

Age, sex, and breeding status shape a complex foraging pattern in an extremely long-lived seabird

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Abstract. Evidence of age-dependent changes in foraging behavior of free-ranging individuals is scarce, especially at older stages. Using the isotopic niche as a proxy of the trophic niche during both the breeding (blood) and inter-nesting (feather) periods, we report here empirical evidence for age-, gender-, and breeding status-dependent foraging ecology and examine its potential consequences on subsequent reproduction and survival in an extremely long-lived species, the Wandering Albatross (*Diomedea exulans*). Immature Wandering Albatrosses of both sexes forage in the subtropics ($\delta^{13}\text{C}$) and feed at the same trophic position ($\delta^{15}\text{N}$) as the adults. In contrast to immature birds, adult females forage, on average, at more northern latitudes than males, with both sexes feeding in the subtropics during the inter-nesting period, and males, not females, favoring subantarctic waters during incubation. In contrast to adult females, males show a unique pattern among birds and mammals of a continuous change with age in their main feeding habitat by foraging progressively farther south in colder waters during both the breeding and inter-nesting periods. In males, foraging at higher latitudes (lower feather $\delta^{13}\text{C}$ values) is associated with a lower probability of breeding during the following years compared to other birds, but with no effect on their probability of surviving. Foraging in cold and windy waters may be linked to foraging impairment that might explain different life history trade-offs and lower investment in reproduction with age. This key point requires further longitudinal investigations and/or studies examining foraging success and the energy budget of birds feeding in different water masses.

Key words: breeding; capture–recapture models; Crozet Archipelago; *Diomedea exulans*; foraging behavior; inter-nesting; senescence; stable isotopes; Wandering Albatross.

INTRODUCTION

Age-specific reproduction and survival are critical factors for understanding in many fields of evolutionary ecology, such as individual behavioral strategies and population dynamics (Forslund and Pärt 1995). The general pattern of iteroparous organisms is that reproductive success and survival increase with age during the first years, reach a plateau at middle age, and then decline at old age as a result of senescence (Forslund and Pärt 1995, Jones et al. 2008). The proximate causes of this general pattern are not well understood, and studies have focused mainly on the first reproductive years (Forslund and Pärt 1995). Reproductive and survival improvements are considered to result from selection of better individuals, learning processes, or a combination of both factors (Curio 1983). Learning processes include increasing foraging abilities, namely searching, finding, capturing, and

handling food (Wunderle 1991, Daunt et al. 2007). Hence, foraging ecology has a key role in shaping individual fitness early in reproductive life, but surprisingly little information is available for old individuals in wild populations (MacNulty et al. 2009). A pivotal question is to determine if foraging behavior varies in old individuals, and if this change has consequences for reproductive output and survival rate.

Birds are predominant models for studying aging because they live considerably longer than similar-sized mammals (Holmes and Martin 2009), and senescence is experienced by more individuals in the longest-lived taxa (Turbill and Ruf 2010). Demographic parameters of birds follow the general age-related pattern (Forslund and Pärt 1995, Holmes and Martin 2009) and their reproductive performances early in life are causally linked to their food and feeding ecology (Wunderle 1991, Rutz et al. 2006). Seabirds, together with flamingos and parrots, reach the longest maximum life spans among birds, with some petrels and albatrosses living >30 years (Wasser and Sherman 2010). Foraging strategies of old seabirds have been documented recently using conventional means, bio-logging, and intrinsic

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markers. Compared to mid-aged seabirds, the few existing studies suggest that old breeders feed on different proportions of prey (Navarro et al. 2010), perform longer foraging trips with reduced activity and lower mass gain (Catry et al. 2006, 2011), and dive longer with the same prey pursuit rate (Zimmer et al. 2011). An unexpected pattern of spatial segregation by age was recently documented in satellite-tracked Wandering Albatrosses *Diomedea exulans*, with old breeding males foraging farther south than females and young and mid-aged males (Lecomte et al. 2010). However, this pioneer work was conducted on a single foraging trip of incubating birds, with no available trophic information.

Due to logistic limitations in terms of instrument costs and time available for fieldwork, most telemetric investigations have been conducted on relatively small numbers of individuals during short periods. Hence, alternative biochemical methods such as stable isotopes are now increasingly used to gain further relevant ecological information. Different avian tissues (e.g., blood, feathers) can be easily sampled during the breeding season on a large number of individuals (Cherel et al. 2013), which allows recording of isotopic information on their feeding ecology at different time scales (Dalerum and Angerbjörn 2005, Cherel et al. 2008). Here we measured the isotopic niche as a proxy of the trophic niche (Newsome et al. 2007) on a unique data set of Wandering Albatrosses of known age, sex, and breeding status, using one of the few long-term study populations of very long-lived animals. Wandering Albatrosses are among the longest-lived birds, with some free-living individuals being ≥ 50 years old (Wasser and Sherman 2010), and the species presents strong age dependence in reproduction and survival (Lecomte et al. 2010, Pardo et al. 2013). Our objective was firstly to investigate the age-related variations of foraging niche during both the breeding and inter-nesting periods of male and female albatrosses, and secondly to test the effect of the isotopic niche on their subsequent survival and breeding performances using capture–recapture models.

METHODS

Field study

Fieldwork was carried out at Possession Island, Crozet Archipelago (46–47° S, 52° E). All Wandering Albatrosses from the island had been sexed and banded as part of a long-term mark–recapture program, with chicks being banded before fledging and pairs being monitored throughout the breeding cycle since 1966. Because some birds had been banded as adults in the early part of the long-term study, their minimum age was calculated from the year of banding plus the minimum age at first breeding, which is seven years in Wandering Albatrosses (Lecomte et al. 2010). All albatrosses were handled in January–March 2008, corresponding to the incubation stage of breeding birds. Wandering Albatrosses of the present isotopic investi-

gation included adult individuals that were also tracked using satellite transmitters (Jaeger et al. 2010, Lecomte et al. 2010).

Stable isotope method and analysis

The stable isotope method was validated in the southwestern Indian Ocean, with $\delta^{13}\text{C}$ values of seabirds indicating their latitudinal (but not their longitudinal) feeding grounds (Jaeger et al. 2010) and their $\delta^{15}\text{N}$ values increasing with trophic level (Cherel et al. 2010). The albatross isotopic niche was investigated by collecting blood and feathers, two complementary tissues that record trophic information corresponding to the breeding and inter-nesting periods, respectively (Cherel et al. 2008). In *Diomedea* albatrosses, feather isotope values represent the foraging habits during the inter-nesting period, because adult birds gradually replace their plumage at that time (Battam et al. 2010).

Whole blood (1 mL per bird) was sampled from the tarsus vein of 172 individuals, centrifuged, and blood cells (hereafter blood) were subsequently stored at -20°C until isotopic analysis. Body feathers were collected from 202 individuals and then stored dry in plastic bags. Four body feathers per individual were pooled to obtain an average isotopic signature for the whole plumage (Jaeger et al. 2009). Feathers were cleaned of surface lipids and contaminants using a 2:1 chloroform:methanol solution for two minutes, followed by two successive methanol rinses. The four feathers were air-dried and then homogenized by cutting them into small pieces. Blood samples were air-dried in an oven at $+60^\circ\text{C}$. The consistently low C:N mass ratio (3.24 ± 0.06 , mean \pm SD) verified that the low lipid content of blood cells does not necessitate lipid extraction (Cherel et al. 2005). One subsample of blood or feathers was then weighed (~ 0.4 mg) with a microbalance, packed into a tin container, and nitrogen and carbon isotope ratios were determined by a continuous-flow mass spectrometer (Thermo Scientific Delta V Advantage, Thermo Fisher Scientific, Waltham, Massachusetts, USA) coupled to an elemental analyzer (Thermo Scientific Flash EA 1112). Results are presented in the usual δ notation relative to Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate measurement errors $< 0.10\%$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

Stable isotope data analyses

The Southern Ocean is marked by a well-defined latitudinal baseline $\delta^{13}\text{C}$ gradient that is reflected in the tissue of consumers, including the Wandering Albatross (Jaeger et al. 2010, Quillfeldt et al. 2010). The isotopic consumer data allowed us to estimate the carbon position of the main oceanic fronts within the southern Indian Ocean, and thus to delineate robust isoscapes of the main foraging zones for top predators, depending on the targeted tissues. Based on blood (feather) $\delta^{13}\text{C}$

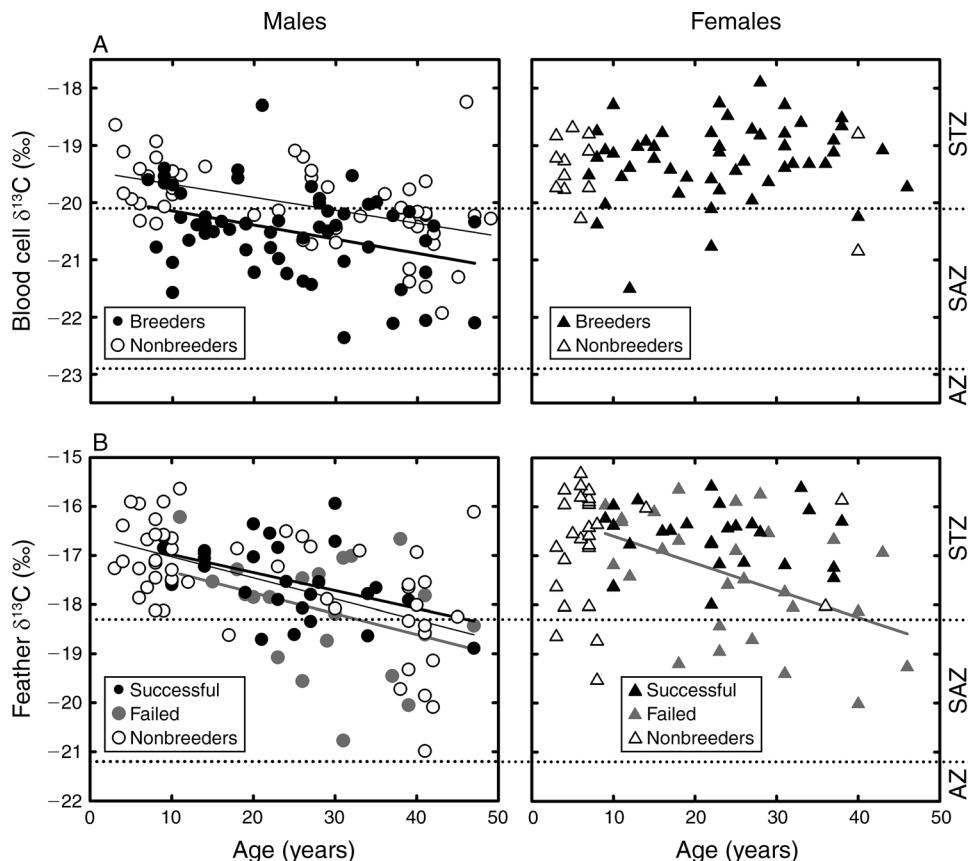


FIG. 1. Effect of age on $\delta^{13}\text{C}$ values of male (circles, left panels) and female (triangles, right panels) Wandering Albatrosses (*Diomedea exulans*). (A) Blood $\delta^{13}\text{C}$ values (corresponding to the breeding period); birds were grouped according to their breeding status in 2008, either breeders (black symbols, thick regression line) or nonbreeders (white symbols, thin regression line). (B) Feather $\delta^{13}\text{C}$ values (corresponding to the nonbreeding period); birds were grouped according to their past breeding status, i.e., successful breeders (black symbols and thick regression line), failed breeders (gray symbols and regression line), or nonbreeders (white symbols, thin regression line). Only regression lines that were statistically significant ($P < 0.05$) are shown. Abbreviations are: STZ, subtropical zone; SAZ, subantarctic zone; AZ, antarctic zone (see *Methods: Stable isotope data analyses* for their isotopic delineation).

isoscapes, values less than -22.9‰ (-21.2‰), -22.9‰ to -20.1‰ (-21.2‰ to -18.3‰), and greater than -20.1‰ (-18.3‰) were considered to correspond to the Antarctic (AZ), Subantarctic (SAZ), and subtropical (STZ) Zones, respectively (Fig. 1; see Jaeger et al. 2010).

The breeding cycle of Wandering Albatrosses lasts a complete year and most individuals that are successful in fledging a chick breed in alternate years, whereas those failing during incubation or during the early stages of chick-rearing breed again in the following year (Tickell 1968). Because the age, sex, and breeding status of each individual from Possession Island was known, birds were selected to obtain a data set distribution as homogeneous as possible (Table 1). For statistical analyses of blood isotopic data, albatrosses were first grouped according to their breeding status in 2008: either (1) breeding (incubating) or (2) nonbreeding (non-incubating) birds. For statistical analyses of feather isotopic data, albatrosses were grouped according to their past breeding status: (1) failed breeders that failed

early in the 2007 breeding cycle, thus allowing them to breed again in 2008; (2) successful breeders that fledged a chick in 2006 and consequently did not breed in 2007; and (3) nonbreeders that did not breed in 2007 and 2006. The effects of sex, age, and breeding status in 2008 on blood isotopic ratios and the effects of sex, age, and past breeding status on feather isotopic ratios were investigated using generalized linear models. Date of sampling was included as a covariate in statistical analysis of blood isotopic ratios, because the foraging ecology of Wandering Albatrosses changes over the incubation period, with birds reducing the duration of the foraging trips as the season progresses (Weimerskirch et al. 1993). The resulting models for blood and feather data were thus: $\delta X \sim \text{sex} + \text{age} + \text{status 2008} + \text{sex} \times \text{age} + \text{age} \times \text{status 2008} + \text{date}$, and: $\delta X \sim \text{sex} + \text{age} + \text{past status} + \text{sex} \times \text{age} + \text{age} \times \text{past status}$, respectively. A second-order Akaike information criterion (AIC_c) was used to select the most parsimonious model. The effects of variables present in the most parsimonious model were

TABLE 1. Number of blood- and feather-sampled Wandering Albatrosses (*Diomedea exulans*) according to their sex, age, and breeding status.

Tissue and status	Females				Males			
	3–14 yr	15–29 yr	>29 yr	NA	0–14 yr	15–29 yr	>29 yr	NA
Blood								
Nonbreeders	11	0	2	0	17	10	22	0
Breeders	13	22	15	3	15	23	18	1
Total	66				106			
Feathers								
Nonbreeders	25	1	2	0	26	7	18	0
Successful	7	13	6	1	6	14	7	1
Failed	5	14	8	1	1	10	10	1
NA	1	1	2	1	1	6	2	0
Total	90				112			

Notes: Blood-sampled individuals were split into breeding (incubating) and nonbreeding (non-incubating) birds in 2008, and feather-sampled individuals were split into nonbreeders, successful, and failed breeders according to their past breeding status (see *Methods: Stable isotope data analyses*). NA indicates no available data.

then tested using *F* statistics. Birds were also grouped by sex according to their breeding history and age: (1) immature birds refer to young Wandering Albatrosses (3–11 years) that never bred; breeding albatrosses, i.e., those that bred at least once, were split into two groups: (2) breeders (7–29 years old) and (3) old breeders (>29 years old). All calculations and statistical modeling were carried out using R Version 2.11.1 (R Development Core Team 2010). Isotopic values are means \pm SD.

Stable isotopic values and demographic parameters

The effect of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values on demographic parameters was investigated using capture–recapture data of blood- and feather-sampled individuals over the period 2008–2012. Only sexually mature albatrosses were included in the analyses ($n = 167$). A recent multistate mark–recapture (MSMR) model that took into account the probability of detecting individuals according to their return to the colony and previous breeding status was used (Pardo et al. 2013), because it is a key point to calculate unbiased estimates of demographic parameters (Lebreton and Pradel 2002). Details of the model are given in the Appendix. The model was parameterized in terms of the probability of survival (s); the probability of returning to the colony, given survival (r); the probability of breeding, given return to the colony (β); the probability of successful hatching, given breeding (ω); the probability of successful fledgling, given hatching (γ); and the detection probability (p). Transition probabilities between states were thus modeled with a four-step procedure where s , r , β , ω , and γ were considered as four successive steps in transition matrices.

The hypothesis that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in one breeding season can influence the survival and breeding outputs of an individual over the four following years was tested by building MSMR models in which each demographic parameter θ was modeled as a function of an individual covariate C (standardized $\delta^{13}\text{C}$ or standardized $\delta^{15}\text{N}$ value) using a logit-link function:

$\text{logit}(\Theta) = a + b \times C_i$, where a is an intercept, b is a slope, and C_i is the value of standardized stable isotopic value for individual i . The covariate C has a negative or positive effect on demographic parameter when $b < 0$ or $b > 0$, respectively. The 95% confidence interval of the slope parameters and AIC_c (Burnham and Anderson 2002) for inference was used, keeping in mind the minimum recommended AIC_c difference of 2. Then, a composite model combining all of the covariates that were detected to have an effect on demographic parameters was built, and the goodness of fit (GOF) of the time-dependent MSMR model was tested using U-CARE (Choquet et al. 2009a). Model selection was based on AIC_c (Burnham and Anderson 2002) and all models were run under program E-SURGE 1.8.5, allowing the splitting of transition probabilities between states (Choquet et al. 2009b). To avoid estimating parameters at a local minimum of the likelihood function, each model was run five times with random initial values.

RESULTS

Gender effect on blood and feather isotopic values

Using the latitudinal $\delta^{13}\text{C}$ decrease of marine organisms in the Southern Hemisphere (Jaeger et al. 2010, Quillfeldt et al. 2010), the data indicate that Wandering Albatrosses forage from subtropical to subantarctic waters during both the incubation and inter-nesting periods (Fig. 1). Modeling reveals a marked gender effect on blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and on feather $\delta^{13}\text{C}$ values (Table 2), with males foraging in more southern latitudes than females. Indeed, blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were higher in females than in males (females, $-19.3\text{‰} \pm 0.7\text{‰}$ and $14.2\text{‰} \pm 0.6\text{‰}$, $n = 66$; vs. males, $-20.3\text{‰} \pm 0.8\text{‰}$ and $13.5\text{‰} \pm 0.5\text{‰}$, $n = 106$; two-sample *t* test, $t = 9.01$ and 8.15 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively; both $P < 0.0001$). Feather $\delta^{13}\text{C}$ values were also higher in females than in males, but their $\delta^{15}\text{N}$ values were not statistically different (females, -16.9‰

TABLE 2. Effects of sex, age, and breeding status (in 2008 and Past status, see *Methods: Stable isotope data analyses*) on blood and feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of Wandering Albatrosses.

Explanatory variable	Blood				Feather			
	$\delta^{13}\text{C}$ (df = 1, 162)		$\delta^{15}\text{N}$ (df = 1, 164)		$\delta^{13}\text{C}$ (df = 1, 177)†		$\delta^{15}\text{N}$ (df = 1, 179)‡	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Sex	83.333	<0.0001	67.285	<0.0001	13.040	0.0004		
Age	9.204	0.003	5.916	0.016	45.549	<0.0001	13.370	0.0003
Status 2008	4.767	0.030			nt		nt	
Age × Sex	17.051	<0.0001	4.621	0.033	2.620	0.107		
Age × Status 2008					nt		nt	
Date	1.324	0.252			nt		nt	
Past status	nt		nt		5.215	0.002	4.186	0.007
Age × Past status	nt		nt					

Notes: The most parsimonious model was selected with a second-order Akaike information criterion (AIC_c). Effects of variables present in the most parsimonious model were tested using *F* statistics. Abbreviation: nt, not tested. Cells are blank where a factor was not included in the best model. Best models for each tissue type and isotope were as follows. For blood $\delta^{13}\text{C}$: $\sim\text{Sex} + \text{Age} + \text{Status 2008} + \text{Age} \times \text{Sex} + \text{Date}$. For blood $\delta^{15}\text{N}$: $\sim\text{Sex} + \text{Age} + \text{Age} \times \text{Sex}$. For feather $\delta^{13}\text{C}$: $\sim\text{Sex} + \text{Age} + \text{Past status} + \text{Age} \times \text{Sex}$. For feather $\delta^{15}\text{N}$: $\sim\text{Age} + \text{Past status}$.

† For Past status, df = 3, 177.

‡ For Past status, df = 3, 179.

$\pm 1.0\text{‰}$ and $15.9\text{‰} \pm 1.0\text{‰}$, $n = 90$; vs. males, $-17.6\text{‰} \pm 1.1\text{‰}$ and $15.7\text{‰} \pm 0.9\text{‰}$, $n = 112$; $t = 4.54$ and 1.18 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$; $P < 0.0001$ and $P = 0.240$, respectively).

Excluding immature albatrosses, sex-related $\delta^{13}\text{C}$ segregation occurred for blood and feathers whatever the birds' breeding status (two-sample *t* tests, all $P < 0.044$; Figs. 2 and 3, respectively). Female breeders and old breeders also had higher blood $\delta^{15}\text{N}$ values than did males (both $P < 0.001$), whereas female and male feather $\delta^{15}\text{N}$ values did not differ significantly for breeders and old breeders ($P = 0.623$ and 0.976 , respectively). Interestingly, immature birds were the only group that did not present sex-related differences in blood and feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($P = 0.137$ and $P = 0.286$, respectively; Fig. 3).

Effects of breeding status and age on blood and feather isotopic values

Modeling indicates that breeding status affects both blood and feather isotopic values (Table 2). Blood $\delta^{13}\text{C}$ values, unlike blood $\delta^{15}\text{N}$ values, were significantly affected by the birds' breeding status in 2008 (Table 2), with breeding males having lower $\delta^{13}\text{C}$ values than nonbreeders (two-sample *t* test, $t = 3.13$, $P = 0.002$; Fig. 2). Feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were significantly affected by the birds' past breeding status (Table 2). Failed breeders of both sexes exhibited significantly lower feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than both successful breeders and nonbreeders (Tukey HSD multiple comparison tests, all $P < 0.049$, except for $\delta^{15}\text{N}$ of males, with both $P > 0.299$; Fig. 2).

Modeling indicates a marked age effect on blood and feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, but a significant interaction between age and sex highlights a gender difference in the effect of aging on blood, but not feather, isotopic signatures (Table 2). Indeed, female blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were not significantly affected by age, while

males showed a well-defined age-related pattern. Both breeding and nonbreeding males exhibited significant decreases in their blood $\delta^{13}\text{C}$ values with age (Fig. 1), with nonbreeding birds, but not breeding ones, also showing a significant $\delta^{15}\text{N}$ decrease with age (linear

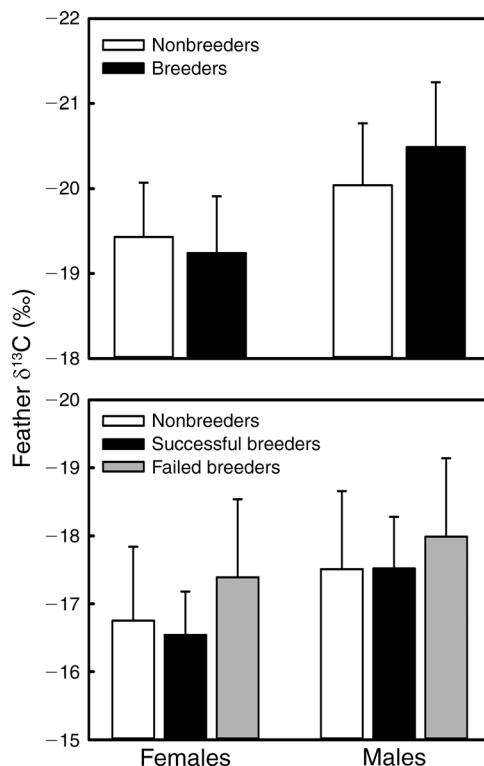


FIG. 2. Effect of breeding status on $\delta^{13}\text{C}$ values (mean \pm SD) of male and female Wandering Albatrosses. Birds were grouped according to their 2008 breeding status (blood $\delta^{13}\text{C}$ values, upper panel) and past breeding status (feather $\delta^{13}\text{C}$ values, lower panel) (see *Methods: Stable isotope data analyses* for definitions and statistics).

regressions, all $P < 0.007$, except for breeder $\delta^{15}\text{N}$ values, where $P = 0.248$). In contrast to blood isotopic values, well-defined age-related patterns were found for feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in both sexes (Table 2). Feather $\delta^{13}\text{C}$ values decreased with age, whatever the breeding status of males (linear regressions, all $P < 0.024$; Fig. 1), but $\delta^{15}\text{N}$ values decreased with age only in nonbreeders, but not in failed and successful breeders ($P = 0.040$, 0.207, and 0.764, respectively). In females, although failed breeders showed significant decreases in both their feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with age ($P = 0.016$ and 0.024 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively; Fig. 1), nonbreeders and successful breeders did not (for $\delta^{13}\text{C}$, $P = 0.972$ and 0.946; for $\delta^{15}\text{N}$, $P = 0.717$ and 0.950, respectively).

Effects of stable isotopic values on demographic parameters

The GOF of the MSMR model was overall not significant (for males, $\chi^2 = 16.327$, $\text{df} = 22$, $P = 0.799$; for females, $\chi^2 = 7.078$, $\text{df} = 16$, $P = 0.972$). There were no effects of blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values on demographic parameters (Table 3). In contrast, model selection suggested an effect of feather $\delta^{13}\text{C}$ values on breeding decision in the following years, with no effects on other demographic parameters (return and survival rate, and hatching and fledging success; Table 4). The relationship between feather $\delta^{13}\text{C}$ values and future breeding probability was positive (estimated slope and 95% confidence interval 1.07 [0.32 to 1.82]) in nonbreeding males, but not in breeding males and in females (confidence intervals include 0; statistics not shown). Model selection also suggested an effect of feather $\delta^{15}\text{N}$ values on the return rate to the colony, with no effects on other demographic parameters (Table 4). The relationship between feather $\delta^{15}\text{N}$ values and the probability of returning to the colony was negative in successful breeders (estimated slope and confidence interval -0.40 [-0.76 to -0.04]), but not in failed breeders and nonbreeders (confidence intervals include 0, statistics not shown).

DISCUSSION

Evidence of age-dependent changes in the food and feeding ecology of free-ranging individuals is scarce, especially at older stages (MacNulty et al. 2009). Here, we report empirical evidence for age-, gender-, and breeding status-dependent trophic niche in the Wandering Albatross. The most notable result of this study is the age-related and male-specific pattern in foraging behavior during both the breeding and inter-nesting periods, and the consequences of foraging in some habitats for subsequent reproductive status. The isotopic investigation reveals a more complex foraging pattern of Wandering Albatrosses than previously thought, thus verifying and expanding considerably the data gathered using satellite tracking during a single incubation trip (Lecomte et al. 2010). Satellite tracking of a subset of the

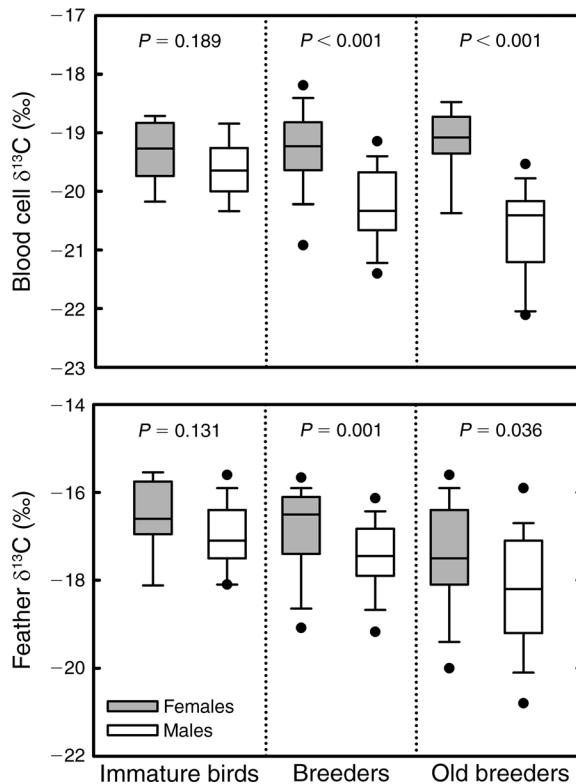


FIG. 3. Effect of sex on blood (upper panel) and feather (lower panel) $\delta^{13}\text{C}$ values of Wandering Albatrosses that were grouped according to their breeding history: immature birds, breeders (7–29 years old), and old breeders (>29 years old). Boxplots show the median, with box endpoints at the 25th and 75th percentiles, error bars show the 90th and 10th percentiles, and the outlier points represent the 95th and 5th percentiles. P values correspond to the statistical results of two-sample t tests.

sampled birds validated the use of $\delta^{13}\text{C}$ values to depict the latitudinal foraging areas of Wandering Albatrosses (Jaeger et al. 2010), but, in apparent contradiction with tracking of the birds (Lecomte et al. 2010, Weimerskirch et al. 2012), no very low antarctic $\delta^{13}\text{C}$ values were recorded in our large isotopic data set. Because breeding Wandering Albatrosses feed all along their foraging trips (Weimerskirch et al. 2005), blood signature integrates not only prey taken in Antarctica, but also elsewhere and during several consecutive trips, thus diluting the low $\delta^{13}\text{C}$ values of antarctic food by the higher $\delta^{13}\text{C}$ values of prey caught farther north. Such a “dilution effect” lowers differences among individuals and groups and underlines the strength of age-, sex-, and breeding status-related foraging strategies depicted here. On the other hand, the dilution effect precludes the isotopic recording of maximum foraging ranges measured by telemetry.

Sexual segregation in trophic niche is well documented in seabirds, including albatrosses (Catry et al. 2005, Wearmouth and Sims 2008). Although both sexes overlap, incubating male Wandering Albatrosses prefer colder waters at the latitude of Crozet or to the south,

TABLE 3. Modeling the effects of standardized blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values on demographic parameters.

Hypothesis	Model no.	Rank	Deviance	ΔAIC_c
A) Effects of blood $\delta^{13}\text{C}$ values on demographic parameters				
No effect of $\delta^{13}\text{C}$	1	23	1421.00	0.00
Effect of $\delta^{13}\text{C}$ on survival rate the following years	6	25	1418.12	1.62
Effect of $\delta^{13}\text{C}$ on hatching success the following years	3	25	1418.61	2.11
Effect of $\delta^{13}\text{C}$ on fledgling success the following years	2	25	1418.89	2.40
Effect of $\delta^{13}\text{C}$ on breeding decision the following years	4	31	1405.20	2.49
Effect of $\delta^{13}\text{C}$ on return rate the following years	5	26	1420.79	6.57
B) Effects of blood $\delta^{15}\text{N}$ values on demographic parameters				
No effect of $\delta^{15}\text{N}$	1	23	1421.00	0.00
Effect of $\delta^{15}\text{N}$ on survival rate the following years	11	25	1419.18	2.68
Effect of $\delta^{15}\text{N}$ on fledgling success the following years	7	25	1419.61	3.11
Effect of $\delta^{15}\text{N}$ on hatching success the following years	8	25	1419.68	3.18
Effect of $\delta^{15}\text{N}$ on breeding decision the following years	9	31	1408.98	6.27
Effect of $\delta^{15}\text{N}$ on return rate the following years	10	26	1420.99	6.76

whereas females favor warmer waters to the north (Weimerskirch et al. 1993, 2012). The different foraging zones are related to sexual size dimorphism, with greater wing loadings allowing larger males to be more efficient in the windier southern latitudes (Shaffer et al. 2001). Accordingly, blood $\delta^{13}\text{C}$ values confirm that a majority of males (71%) favored the subantarctic zone, whereas most adult females (89%) foraged in the subtropics during incubation. Much of what is known about seabird sexual segregation is generally restricted to the breeding period (Wearmouth and Sims 2008, Mancini et al. 2013), but a preliminary tracking investigation on a few failed breeders suggests that Wandering Albatrosses also segregate sexually between breeding attempts (Weimerskirch and Wilson 2000). Overall, feather isotopic values confirm this pattern on failed breeders and expand it to both successful breeders and non-breeders. Hence, sexual segregation also occurs during the molting period, with females foraging consistently farther north than males within the Subtropical Zone, as shown in this study and in Jaeger et al. (2009). Interestingly, comparison of blood and feather $\delta^{13}\text{C}$ values indicates a northern shift in foraging grounds of adult males between the breeding and inter-nesting

periods, with most males (72%) molting in subtropical waters, as females (88%) do. Wandering Albatrosses are apex predators that feed mainly on large squids (Cherel and Weimerskirch 1999, Blévin et al. 2013). Blood and feather $\delta^{15}\text{N}$ values showed no biologically relevant sex-related dietary differences in terms of trophic position, the higher female $\delta^{15}\text{N}$ values being likely to result from higher $\delta^{15}\text{N}$ baseline levels (that propagate up the food web) in the subtropics than in subantarctic waters (Altabet and François 1994, Jaeger et al. 2010). However, this does not preclude some dietary differences in terms of prey items, because most marine organisms, including oceanic cephalopods, are related to specific water masses.

There is a general paucity of individual-based study on the foraging strategies of young birds after their first year at sea and, except for a pioneer investigation in the Benguela Current (Petersen et al. 2008), no tracking information is available on immature albatrosses. In Wandering Albatrosses, postnatal dispersal of juveniles of both sexes occurs in the subtropics (Weimerskirch et al. 2006), and at-sea observations of birds of unknown status showed that darker (younger) individuals occur in the northern part of the species' range (Weimerskirch et

TABLE 4. Modeling the effects of standardized feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values on demographic parameters.

Hypothesis	Model no.	Rank	Deviance	ΔAIC_c
A) Effects of feather $\delta^{13}\text{C}$ values on demographic parameters				
Effect of $\delta^{13}\text{C}$ on breeding decision the following years	4	31	1613.57	0.00
No effect of $\delta^{13}\text{C}$	1	23	1640.38	8.85
Effect of $\delta^{13}\text{C}$ on fledgling success the following years	2	25	1638.43	11.33
Effect of $\delta^{13}\text{C}$ on return rate the following years	5	26	1636.32	11.45
Effect of $\delta^{13}\text{C}$ on hatching success the following years	3	25	1639.02	11.92
Effect of $\delta^{13}\text{C}$ on survival rate the following years	6	25	1640.30	13.21
B) Effects of feather $\delta^{15}\text{N}$ values on demographic parameters				
Effect of $\delta^{15}\text{N}$ on return rate the following years	10	26	1631.23	0.00
No effect of $\delta^{15}\text{N}$	1	23	1640.38	2.49
Effect of $\delta^{15}\text{N}$ on fledgling success the following years	7	25	1638.03	4.58
Effect of $\delta^{15}\text{N}$ on survival rate the following years	11	25	1639.29	5.83
Effect of $\delta^{15}\text{N}$ on hatching success the following years	8	25	1639.60	6.14
Effect of $\delta^{15}\text{N}$ on breeding decision the following years	9	31	1632.91	12.98

al. 1989). Accordingly, blood and feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of immature Wandering Albatrosses presented no sex-related differences and were identical to those of adult females. Immature birds at least two years old thus foraged mainly in the subtropics, where they fed at the same trophic position as the adults. A consequence of feeding in the subtropics is that young males, not females, change their main latitudinal foraging grounds when they recruit into the breeding populations. Hence, breeding status drives the foraging strategy of males early in their reproductive life, but whether it is an abrupt or progressive shift remains to be investigated.

In contrast to sex-related resource partitioning, very few studies have documented the influence of breeding status on trophic segregation in adult seabirds (Awkerman et al. 2007). Interestingly, their breeding status affects the main foraging areas of adult Wandering Albatrosses of both sexes. Firstly, nonbreeding adult males had higher blood $\delta^{13}\text{C}$ values than breeders, thus indicating that they overall fed in northern latitudes, whatever their age during the incubation period (Fig. 1). The ecological origins of this segregation can be manifold, as competitive exclusion, energy constraint linked to reproduction, or physiological or phenotypic differences. Nonbreeding males of various ages, and particularly old birds, were observed interacting with immature females. Although breeding males perform long trips during the incubation period (Weimerskirch et al. 1993), colony monitoring of nonbreeding males suggests that they performed short trips in the vicinity of the colony at that time (authors' unpublished data), a foraging behavior that requires further tracking investigation. Secondly, failed breeders of both sexes had lower feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, thus resulting in more failed breeders than successful and nonbreeders foraging in subantarctic waters during the inter-nesting period (30%, 9%, and 17%, respectively). Because early failed breeders reproduce in the following year, their inter-nesting period is shortened (6–11 months) when compared to the complete sabbatical year of successful breeders. A shorter inter-nesting period probably drives the birds' behavior to stay more in waters closer to the colony (Weimerskirch and Wilson 2000) rather than to engage in longer term migration in the subtropics.

The most innovative finding of the present work is the effect of age on the foraging strategies of adult Wandering Albatrosses with, again, variations associated with sex and periods of the cycle, the result being an intricate use of foraging latitudes by the species over time. During both the incubation and inter-nesting periods, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values showed that, whatever their breeding status, males foraged progressively farther south with age, with no associated biologically significant changes in trophic level. In contrast, no age effect was detected in females, except that old failed breeders favored more southern foraging latitudes during the inter-nesting period. A direct and noticeable consequence of this differential age- and gender-related effect

is that the isotopic niches of both sexes diverge more and more with age, from no differences in immature birds to almost no overlap in the foraging latitudes of old (>30 years) females and males during incubation. At-sea observations of birds of unknown sex and status are in general agreement with this pattern, with the whitest individuals (most likely corresponding to the oldest males) being consistently reported over years at higher latitudes than any other stages of plumage maturation (Weimerskirch et al. 1989).

Because age per se is not known to intrinsically affect the stable isotope signature of adult organisms, the foraging pattern raises a series of fascinating questions about the effect of age on the evolution of feeding behavior and of resource partitioning within a long-lived species. For example, *why do males progressively forage in more southern latitudes, and is the age effect related to male foraging senescence?* At least two nonexclusive explanations may account for this foraging pattern. Firstly, competitive exclusion can occur among different age classes. If younger males outcompete older individuals at the latitude of the colonies, while females forage in warmer waters, colder waters appear a viable alternative habitat for old males, with higher costs of traveling farther south from the breeding sites, and thus of being at risk of nest desertion by their mate. Secondly, as they age, males may reduce the cost of foraging by flying in windier areas, where they decrease the frequency of costly landings and takeoffs. Noticeably, the male age-related pattern also occurred in nonbreeders and during the inter-nesting period, suggesting that the energy-saving strategy may be used all year long and is thus intrinsically linked to the birds' age. Older males also had high stress-hormone levels when returning from the sea during incubation, suggesting low foraging success (Lecomte et al. 2010), which is in agreement with reduced foraging performance in old male Grey-headed Albatrosses (Cathy et al. 2006). As a consequence of aging induced by impairment of cognitive or locomotory capacities, males may forage farther south, but with low success in terms of food intake compared to energy expenditure. A decrease in resources acquisition through this "foraging senescence" should modify life history trade-offs and explain other aspects of senescence such as as decrease of reproduction or survival. Accordingly, male Wandering Albatrosses with low feather $\delta^{13}\text{C}$ values (i.e., foraging at higher latitudes during the inter-nesting period) have a lower probability of reproducing in the following years, especially if they were previously observed as nonbreeders. However, foraging at higher latitudes had no effect on survival rate. A recent theory speculates that individuals invest less in reproduction with age in order to maintain a high level of fitness until old age (McNamara et al. 2009).

Why does age affect the foraging strategy of males and not of females? Recent demographic investigations in Wandering Albatrosses from the Crozet Islands showed a complex sex- and age-related pattern in life history

traits that chronologically fit with the foraging pattern. Reproductive senescence occurs in both sexes from 30 years onward, but adult survival drops with age in males, whereas it remains stable in females (Lecomte et al. 2010, Pardo et al. 2013). Male-biased mortality and accelerated aging occur with higher reproductive investment (Bonduriansky et al. 2008) and with intense male competition for access to resources in monogamous species, including humans (Møller et al. 2009). Indeed, male Wandering Albatrosses invest more in reproduction than females (Weimerskirch and Lys 2000), and male age-related foraging strategies can be explained by competitive exclusion on foraging grounds.

To our knowledge, a continuous change with age in the ecological niche of a species has not been reported previously in any species of birds and mammals. Hence, the isotopic approach opens new perspectives for gathering relevant foraging information quickly and cheaply for a large number of simultaneously sampled individuals of different ages. However, a main intrinsic limitation of the method is that the isotopic niche is only a part of the ecological niche and, consequently, it is at its most powerful when combined with other methods. The study points out the need for more integrated investigations for a better evolutionary understanding of the age effect on the foraging behavior of male Wandering Albatrosses. Specifically, the use of bio-logging to record energy expenditure and food intake (Weimerskirch et al. 2000, 2005) of different age classes would help to clarify the energy consequences of foraging progressively to more southern waters with age, and its potential consequences in terms of reproductive success and survival.

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SUPPLEMENTAL MATERIAL

Appendix

Construction of the multistate mark–recapture model ([Ecological Archives E095-206-A1](#)).

Ecological Archives E095-206-A1

Audrey Jaeger, Aurélie Goutte, Vincent J. Lecomte, Pierre Richard, Olivier Chastel, Christophe Barbraud, Henri Weimerskirch, and Yves Cherel. 2014. Age, sex, and breeding status shape a complex foraging pattern in an extremely long-lived seabird. *Ecology* 95:2324–2333. <http://dx.doi.org/10.1890/13-1376.1>

APPENDIX A. Construction of the multistate mark–recapture model.

The effects of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values on demographic parameters were tested using a multistate mark-recapture (MSMR) model developed by Pardo et al. (2013). The model includes eight states: dead, failed breeder on egg (FBE, defined as an individual that was observed with one egg that failed to hatch), failed breeder on chick (FBC, defined as an individual that was observed with one chick but that failed to fledge the chick), successful breeder (SB, defined as an individual that fledged one chick), observable non-breeder (ONB, defined as an individual that was observed at the colony, but that was not observed with an egg or chick), and three unobservable states consisting of non-breeders that were observed at the colony during the previous breeding attempt (PONB), non-breeders whose previous breeding attempt failed (PFB) and non-breeders whose previous breeding attempt was successful (PSB). The state dead (\dagger) was an absorbing state representing death or permanent emigration from the study area. The unobservable states account for temporary absence corresponding to birds that skip breeding after breeding either unsuccessfully or successfully.

States occupied are not directly observed; rather, at each occasion t , an event happens and it is recorded leading to an observed encounter history. In our case, we thus considered five events; 0 = "not observed", 1 = "seen as a failed breeder on egg", 2 = "seen as a failed breeder on chick", 3 = "seen as a successful breeder", 4 = "seen as a non-breeder", which were used to build capture histories. Events and states are considered as random variables, and it is assumed that an event at occasion t depends only on an underlying state (which is not observed) of the individual at the moment, and that successive states obey a Markov chain. Models were parameterized in terms of the probability of survival (s), the probability to return at the colony given survival (r), the probability of breeding given return at the colony (β), the probability of successful hatching given breeding (ω), the probability of successful fledgling given hatching (γ), and the detection probability (p). Transition probabilities between states were thus modeled with a five-step procedure where s , r , β , ω and γ were considered as five successive steps in transition matrices. Parameters of the model are defined in the following table:

Parameter	Definition
s^t_s	Probability that an individual in state s at time t survives to time $t + 1$ and does not permanently emigrate from the study area
r^t_s	Probability that an individual in state s at time t returns to the colony to time $t + 1$ given that it survives to $t + 1$
β^t_s	Probability that an individual in state s at time t breeds at time $t + 1$ given that it survives to and returns to the colony at time $t + 1$
γ^t_s	Probability that an individual in state s at time t incubates successfully at time $t + 1$ given that it survives to, returns to the colony and breeds at time $t + 1$
δ^t_s	Probability that an individual in state s at time t raises successfully one chick at

	time $t + 1$ given that it survives to, returns to the colony and incubates successfully at time $t + 1$
p^t_s	Probability that an individual in state s at time t is encountered at time $t + 1$

Several constraints were made to ensure that the parameters of the model were estimable. The state dead being explicitly included in the model but being never encountered, initial encounter probability was fixed to 0, transition probabilities from the state dead to the other states were fixed to 0 and capture probability was fixed to 0 (Pradel 2005, Choquet et al. 2009). The probability of seeing individuals in unobservable states and transitions between unobservable states were constrained to 0. β_{SB} was not constrained to 0, because some individuals were observed breeding in the year consecutive to a successful breeding event (Barbraud and Weimerskirch, 2012). Models in which all survival probabilities varied separately were not considered to limit redundancy in survival parameters (Hunter and Caswell 2009). Because our capture-recapture analyses relied on a limited number of individual capture histories, a limited number of recapture occasions and a relatively large number of unobservable states we constrained: (i) parameters s , r , β , ω , γ and p to be constant over time, (ii) return rates to be similar for ONB, PFB, PSB, and PONB, and (iii) breeding probabilities to be similar for PFB, PSB, and PONB. With these constraints the initial model was full-rank. Note that a model in which all demographic parameters were time and state dependent was run, but this model was highly rank deficient.

This MSMR model was parameterized by the survival–transition probabilities matrix:

	FBE	FBC	SB	ONB	PFB	PSB	PONB	\dagger	
FBE	$sr\beta(1-\omega)$	$sr\beta\omega(1-\gamma)$	$sr\beta\omega\gamma$	$sr(1-\beta)$	$s(1-r)$	-	-	*	
FBC	$sr\beta(1-\omega)$	$sr\beta\omega(1-\gamma)$	$sr\beta\omega\gamma$	$sr(1-\beta)$	$s(1-r)$	-	-	*	
SB	$sr\beta(1-\omega)$	$sr\beta\omega(1-\gamma)$	$sr\beta\omega\gamma$	$sr(1-\beta)$	-	$s(1-r)$	-	*	
ONB	$sr\beta(1-\omega)$	$sr\beta\omega(1-\gamma)$	$sr\beta\omega\gamma$	$sr(1-\beta)$	-	-	$s(1-r)$	*	
PFB	$sr\beta(1-\omega)$	$sr\beta\omega(1-\gamma)$	$sr\beta\omega\gamma$	$sr(1-\beta)$	-	-	-	*	
PSB	$sr\beta(1-\omega)$	$sr\beta\omega(1-\gamma)$	$sr\beta\omega\gamma$	$sr(1-\beta)$	-	-	-	*	
PONB	$sr\beta(1-\omega)$	$sr\beta\omega(1-\gamma)$	$sr\beta\omega\gamma$	$sr(1-\beta)$	-	-	-	*	
\dagger	-	-	-	-	-	-	-	*	

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[\[Back to E095-206\]](#)