



# Stable isotope analysis of baleen from North Atlantic right whales *Eubalaena glacialis* reflects distribution shift to the Gulf of St. Lawrence

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**ABSTRACT:** Seasonal migration of the Critically Endangered North Atlantic right whale *Eubalaena glacialis* along the eastern seaboard of North America has been well studied. Since 2010, however, right whales have shifted their summer foraging location from the Bay of Fundy to the Gulf of St. Lawrence. There is a need to better understand right whale distribution to manage anthropogenic activities and mitigate impacts on whales. Stable isotope ratios of baleen plates can provide details about migration and foraging behaviour of an individual over a period of several years. We interpreted  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  cycles, examined whether stable isotope ratios of baleen could detect the right whale distribution shift, and compared variation within and among individuals before and after 2010.  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were compared between 8 right whales that died between 1992 and 2005 (pre-2010) and 5 right whales that died in 2019 (post-2010). The correlation between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  varied considerably between individuals, indicating no clear pattern of annual migration in  $\delta^{13}\text{C}$  among whales. We observed a change in both isotope ratios after 2010, whereby the post-2010 whales were enriched in  $^{13}\text{C}$  and  $^{15}\text{N}$  relative to the pre-2010 whales (mean  $\pm$  SE:  $0.5 \pm 0.1$  and  $0.9 \pm 0.2\%$ , respectively). The isotopic variance among and within whales did not change after 2010. These results suggest that a range shift observed in sighting data is also reflected in the isotope ratios of right whale baleen. Detecting shifts in right whale migration is essential for protecting this species, and stable isotope analyses may be useful in future conservation efforts.

**KEY WORDS:** North Atlantic right whale · Baleen · Stable isotopes · Carbon · Nitrogen · Distribution

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## 1. INTRODUCTION

The North Atlantic right whale *Eubalaena glacialis*, hereafter 'right whale', is a Critically Endangered species (Cooke 2020); current estimates indicate that there are approximately 340 individuals left in the world (Pettis et al. 2023). Right whales were hunted almost to extinction following centuries of whaling that ended in 1935, when international protection for this species commenced (Reeves et al. 2007). In the absence of whaling, the western North Atlantic population had increased to 476 individuals by 2010 (Davis et al. 2017). However, population size has since been

declining due to other anthropogenic stressors (Sharp et al. 2019); ship strikes and entanglement in fishing gear have been the leading causes of right whale death for the past 30 yr (Kraus et al. 2016, Pettis et al. 2022). Right whales are likely to become extinct if drastic conservation measures are not initiated (Kraus et al. 2016, Meyer-Gutbrod & Greene 2017, Stokstad 2017).

Right whales are one of the most intensively studied whale species due to their endangered status; however, their distribution is not completely understood. Right whales are known to migrate seasonally along the eastern coast of North America, but their route

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may vary between individuals and sex (Kraus et al. 2007). The seasonal distribution of right whales is linked to the distribution of their preferred prey, the calanoid copepod *Calanus finmarchicus* (Mayo & Marx 1990, Pendleton et al. 2012). In the spring and summer, the population tends to migrate to foraging grounds off the coast of Atlantic Canada, but the whales do not demonstrate strong fidelity to these locations (Baumgartner & Mate 2005, Davis et al. 2017). The 5 major foraging locations include Cape Cod Bay in winter and early spring; the Great South Channel in late spring and summer; and the Bay of Fundy, Roseway Basin, and in recent years, the Gulf of St. Lawrence, in the summer and autumn (Fig. 1; Hlista et al. 2009, Davis et al. 2017, Pettis et al. 2022). During the winter, most pregnant females consistently travel south to their calving grounds off the coasts of Florida and Georgia (Davis et al. 2017). The winter range for non-reproductive individuals can include waters from the Gulf of Maine south to the calving grounds (Kraus

& Rolland 2007, Davis et al. 2017). Although right whale migration is well studied, individuals may go for months (especially in the winter) or years without being sighted (Hamilton et al. 2007). Cole et al. (2013) suggested that lack of right whale sightings in the winter may be associated with use of alternative breeding grounds. Further, sporadic sightings of individuals from this population have been reported in the central and eastern North Atlantic in historic feeding grounds (Smith et al. 2006). Given the patchiness of such sighting data, additional methods of estimating right whale distribution will be valuable to furthering conservation efforts.

Since 2010, the summer right whale distribution has shifted northward from the Bay of Fundy into the Gulf of St. Lawrence (Davies et al. 2019, Right Whale Consortium 2020, Meyer-Gutbrod et al. 2021, 2023; Fig. 1). Historically, the Gulf of St. Lawrence was a known whaling region (Reeves et al. 2007); however, only a small number of right whales has been recorded in this region until recent years

(Brown et al. 2007). In addition to the summer distribution shift, more right whales are spending their winter and spring months in southern New England shelf waters since 2015 (O'Brien et al. 2022). These distribution shifts, which also occurred for other baleen whale species in this region around 2010 (Davis et al. 2020), are due to climate change and the shift in distribution of their prey (Record et al. 2019, Meyer-Gutbrod et al. 2023). The abundance of *C. finmarchicus* in the Gulf of Maine has decreased in the past 10 yr due to rapid ocean warming (Record et al. 2019, Meyer-Gutbrod et al. 2021). Right whales have been known to shift their feeding grounds when the zooplankton communities change (Patrician & Kenney 2010). The distribution shift that began in 2010 is considered to be atypical because the species has never been recorded in large abundance so far north on a yearly basis; up to half of the population is now venturing into the Gulf of St. Lawrence every summer (Right Whale Consortium 2020, Crowe et al. 2021, Pettis et al. 2021).

Increased presence of right whales in the Gulf of St. Lawrence has resulted in significant concern regarding

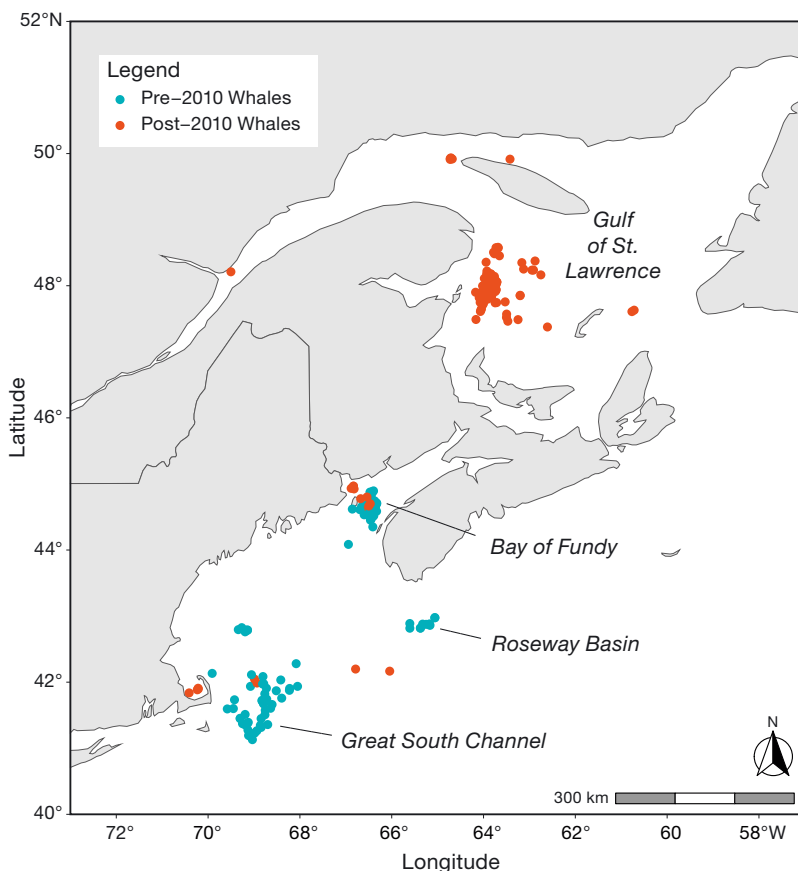


Fig. 1. Locations of summer (May to October) sightings of 12 right whales included in our analysis. There were no summer sightings of Eg#1014. Blue points represent sightings before 2010 when whales frequented the Bay of Fundy. Orange points represent sightings after 2010, indicating a northward shift in summer range. Sighting data were obtained from the North Atlantic Right Whale Consortium

the viability of the species. Between 2017 and 2022, 21 right whales died in these and nearby waters from ship strikes, entanglement, or undetermined causes (Daoust et al. 2018, Sharp et al. 2019, Bourque et al. 2020). Recently, new regulations on ship speed and fishing zones have been enacted in the Gulf of St. Lawrence (Davies & Brillant 2019). However, population models indicated that the species was already at significant risk of extinction prior to 2005 and that risk will have only increased as the population has continued to decrease in recent years (Kraus et al. 2005, NOAA Fisheries 2022). Because the fishing and shipping industries use the same areas as the whales, and compatibility seems to be limited, there is an urgent need to identify all locations critical for right whale persistence.

Our understanding of right whale distribution and movement patterns is imperfect because it is based on tracking methods, such as passive acoustic monitoring, visual observations, and satellite tagging, all of which have many uncertainties (Baumgartner & Mate 2005, Moore et al. 2013, Davis et al. 2017). Passive acoustic monitoring can only detect whales when they are vocalizing within 8–16 km from the receivers, and variation in whale behaviour and environmental conditions can alter sound detection and propagation, thus impacting the results (Davis et al. 2017, Durette-Morin et al. 2019). Visual surveys are helpful for knowing an individual's location at specific periods of time, but the data rely on chance that researchers, fishers, whale-watching tours, or others encounter them at the surface. Lastly, satellite tagging is the least common method for tracking right whales, although its use on right whales has increased in recent years. Satellite tagging can be difficult due to logistical challenges, and its use has raised concerns due to its invasiveness and potential to cause harmful wounds (Moore et al. 2013). Other methods have thus been developed to understand the right whales' distribution when they are not within distance of acoustic receivers and when they are not being observed via visual surveys.

Stable isotope analysis (SIA) is a tool that is widely used in migration and distribution studies and is particularly useful for identifying habitat of species that are wide-ranging but difficult to locate (Jennings & Warr 2003, Trueman & Glew 2019, Wassenaar 2019). The stable isotope values of an animal's tissues reflect those of its prey in a predictable manner (Busquets-Vass et al. 2017). The geographical origin of an organism can sometimes be inferred from stable isotope values of its tissues, based on spatially explicit patterns in isotope values ('isoscapes') of e.g. particulate

organic matter (Wassenaar 2019). Isotopes can also be used to quantify bionomic elements of an organism's ecological niche by measuring the area (in  $\delta$ -space) of the isotopic values as coordinates, known as the isotopic niche (Newsome et al. 2007). The isotopic niche is a powerful tool to understand the ecology of organisms, as it is reflective of both trophic niche and the scenopoetic dimensions of the ecological niche, such as habitat characteristics (e.g. environmental temperature) (Newsome et al. 2007, Jackson et al. 2011). Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope ratios are commonly used for investigating marine animal migration and foraging ecology (Larson & Hobson 2009, Hobson 2019, Trueman & Glew 2019). Of interest in our study is the capacity to use isotopic profiles in whale baleen plates to explore the habitat use and distribution of these right whales before and after a major distribution shift (Best & Schell 1996, Summers et al. 2006, Lysiak 2008, Busquets-Vass et al. 2017, Das et al. 2017, Reiss et al. 2020, Teixeira et al. 2022).

Right whale mouths contain 2 rows of piliferous baleen plates that filter zooplankton from the water column. Baleen is made of keratin and grows continuously. As whales forage, they incorporate isotopes from assimilated prey into the actively growing base of the baleen plate so that the newest tissue growth reflects the food sources over the last 2 wk (Best & Schell 1996, Lysiak 2008, Matthews & Ferguson 2015, Eisenmann et al. 2016). Because keratin in baleen plates is metabolically inert after erupting from the whale gum, the isotopic record is conserved for as long as the baleen remains intact (Busquets-Vass et al. 2017, Werth et al. 2020). Adult right whale baleen grows at a stable rate of approximately 24 cm  $\text{yr}^{-1}$  to a length of ~2 m, offering a time series that can provide insight into the last 10 yr of a whale's life (Hunt et al. 2016, Lysiak et al. 2018).

Stable isotope ratios along the length of the baleen plate generally form an annual oscillating pattern which has been attributed to migration of whales through isotopically distinct regions of their range (Best & Schell 1996, Lysiak 2008). Spatial variation in the isotopic composition of their zooplankton prey is thought to drive isotopic oscillations observed in right whale baleen (Lysiak 2008, McMahan et al. 2013, Oczkowski et al. 2016). Zooplankton in the western North Atlantic tends to be enriched in  $^{15}\text{N}$  at higher latitudes, and  $\delta^{13}\text{C}$  varies in patches across the right whale migratory range (McMahan et al. 2013). Both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  are elevated closer to shore due to nutrient runoff (Oczkowski et al. 2016). There is uncertainty on the interpretation of the isotope profiles of baleen because factors other than migra-

tion can be influencing the oscillating pattern, such as the effect of consumer metabolism (Post 2002, Lysiak 2008, McMahon & Newsome 2019). During the winter, zooplankton is limited, and the whales that travel to southern waters go through a fasting period (Pendleton et al. 2012, Record et al. 2019). These periods may affect isotopic profiles of the baleen (e.g. elevating  $\delta^{15}\text{N}$  values) because the whales may catabolize endogenous proteins and fats to meet energetic needs when zooplankton are scarce (Hobson et al. 1993, Best & Schell 1996).

Previous studies on mysticetes showed correlated and non-correlated  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  cycles along their baleen plates (Best & Schell 1996, Caraveo-Patiño et al. 2007, Matthews & Ferguson 2015, Hunt et al. 2018, Pomerleau et al. 2018, Reiss et al. 2020). For example, bowhead whales *Balaena mysticetus* and sei whales *Balaenoptera borealis* have synchronous  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  cycles, which indicates that they forage continuously in isotopically distinct regions throughout their distribution (Matthews & Ferguson 2015, Pomerleau et al. 2018, Reiss et al. 2020). On the other hand, gray whales *Eschrichtius robustus* and blue whales *Balaenoptera musculus* showed no correlation between  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (Caraveo-Patiño et al. 2007, Hunt et al. 2018). Such distinct  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  oscillations indicate that whales either (1) migrate annually between  $\delta^{15}\text{N}$  distinct regions, but not  $\delta^{13}\text{C}$ , (2) shift the trophic level of their diet annually, or (3) fast during seasonal changes in food availability (Hobson et al. 1993, Hobson & Schell 1998, Aguilar et al. 2014, Matthews & Ferguson 2015). Isotope data on North Atlantic right whales is scarce (Summers et al. 2006, Hunt et al. 2016, 2018, Lysiak et al. 2018), although Lysiak (2008) did find a weak positive correlation between  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , which was attributed to foraging in isotopically distinct regions. There is a need to further explore the relationship between  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in baleen so that we can infer right whale migration and feeding behaviours, which may provide valuable information for management and conservation efforts.

Many ecological studies investigate resource use and population dynamics at the population scale, assuming that conspecifics are identical (Bolnick et al. 2003). However, it is important to consider individual variation in foraging and behaviour across the population, as it has potentially significant ecological and conservation implications (Bolnick et al. 2003). Since right whales are zooplankton specialists that feed primarily on *C. finmarchicus*, it is assumed that their isotopic niche width will be sim-

ilar between individuals. However, individual right whales have plastic migratory behaviours, meaning there is considerable variation in habitat use between individuals and inter-annually within individuals (Lysiak 2008, Right Whale Consortium 2020, Pettis et al. 2021). Individual variation facilitates the ability of a population to adapt to environmental change (Bolnick et al. 2003), which is critical for right whales as they adapt to climate change. Assessing individual differences in the isotopic niche width of whales will provide an improved understanding of how migration and feeding behaviours differ between individuals faced with a rapidly changing environment.

The shift in right whale distribution identified in 2010 was a dramatic event that has implications for the conservation, ecology, and stable isotope composition of right whales (Bishop et al. 2022, Ganley et al. 2022, O'Brien et al. 2022). This paper addresses 3 questions regarding how stable isotope ratios of whale baleen may reveal the implications of these changing migration routes: (1) Do  $\delta^{13}\text{C}$  cycles in right whale baleen plates correlate with  $\delta^{15}\text{N}$  cycles, and therefore are the whales migrating through and feeding within isotopically distinct regions? (2) Do the isotopic profiles in the baleen plates reflect the observed distribution shift? (3) Has individual isotopic variation changed since the whales shifted their summer feeding grounds? To investigate these questions, we used stable isotope analyses ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of baleen plates collected from right whales that died before and after 2010.

Previous research has shown that stable isotope ratios cycle annually along right whale baleen plates, with typically a clearer  $\delta^{15}\text{N}$  oscillating pattern (Summers et al. 2006, Lysiak 2008); therefore, if the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  cycles correlate, then we have strong evidence of annual migration in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. If there is no strong correlation between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , then there is no clear annual migration in  $\delta^{13}\text{C}$  and some other factor is influencing  $\delta^{13}\text{C}$ . We predicted that the post-2010 whales would differ in stable isotope ratios due to a large proportion of the population foraging in a new region from previous feeding grounds. Finally, we predicted that intra-annual individual variation has changed since the whales shifted their summer feeding grounds in 2010. Since the whales are now travelling to farther locations for summer feeding, it is possible individuals have a larger isotopic niche that reflects this movement. This study can help us better understand the sensitivity of stable isotopes regarding changes in right whale distribution.

## 2. MATERIALS AND METHODS

### 2.1. Baleen collection and sample preparation

For this study, a single baleen plate was collected during necropsies of 6 adult North Atlantic right whales that had died from ship strike or unknown causes, 5 of which died in the Gulf of St. Lawrence in the summer of 2019 and 1 individual (NARWC ID: Eg#1223) died in the Bay of Fundy in 1992. All baleen plates collected in 2019 were legally obtained under a Species at Risk Act permit as issued to the Marine Animal Response Society (Permit No. DFO-GLF-2014-2019-01). The plates were collected opportunistically with non-standardized methods; however, the sampled plates were the longest plates in the whales' mouths and were likely taken from the same central region of the baleen racks between individuals. The position of the plates within the mouth should not greatly influence the data because the stable isotope ratios and growth rate remain relatively the same between the central plates of the baleen rack, compared to plates within the anterior and posterior regions (Werth et al. 2021).

We removed the gum from the 5 baleen plates collected in 2019 and scrubbed them with steel wool and water to remove surface dirt. The plates were then cleaned with a chloroform/methanol (2:1) solution to remove any surface lipids or oils. We measured the baleen plates from the base (new growth) to the tip (old growth) and marked sample locations every 2 cm along the outside edge of the plate. We drilled the baleen along the sample intervals using a flexible shaft rotary drill and collected the resulting

keratin powder for SIA. The baleen plates, table, and drill were cleaned with 95% ethanol between every sample to prevent cross-contamination.

Additional isotopic data from 8 individuals that died between 1992 and 2005 were obtained from Lysiak (2008); these data represent the 'pre-2010' whales ( $n = 8$ ), and the individuals that died in the summer of 2019 represent the 'post-2010' whales ( $n = 5$ ). Further details on the individual whales included in this study are provided in Table 1. To ensure comparability of measurements, we analysed a baleen plate from a whale (Eg#1223, aka 'Delilah') included in the Lysiak (2008) dataset. We performed a paired-sample  $t$ -test of the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  data from individual Eg#1223 with Lysiak's (2008) isotopic data from the same individual. Results of this analysis indicate that our measurements are comparable, and therefore any differences between the pre-2010 and post-2010 groups are not related to instrument bias (Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m722\\_p177\\_supp.pdf](http://www.int-res.com/articles/suppl/m722_p177_supp.pdf)). We used Eg#1223 data of Lysiak (2008) in the final dataset, as it had a longer time series compared to the smaller plate that we sampled.

### 2.2. Stable isotope analysis (SIA)

We weighed 1.0–1.2 mg of each powdered sample into  $5 \times 3.5$  mm tin capsules and crimped them shut. Samples were analysed at the Stable Isotope in Nature Laboratory (SINLAB) at the University of New Brunswick, Canada. Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope values were analysed with an Elemental Combustion System (ECS) 4010 elemental

Table 1. Individual characteristics, mortality information (Bourque et al. 2020, Right Whale Consortium 2020), and Spearman correlation coefficients comparing  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in the baleen of the 13 studied North Atlantic right whales. \* $p < 0.05$ . Dates are given as mo/d/yr; nd: no data (age not available)

Category	Whale ID	Sex	Age (yr)	Confirmed mortality	Mortality location	Necropsy notes	$\delta^{15}\text{N}$ & $\delta^{13}\text{C}$ correlation coefficient
Pre-2010	Eg#1223	F	12	09/05/1992	Bay of Fundy	Vessel collision, nursing	0.19
Pre-2010	Eg#1623	M	12	01/30/1996	Georgia	Vessel collision	-0.20
Pre-2010	Eg#1014	F	30	04/20/1999	Cape Cod Bay	Vessel collision	-0.23*
Pre-2010	Eg#1238	M	19	10/29/2001	Gulf of St. Lawrence	Acute fishing gear entanglement	0.45*
Pre-2010	Eg#1004	F	34	02/07/2004	Virginia/North Carolina	Vessel collision, pregnant	0.07
Pre-2010	Eg#2143	F	14	01/12/2005	Georgia/Florida	Vessel collision, pregnant	-0.02
Pre-2010	Eg#2301	F	12	03/03/2005	Virginia	Chronic fishing gear entanglement	0.13
Pre-2010	Eg#2617	F	9	04/28/2005	Great South Channel	Vessel collision	0.20
Post-2010	Eg#4023	M	9	06/04/2019	Gulf of St. Lawrence	Vessel collision	0.16
Post-2010	Eg#1281	F	38+	06/20/2019	Gulf of St. Lawrence	Vessel collision	0.55*
Post-2010	Eg#1514	M	30+	06/25/2019	Gulf of St. Lawrence	Vessel collision	0.47*
Post-2010	Eg#3450	F	nd	06/27/2019	Gulf of St. Lawrence	Vessel collision	0.19
Post-2010	Eg#3421	M	15	07/18/2019	Gulf of St. Lawrence	Undetermined	0.43*



analyser coupled to a Delta Plus XP continuous-flow isotope-ratio mass spectrometer. The analytical error ( $<0.2\%$  for both carbon and nitrogen) was calculated based on repeat analyses of in-house standards: nicotinamide ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  mean  $\pm$  SD:  $-32.3 \pm 0.03$  and  $2.0 \pm 0.06\%$ , respectively), bovine liver ( $-18.8 \pm 0.05$  and  $7.2 \pm 0.02\%$ ), muskellunge muscle ( $-22.3 \pm 0.1$  and  $14.0 \pm 0.1\%$ ) and USGS 61 (USGS, Reston, VA) ( $-34.8 \pm 0.08$  and  $-2.9 \pm 0.1\%$ ). Equipment was calibrated to international standards Vienna-Pee Dee belemnite carbonate for  $\delta^{13}\text{C}$  and atmospheric nitrogen for  $\delta^{15}\text{N}$ . Stable isotope compositions are presented in permille (‰) using standard  $\delta$  notation (Peterson & Fry 1987).

### 2.3. Data analysis

We obtained sighting locations of studied whales during the years represented in our baleen plates in order to try and relate isotopic profiles of whales to locations where they were sighted (Oczkowski et al. 2016, Right Whale Consortium 2020). Summer (May to October) sightings of studied whales were plotted on a map to demonstrate the shift in distribution between the pre- and post-2010 whales (Fig. 1). There were no summer sightings of Eg#1014. Sightings were mapped using the world basemap from the *rnatuarearth* package in R (Massicotte & South 2023).

We tested whether individuals'  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values were correlated using non-parametric Spearman's correlation tests. We used  $\delta^{15}\text{N}$  data to analyse the time series of the whales' migration history because the annual oscillations in  $\delta^{15}\text{N}$  are more consistent than those observed in  $\delta^{13}\text{C}$  (Lysiak 2008; see Fig. 2). We counted the number of data points between each consecutive peak and each consecutive valley of the  $\delta^{15}\text{N}$  profiles to estimate the average growth rate (Lysiak 2008). We used the date the animal was first reported dead and the annual  $\delta^{15}\text{N}$  oscillations to anchor the isotopic time-series at the known date of death. In each of the 5 whales sampled in summer of 2019, the first  $\delta^{15}\text{N}$  measurement under the gum (i.e. closest to time of death) was  $^{15}\text{N}$  depleted relative to preceding values, indicating that the summer period is associated with depleted  $\delta^{15}\text{N}$  values. Since this conflicts with previous findings (Lysiak et al. 2018) and the presumed enrichment of  $^{15}\text{N}$  in northern latitudes, we avoided inferring seasonality within the isotopic dataset, and rather used the full isotopic profile of the baleen plates when comparing between individuals to take advantage of the large dataset.

To test whether the stable isotope ratios differed in the whales before and after the shift in distribution, we performed a linear mixed-effects model of the full  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  dataset with 2 independent variables (i.e. time and sex) using the 'nlme' package in R (Pinheiro et al. 2020), including individual whales as a random effect. 'Time' and 'sex' were categorical variables listed as pre- and post-2010, and female and male. Model selection was based on the chi-squared test within the 'drop1' function of the 'lme4' package in R (Bates et al. 2015). Interaction terms amongst the independent variables were selected against, and therefore not included in the final model. Variation in the distribution of isotope values among whale samples from different years in both pre- and post-2010 groups was assessed using the Bayesian Layman metrics approach, which estimates semi-quantitative metrics to compare stable isotope structure between communities (Layman et al. 2007, Jackson et al. 2011). We used the 'SIBER' package in R to analyse the overall convex hull size (i.e. total area), range of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, and the isotopic similarity among individuals (i.e. centroid distance) for pre- and post-2010 whales (Jackson & Parnell 2021).

Isotopic niche width was estimated using the 'SIBER' package in R (Layman et al. 2007, Jackson et al. 2011, Jackson & Parnell 2021). We calculated the standard ellipse area corrected for small sample size (SEAc) for each year per individual using a complete year of isotope data, where a year was defined as all datapoints between annual  $\delta^{15}\text{N}$  peaks. We then performed a linear mixed-effects model of the SEAc data with time (pre-/post-2010), sex (female/male), and count (number of data points per year) as independent variables, including individual whales as a random effect. Model selection was based on the chi-squared test, and the variables count, time, and interaction terms amongst the independent variables were selected against during model selection. All model assumptions were checked (Figs. S2 & S3). The critical p-value was set to 0.05. All statistical tests were performed using the software R (R Core Team 2022).

## 3. RESULTS

### 3.1. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ cycles in baleen

In total, our pre-2010 dataset included 2 males and 6 females ranging from 9 to 34 yr old, and our post-2010 dataset included 3 males and 2 females ranging from 9 to 38+ yr old (Table 1). The carbon and nitro-

gen isotopic profiles of the right whales ( $n = 13$ ) varied between and within individuals;  $\delta^{13}\text{C}$  ranged from  $-21.9$  to  $-16.7$ ‰ and  $\delta^{15}\text{N}$  ranged from  $7.0$  to  $13.1$ ‰. The  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  records along the baleen plates showed oscillating patterns for each individual (e.g. for whale Eg#4023 shown in Fig. 2). The  $\delta^{15}\text{N}$  dataset had clearer and more consistent oscillations that are believed to be annual, compared to the  $\delta^{13}\text{C}$  oscillations; thus we used the  $\delta^{15}\text{N}$  oscillations to determine the annual growth rate and time series. The mean ( $\pm$ SD) annual growth rate of the baleen was  $27 \pm 5 \text{ cm yr}^{-1}$ , based on the assumption that the oscillating  $\delta^{15}\text{N}$  values represent annual patterns. Due to the variable baleen growth rate among years and individuals, we structured the time series by defining a year as  $\delta^{15}\text{N}$  peak to peak rather than using the mean annual growth rate.

The oscillating  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  patterns for each individual show a similar trend, where most of the peaks,

and valleys, occur at or near the same time between individuals (Fig. 3). The carbon isotope data demonstrated a decreasing trend between 2001 to 2005, with the lowest value being  $-21.9$ ‰ (Fig. 3). By mid-2012, the mean  $\delta^{13}\text{C}$  value had increased to  $-19$ ‰, which was a similar value to the isotopic levels in the whales before 2000 (Fig. 3). Post-2010 whales showed a similar 2 to 3 yr oscillating cycle in the  $\delta^{13}\text{C}$  data, whereas  $\delta^{15}\text{N}$  consistently oscillated on an annual cycle.

We observed limited evidence of temporal correlation between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  across all whales, with considerable variation among individual whales (rho values ranged from  $-0.23$  to  $0.55$ ; Table 1). Some individuals had  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values that aligned well (e.g. Eg#1238 and Eg#1281; Fig. 4), while other whales had contrasting  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values (e.g. Eg#2143 and Eg#1623; Fig. 4). Most individuals had a weak positive correlation between  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ; 3 individuals had a weak negative correlation (Table 1, Fig. 4).

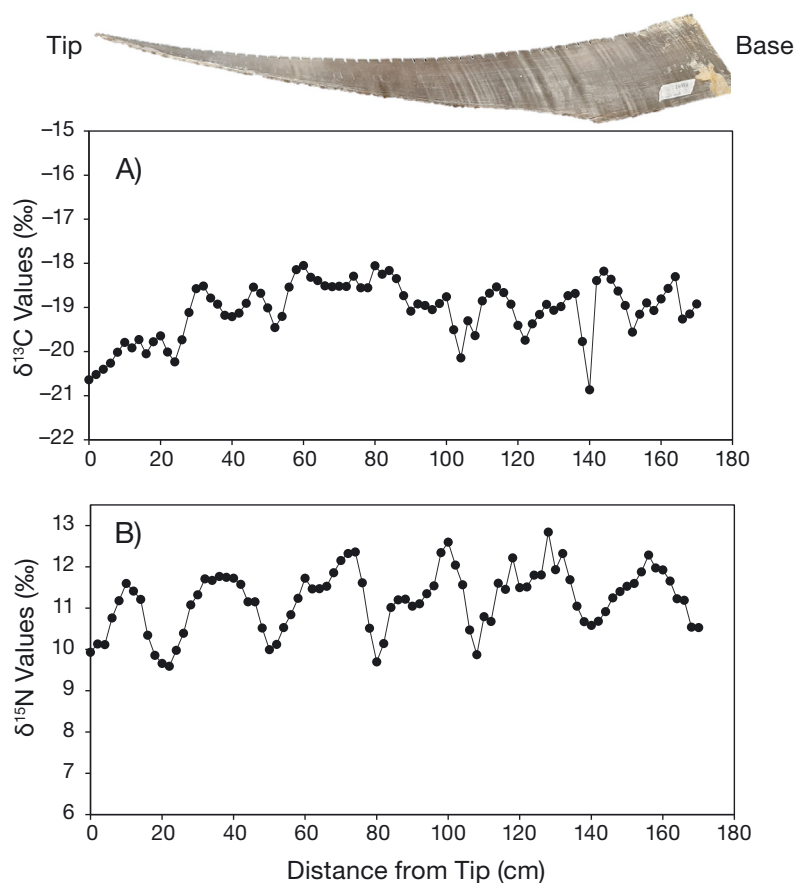


Fig. 2. (A)  $\delta^{13}\text{C}$  and (B)  $\delta^{15}\text{N}$  values along the length of a North Atlantic right whale baleen plate from individual Eg#4023. Subsamples ( $n = 86$ ) were taken every 2 cm. Subsample 0 was taken from the oldest growth at the tip of the baleen, and subsample 86 was taken from the most recent growth at the base of the baleen plate. Image is of right whale baleen (Eg#1223) aligned from oldest (tip) to most recent growth (base)

### 3.2. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ enrichment in post-2010 whales

Pre- and post-2010 baleen samples showed shifts in stable isotope ratios, with the greatest shift occurring in the  $\delta^{15}\text{N}$  data (Fig. 5). Post-2010 whales had significantly higher nitrogen and carbon isotope ratios than pre-2010 whales: post-2010 whales were  $0.5 \pm 0.1$ ‰ more enriched in  $\delta^{13}\text{C}$  and  $0.9 \pm 0.2$ ‰ more enriched in  $\delta^{15}\text{N}$  compared to pre-2010 whales (Table 2). Sex did not have a significant influence on either isotope at an alpha level of 0.05; however, sex significantly affected the  $\delta^{15}\text{N}$  data at an alpha level of 0.1, where the males had slightly higher  $\delta^{15}\text{N}$  ratios compared to females (Table 2). Post-2010 whales had a larger convex hull size (i.e. total distribution of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values) than pre-2010 whales (total area =  $5.4 \pm 0.7$ ‰<sup>2</sup> and  $3.5 \pm 0.6$ ‰<sup>2</sup>, respectively, Fig. 5). Post-2010 whales had a larger range of  $\delta^{15}\text{N}$  values (post-2010:  $2.8 \pm 0.3$ ‰; pre-2010:  $2.2 \pm 0.4$ ‰), and their stable isotope ratios were less tightly packed (i.e. the distance to the centroid was greater) than the pre-2010 whales (centroid distance =  $0.9 \pm 0.04$  and  $0.6 \pm 0.05$ ‰, respectively). The  $\delta^{13}\text{C}$  range was similar between pre- and post-2010 whales ( $2.7 \pm 0.3$  and  $2.9 \pm 0.3$ ‰, respectively).

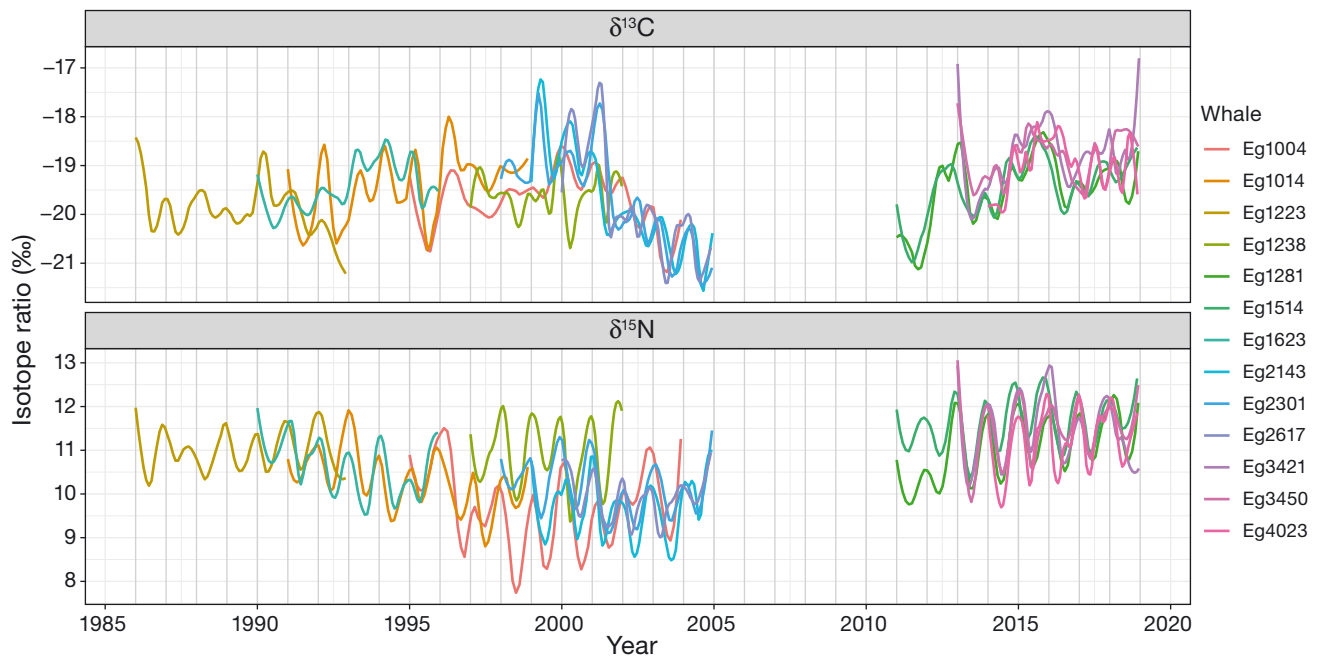


Fig. 3. Temporal variation in the carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope ratios in baleen-plate samples from 13 North Atlantic right whales. Lines represent locally estimated scatterplot smoothing (LOESS) smoothers fitted to  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values of individual right whales

### 3.3. Variability in isotopic niche width

SEAc from the SIBER analysis output measures the variance of stable isotopes in an individual per year. SEAc varied between individuals and years (Fig. 6), e.g. it varied greatly between individuals in 2001 ( $\text{SEAc} = 0.5\text{--}3.2\text{‰}^2$ ,  $n = 4$ ), but was similar between individuals in 2015 ( $\text{SEAc} = 0.6\text{--}1.1\text{‰}^2$ ,  $n = 5$ ). There was a slight decrease in female SEAc over time, and an increase in male SEAc over time (Fig. 6); however, SEAc was not significantly different between pre- and post-2010 whales. The largest SEAc values were mostly from pre-2010 adult females, with some of those whales having been pregnant or entangled during that given year (Table 3). One female (Eg#1014) had 3 out of the 7 largest SEAc values (Table 3). Although female whales had larger and more varied SEAc values compared to males, the difference was not significant (male value from intercept =  $-0.3 \pm 0.2\text{‰}^2$  (11),  $t = -1.37$ ,  $p = 0.20$ ). There was a slight decreasing trend in SEAc with count due to the effect of sample size, i.e. as sample size increased, the standard deviation decreased (Fig. S4). However, there was no significant relationship between the SEAc and the number of data points per year (i.e. count); therefore, we do not believe this to have had a confounding effect on our analysis.

## 4. DISCUSSION

In this paper we posed 3 questions: (1) Do  $\delta^{13}\text{C}$  cycles in right whale baleen plates correlate with  $\delta^{15}\text{N}$  cycles, and therefore are the whales migrating through and feeding within isotopically distinct regions? (2) Do the isotopic profiles in the baleen plates reflect the observed distribution shift? (3) Has individual isotopic variation changed since the whales shifted their summer feeding grounds?  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  cycles along right whale baleen were not strongly correlated; therefore, there is no clear pattern of annual migration evident in  $\delta^{13}\text{C}$  values. Right whales sampled post-2010 were more enriched in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in their baleen plates compared to the individuals that died before 2010; however, the intra-annual individual isotopic variance did not change between pre- and post-2010 whales. We explore each of these results further to better understand the link between right whale stable isotope ratios and right whale distribution and foraging behaviour.

### 4.1. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ cycles in baleen

Pronounced annual cycles in  $\delta^{15}\text{N}$  were among the clearest results of this study; however, interestingly, these cycles were typically asymmetric, involving a



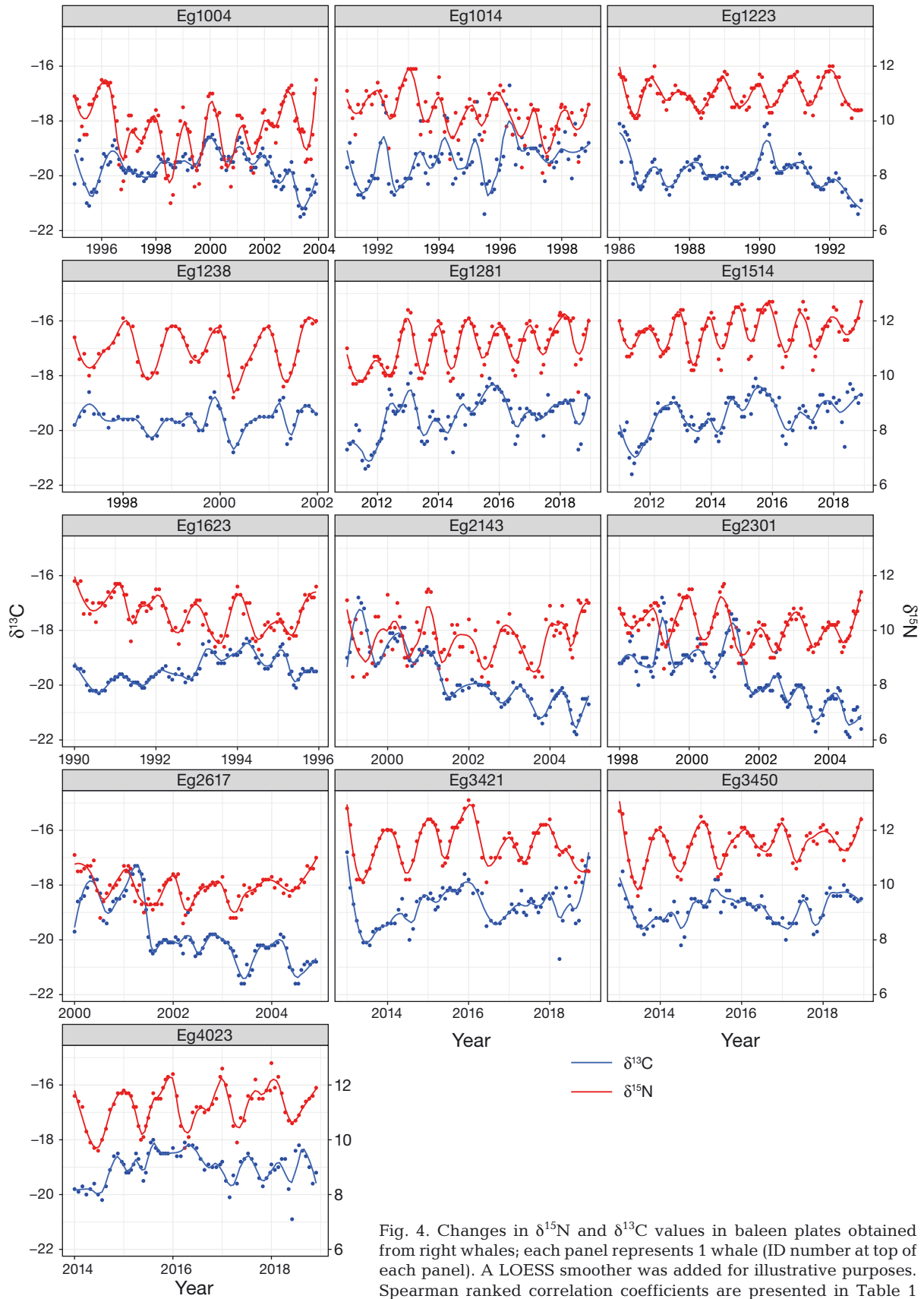


Fig. 4. Changes in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in baleen plates obtained from right whales; each panel represents 1 whale (ID number at top of each panel). A LOESS smoother was added for illustrative purposes. Spearman ranked correlation coefficients are presented in Table 1

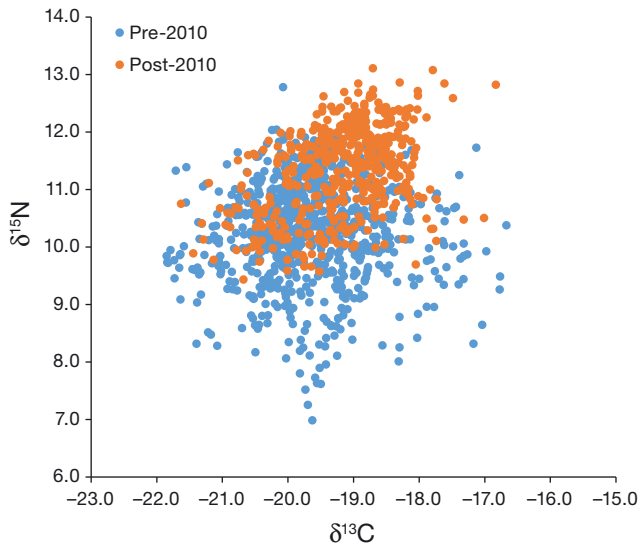


Fig. 5.  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in 8 pre-2010 right whale baleen plates and 5 post-2010 right whale baleen plates

slow, steady enrichment in  $^{15}\text{N}$  over several months, followed by a rapid depletion. Slow increases in  $\delta^{15}\text{N}$  could be related to migration towards increasingly  $\delta^{15}\text{N}$ -enriched areas (Aguilar et al. 2014). Conversely, intensive feeding in summer months might also increase diet–tissue isotopic offsets, as nitrogen excretion increases lead to  $^{15}\text{N}$  enrichment in whale tissues (Florin et al. 2011). Changes in nitrogen isotope ratios are often attributed to changes in trophic level. However, previous work has shown that right whales consistently prefer to forage on *Calanus finmarchicus* (Mayo & Marx 1990), and significant changes in trophic level over the course of 1 yr seem unlikely in this species. Therefore, observed changes in  $\delta^{15}\text{N}$  oscillation patterns may be more influenced by changes in physiology throughout the year. For example, increases in fat catabolism during periods of low foraging may deplete  $\delta^{15}\text{N}$  (Hobson & Schell 1998, Aguilar et al. 2014, Matthews & Ferguson 2015).

Assuming  $\delta^{15}\text{N}$  oscillations represent annual cycles, we predicted that a strong correlation between  $\delta^{15}\text{N}$

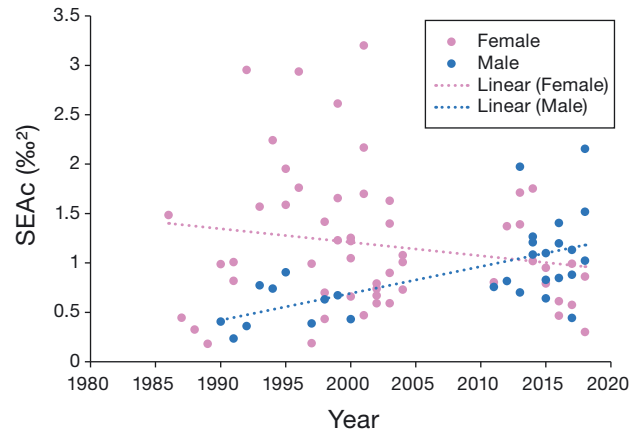


Fig. 6. Annual corrected standard ellipse area (SEAc) values ( $\%^{2}$ ) of 13 North Atlantic right whales, with male and female linear trendlines. Further details are provided in Table 3

and  $\delta^{13}\text{C}$  cycles would be evidence of annual migration in  $\delta^{13}\text{C}$ . However,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  were not strongly correlated, which may indicate that right whales do not continuously forage across a large carbon gradient on an annual basis. Decoupled  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in most whales suggest that the biogeochemical processes driving these values are also decoupled. While  $\delta^{15}\text{N}$  is likely driven by annual cycles in foraging behaviour, variation in  $\delta^{13}\text{C}$  is expected to relate to spatial variation in the  $\delta^{13}\text{C}$  values of prey. Even though the right whales are moving through isotopically distinct areas (Magozzi et al. 2017), our results indicate that the range in  $\delta^{13}\text{C}$  is not great enough to pinpoint exactly where the whales travelled. Keratin generally has a fast tissue turnover rate of 1 to 7 d (Ayliffe et al. 2004); however, right whales can move  $>75 \text{ km d}^{-1}$ , easily traversing isotopically distinct regions over shorter time frames than isotopes in baleen integrate (Baumgartner & Mate 2005). Using the baleen growth rate, we know that each baleen isotope sub-sample contains  $\sim 2 \text{ wk}$  of data ( $\sim 1 \text{ cm}$  growth every 2 wk), which equates to potentially 1000s of kms distance (Lysiak 2008). Their movement patterns could muddle seasonal differences in  $\delta^{13}\text{C}$  and wash out a clear migration signal.

Table 2. Linear mixed-effects model results of the stable isotope ratios in right whale baleen ( $n = 13$ ). Individual whales were set as a random effect. Time represents pre- and post-2010 whales, and sex represents males and females

Isotope	Fixed effects	Value	SE	df	<i>t</i>	<i>p</i>
$\delta^{13}\text{C}$	Intercept	-19.1	0.1	1156	-179.74	<0.01
	Time: pre-2010	-0.5	0.1	11	-4.02	<0.01
$\delta^{15}\text{N}$	Intercept	-18.9	0.2	1156	-82.95	<0.01
	Time: pre-2010	-0.9	0.2	10	-3.80	<0.01
	Sex: Male	0.5	0.2	10	1.89	0.09

The variation in correlation between isotopes among individual whales further attests to variation in migration routes and strategies among individuals. Durette-Morin et al. (2022) recently discovered that right whales occupy the Scotian Shelf year-round, although their presence is lower in the winter compared to the warmer months. This study further attests to the variable mi-

Table 3. Largest corrected standard ellipse area (SEAc) values ( $\geq 2\%$ ) of studied right whales with notes about the corresponding individual during that year

Individual	Sex	Age	Year	SEAc	Notes
Eg#1014	F	23	1992	2.9	Finished nursing fifth calf (out of 6) in 1991. No sightings in 1992.
Eg#1014	F	25	1994	2.2	No sightings in 1994.
Eg#1014	F	27	1996	2.9	Pregnant for the full year (calved in December 1996). Minor entanglement injury at the start of 1996 and remained entangled for the full year. Seen in Cape Cod Bay, Georgia, and Florida waters in 1996.
Eg#2301	F	8	2001	3.2	Pregnant in late 2001 (calved in December 2002). Seen in the Great South Channel and Bay of Fundy in 2001.
Eg#2143	F	8	1999	2.6	Seen in the Great South Channel and Bay of Fundy in 1999.
Eg#2617	F	5	2001	2.2	Seen in Cape Cod Bay, Gulf of Maine, and Bay of Fundy in 2001.
Eg#3421	M	14	2018	2.2	Seen in the Great South Channel, Gulf of St. Lawrence, and Georges Basin in 2018.

gratory behaviours between individuals, which could explain why we saw such diverse  $\delta^{13}\text{C}$  patterns between individuals. Additionally, the 5 whales that died in June and July of 2019 in the Gulf of St. Lawrence did not show similar  $\delta^{13}\text{C}$  values in their most recent baleen growth, even though these whales all died in the same isotopically distinct area during the same time period. Their  $\delta^{13}\text{C}$  values ranged considerably from  $-17.9$  to  $-19.3\%$ , a  $1.4\%$  difference, which is  $1/3$  of the total isotopic range observed across this study. It is unknown how long the whales were feeding in the Gulf of St. Lawrence before they died; therefore, their most recent isotopic signatures may not reflect the isotopic signature of the Gulf. This individual variation indicates that  $\delta^{13}\text{C}$  values in whale baleen are influenced by a combination of extrinsic environmental and endogenous biochemical processes. This presents obvious challenges for studies aiming to recreate whale migration using  $\delta^{13}\text{C}$  values alone, as the offset between whale and prey  $\delta^{13}\text{C}$  values, i.e. fractionation, and isotopic differences relating to reproductive status, may differ considerably among individuals. Ultimately, due to the number of independent drivers influencing the stable isotope ratios of right whale baleen, this type of isotope data must be interpreted carefully.

#### 4.2. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ enrichment in post-2010 whales

We demonstrated that carbon and nitrogen stable isotope ratios in right whale baleen shifted after the population changed their summer foraging grounds in 2010. Post-2010 whales were enriched in  $^{15}\text{N}$  and  $^{13}\text{C}$  compared to pre-2010 whales. Further, post-2010 whales had a larger convex hull size and a larger

$\delta^{15}\text{N}$  range, and their  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values were less tightly packed than the pre-2010 whales. Interpretation of such changes in the stable isotope ratios in right whales since 2010 can be difficult, as there are many factors that could be influencing the stable isotope ratios in baleen plates. Firstly, temporal differences could be related to feeding location as the whales migrate to isotopically distinct areas. Secondly, limited foraging may be another explanation for the shift in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  after 2010. Right whales may be acquiring less food from the environment due to climate change. It is not likely that right whales have shifted their prey type since they consistently prefer to forage on *Calanus* spp. copepods (Mayo & Marx 1990, Sorochan et al. 2021). Lastly, the isotope baseline may have shifted in the past decade, which would result in an isotopic shift in right whales. We explore these possible factors affecting the isotopic change in post-2010 whales in greater detail in the following paragraphs.

A marine isoscape developed by McMahan et al. (2013) indicates that  $\delta^{15}\text{N}$  in zooplankton increases with latitude across the range where right whales are known to migrate, to a maximum of  $\sim 9\%$  in the Gulfs of Maine and St. Lawrence. Furthermore, the Gulf of St. Lawrence is  $\sim 1.5$ – $2.5\%$  more enriched in  $^{13}\text{C}$  than the Bay of Fundy (McMahan et al. 2013). As post-2010 right whales moved northward to new feeding grounds in the Gulf of St. Lawrence, their  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values increased by  $0.9$  and  $0.5\%$ , respectively, relative to pre-2010 whales, which aligns well with the isoscape (McMahan et al. 2013). The isoscape of McMahan et al. (2013) used for comparison was based on plankton in different locations within the Atlantic Ocean over the span of many years. Although localized isoscapes within the ocean can vary

over time, large-scale isoscape patterns along the eastern Atlantic seaboard remain largely stable (McMahon et al. 2013, Oczkowski et al. 2016, Magozzi et al. 2017, Wassenaar 2019). We currently lack a robust isoscape for the Bay of Fundy and the Gulf of St. Lawrence, habitats which may become increasingly important for right whales. Future research should focus on increasing the resolution of isoscapes in these regions.

It is possible that a reduction in nutrient intake due to anthropogenic stressors (e.g. fishing gear entanglements) and decreasing plankton abundance has affected the stable isotope ratios of right whale baleen in recent years. Approximately 83% of the right whale population has been entangled at least once (Knowlton et al. 2012). Some of these entanglements have become chronic and have prevented the whales from feeding properly for several months (Knowlton et al. 2012), which would have an effect on the starving whales' stable isotopes. Changes in ocean circulation are known to affect plankton abundance (Patrićian & Kenney 2010, Meyer-Gutbrod et al. 2015). In 2010, the Gulf of Maine and the western Scotian Shelf region underwent a physical oceanographic regime shift (Meyer-Gutbrod et al. 2021). Zooplankton abundance in the Scotian shelf and eastern Gulf of Maine decreased greatly between 2011 and 2016, with almost half (43%) of monitoring stations detecting a decline of  $\geq 2$  SD compared to the previous 10 yr (Johnson et al. 2017). The decrease in zooplankton abundance in these areas likely explains why right whales are now travelling to the Gulf of St. Lawrence. There is evidence that right whales are becoming less fit over time; their body lengths have been decreasing since 1981 due to anthropogenic stressors and climate-driven changes to prey dynamics (Stewart et al. 2021). Given that many of the whales in our study were actively or historically entangled, it is likely that they were malnourished. If whales face considerable nutritional stress, protein catabolism could result in  $^{15}\text{N}$  enrichment (Hobson et al. 1993). The 2 right whales in our study that died due to fishing gear entanglement (Eg#1238 and Eg#2301) had increased  $\delta^{15}\text{N}$  values in the last few months of their life (Fig. 4). This spike in  $\delta^{15}\text{N}$  could indicate a depletion in food intake and an increased reliance on protein catabolism (Hobson et al. 1993, Lysiak et al. 2018). More studies on the abundance and energy levels of zooplankton in the Gulf of St. Lawrence would be beneficial to understand if right whales may be nutrient depleted in recent years.

The third explanation for the difference seen in stable isotopes of pre- and post-2010 whales is that

the isotopic baseline may have shifted in recent years. The carbon and nitrogen isotopic composition of plankton at the base of the food web is shaped by factors like the availability and speciation of nutrients, as well as rates of photosynthesis (Trueman & Glew 2019). Plankton can vary in nutrient enrichment levels across location and time, thus affecting the isotopic baseline (Tiselius & Fransson 2016, Trueman & Glew 2019). With the recent regime shift in the Scotian Shelf (Meyer-Gutbrod et al. 2021), we speculate that the zooplankton in the past decade could have different  $^{15}\text{N}$  and  $^{13}\text{C}$  enrichment levels, which may affect the isotope ratios seen in right whales, although it is unclear which direction this would influence isotope variability. In conclusion, the enrichment in  $^{15}\text{N}$  and  $^{13}\text{C}$  observed in post-2010 whales was likely due to a combination of these 3 theories, since it is difficult to separate the intrinsic and extrinsic factors that influence the stable isotope ratios in organisms.

### 4.3. Variability in isotopic niche width

Individual whales can have a profound effect on population dynamics due to inter- and intra-individual variability (Bolnick et al. 2003). Individual variation facilitates frequency-dependent interactions that directly impact a population's resilience to change (Wilson 1998, Bolnick et al. 2003), which will be crucial for right whale perseverance in the face of climate change. We expected the inter-annual variation on an individual level to increase over time as the whales travelled to new locations; however, there were no significant differences in isotopic niche width for individual whales over time. Estimates for SEAc varied greatly between individuals during certain years, and this could be explained by irregular oscillations in  $\delta^{13}\text{C}$ . In some years,  $\delta^{13}\text{C}$  peaks and valleys matched with  $\delta^{15}\text{N}$  peaks and valleys well, while in other years, the oscillations did not align well; when  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  are correlated, standard ellipses become small and thin, while decoupling of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  produces relatively wide circular ellipse estimates.

Varied SEAc values could also be explained by differing migration routes among individuals, assuming that they are feeding while travelling. Individual whales do not always travel to the same summer and wintering grounds, and the migration route can be different among the population depending on sex (Davis et al. 2017, Davies et al. 2019, Right Whale Consortium 2020). Although there was no significant difference in stable isotope ratios between male and

female whales at an alpha level of 0.05, males had slightly higher  $\delta^{15}\text{N}$  ratios compared to females at an alpha level of 0.1. Considering the small sample size in our study, it is likely that sex has a real effect on  $\delta^{15}\text{N}$  in right whales. We found that females had the largest SEAc values in pre-2010 and that males became slightly more variable post-2010. A possible explanation for this pattern is that the calving rate has reduced in recent years (Pettis et al. 2022), and therefore, fewer females are going through the metabolic changes related to a full pregnancy term and nursing period (Lysiak et al. 2018). Mother right whales undergo periods of prolonged and intensive nutritional stress as they fast and nurse their calves for up to a year (Kraus 2002, Hunt et al. 2016). These metabolic changes could lead to  $^{15}\text{N}$  enrichment in the nursing mother due to reduced nutrient intake (Hobson et al. 1993). Not only are the pregnant females undergoing more physiological stress than males and non-pregnant females, but they also must travel farther distances to the calving grounds off the coast of Florida (Right Whale Consortium 2020). Males and non-breeding females typically do not travel as far south as pregnant females (Right Whale Consortium 2020). This could explain the larger isotopic variance seen in the pre-2010 adult females.

It is important to note a few caveats related to our study. Firstly, we are inferring patterns in community and individual variability from a small sample size ( $n = 13$ ); therefore, our findings do not accurately represent the whole right whale population and our results must be interpreted carefully. Further, all of the post-2010 whales in our study displayed strong site fidelity to the Gulf of St. Lawrence. As such, these individuals do not represent the other half of the population with unknown summer locations. Comparisons between the isotopic niches of more right whale individuals would be beneficial to understand this highly mobile species. Secondly, the temporal distribution in pre-2010 whales is much greater than post-2010, which would affect the variation in isotope ratios between these 2 periods in the linear mixed-effects models. However, the Layman metrics comparisons are robust against variation in sample size because they are based on a Bayesian approach using isotopic distributions rather than specific values (Jackson et al. 2011). Thirdly, there is the potential that the Suess effect, which is the depletion of  $^{13}\text{C}$  in the atmosphere over time due to increased anthropogenic  $\text{CO}_2$  emissions (Eide et al. 2017), could have an effect on the stable isotope ratios of the whales in our study, since our data span a 33 yr period. However, applying a Suess effect correction can add more

uncertainties to our data because the degree of Suess effect varies by location and depth (Eide et al. 2017). Since the whales travel and feed throughout many regions and can dive as deep as 200 m (Baumgartner & Mate 2003), the Suess effect correction might make the data worse and harder to interpret. Individual whales travel variably within and between years, so it is difficult to apply a constant Suess effect value to all data. This is a big issue for this study and currently a limitation of the technique that we cannot adequately incorporate into our analyses. Lastly, we compared right whale stable isotopes to the isoscape along the core known right whale range in the western North Atlantic; however, right whales have been acoustically detected and occasionally sighted in the central and eastern North Atlantic, such as the historic feeding ground 'Cape Farewell Ground' east of southern Greenland (Smith et al. 2006, Mellinger et al. 2011). Although it is possible for the whales in our study to have travelled outside of American and Canadian waters during the study period, most of the individuals were seen every year along the eastern Atlantic seaboard (Right Whale Consortium 2020); therefore, we decided to limit the isoscape to their known range. Ultimately, right whale distribution outside of the western North Atlantic remains a key knowledge gap, and there is a potential use for SIA to find further information on where the whales may be travelling outside of their known range.

In summary,  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  cycles along right whale baleen were not strongly correlated; therefore,  $\delta^{13}\text{C}$  does not show clear annual migration, and  $\delta^{13}\text{C}$  values alone may not be a useful predictor of the migration route of right whales. Right whales sampled post-2010 were more enriched in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in their baleen plates compared to the individuals that died before 2010; however, the isotopic variance did not change between pre- and post-2010 whales. Although there could be many factors that influenced this pattern, it is likely that the shift in isotopes can be explained by the right whales' summer distribution shift to the Gulf of St. Lawrence in 2010. If the stable isotope shift was due to migration, we were able to detect a difference from the Bay of Fundy to the Gulf of St. Lawrence, which attests to the environmental variation between these 2 regions.

Further research that applies compound-specific isotope analysis (McMahon & Newsome 2019) would be helpful to determine how whale metabolism during winter versus summer affects the isotopic profile in baleen. Other methods, such as performing SIA on barnacles on whales (Taylor et al. 2019) or whale earwax (Robinson et al. 2013), show promise in deter-



mining whale life history and should be compared to baleen datasets. Our study, among many others, clearly shows the importance of performing necropsies to collect valuable research samples. Right whale studies tend to have small sample sizes because of the whales' small population size and endangered status. Our dataset comprised 13 right whale individuals that contained isotopic data from 1986–2005 and 2011–2019. It would be beneficial to have isotopic data of individuals that died recently after the distribution shift so that we could compare the isotopes within the same individual before and after 2010. Future research projects regarding right whales should consider using a combination of past isotope datasets from other researchers to get a larger sample size. Given that stable isotopes appear to show distribution shifts, there is the potential to identify unknown critical habitat of whales.

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#### LITERATURE CITED

- ✦ Aguilar A, Giménez J, Gómez-Campos E, Cardona L, Borrell A (2014)  $\delta^{15}\text{N}$  value does not reflect fasting in mysticetes. *PLOS ONE* 9:e92288
- ✦ Ayliffe LK, Cerling TE, Robinson T, West AG and others (2004) Turnover of carbon isotopes in tail hair and breath  $\text{CO}_2$  of horses fed an isotopically varied diet. *Oecologia* 139:11–22
- ✦ Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
- ✦ Baumgartner MF, Mate BR (2003) Summertime foraging ecology of North Atlantic right whales. *Mar Ecol Prog Ser* 264:123–135
- ✦ Baumgartner MF, Mate BR (2005) Summer and fall habitat of North Atlantic right whales (*Eubalaena glacialis*) inferred from satellite telemetry. *Can J Fish Aquat Sci* 62: 527–543
- ✦ Best PB, Schell DM (1996) Stable isotopes in southern right whale (*Eubalaena australis*) baleen as indicators of seasonal movements, feeding and growth. *Mar Biol* 124: 483–494
- ✦ Bishop AL, Crowe LM, Hamilton PK, Meyer-Gutbrod EL (2022) Maternal lineage and habitat use patterns explain variation in the fecundity of a critically endangered baleen whale. *Front Mar Sci* 9:880910
- ✦ Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulseley CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. *Am Nat* 161:1–28
- Bourque L, Wimmer T, Lair S, Jones M, Daoust PY (2020) Incident report: North Atlantic right whale mortality event in Eastern Canada, 2019. Collaborative report produced by Canadian Wildlife Health Cooperative and Marine Animal Response Society, Charlottetown, Prince Edward Island
- Brown MW, Kraus SD, Slay CK, Garrison LP (2007) Surveying for discovery, science, and management. In: Kraus SD, Rolland RM (eds) *The urban whale: North Atlantic right whales at the crossroads*. Harvard University Press, Cambridge, MA, p 105–137
- ✦ Busquets-Vass G, Newsome SD, Calambokidis J, Serravalente G, Jacobsen JK, Aguiñiga-García S, Gendron D (2017) Estimating blue whale skin isotopic incorporation rates and baleen growth rates: implications for assessing diet and movement patterns in mysticetes. *PLOS ONE* 12:e0177880
- ✦ Caraveo-Patiño J, Hobson KA, Soto LA (2007) Feeding ecology of gray whales inferred from stable-carbon and nitrogen isotopic analysis of baleen plates. *Hydrobiologia* 586:17–25
- ✦ Cole TVN, Hamilton P, Henry AG, Duley P, Pace RM III, White BN, Frasier T (2013) Evidence of a North Atlantic right whale *Eubalaena glacialis* mating ground. *Endang Species Res* 21:55–64
- Cooke JG (2020) *Eubalaena glacialis* (errata version published in 2020). IUCN Red List of Threatened Species 2020: e.T41712A178589687. <https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T41712A178589687.en> (accessed 3 Nov 2023)
- ✦ Crowe LM, Brown MW, Corkeron PJ, Hamilton PK and others (2021) In plane sight: a mark–recapture analysis of North Atlantic right whales in the Gulf of St. Lawrence. *Endang Species Res* 46:227–251
- Daoust PY, Couture E, Wimmer T, Bourque L (2018) Incident report: North Atlantic right whale mortality event in the Gulf of St. Lawrence, 2017. Collaborative report produced by Canadian Wildlife Health Cooperative, Marine Animal Response Society and Fisheries and Oceans Canada, Charlottetown, Prince Edward Island
- ✦ Das K, Holleville O, Ryan C, Berrow S, Gilles A, Ody D, Michel LN (2017) Isotopic niches of fin whales from the Mediterranean Sea and the Celtic Sea (North Atlantic). *Mar Environ Res* 127:75–83
- ✦ Davies KTA, Brillant SW (2019) Mass human-caused mortality spurs federal action to protect endangered North Atlantic right whales in Canada. *Mar Policy* 104:157–162
- ✦ Davies KTA, Brown MW, Hamilton PK, Knowlton AR, Taggart CT, Vanderlaan ASM (2019) Variation in North Atlantic right whale *Eubalaena glacialis* occurrence in the Bay of Fundy, Canada, over three decades. *Endang Species Res* 39:159–171
- ✦ Davis GE, Baumgartner MF, Bonnell JM, Bell J and others (2017) Long-term passive acoustic recordings track the changing distribution of North Atlantic right whales (*Eubalaena glacialis*) from 2004 to 2014. *Sci Rep* 7:13460

- Davis GE, Baumgartner MF, Corkeron PJ, Bell J and others (2020) Exploring movement patterns and changing distributions of baleen whales in the western North Atlantic using a decade of passive acoustic data. *Glob Change Biol* 26:4812–4840
- Durette-Morin D, Davies KTA, Johnson HD, Brown MW, Moors-Murphy H, Martin B, Taggart CT (2019) Passive acoustic monitoring predicts daily variation in North Atlantic right whale presence and relative abundance in Roseway Basin, Canada. *Mar Mamm Sci* 35:1280–1303
- Durette-Morin D, Evers C, Johnson HD, Kowarski K and others (2022) The distribution of North Atlantic right whales in Canadian waters from 2015–2017 revealed by passive acoustic monitoring. *Front Mar Sci* 9:976044
- Eide M, Olsen A, Ninnemann US, Eldevik T (2017) A global estimate of the full oceanic  $^{13}\text{C}$  Suess effect since the preindustrial. *Global Biogeochem Cycles* 31:492–514
- Eisenmann P, Fry B, Holyoake C, Coughran D, Nicol S, Bengtson Nash S (2016) Isotopic evidence of a wide spectrum of feeding strategies in Southern Hemisphere humpback whale baleen records. *PLOS ONE* 11:e0156698
- Florin ST, Felicetti LA, Robbins CT (2011) The biological basis for understanding and predicting dietary-induced variation in nitrogen and sulphur isotope ratio discrimination. *Funct Ecol* 25:519–526
- Ganley LC, Byrnes J, Pendleton DE, Mayo CA and others (2022) Effects of changing temperature phenology on the abundance of a critically endangered baleen whale. *Glob Ecol Conserv* 38:e02193
- Hamilton P, Knowlton A, Marx M (2007) Right whales tell their own stories: the photo-identification catalog. In: Kraus SD, Rolland RM (eds) *The urban whale: North Atlantic right whales at the crossroads*. Harvard University Press, Cambridge, MA, p 75–104
- Hlista BL, Sosik HM, Martin Traykovski LV, Kenney RD, Moore MJ (2009) Seasonal and interannual correlations between right-whale distribution and calving success and chlorophyll concentrations in the Gulf of Maine, USA. *Mar Ecol Prog Ser* 394:289–302
- Hobson KA (2019) Application of isotopic methods to tracking animal movements. In: Hobson KA, Wassenaar LI (eds) *Tracking animal migration with stable isotopes*, 2nd edn. Academic Press, London, p 85–116
- Hobson KA, Schell DM (1998) Stable carbon and nitrogen isotope patterns in baleen from eastern Arctic bowhead whales (*Balaena mysticetus*). *Can J Fish Aquat Sci* 55:2601–2607
- Hobson KA, Alisauskas RT, Clark RG (1993) Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. *Condor* 95:388–394
- Hunt KE, Lysiak NS, Moore MJ, Rolland RM (2016) Longitudinal progesterone profiles in baleen from female North Atlantic right whales (*Eubalaena glacialis*) match known calving history. *Conserv Physiol* 4:cow014
- Hunt KE, Lysiak NSJ, Matthews CJD, Lowe C and others (2018) Multi-year patterns in testosterone, cortisol and corticosterone in baleen from adult males of three whale species. *Conserv Physiol* 6:coy049
- Jackson AL, Parnell AC (2021) SIBER: stable isotope Bayesian ellipses in R. R package version 2.1.6. <https://CRAN.R-project.org/package=siber>
- Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *J Anim Ecol* 80:595–602
- Jennings S, Warr KJ (2003) Environmental correlates of large-scale spatial variation in the  $\delta^{15}\text{N}$  of marine animals. *Mar Biol* 142:1131–1140
- Johnson C, Devred E, Casault B, Head E, Spry J (2017) Optical, chemical, and biological oceanographic conditions on the Scotian Shelf and in the Eastern Gulf of Maine in 2015. *DFO Can Sci Advis Sec Res Doc* 2017/012
- Knowlton AR, Hamilton PK, Marx MK, Pettis HM, Kraus SD (2012) Monitoring North Atlantic right whale *Eubalaena glacialis* entanglement rates: a 30 yr retrospective. *Mar Ecol Prog Ser* 466:293–302
- Kraus SD (2002) Birth, death and taxis: North Atlantic right whales in the twenty-first century. PhD dissertation, University of New Hampshire, Durham, NH
- Kraus SD, Rolland RM (2007) Right whales in the urban ocean. In: Kraus SD, Rolland RM (eds) *The urban whale: North Atlantic right whales at the crossroads*. Harvard University Press, Cambridge, MA, p 1–38
- Kraus SD, Brown MW, Caswell H, Clark CW and others (2005) North Atlantic right whales in crisis. *Science* 309:561–562
- Kraus S, Pace R, Frasier T (2007) High investment, low return: the strange case of reproduction in *Eubalaena glacialis*. In: Kraus SD, Rolland RM (eds) *The urban whale: North Atlantic right whales at the crossroads*. Harvard University Press, Cambridge, MA, p 172–199
- Kraus SD, Kenney RD, Mayo CA, McLellan WA, Moore MJ, Nowacek DP (2016) Recent scientific publications cast doubt on North Atlantic right whale future. *Front Mar Sci* 3:137
- Larson KW, Hobson KA (2009) Assignment to breeding and wintering grounds using stable isotopes: a comment on lessons learned by Rocque et al. *J Ornithol* 150:709–712
- Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88:42–48
- Lysiak NSJ (2008) Investigating the migration and foraging ecology of North Atlantic right whales with stable isotope geochemistry of baleen and zooplankton. PhD dissertation, Boston University, Boston, MA
- Lysiak NSJ, Trumble SJ, Knowlton AR, Moore MJ (2018) Characterizing the duration and severity of fishing gear entanglement on a North Atlantic right whale (*Eubalaena glacialis*) using stable isotopes, steroid and thyroid hormones in baleen. *Front Mar Sci* 5:168
- Magozzi S, Yool A, Vander Zanden HB, Wunder MB, Trueman CN (2017) Using ocean models to predict spatial and temporal variation in marine carbon isotopes. *Ecosphere* 8:e01763
- Massicotte P, South A (2023) rnatuarearth: World Map Data from Natural Earth. <https://docs.ropensci.org/rnatuarearth/> (accessed 24 Sep 2023)
- Matthews CJD, Ferguson SH (2015) Seasonal foraging behaviour of Eastern Canada–West Greenland bowhead whales: an assessment of isotopic cycles along baleen. *Mar Ecol Prog Ser* 522:269–286
- Mayo CA, Marx MK (1990) Surface foraging behaviour of the North Atlantic right whale, *Eubalaena glacialis*, and associated zooplankton characteristics. *Can J Zool* 68:2214–2220
- McMahon K, Newsome S (2019) Amino acid isotope analysis: a new frontier in studies of animal migration and for-

- aging ecology. In: Hobson KA, Wassenaar LI (eds) Tracking animal migration with stable isotopes, 2nd edn. Academic Press, London, p 173–190
- ✦ McMahon KW, Hamady LL, Thorrold SR (2013) A review of ecogeochemistry approaches to estimating movements of marine animals. *Limnol Oceanogr* 58:697–714
- ✦ Mellinger DK, Nieuwkerk SL, Klinck K, Klinck H, Dziak RP, Clapham PJ, Brandsdóttir B (2011) Confirmation of right whales near a nineteenth-century whaling ground east of southern Greenland. *Biol Lett* 7:411–413
- Meyer-Gutbrod EL, Greene CH (2017) Uncertain recovery of the North Atlantic right whale in a changing ocean. *Glob Change Biol* doi:10.1111/gcb.13511
- ✦ Meyer-Gutbrod EL, Greene CH, Sullivan PJ, Pershing AJ (2015) Climate-associated changes in prey availability drive reproductive dynamics of the North Atlantic right whale population. *Mar Ecol Prog Ser* 535:243–258
- ✦ Meyer-Gutbrod E, Greene C, Davies K, Johns D (2021) Ocean regime shift is driving collapse of the North Atlantic right whale population. *Oceanography* 34:22–31
- ✦ Meyer-Gutbrod EL, Davies KTA, Johnson CL, Plourde S and others (2023) Redefining North Atlantic right whale habitat-use patterns under climate change. *Limnol Oceanogr* 68:S71–S86
- Moore M, Andrews R, Austin T, Bailey J and others (2013) Rope trauma, sedation, disentanglement, and monitoring-tag associated lesions in a terminally entangled North Atlantic right whale (*Eubalaena glacialis*). *Mar Mamm Sci* 29:E98–E113
- ✦ Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. *Front Ecol Environ* 5: 429–436
- NOAA Fisheries (2022) 2017–2022 North Atlantic right whale unusual mortality event. <https://www.fisheries.noaa.gov/national/marine-life-distress/2017-2022-north-atlantic-right-whale-unusual-mortality-event> (accessed 12 Jun 2022)
- ✦ O'Brien O, Pendleton DE, Ganley LC, McKenna KR and others (2022) Repatriation of a historical North Atlantic right whale habitat during an era of rapid climate change. *Sci Rep* 12:12407
- ✦ Oczkowski A, Kreakie B, McKinney RA, Prezioso J (2016) Patterns in stable isotope values of nitrogen and carbon in particulate matter from the Northwest Atlantic continental shelf, from the Gulf of Maine to Cape Hatteras. *Front Mar Sci* 3:252
- ✦ Patrician MR, Kenney RD (2010) Using the Continuous Plankton Recorder to investigate the absence of North Atlantic right whales (*Eubalaena glacialis*) from the Roseway Basin foraging ground. *J Plankton Res* 32: 1685–1695
- ✦ Pendleton DE, Sullivan PJ, Brown MW, Cole TVN and others (2012) Weekly predictions of North Atlantic right whale *Eubalaena glacialis* habitat reveal influence of prey abundance and seasonality of habitat preferences. *Endang Species Res* 18:147–161
- ✦ Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annu Rev Ecol Syst* 18:293–320
- ✦ Pettis HM, Pace RM, Hamilton PK (2021) North Atlantic Right Whale Consortium 2020 annual report card. North Atlantic Right Whale Consortium, Boston, MA
- ✦ Pettis HM, Pace RM, Hamilton PK (2022) North Atlantic Right Whale Consortium 2021 annual report card. North Atlantic Right Whale Consortium, Boston, MA
- ✦ Pettis HM, Pace RM, Hamilton PK (2023) North Atlantic Right Whale Consortium 2022 annual report card. North Atlantic Right Whale Consortium, Boston, MA
- ✦ Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2020) nlme: Linear and nonlinear mixed effects models. R package version 3.1-147. <https://CRAN.R-project.org/package=nlme>
- ✦ Pomerleau C, Matthews CJD, Gobeil C, Stern GA, Ferguson SH, Macdonald RW (2018) Mercury and stable isotope cycles in baleen plates are consistent with year-round feeding in two bowhead whale (*Balaena mysticetus*) populations. *Polar Biol* 41:1881–1893
- ✦ Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83: 703–718
- R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- ✦ Record NR, Runge JA, Pendleton DE, Balch WM and others (2019) Rapid climate-driven circulation changes threaten conservation of endangered North Atlantic right whales. *Oceanography* 32:162–169
- Reeves RR, Smith TD, Josephson EA (2007) Near-annihilation of a species: right whaling in the North Atlantic. In: Kraus SD, Rolland RM (eds) The urban whale: North Atlantic right whales at the crossroads. Harvard University Press, Cambridge, MA, p 39–74
- ✦ Reiss L, Häussermann V, Mayr C (2020) Stable isotope records of sei whale baleens from Chilean Patagonia as archives for feeding and migration behavior. *Ecol Evol* 10:808–818
- Right Whale Consortium (2020) North Atlantic Right Whale Consortium sightings database 07/23/2020. New England Aquarium, Boston, MA
- ✦ Robinson EM, Trumble SJ, Subedi B, Sanders R, Usenko S (2013) Selective pressurized liquid extraction of pesticides, polychlorinated biphenyls and polybrominated diphenyl ethers in a whale earplug (earwax): a novel method for analyzing organic contaminants in lipid-rich matrices. *J Chromatogr A* 1319:14–20
- ✦ Sharp SM, McLellan WA, Rotstein DS, Costidis AM and others (2019) Gross and histopathologic diagnoses from North Atlantic right whale *Eubalaena glacialis* mortalities between 2003 and 2018. *Dis Aquat Org* 135:1–31
- ✦ Smith TD, Barthelmess K, Reeves RR (2006) Using historical records to relocate a long-forgotten summer feeding ground of North Atlantic right whales. *Mar Mamm Sci* 22: 723–734
- ✦ Sorochan KA, Plourde S, Baumgartner MF, Johnson CL (2021) Availability, supply, and aggregation of prey (*Calanus* spp.) in foraging areas of the North Atlantic right whale (*Eubalaena glacialis*). *ICES J Mar Sci* 78: 3498–3520
- ✦ Stewart JD, Durban JW, Knowlton AR, Lynn MS and others (2021) Decreasing body lengths in North Atlantic right whales. *Curr Biol* 31:3174–3179
- ✦ Stokstad E (2017) Surge in right whale deaths raises alarms. *Science* 357:740–741
- ✦ Summers EL, Estrada JA, Zeeman SI (2006) A note on geographic and seasonal fluctuations in the isotopic composition of baleen in four North Atlantic right whales (*Eubalaena glacialis*). *J Cetacean Res Manag* 8:241–245
- ✦ Taylor LD, O'Dea A, Bralower TJ, Finnegan S (2019) Isotopes from fossil coronulid barnacle shells record evo-

- dence of migration in multiple Pleistocene whale populations. *Proc Natl Acad Sci USA* 116:7377–7381
- ✦ Teixeira CR, Troina GC, Daura-Jorge FG, Simões-Lopes PC, Botta S (2022) A practical guide on stable isotope analysis for cetacean research. *Mar Mamm Sci* 2022:1200–1228
- ✦ Tiselius P, Fransson K (2016) Daily changes in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  stable isotopes in copepods: equilibrium dynamics and variations of trophic level in the field. *J Plankton Res* 38: 751–761
- ✦ Trueman CN, Glew KSJ (2019) Isotopic tracking of marine animal movement. In: Hobson KA, Wassenaar LI (eds) *Tracking animal migration with stable isotopes*, 2nd edn. Academic Press, London, p 137–172
- ✦ Wassenaar LI (2019) Introduction to conducting stable isotope measurements for animal migration studies. In: Hobson KA, Wassenaar LI (eds) *Tracking animal migration with stable isotopes*, 2nd edn. Academic Press, London, p 25–51
- ✦ Werth AJ, Sformo TL, Lysiak NS, Rita D, George JC (2020) Baleen turnover and gut transit in mysticete whales and its environmental implications. *Polar Biol* 43:707–723
- ✦ Werth AJ, Sformo TL, Lysiak NS, Rita D, George JC (2021) Differential baleen growth and its consequences. *Polar Biol* 44:1227–1228
- ✦ Wilson DS (1998) Adaptive individual differences within single populations. *Philos Trans R Soc B* 353:199–205

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