

Foraging ecology of yellow-legged gulls with a marine strategy

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Roberto Filipe Afonso Mendes

Departamento de Ciências da Vida
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Abstract

Seagulls are opportunistic seabirds that can feed on a wide variety of food, including anthropogenic resources, traveling even for dozens kilometers in that demand. This work focuses on the foraging strategies (particularly the marine strategy) of the yellow - legged gull (*Larus michaellis*) in two distinct colonies (Berlenga – from 2011 to 2016 and Deserta – in 2015 and 2016) during the breeding season (May - June). In addition, the strategies of yellow-legged gulls were compared with the foraging strategy of Audouinii gull (*Larus audouinii*) in Deserta, since this is a species that has a strictly marine foraging strategy. Stable isotope analyses of blood and plasma were measured to detect differences in foraging at breeding season between the years and colonies, as well as GPS loggers to assess foraging behavior performed by gulls of the two species. The objectives were to define the general foraging strategy of the yellow-legged gulls during the breeding season in each year and local, and relate their marine, mix and terrestrial strategies with foraging behavior, niche width and oceanographic conditions. Overall, the results indicated differences in foraging strategies over the years and colonies, and differences in the isotopic niche between the two species of seagulls. It was possible to define the 3 predictable feeding strategies for yellow-legged gulls (marine, mixed and terrestrial). In 2013 in Berlenga, individuals preferred a more terrestrial foraging strategy, supposedly due to the lower NAO values observed during this year. In contrast, 2015 was the year in which the marine foraging strategy was most used. It should be noted that in only some years in Berlenga, mixed trips (2011, 2012 and 2015) were carried out. Results show that the isotopic niche of gulls with a marine foraging strategy was much smaller than the niche of gulls with a terrestrial foraging strategy. Gulls adopting a terrestrial foraging strategy may feed on a wide variety of foods, which greatly influence the amplitude of the isotopic values. It could also be verified that the niche of the audouinii gulls was small and similar to the yellow-legged gulls that used a marine foraging strategy. In conclusion, the feeding strategies of yellow-legged gulls during the breeding season can differ greatly according with the year and location of the colony, and should be influenced by oceanographic conditions and availability of terrestrial and marine food sources.

Keywords: Berlenga; Breeding season; Deserta; Foraging strategy; GPS tracking; Isotopic niche; *Larus audouinii*; *Larus michaellis*; NAO

Resumo

As gaivotas são aves marinhas oportunistas que se alimentam de uma grande variedade de alimentos, incluindo recursos antropogénicos, viajando mesmo dezenas de quilómetros em busca de alimento. Este trabalho incide nas estratégias de alimentação (particularmente a estratégia marinha) da gaivota de patas amarelas (*Larus michaellis*) em duas colónias distintas (Berlenga - de 2011 a 2016 e Deserta - em 2015 e 2016) durante a época de reprodução (Maio a Junho). Além disso, as estratégias de gaivotas de pernas amarelas foram comparadas com a estratégia de alimentação da gaivota de Audouinii (*Larus audouinii*) na Deserta, uma vez que esta é uma espécie que possui uma estratégia de alimentação estritamente marinha. As análises de isótopos estáveis do sangue e plasma foram medidas para detectar diferenças na alimentação na época de reprodução entre os anos e colónias, bem como GPS loggers para avaliar o comportamento na procura de alimentação realizado pelas gaivotas das duas espécies. Os objectivos foram definir a estratégia geral de alimentação das gaivotas de patas amarelas durante a época de reprodução em cada ano e local e relacionar as suas estratégias marinhas, mistas e terrestres com o comportamento na procura de alimento, largura de nicho e condições oceanográficas. No geral, os resultados indicaram diferenças nas estratégias de alimentação ao longo dos anos e colónias e diferenças no nicho isotópico entre as duas espécies de gaivotas. Foi possível definir as 3 estratégias de alimentação previsíveis para as gaivotas de patas amarelas (marinha, mista e terrestre). Em 2013, os indivíduos da Berlenga preferiram uma estratégia de alimentação mais terrestre, provavelmente devido aos menores valores de NAO observados durante esse ano. Em contraste, 2015 foi o ano em que a estratégia de alimentação marinha foi mais utilizada. É de salientar que em apenas alguns anos na Berlenga, foram realizadas viagens mistas (2011, 2012 e 2015). Os resultados mostram que o nicho isotópico das gaivotas com uma estratégia de alimentação marinha foi muito menor que o nicho das gaivotas com uma estratégia de alimentação terrestre. As gaivotas que adoptam uma estratégia de alimentação terrestre podem alimentar-se de uma grande variedade de alimentos, que influenciam muito a amplitude dos valores isotópicos. Pode também verificar-se que o nicho das gaivotas audouinii é pequeno e semelhante ao das gaivotas de patas amarelas que usaram uma estratégia de alimentação marinha. Em conclusão, as estratégias de alimentação das gaivotas de patas amarelas durante a época de reprodução podem diferir muito de acordo com o ano e localização da colónia, e podem ser influenciadas pelas condições oceanográficas e a disponibilidade de fontes de alimento terrestres e marinhas.

Palavras-chave: Berlenga; Deserta; Época de reprodução; GPS tracking; *Larus audouinii*;
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1. Introduction



1.1. Seabirds as ecological indicators

Marine ecosystems include hundreds of types of organisms such as bacteria, phytoplankton, zooplankton, fish, mammals and birds, and all these are interconnected in a complex trophic network and in permanent mutation and adaptation (Cury et al., 2003). Marine ecosystems encompass an array of processes which provide essential goods and services (Costanza et al., 1997). Therefore, it is essential to understand its dynamics in order to predict and manage the consequences and impacts of human exploration, with the aim of maintaining its sustainability (Cury et al., 2003). It is essential to obtain updated information on fluctuations in marine ecosystems for their effective management (Piatt & Sydeman, 2007). In that sense, there are several approaches to study ecosystems, among which, empirical or historical approaches. These consist in the long-term observation and description of several environmental parameters, in order to establish standards. On the other hand, there is also an experimental approach which consists in manipulating the structural or functional components of an ecosystem, and studying how it reacts to such controlled manipulation (Likens, 1992). However, manipulating an entire ecosystem is very difficult if not impossible, and often “natural experiments” (i.e. using the natural oscillations) and ecological indicators are used.

Ecological indicators are used to detect changes in ecosystems in order to evaluate their condition. Due to the general high complexity of ecosystems, ecological indicators are very useful tools to adopt strategies and make decisions regarding ecosystem management, quickly and efficiently (Durant et al., 2009). The use of some species as ecological indicators is a recurring practice in Ecology. This concept presumes that a single species or group of species represent all species with the same requirements in a given ecosystem (Landres et al., 1988; Niemi & McDonald, 2004). Typically, the species used as indicators belong to macroflora, mainly vascular plants, and macrofauna, such as marine macroinvertebrates, fish, mammals and birds (Niemi & McDonald, 2004). The main reasons for the choice of some species as ecological indicators are that they are relatively easy to identify, awaken the interest of the general public, are relatively easy to monitor, there is sufficient scientific information about these species, particularly how they react to disturbances, and also the fact that such evaluation has relatively low costs (Niemi & McDonald, 2004). However, it is noteworthy that the ecology of these indicators should be well known and studied, in order to separate clearly the natural dynamics of the species concerned and the effects caused by the alteration of the ecosystem (Koskimies, 1989).

Birds are often used as ecological indicators, not only for being a well-studied group, but also because they are easy to monitor compared to other groups of organisms, and are ecologically very versatile, exploring diverse habitats in different ways (Gregory et al., 2009; Koskimies, 1989). Birds can detect environmental changes, such as prey availability, which would not be possible to detect by monitoring physical and chemical parameters of the ecosystem, often cumulative of different environmental changes that act simultaneously and which would not be detected otherwise (Koskimies, 1989). When using birds as bio-indicators, it is possible to evaluate the changes that occur in a given ecosystem not only in a quantitative manner but also in a qualitative way (Koskimies, 1989).

As marine species, seabirds have several unique attributes when compared to other marine taxa. Seabirds are readily observed in an environment where most species are immersed, and are often on top of trophic chains thus reflecting changes that occur in the lower trophic levels (Cury et al., 2003). Seabirds are also quite affected by anthropogenic pressures such as pollution and over-exploitation of available marine resources. They usually concentrate a great interest by the public, which helps raising awareness for environmental problems, such as climate change and excessive pollution (Piatt & Sydeman, 2007). Due to its mobility and longevity, seabirds will respond differently to changes in the marine ecosystem at both spatial and temporal scales. For instance, during the breeding season, most seabirds are limited to search for food in the surrounding areas of their breeding grounds, i.e. they become central-place foragers. When relieved from breeding duties, seabirds can perform migrations and explore other sources of food, thus reflecting quite distinct conditions and habitats, which would otherwise be difficult to access (Diamond & Devlin, 2003). When using seabirds as ecological indicators, one should consider quick parameters to measure, sensitive to stress and changes in the ecosystem; these should also be integrative (Iverson et al., 2007). Additionally, to select the most informative parameters one should take into account the time scale, i.e., some parameters might reflect short-term changes such as individual body condition, while others reflect the long-term changes such as population size. We must also take into account the spatial scale, as there are species which forage over a larger spatial scale, such as pelagic seabirds while others are confined to a narrower spatial scale, such as shorebirds, and thus reflect changes in marine ecosystems at a local scale. Demographic, physiological or behavioral parameters can be measured and evaluated, providing information on the ecological status of a particular ecosystem (Piatt & Sydeman, 2007). However, the behavioral and physiological parameters are more sensitive to environmental changes (Durant et al., 2009; Mallory et al., 2010). The population size, breeding success, survival of individuals and feeding and foraging

ecology of seabirds, are some of the parameters used to assess the condition of marine ecosystems (Diamond & Devlin, 2003; Iverson et al., 2007)

1.2. Feeding and foraging ecology of seabirds

Dietary studies provide relevant information on prey abundance at different spatial and temporal scales, evaluate the predator / prey dynamics, assess the degree of niche overlap and competition between species, populations and/or individuals, and investigate individual specialization, among others (Ceia et al., 2015; Weiser & Powell, 2010). Together with complementary data, such information is important to understand the distribution of marine birds, their population dynamics and also the ecosystem structure and its changes over time (Iverson et al. 2007) .

There are several approaches to study the trophic ecology of seabirds (Iverson et al., 2007). For instance, the analysis of stomach contents is a fairly common approach and this can be achieved by using regurgitated items or analysing dead birds. However, both have their disadvantages since both methods contain dietary choices only for the most recent meal, not reflecting the long-term diet, and in the case of dead birds, it eliminates the opportunity of performing a continuous study. Moreover, some prey might be over-represented, due to specific parts that are resistant to digestion (Iverson et al., 2007). Another method often used to reconstruct the diet of seabirds is the analysis of droppings (Barrett et al., 2007), but this is often more limited in the time-scale. The analysis of excrements is useful because it is a non-invasive method and reveals different types of prey that are eaten by birds, but as in regurgitated analysis this does not identify all prey items eaten by the predator, because in this case some are completely destroyed during digestion (Barrett et al., 2007). Currently, molecular biological techniques are increasingly being used to determine seabirds' diet (Barrett et al., 2007), although their relative high cost. However, techniques such as stable isotopes analysis (SIA) are probably the most used nowadays to study foraging and feeding ecology of seabirds, especially when combined with the distribution of the individual tagged with a tracking device (e.g. GPS-logger; (Ceia et al., 2015)). These are robust and powerful techniques, relatively cheap, to examine feeding strategies in seabirds, as they allow the

collection of temporally and spatially structured information (Barrett et al., 2007; Iverson et al., 2007)

1.3. Factors influencing feeding strategies of seabirds

Generally, seabirds are top marine consumers, highly mobile and often exploring the marine environment in extended spatial and temporal scales. Most species reproduce, forage and feed around the most productive marine areas typically characterized by shallow waters, relatively lower sea surface temperatures and higher chlorophyll *a* concentration. These oceanographic characteristics are often present in upwelling areas or convergence zones between different water bodies (i.e. oceanographic fronts), offshore seamounts, neritic and coastal areas, estuarine areas, among others (Monticelli et al., 2007). In general, the most usual prey in the diet of the seabirds are small pelagic fish, squid and crustaceans (Montevecchi & Myers, 1996). However, coastal species such as gulls (i.e. Family Laridae), also feed along the coast and can often turn to estuarine and terrestrial habitats. Most species of gulls have an opportunistic and generalist feeding behavior, which gives them a high plasticity in food demand (Christel et al., 2012; Moreno et al., 2010).

Accounting for factors such as the geographical location of the colony, abundance of resources at sea or the time of year, seagull feeding strategies can differ (Arizaga et al., 2014). For instance, Yellow-legged gulls *Larus michahellis* (hereafter YLG) can pursue for a more marine or terrestrial strategy, in relation to the resources that are available. However, it seems that YLGs adopt a more marine feeding strategy when marine resources are abundant, especially during the breeding season (Alonso et al., 2015; Ceia et al., 2015).

The abundance of marine resources is, among others, related to climatic variation, which can be depicted by climatic indexes such as the North Atlantic Oscillation (NAO) index. The NAO refers to a north–south alternation in atmospheric mass between the subtropical Atlantic and the Arctic, and thus involves out-of-phase behavior between the climatological low-pressure centre near Iceland and the high-pressure centre near the Azores. It is the most robust pattern of recurrent atmospheric behavior in the North Atlantic region, including the Iberian Peninsula. During the positive phase of the NAO index the westerly winds strengthen and move northwards, inducing increased precipitation and sea-surface temperature in

northern Europe and opposite conditions in Southern Europe. During the negative phase of the NAO the storm track is diverged towards southern Europe, leading to an increase in warm conditions, wind speed and vertical water mixing along the Iberian Peninsula and in Southern Europe (Paiva et al., 2013). Local climatic conditions are influenced by the NAO index, and for the Iberian Peninsula there is usually a negative relationship between NAO and sea-surface temperature (SST), although local climatic conditions cannot always be clearly predicted by the NAO (Ramos et al., 2013). So, presumably, NAO can influence seagull feeding strategies. However, depending on the species, and corresponding feeding strategies, gulls can be more or less influenced by climatic oscillations depicted by NAO.

1.4. Feeding strategies of gulls

Gulls, including YLGs, are adapted to capture a high diversity of marine prey such as crustaceans, molluscs, and planktonic organisms, but for most gull species the main prey are fish. However, its flexibility in food demand allows them to further modify their strategies and have access to a large number of food sources of anthropogenic origin, such as bins, surplus fisheries, refuse dumps, agricultural fields, among others (Christel et al., 2012). Thus, there is a large variation in respect of feeding strategies among the different species or populations of gulls, or even among years. These may have a more terrestrial or marine influence depending on the resources available within the foraging area (Ceia et al., 2014). The trophic ecology of gulls may vary seasonally, as gulls display distinct feeding behaviors during the breeding season and the non-breeding season (Ceia et al., 2014). Typically, gulls such as the YLG feed during the day, but some species, such as the Audouin's gull *Larus Audouinii* (hereafter AG), which is regarded as a specialist on epipelagic fish (Mañosa et al., 2004), may feed also at night.

Gulls are typically opportunistic and as such, there are variations in their diet throughout the seasons and the years. Depending on the abundance and availability of food sources, YLGs may have a more specialist or generalist behavior (Ceia et al., 2014). Thus, and due to their plasticity, feeding strategies of YLGs may vary greatly according to the year and/or season and geographic location. An example of consistency in the diet of YLGs during the breeding period arises when the availability of the swimming crab *Polybius henslowii* is very high. According to

Ceia et al. (2014) and Alonso (2015), YLGs prefer to feed mostly on these crabs, demonstrating a high rate of specialization, during years of higher availability of this prey. A study carried out on the coasts of Galicia has shown that the swimming crab *Polybius henslowii* is predominant in the YLG diet and also influences its breeding success (Munilla, 1997).

Studies on the feeding ecology of gulls are largely restricted to the breeding season, when birds are accessible for sampling (Arizaga et al., 2013) . During the breeding season YLGs tend to agglomerate and form large colonies. They forage preferably near the colony, but can travel longer distances (up to 100 km) in search of food (Asello et al., 2010; Ceia et al., 2014). Overall, there little information on the feeding of gulls outside the breeding season, including YLGs, especially during the migratory and wintering seasons (Quillfeldt et al., 2005). During the non-breeding season (i.e. autumn and winter) most gull species such as YLGs use terrestrial food sources, particularly from anthropogenic sources, but also feed in shallow coastal waters and in rocky coasts during low tide (Arizaga et al., 2014; Poot, 2003). However, AG is regarded as an strictly marine species, and its foraging trips to land are extremely rare (Mañosa et al., 2004). In recent decades, there have been some methodologies to address foraging ecology of seabirds, such as SIA, which allow to integrate the trophic information from different seasons (Hobson, 1994). However, the fact that food resources consumed by gulls differ seasonally may have consequences for the consistency of their diet (Ceia et al., 2014).

Owing to their opportunistic and generalist behavior, YLGs tend to explore different locations both on land and sea, using often a mix strategy. These foraging areas can include refuse dumps, agricultural fields, among other anthropogenic food sources which may range from marine origin such as fishery discards or in fishing ports in order to get easier meals. Therefore, YLGs may adopt a marine, mix or a terrestrial strategy depending on extrinsic factors, such as the year (i.e. oceanographic factors), geographic area or prey abundance. However, AGs supposedly present a strictly marine strategy, not venturing to refuse dumps or agricultural fields in search of food (García-Tarrasón et al., 2014).

1.5. The use of SIA and biologging to study the foraging strategies of gulls

The classical techniques to study diet such as analysis of stomach contents, direct observations or collection of prey remains in breeding colonies has some limitations, although they provide an exceptional detail in the identification and measurement of prey items. These techniques, often time-consuming and limited to the breeding period, reflect the diet only during specific time-periods and some types of prey may be under- and/or over-represented. Thus, over the past recent decades, new techniques have been developed and adopted, aiming to complement the information given by more traditional methods such as SIA and biologging (Barrett et al., 2007).

There are several classical techniques that allow us to evaluate the feeding ecology such as the daily visual analysis of the diet and analyses of stomach contents. However, currently there are new techniques to evaluate the feeding ecology individual consistency such as the stable isotope analysis (SIA) and tracking devices. In this way studies on foraging and feeding ecology of seabirds increased substantially since 2000 (Ceia et al., 2015). These new techniques represent a major advance in the study of gulls' foraging ecology, and particularly their feeding strategies.

Stable isotope analysis has been recognized as an important methodology for ecological studies since the mid-80s (Peterson & Fry, 1987). However, only during the 1990s, SIA began to be widely used in trophic ecology studies (Bond & Jones, 2009) The use of stable isotopes in trophic ecology studies is based on two assumptions: firstly, the fact that the ratios of stable isotopes in the tissues of consumers reflect in a predictable way the ratios of isotopes in their prey secondly, the fact that the isotopes present a cumulative performance over the trophic levels in marine (and terrestrial) ecosystems. Stable isotopes most frequently used in studies of trophic ecology in marine ecosystems are nitrogen ($^{15}\text{N}/^{14}\text{N}$; i.e. $\delta^{15}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$; i.e. $\delta^{13}\text{C}$) (Quillfeldt et al., 2005). The use of $\delta^{15}\text{N}$ is based on the trophic enrichment of ^{15}N as it ascends along trophic levels in a predictable manner. Thus, consumers' tissues tend to be enriched in $\delta^{15}\text{N}$ relative to the tissues of their prey typically increasing from 3 - 5‰ in the marine environments (Forero & Hobson, 2003). This increase occurs because the light isotope (i.e. ^{14}N) is preferably excreted when compared with the heavy isotope (i.e. ^{15}N) (Bond & Jones, 2009). On the other hand, the use of $\delta^{13}\text{C}$ is often used as a geographic identifier (i.e. habitat), as there is a typical enrichment of $\delta^{13}\text{C}$ from terrestrial to marine environments, from oceanic

to neritic environments, from lower to higher latitudes, and from pelagic to benthic communities. Typically, $\delta^{13}\text{C}$ levels increase around 1‰ in each trophic level (Catry et al., 2012; Forero & Hobson, 2003; Quillfeldt et al., 2005). Thus, with the analyses of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, it is possible to evaluate the interactions in the trophic chains, the trophic positions of the species and their spatial and temporal variations in the isotopic niches (Forero & Hobson, 2003). Isotopic niche is a space defined by stable isotope values that are placed on each axis in a graph, and through this space as a proxy, it is possible to evaluate the ecological niche.

Seabirds are top predators, consuming a wide variety of prey species. This variation presents a problem in estimating the proportion of each prey item in the consumer's diet, especially for generalist species, because different combinations of prey species and proportions may result in the same isotope signature in the consumer. Thus, it is possible that two individual seabirds which explore two different food sources to present identical stable isotope values. Moreover, many seabird diets overlap during the breeding season when species breed in sympatry (Bearhop et al., 2004) which is the case for YLG and AG in Ria Formosa-Algarve, Portugal. Knowledge about the isotopic composition of the food chain of interest is therefore necessary (Post, 2013). For example, a seagull that feeds mainly in the marine environment, theoretically should present higher $\delta^{13}\text{C}$ value than a seagull feeding on terrestrial resources. However, the consumption of terrestrial food that has in their composition large amount of different plants (e.g. C3 vs C4, or mixture of both) can present very different $\delta^{13}\text{C}$ values. Food webs with a high content of C3 plants in the food web basis present a lower signature with regard to $\delta^{13}\text{C}$, whereas food webs with a high C4 plant content have typically a higher signature (Newsome et al., 2007). When there is a mixture of both, the values of $\delta^{13}\text{C}$ could be on average similar to the value of marine $\delta^{13}\text{C}$. Thus it is necessary to use other types of devices such as GPS loggers that allow us to obtain other data regarding the feeding behavior of gulls, in particular to identify the sources of food consumed.

Through the analysis of different tissues of the same individual, SIA allows obtaining information on trophic ecology at different time scales, because the isotopic value of each tissue reflects the time at which it was synthesized (Bond & Jones, 2009; Forero & Hobson, 2003). Thus, when analyzing different tissues of an individual, it is possible to evaluate its diet at different times of the year, even when it is not commonly accessible, during migration or outside the breeding season (Quillfeldt et al., 2005). Depending on the ecological issue to be evaluated, different types of tissue may be used to perform SIA. The tissues that are most commonly used in seabirds, as non-invasive techniques, are feathers, blood, nails and eggs (Bond & Jones, 2009). These tissues provide great detail of dietary information, without the

need to sacrifice birds to evaluate their diet (Bearhop et al., 2004; Forero & Hobson, 2003). Tissues such as plasma or blood cells have a rapid isotopic turnover rate and will reflect a more recent diet, while tissues with slower isotopic turnover such as muscle will reflect the long-term diet (Hobson et al., 1994). Blood can be centrifuged and red blood cells (RBC) and plasma fractions can be separated, and so its isotopic analysis can be performed separately. Blood cells reflect the diet of the 2-3 weeks and the plasma mainly reflects the diet over the last week (Votier et al., 2010).

SIA allows to evaluate the spatio-temporal variation in the isotopic niche (and hence in the foraging and trophic niche) throughout the seasons and years, thus allowing to reconstruct the history of the diet of a particular individual or population along the year (Hobson et al., 1994). However, like other methodologies, this technique also has some limitations. The main limitations of SIA are related to the lack of knowledge on the fractionation or alteration of stable isotopes in consumer tissues, isotopic composition of prey and regional isotopic gradients (i.e. isoscapes) (Hobson & Clark, 1992).

Tracking devices are efficient techniques used to assess the feeding strategies of seabirds, which in conjunction with SIA can provide powerful data analyses. For instance, with GPS devices, it is possible to record with great precision the position of an individual bird, assessing its foraging behavior and foraging grounds, and inferring the possible food sources. These devices are relatively lightweight, causing no hindrance to the flight or any other task performed by the bird. Potentially, it is possible to assess several key parameters such as the duration of each trip, geographic positions, nature of the trip, namely whether it was a marine, mix or terrestrial trip, among others. So, the use of SIA associated with tracking devices should be a powerful technique to assess the foraging and feeding strategies of gulls (Bouten et al., 2013; Caron-Beaudoin et al., 2013; Ceia et al., 2014)

1.6. Objectives

The main goal of this study was to investigate how relevant is the marine, mix and terrestrial strategies for the YLGs. For that, both SIA and biologging techniques were applied conjunctly across 2011-2016, in two different populations of YLGs (i.e. Berlenga and Deserta

Islands). Moreover, the same methodology was applied in AGs at Deserta Island (where both species breed in sympatry), which were used as indicators of a strictly marine strategy. Specifically, this study addresses the following issues:

- Are the population of marine gull strategists consistent in the long term (i.e. across years)?
- Will the isotopic niche of marine gull strategists be narrower than that of mix and terrestrial strategists?
- Which factors may determine a more marine/terrestrial strategy adopted by yellow-legged-gulls?

This study will address the extent to which the extreme plasticity of YLGs allows individuals (from both populations) to respond to inter-annual variations during the breeding period, namely in their foraging strategies. It is expected that foraging strategies adopted by YLGs could vary annually according with oceanographic processes, supposedly leading to different marine prey availability. It is also expected that YLG marine strategists have a similar isotopic niche to those presented by AGs.

2. Material and Methods



2.1. Study sites

Fieldwork was carried out in two distinct sites (Berlenga and Deserta Islands). In Berlenga Island, data was gathered yearly on YLG between 2011 and 2016, and in Deserta Island on both YLG and AG in 2015 and 2016.

Berlenga Island is part of the natural reserve of Berlengas archipelago and is located 11 km off the western Portugal coast, Carvoeiro Cape, near the city of Peniche. Berlengas archipelago is made up of 3 sets of small islands: Berlenga Grande (i.e. Berlenga Island), Estelas and Farilhões. Considered a UNESCO World Biosphere Reserve since 30 June 2011, this archipelago has a great biological and ecological value. It comprises a vast marine reserve area with about 104 ha of land and 9456 ha of marine area. The archipelago is located on the continental shelf of the west front of the Iberian Peninsula being largely influenced by the Atlantic in the northern and northwestern areas and by the Mediterranean, especially in the southern and southeastern regions. Due to the climatic and geographical characteristics, this archipelago has presents unique terrestrial and marine habitats. Berlenga Island is the largest of the archipelago and the only one that is inhabited. In total it has about 78.8 ha, with 1.5 km length, 0.8 km width and a maximum height of 85 m. The Berlengas Nature Reserve is an important nesting area for seabirds, among which are Cory's shearwater (*Calonectris borealis*), European shag (*Phalacrocorax aristotelis*), common murre (*Uria aalge*; virtually extinct), Madeiran storm petrel (*Hydrobates castro*), yellow-legged gull (*Larus michahellis*) and some breeding pairs of lesser black-backed gull (*Larus fuscus*). At Berlenga Island, YLG has the largest breeding population of the Portuguese coast, with about 16000 nesting birds, and is the dominant species throughout the year in the island (ICNF, 2016 pers. comm.).

Deserta (or Barreta) Island belongs to the Ria Formosa Natural Park in the Algarve. Ria Formosa is situated in the eastern Algarve encompassing an important lagoon area, covering an area of about 18 000 ha, and a group of 5 barrier-islands (including Deserta Island) and two peninsulas, that separate the lagoon from the Atlantic Ocean. This barrier-island system (from west to east) is composed by the Ancão peninsula (Faro beach), the Deserta, Culatra, Armona, Tavira and Cabanas islands, and Cacela peninsula. These barrier islands (composed exclusively by sand) are constantly changing due to the dynamic inlets that separate them. Ria Formosa is a very dynamic ecosystem and islands have different characteristics depending on whether they meet west or east of the Cape of Santa Maria located in Deserta Island (Ceia et al., 2010).

This barrier-island system is characterized by an extension of beaches and dunes that protect the lagoon. The Ria Formosa Natural Park is home to a wide variety of habitats that include: barrier-islands, salt marshes, sand and basin, dunes, freshwater and brackish ponds, water courses, agricultural areas and forests. These distinct habitats lead to an enormous diversity of flora and fauna in the region. The human presence accompanies the Ria Formosa in all its extension, materializing in small clusters or in cities, but is almost absent on Deserta Island. About 14% of the lagoon surface is permanently submerged and about 80% of the bottoms emerge during low tide conditions, which averages in depth around 2 m. Ria Formosa is fed almost exclusively by the ocean since the rivers that flow into it are small and of seasonal characteristics. This system is characterized by a semi-arid Mediterranean climate with a prolonged dry season during the summer months.

The breeding seabird community is characterized by YLGs, AGs and little terns (*Sternula albifrons*). The presence of some domestic cats (*Felis catus familiaris*) introduced by humans, is a threat to breeding birds, particularly little terns. There are two distinct sub-colonies of YLG distanced by ca. 400 m, one on each side of the walkway, and two sub-colonies of AG distanced by ca. 200 m that are separated from each other by a dune.

2.2. Study species

2.2.1. Yellow-legged gull (YLG) *Larus michaellis*

Yellow-legged gull (YLG) *Larus michaellis* (Naumann, 1840), is a coastal seabird belonging to the order Charadriiformes and the family Laridae. There are no marked morphological differences between the sexes, although males are in average slightly larger and heavier than females (Arizaga et al., 2010). The breeding period starts in April and lasts until the mid-June. Both parents participate in the incubation (usually three eggs), which lasts approximately 30 days, and feeding the chicks. The emancipation of juveniles occurs after 35 to 40 (Ouarab et al., 2009; Ramírez et al., 2010)

Typically, this species forms large colonies during the breeding season, but in some cases there may be some dispersion in situations where food sources are unpredictable

(Arizaga et al., 2010). It has a preference for coastal habitats; however, due to its opportunistic behavior and great adaptive and competitive plasticity, it has the capacity to colonize several habitats, such as estuaries and inland water bodies. It can be found breeding in urban environments, particularly in coastal cities. In recent decades, the populations of this species have prospered in a notorious way, so much that in many places they reached a status of pest species (Oro & Mart, 2007; Skórka et al., 2005) and their populations are often object of control such as in Berlenga Island with the culling of the eggs. It is resident in much of southern Europe (including Portugal), on the Mediterranean coast, in the Black Sea and Caspian Sea, and in the islands of the Canaries, Selvagens, Madeira and Açores. Its wintering sites include the coast of Southwest Asia, most of the European coast, and the coast of Africa (BirdLife International, 2011). In mainland Portugal this species can be found throughout the coast, and its main nesting site occurs on the island of Berlenga, where there is a colony with nearly 8000 breeding pairs. It is also common in the islands of the Azores and Madeira, where the colonies are increasing substantially (Ramírez et al., 2010).

Yellow-legged gull is an opportunistic species, with an omnivorous feeding behavior and the capacity to feed on a great variety of resources (both from marine and terrestrial origins). These animals are extremely versatile in the search for food, which allows them to explore different habitats both on land and at sea, thus highly increasing the potential food sources. As top-level generalist predators, YLGs have the ability to capture various types of prey, from fish near shore, marine and terrestrial invertebrates, small mammals, small reptiles and even other seabirds. Usually, during the breeding seasons, eggs of other birds and offspring recently hatched can be also preyed (Matias & Catry, 2010). Additionally, litter from refuse dumps is also often consumed (Ceia et al., 2014). These birds also practice the so-called kleptoparasitism, that is, they frequently steal food from other animals (Oro & Mart, 2007). With the increasing pressure of the human population and the reduction of available natural resources, YLGs are increasingly foraging for food sources of anthropogenic origin, such as dumps, discharges from fishing activity, among others (Matias & Catry, 2010). These anthropogenic food sources decisively influence positively the dynamics of some populations of YLG, influencing for instance the survival of immature individuals, reproductive success, geographical distribution patterns, and changing the expected mortality rates. It is known that the availability of food resulting from human activity leads to an increase in the populations of this species (Ramos et al., 2009). Due to a rich protein/energy content, these anthropogenic food sources allow YLGs to have a higher survival rate. However, an exclusively anthropogenic food source diet could be deficient of essential nutrients necessary for a healthy development

of these birds, especially during the breeding period, where marine prey is often preferred (Ceia et al., 2014). It should also be noted that YLG's diet can vary considerably according with geographical location and distance from the main sources of food (Arizaga et al., 2010).

2.2.2. Audouin gull (AG) *Larus audouinii*

The Audouin gull (AG) *Larus audouinii* (Payraudeau, 1826) is a medium-sized bird, smaller, and slender than YLG. Like YLGs, this species shows slight morphological sexual dimorphism, with males about 20% larger than females. As in other gull species, juveniles present the typical brown-spotted plumage, distinguishing from the adults by the U-shaped white spot on the uropygium. It is estimated that the world's population of AG is about 22,000 pairs, 90% of which nest in Spain. During the winter, this species migrates to the north and west coast of Africa (BirdLife International, 2012, 2014). Although it is currently classified as Vulnerable by the Portuguese Red Book of Vertebrates, in recent years there has been an increase in the Portuguese population of AG at Deserta Island.

Audouin gulls are colonial seabirds, normally reproducing in rocky cliffs, small islands or coastal areas. Colonies can be composed by a few individuals to 10,000 pairs. The distribution of AG is almost exclusively confined to the Mediterranean basin including southern Portugal, although limited to breed in Deserta Island (BirdLife International, 2014). Thus, its general distribution is much more restricted compared to that of YLG, and this species essentially exploit marine environments, contrasting with the mixed strategy (i.e. both terrestrial and marine environments) of YLGs (BirdLife International, 2014). Contrasting with YLG, which has a more diversified diet, AG presents a diet mostly based on fish and cephalopods, foraging most exclusively in the marine environment and more offshore than YLGs. The studies carried out on the feeding strategies of AGs suggest that most fish is opportunistically caught from fishing discards by local fishing fleets, especially fish of low commercial value, although they can adopt both natural and opportunistic (i.e. in association with fisheries) feeding strategies (García-Tarrasón et al., 2014; Navarro et al., 2010).

2.3. Sampling procedures

On Berlenga and Deserta Islands, sampling was performed yearly over six (2011-2016) and two years (2015-2016), respectively, during approximately two weeks in May/June, i.e. during the incubation stage of the breeding season of both species. A total of 105 individuals of YLG were sampled in Berlenga Island, and 54 individuals of both YLGs and AG were sampled in Deserta Island (27 individuals of each species) for isotopic analyses. In total, 159 individuals from both species and locations were captured and sampled throughout 2011-2016 (see Table 1 and 2). In addition, GPS loggers were deployed in a total of 47 individuals from both gull species (from which 45 were sampled for isotopic analyses) throughout the study period (see Table 3 and 4), and removed after 5.4 (± 3.0) days during recapture. Adults with 3 egg clutches were chosen randomly and trapped by setting square traps over their nests during both capture and recapture procedures. Individuals caught in the traps were ringed and body mass (to the nearest 10 g), wing (to the nearest 1 mm) and tarsus length (to the nearest 0.1 mm) were measured. Blood samples (ca. 0.5 ml from the tarsal vein) were collected from each bird using 27G needles and, within 2 to 3 h, separated into plasma and blood cells (BC) using a centrifuge (15 min at $1250 \times g$), and then stored frozen until isotopic analyses. All the process of capture, sampling and release took around 10 minutes, thus minimizing the overall stress to the animal.

2.4. Stable isotope analysis

Because high lipid concentrations in plasma can lead to depleted $\delta^{13}\text{C}$ values, lipids were removed using successive rinses in a 2:1 chloroform-methanol solution (Cherel et al., 2003). The low lipid content of whole blood (or RBC) does not typically require lipid extraction (Cherel et al., 2003). The carbon and nitrogen stable isotopic composition of the blood samples were determined using a Flash EA1112 Series elemental analyser coupled on line via Finnigan conflo II interface to a Thermo Delta V S mass spectrometer. Approximately 0.3 mg of each sample was combusted in a tin cup for the simultaneous determination of nitrogen and carbon isotope

ratios. Isotope ratios are presented in the usual δ notation based on the Vienna-PeeDee Belemnite (V-PDB) for carbon and atmospheric N₂ (AIR) for nitrogen, and expressed as ‰. $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$, where $R = {}^{13}\text{C} / {}^{12}\text{C}$ or ${}^{15}\text{N} / {}^{14}\text{N}$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate precision <0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Different tissues present different values, also reflecting the temporal changes, the trophic position and the abundance of available resources in the habitat (Newsome et al., 2007). The $\delta^{13}\text{C}$ values typically reflect the consumer's use of the habitat / resource, while the $\delta^{15}\text{N}$ values reflect the trophic level of the consumers. The complete turnover rate of plasma in birds is high (ca. 20 days), with a half-life of components of around 3 days, thus plasma retaining diet information during the last week before sampling (and during tracking for birds equipped with a GPS), while RBC retains information up to 3 to 4 weeks (Hobson & Clark, 1992), representing the diet of individuals from the incubation and pre-laying period, respectively.

2.5. GPS Tracking

Overall 47 breeding adults were equipped with GPS loggers (CatTraq GT-120, Perthold Engineering LLC) to assist in the definition of the terrestrial, mix and marine strategies adopted by gulls of both species and colonies during the different years. The total mass of the device (17 g) was between 1.3 and 2.6% in YLGs and 2.2 and 3.2% in AGs of adult mass. The GPS loggers were attached to feathers in the mantle region with Tesa® tape, and set to record position (median error of <10 m) every 2 min, in order to have a detailed report of the gulls' movements.

2.6. Data analyses (statistical analyses)

Although plasma samples were all delipidated using a 2:1 chloroform-methanol solution, some samples (i.e. 84 samples) still showed mass ratios higher than the 3.5 threshold which correspond to a low lipid concentration in tissue. Thus, the method suggested by Post et al. (2007) was used to normalize the $\delta^{13}\text{C}$ values of the samples with > 3.5 C:N according to the formula:

$$\delta^{13}\text{C normalized} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \times \text{C:N}$$

SIA results were then compared among years and study areas using an ANOVA or a Kruskal Wallis test, depending on the distribution of the data. To test the homogeneity of variances in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which provides a measure of niche width (see Bearhop et al., 2004 for more details), we used Levene's test. However, to analyse stable isotope data in the context of isotopic niche width between years and among seasons and periods, we adopted the recent metrics based in a Bayesian framework (Stable Isotope Bayesian Ellipses in R: SIBER; Jackson et al. 2011), which allows for robust statistical comparisons. The area of the standard ellipse (SEAc, an ellipse obtained by Bayesian inference that contains 40 % of the data regardless of sample size and corrected for small sample sizes) was adopted to compare niche width between species, years, colonies and strategies, and a Bayesian estimate of the standard ellipse and its area (SEAB) to test whether there are differences among these groups. The convex hull area (TA) (Layman et al., 2007), although much more sensitive to sample size, was also employed to compare among groups. We used the computational code to calculate the metrics from SIBER implemented in the package SIAR (Parnell et al. 2010) under R 2.15.2.

GPS data were separated into individual foraging trips. GPS locations at the colony were excluded from the analyses, and we defined foraging trips from the time the birds departed from the colony until their return. All trips with less than 15 minutes duration were withdrawn (Ceia et al., 2014). Foraging trips were classified according with the strategy adopted, i.e. marine, mix or terrestrial. This was performed according with the destination of the trip, and thus the potential resource use during that foraging trip (i.e. diet). Hence, foraging trips to the sea, harbours, beaches and lagoon, were classified as marine. On the other hand, trips to the treatment stations, fields, dumps, salinas and dams were classified as terrestrial. Trips with a

portion of both strategies were classified as mix. This analysis was performed using excel, QGIS 2.18.0 and Google Earth that allowed to verify specifically all the points of the foraging trips.

The nonparametric fixed kernel density (FKD) estimator was used to calculate the 25, 50, 75 and 95% density contour areas of each individual gull using functions ('kernelUD', 'getvolumeUD', 'getverticeshr' and 'kernel.area') of the adehabitat package ($h = 0.03$, grid = 500; Calenge 2006) under R 2.15.2. Although areas were statistically analyzed per individual, maps showing the kernel densities are presented per year for better representation using QGIS 2.18.0.

A set of 13 variables based on GPS data were chosen to assess the strategy of individual gulls across years. Our tracking variables were estimated for each individual with a GPS logger and they were composed by the (1) total time of tracking (days); (2) trip duration; (3) maximum latitude (degrees); (4) maximum longitude (degrees); (5) maximum distance from colony (km); (6) cumulative distance travelled (km); (7) number of trips per day (total) (8) number of trips at sea (%); (9) number of trips at both sea and land (i.e. mix) (%); (10) number of trips at land (%) (11) time at sea (%) (12) time at land (%) and (13) time at colony (%). Variables 2 to 6 were calculated for each foraging trip and means were then calculated for each individual. All data were tested for normality and homoscedasticity and the variables (8-13) were arcsine transformed. All variables were compared among years within each colony using an ANOVA or a Kruskal Wallis test. These analyses were performed using STATISTICA 7.

For this study, GPS data from Berlenga's YLGs (2011-2016) and Deserta's YLGs and AGs (2015-2016) were used. For AG we were not able to collect tracking data in 2016, but GPS data from 2015 corroborate that this species was almost exclusively marine, with only 3 out of 91 foraging trips to a terrestrial feature, specifically a water treatment station (to rest and presumably drink fresh water). In line with the aim and hypotheses of this study, AGs were used only as an indicator of marine strategy use and tracking data corroborated this expectation (see results). A feeding strategy was defined for each YLG (i.e. marine, mix or terrestrial strategy) with GPS data. This was performed based on the cumulative time spend at sea, which corresponds to all the foraging trips with a marine strategy plus the marine strategy adopted during the mix foraging trips, and the cumulative time spend on land, which corresponds to the all the foraging trips with a terrestrial strategy plus the terrestrial strategy adopted during the mix foraging trips, of each individual (variables 11 and 12). If the proportion of time spend at sea or at land was higher than 0.66, a marine and terrestrial strategy was assumed, respectively. In the other hand, if this proportion was between 0.33 and 0.66, the strategy adopted by the individual was considered as mix. This categorization was supported with the histogram of frequencies of time spent at sea and land during foraging

trips of each individual (see Fig. 1, in appendix). Subsequently, a discriminant analysis was performed to define a strategy for all YLGs individuals based on their isotopic values. For this analysis only birds with more than 3 days tracking record were used. Hence, the isotopic signature of plasma on recapture was largely representative of diet during the trips in which each bird was tracked, according to plasma's turnover rate (Hobson & Clark, 1992). Additionally, two individuals with more than 3 days of tracking record but no corresponding isotopic values were discarded from the analysis. This resulted in a total of 30 YLG individuals used in the discriminant analysis to assess the strategy (i.e. marine, mix or terrestrial) of the remaining 102 individual YLGs with a plasma isotopic value (including the 9 birds with less than 3 days tracking period). The strategy was used as the grouping variable and both plasma $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as independent variables. The option 'same for all groups' was adopted as a priori classification probabilities. Then probability indicating the strategy adopted by each individual based on its isotopic values was calculated. This model was highly significant ($F_{4,52} = 9.0$, $p < 0.001$), with an overall error (i.e. the definition of the strategy) of only 16.7% corresponding to 5 out of 30 individuals identified as being poorly categorized (from which 60% marine, 20% mix and 20% terrestrial).

To assess correlations between the variables, these were accordingly separated into explanatory and response variables. The explanatory variables included NAO and tracking variables. Two groups were selected within the tracking variables according to their nature (i.e. by trip or by individual). In the first group, the maximum distance from colony (Km), cumulative distance traveled (Km) and variables resulted from Kernel analyses were included. In the second group, number of trips at sea (%), number of trips at both sea and land (i.e. mix) (%), number of trips at land (%), time at sea (%), time at land (%) and time at colony (%). On the other hand, response variables included plasma $\delta^{13}\text{C}$, plasma $\delta^{15}\text{N}$, SEAc, TA, SEA.B, terrestrial strategy, mix strategy and marine strategy. The correlations between the explanatory and response variables were addressed per year using the overall annual value for the variables: NAO, SEAc, TA, SEA.B, terrestrial strategy, mix strategy and marine strategy, and were performed per individual wherever individual values were obtained for the variables: plasma $\delta^{13}\text{C}$, plasma $\delta^{15}\text{N}$, maximum distance from colony (Km), cumulative distance traveled (km), number of trips at sea (%), number of trips at both sea and land (i.e. mix) (%), number of trips at land at sea (%), time at land (%) and time at colony (%). These analyses were performed using STATISTICA 7.

3. Results



3.1. Isotopic values of YLGs and AGs at Berlenga and Deserta Islands

In Berlenga Island, the $\delta^{13}\text{C}$ values for the 107 YLGs analysed varied between -24.7 and -17.7 ‰ (-18.9 ‰ \pm 0.9) in plasma and between -21.6 and -17.8 ‰ (-19.1 ‰ \pm 0.7) in RBC (Table 1). In 2013, this population showed the lower values in the mean plasma $\delta^{13}\text{C}$ values (i.e. -20.6 ‰), but also the highest standard deviation (i.e. 2.0 ‰) that was also observed in RBC standard deviation $\delta^{13}\text{C}$ values (i.e. 1.3 ‰) (table 1). Important to note that in 2013 was also the year with the lowest number of individuals analyzed (i.e. 6 individuals). The $\delta^{15}\text{N}$ values ranged from 10.0 to 15.5 ‰ (12.7 ‰ \pm 1.2) in plasma and from 9.3 to 14.8 ‰ (12.1 ‰ \pm 1.2) in RBC. In 2014 was the year in which plasma $\delta^{15}\text{N}$ values were higher with mean values of 13.4 ‰ and lower standard deviation (\pm 0.5).

Table 1 *Larus michahellis*. Stable isotopic values of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) of plasma and red blood cells (RBC) of yellow-legged gulls between 2011 and 2016, and total at Berlenga Island, West Portugal. Upper letters indicate the significant differences between years according to a Kruskal-Wallis test, followed by for multiple comparisons. Values are means \pm SD. For more details on statistical results and min-max values, see table I in appendix.

	<i>Larus michahellis</i> (Berlenga)						
	2011 (N=26)	2012 (N=26)	2013 (N=6)	2014 (N=18)	2015 (N=9)	2016 (N=22)	Total (N=107)
$\delta^{13}\text{C}$ (‰) Plasma	-18.9 \pm 0.8 ^a	-18.7 \pm 0.5 ^b	-20.6 \pm 2.0 ^{abc}	-18.4 \pm 0.4 ^{cd}	-18.8 \pm 0.3	-19.1 \pm 0.7 ^d	-18.9 \pm 0.9
$\delta^{15}\text{N}$ (‰) Plasma	12.9 \pm 1.5	12.2 \pm 1.0 ^a	12.4 \pm 1.9	13.4 \pm 0.5 ^{ab}	12.0 \pm 0.9 ^b	12.7 \pm 1.1	12.7 \pm 1.2
$\delta^{13}\text{C}$ (‰) RBC	-19.3 \pm 0.7 ^{ac}	-19.2 \pm 0.6 ^b	-19.1 \pm 1.3	-18.6 \pm 0.6 ^{abd}	-18.5 \pm 0.2 ^{ce}	-19.5 \pm 0.7 ^{de}	-19.1 \pm 0.7
$\delta^{15}\text{N}$ (‰) RBC	12.7 \pm 1.4 ^a	11.4 \pm 1.1 ^{ab}	11.6 \pm 1.2	12.5 \pm 0.9 ^b	11.7 \pm 0.7	12.0 \pm 1.2	12.1 \pm 1.2

In Deserta Island, $\delta^{13}\text{C}$ values for the 27 YLGs analysed varied between -21.4 and -15.7 ‰ (-18.0 ‰ \pm 1.1) in plasma and between -20.4 and -16.4 ‰ (-18.0 ‰ \pm 0.8) in RBC (Table 2). The $\delta^{15}\text{N}$ values ranged from 9.4 to 14.8 ‰ (13.2 ‰ \pm 1.2) in plasma and from 9.6 to 13.9 ‰ (12.5 ‰ \pm 1.0) in RBC (Table 2). For AGs, $\delta^{13}\text{C}$ values for the 27 YLGs analysed varied between -19.4 and -17.7 ‰ (-18.5 ‰ \pm 0.4) in plasma and between -19.0 and -17.5 ‰ (-18.3 ‰ \pm 0.3) in RBC (Table 2). The $\delta^{15}\text{N}$ values ranged from 11.5 to 13.7 ‰ (12.9 ‰ \pm 0.5) in plasma and from 11.7 to 13.1 ‰ (12.4 ‰ \pm 0.3) in RBC (Table 2). Note that in all parameters, the standard deviation of stable isotopic values is smaller in the AGs than in the YLGs. No differences between the years were found for both species in mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of plasma and RBC (Table II, appendix).

Table 2: *Larus michahellis* and *Larus Audouinii*. Stable isotopic values of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) of plasma and red blood cells (RBC) of yellow-legged gulls by year (2015-2016) and total at Deserta Island, South of Portugal. Values are means \pm SD. For more details on statistical results and min-max values, see table II in appendix.

	<i>Larus michaellis</i> (Deserta)			<i>Larus Audouinii</i> (Deserta)		
	2015 (N=12)	2016 (N=13)	Total (N=27)	2015 (N=15)	2016 (N=12)	Total (N= 27)
$\delta^{13}\text{C}$ (‰) Plasma	-18.0 \pm 0.5	-18.0 \pm 1.4	-18.0 \pm 1.1	-18.6 \pm 0.4	-18.5 \pm 0.3	-18.5 \pm 0.4
$\delta^{15}\text{N}$ (‰) Plasma	13.2 \pm 0.5	13.3 \pm 1.7	13.2 \pm 1.2	12.8 \pm 0.5	13.0 \pm 0.4	12.9 \pm 0.5
$\delta^{13}\text{C}$ (‰) RBC	-18.2 \pm 0.5	-17.9 \pm 1.0	-18.0 \pm 0.8	-18.2 \pm 0.3	-18.3 \pm 0.3	-18.3 \pm 0.3
$\delta^{15}\text{N}$ (‰) RBC	12.3 \pm 0.7	12.7 \pm 1.2	12.5 \pm 1.0	12.4 \pm 0.3	12.3 \pm 0.4	12.4 \pm 0.3

3.2. Foraging behavior of gulls at Berlenga and Deserta Islands

The foraging parameters obtained from the 30 individuals of YLGs over the 6 years of study (2011-2016) in Berlenga Island showed that in 2016 more trips were performed per day (i.e. 4.2. trips/day), contrasting with 2013 when only 1.8 trips per day were performed. In 2012 the duration of the trips was, on average, 0.33 days, in contrast to 2016, the year in which the duration of the trips was shorter (i.e. 0.02 days) (Table 3). It is also important to note the difference between the values of the maximum distance traveled in each year, which were higher in 2013 (i.e. 21.0 Km) and lower in 2016 (i.e. 1.7 Km), as well as the difference between cumulative distance values, also larger in 2013 (i.e. 57.2. Km) and lower in 2016 (i.e. 4.2. Km) (Table 3).

Table 3: *Larus michahellis*. Foraging parameters derived from GPS data of yellow-legged gulls breeding in Berlenga Island, West Portugal, between 2011 and 2016, and in total. Values are means \pm SD. For more details on statistical results and min-max values, see table III in appendix.

	<i>Larus michahellis</i> (Berlenga)						
	2011 (N=4)	2012 (N=7)	2013 (N=6)	2014 (N=5)	2015 (N=4)	2016 (N=4)	Total (N=30)
Tracking days_total	5.7 \pm 2.3	3.8 \pm 2.1	3.0 \pm 1.1	6.1 \pm 2.6	4.4 \pm 0.5	2.9 \pm 1.0	4.2 \pm 2.1
Trip duration (days_mean)	0.19 \pm 0.03	0.33 \pm 0.53	0.18 \pm 0.11	0.09 \pm 0.04	0.15 \pm 0.02	0.02 \pm 0.01	0.18 \pm 0.27
Trips/day (total)	1.89 \pm 0.17	3.87 \pm 3.18	1.82 \pm 0.47	2.60 \pm 0.66	1.78 \pm 0.21	4.23 \pm 0.83	2.76 \pm 1.81
Latitude max (mean)	39.37 \pm 0.09	39.38 \pm 0.03	39.41 \pm 0.10	39.40 \pm 0.04	39.39 \pm 0.04	39.4 \pm 0.00	39.4 \pm 0.06
Longitude max (mean)	-9.40 \pm 0.05	-9.46 \pm 0.11	-9.39 \pm 0.20	-9.46 \pm 0.05	-9.49 \pm 0.12	-9.50 \pm 0.01	-9.45 \pm 0.11
Max distance (mean)	14.2 \pm 4.8	11.7 \pm 8.2	21.0 \pm 9.4	10.7 \pm 6.2	16.5 \pm 4.9	1.7 \pm 0.5	13.0 \pm 8.6
Cumulative distance (mean)	42.1 \pm 9.5	37.5 \pm 26.9	57.2 \pm 23.0	32.2 \pm 19.1	50.2 \pm 10.9	4.2 \pm 1.2	38.4 \pm 24.0

In Deserta Island, AGs showed higher trip duration (i.e. 0.19 days) than YLGs during both years (table 4). YLGs performed more trips per day in 2015 with an average of 3.08 trips per day (Table 4).

In general, YLGs made more trips per day than AGs (i.e. 2.21 trips per days). In 2016 the maximum distance of YLGs was higher (i.e. 11.1 Km) than in 2015, but when comparing the values between species, AGs show a greater average of maximum distance values (i.e. 14.9 Km) than the YLGs. The same pattern was present in the cumulative distance (Table 4).

Table 4: *Larus michahellis* and *Larus Audouinii*. Foraging parameters derived from GPS data of yellow-legged gulls breeding in Deserta Island, South Portugal, between 2015 and 2016, and in total, and foraging parameters derived from GPS data of Audouinii gulls breeding in Deserta Island, South Portugal in 2015. Values are means \pm SD. For more details on statistical results and min-max values, see table IV in appendix.

	<i>Larus michahellis</i> (Deserta)			<i>Larus Audouinii</i> (Deserta)
	2015 (N=6)	2016 (N=5)	Total (N=11)	2015 (N=6)
Tracking days_total	6.6 \pm 2.4	9.7 \pm 5.0	8.0 \pm 4.0	6.9 \pm 1.3
Trip dur (days_mean)	0.09 \pm 0.02	0.12 \pm 0.03	0.11 \pm 0.03	0.19 \pm 0.04
Trips/day (total)	3.08 \pm 1.37	2.24 \pm 0.35	2.70 \pm 1.09	2.21 \pm 0.47
Lat max (mean)	36.97 \pm 0.04	37.00 \pm 0.02	36.99 \pm 0.04	36.98 \pm 0.04
Long max (mean)	-7.89 \pm 0.09	-7.87 \pm 0.04	-7.88 \pm 0.07	-7.81 \pm 0.07
Max dist (mean)	9.0 \pm 4,7	11.1 \pm 6.6	10.0 \pm 5.5	14.9 \pm 2.9
Comul dist (mean)	25.2 \pm 11.1	28.8 \pm 19.6	26.9 \pm 14.8	48.8 \pm 12.5

3.3. Spatial patterns and habitat selection

In Berlenga Island, we documented a total of 311 foraging trips from 30 individuals (2011: 42 trips of 4 individuals, 2012: 79 trips of 7 individuals, 2013: 31 trips of 6 individuals, 2014: 78 trips of 5 individuals, 2015: 31 trips of 4 Individuals, 2016: 50 trips of 4 individuals). Overall, the spatial patterns of selection of foraging habitat differed among the years of study. For example in 2011 and 2013 individuals showed a greater urge to travel to land, with more core foraging areas (i.e. 25 and 50%) within terrestrial habitats (Fig. 1A and Fig. 1C). On the other hand, in 2014, 2015 and 2016 gulls' overall preferred habitat was at sea (Fig. 1D, Fig. 1E and Fig. 1F). In 2016 YLGs foraged at sea mostly near to the colony, only with some trips to the port of Peniche (Fig. 1F).

YLGs then used different foraging sites in different years. In the years 2011 and 2013 individuals explored more terrestrial habitats such as dumps and landfills (Marinha grande and Cadaval) (Fig. 1A and Fig. 1C). In 2012 and 2014 despite some trips to land, they engaged mostly on core areas at sea (Fig. 1B and Fig. 1D). In 2015 and 2016, the YLGs foraged almost exclusively at sea or looked for trawls in ports (Fig. 1E and Fig. 1F).

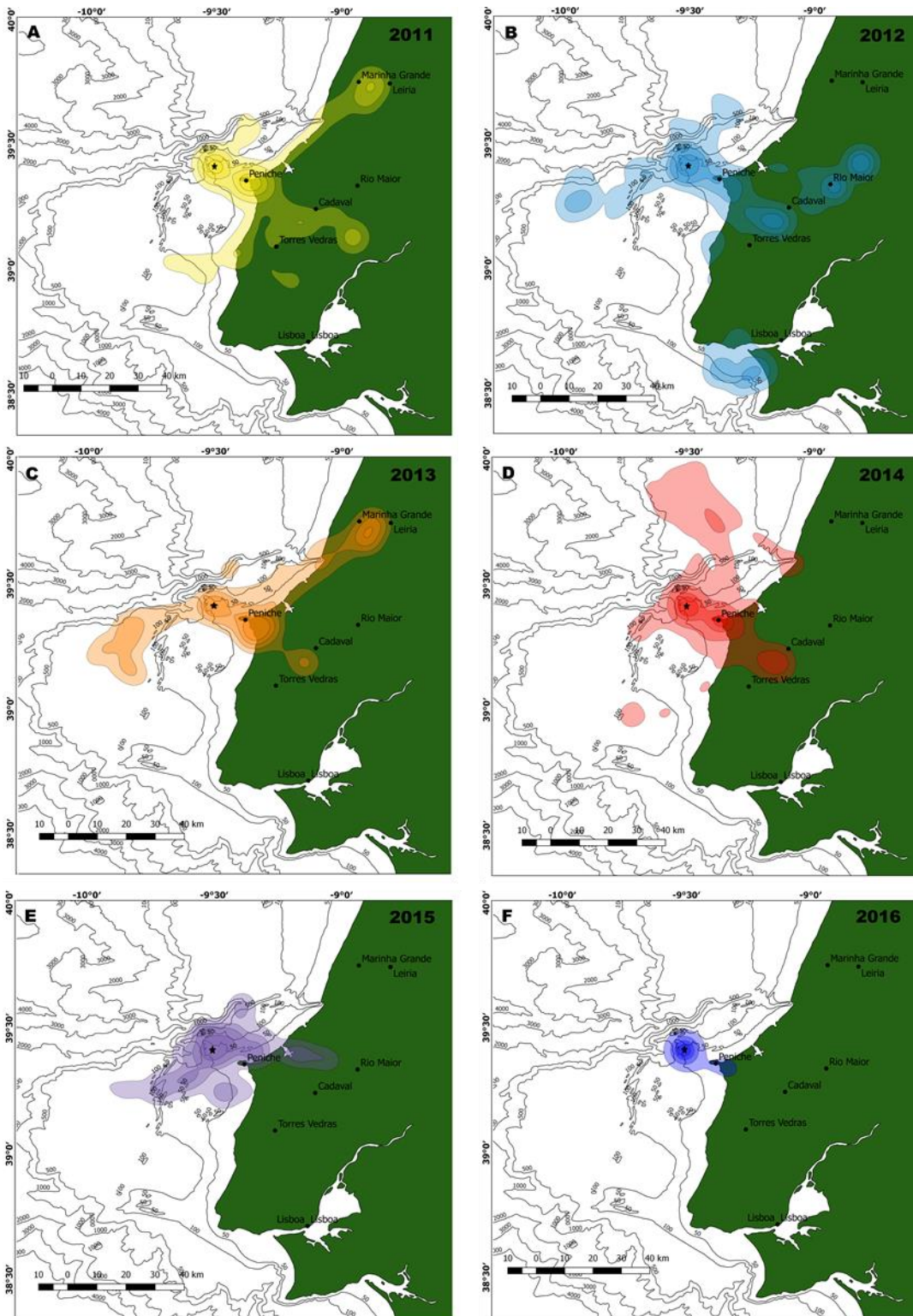


Figure 1: *Larus michahellis*. Foraging distributions of yellow-legged gulls from Berlenga Island during the incubation period in (A) 2011, (B) 2012, (C) 2013, (D) 2014, (E) 2015 and (F) 2016. Decreasing kernel polygon shades represent 25, 50, 75 and 95% foraging home ranges. Star indicates the location of the colony

At Deserta Island, it was documented a total of 240 foraging trips of 11 individuals of YLGs (2015: 136 trips of 6 individuals, 2016: 104 trips of 5 individuals) and 91 trips of 6 individuals from AGs in 2015. In 2015, YLGs used more core foraging areas at sea (Fig. 2A) than in 2016, where, the Loulé refuse dump was visited (Fig. 2B) by one individual. On the other hand, AGs showed a strictly marine habitat use corroborating their marine feeding strategy (Fig. 2C).

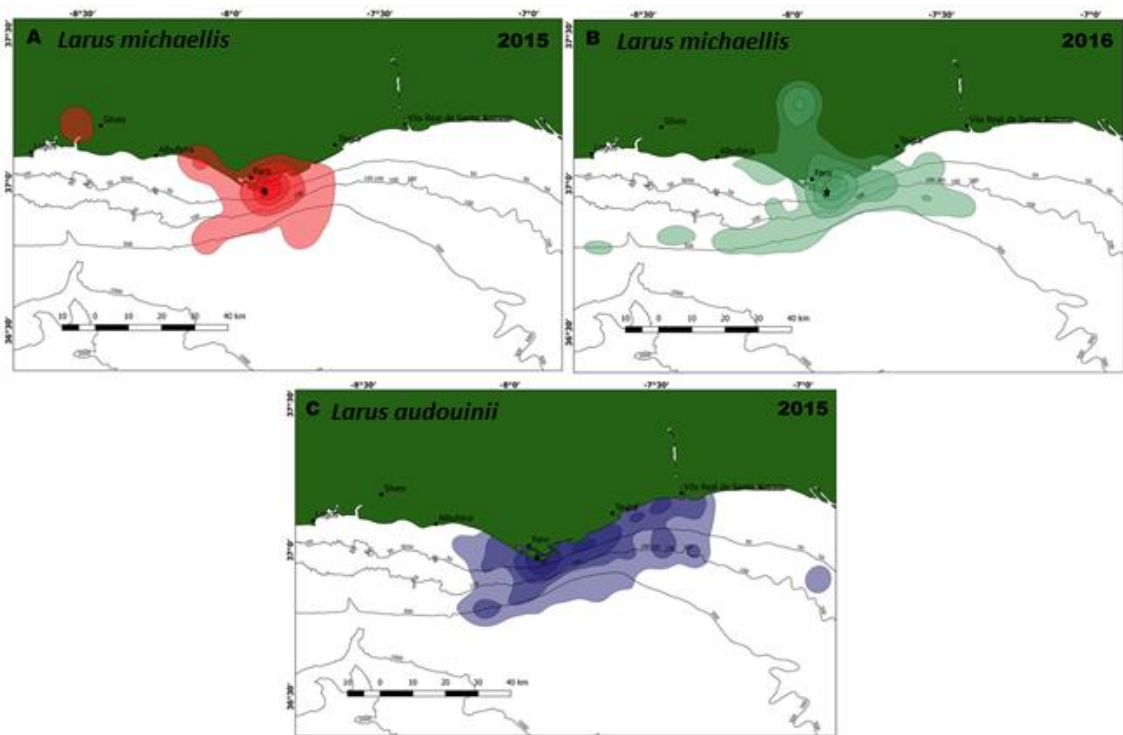


Figure 2: *Larus michaellis* and *Larus Audouinii*. Foraging distributions of yellow-legged gulls in (A) 2015 and (B) 2016, and Audouinii gulls in (C) 2015 from Deserta Island during the incubation period. Decreasing kernel polygon shades represent 25, 50, 75 and 95% foraging home ranges. Star indicates the location of the colony

3.4. Foraging strategies of YLGs

Seagulls performed different foraging trips resulting into different strategies according with their destinations. The three foraging strategies (i.e. marine, terrestrial and mix) were adopted by gulls across the years of study, although mix foraging trips (i.e. trips with simultaneous marine and terrestrial destinations) were only eight. Only the years 2011, 2012 (Berlenga) and 2015 (Deserta) present individual mixed trips, so YLGs most often adopt either a marine or a terrestrial strategy during a single trip. It is evident that most of the trips were within a marine strategy in all years, but in 2013 a high proportion in the number of terrestrial foraging trips was recorded (i.e. 43 %) comparing with other years (Fig. 3). It should also be noted that Berlenga's YLGs in 2016 have an average percentage of marine foraging trips of 99% (Figure 3).

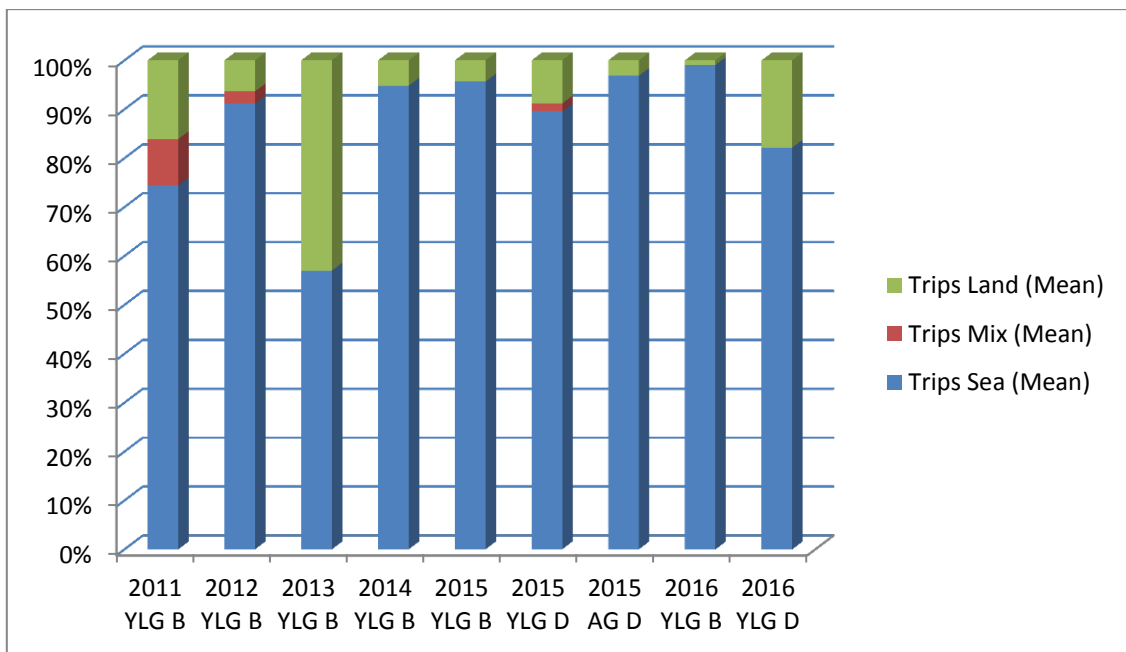


Figure 3: Percentage of marine, terrestrial and mix trips by year, species and island. YLG: yellow legged gull; AG: Audouinii gull; B: Berlenga Island; D: Deserta Island.

YLGs and AGs spent their time differently, depending on the year and location. In 2011 and 2013 YLGs from Berlenga Island spent most of their time engaging on a terrestrial strategy during foraging trips than on a marine strategy (Fig. 4). In contrast, in YLGs from Berlenga in 2016 were those that were less time pursuing terrestrial foraging trips, on average less than 0.01%, a similar pattern adopted by AGs. However, contrasting with AGs, YLGs from Berlenga spent the longest time in the colony in 2016 with values averaging 91% of the time. On the other hand, AGs spent less time in the colony, on average 59% of the time. AGs spent most of their foraging time at sea, with an average proportion of 40% (Figure 4).

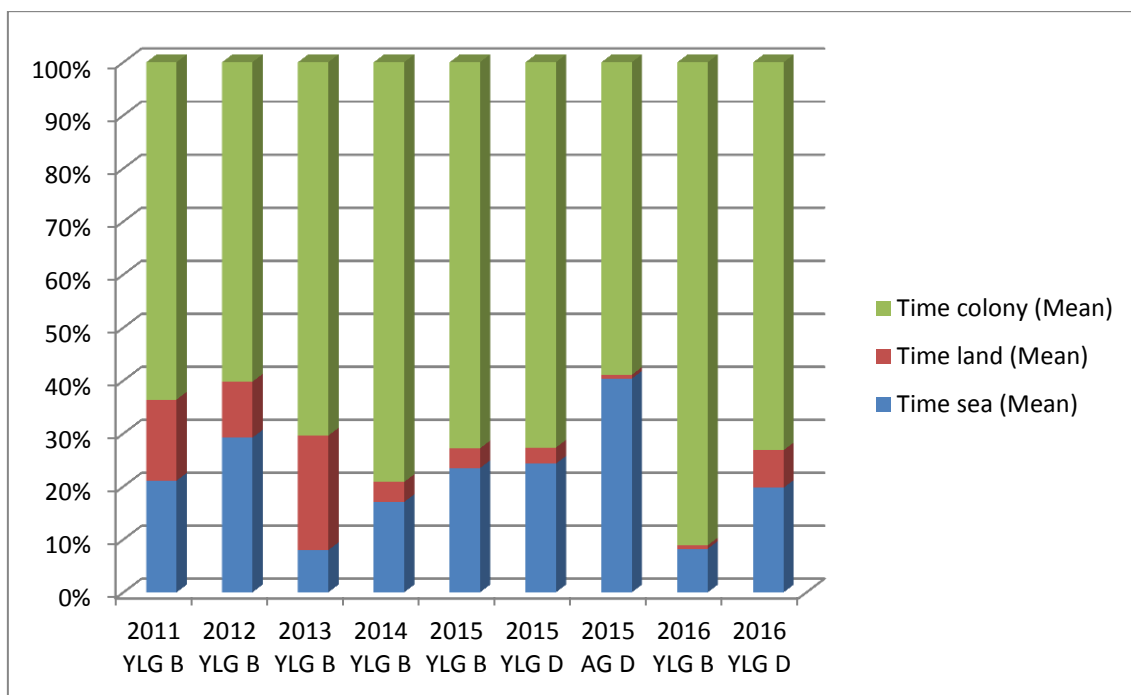
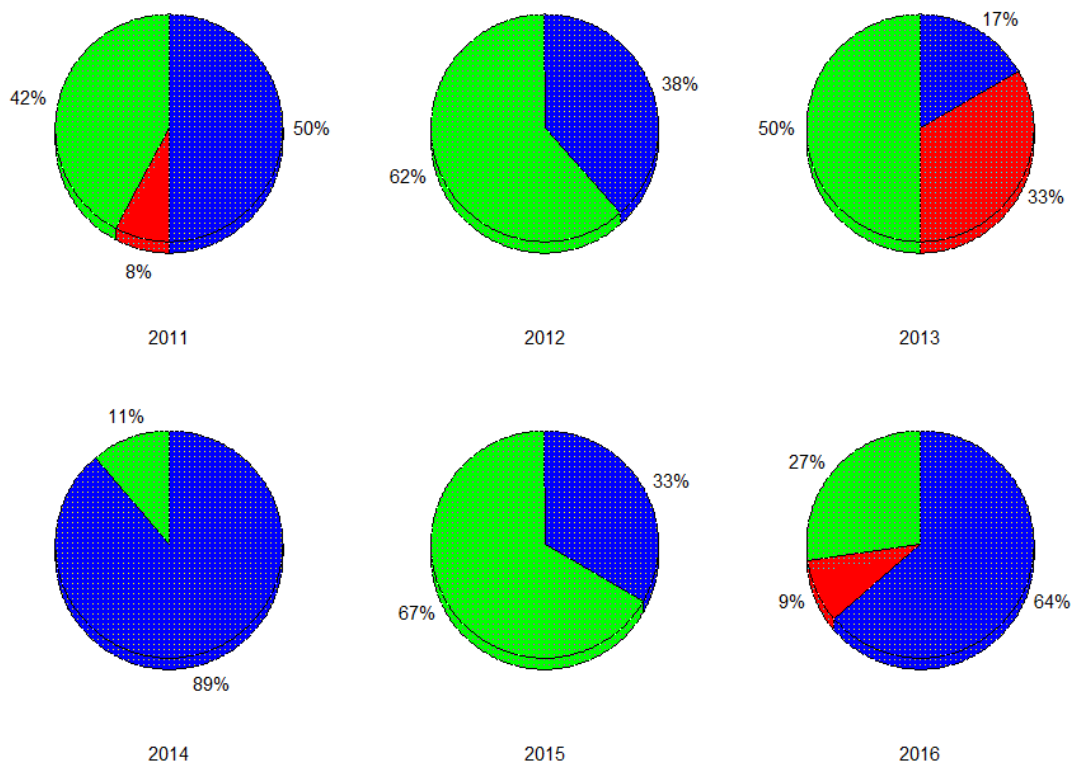


Figure 4: Percentage of time spent during the tracking period (i.e. during the incubation period) by year, species and island. YLG: yellow legged gull; AG: Audouinii gull; B: Berlenga Island; D: Deserta Island

In relation to the feeding strategy used by the YLGs over the 6 years of study in Berlenga Island, based on discriminant analyses, results show that the years 2014 and 2016 were those in which the marine strategy was used by the great majority of the individuals (89% and 64% respectively). In contrast, in 2013, when the marine strategy was less used, only about 17% of the individuals used this foraging strategy. The mixed strategy was mostly used in 2015 and 2012 with values of 67% and 62% respectively and less used in 2014, where only 11% of the individuals adopted the mix foraging strategy. On the other hand, the terrestrial strategy was only adopted during three years (2011, 2013 and 2016) within the population. 2013 was the year in which the YLGs most used this strategy (33%). In 2011 and 2016 the terrestrial strategy was only used by 8 and 9% respectively (Figure 5).



Blue – Marine Green – Mix Red – Terrestrial

2011 – 26 Ind. 2012 – 26 Ind. 2013 – 6 Ind. 2014 – 18 Ind. 2015 – 9 Ind. 2016 – 22 Ind.

Figure 5: *Larus michahellis*: Percentage of yellow legged gulls engaged in foraging trips with marine, terrestrial and mix strategies between 2011 and 2016 on Berlenga Island, Western Portugal.

With regard to the feeding strategy used by YLGs in Deserta island, results show that there were no large variations in the strategies adopted by YLGs over the 2 years (Figure 6). The terrestrial strategy was not adopted by the population during these years. The marine foraging strategy was the most used in both years, with 75% (2015) and 77% (2016) of individuals adopting for this strategy, respectively. The mixed strategy was also adopted in these 2 years with around 25% (2015) and 23% (2016) of the individuals within the population, respectively. It should be noticed that 100% of the AGs were considered to pursue a marine strategy during this study.

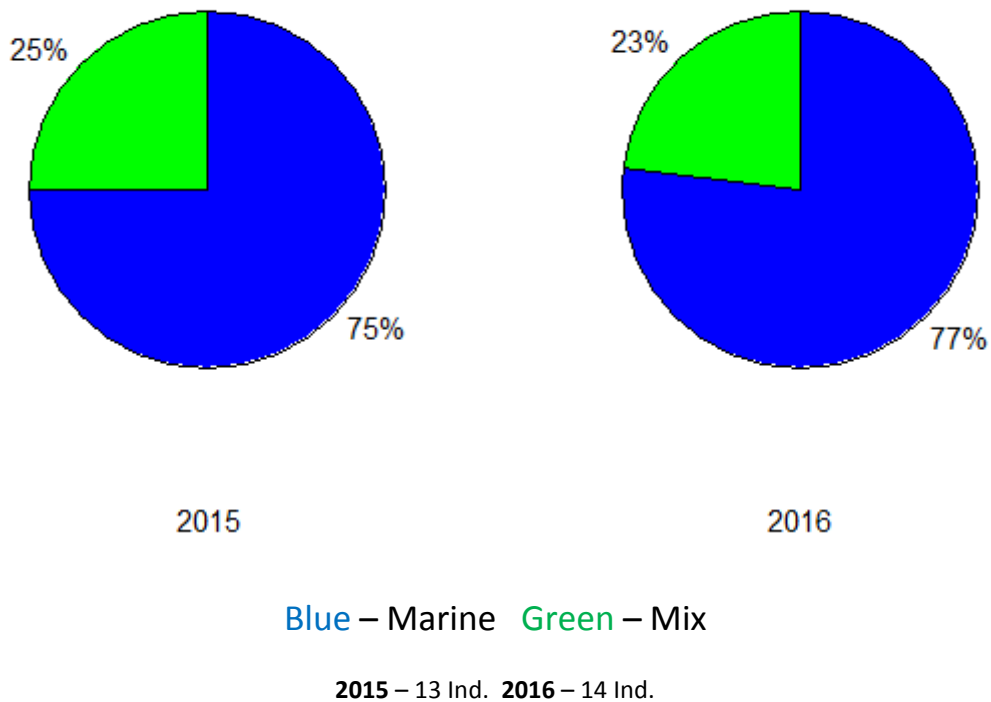


Figure 6: *Larus michahellis*: Percentage of yellow legged gulls engaged in foraging trips with marine and mix strategies in 2015 and 2016 on Deserta Island, South Portugal. The terrestrial strategy was not adopted by none of the sampled gulls in the two years.

3.5. Isotopic niche and identification of foraging strategies

The metrics SEAc, TA and SEA.B values were obtained for each year and species and showed that the higher values corresponded to YLGs sampled in Berlenga in 2013 (Table 5). On the other hand, 2014 and 2015 were the years in which the SEAc, TA and SEA.B values were lower (Table 5). It is important to highlight that in the AGs, both in 2015 and 2016, the SEAc, TA and SEA.B values were very low in comparison with general YLGs' metric values.

Table 5: *Larus michahellis* and *Larus Audouinii*. SEAc, TA, SEA.B (mean and SD) and NAO (Winter) values by year (2011-2016), species (YLG/AG), and Island (Berlenga/Deserta)

Year	Species	Island	N (total)	SEAc	TA	SEA.B	NAO (Winter)
2011	YLG	Berlenga	26	3.0	8.1	3.2 ± 0.7	-1.57
2012	YLG	Berlenga	26	1.5	4.7	1.8 ± 0.4	3.17
2013	YLG	Berlenga	6	12.9	10.3	9.9 ± 4.5	-1.97
2014	YLG	Berlenga	18	0.6	1.6	1.0 ± 0.2	3.1
2015	YLG	Berlenga	9	1.2	2.1	1.9 ± 0.7	3.56
2015	YLG	Deserta	12	0.7	1.1	1.2 ± 0.3	3.56
2015	AG	Deserta	15	0.8	2.0	1.1 ± 0.3	3.56
2016	YLG	Berlenga	22	2.3	5.6	2.4 ± 0.5	0.98
2016	YLG	Deserta	13	3.9	9.3	4,3 ± 1.2	0.98
2016	AG	Deserta	12	0.3	0.7	0.9 ± 0.2	0.98

Based on the discriminant analyses, plasma $\delta^{13}\text{C}$ values of YLGs (N = 132) were lower in gulls pursuing a terrestrial foraging strategy (mean = -20.6 ‰) with a range between -24.5 and -19.6 ‰ and with a higher standard deviation (i.e. ± 1.9 ‰). Individuals adopting a mix strategy showed relatively higher plasma $\delta^{13}\text{C}$ values (-19.0 ‰) with a range between -20.9 and -17.7 ‰ and with a standard deviation (i.e. ± 0.7 ‰). Finally, individuals which adopt a marine strategy showed the highest plasma $\delta^{13}\text{C}$ values (-18.0 ‰), with a range between -19.4 and -15.0 ‰ and a standard deviation of 0.7 ‰. Important to note the higher standard deviation of gulls with a terrestrial strategy in comparison with the other strategies. AGs (N = 27) had an average of plasma $\delta^{13}\text{C}$ values of -18.1 ‰, with a range between -19.2 and -17.2 ‰

and a standard deviation of 0.5 ‰ (Figure 7), thus within the values of YLGs with a marine strategy.

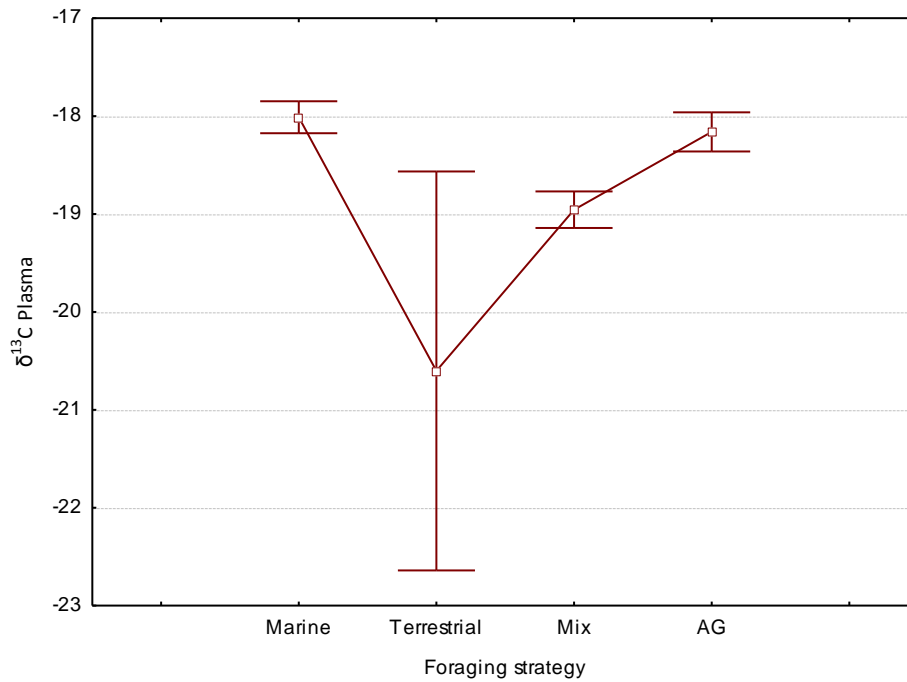


Figure 7: Plasma $\delta^{13}\text{C}$ (‰) values of yellow legged gulls (N=132) and Audouinii gulls (N=27) for each strategy adopted (terrestrial, mix or marine). Values are means \pm 0.95 confidence interval.

Plasma $\delta^{15}\text{N}$ values of YLGs (N = 132) were lower in gulls adopting a mix foraging strategy (mean = 11.7 ‰ \pm 0.9), followed by the terrestrial strategy (13.2 ‰ \pm 1.1) and the marine strategy (13.5 ‰ \pm 0.8). Similar to plasma $\delta^{13}\text{C}$ values, plasma $\delta^{15}\text{N}$ values also showed the higher standard deviation of gulls with a terrestrial strategy in comparison with the other strategies. AGs (N = 27) had an average of plasma $\delta^{15}\text{N}$ of 12.9 ‰, with a range between 11.5 and 13.7 ‰ and a small standard deviation of 0.5 ‰ (Figure 8).

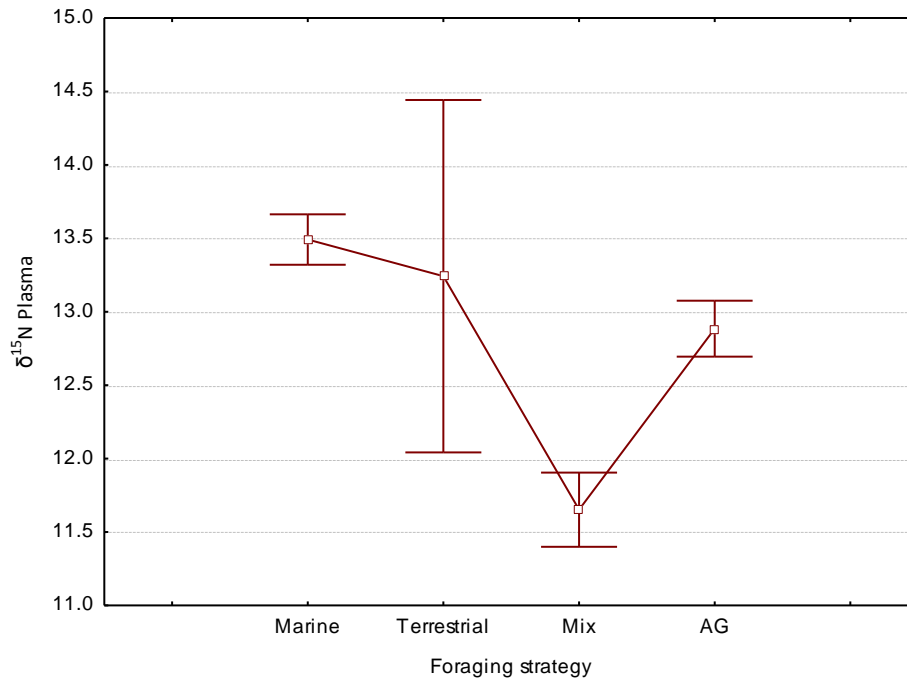


Figure 8: Plasma $\delta^{15}\text{N}$ (‰) values of yellow legged gulls (N=132) and Audouinii gulls (N=27) for each strategy adopted (terrestrial, mix or marine). Values are means \pm 0.95 confidence interval.

The SEAC overlap on the isotopic niche was lower for the YLGs with a mix foraging strategy and YLGs with a marine foraging strategy (<0.001), and YLGs with a marine foraging strategy and YLGs with a terrestrial foraging strategy (0.002). On the other hand, the overlap was higher for the YLGs with a marine strategy and AGs (0.46) and for YLGs with a mix foraging strategy and YLGs with a terrestrial strategy (0.31). Isotopic niche was higher for YLGs with a terrestrial foraging strategy (7.01) and lower for the AGs (0.76) (figure 9).

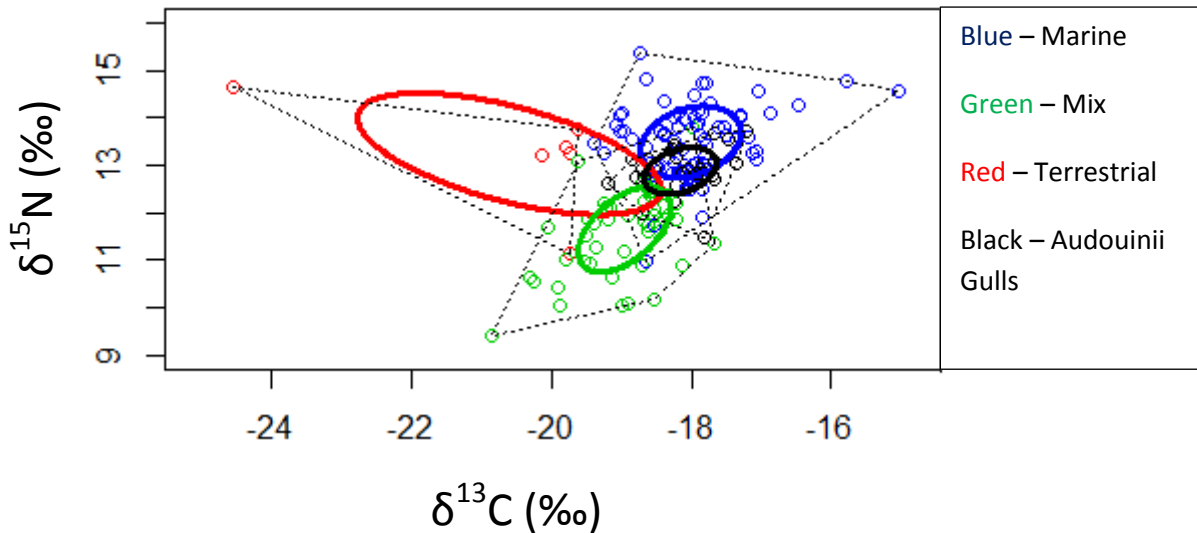


Figure 9: Isotopic niches of yellow legged gulls (YLGs) and Audouin gulls (AGs), based on Jackson et al. (2011) applied to Stable Isotopic ratios in plasma. The area of the standard ellipses (SEAc) is represented.

3.6. Factors which may determine the foraging strategies adopted by yellow legged gulls

Plasma $\delta^{13}\text{C}$ values were positively correlated with trips at sea (Pearson correlation $N=45$, $r=0.36$, $p=0.02$) and time at sea (Pearson correlation $N=45$, $r=0.35$, $p=0.02$) (Figure 10), and negatively correlated to time at land (Pearson correlation $N=45$, $r=-0.38$, $p=0.01$) (Figure 11). However, no relationship was found between plasma $\delta^{13}\text{C}$ values and trips at land (Spearman correlation $N=45$, $r=-0.26$, $p=0.08$). No relationship was found with trips mix, neither with time at colony. However, no relationships were found between plasma $\delta^{15}\text{N}$ values and any of the explanatory variables (Spearman correlation all $p>0.05$). No relationships were found between plasma $\delta^{13}\text{C}$ values and maximum distance from colony (Km), cumulative distance traveled (Km) and Kernel variables (Spearman correlation all $p>0.05$).

Per year, the terrestrial strategy was negatively correlated with NAO (Pearson's correlation $N=8$, $r=-0.78$, $p=0.02$) (Figure 12). However, no relationship was found between marine strategy (Pearson's correlation $N=8$, $r=0.39$, $p=0.34$) (Figure 13) nor mix strategy with NAO. SEAc, TA and SEA.B were negatively correlated with NAO was negatively correlated with the isotopic niche metrics, SEAc (Pearson correlation $N=10$, $r=-0.73$, $p=0.02$, Figure 14), TA

(Pearson correlation N=10, $r=-0.79$, $p=0.007$, Figure 15) for TA and SEA.B (Pearson correlation N=10, $r=-0.74$, $p=0.01$).

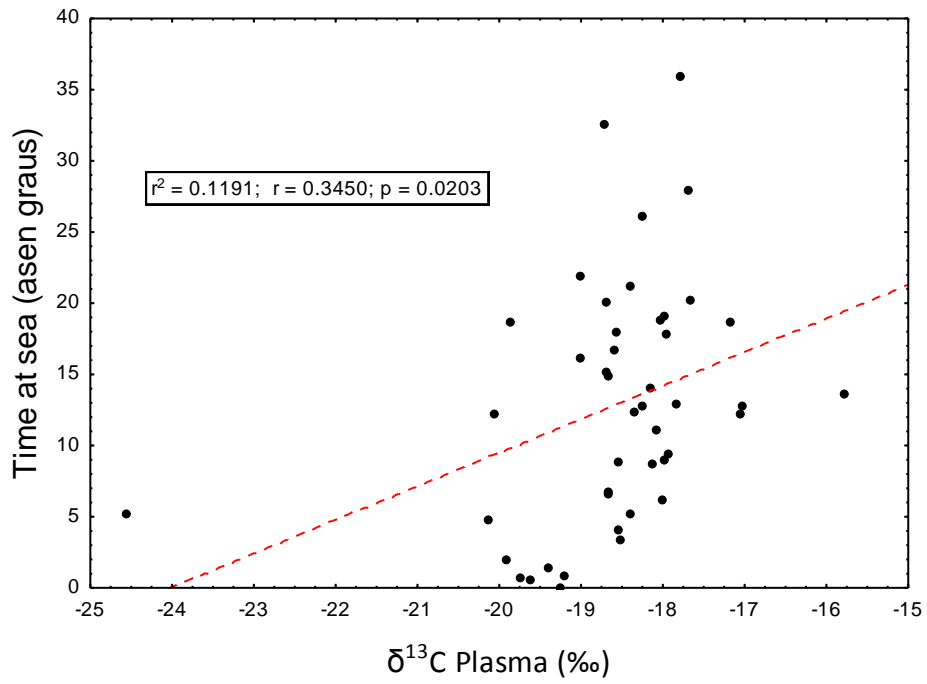


Figure 10: *Larus michahellis* and *Larus audouinii*: Pearson correlation between values of $\delta^{13}\text{C}$ Plasma (‰) and values of time at sea (% arcsin) of yellow-legged gulls and Audouinii gulls.

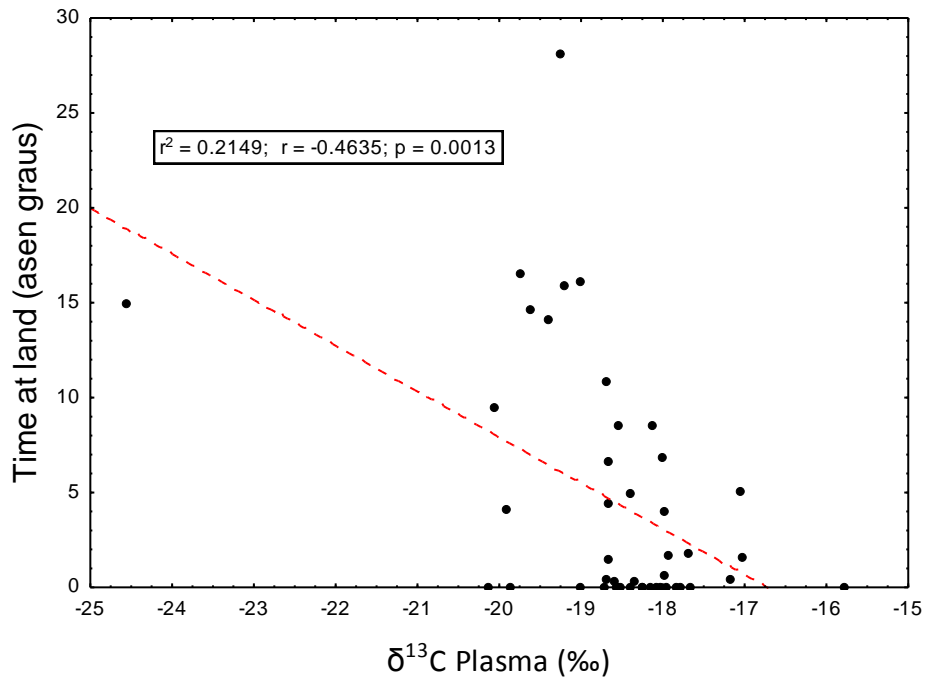


Figure 11: *Larus michahellis* and *Larus audouinii*: Pearson correlation between values of $\delta^{13}\text{C}$ Plasma (‰) and values of time at land (% arcsin) of yellow-legged gulls and Audouinii gulls.

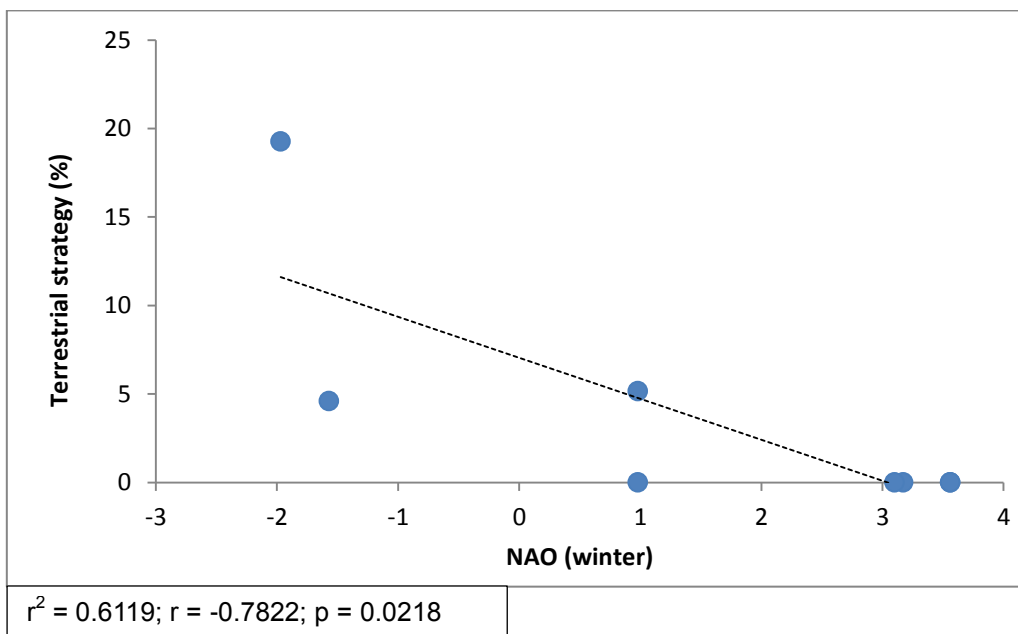


Figure 12: *Larus michahellis* and *Larus audouinii*: Pearson correlation between values of NAO (winter) and values of terrestrial strategy (% arcsin) of yellow-legged gulls and Audouinii gulls.

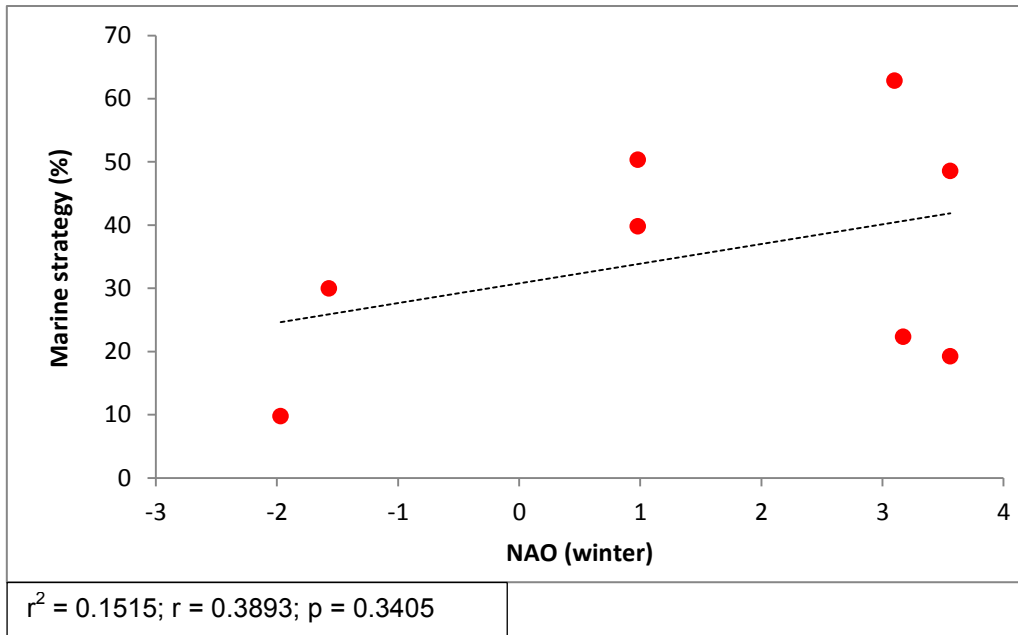


Figure 13: *Larus michahellis* and *Larus audouinii*: Pearson correlation between values of NAO (winter) and values of marine strategy (% arcsin) of yellow-legged gulls and Audouinii gulls.

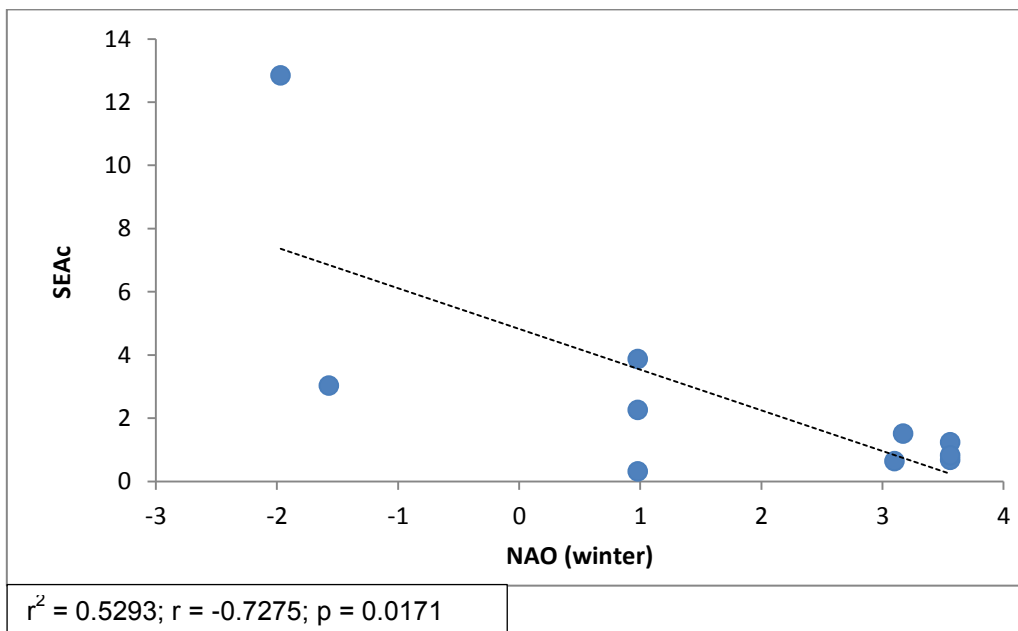


Figure 14: *Larus michahellis* and *Larus audouinii*: Pearson correlation between values of NAO (winter) and values of SEAc

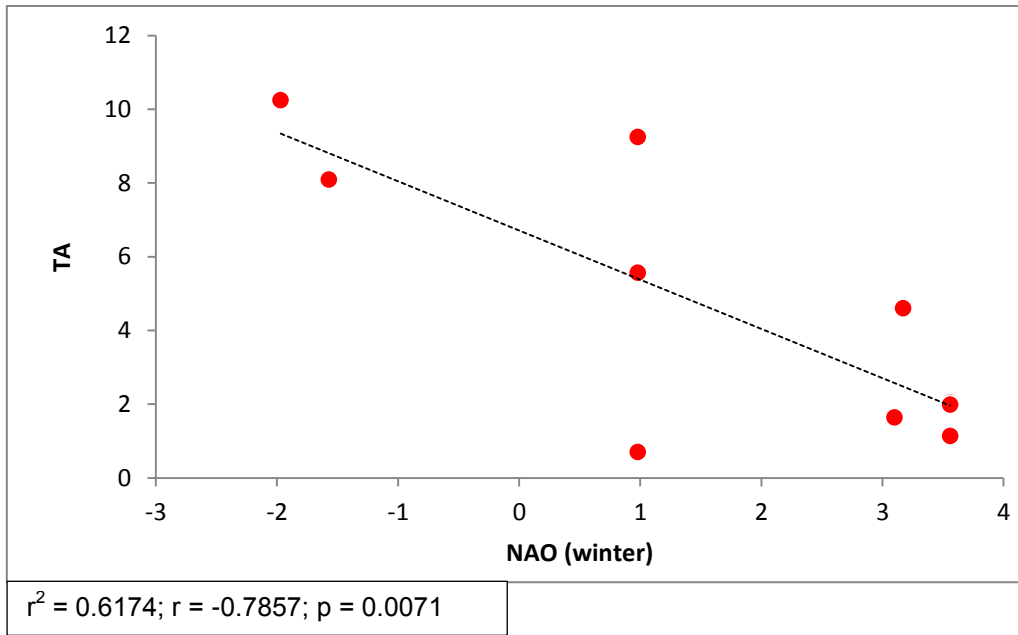


Figure 15: *Larus michahellis* and *Larus audouinii*: Pearson correlation between values of NAO (winter) and values of TA

4. Discussion



Yellow-legged gulls were used as a model of generalist and opportunistic species to infer the foraging strategies adopted by the individuals in Berlenga (2011-2016) and Deserta (2015-2016) Islands. The foraging behavior and niche width of YLGs differed markedly between years and colonies during the incubation period, matching the strong variation in the oceanographic conditions, and supposedly baseline diet among years during the same period (Christel et al., 2012; Moreno et al., 2010). The present work reports on spatio-temporal differences in the foraging distribution of AGs and YLGs during the breeding period. This study also confirmed the marine foraging behavior of AGs, while YLGs had a more generalist foraging behavior, particularly during years with lower NAO (winter) index values. AGs and YLGs were active on at-sea foraging areas that matched mainly with the marine foraging strategy. It is clear that both gull species learned to exploit marine resources, presumably due to the high availability of discards - the super-abundant and predictable food source - easier to obtain than capturing natural prey. Although the YLGs also foraged on land, mostly refuse dumps, they concentrated their foraging activity at-sea and fishing harbors, especially during years of higher NAO (winter) values.

Stable isotope analysis allows to evaluate the spatio-temporal variation in the isotopic niche (and hence in the foraging and trophic niche) throughout seasons and years, thus allowing to reconstruct the history of a particular individual or population along the year (Hobson et al., 1994). SIA in Berlenga showed a general large variation between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in both plasma and RBC, which shows that YLGs were feeding on a wide variety of foods in the 15 days prior to sample collection, which is reflected in such large variation. In 2013 the lowest values of $\delta^{13}\text{C}$ were registered, indicating a predominantly terrestrial foraging strategy, probably more based on foods derived from a baseline of C3 plants (Newsome et al., 2007). Moreover, in 2013 the value of the standard deviation was higher, although the small number of samples in such year. SIA also indicated that a large range of values occurred in $\delta^{15}\text{N}$ in both plasma and RBC, which shows that individuals fed on food of various trophic levels. Thus, the higher the trophic level of the food, the greater the value of $\delta^{15}\text{N}$ represented in RBC or plasma. In the Deserta Island, the variation between the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the 2 years of study was not as great as the Berlenga variation during the same years, which shows that there was a greater consistency in the feeding strategy adopted each year. The AGs presented values of $\delta^{13}\text{C}$ slightly lower than the YLGs of Deserta, and given that they adopted an exclusively marine feeding strategy, we can easily draw conclusions about the feeding strategy of YLGs of Deserta. Although the close values, the YLGs of Deserta did not present in the study period a strategy of feeding as marine as the AGs. Regarding the values of $\delta^{15}\text{N}$, the YLGs

presented slightly higher values than the AGs, which suggests the consumption of items of higher trophic levels by YLGs, compared to AGs.

In Deserta Island, SIA results revealed no differences between AG and YLG species, which suggests that both species foraged in similar habitats and consumed similar prey species, thus exhibiting a similar trophic ecology. This was corroborated with the tracking information, with both species exploiting the marine environment, though some YLG individuals foraged over refuse dumps, which might explain the slight higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Regarding trophic ecology, the diet overlapped between the two gulls species and could be explained by the consumption of similar prey or the consumption of different prey but with similar isotopic signatures (Bearhop et al., 2004). Conventional methods (i.e. identification of prey from pellets) indicate a high percentage of fish prey in both species' diet in Deserta Island, but more pronounced in AGs than YLGs, besides fish represented in more than half of the YLGs diet composition (Matos, 2016).

Although the sample size of tracked birds was relatively low, our results suggest substantial inter-annual variation in foraging behavior and effort of yellow-legged gulls during the incubation period on Berlenga and Deserta Islands. There were differences in both spatial and temporal patterns of the trips, and in their frequency. Apparently, this variability was strongly related to the gulls' diet, which differed markedly between years and colonies. Our results suggest that foraging behavior of this opportunistic species is influenced to a large extent by prey conditions around the colony (Schwemmer & Garthe, 2008). Moreover, the annual variation in the foraging trip parameters for individuals sampled at Berlenga show that YLGs made several trips to different locations, indicating variability in the availability of food around the colony. Trip duration was much longer in 2012, however many of these trips were to harbors, and a preference for a marine feeding strategy. YLGs adopt a more marine feeding strategy when marine resources are abundant, especially during the breeding season (Alonso et al., 2015; Ceia et al., 2014). The number of trips per day was higher in 2016, however these trips were very short (tens of km) which suggests a high food availability close to the colony. On the other hand, 2013 was the year in which fewer foraging trips were performed by individuals. However, a higher proportion of these trips were long, to dumps and landfills, suggesting a lower food abundance around the colony. Thus, a more terrestrial feeding strategy was adopted by individuals in 2013. The maximum and cumulative distance traveled were also higher in 2013 (indicating higher foraging effort), which shows a higher demand for food in areas away from the colony during the study period. Birds forage preferably near the colony, but can travel longer distances (up to 100 km) in search of food if necessary (Asello et

al., 2010; Ceia et al., 2014). Moreover, it is interesting to notice that the main prey of YLGs breeding in Berlenga and Galicia is the Henslow's swimming crab *Polybius henslowii* (Alonso et al., 2015; Ceia et al., 2014; Munilla, 1997): in years of low availability of such prey, birds increased the consumption of refuse waste and terrestrial invertebrates, investing on a more generalist diet. Regarding the Deserta Island, results show that AGs performed longer trips than YLGs, which shows that they searched for food in marine areas further away from the colony. However YLGs from Deserta in 2015 made more trips per day, which suggests a greater demand for food in that year. Moreover, the maximum and cumulative distance traveled were higher in AGs than in YLGs.

Gulls are adapted to capture a high diversity of marine prey such as crustaceans, molluscs, and planktonic organisms, but for most gull populations the main prey are fish. However, the flexibility in food demand of YLGs allows to further modify their foraging strategies and have access to a large number of food sources of anthropogenic origin, such as general human waste, surplus fisheries, refuse dumps, agricultural fields, among others (Christel et al., 2012).

In Berlenga, the YLGs opted for different foraging strategies in the various years of study. In 2011 and 2013 they adopted a more terrestrial foraging strategy, contrary to the years of 2014, 2015 and 2016, in which they mostly adopted a marine strategy. These differences between foraging strategies are very much related to the abundance of marine food resources. If there are few marine resources available, YLGs seek other food sources, resorting to dumps, agricultural fields and landfills, even if they have to cover many kilometers (Ceia et al., 2014). In Deserta, these differences between years were not so marked (although data available only for two years), with YLGs preferring a more marine feeding strategy both in 2015 and 2016. Most of the foraging areas of the YLGs were similar to the foraging areas of the AGs, which are exclusively marine (Mañosa et al., 2004). It is important to note that in some years (2011, 2012 and 2015) mixed trips (marine and terrestrial during the same trip) occurred, but overall these are not very common. It should also be noted that, taking into account the trips performed by individuals, the time available in each strategy was different across years. For example, in the Berlenga colony in 2015, the time spent in the marine foraging strategy was higher than in 2013, which again supports the fact that 2013 YLGs choose a more terrestrial foraging strategy. In the Deserta colony, the YLGs did not adopt a full terrestrial strategy, but rather a mixed foraging, which suggests a great availability of marine resources near the colony.

As expected, AGs presented a small isotopic niche, because their diet is exclusively marine and does not present much variability (García-Tarrasón et al., 2014). We can verify that SEAc index corresponding to the strategy of terrestrial foraging in YLGs is larger than the others, which indicates the consumption of a larger variability of food resources with distinct isotopic signatures. The SEAc index of AGs is small compared with YLGs. However, for YLGs which adopted a marine strategy, SEAc index was also small (indicating a small isotopic niche width) and greatly overlapped with AGs, indicating a small variability of foods with similar signatures.

Relationships between response and explanatory variables during this study indicate which factors may determine the foraging strategies adopted by YLGs and the respective correspondent isotopic values. It is possible to verify that the $\delta^{13}\text{C}$ values of the plasma correlated positively with the time spent at sea, that is, the higher the values of $\delta^{13}\text{C}$, the longer the YLGs spent at sea. On the other hand, there is a negative correlation between the values of the plasma $\delta^{13}\text{C}$ and the time spent on land, that is, the lower the values of $\delta^{13}\text{C}$, the longer the YLGs spent on land. Oceanographic conditions, such as the NAO index is also important to explain the choice of a more terrestrial, mixed or marine foraging strategy (Monticelli et al., 2007). During this study, the NAO (winter) index was negatively correlated with the terrestrial strategy, that is, the lower the NAO the greater the probability of the strategy being terrestrial. When NAO values are very low (i.e. around -2), the upwelling along the Portuguese coast decreases which contributes to a reduction in marine productivity around the colonies, forcing individuals to search for food farther and adopt a Terrestrial strategy, as it occurred in 2013. On the other hand, higher NAO (winter) index values were correlated with a more marine strategy. Higher NAO index values are related with stronger upwelling events, supposedly increasing marine productivity. NAO values were negatively correlated with SEAc and TA values, thus the smaller the NAO values, the higher the SEAc and the TA index values, characterized by a larger variability in food sources and hence a terrestrial foraging strategy.

In conclusion, this study demonstrated that the population of YLG adopting a marine strategy in Berlenga Island was not consistent across years. However, the population of YLGs in Deserta Island was more consistent in adopting a marine strategy, although only two years of data were collected. This suggests that marine resources availability around the colonies has a strong influence in such foraging decisions, complemented with resources available from terrestrial sources. This study also corroborates that the isotopic niche width of marine strategists is much lower than gulls that adopt a terrestrial strategy, as expected. However,

and surprisingly, gulls adopting a mixed strategy also showed an overall small isotopic niche, only slightly higher than gulls adopting a marine strategy. A diet based on marine sources may buffer isotopic signatures of some prey from terrestrial origins resulting in different averages but small isotopic standard deviations. Another possibility is that gulls adopting a mixed strategy can also exploit (and opt) for marine resources at refuse dumps. Although some overlap and bias in the definition of the different foraging strategies, isotopic values (and especially $\delta^{13}\text{C}$) performed well in the model (discriminant analyses) conducted. This allowed assessing the influence of oceanographic conditions (based on NAO index values), which are the base of the overall availability in the marine food sources, and a major driver of foraging strategies adopted by YLG.

Further studies should evaluate the foraging consistency in the strategies of populations of YLGs at the individual level. It is known that within a generalist population there are individuals which specialize in a specific diet. It is crucial a better understanding of variation in foraging strategies within and between individuals to determine the key factors that contribute to the niche variation at the individual level. The foraging niche variation and hence on foraging strategies adopted by different individuals should have implications on the degree of intraspecific competition and thus in ecological and evolutionary processes.

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Appendix

Table 1: *Larus michahellis*. Stable isotopic values of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) of plasma and red blood cells (RBC) of yellow-legged gulls between 2011 and 2016, and total at Berlenga Island, West Portugal. Statistical results from Kruskal-Wallis and Levene's tests are shown. Upper letters indicate the significant differences between years according to a Kruskal-Wallis test, followed by a pos-hoc Dunn's test for multiple comparisons. Values are means \pm SD (min-max).

	<i>Larus michaellis</i> (Berlenga)							Kruskal-Wallis Test		Levene's Test	
	2011 (N=26)	2012 (N=26)	2013 (N=6)	2014 (N=18)	2015 (N=9)	2016 (N=22)	Total (N=107)	H _(5,107)	P	F _(5,101)	P
$\delta^{13}\text{C}$ (‰) Plasma	-18.9 \pm 0.8 ^a (-20.3 - -17.7)	-18.7 \pm 0.5 ^b (-19.5 - -17.8)	-20.6 \pm 2.0 ^{abc} (-24.7 - -19.6)	-18.4 \pm 0.4 ^{cd} (-19.3 - -17.9)	-18.8 \pm 0.3 (-19.4 - -18.4)	-19.1 \pm 0.7 ^d (-20.8 - -18.0)	-18.9 \pm 0.9 (-24.7 - -17.7)	23.3	<0.001	6.0	<0.001
$\delta^{15}\text{N}$ (‰) Plasma	12.9 \pm 1.5 (10.5 - 15.4)	12.2 \pm 1.0 ^a (10.0 - 14.0)	12.4 \pm 1.9 (10.1 - 14.6)	13.4 \pm 0.5 ^{ab} (12.6 - 14.5)	12.0 \pm 0.9 ^b (10.9 - 13.4)	12.7 \pm 1.1 (-10.1 - 14.3)	12.7 \pm 1.2 (10.0 - 15.4)	16.2	0.006	5.6	<0.001
$\delta^{13}\text{C}$ (‰) RBC	-19.3 \pm 0.7 ^{ac} (-20.8 - -18.0)	-19.2 \pm 0.6 ^b (-20.4 - -18.2)	-19.1 \pm 1.3 (-21.6 - 17.8)	-18.6 \pm 0.6 ^{abd} (-20.4 - 18.0)	-18.5 \pm 0.2 ^{ce} (-18.8 - 18.1)	-19.5 \pm 0.7 ^{de} (-21.6 - -18.1)	-19.1 \pm 0.7 (-21.6 - 17.8)	30.0	<0.001	2.0	0.08
$\delta^{15}\text{N}$ (‰) RBC	12.7 \pm 1.4 ^a (9.8 - 14.8)	11.4 \pm 1.1 ^{ab} (9.7 - 13.5)	11.6 \pm 1.2 (9.8 - 12.7)	12.5 \pm 0.9 ^b (10.8 - 14.0)	11.7 \pm 0.7 (10.9 - 13.0)	12.0 \pm 1.2 (9.3 - 13.8)	12.1 \pm 1.2 (9.3 - 14.8)	17.8	0.003	1.9	0.10

Table II: *Larus michahellis* and *Larus Audouinii*. Stable isotopic values of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) of plasma and red blood cells (RBC) of yellow-legged gulls by year (2015-2016) and total at Deserta Island, South of Portugal. Statistical results from ANOVA and Levene's tests are shown. Values are means \pm SD (min-max).

	<i>Larus michaellis</i> (Deserta)			ANOVA		Levene's Test		<i>Larus audouinii</i> (Deserta)			ANOVA		Levene's Test	
	2015 (N=12)	2016 (N=13)	Total (N=25)	$F_{(1,23)}$	P	$F_{(1,23)}$	P	2015 (N=15)	2016 (N=12)	Total (N=27)	$F_{(1,25)}$	P	$F_{(1,25)}$	P
$\delta^{13}\text{C}$ (‰) Plasma	-18.0 \pm 0.5 (-18.7 - -17.3)	-18.0 \pm 1.4 (-21.4 - -15.7)	-18.0 \pm 1.1 (-21.4 - -15.7)	0.0	0.97	3.6	0.07	-18.6 \pm 0.4 (-19.4 - -17.7)	-18.5 \pm 0.3 (-18.9 - -17.9)	-18.5 \pm 0.4 (-19.4 - -17.7)	0.2	0.67	0.1	0.77
$\delta^{15}\text{N}$ (‰) Plasma	13.2 \pm 0.5 (12.4 - 13.8)	13.3 \pm 1.7 (9.4 - 14.8)	13.2 \pm 1.2 (9.4 - 14.8)	0.0	0.87	3.6	0.03	12.8 \pm 0.5 (11.5 - 13.7)	13.0 \pm 0.4 (12.2 - 13.7)	12.9 \pm 0.5 (11.5 - 13.7)	1.1	0.30	0.9	0.34
$\delta^{13}\text{C}$ (‰) RBC	-18.2 \pm 0.5 (-19.1 - -17.6)	-17.9 \pm 1.0 (-20.4 - -16.4)	-18.0 \pm 0.8 (-20.4 - -16.4)	0.7	0.36	2.6	0.12	-18.2 \pm 0.3 (-18.8 - -17.5)	-18.3 \pm 0.3 (-19.0 - -18.0)	-18.3 \pm 0.3 (-19.0 - -17.5)	1.7	0.21	0.6	0.44
$\delta^{15}\text{N}$ (‰) RBC	12.3 \pm 0.7 (10.9 - 13.1)	12.7 \pm 1.2 (9.6 - 13.9)	12.5 \pm 1.0 (9.6 - 13.9)	0.9	0.35	1.6	0.22	12.4 \pm 0.3 (11.8 - 13.1)	12.3 \pm 0.4 (11.7 - 12.8)	12.4 \pm 0.3 (11.7 - 13.1)	0.2	0.66	0.1	0.75

Table III: *Larus michahellis*. Foraging parameters derived from GPS data of yellow-legged gulls breeding in Berlenga Island, West Portugal, between 2011 and 2016, and in total. Statistical results from Kruskal-Wallis and Levene's tests are shown. Values are means \pm SD (min-max).

	<i>Larus michaellis</i> (Berlenga)							Kruskal-Wallis Test		Levene's Test	
	2011 (N=4)	2012 (N=7)	2013 (N=6)	2014 (N=5)	2015 (N=4)	2016 (N=4)	Total (N=30)	H _(5,30)	P	F _(5,24)	P
Tracking days_total	5.7 \pm 2.3 (2.5 – 8.1)	3.8 \pm 2.1 (0.4 – 6.7)	3.0 \pm 1.1 (1.1 – 4.3)	6.1 \pm 2.6 (3.3 – 10.1)	4.4 \pm 0.5 (3.8 – 4.8)	2.9 \pm 1.0 (2.0 – 4.0)	4.2 \pm 2.1 (0.4 – 10.1)	10.6	0.0593	1.3	0.31
Trip dur (days_mean)	0.19 \pm 0.03 (0.16 – 0.23)	0.33 \pm 0.53 (0.03 – 1.52)	0.18 \pm 0.11 (0.04 – 0.37)	0.09 \pm 0.04 (0.03 – 0.11)	0.15 \pm 0.02 (0.13 – 0.18)	0.02 \pm 0.01 (0.02 – 0.03)	0.18 \pm 0.27 (0.02 – 1.52)	15.8	0.0073	2.7	0.04
Trips/day (total)	1.89 \pm 0.17 (1.72 – 2.09)	3.87 \pm 3.18 (0.91 – 8.41)	1.82 \pm 0.47 (1.28 – 2.40)	2.60 \pm 0.66 (1.90 – 3.61)	1.78 \pm 0.21 (1.67 – 2.09)	4.23 \pm 0.83 (3.11 – 5.07)	2.76 \pm 1.81 (0.91 – 8.41)	13.3	0.0210	8.4	<0.001
Lat max (mean)	39.37 \pm 0.09 (39.30 – 39.49)	39.38 \pm 0.03 (39.32 – 39.41)	39.41 \pm 0.10 (39.29 – 39.53)	39.40 \pm 0.04 (39.35 – 39.45)	39.39 \pm 0.04 (39.35 – 39.44)	39.4 \pm 0.00 (39.40 – 39.41)	39.4 \pm 0.06 (39.29 – 39.53)	2.1	0.8357	3.4	0.02
Long max (mean)	-9.40 \pm 0.05 (-9.44 – -9.35)	-9.46 \pm 0.11 (-9.64 – -9.30)	-9.39 \pm 0.20 (-9.75 – -9.22)	-9.46 \pm 0.05 (-9.52 – -9.42)	-9.49 \pm 0.12 (-9.66 – -9.41)	-9.50 \pm 0.01 (-9.51 – -9.50)	-9.45 \pm 0.11 (-9.75 – -9.22)	6.3	0.2763	3.0	0.03
Max dist (mean)	14.2 \pm 4.8 (7.2 – 17.9)	11.7 \pm 8.2 (1.6 – 22.5)	21.0 \pm 9.4 (3.6 – 31.1)	10.7 \pm 6.2 (2.4 – 17.7)	16.5 \pm 4.9 (10.7 – 21.7)	1.7 \pm 0.5 (1.2 – 2.3)	13.0 \pm 8.6 (1.2 – 31.1)	14.7	0.0117	1.9	0.14
Comul dist (mean)	42.1 \pm 9.5 (27.9 – 48.1)	37.5 \pm 26.9 (4.4 – 66.8)	57.2 \pm 23.0 (14.6 – 78.0)	32.2 \pm 19.1 (6.5 – 52.9)	50.2 \pm 10.9 (39.2 – 64.1)	4.2 \pm 1.2 (3.0 – 5.7)	38.4 \pm 24.0 (3.0 – 78.0)	13.3	0.0205	4.2	0.007

Table IV: *Larus michahellis* and *Larus Audouinii*. Foraging parameters derived from GPS data of yellow-legged gulls breeding in Deserta Island, South Portugal, between 2015 and 2016, and in total, and foraging parameters derived from GPS data of Audouinii gulls breeding in Deserta Island, South Portugal in 2015. Statistical results from ANOVA and Levene's tests are shown. Values are means \pm SD (min-max).

	Larus michaellis (Deserta)			ANOVA		Levene's Test		Larus audouinii (Deserta)
	2015 (N=6)	2016 (N=5)	Total (N=11)	$F_{(1,9)}$	P	$F_{(1,9)}$	P	2015 (N=6)
Tracking days_total	6.6 \pm 2.4 (4.1 – 11.2)	9.7 \pm 5.0 (1.1 – 13.0)	8.0 \pm 4.0 (1.1 – 13.0)	1.9	0.20	1.7	0.22	6.9 \pm 1.3 (4.7 – 8.7)
Trip dur (days_mean)	0.09 \pm 0.02 (0.06 – 0.13)	0.12 \pm 0.03 (0.10 – 0.18)	0.11 \pm 0.03 (0.06 – 0.18)	2.9	0.12	1.1	0.32	0.19 \pm 0.04 (0.12 – 0.22)
Trips/day (total)	3.08 \pm 1.37 (2.04 – 5.78)	2.24 \pm 0.35 (1.69 – 2.66)	2.70 \pm 1.09 (1.70 – 5.78)	1.7	0.22	2.5	0.14	2.21 \pm 0.47 (1.65 – 2.90)
Lat max (mean)	36.97 \pm 0.04 (36.91 – 37.03)	37.00 \pm 0.02 (36.97 – 37.03)	36.99 \pm 0.04 (36.91 – 37.03)	2.0	0.23	0.7	0.44	36.98 \pm 0.04 (36.94 – 37.03)
Long max (mean)	-7.89 \pm 0.09 (-8.02 – -7.82)	-7.87 \pm 0.04 (-7.93 – -7.83)	-7.88 \pm 0.07 (-8.02 – -7.82)	0.4	0.55	6.1	0.04	-7.81 \pm 0.07 (-7.89 – -7.72)
Max dist (mean)	9.0 \pm 4.7 (3.5 – 15.5)	11.1 \pm 6.6 (5.9 – 22.3)	10.0 \pm 5.5 (3.5 – 22.3)	0.4	0.57	0.1	0.77	14.9 \pm 2.9 (9.9 – 18.1)
Comul dist (mean)	25.2 \pm 11.1 (10.6 – 39.3)	28.8 \pm 19.6 (12.9 – 61.7)	26.9 \pm 14.8 (10.6 – 61.7)	0.1	0.71	0.7	0.43	48.8 \pm 12.5 (27.5 – 63.9)

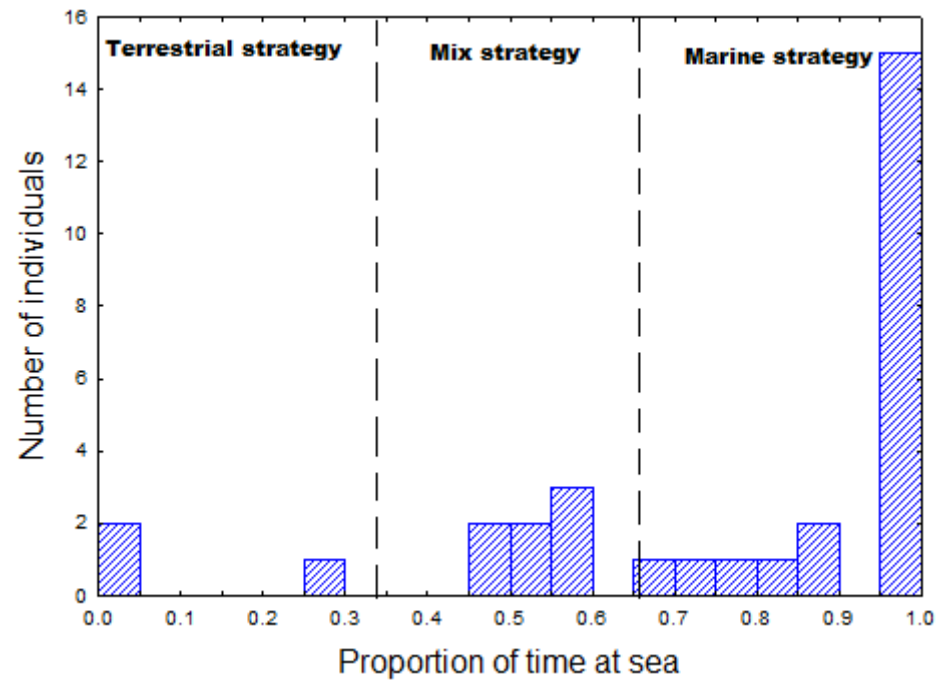


Figure 1: *Larus michaellis*. Histogram of proportion of time at sea during foraging trips (time at sea / total time during foraging trips; for gulls with > 3 days tracking duration) by Yellow legged gulls breeding in Berlenga and Deserta islands from 2011 to 2016. Dashed lines indicate the thresholds separating the 3 different strategies adopted by gulls during this study (i.e. 0.33 and 0.66).