



Isotopic niches of fin whales from the Mediterranean Sea and the Celtic Sea (North Atlantic)



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ABSTRACT

The fin whale (*Balaenoptera physalus*) is the most abundant and widespread mysticete species in the Mediterranean Sea, found mostly in deep, offshore waters of the western and central portion of the region. In the Mediterranean, this species is known to feed mainly on krill, in contrast to its Atlantic counterpart, which displays a more diversified diet. The International Whaling Commission recognizes several managements units in the Atlantic and the Mediterranean Sea and the connectivity between these populations is still being debated. Questions remain about inter-individual feeding strategies and trophic ecology.

The goal of this study was to compare isotopic niches of fin whales from the Mediterranean Sea and the Celtic Sea (North Atlantic).

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were analysed in 136 skin biopsies from free-ranging Mediterranean fin whales sampled in 2010 and 2011 during campaigns at sea.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ranged from -20.4 to -17.1‰ and from 5.9 to 8.9‰, respectively. These values are in good agreement with those estimated previously from baleen plates from Mediterranean and North Atlantic fin whales. The narrow isotopic niche width of the Mediterranean fin whale (Standard Ellipses area SEAc) compared to the North Atlantic fin whale raises many concerns in the context of global changes and long-term consequences.

One could indeed expect that species displaying narrow niches would be more susceptible to ecosystem fragmentation and other anthropogenic impacts.

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1. Introduction

The fin whale, *Balaenoptera physalus* (Linnaeus, 1758), is the most abundant and widespread mysticete species in the Mediterranean Sea, found mostly in deep, offshore waters of the western and central portions of the region (Notarbartolo-di-Sciara et al., 2003). While fin whale populations are classified as endangered by the International Union for Conservation of Nature (IUCN) Red List, they are not considered threatened in the North Atlantic (Reilly

et al., 2013).

Mediterranean fin whales are currently defined as a distinct subpopulation from those in the North Atlantic (IWC, 2009; Notarbartolo-di-Sciara et al., 2003; Panigada and Di Sciara, 2012). The International Whaling Commission recognizes seven management units in the Atlantic and one in the Mediterranean Sea, comprising three breeding populations (IWC, 2016, 2007). Depending on the subpopulation they belong to, fin whales may face various anthropogenic threats, including ship strikes, entanglement in fishing gear, exposure to noise, chronic exposure to a variety of toxins and pollutants, and possible impacts of global climate change that include potential shifts in prey availability (Aguilar, 2009; Clapham et al., 1999; Davidson et al., 2012; Doney et al., 2012; Pinzone et al., 2015; Pompa et al., 2011). The

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connectivity between these subpopulations is still being debated. Although highly mobile, cetaceans including fin whales can show high levels of population structure in the absence of contemporary geographical barriers as the result of historical processes, social structure and ecological specializations (Bérubé et al., 1998; Roman and Palumbi, 2003). Genetic analyses based on both mitochondrial and nuclear DNA indicated differences between fin whales in the Mediterranean Sea, largely resident in the basin, and fin whales sampled in the Atlantic (Bérubé et al., 1998; Palsbøll et al., 2004). However, acoustic analyses have demonstrated some inter-population movements, prompting debate on the extent to which the two putative populations are geographically isolated (Castellote et al., 2014, 2012; Gimenez et al., 2014). Stable isotope analyses of baleen plates from stranded whales suggest that whales from the Mediterranean and North Atlantic are largely discrete but with occasional exchange (Bentaleb et al., 2011; Giménez et al., 2013; Ryan et al., 2013). The results of $\delta^{18}\text{O}$ values analysed in bones of fin whales from northwestern Spain and Iceland suggested intricate structure of fin whale subpopulations exploiting different habitats and with latitudinal migrations that are still far to be completely understood (Vighi et al., 2016).

The small Mediterranean Sea population has been proposed as vulnerable (VU) in IUCN's Red List of threatened species based on (a) the genetic distinction from the North Atlantic population, (b) it containing fewer than 10,000 mature individuals, (c) all mature individuals being in the one population, and (d) an inferred decline in numbers of mature individuals (Panigada and Di Sciara, 2012). The size of the population has been estimated at approximately 3583 individuals (95% CI = 2130–6027) in the western Mediterranean (except for the Tyrrhenian Sea) in 1991 (Forcada et al., 1996) and 901 (95% CI = 591–1374) in the Corsican-Ligurian-Provençal Basin in 1992 (Forcada et al., 1996), which is very low compared to the current estimate of 56,000 whales in the North Atlantic (Roman and Palumbi, 2003). In 2001, the abundance in the Pelagos Sanctuary (Western Mediterranean Sea; Fig. 1a) was estimated at 715 individuals (CV = 31.2%) (Gannier, 2006). Surveys carried out in summer 2009 in the Pelagos Sanctuary estimated abundance of fin whales at 148 (95% CI = 87–254), pointing towards an appreciable decrease in summer abundance and density since the early 1990s (Panigada et al., 2011).

Studies on Mediterranean fin whales feeding habits inferred from surface feeding visual observations from stomach content and faeces analyses suggested that the euphausiid *Meganyctiphanes norvegica* is the main food item in the western Mediterranean Sea (Canese et al., 2006; Notarbartolo-di-Sciara et al., 2003; Orsi Relini and Giordano, 1992). Off northwest Spain, stomach contents of captured whales during past whaling industry contained exclusively krill *M. norvegica* (Aguilar, 2009, 1985; Mizroch et al., 1984). In some areas from the North Atlantic, fin whales supplement their diet with small schooling fishes such as capelin, anchovies, sprat and herring (Mizroch et al., 1984; Ryan et al., 2014). Indeed, in the Celtic Sea sprat and herring account for half of the estimated diet composition which may account for the higher apparent trophic level compared with fin whales in the Bay of Biscay, the Mediterranean Sea and Icelandic waters (Ryan et al., 2014, 2013; Víkingsson, 1997). How these differences in diet influence species susceptibility, adaptability and conservation remains an open question and it is crucial to understand how fin whales respond to changes in prey availability, as well as how prey is affected by changing environmental conditions (Víkingsson et al., 2015). The potential effects of global environmental changes on Mediterranean fin whales may influence the entire population, with virtually no space to move to northern latitudes (Evans et al., 2010).

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were previously investigated in baleen plates from fin whales sampled off Ireland ($n = 7$) (Ryan et al., 2013) and from the Mediterranean Sea ($n = 9$) (Bentaleb et al., 2011). Analysis of different tissues comes with certain caveats. Skin biopsies ensure known provenance, however the tissue turnover rate is estimated to be 8–10 weeks (Hicks et al., 1985; St. Aubin et al., 1990), during which time a highly mobile animal may move considerable distances. Baleen can only be sampled from dead (usually stranded) whales that are subject to wind and currents over potentially large distances, which usually precludes knowledge of fine-scale provenance. Skin is metabolically active and therefore provides a relatively temporally discreet insight into isotopic niche. Baleen however, due to it being an inert tissue, provides time-integrated data over which spatio-temporal reference points are difficult to discern given that growth rates and provenance are usually unknown (Ryan et al., 2013). Therefore, skin biopsies are preferable for the purposes of the present study where the key aim is to describe the isotopic niche of contemporary fin whales in the Mediterranean.

Stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$ reported as $\delta^{13}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$ reported as $\delta^{15}\text{N}$) values have become widespread and powerful trophic markers, as the stable isotope composition of consumer tissues are mostly derived from those of their food (DeNiro and Epstein, 1981, 1978). Contribution of each assimilated prey source are proportionally reflected in the tissues of a predator, after accounting for isotopic fractionation in the digestion and assimilation process (DeNiro and Epstein, 1981, 1978). This trophic fractionation typically results in enrichment in the heavier isotope (i.e. increase in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) whose magnitude depends on the considered element. Trophic enrichment in ^{13}C is usually low (i.e. less than 1‰; Mccutchan et al., 2003). The $\delta^{13}\text{C}$ value of a consumer is therefore close to that of the diet and is typically used to indicate relative contributions to the diet of different potential primary producers in a trophic network, indicating for example the aquatic vs. terrestrial, inshore vs. offshore or pelagic vs. benthic contribution to food intake (Louis et al., 2014; Smith et al., 1996). ^{15}N trophic enrichment is more variable, but typically more marked than for ^{13}C , leading to a greater stepwise enrichment in ^{15}N with increasing trophic level (DeNiro and Epstein, 1981; Minagawa and Wada, 1984). Nitrogen stable isotopes are therefore mostly used to estimate an animal's trophic level (Post, 2002). The above-mentioned enrichment factors have been measured for several marine mammal species (Caut et al., 2011; Giménez et al., 2016; Hobson et al., 1996) including fin whales (Borrell et al., 2012). Bentaleb et al. evaluated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in muscle and skin of 65 fin whales from the Mediterranean Sea and calculated the difference with data published previously for krill (Bentaleb et al., 2011).

Since the first conceptualization of the ecological niche as an n -dimensional hypervolume of which each dimension represent an environmental and/or resource requirement (Hutchinson, 1957), use of this concept has expanded in the ecological literature. It was proposed that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values can be used as a proxy to characterize the ecological niche of animals, given the effects of habitat and resource use on these isotopic patterns (e.g. Bearhop et al., 2004; Flaherty and Ben-David, 2010; Newsome et al., 2007). Examining variance in intra- and inter-individual isotope values can be an effective way to investigate resource specialization. This approach allows one to estimate a proxy ecological niche known as the 'isotopic niche' (Newsome et al., 2007).

Here, we provide (1) an analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in skin biopsies of 136 fin whales sampled in the North-western Mediterranean Sea and (2) a comparison of isotopic niches of

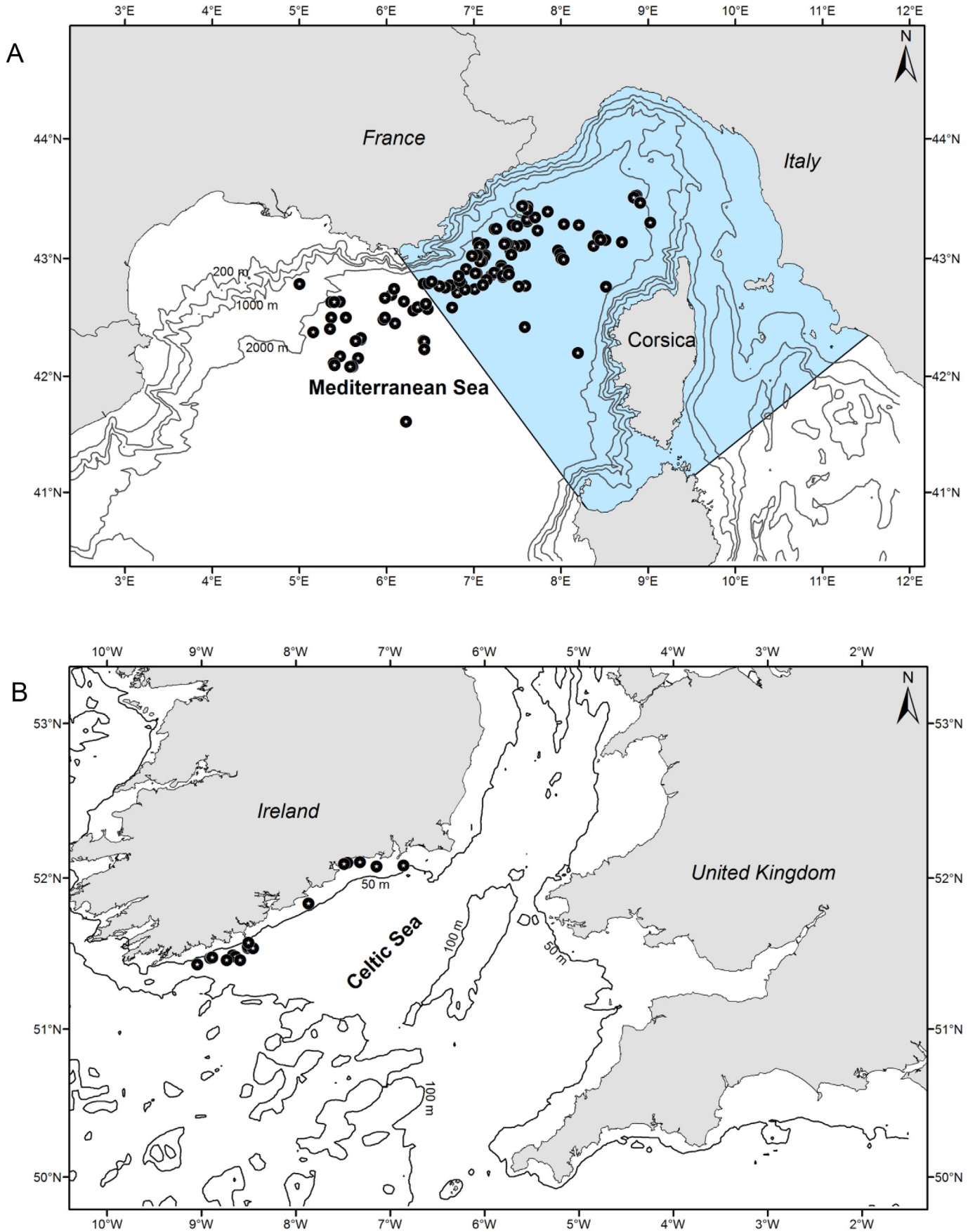


Fig. 1. a. Sampling locations of 136 fin whale *Balaenoptera physalus* skin biopsies in the Mediterranean Sea. Some locations overlap. The blue area represents the Pelagos Sanctuary. b. Sampling locations of 21 fin whale *Balaenoptera physalus* skin biopsies in the Celtic Sea (North Atlantic). Some locations overlap. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Mediterranean Sea and Celtic Sea fin whale populations.

2. Material and methods

2.1. Sample collection and analysis

Skin biopsies of 136 fin whales were sampled in 2010 and 2011 (June–October) during WWF campaigns at sea (North-western Mediterranean Sea, Fig. 1). The biopsies of skin and the first 3–4 cm of blubber of the whale were operated using a 150 lb crossbow (Panzer, US) with a sampling head of 10 mm in diameter and 50 mm in length as described previously (Pinzone et al., 2015). The sampling heads were sterilized with 90% alcohol before the use. Additional information on the time and date of sampling, the geographical coordinates and the structure of the group was registered.

Samples were frozen on board and were kept frozen at -20°C until analyses.

Skin was freeze-dried (Cosmos 2) and ground to a powder with mortar and pestle. Since lipids may be a bias for carbon stable isotope ratio analysis they were removed from the samples by sequentially soaking them with chloroform:methanol (2:1, v/v) (Post et al., 2007; Ryan et al., 2012). Samples were analysed in duplicate: before and after lipid-extraction. Stable isotope ratios of carbon and nitrogen in skin biopsies were determined by analysing approximately 1.5 mg of powdered samples using an automatized vario MICRO Cube N-C-S elemental analyser (Elementar, Hanau, Germany) coupled to a continuous flow IsoPrime100 isotope ratio mass spectrometer (Isoprime, Cheadle, United Kingdom).

Isotopic ratios were expressed using the widespread δ relative notation (Coplen, 2011). Sucrose (IAEA-C6, $\delta^{13}\text{C} = -10.8 \pm 0.2\%$) and ammonium sulphate (IAEA-N1, $\delta^{15}\text{N} = 0.4 \pm 0.2\%$) were used as certified reference material for the measurement of isotopic ratios. Both of these certified materials are calibrated against the international isotopic references Vienna Pee Dee Belemnite (for carbon) and Atmospheric Air (for nitrogen). Standard deviations on replicate measurements of glycine and fin whale skin (one replicate standard every 15 analyses) were 0.1‰ for $\delta^{13}\text{C}$ and 0.3‰ for $\delta^{15}\text{N}$.

2.2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data from the Celtic Sea

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values analysed previously in 21 skin biopsies from individual fin whales sampled in the Celtic Sea between 2008 and 2011 (Fig. 1b) (Ryan et al., 2012) were integrated in the present study for isotopic niche comparison (Table 2). Storage and

Table 1
 $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and C:N ratio in non-lipid extracted and lipid-extracted skin samples of the fin whale *Balaenoptera physalus* from the Mediterranean Sea (n = 136).

	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C:N
Non-treated	-21.6 ± 0.8	7.7 ± 0.5	5.6 ± 1.2
Lipid-extracted	-18.7 ± 0.4	7.9 ± 0.5	3.1 ± 0.1

Table 2
 $\delta^{13}\text{C}$ (lipid-extracted samples) and bulk $\delta^{15}\text{N}$ values in fin whale *Balaenoptera physalus* skin from the Mediterranean Sea and the Celtic Sea (Ryan et al., 2012). Values are expressed as mean \pm standard deviation; and n = number of analysed samples.

	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Mediterranean Sea	-18.7 ± 0.4	7.7 ± 0.5
This work	n = 136	n = 136
Celtic Sea	-18.2 ± 0.5	12.1 ± 1.1
Ryan et al., 2012	n = 21	n = 21

analytical procedures in these of skin samples were detailed previously (Ryan et al., 2012). Lipid extraction procedures differed between studies with respect to the solvents used, which have different polarities. Following lipid extraction, solvent polarity can bias $\delta^{15}\text{N}$ values due to differential extraction of nitrogenous lipid components (Logan and Lutcavage, 2008; Ryan et al., 2012). This issue was circumvented by only using $\delta^{15}\text{N}$ values for control samples. For both datasets, C:N ratios were used to confirm that lipid-extraction was complete. $\delta^{13}\text{C}$ values from delipidated samples and $\delta^{15}\text{N}$ from control samples were used for analysis, ensuring that results were directly comparable between the studies.

2.3. Comparison of isotopic niches

Isotopic niches of fin whales from each population were compared using the SIBER (Stable Isotope Bayesian Ellipses in R) version 2.0 package (Jackson et al., 2011). Delipidated individual $\delta^{13}\text{C}$ and untreated $\delta^{15}\text{N}$ values were used as model inputs. SIBER was used to generate bivariate standard ellipses that represent isotopic niches of consumers. The standard ellipse area (SEA) is a bivariate equivalent of standard deviation. SEA contains only the “typical” members of a population (but may not encompass outlier individuals in isotopic space). For this reason, it has been termed “core isotopic niche”, as it can be used as a proxy of the trophic and habitat resources most commonly used by the population (Layman and Allgeier, 2012). SEA can be estimated using a correction for small sample size (SEAc; Jackson et al., 2011). SEAc is a robust approach when comparing small and/or unbalanced samples. While formal evaluations of what should be considered a “small sample size” for isotopic niche modelling are scarce, Syväranta et al. (2013) suggested that sample sizes inferior to 30 individuals are subject to bias when calculating SEA (Syväranta et al., 2013). Since one of the studied populations (Celtic Sea whales) contains only 21 individuals, we accordingly applied SEAc. This choice does not cause bias in standard ellipse area estimation of the Mediterranean population, as SEA and SEAc tend to converge when sample size increases (Jackson et al., 2011).

Areas of the ellipses associated to each population were also estimated using Bayesian modelling (SEAB; 10^6 iterations). SEAB involves the use of an iterative model based on Bayesian inference to estimate the covariance matrix from the data. SEAB takes into account variability in the data (caused by both natural variations and analytical error) more efficiently and provides a distribution of solutions rather than a single value, therefore allowing error estimates as well as pairwise comparisons. Here, the number of iterations was set to 10^6 . Model solutions were presented using credibility intervals of probability density function distributions. Direct pairwise comparisons were performed, and were considered meaningful when probability of occurrence (i.e. number of model solutions where a given situation was found) exceeded 95%.

3. Results

3.1. Effects of lipid extraction

Lipid-extracted samples were enriched in ^{13}C over untreated samples by an average $\Delta^{13}\text{C}$ of 2.9‰ (Table 1; Wilcoxon test, $p < 0.0001$). The progressive reduction in effects of lipid extraction with increasing $\delta^{13}\text{C}$ values resulted from a decrease in fat content (inferred from a decrease in C:N ratios). Effect of lipid extraction was smaller but statistically significant (Table 1; Wilcoxon test, $p < 0.0001$) for $\delta^{15}\text{N}$ values, and there was a slight increase of 0.14‰.

3.2. Isotopic niche variation

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values measured in skin of fin whales from the Mediterranean Sea and the Celtic Sea ranged from -20.4 to -17.1 ‰ and from 5.9 to 14.3 ‰, respectively (Table 2).

Standard ellipses of the two fin whale populations were markedly separated (Fig. 2).

Standard ellipse areas (SEA_C) of the Mediterranean and Celtic Sea populations were 0.63‰^2 and 1.42‰^2 , respectively (Fig. 3). Model-estimated standard ellipse area (SEA_B) of Mediterranean Sea whales was smaller than the one of Celtic Sea whales in more than 99.99% of model runs, evidencing that the narrower trophic niche trend associated to the Mediterranean population was meaningful (Fig. 3).

4. Discussion

Our results provided the first published records of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in skin from free-ranging fin whales from the Mediterranean Sea revealing intra-population fluctuations and different isotopic niches between populations.

4.1. Intra-population variations

All fin whale samples from the Mediterranean were sampled during summer season between June and October of 2010 and 2011 and therefore we assume that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values determined in skin of fin whales likely reflect their diet during the spring and the summer periods. Although the turnover rate of fin whale skin has never been estimated, turnover rate measured for the beluga whale *Delphinapterus leucas* (St. Aubin et al., 1990) and the common bottlenose dolphin *Tursiops truncatus* (Hicks et al., 1985) suggest that skin integrates the diet of the last 8–10 weeks prior to sampling. Half-life turnover rates were estimated to be 24.16 ± 8.19 days for carbon and 47.63 ± 19 days for nitrogen in skin of bottlenose dolphins (Giménez et al., 2016).

A krill-skin isotope enrichment was previously calculated for fin whales ($\Delta^{15}\text{N} = 2.8\text{‰}$) (Borrell et al., 2012). We observed a wide distribution of $\delta^{13}\text{C}$ values (range -20.4 to -17.1‰) between

individual whales from the Mediterranean Sea reflecting intra-population variability (Fig. 2). Given the large geographical ranges across which fin whales typically travel (Mouillot and Viale, 2001; Ray et al., 1978), it is likely that some isotopic variation arises from geographical differences in foraging locations in the Mediterranean Sea. Furthermore, migration of fin whale individuals from the Atlantic to the Mediterranean Sea cannot be excluded (Bentaleb et al., 2011; Castellote et al., 2014; Giménez et al., 2013). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values analysed in baleen plates from individuals stranded in the Mediterranean Sea (Bentaleb et al., 2011) and from individuals caught off north-western Spain (Giménez et al., 2013) suggest that, while the two subpopulations generally forage in well-differentiated areas, some individuals with characteristic North Atlantic values do penetrate into the Mediterranean Sea (Giménez et al., 2013). Spatial and temporal overlap may exist between this subpopulation and the Mediterranean subpopulation (Castellote et al., 2012). However, connectivity between subpopulations or management units of whales inhabiting the eastern North Atlantic and the Mediterranean Sea is the subject of ongoing debate (Gimenez et al., 2014).

4.2. Isotopic niche analysis

The isotopic niche of a population is a quantitative approach used to describe trophic space using stable isotope values (Newsome et al., 2007). We present two metrics that can be used to characterize the isotopic niche for comparing two samples. Niche area captures resource specialization: small and large areas indicating specialist and generalist organisms respectively. Niche overlap between samples can indicate shared resources. Both fin whale samples in the present study differed with respect to both niche area and overlap. Therefore, fin whales in the Mediterranean Sea are stenophagous by comparison with whales sampled elsewhere in the eastern North Atlantic.

M. norvegica is the only known prey species common to fin whales from the Celtic Sea and the Mediterranean Sea. Using previously published $\delta^{15}\text{N}$ values for whole krill (Bentaleb et al., 2011; Ferraton, 2007; Ryan et al., 2014), a latitudinal cline is apparent whereby values decrease between the Med, Iberian Atlantic and

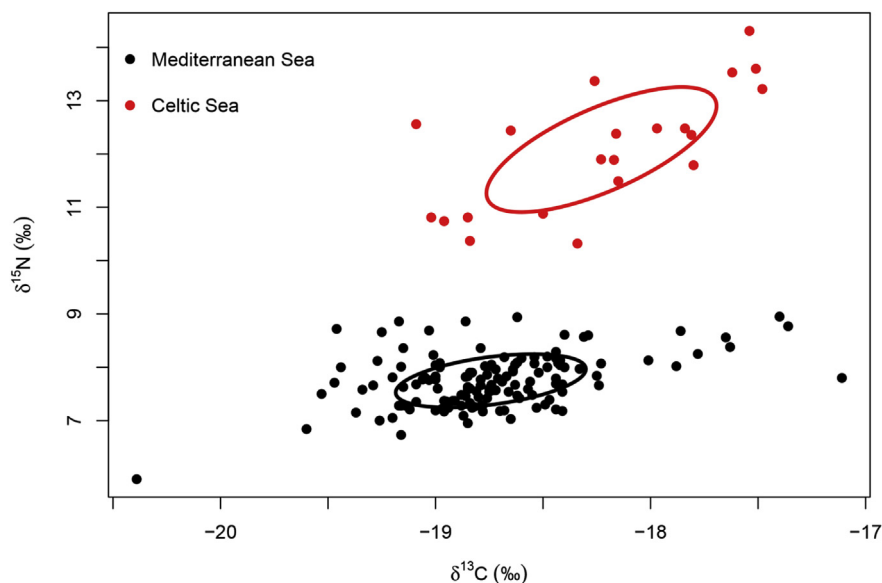


Fig. 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ biplot in skin of fin whales *Balaenoptera physalus* individuals from the Mediterranean Sea (present work), and the Celtic Sea (Ryan et al., 2012). Solid lines represent the standard ellipses associated to each population.

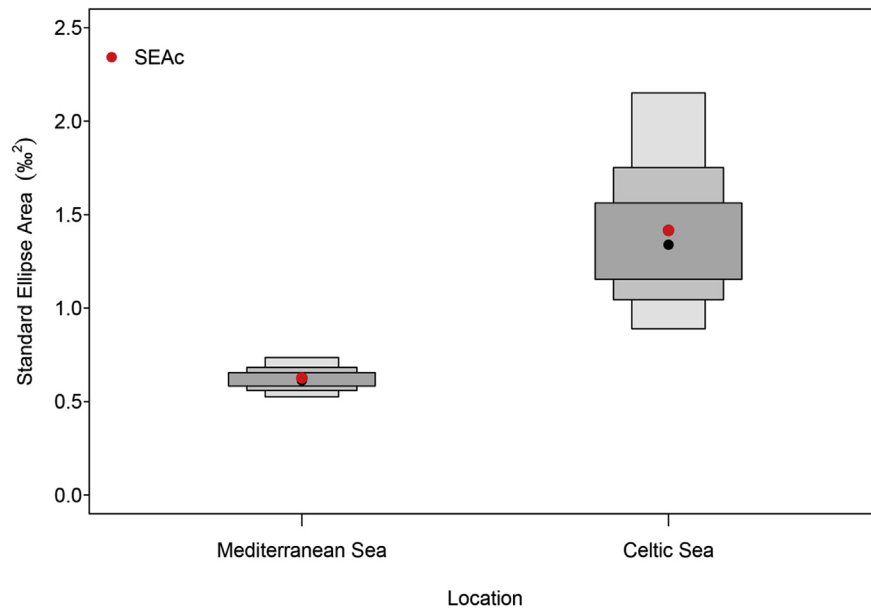


Fig. 3. Estimates of standard ellipse area (SEA) for each fin whale population. Boxplots are posterior probability distributions of model estimations of standard ellipse areas (SEA_B). The dark, intermediate and light grey boxes are the 50%, 75% and 95% credibility intervals, respectively, and the black dot is the mode of each distribution. The red dot is the standard ellipse area calculated using correction for small sample size (SEA_C). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Celtic Sea by ~ 3.1 ppt (Table 3).

The magnitude of this baseline trend is insufficient to account for the difference in fin whale values between the Celtic Sea and the Mediterranean observed in the current study which range from (mean \pm SD) $11.9 \pm 1.0\text{‰}$ to $7.9 \pm 0.5\text{‰}$ respectively. Rather, dietary differences more likely explain the observed results, corroborated by previous findings by Ryan et al. (2013) and observed isotopic niche widths in the present study.

The isotopic niche of fin whales was narrower for Mediterranean than for North Atlantic whales. Indeed, SEA showed that the two sampling areas graphically differentiated for $\delta^{13}\text{C}$ and for $\delta^{15}\text{N}$ (Fig. 3). Ellipses did not overlap for the two sampling locations. As expected, wider $\delta^{15}\text{N}$ variations were observed for whales sampled in the Celtic Sea because of their mixed-diet composed of krill and fish (Ryan et al., 2014) (Fig. 3). Our finding is consistent with a more stenophagous diet of Mediterranean whales, which likely focus mostly on krill (Borrell et al., 2012). Tissues that integrate over weeks, such as skin, are much more likely to discriminate generalist diets than discrete samples from tissues which integrate variation over much longer time-scales, such as baleen plates (Bearhop et al., 2004). In a population of specialists, little or no change in variance of stable isotopes values can be predicted between long- and short-term integrators (Bearhop et al., 2004). In fin whales from the Celtic Sea, standard ellipse area is markedly higher in baleen plates ($SEA_C = 3.89\text{‰}^2$; (Ryan et al., 2013); than in skin ($SEA_C = 1.42\text{‰}^2$). Conversely, in Mediterranean whales, SEA_C previously measured in baleen plates (0.93‰^2 ; (Bentaleb et al., 2011; Ryan et al., 2013); is comparatively closer to SEA_C determined in skin in the present study (0.63‰^2). These geographical discrepancies in inter-tissue

variance further suggest a more specialist diet for Mediterranean fin whales when compared to their North Atlantic counterparts.

4.3. Conservation of the fin whale in the Mediterranean Sea

Our results have important implications for the conservation of vulnerable fin whales. In the event of environmental perturbations, resource specialization can be a disadvantageous evolutionary strategy. Indeed the majority of ecological studies (over both neo- and palaeo- timescales) conclude that resource specialization elevates risk of extinction (Colles et al., 2009). Generalists have access to a wider range of resources. Individual niche width is expected to expand to match the population niche width, but only if there are no biomechanical, physiological, cognitive or other constraints that restrict the variety of different prey resources (Foote et al., 2013). Niche variation owing to individual differences in ecology has been hypothesized to be an early stage of sympatric speciation (Foote et al., 2013). Environmental variation is a major driver of evolutionary divergence (Louis et al., 2014). It can lead to natural selection on environment-associated traits, limiting gene flow and facilitating local adaptation of ecologically distinct groups of individuals (Kawecki and Ebert, 2004; Schluter, 2001).

How climate change-related effects, like seawater temperature rise and ocean acidification, might affect krill (*Meganyctiphanes norvegica* and *Nyctiphanes couchii*) and, in turn, abundance and fitness of fin whales in the Mediterranean Sea remains a pertinent question (Gambaiani et al., 2008). Populations could respond to changing habitats by adapting (through natural selection or phenotypic plasticity), moving (to avoid habitat of reduced

Table 3

$\delta^{15}\text{N}$ value in krill *Meganyctiphanes norvegica* from the Mediterranean Sea (Ferraton, 2007), West of Portugal (Bentaleb et al., 2011) and Celtic Sea (Ryan et al., 2014).

Sampling location	Sampling year	Mean $\delta^{15}\text{N}$ value	SD	Reference
Mediterranean Sea	2002–2004	4.4	0.6	Ferraton 2007
West of Portugal (N38 - 45; W12 - 13)	2001	6.6	1.1	Bentaleb et al., 2011
Celtic Sea (<100 m depth)	2010	7.9	0.1	Ryan et al., 2014

suitability, or take advantage of emerging habitat), by adjusting population size or some combination of the above (Fontaine et al., 2010). Both natural selection and genetic drift can shape populations as they evolve in this context (Fontaine et al., 2010). In the Mediterranean Sea, *M. norvegica* displays a high growth rate in summer, reproduction in winter and recruitment in spring, when the primary production is at maximum, together with a rather low mortality rate (Labat and Cuzin-Roudy, 1996). These biotic features can be viewed as a response to the relatively warm and constant environment of this part of the Mediterranean Sea (13 °C all year round in the Ligurian Sea under the thermocline) (Labat and Cuzin-Roudy, 1996). The relationship between krill and whale abundance is complex as illustrated by a study on fin whales and minke whales from Iceland (Vikingsson et al., 2015). Pronounced oceanographic changes have occurred in Icelandic waters since the mid-1990s, including a rise in seawater temperature and increased flow of warm Atlantic water into the waters north of Iceland (Vikingsson et al., 2015). Assuming that the diet of fin whales in this area consists >90% of euphausiids, mainly *M. norvegica* (Vikingsson, 1997), it was expected that the increased temperatures would have facilitated growth in euphausiid abundance and thereby increased carrying capacity for fin whales (Vikingsson et al., 2009). However, there has been a decrease in euphausiids in shelf and oceanic habitats off Iceland from 1958 to 2007, despite increasing primary production in terms of phytoplankton in those areas (Vikingsson et al., 2015). Seawater temperature warming in the eastern North Atlantic has led to the migration of several marine organisms to higher latitudes (Beaugrand et al., 2002). In the Mediterranean Sea, *M. norvegica* will not be able to extend its range northward because of the land barrier and is likely to share its environment with more thermophilic invasive species in the future (Gambaiani et al., 2008). It seems inevitable that marine predators will need to adapt to a changing spatial distribution of primary and secondary production within pelagic marine ecosystems as they did in the past (Marx and Uhen, 2010). Indeed this is already occurring for baleen whales in the western North Atlantic (Ramp et al., 2015).

During the last glacial maximum (from 26,500 to 19,000 years ago (Clark, 2009)), habitat conditions in the Mediterranean Sea were strikingly different from the current oligotrophic state, with colder conditions (Fontaine et al., 2014, 2010). The Mediterranean Sea was a suitable habitat for cold-water species such as the harbour porpoise (Fontaine et al., 2014, 2010). The postglacial warming presumably led to habitat fragmentation and eventually to the retreat of the harbour porpoise from most of the Mediterranean Sea (Cucknell et al., 2016; Fontaine et al., 2014, 2010). The study of the genetic isolation process of the fin whale from the Mediterranean Sea from its Atlantic counterpart is yet to be investigated but a similar continuum of events could be envisaged. The differences observed between fin whales from the Atlantic and the Mediterranean Sea might reflect the adaptation of fin whales to an environment characterised by specific climatic conditions as well as primary (and secondary) production.

To conclude, our results using skin biopsies complement $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ studies using baleen plates of fin whales, supporting the current International Whaling Commission stock assessment of an isolated Mediterranean population (Ryan et al., 2013; Giménez et al., 2013). The narrow width of the isotopic niche of the Mediterranean fin whales compared to the North Atlantic specimens, as well as the temporally stable trend to higher specialism in the Mediterranean population, raise many concerns in the context of global changes and long-term consequences.

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