Journal of Zoology

Journal of Zoology. Print ISSN 0952-8369

Ontogenic dietary changes in South American sea lions

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Keywords
South American sea lion; *Otaria flavescens*; diet ontogeny; bone; stable isotopes.

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Editor: Nigel Bennett

Received 22 January 2009; revised 22 May 2009; accepted 17 June 2009

doi:10.1111/j.1469-7998.2009.00613.x

Abstract

Stable isotopes of carbon and nitrogen in the skull bones of South American sea lions *Otaria flavescens* from the Chubut province (Argentina) were analysed to determine whether their feeding habits change during ontogeny. The stable isotope analysis showed that $\delta^{13}C$ steadily increased in males and females with their developmental stage (young, first adult, adult and senile), except in senile males whose $\delta^{13}C$ decreased to a value close to that of first adults. Pairwise comparison of bone stable isotope ratio in each developmental stage revealed differences between males and females only for the $\delta^{13}C$ values relative to first adults and adults. Overall, results indicate that the contribution of benthic prey items to the diet of both sexes increases with the developmental stage, except in senile males, and that first adult and adult males have a more benthic diet than females at the same developmental stage. No differences exist between males and females at younger and older developmental stages. With respect to $\delta^{15}N$, the only difference was in young female skulls, which were more enriched than those of any other group. Consequently, the trophic level of sea lions is roughly the same throughout life, independent of the developmental stage and sex, except for young females. The growth curve analysis revealed statistically significant differences in the condylobasal length of the skull between the sea lions in both sexes of the young stage and those of the other three developmental stages considered here but not among the individuals of the three later stages. This result indicates that the dietary differences between individuals in the young stage and those in the successive stages is likely due to differences in body size, whereas dietary differences among individuals of the later three stages might be due to different foraging skills that are progressively acquired during their life span.

Introduction

The foraging strategies of most air-breathing marine vertebrates are highly dependent on their diving skills, as they often forage underwater (Bjorndal, 1997; Berta & Sumich, 1999; Schreiber & Burger, 2001). Body mass is a critical parameter for diving vertebrates, not only because oxygen stores increase with body size (Schmidt-Nielsen, 1984; Gentry, Kooyman & Goebel, 1986; Kooyman, 1989; Costa, 1993; Fowler *et al*., 2007*b*) but also because of a faster use of oxygen stores in smaller species due to a higher mass-specific rate of metabolism (Brody, 1945; Miller & Irving, 1975; Ashwell-Erickson & Elsner, 1981; Schmidt-Nielsen, 1984; Thorson & Le Boeuf, 1994).

The influence of body size on diving skills is well exemplified in pinnipeds, as the adults of those species with a large body mass often exploit deep, benthic habitats, whereas the adults of species with a smaller body size typically behave as epipelagic predators (Gentry *et al*., 1986; Kooyman, 1989; Costa, 1991, 1993; Costa *et al*., 2004). Similarly, females of some highly dimorphic species have a more pelagic diet than males throughout their life, due to their smaller body size (Le Boeuf *et al*., 1996, 2000; Meynier *et al*., 2008). Nevertheless, the relationship between body size and habitat use is not univocal, as both sexes of some dimorphic species behave as pelagic predators (Costa *et al*., 2004). This might be because animals with a better diving capacity choose to stay for longer in pelagic prey-rich patches instead of diving deeper or because a virtually non-existent continental shelf limits the availability of benthic habitats shallow enough to be accessed even by the best divers in the population (Hückstädt, Rojas & Antezana, 2007).

Experimental studies on the diving ontogeny of pinnipeds have also revealed a consistent increase in dive depth, dive time, travelling distance and swimming speed with age both in phocids (Lydersen, 1991; Lydersen & Hammill, 1993; Lydersen, Hammill & Kovacs, 1994; Thorson & Le Boeuf, 1994; Le Boeuf *et al*., 1996; Burns, 1999; Bekkby & Bjørge, 2000; Jørgensen *et al*., 2001) and otariids (Horning & Trillmich, 1997; McCafferty, Boyd & Taylor, 1998; Baker & Donohue, 2000; Baylis *et al*., 2005; Pitcher *et al*., 2005;

Chilvers *et al.*, 2006; Fowler *et al.*, 2006; Spence-Bailey, Verrier & Arnould, 2007). This is probably because oxygen stores increase as the body mass of young pinnipeds increases during growth (Fowler *et al.*, 2006), but also because pinnipeds improve their control of oxygen demand with age (Rea & Costa, 1992; Ponganis, Kooyman & Castellini, 1993; Greaves *et al.*, 2005; Fowler, Costa & Arnould, 2007*a*; Fowler *et al.*, 2007*b*).

Improved diving skills with age are not expected to lead to an increase in the consumption of benthic prey items in obligate benthic foragers (e.g. Fowler *et al.*, 2007*a*,*b*) or in oceanic species unlikely to reach the seabed (e.g. Lewis *et al.*, 2006). Conversely, improved diving skills with age are expected to allow facultative foragers inhabiting the continental shelf to increase their access to the seabed and the time spent there as they grow, thus resulting in an increased contribution of benthic prey items to their diet (Le Boeuf *et al.*, 1996). Unfortunately, ontogenic dietary changes in pinnipeds are poorly documented (Hobson & Sease, 1998; Newsome *et al.*, 2006), and further research is needed to test the hypothesis that facultative foragers increase their consumption of benthic prey with increasing body size and age.

The South American sea lion *Otaria flavescens* is a highly dimorphic species, with adult males weighing 300–350 kg and adult females weighing 100–150 kg (Cappozzo, 2002). Both sexes have a pelagic diet in the eastern Pacific (Soto, Trites & Arias-Schreiber, 2006; Hückstädt *et al.*, 2007), where pelagic prey occur at a high density; however, in the south-western Atlantic they are able to forage both close to the seabed and in the middle of the water column (Werner & Campagna, 1995; Thompson *et al.*, 1998), with males exploiting deeper habitats than females (Campagna *et al.*, 2001). Accordingly, mixed diets have been reported from northern Patagonia (Koen Alonso *et al.*, 2000) and the Falkland (Malvinas) islands (Thompson *et al.*, 1998). This dietary flexibility makes the South American sea lion a good subject to test the hypothesis that the consumption of benthic prey is related to body size and increases with age in facultative foragers.

Stable isotope analysis is a method especially well suited for this kind of study, as the stable isotope ratio in the consumer's tissues integrates the stable isotope ratio of its prey items in a predictable manner over a long period of time (DeNiro & Epstein, 1978, 1981). Stable isotope analysis offers less detailed information on dietary composition than scat analysis; however, because it provides information on assimilated food, it has become a standard method in the study of the foraging ecology of pinnipeds (Aurioles, Koch & Le Bœuf, 2006; Newsome *et al.*, 2006; Hückstädt *et al.*, 2007; Ducatez *et al.*, 2008; Porras-Peters *et al.*, 2008). The ratio $^{15}N/^{14}N$ (expressed as $\delta^{15}N$) increases with each trophic level due to the preferential excretion of the lighter stable isotope (Minagawa & Wada, 1984) and, therefore, is used to assess the trophic level (McCutchan *et al.*, 2003). Differences in the stable carbon isotope ratios between the pelagic and benthic primary producers are usually much larger than those observed among trophic levels (Cardona *et al.*, 2007); therefore, $\delta^{13}C$ is often used to discriminate between habitats, because benthic species are usually enriched in ^{13}C relative to pelagic species. Consequently, stable isotopes cannot be used to determine the depth of the foraging habitat but do allow for differentiating benthic from epipelagic predators by analysing a tiny tissue sample.

Following this reasoning, here we analyse stable carbon and nitrogen isotopes in skull bone fragments from the South American sea lion to test three predictions emerging from the hypothesis that the consumption of benthic prey items is related to body size and age in facultative foragers: (1) the consumption of benthic prey items will increase from post-weaning to adulthood within each sex; (2) adult females will have a more pelagic diet than adult males; (3) the consumption of benthic prey items will also increase with age in non-growing adults.

Materials and methods

Sampling

Samples (40 males and 40 females for stable isotope analyses and 116 males and 84 females for the length–age relationship) were collected from sea lion skulls of the scientific collection of Centro Nacional Patagonico (CENPAT) at Puerto Madryn, Argentina. Skulls selected for sampling were restricted to sea lions that were incidentally captured by fishermen or stranded and died along the coast off the Chubut province in northern Patagonia (Fig. 1) from 1990 to 2000 to avoid the possible confounding effects of long-term changes in growth rate and/or stable isotope baseline. The age of all the sampled individuals had previously been assessed by counting growth layers in the dentine of the canines (Crespo, 1988; Crespo *et al.*, 1994), and the age ranged from 1 to 19 years for stable isotope analysis (Table 1) and from 1 month to 20 years for the length–age relationship analysis (Fig. 2).

The life span of South American sea lions is *c.* 18–20 years (King, 1983; Crespo, 1988), with females reaching adulthood at about 4 years of age and males at about 6 years of age (Vaz-Ferreira, 1981; Cappozzo, 2002). Based on these data, we established four developmental stages (young, first adult, adult and senile). Accordingly, we selected the following from the above-mentioned skulls to analyse the $\delta^{13}C$ and $\delta^{15}N$ in the bone: 10 young individuals of each sex (post-weaned and not yet sexually mature individuals between 1 and 5 years of age for males and between 1 and 3 years of age for females), 10 first adult individuals of each sex (sexually mature individuals between 7 and 8 years of age for males and between 5 and 7 years of age for females), 10 adult individuals of each sex (sexually mature individuals between 9 and 12 years of age for males and between 8 and 12 years of age for females) and 10 senile individuals of each sex (sexually mature individuals >12 years old). The main difference between first adults and adults is that the former can still grow in length, whereas the latter are thought to have ceased length growth. The term subadult was not used because it implies that the individual is not sexually mature.

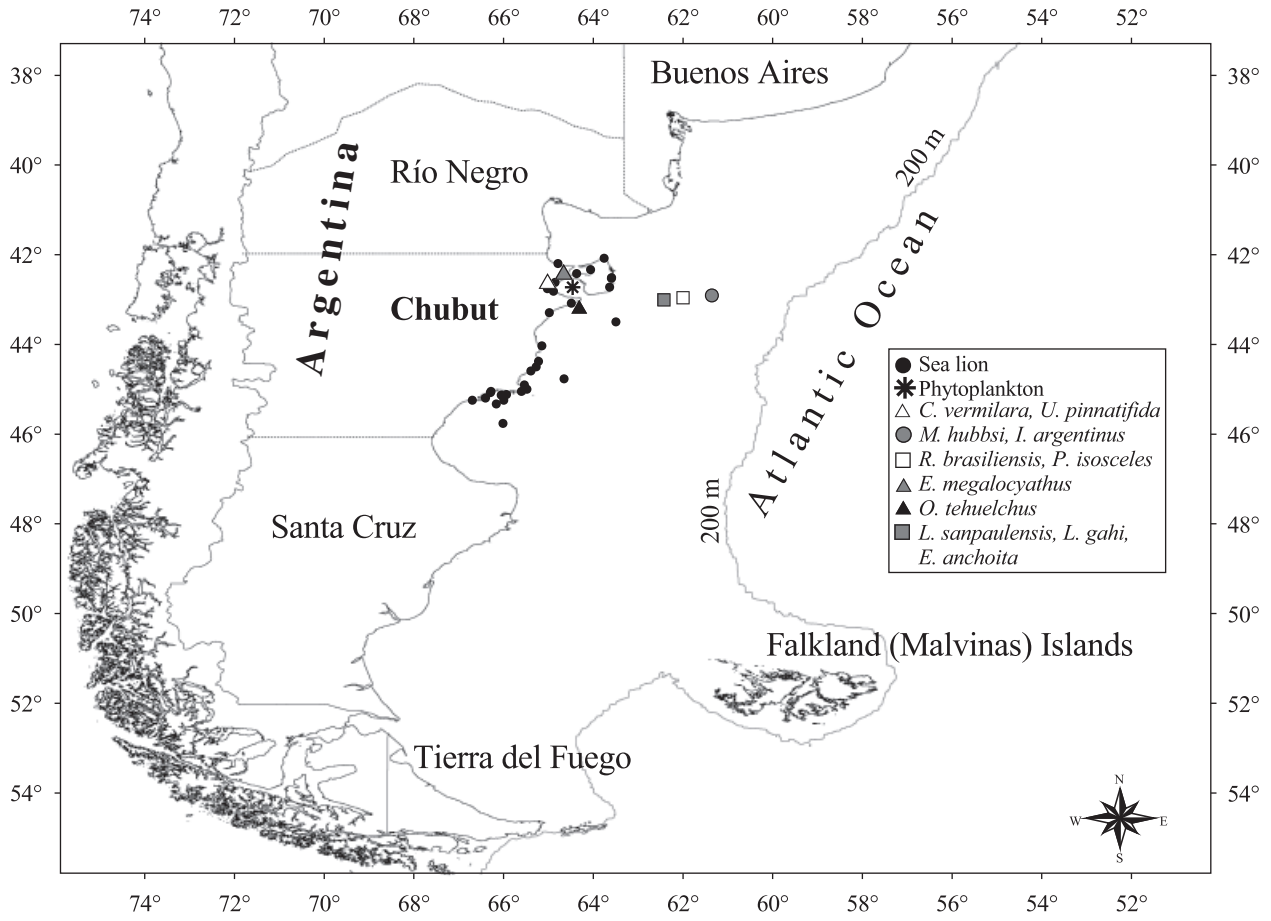

Figure 1 Atlantic coast of Argentina and location of the Chubut province. Symbols show the sampling location of primary producers, South American sea lions *Otaria flavescens* and potential prey.

The skulls were first cleaned using dermestid beetles, washed with water and soap, thoroughly rinsed with water and air dried. A small fragment of turbinate bones from the nasal cavity was collected from each skull. This bone type was selected because it is easy to crush and its sampling does not damage the skull for subsequent studies. The condylobasal length of each skull was also measured, as it is highly correlated with standard length in South American sea lions (Rosas, Haimovici & Pinedo, 1993) and can thus be used as a proxy for body length. The condylobasal length was also measured in additional skulls in order to obtain a larger sample to study the length–age relationship.

Samples of the most important potential prey species for South American sea lions off the Chubut province (Koen Alonso *et al.*, 2000) were collected in January and February 2006 (Table 2). Pelagic species were represented by Argentine short-fin squid *Illex argentinus*, Argentine anchovy *Engraulis anchoita*, South-American long-fin squid *Loligo sanpaulensis*, Argentine hake *Merluccius hubbsi* and Patagonian squid *Loligo gahi*, whereas benthic species were represented by red octopus *Enteroctopus megalocyathus*, tehuelche octopus *Octopus tehuelchus*, flounder *Paralichthys isosceles* and banded cusk eel *Raneya brasiliensis*. White muscle and mantle were collected from fish and cephalopods, respectively. Samples of benthic primary producers (*Codium vermilara* and *Undaria pinnatifida*) and phytoplankton (diatoms and dinoflagellates) were also collected to determine their stable isotope ratios and to produce a complete and better description of the isotopic landscape off the Chubut province. The samples of the potential prey items and primary producers were provided by local fishermen or collected by the staff of the Laboratory of Marine Mammals of CENPAT. Phytoplankton was collected with a 20 μm mesh-size plankton net and, once in the laboratory, filtered in a pre-combusted GF/C filter.

All skull bone samples were stored dry, whereas all potential prey items and primary producer samples were stored in a freezer at $-20\,^{\circ}$C.

Stable isotope analysis

Following initial sampling, cleaning and preparation, the skull bone fragments and the other samples (primary producers and potential prey items) were dried at 60 °C and ground into a fine powder using a mortar and pestle. Lipids were extracted with a chloroform/methanol (2:1) solution

Table 1 Stable isotope values of the South American sea lion *Otaria flavescens* skull sample from Chubut province investigated in this study: age (in years) and sampling date (year of collection)

	♂				♀			
Developmental stage	Age	Sampling date	δ^{13}C (‰)	δ^{15}N (‰)	Age	Sampling date	δ^{13}C (‰)	δ^{15}N (‰)
Young	1	1993	−13.0	24.3	1	1998	−13.3	22.7
	1	1993	−12.8	26.2	1	1996	−12.6	23.9
	1	1995	−13.5	24.5	1	1999	−12.9	25.5
	2	1994	−13.1	23.2	1	1993	−13.0	24.8
	3	1994	−13.1	21.1	1	1999	−12.9	25.9
	3	1991	−12.9	20.9	1	1995	−14.8	25.3
	3	1994	−13.6	19.9	2	1998	−14.4	24.3
	5	1997	−13.1	21.1	3	1996	−12.7	22.5
	5	2000	−12.7	21.3	3	1991	−12.4	23.1
	5	2000	−12.6	21.9	3	1990	−12.4	21.9
First adult	7	1991	−11.3	24.1	5	2000	−13.5	20.9
	7	1992	−12.1	21.8	5	2000	−13.0	20.1
	7	2000	−11.7	21.5	5	1994	−12.9	21.7
	7	1994	−12.8	21.7	6	1993	−12.6	23.3
	7	2000	−12.1	22.0	6	1993	−12.7	22.8
	8	1994	−12.5	22.7	6	2000	−13.1	21.0
	8	1997	−12.9	21.9	7	1991	−12.3	22.1
	8	1998	−12.3	22.7	7	1992	−13.0	21.9
	8	2000	−10.7	21.6	7	1990	−11.6	22.4
	8	2000	−12.7	21.7	7	1996	−13.3	21.7
Adult	9	1999	−11.4	22.9	8	1990	−12.3	22.2
	9	1990	−11.4	19.1	8	1994	−12.1	22.2
	9	1993	−11.9	23.2	9	1993	−12.0	23.3
	10	1994	−11.3	22.9	9	2000	−13.0	22.4
	10	1993	−11.6	23.4	9	1994	−12.0	22.6
	10	2000	−10.9	23.5	10	1995	−11.8	22.4
	11	1996	−11.2	22.3	10	2000	−12.6	22.0
	11	1990	−11.6	22.0	11	1994	−12.3	22.3
	12	1990	−11.9	23.0	12	1995	−12.5	21.8
	12	1990	−11.0	22.4	12	1990	−13.1	21.6
Senile	13	1994	−11.5	22.5	13	1996	−11.6	22.0
	13	2000	−12.5	22.1	13	1996	−11.5	23.4
	13	2000	−12.5	21.5	13	1990	−11.7	22.2
	13	2000	−11.4	22.3	14	1993	−11.5	23.3
	16	1998	−11.5	22.2	15	1995	−12.5	21.6
	16	1994	−12.3	21.0	15	2000	−11.1	23.2
	16	2000	−12.4	22.9	16	1998	−12.1	22.3
	17	1995	−11.8	22.6	17	2000	−12.1	23.0
	18	1998	−11.6	22.3	18	1994	−12.3	22.0
	19	2000	−12.6	21.1	19	2000	−11.8	22.6

(Bligh & Dyer, 1959), because lipids are depleted in ^{13}C compared with other molecules, thus confounding the results by decreasing the δ^{13}C value (DeNiro & Epstein, 1977; Tieszen *et al.*, 1983). Bone and phytoplankton samples contain a high concentration of inorganic carbon that may add undesirable variability to δ^{13}C (Lorrain *et al.*, 2003). Consequently, they were previously treated by soaking for 24 h in 0.5 N (bone) and 0.05 N (phytoplankton) hydrochloric acid (HCl) to decarbonize them (Ogawa & Ogura, 1997; Newsome *et al.*, 2006). Because HCl treatment adversely affects δ^{15}N (Bunn, Loneragan & Kempster, 1995), each of the samples was divided into two sub-samples, respectively, used for C analyses after decarbonation and for N analyses without decarbonation.

Approximately 1 mg of dried bone, 4 mg of homogenized seaweeds, 16 mg of homogenized phytoplankton with filter and 0.6 mg of white muscle from fish and of mantle from cephalopods were weighed into tin cups (3.3 × 5 mm), combusted at 900 °C and analysed in a continuous flow stable isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA; Thermo Finnigan, Bremen, Germany). Atropine was used as a system check for elemental analyses. Samples were processed at Scientific-Technical Services of the University of Barcelona.

Stable isotope abundances, expressed in delta (δ) notation, where the relative variations of stable isotope ratios are expressed in permil (‰) deviations from pre-defined international standards, were calculated as:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

where X is ^{13}C or ^{15}N, R_{sample} is the heavy–light stable isotope ratio of the sample ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) and R_{standard} is the heavy–light stable isotope ratio in reference standards, which were V-PDB (Vienna Pee Dee Belemnite) calcium carbonate for ^{13}C and the atmospheric nitrogen (air) for ^{15}N. International stable isotope secondary standards of known $^{13}C/^{12}C$ ratios, as given by the International Atomic Energy Agency (IAEA, Vienna), namely polyethylene (IAEA CH_7, $\delta^{13}C = -31.8‰$), graphite (IAEA $USGS_{24}$, $\delta^{13}C = -16.1‰$) and sucrose (IAEA CH_6, $\delta^{13}C = -10.4‰$), were used for calibration at a precision of 0.2‰. For nitrogen, the international stable isotope secondary standards of known $^{15}N/^{14}N$ ratios, namely $(NH_4)_2SO_4$ (IAEA N_1, $\delta^{15}N = +0.4‰$ and IAEA N_2, $\delta^{15}N = +20.3‰$) and KNO_3 (IAEA NO_3, $\delta^{15}N = +4.7‰$), were used to a precision of 0.3‰.

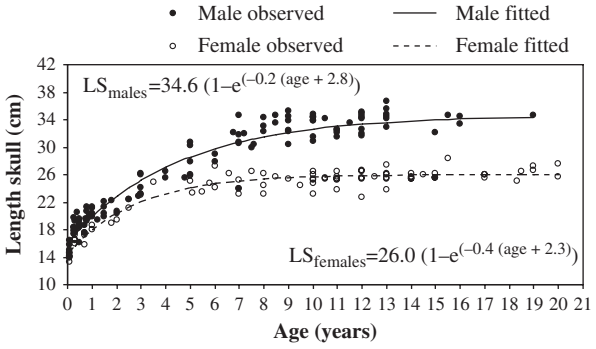

Figure 2 Growth curves of the male and female South American sea lions *Otaria flavescens* from Chubut province, calculated according to the von Bertalanffy equation. Sample size: $n = 116$ for male and $n = 84$ for female.

Data analyses

The length–age relationship was calculated according to the von Bertalanffy growth curve:

$$L_t = L_\infty(1 - \exp[-K(t - t_0)])$$

where L_t is the length at age t, L_∞ is the theoretical maximum (or asymptotic) length that individuals would reach if lived indefinitely, K is a growth coefficient and t_0 is the theoretical age at zero length.

One-way ANOVA, followed by the Scheffe *post hoc* test, was used to detect differences in the skull length of the individuals of each sex in each developmental stage (young, first adult, adult and senile), because the sample size for condylobasal length was not constant. Nested ANOVA was used to test the influence of habitat type (benthic vs. pelagic) and species identity on the $\delta^{13}C$ and $\delta^{15}N$ of prey species.

Table 2 Mean and standard deviation of the stable isotope values of primary producers and potential prey of the South American sea lion *Otaria flavescens* off Chubut province (northern Patagonia, Argentina)

Scientific name	Common name	Habitat	Sampling date	*n*	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Primary producers						
Phytoplankton		P	January 2006	2[a]	-21.0 ± 0.1	13.4 ± 0.6
Seaweed						
Codium vermilara		B	January 2006	5	-14.9 ± 1.3	11.6 ± 0.4
Undaria pinnatifida	Wakame	B	January 2006	5	-19.1 ± 1.2	10.4 ± 0.5
Potential prey						
Fish						
Merluccius hubbsi (>30 cm)	Argentine hake	P	February 2006	5	-17.0 ± 0.5	17.1 ± 0.4
Merluccius hubbsi (<30 cm)	Argentine hake	P	February 2006	5	-17.7 ± 0.6	15.9 ± 0.5
Engraulis anchoita	Argentine anchovy	P	January 2006	5	-17.9 ± 0.2	15.7 ± 0.8
Paralichthys isosceles	Flounder	B	January 2006	5	-15.9 ± 0.4	18.0 ± 0.6
Raneya brasiliensis	Banded cusk eel	B	January 2006	5	-15.3 ± 0.6	18.8 ± 0.5
Cephalopod						
Illex argentinus	Argentine short-fin squid	P	February 2006	5	-17.0 ± 0.6	13.7 ± 0.8
Loligo sanpaulensis	South American long-fin squid	P	January 2006	5	-16.8 ± 0.2	17.2 ± 0.3
Loligo gahi	Patagonian squid	P	January 2006	4	-17.6 ± 0.4	15.7 ± 0.6
Enteroctopus megalocyathus	Red octopus	B	February 2006	5	-14.6 ± 0.7	18.9 ± 0.9
Octopus tehuelchus	Tehuelche octopus	B	February 2006	5	-14.8 ± 0.2	19.9 ± 0.4
Benthic prey[b]				4	-15.1 ± 0.6	18.9 ± 0.8
Pelagic prey[c]				6	-17.3 ± 0.5	15.9 ± 1.3

[a]Collective samples of diatoms and dinoflagellates, including several individuals.
[b]Gross mean of the benthic prey. Sample size refers to the number of species.
[c]Gross mean of the pelagic prey. Sample size refers to the number of species.
Habitat type: P, pelagic; B, benthic; *n*, sample size.

Two-way ANOVA was used to assess the effect of sex and developmental stage in bone stable isotope ratios (δ^{13}C and δ^{15}N). One-way ANOVA, followed by the Tukey *post hoc* test, was later used to compare bone stable isotope ratios (δ^{13}C and δ^{15}N) of different developmental stages within each sex. Furthermore, Student's *t*-test was used to investigate differences in bone stable isotope ratios (δ^{13}C and δ^{15}N) of both sexes in each different developmental stage.

Data are shown as mean ± standard deviation, unless otherwise stated. All statistical analyses were conducted with the SPSS 15 software package. Before all other analyses, normality was tested by means of the Lilliefors test and homoskedasticity by means of the Levene test.

Results

The von Bertalanffy growth curves for both sexes (Fig. 2) confirmed the marked sexual dimorphism of the South American sea lion, as males had an asymptotic condylobasal length of 34.6 cm, whereas that of females was 26.0 cm. Furthermore, the period of fast growth before the adulthood stasis was longer in males (7–8 years) than in females (5–7 years). Nevertheless, in both sexes there was no measurable skull growth after the sexual maturity. As a consequence, one-way ANOVA (females: $F_{3,79} = 158.206$, $P < 0.001$; males: $F_{3,110} = 159.785$, $P < 0.001$) and a Scheffe *post hoc* test (Fig. 3) revealed that the skull length of young sea lions of each sex was significantly smaller than that of sea lions at the other three developmental stages here considered, whereas no statistically significant difference was found among the individuals of each sex in the first adult, adult and senile developmental stages.

The δ^{13}C values of the primary producers ranged from -14.9 ± 1.3‰ for seaweeds to -21 ± 0.1‰ for phytoplankton, whereas those of the potential prey items ranged from -14.6 ± 0.7‰ for benthic species, like the red octopus, to -17.9 ± 0.2‰ for pelagic species, like the Argentine anchovy

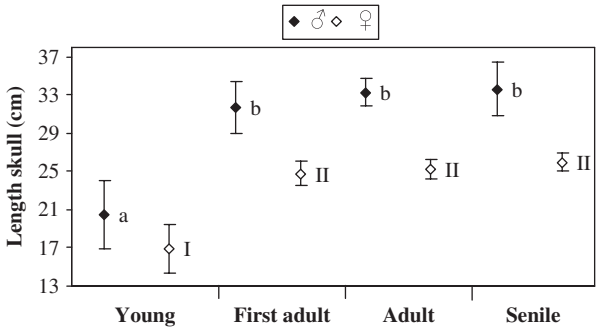

Figure 3 Mean and standard deviation of the skull length of South American sea lions *Otaria flavescens* at the four developmental stages. Developmental stages within each sex with different letters (males) or Roman numerals (females) differ in their mean values. Sample size: $n = 60$ for young males, $n = 14$ for first adult males, $n = 28$ for adult males, $n = 12$ for senile males, $n = 20$ for young females, $n = 11$ for first adult females, $n = 26$ for adult females and $n = 26$ for senile females.

(Table 2 and Fig. 4). Accordingly, benthic potential prey species (δ^{13}C: -15.1 ± 0.6‰; δ^{15}N: 18.9 ± 0.8‰) were, on average, more enriched both in ^{13}C (nested ANOVA: $F_{9,39} = 235.170$, $P < 0.001$) and ^{15}N (nested ANOVA: $F_{9,39} = 318.709$, $P < 0.001$) than pelagic species (δ^{13}C: -17.3 ± 0.5‰; δ^{15}N: 15.9 ± 1.3‰), although the δ^{15}N primarily increased with trophic level (Fig. 4).

The δ^{13}C of skull bone ranged from -13.6 to -10.7‰ for males and from -14.8 to -11.1‰ for females, whereas the δ^{15}N of skull bone ranged from 19.1 to 26.2‰ for males and from 20.1 to 25.9‰ for females (Table 1). The average δ^{13}C of skull bone ranged from -13.0 ± 0.3‰ in young males to -11.4 ± 0.3‰ in adult males and from -13.1 ± 0.8‰ in young females to -11.8 ± 0.4‰ in senile females. The average δ^{15}N of skull bone ranged from 22.0 ± 0.6‰ in senile males to 22.5 ± 1.3‰ in adult males and from 21.8 ± 1.0‰ in first adult females to 24.0 ± 1.4‰ in young females (Fig. 5). Two-way ANOVA (sex × developmental stage) revealed statistically significant differences in the average δ^{13}C of males and females ($F_{7,72} = 10.477$, $P = 0.002$) and also among the average δ^{13}C of the developmental stages ($F_{7,72} = 22.196$, $P < 0.001$). As well, there was a statistically significant interaction term ($F_{7,72} = 4.791$, $P = 0.004$), thus pointing out that the pattern of the ontogenetic change of the δ^{13}C is not the same in both sexes. This is because the δ^{13}C of both females and males increased steadily with the developmental stage, except in senile males, whose δ^{13}C decreased to a value close to that of first adults according to the Tukey *post hoc* test (Fig. 5). Pairwise comparison of the bone δ^{13}C values of males and females in the same developmental stage revealed differences for first adults and adults but not for young and senile individuals (Fig. 5).

Two-way ANOVA (sex × developmental stage) revealed statistically significant differences in δ^{15}N among the developmental stages considered ($F_{7,72} = 4.354$, $P = 0.007$) without statistically significant differences between sexes ($F_{7,72} = 2.180$, $P = 0.144$) but with a statistically significant interaction term ($F_{7,72} = 2.996$, $P = 0.036$). Such differences were because the skulls of young females were more enriched in ^{15}N than those of the individuals of the other three developmental stages (Fig. 5), as revealed by the Tukey *post hoc* test. As a consequence, the trophic level of sea lions remained roughly the same throughout their life, independent of developmental stage and sex, with the exception of young females (Fig. 5).

Discussion

The isotopic data presented here do not allow for a precise reconstruction of the composition of the diet of South American sea lions, because prey-to-predator bone fractionation factors have not been experimentally determined for this species and those determined experimentally for other pinniped species are for tissues other than bone (Hobson *et al.*, 1996; Kurle, 2002). However, the stable isotope data presented here are useful for detecting changes in the relative contribution of benthic and pelagic prey items to the diet of South American sea lions, as long as the δ^{13}C and δ^{15}N

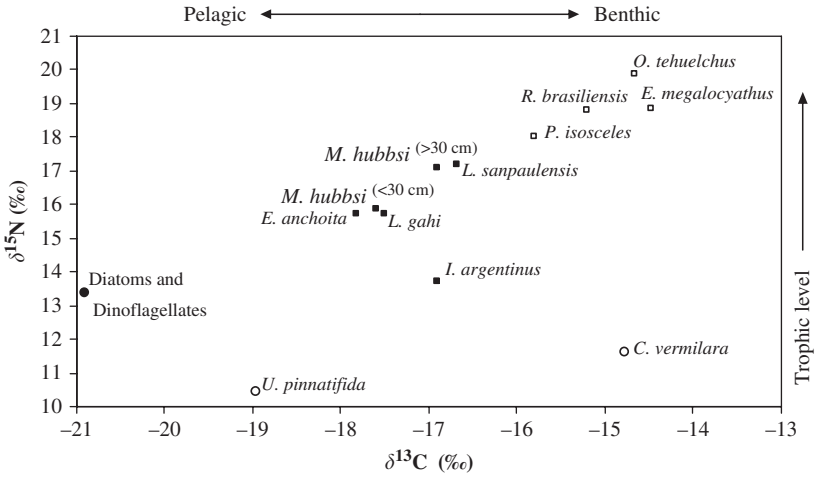

Figure 4 Mean bivariated stable isotope values of the primary producers and the main prey of the South American sea lion *Otaria flavescens* off the Chubut province. Primary producers: seaweeds (○) and phytoplankton (●). Main prey: benthic species (□) and pelagic species (■). Sample size: $n=5$ for all the species, except for the *Loligo gahi* ($n=4$) and phytoplankton ($n=2$; collective samples).

gradients in the local ecosystem have not been inverted from the time the sea lions were stranded (1990–2000) and when the samples of the potential prey species were collected (2006). More precisely, the stable isotope landscape off the Chubut province indicates that changes in the $\delta^{13}C$ of the bone material should primarily reflect changes in the proportion of benthic and pelagic prey items in the diet, whereas changes in the $\delta^{15}N$ should be primarily linked to changes in trophic level.

Results suggest that consumption of benthic prey items increased from post-weaning to adulthood in both sexes, except in senile males, thus supporting the hypothesis that the early foraging ontogeny of the South American sea lion is tightly linked to the improvement of diving skills resulting from an increase in body mass (Le Boeuf *et al.*, 1996; Horning & Trillmich, 1997). Differences in body mass explain not only why diet changed with age, but also, why first adult males and adult males had a much more benthic diet than females of the same developmental stage.

However, this interpretation of the ontogenic changes in the stable isotope ratio of skull bone is highly dependent on the actual rate of bone turnover and discrimination between age classes (Tieszen *et al.*, 1983; Hobson & Clark, 1992; Hobson, 1993). Suckling pinniped pups are more enriched in ^{15}N than their mothers, whereas the relationship between suckling pups and their mothers is less clear for ^{13}C and may be species dependent (Newsome *et al.*, 2006; Ducatez *et al.*, 2008). Experimental evidence indicates that suckling pups of the South American sea lion are more enriched in ^{15}N than their mothers are, without any significant mother-to-pup fractionation for carbon (M. Drago, unpubl. data). At least in other pinniped species, the suckling signal decays after weaning and is completely turned over from bone 10 months later (Newsome *et al.*, 2006). Conversely, bone turnover is likely to be substantially slower in the other age classes and hence stable isotope ratios in bone may be much less discernable between the older age classes than between young and first adult sea lions.

The persistence of the suckling signal may have affected the $\delta^{15}N$ values of some of the young individuals analysed

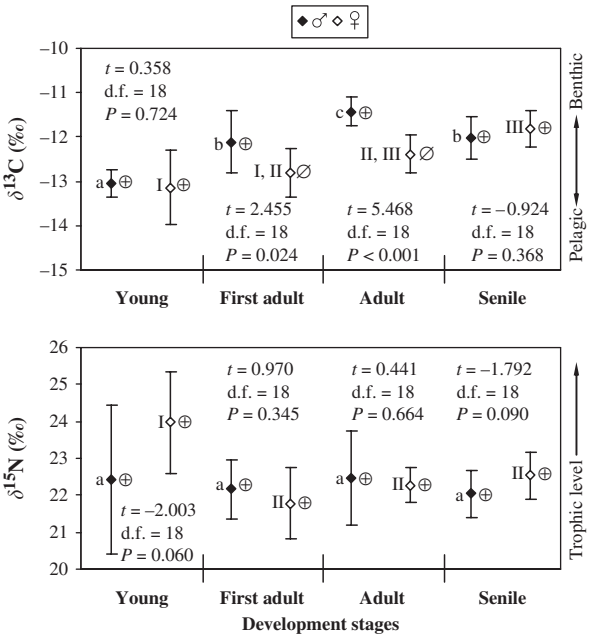

Figure 5 Mean and standard deviation of the bone $\delta^{13}C$ and $\delta^{15}N$ of males and females at the four developmental stages. Developmental stages of each sex with different letters (males) or Roman numerals (females) differ in their mean values according to the Tukey *post hoc* test. The summary statistics of the corresponding ANOVA are shown in the text. Males and females of each developmental stage with a different symbol (⊕ vs. ∅) differ in their mean values according to Student's *t*-test. Sample size: $n=10$ for each sex and developmental stage.

here, because South American sea lions are weaned when they are 6–10 months old, with males being weaned earlier than females (Crespo, 1988). Consequently, South American sea lions older than 20 months (1.8 years) are expected to have completely turned over the suckling signal, with the stable isotopic ratios of younger individuals being a mixture of the suckling signal and that of their own diet. Only three of the 10 young males included in the present study were

younger than 2 years and, hence, susceptible of exhibiting traces of the suckling signal, but up to six young females may have exhibited it. The persistence of some traces of the suckling signal in some of the young analysed probably explains why the standard deviation of the δ^{15}N of young sea lions of each sex was larger than that of other developmental stages and why the δ^{15}N of young females was higher than that of the females in other developmental stages. However, the interpretation of the ontogenic changes in the diving skills of the South American sea lions is derived from the δ^{13}C data, not affected by the persistence of traces of the suckling signal.

Length growth may explain increased consumption of benthic prey items during the early ontogeny of each sex and the differences between sexes, but the consumption of benthic prey items continued to increase steadily in both sexes after puberty, although South American sea lions have determinate length growth (Rosas *et al.*, 1993; present study). Consequently, continued improvement of diving skills through life cannot be explained only by length growth. Nothing is known about weight gain in the South American sea lion, but weight stabilizes after puberty much later than length in Steller sea lions *Eumetopias jubatus* (Winship, Trites & Calkins, 2001). Weight also increases with age in adult female New Zealand sea lions *Phocarctos hookeri* that range from 10 to 17 years old, although age explains only 7% of the weight variability (Chilvers *et al.*, 2006).

A similar weight–age pattern in South American sea lions may explain the increased access to benthic prey items of the first adult, adult and senile individuals as compared with young individuals. However, it is unlikely that it explains the steady increase in the consumption of benthic prey items in females after puberty, considering the high variability in the body weight of adult sea lions of other species (Winship *et al.*, 2001; Chilvers *et al.*, 2006), the absence of a correlation between age and dive depth in adult female New Zealand sea lions (Chilvers *et al.*, 2006) and the wide weight variability expected for female South American sea lions in agreement with the length variability (Rosas *et al.*, 1993; present study).

We believe that increased access to benthic prey items with age after puberty cannot be explained only by weight growth, although bigger individuals can dive deeper. Young pinnipeds have limited access to deep, benthic resources, not only because they have smaller oxygen stores but also because they appear unable to regulate heart rate, respiration, vasoconstriction or body temperature as effectively as adults (Rea & Costa, 1992; Ponganis *et al.*, 1993; Greaves *et al.*, 2005; Fowler *et al.*, 2007*a*,*b*). As a consequence, young pinnipeds rely on energy produced anaerobically after long/deep dives more often than adults do (Kooyman *et al.*, 1983; Burns, 1999), although adult pinnipeds foraging on the seabed often exceed their calculated aerobic dive limit (Costa & Gales, 2000, 2003; Costa, Gales & Goebel, 2001; Chilvers *et al.*, 2006). This is because tight control of the cardiorespiratory function allows adult pinnipeds to significantly reduce their rate of metabolism while submerged (Hurley & Costa, 2001), thus enabling them to have access to larger and more rewarding prey items than those available for epipelagic foragers and also reducing competition with younger individuals (Costa & Gales, 2003; Page, McKenzie & Goldsworthy, 2005).

We hypothesize that increased consumption of benthic prey items with age might depend on age-related learning. Furthermore, if improvement of those skills continues through life, pinnipeds are expected to increase dive depth and dive time with age, even after reaching final adult body size. The reduced consumption of benthic prey items by senile males is, however, intriguing and suggests a decrease in diving performance, perhaps due to a physiological debilitation caused by a very high energetic investment in breeding (Campagna & Le Boeuf, 1988). Such a hypothesis is supported by a mortality peak for 11-year-old males (Crespo, 1988) and also by a possible reduction in body weight, as reported for the Steller sea lion (Winship *et al.*, 2001). However, weight-at-age data are urgently needed to test this hypothesis.

Acknowledgements

Thanks are due to the staff of the Marine Mammal Laboratory of the CENPAT-CONICET, particularly to S. Ameghino, N. García, L. Hardtke, S. Leonardi and D. Vales for the fieldwork, to S.L. Dans and M.F. Grandi for the age assessment of the sampled individuals and to C. Gambuzza for assistance with the English. The Ministry of Education and Science (MEC) of Spain supported M.D. through a PhD fellowship. The study was funded by the Fundación BBVA through the project 'Estudio de las amenazas para la conservación de mamíferos marinos de Patagonia' (BIOCON 04), Programa Nacional de Biodiversidad, Ciencias de la Tierra y Cambio Global of the MEC of Spain through the project 'CGL2005-00922/BOS', GEF/PNUD through the project 'Conservación de la Diversidad Biológica Marina y Prevención de la Contaminación en Patagonia' (ARG 02/018) and the Zoo d'Amneville, France.

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