



Short Communication

Intra-specific trophic variation in false killer whales (*Pseudorca crassidens*) from the southwestern South Atlantic Ocean through stable isotopes analysis

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ABSTRACT

The false killer whale (*Pseudorca crassidens*) is a highly social top predator difficult to study in the wild because of its wide-ranging oceanic habits. Mass strandings offer good opportunities to gather ecological information about cetacean species. In this study we analyze a possible isotopic ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) variation in bone collagen among individual false killer whales that mass stranded on the south shore of the Strait of Magellan, Chile, in 1989, in relation to their ontogenetic classes, sex and total body length. We found an isotopic enrichment in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from young and smaller to older and larger individuals, respectively. These isotopic shifts may reflect differences in foraging and diving capabilities, enabling older and larger individuals to feed more deeply in the water column and/or on larger prey. The lack of isotopic differences between females and males may suggest little evidence for sex-related resource partitioning in this group, as result of a possible coordination during feeding activities, e.g. food sharing as previous studies have found. We also found an important isotopic effect of lactation in both the carbon and nitrogen isotope composition of nursing calves, probably due to a prolonged nursing period (from 19 months to two years). This study integrate ecological information from several years to lifetime in relation to sex and total body length, obtaining information on possible changes linked to the development of foraging capabilities in false killer whale.

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The false killer whale, *Pseudorca crassidens*, can be found worldwide in tropical, subtropical and warm temperate oceans (Baird, 2002). Despite its known distribution, this species usually does not range beyond 50° of latitude in both hemispheres (Stacey and Baird, 1991). In the southwestern South Atlantic Ocean its presence has been reported (as strandings) from Brazil (33°00'S, 52°40'W) to the Strait of Magellan (52°27'S, 69°31'W), Falkland (Malvinas) Islands and the Beagle Channel (54°53'S, 67°18'W) (Koen Alonso et al., 1999; Andrade et al., 2001; Zylber et al., 2002; Goodall et al., 2008).

A major problem in studying this species in the wild is because of its wide-ranging oceanic habits; thus little is known about false killer whales in the southwestern South Atlantic Ocean. Because of their extremely social behavior, false killer whales frequently

strand in large numbers (Odell et al., 1980; Stacey and Baird, 1991), offering good opportunities to gather biological and ecological information on this cetacean species.

False killer whales are known to occur in socially cohesive herds of ~20–50 animals, in which both sexes are often equally represented, but larger aggregations may also occur, associated with foraging events (Stacey et al., 1994; Baird, 2002). Stomach content analyses performed on individuals that mass-stranded along the western and southwestern South Atlantic Ocean suggest that this species may have an adaptable foraging behavior. Depending on location, stomach contents have included coastal fish (e.g. Serranidae and Scianidae, Pinedo and Rosas, 1989); epipelagic squids (e.g. *Ommastrephes batramii*, Andrade et al., 2001); oceanic-neritic squids (*Illex argentinus*, *Martialia hyadesi*) and demersal-benthic fish *Macruronus magellanicus* (Koen Alonso et al., 1999).

Based on these stomach content studies, Andrade et al. (2001) suggested a possible sex-related resource partitioning (in feeding grounds or in prey selection) between males and females. Despite that gut contents are the best snapshot of what an individual have been eating recently, is not always a good reflection of truly

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individual, sexual or ontogenetic trophic differences due to widely recognized biases of this method when applied to cetaceans. Gut content can vary greatly among stranded individuals and provide data only from recent meals. In many cases prey items are regurgitated during the stranding process, and the stomach appears empty (Pierce et al., 2004). Also, differential digestion of different types of prey can result in under-representation of some common item such as soft body prey (Sheffield et al., 2001; McLeod et al., 2003). Thus, to evaluate intra-specific trophic differences, a good collection of prey items from a broad range of individuals is essential.

Nevertheless, studies on captive individuals and measurements taken at mass stranding events have shown that males became more robust than females at the same age, with higher annual food consumption (Kastelein et al., 2000; Ferreira et al., 2014). Little is known about the diving behavior of this species in the wild (Baird, 2002), but the age and size of individuals are known to influence diving capability in marine mammals. Larger bodies (larger animals) have a higher oxygen storage capacity in blood and muscle, allowing better diving capabilities, enabling them to search for larger prey in deeper water and/or spend more time in apnea during diving in the wild (Noren et al., 2001). Also, the limited diving capacity of young dolphins may influence their foraging behavior, not only of newly weaned calves but also of females accompanied by calves (Noren et al., 2002). Thus, differences in physiology, energetic requirements and hunting experiences within different age and sex classes may result in resource partitioning, e.g. different patterns of diet and/or habitat use, as has been observed in other species of marine mammals (e.g. Drago et al., 2010; Orr et al., 2011; Riccialdelli et al., 2013; among others).

Stable isotope analysis (SIA) of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) has proven to be a valuable tool for determining a wide variety of trophic aspects of the ecology of animal taxa along present and historical contexts (e.g. Kelly, 2000; Koch, 2007; Michener and Kaufman, 2007). Indeed, intraspecific trophic differences among age and sex classes have been successfully studied through SIA (e.g. Knoff et al., 2008; Valenzuela et al., 2010; Riccialdelli et al., 2013, among others). Isotopic composition of consumer tissues reflects the composition of their food (e.g. milk for purely lactating and prey for weaning individuals) plus a trophic discrimination factor ($\sim 0\text{--}2\text{‰}$ for $\delta^{13}\text{C}$ and $\sim 2\text{--}5\text{‰}$ for $\delta^{15}\text{N}$) (DeNiro and Epstein, 1978, 1981; Minagawa and Wada, 1984; Fogel et al., 1989). Therefore, by analyzing the isotopic composition of false killer whale tissues from stranded individuals, we can evaluate possible dietary shifts that may occur as animals mature, e.g. from nursing periods to independent foraging, as well as diet differences attributed to physiology or morphology (Newsome et al., 2010; Orr et al., 2011). Bone collagen has a slow (multi-year) turnover rate and represents a long-term integrator of ecological information, which has its advantages in determining long-term resource and habitat use in marine mammals. Thus, its isotope values are not influenced by periodic (seasonal) or sporadic fluctuations in resource or habitat use (Koch 2007). Because of this, bone collagen is a useful tissue in order to compare the main trophic behavior between sex and ontogenetic classes.

In order to better understand the trophic ecology of this species in this area, we investigated a possible isotopic ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) variation among individual false killer whales that mass stranded along the southern shore of the Strait of Magellan in 1989, in relation to ontogenetic classes, sex and total body length. We hypothesize that (1) isotopic differences between nursing calves and older classes are related to the isotopic effect of lactation. We expected to measure low $\delta^{13}\text{C}$ values in calves due to the high lipid content in the ^{13}C depleted milk and high $\delta^{15}\text{N}$ values in respect to adult individuals, since the calf is actually feeding on breast milk with similar isotopic compositions to their mother's tissues (Fogel et al., 1989), and (2) isotopic differences between

age and sex classes are related to differences in foraging habits that result in resource partitioning, probably due to body size and diving capabilities. In general, body size and isotope values are positively correlated for several prey species (e.g. squid, Cherel and Hobson, 2005); thus an individual false killer whale that is feeding deeper in the water column and/or on larger prey is expected to have enriched ^{13}C and ^{15}N compositions in its tissues.

We analyzed bone cranial samples of 29 individual false killer whales from the mass-stranding event that occurred along the Strait of Magellan in 1989 (Goodall et al., 2008). The specimens sampled are held in the Museo Acatushun de Aves y Mamíferos Marinos Australes (RNP Goodall collection), Estancia Harberton, Tierra del Fuego (Argentina).

The data on sex and total body lengths (TBLs) were determined by external examination during the field necropsy. Sexual maturity was determined by TBL or the presence of fetuses. For southern stocks, body lengths at birth are about 155 cm, and both sexes appear to reach sexual maturity between 8 and 14 years, with a body length of 325 cm in females and >360 cm in males (Ferreira et al., 2014). Although weaning was not recorded, calves may begin eating solid food between six to eight months of age and lactate for 19–24 months (Clark and Odell, 1999).

Based on the average TBLs at attainment of sexual maturity of southern stock animals, two individuals analyzed that measured 332 and 360 cm were classified as subadult males, and 24 were classified as adults. One pregnant female lacked a TBL measurement, but for its gestational stage it was obviously sexually mature. The other adult females ranged from 404 to 448 cm ($n = 13$) and adult males ranged from 491 to 548 cm ($n = 10$). Three of the individuals analyzed were classified as nursing calves, based on a combination of (a) their TBLs, that ranged from 207 to 253 cm; (b) the state of physical maturity for two of this individuals (PhM = 0, fetus or neonates, with at least some neural spines unfused to the centra, according to Goodall et al., 1988) and lastly (c) the estimated age for the larger one (0–1 year old, age estimated by ACM Schiavini and EA Crespo, pers. comm.). The individuals classified in this study as subadult were probably maturing. However, the isotopic composition of bone collagen is derived from food assimilated over a period of time that depends on the turnover rate of the tissue. Bone collagen, due to its slow isotopic turnover, integrates ecological information over several years, five to ten years depending on the ontogenetic stage of the animal (Hirons et al., 2001; Koch, 2007), thus SIA on subadult individuals gives us information on their foraging behavior prior to this stage. Also, the superior preservation qualities of bone in comparison to soft tissues (skin, muscle) allow for a post-mortem assessment of the ecological characteristics at the individual level (Hare et al., 1991; Newsome et al., 2010).

Bone samples were treated according to Riccialdelli et al. (2010); during this procedure each sample was demineralized in an 0.2 N HCl solution for ~ 96 h and then lipid extracted with a 2:1 chloroform:methanol solution. The collagen extraction was dried in an oven at 60°C for ~ 48 h. Results are expressed in delta notation (δ) using the equation:

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

where R_{sample} and R_{standard} are the $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$ ratios of the sample and standard, respectively. The standards are Vienna-Pee Dee Belemnite limestone (V-PDB) for carbon and atmospheric N_2 for nitrogen. The units are expressed as parts per thousand or per mil (‰). The within-run standard deviation (SD) of an acetanilide standard was $\leq 0.2\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

We assessed isotopic variation for false killer whales in relation to ontogenetic class (calves, subadult and adult individuals), sex and TBLs. Due to the small sample size of our data set we use a

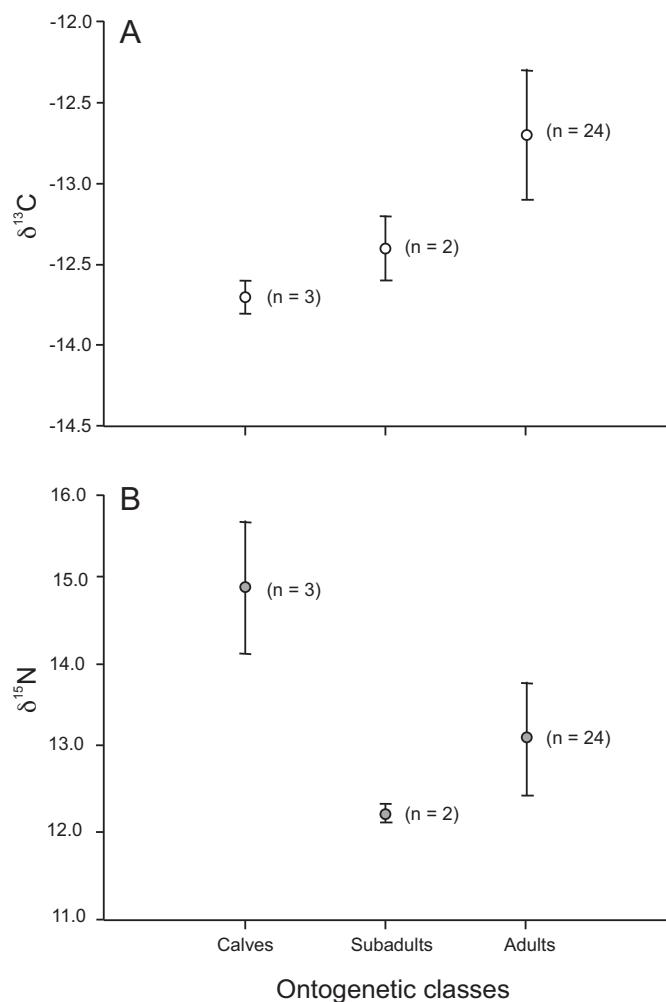


Fig. 1. Mean bone collagen $\delta^{13}\text{C}$ (A) and $\delta^{15}\text{N}$ (B) values of calves, subadult and adult false killer whales (*Pseudorca crassidens*). Error bars represent standard deviation (SD), number in parenthesis represent sample size (n).

non-parametric Mann–Whitney test (*U* test) to test for categorical differences in isotope values and Levene's test was used to test homogeneity of variance. We also evaluated a possible relationship between the isotopic variability found in false killer whale individuals with TBLs through Spearman rank correlation coefficient (r_s , Spearman correlation coefficient) using all individuals except nursing calves. For all calculations, we tested significance at the $\alpha = 0.05$ level.

The bone collagen from the 29 individual false killer whales analyzed had a mean (\pm SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of -13.0‰ ($\pm 0.6\text{‰}$) and 13.6‰ ($\pm 1.6\text{‰}$), respectively, with a mean C:N of 2.8 (± 0.1) indicative of pure protein (Ambrose, 1990) (see Electronic Appendix 1).

Due to very small sample sizes of calves and subadults we only provide descriptive comparisons in relation to the isotopic results of the ontogenetic classes. An important enrichment in ^{13}C content from calves to adult class can be observed (Fig. 1). Calves showed the lowest mean $\delta^{13}\text{C}$ values among the classes, with mean differences of 0.3‰ and 1.0‰ , with respect to subadults and adults, respectively. Also, subadult animals had a mean difference of 0.7‰ with adult individuals. $\delta^{15}\text{N}$ values were also different between ontogenetic classes. Calves showed an enrichment of 2.8‰ and 1.9‰ in $\delta^{15}\text{N}$ values with respect to subadults and adults, respectively, whereas subadult individuals had lower mean $\delta^{15}\text{N}$ values respect to adults (mean difference of 0.9‰) (Fig. 1).

Sex classes were only compared in adult individuals due to the small number of individuals of different sexes in younger classes (calves and subadults). We did not find any statistical difference between adult females and adult males in $\delta^{13}\text{C}$ (*U*-test, $p = 0.23$) or $\delta^{15}\text{N}$ values (*U*-test, $p = 0.06$). Also, isotopic variances did not differ significantly (Levene's test = 0.58 , $p = 0.453$ for $\delta^{13}\text{C}$ and Levene's test = 0.32 , $p = 0.578$, for $\delta^{15}\text{N}$).

We found a significant positive correlation between TBLs and $\delta^{13}\text{C}$ values ($r_s = 0.464$, $p = 0.01$, $n = 25$). There was also a significant positive correlation between TBLs and $\delta^{15}\text{N}$ values ($r_s = 0.471$, $p = 0.01$, $n = 25$) (see Electronic Appendix 2).

It should be noted that the data set analyzed in this study is low, especially for calves and subadults, and also that bone collagen integrates diet over a long time scale and may mask short-term dietary shifts (Hedges et al., 2005). Nevertheless, we found isotopic differences between classes, which are likely due to individual dietary variation. The diet of nursing individual false killer whales (e.g. milk) differs greatly from that of subadult and adult animals. The isotopic differences found between calves and older individuals reflect the isotopic effect of lactation expected for both isotope values. This effect was also observed in other mammalian species, such as bottlenose dolphins, killer whales, Commerson's dolphins (Knoff et al., 2008; Newsome et al., 2009; Riccialdelli et al., 2013), otariids (Newsome et al., 2006; Orr et al., 2011) and even humans (Fogel et al., 1989). A large variability in isotope fractionation between mothers and offspring may occur, which is influenced by many factors, e.g. the lactation period, the lipid content of the milk, and the tissue analyzed, among others (Jenkins et al., 2001; Valenzuela et al., 2010). For $\delta^{13}\text{C}$ values, we found a difference between calves and adults as expected, for a mean difference in carbon isotopes of one trophic level. Also, calves had higher $\delta^{15}\text{N}$ values compared to subadult and adult individuals, respectively, but the differences was smaller than the mean difference expected ($\sim 3.4\text{‰}$) for one trophic level of nitrogen isotopes.

Botta et al. (2012) also measured enriched ^{13}C and ^{15}N values in the teeth of one nursing calf false killer whale of 165 cm that was stranded alone in southern Brazil (-13.1‰ and 19.4‰ in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively). False killer whales have a long nursing period – up to two years – and a gradual weaning period where calves start to eat solid food, which occurs between 6 to 8 months of age (Clark and Odell, 1999). A gradual shift from maternal dependency to independent foraging is concomitant with a decrease in lactation to induce weaning (Eichelberger et al., 1940), which could contribute to (1) the small differences in $\delta^{15}\text{N}$ values between the calves and older individuals and (2) the isotope differences observed between the calf measured by Botta et al. (2012) and the calves measured in this study, since they seemed to have had different ages due to their total body length.

Polito and Goeble (2010) have found that the isotope composition of milk secreted by mothers reflects dietary intake during nursing periods in marine mammals (e.g. Otariids). Also, a gradient in isotope baseline values (e.g. particulate organic matter or plankton) measured along longitudinal and latitudinal regions (Goerike and Fry, 1994; Lara et al., 2010) can cascade up food webs to top marine consumers (Best and Schell, 1996; Graham et al., 2010). Thus differences in isotope values measured in calves can also be influenced by a combination of differences in prey selection by their mothers and/or the effect of isotope baseline differences, if foraging grounds remain distant during the nursing period.

Despite of the small sample size ($n = 2$) for subadults, we found differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and a positive trend in both isotope values with TBLs. Different foraging habits, probably associated with diving capacities, hunting skills or prey preferences between the classes analyzed, may be possible explanations for these differences. The isotopic composition of the potential input

(e.g. fish and squids) may vary depending on the species and/or size of the individual prey, which could also be available at different depths in the water column (e.g. Jennings et al., 2001; Cherel and Hobson, 2005). Stomach content analyses performed on adult individuals (we have no information for subadults) that we analyzed in this study has shown that they feed on a variety of species of squids and demersal-benthic fish (Koen Alonso et al., 1999). Thus, older and larger individuals could have been feeding more deeply in the water column and/or on larger prey or even feeding on different proportions of the same prey.

In addition, for diving foraging species, the greater aerobic capacity of adult males allows them to dive longer and deeper and breathe less often while in search and attack of deep-sea prey, than that of female animals (Noren et al., 2002; Miller et al., 2010). However, in social groups of cetaceans such as mammal-eating killer whales (*Orcinus orca*), where a pronounced division of labor and cooperative hunting is known, individuals of different age and sex classes showed similar diving activities (Miller et al., 2010). False killer whales are social cetaceans that live in groups with individuals of mixed age and sex classes (Stacey and Baird, 1991) (although subadults are often missing in large herds) and food sharing has been observed in the wild (Stacey et al., 1994). Although little is known about the foraging strategies of false killer whales in the wild, the lack of isotopic differences in bone collagen between males and females may suggest similarities at least in the long-term foraging habits (e.g. type of prey consumed and foraging areas).

In conclusion, the use of stable isotopes in this study permits us to integrate the chemical signals acquired from their main inputs (milk vs. solid food), reflecting a dietary shift from nursing to mature animals. By analyzing bone collagen, a tissue with a slow turnover rate, we could also integrate ecological information from several years to lifetime in relation to sex and total body length, obtaining information on possible changes linked to the development of foraging capabilities. These results were based on the best available data and should be refined as additional data become available. In the meantime, our data could be combined in further studies with possible prey at different habitats in a latitudinal and longitudinal gradient in order to characterize this species' main diet and habitat use.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2015.01.003>

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