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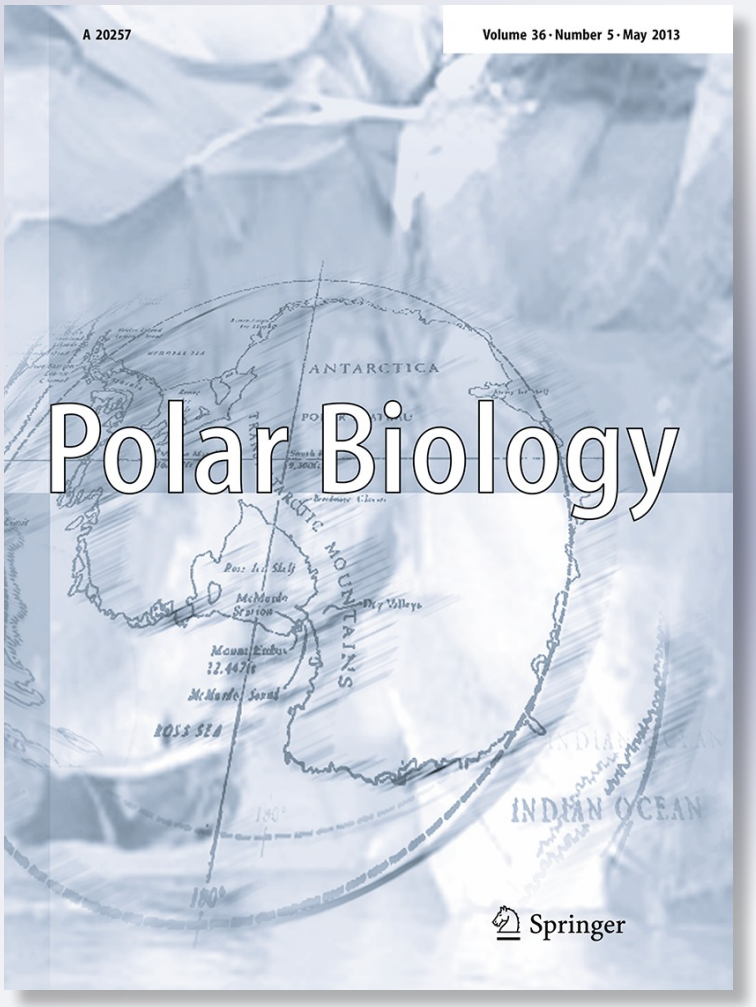

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ORIGINAL PAPER

Ontogenetic diet shift in Commerson's dolphin (*Cephalorhynchus commersonii commersonii*) off Tierra del Fuego

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Abstract The Commerson's dolphin (*Cephalorhynchus c. commersonii*, Lacépède, 1804) is the most common endemic dolphin of the coastal waters of Tierra del Fuego incidentally caught in artisanal coastal gill nets. A better understanding of its trophic ecology is essential to facilitate the effective management and conservation of its population. The aim of this study was to analyze possible shifts in diet among age and sex classes by analyzing bone collagen $\delta^{13}C$ and $\delta^{15}N$ values collected from 220 individuals along the coast of Tierra del Fuego. Additional analysis of potential prey allowed us to use a stable isotope mixing model to quantify resource use. Isotopic comparisons suggest that all age classes share the same foraging areas. We found, however, a significant dietary shift: juveniles consume a higher mean (±SD) proportion (60 ± 7 %) of pelagic *Sprattus fuegensis* than adults (36 ± 10 %), and the consumption of benthopelagic species such as *Illex argentinus* and *Loligo gahi* is higher in adults (33 ± 12 %) than juveniles (20 ± 7 %). This may result from an improvement in foraging skills and expansion of habitats in adulthood. While males move greater distances in search of mates and resources, a lack of isotopic differences between the sexes suggests little evidence for sex-related resource partitioning. A significant decrease in $\delta^{15}N$ values between calves and juveniles indicates a weaning period between 0.5 and 1 year as was shown in previous captive studies on this species. Our results also suggest that artisanal fisheries, despite being a major source of mortality, do not affect the long-term food habits of Commerson's dolphin since they showed a weak trophic overlap.

Keywords Stable isotopes · Diet · *Cephalorhynchus commersonii commersonii* · Subantarctic waters

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Introduction

Commerson's dolphin (*Cephalorhynchus commersonii commersonii*, Lacépède 1804) is one of the most common endemic dolphins in the coastal waters of the southwest South Atlantic Ocean (Goodall 1994; Garaffo et al. 2011). Along the southern margin of its distribution around Tierra del Fuego, Commerson's dolphins likely number in the thousands of individuals (Lescrauwaet et al. 2000; Pedraza 2008). This species is incidentally caught in gill nets in southern Patagonia, which is considered to be a major source of mortality and threat to the species in this region (Goodall et al. 1988, 1994; Iñíguez et al. 2003).

Commerson's dolphin appears to move seasonally in small groups (~2–10 individuals) between inshore and

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offshore habitats and make diurnal movements that coincide with those of their main prey (Goodall 1994; Pedraza 2008; Coscarella et al. 2010). Also some segregation has been proposed during certain times of the year such as after the reproduction period, with females and calves feeding in offshore areas or in coastal habitat but separated from juveniles and adults (Pedraza 2008). In general, reproduction takes place from the austral spring (September) to summer (February) (Goodall 1994; Kastelein et al. 1993a) during which females give birth to a single calf. The length of lactation in dolphins, with Commerson's dolphin being no exception, has been poorly studied in comparison with other marine mammals such as pinnipeds and baleen whales (Eichelberger et al. 1940; Oftedal 1997). While it is known that the lactation period of Commerson's dolphin lasts at least 6 months, studies of captive individuals indicate that calves can begin to eat solid food at ~2 months and by ~8–12 months nursing ceases completely (Joseph et al. 1987; Kastelein et al. 1993b). Kastelein et al. (1993b) reported that adult females vary their food intake during the lactation period. After weaning, females must increase their food consumption, and they may compete with their calves for resources if food is limited (Kastelein et al. 1993b). Thus, some have hypothesized that adults and juveniles may consume different resources as a way to reduce the possible competition between individuals (Lockyer et al. 1988; Kastelein et al. 1993b; Pedraza 2008). Despite the low rates of dispersion determined for both sexes (Pimper et al. 2010; Cipriano et al. 2011), males have greater mobility than females (Pimper et al. 2010) and therefore the possibility of the exploitation of different prey and/or habitats.

Using traditional approaches such as direct observation, stomach content and parasitological analysis, studies of the dietary preferences and variation in the seasonal abundance of Commerson's dolphins in the waters off Patagonia (Bastida et al. 1988; Berón Vera et al. 2001; Iñíguez and Tossenberger 2007; Pedraza 2008; Coscarella et al. 2010; among others) suggest that this species is an opportunistic predator that feeds primarily in coastal waters over the continental shelf on pelagic and benthic prey. In the waters off Tierra del Fuego, Commerson's diet is primarily composed of fish such as the Fuegian spratt (*Sprattus fuegensis*), Patagonian grenadier (*Macruronus magellanicus*), nototenids (*Patagonotothen tesellata*, *P. sima*, *P. cornucula*), Patagonian blenny (*Eleginops maclovinus*) and silversides (*Odonthestes* spp.). Cephalopods such as Patagonian squid (*Loligo gahi*), Argentine shortfin squid (*Illex argentinus*), red octopus (*Enteroctopus megalocyathus*) and crustaceans such as the squat lobster (*Munida gregaria*), marine crab (*Halicarcinus planatus*) and euphausids (Bastida et al. 1988; Clarke and Goodall 1994; Rosero Caicedo 2005) are also common dietary components.

Stable isotope analysis (SIA) has rapidly become a widespread technique since can evaluate the relative importance of different dietary components over time and complemented with the information raised with conventional dietary analysis offers valuable information about the foraging and trophic ecology of marine mammals (Newsome et al. 2010). The technique is based on the established relationship between the isotopic composition of a consumer's tissues and that of its prey, a process known as trophic discrimination (Cerling and Harris 1999). The isotopic differences among consumer tissues and their prey (trophic discrimination factors) are ~2–5 and 0–2 ‰ for $\delta^{15}N$ and $\delta^{13}C$, respectively (DeNiro and Epstein 1978, 1981; Minagawa and Wada 1984). This approach has been successfully used to characterize sex- or age-related resource segregation and ontogenetic dietary shifts that inform questions regarding nursing strategies and lactating periods in marine mammals (e.g., Newsome et al. 2006; Mendes et al. 2007; Newsome et al. 2009a, b; Drago et al. 2010; Young et al. 2010).

Different foraging strategies among age and/or sex classes may also produce distinctive isotope signals that provide information on the relative trophic position (Minagawa and Wada 1984), primary prey sources (DeNiro and Epstein 1978), length of the nursing period (Richards et al. 2002; Newsome et al. 2006) and general habitat preferences of individuals (Clementz and Koch 2001; Graham et al. 2010; Riccialdelli et al. 2010). Also, exploring the lactating period and weaning age through SIA could serve to indicate when calves could become potentially competitive with their parents for the consumption of the same preys. For example, isotopic differences between lactating calves and adult females have been reported in several SIA-based studies of marine mammals (e.g., Hobson and Sease 1998; Knoff et al. 2008; Newsome et al. 2009b; Valenzuela et al. 2010). In general, nursing calves have higher $\delta^{15}N$ and lower $\delta^{13}C$ values in comparison with their mothers (Fogel et al. 1989). Breast milk consists of nutrients catabolized from mother's tissues (fat and protein), thus offspring that solely consume milk appear to be feeding approximately one trophic level higher than adult females and typically have higher $\delta^{15}N$ values by ~1.5–4.0 ‰. In some cases, nursing calves also have lower $\delta^{13}C$ values than adult females, a pattern that has been attributed to the influence of the high lipid content of the marine mammal milk. Lipids have lower $\delta^{13}C$ values in comparison with other macromolecular components, such as proteins (DeNiro and Epstein 1978). Nevertheless, differences in the isotopic values between adult females and their offspring depend on many factors, including the type of tissue analyzed, the lipid content of the milk, the length of the lactation period and other physiological processes (Jenkins et al. 2001; Valenzuela et al. 2010).

The main objective of this study was to investigate intraspecific variation in the trophic habits of Commerson's

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dolphin in relation to the ontogenetic classes, sex and total body length of the individuals analyzed. First, we hypothesized that the bone collagen of nursing calves that depend entirely on milk will have higher $\delta^{15}N$ and lower $\delta^{13}C$ values than adults. Second, according to information obtained during captive studies that estimated weaning age, bone collagen from older (juvenile to adult) age classes would not show any isotopic effects of lactation. Thus, isotopic differences between older age and sex classes may be related to differences in hunting and diving capability or competition that results in habitat and resource partitioning. Since Commerson's dolphins consume some prey species targeted by coastal fisheries (*E. maclovinus* and *Odonthestes* spp.) and bycatch-induced mortality is a major threat to its population viability, the identification of primary prey and habitat preferences would be useful information for the development of management and conservation strategies for this marine mammal species in the southwestern South Atlantic Ocean.

Materials and methods

Cetacean samples

We analyzed bone collagen samples of 220 specimens of Commerson's dolphins from Tierra del Fuego. These samples were obtained from the Goodall collection at the Museo Acatushún de Aves y Mamíferos Marinos Australes, Estancia Harberton, Tierra del Fuego, Argentina. The specimens were by-caught and beach-cast along the eastern and southern coast of Tierra del Fuego (52–54° S and 68–69° W) (Fig. 1), during the years 1974–2009 as part of an ongoing long-term study (Goodall et al. 2008).

Sex

Bone fragments were sampled from 121 males, 68 females and 31 individuals of unknown sex. Sex was determined by external examination of the genital pigmentation (Goodall et al. 1988), by DNA analysis (Pimper 2010; Pimper et al. 2010) or in some cases by pelvic bone morphology; pelvic bones of males are larger and have a different shape than those of females (Goodall et al. 1988; Collet and Robineau 1988). Sex identifications obtained by morphological characters have been confirmed by DNA analysis (Pimper et al. 2009, 2010; Pimper 2010).

Age and total body length

Age was estimated for 192 specimens following the methodology described in Dellabianca et al. (2012). One growth layer group (GLG, Perrin and Myrick 1980) was assumed to represent 1 year, as in Lockyer et al. (1981, 1988) and Dellabianca et al. (2012). In addition, external measurements (e.g., total body length, TBL) were taken for each specimen at the time of the collection (Norris 1961).

Physical maturity

We also assessed the state of epiphyseal fusion of the vertebra as a level of physical maturity for 208 specimens: where 0 = fetus or neonate ($n = 24$ individuals), with at least some neural spines unfused to the centra; 1 = juvenile ($n = 27$

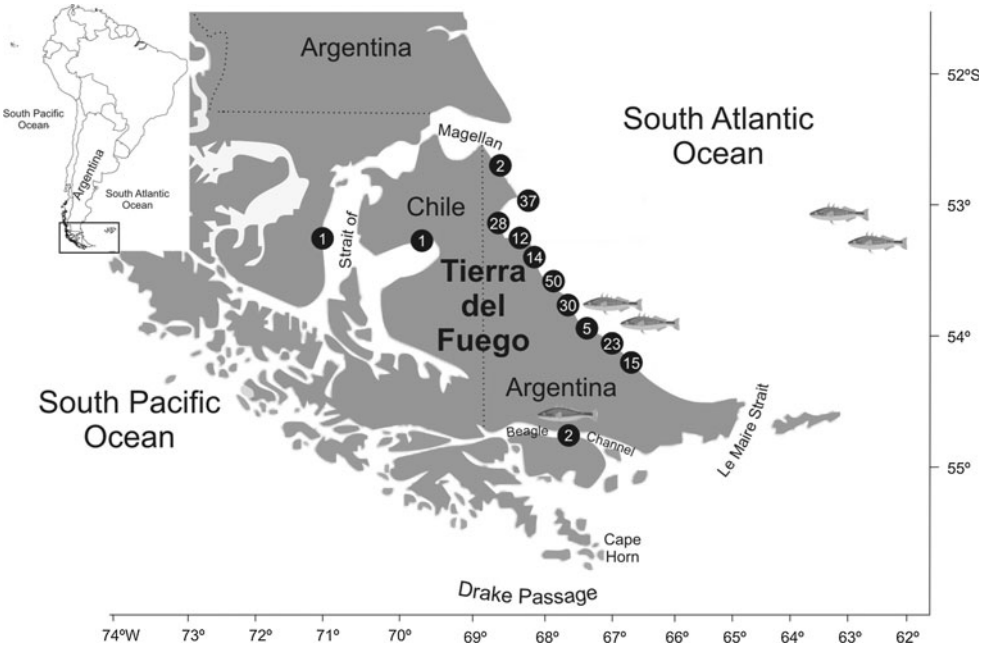

Fig. 1 Commerson's dolphin (*Cephalorhynchus c. commersonii*) bycatch/stranding (*filled circle*) and prey sampling sites (( )) in coastal areas of Tierra del Fuego, Argentina in the southwestern South Atlantic Ocean. The number of bycatch/stranding per general area is shown inside each *circle*

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individuals), all neural spines fused but epiphyses unfused to the centra; 2 = subadult ($n = 111$ individuals), some or nearly all of the epiphyses fused; and 3 = adult ($n = 46$ individuals), all epiphyses fused (Goodall et al. 1988).

Prey samples

Using stomach content dietary studies of Commerson's dolphin diet as a guide (e.g., Bastida et al. 1988; Clark and Goodall 1994; Rosero Caicedo 2005), benthic and pelagic prey were collected along the coast of Tierra del Fuego for SIA from January to May 2007 (Fig. 1). Benthic prey were obtained by hand, and pelagic prey were obtained by artisanal shore-set fixed gillnets in coastal habitats (53°57′ S–67° 27′ W/54°17′ S–66°41′ W) and from commercial fishing vessels operating in pelagic habitats (53° 09′ S–62° 48′ W) over the southern Patagonian shelf. In addition, a few items (fish bones) were sampled from the stomachs of incidentally caught dolphins. Prey species ($n = 17$) were grouped following ecological and taxonomic characteristics into 4 major types: coastal and benthic fish (*Patagonothothen ramsayi*, *P. tessellata*, *P. sima*, zoarcids, *E. maclovinus*); coastal and pelagic fish (*Odontesthes* spp., *S. fuegensis*); benthopelagic species (*M. magellanicus*, *L. gahi*, *I. argentinus*) and benthic invertebrates (*M. gregaria*, *Campylognothus vagans*, *H. planatus*, *Enteroctopus magalocyathus*, octopus unidentified).

Stable isotope analysis (SIA)

Degradation processes can rapidly change the isotopic composition of soft tissues (e.g., muscle), however, bone collagen is more resilient to degradation (Tuross et al. 1988) and has been routinely sampled from marine mammals entangled in nets or stranded on beaches. Cetacean bone and prey bone, beaks and/or muscle samples were processed and analyzed according to Riccialdelli et al. (2010). Results are expressed in delta notation (δ) using the equation:

$$\delta^{13}\mathrm{C}\ or\ \delta^{15}\mathrm{N} = \left[\left(R_{\text{sample}} \div R_{\text{standard}}\right) - 1\right] \times 1{,}000 \quad ((1))$$

where R_{sample} and R_{standard} are the ^{13}C:^{12}C or ^{15}N:^{14}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 ≤0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$ values.

Since Commerson's dolphin samples were collected from 1974 to 2009, we applied a correction factor of −0.022 ‰ year^{-1} to all sample carbon isotope values to account for the Suess effect, or the anthropogenic decrease in the $\delta^{13}C$ of atmospheric CO_2 due to the burning of fossil fuels (Francey et al. 1999; Idermühle et al. 1999).

Data treatment and statistical analysis

To evaluate isotopic changes related to ontogeny, we created five classes using a combination of the estimated age from counts of GLGs and physical maturity (PM) of each individual: (1) calves ($n = 22$) included individuals classified as neonates by PM and up to 6 month old and were possibly still nursing at the time of death (according to Kastelein et al. 1993a, b; Joseph et al. 1987); (2) juveniles ($n = 75$) included individuals classified as juveniles by PM and ranged in age from 7 months to 2 years (Kastelein et al. 1993a, b). For these first two age categories, we used PM to classify individuals that had GLG counts that assigned them to the age limits of each category; (3) subadults ($n = 22$) included individuals classified by PM and between 3 and 4 years but sexually immature (Lockyer et al. 1988); (4) first adults ($n = 44$) included individuals classified by PM as subadults between 5 and 8 years of age and probably sexually mature or in the process of maturing (Lockyer et al. 1988); and (5) adults ($n = 29$) included individuals classified as subadults and adults by PM and >8 years of age and sexually mature (Lockyer et al. 1988).

We assessed isotopic variation for Commerson's dolphin in relation to sex and ontogenetic class. A Kolgomorov–Smirnov test (K–S test) was used to test normality for the two variables ($\delta^{13}C$, $\delta^{15}N$) for each category. An F test (Levene's test) was used to test homogeneity of variance. One-way ANOVAs and pairwise comparisons using a Student's t test were performed when data met parametric requirements; otherwise, a non-parametric Kruskall–Wallis (H test) and Mann–Whitney test (U test) were used for to test for categorical differences in isotope values. We analyzed possible differences in variance $\delta^{13}C$ and $\delta^{15}N$ among age and sex defined groups using an F test. The estimated ages of the specimens ($n = 192$) ranged between 0 and 18 years with TBLs between 64 cm and 148 cm ($n = 188$). Since foraging habits may change once Commerson's dolphins start consuming solid food, we evaluated a possible correlation between the isotopic variability of individual dolphins with age and TBL through Pearson (r) and Spearman rank correlation coefficients (ρ, Spearman rho coefficient), using all individuals except for nursing calves. For all calculations, we tested significance at the $\alpha = 0.05$ level. Differences in the isotopic composition of prey types were assessed using the same statistical methods as those used to examine cetacean isotope data.

SIAR

We used Stable Isotope Analysis in R (SIAR, Parnell et al. 2010) to quantify differences in the relative consumption of

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prey types by ontogenetic classes; calves were excluded from the analysis because they do not consume solid foods. We quantified diet proportions for each individual dolphin and used the mean (SD) isotope values of different prey groups. Since we analyzed different types of prey tissues (bone, beaks, muscle), we had to account for tissue-specific discrimination (TSD), so prey data could be directly compared to cetacean bone collagen. The model does not account for TSD, so we applied a correction of +4.0 ‰ in $\delta^{13}C$ to account for TSD only for prey muscle, since bone and beaks samples only need a correction for trophic enrichment; also no correction for TSD is required for $\delta^{15}N$ (Hare et al. 1991; Hedges et al. 2005). Trophic discrimination factors (and variance) can be incorporated in the model. To account for trophic discrimination, we applied trophic discrimination factors of 1.0 ‰ (0.5 ‰ SD) and 3.4 ‰ (0.5 ‰ SD) for $\delta^{13}C$ and in $\delta^{15}N$ respectively (Minagawa and Wada 1984; Newsome et al. 2010).

Results

Commerson's dolphin samples

Bone collagen from 220 individuals had mean (±SD) $\delta^{13}C$ and $\delta^{15}N$ values of −13.3 ‰ (±1.2) and 17.4 ‰ (±1.0) respectively, with mean C:N ratios of 2.9 (±0.2) indicative of pure protein (Ambrose 1990). Cetacean isotope results are summarized in Table 1 and are presented in Figs. 2 and 3.

Ontogenetic classes

We did not find significant differences in mean $\delta^{13}C$ values between the ontogenetic classes ($F = 2.31$, $p = 0.06$; Table 1). $\delta^{15}N$ values were significantly different among ontogenetic classes ($H = 41.44$, $df = 4$; $p < 0.001$). Specifically, calves had significantly higher $\delta^{15}N$ values than other ontogenetic classes, with differences of +1.8, +1.9, +1.6 and +1.3 ‰ with juvenile, subadult, first adult and adult individuals, respectively. Also, juveniles had significantly lower $\delta^{15}N$ values than adults (U test; $p = 0.001$). Subadults had significantly lower $\delta^{15}N$ values than first adults and adult individuals (U test; $p = 0.047$ and $p = 0.001$ respectively); see Table 2A for pairwise comparisons. Lastly, ontogenetic classes did not differ significantly in $\delta^{13}C$ variance (Levene's test = 1.795, $p = 0.132$), but calves showed a significantly higher variation in $\delta^{15}N$ values (Levene's test = 8.594, $p = 0.001$) than older age classes.

Table 1 Mean $\delta^{13}C$ and $\delta^{15}N$ values (±SD) of bone collagen of Commerson's dolphins off Tierra del Fuego

Group	$\delta^{13}C$ (± SD)	$\delta^{15}N$ (± SD)	N	C:N
Ontogenetic classes				
Calves	−13.5 (1.3)	18.9 (1.4)	22	2.9
juveniles	−13.5 (1.1)	17.1 (0.7)	75	2.9
Subadults	−13.3 (1.3)	17.0 (0.5)	22	2.9
First adults	−13.3 (1.1)	17.4 (0.7)	44	2.9
Adults	−12.7 (1.7)	17.6 (0.7)	29	2.9
Sex				
Females	−13.3 (1.2)	17.3 (0.9)	68	2.9
Males	−13.3 (1.3)	17.4 (0.8)	121	2.9

N number of individuals analyzed. C:N ratio. Mean $\delta^{13}C$ values are shown corrected for Suess effect

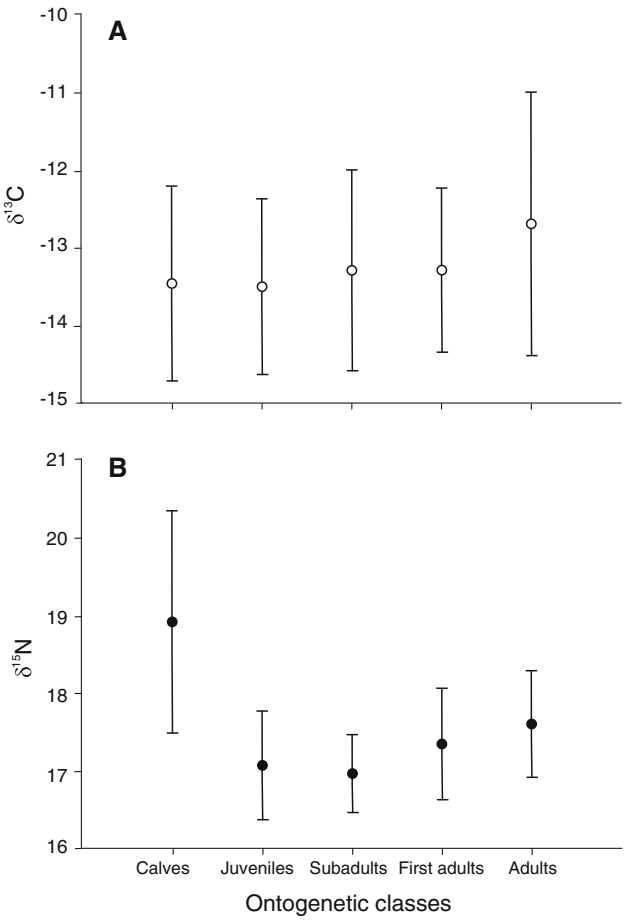

Fig. 2 Mean bone collagen $\delta^{13}C$ (**a**) and $\delta^{15}N$ (**b**) values of different ontogenetic classes of Commerson's dolphins; *error bars* represent standard deviation (*SD*)

Age and total body length

Using Pearson and Spearman rank correlation coefficients, we found a significant positive correlation between estimated ages and both isotope values ($r = 0.212$, $p = 0.005$

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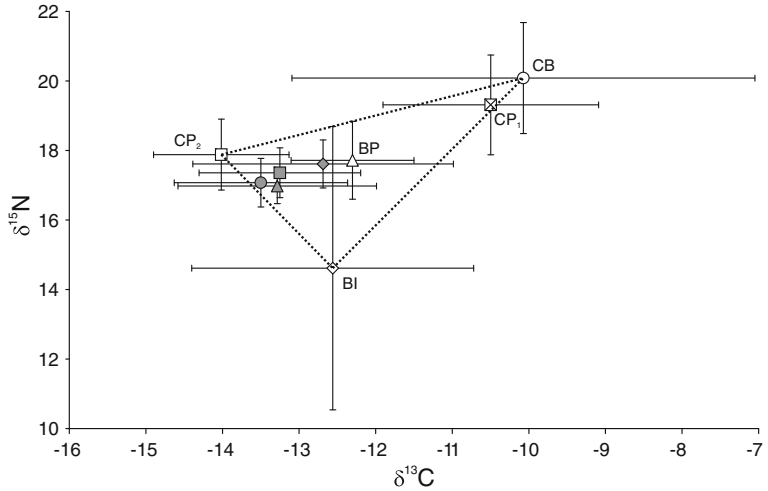

Fig. 3 Mean $\delta^{13}C$ and $\delta^{15}N$ values for ontogenetic classes and potential prey; *error bars* represent SD. Ontogenetic classes include data for juveniles (*filled circle*), subadults (*filled triangle*), first adults (*filled square*) and adults (*filled diamond*). Prey types include coastal and benthic fish (CB—*open circle*), coastal and pelagic fish (CP_1—*square with cross*, CP_2—*open square*), benthopelagic species (BP—*open triangle*), benthic invertebrates (BI—*open diamond*). Mean prey isotope values have been corrected for tissue-specific and trophic isotopic discrimination by adding 5 ‰ to $\delta^{13}C$ and 3.4 ‰ to $\delta^{15}N$ values of muscle and whole body samples and +1 ‰ in $\delta^{13}C$ and +3.4 ‰ to $\delta^{15}N$ values of bone and beak samples

for $\delta^{13}C$ values and $\rho = 0.24$, $p = 0.001$ for $\delta^{15}N$ values, $n = 170$). We also found a small but significant positive correlation between $\delta^{15}N$ values and TBLs ($r = 0.215$, $p = 0.005$, $n = 171$).

Sex

Males ($n = 121$) had mean (±SD) $\delta^{13}C$ values of −13.3 ‰ (±1.3) and mean $\delta^{15}N$ values of 17.4 ‰ (±0.8). Females ($n = 68$) had mean $\delta^{13}C$ values of −13.3 ‰ (±1.2) and mean $\delta^{15}N$ values of 17.3 ‰ (±0.9). Without discriminating by ontogenetic class, we did not find any statistical differences between male and female individuals in $\delta^{13}C$ (t test = −0.41, $df = 149$, $p = 0.684$) or ^{15}N values (U test, $p = 0.367$). Isotopic variance did not significantly differ between the sexes ($\delta^{13}C$: Levene's test = 0.027; $p = 0.871$; $\delta^{15}N$: Levene's test = 2.376, $p = 0.125$). In addition, comparison between sexes in the same ontogenetic class did not show any significant difference in mean $\delta^{13}C$ or $\delta^{15}N$ values (t test, $p > 0.05$ for all comparisons and U $\text{test}_{\text{FvsM}}$, $p = 0.274$ for juvenile $\delta^{13}C$ values). In addition, we found no differences in isotopic variation among ontogenetic classes, except in juveniles where males had higher variation in $\delta^{13}C$ values than females ($F_{\text{FvsM}} = 0.445$, $p = 0.02$).

Prey

Prey isotope results are presented in Fig. 3 and summarized in Table 3. After application of trophic and tissue-specific discrimination corrections (see "Materials and methods"), prey groups showed significant differences in both $\delta^{13}C$ ($H = 33.64$, $df = 4$, $p < 0.001$) and $\delta^{15}N$ values ($H = 44.53$, $df = 4$, $p < 0.001$). In particular, coastal and pelagic fish were divided into two groups, CP1 (*Odontesthes* spp.) and CP2 (*S. fuegensis*) because these species had significantly different isotopic values (see Table 2B for pairwise comparisons). Thus, the 4 original prey groups became 5 potential prey sources for input into the SIAR models. Also, prey groups showed significant differences in $\delta^{13}C$ variances (Levene's test, $p = 0.000$), specifically between coastal and benthic fish and the rest of the prey groups (Levene's test, $p < 0.01$) and CP1 with benthopelagic species (Levene's test, $p = 0.007$), but we found similar variances in $\delta^{15}N$ values among all prey groups (Levene's test = 2.132, $p = 0.083$).

SIAR

The stable isotope mixing model used in this study defined two main prey groups for Commerson's dolphins, *S. fuegensis* (CP2) a coastal and pelagic fish, and benthopelagic (BP) species as the second most important prey, but the relative consumption of these prey change as a function of age class. The consumption of CP2 relative to BP decreases significantly from juvenile to adult classes (see Table 2C for statistical comparisons). Coastal pelagic (CP1) and benthic fish (CB) showed the lowest mean contributions to the diet of each ontogenetic class. Mixing model results are summarized in Table 4.

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Table 2 [A] One-way ANOVA and *U* test pairwise comparison for $\delta^{13}C$ and $\delta^{15}N$ values among Commerson's ontogenetic classes

[A]	Calf	Juveniles	Subadults	First adults
	$\delta^{13}C/\delta^{15}N$	$\delta^{13}C/\delta^{15}N$	$\delta^{13}C/\delta^{15}N$	$\delta^{13}C/\delta^{15}N$
Juveniles	NS/***	–	–	–
Subadults	NS/***	NS/NS	–	–
First adults	NS/***	NS/NS	NS/*	–
Adults	NS/**	NS/**	NS/**	NS/NS

[B]	CB	CP1	CP2	BP
	$\delta^{13}C/\delta^{15}N$	$\delta^{13}C/\delta^{15}N$	$\delta^{13}C/\delta^{15}N$	$\delta^{13}C/\delta^{15}N$
CP1	NS/*	–	–	–
CP2	***/***	***/*	–	–
BP	**/***	***/***	***/NS	–
BI	NS/***	**/***	**/***	NS/**

[C]	Juveniles	Subadults	First adults
CP2			
Subadults	***	–	–
First adults	***	***	–
Adults	***	***	***
BP			
Subadults	***	***	***
First adults	***	***	***
Adults	***	***	***

[B] *U* test pairwise comparison for $\delta^{13}C$ and $\delta^{15}N$ values among the prey groups: coastal and benthic fish (CB), coastal and pelagic fish (CP1 and CP2), benthopelagic species (BP) and benthic invertebrates (BI). [C] Results of analysis of variance and post hoc test for the proportional contributions of pelagic (CP2) and benthopelagic (BP) species, mean prey groups suggested by SIAR, among four ontogenetic classes. Proportional contributions were transformed by arcsin transformation. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, *NS* not significant differences ($P > 0.05$)

Discussion

The isotope effect of lactation

The high mean $\delta^{15}N$ values of calves relative to older ontogenetic classes represent the isotopic effect of lactation on bone collagen in Commerson's dolphins, as observed in bone and dentin collagen of Otariids (Newsome et al. 2006), killer whales (*Orcinus orca*) (Newsome et al. 2009b) and in teeth and skin of bottlenose dolphins (*Tursiops truncatus*) (Knoff et al. 2008). The offset between calves and juveniles was of lesser magnitude ($\sim$1.8 ‰) than that found for bone collagen in California sea lions and northern fur seals ($\sim$3−5 ‰, Newsome et al. 2006). As observed in captive Commerson's dolphins (Joseph et al. 1987; Kastelein et al. 1993b), until 2 months post-partum, high energy costs associated with lactation likely lead to an increase in food intake for adult females resulting in a greater energy transfer to the calf from milk (Eichelberger et al. 1940; Kastelein et al. 1993b; Oftedal 1997). After this full nursing period, adult female food intake decreases to a minimum at around the time the calves start to supplement nursing with solid food and then increases to stabilize at normal rates (Kastelein et al. 1993b). The decrease in food intake can lead to a decrease in lactation by variations in the fat and salt content of milk, which results in a lower energy transfer to the calf and eventually leads to little or no milk production that induces complete weaning (Eichelberger et al. 1940; Kastelein et al. 1993b). A gradual weaning period that occurs at a young age (<6 months) during which calves consume a mixture of both milk and solid food could contribute to (1) the low offset between calves an older age classes and (2) the high variation in $\delta^{15}N$ values in calves observed in this study. During periods of rapid growth, bone collagen isotopic turnover rates are faster than for non-growing adults (Newsome et al. 2006; Martinez del Rio et al. 2009); such rapid turnover likely results in the dilution of the nursing signal and the significant decrease in $\delta^{15}N$ values from calves <6 months of age to juveniles between 6 months and 2 years of age.

The ontogenetic diet shift hypothesis

After weaning, juvenile diets are assumed to gradually equal that of adults, and thus isotopic differences between these individual classes should diminish (Jenkins et al. 2001). A significant and positive increase in $\delta^{15}N$ values with age and total body length supports the gradual change in diet from juveniles to adulthood in Commerson's dolphins. Considering the large variability in the size of the specimens analyzed, total body length is not an appropriate measure to determine the age in this species, but the general size of an animal independent of its age could influence its foraging capabilities. The observed age- and TBL-related trend in $\delta^{15}N$ may be driven by differences in the types of prey consumed and/or the use of different foraging habitats, which can create isotopic differences in similar prey types in different locations. No significant differences in mean $\delta^{13}C$ values between ontogenetic classes were found, which suggests that both juvenile and adult Commerson's forage in the same areas. The small (<1.0 ‰) but significant positive correlation between $\delta^{13}C$ values with age could be related with a possible shift in prey consumed from young individuals to adults.

Stomach content analysis (SCA) showed that the primary diet of Commerson's dolphins in Tierra del Fuego consists of several benthic and pelagic prey species analyzed in this study (Bastida et al. 1988; Clarke and Goodall 1994; Rosero Caicedo 2005). In agreement with previous studies based on SCA, our study also suggests that coastal

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Table 3 Raw mean $\delta^{13}C$ and $\delta^{15}N$ values (±SD) of Commerson's dolphin main prey. Muscle (*M*), whole body (*WB*), bone (*B*) and beak (*BK*) samples. *NA* not available, items from stomach contents. Coastal and benthic fish (*CB*), coastal and pelagic fish (CP1 and CP2), benthopelagic species (*BP*), benthic invertebrates (*BI*)

Species	Group	Geographical coordinates	$\delta^{13}C$ (±SD)	$\delta^{15}N$ (±SD)	C/N	N	Tissue
Patagonotothen spp. (*P. ramsayi, P. tessellata, P. sima*)	CB	53°57′52″ S–67°27′49 ″ W	−13.6 (2.5)	15.7 (1.5)	3.0	12	B
		54°17′52″ S–66°41′33″ W					
		53°57′52″ S–67°27′49″ W	−16.1 (1.6)	15.6 (1.9)	3.2	4	M
		54°17′52″ S–66°41′33″ W					
Zoarcids	CB	54°17′52″ S–66°41′33″ W	−10.4 (1.5)	17.5 (0.5)	3.2	6	B
		54°17′52″ S–66°41′33″ W	−11.1 (1.0)	18.0 (0.4)	3.2	6	M
E. maclovinus	CB	53°57′52″ S–67°27′49″ W	−15.4	13.9	2.9	1	B
		53°57′52″ S–67°27′49″ W	−13.9 (2.2)	17.3 (1.3)	3.1	9	M
Odontesthes spp.	CP1	53°57′52″ S–67°27′49″ W	−12.8 (0.4)	15.2 (1.3)	3.0	8	B
		54°52′31″ S–67°16′35″ W					
		53°57′52″ S–67°27′49″ W	−14.5 (1.0)	16.4 (1.4)	3.2	11	M
		54°52′31″ S–67°16′35″ W					
S. fuegensis	CP2	NA	−15.0 (0.9)	14.5 (1.0)	3.1	10	B
M. magellanicus	BP	53°09′ S–62°48′ W	−13.7 (0.7)	15.0 (1.1)	2.7	9	B
		53°09′ S–62°48′ W	−16.1 (0.4)	15.1 (0.3)	3.1	5	M
I. argentinus	BP	53°09′ S–62°48′ W	−16.6	14.9	3.3	1	M
L. gahi	BP	53°09′ S–62°48′ W	−17.5 (0.3)	13.3 (0.5)	3.2	10	M
M. gregaria	BI	54°17′52″ S–66°41′33″ W	−16.9	12.2	5.2	1	WB
C. vagans	BI	53°09′ S–62°48′ W	−17.2 (0.4)	13.6 (0.5)	3.2	3	M
H. planatus	BI	54°17′52″ S–66°41′33″ W	−16.9	2.4	6.4	1	WB
E. megalocyathus	BI	53°09′ S–62°48′ W	−15.9 (2.7)	10.5 (3.8)	3.3	2	BK
Octopus unidentified	BI	53°09′ S–62°48′ W	−15.5	13.5	3.1	1	M

Table 4 Relative consumption of prey types by the ontogenetic classes of Commerson's dolphins off Tierra del Fuego

Prey group	Juveniles	Subadults	First adults	Adults
CP2	60 ± 7	46 ± 11	55 ± 8	36 ± 10
BP	20 ± 7	28 ± 12	25 ± 10	33 ± 12
BI	17 ± 2	18 ± 4	13 ± 3	13 ± 4
CP1	2 ± 2	5 ± 4	4 ± 3	11 ± 7
CB	1 ± 1	3 ± 3	3 ± 2	7 ± 5

Stable isotope mixing model results (SIAR) are shown as mean contribution (%, ±SD)

and pelagic fish (e.g., *S. fuegensis*) and benthopelagic species (e.g., *L. gahi* and *I. argentinus*) are the primary prey consumed by Commerson's dolphin in this region. As novel, our results also show that the relative consumption of these prey varied among ontogenetic classes. We found an important change in the consumption of pelagic to benthopelagic species from juvenile to adult classes. This dietary shift may result from an improvement in foraging skills and expansion of habitats utilized by older individuals that enable them to search for elusive, fast and larger prey (e.g., benthopelagic species) at depth in coastal and continental shelf environments, as was suggested by Kastelein et al. (1993b). Furthermore, juveniles may be limited to epipelagic prey (e.g., *Sprattus*), as their small body size constrains their diving capabilities to limit benthic prey availability. Similar age- and size-related limitations in diving capability have been observed in other marine mammal species, including Fraser's dolphins (*Lagenodelphis hosei*), spinner dolphins (*Stenella longirostris*), pygmy killer whales (*Feresa attenuata*), bottlenose dolphins (*Tursiops truncatus*), Steller sea lions (*Eumetopias jubatus*), southern sea lions (*Otaria flavescens*) and gray seals (*Halichoerus grypus*), among others (Dolar et al. 1999; Noren et al. 2001, 2002, 2005; Richmond et al. 2006; Drago et al. 2010).

The sexual-resource partitioning hypothesis

Females appear to exhibit greater site fidelity than males which likely move greater distances in search of mates and resources (Pimper et al. 2010). The fusion-fission model proposed by Coscarella (2005) for northern Commerson's dolphin populations suggests the existence of weak social bonds between the sexes, with males moving between groups more often. This could lead to greater dietary diversity in males relative to females, if movement exposes males to

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different foraging sites or habitats. The lack of isotopic differences between the sexes, even among those within each ontogenetic class, however, suggests similarities in habitat preferences and/or types of prey consumed by males and females of any age. The high metabolic rate of Commerson's dolphins implies that this species must continuously forage, so greater mobility and movement in males must be accompanied by suitable availability of prey (Kastelein et al. 1993b). Thus, the lack of isotopic differences between the sexes suggests that while males may move greater distances, females and males have similar diets, and there is little evidence for resource partitioning in this species. Note that the analysis of bone collagen with its relatively slow isotopic turnover integrates ecological information over several years. Future isotopic analysis of other tissues with a higher turnover rate (e.g., skin, blood, or muscle) that are possible to collect from stranded and by-caught individuals could be analyzed to investigate sex- and age-related ecological differences on shorter, intra-annual timescales.

Fishing activities can affect populations of top marine consumers like Commerson's dolphins directly by incidental take of individuals and indirectly through the decline or collapse of commercially targeted species that are important for top marine consumers (Northridge 1985; Matthiopoulos et al. 2008). These direct and indirect interactions can have negative consequences for both top marine consumers and fisherman (Reeves et al. 2003; Lauriano et al. 2009). Changes in the abundance or depletion of food resources from fisheries activities have never been studied in Tierra del Fuego, which hinders the study of how resource availability of commercially exploited fish stocks affects the dolphin foraging habits. Furthermore, most studies that focus on describing dolphin bycatch in these fisheries are qualitative; rigorously collected quantitative data are not currently available (e.g., Goodall et al. 1994, 2008). Our diet study, however, suggests that there is little overlap between the primary prey consumed by Commerson's dophins and those targeted by local commercial (artisanal) fisheries. Our mixing model results suggest that two fish species targeted by coastal artisanal fisheries, *E. maclovinus* and *Odonthestes* spp., are not important prey for Commerson's dolphins of any age in this region. Despite this pattern, a major source of mortality for Commerson's dolphins is entanglement in fishing nets (Goodall et al. 2008); most of the individuals analyzed in this study represent incidental bycatch. In addition, the conflict between Commerson's dolphins and artisanal fishery seems to occur on a seasonal basis (Goodall 1994); thus, future analysis of other dolphin tissues with faster isotopic incorporation rates will permit us to study the possibility of seasonal competition between Commerson's dolphins and fisheries. Nevertheless, the long-term dietary information contained in bone collagen suggests that the potential indirect effects of competition are not effecting this population of Commerson's dolphins. To further reduce the effects of direct incidental take of dolphins in fishing nets, the regional government could promote the use of marine mammal acoustic alarm devices (i.e., pingers) by artisanal fisheries. This may reduce the effects of bycatch mortality without reducing prey availability since our data suggest overlap in prey targeted by Commerson's and local fisheries is minimal, ultimately resulting in benefits for both dolphins and fisherman in this region. However, further studies are needed to explore other hypothesis about other possible causes of incidental entanglement in order to implement the correct measures to reduce this interaction.

Conclusions

Our study quantified dietary preferences of Commerson's dolphins among sexes and age classes in coastal habitats adjacent to Tierra del Fuego. We found that Commerson's dolphins primarily consume two prey types in this region, *S. fuegensis* and benthopelagic species, and that the relative contribution of these prey changes from the juvenile to adult age class. This shift may relate to an increase in foraging and diving capability, which increases access to benthic habitats for older individuals. Lastly, our data suggest that there is a minimal overlap in the prey species targeted by local artisanal fisheries and those primarily consumed by Commerson's in this region. However, previous studies show that incidental take (i.e., bycatch) is a major source of mortality for Commerson's and other coastal marine mammal species in this region. Thus, exploring ways to reduce incidental marine mammal bycatch should become a management and conservation priority along the eastern coast of Tierra del Fuego.

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References

Ambrose SH (1990) Preparation and characterization of bone and tooth collagen for isotopic analysis. J Archaeol Sci 17:431–451

Bastida R, Lichtschein V, Goodall RNP (1988) Food habits of *Cephalorhynchus commersonii* off Tierra del Fuego. Rep Int Whal Comm (Spec Issue) 9:143–160

Berón Vera B, Pedraza SN, Raga JA, Gil de Pertierra A, Crespo EA, Koen Alonso M, Goodall RNP (2001) Gastrointestinal helminthes of Commerson's dolphins *Cephalorhynchus commersonii* from central Patagonia and Tierra del Fuego. Dis Aquat Org 47:201–208

Cerling TE, Harris JM (1999) Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implication for ecological and paleontological studies. Oecologia 120:347–363

Cipriano F, Hevia M, Iñíguez M (2011) Genetic divergence over small geographic scales and conservation implications for Commerson's dolphins (*Cephalorhynchus commersonii*) in southern Argentina. Mar Mamm Sci 27:701–718. doi:10.1111/j.1748-7692.2010.00434.x

Clarke M, Goodall RNP (1994) Cephalopods in the diets of three odontocete cetacean species stranded at Tierra del Fuego, *Globicephala melaena* (Traill, 1809), *Hyperoodon planifrons* Flower, 1882 and *Cephalorhynchus commersonii* (Lacépède, 1804). Antarct Sci 6:149–154

Clementz MT, Koch PL (2001) Differentiating aquatic mammal habitat and foraging ecology with stable isotopes in tooth enamel. Oecologia 129:461–472

Collet A, Robineau D (1988) Data on the genital tract and reproduction in Commerson's dolphin, *Cephalorhynchus commersonii* (Lacépède, 1804) from the Kerguelen Islands. Rep Int Whal Comm (Spec Issue) 9:119–141

Coscarella MA (2005) Ecología, comportamiento y evaluación del impacto de embarcaciones sobre manadas de tonina overa *Cephalorhynchus commersonii* en Bahía Engaño, Chubut. PhD Dissertation, Universidad de Buenos Aires, Argentina (in Spanish)

Coscarella MA, Pedraza SN, Crespo EA (2010) Behaviour and seasonal variation in the relative abundance of Commerson's dolphin (*Cephalorhynchus commersonii*) in northern Patagonia, Argentina. J Ethol 28:463–470. doi:10.1007/s10164-010-0206-4

Dellabianca NA, Hohn AA, Goodall RNP (2012) Age estimation and growth layer patterns in teeth of Commerson's dolphins (*Cephalorhynhcus c. commersonii*) in subantarctic waters. Mar Mamm Sci 28:378–388. doi:10.1111/j.1748-7692.2011.00475.x

DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. Geochim Cosmochim Acta 42:495–506

DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. Geochim Cosmochim Acta 45:341–351

Dolar MLL, Suarez P, Ponganis PJ, Kooyman GL (1999) Myoglobin in pelagic small cetaceans. J Exp Biol 202:227–236

Drago M, Cardona L, Crespo EA, García N, Ameghino S, Aguilar A (2010) Change in the foraging strategy of female South American sea lions (Carnívora: Pinnipedia) after parturition. Sci Mar 74:589–598. doi:10.3989/scimar.2010.74n3589

Eichelberger L, Fetcher ES Jr, Geiling EMK, Vos BJ Jr (1940) The composition of dolphin milk. J Biol Chem 134:171–176

Fogel ML, Tuross N, Owsley DW (1989) Nitrogen isotope tracers of human lactation in modern and archaeological populations. In: Geophysical Laboratory, Carnegie Institution of Washington (publisher). Annual report of the director of the Geophysical Laboratory, Carnegie Institution of Washington, 1988–1989. Washington, DC, pp 111–117

Francey RK, Allison CE, Etheridge DM, Trudinger CM, Enting IG et al (1999) A 1,000 year record of $\delta^{13}C$ in atmospheric CO_2. Tellus B 51:170–193

Garaffo GV, Dans SL, Pedraza SN, Degrati M, Schiavini A, Gonázlez R, Crespo EA (2011) Modeling habitat use for dusky dolphin and Commerson's dolphin in Patagonia. Mar Ecol Prog Ser 421:217–277. doi:10.3354/meps08912

Goodall RNP (1994) Commerson's dolphin *Cephalorhynchus commersonii* (Lacépède 1804). In: Ridgway SH, Harrison SR (eds) Handbook of marine mammals, vol 5., The first book of dolphinsAcademic Press, London, pp 241–267

Goodall RNP, Galeazzi AR, Lichter AA (1988) Exploitation of small cetaceans off Argentina 1979–1986. Rep Int Whal Comm 38:407–410

Goodall RNP, Schiavini ACM, Fermani C (1994) Net fisheries and net mortality of small cetaceans off Tierra del Fuego, Argentina. Rep Int Whal Commn (Spec Issue) 15:295–304

Goodall RNP, Benegas LG, Boy CC, Dellabianca N, Pimper L, Riccialdelli L (2008) Review of small cetaceans stranded or incidentally captured on the coast of Tierra del Fuego, Argentina, over 33 years. Paper SC/60/SM21 presented to the Scientific Committee, International Whaling Commission, June 2008, pp 14 (unpublished). Available from www.iwcoffice.org

Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West J (ed) Isoscapes: understanding movement, pattern, and process on earth through isotope mapping. Springer Science + Business Media BV, New York, pp 299–318

Hare PE, Fogel ML, Stafford TW Jr, Mitchell AD, Hoering TC (1991) The isotopic composition of carbon and nitrogen in individual amino acids isolated from modern and fossil proteins. J Archaeol Sci 18:277–292

Hedges REM, Stevens RE, Koch PL (2005) Isotopes in bones and teeth. In: Leng MJ (ed) Isotopes in palaeoenvironmental research. Springer, Netherlands, pp 117–145

Hobson KA, Sease JL (1998) Stable isotope analyses of tooth annuli reveal temporal dietary records: an example using Steller sea lion. Mar Mamm Sci 14:116–129

Idermühle A, Stocker T, Joos F, Fisher H, Smith H, Wahlen M, Deck B, Mastroianni D, Tschumi J, Blunier T, Meyer R, Stauffer B (1999) Holoce carbon-cycle dynamics based in CO_2 trapped in ice at Taylor Dome, Antarctica. Nature 398:121–126

Iñíguez MA, Tossenberger VP (2007) Commerson's dolphins (*Cephalorhynchus commersonii*) off Ría Deseado, Patagonia, Argentina. Aquat Mamm 33:276–285

Iñíguez MA, Hevia M, Gasparrou C, Tomsin AL, Secchi ER (2003) Preliminary estimate of incidental mortality of Commerson's dolphins (*Cephalorhynchus commersonii*) in an artisanal setnet fishery in La Angelina beach and Ría Gallegos, Santa Cruz, Argentina. LAJAM 2:87–94. doi:10.5597/lajam00036

Jenkins SG, Partridge ST, Stephenson TR, Farley SD, Robbins CT (2001) Nitrogen and carbon isotope fractionation between mothers, neonates and nursing offspring. Oecologia 129:336–341

Joseph BE, Antrim JE, Cornell LH (1987) Commerson's dolphin (*Cephalorhynchus commersonii*): a discussion of the first live birth within a marine zoological park. Zoo Biol 6:69–77

Kastelein RA, McBain J, Neurohr B (1993a) Information on the biology of Commerson's dolphins (*Cephalorhynchus commersonii*). Aquat Mamm 19:13–19

Kastelein RA, McBain J, Neurohr B, Mohri M, Saijo S, Wakabayashi I, Wiepkema PR (1993b) The food consumption of Commerson's dolphins (*Cephalorhynchus commersonii*). Aquat Mamm 19:99–121

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Knoff A, Hohn A, Macko SA (2008) Ontogenetic diet changes in bottlenose dolphins (*Tursiops truncatus*) reflected through stable isotopes. Mar Mamm Sci 24:128–137. doi:10.1111/j.1748-7692.2007.00174.x

Lauriano G, Caramanna L, Scarno M, Andaloro F (2009) An overview of dolphin depredation in Italian artisanal fisheries. J Mar Biol Assoc UK 89:921–929. doi:10.1111/j.1748-7692.2007.00174.x

Lescrauwaet AC, Gibbons J, Guzman L, Schiavini ACM (2000) Abundance estimation of Commerson's dolphin in the eastern area of the strait of Magellan—Chile. Rev Chil Hist Nat 73:473–478

Lockyer C, Smellie GG, Goodall RNP, Cameron IS (1981) Examination of teeth of Commerson's dolphin, *Cephalorhynchus commersonii*, for age determination. J Zool Soc Lond 195:123–131

Lockyer C, Goodall RNP, Galeazzi AR (1988) Age and body length characteristics of *Cephalorhynchus commersonii* from incidentally-caught specimens off Tierra del Fuego. Rep Int Whal Comm (Spec Issue) 9:103–118

Martínez del Rio C, Wolf N, Carleton SA, Gannes LZ (2009) Isotopic ecology ten years after a call for more laboratory experiments. Biol Rev 84:91–111. doi:10.1111/j.1469-185X.2008.00064.x

Matthiopoulos J, Smout S, Winshio AJ, Thompson D, Boyd IL, Harwood J (2008) Getting beneath the surface of marine mammal—fisheries competition. Mammal Rev 38:167–188

Mendes S, Newton J, Reid RJ, Frantzis A, Pierce GJ (2007) Stable isotope profiles in sperm whale teeth: variations between areas and sexes. J Mar Biol Ass UK 87:621–627. doi:10.1017/S0025315407056019

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochim Cosmochim Acta 48:1135–1140

Newsome SD, Koch PL, Etnier MA, Aurioles-Gamboa D (2006) Using carbon and nitrogen isotope values to investigate maternal strategies in Northeast Pacific otariids. Mar Mamm Sci 22:556–572. doi:10.1111/j.1748-7692.2006.00043.x

Newsome SD, Etnier MA, Monson DH, Fogel ML (2009a) Retrospective characterization of ontogenetic shifts in killer whale diets via δ^{13}C and δ^{15}N analysis of teeth. Mar Ecol Prog Ser 374:229–242. doi:10.3354/meps07747

Newsome SD, Tinker MT, Monson DH, Oftedal OT, Ralls K, Staedler MM, Fogel ML, Estes JA (2009b) Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). Ecology 90:961–974

Newsome SD, Clementz MT, Koch PL (2010) Using stable isotope biogeochemistry to study marine mammal ecology. Mar Mamm Sci 26:509–572. doi:10.1111/j.1748-7692.2009.00354.x

Noren SR, Williams TM, Pabst DA, McLellan WA, Dearolf JL (2001) The development of diving in marine endotherms: the skeletal muscles of dolphins, penguins, and seals for activity during submergence. J Comp Physiol B 171:127–134. doi:10.1007/s003600000161

Noren SR, Lacave G, Wells RS, Williams TM (2002) The development of blood oxygen stores in bottlenose dolphins (*Tursiops truncatus*): implications for diving capacity. J Zool Lond 258:105–113. doi:10.1017/S0952836902001243

Noren SR, Iverson SJ, Boness SJ (2005) Development of the blood and muscle oxygen stores in gray seals (*Halichoerus grypus*): implications for juvenile diving capacity and the necessity of a terrestrial postweaning fast. Physiol Biochem Zool 78:482–490

Norris K (1961) Standardized methods for measuring and recording data on the smaller cetaceans. J Mammal 42:471–476

Northridge SP (1985) Estudio mundial de las interacciones entre los mamíferos marinos y la pesca. FAO Documento Técnico de Pesca 251 FIRM/T251 (in Spanish)

Oftedal OT (1997) Lactation in whales and dolphins: evidence of divergence between baleen- and toothed-species. J Mammary Gland Biol Neoplasia 2:205–230

Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. PLoS One 5:e9672

Pedraza SN (2008) Ecología de la tonina overa (*Cephalorhynhcus commersonii*) en el litoral patagónico. PhD Dissertation, Universidad de Buenos Aires, Argentina (in Spanish)

Perrin WF, Myrick AC (eds) (1980) Age determination of toothed whales and sirenians. Rep Int Whal Comm (Spec Issue) 3, pp 229

Pimper LE (2010) Estructura poblacional y conservación de la tonina overa, *Cephalorhynchus commersonii*, en Tierra del Fuego y zonas aledañas. PhD Dissertation, Universidad de Buenos Aires, Argentina (in Spanish)

Pimper LE, Remis MI, Goodall RNP, Baker SC (2009) Teeth and bones as sources of DNA for genetic diversity and sex identification of Commerson's dolphins (*Cephalorhynchus commersonii*) from Tierra del Fuego, Argentina. Aquat Mamm 35:330–333. doi:10.1578/AM.35.3.2009.330

Pimper LE, Baker CS, Goodall RNP, Olavarría C, Remis MI (2010) Mitochondrial DNA variation and population structure of Commerson's dolphins (*Cephalorhynchus commersonii*) in their southernmost distribution. Conservat Genet 11:2157–2168. doi:10.1007/s10592-010-0102-z

Reeves RR, Smith BD, Crespo EA, Notarbartolo di Sciara G (compilers) (2003) Dolphins, whales and porpoises: 2002–2010 conservation action plan for the world's cetaceans. IUCN/SSC Cetacean Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK, pp 139

Riccialdelli L, Newsome SD, Fogel ML, Goodall RNP (2010) Isotopic assessment of prey and habitat preferences of a cetacean community in the southwestern South Atlantic Ocean. Mar Ecol Prog Ser 418:235–248. doi:10.1578/AM.35.3.2009.330

Richards MP, Mays S, Fuller BT (2002) Stable carbon and nitrogen isotope values of bone and teeth reflect weaning age at the medieval Wharram Percy site, Yorkshire, UK. Am J Phys Anthropol 119:205–210

Richmond JP, Burns JM, Rea LD (2006) Ontogeny of total body oxygen stores and aerobic dive potential in Steller sea lions (*Eumetopias jubatus*). J Comp Physiol B 176:535–545. doi:10.1007/s00360-006-0076-9

Rosero Caicedo DM (2005) Dieta de la tonina overa, *Cephalorhynchus commersonii* (Lacépède, 1804) en Tierra del Fuego, Argentina. Bs. Dissertation, Pontificia Universidad Javeriana, Bogota DC, Colombia (in Spanish)

Tuross N, Fogel ML, Hare PE (1988) Variability in the preservation of the isotopic composition of collagen from fossil bone. Geoquim Comsoquim Acta 52:929–935

Valenzuela LO, Sironi M, Rowntree VJ (2010) Interannual variation in the stable isotope differences between mothers and their calves in southern right whales (*Eubalaena australis*). Aquat Mamm 36:138–147. doi:10.1578/AM.36.2.2010.138

Young BG, Loseto LL, Ferguson SH (2010) Diet differences among age classes of Arctic seals: evidence from stable isotope and mercury biomarkers. Polar Biol 33:153–162. doi:10.1007/s00300-009-0693-3