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ORIGINAL PAPER

Long-term changes in Black-browed albatrosses diet as a result of fisheries expansion: an isotopic approach

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Abstract Ecological changes due to fishing activities appear to be similar across marine ecosystems; in this context the application of retrospective studies could help understand the magnitude of such impact on apex predators. Carbon and nitrogen stable isotopic values of feathers were used to evaluate if the observed expansion in Argentine fisheries operating in the Patagonian Continental Shelf affected Black-browed albatrosses (BBAs) diet. Feather samples from museum skins and from contemporary birds captured at sea were compared. Samples from the "pre-expansion" period showed enriched carbon values compared to recent samples. No differences in δ^{15}N were observed between periods, suggesting that if a diet change occurred it did not affect trophic levels exploited by BBAs. Isotopic niche width of contemporary BBAs was wider than the one for historic albatrosses suggesting, for the former, a more variable diet. Given that cephalopods from the Patagonian Continental Shelf showed enriched carbon values compared to pelagic and demersal prey, our results suggest a trend from a cephalopod-based diet during the pre-fisheries expansion period towards a demersal prey-based diet in a contemporary fishing context. Despite the limitations imposed by retrospective studies, our results show that a shift in the diet of the Black-browed albatross in waters of the Patagonian Continental Shelf could have occurred as a result of ecosystem changes promoted by the expansion of industrial fisheries and mostly through the emergence of discards as an abundant and predictable food source.

Introduction

Human activities, and particularly industrial fishing, have heavily impacted on the marine ecosystem worldwide (Halpern et al. 2008). These impacts involve from changes in productivity and abundance of resources, to the modification of not only the community structure but the whole ecosystem (Trites and Donnelly 2003; Hiddink et al. 2006; Jaureguizar and Milessi 2008; Grafton et al. 2010). Ecological changes due to fishing and overfishing tend to be similar across ecosystems but can only be understood through historical analysis. The retrospective evaluation of these changes allows visualizing the magnitude of that impact on every component of marine communities, including apex predators (Jackson et al. 2001; Zenteno et al. 2015). Many recent studies have evaluated this in order to understand the role of climate change, fisheries and food web alteration in modelling the demography and ecology of marine top predators, including mammals and seabirds (Crespo and Hall 2002; Becker and Beissinger 2006; Drago et al. 2009; Vales et al. 2014). This kind of studies have evidenced that population and breeding success declines in many seabird species as a result of diet shifts towards ones of lower trophic status (Hilton et al. 2006; Emslie and Patterson 2007; Norris et al. 2007; Gutowsky et al. 2009).

Covering about 1.2 million square kilometres, the Patagonian Continental Shelf is ground for medium to large high-seas industrial fisheries, including longliners, trawlers, and jiggers (PNA-Aves 2010). As other marine

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areas around the globe, the evolution of fisheries in this particular area has suffered several expansive cycles. During the 1970s a big expansion occurred with the incorporation of ice- and freezer-trawlers (moving from 36 to 160 vessels) and a consequent large increment in landings (moving from 38,000 metric tonnes in 1961 to ca. 428,000 metric tonnes in 1979, Fig. 1) mostly based on Argentine hake (*Merluccius hubbsi*, 30–76% of landings between 1971 and 2010) and cephalopods (mostly *Illex argentinus*, up to 34% of landings). These figures largely exceed the captures by the coastal fleet (chiefly ice-trawlers) that supplied the market since the beginning of the twentieth century (Bertolotti et al. 2001; Sánchez et al. 2012). This evolution of the industrial fleet had detrimental impact through the region where biomass and mean trophic levels of landings declined in the mid-1990s, where many stocks became fully exploited or over-exploited (Aubone et al. 2004; Jaureguizar and Milessi 2008; Milessi and Jaureguizar 2013). By the end of 1997, among other mitigation measures, an extensive fishing closure (*c*. 120,000 km^2) was implemented in the Patagonian Shelf Area in order to protect Argentine hake juveniles and spawners (Aubone et al. 2004). Particularly this measure has impacted positively not only on the hake but on other targeted and non-targeted species (Alemany et al. 2013). Another side effect of fisheries expansions and its concomitant increment in overall catches has been the rise of fishery discards and offal (Cañete et al. 2000; Dato et al. 2003; Aubone et al. 2004). These fishery by-products, together with the occurrence of facilitation processes of bottom prey associated to fishing operations (chiefly net hauling) have heavily impacted on the foraging ecology of seabirds (Furness 2003; Votier et al. 2004, 2010; Bicknell et al. 2013). Particularly discards, including non-target species and undersized fish, and offal (e.g. guts, heads, tails), constitute an abundant and predictable source of food for a range of seabirds and marine mammal species (Watkins et al. 2008; Abraham et al. 2009;

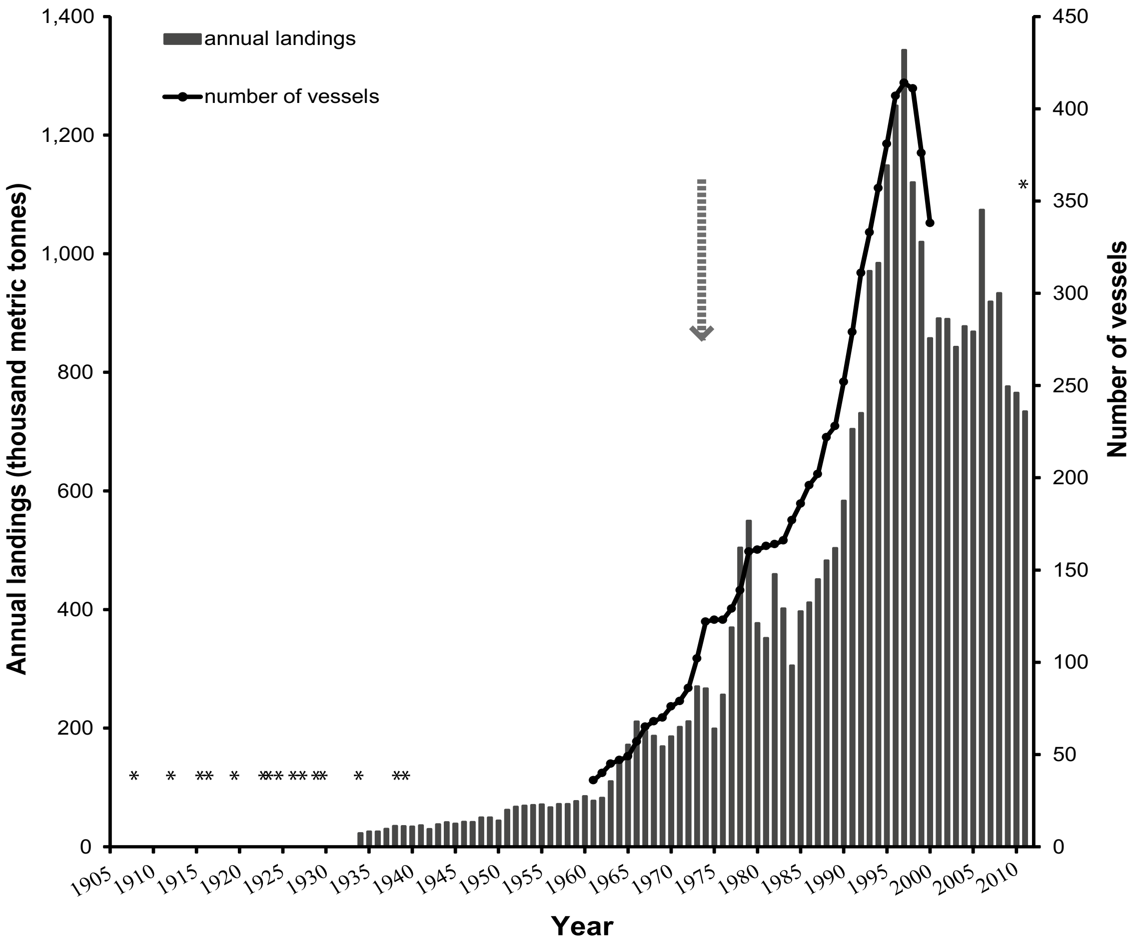

Fig. 1 Total annual landings of Argentinean marine fisheries (Sánchez et al. 2012) and number of industrial vessels (Bertolotti et al. 2001; Sánchez et al. 2012) operating in Argentinean waters between 1934 and 2011. *Asterisks* indicate the temporal correspondence of museum and contemporary samples, the *grey dotted arrow* indicates the onset of Argentinean industrial fisheries expansion

Bartumeus et al. 2010; Favero et al. 2011; Mariano-Jelicich et al. 2014).

Among local resident seabirds in the target area, the Black-browed albatross (*Thalassarche melanophris*, herein BBA) is of particular concern given its occurrence as part of the by-catch of several fisheries in the Patagonian Continental Shelf (Favero et al. 2011, 2013). Individuals breeding in Malvinas (Falkland) Island migrate north during the austral winter distributing in the Southwestern Atlantic from 29° to 51°S and from 48° to 66°W, a foraging area of about 1,100,000 km^2 (Copello et al. 2013). This wide use of the Patagonian Continental Shelf results in a high spatial overlap between BBAs and the trawler fleet in these waters during the austral winter (Copello et al. 2014). Historical reports about spatial distribution of this species are almost inexistent. However, historic information on recoveries of BBAs ringed as nestlings in Malvinas (Falkland) Islands highlights the importance of waters off Southern South America north from 40°S and up to ca. 22°S, with waters adjacent to the La Plata River being an hotspot of recoveries (Tickel 1967). These waters have been recently highlighted for its importance for BBAs and other apex predators during their non-breeding season (Croxall and Wood 2002; Copello et al. 2014; González Cárman et al. 2016).The diet of BBAs has been better documented during the breeding season where several authors reported the occurrence of epipelagic fish, crustaceans and cephalopods together with gelatinous components of plankton, but also suggesting the occurrence of demersal fish as coming from their association with fisheries (Thompson 1992; Weiss et al. 2009; Suazo 2008; Granadeiro et al. 2014). However, the diet of the species during the non-breeding season is poorly known; for instance, studies performed in the late 1970s in waters off the Benguela region were only focused on the cephalopod fraction of the diet (Lipinsky and Jackson 1989). More recent information on BBAs' diet during the inter-breeding season has been collected through the analysis of carcasses and bird specimens killed in fisheries (Colabuono and Vooren 2007; Petry et al. 2007). However, these methodologies are not appropriate to test long-term variation in food resources since they provide only a "snapshot" of the diet of each individual. Moreover, in the case of birds by-caught in fisheries a strong bias towards preys coming from such source should be expected (Barrett et al. 2007; Karnovsky et al. 2012). More recently, studies conducted in the Southwestern Atlantic Ocean using biogeochemical techniques such as stable isotopes analysis revealed a high contribution of fishery discards to the diet of Procellariform birds, including BBAs (Bugoni et al. 2010; Mariano-Jelicich et al. 2014; but see Granadeiro et al. 2014). Stable isotope analysis offers an alternative method to reconstruct dietary changes in marine predators over long periods of time (Newsome et al. 2010). This method is based on the assumption that the stable isotope ratio in the consumer's tissues integrates the stable isotope ratio of its prey items in a predictable manner over a certain period of time (DeNiro and Epstein 1978; Kelly 2000). This methodology has been widely used to evaluate historical changes in the diet of several marine top predators including seabirds (Becker and Beissinger 2006; Norris et al. 2007; Drago et al. 2009; Jaeger and Cherel 2011; Saporiti et al. 2014). The aim of this study was to explore whether the diet of the Black-browed albatross in waters of the Patagonian Shelf has historically changed as the expansion of Argentinean industrial fisheries generated changes both in the ecosystem and prey availability for this surface predator. We hypothesise that the above-referred differences in prey availability will be reflected in variations of carbon and nitrogen isotopic values of Black-browed albatross tissues. In this context, we expect a shift towards enriched carbon and nitrogen values of Black-browed albatross tissues with passing time, reflecting a contribution of demersal prey of higher trophic level as a result of fisheries expansion.

Materials and methods

Feathers are used extensively in avian ecology studies because they are metabolically inert after synthesis, they can be easily collected and its collection is relatively non-invasive; furthermore, they are easily stored and transported. Among its many utilities, feathers from bird skins housed in museum collections have been the chosen tissue used to depict historical changes in birds' foraging ecology (Becker and Beissinger 2006; Hilton et al. 2006; Norris et al. 2007; Gutowsky et al. 2009; Jaeger and Cherel 2011). Body feathers of Procellariforms are gradually replaced over several months mainly during the non-breeding period (Bugoni et al. 2015); particularly mantle feathers of the Black-browed albatross are moulted between breeding seasons and not during incubation (Granadeiro et al. 2014; but see Catry et al. 2013). As a result, the use of body feathers has been described as a powerful tool to gather useful information on the entire inter-breeding period by means of stable isotope analysis (Jaeger et al. 2010; Cherel et al. 2016).

In relation to a more comprehensive study, 16 adult Black-browed albatrosses (*T. melanophris*) were captured during austral winter 2011 from Argentine industrial fishing vessels operating in jurisdictional waters between 41 and 43°S and 57–59°W (Mariano-Jelicich et al. 2014; Table 1). Adult birds close to the vessel were captured with an adapted dip net. Three to four body feathers were collected from birds by gentle pulling. Birds were marked to avoid recapture. These samples

Table 1 Stable isotope ratios (mean ± SD) of feathers from Black-browed albatrosses used in the present study

Sample number	Location	Sex	Dead/captured year	δ^{13}C ‰[a]	δ^{15}N ‰
TM9452	Montevideo, Uruguay	M	1908	−15.5	15.5
TM8540	Mar del Plata, Argentina	–	1914	−14.7	19.2
TM45132	Buenos Aires, Argentina	–	1915	−15.1	16.5
T4196	Isla de los Estados, Argentina	–	1915	−14.3	18.3
TM1003	Mar del Plata, Argentina	F	1919	−14.9	16.1
TM80a	Quequén, Argentina	M	1921	−14.4	16.8
T71a1	Mar del Plata, Argentina	–	1921	−15.5	15.6
T176a-1	Escobar, Argentina	–	1923	−15.1	16.7
T176a	Escobar, Argentina	–	1923	−14.7	19.1
TM979a	Mar del Plata, Argentina	–	1926	−14.4	19.2
TM1037	Buenos Aires, Argentina	F	1926	−15.1	14.3
T1037a-3	Buenos Aires, Argentina	F	1926	−14.5	17.6
T1037a-2	Buenos Aires, Argentina	M	1926	−15.6	15.5
T1037a-1	Buenos Aires, Argentina	M	1926	−14.9	16.4
T73235	Montevideo, Uruguay	M	1927	−14.9	16.7
TM1952	Montevideo, Uruguay	–	1928	−15.0	15.7
T1573a-4	Mar del Plata, Argentina	–	1928	−14.2	17.3
T1573a-1	Mar del Plata, Argentina	–	1928	−15.9	16.6
TM4533	Rio de la Plata, Argentina	F	1937	−15.6	16.2
ACN2	41°32′32.0″S 58°00′24.8″W	F	2011	−15.4	15.6
ACN9	42°13′32.3″S 58°44′41.0″W	F	2011	−15.8	17.7
ACN1	41°32′32.0″S 58°00′24.8″W	F	2011	−15.4	16.4
ACN41135	42°15′32.9″S 58°32′30.9″W	F	2011	−16.5	16.6
ACN25	42°33′50.1″S 58°53′13.7″W	F	2011	−15.4	17.6
ACN41120	42°00′35.2″S 58°27′46.5″W	F	2011	−17.1	14.3
ACN22	42°33′50.1″S 58°53′13.7″W	F	2011	−15.8	17.8
ACN41132	41°37′57.4″S 57°35′45.6″W	F	2011	−15.7	15.8
ACN11	42°13′32.3″S 58°44′41.0″W	M	2011	−16.1	17.8
ACN21	42°33′50.1″S 58°53′13.7″W	M	2011	−18.7	14.5
ACN3	41°32′32.0″S 58°00′24.8″W	M	2011	−16.1	15.6
ACN41130	42°15′45.5″S 58°32′48.4″W	M	2011	−15.7	16.2
ACN5	42°02′42.6″S 58°32′40.4″W	M	2011	−15.7	17.2
ACN6	42°02′42.6″S 58°32′40.4″W	M	2011	−15.7	17.9
ACN7	42°02′42.6″S 58°32′40.4″W	M	2011	−15.9	16.5
ACN8	42°17′18.2″S 58°46′17.2″W	M	2011	−15.8	18.0

Samples from 1908 to 1937 correspond to museum skins; samples from 2011 correspond to birds captured at sea

[a] Carbon raw values

were used to represent current isotopic values. Since only birds attending vessels were sampled there is a possibility of bias towards individuals specialized on discards. However, observations of marked birds, suggests that individual birds only remain for short time periods attending the same vessel (Bugoni et al. 2010). BBAs are known to cover vast areas in short periods of time (Copello et al. 2013, 2014), and therefore have potential access to a wide range of natural prey and food source coming from anthropogenic activities. Historical values came from body feathers sampled from 19 adult museum specimens deposited in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (specimens coding included bird #TM9452, #TM80a, #TM45132, #TM1003, #TM979a, #TM1037, #TM1952, #TM4533, #TM8540, #T1037a3, #T176a1, #T1573a4, #T1573a1, #T176a, #T1037a2, #T1037a1, #T4196, #T73235, #T71a1; Table 1). All feathers included in this study were considered to come from adult birds (Onley and Bartle 1999).

Prey data

Comparison among potential preys was performed using isotopic values of representative fish and invertebrate species reported in BBAs' trophic spectrum (Thompson 1992; Weiss et al. 2009; Granadeiro et al. 2014). Components assumed in the "natural" diet (in relation to the prey distribution in the water column and albatross diving capabilities following Prince et al. 1994; Sakamoto et al. 2009) included epipelagic species like Argentine anchovy *Engraulis anchoita*, Fueguian spratt *Sprattus fuegensis*, lobster krill *Munida* sp., and young age-classes of Ommastrephid and Loliginid squids (*Illex argentinus, Loligo sanpaulensis, Loligo gahi*). In addition, demersal, and semi-demersal species often discarded by trawlers operating in the Patagonian Continental Shelf were also considered. The discards in these fisheries mostly involve undersized and non-target demersal species generally discarded unprocessed, and offal from processed target species, mainly Argentine hake *Merluccius hubbsi*, Longtail southern cod *Patagonotothen ramsayii*, hoki *Macruronus magellanicus,* and the Patagonian toothfish *Dissostichus eleginoides* among other demersal predatory finfish, and the Argentinian shortfin *I. argentinus* (González-Zevallos and Yorio 2006; Granadeiro et al. 2011; Mariano-Jelicich et al. 2014). Long-term onboard observations on foraging behaviour of BBA attending fishing vessels allowed us to identify the Argentine hake, the Longtail southern cod, and the Argentine shortfin squid as both the most commonly discarded species in the demersal trawlers (Seco Pon 2014) as well as the most consumed items by BBA (Mariano-Jelicich et al. 2014). Representative samples of main fish and invertebrate species discarded, including non-commercial species and undersized fish and squid, were collected onboard trawlers and longliners during autumn and winter months 2011 (latitude range 38–54°S, longitude range 56–63°W). A portion of white muscle from the lateral region of fishes, crustacean muscle and the mantle of squids was sampled. The inventory of potential food sources was completed with isotopic data of fish species previously reported for northern Patagonia (Forero et al. 2004; Ciancio et al. 2008; Drago et al. 2009, see Table 2). Potential prey species were

Table 2 Sample size, stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of Black-browed albatross (PRE—pre-fisheries expansion, 1908–1937 and POST—post-fisheries expansion, 2011), potential prey considered in the study and its corresponding food source category

		N	$\delta^{13}C$	$\delta^{15}N$
Black-browed albatross PRE		19	−15.2 ± 0.5	16.8 ± 1.4
Black-browed albatross POST		16	−16.1 ± 0.8	16.6 ± 1.2
Cephalopods		14	−16.8 ± 0.3	16.3 ± 0.3
	Illex argentinus Argentine shortfin squid	5	−16.4 ± 0.1	16.0 ± 0.4
	Loligo sanpaulensis[a] Argentine longfin squid	5	−16.8 ± 0.3	17.2 ± 0.2
	Loligo gahi[a] Patagonian shortfin squid	4	−17.6 ± 0.6	15.7 ± 0.4
Demersal species (Trawl)		19[d]	−17.2 ± 0.7	15.8 ± 0.6
Fish	*Merluccius hubbsi* Argentine hake	7	−17.5 ± 0.3	16.2 ± 0.4
Fish	*Patagonotothen ramsayii* Longtail southern cod	8	−17.3 ± 0.7	15.5 ± 0.8
Fish	*Macruronus magellanicus*[b] Hoki	2	−17.4 ± 0.1	16.2 ± 0.2
Fish	*Dissostichus eleginoides* Patagonian toothfish	2	−20.8 ± 1.1	12.4 ± 0.2
Crustacea	*Pleoticus muelleri* Argentinean red shrimp	2	−15.8 ± 0.4	15.7 ± 0.5
Epipelagic species		7	−17.5 ± 0.5	14.7 ± 1.0
Fish	*Sprattus fuegensis*[c] Fueguian spratt	1	−18.1	12.3
Fish	*Engraulis anchoita* Argentine anchovy	5	−17.5 ± 0.5	15.3 ± 0.2
Crustacea	*Munida* sp., Lobster krill	1	−17.3	13.4

Values expressed as mean ± SD

[a] Drago et al. (2009), [b] from Forero et al. (2004), [c] from Ciancio et al. (2008). [d] Not including values for the Patagonian toothfish

grouped into three categories: epipelagic species; demersal species and cephalopods.

Sample preparation

All feathers were cleaned for any contaminant and surface lipids using a 2:1 chloroform–methanol solution followed by two successive rinses in methanol (Jaeger et al. 2010). Samples were left to dry at ambient temperature. Then two to four feathers per sample were cut into small fragments with a stainless-steel scissor, homogenised and sub-samples of ~0.5 mg were packed in tin capsules for stable isotope analysis.

Prey tissue samples were dried in an oven at 60 °C and grounded using a hand mortar (Hobson et al. 1997; Cherel and Hobson 2007). In order to reduce carbon variability due to lipid variation between tissues, we conducted lipid extraction from potential prey sample using successive rinses in a 2:1 chloroform–methanol solution (Bligh and Dyer 1959). Samples were homogenised and sub-samples of ~0.8 mg packed in tin capsules for stable isotope analysis. Stable isotope values were determined by mass spectrometry at the Stable Isotope Facility at UC Davis. Results are presented in the usual δ notation relative to Vienna Pee Dee Belemnite and atmospheric N2 (Air) for δ13C and δ15 N, respectively. Based on the internal standards (G-11 nylon, G-13 bovine liver, G-17 USGS-41 glutamic acid, and G-9 glutamic acid), the analytical precision (±1 SD) was estimated as <0.2‰ and for both δ13C and δ15 N.

Data analysis

Two periods were established considering the evolution of the total annual marine landings (Sánchez et al. 2012) and the industrial fishery (i.e. number of vessels) in Argentina (Bertolotti et al. 2001; Sánchez et al. 2012) as shown in Fig. 1. These periods were: a "pre-fisheries expansion" period characterized by low annual landings and vessel numbers (previous to 1975, Fig. 1) and a "post-fisheries expansion" period characterized by a marked increment in both annual landings and number of industrial vessels (from 1975 onwards). Historic data (i.e. BBAs specimens from museum) was obtained from albatrosses collected between 1908 and 1937 ($n = 19$, Fig. 1). A Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson 2001; Anderson et al. 2008) in PRIMER 6 (Clarke and Gorley 2006) was used to evaluate if δ^{13}C and δ^{15}N of historic BBAs varied over time (i.e. years of collection). No differences among historic isotopic values were observed (PERMANOVA *Pseudo-F* (1,18) = 0.28, $P = 0.66$) Consequently, long-term changes in δ^{13}C and δ^{15}N were evaluated by comparing two groups, the "pre-fisheries expansion" (i.e. early 1900s samples, herein PRE, Fig. 1) and "post-fisheries expansion" (birds sampled on the austral winter 2011, herein POST, Fig. 1).

Raw δ^{13}C values of seabirds' feathers were adjusted to take into account the effect of the increase in atmospheric CO_2 as a result of human fossil fuel burning; the Suess effect (Hilton et al. 2006). This increment in the atmosphere CO_2 concentration has resulted in an increasing concentration of dissolved CO_2 in the ocean, what in turn resulted in increasing δ^{13}C values in phytoplankton during the last 150 years. To account for the Suess effect, δ^{13}C data from historical feathers were normalized by subtracting a year-specific factor $\delta^{13}C_{\text{suess}} = -1 + 1.1^{(2011-\text{year}) * 0.027}$ following Quillfeldt et al. (2010). The comparison of isotopic values between PRE and POST feathers was performed with parametric statistics (Zar 1999).

Samples of 11 potential prey species were evaluated but, because of small isotopic differences among several preys, they were pooled into three categories: cephalopods, demersal species (assumed to be facilitated during trawl operations and/or components of trawl discards) and epipelagic species. Isotopic values were compared among potential prey categories through a PERMANOVA (Anderson 2001; Anderson et al. 2008) in PRIMER 6 (Clarke and Gorley 2006) and pairwise post hoc comparisons. Values for the Patagonian toothfish *Dissostichus eleginoides* were excluded from the analysis given the extreme depleted values. Stable Isotope Bayesian Ellipses in R (SIBER) (Jackson et al. 2011) was used to define the isotopic niche space among BBAs from the two studied periods as a measure of their isotopic resource use area. This method is a Bayesian version of Layman metrics (Layman et al. 2007) that incorporates uncertainties such as sampling biases and small sample sizes into niche metrics (Jackson et al. 2011). We used standard ellipse areas corrected for small sample size (SEAc) to represent the BBAs from the two periods analysed in the isotopic space and estimated the width of their isotopic niche using the Bayesian standard ellipse areas (SEAb). Furthermore, we calculated the magnitude of the isotopic overlap among BBAs parameters (Jackson et al. 2011).

Data are always expressed as mean ± standard deviation (SD). Previous to any statistical analysis normality of the data was tested by Kolmogorov–Smirnov tests and visual inspection, and homoscedasticity by means of Levene test. Statistical analyses were carried out in Statistica v7 and free software R 3.3.2 (R Development Core Team 2016) and all functions for SIBER analyses were contained in the library Stable Isotope Analysis in R (SIAR) (Parnell et al. 2010).

Results

Carbon values of BBAs' potential prey ranged from −20.8‰ for the Patagonian toothfish to −15.8‰ for the Argentinean red shrimp (*Pleoticus muelleri)* (Table 2). Demersal species like Argentine hake and Longtail southern cod showed carbon values close to epipelagic species like the Argentine anchovy (Table 2). Nitrogen values of prey ranged from 12‰ in the Fueguian spratt to 17.2‰ for longfin squid (Table 2). The comparison between prey categories (i.e. epipelagic species, demersal species and cephalopods) showed significant differences in $\delta^{13}C$ and $\delta^{15}N$ (PERMANOVA *Pseudo-F*(2,38) = 7.24, $P < 0.001$). Posterior pairwise comparisons showed significant differences in all the cases (Pseudo-F(1, 32) = 3.39, $P = 0.03$ for cephalopods vs demersal species, Pseudo-F(1,20) = 14.05, $P < 0.001$ for cephalopods vs epipelagic species; Pseudo-F(1,24) = 6.15, $P < 0.01$ for epipelagic species vs demersal species). These differences were largely driven by enriched $\delta^{13}C$ in cephalopods compared to epipelagic and demersal species (Tukey post hoc test $P < 0.05$ in all cases), and depleted Nitrogen values in epipelagic species compared to demersal species and cephalopods (Tukey post hoc test $P < 0.05$ in all cases).

Regarding the isotopic values for BBAs, PRE carbon isotopic values ranged from −16.20 to −14.18‰, while nitrogen values ranged from 14.34 to 19.26‰. POST carbon values ranged from −18.71 to −15.40‰, while nitrogen values ranged from 14.31 to 18.06‰ (Table 2; Fig. 2). PRE and POST feathers were isotopically different (Wilk's $\lambda = 0.64$, $P = 0.0009$), largely due to enriched carbon isotope values in PRE feathers (−15.24 ± 0.5‰ vs. −16.08 ± 0.82‰, $t_{33} = 3.72$, $P < 0.001$, Fig. 2). Nitrogen isotope ratios remained similar over time (16.83 ± 1.36‰ vs. 16.62 ± 1.18‰), showing no significant differences ($t_{33} = 0.49$, $P = 0.62$, Fig. 2).

The Bayesian ellipse area corrected for samples size (SEAc) of POST albatrosses overlapped with that of the PRE group (Fig. 2). The overlap area (0.18‰^{2}) of the Bayesian ellipses from both periods represented the 10% of the ellipse surface of the PRE group and the 7% of the ellipse surface of the POST group (Fig. 2). Bayesian estimates for isotopic niche width (SEAb) showed that POST mean isotopic niche width was larger (2.84‰^{2}, 95% credibility interval of 1.52–4.36‰^{2}) with 93% probability of difference than PRE isotopic niche width (SEAb mean = 1.70‰^{2}, 95% credibility interval of 0.99–2.49‰^{2}).

Discussion

The available information about BBAs' diet during the non-breeding season is scarce. In recent years, reports from southern Brazil highlighted the importance of small cephalopods and finfish (Sciaenidae) species in the trophic spectrum of BBAs beached and longline by-caught (Colabuono and Vooren 2007; Petry et al. 2007).This latter fact supposes certain degree of bias given that while small cephalopods belong to the group of oceanic species that could be naturally available to BBAs, the bulk of fish species reported in those studies corresponded to demersal species targeted by fisheries and present in the discards. Moreover, isotopic approaches to the evaluation of diet composition of BBAs have reported an important contribution to its diet of demersal species abundant in discards from trawlers operating in the Patagonian Continental Shelf (Mariano-Jelicich et al. 2014). Indeed, estimations on discard consumption, based on direct on-board observations and experimental discard, estimated the subsidy in terms of biomass of

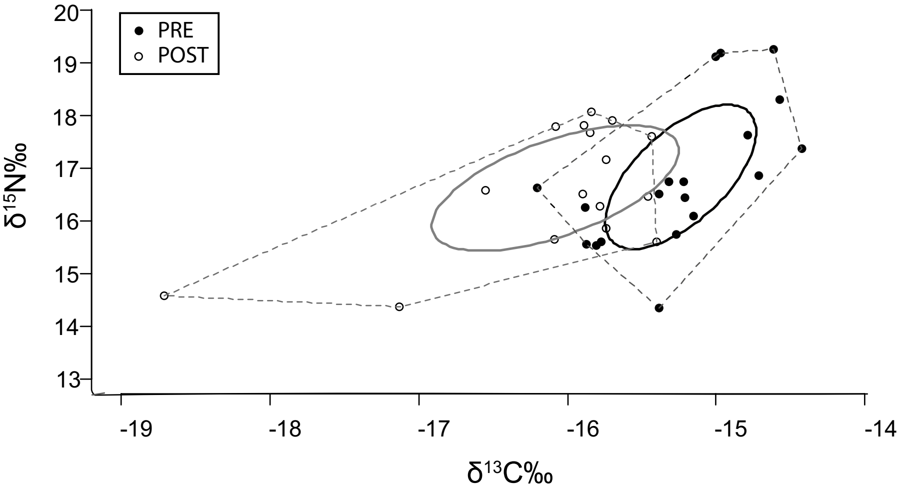

Fig. 2 Isotopic niche area based on stable isotope ratios of Black-browed albatrosses' feathers. *Black* symbols correspond to museum samples (*PRE* pre-fisheries expansion, 1908–1937), *white* symbols correspond to contemporary samples (*POST* post-fisheries expansion, 2011). *Solid lines* enclose the area of the standard ellipses (SEACc, 40% credible interval), and *dotted lines* represent the layman metric of convex hull area of BBAs for each period. Values from pre-fisheries feathers are shown with correction for Suess effect

fisheries discards used by the BBAs in ca. 3280 tons per year (Seco Pon 2014). These reports are in line with the high spatial overlap of BBAs and fisheries observed along the Patagonian Shelf (Copello et al. 2014; 2016). Unlikely, historic reports of diet prior to fisheries expansion are scarce or almost inexistent (Lipinsky and Jackson 1989; Thompson 1992). Several BBAs ringed in Malvinas (Falkland) Islands were recovered in waters adjacent to the La Plata River (Tickel 1967). This information highlights the use of these productive waters by the study species. Based on this information on ring recoveries we assume that this species did not change substantially its non-breeding areas over the study period, and so differences found in carbon values are not related to a change in distribution but on their diet. The increase availability of demersal fish via fisheries offal and discards in years after fisheries expansion (Cañete et al. 2000; Dato et al. 2003) and its concomitant consumption (Mariano-Jelicich et al. 2014; Seco Pon 2014), led us to hypothesise that such changes should be evident in trophic differences among top predators. Our results show, that, although the isotopic niche of both evaluated groups overlap, the larger niche width of albatrosses in present times (POST) could reflect an increase in resource utilization (i.e. more variable diet) as a result of discard consumption (Fig. 2). In this context, BBAs under study were expected to have historically moved from more pelagic low trophic level "natural" trophic spectrum to a diet biased towards demersal high trophic level prey as a result of their association to fisheries, hence showing an increment in δ^{15}N values. However, no differences in δ^{15}N were observed, implying that, if a change in diet occurred, this should have involved similar trophic-level prey species.

Considering the depleted carbon isotopic values reported for epipelagic species compared to demersal and benthic species (Forero et al. 2004; Ciancio et al. 2008; Botto et al. 2011), a shift from depleted towards enriched carbon values in BBA feathers was foreseeable. Nevertheless, the change in δ^{13}C of feathers reported here was opposite to the expected. Isotopic values of potential prey from Northern Patagonia compared in this study showed that demersal fish species like the Argentine hake and the Longtail southern cod showed carbon values close to epipelagic fish species like the Argentine anchovy (Table 2). This could be related to the fact that the Argentine hake spends diurnal hours closer to the sea bed, but moves towards upper layers in the water column during nocturnal hours to feed on pelagic species (Angelescu and Fuster de Plaza 1965; Drago et al. 2009). Despite their diet, the diurnal demersal ecology of the Argentine hake makes this species unavailable for BBA as it is unfeasible that the predatory behaviour of hakes occurs within the first 2–3 m of the water column (i.e. rough maximum diving depth for BBAs, Brooke 2004). So, its occurrence as well as the Longtail southern cod is unlikely without considering fisheries facilitation and/or other facilitation process (i.e. association with marine mammals). Cephalopods, in turn, tend to have enriched carbon values compared to demersal fish species (but with similar δ^{15}N). Therefore, the observed changes in isotopic values could be seen as a result of a shift from a cephalopod-based diet with an epipelagic fish component to a demersal fish-based one. Particularly cephalopods have been described as an important component of BBAs' diet, captured during their diel movements and so connecting benthic and pelagic webs (Lipinsky and Jackson 1989). Moreover, no differences were observed between cephalopods and demersal fish species in δ^{15}N but in δ^{13}C.

This shift from a 'squid and pelagic fish-based' to a 'demersal fish-based' diet, even though not affecting the trophic position of BBAs, could have an important effect in terms of food quality (Romano et al. 2006; Grémillet et al. 2008). Nevertheless, not such effect results evident as the energetic value of mainly discarded species are not far away from those of cephalopods (mean energetic value for fish species in fishery discards = 5.9 kJ g^{-1}, mean energetic value for cephalopods = 5.8 kJ g^{-1}; Eder and Lewis 2005; Drago et al. 2009). However, a fall in the consumption of pelagic clupeids (i.e. Argentine anchovy, Fueguian spratt) could have impacted the energetic value of BBAs' diet given the high nutritional quality of this species (8.4 kJ g^{-1}; Drago et al. 2009).

The retrospective evaluation of ecological changes forced by fisheries expansion allows visualizing the magnitude of that impact on different components of marine communities (Jackson et al. 2001; Zenteno et al. 2015). However, this approach is not free from problems. Available evidence revealed no major changes in primary productivity in waters off southern Brazil during the period 1998–2006 (Heileman and Gasalla 2008), and so, no major change in the δ^{15}N baseline is expected, as both parameters are strongly correlated along the coasts of the southwestern Atlantic (Saporiti et al. 2014). Moreover, different sources of evidence show no remarkable changes in particulate organic matter δ^{13}C values at waters off the Northern Patagonia between 2001 and 2011(Lara et al. 2010; Botto et al. 2011; Saporiti et al. 2015). The access to historic prey samples would be the key to exclude any bias resulting from potential changes in baseline isotopic values over the period studied.

Another drawback of retrospective studies could be the uneven spatio-temporal distribution of specimens (Saporiti et al. 2014). Despite the contemporary (POST) period was represented by a single-year samples, POST feather values reported in this study were in line with those reported for BBAs breeding in Malvinas (Falkland) Islands ($\delta^{13}C = -16.0 \pm 0.2$ $\delta^{15}N = 16.9 \pm 0.2$ for period 2003−2006, Weiss et al. 2009; range δ^{13}C: −16.7 to −15.5 and range values for δ^{15}N: 15.5–20.0, Granadeiro et al.

2014). This was expected given that BBAs feeding in the Patagonian Continental Shelf during the austral winter are largely individuals from breeding populations in Malvinas (Falkland) Islands (Tickel 1967; Grémillet et al. 2000; Copello et al. 2014).

Historic (PRE) BBAs feather $\delta^{13}C$ values reported here were similar to values from White-chinned petrels breeding in Malvinas (Falkland) Islands ($\delta^{13}C$: $-15.4 \pm 1.6‰$, Weiss et al. 2009). This species was known to forage mainly on squids and fish during its non-breeding season (Jackson 1988), including epipelagic crustaceans during its breeding season (Croxall et al. 1995 and references therein). Given the similar values of actual White-chinned petrels' isotopic values with those of historic BBA, this could also suggest a prevalence of a squid-based diet during this pre-fisheries expansion period.

Regarding other marine apex predators, a similar trend of depleted carbon values from historic to current diet has also been reported for the South American sea lion (*Otaria flavescens*) from northern and central Patagonia. This change has been described as a result of the consumption of Argentine hake given its availability (in the form of fishery discards) and as a response to an increase in intraspecific competition for benthic resources (Drago et al. 2009). However, it should be take into account that differences in the time period from each study (i.e. 1908–2011 in this study vs 1940–2007 in Drago et al. 2009) could probably imply uncertainty on the isotopic profile of trophic chains given that no historical food reference samples from any period were available.

Both the El Niño Southern Oscillation (ENSO) and the rotation of the Subtropical anticyclone influence the primary production in the Southwestern Atlantic Ocean (Behrenfeld et al. 2001; Drago et al. 2009). A reduction in primary production in turns reduces the $\delta^{13}C$ of primary producers and hence the entire food web (Graham et al. 2010). In this regard, the reported fall in $\delta^{13}C$ of BBAs feathers might reflect the periodicity of these climatic processes if samples were collected in periods of contrasting productivity. This is an unlikely explanation, given that despite these climatic processes have a cyclic frequency and our historic (PRE) dataset spans over 30 years with somehow evenly distributed samples; no differences were observed in carbon values within this group. Moreover, if a major change in $\delta^{13}C$ occurred given a reduction in primary productivity, a drop in $\delta^{15}N$ should be expected, as both parameters are strongly correlated along the coasts of the southwestern Atlantic (Saporiti et al. 2014).

Although several shortcomings in relation to retrospective studies should be considered in future analysis, our results suggest that a shift in the diet of the Black-browed albatross in waters of the Patagonian Continental Shelf could have occur as a result of ecosystem changes favoured by the expansion of industrial fisheries and mostly through the appearance of discards as a predictable and abundant food source.

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Compliance with Ethical Standards

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Ethical approval All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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