



Long-Term Stability in the Trophic Ecology of a Pelagic Forager Living in a Changing Marine Ecosystem

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Natural or human-induced environmental changes can modify the structure of ecological communities and thus alter food web interactions. After the collapse of hake stocks (*Merluccius hubbsi*) provoked by fisheries over the Patagonian shelf in 1997 profound changes have taken place in the community, including long-term dietary shifts in some marine vertebrate predators. Stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios in bone collagen of subadult and adult male South American fur seals (*Arctocephalus australis*) were measured for the period 1976–2017 to investigate if the changes occurred in the marine community from northern and central Patagonia affected the diet of this predator. Suess corrected $\delta^{13}\text{C}$ values and $\delta^{15}\text{N}$ values in bone collagen of fur seals did not change significantly over the study period. According to this, male fur seals have remained as pelagic foragers without changing their trophic position nor switching their main preys in the Patagonian food web over the last four decades. This long-term stability in the diet of fur seals contrasts with dietary changes reported for benthic foragers in the region. Although long-term diet studies are restricted to a few marine predators in the region, current evidence suggests that benthic-demersal foragers were more prone to dietary shifts than pelagic ones after perturbations that occurred in the marine community of northern and central Patagonia.

Keywords: high trophic level marine predator, Patagonian shelf, South American fur seals, dietary reconstruction, stable isotope analysis, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, collagen

INTRODUCTION

Heavy perturbations, either natural or anthropogenic, can modify the structure of ecological communities and thus alter food web interactions. The South Atlantic Ocean has a long history of large-scale removal of predators as a consequence of whaling, sealing and fishing. Populations of southern right whales *Eubalaena australis*, southern elephant seals *Mirounga leonina*, South American fur seals *Arctocephalus australis*, South American sea lions *Otaria flavescens*, and tope sharks *Galeorhinus galeus*, among other marine predators, were reduced from the Patagonian waters between end-18th and mid-20th centuries (Mateo, 2015; Würsig et al., 2018). This reduction in the biomass of large marine vertebrates is thought to be the main cause of changes in the regional food web structure, as modern food webs are longer, less redundant and less overlapping than ancient ones (Saporiti et al., 2014).

The Patagonian Shelf Large Marine Ecosystem is one of the most productive and complex marine regions in the Southern Hemisphere (Heileman, 2009). Approximately bounded by 41° and 48° S, the marine food web of northern and central Patagonia is organized around the anchovy *Engraulis anchoita*, hake *Merluccius hubbsi* and shortfin squid *Illex argentinus* (Angelescu and Prenski, 1987). These three core species support a large number of high trophic level predators (Croxall and Wood, 2002; Favero and Silva Rodríguez, 2005; Koen-Alonso and Yodzis, 2005, and references therein; Romero et al., 2012), and hake and shortfin squid also support intensive fishing (Brunetti et al., 1998; Bertolotti et al., 2001). On the other hand, the anchovy fishery is very underdeveloped in Patagonian waters and the main fishing grounds have been concentrated traditionally off Buenos Aires province (Hansen, 2000). In addition, there is an important fishery targeting the red shrimp *Pleoticus muelleri* (Figure 1A).

Over the Patagonian shelf, far more than 70% of hake catches have been extracted historically south of 41° S (MPyT-SA, 2020). Since 1960s, the landings of hake by the Argentine fleet increased steadily, peaking in the mid 1990s and resulting on the overfishing of regional stocks (Bertolotti et al., 2001). On the other hand, fishing for red shrimp occurs mainly in coastal waters off northern and central Patagonia, between 43° and 46° S (Bertuche et al., 2000). This shrimp fishery generates high revenues and is yielding record catches in recent years, with 254,905.9 tonnes landed in 2018 (MPyT-SA, 2020). Hake smaller than 30 cm and anchovies are largely discarded by the shrimp fishery (Crespo et al., 1997; Gandini et al., 1999), as well as large amounts of lobster krill *Munida gregaria* (Varisco and Vinuesa, 2007). For the hake fishery operating south of the 41° S parallel, hake discards during the period 1986–1997 increased from 15,563 tonnes (1986) to 104,592 tonnes (1997), whereas these figures decreased and varied between 6,000 and 22,000 tonnes during the period 1998–2004 (Góngora et al., 2012). For its part, hake discards by the shrimp fishery varied between 17,195 and 46,452 tonnes during the period 1998–2004 (Góngora et al., 2012). Additionally, it is estimated that around 310,000 tonnes per year of several species of bony fishes and elasmobranchs were returned dead to the ecosystem as part of the by-catch of the hake bottom-trawl and shrimp fisheries in the region during the mid-1990s (LAMAMA, unpublished data).

Following the collapse of hake catches in 1997, an extensive year-round fishing closure, the Patagonian Closed Area, was created to protect juveniles and spawners of the species. After a decade of protection, the structure of the demersal fish assemblage changed in this offshore marine protected area (Alemany et al., 2013). Among the main changes, Alemany et al. (2013) detected a greater abundance of hake and other demersal fish species, increasing hake juvenile size, and a higher proportion of juveniles aged 2+ inside the protected area. In parallel, several high trophic level predator populations began to recover during the 20th century after the implementation of various legal protections (Croxall and Wood, 2002; Schiavini et al., 2005; Crespo et al., 2012, 2015; Ferrari et al., 2013; Raya Rey et al., 2014; Grandi et al., 2015; Baylis et al., 2019).

Massive extraction of marine fauna biomass seems to have produced heavy perturbations in the regional ecosystem. For

instance, the harvesting of South American sea lions that took place between 1930 and 1960, together with the removal of large quantities of hake biomass by fisheries during mid-1990s, are thought to have caused a severe reorganization of the whole marine ecosystem in northern and central Patagonia (Koen-Alonso and Yodzis, 2005). In addition, there is evidence of long-term changes in the diet of some large marine vertebrates as a result of fisheries activities, such as in spiny dogfish *Squalus acanthias* (Koen-Alonso et al., 2002), yellownose skates *Zearaja chilensis* (Buren, 2004), South American sea lions (Drago et al., 2009), and black-browed albatrosses *Thalassarche melanophris* (Mariano-Jelicich et al., 2017).

The South American fur seal *A. australis* (von Zimmermann, 1783) is a high trophic level predator in the ecosystems of the southwestern South Atlantic and the southeastern South Pacific oceans. This predator is considered a generalist feeder (Franco-Trecu et al., 2014), foraging upon a wide variety of prey (Naya et al., 2002; Crespo et al., 2008; Oliveira et al., 2008; Baylis et al., 2014). Individuals of the species forage over both the continental shelf and the shelf-break (Dassis et al., 2012; Mandiola et al., 2015; Baylis et al., 2018). The existence of some degree of competition for shared resources between fur seals and fisheries has been suggested through all its distribution range (Naya et al., 2002; Szteren et al., 2004; Crespo et al., 2008; Vargas Hernández, 2012; Baylis et al., 2014, 2018; Vales et al., 2015). In northern and central Patagonian waters, male fur seals forage mainly on shortfin squid, anchovy, juvenile hake and decapod crustaceans (red shrimp and lobster krill) (Vales et al., 2015). With the exception of lobster krill, all these prey species are of commercial interest (Figure 1A). Shortfin squid and hake consumed by fur seals seem to be smaller than those exploited by fisheries (LAMAMA, unpublished data), although this result can be biased if fur seals break-up larger individuals and consume only some parts. In any case, the use of the same resource with different sizes (or differences in space and time) does not necessarily mitigate the intensity of the interaction (Harwood, 1987). Therefore, some degree of interaction between fisheries and fur seals is expected, although it is unknown how this might affected the long-term diet of this predator in the region.

Stable isotope analysis has become a valuable tool for the study of marine mammal ecology, allowing the reconstruction of dietary changes in some species through the analysis of specimens deposited in museum and scientific collections (Newsome et al., 2010). Stable isotope ratios of N and C are based on a predictable relation between the isotopic composition of a consumer and its diet (DeNiro and Epstein, 1978, 1981). For aquatic organisms, $\delta^{15}\text{N}$ values can provide data on trophic level (Minagawa and Wada, 1984; Post, 2002), while $\delta^{13}\text{C}$ values can reveal information on feeding locations, including the relative use of benthic vs. pelagic and coastal vs. oceanic prey (Hobson et al., 1994; France, 1995). This general pattern also applies for the Patagonian marine ecosystem, where benthic prey are more enriched in both ^{15}N and ^{13}C than pelagic ones (Forero et al., 2004; Ciancio et al., 2008; Drago et al., 2009; Vales et al., 2015). By using stable isotope ratios in bone collagen, it is possible to study the long-term trends in dietary patterns of vertebrates.

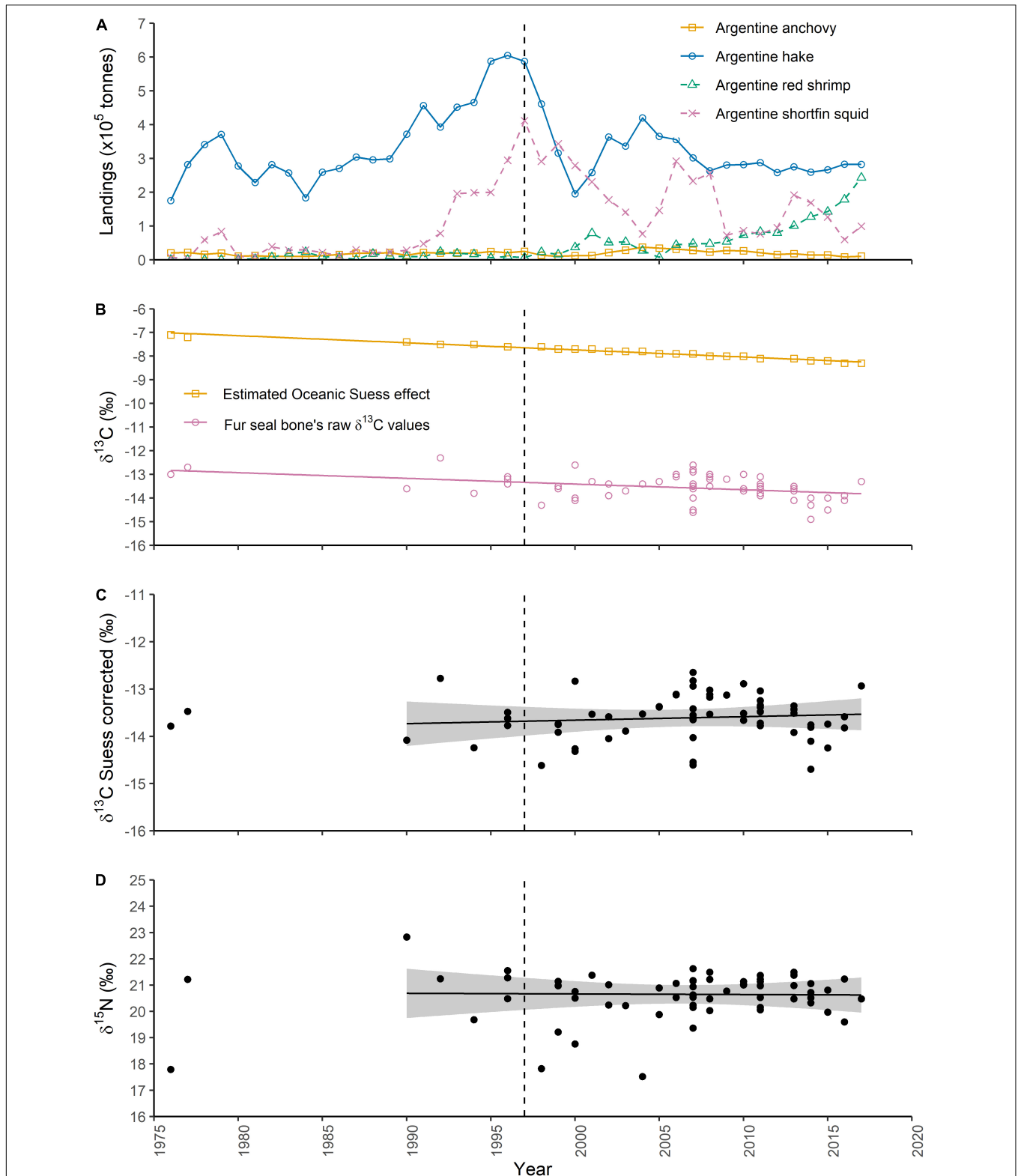


FIGURE 1 | (A) Fishery landings of short-fin squid, hake, anchovy and red shrimp off Argentine coast (Sánchez et al., 2012; Navarro et al., 2014, 2019; MPyT-SA, 2020). The dashed vertical line in 1997 indicates when the hake fishery collapsed. Temporal trend in the stable isotope ratios in bone collagen of subadult and adult male South American fur seals from northern and central Patagonia: **(B)** raw $\delta^{13}\text{C}$ values (empty pink circles) and the expected change in $\delta^{13}\text{C}$ in the ocean caused by anthropogenic activity, namely the Oceanic Suess effect (empty orange squares); **(C)** Suess corrected $\delta^{13}\text{C}$ values; and **(D)** $\delta^{15}\text{N}$ values. The shaded gray bands surrounding the estimated trends in **(C,D)** are approximate 95% across-the-function confidence intervals.

Bone collagen has a slow turnover rate and integrates the stable isotope ratios over several years in marine mammals (Hirons et al., 2001; Riofrío-Lazo and Aurióles-Gamboa, 2013), allowing the comparison of the isotope ratios of many individuals over long periods of time (Schoeninger and DeNiro, 1984; Lee-Thorp et al., 1989; Hirons et al., 2001; Dalerum and Angerbjörn, 2005). Therefore, any change in the diet of the fur seal population over a long timescale should be reflected in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of their bone tissues.

This study uses stable carbon and nitrogen isotope ratios in bone collagen of South American fur seals to investigate if the reorganization of the marine community in Patagonian waters (Koen-Alonso and Yodzis, 2005; Saporiti et al., 2014) affected the diet of this predator over the last four decades. More precisely, we test the hypothesis that decreasing availability of hake resulted in a decrease in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of the bone tissues of fur seals, because of increased consumption of anchovies and squids (preys depleted in ^{15}N and ^{13}C).

MATERIALS AND METHODS

Sampling

Sixty-two skulls of male South American fur seals were sampled from individuals collected between 1976 and 2017 along the Atlantic coast of northern and central Patagonia (between 41° and 46° S). However, it is important to mention that samples are not distributed evenly over time. Two samples correspond to the years 1976 and 1977, some are scattered between the years 1990 and 1995, and the remaining correspond to the more recent years (i.e., 1996–2017). Specimens are deposited at the osteological collection of the Marine Mammal Laboratory (CESIMAR, CONICET). For this study, only male individuals older than 5 years (sub-adult and adult age classes) were considered, this is because juvenile males have a different diet than the subsequent age classes (Vales et al., 2015). Individual ages were estimated from counts of growth layer groups (GLGs) in the dentine and/or in the cementum of teeth assuming that one GLG is deposited per year (Schiavini et al., 1992; Crespo et al., 1994; Molina-Schiller and Pinedo, 2004). In order to prevent damage to the skulls, a small fragment of maxillo-turbinal bone from the nasal cavity was sampled (Drago et al., 2009), and then stored dry until isotope analysis.

The analysis of stomach contents, scats and C and N stable isotope ratios point to squids (*I. argentinus* and *Doryteuthis gahi*), anchovies (*E. anchoita*), juvenile hakes (*M. hubbsi*), and decapod crustaceans (*P. muelleri* and *M. gregaria*) as the main prey in the diet of fur seals in northern and central Patagonia (Vales et al., 2015). Accordingly, these prey species were sampled from January 2006 to April 2010 from the study region for isotope analysis. White dorsal muscle was sampled for fish, muscle for shrimp, and mantle for squid; whereas in the case of lobster krill (*M. gregaria*) the whole body was sampled due to its small size. All prey samples were stored in a freezer at -20°C until analysis. Fish, cephalopod, crustacean, and some of the isotope values in bone of fur seals have been published in previous papers (Drago et al., 2009; Vales et al., 2015) (Tables 1, 2).

Stable Isotope Analysis

Maxillo-turbinal bone and prey samples were dried in a stove at 60°C for 36–48 h and ground to a fine powder with a mortar and pestle. Lipids were extracted from samples through sequential washes with a chloroform/methanol (2:1) solution (Folch et al., 1957). Since bone samples contain a high concentration of inorganic carbon that may add undesirable variability to $\delta^{13}\text{C}$ (Lorrain et al., 2003), they were treated by soaking for 24 h in 0.5 N hydrochloric acid (HCl) to decarbonize them (Newsome et al., 2006). Given that HCl treatment may affect $\delta^{15}\text{N}$ (Bunn et al., 1995), each sample was divided into 2 subsamples: one was used for ^{13}C analysis after decarbonizing and the other one was used for ^{15}N analysis without decarbonizing.

Approximately 0.5–1 mg of dried bone and 0.3 mg of prey tissues were weighed into tin cups. Then, samples were combusted at 900°C , and analyzed in a continuous flow isotope ratio mass spectrometer. Samples were analyzed at the Centres Científic i Tecnològics of the University of Barcelona (CCiT-UB), the Instituto de Geocronología y Geología Isotópica (INGEIS-CONICET/UBA), and the University of New Mexico Center for Stable Isotopes (UNM-CSI). In all cases, international isotope secondary standards given by the International Atomic Energy Agency (IAEA) were used for calibration at a precision equal to or less than 0.3 ‰ for nitrogen and 0.2 ‰ for carbon. Stable isotope values of paired bone samples ($n = 5$) analyzed at the CCiT-UB and the INGEIS-CONICET/UBA laboratories proved to be not statistically significant (Vales et al., 2015). On the other hand, we did not have paired samples to test potential biases among the isotope values reported by these two laboratories and the UNM-CSI, thus we had to rely on the assumption that measurements conducted at these three labs are comparable. Stable isotope abundance is expressed in standard δ notation relative to carbonate Pee Dee Belemnite and atmospheric nitrogen. Carbon to nitrogen (C:N) atomic ratio was used as proxy for data quality (e.g., conservation status of the isotopic ratio in bone collagen and adequate lipid extraction; DeNiro, 1985; Newsome et al., 2010).

The Suess Effect Correction

During the last three centuries, the accelerating release of anthropogenic CO_2 to the atmosphere due to fossil fuel burning and deforestation has been decreasing rapidly the content of ^{13}C in atmospheric CO_2 , and this is called the Suess effect (Keeling, 1979). In turn, CO_2 is exchanged between air and water and the isotope values of atmospheric CO_2 and aqueous CO_2 equilibrate. In this way, the global oceanic ^{13}C Suess effect follows the atmospheric ^{13}C Suess effect record, although with a roughly decadal lag due to the long equilibration time-scale of ^{13}C (Gruber et al., 1999; Körtzinger et al., 2003; Quay et al., 2003). In turn, as ^{13}C -depleted oceanic aqueous CO_2 increases, phytoplankton fractionation increases, and thus phytoplankton $\delta^{13}\text{C}$ decreases through time (Mizutani and Wada, 1982; Laws et al., 1995). Because of this, the Suess effect needs to be accounted when interpreting temporal changes in $\delta^{13}\text{C}$ in the aquatic environment (Verburg, 2007). Accordingly, raw $\delta^{13}\text{C}$ values of the skeletal material of fur seals were corrected applying the

TABLE 1 | Stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), and the C:N mass ratio (mean \pm SD) of the main prey of South American fur seals.

Prey species	Common name	Ecological group	n	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C:N mass ratio
<i>Engraulis anchoita</i> ^a	Argentine anchovy	SPF	5	-17.9 \pm 0.2	15.7 \pm 0.8	3.1 \pm 0.0
<i>Merluccius hubbsi</i> (<30 cm) ^b	Argentine hake	SPF	4	-16.8 \pm 0.2	16.6 \pm 0.1	3.1 \pm 0.0
<i>Illex argentinus</i> ^a	Argentine shortfin squid	DPC	5	-17.0 \pm 0.6	13.7 \pm 0.8	3.0 \pm 0.0
<i>Doryteuthis gahi</i> ^a	Patagonian squid	DPC	4	-17.6 \pm 0.4	15.7 \pm 0.6	3.0 \pm 0.0
<i>Pleoticus muelleri</i> ^b	Argentine red shrimp	DBCcr	5	-15.9 \pm 0.4	16.7 \pm 0.3	2.9 \pm 0.0
<i>Munida gregaria</i> morph <i>subrugosa</i> ^b	Lobster krill	BCr	5	-15.7 \pm 0.8	16.8 \pm 0.3	3.3 \pm 0.1

Abbreviations for ecological groups are as follows: SPF, small pelagic fish; DPC, demersal pelagic cephalopod; DBCcr, demersal benthic crustacean; BCr, benthic crustacean. Sample size (n). Data sourced from Drago et al. (2009) and Vales et al. (2015) are indicated with the superscript letters "a" and "b," respectively.

equation developed by Verburg (2007) for correcting the Suess effect in organic matter from lacustrine environments. However, this equation was modified in the present study to consider the 10 years lag existing for isotopic equilibration between atmospheric CO_2 and oceanic aqueous CO_2 :

Oceanic Suess effect correction factor_(year Y)

$$= 7.7738118 \times 10^{-16} \times (Y - 10)^6 - 1.2222044 \times 10^{-11} \\ \times (Y - 10)^5 + 7.1612441 \times 10^{-8} \times (Y - 10)^4 - 2.1017147 \\ \times 10^{-4} \times (Y - 10)^3 + 3.3316112 \times 10^{-1} \times (Y - 10)^2 \\ - 273.715025 \times (Y - 10) + 91703.261$$

where Y is the year when the fur seal died and was found beach stranded. The result of the equation, which is expressed in per mille units (‰), is added to the raw $\delta^{13}\text{C}$ data. All Suess corrected $\delta^{13}\text{C}$ values were referenced to the year 2008, as this is the average year for the prey-sampling period (2006–2010) (Figure 1B).

Data Analysis

Generalized additive mixed models (GAMMs) were used to test temporal trends in the $\delta^{15}\text{N}$ and Suess corrected $\delta^{13}\text{C}$ values of skull bone samples between 1990 and 2017 years. By using GAMMs, it is possible to observe the tendency of stable isotope ratios to change over time without defining a particular curve order *a priori*, while also accounting for temporal correlation (Wood, 2017; Simpson, 2018). GAMMs were fitted using a Gaussian distribution with an identity link function in the Mixed GAM Computation Vehicle (mgcv version 1.8–28) package with the restricted maximum likelihood (REML) smoothing method (Wood, 2017) in R 3.6.0 (R Development Core Team, 2019). Models for $\delta^{15}\text{N}$ and Suess corrected $\delta^{13}\text{C}$ data were fitted using basis dimensions (k) of 20 and 5, respectively, after checking via the gam.check() function in mgcv that these basis functions were sufficiently large to capture the wiggleness in the data (i.e., p -value > 0.05). To account for residual temporal autocorrelation, a continuous-time first-order autoregressive [CAR(1)] process was introduced to models by selecting the corCAR1() function in the correlation argument of the gamm() function. The time series were constructed by using the weighted average of the isotopic values per year and by computing the normalization of these values, as explained by Wood (2017). Model assumptions were verified by observing

the plots provided by the gam.check() function (e.g., plotting residuals versus fitted values, etc.).

The carbon and nitrogen isotope ratios of fur seal tissues were compared to those of its main prey in a $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplot through the application of trophic discrimination factors (TDFs) to consumer isotopic values. Estimated TDFs from diet to bone reported for adult male fur seals were used ($\delta^{15}\text{N} = +5.1$ ‰; $\delta^{13}\text{C} = +3.6$ ‰; Vales et al., 2014).

RESULTS

The $\delta^{15}\text{N}$ and Suess corrected $\delta^{13}\text{C}$ values of skull bone ranged from +17.5 to +22.8 ‰ (mean = +20.6 ‰, SD = 0.9) and from -14.7 to -12.6 ‰ (mean = -13.6 ‰, SD = 0.5), respectively (Table 2). Carbon to nitrogen (C:N) atomic ratio ranged from 3.2 to 3.6 (mean = 3.3, SD = 0.1), falling within the expected range (from 2.9 to 3.6) for unaltered bone samples (DeNiro, 1985).

No temporal trend was found in the stable isotope ratios of subadult and adult male fur seals during the period 1990–2017 [$\delta^{15}\text{N}$: effective degrees of freedom (edf) = 1, $F = 0.008$, p -value = 0.929, $N = 23$; Suess corrected $\delta^{13}\text{C}$: edf = 1, $F = 0.329$, p -value = 0.572, $N = 23$] (Figures 1C,D). After correcting the $\delta^{15}\text{N}$ and the Suess corrected $\delta^{13}\text{C}$ values for diet-to-bone discrimination, the bivariate signal of most subadult and adult male fur seals lay within a polygon formed by shortfin squid, anchovy, Patagonian squid, juvenile hakes, and decapod crustaceans (red shrimp and lobster krill) (Figure 2).

DISCUSSION

The present study reveals no major changes in the trophic ecology of subadult and adult male fur seals in Patagonian waters during at least the past three decades (period 1990–2017), as Oceanic Suess corrected carbon and nitrogen isotope ratios in bone collagen were remarkably stable during this period. Moreover, isotopic values from two individuals collected in 1976 and 1977 suggest that the long-term stability in the diet may have extended further in time. Unfortunately, the gap existing in our isotopic dataset over the period 1978–1989 prevents us from modeling the data beyond the 1990s and assessing this last hypothesis. Nevertheless, in spite of the uneven distribution of the data over time, the 1990–2017 dataset allow us to test potential shifts in the diet of fur seals around 1997 due to the hake stock reduction

TABLE 2 | Stable isotope ratios ($\delta^{15}\text{N}$, raw $\delta^{13}\text{C}$, and Suess corrected $\delta^{13}\text{C}$) in bone collagen of subadult and adult male South American fur seals dead stranded during the period 1976–2017 in northern and central Patagonia.

Sample ID	Stranding year	$\delta^{15}\text{N}$ (‰)	Raw $\delta^{13}\text{C}$ (‰)	Suess corrected $\delta^{13}\text{C}$ (‰)	C:N atomic ratio
LAMAMA Aa 011	1976	17.8	-13.0	-13.8	3.2
LAMAMA Aa 010	1977	21.2	-12.7	-13.5	3.3
LAMAMA Aa 001 ^a	1990	22.8	-13.6	-14.1	3.2
LAMAMA Aa 003 ^a	1992	21.2	-12.3	-12.8	3.2
LAMAMA Aa 005 ^a	1994	19.7	-13.8	-14.2	3.3
LAMAMA Aa 012 ^a	1996	21.3	-13.1	-13.5	3.3
LAMAMA Aa 015 ^a	1996	21.5	-13.4	-13.8	3.3
LAMAMA Aa 018 ^a	1996	20.5	-13.2	-13.6	3.3
LAMAMA Aa 022 ^a	1998	17.8	-14.3	-14.6	3.3
LAMAMA Aa 019 ^a	1999	19.2	-13.5	-13.7	3.2
LAMAMA Aa 023 ^a	1999	21.0	-13.5	-13.7	3.4
LAMAMA Aa 024 ^a	1999	21.1	-13.6	-13.9	3.4
LAMAMA Aa 026 ^a	2000	20.5	-14.1	-14.3	3.4
LAMAMA Aa 027 ^a	2000	18.8	-12.6	-12.8	3.2
LAMAMA Aa 028 ^a	2000	20.8	-14.0	-14.3	3.3
LAMAMA Aa 029	2001	21.4	-13.3	-13.5	3.3
LAMAMA Aa 032 ^a	2002	20.2	-13.9	-14.0	3.2
LAMAMA Aa 036 ^a	2002	21.0	-13.4	-13.6	3.2
LAMAMA Aa 033 ^a	2003	20.2	-13.7	-13.9	3.2
LAMAMA Aa 035 ^a	2004	17.5	-13.4	-13.5	3.2
LAMAMA Aa 038 ^a	2005	19.9	-13.3	-13.4	3.2
LAMAMA Aa 044 ^a	2005	20.9	-13.3	-13.4	3.2
LAMAMA Aa 045 ^a	2006	21.1	-13.1	-13.1	3.3
LAMAMA Aa 002	2006	20.5	-13.0	-13.1	3.3
LAMAMA Aa 048 ^a	2007	20.2	-13.6	-13.6	3.3
LAMAMA Aa 050 ^a	2007	20.2	-12.9	-12.9	3.2
LAMAMA Aa 051 ^a	2007	20.9	-12.6	-12.6	3.2
LAMAMA Aa 052 ^a	2007	20.6	-14.6	-14.6	3.2
LAMAMA Aa 056 ^a	2007	21.2	-14.5	-14.5	3.5
LAMAMA Aa 059 ^a	2007	21.6	-12.8	-12.8	3.2
LAMAMA Aa 060 ^a	2007	21.2	-13.4	-13.4	3.3
LAMAMA Aa 061 ^a	2007	19.4	-13.6	-13.6	3.3
LAMAMA Aa 062 ^a	2007	20.5	-13.5	-13.6	3.3
LAMAMA Aa 058 ^a	2007	20.6	-14.0	-14.0	3.5
LAMAMA Aa 020 ^a	2008	20.0	-13.1	-13.1	3.3
LAMAMA Aa 021	2008	20.5	-13.5	-13.5	3.2
LAMAMA Aa 042 ^a	2008	21.2	-13.2	-13.2	3.3
LAMAMA Aa 043 ^a	2008	21.5	-13.0	-13.0	3.4
LAMAMA Aa 073 ^a	2009	20.8	-13.2	-13.1	3.2
LAMAMA Aa 074 ^a	2010	21.0	-13.0	-12.9	3.2
LAMAMA Aa 078	2010	21.0	-13.6	-13.5	3.2
LAMAMA Aa 079 ^a	2010	21.1	-13.7	-13.7	3.4
LAMAMA Aa 081 ^a	2011	21.2	-13.1	-13.0	3.4
LAMAMA Aa 083 ^a	2011	20.2	-13.9	-13.8	3.5
LAMAMA Aa 084 ^a	2011	20.1	-13.6	-13.5	3.4
LAMAMA Aa 085 ^a	2011	21.1	-13.5	-13.3	3.4
LAMAMA Aa 086 ^a	2011	21.4	-13.4	-13.2	3.5
LAMAMA Aa 088 ^a	2011	21.0	-13.8	-13.7	3.6
LAMAMA Aa 087	2011	20.5	-13.5	-13.4	3.4
LAMAMA Aa 090 ^a	2013	20.5	-13.6	-13.4	3.4

(Continued)

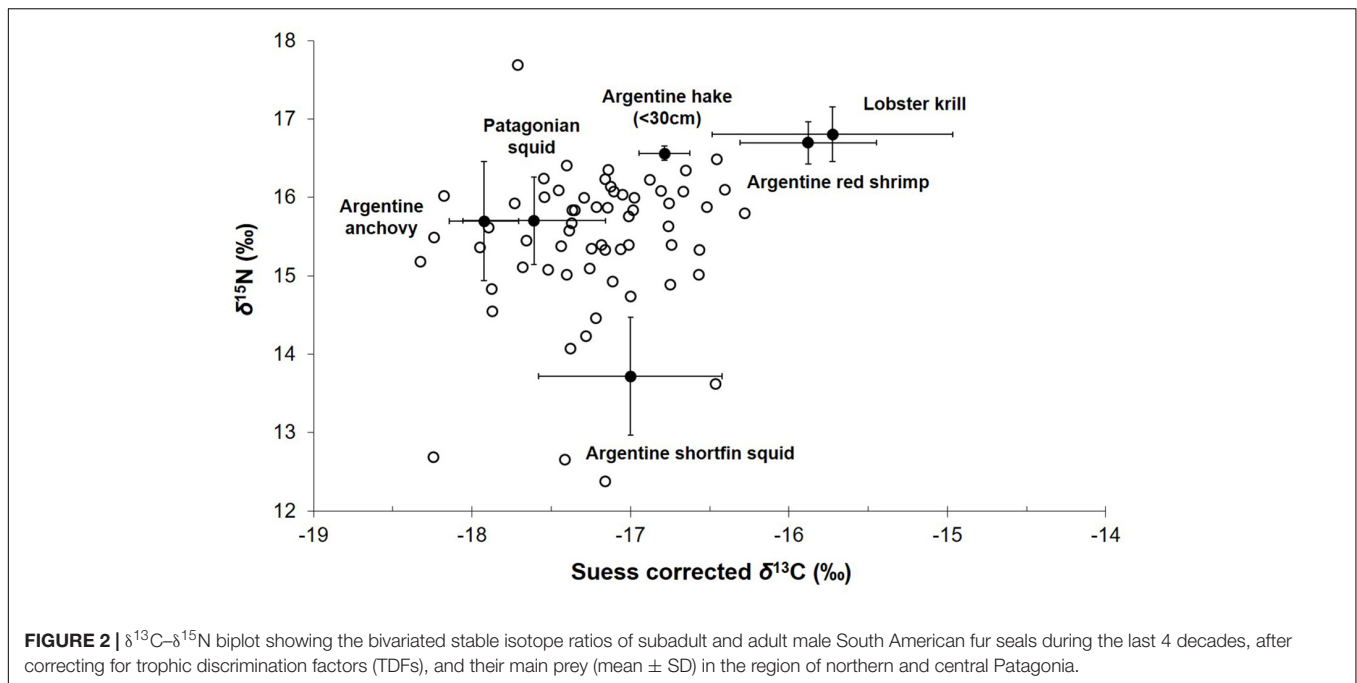
TABLE 2 | Continued

Sample ID	Stranding year	$\delta^{15}\text{N}$ (‰)	Raw $\delta^{13}\text{C}$ (‰)	Suess corrected $\delta^{13}\text{C}$ (‰)	C:N atomic ratio
LAMAMA Aa 094	2013	21.4	-14.1	-13.9	3.2
LAMAMA Aa 091	2013	21.0	-13.5	-13.4	3.4
LAMAMA Aa 103	2013	21.5	-13.7	-13.5	3.3
LAMAMA Aa 107	2014	21.1	-14.3	-14.1	3.3
LAMAMA Aa 108	2014	20.7	-14.0	-13.8	3.3
LAMAMA Aa 109	2014	20.3	-14.9	-14.7	3.5
LAMAMA Aa 105	2014	20.5	-14.0	-13.8	3.2
LAMAMA Aa 111	2015	20.0	-14.5	-14.2	3.6
LAMAMA Aa 136	2015	20.8	-14.0	-13.7	3.5
LAMAMA Aa 125	2016	19.6	-13.9	-13.6	3.3
LAMAMA Aa 133	2016	21.2	-14.1	-13.8	3.5
LAMAMA Aa 131	2017	20.5	-13.3	-12.9	3.4

Data sourced from Vales et al. (2015) are indicated with the superscript letter "a."

provoked by the fishery. As a result, the isotope ratios in bone of fur seals, which are expected to reflect the diet over the last years of life of individuals, did not evidence significant changes in the temporal trend. Such temporal stability in the diet of fur seals at first seem surprising, as profound changes have taken place in the marine community of northern and central Patagonia (Koen-Alonso and Yodzis, 2005).

The long-term reconstruction of predator diets through stable isotope analysis requires, in parallel, to account for changes over time in the stable isotope baseline of the ecosystem. This is because any change affecting the stable isotope ratios in primary producers is expected to be transferred upwards in the food web and be reflected in top consumers (Hirons et al., 2001). Unfortunately, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ baseline time series are not available for Patagonian waters and hence natural environmental changes potentially affecting the isotope signature at the base of the food web over time cannot be considered. On the other hand, the Oceanic Suess effect could be corrected for $\delta^{13}\text{C}$ values in bone collagen of fur seals by using the equation developed by Verburg (2007) for $\delta^{13}\text{C}$ values in atmospheric CO_2 for the period 1700–2000. This equation was modified in the present study to account for the 10 years lag existing for isotopic equilibration between atmospheric CO_2 and oceanic aqueous CO_2 (Gruber et al., 1999; Körtzinger et al., 2003; Quay et al., 2003). However, this adjustment in the equation produced no relevant changes in the results, as differences between paired atmospheric and oceanic Suess corrected $\delta^{13}\text{C}$ values were in the order of 0.004–0.007 ‰. In addition, it is important to note that the dataset presented here spans beyond the year 2000. Nevertheless, $\delta^{13}\text{C}$ values obtained from the Verburg's equation during the first two decades of the 21st century agree with the more recent atmospheric $\delta^{13}\text{C}$ records that extend to the year 2015 (Graven et al., 2017). Therefore, we understand that the Verburg's equation is a reliable method for correcting the carbon dataset. Using this equation, we estimated the overall Suess effect from 1976 to 2017 in 1.16 ‰. This figure is consistent with the reported by Graven et al. (2017), although is several times higher than the estimation developed by Hilton et al. (2006) to account



for the Suess effect in marine predators during the same period (0.11 ‰). Because of this, Suess corrected $\delta^{13}\text{C}$ values reported in this study for fur seals are not directly comparable with values from other studies using the Hilton's equation (e.g., Quillfeldt et al., 2010; Mariano-Jelicich et al., 2017).

After accounting for the Oceanic Suess effect, $\delta^{13}\text{C}$ values in bone collagen of male fur seals showed no temporal trend. This implies that the decreasing trend observed in raw $\delta^{13}\text{C}$ values reflects the input of anthropogenic CO_2 in the marine aquatic environment of the region over time, rather than a dietary shift in fur seals. Likewise, $\delta^{15}\text{N}$ values did not exhibit any temporal shifts throughout the study period. According to this, male fur seals from northern Patagonia have remained at the same trophic position and have not switched their main prey species over the last four decades. However, this does not mean that the diet of fur seals has not changed at all, because different proportions of assimilated prey may result into similar average stable isotope ratios in the tissues of the predator. Nevertheless, major changes in the relative contribution of pelagic and demersal prey to the diet of fur seals over the Patagonian shelf in the period studied can be ruled out.

Likewise, male fur seals inhabiting the neighbor ecosystem of the Río de la Plata estuary and surroundings had steady $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values during the period 1994–2011, despite the varying abundance of demersal-benthic prey induced by fisheries in the region (Vales et al., 2014). Nonetheless, such stability throughout time in the stable isotope ratios of fur seals from the Río de la Plata and adjoining waters does not hold when the carbon and nitrogen isotope data set span a longer period of time and shifts in the isotopic baseline are considered. Baseline corrected carbon and nitrogen stable isotope ratios were found to increase significantly in male and female fur seals in the Río de la Plata from 1944 to 2012, probably as a consequence of the increased consumption of

high trophic level demersal prey over time (Drago et al., 2017). On the other hand, demersal sciaenid fishes do not abound in the Patagonian waters and the fur seals rely upon other trophic resources available (see below). This may explain in part the different responses of fur seal populations over time between the Río de la Plata and the Patagonian ecosystems.

According to the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplot, the main prey targeted by male fur seals over the last four decades were pelagic squid, small pelagic fishes and decapod crustaceans (Vales et al., 2015; this study). Most of these trophic resources are shared between fisheries and fur seals in the Patagonian region (see section "Introduction"). Nevertheless, the collapse of hake stocks caused by fisheries development seems to have not affected the diet of male fur seals, despite juvenile hakes being one of the main prey of this predator (Vales et al., 2015).

In any case, the long-term stability in the trophic ecology recorded in fur seals from Patagonia is remarkable, as other predators have undergone marked dietary shifts in recent decades. For instance, mature and large individuals of the spiny dogfish are predators feeding mostly of demersal and benthic species (Koen-Alonso et al., 2002). Diet studies on these sharks over the period 1984–1998 indicated a switch from hake as the main prey in 1984–1985 and 1994 to shortfin squids in 1998 (Koen-Alonso et al., 2002). Such a dietary shift was related to the major decrease of the hake population in 1997 due to overfishing and the increase of squid abundance between 1994 and 1999 (Koen-Alonso et al., 2002). In a similar way, yellownose skates that are predators with demersal and benthic feeding habits, switched their diet between 1996–1998 and 2000–2001 periods. The main changes involved a delay in the size at which these skates shift from a carcinophagous diet to a piscivorous diet, and the increase in the consumption of invertebrates to the detriment of fish relevance in diet (Koen-Alonso et al., 2001;

Buren et al., 2003; Buren, 2004). For its part, South American sea lions exhibit differences in diet between the sexes, with males feeding mainly on benthic resources, and females consuming more pelagic prey than adult males throughout the year (Drago et al., 2009, 2010). During the period 1974–2002, sea lions revealed a decreasing trend in $\delta^{13}\text{C}$ values, which was interpreted as a dietary switch from benthic to pelagic prey (Drago et al., 2009). Such a change in diet was less marked in adult females than in adult males, as females had a more pelagic diet through all the study period. In this case, the dietary shift was triggered by the reduction of the hake biomass resulting from overfishing, massive discard of pelagic fish and the sea lion population recovery in the region (Drago et al., 2009). In short, dietary shifts seem to have been more profound in adult male sea lions, less marked in adult female sea lions, and absent in subadult and adult male fur seals; whereas yellownose skates, and mature and large spiny dogfishes, also exhibited some degree of dietary change through time. According to these, we suggest that predators relying on benthic and demersal resources were more prone to suffer dietary shifts than those depending on pelagic prey after the changes induced by fisheries activity in the marine community of northern and central Patagonia. Nevertheless, more long-term diet studies are needed in a greater variety of high trophic level predators to contrast this hypothesis.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/supplementary material.

ETHICS STATEMENT

No manipulation of living animals occurred in this study, as bone samples come from fur seals found dead on beaches, and prey samples were obtained from fishery discards. Research authorizations and collection of dead and stranded fur seals were approved by the Argentine Government through the “Secretaría de Turismo” and the “Dirección de Fauna y Flora Silvestre”

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from the Chubut Province, the “Dirección de Areas Protegidas” from the Río Negro Province, and the “Administración de Parques Naturales” to work in the marine protected area “Parque interjurisdiccional Marino Costero Patagonia Austral.”

AUTHOR CONTRIBUTIONS

DV, LC, and EC conceived and designed the experiments. DV, NG, RL, and EC conducted the fieldwork. DV and RL processed the samples for stable isotope analysis. DV processed the data, performed the statistical analysis and wrote the manuscript with contributions from all authors. DV and LC analyzed the data. All authors gave final approval for publication.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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