Wait your turn, North Atlantic fin whales share a common feeding ground sequentially

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1. ABSTRACT

Highly migratory marine species pose a challenge for the identification of management units due to the absence of clear oceanographic barriers. The population structure of North Atlantic fin whales has been investigated since the start of whaling operations but is still the subject of an ongoing scientific debate. Here we measured stable isotopes of carbon, nitrogen and oxygen in skin samples collected from 151 individuals from western Iceland, Galicia (NW Spain), the Azores archipelago and the Strait of Gibraltar (SoG). We found spatiotemporal differences in stable isotope ratios suggesting that fin whales sampled in these four areas may share a common feeding ground within the Northeast Atlantic at different times during the year. Our results also suggest that SoG whales use this common feeding ground in summer but exploit Mediterranean resources during the winter months, further supporting the existence of a limited but current exchange of individuals between these two basins.

1. Introduction

Species that occur over wide ranges present diverse distribution patterns. These encompass from a discrete distribution of small home ranges with limited overlap for highly territorial species (Ables, 1969; Herfindal et al., 2005), to a continuous distribution characterized by large home ranges shared with other conspecifics and often including migratory movements between breeding and feeding areas (Guilford et al., 2012; Harris et al., 2009). In the latter case, drawing boundaries between different populations, subpopulations or stocks can be especially challenging, particularly in the marine environment. The lack of well-defined geographical barriers and the presence of dynamic oceanographic processes may result in pelagic species spanning over entire ocean basins (e.g. Horton et al., 2017). Moreover, divergent subpopulations may share the same feeding grounds (Ansmann et al., 2015; Lahanas et al., 1998) and, conversely, one panmictic subpopulation may forage in separate areas, a fact that is sometimes associated to sex or age segregation (Breed et al., 2006; Caut et al., 2008; Engelhaupt et al., 2009). Additionally, spatiotemporal distribution and migration patterns can depend on habitat quality and availability which, in turn, are affected by natural changes such as periodic environmental oscillations (e.g. El Niño) (Barbraud and Weimerskirch, 2003; Salvadeo et al., 2011), and direct or indirect anthropogenic factors such as habitat degradation, harassment by whale watching boats, maritime shipping or climate change (Ramp et al., 2015; Rolland et al., 2012). Uncontrolled whaling is another demonstrated cause for disruption of migratory routes and

abandonment of feeding or breeding grounds by marine mammals (Clapham et al., 2008). In some areas where whales went commercially extinct no recolonization of relatively small geographic territories has occurred. This may be explained by the loss of cultural memory about these habitats, by adjacent stocks being too small or too distant to allow recolonization and/or by post-whaling segregation that would produce the abandonment of particular areas (Clapham et al., 2008).

The fin whale (*Balaenoptera physalus*) is a cosmopolitan species present from polar to subtropical regions (Edwards et al., 2015) where it exhibits different migration strategies (Geijer et al., 2016). Its subpopulation structure has been extensively studied in the North Atlantic associated to the intense whaling operations that took place since the last quarter of the 19th century (Aguilar, 2013; Jonsgård, 1966; Tønnessen and Johnsen, 1982). From 1864 until the moment when the moratorium on commercial whaling established by the International Whaling Commission (IWC) came into force in 1985, around 100,000 fin whales were caught in the North Atlantic, causing a drastic decrease in the abundance of the species in the basin (International Whaling Commission, 2009; Tønnessen and Johnsen, 1982). Since the 1990s, about 1000 individuals have been caught; 700 off Iceland as commercial catches taken under reservation to the moratorium, and 300 off West Greenland as aboriginal subsistence catches (data available until 2015 https://iwc.int/catches). Since the initiation of regular surveys in the mid 1980s, population trends indicate increasing population numbers (Pike et al., 2019; Víkingsson et al., 2009) and it has been proposed that the full recovery of the species in the North Atlantic had been completed by 2000 (Cooke, 2018; Víkingsson et al., 2009, 2015). This has led the International Union for the Conservation of Nature to change the species global conservation status from Endangered to Vulnerable in 2018 (Cooke, 2018). However, not all areas show the same recovery capacity within the North Atlantic Ocean. While there seems to be a substantial increase around East Greenland–Iceland–Faroe islands (Pike et al., 2019; Víkingsson et al., 2009), little change was observed in the Bay of Biscay since 1989 (Hammond et al., 2017; Lens et al., 1989). More strikingly, currently few animals are recorded in the once frequently-used area near the Strait of Gibraltar (SoG) (Gauffier et al., 2018; Sanpera and Aguilar, 1992). In its assessment work on North Atlantic fin whales using the Revised Management Procedure (RMP), the IWC has incorporated seven stock structure hypotheses for the North Atlantic based on a suite of genetic and non-genetic information (International Whaling Commission, 2017, 2009). These hypotheses include 2–6 breeding stocks/sub-stocks and up to seven feeding sub-areas allowing for varying degrees of mixing and/or dispersions between these areas (Fig. 1); within this framework, the eastern North Atlantic is split into four feeding sub-areas: West-Iceland (WI), East-Iceland-Faroe-islands (EI + F) and Norway (N) above 50-52°N, and the Spain-Portugal-British-Isles (S) below 50-52°N. The latter encompasses southern Ireland and the UK, the entire Bay of Biscay, Portuguese waters (mainland Portugal, Madeira and most of the Azores archipelago), the SoG and the northern Atlantic waters of Morocco. To these should be added the Mediterranean Sea subpopulation, which is considered a separate unit based on genetic, isotopic and contaminant differences (Aguilar et al., 2002; Bérubé et al., 1998; Das et al., 2017; Giménez et al., 2013; Palsbøll et al., 2004). However, the connectivity of this last unit with the S sub-area has been under debate for decades (Castellote et al., 2012; Gauffier et al., 2018; Giménez et al., 2013; Notarbartolo di Sciara et al., 2016). Recent evidence has linked specimens from the Azores archipelago, currently included in the S feeding sub-area, to eastern Greenland and western Iceland summer feeding grounds (Silva et al., 2013).

Clapham et al. (2008) recommended to base successful management on both genetic and non-genetic evidence of population substructure and to define stocks on a smaller scale than they currently are. Indeed, while genetic markers can be enough to assess the structure of differentiated subpopulations (Palsbøll et al., 2007), ecological tracers (stable isotopes, fatty acid, contaminants, etc.), life-history traits and demographic parameters might contribute to revealing finer and more dynamic population structure within genetically homogeneous subpopulations. These techniques provide information over a shorter time-scale and may allow the definition of ecologically meaningful subpopulations or ecological management units, which comprise individuals with ecologically similar behavior co-occurring in space and time (Esteban et al., 2016; Giménez et al., 2018; Murphy et al., 2009; Waples and Gaggiotti, 2006). The combination of modern methodologies and contemporary samples can provide further resolution of current habitat use and migration patterns of a formerly heavily exploited marine mammal such as the North Atlantic fin whale. The Scientific Committee of the IWC has also recommended the use of both genetic and
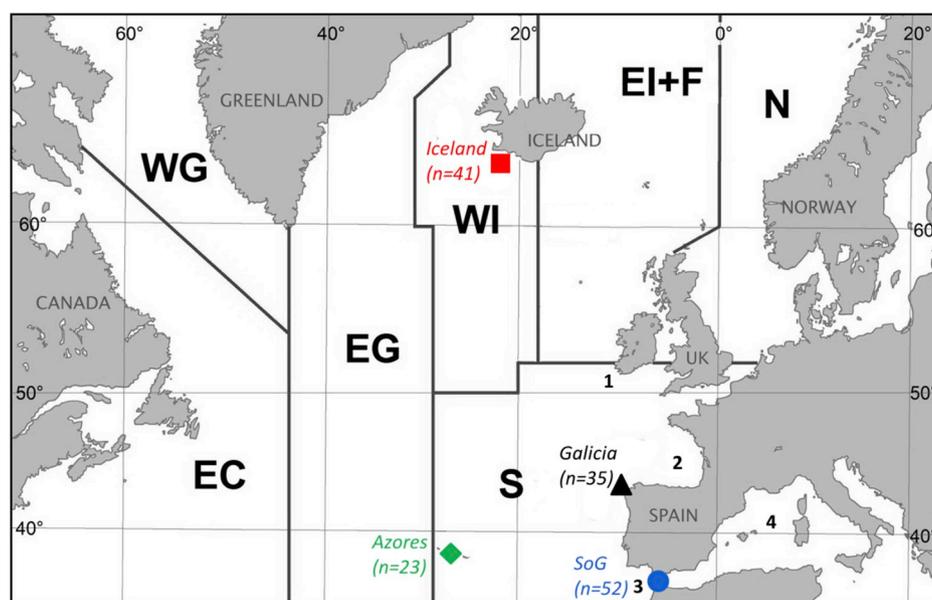
Fig. 1. Origin of fin whale samples (SoG: Strait of Gibraltar) within the IWC stock subdivision of the North Atlantic fin whale population, EC: eastern Canada/USA; WG: West Greenland; EG: East Greenland, WI: West Iceland; EI + F: East Iceland + Faroe Islands; N: Norway; S: Spain + Portugal + France + British Isles (International Whaling Commission, 2009). Other locations mentioned in text 1: Celtic Sea, 2: Bay of Biscay, 3: Gulf of Cadiz, 4: NW Mediterranean Sea.

non-genetic information and applied a suite of such techniques when establishing the stock structure hypothesis for management of North Atlantic fin whales mentioned above (International Whaling Commission, 2017, 2009).

Stable isotopes have been extensively used to investigate marine mammal population structure, trophic ecology, habitat use and migration patterns (e.g. Aguilar et al., 2014; Esteban et al., 2016; Giménez et al., 2018, 2013; Graham et al., 2010; Newsome et al., 2010). Most studies have focused on carbon and nitrogen isotope compositions as proxies of habitat use and trophic level because the $\delta^{15}N$ value increases with trophic level and the $\delta^{13}C$ value is linked to the type of primary production (Newsome et al., 2010). However, researchers are increasingly incorporating stable isotopes of oxygen $^{18}O/^{16}O$ for marine vertebrate studies (Borrell et al., 2018a; Killingley, 1980). This is mainly due to the well-defined latitudinal gradient of the $\delta^{18}O$ value, highly correlated to seawater temperature and especially salinity, which are both higher in regions with positive net evaporation rates and lower in regions where freshwater inputs by river runoff, rain or glacial meltwater are abundant (Bowen, 2010; McMahon et al., 2013). Correlations have been shown mainly with bone samples (Vighi et al., 2016; Zenteno et al., 2013), but recent studies have also investigated $\delta^{18}O$ variations in cetacean and fish organic tissues (Borrell et al., 2018a; deHart and Picco, 2015; Endo et al., 2014, 2012; Soto et al., 2013). For most animals, it is assumed that carbon and nitrogen are supplied by diet while oxygen is supplied mostly by the water that is drunk (Newsome et al., 2010) or, in the case of marine mammals, that is contained in their food (Ortiz, 2001). In the central and east North Atlantic and the Mediterranean Sea, fin whales feed predominantly on the northern krill (*Meganyctiphanes norvegica*), although other zooplankton species or schooling fish may constitute a fractional part of their diet (Aguilar and García-Vernet, 2018).

In this study, we examined potential differences in stable isotope profiles among fin whales sampled at different locations in the North Atlantic. We investigated whether these differences are related to the known baseline $\delta^{13}C$, $\delta^{15}N$ and/or $\delta^{18}O$ values over the region, as calculated for their potential prey, with the ultimate objective of deepening into the subpopulation structure and migrations of the species in that Ocean. For this, we used skin samples from four locations, the SoG, Galicia (NW Spain), the Azores archipelago and Iceland. Cetacean skin has a full isotopic incorporation rate of about three to six months (Busquets-Vass et al., 2017; Giménez et al., 2016), thus it can provide information about the environment in which the individuals lived and fed during the previous semester before sampling. The results are discussed in relation to the connectivity between the feeding sub-areas defined by the IWC.

2. Material and methods

2.1. Data collection

A sample of skin was collected from 151 fin whales examined in 4 areas of the North-East Atlantic, *i.e.* western Iceland, Galicia in NW Spain, the Azores Archipelago and the SoG taking advantage of biopsy sampling studies, strandings, or commercial whaling operations (Table 1, Fig. 1). In the SoG and Galicia, samples were collected from three age classes (calf <12 m, juvenile 12–16 m, adult>16 m) all year long; in the Azores and Iceland only large, supposedly adult individuals were sampled, and the periods of collection were April–July in the former and June–September in the latter (Table S2). Although body location appears not to influence the isotopic ratios of skin (Borrell et al., 2018b), most samples were collected from the dorsal region around and below the dorsal fin.

2.2. Sample processing

All samples were preserved frozen at −20 °C until analysis. Then, 1 g

Table 1
Origin of fin whale skin samples and mean ± SD of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{18}O$ values.

Area	Season	Age class	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{18}O$ (‰)
Azores[a]	summer	Adult	23	−19.9 ± 0.3	9.4 ± 0.3	18.3 ± 0.5
Galicia[b]	summer	Adult	21	−19.1 ± 0.4	9.8 ± 0.7	18.2 ± 0.9
		Juvenile	3	−20.0 ± 0.5	9.6 ± 0.7	18.6 ± 0.7
	winter	Adult	3	−17.8 ± 1.0	10.9 ± 1.2	19.0 ± 0.7
		Juvenile	1	−18.0	10.9	15.2
		Calf	7	−19.0 ± 0.5	11.1 ± 0.4	18.0 ± 1.3
SoG	summer	Adult	40	−19.4 ± 0.3	8.1 ± 0.6	18.7 ± 0.7
		Juvenile	3	−19.2 ± 0.2	9.4 ± 1.6	18.0 ± 0.9
		Calf	2	−19.2 ± 0.0	9.3 ± 0.2	18.5 ± 0.3
	winter	Adult	4	−19.4 ± 0.7	9.7 ± 0.3	17.6 ± 1.5
		Juvenile	3	−19.1 ± 1.3	10.7 ± 0.7	15.1 ± 1.2
Iceland[b]	summer	Adult	41	−19.5 ± 0.3	9.8 ± 0.6	19.4 ± 0.8

[a] Samples partially included in Silva et al. (2019).
[b] Samples partially included in Borrell et al. (2018a).

of skin including all epidermal layers was dried for 48 h at 70 °C and ground to powder with mortar and pestle. Lipids were removed from the samples by several rinses with a 2:1 chloroform:methanol solution. The C:N ratio of delipidated samples varied between 2.73 and 3.49, showing that the lipid extraction process was effective and consistent (Giménez et al., 2017; Ryan et al., 2012). Powdered samples of 0.30–0.40 mg were analyzed separately for carbon-nitrogen and for oxygen in the "Centres Científics i Tecnològics of the University of Barcelona (CCiT-UB)" following the protocol described in Borrell et al. (2018a).

The analytical results are presented according to the delta (δ) notation, where the relative variations of stable isotope ratios are expressed in parts-per-thousand (‰) compared to predefined standards:

$$\delta^{13}C \ or \ \delta^{15}N \ or \ \delta^{18}O = \left[\left(\frac{R_{sample}}{R_{standard}} \right) - 1 \right] *1000$$

where R_{sample} and $R_{standard}$ are the heavy-to-light isotope ratios ($^{13}C/^{12}C$, $^{15}N/^{14}N$ or $^{18}O/^{16}O$), in the sample and in the reference standard respectively. International isotope secondary standards distributed by the International Atomic Energy Agency (IAEA) of known $^{13}C/^{12}C$, $^{15}N/^{14}N$ and $^{18}O/^{16}O$ ratios, in relation to the Vienna Pee Dee Belemnite (V-PDB) calcium carbonate, the atmospheric nitrogen (air) and the Vienna-Standard Mean Ocean Water (V-SMOW) respectively, were used to calibrate the system and compensate for any analytical drift over time. These consisted in polyethylene (IAEA CH7: $\delta^{13}C = −31.8$‰), sucrose (IAEA CH6: $\delta^{13}C = −10.4$‰; $\delta^{18}O = +36.4$‰), ammonium sulphate (IAEA N1: $\delta^{15}N = +0.4$‰ and IAEA N2: $\delta^{15}N = +20.3$‰), potassium nitrate (USGS 34: $\delta^{15}N = −1.7$‰), L-glutamic acid (USGS 40: $\delta^{15}N = −4.6$‰; $\delta^{13}C = −26.2$‰), caffeine (IAEA 600: $\delta^{15}N = 1.0$‰; $\delta^{13}C = −27.7$‰), benzoic acid (IAEA 601: $\delta^{18}O = +23.3$‰), cellulose (IAEA CH3: $\delta^{18}O = +31.9$‰). Analytical precision for repeat measurements of the reference material run in parallel with the skin samples was 0.3‰ for $\delta^{18}O$ and 0.1‰ for $\delta^{13}C$ and $\delta^{15}N$ (1 S.D., n = 10).

$\delta^{13}C$ values from 1985 to 1986 in Galicia and Iceland were adjusted for the Suess effect based on Borrell et al. (2018a). The Suess effect is a $\delta^{13}C$ decrease over time caused by the invasion of isotopically light anthropogenic CO_2 into the ocean attributed to the burning of fossil fuels and the increased deforestation worldwide (Gruber et al., 1999). Here we applied a $\delta^{13}C$ decrease of 0.027‰ yr^{-1} in Iceland and 0.016‰ yr^{-1} in Galicia, using 2014 as the reference for the adjustment (Borrell et al., 2018a).

2.3. Statistical analysis

Mean and standard deviation (SD) values of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{18}O$ values were calculated for each area, season and age class. However, due to heterogeneous composition in age classes between areas, most analyses were also performed on a subset containing only adult individuals sampled all year long or on a subset containing only adult individuals

sampled during the period April–October, as this last category was present in all four areas. This latter group is hereafter named the *reduced adult summer dataset*.

Data normality and homoscedasticity were verified using Kolmogorov-Smirnov and Fligner tests and failed to show neither normality nor homoscedasticity. In the complete dataset, univariate isotopic ratios of carbon, nitrogen and oxygen were compared to examine differences among sampling areas (Iceland, Azores, Galicia, and the SoG) and seasons (April–October and November–March) by means of Kruskal-Wallis tests and post-hoc Dunn tests with Benjamini-Hochberg correction (Benjamini and Hochberg, 1995).

Differences in trivariate isotopic signals (δ^{13}C-δ^{15}N-δ^{18}O) were assessed through a "non-parametric" permutational multivariate analysis of variance, PERMANOVA (Anderson, 2001), using the R package 'vegan' version 2.5–3 (Oksanen et al., 2018) with 999 permutations. A PERMANOVA using distance matrices was performed by fitting the 'adonis2' function to two factor covariates, *i.e.* sampling area and season.

In the *reduced adult summer dataset*, tridimensional isotopic niche region and pairwise niche overlap were computed among sampling areas based on δ^{13}C-δ^{15}N-δ^{18}O isotopic values using the probabilistic method developed by Swanson et al. (2015), available as the R package 'nicheROVER' v1.0 (Lysy et al., 2015). Niche region (N_R) was defined as the 40% probability region of the tridimensional stable isotopes niche, representing the core N_R, as for the widely used bivariate Standard Ellipse Areas (Jackson and Parnell, 2017). Uncertainty was accounted for in a Bayesian framework in three dimensions. Directional estimates of niche overlap and unique and consistent bivariate projections of the multivariate niche region were also produced. Niche overlap was defined as the probability that an individual from one group could be found within the isotopic niche region of another group. Uncertainty in niche overlap was reported as the posterior distribution (as Pr(D|M), given data (D) and a model (M)) of the overlap percentage along with the Bayesian 95% credible intervals for each pairwise comparison. 10,000 runs were performed for all analyses. Additionally, the methodology provided by Rossman et al. (2016) was used to estimate the standard ellipsoid volume (SEV) of each area as a proxy of its tridimensional trophic niche size, as well as the Euclidean distance in the δ-space between centroid locations (CL) as a proxy for trophic segregation. Then the probabilities of centroids having a different location and of ellipsoids having a different size were calculated for each pair of areas as the number of posterior samples for which CL or SEV was larger in area 1 than in area 2, divided by the total number of posterior samples. Finally, the percentage of overlap between areas 1 and 2 was calculated as the geometric volume of overlap between ellipsoids divided by the SEV of area 1 or area 2 and compared to the estimates from nicheROVER. These calculations were made in a Bayesian framework, with the script provided by Rossman et al. (2016), and default values.

Mean and SD values of carbon and nitrogen isotope ratios of adult individuals from all 4 areas and 2 seasons sampled in our study were plotted against data available in the literature for fin whale skin and northern krill, the fin whale main prey species. Prey values were adjusted with the discriminant factor obtained by Borrell et al. (2012), *i. e.* 2.82 ± 0.30 for nitrogen and 1.28 ± 0.38 for carbon. Prey and fin whale values were adjusted for the Suess effect when possible, with 2014 as the reference year. Original published values can be found in Table S2.

Finally, for adult samples from Galicia and the SoG, the two areas in which samples were collected along the year, the relationships between δ^{13}C, δ^{15}N or δ^{18}O values and Julian day were modeled as a cyclic continuous variable using Generalized Additive Models (GAM (Hastie and Tibshirani, 1990); by means of the R package 'mgcv' version 1.8–26 (Wood, 2018). A Gaussian distribution and logit link function with gamma = 1.4 and smoothers constrained to a maximum of 4 degrees of freedom (k = 5) were used to prevent overfitting (Wood, 2006). Each model was checked to detect any obvious deviation from normality and patterns in the residuals.

All analyses were performed in R 3.5.1 (R Core Team, 2018). All graphs (except nicheROVER) were drawn with the 'ggplot2' package (Wickham, 2016).

2.4. Ethics statement

Samples obtained through biopsy from live animals or from stranded whales from the Azores archipelago, the SoG and Galicia were collected under specific permits issued by the respective national and regional administrations. Samples from NW Spain and Iceland obtained from captured whales were collected from legal whaling operations; Icelandic samples were legally imported into Spain under CITES permit ES-BB_00207/15I.

3. Results

Overall, mean ± SD isotopic values of the 151 fin whale skin samples were −19.41 ± 0.53‰ for carbon, 9.37 ± 1.02‰ for nitrogen and 18.63 ± 1.09‰ for oxygen. Univariate isotopic ratios were significantly different by area (all Kruskal-Wallis K–W X^2 tests p $< 10^{-8}$). Galicia whales had the highest δ^{13}C values, followed by SoG/Iceland (Dunn test $Z_{SoG\text{-}Iceland} = 1.72$, p = 0.08) and then Azores individuals; SoG animals had the lowest δ^{15}N values, followed by Azores ($Z_{Azores\text{-}Iceland} = -1.97$, p = 0.06) and then Iceland/Galicia whales ($Z_{Galicia\text{-}Iceland} = 1.68$, p = 0.09); δ^{18}O values were similar for Galicia/Azores/SoG whales (all Dunn tests p $>$ 0.54) and all lower than Icelandic animals (Table 1). A similar pattern was observed for summer adult individuals, for which univariate isotopic ratios were also significantly different by area (all K–W X^2 tests p $< 10^{-10}$) (Fig. 2). On the full dataset, the season effect was significant for isotope ratios of carbon in Galicia (K–W $X^2 = 9.2$, df = 1, p = 0.002), of oxygen in the SoG (K–W $X^2 = 13.9$, df = 1, p $<$ 0.001) and of nitrogen in whales from both areas (K–W X^2 tests p $<$ 0.001). In general, November–March isotope ratios showed more variations than April–October and were higher for carbon and nitrogen (Fig. 2). One possible mother-calf pair (adult travelling with a small calf) was sampled in the SoG and the calf had a difference of −0.1‰ δ^{13}C, 1‰ δ^{15}N and −0.3‰ δ^{18}O with the adult.

According to the results of the trivariate PERMANOVA, the explanatory variables area ($R^2 = 0.29$, p = 0.001), season ($R^2 = 0.21$, p = 0.001) and age class ($R^2 = 0.14$, p = 0.001) had a significant effect both separately and combined. In the reduced adult summer dataset, the variable area was significant ($R^2 = 0.42$, p = 0.001). Stable isotope ratios were also different between seasons for adult whales in the SoG ($R^2 = 0.18$, p = 0.001) and in Galicia ($R^2 = 0.39$, p = 0.008).

Overall there was little overlap between 40% niche regions of summer adult whales as indicated by the 2D ellipses projections and overlap metrics (Fig. 3, Table 2D). As detected by the univariate analyses, nitrogen stable isotope differentiated SoG whales from individuals in the other areas, while carbon did the same for the Azores samples and oxygen for Icelandic animals. Tridimensional N_R sizes estimated as SEV were the largest for samples from Galicia, then from the SoG and Iceland and finally smallest for Azores whales (Fig. 4, Table 2A). Pairwise SEV size differences had all more than 90% probability to be different from zero, except for the difference between samples from the SoG and Iceland (Table 2B). Ranking order and magnitude of SEV agree well with the visual assessment of 2D elliptical projections from nicheROVER (Fig. 3). The probabilities that the distance between trivariate centroid locations was not zero were all over 90% except between Galicia and Azores whales. Percentages of NicheROVER and SEV overlap estimates were consistent and mostly low (Table 2CD). SEV overlap estimates were generally smaller and had wider confidence intervals, probably caused by small sample size (Rossman et al., 2016; Swanson et al., 2015).

All values from our study fell within the range of published carbon and nitrogen isotope compositions from whales and their prey in the
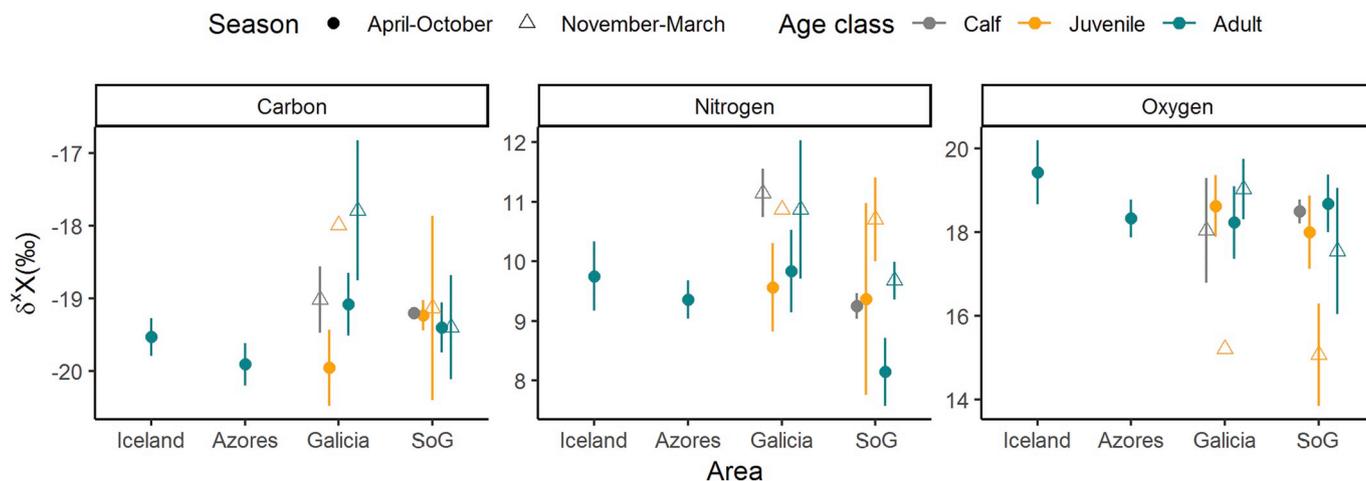
Fig. 2. Mean ± SD of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{18}O$ values per sampling area. When available, results are presented by season and age class.
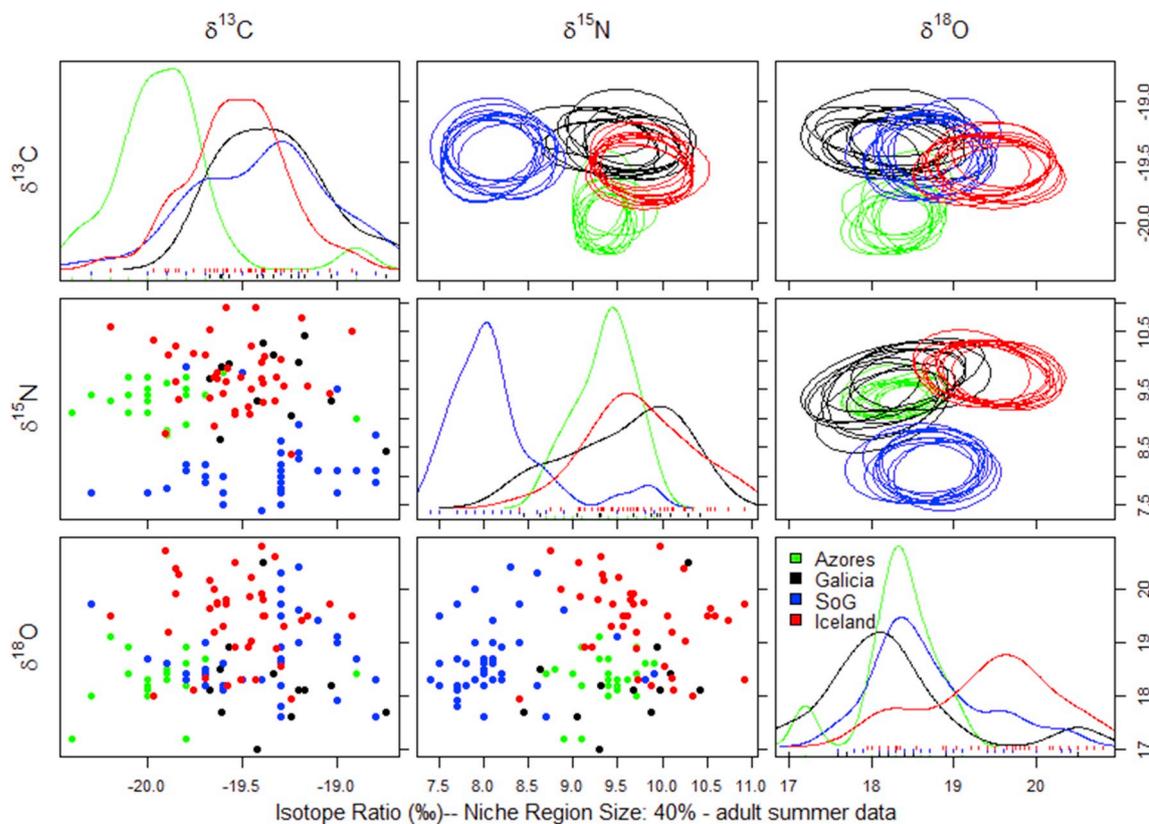
Fig. 3. NicheROVER plots at 40% trophic niche region (N_R) for $\delta^{13}C$, $\delta^{15}N$ and $\delta^{18}O$ values in the 4 areas for the *reduced adult summer dataset*. Top-right: 2D-elliptical projections of N_R; diagonal: 1D-density distributions; bottom-left: 2D-scatterplots of raw data.

northeast Atlantic and Mediterranean. In general, nitrogen isotopic composition of fin whale skin and northern krill showed a latitudinal gradient of enrichment towards the poles, covering a range of more than 7‰ (Fig. 5). Conversely, most $\delta^{13}C$ values were within 3‰. Krill and whale values showed a great variation within and among sampling areas. Indeed, the highest $\delta^{15}N$ and lowest $\delta^{13}C$ values were from Svalbard krill (n°2 in Fig. 5), while the lowest $\delta^{15}N$ value was from Mediterranean krill (n°20) and the highest $\delta^{13}C$ value from Gulf of Cadiz krill (n°16). Within areas sampled in different seasons, fin whales and krill $\delta^{15}N$ values were higher in November–March than in April–October. Mediterranean samples were the most ^{15}N-depleted. Adult whales sampled in summer in the SoG were consistent with these low

Mediterranean $\delta^{15}N$ signatures and in their lower $\delta^{13}C$ range. Conversely, $\delta^{15}N$ and $\delta^{13}C$ values of adult whales from winter in the SoG were similar to Icelandic values and close to summer values of individuals from Galicia and the Azores. Adult whales sampled in Galicia in winter had the highest values of our samples.

Fig. 6 shows $\delta^{13}C$, $\delta^{15}N$ or $\delta^{18}O$ values of adult samples from the four areas plotted against Julian Day for illustration purpose, as well as GAMs with significant smooth terms for Galicia and SoG samples. Univariate GAM models for $\delta^{15}N$ values along Julian days showed a cyclic pattern of decrease, reaching minimum values in summer and maximum values in winter for both whales from Galicia and the SoG (Fig. 6, Table S1). In samples from Galicia, carbon isotopic ratios presented a cyclic evolution

Table 2

Reduced adult summer dataset (A) Estimated standard ellipsoid volume (SEV) and centroid location (CL) values for each area. (B) First column is the probability that Area$_1$ has a greater SEV value than Area$_2$. The second column shows the estimated differences in CL values between Area$_1$ and Area$_2$, while the final column lists the probability this difference is not 0. (C) The percentage of niche overlap calculated as the overlap between each area divided by the SEV of Area$_1$. (D) The percentage of niche overlap from nicheROVER. When appropriate, values are given as median (95% CI min, 95% CI max).

(A)	Standard Ellipsoid Volume (SEV)	Centroid Location (CL)		
Area	Median (‰)^3	δ^{13}C (‰)	δ^{15}N (‰)	δ^{18}O (‰)
Azores	0.49 (0.31, 0.82)	−19.9 (−20.1, −19.7)	9.3 (9.1, 9.5)	18.3 (18.0, 18.5)
Galicia	1.51 (0.81, 3.08)	−19.3 (−19.6, −18.9)	9.5 (9.1, 10.1)	18.2 (17.6, 18.8)
SoG	0.80 (0.56, 1.18)	−19.4 (−19.5, −19.2)	8.1 (7.9, 8.3)	18.6 (18.4, 18.9)
Iceland	0.75 (0.52, 1.10)	−19.5 (−19.6, −19.4)	9.7 (9.5, 9.9)	19.4 (19.1, 19.6)

(B)	SEV difference	CL difference	
Area$_1$, Area$_2$	$P[D_{SEV1,SEV2}]>0$	Estimate (‰)	$P[D_{\mu1,\mu2}] > 0$
Azores, Galicia	0.00	0.7 (0.4, 1)	0.52
Azores, SoG	0.06	1.4 (1.1, 2)	1.00
Azores, Iceland	0.09	1.2 (0.9, 2)	1.00
Galicia, SoG	0.96	1.6 (1.1, 2)	0.98
Galicia, Iceland	0.97	1.3 (0.7, 2)	0.89
SoG, Iceland	0.59	1.8 (1.5, 2)	1.00

(C)	Percent of SEV niche overlap			
	Area$_2$			
Area$_1$	Azores	Galicia	SoG	Iceland
% Azores	*	19 (0, 81)	0 (0, 0)	0 (0, 12)
% Galicia	6 (0, 26)	*	0 (0, 5)	5 (0, 27)
% SoG	0 (0, 0)	0 (0, 10)	*	0 (0, 0)
% Iceland	0 (0, 8)	10 (0, 60)	0 (0, 0)	*

(D)	% nicheROVER overlap			
	Azores	Galicia	SoG	Iceland
Azores	*	42 (5, 87)	22 (6, 46)	7 (1, 19)
Galicia	2 (1, 3)	*	8 (3, 15)	4 (2, 7)
SoG	2 (1, 3)	15 (5, 29)	*	2 (0, 3)
Iceland	2 (0, 5)	34 (12, 62)	7 (1, 16)	*

similar to that of nitrogen (Fig. 6, Table S1). In the SoG, δ^{18}O showed a cyclic pattern, opposite to the δ^{15}N pattern, with maximum values in summer (Fig. 6).

4. Discussion

The stable isotope values of skin from the fin whales examined show that individuals from different locations exhibit heterogeneous isotopic niche sizes and little niche overlap. Differences in isotopic niche space
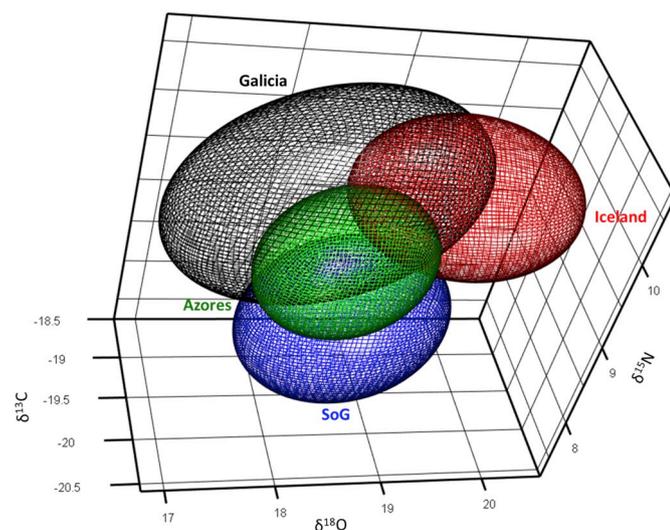
Fig. 4. 3D isotopic niches for each area of the *reduced adult summer dataset*. This figure is also available as a video file.

were mainly due to relatively lower δ^{13}C values in the Azores, lower δ^{15}N values in the SoG and higher δ^{18}O values in Iceland. Little overlap in isotopic niche space can be explained by predators feeding on different prey or on the same prey in areas or times of the year with dissimilar isotopic baseline values. As fin whales from Iceland, Galicia, Azores and the Mediterranean Sea are believed to feed mainly on *Meganyctiphanes norvegica* (Aguilar, 1985; Bentaleb et al., 2011; Sigurjónsson and Víkingsson, 1997; Silva et al., 2019), these differences are most probably due to variations in local baseline values or to differences in the body composition of *M. norvegica*'s, which, in turn, may be caused by variations in its diet (Schmidt, 2010). Despite a reduced sample size for young individuals, we observed some variation in isotopic compositions from calves, juveniles and adults from Galicia and the SoG. Thus, sampling specimens from different age classes and seasons was found to contribute to greater variability of δ^{13}C, δ^{15}N and δ^{18}O values in Galicia and the SoG. Indeed, isotopic niche size increases when segments of the subpopulation feed on different resources (Bearhop et al., 2004). As a consequence, subsequent analyses were undertaken only for summer adult individuals, so that the comparison between the four sampled areas would not be confounded by the effects of age and season on stable isotope composition.

Despite very low genetic divergence (Bérubé et al., 1998; Olsen et al., 2014), ecological differences between fin whales from Galicia and Iceland have been extensively demonstrated through molecular markers, morphologic data and mark-recapture (International Whaling Commission, 2009; Jover, 1992; Lockyer, 1982; Sanpera et al., 1996; Vighi et al., 2019, 2017, 2016). These were corroborated in our study by the differences in carbon and oxygen isotopic composition, thus further giving support to traditional stock boundaries previously used by the IWC (Donovan, 1991; International Whaling Commission, 2009). Interestingly, our results from fin whale skin are opposite to previous studies from bone samples from these locations, where δ^{18}O value was
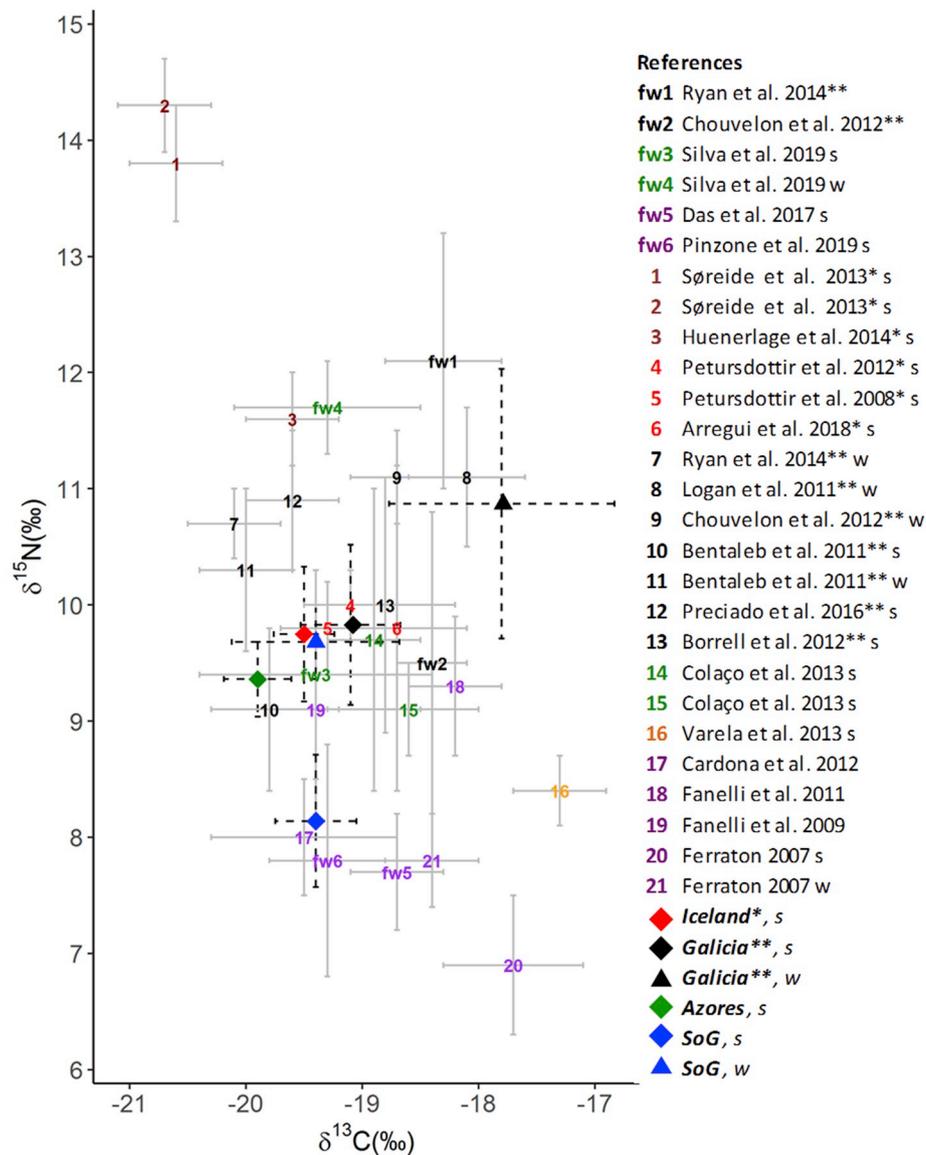
Fig. 5. Biplot of mean ± SD of δ^{13}C and δ^{15}N values for adult fin whales (shapes). Numbers refer to Table S2, fw for fin whale skin, numbers for northern krill values adjusted with the discriminant factor from Borrell et al. (2012); s: sampled in April–October, w: sampled in November–March. Colors indicate sampling area, dark red: Svalbard archipelago, red: Iceland, black: Ireland/Bay of Biscay/Galicia, green: Azores, orange: Gulf of Cadiz, blue: SoG, purple: Mediterranean. When possible, δ^{13}C values were adjusted for Suess effect (with a decrease of *0.027‰ yr^{-1} and **0.016‰ yr^{-1}), using 2014 as the reference for the adjustment (Borrell et al., 2018a). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

significantly higher in Galicia (Vighi et al., 2016) and followed the oxygen isoscapes of seawater (McMahon et al., 2013). These differences may be related to the capacity of bone to integrate long-term isotopic fluctuations while skin samples typically reflect the environment where the whales have been feeding during the previous months (Newsome et al., 2010) or to a different correlation between seawater and the various tissues. Oxygen isotopic composition has been studied in cetacean bones and teeth and was found to be highly correlated to oceanic water (Clementz and Koch, 2001; Yoshida and Miyazaki, 1991), with cetacean species from higher latitudes exhibiting lower δ^{18}O value due to ^{18}O-depleted polar meltwater (Vighi et al., 2016; Yoshida and Miyazaki, 1991). However, while δ^{18}O values have been measured in several tissues from terrestrial and aquatic organisms (Borrell et al., 2018a; Pietsch et al., 2011; Soto et al., 2013), the processes regulating oxygen isotope ratios variations in cetacean skin have yet to be fully understood. Fluxes of oxygen into marine mammals include preformed water in food, seawater consumed when eating, metabolic water produced from fat, active drinking and flux of water through the skin, in different proportions for each species (Clementz and Koch, 2001; Ortiz, 2001). Although not properly studied, these processes are not believed to strongly fractionate oxygen (Newsome et al., 2010). Moreover,

turnover rates have been shown to be species, tissue and isotope dependent (Busquets-Vass et al., 2017; Giménez et al., 2016), and can even vary with environmental conditions (Busquets-Vass et al., 2017; Durban and Pitman, 2012). Thus, as δ^{18}O incorporation rates have not been assessed for cetacean skin, it is challenging to interpret the temporal, and therefore potentially spatial coverage, reflected by the samples analyzed here. However, as we found differences in δ^{18}O between areas, as well as along the year in some areas (see below), we argue that oxygen stable isotope composition in whale skin could be a useful marker to differentiate populations, and therefore future experimental research should focus on unveiling the underlying processes of its incorporation (Vander Zanden et al., 2016).

Fin whales are regularly found in western Icelandic waters during May–October, with the highest densities in June–August (Sigurjónsson and Víkingsson, 1997). The samples analyzed here had been collected in August–September and are likely to reflect the signatures acquired from recent but previous feeding grounds that could encompass from three to six months. Mark-recapture studies showed very limited movements between western Icelandic grounds and the western North Atlantic and none with the eastern grounds (International Whaling Commission, 2009). However, fin whales may spend some time outside the summer in
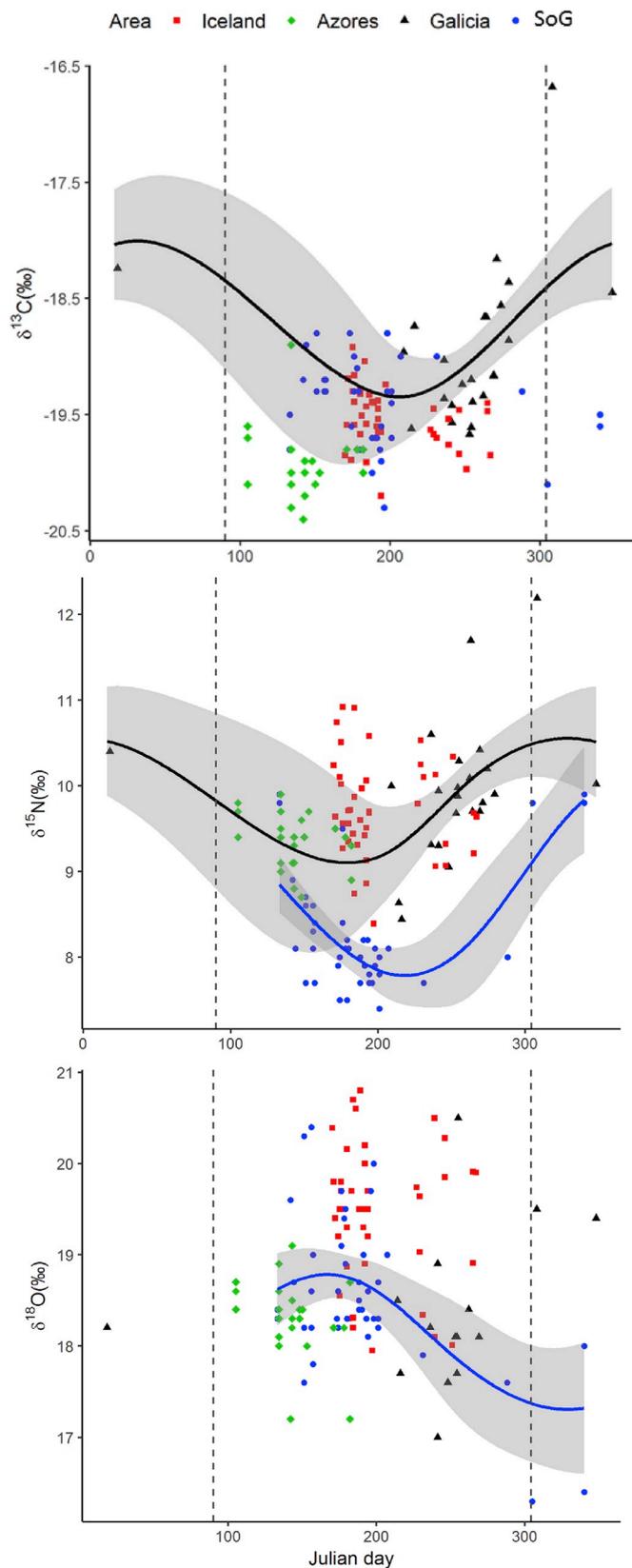
Fig. 6. $\delta^{15}N$, $\delta^{13}C$ and $\delta^{18}O$ values for adult fin whales along Julian day in the 4 areas plotted for illustration purpose. GAMs were fitted to Galicia and SoG samples only, lines and shades indicate mean and 95% CI predictions for significant smooth terms. Vertical dashed lines separate the two periods April–October and November–March. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

lower latitudes of the central North Atlantic, where seawater $\delta^{18}O$ is higher (McMahon et al., 2013). In fact, satellite tagging and encounter rates in the Azores show that some whales feed in the Azores archipelago in spring-early summer (Silva et al., 2013; Visser et al., 2011) and then migrate to subpolar feeding grounds, in particular to western Iceland and eastern Greenland (Silva et al., 2013). Moreover, although no satellite information is available on the origin of fin whales returning to the Azores in late autumn-winter, their nitrogen stable isotope compositions are consistent with feeding on krill at high latitudes during the previous months (Huenerlage et al., 2016; Silva et al., 2019). This finding effectively provides a transboundary link between IWC feeding sub-area S and the EG/EI sub-areas (International Whaling Commission, 2009). In turn, whales sampled in the Azores in spring-early summer were on their northwards stopover and had lower $\delta^{15}N$ and $\delta^{13}C$ values, that could reflect late autumn-winter feeding grounds with values more similar to the krill sampled in oceanic waters off Iberia and the Azores (this study, Silva et al., 2019)). They were also the most ^{13}C-depleted among the samples analyzed here, which would be consistent with feeding in pelagic ecosystems (Newsome et al., 2010), such as those along the Mid-Atlantic Ridge, where fin whales are regularly detected (Lacey, 2019; Nieukirk et al., 2012; Pike et al., 2019).

The fin whales occurring at the SoG have been at the center of the scientific debate for decades, as to whether the Strait represents a physical barrier that isolates individuals present in the Mediterranean Sea from those in the eastern North Atlantic. Most studies seem to point towards a distinctiveness of NW Mediterranean individuals (Bérubé et al., 1998; Castellote et al., 2012; Das et al., 2017; Giménez et al., 2013; Ryan et al., 2013), but do not exclude some degree of connectivity through the SoG (Bentaleb et al., 2011; Gauffier et al., 2018; Giménez et al., 2014; Notarbartolo di Sciara et al., 2016; Palsbøll et al., 2004). In our study, SoG whales were sampled both during their western migration towards the Atlantic Ocean in May–October (peaking in June–July) and during their eastern migration entering the Mediterranean Sea in November–March (Gauffier et al., 2018). Results show significant differences in $\delta^{15}N$ and $\delta^{18}O$ values between the two periods. The nitrogen isotope composition of the whales sampled during the western migration was similar to Mediterranean values, which would be consistent with spending the winter months inside the Mediterranean Sea. Winter feeding has been observed within the Mediterranean Sea (Canese et al., 2006), therefore contradicting the common belief that baleen whales fully fast in winter. Conversely, the $\delta^{15}N$ autumn values were similar to those of individuals from the North Atlantic, especially Icelandic whales, but also close to the values of the whales sampled at the Azores and Galicia in the summer. This suggests that the whales sampled in the SoG may feed in the summer in the same area as the Icelandic whales had been feeding during the previous months (winter-spring). This would indicate a common feeding ground for whales migrating from the Azores to Iceland and back, with the SoG whales, but not at the same time. Although the extent of winter feeding is unknown (Aguilar et al., 2014), this finding, together with the observations of seasonal movements through the SoG (Gauffier et al., 2018), seem to confirm that some whales perform annual migrations between North Atlantic summer feeding grounds and Mediterranean winter feeding grounds. Additionally, whales sampled in the SoG exhibit $\delta^{18}O$ oscillations, however, these oscillations show an opposite pattern to those of $\delta^{15}N$. A negative correlation between these two isotopes was also found in muscle samples from other cetacean species (Endo et al., 2014, 2012), but, conversely, a synchronized positive oscillation pattern was found in baleen plates from another whale species (deHart and Picco, 2015). Therefore, this is challenging to interpret due to the lack of information about fractionation and turnover of the oxygen stable isotopes discussed previously and the absence of comparable references for $\delta^{18}O$ values in fin whale skin and their prey. If the turnover for oxygen in skin was similar to that of nitrogen, then this pattern could correspond to whales spending the winter in Mediterranean waters, which are ^{18}O-enriched by almost 2‰ as compared to the North Atlantic, and the summer in the Bay of Biscay

([McMahon et al., 2013](#)). In this case, this migration pattern would be consistent with the one suggested by $\delta^{15}N$ values. However, more information on physiological processes is needed to link $\delta^{18}O$ oscillation patterns in skin to whale migration.

About 18,000 fin whales are believed to visit the Bay of Biscay in summer ([Hammond et al., 2017](#)) and, although density sharply declines during winter ([Aguilar and Sanpera, 1982](#)), part of the subpopulation appears to be staying in these latitudes all year round ([Laran et al., 2017](#)). Indeed, as some of our Galician samples included stranded calves, some individuals may spend the winter in an unidentified breeding ground near the Galician coast. Others could even migrate further north towards the Celtic Sea ([Baines et al., 2017](#); [Ryan et al., 2013](#)). However, most individuals could migrate to wintering grounds located in lower latitudes, maybe to the early 20th-century whaling grounds located off the Gulf of Cadiz or northern Africa ([Sanpera and Aguilar, 1992](#)), which have not been properly surveyed since whaling ended in this area. This appears to be confirmed by the fact that whalers did observe whales migrating north along the western Iberian Peninsula in spring-summer ([Best, 1992](#)). These movements between offshore and more coastal waters could also explain the oscillations found in $\delta^{13}C$ values of whales sampled in Galicia, and could include seasonally feeding on other species, such as inshore foraging fish that present higher $\delta^{13}C$ values ([Ryan et al., 2014](#)). $\delta^{15}N$ values of Galician whales showed similar oscillations as those of animals in the SoG but of lower amplitude.

Most information available on fin whales comes from their summer feeding grounds and little is known about their wintering areas ([Aguilar and García-Vernet, 2018](#)), with the exception to the Celtic Sea ([Baines and Reichelt, 2014](#)). The SoG aggregation of fin whales is indeed the only unit that was historically subject to whaling in winter ([Aguilar, 2013](#)). In this study, we sampled whales throughout the year in the SoG and Galicia and found cyclic stable isotope values oscillations. Seasonal oscillations in stable isotope compositions have previously been found in fin whale baleen plates ([Aguilar et al., 2014](#); [Bentaleb et al., 2011](#)). [Aguilar et al. (2014)](#) found that $\delta^{15}N$ values in Galicia samples from both baleen plates and muscle tissue progressively increased during the summer period of intense feeding and decreased during winter, when whales fast or at least decrease their food consumption, contrary to previous assumptions that ^{15}N enriched during fasting. They attributed this apparent inconsistency to the combined effects of some degree of winter-feeding together with lipid-dominated catabolism, reduced excretion and/or animals moving between different isoscapes. In our study, we compared seasonally-collected samples of fin whales and northern krill from the eastern North-East Atlantic and the Mediterranean Sea and found ^{15}N enrichment occurring from summer to winter, which matches the apparent opposite results from the baleen plates when taking into account $\delta^{15}N$ full incorporation rate of about six months in cetacean skin ([Busquets-Vass et al., 2017](#); [Giménez et al., 2016](#)). Limited winter feeding in areas with ^{15}N-depleted prey ([Aguilar et al., 2014](#)) is consistent with our findings for whales sampled in Galicia and the SoG. Additionally, our study would benefit from getting more adult whale and prey samples from outside of the summer months to increase the resolution of the oscillation patterns along the year and better understand the use that fin whales make of their resource in the different areas.

5. Conclusion

We can conclude that the pattern of movements and the habitat use of fin whales in the North Atlantic appear to be more complex than implied by some previous research and the subdivisions applied by the International Whaling Commission until the 1990s ([Donovan, 1991](#)). Indeed, the transboundary movements undertaken by a significant segment of the subpopulations and the bidirectional crossing of individuals between the Mediterranean Sea and the Atlantic Ocean through the SoG provide an important new insight into the biology and

population structure that should be incorporated into future assessments of North Atlantic fin whales.

Declaration of competing interest

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

CRediT authorship contribution statement

Pauline Gauffier: Conceptualization, Investigation, Formal analysis, Data curation, Visualization, Writing - original draft, Writing - review & editing. **Asunción Borrell:** Conceptualization, Investigation, Writing - review & editing, Supervision. **Mónica A. Silva:** Investigation, Writing - review & editing. **Gísli A. Víkingsson:** Investigation, Writing - review & editing. **Alfredo López:** Investigation, Writing - review & editing. **Joan Giménez:** Investigation, Writing - review & editing. **Ana Colaço:** Investigation, Writing - review & editing. **Sverrir Daníel Halldórsson:** Investigation, Writing - review & editing. **Morgana Vighi:** Investigation, Writing - review & editing. **Rui Prieto:** Investigation, Writing - review & editing. **Renaud de Stephanis:** Conceptualization, Investigation, Writing - review & editing. **Alex Aguilar:** Conceptualization, Investigation, Writing - review & editing, Supervision.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2020.104884.

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