

Foraging behaviour of southern right whales (*Eubalaena australis*) inferred from variation of carbon stable isotope ratios in their baleen

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ABSTRACT

The isotopic composition of a whale's diet is recorded in its tissues including its baleen. The longest baleen plates of an adult right whale contain a 6- to 7-year record of the isotopic composition of its prey (copepods and krill). The stable carbon isotope ratios of prey change with water temperature (latitude), depth, freshwater inputs and current systems, so the isotopic signals in baleen provide information about the annual foraging paths of individuals. Baleen from five adult southern right whales (*Eubalaena australis*) that died and stranded on their nursery ground at Península Valdés, Argentina, were sampled at 2 cm intervals from the gum line to the tip of the baleen plate. The stable carbon isotope ratios ($\delta^{13}\text{C}$) in the baleen oscillate between high and low values on annual cycles. Higher values of $\delta^{13}\text{C}$ appear to indicate feeding on warmer-water prey (Patagonian Shelf, -18 to -23‰) while lower values indicate colder-water prey (South Georgia, -24 to -29‰). Each annual cycle was analyzed to determine the distances (in centimetres of baleen growth) between peaks, the highest and lowest values of $\delta^{13}\text{C}$, the rates of change in $\delta^{13}\text{C}$ between peaks and troughs, and the $\delta^{13}\text{C}$ values at plateaus where signals remained approximately constant. Baleen grew an average of 31 cm/yr with large interannual variation (sd 5.8 cm) within individuals but no significant differences between individuals. Baleen growth in a given year was positively correlated with the lowest (most southerly) $\delta^{13}\text{C}$ value in that year. Individuals differed significantly in their mean isotopic ratios and in the ranges of their annual oscillations (latitudinal foraging ranges). Two whales had narrow ranges (spanning 3.0 and 2.7‰ $\delta^{13}\text{C}$), but one fed in warm waters at higher latitudes (mean $\delta^{13}\text{C} = -18.2\text{‰}$) while the other fed in cool waters at lower latitudes (mean $\delta^{13}\text{C} = -23.8\text{‰}$). The other three whales had significantly broader ranges (spanning 5.1 to 6.8‰ $\delta^{13}\text{C}$). $\delta^{13}\text{C}$ values change more rapidly in spring ($\sim 0.3\text{‰/wk}$) than in fall ($\sim 0.2\text{‰/wk}$). We conclude that carbon isotope ratios in baleen record individual differences in foraging and distribution, and that they also record each individual's yearly responses to changing environmental conditions, possibly including fluctuations in the abundances of copepods and krill.

KEYWORDS: DISTRIBUTION, FEEDING GROUNDS, MIGRATION, MOVEMENTS

INTRODUCTION

Southern right whales (*Eubalaena australis*) are major consumers of copepods and krill with seasonal foraging paths that cover vast expanses of the southern oceans. They migrate between nursery and feeding grounds that are thousands of kilometers apart (Best *et al.*, 1993). The population of southern right whales that uses the gulfs surrounding Península Valdés, Argentina as a nursery ground has fewer calves than expected following years of low krill (*Euphausia superba*) abundance in the waters off South Georgia (Leaper *et al.*, 2006). Krill abundance declines following El Niño years when sea surface temperatures around South Georgia are higher than normal (Trathan *et al.*, 2006). Krill are a key component of the Southern Ocean food web. Their larvae feed extensively on ice-algae that grow on the undersurfaces of ice sheets. Global warming is melting Antarctic ice sheets and could have profound effects on krill and as a consequence on their predators including the great whales. Murphy *et al.* (2007) have argued that a regional warming of only 1°C over the next century could lead to a 95% reduction in krill biomass across the Scotia Sea.

Can krill-dependent predators adapt to declines in krill abundance? A combination of genetic and stable-isotope analyses of skin biopsies from the Patagonian right whales has suggested that members of this population learn particular foraging locations from their mothers and then continue to forage in the same places, giving rise to potentially conservative matrilineal family foraging 'traditions' (Valenzuela *et al.*, SC/60/BRG13). To understand the potential consequences of this and other aspects of right-whale foraging strategies, we need first to understand where right whales go, individually and collectively, when they leave their nursery grounds in early spring. Here we describe a method for studying the foraging paths of individual right whales by measuring changes in carbon isotope ratios along the length of a baleen plate. Analysis of such records for five whales suggests that the whales used at least three different foraging strategies and that individual foraging paths also varied from year to year. Continuing such analyses through years with known climate and prey-abundance anomalies may suggest how right whales will respond to longer-term changes in climate and prey abundance.

BACKGROUND

Baleen as an indicator of foraging behavior. Regional variations in stable isotopes have been used to identify the feeding locations and migratory patterns of many species of birds and mammals including whales (Rubenstein and Hobson, 2004; Kunito *et al.*, 2000; Schell *et al.*, 1989; Abend and Smith, 1997; Schoeninger *et al.*, 1999). Schell *et al.* (1989) documented annual cycles of $\delta^{13}\text{C}$ values in the baleen of bowhead whales and showed that these values matched those of the whales' prey at locations along their migratory path between the Bering, Chukchi and Beaufort Seas. Best and Schell (1996) showed that southern right whale baleen plates also have annual isotopic cycles, and reported that baleen plates from adult whales contain a continuous six to seven year record of their foraging paths in the South Atlantic. Best and Schell (1996) hypothesized that for these baleens from South Africa, each annual cycle corresponds to regular north-south movements across the subtropical convergence (STC). Rowntree *et al.* (2001) report the mean isotope values of seven baleen plates from Península Valdés, Argentina. Rowntree *et al.* (2001) found that the mean isotopic values of four baleen plates from Argentina were similar to the mean values of six plates from South Africa, but that the other three plates had higher mean values.

Why $\delta^{13}\text{C}$ in the ocean is a good indicator of feeding locations. Isotopes with different masses respond differently to various biological and biogeochemical processes, giving rise to location-specific source ratios that then propagate through food chains (often with small predictable offsets caused by metabolic pathways). Primary producers and water temperatures influence carbon stable isotope ratios. Algae preferentially use the lighter carbon dioxide molecule ($^{12}\text{CO}_2$) for photosynthesis, resulting in organic molecules enriched in ^{12}C (hence depleted in ^{13}C). This 'organic fractionation' through photosynthesis in the ocean lowers the $^{13}\text{C}/^{12}\text{C}$ ratio of organic molecules synthesized by primary producers, relative to the isotopic ratio of dissolved inorganic CO_2 . (The isotopic ratio is conventionally expressed in a standardized form called $\delta^{13}\text{C}$, whose units are parts per thousand, denoted '‰' or 'per mil'.) Water temperature influences the $\delta^{13}\text{C}$ values of primary production by changing the strength of the organic fractionation process. At high temperatures, relatively little CO_2 dissolves in seawater and therefore relatively little is available to the phytoplankton. Under these conditions the fractionation is relatively weak because phytoplankton consume most of the available CO_2 . At low temperatures CO_2 dissolves more readily, and more is therefore available to phytoplankton, resulting in much more robust fractionation. As a consequence of these processes that couple temperature to the CO_2 content of surface waters, the carbon isotope ratios ($\delta^{13}\text{C}$, reflecting $^{13}\text{C}/^{12}\text{C}$) of primary producers decrease with latitude.

Carbon isotope ratios measured in the tissues of a predator reflect those of its prey with minor (and predictable) offsets (Kelly, 2000). Based on this 'you are what you eat' principle, $\delta^{13}\text{C}$ has been used to identify feeding locations and prey types by matching the isotope values of consumers with those of potential foods (Hobson, 1999). As carbon is assimilated into the tissues of a consumer, the lighter isotope (^{12}C) is used preferentially in many metabolic processes such that the $^{13}\text{C}/^{12}\text{C}$ ratio that remains in the consumer's tissues is about 1‰ higher than in its food (Deniro and Epstein, 1978; Fry and Sherr, 1984). However, recent papers argue that in keratin-rich tissues (like hair or baleen) this fractionation factor may be as high as 3‰ (Cerling *et al.*, 2004).

Right whale feeding locations as indicated by whaling records. Whaling records and resightings of known individuals have provided what we know about the whales' foraging routes. Eighteenth-century whalers in the South Atlantic found right whales farthest north (30°S) from August to December and farthest south (40-55°S) from January through July (Townsend, 1935). From August-October (winter and early spring), much of the population is on the nursery ground at Península Valdés (42°S, 64°W) (Payne, 1986). In one season (1961-62) a Soviet whaling ship illegally took 1,312 right whales to the east of Argentina (Tormosov *et al.*, 1998) (Fig. 1). Most of the whales were killed in November and December on the Patagonian Shelf, east and northeast of Península Valdés. The number of right whales at Península Valdés begins to decline in late October and most have gone by December making it likely that many of these whales had just arrived in this area after leaving the nursery ground. This region of the Patagonian shelf is where the warm southward-flowing waters of the Brazil Current meet the cold northward flow of the Falklands/Malvinas Current. The temperature stratification in this confluence makes it an extremely productive fishing ground. Other than sporadic feeding on the Valdés nursery, the confluence is probably the first feeding location that many of the whales visit after leaving Península Valdés.

The stomach contents of 249 right whales taken by the Soviets from November through April show that the diet of southern right whales changes with latitude. The stomachs of whales taken north of 40°S contained mostly copepods (92%) while those south of 50°S contained mostly krill (99%) and those in between contained mixtures of krill (71%) and copepods (24%). Stomachs were fullest in summer (January to March). The latitudinal change in diet appears related to the occurrence and distribution of dense swarms of krill. Antarctic krill (*Euphausia superba*) are distributed in high latitudes between the Polar Front (Fig. 2) and the Antarctic Shelf (Atkinson *et al.*, 2004). Krill densities are highest in summer and are correlated with high concentrations of chlorophyll *a* (Atkinson *et al.*, 2004).

Fig. 1. Locations of right whales taken by a Soviet whaling ship in 1960s. The large white dots indicate positions where 80-100 whales were taken; medium dots indicate 40-70 whales, and small dots indicate 1-10 whales. Note that most catches are on or just off the edge of the Patagonian Shelf. Peninsula Valdés is near the westernmost of the medium dots; its southern bay (Golfo Nuevo) can be seen clearly in this image and is approximately the same size as the medium dot. The northern bay (Golfo San Jose) is partly obscured by light colored pixels representing the land surface.

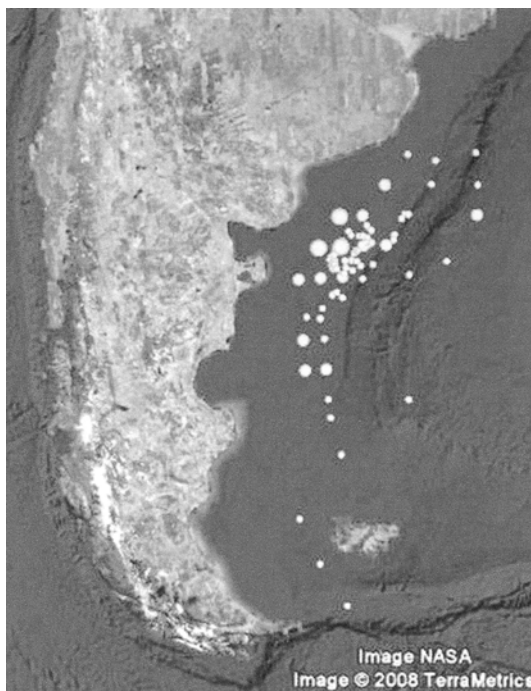
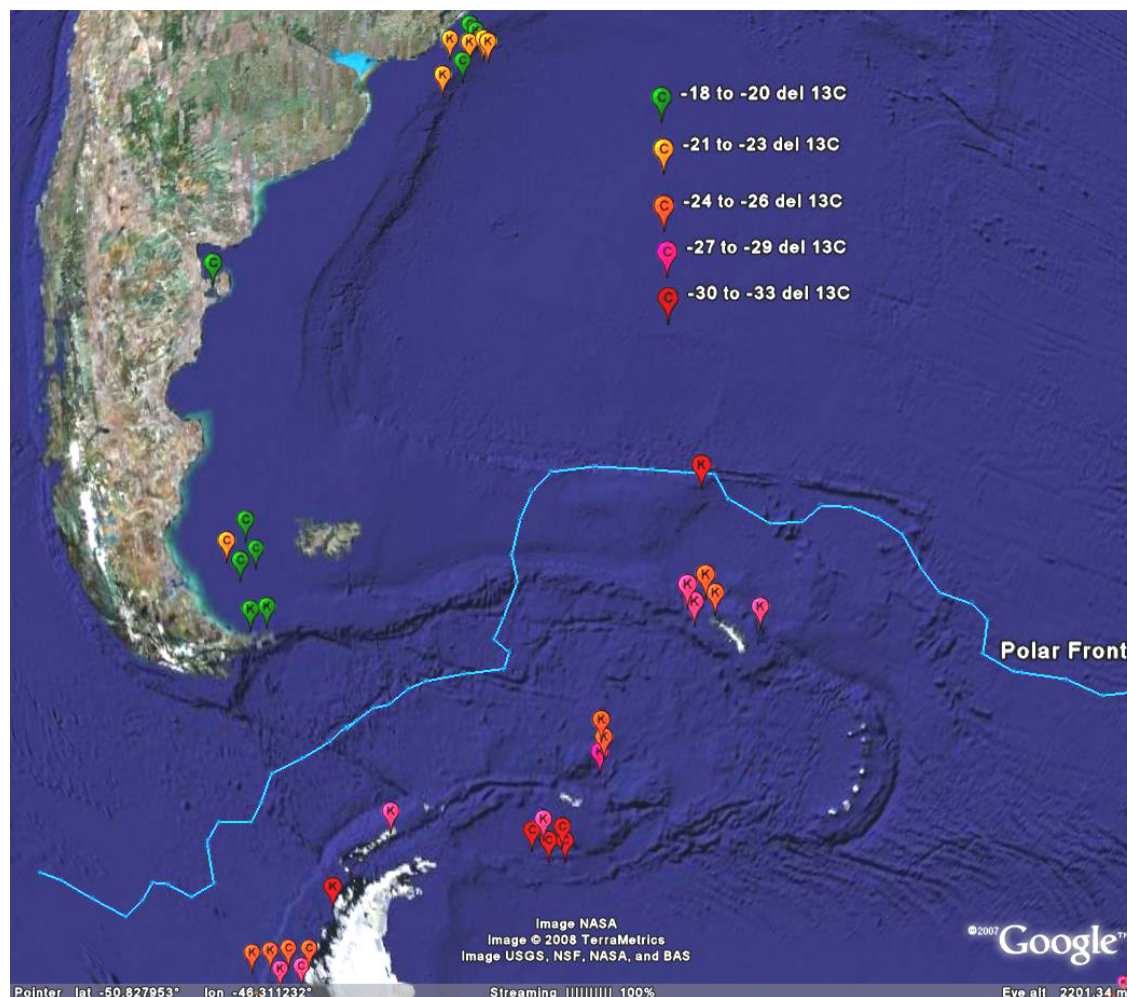


Fig. 2. Locations of prey samples and their carbon stable isotope ratios. Pins are marked 'C' for copepods and 'K' for krill. Five $\delta^{13}\text{C}$ ranges are indicated by colors (as keyed by the inset legend). Ratios from prey below the Polar Front are very low, and those from the Patagonian shelf are relatively high. Published data are from Dunton (2001), Rau *et al.* (1991a,b), Rowntree *et al.* (2001), Schmidt *et al.* (2003), and Wada *et al.* (1987).



From January through March (summer), right whales have been sighted south of 50°S (Oshumi and Kasamatsu, 1986; Hamner *et al.*, 1988). In these months the biomass of mesozooplankton and krill around South Georgia (53°S, 36°W) is greater than anywhere else in the Southern Ocean (Atkinson *et al.*, 2001), making it another likely feeding destination for the Patagonian right whales. Whalers took over 175,000 baleen whales near South Georgia in the early 1900s (Moore *et al.*, 1999). Today, right whales are the predominant species seen off South Georgia with a peak in sightings from January through May (Moore *et al.*, 1999). The most concrete evidence linking the Península Valdés right whales to South Georgia is three resightings of known individuals that had been photographed previously at the Península (Rowntree *et al.*, 2001).

During the six months when the whales are neither fasting nor feeding on krill, they are likely to feed on copepods. Copepod abundances are more strongly seasonal at higher latitudes (Woodd-Walker *et al.*, 2002), suggesting that right whales might profitably consume them at lower latitudes both before and after the peak of krill abundance at high latitudes. Some species of *Calanoides* and *Calanus* with polar distributions store lipids (Woodd-Walker *et al.*, 2002), which could make them a valuable resource for replenishing blubber reserves. SeaWiFS maps in Atkinson *et al.* (2001) show a geographic progression of high chlorophyll *a* concentrations from October to January. If copepod blooms follow the spatio-temporal distribution of chlorophyll *a*, then right whales might follow the blooms by foraging first on the Patagonian Shelf and then moving, as spring advances, southward along the Shelf, then east to South Georgia.

MATERIALS AND METHODS

Baleen plates were collected from five adult right whales that stranded at Península Valdés, Argentina. Sex, size and year information about the stranded animals is shown in Figs 3 and 6 where known (O95, Ea32-05 and Ea43-05). Two of the plates were contributed to the study in 1995 and we know only that their years of death were prior to 1995. The plate from whale F95 is short (90cm) and contains only two complete annual cycles. These cycles are sharp and of high amplitude, so we infer that F95 was an adult and that the plate is from the front of the mouth. Baleen plates from juveniles are also short, but the annual cycles of $\delta^{13}\text{C}$ are more spread out than in adults because juvenile baleen grows more rapidly (see Fig. 2 in Best and Schell, 1996).

The plates were washed with household detergent, scraped to remove foreign material (*e.g.*, diatom films) and dried. They were then sampled using a motorized engraving tool at 2cm intervals along the external edge, from the base of the plate where it was forming within the gum to the end of the longest hairs at the distal tip. Ten to 20mg of tissue was extracted from each sampling location. Three plates (O95, PRW95 and F95) were analysed as described by Rowntree *et al.* (2001), and two plates (Ea32-05 and Ea43-05) were analysed at the Stable Isotope Ratio Facility for Environmental Research (SIRFER) at the University of Utah. For plates analyzed at SIRFER, one milligram of each sample was ionized on an elemental analyzer coupled to an isotope ratio mass spectrometer. Isotope ratios are expressed as $\delta^{13}\text{C}$ (‰) = $[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where *R* is the ratio $^{13}\text{C}/^{12}\text{C}$. The standard for carbon was referenced to Pee Dee Belemnite. The reproducibility of these measurements is 0.2‰ based on repeated analyses of an internal laboratory standard (yeast).

The succession of $\delta^{13}\text{C}$ values along the length of each plate was plotted using Canvas 8 (Fig. 3), and the program's dimensioning tools were then used to measure features of interest for subsequent statistical analysis. The measurements made for each annual cycle are diagrammed in Fig. 4. Only complete cycles were measured (*i.e.*, partial cycles at the beginning and end of each baleen plate were excluded). Places in a cycle where $\delta^{13}\text{C}$ values did not change more than 0.25‰ over a 2cm interval were interpreted as times when the whale fed on a relatively constant diet (marked by a circle in Fig. 4). Each cycle was measured for the following variables:

1. interval (cm) between the peaks (highest $\delta^{13}\text{C}$ values) at the beginning and end of the cycle;
2. change in $\delta^{13}\text{C}$ (‰) from the first peak to the lowest point in the following trough;
3. change in $\delta^{13}\text{C}$ from the lowest point in the trough to the following peak;
4. interval (cm) between the first peak and the lowest point in the trough, excluding 2cm intervals where $\delta^{13}\text{C}$ values did not change more than 0.25‰;
5. interval (cm) between the lowest point in a trough to the following peak, excluding 2cm intervals where $\delta^{13}\text{C}$ values did not change more than 0.25‰;
6. interval (cm) where $\delta^{13}\text{C}$ values did not change more than 0.25‰ just prior to the final peak;
7. highest and lowest $\delta^{13}\text{C}$ values in a cycle.

Statistical analyses of these data were conducted using JMP statistical software. Formal significance levels are for one-way ANOVAs unless otherwise indicated.

A map was constructed using Google Earth Plus to show the distribution of $\delta^{13}\text{C}$ values in copepods and krill collected throughout the potential foraging range of the Península Valdés population. Most of the isotope values are from published literature, but some data for locations on the Patagonian Shelf and off Uruguay are unpublished observations by the authors and colleagues whose contributions are acknowledged below. The resulting map (Fig. 2) shows mean $\delta^{13}\text{C}$ values binned to a resolution of 3‰.

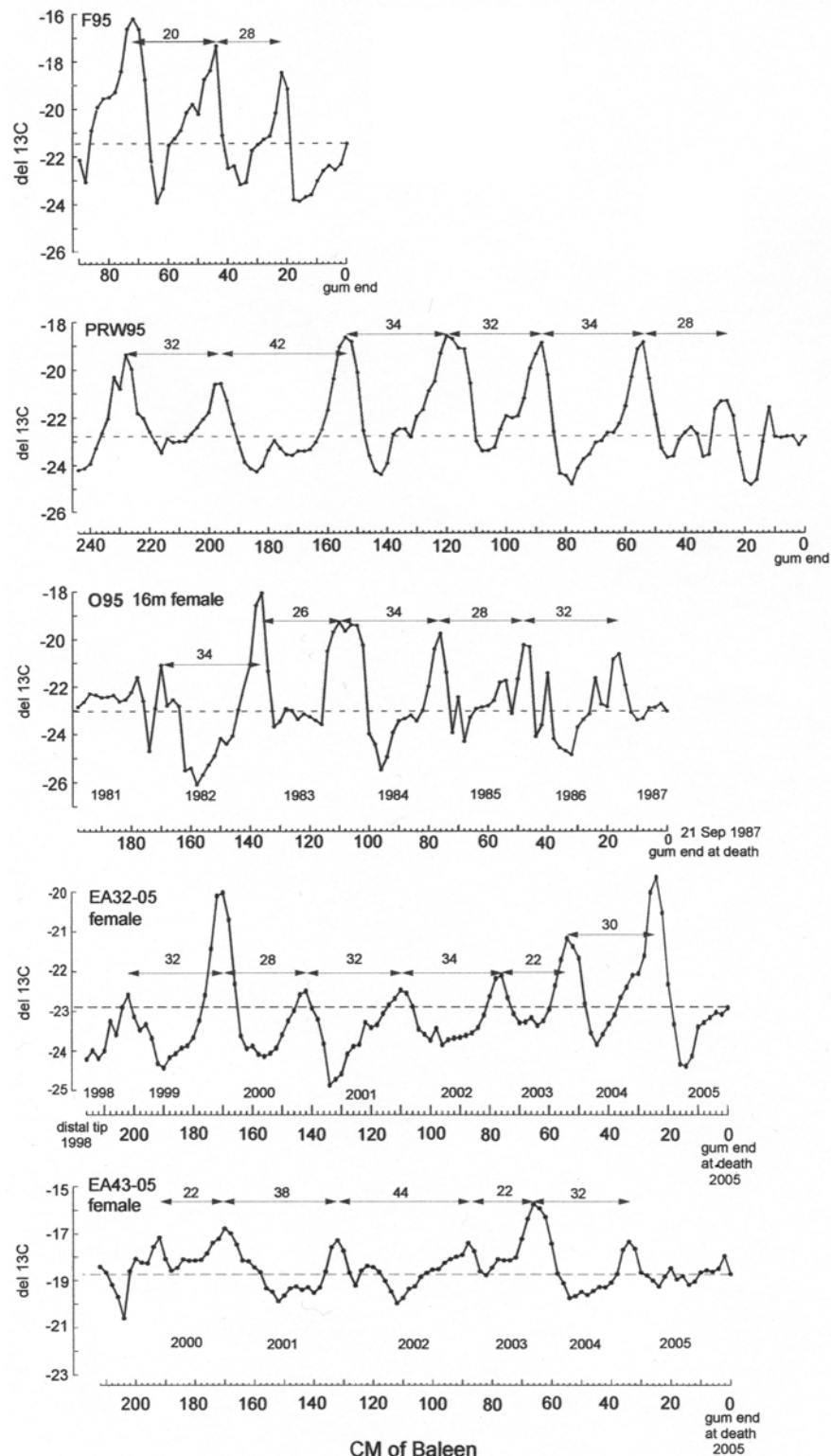


Fig. 3. Carbon stable isotope ratios ($\delta^{13}\text{C}$) along baleen plates from five southern right whales. The horizontal axes represent centimetres from the base of each plate, increasing from right to left so that time runs in the familiar sense from left to right. The vertical axes cover different ranges of $\delta^{13}\text{C}$, so as to maximize the visibility of the record for each individual whale. The dashed lines indicate $\delta^{13}\text{C}$ values at the base of each plate, representing the isotopic signature when the whale died at Peninsula Valdés.

RESULTS AND DISCUSSION

Regular but variable cycles in the $\delta^{13}\text{C}$ values of Patagonian right whale baleen. Fig. 3 summarizes the observed carbon isotope ratios at 2-cm intervals along each of the five baleen plates analyzed. Most $\delta^{13}\text{C}$ cycles show four distinct features or landmarks: (1) the initial peak; (2) the low point at the bottom of the trough; (3) a region where $\delta^{13}\text{C}$ remains roughly constant at an intermediate value, just before the final peak; and (4) the final peak, which is the initial peak of the next cycle. We interpret landmark 3 (the plateau interrupting the rise from the trough to the final peak) as a signal of the late-winter fast, when little if any feeding occurs. Typical $\delta^{13}\text{C}$ values for these plateaus are similar to those at 0cm (at the base of the plate in the gum, representing times immediately prior to the whale's death), which is similar to the average $\delta^{13}\text{C}$ of the whale. On this interpretation, the plateau represents growth supported entirely by metabolism of stored tissue reserves (blubber, muscle, etc.) and not by any current food intake. This idea is consistent with recent research on horses. Ayliffe *et al.* (2004) suggested that the isotopic composition of a horse's developing tail-hair shaft is determined by the mixing of contributions from different carbon pools, the two most important being a 'fast' pool derived from the current diet and a 'slow' pool derived from stored muscle proteins. This implies that during starvation (fasting), the only available pool would be the 'slow' one, which would contribute carbon isotopically reflective of the animal's long-term average.

To the best of our knowledge, feeding has not been observed at Península Valdés in winter (August through September), but whales are seen skim-feeding sporadically in October. The $\delta^{13}\text{C}$ values of prey (euphausiids and mysids) collected in October in the paths of skim-feeding whales at the Península ranged from -19.2 to -17.8‰ , which is the high end of the range in $\delta^{13}\text{C}$ values for the Patagonian Shelf (-18 to -23‰) (Fig. 2). Shortly after the first peak in a cycle, $\delta^{13}\text{C}$ values drop steeply to their lowest levels. Whales with extremely low values of $\delta^{13}\text{C}$ in their baleen are inferred to be feeding in colder waters south of the Polar Front where prey values range from -27 to -33‰ (Fig. 2). Tormosov *et al.* (1998) report that right whale stomachs contained mostly krill south of 50°S and were most full in summer (January through March).

Baleen growth. Averaged over all years and all whales, the mean baleen growth per cycle was 31cm (sd 5.81cm) with a range of 22–44 cm. PRW95 had the highest mean growth rate (33.7cm/cycle) and F95 had the lowest (25cm/cycle), but there was no indication of any real difference among the whales in the average rate of growth ($P=0.47$). However, the distances between peaks in the baleen of any given individual vary considerably. These distances tend to be larger in years with lower minimum $\delta^{13}\text{C}$ values, implying that the whale obtained relatively large amounts of food from the southern part of its range. A regression model with 'whale' as a factor (ANCOVA) explains more than half of the variance in apparent yearly baleen growth and is highly significant ($P < 0.005$), as are the separate effects of 'whale' ($P < 0.005$) and minimum $\delta^{13}\text{C}$ value ($P < 0.001$) (Fig. 5).

There are several different reasons why cycles might be of different lengths. One possibility is that baleen grows at a roughly constant rate (Best and Schell, 1996). In this case, the peaks would occur at somewhat different times of year (a month or so earlier in some years, a month or so later in others). Such variation might be caused by variation in a whale's foraging schedule. For example, nursing mothers are known to stay at Península Valdés longer than resting or weaning mothers. Similarly, if a whale found that prey were still unusually abundant late in the season at the southern end of its range, then it might decide to feed there for an extra month or two. The resulting accumulation of light carbon in the whale's tissues might then delay the occurrence of the subsequent (post-fasting) peak, by diluting the high- $\delta^{13}\text{C}$ signal acquired from spring feeding at northern latitudes. Thus the distance between successive $\delta^{13}\text{C}$ peaks in the whale's baleen might be increased without any real increase in the rate of baleen growth.

An alternative hypothesis is that baleen grows faster when a whale is foraging on highly abundant or nutritious prey and when it is relatively free from stresses caused by reproduction or disease, and conversely, that baleen tends to grow more slowly when a whale is subject to nutritional or other stresses, including fasting. The pattern illustrated in Fig. 5 is consistent with this interpretation, as well as with the previous one. More data and other kinds of analyses will be needed to evaluate the relative importance of these two effects. For example, the constant-growth-rate/variable-peak-time effect is predicted to cause a distinctive pattern of apparent compensations in the lengths of successive cycles. In either case, the isotopic peaks can be taken to represent the beginnings and ends of *approximately* annual cycles.

Fig. 6 shows the same information as Fig. 3, but with all the cycles for each whale superimposed to highlight the form and extent of year-to-year variation in growth and carbon isotope ratios. Each yearly cycle begins at the highest $\delta^{13}\text{C}$ value (0 cm on the horizontal axis). The vertical axis in Fig. 6 is the same for all whales, so as to facilitate comparison of their foraging ranges. Ea43-05 shows a notably high mean value of $\delta^{13}\text{C}$ and a notably narrow range of values, indicating that it fed almost exclusively in warmer waters. The whales with broader ranges show very different minimum $\delta^{13}\text{C}$ values in different years.

Fig. 4. Measurements extracted from the stable isotope ratio traces shown in Fig. 3. Arrows and the ellipse highlight the positions and dimensions of features discussed in the text.

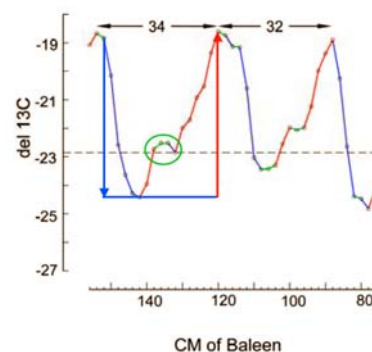


Fig. 5. Dependence of yearly cycle length (apparent baleen growth) on the lowest carbon isotope ratio seen within that year. Whales are treated as factors in this analysis of covariance (ANCOVA), and are therefore fitted to lines with the same slope but different intercepts.

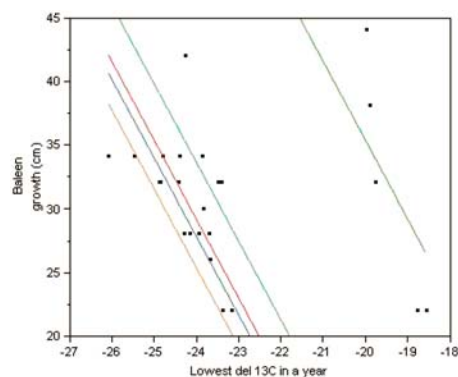


Fig. 6. Superimposed yearly carbon isotope cycles for each whale. The peak beginning each cycle is set to 0 cm on the horizontal axis. Years are identified by numbers, and are drawn in different colors.

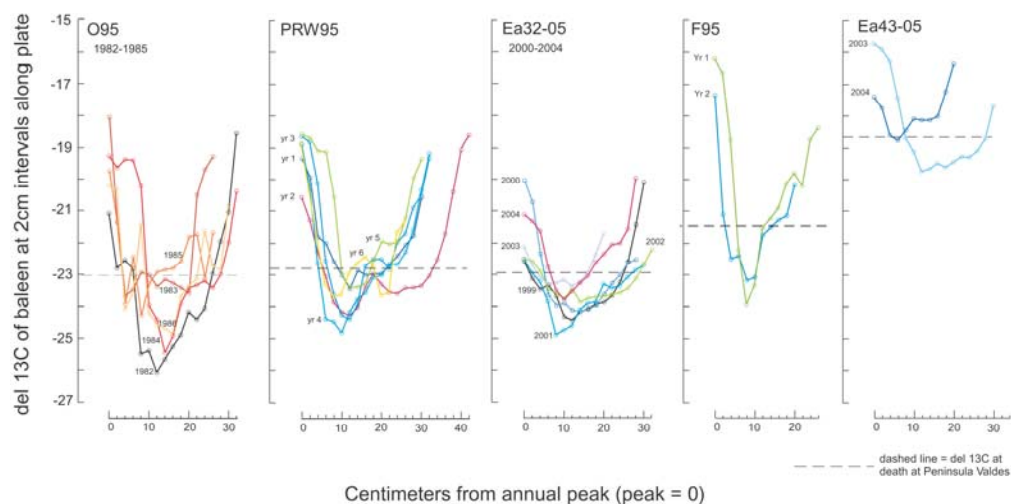
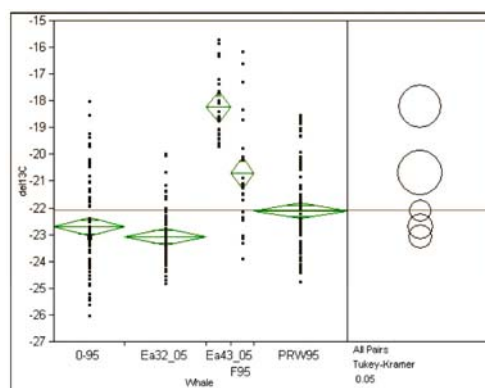


Fig 7. Overall distributions of $\delta^{13}\text{C}$ for the samples taken from each whale. Ea43-05 and F95 have means that are formally significantly higher than those of the other three whales, but this result should be viewed with some caution because there are several senses in which baleen samples from the same whale (especially those separated by only a few centimetres) are not independent of each other.



Mean and range of $\delta^{13}\text{C}$ in individual whales. The distributions of all sampled $\delta^{13}\text{C}$ values for each whale are compared in Fig. 7. Ea 43-05 and F95 had higher mean $\delta^{13}\text{C}$ values than the three other whales and their means also differ significantly from each other ($P < 0.05$) if the samples taken from a single baleen plate are viewed as statistically independent of each other. (For some purposes this makes sense, but for others it clearly does not.) There were no significant differences between the mean $\delta^{13}\text{C}$ values of the other three whales. Ea43-05 and F95 appear to have spent more time feeding on prey with higher $\delta^{13}\text{C}$ values than the other three whales, probably on the Patagonian Shelf or other low-latitude sites. The average annual isotopic ranges of individuals (highest minus lowest $\delta^{13}\text{C}$ values within each year) also vary significantly (6.78‰ for F95, 5.70‰ for O95, 5.11‰ for PRW96, 3.00‰ for Ea32-05 and 2.72‰ for Ea43-05; $P < 0.0001$). The whales with apparently narrow foraging ranges both died in 2005, while the three with much broader ranges all died before 1995. No conclusions can be drawn from this pattern given the very small number of individuals, but it shows that if secular changes in foraging patterns were to occur, then this technique could be used (even retrospectively) to detect them.

Speed and direction of migrations. For the purpose of this analysis, a whale was considered to be ‘migrating’ when $\delta^{13}\text{C}$ values changed by at least 0.25‰ between successive (2cm) samples. Total change in $\delta^{13}\text{C}$ value was defined as the difference between the highest and lowest values of $\delta^{13}\text{C}$ at the beginning (North to South) and the end (South to North) of each cycle. The time required to make that change was estimated as the baleen growth (cm) during the ‘migration’ (as defined in the first sentence) between the highest and lowest values of $\delta^{13}\text{C}$. Because cycles varied in total length, distance along the baleen plate was converted to apparent ‘time’ by assuming that a given cycle represented 52 weeks, and apparent rates of ‘movement’ were estimated (for each 2cm sampling interval) in units of change in $\delta^{13}\text{C}$ per ‘week’.

The average rate of change on the way down (from the highest to lowest values of $\delta^{13}\text{C}$) is much higher than the rate on the way up (0.3‰ per week on the way down *versus* 0.2‰ per week on the way up), and this difference is formally significant ($P < 0.01$). This contrast suggests that after the whales have fed on the Patagonian Shelf, they rapidly change to feeding on prey with much lower $\delta^{13}\text{C}$ values and then return more slowly to feed on prey in warmer waters with higher $\delta^{13}\text{C}$ values. Given that krill densities are highest in summer, that swarms occur only south of 50°S (Atkinson *et al.*, 2004) and that the Península Valdés right whales appear to be krill dependent, it is likely that after feeding on the Patagonian Shelf some of the whales travel south to feed on krill as they become more abundant in January. The slower return to higher values of $\delta^{13}\text{C}$ may indicate feeding along the way and/or a reduction in prey availability as winter approaches. To distinguish among these possibilities will require the development of additional markers that can be used in combination with carbon isotopes to more precisely identify the feeding locations of individual whales.

CONCLUSIONS

Carbon isotope analysis along baleen plates can provide insight into the foraging ecology of baleen whales. Southern right whales at Península Valdés appear to have three different foraging (and migratory) strategies. Some whales (*e.g.*, Ea32-05 and Ea43-05) show cycles that have relatively small isotopic ranges, but the mean of one of these whale’s range was low (Ea32-05) and the mean of the other’s range was high (Ea43-05). Ea43-05 apparently migrated north of Península Valdés to lower latitudes where food is isotopically depleted in ^{13}C ; data on stable nitrogen isotopes (not shown) indicate that Ea43-05 may have consumed food that is isotopically very similar to prey collected off Uruguay. A third group of whales (*e.g.*, F95, PRW95 and O95) appear to use feeding grounds spread over larger distances, as evidenced by their very large isotopic ranges, at least in some years.

Future applications. When we understand better how to interpret the apparent variation in baleen growth rates from year to year in individual animals, and when we also better understand the meaning of year-to-year variation in carbon isotope profiles, then we are likely to have a very sensitive indicator of the effects of environmental fluctuations on health and reproduction of right whales. These may provide insights into the flexibility of animals confronted with reductions of food abundance due to global warming. Furthermore, a baleen plate from a right whale calf contains information from the time the plate began development *in utero*, and it represents, isotopically, the region where the mother was feeding before giving birth. Comparing the carbon isotopes from calves born in years with high and low krill abundances will provide evidence of the ways in which pregnant females adapt to years of low krill abundance.

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