19.0 ± 0.9 |
| Male | Pessegueiro | 13.9 ± 0.6 | -16.5 ± 0.4 | 13.7 ± 1.1 | -16.9 ± 1.0 | 11.7 ± 1.0 | -18.1 ± 0.8 | 12.7 ± 0.3 | -17.8 ± 0.6 |
| Female | Pessegueiro | 13.2 ± 0.9 | -17.7 ± 1.2 | 13.4 ± 1.1 | -17.1 ± 0.8 | 11.2 ± 0.9 | -18.6 ± 0.6 | 11.9 ± 0.5 | -18.3 ± 0.4 |
| Male | Deserta | 14.4 ± 1.1 | -16.2 ± 0.6 | 14.0 ± 1.0 | -17.0 ± 0.5 | 10.9 ± 1.0 | -18.6 ± 0.6 | 12.0 ± 1.0 | -19.2 ± 1.2 |
| Female | Deserta | 13.6 ± 2.1 | -16.7 ± 1.0 | 13.6 ± 0.9 | -15.6 ± 2.4 | 10.8 ± 0.4 | -18.6 ± 0.6 | 12.2 ± 0.4 | -18.3 ± 0.6 |
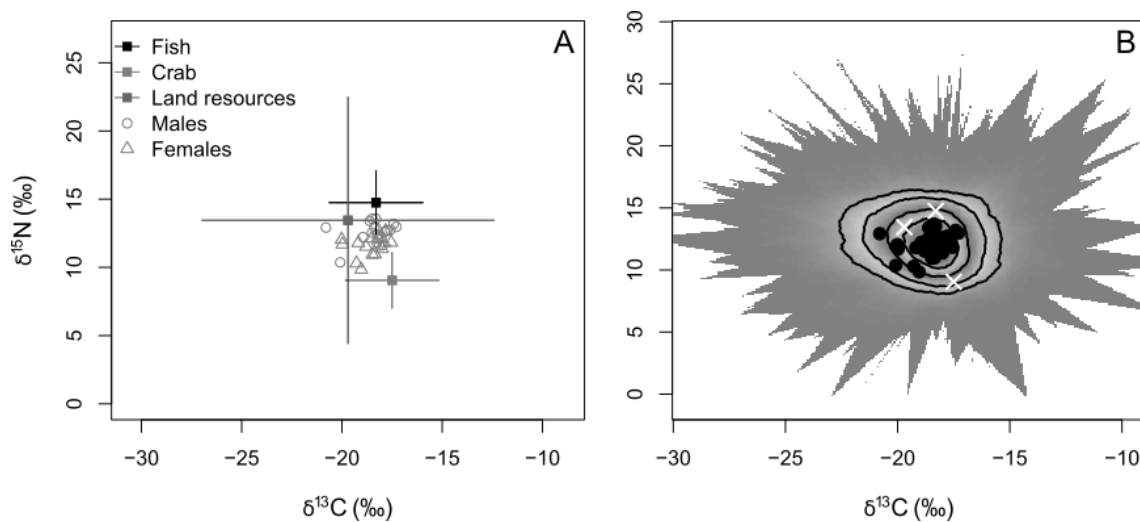
**Figure S2.1.** (A) Biplot of stable isotope values for male (open circle) and female (open triangles) yellow-legged gulls and of prey (mean ± SD) corrected for trophic enrichment, created using SIAR (Parnell et al. 2010). (B) Simulated mixing region for the biplot in (A), created using metrics provided by Smith et al. (2013). The positions of yellow-legged gulls (black dots) and of prey (white crosses) are shown, as well as the probability contours at the 5% level (outermost contour) and at every 10% level.

**Table S3.1.** Fishery landings (tonnes) in Peniche fishing harbour.

| Year | Total | *Sardina pilchardus* | *Scomber colias* |
|------|-------|----------------------|------------------|
| 2016 | 10741 | 2051 | 969 |
| 2017 | 13177 | 4575 | 980 |
| 2018 | 11872 | 3269 | 1780 |

**Text A4.1.** Stable isotope analysis (SIA) laboratory procedures and determination.

Successive rinses of a 2 chloroform: 1 methanol solution were used to extract lipids from plasma samples, and to clean feathers from surface lipids and contaminants (Kojadinovic et al. 2008). Feathers were cut with stainless steel scissors into small fragments. All tissue samples were dried in an oven for at least 48 h at 50°C to a constant mass and homogenized. Sub-samples of approximately 0.35 mg for nitrogen and carbon, and of 1.5 mg for sulphur were weighed in a microbalance, placed in a tin cup, and crimped for combustion. Isotopic ratios were determined by Continuous-Flow Isotope Ratio Mass Spectrometry (CF-IRMS). Results are expressed in the usual $\delta$ notation as parts per thousand (‰) deviation from the international standards atmospheric nitrogen ($N_2$) for $\delta^{15}N$, Vienna-PeeDee Belemnite (V-PDB) for $\delta^{13}C$, and Vienna Cañon Diablo Troilite (VCDT) for $\delta^{34}S$, according to the following equation: $\delta^{15}N$, $\delta^{13}C$ or $\delta^{34}S = [(Rsample /Rstandard) - 1]$, where $R = {}^{15}N/{}^{14}N$, ${}^{13}C/{}^{12}C$ or ${}^{34}S/{}^{32}S$, respectively (Bond and Hobson 2012). Replicate measurements of internal laboratory standards indicate precision < 0.2‰ for the three stable isotopes.

**Table A4.1**. Linear Mixed Models (LMM) testing the effect colony (yellow-legged gulls from Sálvora, Berlenga, Pessegueiro, and Deserta islands and Audouin's gulls) and tissue (P1 feathers – late breeding, S8 feathers – non-breeding, RBC – breeding, chick feathers) on the $\delta^{15}N$ and $\delta^{13}C$ values of gulls sampled in 2017. Bird identity included as a random effect to control for pseudo-replication issues. Correction factors were applied on stable isotope values of feathers to allow direct comparisons between periods (see Methods). Significant P values are shown in bold.

| Response | Colony F | Colony P | Tissue F | Tissue P | Colony*Tissue F | Colony*Tissue P |
|---|---|---|---|---|---|---|
| $\delta^{15}N$ | 4.3 | **0.003** | 34.1 | **< 0.001** | 4.0 | **< 0.001** |
| $\delta^{13}C$ | 11.7 | **< 0.001** | 16.7 | **< 0.001** | 6.6 | **< 0.001** |

**Table S4.1.** Percentage of occurrence (PO) of the main fish species, i.e. at least once PO > 5%, and of each prey category in yellow-legged gull (Deserta) and Audouin's gull pellets in the breeding season of 2014 and 2015. Sampling months and total fish landing quantities (N = tonnes/month) and their percentages by species are also shown.

| | Breeding | | | | | |
|---|---|---|---|---|---|---|
| | 2014 (May-Jun) | | | 2015 (May-Jun) | | |
| | Deserta | Audouin's gull | Landings | Deserta | Audouin's gull | Landings |
| | Diet | Diet | | Diet | Diet | |
| | N = 121 | N = 182 | N = 1,201 | N = 105 | N = 107 | N = 1,489 |
| **Pelagic fish** | 67.8 | 86.3 | 88.5 | 57.1 | 86.9 | 87.6 |
| *Belone belone* | 0.8 | 7.7 | 0.1 | 1.9 | 6.5 | 0.1 |
| *Chelon* sp. | 2.5 | — | <0.1 | 2.9 | — | <0.1 |
| *Engraulis encrasicolus* | — | 0.5 | 0.2 | 1.0 | 1.9 | <0.1 |
| *Gadiculus argenteus* | 0.8 | 2.2 | — | 3.8 | 9.3 | — |
| *Micromesistius poutassou* | 19.0 | 7.7 | 3.5 | 22.9 | 23.4 | 1.0 |
| *Myctophum* sp. | 1.7 | 8.8 | — | 2.9 | 2.8 | — |
| *Sardina pilchardus* | 25.6 | 23.1 | 21.3 | 18.1 | 21.5 | 14.0 |
| *Scomber* sp. | 17.4 | 15.4 | 40.2 | 20.0 | 13.1 | 56.6 |
| *Scomberosox saurus* | 7.4 | 52.2 | — | 5.7 | 45.8 | — |
| *Trachurus* sp. | 18.2 | 6.0 | 22.9 | 10.5 | 9.3 | 15.7 |
| **Demersal fish** | 43.0 | 31.9 | 11.5 | 41.9 | 45.8 | 12.4 |
| *Boops boops* | 9.9 | 4.4 | 0.2 | 2.9 | 6.5 | 0.5 |
| *Callionymus lyra* | — | — | — | — | — | — |
| *Cepola rubescens* | 1.7 | — | — | — | 0.9 | — |
| *Chelidonichthys* sp. | — | — | <0.1 | — | — | 0.1 |
| *Coelorinchus* sp. | 2.5 | 4.4 | — | 2.9 | 4.7 | — |
| *Conger conger* | 3.3 | 0.5 | 0.5 | 1.0 | 5.6 | 0.3 |
| *Diplodus* sp. | 14.9 | 19.2 | 1.7 | 18.1 | 19.6 | 1.1 |
| *Galeus melastomus* | — | — | <0.1 | — | — | <0.1 |
| *Lepidotrigla cavillone* | — | — | <0.1 | — | — | 4.0 |
| *Lesueurigobius* sp. | — | — | — | — | — | — |
| *Lithognathus mormyrus* | 0.8 | — | <0.1 | 2.9 | 1.9 | 0.1 |
| *Malacocephalus laevis* | — | — | — | — | — | — |
| *Merluccius* sp. | 6.6 | 2.7 | 1.5 | 6.7 | 2.8 | 1.6 |
| *Microchirus* sp. | 1.7 | 0.5 | 0.5 | — | — | 0.5 |
| *Nezumia* sp. | — | — | — | — | — | — |
| *Phycis* sp. | — | — | 0.1 | 2.9 | — | 0.1 |
| *Sarpa salpa* | — | — | 0.7 | — | — | 0.3 |
| *Serranus* sp. | 2.5 | 2.7 | <0.1 | 4.8 | 13.1 | <0.1 |
| *Trachinus* sp. | — | — | 0.1 | — | — | 0.1 |
| *Trisopterus* sp. | — | — | <0.1 | — | — | 0.1 |
| **Unidentified fish** | 24.0 | 15.4 | — | 30.5 | 33.6 | — |
| **Total fish** | 89.3 | 100 | 100 | 73.3 | 100 | 100 |
| **Marine invertebrates** | 14.0 | 6.6 | — | 10.5 | 7.5 | — |
| **Vegetal matter** | 11.6 | — | — | 12.4 | — | — |
| **Refuse** | 14.9 | 0.5 | — | 29.5 | 1.9 | — |
| **Others** | 19.8 | 8.8 | — | 41.9 | 23.4 | — |

**Table S4.2.** Percentage of occurrence (PO) of the main fish species, i.e. at least once PO > 5%, and of each prey category in yellow-legged gull pellets in each season of 2016 at Berlenga and Pessegueiro islands. Sampling months and total fish landing quantities (N = tonnes/month) and their percentages by species are also shown.

| | 2016 | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | Berlenga | | | | | | Pessegueiro | |
| | Pre-breeding (Feb-Mar) | | Breeding (May-Jun) | | Post-breeding (Aug) | | Pre-breeding (Feb) | |
| | Diet | Landings | Diet | Landings | Diet | Landings | Diet | Landings |
| | N = 77 | N = 898 | N = 106 | N = 1,712 | N = 31 | N = 1,336 | N = 29 | N = 121 |
| **Pelagic fish** | — | 71.4 | 7.5 | 85.7 | 16.1 | 77.8 | 13.8 | 67.3 |
| *Belone belone* | — | — | — | — | — | — | 6.9 | — |
| *Chelon* sp. | — | <0.1 | — | <0.1 | — | <0.1 | — | 0.5 |
| *Engraulis encrasicolus* | — | <0.1 | — | <0.1 | — | 0.1 | — | — |
| *Gadiculus argenteus* | — | — | — | — | — | — | — | — |
| *Micromesistius poutassou* | — | 0.1 | 1.9 | 0.2 | 3.2 | 0.3 | — | 45.4 |
| *Myctophum* sp. | — | — | — | — | — | — | — | — |
| *Sardina pilchardus* | — | <0.1 | 4.7 | 30.0 | 9.7 | 24.1 | 3.4 | — |
| *Scomber* sp. | — | 4.2 | — | 9.4 | — | 10.3 | 3.4 | 4.2 |
| *Scomberosox saurus* | — | — | — | <0.1 | — | — | — | — |
| *Trachurus* sp. | — | 55.8 | 1.9 | 45.1 | 6.5 | 42.1 | 3.4 | 17.1 |
| **Demersal fish** | 1.3 | 28.6 | 9.4 | 14.3 | — | 22.2 | 13.8 | 32.7 |
| *Boops boops* | — | 0.8 | 3.8 | 0.1 | — | 0.1 | — | 5.3 |
| *Callionymus lyra* | — | — | — | — | — | — | — | — |
| *Cepola rubescens* | — | — | — | — | — | — | — | — |
| *Chelidonichthys* sp. | — | 0.4 | — | 0.2 | — | 0.2 | 3.4 | 0.1 |
| *Coelorinchus* sp. | — | — | — | — | — | — | — | — |
| *Conger conger* | — | 1.1 | 0.9 | 1.7 | — | 3.1 | — | 1.5 |
| *Diplodus* sp. | — | 1.3 | 0.9 | 0.3 | — | 0.3 | — | 2.4 |
| *Galeus melastomus* | — | 0.1 | — | <0.1 | — | 0.1 | — | — |
| *Lepidotrigla cavillone* | — | 0.4 | — | 0.1 | — | 0.1 | 6.9 | — |
| *Lesueurigobius* sp. | — | — | — | — | — | — | — | — |
| *Lithognathus mormyrus* | — | — | — | — | — | — | — | <0.1 |
| *Malacocephalus laevis* | — | — | — | — | — | — | — | — |
| *Merluccius* sp. | — | 3.7 | 1.9 | 2.8 | — | 3.9 | — | 0.6 |
| *Microchirus* sp. | — | 0.2 | — | 0.2 | — | 0.2 | 3.4 | 1.2 |
| *Nezumia* sp. | — | — | — | — | — | — | — | — |
| *Phycis* sp. | — | 0.3 | — | 0.4 | — | 0.6 | — | 0.4 |
| *Sarpa salpa* | — | <0.1 | — | 0.1 | — | 0.1 | — | 0.1 |
| *Serranus* sp. | — | <0.1 | 1.9 | <0.1 | — | 0.1 | — | — |
| *Trachinus* sp. | — | <0.1 | — | <0.1 | — | <0.1 | — | <0.1 |
| *Trisopterus* sp. | 1.3 | 2.6 | 2.8 | 1.8 | — | 2.7 | — | 0.7 |
| **Unidentified fish** | 2.6 | — | 8.5 | — | — | — | 13.8 | — |
| **Total fish** | 3.9 | 100 | 21.7 | 100 | 16.1 | 100 | 31.0 | 100 |
| **Marine invertebrates** | 88.3 | — | 90.6 | — | 83.9 | — | 86.2 | — |
| **Vegetal matter** | 10.4 | — | 2.8 | — | 6.5 | — | 3.4 | — |
| **Refuse** | 15.6 | — | 8.5 | — | 22.6 | — | — | — |
| **Others** | 5.2 | — | 9.4 | — | 6.5 | — | — | — |

**Table S4.3.** Percentage of occurrence (PO) of the main fish species, i.e. at least once PO > 5%, and of each prey category in yellow-legged gull pellets in each season of 2016 at Deserta Island. Sampling months and total fish landing quantities (N = tonnes/month) and their percentages by species are also shown.

| | 2016 | | | | | |
| --- | --- | --- | --- | --- | --- | --- |
| | Deserta | | | | | |
| | Pre-breeding (Feb-Mar-Apr) | | Breeding (May) | | Post-breeding (Sep) | |
| | Diet | Landings | Diet | Landings | Diet | Landings |
| | N = 224 | N = 894 | N = 163 | N = 1,315 | N = 112 | N = 1,408 |
| **Pelagic fish** | 47.8 | 80.2 | 60.7 | 88.4 | 68.8 | 84.8 |
| *Belone belone* | 0.4 | <0.1 | 3.7 | 0.1 | — | <0.1 |
| *Chelon* sp. | 8.5 | 0.1 | 5.5 | — | 2.7 | <0.1 |
| *Engraulis encrasicolus* | — | 0.5 | 0.6 | <0.1 | — | <0.1 |
| *Gadiculus argenteus* | 0.4 | — | 3.7 | — | 1.8 | — |
| *Micromesistius poutassou* | 6.7 | 1.6 | 22.1 | 2.3 | 40.2 | 1.3 |
| *Myctophum* sp. | 0.9 | — | — | — | — | — |
| *Sardina pilchardus* | 24.1 | 0.3 | 11.7 | 27.2 | 8.9 | 9.9 |
| *Scomber* sp. | 9.8 | 50.9 | 9.8 | 44.4 | 8.9 | 48.0 |
| *Scomberosox saurus* | 0.4 | — | 11.7 | — | — | — |
| *Trachurus* sp. | 14.3 | 26.8 | 23.3 | 14.4 | 27.7 | 14.1 |
| **Demersal fish** | 64.3 | 19.8 | 36.2 | 11.6 | 44.6 | 15.2 |
| *Boops boops* | 8.9 | 2.2 | 3.7 | 0.8 | 8.0 | 0.6 |
| *Callionymus lyra* | — | — | — | — | — | — |
| *Cepola rubescens* | 0.4 | — | — | — | — | — |
| *Chelidonichthys* sp. | — | 0.1 | — | 0.1 | 0.9 | <0.1 |
| *Coelorinchus* sp. | 0.4 | — | — | — | — | — |
| *Conger conger* | 2.7 | 0.4 | 2.5 | 0.2 | 0.9 | 0.5 |
| *Diplodus* sp. | 37.9 | 2.6 | 10.4 | 0.8 | 10.7 | 1.8 |
| *Galeus melastomus* | 0.9 | <0.1 | 0.6 | — | — | <0.1 |
| *Lepidotrigla cavillone* | — | <0.1 | — | <0.1 | 0.9 | <0.1 |
| *Lesueurigobius* sp. | — | — | — | — | — | — |
| *Lithognathus mormyrus* | 0.4 | 0.1 | 0.6 | <0.1 | 0.9 | <0.1 |
| *Malacocephalus laevis* | 1.3 | — | 1.2 | — | 6.3 | — |
| *Merluccius* sp. | 4.5 | 2.1 | 1.8 | 1.9 | 8.0 | 2.7 |
| *Microchirus* sp. | — | 1.2 | — | 0.6 | 0.9 | 1.1 |
| *Nezumia* sp. | — | — | — | — | 0.9 | — |
| *Phycis* sp. | 0.9 | 0.2 | 0.6 | 0.1 | 0.9 | 0.2 |
| *Sarpa salpa* | 4.0 | 0.5 | 1.2 | 0.5 | 0.9 | 0.4 |
| *Serranus* sp. | 3.1 | <0.1 | 5.5 | <0.1 | 0.9 | <0.1 |
| *Trachinus* sp. | — | 0.1 | — | 0.1 | 6.3 | 0.1 |
| *Trisopterus* sp. | 0.4 | 0.1 | 0.6 | <0.1 | 0.9 | 0.1 |
| **Unidentified fish** | 24.6 | — | 27.0 | — | 16.1 | — |
| **Total fish** | 93.3 | 100 | 80.4 | 100 | 94.6 | 100 |
| **Marine invertebrates** | 6.7 | — | 19.6 | — | 3.6 | — |
| **Vegetal matter** | 13.8 | — | 13.5 | — | — | — |
| **Refuse** | 12.9 | — | 19.0 | — | 2.7 | — |
| **Others** | 18.3 | — | 17.8 | — | 8.0 | — |

**Table S4.4.** Percentage of occurrence (PO) of the main fish species, i.e. at least once PO > 5%, and of each prey category in Audouin's gull pellets in each season of 2016. Sampling months and total fish landing quantities (N = tonnes/month) and their percentages by species are also shown.

| | 2016 | | | | | |
|---|---|---|---|---|---|---|
| | Audouin's gull | | | | | |
| | Pre-breeding (Mar-Apr) | | Breeding (May) | | Post-breeding (Sep) | |
| | Diet | Landings | Diet | Landings | Diet | Landings |
| | N = 32 | N = 1,062 | N = 279 | N = 1,315 | N = 117 | N = 1,408 |
| **Pelagic fish** | 81.3 | 81.8 | 93.5 | 88.4 | 85.5 | 84.8 |
| *Belone belone* | 12.5 | <0.1 | 7.2 | 0.1 | 2.6 | <0.1 |
| *Chelon* sp. | — | 0.1 | — | — | — | <0.1 |
| *Engraulis encrasicolus* | — | 0.3 | 3.2 | <0.1 | 0.9 | <0.1 |
| *Gadiculus argenteus* | 12.5 | — | 3.9 | — | 4.3 | — |
| *Micromesistius poutassou* | 25.0 | 2.0 | 19.4 | 2.3 | 41.9 | 1.3 |
| *Myctophum* sp. | 15.6 | — | 2.2 | — | — | — |
| *Sardina pilchardus* | 28.1 | 0.3 | 1.8 | 27.2 | 4.3 | 9.9 |
| *Scomber* sp. | 9.4 | 56.2 | 3.2 | 44.4 | 15.4 | 48.0 |
| *Scomberosox saurus* | 12.5 | — | 84.2 | — | 29.9 | — |
| *Trachurus* sp. | 12.5 | 22.9 | 2.5 | 14.4 | 7.7 | 14.1 |
| **Demersal fish** | 28.1 | 18.2 | 19.0 | 11.6 | 37.6 | 15.2 |
| *Boops boops* | 3.1 | 2.2 | 1.4 | 0.8 | 6.8 | 0.6 |
| *Callionymus lyra* | — | — | — | — | — | — |
| *Cepola rubescens* | — | — | 0.4 | — | — | — |
| *Chelidonichthys* sp. | — | 0.1 | — | 0.1 | — | <0.1 |
| *Coelorinchus* sp. | — | — | 0.4 | — | 1.7 | — |
| *Conger conger* | — | 0.4 | 3.9 | 0.2 | 1.7 | 0.5 |
| *Diplodus* sp. | 12.5 | 2.6 | 5.4 | 0.8 | 19.7 | 1.8 |
| *Galeus melastomus* | — | <0.1 | — | — | — | <0.1 |
| *Lepidotrigla cavillone* | — | <0.1 | — | <0.1 | — | <0.1 |
| *Lesueurigobius* sp. | — | — | — | — | — | — |
| *Lithognathus mormyrus* | — | 0.2 | — | <0.1 | — | <0.1 |
| *Malacocephalus laevis* | 3.1 | — | 1.4 | — | 1.7 | — |
| *Merluccius* sp. | — | 2.0 | 2.9 | 1.9 | 0.9 | 2.7 |
| *Microchirus* sp. | — | 0.9 | — | 0.6 | — | 1.1 |
| *Nezumia* sp. | — | — | — | — | — | — |
| *Phycis* sp. | — | 0.2 | — | 0.1 | — | 0.2 |
| *Sarpa salpa* | — | 0.5 | — | 0.5 | — | 0.4 |
| *Serranus* sp. | — | <0.1 | 4.3 | <0.1 | — | <0.1 |
| *Trachinus* sp. | — | 0.1 | — | 0.1 | — | 0.1 |
| *Trisopterus* sp. | 3.1 | 0.1 | 0.4 | <0.1 | — | 0.1 |
| **Unidentified fish** | 43.8 | — | 24.0 | — | 11.1 | — |
| **Total fish** | 93.8 | 100 | 97.1 | 100 | 100 | 100 |
| **Marine invertebrates** | 15.6 | — | 14.7 | — | — | — |
| **Vegetal matter** | 6.3 | — | — | — | 3.4 | — |
| **Refuse** | — | — | 1.1 | — | — | — |
| **Others** | 3.1 | — | 14.7 | — | — | — |

**Table S4.5.** Percentage of occurrence (PO) of the main fish species, i.e. at least once PO > 5%, and of each prey category in yellow-legged gull pellets in each season of 2017 at Sálvora and Berlenga islands. Sampling months and total fish landing quantities (N = tonnes/month) and their percentages by species are also shown.

| | 2017 | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Sálvora | | Berlenga | | | | | |
| | Breeding (May) | | Pre-breeding (Feb-Mar) | | Breeding (May-Jun) | | Post-breeding (Sep) | |
| | Diet | Landings | Diet | Landings | Diet | Landings | Diet | Landings |
| | N = 101 | N = 5,453 | N = 84 | N = 946 | N = 204 | N = 2,189 | N = 42 | N = 1,450 |
| **Pelagic fish** | 17.8 | 56.4 | 38.1 | 70.1 | 20.6 | 87.4 | 23.8 | 84.0 |
| *Belone belone* | — | <0.1 | 3.6 | — | — | — | — | — |
| *Chelon* sp. | — | — | — | 0.1 | — | <0.1 | — | 0.1 |
| *Engraulis encrasicolus* | 1.0 | <0.1 | — | <0.1 | — | 0.1 | — | 0.5 |
| *Gadiculus argenteus* | — | — | — | — | 0.5 | — | — | — |
| *Micromesistius poutassou* | 7.9 | 19.6 | 6.0 | 0.7 | 5.4 | 0.6 | — | 0.5 |
| *Myctophum* sp. | — | — | — | — | — | — | — | — |
| *Sardina pilchardus* | 4.0 | 1.9 | 7.1 | 0.1 | 8.3 | 41.6 | 16.7 | 42.2 |
| *Scomber* sp. | 3.0 | 11.4 | 8.3 | 6.5 | 4.4 | 10.5 | 7.1 | 10.2 |
| *Scomberosox saurus* | — | <0.1 | 9.5 | — | 1.5 | — | — | — |
| *Trachurus* sp. | 5.9 | 13.7 | 11.9 | 56.9 | 10.3 | 33.6 | 2.4 | 27.9 |
| **Demersal fish** | 12.9 | 43.6 | 25.0 | 29.9 | 10.8 | 12.6 | 2.4 | 16.0 |
| *Boops boops* | 7.9 | 1.3 | 4.8 | 0.2 | 2.0 | 0.1 | 2.4 | 0.2 |
| *Callionymus lyra* | — | <0.1 | — | — | — | — | — | — |
| *Cepola rubescens* | — | — | — | — | — | — | — | — |
| *Chelidonichthys* sp. | 1.0 | 0.1 | 4.8 | 0.5 | 1.0 | 0.1 | — | 0.1 |
| *Coelorinchus* sp. | — | — | — | — | — | — | — | — |
| *Conger conger* | 1.0 | 1.7 | — | 1.3 | 2.5 | 1.8 | — | 1.5 |
| *Diplodus* sp. | 1.0 | 0.3 | 2.4 | 1.7 | — | 0.4 | — | 0.4 |
| *Galeus melastomus* | — | 0.1 | — | 0.1 | — | 0.1 | — | 0.1 |
| *Lepidotrigla cavillone* | 1.0 | — | 3.6 | 0.5 | 2.9 | <0.1 | — | 0.1 |
| *Lesueurigobius* sp. | — | — | — | — | — | — | — | — |
| *Lithognathus mormyrus* | — | — | — | — | — | — | — | — |
| *Malacocephalus laevis* | — | — | — | — | — | — | — | — |
| *Merluccius* sp. | 1.0 | 6.6 | 8.3 | 3.9 | 1.0 | 1.8 | — | 2.3 |
| *Microchirus* sp. | — | <0.1 | 1.2 | 0.4 | 0.5 | 0.1 | — | 0.1 |
| *Nezumia* sp. | — | — | — | — | — | — | — | — |
| *Phycis* sp. | — | <0.1 | — | 0.3 | — | 0.4 | — | 0.2 |
| *Sarpa salpa* | — | <0.1 | — | <0.1 | — | 0.1 | — | 0.2 |
| *Serranus* sp. | — | 0.1 | 2.4 | <0.1 | — | <0.1 | — | <0.1 |
| *Trachinus* sp. | — | — | — | <0.1 | — | <0.1 | — | <0.1 |
| *Trisopterus* sp. | 2.0 | 1.0 | 3.6 | 2.6 | 2.0 | 1.1 | — | 1.3 |
| **Unidentified fish** | 8.9 | — | 16.7 | — | 10.3 | — | 4.8 | — |
| **Total fish** | 23.8 | 100 | 60.7 | 100 | 26.0 | 100 | 26.2 | 100 |
| **Marine invertebrates** | 68.3 | — | 21.4 | — | 85.2 | — | 69.0 | — |
| **Vegetal matter** | 25.7 | — | 2.4 | — | 3.7 | — | 4.8 | — |
| **Refuse** | 20.8 | — | 26.2 | — | 6.9 | — | 9.5 | — |
| **Others** | 17.8 | — | 26.2 | — | 18.5 | — | 19.0 | — |

**Table S4.6.** Percentage of occurrence (PO) of the main fish species, i.e. at least once PO > 5%, and of each prey category in yellow-legged gull pellets in each season of 2017 at Pessegueiro Island. Sampling months and total fish landing quantities (N = tonnes/month) and their percentages by species are also shown.

| | 2017 | | | |
|---|---|---|---|---|
| | Pessegueiro | | | |
| | Breeding (May & Jul) | | Post-breeding (Oct) | |
| | Diet | Landings | Diet | Landings |
| | N = 58 | N = 629 | N = 87 | N = 666 |
| **Pelagic fish** | 46.6 | 88.4 | 43.7 | 89.7 |
| *Belone belone* | — | — | — | — |
| *Chelon* sp. | — | <0.1 | — | 0.2 |
| *Engraulis encrasicolus* | — | — | — | — |
| *Gadiculus argenteus* | 1.7 | — | — | — |
| *Micromesistius poutassou* | 12.1 | 10.5 | 2.3 | 9.4 |
| *Myctophum* sp. | — | — | — | — |
| *Sardina pilchardus* | 22.4 | 19.8 | 16.1 | 23.7 |
| *Scomber* sp. | 12.1 | 45.0 | 31.0 | 54.1 |
| *Scomberosox saurus* | — | — | — | — |
| *Trachurus* sp. | 13.8 | 13.1 | 4.6 | 2.1 |
| **Demersal fish** | 48.3 | 11.6 | 20.7 | 10.3 |
| *Boops boops* | 31.0 | 2.3 | 4.6 | 1.2 |
| *Callionymus lyra* | — | — | — | — |
| *Cepola rubescens* | — | — | — | — |
| *Chelidonichthys* sp. | — | <0.1 | 1.1 | <0.1 |
| *Coelorinchus* sp. | — | — | — | — |
| *Conger conger* | 1.7 | 1.0 | — | 0.8 |
| *Diplodus* sp. | 3.4 | 1.2 | 5.7 | 1.2 |
| *Galeus melastomus* | — | <0.1 | — | — |
| *Lepidotrigla cavillone* | 5.2 | — | 3.4 | — |
| *Lesueurigobius* sp. | — | — | — | — |
| *Lithognathus mormyrus* | 5.2 | <0.1 | — | <0.1 |
| *Malacocephalus laevis* | — | — | — | — |
| *Merluccius* sp. | 3.4 | 1.8 | 1.1 | 1.6 |
| *Microchirus* sp. | — | <0.1 | — | <0.1 |
| *Nezumia* sp. | — | — | — | — |
| *Phycis* sp. | — | 0.4 | — | 0.2 |
| *Sarpa salpa* | — | 0.9 | — | 0.5 |
| *Serranus* sp. | 6.9 | — | — | — |
| *Trachinus* sp. | — | <0.1 | 2.3 | <0.1 |
| *Trisopterus* sp. | 1.7 | 0.1 | — | 0.1 |
| **Unidentified fish** | 20.7 | — | 10.3 | — |
| **Total fish** | 72.4 | 100 | 58.6 | 100 |
| **Marine invertebrates** | 10.3 | — | 29.9 | — |
| **Vegetal matter** | 12.1 | — | 59.8 | — |
| **Refuse** | 1.7 | — | 4.6 | — |
| **Others** | 31.0 | — | 13.8 | — |

**Table S4.7.** Percentage of occurrence (PO) of the main fish species, i.e. at least once PO > 5%, and of each prey category in yellow-legged gull pellets in each season of 2017 at Deserta Island. Sampling months and total fish landing quantities (N = tonnes/month) and their percentages by species are also shown.

| | 2017 | | | | | |
|---|---|---|---|---|---|---|
| | Deserta | | | | | |
| | Pre-breeding (Feb-Mar) | | Breeding (May-Jun) | | Post-breeding (Oct) | |
| | Diet | Landings | Diet | Landings | Diet | Landings |
| | N = 184 | N = 545 | N = 262 | N = 834 | N = 119 | N = 639 |
| **Pelagic fish** | 58.2 | 70.3 | 51.1 | 80.0 | 71.4 | 72.6 |
| *Belone belone* | 0.5 | <0.1 | 0.4 | <0.1 | — | <0.1 |
| *Chelon* sp. | 3.8 | <0.1 | 7.6 | <0.1 | 5.0 | <0.1 |
| *Engraulis encrasicolus* | 1.1 | 0.7 | — | 0.1 | 0.8 | 0.1 |
| *Gadiculus argenteus* | 4.3 | — | 3.1 | — | 8.4 | — |
| *Micromesistius poutassou* | 13.0 | 5.8 | 25.6 | 5.8 | 45.4 | 10.0 |
| *Myctophum* sp. | — | — | 1.1 | — | — | — |
| *Sardina pilchardus* | 21.2 | 0.2 | 9.9 | 35.1 | 18.5 | 29.3 |
| *Scomber* sp. | 13.0 | 8.4 | 3.1 | 8.3 | 9.2 | 8.0 |
| *Scomberosox saurus* | 0.5 | — | 1.1 | — | 3.4 | — |
| *Trachurus* sp. | 24.5 | 55.2 | 17.6 | 30.0 | 16.0 | 21.6 |
| **Demersal fish** | 62.5 | 29.7 | 34.7 | 20.0 | 53.8 | 27.4 |
| *Boops boops* | 5.4 | 1.4 | 5.0 | 1.4 | 6.7 | 1.2 |
| *Callionymus lyra* | 0.5 | — | — | — | 3.4 | — |
| *Cepola rubescens* | — | — | — | — | — | — |
| *Chelidonichthys* sp. | 1.1 | 0.4 | 1.1 | 0.1 | — | 0.1 |
| *Coelorinchus* sp. | — | — | — | — | 0.8 | — |
| *Conger conger* | 3.3 | 0.6 | 0.8 | 0.7 | 4.2 | 0.8 |
| *Diplodus* sp. | 35.9 | 4.3 | 16.4 | 2.4 | 21.8 | 2.4 |
| *Galeus melastomus* | — | <0.1 | 0.8 | 0.1 | — | — |
| *Lepidotrigla cavillone* | 0.5 | 0.1 | 0.8 | <0.1 | 0.8 | 0.1 |
| *Lesueurigobius* sp. | — | — | — | — | — | — |
| *Lithognathus mormyrus* | — | 0.4 | 0.4 | 0.1 | 2.5 | <0.1 |
| *Malacocephalus laevis* | 3.8 | — | 2.7 | — | 4.2 | — |
| *Merluccius* sp. | 4.9 | 3.3 | 5.3 | 1.7 | 7.6 | 1.5 |
| *Microchirus* sp. | 4.9 | 1.9 | 1.5 | 0.9 | 1.7 | 0.7 |
| *Nezumia* sp. | — | — | — | — | 1.7 | — |
| *Phycis* sp. | 0.5 | 0.3 | 0.8 | 0.1 | — | 0.2 |
| *Sarpa salpa* | 0.5 | 2.3 | 0.4 | 1.0 | 0.8 | 1.4 |
| *Serranus* sp. | 3.3 | <0.1 | 1.9 | <0.1 | 6.7 | <0.1 |
| *Trachinus* sp. | 2.2 | 0.1 | 2.7 | 0.1 | 2.5 | <0.1 |
| *Trisopterus* sp. | 2.7 | 0.1 | 0.8 | <0.1 | 10.1 | 0.1 |
| **Unidentified fish** | 24.5 | — | 24.8 | — | 26.1 | — |
| **Total fish** | 92.4 | 100 | 76.7 | 100 | 93.3 | 100 |
| **Marine invertebrates** | 4.9 | — | 9.2 | — | 8.4 | — |
| **Vegetal matter** | 4.9 | — | 5.3 | — | 4.2 | — |
| **Refuse** | 23.9 | — | 36.6 | — | 11.8 | — |
| **Others** | 12.0 | — | 14.5 | — | 9.2 | — |

**Table S4.8.** Percentage of occurrence (PO) of the main fish species, i.e. at least once PO > 5%, and of each prey category in Audouin's gull pellets in each season of 2017. Sampling months and total fish landing quantities (N = tonnes/month) and their percentages by species are also shown.

| | 2017 | | | | | |
|---|---|---|---|---|---|---|
| | Audouin's gull | | | | | |
| | Pre-breeding (Mar) | | Breeding (May-Jun) | | Post-breeding (Oct) | |
| | Diet | Landings | Diet | Landings | Diet | Landings |
| | N = 94 | N = 614 | N = 280 | N = 834 | N = 48 | N = 639 |
| **Pelagic fish** | 78.7 | 70.8 | 86.4 | 80.0 | 75.0 | 72.6 |
| *Belone belone* | 10.6 | <0.1 | 12.9 | <0.1 | 4.2 | <0.1 |
| *Chelon* sp. | — | <0.1 | — | <0.1 | — | <0.1 |
| *Engraulis encrasicolus* | — | 1.2 | 2.1 | 0.1 | 8.3 | 0.1 |
| *Gadiculus argenteus* | 14.9 | — | 9.6 | — | 2.1 | — |
| *Micromesistius poutassou* | 30.9 | 7.4 | 21.1 | 5.8 | 25.0 | 10.0 |
| *Myctophum* sp. | 3.2 | — | 2.5 | — | — | — |
| *Sardina pilchardus* | 26.6 | 0.3 | 20.7 | 35.1 | 25.0 | 29.3 |
| *Scomber* sp. | 8.5 | 4.9 | 5.0 | 8.3 | 8.3 | 8.0 |
| *Scomberosox saurus* | 20.2 | — | 52.9 | — | 18.8 | — |
| *Trachurus* sp. | 18.1 | 57.0 | 6.1 | 30.0 | 6.3 | 21.6 |
| **Demersal fish** | 68.1 | 29.2 | 44.3 | 20.0 | 72.9 | 27.4 |
| *Boops boops* | 10.6 | 1.6 | 4.3 | 1.4 | 8.3 | 1.2 |
| *Callionymus lyra* | 3.2 | — | 7.1 | — | 12.5 | — |
| *Cepola rubescens* | 1.1 | — | 7.1 | — | — | — |
| *Chelidonichthys* sp. | 1.1 | 0.2 | 0.4 | 0.1 | — | 0.1 |
| *Coelorinchus* sp. | — | — | — | — | — | — |
| *Conger conger* | 5.3 | 0.6 | 3.9 | 0.7 | 2.1 | 0.8 |
| *Diplodus* sp. | 34.0 | 4.4 | 13.2 | 2.4 | 25.0 | 2.4 |
| *Galeus melastomus* | 1.1 | <0.1 | 0.4 | 0.1 | — | — |
| *Lepidotrigla cavillone* | 1.1 | 0.1 | 0.7 | <0.1 | 4.2 | 0.1 |
| *Lesueurigobius* sp. | — | — | 0.7 | — | 8.3 | — |
| *Lithognathus mormyrus* | — | 0.5 | — | 0.1 | — | <0.1 |
| *Malacocephalus laevis* | 4.3 | — | 3.2 | — | 8.3 | — |
| *Merluccius* sp. | 5.3 | 3.5 | 2.5 | 1.7 | 6.3 | 1.5 |
| *Microchirus* sp. | 2.1 | 1.8 | 1.4 | 0.9 | — | 0.7 |
| *Nezumia* sp. | 1.1 | — | — | — | 6.3 | — |
| *Phycis* sp. | — | 0.3 | 1.1 | 0.1 | — | 0.2 |
| *Sarpa salpa* | — | 2.3 | — | 1.0 | — | 1.4 |
| *Serranus* sp. | 11.7 | <0.1 | 8.9 | <0.1 | 14.6 | <0.1 |
| *Trachinus* sp. | — | <0.1 | 0.4 | 0.1 | — | <0.1 |
| *Trisopterus* sp. | 3.2 | 0.1 | 2.5 | <0.1 | 2.1 | 0.1 |
| **Unidentified fish** | 30.9 | — | 22.9 | — | 35.4 | — |
| **Total fish** | 97.9 | 100 | 99.6 | 100 | 100 | 100 |
| **Marine invertebrates** | 16.0 | — | 2.9 | — | 6.3 | — |
| **Vegetal matter** | 1.1 | — | 0.4 | — | — | — |
| **Refuse** | — | — | — | — | 2.1 | — |
| **Others** | 4.3 | — | 3.2 | — | — | — |

**Table S4.9.** Percentage of occurrence (PO) of the main fish species, i.e. at least once PO > 5%, and of each prey category in yellow-legged gull pellets in each season of 2018 at Sálvora Island. Sampling months and total fish landing quantities (N = tonnes/month) and their percentages by species are also shown.

| | 2018 | | | |
| | Sálvora | | | |
| | Pre-breeding (Jan) | | Breeding (May) | |
| | Diet | Landings | Diet | Landings |
| | N = 65 | N = 3,329 | N = 51 | N = 5,036 |
| **Pelagic fish** | 9.1 | 56.2 | 2.8 | 57.5 |
| *Belone belone* | — | <0.1 | — | <0.1 |
| *Chelon* sp. | — | — | — | — |
| *Engraulis encrasicolus* | — | 0.1 | — | 2.4 |
| *Gadiculus argenteus* | — | — | — | — |
| *Micromesistius poutassou* | 3.8 | 33.0 | 2.8 | 28.4 |
| *Myctophum* sp. | — | — | — | — |
| *Sardina pilchardus* | 1.1 | <0.1 | — | 0.6 |
| *Scomber* sp. | 2.7 | 7.2 | — | 4.3 |
| *Scomberosox saurus* | — | — | — | — |
| *Trachurus* sp. | 1.6 | 6.4 | — | 13.0 |
| **Demersal fish** | 11.8 | 43.8 | 2.4 | 42.4 |
| *Boops boops* | 3.8 | 2.2 | 0.4 | 1.6 |
| *Callionymus lyra* | — | <0.1 | — | <0.1 |
| *Cepola rubescens* | — | — | — | — |
| *Chelidonichthys* sp. | — | 0.4 | — | 0.1 |
| *Coelorinchus* sp. | — | — | — | — |
| *Conger conger* | 2.2 | 1.8 | — | 1.9 |
| *Diplodus* sp. | 0.5 | 0.2 | — | 0.6 |
| *Galeus melastomus* | — | 0.1 | — | 0.1 |
| *Lepidotrigla cavillone* | 0.5 | — | — | — |
| *Lesueurigobius* sp. | — | — | — | — |
| *Lithognathus mormyrus* | — | — | — | — |
| *Malacocephalus laevis* | — | — | — | — |
| *Merluccius* sp. | — | 3.6 | 0.4 | 5.6 |
| *Microchirus* sp. | — | <0.1 | — | <0.1 |
| *Nezumia* sp. | — | — | — | — |
| *Phycis* sp. | — | <0.1 | — | 0.1 |
| *Sarpa salpa* | — | — | — | <0.1 |
| *Serranus* sp. | 0.5 | <0.1 | 1.6 | <0.1 |
| *Trachinus* sp. | — | <0.1 | — | — |
| *Trisopterus* sp. | 4.3 | 1.0 | — | 0.7 |
| **Unidentified fish** | 3.2 | — | 3.6 | — |
| **Total fish** | 24.2 | 100 | 8.7 | 100 |
| **Marine invertebrates** | 80.0 | — | 86.3 | — |
| **Vegetal matter** | 15.4 | — | 13.7 | — |
| **Refuse** | 6.2 | — | 9.8 | — |
| **Others** | — | — | 17.6 | — |

**Table S4.10.** Percentage of occurrence (PO) of the main fish species, i.e. at least once PO > 5%, and of each prey category in yellow-legged gull pellets in season of 2018 at Berlenga Island. Sampling months and total fish landing quantities (N = tonnes/month) and their percentages by species are also shown.

| | 2018 | | | | | |
|---|---|---|---|---|---|---|
| | Berlenga | | | | | |
| | Pre-breeding (Feb) | | Breeding (May & Jul) | | Post-breeding (Sep) | |
| | Diet | Landings | Diet | Landings | Diet | Landings |
| | N = 109 | N = 692 | N = 156 | N = 2,053 | N = 259 | N = 1,282 |
| **Pelagic fish** | 3.7 | 64.9 | 9.0 | 86.1 | 13.1 | 80.9 |
| *Belone belone* | 0.9 | — | — | — | 0.4 | — |
| *Chelon* sp. | — | 0.1 | — | <0.1 | — | <0.1 |
| *Engraulis encrasicolus* | — | 3.3 | — | <0.1 | — | 1.5 |
| *Gadiculus argenteus* | — | — | — | — | — | — |
| *Micromesistius poutassou* | 0.9 | 0.6 | 1.9 | 0.6 | 2.7 | 0.3 |
| *Myctophum* sp. | — | — | — | — | — | — |
| *Sardina pilchardus* | 0.9 | — | 2.6 | 28.0 | 7.7 | 31.1 |
| *Scomber* sp. | — | 1.5 | 3.2 | 24.7 | 2.7 | 22.3 |
| *Scomberosox saurus* | 1.8 | — | — | — | 1.9 | — |
| *Trachurus* sp. | — | 51.5 | 3.2 | 30.6 | 2.7 | 23.0 |
| **Demersal fish** | 2.8 | 35.1 | 1.9 | 13.9 | 3.9 | 19.1 |
| *Boops boops* | 1.8 | 0.1 | — | <0.1 | 1.2 | <0.1 |
| *Callionymus lyra* | — | — | — | — | — | — |
| *Cepola rubescens* | — | — | — | — | — | — |
| *Chelidonichthys* sp. | — | 0.4 | — | 0.1 | — | 0.2 |
| *Coelorinchus* sp. | — | — | — | — | — | — |
| *Conger conger* | — | 1.5 | — | 1.7 | 0.4 | 1.5 |
| *Diplodus* sp. | — | 3.1 | 0.6 | 0.2 | 0.4 | 0.2 |
| *Galeus melastomus* | — | 0.1 | — | 0.1 | — | 0.1 |
| *Lepidotrigla cavillone* | — | 1.0 | — | <0.1 | 0.4 | 0.1 |
| *Lesueurigobius* sp. | — | — | — | — | — | — |
| *Lithognathus mormyrus* | — | — | — | — | — | <0.1 |
| *Malacocephalus laevis* | — | — | — | — | — | — |
| *Merluccius* sp. | — | 3.9 | 1.3 | 3.1 | 0.8 | 4.2 |
| *Microchirus* sp. | — | 0.3 | — | 0.1 | — | 0.1 |
| *Nezumia* sp. | — | — | — | — | — | — |
| *Phycis* sp. | — | 0.3 | — | 0.3 | — | 0.5 |
| *Sarpa salpa* | — | <0.1 | — | <0.1 | — | 0.1 |
| *Serranus* sp. | 0.9 | <0.1 | — | <0.1 | 0.8 | <0.1 |
| *Trachinus* sp. | — | <0.1 | — | <0.1 | — | <0.1 |
| *Trisopterus* sp. | — | 4.6 | — | 0.9 | 0.4 | 1.2 |
| **Unidentified fish** | 2.8 | — | 3.8 | — | 6.6 | — |
| **Total fish** | 6.4 | 100 | 13.5 | 100 | 18.1 | 100 |
| **Marine invertebrates** | 94.5 | — | 94.2 | — | 89.6 | — |
| **Vegetal matter** | 1.8 | — | 2.6 | — | 6.2 | — |
| **Refuse** | 6.4 | — | 1.9 | — | 6.6 | — |
| **Others** | 6.4 | — | 9.0 | — | 10.4 | — |

**Table S4.11.** Percentage of occurrence (PO) of the main fish species, i.e. at least once PO > 5%, and of each prey category in yellow-legged gull pellets in each season of 2018 at Pessegueiro Island. Sampling months and total fish landing quantities (N = tonnes/month) and their percentages by species are also shown.

| | 2018 | | | | | |
|---|---|---|---|---|---|---|
| | Pessegueiro | | | | | |
| | Pre-breeding (Feb) | | Breeding (May) | | Post-breeding (Oct) | |
| | Diet | Landings | Diet | Landings | Diet | Landings |
| | N = 26 | N = 236 | N = 54 | N = 652 | N = 39 | N = 502 |
| **Pelagic fish** | 38.5 | 83.2 | 55.6 | 88.8 | 38.5 | 85.4 |
| *Belone belone* | — | — | — | — | — | <0.1 |
| *Chelon* sp. | — | 0.1 | — | <0.1 | — | 0.2 |
| *Engraulis encrasicolus* | — | — | — | — | — | — |
| *Gadiculus argenteus* | — | — | 1.9 | — | — | — |
| *Micromesistius poutassou* | 15.4 | 5.7 | 7.4 | 11.9 | 7.7 | 12.9 |
| *Myctophum* sp. | — | — | — | — | — | — |
| *Sardina pilchardus* | 15.4 | — | 9.3 | 8.7 | 23.1 | — |
| *Scomber* sp. | 11.5 | 67.8 | 20.4 | 45.9 | 10.3 | 50.4 |
| *Scomberosox saurus* | 7.7 | — | 1.9 | — | 5.1 | — |
| *Trachurus* sp. | 3.8 | 9.1 | 29.6 | 22.1 | 15.4 | 21.7 |
| **Demersal fish** | 30.8 | 16.8 | 53.7 | 11.2 | 41.0 | 14.6 |
| *Boops boops* | — | 6.2 | 35.2 | 3.2 | 5.1 | 4.2 |
| *Callionymus lyra* | 7.7 | — | — | — | — | — |
| *Cepola rubescens* | — | — | — | — | — | — |
| *Chelidonichthys* sp. | — | 0.2 | 1.9 | <0.1 | — | <0.1 |
| *Coelorinchus* sp. | — | — | — | — | — | — |
| *Conger conger* | — | 1.6 | 1.9 | 1.3 | — | 0.4 |
| *Diplodus* sp. | 11.5 | 0.5 | 11.1 | 1.3 | 2.6 | 0.6 |
| *Galeus melastomus* | — | — | 1.9 | <0.1 | — | — |
| *Lepidotrigla cavillone* | — | — | 9.3 | — | 5.1 | — |
| *Lesueurigobius* sp. | — | — | — | — | — | — |
| *Lithognathus mormyrus* | — | <0.1 | — | <0.1 | — | <0.1 |
| *Malacocephalus laevis* | — | — | — | — | — | — |
| *Merluccius* sp. | — | 0.1 | — | 0.3 | 5.1 | 2.3 |
| *Microchirus* sp. | — | 0.4 | 1.9 | 0.1 | — | <0.1 |
| *Nezumia* sp. | — | — | — | — | — | — |
| *Phycis* sp. | — | 0.6 | 1.9 | 0.7 | — | 0.2 |
| *Sarpa salpa* | — | <0.1 | — | <0.1 | — | 2.2 |
| *Serranus* sp. | 7.7 | — | 11.1 | — | 15.4 | — |
| *Trachinus* sp. | — | <0.1 | — | 0.1 | 5.1 | <0.1 |
| *Trisopterus* sp. | 3.8 | 0.5 | — | 0.1 | 7.7 | <0.1 |
| **Unidentified fish** | 26.9 | — | 35.2 | — | 17.9 | — |
| **Total fish** | 65.4 | 100 | 83.3 | 100 | 76.9 | 100 |
| **Marine invertebrates** | 50.0 | — | 25.9 | — | 43.6 | — |
| **Vegetal matter** | 23.1 | — | 64.8 | — | 56.4 | — |
| **Refuse** | 3.8 | — | 13.0 | — | 2.6 | — |
| **Others** | 42.3 | — | 16.7 | — | 38.5 | — |

**Table S4.12.** Percentage of occurrence (PO) of the main fish species, i.e. at least once PO > 5%, and of each prey category in yellow-legged gull pellets in each season of 2018 at Deserta Island. Sampling months and total fish landing quantities (N = tonnes/month) and their percentages by species are also shown.

| | 2018 | | | | | |
|---|---|---|---|---|---|---|
| | Deserta | | | | | |
| | Pre-breeding (Apr) | | Breeding (May) | | Post-breeding (Oct) | |
| | Diet | Landings | Diet | Landings | Diet | Landings |
| | N = 92 | N = 410 | N = 150 | N = 1,884 | N = 39 | N = 664 |
| **Pelagic fish** | 26.1 | 72.0 | 50.0 | 94.0 | 71.8 | 72.0 |
| *Belone belone* | — | <0.1 | — | <0.1 | — | <0.1 |
| *Chelon* sp. | — | 0.1 | 2.0 | <0.1 | 2.6 | 0.5 |
| *Engraulis encrasicolus* | 1.1 | — | — | 0.6 | — | <0.1 |
| *Gadiculus argenteus* | 1.1 | — | 4.7 | — | 15.4 | — |
| *Micromesistius poutassou* | 5.4 | 7.2 | 26.7 | 1.4 | 20.5 | 4.1 |
| *Myctophum* sp. | — | — | — | — | 2.6 | — |
| *Sardina pilchardus* | 2.2 | — | 7.3 | 7.7 | 10.3 | — |
| *Scomber* sp. | 7.6 | 13.9 | 10.0 | 70.8 | 30.8 | 34.6 |
| *Scomberosox saurus* | — | — | 1.3 | — | 5.1 | — |
| *Trachurus* sp. | 14.1 | 50.6 | 18.7 | 13.3 | 15.4 | 29.0 |
| **Demersal fish** | 25.0 | 28.0 | 38.7 | 6.0 | 76.9 | 28.0 |
| *Boops boops* | 5.4 | 1.0 | 8.0 | 0.3 | 2.6 | 2.1 |
| *Callionymus lyra* | — | — | — | — | — | — |
| *Cepola rubescens* | — | — | — | — | — | <0.1 |
| *Chelidonichthys* sp. | 1.1 | 0.3 | 2.0 | <0.1 | — | 0.1 |
| *Coelorinchus* sp. | — | — | — | — | — | — |
| *Conger conger* | 1.1 | 0.1 | 5.3 | 0.3 | 7.7 | 0.4 |
| *Diplodus* sp. | 2.2 | 2.4 | 6.7 | 0.6 | 23.1 | 2.9 |
| *Galeus melastomus* | — | — | 0.7 | — | — | <0.1 |
| *Lepidotrigla cavillone* | — | 0.1 | 1.3 | | — | 0.1 |
| *Lesueurigobius* sp. | — | — | — | — | — | — |
| *Lithognathus mormyrus* | 2.2 | 0.3 | 1.3 | <0.1 | 7.7 | <0.1 |
| *Malacocephalus laevis* | — | — | 0.7 | — | 10.3 | — |
| *Merluccius* sp. | 3.3 | 2.8 | 6.7 | 0.7 | 17.9 | 1.9 |
| *Microchirus* sp. | 4.3 | 1.5 | 3.3 | 0.2 | — | 1.9 |
| *Nezumia* sp. | — | — | — | — | 5.1 | — |
| *Phycis* sp. | — | 0.3 | — | 0.1 | 5.1 | 0.1 |
| *Sarpa salpa* | — | 1.1 | 0.7 | 0.3 | 10.3 | 4.7 |
| *Serranus* sp. | 4.3 | <0.1 | 3.3 | <0.1 | — | <0.1 |
| *Trachinus* sp. | 1.1 | 0.1 | 3.3 | <0.1 | 15.4 | 0.1 |
| *Trisopterus* sp. | 1.1 | 0.2 | 1.3 | 0.1 | 10.3 | 0.1 |
| **Unidentified fish** | 29.3 | — | 24.0 | — | 25.6 | — |
| **Total fish** | 60.9 | 100 | 78.0 | 100 | 100.0 | 100 |
| **Marine invertebrates** | 26.1 | — | 37.3 | — | 10.3 | — |
| **Vegetal matter** | 60.9 | — | 12.0 | — | — | — |
| **Refuse** | 77.2 | — | 12.7 | — | 7.7 | — |
| **Others** | 17.4 | — | 8.7 | — | 15.4 | — |

**Table S4.13.** Percentage of occurrence (PO) of the main fish species, i.e. at least once PO > 5%, and of each prey category in Audouin's gull pellets in each season of 2018. Sampling months and total fish landing quantities (N = tonnes/month) and their percentages by species are also shown.

| | 2018 | | | | | |
|---|---|---|---|---|---|---|
| | Audouin's gull | | | | | |
| | Pre-breeding (Apr) | | Breeding (May) | | Post-breeding (Oct) | |
| | Diet | Landings | Diet | Landings | Diet | Landings |
| | N = 44 | N = 410 | N = 191 | N = 1,884 | N = 60 | N = 664 |
| **Pelagic fish** | 88.6 | 72.0 | 88.0 | 94.0 | 95.0 | 72.0 |
| *Belone belone* | 11.4 | <0.1 | 3.7 | <0.1 | 1.7 | <0.1 |
| *Chelon* sp. | — | 0.1 | — | <0.1 | — | 0.5 |
| *Engraulis encrasicolus* | — | — | 4.7 | 0.6 | — | <0.1 |
| *Gadiculus argenteus* | 22.7 | — | 5.8 | — | 3.3 | — |
| *Micromesistius poutassou* | 18.2 | 7.2 | 22.5 | 1.4 | 18.3 | 4.1 |
| *Myctophum* sp. | 6.8 | — | 8.9 | — | 13.3 | — |
| *Sardina pilchardus* | 11.4 | — | 15.7 | 7.7 | 8.3 | — |
| *Scomber* sp. | 6.8 | 13.9 | 14.1 | 70.8 | 8.3 | 34.6 |
| *Scomberosox saurus* | 63.6 | — | 68.6 | — | 88.3 | — |
| *Trachurus* sp. | 9.1 | 50.6 | 4.7 | 13.3 | 5.0 | 29.0 |
| **Demersal fish** | 40.9 | 28.0 | 39.8 | 6.0 | 28.3 | 28.0 |
| *Boops boops* | 15.9 | 1.0 | 3.1 | 0.3 | 3.3 | 2.1 |
| *Callionymus lyra* | 4.5 | — | — | — | — | — |
| *Cepola rubescens* | 2.3 | — | 0.5 | — | — | <0.1 |
| *Chelidonichthys* sp. | — | 0.3 | — | <0.1 | — | 0.1 |
| *Coelorinchus* sp. | — | — | — | — | — | — |
| *Conger conger* | — | 0.1 | 7.9 | 0.3 | 3.3 | 0.4 |
| *Diplodus* sp. | 2.3 | 2.4 | 11.0 | 0.6 | 10.0 | 2.9 |
| *Galeus melastomus* | 4.5 | — | — | — | — | <0.1 |
| *Lepidotrigla cavillone* | 2.3 | 0.1 | — | — | — | 0.1 |
| *Lesueurigobius* sp. | — | — | — | — | — | — |
| *Lithognathus mormyrus* | — | 0.3 | — | <0.1 | — | <0.1 |
| *Malacocephalus laevis* | 13.6 | — | 7.3 | — | 6.7 | — |
| *Merluccius* sp. | 4.5 | 2.8 | 8.4 | 0.7 | 6.7 | 1.9 |
| *Microchirus* sp. | — | 1.5 | 0.5 | 0.2 | — | 1.9 |
| *Nezumia* sp. | — | — | — | — | 1.7 | — |
| *Phycis* sp. | — | 0.3 | — | 0.1 | — | 0.1 |
| *Sarpa salpa* | — | 1.1 | — | 0.3 | — | 4.7 |
| *Serranus* sp. | 2.3 | <0.1 | 9.9 | <0.1 | 1.7 | <0.1 |
| *Trachinus* sp. | — | 0.1 | 0.5 | <0.1 | — | 0.1 |
| *Trisopterus* sp. | — | 0.2 | 1.0 | 0.1 | 1.7 | 0.1 |
| **Unidentified fish** | 25.0 | — | 32.5 | — | 23.3 | — |
| **Total fish** | 95.5 | 100 | 96.3 | 100 | 100.0 | 100 |
| **Marine invertebrates** | 13.6 | — | 21.5 | — | — | — |
| **Vegetal matter** | — | — | — | — | — | — |
| **Refuse** | — | — | 1.0 | — | — | — |
| **Others** | — | — | 8.4 | — | 3.3 | — |

**Table S4.14.** $\delta^{15}N$, $\delta^{13}C$, and $\delta^{34}S$ values in each tissue (P1 – innermost primary feathers, S8 – eighth secondary feathers, RBC – red blood cells, Br – breast feathers, Chicks – chick feathers) of yellow-legged (from Sálvora, Berlenga, Pessegueiro, and Deserta islands) and Audouin's gulls in 2017 and 2018. Values are mean ± SD. Pelagic and demersal fish landing quantities (tonnes/month) are also shown.

| Year | Tissue | N | $\delta^{15}N$ | $\delta^{13}C$ | $\delta^{34}S$ | Pelagic fish landings | Demersal fish landings |
|---|---|---|---|---|---|---|---|
| | | | | **Sálvora** | | | |
| 2017 | P1 | 9 | 13.8 ± 0.8 | -18.4 ± 0.8 | — | | |
| | S8 | 9 | 12.9 ± 1.3 | -17.9 ± 1.4 | — | | |
| | RBC | 9 | 12.6 ± 0.7 | -18.9 ± 0.8 | — | | |
| | Chicks | 15 | 13.4 ± 0.6 | -16.9 ± 0.5 | — | | |
| | | | | **Berlenga** | | | |
| 2017 | P1 | 16 | 13.7 ± 0.7 | -17.2 ± 0.4 | — | | |
| | S8 | 16 | 14.4 ± 1.3 | -16.8 ± 1.1 | — | | |
| | Br | 16 | 12.9 ± 0.6 | -16.8 ± 0.5 | 18.7 ± 1.0 | 956 | 291 |
| | RBC | 16 | 12.6 ± 0.7 | -18.8 ± 0.7 | — | | |
| | Chicks | 10 | 12.8 ± 0.7 | -17.0 ± 0.6 | 17.0 ± 0.7 | 1,990 | 243 |
| 2018 | P1 | 16 | 14.7 ± 0.6 | -16.7 ± 0.5 | — | | |
| | S8 | 16 | 14.6 ± 0.8 | -17.0 ± 0.8 | — | | |
| | Br | 16 | 13.9 ± 0.9 | -16.8 ± 0.4 | 18.0 ± 1.0 | 1,133 | 256 |
| | RBC | 16 | 11.6 ± 0.9 | -18.4 ± 0.4 | — | | |
| | Chicks | 10 | 13.0 ± 0.6 | -16.5 ± 0.3 | 16.4 ± 0.7 | 1,733 | 232 |
| | | | | **Pessegueiro** | | | |
| 2017 | P1 | 7 | 14.3 ± 0.9 | -16.1 ± 1.0 | — | | |
| | S8 | 7 | 14.8 ± 0.7 | -16.1 ± 0.5 | — | | |
| | Br | 7 | 13.3 ± 0.4 | -15.9 ± 0.4 | 18.5 ± 0.9 | 649 | 70 |
| | RBC | 7 | 13.5 ± 0.6 | -18.0 ± 0.4 | — | | |
| | Chicks | 13 | 13.7 ± 0.2 | -16.7 ± 0.3 | 17.6 ± 0.6 | 298 | 41 |
| 2018 | P1 | 11 | 13.6 ± 0.8 | -17.0 ± 1.0 | — | | |
| | S8 | 11 | 13.6 ± 1.1 | -17.0 ± 0.9 | — | | |
| | Br | 11 | 13.7 ± 0.7 | -16.8 ± 0.6 | 17.1 ± 1.6 | 374 | 57 |
| | RBC | 11 | 11.5 ± 1.0 | -18.3 ± 0.7 | — | | |
| | Chicks | 10 | 13.4 ± 0.3 | -16.1 ± 0.2 | 17.5 ± 0.3 | 472 | 51 |
| | | | | **Deserta** | | | |
| 2017 | P1 | 10 | 15.0 ± 0.8 | -15.7 ± 0.4 | — | | |
| | S8 | 10 | 14.3 ± 1.0 | -16.5 ± 1.0 | — | | |
| | Br | 10 | 13.0 ± 0.8 | -16.2 ± 0.7 | 17.3 ± 1.5 | 745 | 169 |
| | RBC | 10 | 11.9 ± 1.4 | -18.6 ± 0.8 | — | | |
| | Chicks | 14 | 13.2 ± 0.7 | -16.6 ± 0.9 | 15.9 ± 2.0 | 677 | 147 |
| 2018 | P1 | 8 | 14.0 ± 1.6 | -16.6 ± 0.8 | — | | |
| | S8 | 8 | 13.8 ± 1.0 | -16.3 ± 1.7 | — | | |
| | Br | 8 | 13.2 ± 1.1 | -16.8 ± 0.5 | 15.7 ± 3.0 | 583 | 128 |
| | RBC | 8 | 10.9 ± 0.8 | -18.6 ± 0.6 | — | | |
| | Chicks | 10 | 13.0 ± 0.4 | -16.4 ± 0.2 | 17.5 ± 0.4 | 781 | 98 |
| | | | | **Audouin's gull** | | | |
| 2017 | P1 | 12 | 14.1 ± 0.3 | -16.3 ± 0.3 | — | | |
| | S8 | 12 | 15.0 ± 1.3 | -14.4 ± 1.4 | — | | |
| | RBC | 12 | 12.9 ± 0.3 | -18.4 ± 0.5 | — | | |
| | Chicks | 15 | 12.9 ± 0.2 | -17.3 ± 0.3 | — | | |
| 2018 | P1 | 14 | 13.6 ± 0.7 | -17.0 ± 0.5 | — | | |
| | S8 | 14 | 13.3 ± 0.6 | -15.3 ± 1.7 | — | | |
| | RBC | 14 | 11.2 ± 0.3 | -18.6 ± 0.3 | — | | |
| | Chicks | 11 | 12.9 ± 0.3 | -16.5 ± 0.1 | — | | |

**Table S4.15.** $\delta^{15}N$ and $\delta^{13}C$ values and biochemical parameters in the plasma of yellow-legged (from Berlenga, Pessegueiro, and Deserta islands) and Audouin's gulls in 2017 and 2018. Values are mean ± SD. Pelagic and demersal fish landing quantities (tonnes/month) are also shown.

| Year | N | $\delta^{15}N$ | $\delta^{13}C$ | Triglycerides (mg/dL) | Uric acid (mg/dL) | Carotenoids (mg/dL) | Total protein (g/dL) | Pelagic fish landings | Demersal fish landings |
|---|---|---|---|---|---|---|---|---|---|
| Berlenga | | | | | | | | | |
| 2017 | 16 | 13.0 ± 0.6 | -18.7 ± 0.6 | 102.5 ± 62.1 | 10.1 ± 5.9 | 2.9 ± 0.9 | 4.3 ± 0.8 | 1,988 | 245 |
| 2018 | 16 | 11.8 ± 0.3 | -18.5 ± 0.4 | 306.6 ± 111.5 | 16.1 ± 12.2 | 1.9 ± 1.1 | 4.3 ± 2.9 | 2,385 | 326 |
| Pessegueiro | | | | | | | | | |
| 2017 | 7 | 12.2 ± 1.5 | -19.0 ± 1.2 | 52.3 ± 26.7 | 13.7 ± 9.6 | 1.7 ± 0.5 | 3.7 ± 1.1 | 562 | 62 |
| 2018 | 11 | 12.0 ± 0.8 | -18.8 ± 1.1 | 261.0 ± 75.3 | 16.0 ± 6.6 | 2.4 ± 0.7 | 3.2 ± 0.5 | 423 | 97 |
| Deserta | | | | | | | | | |
| 2017 | 10 | 13.0 ± 0.7 | -18.4 ± 0.4 | 129.9 ± 61.9 | 13.0 ± 4.2 | 2.4 ± 0.6 | 4.9 ± 1.0 | 709 | 189 |
| 2018 | 8 | 12.4 ± 0.6 | -18.0 ± 0.5 | 311.4 ± 56.2 | 11.0 ± 4.0 | 1.5 ± 0.5 | 4.1 ± 0.5 | 1,768 | 120 |
| Audouin's gull | | | | | | | | | |
| 2017 | 12 | 12.1 ± 1.4 | -19.3 ± 0.5 | 137.9 ± 27.4 | 10.1 ± 5.8 | 2.2 ± 0.4 | 4.0 ± 0.4 | 709 | 189 |
| 2018 | 14 | 12.1 ± 1.2 | -18.8 ± 0.7 | 466.9 ± 74.5 | 7.7 ± 2.5 | 2.3 ± 0.8 | 4.3 ± 0.6 | 2,259 | 120 |

**Table S5.1.** List of sampled locations by year for pellets of yellow-legged gull *Larus michahellis*.

| 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | 1994 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | 2016 | 2017 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Arousa | Cíes | Arousa | Arousa | Arousa | Cíes | Cíes | Xuño | Arousa | Arousa | Arousa | Arousa | Arousa | Arousa | Cíes | Arousa | Arousa | Arousa | Arousa | Arousa | Arousa | Arousa |
| Cíes | | Cíes | Cíes | Cíes | Xuño | Farallóns | | Ansarón | Ansarón | Cíes | Ansarón | Cíes | Cíes | | Cíes | | Cíes | Cíes | Cíes | Cíes | Ansarón |
| Farallóns | | Farallóns | Malpica | Estelas | | Ons | | Cíes | Cíes | | Cíes | Ons | | | Ons | | Ons | Ons | Ons | Ons | Cíes |
| Lobeiras | | Lobeiras | Ons | Farallóns | | | | Coelleira | Lobeiras | | Ons | | | | | | Sisargas | | | | Ons |
| Ons | | Ons | Sisargas | Lobeiras | | | | Lobeiras | Ons | | Sisargas | | | | | | | | | | Sisargas |
| Sisargas | | Traba | | Ons | | | | Ons | | | | | | | | | | | | | |
| | | Vilán | | Sisargas | | | | Pantorgas | | | | | | | | | | | | | |

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**Table S5.2.** List of general additive mixed models (GAMMs) explaining sardine occurrence in yellow-legged gull pellets. Models are ordered by increasing Akaike Information Criterion corrected for small sample sizes (AICc) and include all possible combinations of explanatory variables and the missing values imputation. Explanatory variables tested were sardine landings, fishery landings, North Atlantic Oscillation index (NAO), and Sea Surface Temperature anomaly (SSTa). Number of estimated parameters (df), log likelihood (LogLik), and Akaike weight (Wi) are also shown. All models include colony as a random effect. Best supported models (ΔAICc < 2) are highlighted in bold.

| (Intercept) | sardine landings | fishery landings | NAO index | SSTa | missing values imputation | df | logLik | AICc | ΔAICc | Wi |
|---|---|---|---|---|---|---|---|---|---|---|
| **8.21** | **+** | **+** | | | | **8** | **-263.49** | **545.03** | **0.00** | **0.34** |
| **8.12** | **+** | **+** | **+** | | | **10** | **-261.43** | **546.10** | **1.07** | **0.20** |
| **8.41** | **+** | | | | | **6** | **-266.87** | **546.90** | **1.87** | **0.13** |
| 8.21 | + | + | | | + | 9 | -263.49 | 547.59 | 2.55 | 0.09 |
| 8.44 | + | | + | | | 8 | -265.27 | 548.59 | 3.56 | 0.06 |
| 8.12 | + | + | + | | + | 11 | -261.43 | 548.81 | 3.78 | 0.05 |
| 8.29 | + | + | | + | | 10 | -262.87 | 548.97 | 3.94 | 0.05 |
| 8.41 | + | | | | + | 7 | -266.87 | 549.31 | 4.28 | 0.04 |
| 8.44 | + | | + | | + | 9 | -265.27 | 551.14 | 6.11 | 0.02 |
| 8.12 | + | + | + | + | | 12 | -261.43 | 551.60 | 6.56 | 0.01 |
| 8.29 | + | + | | + | + | 11 | -262.87 | 551.68 | 6.65 | 0.01 |
| 8.47 | + | | + | + | | 10 | -265.24 | 553.71 | 8.67 | 0.00 |
| 8.12 | + | + | + | + | + | 13 | -261.43 | 554.47 | 9.44 | 0.00 |
| 8.47 | + | | + | + | + | 11 | -265.24 | 556.41 | 11.38 | 0.00 |
| 7.55 | | + | | | + | 7 | -276.88 | 569.34 | 24.31 | 0.00 |
| 7.57 | | + | + | | + | 9 | -275.77 | 572.14 | 27.11 | 0.00 |
| 7.54 | | + | | + | + | 9 | -276.65 | 573.92 | 28.88 | 0.00 |
| 7.59 | | + | + | + | + | 11 | -275.72 | 577.38 | 32.35 | 0.00 |
| 8.76 | | + | | + | | 8 | -287.22 | 592.51 | 47.47 | 0.00 |
| 8.76 | | + | + | + | | 10 | -287.22 | 597.68 | 52.65 | 0.00 |
| 8.39 | | | + | | + | 7 | -291.78 | 599.15 | 54.11 | 0.00 |
| 8.17 | | | + | + | + | 9 | -289.89 | 600.38 | 55.35 | 0.00 |
| 8.49 | | | | | + | 5 | -294.78 | 600.38 | 55.35 | 0.00 |
| 8.30 | | | | + | + | 7 | -293.62 | 602.81 | 57.78 | 0.00 |
| 9.33 | | | | | | 4 | -298.54 | 605.63 | 60.60 | 0.00 |
| 9.06 | | | | + | | 6 | -297.68 | 608.52 | 63.49 | 0.00 |
| 9.44 | | | + | | | 6 | -298.42 | 610.00 | 64.96 | 0.00 |
| 9.21 | | | + | + | | 8 | -297.06 | 612.17 | 67.13 | 0.00 |

**Table S5.3.** List of general additive mixed models (GAMMs) explaining total fish occurrence in yellow-legged gull pellets. Models are ordered by increasing Akaike Information Criterion corrected for small sample sizes (AICc) and include all possible combinations of explanatory variables and the missing values imputation. Explanatory variables tested were sardine landings, fishery landings, North Atlantic Oscillation index (NAO), and Sea Surface Temperature anomaly (SSTa). Number of estimated parameters (df), log likelihood (LogLik), and Akaike weight (Wi) are also shown. All models include colony as a random effect. Best supported models (ΔAICc < 2) are highlighted in bold.

| (Intercept) | sardine landings | fishery landings | NAO index | SSTa | missing values imputation | df | logLik | AICc | ΔAICc | Wi |
|---|---|---|---|---|---|---|---|---|---|---|
| **26.51** | **+** | **+** | | | | **8** | **-302.28** | **622.62** | **0.00** | **0.36** |
| **26.53** | **+** | | | | | **6** | **-305.27** | **623.71** | **1.09** | **0.21** |
| 26.51 | + | + | | | + | 9 | -302.28 | 625.17 | 2.55 | 0.10 |
| 26.53 | + | | | | + | 7 | -305.27 | 626.12 | 3.50 | 0.06 |
| 26.12 | + | + | + | | | 10 | -301.49 | 626.22 | 3.60 | 0.06 |
| 26.31 | + | | + | | | 8 | -304.30 | 626.67 | 4.04 | 0.05 |
| 26.61 | + | | | + | | 8 | -304.31 | 626.67 | 4.05 | 0.05 |
| 26.34 | + | + | + | | | 10 | -302.06 | 627.36 | 4.74 | 0.03 |
| 26.35 | + | | + | + | | 10 | -302.71 | 628.65 | 6.03 | 0.02 |
| 26.12 | + | + | | + | + | 11 | -301.49 | 628.92 | 6.30 | 0.02 |
| 26.31 | + | | + | | + | 9 | -304.30 | 629.22 | 6.60 | 0.01 |
| 26.61 | + | | + | | + | 9 | -304.31 | 629.22 | 6.60 | 0.01 |
| 25.86 | + | + | + | + | | 12 | -300.46 | 629.66 | 7.03 | 0.01 |
| 26.34 | + | + | + | | + | 11 | -302.06 | 630.07 | 7.45 | 0.01 |
| 26.35 | + | | + | + | + | 11 | -302.71 | 631.36 | 8.73 | 0.00 |
| 25.86 | + | + | + | + | + | 13 | -300.46 | 632.53 | 9.91 | 0.00 |
| 25.76 | | + | | | + | 7 | -310.36 | 636.29 | 13.67 | 0.00 |
| 25.48 | | + | | + | + | 9 | -309.58 | 639.76 | 17.14 | 0.00 |
| 25.80 | | + | + | | + | 9 | -310.10 | 640.80 | 18.18 | 0.00 |
| 25.54 | | + | + | + | + | 11 | -309.06 | 644.06 | 21.44 | 0.00 |
| 26.76 | | + | | | | 6 | -316.10 | 645.37 | 22.75 | 0.00 |
| 25.90 | | + | | + | | 8 | -313.97 | 646.00 | 23.38 | 0.00 |
| 26.68 | | + | + | | | 8 | -315.98 | 650.02 | 27.40 | 0.00 |
| 25.89 | | + | + | + | | 10 | -313.97 | 651.18 | 28.56 | 0.00 |
| 26.29 | | | + | + | + | 7 | -321.72 | 659.01 | 36.39 | 0.00 |
| 26.71 | | | | | + | 5 | -324.20 | 659.22 | 36.59 | 0.00 |
| 26.21 | | + | + | + | + | 9 | -319.37 | 659.35 | 36.73 | 0.00 |
| 26.70 | | | | + | | 6 | -323.17 | 659.51 | 36.89 | 0.00 |
| 27.31 | | | | | | 4 | -325.78 | 660.10 | 37.48 | 0.00 |
| 26.71 | | | + | | + | 7 | -322.96 | 661.49 | 38.87 | 0.00 |
| 26.81 | | | + | + | | 8 | -322.47 | 662.99 | 40.37 | 0.00 |
| 27.38 | | | + | | | 6 | -325.73 | 664.63 | 42.00 | 0.00 |

**Table S5.4.** Pearson correlation coefficients between explanatory variables.

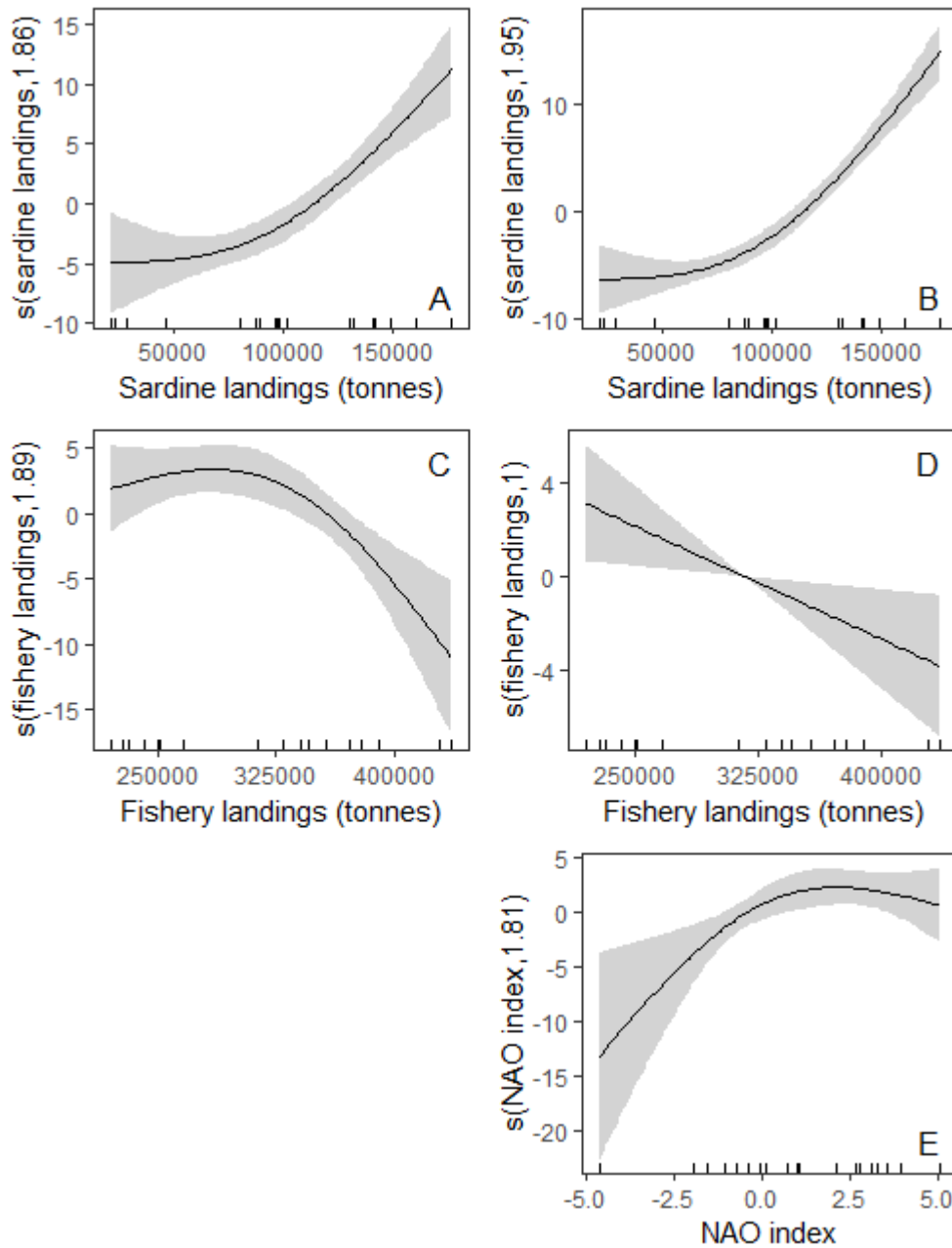|                  | SSTa  | NAO index | fishery landings | sardine landings |
|------------------|-------|-----------|------------------|------------------|
| SSTa             | 1.0   | -0.03     | 0.3              | -0.4             |
| NAO index        | -0.03 | 1.0       | -0.3             | 0.1              |
| fishery landings | 0.3   | -0.3      | 1.0              | -0.5             |
| sardine landings | -0.4  | 0.1       | -0.5             | 1.0              |

**Figure S5.1.** Response curves of the variables explaining the temporal trends of fish prey (percentage of occurrence (PO %), arcsine square root transformed) of yellow-legged gulls based on general additive models (GAMs) outputs considering only Cíes colony. Plots show the predicted curve (black solid lines), 95% confidence intervals (grey shaded areas). A - Sardine landings effect on sardine occurrence, B - Sardine landings effect on total fish occurrence, C - Fishery landings effect on sardine occurrence, D - Fishery landings effect on total fish occurrence, E - North Atlantic Oscillation (NAO) index effect on total fish occurrence.