



Trophic ecology of northern gannets *Morus bassanus* highlights the extent of isotopic niche overlap with other apex predators within the Bay of Biscay

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Abstract

Understanding the linkages within complex and evolving marine food webs is essential to comprehend marine ecosystem structure and dynamics. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope signatures are recognized to be powerful descriptors of the trophic ecology and trophic relationships within marine communities. Apex predators such as seabirds can influence the structure of communities by predating in lower trophic levels. They also convey information both over a range of spatial and temporal scales due to their high mobility and longevity, respectively. For this reason, here, we studied the trophic ecology of northern gannets and the extent of niche overlap with other apex predators within the Bay of Biscay (North-East Atlantic), a key feeding area for numerous predatory species. Mixing models indicated that northern gannets fed primarily on European anchovy *Engraulis encrasicolus* and on a mixed group composed of European sardine *Sardina pilchardus*, European sprat *Sprattus sprattus*, juvenile hake *Merluccius merluccius*, Atlantic mackerel *Scomber scombrus* and Atlantic horse mackerel *Trachurus trachurus*. Within the apex predator community, the northern gannets trophic niche overlapped the most with common guillemots *Uria aalge* (15.58%, based on Stable Isotope Bayesian Ellipses (SIBER)) and overlapped to a lesser extent with cetacean species occupying shelf habitats (i.e., the harbour porpoise *Phocoena phocoena* (9.99%) and the short-beaked common dolphin *Delphinus delphis* (10.37%)). Overall, the overlap found was moderate indicating trophic similarities and dissimilarities between these species. Information on trophic interactions between co-existing species is necessary for holistic environmental management, particularly in areas where several megafauna species share their foraging grounds with fisheries activity.

Keywords Marine ecology · Megafauna · Seabirds · Migration · Stable isotopes · Isotopic mixing models

Introduction

The study of apex predators' trophic ecology can reveal a great deal of information due to the importance of predator-prey relationships and their dynamics on the evolution and

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structure of animal communities (Forero et al. 2004). Apex predators such as cetaceans, seabirds and large predatory fish constitute an ideal model for studying trophic relationships, as they tend to integrate long-term and large-scale ecosystem signals due to their high position in food webs (Einoder 2009; Abreu et al. 2020). Each component (i.e., functional group) in the food web occupies a trophic niche which can be shared among different species (Cury et al. 2003). Identifying the trophic niche of apex predators and the linkages between them is necessary to understand the non-linear dynamics, structure and functioning of marine ecosystems (Boyd et al. 2006; Speed et al. 2012; Giménez et al. 2017a; García-Barón et al. 2019).

Among apex predators, the northern gannet (*Morus bassanus*) is a large migratory seabird widely distributed in the North Atlantic, breeding in colonies in latitudes ranging between 48° and 74°N (Nelson 2002; Barrett et al. 2017). Northern gannets individuals exhibit a southward-oriented chain migration from the breeding grounds to wintering areas (Fort et al. 2012), showing high site fidelity to their non-breeding destination over the years (Grecian et al. 2019). The pre-winter period, which takes place in September and October, is when birds are assumed to migrate to their wintering area (Nelson 2002; Fort et al. 2012; Grecian et al. 2019). They stay from October to March in the Bay of Biscay (Louzao et al. 2020) and they return to their breeding grounds during February and March (Fort et al. 2012). Northern gannets have a flexible feeding behaviour (Hamer et al. 2007), as they search for food both near the coast and further out in the open sea, in addition to taking advantage of discards from fishing vessels (Valeiras 2003; Votier et al. 2010; Stauss et al. 2012; Le Bot et al. 2019; Louzao et al. 2020; Giménez et al. 2021). The trophic ecology of northern gannets during the breeding season is relatively well-known and widely studied using carbon and nitrogen stable isotopes (Hamer et al. 2000, 2007; Lewis et al. 2003; Grémillet et al. 2006; Stauss et al. 2012; Cleasby et al. 2015; Barrett 2016; Giménez et al. 2021; Clark et al. 2021). However, knowledge of their trophic ecology in wintering areas, particularly in the eastern North Atlantic, remains limited. Grecian et al. (2019) studied the dietary flexibility in the migratory behaviour of northern gannets wintering in the Northeast Atlantic. They identified alternative trophic strategies using stable isotopes analysis. Northern gannets can specialize in fisheries discards or become small forage fish specialists, showing consistencies in diet during the non-breeding season across years. Individuals that wintered in the Bay of Biscay were all assigned to the first trophic strategy (i.e., fisheries discards). However, the specific diet of this species is completely unknown in the Bay of Biscay.

For numerous megafauna species, the Bay of Biscay constitutes a key feeding area during certain periods of the year when marine apex predators, including seabirds, undertake

seasonal feeding migrations into the area (Lezama-Ochoa et al. 2010; Stenhouse et al. 2012). Among those species, the northern gannet has been identified as a central species, as it presents a high number of associations within the marine megafauna and pelagic prey community of the Bay of Biscay during the migration period (Astarloa et al. 2019). Traditionally, stomach contents have been one of the main methods applied to study trophic interactions. While it provides a 'snapshot' of the diet with potential biases (e.g., in favour of species whose hard parts are accumulated in the gut), it allows a detailed taxonomic identification of prey species as well as an estimation of prey size (Pierce and Boyle 1991; Gannon et al. 1997; Spitz et al. 2011; Kiszka et al. 2014). Studying trophic interactions of migratory seabirds in non-breeding areas can be very complex in relation to individual monitoring and trophic data acquisition. Therefore, alternative methods such as stable isotope analysis of nitrogen and carbon in animal tissues are commonly used to study marine predators' trophic ecology (Giménez et al. 2017a; Tixier et al. 2019). Animal tissues can integrate dietary components over different time-frames, depending on the specific turn-over rate of the chosen tissue. Muscle is one of the tissues that integrate for a relatively long period of time (Hesslein et al. 1993; Pinnegar and Polunin 1999), allowing us to investigate the diet of northern gannets focusing on long-term feeding behaviours. The isotopic signature of a consumer's tissues reflects the isotopic signatures of food sources (plus a diet-to-tissue discrimination factor) proportional to their dietary contribution (Bond and Jones 2009; Alexandre 2020). $\delta^{13}\text{C}$ values are generally used as a tracer of the feeding habitat or feeding zone, while $\delta^{15}\text{N}$ values are mainly used as an indicator of the trophic position (France 1995; Hobson 1999). Computational developments such as stable isotope mixing models can also be used to estimate the contribution of sources (prey) to a mixture (predator) (Moore and Semmens 2008). Moreover, it is possible to compare isotopic niche widths and overlap among and within communities using Stable Isotope Bayesian Ellipses (SIBER) (Jackson et al. 2011), which provides insights into how co-occurring species share the resources and the isotopic variance of consumer's diet.

Here, we used stable isotope analysis of carbon and nitrogen to study the trophic ecology of northern gannets and the extent of niche overlap with other apex predators within the Bay of Biscay. Firstly, we estimated the assimilated diet of northern gannets using stable isotope mixing models. We hypothesised that their diet in the Bay of Biscay during the non-breeding period would differ from their diet in northern areas during the breeding period, as the pelagic food web is dominated by different forage fish and northern gannets are known to exhibit great trophic plasticity (Hamer et al. 2007). Then, we assessed the trophic overlap of northern gannets with other apex predators within the megafauna community,

including another seabird species (the common guillemot *Uria aalge*), one large predatory fish (the Atlantic bluefin tuna *Thunnus thynnus*), and five cetaceans (the long-finned pilot whale *Globicephala melas*, the harbour porpoise *P. phocoena*, the striped dolphin *Stenella coeruleoalba*, the short-beaked common dolphin *D. delphis* and the Cuvier's beaked whale *Ziphius cavirostris*). We hypothesised that trophic overlap would exist between different predators foraging in the same habitat and that the two seabird species would present the highest overlap between them. We also expected some overlap between northern gannets and cetaceans foraging near the sea surface, such as the short-beaked common dolphin. Such information on the trophic interactions between co-existing species is needed to improve our understanding of ecosystem structure and functioning.

Materials and methods

Predator data collection

The selection of bird and cetacean species analysed in this study was based on the availability of carcasses, which allowed us to obtain trophic information from species otherwise very difficult to sample. Twenty-nine non-breeding northern gannets collected between 2016 and 2017 on the southern coast of the Bay of Biscay (from Asturias to the Basque Country, North of Spain) were used, see Table S1 (a). Samples were obtained from wildlife recovery centres (only individuals staying alive less than 24 h were sampled to avoid the bias derived from feeding in the recovery centre), stranded bird surveys and beach cleaning services (Franco et al. 2019). Dissections were performed following the methodology of van Franeker (2004). Age and sex were determined according to plumage and the maturity of sexual organs. Information on location, sex (female and male), and maturity stage (juvenile, immature or adult) were registered when possible. In the case of data from wildlife recovery centres, detailed information can be found in García-Barón et al. (2019). Birds were kept frozen (-20°C) until dissection. At the laboratory, northern gannets were dissected and pectoral muscle was sampled for stable isotope analyses.

Concerning other apex predators present in the Bay of Biscay, stable isotope data were obtained for: (a) common guillemots (*Uria aalge*; $n = 50$), from the same previous sampling programme as northern gannets (Franco et al. 2019), (b) Atlantic bluefin tunas (*T. thynnus*; $n = 120$), from commercial fishing in the oceanic waters of the Bay of Biscay in 2009 (Goñi et al. 2010), and (c) five cetacean species stranded along the French coast of the Bay of Biscay, recovered and examined by members of the French Stranding Network between 2000 and 2009: long-finned pilot whales (*G. melas*; $n = 16$), harbour porpoises (*P. phocoena*;

$n = 10$), striped dolphins (*S. coeruleoalba*; $n = 11$), short-beaked common dolphins (*Delphinus delphis*; $n = 26$) and Cuvier's beaked whales (*Z. cavirostris*; $n = 11$) (Chouvelon et al. 2012). Atlantic bluefin tunas were divided into two separate groups, juveniles vs. adults. Seabird and cetacean muscles were delipidated before stable isotope analyses as lipids can affect the $\delta^{13}\text{C}$ values (Bond and Jones 2009; Giménez et al. 2017b), whereas tuna samples were not originally delipidated before stable isotope analyses. Therefore, a posterior mathematical correction was applied on $\delta^{13}\text{C}$ values of tunas, following Logan et al. (2008).

Prey data collection

The diet of northern gannets is not fully known in the Bay of Biscay, but it has been studied in northern European breeding locations (Hamer et al. 2000, 2007; Lewis et al. 2003; Grémillet et al. 2006; Barrett 2016). Therefore, potential prey species were selected according to the following five criteria (see Table 1);

- Taxonomically similar (at the family level) prey species, identified based on regurgitates from the breeding colonies (Hamer et al. 2000, 2007; Lewis et al. 2003; Grémillet et al. 2006; Barrett 2016), showing a medium or high abundance in the Bay of Biscay using AquaMaps information (Kaschner et al. 2019) and AZTI abundance database. Therefore, we excluded absent and scarce species in our study area. The selected species included the Atlantic mackerel (*S. scombrus*), the European sprat (*S. sprattus*), the whiting (*Merlangius merlangius*) and the red gurnard (*Aspitrigla cuculus*);
- Distributional co-occurrence patterns validated with trophic evidence (Astarloa et al. 2019), which included the Atlantic horse mackerel (*T. trachurus*) and the European sardine (*S. pilchardus*);
- Alternative prey species of the Gadidae and Triglidae families, as these families were detected in the diet information on the breeding colonies (Hamer et al. 2000, 2007; Lewis et al. 2003; Grémillet et al. 2006), with medium to high abundance in the Bay of Biscay. These species corresponded to the pouting (*Trisopterus luscus*), the poor cod (*T. minutus*), the blue whiting (*Micromesistius poutassou*), the tub gurnard (*Chelidonichthys lucerna*) and the grey gurnard (*Eutrigla gurnardus*);
- Important discarded species in terms of biomass in the Bay of Biscay (i.e., the juvenile European hake) (Rochet et al. 2014; Valeiras et al. 2015); and
- The European anchovy (*E. encrasicolus*) as it is a highly abundant pelagic species in the Bay of Biscay (Boyra et al. 2013; Masse et al. 2018). This species has not been reported in the diet of northern gannets during the breed-

Table 1 Descriptive table of prey stable isotope data used in mixing models

Family	Species common name	Species scientific name	Abundance Bay of Biscay	<i>n</i>	Mean $\delta^{13}\text{C} \pm \text{SD}$	Mean $\delta^{15}\text{N} \pm \text{SD}$	Source
a) Diet evidence in breeding areas							
Scombridae	Atlantic mackerel	<i>Scomber scombrus</i>	High	30	-18.31 ± 0.67	11.81 ± 0.55	JUVENA survey
Clupeidae	European sprat	<i>Sprattus sprattus</i>	Medium–high	10	-17.91 ± 0.19	11.99 ± 0.40	JUVENA survey
Gadidae	Whiting	<i>Merlangius merlangus</i>	Medium-high	32	-16.80 ± 0.30	14.30 ± 0.60	Chouvelon et al. (2012)
Triglidae	Red gurnard	<i>Aspitrigla cuculus</i>	High	10	-17.20 ± 0.30	13.10 ± 0.60	Chouvelon et al. (2012)
b) Co-occurrence							
Carangidae	Atlantic horse mackerel	<i>Trachurus trachurus</i>	High	41	-18.52 ± 0.32	12.11 ± 0.42	JUVENA survey
Clupeidae	European sardine	<i>Sardina pilchardus</i>	High	30	-17.89 ± 0.71	11.78 ± 0.41	JUVENA survey
c) Alternative prey							
Gadidae	Pouting	<i>Trisopterus luscus</i>	High	14	-16.60 ± 0.30	14.10 ± 0.20	Chouvelon et al. (2012)
Gadidae	Poor cod	<i>Trisopterus minutus</i>	Medium-high	65	-17.10 ± 0.40	13.10 ± 0.60	Chouvelon et al. (2012)
Gadidae	Blue whiting	<i>Micromesistius poutassou</i>	High	78	-18.20 ± 0.50	11.10 ± 0.70	Chouvelon et al. (2012)
Triglidae	Tub gurnard	<i>Chelidonichthys lucerna</i>	High	5	-16.80 ± 0.60	13.20 ± 0.50	Chouvelon et al. (2012)
Triglidae	Grey gurnard	<i>Eutrigla gurnardus</i>	High	18	-16.90 ± 0.30	13.10 ± 0.50	Chouvelon et al. (2012)
d) Discards (with trophic evidence)							
Merlucciidae	European hake	<i>Merluccius merluccius</i>	High	57	-18.10 ± 0.40	12.20 ± 0.70	Chouvelon et al. (2012)
e) High abundance species							
Engraulidae	European anchovy	<i>Engraulis encrasicolus</i>	High	50	-18.82 ± 0.53	10.55 ± 1.16	JUVENA survey

Only potential prey with medium to high abundance in the Bay of Biscay were considered based on: (a) diet evidence in breeding areas, (b) spatial co-occurrence in the Bay of Biscay (Astarloa et al. 2019), (c) alternative prey of the same family of the species consumed in the breeding areas with medium to high abundance in the Bay of Biscay, (d) discarded species with trophic evidence, and (e) highly abundant species in the Bay of Biscay. *SD* standard deviation

ing season as anchovies are relatively scarce in the areas where northern gannets breed. However, anchovies do represent an important feeding resource for similar taxonomic species in other biogeographical areas (e.g., the cape gannet *Morus capensis* in the southern hemisphere) (Pichegru et al. 2007; Connan et al. 2017). Therefore, it was considered as a potential prey.

In summary, 13 species were considered as potential prey species of non-breeding northern gannets in the Bay of Biscay (Table 1). Pelagic prey samples (European anchovy, European sardine, Atlantic horse mackerel, Atlantic mackerel and European sprat) were obtained from the JUVENA annual integrated ecosystem surveys in September 2013. From each specimen, a sample of white muscle from the dorsal myotome (away from the dorsal fin) was taken and then stored frozen at $-20\text{ }^{\circ}\text{C}$. For the remaining potential prey

species, stable isotope values were taken from (Chouvelon et al. 2012). For detailed information about the number of individuals collected per year for each of these prey species (collection in autumn (October) each year, on “EVHOE” fishery surveys, Chouvelon et al. 2012), see Table S1 (b). For whiting and hake species, individuals $\leq 350\text{ mm}$ were selected and for blue whiting $< 300\text{ mm}$. We assumed that larger prey would be rarely consumed based on the diet consumed on colonies (Hamer et al. 2000, 2007; Lewis et al. 2003; Barrett 2016).

North Norwegian gannets target four main prey during the chick-rearing period; herring *Clupea harengus*, mackerel, sandeels and saithe *Pollachius virens* (Barrett 2016). However, herring, sandeels and saithe were not considered as potential prey species in the Bay of Biscay. Herring is absent in the southern part of the Bay of Biscay and their abundance in the northern part is low. Although sandeels are an important component ($> 25\%$) of the diet of breeding

gannets in northern Europe, they were not considered in the mixing model as the species has a very low abundance or is even absent in some areas of the Bay of Biscay. Saithe ranges from the Barents Sea to the north of the Bay of Biscay in the eastern Atlantic. However, the abundance in the Bay of Biscay is negligible (Kaschner et al. 2019). Garfish *Belone belone* has also been detected in the diet of northern gannets. In the Rouzic Island colony, in France, it appears to be an important prey item (Grémillet et al. 2006). However, its occurrence and biomass are documented as low in the Bay of Biscay (Hamer et al. 2000, 2007; Lewis et al. 2003), as it is only found in the northern part and with rather low abundance (Kaschner et al. 2019). In the Western hemisphere, capelin *Mallotus villosus* is a large contributor to the biomass of prey in the north-west Atlantic (Monteverchi 1997). However, this species is not found in the Bay of Biscay (Kaschner et al. 2019).

Stable isotope analyses

Northern gannets, common guillemots and pelagic prey stable isotope analyses were carried out at the “Laboratorio de Isótopos Estables–Estación Biológica de Doñana” (LIE-EBD, Spain; www.ebd.csic.es). All samples were delipidated previously to stable isotope measurements by sequential extractions with 2:1 chloroform:methanol solution. Isotopic analysis was performed using a continuous-flow isotope-ratio mass spectrometry system by means of Flash HT Plus coupled to an elemental analyser, Delta-V Advantage isotope ratio mass spectrometer via a CONFLO IV interface (Thermo Fisher Scientific, Bremen, Germany). Replicate assays of standards routinely inserted within the sampling sequence indicated analytical measurement errors of ± 0.1 ‰ and ± 0.2 ‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

Atlantic bluefin tuna muscle samples were thawed, lightly rinsed with deionized water, and dried in glass scintillation vials at 60 °C for at least 48 h. Samples were homogenized to obtain a fine powder. Aliquots of the homogenized samples (0.6–1.2 mg) were packed into tin cups and analysed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ by continuous flow, using an elemental analyser coupled with an isotope ratio mass spectrometer.

With the exception of European anchovy, European sardine, Atlantic horse mackerel, Atlantic mackerel and European sprat, prey samples and also cetacean muscle samples were freeze-dried, homogenised to powder and delipidated using cyclohexane, as described by Chouvelon et al. (2011). Then 0.40 ± 0.05 mg subsamples of lipid-free powder were weighed for stable isotope analyses. Isotopic analyses were performed with an elemental analyser coupled to a Thermo Scientific Delta V Advantage mass spectrometer coupled to a Thermo Scientific Flash EA1112 elemental analyser. Based on replicate measurements of internal laboratory standards,

the experimental precision was ± 0.15 ‰ and ± 0.20 ‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively (Chouvelon et al. 2012).

All isotopic compositions are reported in delta (δ) per mil notation (‰), relative to Vienna Pee Dee Belemnite and atmospheric N_2 .

Isotopic mixing models

Bayesian isotopic mixing models were applied using the R-package “MixSIAR” (Stock and Semmens 2016a) to estimate the proportional contribution of potential prey taxa to the diet of northern gannets. As the discrimination power declines remarkably with an increasing number of potential prey sources (Phillips et al. 2014), a priori aggregation of isotopically similar sources was done. Ward’s Hierarchical cluster analysis based on the similarities of isotopic values was conducted to group prey species before model fitting, as recommended by Phillips et al. (2014).

When studying the trophic ecology of migratory species, the tissue turnover must be taken into consideration. The period for which isotopic values reflect diet depends upon the isotopic turnover rate in that tissue (Hobson and Clark 1993). Tissues with high turnover rates, such as liver and plasma, reflect recent diet while tissues such as muscle present slower turnover rates and reflect longer-term dietary average (Hobson and Clark 1993). However, isotopic turnover rates in birds are poorly understood. In the case of the bird muscle tissue, Hobson and Clark (1992) established a half-life turnover rate of 12.4 days for $\delta^{13}\text{C}$ in captive individuals of the grown Japanese quail (*Coturnix japonica*). Similar estimates were found for other species such as the zebra finch (*Taeniopygia guttata*), the house sparrow (*Passer domesticus*) or chickens (*Gallus gallus domesticus*), with turnover rates varying between 14.5–18.1, 23.5, and 2.4–10 days respectively (Cruz et al. 2005; Carleton et al. 2008; Bauchinger and McWilliams 2009). Accordingly, we only selected muscle for northern gannets during the non-breeding period, from October to March, considering a complete turnover of one month.

As no specific experimental diet to muscle discrimination factor is available for gannets, we used the taxonomically closer value available. Thus, mixing models were fitted with the diet to muscle discrimination factor obtained from Ring-billed gulls (*Larus delawarensis*) (Hobson and Clark 1992). Values used were 0.3 ± 0.4 ‰ for $\delta^{13}\text{C}$ and 1.4 ± 0.1 ‰ for $\delta^{15}\text{N}$ (Hobson and Clark 1992). A mixing polygon following Smith et al. (2013) was constructed to evaluate the isotopic mixing model and to identify consumers whose isotopic signature is unlikely to be explained by the proposed putative prey. Consumers that are not within the 95% mixing region ($n = 8$) must be removed from the mixing model to proceed, as recommended by Smith et al. (2013). The reasons why a consumer falls outside the mixing polygon can be diverse,

such as the inaccuracy of the diet-to-tissue discrimination factor, the lack of a consumed prey, individual specialization or simply some outliers due to contamination, to an error in the isotopic measurement or during the sampling process. We used an “uninformative”/generalist prior to run the mixing models because we did not have previous knowledge about the proportions of each species consumed by northern gannets in the Bay of Biscay. The model was run in a long setting (300,000 chains, using the Markov chain Monte Carlo (MCMC) technique and a burn-in of 200,000 draws, a thinning of 100 and 3 chains) (Stock and Semmens 2016a).

Sex (female or male) and maturity stage (juvenile, immature and adult) were included in the models as fixed covariates (Table S2). Then, we evaluated the relative support for each model. The multiplicative residual \times process error structure was used in all cases as recommended by Stock and Semmens (2016a, b). The function `compare_models` from the “MixSIAR” R-package was used to compare the predictive accuracy of the models constructed (Stock and Semmens 2016a). The relative support for each model was calculated using Leave-One-Out cross-validation (LOO) weights (Vehtari et al. 2017). Model convergence was assessed with the Gelman-Rubin diagnostic, which compares estimates of variance between and within Markov chains, with values < 1.01 indicating convergence (Gelman et al. 2013).

Isotopic niche area and overlap

To investigate isotopic niche space and isotopic niche overlap among predator species, we used Stable Isotope Bayesian

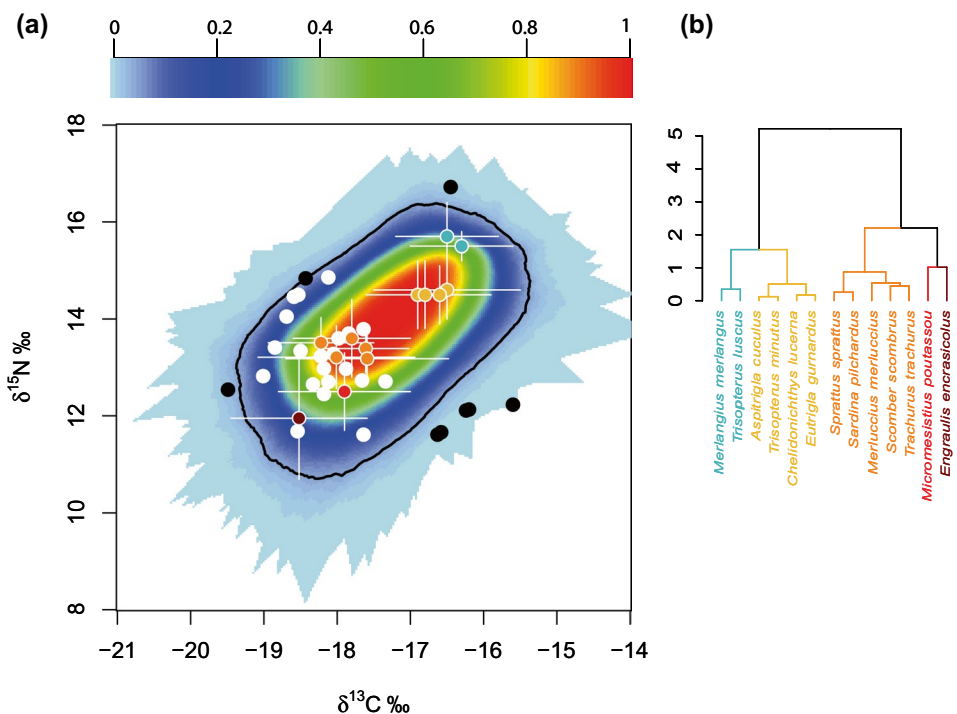
Ellipses in the “SIBER” R-package (Jackson et al. 2011). Standard ellipses represent the core isotopic niche for a species (*ca.* 40% of the data). Standard ellipses areas were corrected for small sample sizes (SEA_c) to be able to compute the overlap of species. Furthermore, its Bayesian equivalent (SEA_b) was also calculated to have a measure of uncertainty through computing credible intervals around the measurement, with the aim of evaluating the variability in the isotopic niche area (Jackson et al. 2011).

Results

Isotopic mixing models

Twenty-one out of the twenty-nine isotopic signatures from northern gannets fell inside the 95% mixing region defined by potential prey adjusted by diet-to-tissue discrimination factors (DTDF) and were kept for the analysis (Fig. 1a). In addition, two additional individuals were not included in the models as information on sex was missing. Then, from the original 29 individuals, only 19 could be included in the mixing model analysis (12 females and 7 males of those 6 were immature, 11 juvenile and 2 adult individuals). Ward’s hierarchical clustering of the stable isotope values of potential prey identified 5 isotopically different clusters (Fig. 1b). Cluster 1 was composed by whiting and pouting, Cluster 2 by red gurnard, poor cod, tub gurnard and grey gurnard, Cluster 3 by European sardine, European sprat, juvenile

Fig. 1 **a** Mixing polygon for predator-prey $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data. Northern gannets are represented as white and black dots corresponding to analysed and excluded individuals, respectively. The potential prey sources (mean \pm SD) are represented as colour dots (corresponding to the species present in the dendrogram) and white error bars. Probability contours are coloured every 10% level. **b** Ward’s hierarchical clustering of the potential prey species, aggregated into 5 groups



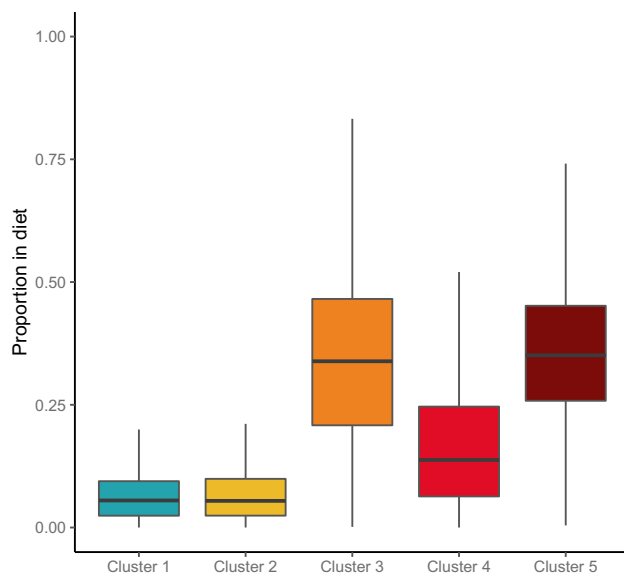


Fig. 2 Diet proportions in the different clusters of wintering northern gannets in the Bay of Biscay. Cluster 1: whiting (*M. merlangus*), pouting (*T. luscus*); Cluster 2: red gurnard (*A. cuculus*), poor cod (*T. minutus*), tub gurnard (*C. lucerna*), grey gurnard (*E. gurnardus*); Cluster 3: European sprat (*S. sprattus*), European sardine (*S. pilchardus*), European hake (*M. merluccius*), Atlantic mackerel (*S. scombrus*), Atlantic horse mackerel (*T. trachurus*); Cluster 4: blue whiting (*M. poutassou*); Cluster 5: European anchovy (*E. encrasicolus*). Black horizontal line depicts the median value

hake, Atlantic mackerel and Atlantic horse mackerel, Cluster 4 by blue whiting and finally Cluster 5 by European anchovy.

Among the four models tested (see Table S2), the best model did not include any covariate (model weight: 33.7%). According to the best model, the highest median contributions to the diet of northern gannets in the Bay of Biscay were those of Cluster 3 and Cluster 5, with a median contribution of 33.9% (5.5–63.1) and 35% (12.3–60.4), respectively (Fig. 2).

Predator isotopic niche area

Some niche overlap (> 10%) was found between northern gannets' isotopic niche and other predator species niches. Specifically, the northern gannets isotopic niche overlapped the most with those of common guillemots (15.6%), followed by the short-beaked common dolphin (10.4%) and the harbour porpoise (10%) (Fig. 3a, Table S3). For all niche overlaps see Table S3. Remaining species showed low overlap with northern gannets (< 10%) such as the long-finned pilot whale (6.5%), the striped dolphin (2%), the Cuvier's whale (0.2%) and both adults (0%) and juveniles of the Atlantic bluefin tuna (0.1%). Among the megafauna community, northern gannets had the largest isotopic niche area (3.5 ‰²), followed by the long-finned pilot whale (2.7 ‰²) and the Atlantic bluefin tuna (adults: 2 ‰²; juveniles: 1.3 ‰²), while common guillemots (0.6 ‰²) and the Cuvier's beaked whale (0.3 ‰²) occupied the smallest isotopic niche areas

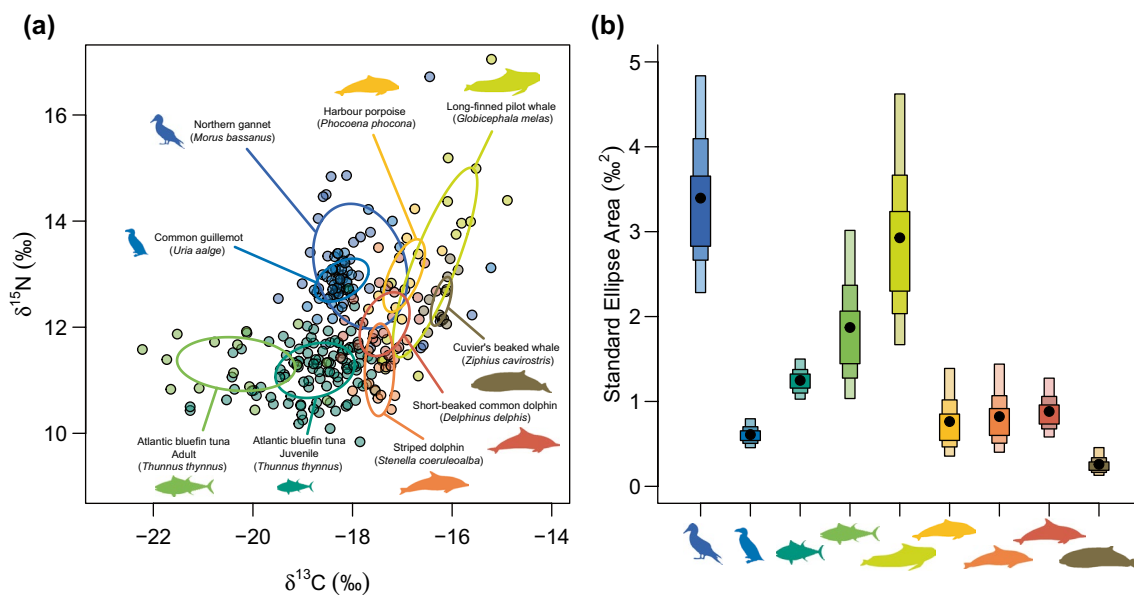


Fig. 3 **a** Standard Ellipse Area corrected (SEAc) for the top predator community of the Bay of Biscay. Northern gannet (*M. bassanus*), common guillemot (*U. aalge*), Atlantic bluefin tuna (*T. thynnus*) juveniles (j) and adults (a) groups, long-finned pilot whale (*G. melas*), harbour porpoise (*P. phocoena*), striped dolphin (*S. coeruleoalba*),

short-beaked common dolphin (*D. delphis*) and Cuvier's beaked whale (*Z. cavirostris*). **b** Density plot showing Bayesian estimated posterior distributions of isotopic niche size (SEAb) with 50, 75 and 95% credible intervals in shaded boxes, and mean values of SEAb indicated by black dots

(Fig. 3b, Table S4). The Kruskal–Wallis rank-sum test and the Dunn's posthoc test indicated the existence of statistical differences between all species considered (Kruskal–Wallis test: Chi square = 31,974, $p > 0.01$, $df = 8$, Dunn's posthoc test: all p -values < 0.01).

Discussion

Elucidating the diet of northern gannets in time and space is fundamental to fully understand the trophic ecology of this species. In this study, we estimated that pelagic fish are the main contributors to northern gannets' diet in the Bay of Biscay. We also found that northern gannets trophic niche overlapped the most with common guillemots and overlapped to a lesser extent with cetacean species occupying shelf habitats. These results improve our knowledge of how northern gannets interacts with prey and other predators in the Bay of Biscay, which is essential to discern the structure of the pelagic community (Boyd et al. 2006; Speed et al. 2012).

Trophic ecology of northern gannets

In the Bay of Biscay, mixing models suggested that northern gannets primarily consumed European anchovies and a mixed group of species composed by the European sardine, the European sprat, juveniles of the European hake, the Atlantic mackerel and the Atlantic horse mackerel. The European anchovy was identified as an important potential prey, as it is highly abundant in the Bay of Biscay (Boyra et al. 2013; Masse et al. 2018), and northern gannets and European anchovies share the same habitats, with both species feeding in both neritic and offshore areas (Chouvelon et al. 2014). The Atlantic mackerel and the European sprat are also common and abundant prey consumed by northern gannets in their breeding locations (Hamer et al. 2000, 2007; Lewis et al. 2003; Grémillet et al. 2006; Barrett 2016), and these two prey species also share similar habitat preferences (i.e., pelagic and neritic habitats) with northern gannets in the Bay of Biscay (Astarloa et al. 2019). The Atlantic horse mackerel and juveniles of the European hake have been described to be less relevant species in the diet of northern gannets from northern Europe (Lewis et al. 2003), although they are still present in their diet. The Atlantic horse mackerel, together with the European sardine, represent potential prey species of northern gannets in the Bay of Biscay according to co-occurrence analysis (Astarloa et al. 2019), while the European hake is the most abundant predatory fish in the demersal community of the Bay of Biscay (ICES 2019), available to northern gannets mostly through fisheries discards of the commercial trawling fleet (Rochet et al. 2014; Valeiras et al. 2015).

Remaining potential prey groups contributed less than 20% to the overall northern gannets' diet. One of the clusters was composed of the blue whiting, which is an abundant species in the area (Sánchez et al. 2002) and one of the most discarded species in the Bay of Biscay (Valeiras 2003). Blue whiting is a species inhabiting deeper waters of the continental shelf and slope, which may be consumed by northern gannets mostly when feeding on fishing discards. Remaining clusters were composed of demersal species of the Gadidae and Triglidae families and contributed the least to the diet of northern gannets in the Bay of Biscay. Most of the analysed species from these families were identified in the diet of northern gannets in northern Europe, such as whiting and red and grey gurnards (Hamer et al. 2000, 2007; Lewis et al. 2003). Gadoids are an important food resource in other foraging areas (Hamer et al. 2000, 2007; Lewis et al. 2003), but their contribution to the diet of northern gannets in the Bay of Biscay in winter appeared to be negligible.

Apex predator community

The comparison of isotopic niche areas among the apex predator community allowed us to determine differences and similarities in trophic niche space utilization (Jackson et al. 2011; Giménez et al. 2018). Northern gannets had the largest isotopic niche area, followed by the long-finned pilot whale. The variation in the isotopic niche width is mainly observed for $\delta^{15}\text{N}$ values, which likely reflects the consumption of prey species of different trophic levels (Bearhop et al. 2004). The long-finned pilot whale had the second-largest isotopic niche area, which can be explained by the fact that this species forages in different habitats, consuming both oceanic and neritic species (Spitz et al. 2011). Common guillemots had the smallest isotopic niche area, indicating a more specialized trophic behaviour. Previous studies showed that during the non-breeding season they consume small readily digestible fish of high energy density (Hislop et al. 1991). The common guillemot' narrower $\delta^{13}\text{C}$ width could also indicate a more restricted feeding zone (Hobson 1999).

Within the analysed megafauna community, some niche overlap ($> 10\%$) was found between northern gannets and other predator species such as common guillemots, harbour porpoises and short-beaked common dolphins. The northern gannet is widely distributed over the continental shelf and frontal areas, and it is possible to observe the species in slope areas as well (Camphuysen 2011; Louzao et al. 2019), coexisting with most of the apex predators considered in this study (Camphuysen and Webb 1999; Veit and Harrison 2017). Northern gannets and common guillemots were the only seabird species considered here and common guillemots had a small niche that overlaps almost entirely with northern gannets' niche. These results are in agreement with at-sea observations, in which northern gannets and common

guillemots have been observed feeding sympatrically in the northwest Atlantic (Bennett et al. 2013). Both species benefit from multispecies flock feeding (Camphuysen and Webb 1999), a strategy in which a group of different seabird species join each other and ‘operate’ together while foraging (Hoffman et al. 1981). In addition, relevant species in the diet of northern gannets in the Bay of Biscay such as the horse mackerel and the sprat were also found in the stomachs of common guillemots (Blake et al. 1985; Ouweland et al. 2004; Sonntag and Hüppop 2005 and Franco pers. comm.). The difference in niche widths could be associated with the more flexible trophic behaviour of northern gannets in comparison with common guillemots, which have a more specialized trophic behaviour. The two seabird species studied here are abundant species, especially during winter. However, further studies including the most abundant seabird species throughout the annual cycle, such as larids and procellariids (Franco et al. 2004; ICES 2019) would help unravel the isotopic niche partitioning among seabird species, and better understand the interactions occurring between them in the Bay of Biscay.

Concerning the overlap with cetaceans, northern gannets have also been reported in association with harbour porpoises, which facilitates feeding resource acquisition by driving prey to the surface (Camphuysen and Webb 1999). The harbour porpoise is a neritic species commonly found on the northern continental shelf of the Bay of Biscay (Lambert et al. 2017; Laran et al. 2017). It feeds on pelagic schooling fish species (e.g. mackerel), but also on demersal (e.g., hake) and benthic fish (e.g., whiting) (Santos and Pierce 2003; Spitz et al. 2006b), which can explain the overlap seen with northern gannets but also with other piscivorous marine predators of this study (Santos and Pierce 2003). The common dolphin can be found in both neritic and oceanic areas (Lambert et al. 2017; Laran et al. 2017), feeding preferentially on small pelagic fish (sardine, anchovy, sprat and horse mackerel) in the neritic area (Meynier et al. 2008), coinciding with the main prey of northern gannets (this study).

Other cetaceans such as the striped dolphin, the long-finned pilot whale, the Cuvier’s beaked whale along with the bluefin tuna, presented low overlap with northern gannets. The habitat of the striped dolphin is mainly oceanic (Spitz et al. 2006a; Ringelstein et al. 2006), but its diet in the Bay of Biscay appears to be a combination of both oceanic and neritic species including fish and cephalopods, maybe due to temporary incursions over the shelf (Spitz et al. 2006a). The oceanic prey species of this dolphin species are all from the vertically migrating mesopelagic community, while the neritic ones are mostly epibenthic (Spitz et al. 2006a). In the case of the long-finned pilot whale, this oceanic cetacean is frequently associated with the continental slope (Abend and Smith 1999; Cañadas and Sagarminaga 2000) and feeds

primarily on small cephalopods, but it also consumes demersal and pelagic fish, such as the hake and the horse mackerel (Spitz et al. 2011). Finally, the highly oceanic habits of both the Cuvier’s beaked whale and the Atlantic bluefin tuna compared to those of northern gannets, together with differences in prey preferences (Spitz et al. 2011; Varela et al. 2013), can explain the low overlap observed with northern gannets.

Limits of the isotopic approach

Our results should be interpreted carefully. Information derived from stable isotope analysis should be combined with information derived from other approaches, such as stomach content analysis (Hamer et al. 2000, 2007; Lewis et al. 2003), fatty acids (Owen et al. 2013) and DNA metabarcoding (Carreiro et al. 2020) to fully elucidate the trophic ecology of the species in the Bay of Biscay. Also, samples were taken from the same biogeographic area but from different years and specific locations, which could potentially generate some biases. At the ecosystem scale, temporal variations found in Chouvelon et al. (2012) suggested that ecological studies conducted using stable isotopes should be sampled over short time periods. However, it may be possible to use individuals sampled over several years to obtain an average value for certain species (Chouvelon et al. 2012) whose biological material is rarely obtained (i.e., strandings of protected species).

Stranded animals could present potential bias in stable isotope analysis due to fasting. Starving animals “feed on themselves” while drawing on their endogenous reserves, the mechanism by which their tissues become enriched in ^{15}N (Gannes et al. 1997). Depending on a bird’s life stage, body condition and strategy for dealing with intermittent food shortages, enrichment in $\delta^{15}\text{N}$ may or may not occur (Sears et al. 2008). A wide variety of birds spontaneously fast in association with breeding, incubation, migration, and moulting (Cherel et al. 1988) or they can be routinely exposed to variable food availability (Durant et al. 2004).

For instance, significant enrichment in $\delta^{15}\text{N}$ occurred in the muscle tissue of both nutritionally stressed captive and fasting wild birds during incubation (Hobson et al. 1993). Nevertheless, other studies failed in finding any evidence of $\delta^{15}\text{N}$ enrichment in response to nutritional stress in birds (Gloutney et al. 1999; Kempster et al. 2007). Species-specific divergences in physiological response to nutritional restriction may be responsible for divergences between studies (Williams et al. 2007). Therefore, although $\delta^{15}\text{N}$ enrichment in response to fasting may not be a universally applicable pattern across all circumstances, we should consider it as a potential bias.

Tissue decomposition could also influence isotopic signatures of stranded individuals. However, changes in the

magnitude of the isotopic signature appeared to be negligible up to eight days in the air and four days under water (Yurkowski et al. 2017; Peiman et al. 2021). Thus, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values derived from tissue rotting for a week are reliable and useable for stable isotope analysis. Meanwhile, Payo-Payo et al. (2013) did not detect any evidence of change over time in decomposing muscle samples exposed to air and reaching an advanced decomposition stage. In our study, the stranded species analysed were fresh or in a moderate decomposition stage, therefore not generating any bias in this study as far as we know.

The muscle samples of northern gannets were collected relying on availability, which led us to a bigger sample of females than males to run the mixing models (12 females vs 7 males), which could result in a sex bias (Fig. S1). Furthermore, no experimental diet to muscle discrimination factor was available for gannets; therefore, we used the value for the taxonomically closer species available, i.e. the ring-billed gull (*Larus delawarensis*) (Hobson and Clark 1992). Despite being the most appropriate discrimination factor currently available, we thus have to be careful when interpreting the results as the use of inappropriate discrimination factors can bias the results (Barton et al. 2019).

Conclusions

The European anchovy, the European sardine, the European sprat, juveniles of the European hake, the Atlantic mackerel and the Atlantic horse mackerel were identified as the main contributors to northern gannets' diet in the Bay of Biscay, with a low contribution of demersal prey species. This indicates that demersal discards are not a big component of the diet within the wintering northern gannets in the Bay of Biscay, suggesting that foraging on small pelagic species is the preferential strategy in this area. However, species such as the Atlantic mackerel and the Atlantic horse mackerel can be discarded due to quota exhaustion or because they are under the minimum landing size (Valeiras et al. 2015). Therefore, in this case, we cannot discern the strategy used when northern gannets forage on these species. Different trophic strategies were detected in this seabird species; northern gannets can specialize on fisheries discards or become small forage fish specialists (Bodey et al. 2018; Grecian et al. 2019), showing consistencies in movement and diet during the non-breeding season over the years (Grecian et al. 2019). Trophic niche overlap was found with common guillemots and, to a lesser extent, with some cetacean species, which can be explained by the similarities in their habitat and prey preferences. We cannot fully elucidate the reason for the large isotopic niche area of northern gannets, but it could be associated with a flexible trophic behaviour due to changes in resource availability, which was already identified in

previous studies, with a more widespread spatial distribution at sea leading to isotopic niche expansion and/or due to a mixture of individuals of variable condition and sampling years. The network of feeding interactions between co-existing species is needed knowledge to improve our understanding of ecosystem structure and functioning. This knowledge can be used in an ecosystem-based management approach, which is critical to predict and manage the consequences of environmental variability and human impacts, particularly in areas such as the Bay of Biscay, where several megafauna species share their foraging grounds with fisheries activity.

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Author contributions ML and JG: conceived the study; ML, JF, TC, NG and CG: collected the data; CG and JG: performed the analysis; JG: produced the plots; CG: led the writing of the manuscript with input from JG and ML: all authors mentioned before and XC, EA, AA, PB and JS: contributed to subsequent revisions, agreed to be listed and approved the submitted version of the manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors have no competing interests to disclose.

Ethical approval No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with carcasses of mammals and seabirds, and fish were obtained from scientific and commercial fishing activities. The seabirds tissue samples were obtained from wildlife recovery centres, stranded bird surveys and beach cleaning services. The five cetacean species stranded were recovered and examined by members of the French Stranding Network. Tissue samples of the Atlantic Bluefin tuna used in this study were collected from commercial fishing in the oceanic waters of the Bay of Biscay within the Total Allowed Catch quotas assigned by the International Commission for the Conservation of Atlantic Tunas (ICCAT). Other fish species tissue samples were obtained from JUVENA, EVHOE and PELGAS surveys.

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