Stable isotope analysis of baleen reveals resource partitioning among sympatric rorquals and population structure in fin whales

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ABSTRACT: Stable isotope analysis is a useful tool for investigating diet, migrations and niche in ecological communities by tracing energy through food-webs. In this study, the stable isotopic composition of carbon and nitrogen in keratin was measured at growth increments of baleen plates from 3 sympatric species of rorquals (*Balaenoptera acutrostrata*, *B. physalus* and *Megaptera novaeangliae*), which died between 1985 and 2010 in Irish and contiguous waters. Bivariate ellipses were used to plot isotopic niches and standard ellipse area parameters were estimated via Bayesian inference using the SIBER routine in the SIAR package in R. Evidence of resource partitioning was thus found among fin, humpback and minke whales using isotopic niches. Highest $\delta^{15}N$ values were found in minke whales followed by humpback, and fin whales. Comparison between Northeast Atlantic (Irish/UK and Biscayan) and Mediterranean fin whale isotopic niches support the current International Whaling Commission stock assessment of an isolated Mediterranean population. Significantly larger niche area and higher overall $\delta^{15}N$ and $\delta^{13}C$ values found in fin whales from Irish/UK waters compared to those sampled in adjacent regions (Bay of Biscay and Mediterranean) suggest inshore foraging that may be unique to fin whales in Ireland and the UK. Isotopic profiles support spatial overlap but different foraging strategies between fin whales sampled in Ireland/UK and the Bay of Biscay. Stable isotope analysis of baleen could provide an additional means for identifying ecological units, thus supporting more effective management for the conservation of baleen whales.

KEY WORDS: Diet · Isotopic niche · Foraging · Stock discrimination · Northeast Atlantic · Bayesian analysis

INTRODUCTION

Following 2 centuries of commercial whaling, the current ecological assemblage and population sizes of rorquals (Family Balaenopteridae) are believed to be very different to those of pre-whaling times (Roman & Palumbi 2003, Baker & Clapham 2004). While we know little of their ecosystem role, the near extirpation of some species of baleen whales may have been associated with subsequent trophic cas-

cades (Springer et al. 2003, Ballance et al. 2006). Poorly managed fisheries may exert top-down control on marine food webs, assuming the functional role of apex predators such as cetaceans, hence replacing them (Trites et al. 2006). Policies for sustainable management of marine resources are attempting to move from single species based approaches to include ecosystem-scale effects, but designing effective ecosystem-based management requires knowledge of species interactions within a spatio-temporal context (Pauly et al. 2002, Gerber et al. 2009). These data are often missing, particularly for highly migratory, high trophic level predators. Basic biological information on foraging strategies, relative trophic positions and resource partitioning is also needed for effective species-based management and maintenance of cetacean populations. In this study, the foraging ecology of 3 species of rorqual — fin whales *Balaenoptera physalus*, humpback whales *Megaptera novaeangliae* and minke whales *B. acutrostratus*, which occur sympatrically in the Northeast Atlantic (NEA) — were investigated using stable isotope analysis of baleen plates.

In the North Atlantic fin, minke and humpback whales are considered to be generalist predators, consuming pelagic schooling fishes, primarily capelin *Mallotus villosus* and herring *Clupea harengus* (Piatt & Methven 1992, Lindstrøm et al. 2002, Laidre et al. 2010, Skern-Mauritzen et al. 2011) and zooplankton such as krill (Euphausiacea) and amphipods (Hobson et al. 2002). Fin whales in the NEA and Mediterranean Sea are known to feed chiefly on northern krill *Meganyctiphanes norvegica* and other zooplankton (Relini et al. 1992, Aguilar 2008, Skern-Mauritzen et al. 2011, Visser et al. 2011). However in Ireland, they occur in inshore waters for up to 10 mo of the year (Whooley et al. 2011), where they associate strongly with an inshore movement of spawning herring (Fairley 1981). Gut content-analysis of fin whales landed at a whaling station in Ireland in 1912 indicated that fin whales were feeding on both clupeids ('herrings') and northern krill (Fairley 1981). Two studies on the diet of minke whales in Scotland yielded consistent findings that minke whales had a piscivorous diet (Macleod et al. 2004, Pierce et al. 2004).

Rorquals are difficult to study as they can be elusive and often occur offshore, ranging over large geographical areas. Rapid onset of autolysis in stranded specimens due to their large body sizes usually renders gut content analysis impractical. A moratorium on whaling, along with conservation and ethical issues, preclude lethal sampling for research.

Given these challenges, stable isotope analysis (SIA) is a tool that is being used with increasing frequency in marine mammal research to address gaps in our knowledge (Newsome et al. 2010, Ramos & González-Solís 2012, Ryan et al. 2012). While conventional diet analyses such as fecal or stomach content analysis may offer high taxonomic resolution, they provide information over a short timescale and are subject to additional sources of uncertainty and bias (Layman et al. 2007, Pierce et al. 2007). Stable isotope values of tissues reflect those of the environment and prey from which the tissues were synthesised (DeNiro & Epstein 1978). SIA can provide information on migratory movements and foraging habits of animals provided that they feed along a known isotopic gradient and that trophic enrichment factors are reliably constrained (e.g. Harrod et al. 2005, Graham et al. 2010, MacKenzie et al. 2011, Trueman et al. 2012a,b). The technique can provide quantitative data to investigate inter alia resource partitioning and other complex processes that govern structure in ecological communities (Jackson et al. 2012).

In the marine environment baseline $\delta^{13}C$ and $\delta^{15}N$ values, i.e. those of particulate organic matter (POM), vary with both latitude and proximity to shore. These broad geographic patterns are driven by variation in the degree of isotopic fractionation during photosynthesis, and the isotopic composition of the inorganic carbon utilised by phytoplankton (Goericke & Fry 1994, Hofmann et al. 2000, Fry 2006, Tagliabue & Bopp 2008, Graham et al. 2010). Because of its sensitivity to plankton growth rates and seawater carbonate chemistry, the isotopic composition of POM is subject to dynamic climatic and oceanographic forcings at all spatiotemporal scales (Newsome et al. 2007a, MacKenzie et al. 2011, Trueman et al. 2012a). Despite predictable gradients in stable carbon isotope ratios at an ocean-basin scale, their usage in assigning geographic location to marine animals is confounded by additional temporal and small-scale spatial variations (due to, e.g. upwelling), which may be difficult to predict (Rau et al. 1992, Hofmann et al. 2000, MacKenzie et al. 2011).

Spatial heterogeneity is also found in the nitrogen stable isotope compositions of marine primary producers due to differential fractionation (Montoya 2007) and differences in the isotopic composition of nitrogen assimilated during cell growth. One study in the inshore seas around the UK showed that 77% of variability in $\delta^{15}N$ values of whiting *Merlangius merlangus* was attributed to differences at the base of the food chain rather than trophic level (Jennings & Warr 2003). Baseline phytoplankton $\delta^{15}N$ values are dic-

tated by the availability and types of nutrients (ammonium, nitrate or N_2) from which they are sourced. Broad latitudinal regions are characterised by specific mechanisms of nitrate utilization, for example N_2-fixation in sub-tropical gyres and nitrate assimilation in vertically-mixed mid to high latitude regions. Considering that nitrogen availability to phytoplankton and its isotopic composition dictates baseline $\delta^{15}N$ values, inputs of terrestrial nitrogen can manifest as a gradient of isotopic enrichment towards the shore in marine food webs (Jennings & Warr 2003).

The ecological niche concept formally defined by Hutchinson (1957) has become fundamental in community ecology theory. Defined as an '*n*-dimensional hypervolume', a niche is a space that encloses *n* limiting dimensions of the environment in which an organism can occur (Hutchinson 1957). The range of stable isotope compositions measured in individuals may be used to quantify trophic niche dimensions, contributing to a resurgence of interest in the niche concept and giving rise to the 'isotopic niche' or 'δ-space' (Newsome et al. 2007b). Theoretically, the isotopic niche approximates the trophic niche (Bearhop et al. 2004, Layman et al. 2007) such that isotopic niche space (the range of isotopic values in ‰) and niche area (the area occupied in bi-plot space in ‰^{2}) provide insight into resource partitioning and specialization respectively. Where baseline isotope values are unknown, the isotopic niche approximates trophic niche with an added component of variation associated with environmental variability in time and space. In this context, differences in isotopic niche space between 2 samples may indicate either differences in the diversity of prey organisms or differences in the area (and/or time) foraged.

Incremental sampling of accretionary tissues can provide a longitudinal record of isotopic proxies for both diet and habitat use (Mendes et al. 2007, Newsome et al. 2009). Synthesized from metabolites of the bloodstream and composed almost exclusively of keratin, baleen is an accretionary tissue suitable for investigating long-term foraging via stable isotope analysis (Schell et al. 1989a). In one study where minke whale baleen was sampled along the growth axis, isotopic values from the most recent 10 mm segment of baleen were found to reach equilibrium with those of muscle (Hobson et al. 2004). Thus baleen isotope values exhibit similar carbon and nitrogen assimilation rates to muscle (several months, although this is not established experimentally) representing metabolic pathways of proteins rather than mobilized lipid stores (Hobson et al. 2004).

The International Whaling Commission (IWC) aims to manage baleen whale populations based on identification of geographically explicit and biologically relevant units (Donovan 1991). However management units are difficult to define. In the management of fin whales in particular, 'stock' discrimination remains poorly resolved in the North Atlantic (IWC 2007). Here we compare isotopic niches estimated via a Bayesian inference framework to infer population connectivity in fin whales sampled in 3 adjacent geographic locations: Ireland/UK, Bay of Biscay and the Mediterranean Sea.

MATERIALS AND METHODS

Baleen plates from adult fin (n = 7), minke (n = 3) and humpback (n = 3) whales found stranded around Ireland and the UK were sampled from collections or taken directly from carcases in the case of recent samples (Fig.1, see Table 1). Samples were also taken from fin whales (n = 3) landed at Caneliñas whaling station in northern Spain before the international moratorium on whaling. These fin whales were killed in the Bay of Biscay near Cape Finisterre at unknown dates between July and August 1985. While length of these animals was unknown, they were assumed to be >17 m in accordance with catch regulations
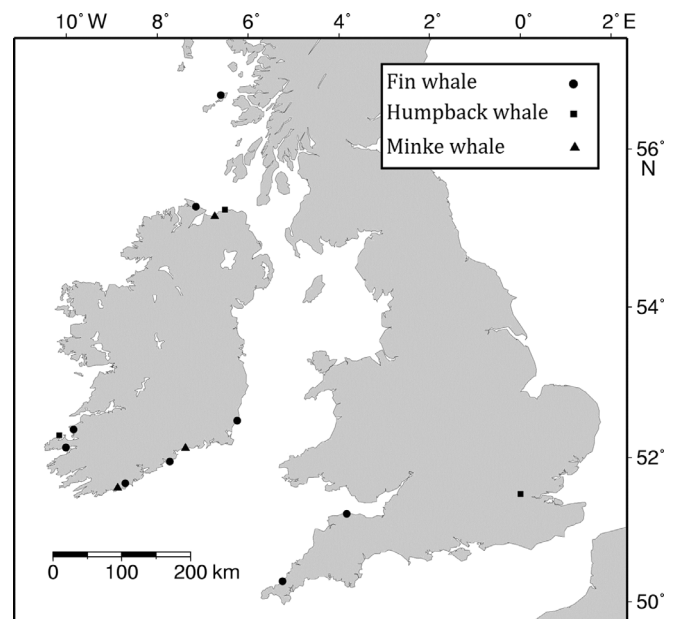

Fig. 1. Whale strandings from which baleen plates were sampled (see Table 1). Bay of Biscay sampling locations were only approximate and therefore not presented here

at that time. In order to ensure that our results were directly comparable with those of a study on Mediterranean fin whales (Bentaleb et al. 2011), a consistent sample preparation was adopted. Baleen plates were air-dried and stored at room temperature, scoured using steel wool and cleaned with 1:1 methanol-chloroform solution to remove any extraneous material such as adhering lipids. As baleen is composed almost exclusively of protein (keratin), tissue treatment such as lipid or carbonate extraction is not necessary. Incremental sampling was carried out longitudinally (i.e. along the growth axis) on each plate at locations measured using demarcated adhesive tape (due to curvature of some plates when dried), from the gingival end to the distal tip. Along the transverse axis, tissue synthesis is uniform (Schell et al. 1989b). Samples were taken within 0 to 20 mm of the non-frilled (outer) edge, where the growth axis is longest (Bentaleb et al. 2011), with increments of 50 mm (fin), 20 mm (humpback) and 10 mm (minke whale). Samples were simultaneously removed and homogenised using a rotary engraving tool with a stainless steel tip (1 mm diameter) that was cleaned between samples using deionised water. Approximately 1.5 (± 0.5) mg of tissue were weighed into tin cups and analysed for carbon and nitrogen isotope ratios by continuous flow elemental analysis isotope ratio mass spectrometry (CF-EA-IRMS). Measurements were carried out using a EuroVector EA 3000 elemental analyzer (EA) interfaced with a Europa Scientific 20-20 isotope ratio mass spectrometer (IRMS) at the University of Southampton. Routine analysis of in-house laboratory standards (Acros L-glutamic acid) was used to estimate instrument accuracy and precision. Carbon and nitrogen isotope ratios were determined against a reference standard, glutamic acid, which itself was referenced with IAEA Vienna Pee Dee Belemnite and atmospheric air.

The elemental carbon to nitrogen ratio (C:N) was used as quality assurance to assess stable isotope values before subsequent analyses. A single fin whale sample with a C:N ratio of 4.2 was outside of the theoretical value of 3.4 ± 0.5 for pure keratin and therefore omitted from all analyses (O'Connell & Hedges 1999, Bentaleb et al. 2011). All plates analysed comprised >1 yr growth according to known or estimated baleen growth rates for the species concerned. A continuous growth rate of baleen was assumed to be 20 cm yr^{-1} for fin (Bentaleb et al. 2011) and 12 cm yr^{-1} for minke (Mitani et al. 2006) whales. The growth rate of humpback baleen is not known; however, based on proportionate body size, it is assumed to be intermediate between fin and minke whales and thus 15 cm yr^{-1} was assumed. Grey whales are of similar body length and weight and are known to have a baleen growth rate of between 10 and 20 cm yr^{-1} (Sumich 2001). Growth rates were used to ensure that samples comprised at least 1 yr of growth for each individual sampled. For some plates, the gingival end was missing, thereby precluding the construction of a time-series from a known point in time.

The use of Euclidean methods, such as convex hulls to define the isotopic niche space of a species in a community (Layman et al. 2007), is subject to sampling biases and sensitive to sample size (Jackson et al. 2011). Standard area ellipses estimated by Bayesian inference can incorporate uncertainties such as sampling biases and small sample sizes into niche metrics (Jackson et al. 2011). Here, resource partitioning is investigated using the Stable Isotope Bayesian Ellipses in R (SIBER) routine in SIAR, a package in the R programming environment, to examine variation in $\delta^{13}C$ and $\delta^{15}N$ values and estimate isotopic niche space (Jackson et al. 2011, R Development Core Team 2011). This approach is similar to bootstrapping in that it iteratively assigns measures of uncertainty, in this case based on Markov-Chain Monte Carlo (MCMC) simulation to construct parameters of ellipses.

Bivariate ellipses and convex hulls were used to delineate isotopic niche space ($\delta^{15}N–\delta^{13}C$ 95 % confidence interval ellipses) and the total extent of isotopic niche respectively among species (Jackson et al. 2011). Bayesian standard ellipses (SEA_C), corrected for small sample sizes by 2 standard deviations (n – 1 for each axis) were then plotted using the SIBER routine in the SIAR package in R (version 2.14.1) (Jackson et al. 2011, R Development Core Team 2011). Niche area and overlap ($‰^2$) were estimated based on 100 000 posterior draws of the SEA_C parameters, which are comparable among and within ecological communities (Jackson et al. 2011). By including bivariate isotopic data for individual whales for increments representing >1 yr of baleen growth (see Table 1), isotopic variation in diet, space and time was incorporated into the posterior distribution. Niche space and area were thus comparable among the 3 species. Similarly, niche space and area were compared between fin whales in order to investigate for evidence of population structure between 3 sampling regions: Ireland/UK, Bay of Biscay (data from present study) and the Mediterranean (Bentaleb et al. 2011).

RESULTS

In order to investigate resource partitioning (niche space) and resource specialization (niche area) among fin, humpback and minke whales from Irish and UK waters, baleen plates were sampled from collections for stable isotope analysis (Fig. 1, Table 1). Only specimens with data on stranding location, date, species and total body length were included (Table 1). From 3 separate runs, the minimum instrumental precision (SD) was <0.2‰ for both $\delta^{15}N$ and $\delta^{13}C$ values respectively for the CF-EA-IRMS. Baleen plates from fin (n = 10), minke (n = 3) and humpback (n = 3) whales were sub-sampled. The mean C:N ratio (range) of baleen subsamples from fin (n = 65), humpback (n = 51) and minke whale (n = 48) was 3.4 (3.2 to 3.7), 3.5 (3.3 to 3.7) and 3.4 (3.2 to 3.5) respectively.

Isotopic niche space

Distinct isotopic niche space was found between the 3 species: fin, humpback and minke whales (Fig. 2). The probabilities that different species occupied distinct niche spaces were estimated as the extent of overlap between ellipses. These probabilities were derived by Bayesian inference where the posterior probability of the model M, given the data D, i.e $Pr(M|D)$, was based on 100 000 MCMC draws. The probability of isotopic niche overlap, estimated from posterior distributions, among these 3 species was very low ($Pr(M|D)$ < 0.001). Significant isotopic niche partitioning was also demonstrated between Mediterranean fin whales and those from other sampling locations (Fig. 3). However, there was considerable overlap in niche space between fin whales from the Bay of Biscay and Ireland/UK (98.7 %) indicating considerable shared isotopic niche space.

Isotopic niche areas

Isotopic niche areas (‰^{2}) for fin, humpback and minke whales from Irish/UK waters, delineated by SEA_C, which is adjusted for sample size, are presented in Fig. 2. Minke whales occupied the smallest isotopic niche area, consistent with high resource specialization, while fin and humpback whales exhibited larger isotopic niche areas (Fig. 2). Probabilities that niche areas differ in extent were derived by Bayesian inference, whereby Pr values imply support of the actual hypothesis presented and not the null hypothesis. The probability, for the posterior distribution (based on 100 000 draws) of the parameters of model M given the prior data D, that humpback

Table 1. Details of whales used in this study for baleen subsamples. Records were sourced from www.iwdg.ie and the British Natural History Museum database. Mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ values from each baleen plate are presented

Specimen	Date	Species	Location	Body length (m)	Baleen length (mm)	Sex	$\delta^{13}C$	$\delta^{15}N$	n
Data in Fig. 2									
IRMn96001	25-Aug-96	Humpback	Brandon Bay, Co. Kerry, Ireland	–	30	F[a]	−18.8 (0.14)	12.5 (0.69)	15
IRMn04001	13-Sep-04	Humpback	Giant's Causeway, Co. Antrim, UK	8	30	M	−19.2 (0.15)	13.4 (0.41)	15
GBMn09001	12-Sep-09	Humpback	QE2 Bridge, London, UK	9.5	42	M	−17.6 (0.76)	12.3 (1.72)	21
IRBa93001	11-Jul-93	Minke	Portstewart, Co. Derry, UK	9.4	19	F	−15.9 (0.42)	13.5 (0.44)	19
IRBa01002	04-Dec-01	Minke	Ballydowane, Co.Waterford, Ireland	7.84	14	M	−16.5 (0.48)	12.7 (0.87)	13
IRBa08001	20-Sep-08	Minke	Duneen, Co. Cork, Ireland	7.47	16	M	−16.8 (0.28)	13.9 (0.38)	16
Data in Figs. 2 & 3									
IRBp94001	01-Apr-94	Fin	Ballyheigue, Co. Kerry, Ireland	24	55	F	−17.9 (0.67)	9.3 (0.75)	10
IRBp01001	05-Dec-01	Fin	Whiting Bay, Co. Waterford, Ireland	18.9	45	M	−16.7 (0.53)	12.2 (0.97)	8
GBBp04001	01-Feb-04	Fin	Isle of Coll, Scotland, UK	17.1	40	F	−17.8 (0.38)	8.5 (0.71)	7
IRBp08012	11-Oct-08	Fin	Inch, Co. Kerry, Ireland	18.5	60	F	−19 (0.22)	8.4 (0.71)	12
IRBp09001	15-Jan-09	Fin	Courtmacsherry, Co. Cork, Ireland	19.7	70	F	−18.6 (0.21)	9.2 (0.6)	13
IRBp09002	01-Feb-09	Fin	Ballyduboy, Co. Wexford, Ireland	16	40	M[a]	−18.8 (0.15)	9.8 (0.29)	8
GBBp10001	23-Feb-10	Fin	Porthtowan, Cornwall, UK	16.9	40	F	−17.8 (0.52)	11.6 (0.99)	7
Data in Fig. 3									
SPBp85001	31-Jul-85	Fin	~100 nm NW Cape Finnistere, Spain	>17	55	–	−17.9 (0.29)	9 (0.41)	12
SPBp85002	31-Jul-85	Fin	~100 nm NW Cape Finnistere, Spain	>17	65	–	−19 (0.35)	10 (0.47)	13
SPBp85003	31-Jul-85	Fin	~100 nm NW Cape Finnistere, Spain	>17	55	–	−18.1 (0.3)	9.8 (0.48)	11

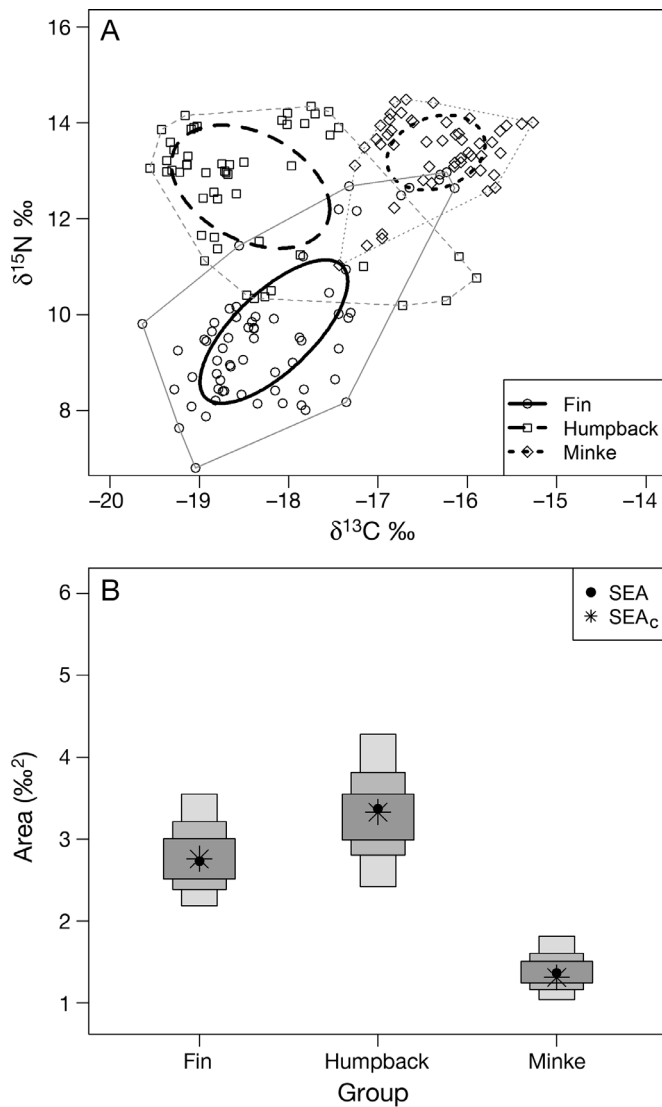[a]Sexes (M: male, F: female) determined genetically from skin samples (see Bérubé & Palsbøll 1996 for methods)

Fig. 2. (A) Variation in $\delta^{13}C$ and $\delta^{15}N$ values for fin (n = 7), humpback (3) and minke (3) whales from Ireland/UK only. Thick black and thin grey lines: 95% CI bivariate ellipses and convex hulls respectively of $\delta^{13}C$ and $\delta^{15}N$ values plotted according to species for adults only (see Table 1), demonstrating the significant isotopic niche partitioning among the 3 rorqual species. (B) Measures of uncertainty and central tendency (black symbols = mode) of Bayesian standard ellipse areas (SEA_C, corrected for small samples in a bivariate distribution for 2 df) based on 100 000 posterior draws of parameters showing 95, 75 and 50% credibility intervals from light to dark grey respectively. See 'Results' section for probabilities of differences in area for species

Fig. 3. (A) $\delta^{13}C$ and $\delta^{15}N$ values plotted according to sampling area. Black and grey lines: show significant isotopic niche partitioning between fin whales from the Mediterranean and other sampling regions (see Fig. 2 for details; Table 1) Fin whales from Bay of Biscay and Ireland/UK occupy common isotopic niche areas. Note: data from a previously published study are included (◇) (Bentaleb et al. 2011). (B) Measures of uncertainty and central tendency of Bayesian standard ellipse areas (SEA_C), see Fig. 2 for details. While fin whales from Ireland/UK share the same isotopic niche space as those from Bay of Biscay, the niche area of the former is significantly greater

whales occupy a greater isotopic niche area than fin whales is $Pr(M|D) = 0.20$. Fin whales sampled in Ireland/UK exhibited a niche area significantly greater than those of both the Mediterranean and the Bay of Biscay ($Pr(M|D) < 99.999\%$). Temporal differences in the samples may account for some of this difference,
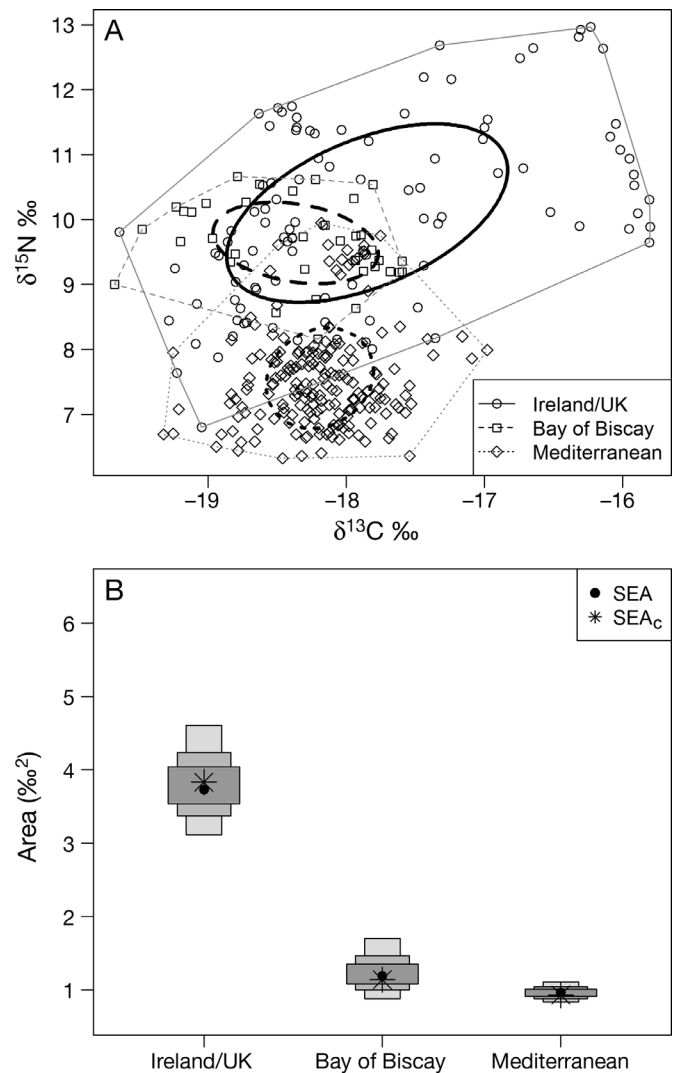
particularly between Bay of Biscay (~4 yr) and other locations (~18 and 30 yr for Ireland/UK and the Mediterranean respectively). However, temporal changes in either $\delta^{13}C$ or $\delta^{15}N$ values are unlikely to be of such a magnitude, that niche areas would increase greatly. The Seuss effect is the reduction in ^{13}C relative to ^{12}C due to anthropogenic burning of ^{12}C rich

fossil fuels, which may account for some differences in $\delta^{13}C$ when comparing samples taken over large timescales. Such changes are likely to be immaterial in the context of this study, e.g. ~−0.45‰ global average over the 30 yr sampling period in the case of fin whale samples (Sonnerup et al. 1999). While the isotopic niche space of Biscayan fin whales overlapped with that of Ireland/UK fin whales, the probability of the latter exhibiting a larger overall niche area was very high ($Pr(M|D) = 1$). The probability that posterior SEA_C of Mediterranean fin whales was less than that of Biscayan fin whales was also high ($Pr(M|D) = 0.92$) indicating a very small isotopic niche for Mediterranean fin whales (Fig. 3).

DISCUSSION

Of the 6 rorqual species occurring sympatrically in the NEA, 3 were considered in this study. Knowledge on the diet of fin and humpback whales from recent times in the NEA is lacking (O'Brien et al. 2009, Wall et al. 2009, Whooley et al. 2011). However fin whales in both the Mediterranean Sea and the Bay of Biscay, and minke whales in Scotland are known to feed preferentially on northern krill and both lesser sand-eel *Ammodytes marinus* and herring respectively (Relini et al. 1992, Pierce et al. 2004, Aguilar 2008). A review of the literature providing evidence of potential resource overlap between fin, humpback and minke whales in the NEA prompted the use of stable isotope analysis to investigate resource partitioning using isotopic niches. Stable isotope analysis of baleen was used to elucidate long-term isotopic niche, which it has been argued is a function of both trophic status and habitat use (Layman et al. 2007). C:N ratios confirmed that the baleen samples were within the theoretical range for pure keratin in 317 out of 318 samples analysed (O'Connell & Hedges 1999). Those C:N ratios presented here are the first in the literature for humpback whale baleen and indicate that a value of 3.4 is conservative across taxa for baleen (cf. skin and blubber, Ryan et al. 2012). This provides a useful reference for quality assurance of corresponding $\delta^{15}N$ and $\delta^{13}C$ values for future studies using CF-EA-IRMS.

By only analysing baleen plates comprising >1 yr of growth, potential variability in stable isotope values arising during migration and annual cycles were captured. As capital breeders, fin, humpback and minke whales are all believed to undergo prolonged migration for reproduction and sometimes show high site fidelity to feeding grounds (Jonsgård 1966, Gill & Fairbainrns 1995, Stevick et al. 2006, Whooley et al. 2011). However the timing, routes taken and location of breeding areas are not known for these species in the NEA (Anderwald et al. 2011). The large range of stable carbon and nitrogen isotope values, particularly for fin and humpback whales from Irish/UK waters, indicates that baleen was synthesised from a broad isotopic source (i.e. probably more than one set of baseline isotope compositions). This could occur due to feeding in more than one area (e.g. during migration) or differential metabolic fractionation of $\delta^{13}C$ and $\delta^{15}N$ such as that associated with catabolism (Schwarcz 1991, Hobson et al. 1993, 2004, Gannes et al. 1997).

Isotopic niche space

Using SEA_C in SIBER, 3 distinct isotopic niches among fin, humpback and minke whales were delineated, indicating significant resource partitioning in Ireland/UK where they occur sympatrically (Fig. 2). This is surprising considering observational evidence of shared resources (namely clupeids) in inshore waters. While SEA_C showed distinct isotopic niches, overlap between convex hulls did occur at $\delta^{15}N$ values of ~11.5‰ and at $\delta^{13}C$ of ~−17‰ indicating that any resource competition that may occur is likely to be short-lived (Fig. 2). The overlapping isotopic niche space shared by Irish/UK and Biscayan fin whales suggests connectivity between whales from these regions. It has been shown that baseline $\delta^{13}C$ values correlate positively with both latitude (Goericke & Fry 1994, Hofmann et al. 2000) and proximity to shore (Fry 2006). All else being equal, Irish/UK fin whales would be expected to exhibit more depleted $\delta^{13}C$ values compared to their southern counterparts considering that $\delta^{13}C$ values generally decrease with latitude, particularly at latitudes >50° N. The opposite was observed however; thus, latitudinal variations in baseline C isotopes cannot explain the distinctive isotopic composition of baleen from Ireland/UK whales. This finding is consistent with an inshore component to their diet, a pattern unique to whales from the Ireland/UK sample.

Isotopic niche area

Although distinct with respect to isotopic niche space, fin and humpback whales exhibited the same isotopic niche areas, which were significantly larger than that of minke whales (Fig. 2). Assuming that

minke whales assimilated nutrients from a baseline subject to similar spatiotemporal variation, the smaller isotopic niche area suggests a more steno-phagous diet for this species in the study area. This result is potentially surprising considering that in the North Atlantic, minke whales exhibit a generalist diet comprising fishes (Lindstrøm et al. 2002, Macleod et al. 2004, Pierce et al. 2004) and zooplankton (Hobson et al. 2002). Thus, the differences in isotopic niche area may reflect differences in spatial foraging. By comparison with fin and humpback whales, the feeding range for minke whales may be restricted either geographically or in terms of the number of food webs from which nutrients are derived. Fin whales exhibited the broadest range of $\delta^{13}C$ values suggestive of feeding over latitudinal gradients (during migration) or in more than one food web, i.e. in both pelagic and inshore waters.

To draw ecological inferences, e.g. on trophodynamics, from a comparison of tissue isotopic variability between species or populations, assumptions concerning spatial variability of basal $\delta^{15}N$ and $\delta^{13}C$ values must be made. At present, our understanding of spatial and temporal variability in marine isotopic baselines is incomplete and more baseline isotopic data are required for a robust interpretation of either isotope niche dimensions or geographic assignment using an isoscapes (stable isotope mapping) approach (West et al. 2010, Trueman et al. 2012b). Compound-specific stable isotope analysis can be used to decouple the relative contributions of trophic and baseline variation in stable carbon and nitrogen isotope compositions (Popp et al. 2007). However, currently these techniques are time consuming and relatively costly, prohibiting routine application to large sample suites.

Implications for conservation and management

Stable isotope values have previously been used as a complementary tool towards resolving population structure (Clegg et al. 2003, Foote et al. 2009, Newsome et al. 2009). Our isotopic niche models indicate that fin whales sampled from Ireland/UK and the Bay of Biscay were spatially explicit from those of the Mediterranean Sea. The isotopic niche area however was different between the 3 groups of fin whales analysed, possibly reflecting either different foraging strategies between fin whales from Ireland/UK and Bay of Biscay or differential variability in isotopic baselines. The IWC recognises a single fin whale management unit ('British Isles–Spain–Portugal') from the sampling regions included in this study

(Donovan 1991, IWC 2007). Our results support the 'British Isles–Spain–Portugal' management unit as ecologically relevant given that considerable overlap in isotopic niche was found in whales from both the Bay of Biscay and Ireland and the UK. Comparing our data with those published by Bentaleb et al. (2011), however, supports the hypothesis that Mediterranean fin whales constitute a distinct population and should be considered as a separate management unit (Bérubé et al. 1998). Interestingly, outliers from the study by Bentaleb et al. (2011) occur within the isotopic niches of both Biscayan and Irish/UK fin whales, supporting the hypothesis that limited exchange does occur between fin whales from the Mediterranean and adjacent waters (Castellote et al. 2012).

Enriched $\delta^{13}C$ values >−17‰ observed in samples from Ireland and the UK but not the Mediterranean or the Bay of Biscay is surprising in light of the expected depletion in baseline $\delta^{13}C$ values with latitude. This pattern is therefore consistent with a significant inshore diet component unique to fin whales from Ireland and the UK, where they have been observed feeding on forage fishes close to shore (Whooley et al. 2011). While direct evidence from satellite telemetry demonstrates that exchange between IWC stocks does occur (Mikkelsen et al. 2007), the geographic range of our samples did not allow for discrimination between the 'Faro–West Norway' and 'British Isles–Spain–Portugal' management units. More research is needed to investigate the range and connectivity of fin whales in the North Atlantic, where population structure remains poorly resolved due to recurrent gene flow between sub-populations (Bérubé et al. 1998, Palsbøll et al. 2004). We propose that stable isotope analysis would complement molecular genetic data towards resolving population structure of fin whales and other rorquals in the North Atlantic (e.g. Clegg et al. 2003).

CONCLUSION

Carbon and nitrogen isotopic niche partitioning was found for fin, humpback and minke whales occurring sympatrically in Irish/UK waters, although based on a small sample size. This somewhat contradicts recent field observations of fin, humpback and minke whales foraging on common prey in Irish waters. Instead, diet overlap between these species may only be short-term, which shows the importance of considering averaged diet over longer time periods, as afforded by stable isotope analysis of accretionary tissues such as baleen. Until such time as

robust estimates of diet solutions can be derived, most promisingly using Bayesian mixing models (Parnell et al. 2010), the isotopic niche concept can progress our understanding of poorly studied ecological communities by helping to formulate pertinent hypotheses on resource partitioning, competition and foraging strategies. We have shown that stable isotope analysis has a role to play in identifying connectivity between fin whales inhabiting adjacent regions in the NEA. Bayesian mixing models complemented by satellite telemetry will be required to clarify resource partitioning and nutrient sources at fine taxonomic and spatial scales among those rorquals occurring sympatrically in the NEA. This would further facilitate informed ecosystems-based management decisions towards more effective conservation of marine resources, including rorquals, which are still recovering from centuries of over-exploitation.

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