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Lifetime foraging patterns of the wandering albatross: Life on the move!

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ABSTRACT

Wandering albatrosses are large long-lived seabirds that inhabit the Southern Ocean. This species uses wind to move at low energetic costs and probably represents one of the best studied life-history models in animals. Here, using both tracking and isotopic data, we report on the lifetime distribution of wandering albatrosses at sea, constructing a synthesis about how their distribution, foraging movements and feeding ecology change throughout all life-history stages (i.e. juvenile, immature, pre breeding adults, breeding adults, sabbatical adults and senescent birds). Males and females exhibit different foraging strategies that change throughout their life. For instance, as males mature from young to old stages, they progressively move from subtropical waters to Antarctic waters. In comparison, females remain in subtropical waters throughout their lives, but increase their speed of travel with age. For both sexes, the first year at sea is a critical period, when the highest mortality occurs. At this stage, juveniles have already fledged and are able to use the wind optimally to maximise movement, but require several months to reach the travelling speed of adults. Immature albatrosses remain in warm subtropical waters, before returning to their birth place and future breeding grounds from where they move as central place foragers. When recruited into the breeding population, they breed every other year. In one year they invest in one long breeding season when males and females use separate foraging zones in the subtropics and sub-Antarctic, respectively. In the subsequent year (termed "sabbatical" year), both sexes disperse across the Southern Ocean, with reduced segregation between sexes. In total, throughout the approximate 50 year lifetime of a wandering albatross, an individual is estimated to travel a mere 8.5 million km. We show that the changes in habitats and foraging strategies observed through the life time of wandering albatrosses are the results of behavioural adjustment to the successive constraints encountered, such as learning processes, breeding or ageing, and have profound consequences on survival and nesting success.

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1. Introduction

Recently, there has been an increasing interest in the lifetime demography of animals (Clutton-Brock, 1988; Newton, 1989), due to increasing numbers of long-term studies of tracked animals (Clutton-Brock and Sheldon, 2010). These studies stress that the breeding activity and survival of animals change markedly over the course of an individual's lifetime. Animals generally improve survival and reproductive output during the first stages of life; these parameters reach a plateau, and then often decline during later age (Jones et al., 2008). This pattern is best demonstrated in long-lived species, such as seabirds, because the pattern spreads across decades. While literature on this subject is accumulating (Berman et al., 2009; Pardo et al., 2013a; Weimerskirch, 1992), the overall number of species for which lifetime demography is known continues to remain limited.

Since survival and reproduction depend entirely on the ability of animals to find resources in the natural environment, and to selectively allocate these resources between reproduction and survival (Stearns,

1992), changes in the foraging pattern of animals are expected to occur through life. For example, it is well known that juvenile animals of most species exhibit dispersive behaviours, during which they search for new environments where competition with congeners is limited, and ultimately settle somewhere to find a mate and start reproducing (Clobert et al., 2001). However, the lifetime foraging movements of animals are basically not known, especially for vertebrates growing throughout their life such as fishes, reptiles or mammals, and are a small size when young, precluding the possibility to track them e.g. Hays et al. (2010). In addition tracking animals in the marine environment is challenging for logistical reasons.

Albatrosses are large sized marine predators whose fledglings are of similar size to adults, making them convenient models to study lifetime foraging. They are wide ranging long-lived marine predators operating large scale movements during the breeding season, when they invest in central place foraging, and outside of the breeding season (Wakefield et al. 2009; Weimerskirch et al., 2000c). The wandering albatross (*Diomedea exulans*) is one of the most wide ranging flying seabirds, rooming over the entire Southern Ocean. It is well known from long-term land-based monitoring programmes that were started more than 50 years ago (Croxall et al., 1990; Weimerskirch and Jouventin, 1987; Weimerskirch et al., 1997a, 1997b, 1997c). Since

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1990, when the first wandering albatrosses were tracked with the Argos system (Jouventin and Weimerskirch, 1990), hundreds of individuals from all life-stages have been tracked from the Crozet islands (52°E, 46°S), which are sub-Antarctic archipelago of small islands in the southern Indian Ocean (Weimerskirch et al., 2012). More recently, the stable isotope method was used to gather further information on the feeding ecology of the same population (e.g. Jaeger et al., 2009, 2010a). The availability of a long-term demographic database combined with large tracking and isotopic databases provides a unique opportunity to examine in detail how animal foraging movements change over the course of a lifetime for this species. Wandering albatrosses have a maximum life span of more than 60 years; consequently, a significant part of the population is made up of old birds that might impact population dynamics (Lecomte et al., 2010; Weimerskirch, 1992). Overall life history parameters, such as survival and breeding success, change extensively through the lifetime of the wandering albatross (Fig. 1); therefore, age effects on demographic parameters might arise from age effects on foraging parameters.

This study aimed to provide the first comprehensive view about how a species forages and distributes over its entire lifetime. We use this information to examine whether the changes observed in the life history traits of the wandering albatross, such as breeding success or survival, are related to differences in foraging behaviour. We place particular focus on sex specific differences, because the wandering albatross exhibits significant sexual dimorphism, with males having noticeably larger body size.

The life cycle of the wandering albatross

Wandering albatrosses are large seabirds (8–12 kg) that are found throughout the Southern Ocean, from Antarctic to subtropical waters. This species nests on the subantarctic islands of South Georgia, Prince Edwards, Crozet, Kerguelen and Macquarie Islands. Breeding lasts a complete year; therefore, most adults that have fledged a chick take a year off breeding (termed a “sabbatical” year), when they remain permanently at sea, before returning to the colony to breed again (Tickell, 1968). Only a few birds breed during two successive years (Barbraud and Weimerskirch, 2012). When the chick fledges after being fed by its parents for 8 months (Tickell, 1968), it will stay at sea continuously for 3 to 7 years before returning to its natal colony, when it will start breeding after several years of visiting the colony (Weimerskirch et al., 1997a, 1997b, 1997c). During the first year after fledging, birds are considered as juveniles, and during the next years until their first breeding attempt, as immatures.

2. Methods

We studied male and female wandering albatross movement, diet and isotopic signature from Possession Island, which is part of the Crozet Islands (46°S, 52°E), with some additional information from the Kerguelen Islands (50°S, 70°E) for comparisons of the juvenile and sabbatical behaviour between the two populations. The Crozet population has been monitored annually at the colony since 1966. All birds, adults and chicks are banded annually; therefore, today, almost all individuals are of known age (Weimerskirch et al., 1997a, 1997b, 1997c). Every year, the identity of individuals present on the colony, their status and breeding success are monitored. Therefore, the survival of all age classes may be estimated on an annual basis (Barbraud and Weimerskirch, 2012; Rolland et al., 2010; Weimerskirch et al., 1987).

2.1. Tracking data

Between 1989 and 2013, more than 600 wandering albatrosses of known sex and age were equipped with one of four different types of transmitters: (1) Argos PTT Satellite Transmitters powered with battery and working in continuous mode (1989–2003), (2) duty-cycled solar

panelled PTTs or GPS/PTTs (2003–2012), (3) GPS (2002–2013) and (4) GLS (Global Location Sensing, 1998–2013). PTTs and GPS were attached to the feathers with adhesive tape, while GLS were fixed on a plastic leg band. Birds were equipped before taking off for the sea, and the devices (PTTs and GPS) were either retrieved after one or several foraging trips from breeding birds, or left on the birds until the logger detached with the moult of feathers for juveniles, immature birds and adult birds in a sabbatical year. GLS was retrieved from the leg band after one sabbatical year or several years. Details of equipment and analysis of data are presented in Weimerskirch et al. (1993, 2000c). The total mass of devices was always far below the recommended 3% threshold (Phillips et al., 2003), and the same procedure of attachment has been consistently used over the last 20 years. The GPS and PTTs have reduced in mass over time, from 180 g in 1989–1992 years, to 50 g in the 1990s, and to 20–30 g in the 2000s. GLS loggers (Mk4 or 15, British Antarctic Survey) weighed 2.5–4.56 g, which is considered as having negligible effects on such a large bird, representing 0.03% of their body mass (Phillips et al., 2003). Long term analysis of the potential effects of telemetry shows that no negative effects of satellite transmitters on wandering albatrosses was found on breeding success, frequency and survival (Barbraud and Weimerskirch, 2011).

Details about the principle of GLS and estimates of positions from daylight levels are presented in Afanasyev and Prince (1992) and Phillips et al. (2004). In addition to daylight, GLS loggers also recorded salt water immersion, allowing the activity of birds to be estimated, such as whether the bird is in flight or sitting on the water.

2.2. Diet and stable isotopes analysis

At the Crozet Islands, wandering albatrosses primarily feed their chicks with squid, followed by fish caught in the vicinity of the colony (Cherel and Weimerskirch, 1999; Ridoux, 1994; Weimerskirch et al., 1997a). Since the diet of albatrosses can only be assessed during the

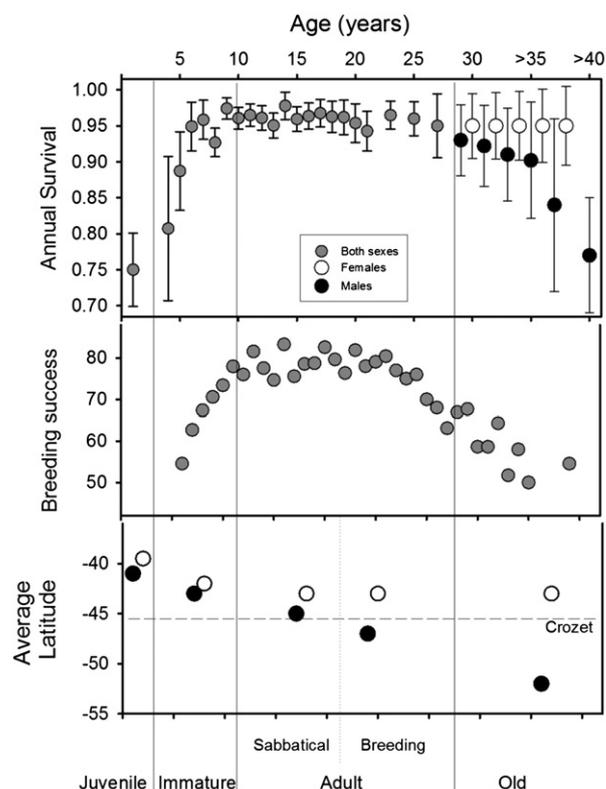


Fig. 1. Changes through age and life history stages in annual survivorship (top), breeding success (middle) and latitude used (lower) by wandering albatrosses.

chick-rearing period, tracking investigations were complemented by measuring the isotopic niche, which served as a proxy of the trophic niche. The isotopic method was validated in the albatross foraging area located within the southern Indian Ocean, in which the $\delta^{15}\text{N}$ values of seabirds increased with trophic level (Cherel et al., 2010), while $\delta^{13}\text{C}$ values indicated latitudinal (but not longitudinal) feeding habitats (Cherel and Hobson, 2007; Jaeger et al., 2010b). The isotopic niche was investigated by collecting blood and feathers that record trophic information that corresponds to the respective breeding and moulting periods (Cherel and Hobson, 2007). As chick food and the foraging ecology of adults during the chick-rearing period are well known (Weimerskirch et al., 1997a), chicks were used as a control group to help interpret the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of immature and adult birds. Special care was taken to compare the same tissue type (blood or feathers) within and between groups, to avoid confounding effects caused by tissue-dependent isotopic values (Dalerum and Angerbjörn, 2005). Sampling was performed on all age classes, except juveniles, because this age class precludes handling and sampling ashore. Fieldwork was carried out at Possession Island on large chicks at the end of the 2007 breeding season, and on immature and incubating birds (hereafter breeders) during the early 2008 breeding season (details in Jaeger et al. submitted). Stable isotope analyses were performed on blood cells (hereafter blood) and on four feathers per individual that were pooled to obtain an average isotopic signature for the whole plumage (Jaeger et al., 2009). Tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were determined by a continuous flow mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyser (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.

3. Results

3.1. At-sea distribution

3.1.1. The juvenile stage

After one of the longest chick rearing periods of birds, nearly 9 months, during which time it is fed by both parents, the fledgling wandering albatross leaves its natal site in November, after the parents reduce the amount of food being provisioned (Weimerskirch and Lys, 2000; Weimerskirch et al., 2000a). The fledglings leave the colony alone, without any contact with their parents, and remain at sea continuously for the following 3 to 7 years. The first year at sea (termed juvenile stage) is critical, as this is the period when most mortality occurs (Riotte-Lambert and Weimerskirch, 2013; Weimerskirch et al., 2006). Although the recruitment rate of wandering albatrosses is relatively high compared to other seabird species, with about 50% of fledglings surviving until recruitment into their natal colony (Gauthier et al., 2010; Weimerskirch et al., 1997a, 1997b, 1997c), about 25% of juveniles die during the first two months at sea (Riotte-Lambert and Weimerskirch, 2013).

After the fledglings leave the colony, they land on the water for variable periods of time (from hours to days) until the southerly winds blow (Weimerskirch et al., 2006). The birds then start a north-north-east direction of movement until they reach subtropical waters, at which point they start large scale movements (Fig. 2). The birds remain in these deep and warm waters for the next year, mainly using large scale looping movements (Fig. 2). During the first months of the juvenile period, the birds progressively increase the distance covered every day, and reduce the proportion of time spent on the water, to eventually reach movement performances similar to those of adults after 5 months at sea (Fig. 2b; Riotte-Lambert and Weimerskirch, 2013). During this first year at sea, juveniles cover an average distance of 185,000 km.

Whereas Crozet juvenile birds remain in the Indian Ocean, with males moving more to the east than females (Fig. 3), Kerguelen juveniles enter in the Pacific Ocean after several months (Åkesson and Weimerskirch, in revision; Weimerskirch et al., unpublished).

3.1.2. The immature stage

After a minimum of 2 years (average 5 years) spent continuously wandering at sea, young immature birds return to their natal colony for the first time for brief visits of a few days interspersed with foraging trips at sea. When on the colony, the birds engage in spectacular courtships, during which they search for a future partner (Jouventin and Lequette, 1990). They spend several hours to a few days on land, and return at sea for several days at sea to feed. When foraging at sea, immature birds behave as central place foragers, making looping movements from the colony, like adults (Fig. 4). These trips may be interpreted as being used by immature birds to become knowledgeable of the environment surrounding the future breeding grounds. Indeed, during the juvenile and immature phase, young individuals are not present in the foraging zone of breeding adults around the breeding grounds, but favour subtropical waters. During these movements from the colony that are shorter in duration compared to those of adults, activity patterns and foraging zones are similar to those of adults, suggesting that when they start visiting the breeding grounds the immature birds have acquired foraging skills similar to those of adults for basal maintenance. However for the additional requirements of breeding, i.e. the energy required for self-maintenance, for fasting during incubation of the egg and for sustaining a chick, young birds must acquire new skills in an environment around the colonies that they are not familiar with, and where competition with congeners is likely to be high. These visits on land alternated with foraging at sea last until March, at which point the young birds leave the environment of the future breeding grounds for the oceanic waters of the Indian Ocean, some individuals travelling as far as the Pacific Ocean (Figs. 3 and 4). During this period of immaturity when they visit the colonies, the birds progressively improve their body condition until they attain a threshold value that allows breeding (Weimerskirch, 1992). When this threshold is attained and a partner selected, breeding starts the next year and the pair bond will be formed for life until the death of one partner.

3.1.3. The adult stage

When they start breeding at the age of 10 years, on average (range 6–15), adult birds must drastically change their life at sea. Specifically, they alternate a complete year of breeding, when they are central place foragers returning regularly to the colony, with a sabbatical year, when they leave the proximity of the nesting grounds for distant foraging grounds.

3.1.4. Breeding season

Throughout the one year breeding cycle, wandering albatrosses alternate periods on land and foraging movements at sea. During incubation, they alternate between long foraging trips lasting 10 days on average (2–30 days) and stints on the nest to incubate the egg where they fast (Weimerskirch, 1995). At this stage, the birds forage up to 3500 km from the nest, with distinct differences between males and females; males forage in sub-Antarctic and Antarctic waters, while females forage in warmer waters (Fig. 5). Wandering albatrosses have been repeatedly tracked since 1989 during the egg incubation period; thus, it is possible to examine the effects of age on foraging performance, and hence fitness. From the age of recruitment (i.e. about 6–15 years old) until old age, breeding success shows a bell shaped curve; specifically, breeding success increases at young ages (6–15), attains a plateau and then decreases above the ages of 25–30 (Fig. 1). The increase in breeding success when young indicates an improvement in foraging ability at sea and, perhaps, synchronisation between partners in the alternation of foraging bouts and breeding

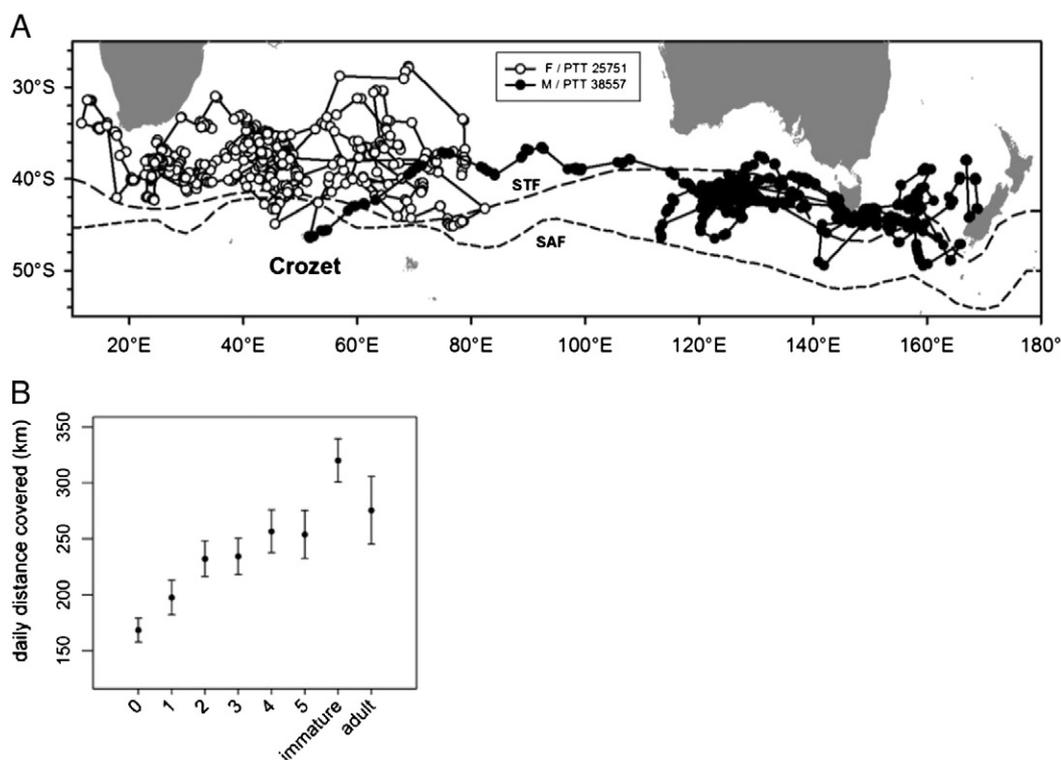


Fig. 2. A movement of two juveniles (aged 8 months at fledging) wandering albatrosses from the Crozet Islands tracked with Argos transmitters during their first 8–10 months at sea (white = female, black = male). B Changes in movement rate of juveniles during the first 6 months after fledging compared to immature individuals and adults outside the breeding season.

duties (incubating, and later in the season brooding, feeding the chick) on land (Weimerskirch et al., 2000a). The decrease in breeding success at old ages, paralleled by a decrease in male survival rates (Fig. 1; Weimerskirch, 1992; Weimerskirch et al., 2005b), indicates that foraging ability declines with age, under the effects of senescence. Long term records of age effects on foraging movements indicate strong sex specific differences. Males appear to be more affected by senescence than females (Lecomte et al., 2010; Pardo et al., 2013b). Tracking shows that a large proportion of males older than 28 years forage in Antarctic waters, whereas younger males remain in sub-Antarctic waters. No age effect was found for female foraging zones (Lecomte et al., 2010) (Fig. 5). Since wandering albatrosses are considered to maximise the distance covered when foraging to increase the probability of encountering prey (Weimerskirch et al., 2005a, 2007), travel rate is considered to be a proxy of foraging success. However, while travel rates increase in females with age, no significant trend was found for males (Fig. 5).

When the chick hatches, both partners continue alternating the periods that they stay on the nest to brood the chick with foraging trips, with intervals lasting 2–4 days. During this period, males and females forage along the shelf edge and outer slope waters around the colony, respectively (Weimerskirch et al., 1993). After one month of brooding the chick is left alone on the nest, and both parents forage independently, visiting the nest for brief periods to feed their offspring (Weimerskirch and Lys, 2000; Weimerskirch et al., 2000a). During this extended chick rearing period, both males and females alternate short trips in neighbouring waters with long trips in oceanic waters, with the proportion of long trips increasing over time until fledging (Weimerskirch and Lys, 2000; Weimerskirch et al., 2000a). In total, over a complete single breeding season, a wandering albatross spends less than 21% of this time on land, completing a total of 70 foraging trips at sea from the colony, and covering 155,000 km on average, equivalent of circumnavigating the southern ocean six times.

3.1.5. Sabbatical period

During the final two months of the chick rearing period, male and female parents reduce the frequency of visits to their offspring, which, by this stage, weighs more than them (Weimerskirch and Lys, 2000). This reduction in visits causes the chick to lose weight and probably to leave the nest for the sea. The final visit to the nest by parents may occur either before or after the chick has left the nest, with males being more likely to visit the nest after fledging than females (Weimerskirch et al., 2000a). Both parents usually leave the colony for a complete year, which is termed the sabbatical period. Strategies during the sabbatical period differ extensively among individuals. Most Crozet Island birds remain in the western Indian Ocean; however, one third of birds move to Australian waters or to the Pacific Ocean (Table 1; Fig. 3). These 'migratory' individuals move to specific sites, restricted in surface, off the coasts of Chile, New Zealand or Australia, where they remain for months, before returning to Crozet again to breed. Birds that follow this type of movement pattern are mainly males (Table 1). Migratory birds that remain in Australia or the Tasman Sea return to Crozet in a westerly direction, i.e. against the westerly winds (Nicholls et al., 1995). Those that winter in the Pacific, off eastern New Zealand or Chile, make a circumpolar trip with the westerly winds (Fig. 6).

Interestingly, some birds circumnavigate Antarctica twice during the sabbatical (Fig. 6), with one bird even performing this trip three times. Birds that make a double circumnavigation, generally do a first rapid (32–45 days) circumnavigation, then start a second one, during which they stop in the staging area for several months, before returning to the breeding colony for a new nesting season (Fig. 6). These double circumnavigations are generally made by birds that travel directly to the eastern Pacific, and then move to the western Pacific, off eastern New Zealand. Instead of flying against the westerly winds through the Pacific from Chile to New Zealand, most birds appear to preferentially circumnavigate Antarctica to reach the western Pacific (Weimerskirch et al. unpublished). The activity patterns of the two strategies are also

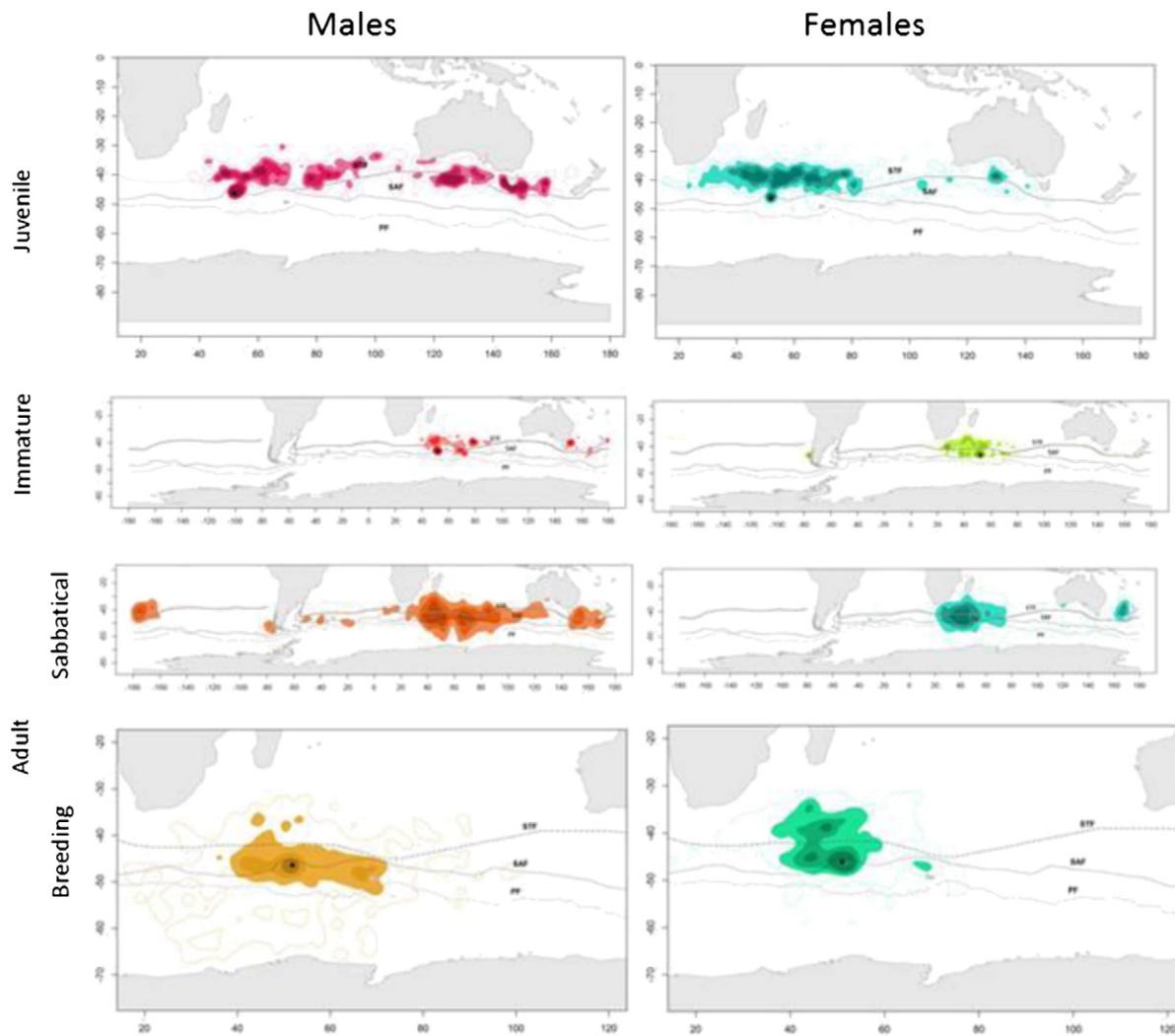


Fig. 3. Kernel utilization distribution (95%, 75%, 50% and 25%) of foraging zones used by male and female juvenile, immature, and adult wandering albatrosses during the breeding season and during the sabbatical period.

very different. For instance, birds wintering off Chile or New Zealand spend up to 6 months in a restricted foraging area of several 1000 km² (Fig. 4), spending average 70–75% of their time on the water during the day. In comparison, those that frequent the Indian Ocean move over a wider surface area (several millions of km²), spending about 50% of their time on the water (Weimerskirch et al. unpublished).

These differences in sabbatical strategies probably have important implications in terms of energetics. The albatrosses moult during the sabbatical period, with this process probably being costly, and potentially reducing flight ability. To limit such costs, albatrosses only replace on average half of the flight feathers every year (Weimerskirch, 1991).

One well known staging area for Crozet birds is the waters off New South Wales, off eastern Australia, where wandering albatrosses have been recaptured at sea over the last five decades (Gibson, 1966). Multiple banding recoveries of Crozet birds off Australia indicate that, every second year, birds return to the same staging area throughout their life time (Weimerskirch and Wilson, 2000; Weimerskirch et al., 1985). We do not know whether such long term fidelity also occurs at other staging areas, such as Chile or New Zealand, but it is likely based on observations of tracks from the same bird in successive sabbatical years.

In addition to the sex specific differences in sabbatical strategies, there are also important site specific differences. All birds from the Kerguelen Islands exhibit migratory movements to Pacific staging

areas off eastern New Zealand or the Chilean coast. In comparison, only a small percentage of Crozet birds exhibit this migratory pattern, with most birds remaining in the Indian Ocean (Weimerskirch et al. unpublished), resulting in a major overlap with the foraging zones of breeding birds. Interestingly, we found no age effects in the behaviour of birds during sabbatical periods.

3.1.6. Stable isotopes

Wandering albatrosses from the Crozet Islands were clustered into five groups according to age, breeding status and sex (chicks, immature females, immature males, female breeders and male breeders). The five groups were segregated by the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the blood and feathers (ANOVA, $F_{4,145} = 48.07$ and 29.96 , and $F_{4,186} = 29.43$ and 24.60 , respectively, all $P < 0.0001$). Chicks had lower blood and feather $\delta^{13}\text{C}$ values compared to the other four groups. In addition, male breeders differed from female breeders and from immature individuals of both sexes (post hoc Tukey Honestly Significant Difference multiple comparison tests, all $P \leq 0.035$). Finally, female breeders and immature individuals of both sexes had identical blood and feather $\delta^{13}\text{C}$ values ($P > 0.5$). Chicks had also lower blood and feather $\delta^{15}\text{N}$ values compared to the other four groups (all $P < 0.0001$). Blood $\delta^{15}\text{N}$ values were lower in male breeders compared to female breeders ($P < 0.0001$); however, feather $\delta^{15}\text{N}$ values were not statistically different ($P > 0.5$) between the immature birds and breeders of both sexes (Fig. 7).

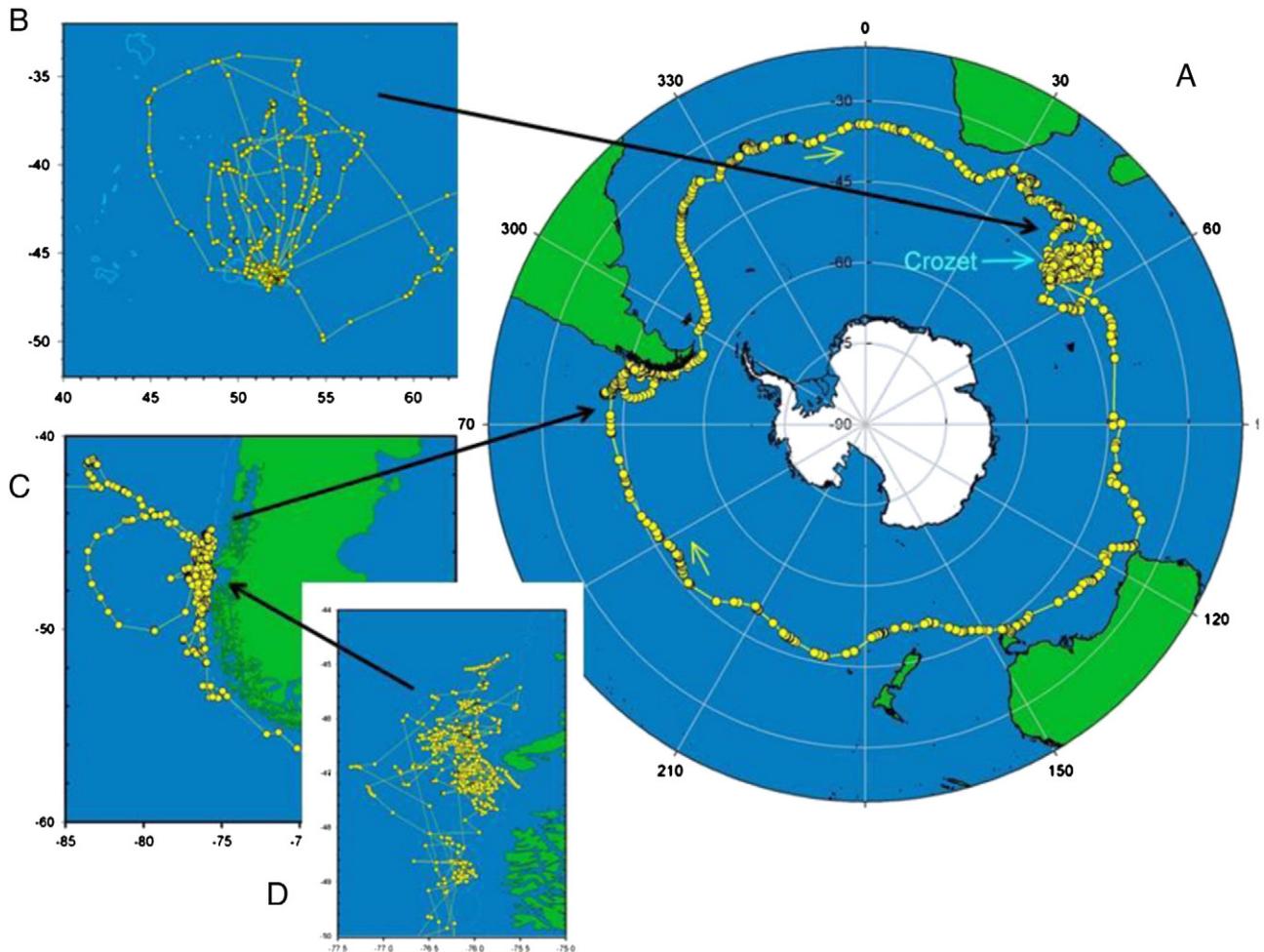


Fig. 4. Movement of an immature female wandering albatross tracked with an Argos transmitter for 1 year (A) circumpolar movement with enlargements of (B) its movement patterns at the breeding grounds on Crozet in January–March 2007, (C) at the wintering area off Chile in May–August 2007, (D) with an enlargement of the main foraging grounds off Chile. The bird returned to Crozet in September 2007, became established at its natal colony in January 2008, and first bred in 2009.

When considering the potential effect of age on the isotopic niche of breeding female and male wandering albatrosses, no age-related pattern was found in the isotopic values of female breeders. In contrast, the blood $\delta^{13}\text{C}$ values (Fig. 8), feather $\delta^{13}\text{C}$ values ($y = -0.05x - 16.54$, $R = 0.48$, $P < 0.0001$) and feather $\delta^{15}\text{N}$ values ($y = -0.03x + 16.35$, $R = 0.31$, $P = 0.012$) of male breeders were negatively and linearly related to age; yet, no significant age-effect was observed for male blood $\delta^{15}\text{N}$ values.

4. Discussion

Throughout its lifetime, a wandering albatross living 50 years covers a distance of more than 8.5 million km! The circumpolar migration of birds during the sabbatical period accounts for only a small amount of this outstanding performance; rather, this distance travelled is due propensity of wandering albatrosses to invest in fast, large scale movements, both during the breeding season and sabbatical period, in addition to during the immature periods. This continuous movement of wandering albatrosses is probably related to the specific foraging strategy of the species, with the maximal distance covered being directly related to the probability of prey encounter (Weimerskirch et al., 1997b, 2005a, 2007). This strategy of maximising the distance covered is observed throughout the life-history of the wandering albatross, and is based on the use of wind, which allows bird to reduce flight costs extensively. Indeed wandering albatrosses rely extensively on wind conditions for their foraging movements, using wind to reduce

the costs of foraging (Weimerskirch et al., 2000c). Therefore, it is no surprise that the overall range of the species is restricted to the windy Southern Ocean.

Although wandering albatrosses are in motion throughout their lives, there is a radical change in the foraging zones used; specifically, from juveniles foraging in warmer waters to the north to the oldest males foraging at the southern limits of the species range in Antarctic waters (Fig. 1). This important change in foraging zone means that this species encounters waters ranging from warm (30 °C) to cold (1 °C) off the Antarctic continent, in addition to very different wind conditions. In the tropical and subtropical waters used by young juveniles after fledging, the wind is much lower than the sub-Antarctic roaring forties and fifties (Weimerskirch et al., 2012). The wing length of juveniles when they fledge is longer than that of adults (Weimerskirch et al., 2000a), which is probably as an adaptation to these calmer conditions, giving them better flight abilities in the calmer sub-tropical waters (Shaffer et al., 2001). In addition, wandering albatrosses are one of the few species that exhibit extensive change in plumage through life, from the chocolate brown plumage of the juvenile, to the almost white plumage of old males (Weimerskirch et al., 1989). This change in plumage is highly progressive, with females whitening less than males. The brown plumage of seabirds has been suggested to be related to submissive behaviour (Bretagnolle, 1993), but could also be considered an adaptation to tropical waters, with dark plumages being more common in warm waters, and whiter plumages in polar species (Weimerskirch et al., 1989).

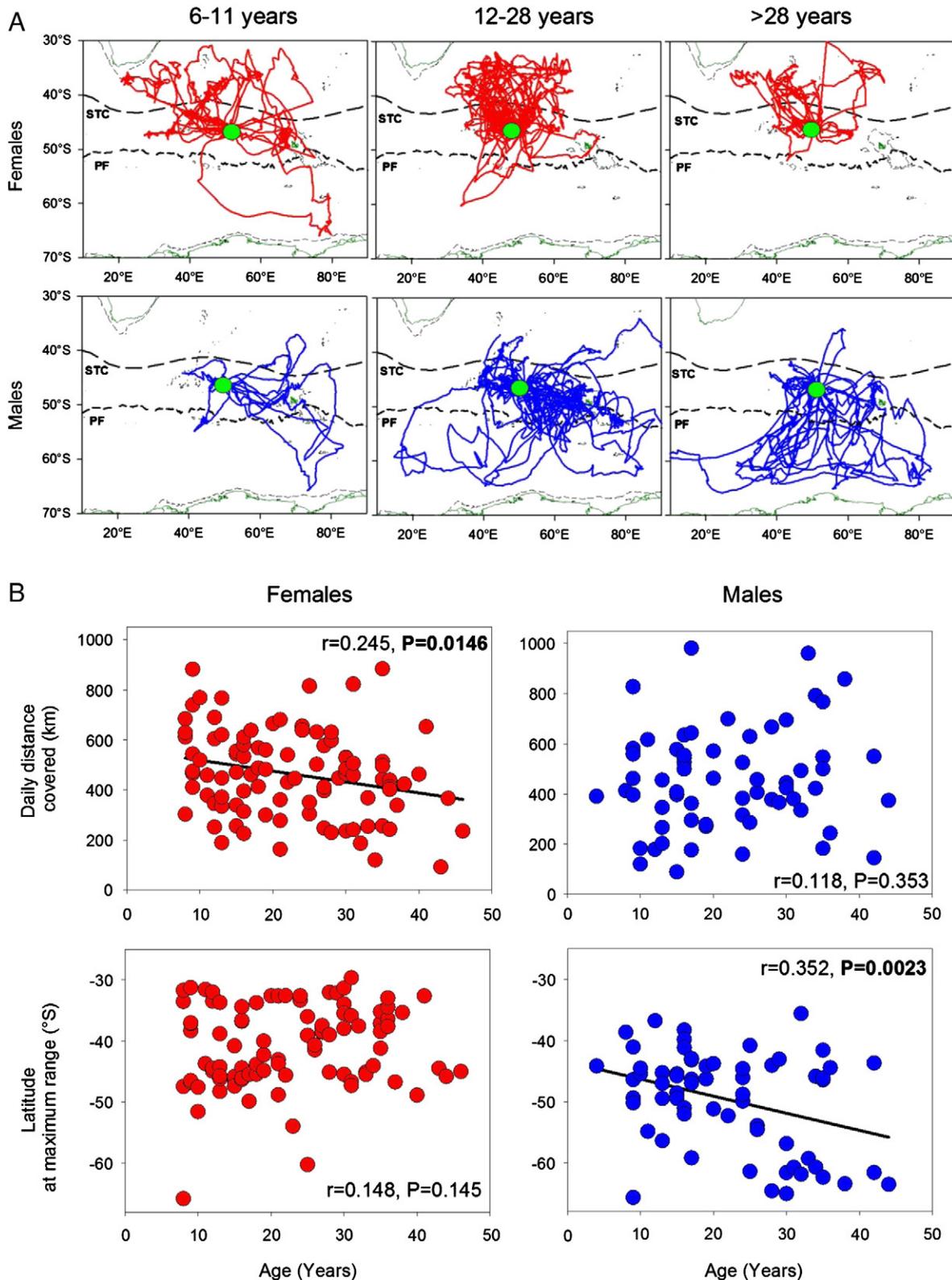


Fig. 5. Foraging trips of young, mid- and old-ages breeding male and female wandering albatrosses during incubation stage, and changes with age in the travel rates and latitude at the maximum ranges of males and females during incubation foraging trips (for this measure only birds foraging outside the Crozet shelf have been considered). Fronts are indicated by dashed lines: to the north, subtropical front, to the south Polar front.

4.1. Changes in foraging strategy and in demographic traits

What are the consequences of the use of different foraging zones and strategies over the life time of an individual on the other life history traits, such as survival, breeding success, age at recruitment and age at

senescence? Changes in foraging are paralleled by changes in demographic parameters (Fig. 1). For instance, young birds, especially during their first year at sea, have much higher mortality compared to adult birds (Fig. 1). The first year at sea, when juveniles move directly from the birth colony to warm subtropical waters, is the period when the

Table 1

Percentage of adult individuals using the major oceanic sectors during the sabbatical period (i.e. non-breeding year) for male and female wandering albatrosses, and the numbers of individuals performing circumnavigation.

	Western Indian Ocean	Australia	Pacific Chile + New Zealand	Circumnavigation
Female (27)	77.8%	22.2%	0%	3.7%
Male (38)	47.4%	18.4%	18.4%	18.4%

highest annual rate of mortality occurs. Based on tracking information (Riotte-Lambert and Weimerskirch, 2013; Weimerskirch et al., 2006), we know that mortality probably occurs during the first two months at sea immediately after fledging (Riotte-Lambert and Weimerskirch, 2013). At fledging, juveniles already have the skills to take advantage of the wind conditions, since they optimally use winds as soon as they leave the natal colony (Riotte-Lambert and Weimerskirch, 2013); however, they progressively increase travel rates over the first 5 months (Fig. 2). These observations suggest that foraging skills to cover long distances to increase the probability of encountering prey, as adult do, are already acquired after 6 months (Fig. 2); yet, the birds only return to land for the first time at an average age of 5 years. This period of immaturity is probably used by young birds to improve their searching skills and ability to detect and handle prey. When they first visit the colonies, young immature birds are 20–30% lighter compared to breeding birds, and improve their body condition until they reach a certain threshold allowing them to breed (Weimerskirch, 1992). However, this second phase of learning is not associated with a higher mortality, since immature birds (aged 5–9 years) have similar survival rates to adults (Fig. 1), and no sex specific differences were found. As

soon as they are recruited into the population, the survival of both males and females is high, and does not change until old age. This observation indicates that the phase of learning to survive has been completed; yet, a long learning phase to breed successfully exists between 7 and 15 years of age (Fig. 1, breeding success). Between 15 and 30 years of age, survival and breeding success peak, indicating that the birds are at their highest performance (Fig. 1). From 30 years of age onward, males appear to suffer senescence, but not females; in fact, the daily distance covered by females during the breeding season foraging trips continues to increase throughout life (Fig. 5).

Thus, as albatrosses grow older, the two sexes are subject to very different ageing effects; female appears to increase daily distance travelled, whereas males tend to shift to a more southerly foraging destination. Interestingly, females appear to be less affected by ageing than males in terms of breeding success, breeding frequency and survival, whereas males are affected by ageing (Pardo et al., 2013b). The exact links between the southward shift of male foraging zones with age and the deterioration of survival and breeding propensity have yet to be clarified.

4.2. Diet and isotopic measures

Like the tracking data, the isotopic values of chicks, immature birds and breeders highlight trophic segregation in relation to age, sex and breeding status of wandering albatrosses. The latitudinal gradient in $\delta^{13}\text{C}$ (Cherel and Hobson, 2007; Jaeger et al., 2010b) together with low chick $\delta^{13}\text{C}$ values indicates that parent birds forage primarily for their chicks in southern sub-Antarctic waters. There, they feed at the top of the pelagic ecosystem, as indicated by the consistently highest chick $\delta^{15}\text{N}$ values of wandering albatrosses within seabird communities

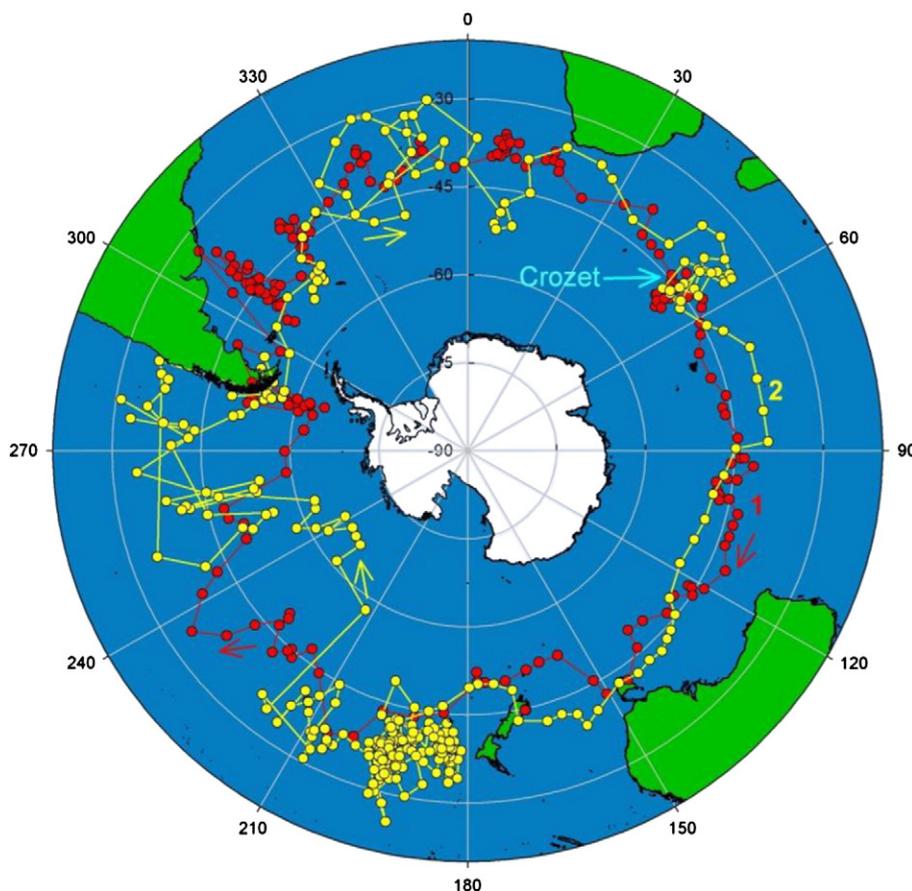


Fig. 6. Double circumpolar movements of a male Crozet wandering albatross during the sabbatical period. The bird did two circumpolar trips around Antarctica, rapidly during the first tour (red), and then stopping off at eastern New Zealand in the second tour (yellow).

(Jaeger et al., 2010a; Phillips et al., 2011). Birds from both the Crozet Islands and Kerguelen Islands occupy the same isotopic niches, indicating that the two populations forage within the same habitats and feed on similar prey with the same changes in their food and feeding ecology in relation to the breeding and non-breeding periods (Cherel et al., 2013; Jaeger et al., in press). However, this similarity does not preclude foraging in spatially distinct areas, because $\delta^{13}\text{C}$ values provide large-scale information restricted to latitude (water masses) and not longitude (Cherel and Hobson, 2007; Jaeger et al., 2010b); this limitation has been confirmed by tracking data, which show that Kerguelen birds favour the subtropical Pacific Ocean during the sabbatical year, whereas Crozet birds favour the subtropical Indian Ocean (Weimerskirch et al. unpublished).

Crozet chicks had consistently lower $\delta^{13}\text{C}$ values compared to the other age-class groups; hence, immature and adult wandering albatrosses forage at lower latitudes during the incubation period and the sabbatical period (Jaeger et al., 2010a). Isotopic investigation, confirmed by tracking, indicates that there were no gender-related differences in the isotopic niche of immature wandering albatrosses, with both sexes foraging at the same high trophic position ($\delta^{15}\text{N}$) in oceanic subtropical waters ($\delta^{13}\text{C}$) during both the sampling summer (blood) and moulting period (feathers). In contrast, the $\delta^{13}\text{C}$ values (and associated $\delta^{15}\text{N}$ values) of breeders showed differences between sexes as those already found with tracking. During the non-breeding period (feathers), both sexes forage within the Subtropical Zone; however, again, females tended to favour lower latitudes compared to males (Jaeger et al., 2009). Hence isotopic studies indicate that males shift their main foraging zone according to their breeding status and/or age, with immature birds foraging primarily and consistently at lower latitudes compared to adult males.

Isotopic studies also support the tracking data showing the differential effect of age on the foraging latitudes of adult male and



Fig. 7. Feather $\delta^{13}\text{C}$ (upper panel) and B $\delta^{15}\text{N}$ (lower panel) values of wandering albatrosses according to their age, breeding status and sex (females white, males black, sex combined grey). Numbers of sampled individuals per group are indicated in parentheses. Values not sharing the same superscript letter are significantly different. Values are means \pm SD. Dotted line illustrates the estimated feather isotopic boundary of the Subtropical Front that delineates the southern Subantarctic Zone (SAZ) from the northern Subtropical Zone (STZ).

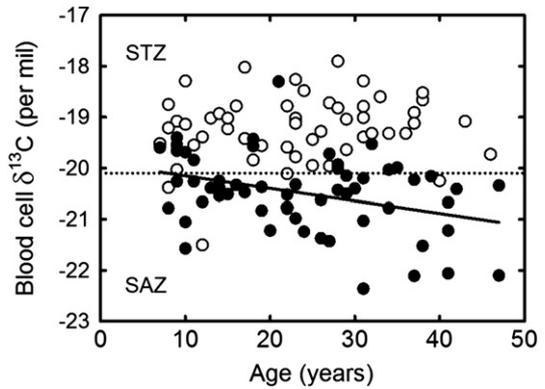


Fig. 8. Individual blood $\delta^{13}\text{C}$ values of breeding wandering albatrosses according to their age and sex (white: females, black: males). Blood $\delta^{13}\text{C}$ values of male breeders are negatively and linearly related to their age ($y = -0.02x - 19.91$, $R = 0.36$, $P = 0.006$). Dotted line illustrates the estimated blood isotopic boundary of the Subtropical Front that delineates the southern Subantarctic Zone (SAZ) from the northern Subtropical Zone (STZ) (see text).

female wandering albatrosses. Blood and feather isotopic ratios did not show any age-related trends in female breeders, whereas males progressively shift to higher latitudes as they age during both the incubation period (blood) and the non-breeding period (feathers). This result is remarkable because several intrinsic methodological limitations partially hinder the potential relationship between the most distant foraging latitudes and the isotopic signatures of the birds. Wandering albatrosses feed along the entire length of their trips (Weimerskirch et al., 2005a), with the blood isotopic signature of large birds representing food assimilated over the last ~2 months before sampling. Hence, the blood signature integrates both the prey taken at the most distant foraging latitudes and elsewhere during several consecutive trips. This dilution effect probably explains the apparent mismatch between satellite-tracking data, indicating that old males foraged in Antarctic waters, and the corresponding blood $\delta^{13}\text{C}$ values, indicating that males foraged in southern sub-Antarctic waters. Hence, the significant negative correlations between $\delta^{13}\text{C}$ values and age are particularly relevant, underlining the strength of the age effect on the latitudinal foraging grounds of adult males. A direct and important consequence of this age- and gender-related effect is that the isotopic niches of both sexes increasingly diverge 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.

4.3. Association with fisheries and conservation implications

Wandering albatrosses are frequent attendees to fishing boats, behind which they aggregate to gather discards (Brothers, 1991; Weimerskirch et al., 2000b). This habit is not recent, since they were known as ship follower since the 18th century, when European sailing boats entered the Southern Ocean, and reported the habit of wandering albatrosses following boats and feeding on discards. Today this habit represents a threat to the survival of the species. Indeed, it was first realised in the late 1980s that wandering albatrosses were threatened by fisheries (Weimerskirch and Jouventin, 1987), with the major causes for mortality being linked to longline fisheries, as birds are attracted to baited hooks and subsequently drown during line setting (Brothers, 1991). This issue has attracted much attention, since it was realised that the problem concerned all albatross species worldwide, with an estimated 100,000 albatrosses and petrels being killed annually. In particular, the population size of wandering albatrosses has decreased as a result of adult mortality in the Indian Ocean, especially females, due to longline fisheries targeting tuna in subtropical waters (Tuck et al., 2001; Weimerskirch et al., 1997a, 1997b, 1997c). However

the different life stages are not similarly affected by the problem of fisheries. For instance, juveniles and young birds that favour subtropical waters are much more likely to encounter longliner targeting tunas (Weimerskirch et al., 2006), the main cause of mortality today (Tuck et al., 2001), whereas, at the other extreme, old males are less likely to be at risk in Antarctic waters. Similarly, adult females that forage northward up to subtropical waters are more threatened than males that favour sub-Antarctic waters. In contrast, males were susceptible to long-line fisheries targeting Patagonian tooth-fish around the breeding grounds of Crozet, a fishery that developed in the late 1990s; however this fishery started in the early 2000 conservation measures aimed at reducing by catch in the CCAMLR (Convention for the Conservation of Antarctic Marine Living Resources) area, which led to very low albatross mortality in these sub-Antarctic waters (Delord et al., 2005).

The present climate change effects on wind conditions have so far favoured wandering albatrosses, with higher wind speeds allowing more rapid movement (Weimerskirch et al., 2012), increasing the likelihood of encountering and capturing prey, which is related to the daily distances individuals are able to cover (Weimerskirch et al., 2005a). However, the observed southward shift of the northern range of wandering albatrosses (Weimerskirch et al., 2012) related to climate change might have also significant consequences in terms of conservation. If the range of breeding females moves southward due to environmental change, they will be less likely to overlap with tuna long-liners, which have not shifted southward during the last 50 years (Tuck et al., 2003).

5. Conclusion

Based on long term demographic and tracking data, this study shows clearly that over their life time wandering albatrosses change extensively their foraging habitats to adjust their foraging strategy to the requirements of their successive life stages, from the period of learning during juvenile and immature ages, through the alternation of central place foraging during breeding and migration or dispersal during the sabbatical, until the southerly movements to Antarctic waters of old ages. Such changes are likely to occur in other marine taxa such as sea-turtles or marine mammals (Field et al., 2005; Hays et al., 2010) but remain overall poorly documented. Likewise the considerable differences in foraging habitats of males and females do also occur for example in seals with high sexual dimorphism (Leboeuf et al., 2000) but how these differences are set over time remains unknown. Although the number of telemetric studies is increasing and applied to a constantly growing number of species, the challenge remains to obtain precise information on the early stage of marine animals such as fish or reptiles for which indirect measures such as isotope signatures remain a precious option.

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