At-sea behavioural ecology of the endangered MacGillivray's prion from Saint Paul Island: combining tracking and stable isotopes

Delord Karine [1, *], Cherel Yves [1], Roy Amédée [2], Bustamante Paco [3, 4], Swadling Kerrie M. [5], Weimerskirch Henri [1], Bost Charles-André [1], Barbraud Christophe [1]

[1] Centre d'Études Biologiques de Chizé (CEBC), UMR 7372 du CNRS-La Rochelle Université, 79360 Villiers-en-Bois, France
[2] Institut de Recherche pour le Développement (IRD), MARBEC (Univ. Montpellier, Ifremer, CNRS, IRD), Avenue Jean Monnet, 34200 Sète, France
[3] Littoral Environnement et Sociétés (LIENSs), UMR 7266 du CNRS-La Rochelle Université, 2 rue Olympe de Gouges, 17000 La Rochelle, France
[4] Institut Universitaire de France (IUF), 1 Rue Descartes, 75005 Paris, France
[5] Institute for Marine and Antarctic Studies and Australian Antarctic Program Partnership (AAPP), University of Tasmania, 20 Castray Esplanade, Battery Point, Tasmania 7004, Australia

* Corresponding author : Karine Delord, email address : karine.delord@cebc.cnrs.fr

Abstract :

Seabirds play important roles as marine ecosystem sentinels. Studying their at-sea ecology is essential for understanding how environmental variability affects their populations. However, the at-sea ecology of small-sized temperate seabirds remains poorly studied. We explored the at-sea ecology of the Critically Endangered MacGillivray's prion Pachyptila macgillivrayi breeding on the subtropical Saint Paul Island. Using global location sensor loggers and stable isotope analysis, we investigated movements, migratory strategies, at-sea activity and moulting period, and characterized the isotopic niche of tracked individuals. During incubation, MacGillivray's prions remained in temperate waters north of the Subtropical Front, possibly feeding on prey caught in cold eddies. During the inter-breeding period, individuals wintered almost equally to the north and south of the Subtropical Front in 2 distinct sectors (Tasman Sea and Southwest Indian Ridge). Daily activity varied seasonally, and individuals overwintering in the Tasman Sea spent more time flying at night when moonlight intensity was high. Moulting occurred after the breeding period and lasted longer compared to other prion species. Isotopic data suggest a higher dietary proportion of low trophic-level prey for MacGillivray's prions than for Antarctic and slender-billed prions, highlighting trophic segregation in relation to bill width. Our study provides new evidence to understand the suite of adaptations allowing the abundant prion species to coexist by feeding on prey of different sizes. Contrary to the majority of seabird species, MacGillivray's prions from Saint Paul Island exhibited 2 migratory tactics with associated differences in at-sea activity, leading to questions about the origin of these differences.

1. INTRODUCTION

Despite the remoteness of the Southern Ocean, there is evidence that human impacts on marine ecosystems have expanded faster in the Southern than in the Northern Hemisphere over recent decades (Halpern et al. 2019). Such impacts include velocity of ocean warming, frequency and intensity of marine heatwaves, pollution and industrial exploitation of marine resources (Halpern et al. 2019, Sydeman et al. 2021). Seabirds play important roles in the functioning of oceanic ecosystems and as sentinels of global changes (Hazen et al. 2019). They may be particularly vulnerable to oceanic changes as they are fully dependent on pelagic trophic webs. In addition, their breeding sites are static in space whereas the availability of their prey varies in space and time. Therefore, studying the behavioural ecology of southern seabirds in the marine realm is essential to understand how environmental changes affect their populations and also for the implementation of adequate conservation measures for southern marine ecosystems. Although considerable progress has been made over the last three decades regarding their at-sea distribution, habitat use and feeding ecology of southern seabirds, the year-round ecology of small-sized seabirds remains poorly studied especially for temperate-water species (Rayner et al. 2016, Mott & Clarke 2018, Berg et al. 2019). This is particularly true concerning information about the non-breeding period, including the location and habitat characteristics of foraging and moulting sites. Furthermore, at-sea activity patterns are lacking for many small-sized species of seabirds.

The prions (*Pachyptila* spp.) are small, planktivorous Procellariiformes and are among the most abundant seabirds in the Southern Ocean (Brooke 2004). Although the

behavioural ecology of four prion species (the slender-billed *P. belcheri*, Antarctic *P. desolata*, MacGillivray's *P. macgillivrayi*, and broad-billed *P. vittata*) has been studied recently (Cherel et al. 2002, Quillfeldt et al. 2015a, Jones et al. 2020), there are many knowledge gaps remaining. This limits our understanding of mechanisms allowing the co-existence of these abundant seabird species issued from a recent adaptive radiation (Masello et al. 2022).

The endangered MacGillivray's prion (BirdLife International 2018) was considered endemic to Saint Paul Island in the Southern Indian Ocean (Roux et al. 1986) until the recent discovery of a large population on a second oceanic island, Gough Island, which is located in the Southern Atlantic Ocean (Ryan et al. 2014, Dilley et al. 2015). The Indian Ocean population of MacGillivray's Prion has been driven to the verge of extinction by introduced predators; e.g, it is extinct on nearby Amsterdam Island. Only a few hundred birds remained on a single offshore stack nearby Saint Paul, but the population is now increasing on Saint Paul island since the eradication of introduced rats in the late 1990s (Barbraud et al. 2021). However, the current relict population is probably at a much lower level than the original one. The marine distribution of MacGillivray's prion is largely unknown, especially for the Indian Ocean population, which is (but see Jones et al. (2020) regarding the Atlantic Ocean population), mainly due to difficulties identifying the species at-sea as prions are very similar in plumage and morphology. The MacGillivray's prion was believed to forage in areas surrounding the breeding colonies for at least part of its seasonal cycle (Brooke 2004). However, Jones et al. (2020) showed that birds from Gough Island migrate westward to distant areas within the Argentine Basin, where they moult their flight feathers. There, MacGillivray's prions appeared to favour sub-Antarctic

and mixed sub-Antarctic and subtropical waters during the non-breeding period and to specifically target sub-Antarctic waters while moulting.

Our aim was to carry out a general exploration of the behavioural ecology of MacGillivray's prions breeding at Saint Paul Island in the marine realm. In particular we investigated movement, foraging, diet, and moult, over the breeding and non-breeding periods and clarified the migratory status of this population. Based on knowledge of other prion species and on the Atlantic population of MacGillivray's prions (Jones et al. 2020), we made the following predictions: i) the MacGillivray's prions breeding at Saint Paul Island are migratory, ii) they should favour sub-Antarctic and mixed sub-Antarctic and subtropical waters, and iii) moulting should occur early during the non-breeding period. First, miniaturized Global Location Sensors (GLS) loggers (Afanasyev 2004) enabled the investigation of year-round movements of tagged individuals. Second, since the at-sea behaviour of petrels is known to be influenced by the phases of the moon (Yamamoto et al. 2008, Dias et al. 2016, Waap et al. 2017), we explored whether the lunar cycle affected the at-sea activity of tracked individuals. Third, combining activity patterns derived from GLS data and stable isotopic profiles of feathers, we investigated moulting and foraging ecology. Fourth, we characterized the isotopic niche using three complementary tissues (plasma, blood cells and feathers) that recorded trophic information at different time scales (Cherel et al. 2014). Finally, on an exploratory basis, some GPS-loggers were also deployed to describe foraging trips during incubation at a finer spatial scale than achieved with GLS.

2. MATERIALS AND METHODS

2.1. Prions

Prions (genus *Pachyptila*) are small (90-250 g) closely-related seabirds restricted to the Southern Hemisphere, where they are one of the most abundant Procellariiformes. Specific identification is mainly based on bill characteristics (size, shape, structure and colour), which are related to the birds' foraging method and diet. Seven species are currently recognized that cluster into two groups (Warham 1990, Masello et al. 2019, 2022). In Antarctic prion, Salvin's prion (*Pachyptila salvini*), MacGillivray's prion and broad-billed prion, the width of the bill is progressively larger. The four species have well-developed, comb-like lamellae inside the upper mandible that are used to filter small particles of food from seawater. The three other species (slender-billed prion, *P. belcheri*, fairy prion (*P. turtur*) and fulmar prion (*P. crassirostris*)) lack palatal lamellae and hence have no specialized filtering apparatus (Prince & Morgan 1987). The MacGillivray's prion has been suggested to feed on small zooplankton, but its diet and foraging ecology is almost unknown (Jones et al. 2020). Its specific status has been debated (Penhallurick & Wink 2004, Rheindt & Austin 2005), as it has been considered as a subspecies of broad-billed prion (Harper 1980) or Salvin's prion (Roux & Martinez 1987), while its bill measurements are closer to those of Salvin's prion (Bretagnolle et al. 1990). Recent works suggests that the MacGillivray's prion is best treated as a separate species (Masello et al. 2022).

The MacGillivray's prion was previously considered as an endemic species to Amsterdam and Saint Paul Island until its recent discovery at Gough Island in the Atlantic

Ocean where approximately 600 000 - 1 000 000 pairs bred in 2000/01 (Ryan et al. 2014, Dilley et al. 2015, Jones et al. 2021). The MacGillivray's prion is now classified as an "Endangered" species (BirdLife International 2018), due to: (i) its decreasing population at Gough Island (Jones et al. 2021), (ii) its small population at Saint Paul ($\approx$ 1 100 breeding pairs; Barbraud et al. 2021), and (iii) its disappearance from Amsterdam Island following the introduction of mammal predators (Worthy & Jouventin 1999).

2.2. Device deployment and retrieval

Fieldwork took place in December 2017 (22-23/12) and 2018 (02-21/12) on Saint Paul Island (38°42"30'S, 77°32"30'E). MacGillivray's prions recolonized Saint Paul Island from the nearby La Roche Quille Islet (Tollu 1984) following the successful eradication of introduced rabbits *Oryctolagus cuniculus* and black rats *Rattus rattus* in the late 1990s (Micol & Jouventin 1998, 2002, Barbraud et al. 2021).

In 2017, 20 geolocator-immersion loggers (GLS Intigeo-C65: 14 × 8 × 6 mm and 1 g; Migrate Technology Ltd, Cambridge, UK) were deployed on birds captured either in their nesting burrow (incubating, n=4) or on the ground at night (breeding status unknown, n=17). The total mass of the GLS device and attachment materials (c. 1.5 g) represented ~1% (0.7-1.0%) of the birds' body mass, well below the 3% threshold recommended for pelagic seabirds (Phillips et al. 2003). Data from all GLS (n = 7) were retrieved successfully. GLS loggers were mounted on plastic leg rings. One year later (2018), seven GLS were retrieved (three out of four deployed on breeding birds and four out of 17 deployed on birds of unknown breeding status). Recaptures were made at the same

nest sites for the birds of known breeding status and via mist netting at night at the breeding colony for the birds of unknown status.

In 2018, miniaturized GPS devices (2.2 g; nanoFix-Geo; PathTrack Limited, Yorkshire, UK) were deployed on four incubating birds. The devices were attached to the four central tail feathers using Tesa® tape and programmed to record a position every 40 min. The total mass of the GPS device and attachment materials (c. 2.5 g) represented <1.5% (1.1-1.2%) of the birds' mass. All birds were handled for <7 min and returned to their nest upon release. Once the devices were deployed, each nest was checked daily to establish departure and return dates, and to recover the loggers. All birds were recaptured, and data from two GPS were downloaded successfully. We were unable to evaluate the influence of handling and tagging on breeding success, due to the short stay on the island.

During GLS and GPS deployment, all birds were weighed (± 5 g) with a Pesola spring balance, and to minimize disturbance they were not handled again before departure. Once the birds had returned to the nest after their foraging trip, they were weighed again and measured: wing length ± 1 mm with a ruler, tarsus length, bill length and bill width ± 0.1 mm with Vernier calipers.

2.3. Geolocator (GLS) data processing

Loggers measured light intensity every 60 s and recorded the maximum light value for every 5 min period. Thresholds in the light curves were used to determine sunrise and sunset. An internal clock in GLS enabled estimation of latitude based on day length and

longitude based on the timing of local mid-day with respect to Universal Time (Afanasyev 2004). GLS light data were analyzed using IntiProc v1.03 (Migrate Technology 2015), which uses the threshold method and BASTrak software (Locator, British Antarctic Survey 2009) to estimate two positions per day, with an average accuracy of ~200 km (Phillips et al. 2004).

Immersion sensors tested for saltwater immersion every 30 s and stored the number of samples wet (> 0) at the end of each 10 min period. We used saltwater immersion to estimate daily activity budgets. The mean percentage of time sitting on the water (wet; immersion data > 0) was calculated to determine variation in combined resting and foraging behaviour, as birds feed while at the sea surface. Conversely, when birds were not on land, the time spent dry was interpreted as flying. Daylight and darkness periods were assessed using sunset and sunrise times and were used to estimate the time spent at the sea surface during day and night.

We defined a proxy for the moulting period of flight feathers by using the same criterion of activity data as that previously used for other seabird species (Gutowsky et al. 2014), especially prions, namely transient peak of daily percentage of time spent wet on water; Mattern et al. (2015) and Cherel et al. (2016). More precisely, we applied generalized additive modelling (GAM) to smooth the "wet" time-series for each individual. We extracted the dates when the fitted "wet" value was above 50% of the maximum, which results in a longer period named the extended moult period, and when the fitted "wet" value exceeded 75% of the maximum, which results in a shorter period named the core moulting period.

General linear mixed-effects models (GLMMs), fitted in the glmmTMB package (Zuur et al. 2010; Douma & Weedon 2019), were used to model activity patterns (daily proportion of time spent on the water during the day and night). Sex, month and two by two interactions were included as independent fixed effects. To account for pseudo-replication individual identity was fitted as a random effect, as the same individual contributed several values. Response variables were visually tested for normality (through Q-Q plots) and homoscedasticity (using Cleveland dotplots; Zuur et al. 2010). A beta family (link = "log"), used for analyzing proportion data (Douma & Weedon 2019) was selected for all models (see Tables S1, S2 and S3). Models including all combinations of variables were then tested and ranked using the Akaike Information Criterion (AIC) values and Akaike weights following the Information-Theoretic Approach (Burnham & Anderson 2002). The model with the lowest AIC was considered the best model. Two models separated by a difference in AIC values < 2 were assumed to fit the data similarly.

Filtered locations were used to generate kernel utilization distribution (UD) estimates with a smoothing parameter (h) of 2° and a 2° x 2° grid cell size (see Delord et al. (2016)). UD is the mean foraging utilization distribution estimated using the locations recorded from each tracked individual. Both h value and grid cell size were based on the mean accuracy of the devices; i.e. ~ 0.4° for longitude and ~ 1.7° for latitude (Phillips et al. 2004). Kernel density estimations were carried out on all individuals for all the inter-breeding period, and for extended and core moult periods of flight feathers. Following Worton (1989) and Montevecchi et al. (2012), we considered the 50% (core foraging area) and the 95% (home range) kernel UD contours. The core areas (50% kernel) were used

to obtain mean latitude and longitude (centroid position). Spatial analyses were performed using the *adehabitatHR* R package (Calenge 2006).

Timing of migration was determined by visual examination of tracks (i.e., longitudinal directional movement during three consecutive days) combined with an index of activity (i.e., comparatively longer periods of no saltwater immersion). During outward migration the birds rapidly reached their destination in the inter-breeding (wintering) zone, after which movements were no longer directional. On the return migration, rapid movement was followed by several days without saltwater immersion, indicative of individuals staying in their burrows. We extracted parameters describing individuals' migration journeys, timing of movements, distance and duration of travel, as well as the location of non-breeding and moulting areas. For each individual, we determined: i) departure date of outward migration, ii) arrival date at the first non-breeding area, iii) departure date of return migration from the last inter-breeding area, and iv) return date at the breeding colony. We calculated the duration of the non-breeding period as the interval between colony departure and return, and the duration of outward and inward migrations as the interval between initiation and end of migratory movements.

Spatial and statistical analyses were performed using QGIS (QGIS Development Team 2020) and R 3.5.2 (R Core Team 2021).

2.4. Exploring periodicity in activity patterns

Wavelet analysis is a well-known tool in ecology for elucidating the frequency contents of noisy, non-linear and non-stationary biological time-series (Cazelles & Stone

2003). It has been used to elucidate spatiotemporal synchrony between organisms (Bertrand et al. 2008), and for exploring periodic patterns of movement of seabirds (Fablet et al. 2013; Roy et al. 2021). In this study, it was used to explore periodicity in MacGillivray's prion activity both during days and nights.

For each bird, the wavelet power coefficients of the time series of flying time during the day (resp. night) were computed by applying the Morlet wavelet transform (Torrence & Compo 1998). Then, the statistical significance of these coefficients was evaluated by simulating random autoregressive time-series following the point-wise procedure presented in Rouyer et al. (2008). We then tested the hypothesis of 29.5 days periodicity in activity time-series at each time step, to identify periods of the year when the birds' activity was significantly synchronized with lunar cycles. The whole procedure was performed using the *WaveletComp* R package (Rösch & Schmidbauer 2018).

2.5. Tissue sampling, molecular sexing and stable isotopes

Twenty-three adults, including those that were recaptured after being equipped with tracking devices (GLS or GPS) were sampled for stable isotope analysis and molecular sexing in December 2018. In addition, incomplete food samples were collected, as prions spontaneously regurgitate when handled. A blood sample from the tarsus vein was collected immediately after capture of the bird upon return from a foraging trip using a 1-mL heparinized syringe and a 25-gauge needle. Collected blood volumes ranged from 0.50 to 0.80 mL. Blood samples were separated into plasma and blood cells (hereafter blood) by centrifuging at 12,000 rpm for 5 min within 2-3 hours after sampling, and

samples were stored frozen at -20 °C until analyses at the laboratory. Isotopic values of plasma and blood cells reflect dietary integration over the short-term (a few days) and medium-term (a few weeks), respectively. We carried out the molecular sexing at the Service "Analyses Biologiques" of the Centre d'Etudes Biologiques de Chizé (CEBC). We conducted a DNA extraction with 2 µl of pellet (red blood cells) and using a chelex resin (Chelex 100 Molecular Biology Resin, BIO-RAD; 10%) associated with Proteinase K (PK) as per the manufacturer's instructions. We then performed a polymerase chain reaction (PCR) with amplification of the CHD gene following a standard procedure as detailed in Fridolfsson and Ellegren (1999).

Six whole body feathers were pulled out from the upper chest of each sampled bird and stored dry in sealed individual plastic bags. Feather sampling was also opportunistically performed on two other groups of MacGillivray's prions. Firstly, body feathers were sampled on 12 large chicks during a short stay on Saint Paul Island in March 2005. Secondly, six pairs of wings, including one from a fledgling (hereafter chick) and five others from specimens of unknown age and status, were collected after prions being preyed by a vagrant peregrine falcon *Falco peregrinus* in 1999 (Jiguet et al. 2007). The tip of each primary feather was cut off, was along with the basal part of the vane of the tenth primary (P10) to obtain sequential isotopic information about the entire primary moult (Quillfeldt et al. 2010, Cherel et al. 2016), i.e. from the distal part of P1 (oldest) to the proximal part of P10 (youngest). Isotopic measurements were also carried out on four body feathers per individual to represent the isotopic niche of adults during moult (Jaeger et al. 2009), or from a single body feather of chicks because their synchronous growth induced little within-individual feather isotopic variations (Carravieri et al. 2014).

Feathers were cleaned to remove surface contaminants using a 2:1 chloroform:methanol solution, followed by two methanol rinses. They were then dried in an oven for 48 h at 50 °C and cut into small pieces with stainless steel scissors. Blood, plasma and food subsamples were freeze-dried and powdered. Avian plasma contains a high and variable lipid content that affects its $\delta^{13}C$ values (Cherel et al. 2005a, b) and food samples contained various amounts of stomach oil. Hence, lipids were removed from plasma and food samples using chloroform/methanol and cyclohexane, respectively. Then, tissue subsamples were weighed using a microbalance, packed in tin cups, and the nitrogen and carbon isotope ratios determined by a continuous flow mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyser (Thermo Scientific Flash 2000). Results are reported in the typical δ notation relative to Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively. Repeated measurements of internal laboratory standards (caffeine) reveal measurement errors <0.10 ‰ and <0.15 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

The Southern Ocean is marked by a well-defined latitudinal baseline $\delta^{13}C$ values gradient that is reflected in the tissue of consumers (Cherel & Hobson 2007, Jaeger et al. 2010, Quillfeldt et al. 2010). The isotopic consumer data allowed the estimation of the $\delta^{13}C$ values of the main oceanic fronts within the Southern Indian Ocean, and thus to delineate robust latitudinal isoscapes of the main foraging zones for top predators, depending on the targeted tissues. Based on blood (feather) $\delta^{13}C$ isoscapes, values less than -22.5 ‰ (-21.2 ‰), -22.5 to -19.7 ‰ (-21.2 to -18.3 ‰), and greater than -19.7 ‰ (-

18.3 ‰) were considered to correspond to the Antarctic (AZ), sub-Antarctic (SAZ) and Subtropical (STZ) Zones, respectively (Cherel and Hobson 2007; Jaeger et al. 2010).

Data were statistically analysed using R (R Core Team 2021). All values are presented as the mean ± SD unless otherwise stated.

3. RESULTS

Seven GLS were successfully retrieved from adults of MacGillivray's prion (*Pachyptila macgillivrayi*) from Saint Paul Island in 2018. The GLS recovery rate was relatively low (35%), due to a combination of a complex burrow structure that made finding and gaining access to nest chambers difficult, and to a short stay in the field that restricted opportunities to check the burrows. The seven loggers provided simultaneous records of location and immersion data during complete annual tracks, all located within the Southern Indian Ocean and Tasman Sea (Figure 1).

3.1. Distribution at-sea during the breeding period

On average birds returned to Saint Paul at the end of September, although there was high individual variation (earliest August 19th, latest November 15th). During breeding, GLS-equipped MacGillivray's prions were distributed over an area centered on Saint Paul Island, thus remaining within the STZ between the northern and the southern Subtropical Fronts (Figure 2). Similarly, the two GPS-tracked birds remained within the STZ during incubation in December 2018 (Figure 2). Prions reached areas > 350 km (355 and 382

km) south from the colony, travelling at a mean speed ~ 9 km/h (8.4 ± 9.3 and 10.1 ± 9.1 km/h) for a trip duration of ≈ 5 days (4.9 and 5.7 days).

3.2. Migration and distribution during the inter-breeding period

Chronology of the 2018 inter-breeding period of the GLS-tracked birds provides the first available data for the phenology and the movements of the species at Saint Paul Island (Table 1). All the seven individuals migrated during the inter-breeding period (Figure 1a). Remarkably, two distinct migratory strategies were observed: four individuals (2 females and 2 males) migrated eastward to winter in the Tasman Sea, while three birds (2 females and 1 undetermined) migrated westward and overwintered mainly over the Southwest Indian Ridge, north of the Del Cano Rise (northward of the Crozet and Prince Edwards Islands). Overall, MacGilligray's prions favored the STZ (≈ 58%), but they also foraged within the Southern Ocean, spending ~ 36% in the SAZ and ~ 5% in the AZ (based on the 95% utilization distribution, not illustrated), regardless of their migratory area. When considering the 75% utilization distribution, differences were related to migratory tactics, with birds wintering in the Tasman Sea and the Southwest Indian Ridge using more subtropical and sub-Antarctic waters, respectively (STZ: 68 and 27%, and SAZ: 30 and 73%, respectively).

3.3. Activity patterns, moulting time and moulting distribution

MacGilligray's prions spent a larger daily proportion of time in flight than sitting on the water during the inter-breeding than during the breeding season (Figure S1).

However, a clear temporal pattern emerged, with birds spending more time on the water right after breeding during the first half of the inter-breeding period, with a peak from March to May (Figure 3, S1, Tables S1, S2 and S3). At that time, MacGillivray's prions spent on average 72% (maximum: 83%; not illustrated) of their time on the water each day, indicating that birds were moulting their flight feathers. During the non-moulting period they only spent ~ 45% on the water. This clear temporal pattern (with a peak in values in March-May) occurred both during the day and at night (Figure S1, Tables S2, S3, S4).

The spatial distribution of MacGillivray's prions during the moult of flight feathers showed two contrasting geographic affinities (the Tasman Sea and the Southwest Indian Ridge), with all birds favouring subtropical waters (~ 46% of utilization distribution; Figure 1b). Again, birds moulting within the Tasman Sea and Southwest Indian Ridge used more subtropical and sub-Antarctic waters, respectively (STZ: 60 and 44%, and SAZ: 40 and 56%, respectively), but the difference was less important than during the whole inter-breeding period (see above). Despite the small sample size, there was low inter-individual variability within the two strategies (Figure 1a).

3.4. Periodicity in activity patterns

The wavelet analysis of daily flying time revealed different patterns for each individual (Figure S2). Three out of six individuals showed a strong relationship between daily flight time and moon cycles, with a significant 29.5 days periodicity (Table 2, Table S5). All three birds overwintered in the Tasman Sea, and these periodic patterns occurred during both daytime and nighttime. Synchronicity was only detected during the non-

breeding period, from the end of April to the beginning of September, and for between one to five lunar cycles. All three birds showed an identical synchronicity in June and July 2018. The birds overwintering over the Southwest Indian Ridge did not exhibit such temporal synchronicity.

3.5. Isotopic values of feathers

All primary samples of the single dead chick had similar isotopic values (Figure S3), which were not statistically different from those of four body feathers from the same bird (Mann-Whitney test, U = 19.5 and 15.0, p = 0.744 and 0.361, for δ^{13}C and δ^{15}N values, respectively). Primaries from the dead chick and body feathers from the 12 live chicks were collected during different years and they showed small but statistically different isotopic values (U = 103.5 and 24.5, p = 0.021 and 0.011, for δ^{13}C and δ^{15}N values, respectively). As expected, all chick feathers (both primaries and body feathers) had δ^{13}C values that characterize the STZ (Table 3).

All 55 primary samples of the five dead adult MacGillivray's prions retained high δ^{13}C and δ^{15}N values that indicate moulting flight feathers in the subtropics (Figure 4, upper panel, Figure S3). In contrast, body feather values of the 23 live adult MacGillivray's prions ranged widely, encompassing 3.3 and 11.2 ‰ differences for δ^{13}C and δ^{15}N, respectively (Table 3). Overall, 33.7% (n = 31) and 66.3% (n = 61) of body feathers were synthesized within the STZ and SAZ, respectively, with no body moult occurring within the AZ. Most of the birds (n = 16, 69.6%) moulted their four body feathers in both the STZ

and SAZ, six (26.1%) within the SAZ only, and a single bird (4.3%) within the STZ only (Figure 4, lower panel).

Body feathers of GLS-carrying MacGillivray's prions that wintered over the Southwest Indian Ridge (n = 12, three birds) and in the Tasman Sea (n = 16, four birds) showed identical $\delta^{13}C$ values (U = 104.5, p = 0.693) and slightly different $\delta^{15}N$ values (U = 52.5, p = 0.043). Interestingly, $\delta^{15}N$ values of body feathers moulted in subtropical waters (n = 3 feathers for birds wintering over the Southwest Indian Ridge and n = 7 in the Tasman Sea,) were significantly lower over the Southwest Indian Ridge than in the Tasman Sea (11.5 ± 2.0 and 15.0 ± 0.6 ‰, respectively, U = 0.0, p = 0.017). A threshold value at 14.5 ‰ discriminated between two groups of birds amongst those that were not GLS tracked and that moulted at least partially in the subtropics (n = 11). Their feather $\delta^{15}N$ values suggest that six birds wintered over the Southwest Indian Ridge and five birds in the Tasman Sea.

3.6. Isotopic values of blood, plasma and food samples

Blood $\delta^{13}C$ and $\delta^{15}N$ values of the 23 incubating MacGillivray's prions averaged -20.6 and 7.1 ‰, respectively (Table 3), with no statistical difference between females and males (Two-sample t-tests, t = 0.67 and 0.39, p = 0.511 and 0.698, respectively). They were lower than the corrected values (from feathers to blood) of large chicks near fledging (t = 24.39 for $\delta^{13}C$ and 49.54 for $\delta^{15}N$, both p < 0.001; Figure 5). The high chick $\delta^{13}C$ values support foraging within the STZ, but the low $\delta^{13}C$ values of incubating adults indicate they fed on sub-Antarctic prey. This unexpected result was confirmed by the low

isotopic values of both birds' plasma (n = 23, -20.7 ± 0.4 and 9.0 ± 0.7 ‰) and food samples (n = 7, -22.4 ± 0.7 and 5.6 ± 1.2 ‰). The presence of higher-trophic level prey (euphausiids and/or fish, see below) increased the $\delta^{15}N$ values of two food samples when compared to the remaining five others (7.2 - 7.4 and 4.9 ± 0.3 ‰, respectively).

Nine spontaneous regurgitations were collected, weighing on average 4.6 ± 2.5 g. All but one of the food samples were dominated by mass by crustaceans (87.3%), with fish accounting for the remaining 12.7%. Crustaceans occurred in all the samples. Copepods constituted by far the main food component by mass and by number, with a predominance of the calanid *Neocalanus tonsus* (mostly stage V copepodites). A few euphausiid remains were found in five samples, with the presence of bilobed eyes indicating the genera *Nematoscelis* and/or *Thysanoessa*. Finally, fish remains were identified in two samples that contained one and six specimens of the phosichthyid genus *Vinciguerria* that were numbered using dentary bones.

3.7. Blood isotopic values and bill width of MacGillivray's, Antarctic and slender-billed prions

Blood isotopic values segregated the three most abundant prion species that breed in the area ($\delta^{13}C$: Kruskal-Wallis, H = 26.17, p < 0.001; $\delta^{15}N$: Anova, $F_{2,52}$ = 164.5, p < 0.001) (Figure 5). MacGillivray's prions had higher blood $\delta^{13}C$ values than the Antarctic (Conover-Inman post hoc test for pairwise comparison, p < 0.001) and slender-billed (p < 0.001) prions from the sub-Antarctic Kerguelen Islands, and $\delta^{15}N$ values significantly decreased in the order slender-billed > Antarctic > MacGillivray's prions (Tukey's post

hoc tests for pairwise comparison, all three p < 0.001). The three prion species segregated by their bill width ($F_{2,52} = 48.8$, p < 0.001, and p < 0.001 for the three pairwise comparisons), with the following increasing order: slender-billed (11.1 ± 0.6 mm) < Antarctic (13.6 ± 0.6 mm) < MacGillivray's (17.9 ± 1.0 mm). Blood $\delta^{15}N$ values were significantly and negatively correlated to bill width amongst species, the larger the bill (MacGillivray's prion), the lower the $\delta^{15}N$ value (Figure 6).

4. DISCUSSION

By combining tracking, activity data and stable isotope we revealed the year-round behavioural ecology through exploration of movement, foraging, feeding and moulting of the MacGillivray's prion (*Pachyptila macgillivrayi*) breeding at Saint Paul Island, Southern Indian Ocean. As expected, and despite a small sample size with relatively few individuals tracked, results showed that the species exhibited a migratory behaviour during which birds favoured sub-Antarctic and subtropical waters where they moulted early during the non-breeding period.

4.1. Food and feeding ecology during the breeding period in relation to bill width

During incubation, the two GPS-equipped MacGillivray's prions foraged south of Saint Paul Island, remaining in temperate waters north of the STF. This was consistent with feather $\delta^{13}C$ values of large chicks, which indicated that adults also forage within the STZ later in the breeding season, during the chick-rearing period. In the Southern Indian Ocean, the $\delta^{15}N$ baseline rises sharply in the vicinity of the STF and this increase

propagates through the food web (Altabet & Francois 1994, Lourey et al. 2003). Consequently, the low plasma and blood $\delta^{13}C$ values of incubating birds, together with the low $\delta^{13}C$ values of food samples, suggest that they feed on sub-Antarctic prey during incubation. Such a mismatch between bio-logging and stable isotopes is rarely reported in the scientific literature and can be explained here by several non-exclusive explanations: (i) the birds effectively foraged within the SAZ, with the STF being located further north than its average latitudinal position during the study period, (ii) prions foraged within cold-water eddies of sub-Antarctic origin that are located within the temperate waters of the STZ, and (iii) prey recently migrated from the SAZ to the STZ, and, hence, still retain the $\delta^{13}C$ values of cold waters. The latter hypothesis seems unlikely, however, because small drifting zooplankton such as copepods generally do not undergo extensive horizontal migrations. These unexpected results illustrate how poorly known is the food and feeding ecology of the MacGillivray's prion, which needs to be further investigated by again combining complementary methods, but for a larger number of birds and during a longer study period.

An interesting aspect of the sub-Antarctic blood isotopic values of MacGillivray's prions is that it allows a comparison between blood $\delta^{15}N$ values and those from prions from the nearby sub-Antarctic Kerguelen Islands without any deleterious $\delta^{15}N$ baseline effect associated with the STF. By contrast, this negative $\delta^{15}N$ baseline effect precludes directly comparing their wing feather $\delta^{15}N$ values (Jones et al. 2020), because MacGillivray's and Antarctic prions moult in the subtropics, while the slender-billed prion moults their primaries in the AZ (Cherel et al. 2016, this study). Consequently, the higher feather $\delta^{15}N$ values of MacGillivray's prions from Gough Island do not translate directly to

a higher trophic level than that of other prions during moult (Jones et al. 2020). Instead, blood isotopic values showed an opposite trend during breeding, with $\delta^{15}N$ values increasing in the order MacGillivray's prions < Antarctic prions < slender-billed prions. All three species feed primarily on crustaceans, but the dietary importance of small-sized zooplankton increases in the order slender-billed prions < Antarctic prions < MacGillivray's prions (Cherel et al. 2002, this study). This trophic segregation is related to the beak morphology of the prions (Klages & Cooper 1992). The larger the beak, the higher the number of palatal lamellae (from none in the slender-billed prion to 136 in the broad-billed prion; Klages & Cooper 1992), the more efficient are the birds at seawater filtering and, hence, the higher is the dietary proportion of copepods and, consequently, the lower the $\delta^{15}N$ values and the birds' trophic position. The negative linear relationship between blood $\delta^{15}N$ values and bill width (Figure 6) illustrates this suite of morphological, behavioural and dietary adaptations that allow the abundant prions from the Southern Indian Ocean to coexist at sea by feeding on prey of different sizes.

Indeed, food samples indicate that the diet of incubating MacGillivray's prion is dominated by 3-4 mm long stage V copepodites of *Neocalanus tonsus*. *N. tonsus* is an abundant circumglobal sub-Antarctic and transition species at the STF, where stage V copepodites form large surface swarm concentrations in spring and summer (Kawamura 1974; Bradford-Grieve & Jillett 1998; Bradford-Grieve et al. 2001). This seasonally predictable mass-occurrence makes *N. tonsus* an ideal prey for filter-feeding predators of various sizes, from the huge southern sei whale (Kawamura 1974) and large basking shark (Bradford-Grieve & Jillett 1998) to comparatively small seabirds such as the broad-billed prion (Imber 1981) and Macgillivray's prion (this study).

4.2. The inter-breeding period

MacGillivray's prions from Saint Paul Island migrated to distant wintering grounds during the inter-breeding period, which is in agreement with the behaviour of other prion species, including the MacGillivray's prion from Gough Island (Quillfeldt et al. 2015a,b, Jones et al. 2020). They wintered almost equally to the north and south of the STF, favouring the STZ and SAZ over the colder waters of the AZ located further south. Accordingly, their δ^{13}C values indicate body feathers were moulted either within the STZ or SAZ, with no feather retaining the lower δ^{13}C values that characterize the AZ. Both GLS tracking and stable isotopes depict inter-individual variations, with most MacGillivray's prions from Saint Paul Island wintering in both the subtropics and the Southern Ocean, while some individuals favored either the STZ or the SAZ.

Seabird species exhibit various overwintering strategies as observed between populations at the intraspecific level: i) entirely migratory (e.g. slender-billed prions (Quillfeldt et al. 2015b), ii) dispersive (e.g. Antarctic prions and blue petrels *Halobaena caerulea*; Quillfeldt et al. 2015a), iii) resident versus migratory (e.g. Fluttering shearwater *Puffinus gavia*; Berg et al. 2019) or iv) migratory movements to different overwintering destinations (e.g. Cook's petrel *Pterodroma cookii* Rayner et al. 2011, south polar skuas *Catharacta maccormicki* Kopp et al. 2011, Weimerskirch et al. 2015). The MacGillivray's prion breeding at Saint Paul Island exhibited clear migratory movements towards two distinct migratory locations (Tasman Sea or the Southwest Indian Ridge), which are not related to at-sea sexual segregation. This strategy is seemingly unique regarding other

prion species (Quillfeldt et al. 2015a,b), even compared to MacGillivray's prions breeding at Gough Island (Jones et al. 2020). Thus, prions either overwinter in a single area for the whole population (slender-billed prion), or a multitude of areas (Antarctic prion), or an in-between strategy (MacGillivray's prion, this study). Few other seabird species are known to have a similar *two-way* strategy (Cook's petrel; Rayner et al. 2011), and genetic differences may be suspected. However, our sample size was small and more individuals need to be tracked to confirm this two-way strategy.

During the inter-breeding period, MacGillivray's prions from Saint Paul exhibited a clear temporal pattern, spending more time on the water right after breeding, during the first half of the inter-breeding period. In addition to this seasonal pattern, the activity appeared to be partly influenced by the moon. The night-time at-sea activity followed repeated cycles according to lunar cycles ($\approx$ 29 days). To our knowledge, a marked within-species variation in response to lunar cycles, or at least a non-region specific response, has not yet been described and needs to be further explored. Prions overwintering in the Tasman Sea were more active during nights with higher moonlight intensity. In a still unexplained way, the birds overwintering over the Southwest Indian Ridge did not exhibit such synchronicity in their cycle of at-sea activity. Among seabirds, the influence of the moon phase on at-sea activity appears poorly marked for some species (Scopoli's shearwaters *Calonectris diomedea* (Ramos 2019); Bulwer's petrel *Bulweria bulwerii* (Dias et al. 2016)), while clearly evidenced in others (e.g. Yamamoto et al. 2008, Mackley et al. 2011, Pinet et al. 2011). Links between at-sea behaviour and the lunar phase during the non-breeding period have been found in several species of albatrosses, petrels, shearwaters or gulls (Phalan et al. 2007, Yamamoto et al. 2008, Pinet et al. 2011, Cruz

et al. 2013, Ramos et al. 2016), with higher nocturnal activity during moonlight nights. The lunar cycle is known to strongly influence the vertical distribution (diurnal vertical migration) of potential prey species such as zooplankton, squid and fish, thereby making them more accessible to foraging seabirds (Brinton 1967, Gliwicz 1986a,b, Luecke & Wurtsbaugh 1993, Benoit-Bird et al. 2009). Prions capture their prey at the surface by pumping water though the filtering lamellae and have access only to the upper first meters of the water column, taking surface prey such as copepods (Imber 1981, Warham 1990). Therefore, vertically migrating prey may become out of reach to prions. Nonetheless, this pattern was not detected for birds overwintering over the Southwest Indian Ridge. This suggests either differences in productivity around the Del Cano Rise compared to the Tasman Sea, and/or different diets and prey behaviour depending on the non-breeding area. Accordingly, $\delta^{13}C$ values indicate that (i) body feathers were synthesized within different water masses (either STZ or SAZ), and (2) for body feathers moulted within the STZ, $\delta^{15}N$ values were lower in the Southwest Indian Ridge than in the Tasman Sea.

4.3. Moult

MacGillivray's prions from Saint Paul exhibited a high seasonality in their at-sea activity pattern, with the daily proportion of time spent on water peaking at the beginning of the inter-breeding period from March to May. This peak in proportion of time spent on water is likely to correspond to the moult of flight feathers (Cherel et al. 2016). Such a transient reduction in flying activity characterizes the intense moult of flight feathers that decreases the flying ability of prions and petrels (Cherel et al. 2016, Jones et al. 2020).

MacGillivray's prions thus showed a post-breeding wing moult, which is in agreement with the timing of moult of the other population of MacGillivray's prions at Gough Island, and of the slender-billed prion and blue petrel, but not of the Antarctic prion that presents a pre-breeding moult of flight feathers (Cherel et al. 2016, Jones et al. 2020).

The isotopic values of the primaries of MacGillivray's prions from Saint Paul are characteristic of the STZ, with a single wing feather moulted within the Southern Ocean. The primary $\delta^{13}C$ values of MacGillivray's prions from Gough Island are slightly different from those from Saint Paul (-16.7 ± 0.7 ‰, n = 72, versus -17.3 ± 0.6 ‰, n= 55, respectively), but they also indicated renewing flight feathers in the subtropics, with again a single feather retaining a sub-Antarctic value (Jones et al. 2021). Prions thus exhibit species-specific moulting areas, with MacGillivray's, Antarctic and broad-billed prions renewing their flight feathers in the subtropics and the slender-billed prion in Antarctic waters (Quillfeldt et al. 2015b, Cherel et al. 2016, Jones et al. 2020). It was estimated that MacGillivray's prions from Gough Island moult primaries in both the STZ and SAZ (Jones et al. 2020). However, the too high feather $\delta^{13}C$ estimation of the STF (Phillips et al. 2009), a key issue to delineate where the prions moult, shifted the moulting zone too far south. In agreement with our interpretation, the primary $\delta^{13}C$ values of MacGillivray's prions were identical to those of the broad-billed prions that moult in the subtropics (-16.6 ± 0.7 ‰, n = 132).

The primary moult of the MacGillivray's prion lasts longer compared to the other prion species (extended moulting duration: MacGillivray's Saint Paul Island ≈ 119 d; MacGillivray's Gough Island ≈ 115 d > Antarctic ≈ 109 d > broad-billed ≈ 96 d > slender-billed ≈ 83 d > blue petrel ≈ 71 d; Cherel et al. 2016, Jones et al. 2020). It is noteworthy

that the species with the longest moulting period are those renewing their flight feathers within the less productive STZ. Interestingly, the high distribution overlap between MacGillivray's prions from Saint Paul and Antarctic prions from Kerguelen (see Figure S4) indicates that both populations renew their plumage in the same oceanic zone. However, Antarctic prions moult before breeding in late winter (July-Nov; Figure 3), while MacGillivray's prions moult after breeding in late summer (Feb-May), creating a temporal mismatch that likely minimizes competition at sea between the two species. Another relevant feature is that the two populations of MacGillivray's prions spend the non-breeding period in different wintering areas, either in the Indian Ocean (Saint Paul) or the Atlantic (Gough; Jones et al. 2021), while the two main populations of the slender-billed prions from the Indian (Kerguelen) and the Atlantic (Falklands) oceans moulted their flight feathers in the same area (Quillfeldt et al. 2015b). Remarkably, however, MacGillivray's prions from Gough Island exhibited very similar timing in departure/arrival at the breeding colony and moulting duration compared to their conspecifics from Saint Paul Island, and both populations appeared to favour the SAZ and STZ during the non-breeding period.

The distribution at sea of the MacGillivray's prion from Saint Paul Island seems relatively small during breeding, but it expands considerably during the inter-breeding period. The oceanic wintering areas of the MacGillivray's prion were already identified as important zones for many pelagic seabird species (Waugh et al. 2012, Delord et al. 2013,2014, Lascelles et al. 2016), and its breeding range is partly included within the Marine Protected Area of Saint Paul and Amsterdam Islands (Southern French Territories; Claudet et al. 2021). Prions are not identified as threatened species by incidental mortality caused by fisheries so far but were found to be influenced by climate

variability (Barbraud & Weimerskirch 2005, Nevoux & Barbraud 2006). Since marine areas used by MacGillivray's prions are impacted by climate change (Sydeman et al. 2021), future studies are needed to understand how climate variability affect the at-sea distribution of this endangered species, and ultimately its population dynamics. Nevertheless, the main issue for Macgillivray's prions remains the presence of house mouse (*Mus musculus*) on Saint Paul, and given the seeming failure of the eradication of mice on Gough, eradicating them on Saint Paul should be a priority (Barbraud et al. 2021).

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Tables

Table 1. Sample sizes of birds tracked using geolocators (GLS), and main characteristics of the inter-breeding and moulting periods of MacGillivray's prions from Saint Paul Island in 2018. Values are indicated as mean ± SD

GLS	Deployment $n = 20$
	Recovery $n = 7$ (35%)
Inter-breeding period	
	Departure date[A] : 22 February ± 13.6 (days)
	Arrival date[A] : 29 September ± 29.6 (days)
	Duration: 189 ± 23.5 (days)
	Distance from the colony: 4839 ± 1954 (4-7550) (km)
	Centroid longitude[B]: 45.1 ± 9.5 - 158.6 ± 0.9 (°E)
	Centroid latitude: -43.9 ± 2.7 (°S)
Migration period	
outward	Arrival date: 6 March ± 12.3 (days)
	Duration: 12 ± 4.1 (days)
inward	Departure date: 11 September ± 24.6 (days)
	Duration: 18 ± 9.0 (days)
Moulting period	Beginning date:
	Extended[C]: 2 March ± 14.1 (days)
	Core[C]: 18 March ± 13.0 (days)
	Duration :
	Extended[C]: 119 ± 38.0 (days)
	Core[C]: 76 ± 30.3 (days)
	Centroid longitude [B]:
	Extended[C]: 48.4 ± 3.0 - 159.5 ± 1.9 (°E)
	Core[C]: 47.4 ± 2.9 - 159.2 ± 1.9 (°E)

Centroid latitude (°S):	
Extended[C]: -43.1 ± 1.5	
Core[C]: -43.9 ± 1.3	

[A] Departure date from the colony at the end of the breeding season *t* and arrival date at the colony at the beginning of the breeding season *t+1*; [B] Refers to the two migratory strategies (see Results Section); [C] Refers to the extended or core moulting area (see Methods Section)

Table 2. Periodicity of at-sea activity during the inter-breeding period of MacGillivray's prions from Saint Paul Island in 2018. Start and End define the period characterized by a significant synchronization between seabird activity and lunar cycles (p-value < 0.05; see Sections 2.4 & 3.4 for details)

	Daytime			Nighttime		
	P^A	Start	End	P	Start	End
BH747	0.435			0.995		
BH754	0.943			0.976		
BH764	0.681			0.959		
BH756	0.989			**0.04**	05/06/2018	30/07/2018
BH757	**<0.001**	05/06/2018	19/08/2018	**0.016**	20/04/2018	10/05/2018
BH758	**0.003**	14/06/2018	05/09/2018	**0.063**	26/06/2018	20/07/2018

[A] The averaged p-value stands for the hypothesis testing that there is a 29.5 periodicity in at-sea activity time-series.

Table 3. Tissue $\delta^{13}C$ and $\delta^{15}N$ values (means ± SD, with ranges in parentheses) of chicks and of incubating adult MacGillivray's prions from Saint Paul Island, and of incubating Antarctic and slender-billed prions from Kerguelen Islands. All the adult birds were sampled after removal of miniaturized saltwater immersion geolocators (for Kerguelen birds, see Quillfeldt et al. (2020)). Blood values for chicks are feather values that were blood corrected according to Cherel et al. (2014). For feathers, n refers to the number of feathers and the number in parentheses to that of birds

Tissues and species	Location	Age	n	Tissue $\delta^{13}C$ (‰)	Tissue $\delta^{15}N$ (‰)	References
Blood cells / whole blood						
MacGillivray's	Saint Paul	chicks	12	-18.8 ± 0.2 (-19.4 to -18.5)	13.3 ± 0.3 (12.5 to 13.7)	this study
	Saint Paul	adults	23	-20.6 ± 0.2 (-21.0 to -20.2)	7.1 ± 0.4 (6.4 to 7.8)	this study
Antarctic	Kerguelen	adults	11	-23.4 ± 1.4 (-24.9 to -19.9)	8.2 ± 0.3 (7.9 to 8.8)	Quillfeldt et al. (2020)
Slender-billed	Kerguelen	adults	23	-23.3 ± 1.2 (-24.6 to -19.6)	8.9 ± 0.3 (8.4 to 9.5)	Quillfeldt et al. (2020)
Body feathers						
MacGillivray's	Saint Paul	chicks	12 (12)	-17.4 ± 0.2 (-17.9 to -17.0)	13.9 ± 0.3 (13.1 to 14.4)	this study
	Saint Paul	adults	92 (23)	-18.7 ± 1.0 (-20.2 to -17.0)	10.4 ± 2.8 (4.9 to 16.0)	this study
Primaries						
MacGillivray's	Saint Paul	chick	11 (1)	-17.5 ± 0.2 (-17.7 to -16.9)	14.2 ± 0.2 (13.9 to 14.4)	this study
	Saint Paul	adults	55 (5)	-17.3 ± 0.6 (-18.3 to -16.2)	13.2 ± 1.7 (10.2 to 16.9)	this study

Figures

Fig. 1. Kernel densities or utilization distribution contours of adult MacGillivray's prions breeding on Saint Paul Island (black triangle), a) during the entire inter-breeding period (50 % UD; blue line; n = 7 individuals), and b) during the moult of flight feathers (n = 6). Darker and lighter green tone areas show the 75 and 90% location densities of the core moult area (i.e., according to the 75% on water moult activity criterion), respectively, while the contours show the 90% location densities of the extended moult area calculated using the 50% on water moult activity criterion. Oceanographic frontal structures are shown: the South Subtropical Front (dark grey line) and Polar Front (grey line) (Belkin & Gordon 1996; Sokolov & Rintoul 2009)

Fig. 2. Kernel densities or utilization distribution contours (25, 50, 75% UD; yellow) calculated from GLS (n = 7) and locations obtained from GPS (n = 2; red) during the breeding period of adult MacGillivray's prions breeding on Saint Paul Island (black triangle). Raw GPS data are illustrated: locations (red circles) and trajectories (red lines). Bathymetry shown in blue. Oceanographic frontal structures are shown: the North Subtropical Front (NSTF; dark grey line) and South Subtropical Front (SSTF; grey line) (Belkin & Gordon 1996; Sokolov & Rintoul 2009)

Fig. 3. Daily activity pattern calculated from GLS for adults of MacGillivray's prion; daily time spent sitting on water as a proxy of daily activity patterns of Antarctic (grey), slender-billed (red; source Cherel et al. (2016) and MacGillivray's (green; this study) prions over

the annual cycle. Months refer to the species-specific inter-breeding period. Birds were equipped with miniaturized saltwater immersion geolocators. Values are means ± SD

Fig. 4. Feather $\delta^{13}C$ and $\delta^{15}N$ values of chicks (red) and adults (blue) of MacGillivray's prion. Upper panel: primary feather isotopic values of one chick and five adults. Values are means ± SD of 11 primary samples (two for P10, see text). Lower panel: body feather isotopic values of chicks and adults that were equipped with miniaturized saltwater immersion geolocators. Values are means ± SD of a single feather for 12 chicks, and of four feathers per adult bird (n = 23). Lower and upper control lines refer to the feather estimated $\delta^{13}C$ location of the Polar Front and Subtropical Front, respectively (Jaeger et al. 2010). Abbreviations: AZ, Antarctic Zone; SAZ, sub-Antarctic Zone; STZ, Subtropical Zone

Fig. 5. Blood $\delta^{13}C$ and $\delta^{15}N$ values of chicks (n = 12, red) and of incubating adults (n = 23, blue) of MacGillivray's prion, and of incubating adults of slender-billed (n = 23, green) and Antarctic (n = 11, grey) prions from Kerguelen Islands. All the adult birds were sampled after removal of miniaturized saltwater immersion geolocators (for Kerguelen birds, see Quillfeldt et al. (2020)). Isotopic values of chicks are feather values that were blood corrected according to (Cherel et al. 2014). Values are means ± SD. Lower and upper control lines refer to the blood estimated $\delta^{13}C$ location of the Polar Front and Subtropical Front, respectively (Cherel & Hobson 2007; Jaeger et al. 2010). Abbreviations: AZ, Antarctic Zone; SAZ, sub-Antarctic Zone; STZ, Subtropical Zone

Fig. 6. Relationship between blood $\delta^{15}N$ value and bill width for prions. All the incubating birds were sampled after removal of miniaturized saltwater immersion geolocators (for Antarctic and slender-billed prions from Kerguelen Islands, see Quillfeldt et al. (2020)). Values include both individual values and means ± SD. Regression line: y = -0.234 x + 11.420 (n = 55, r^2 = 0.78, $F_{1,53}$ = 184.4, p < 0.001)
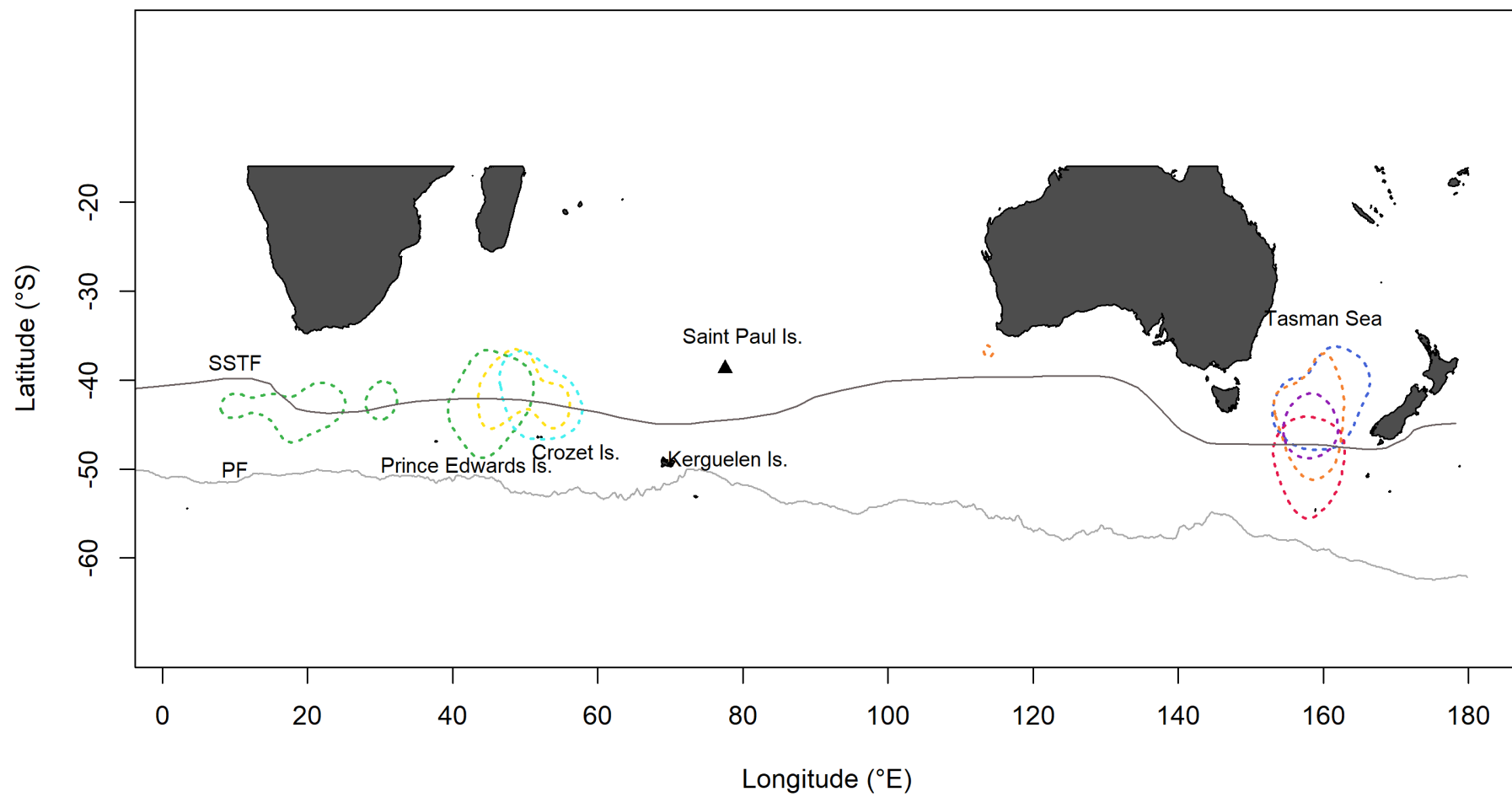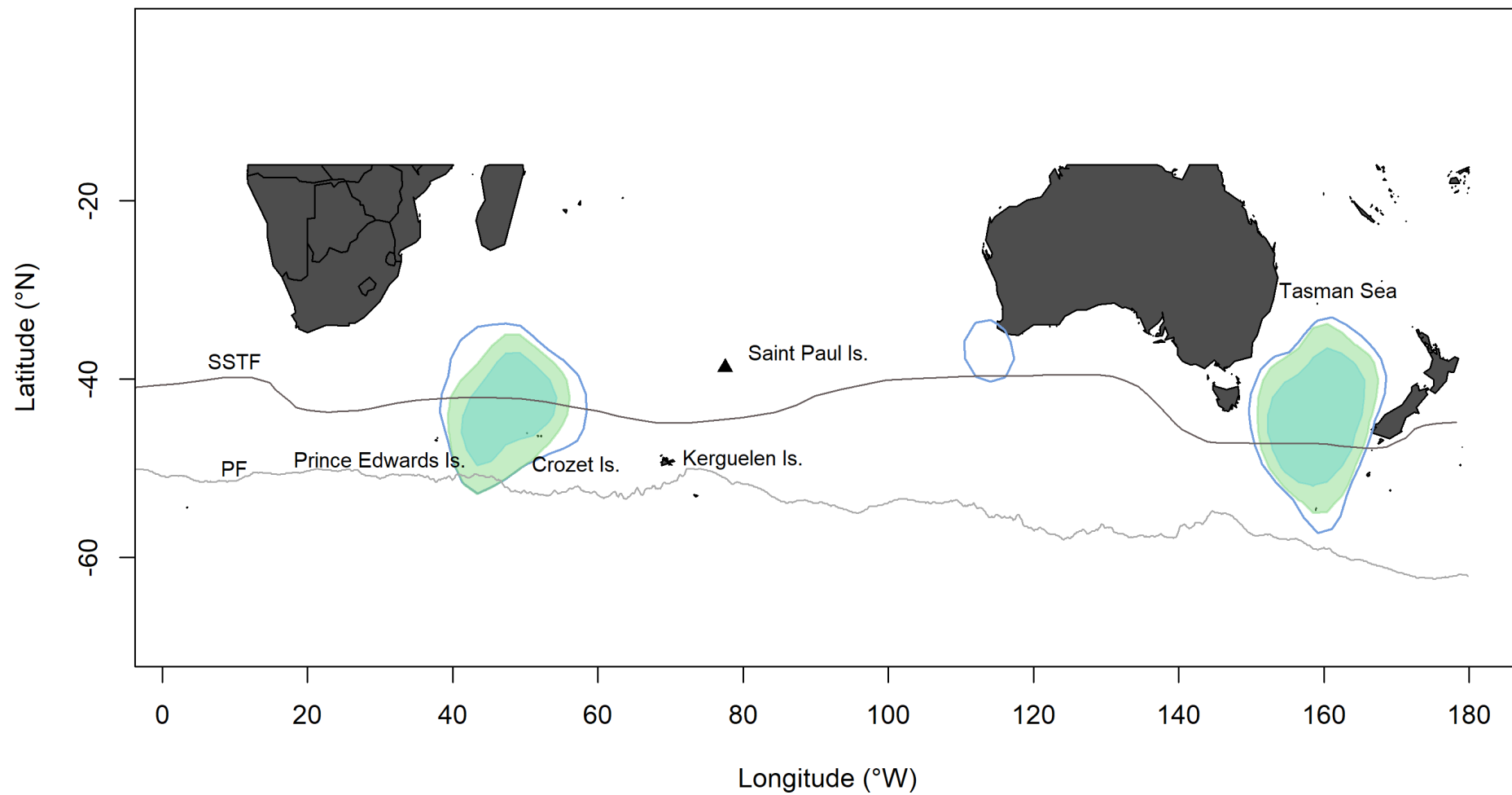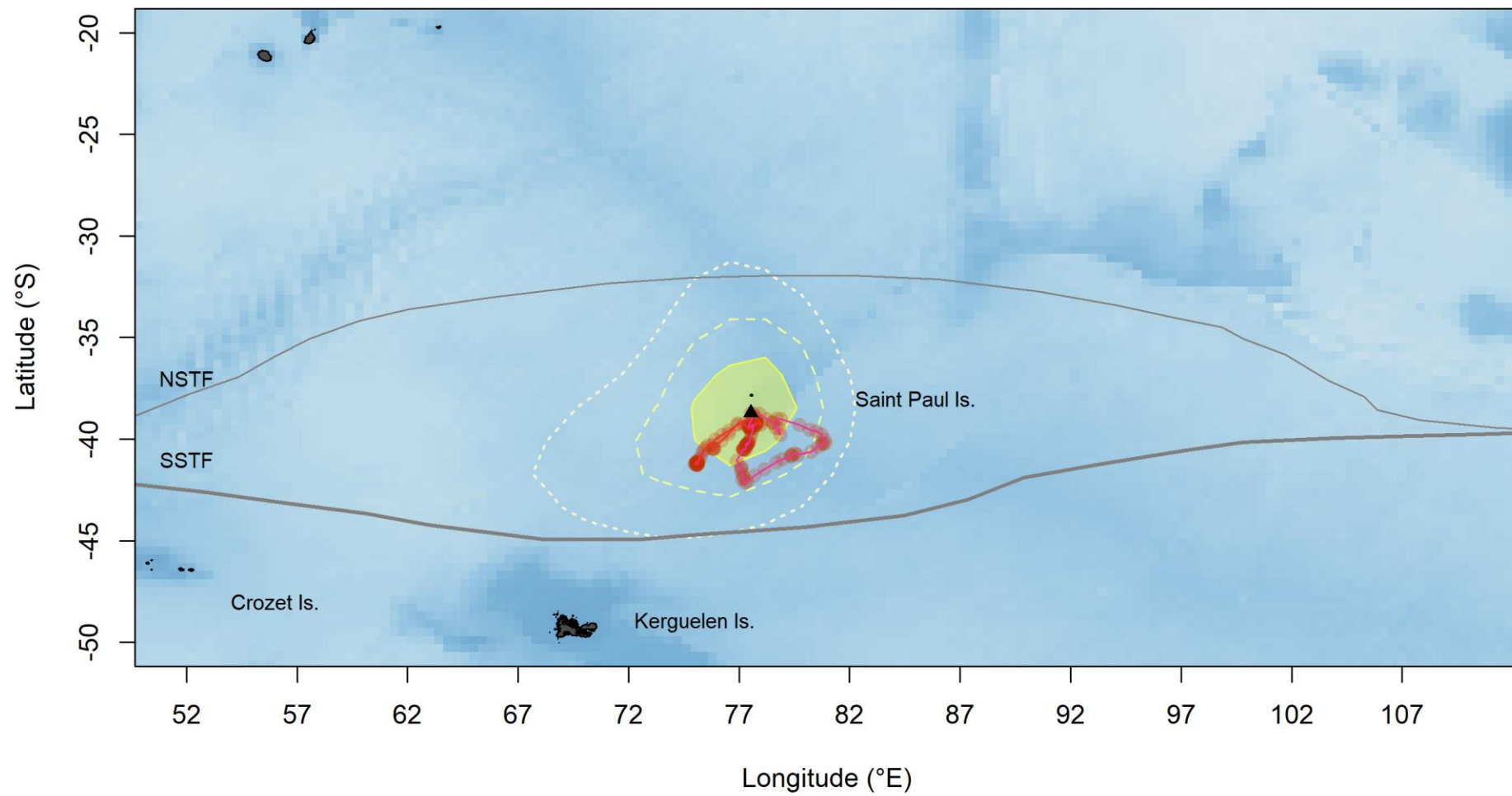
Figure 1a

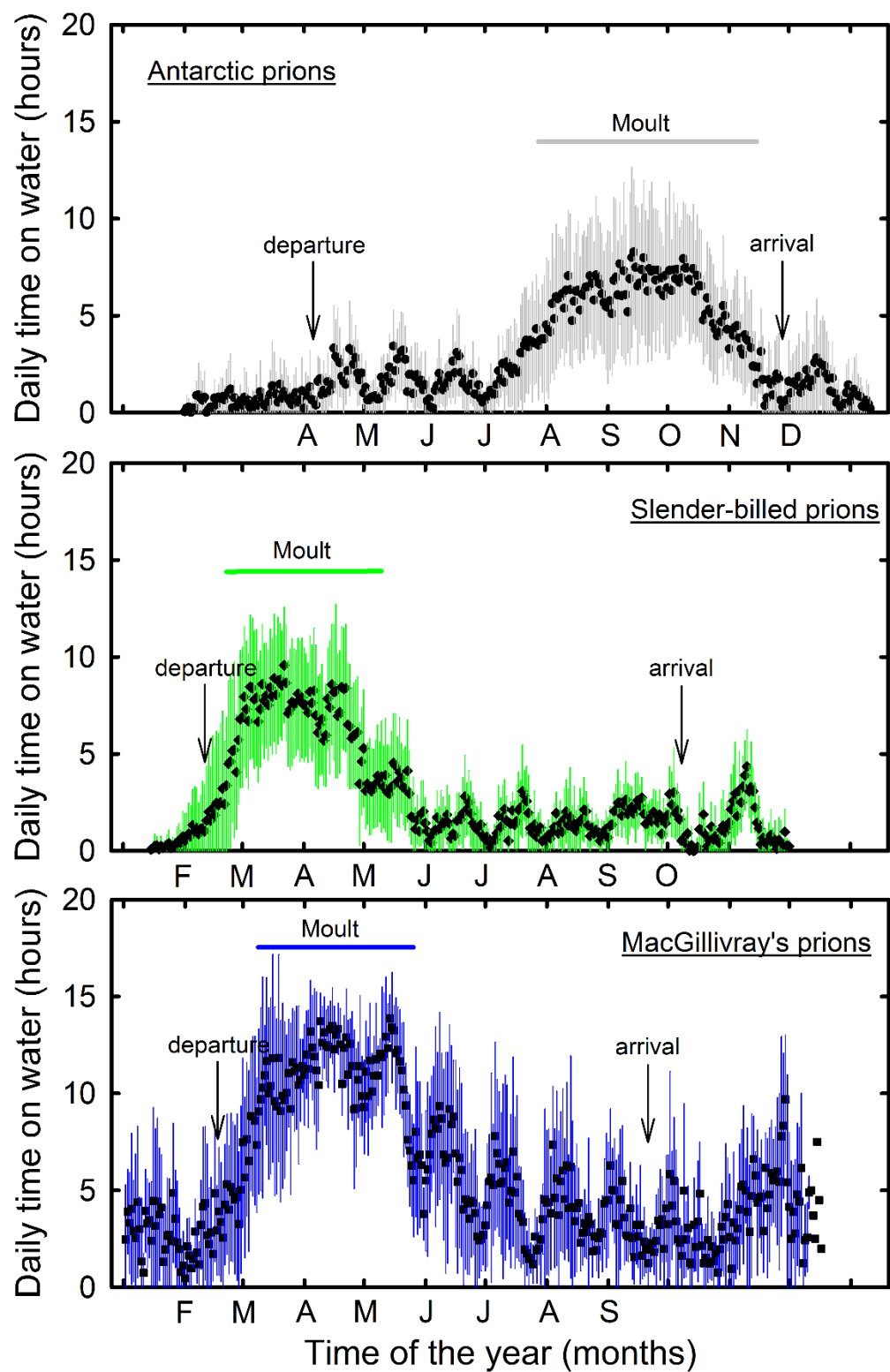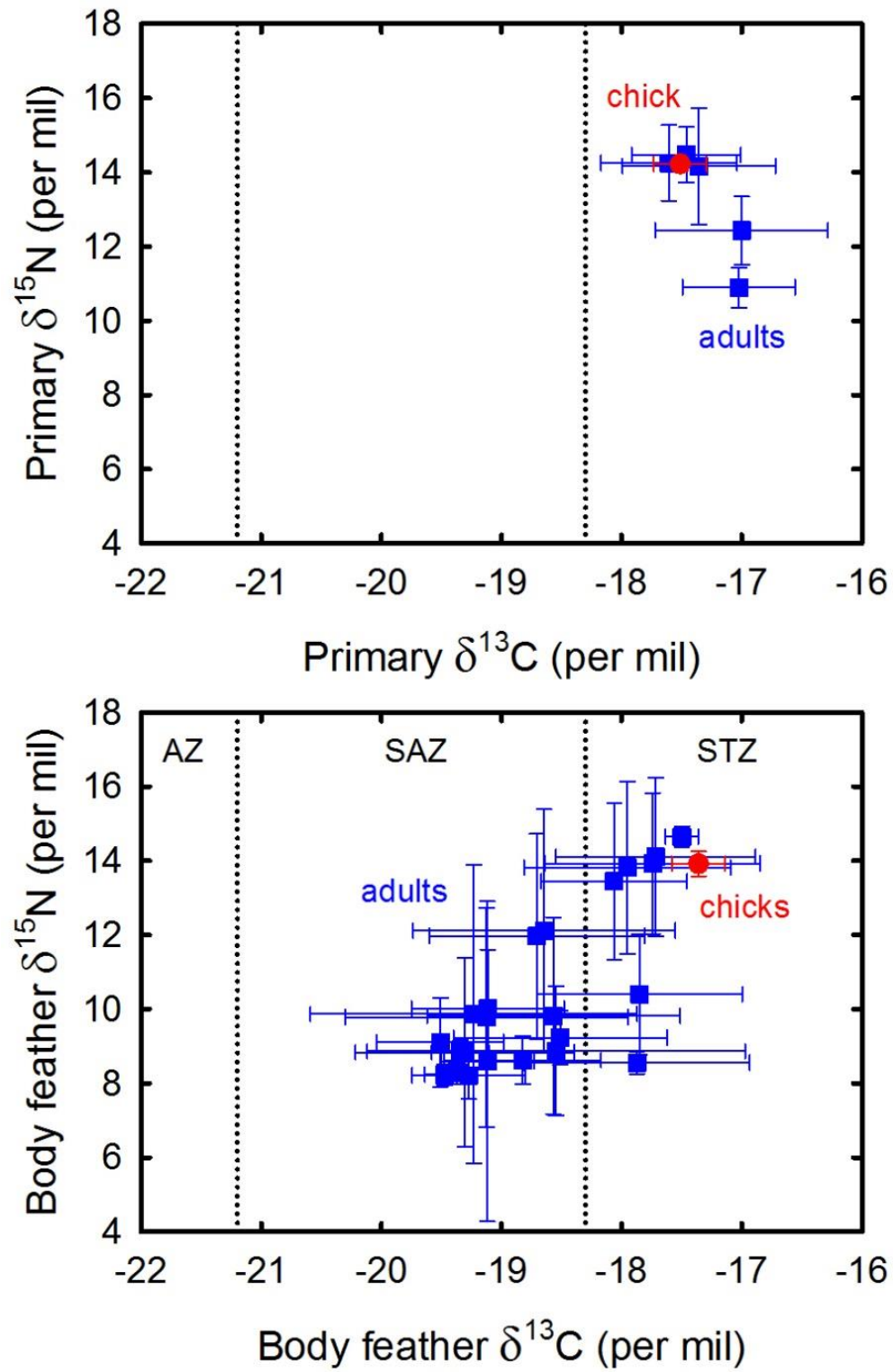Figure 1b

Figure 2

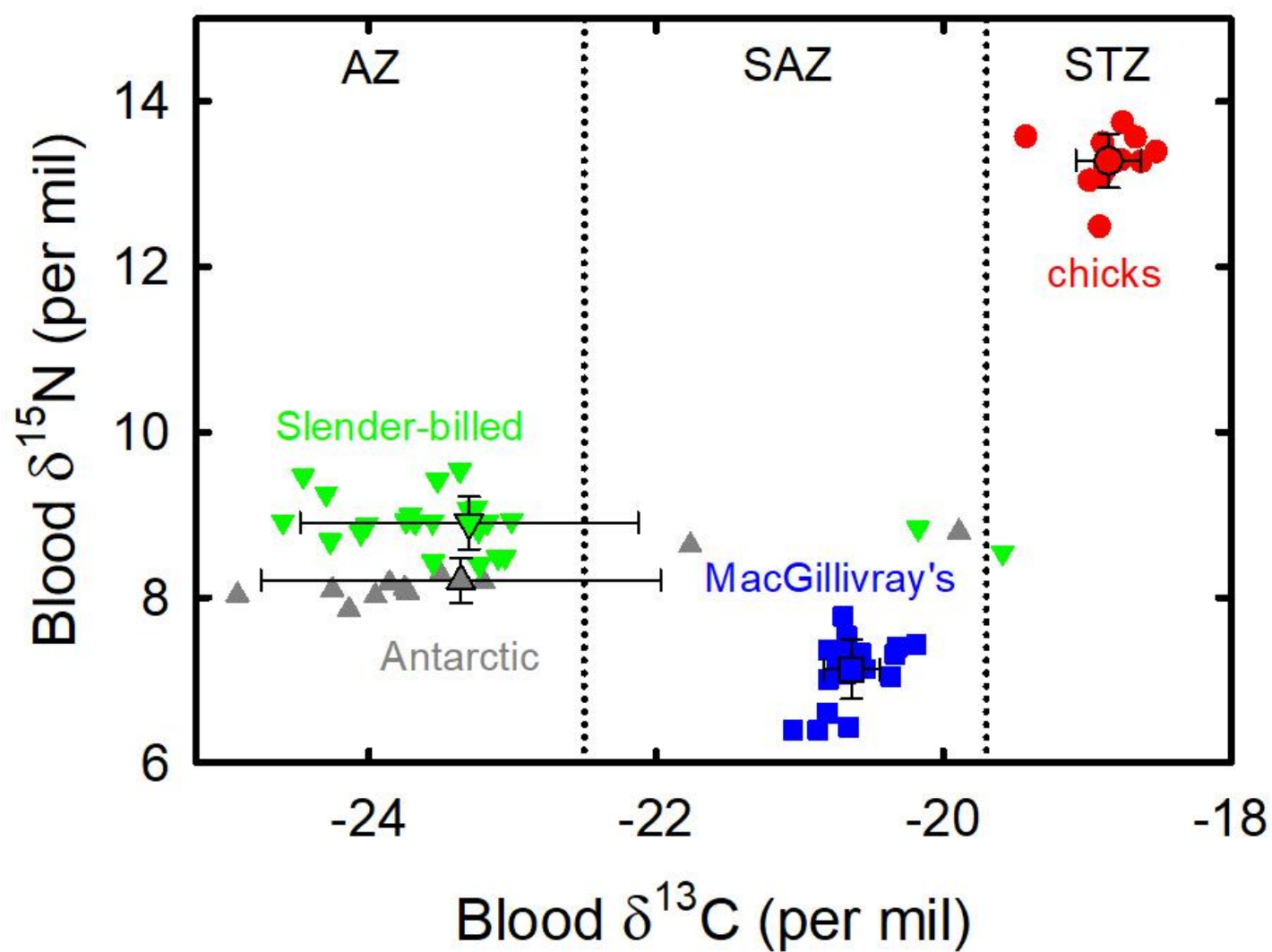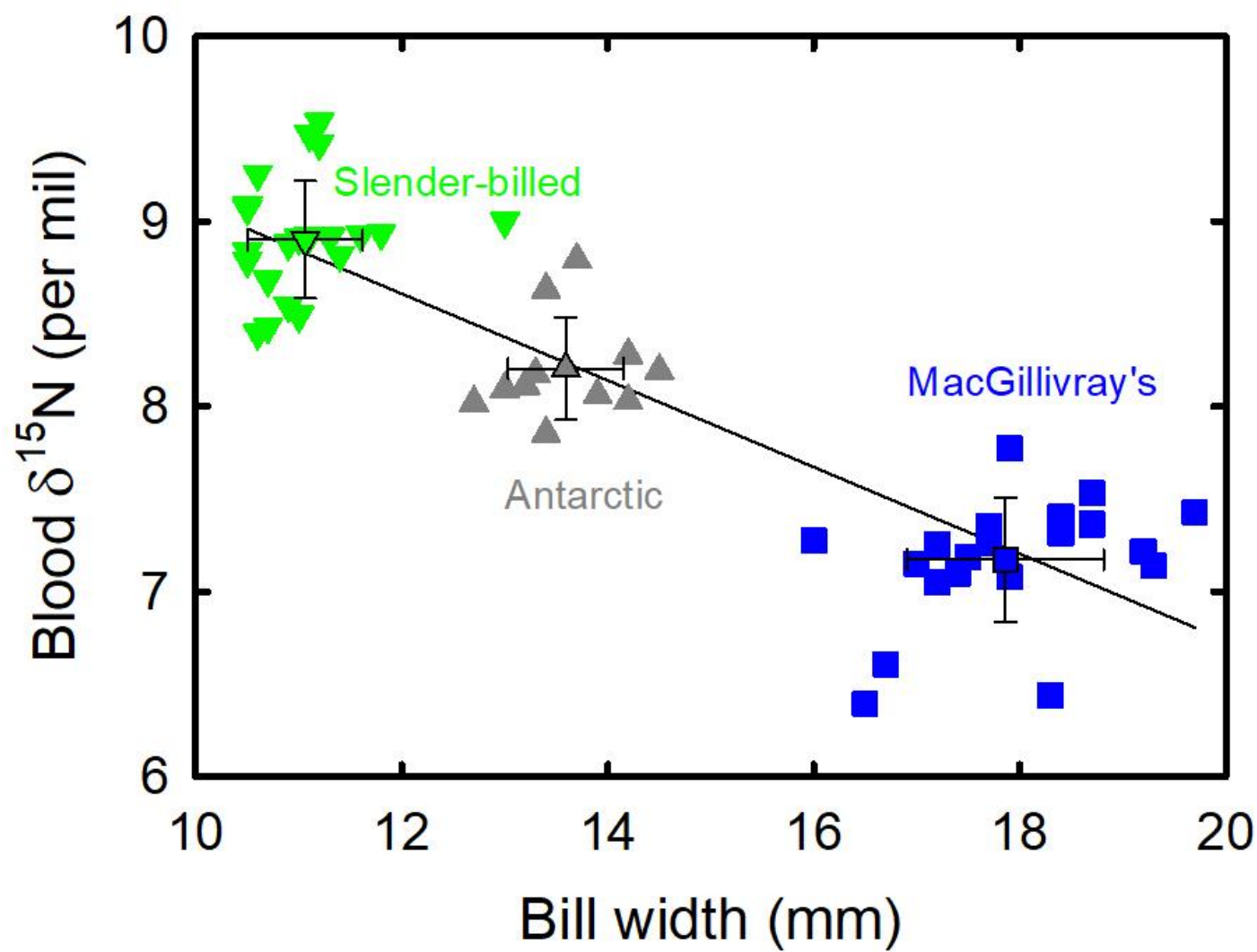Figure 3

Figure 4

Figure 5

Figure 6

Online supplementary materials

Table S1. Detailed list of the analyses performed on the activity data (proportion of time spent wet) for MacGillivray's prions during the inter-breeding period (Generalized Linear Mixed Models, beta binomial with a random factor 'individual').

Study variable: daily proportion of time spent wet	Model selection	AIC	ΔAIC	Sample size
During daytime	~ sex + month + sex:month	**-1746.0**	**0**	1249
	~ sex + month	-1649.9	-96.1	1249
	~ sex	-1260.6	-485,4	1249
	~ month	-1651.8	-94,2	1249
During darkness	~ sex + month + sex:month	**-2086.6**	**0**	1249
	~ sex + month	-1969.3	-117.3	1249
	~ sex	-1569.2	-517.4	1249
	~ month	-1970.6	-116.0	1249

Table S2. Fixed-effect parameters of generalized linear mixed model of the variation in the activity pattern (daily proportion of time spent wet during daytime) for MacGillivray's prions during the inter-breeding period. Variables selected in the best model (see Table S1). Reference value are female (sexfemale) and the proportion of time spent wet during February (month2)

	Value	SE	z-test	P
(Intercept)	-1.321	0.12	10.67	**0.000**
sexmale	-1.064	0.38	-2.79	**0.005**
Month3	0.940	0.10	9.51	**0.000**
Month4	0.975	0.01	9.80	**0.000**
Month5	0.802	0.10	8.06	**0.000**
Month6	0.139	0.10	1.35	0.176
Month7	-0.133	0.10	-1.29	0.198
Month8	0.012	0.10	0.12	0.905
Month9	-0.084	0.11	-0.74	0.457
sexmale :Month3	0.202	0.36	0.56	0.578
sexmale :Month4	0.869	0.36	2.42	**0.016**
sexmale :Month5	1.133	0.36	3.15	**0.002**
sexmale :Month6	1.552	0.36	4.30	**0.000**
sexmale :Month7	1.320	0.36	3.64	**0.000**
sexmale :Month8	1.024	0.36	2.82	**0.005**
sexmale :Month9	1.098	0.38	2.89	**0.004**

Table S3. Fixed-effect parameters of generalized linear mixed model of the variation in the activity pattern (daily proportion of time spent wet during darkness) for MacGillivray's prions during the inter-breeding period. Variables selected in the best model (see Table S1). Reference values are female (sexfemale) and proportion of time spent wet during February (month2)

	Value	SE	z-test	P
(Intercept)	-1.384	0.18	-7.56	**0.000**
sexmale	0.261	0.39	0.68	**0.005**
Month3	0.907	0.10	9.11	**0.000**
Month4	0.950	0.10	9.47	**0.000**
Month5	0.611	0.10	6.11	**0.000**
Month6	-0.021	0.10	-0.20	0.176
Month7	-0.378	0.11	-3.58	0.198
Month8	-0.420	0.11	-3.89	0.905
Month9	-0.330	0.12	-2.87	0.457
sexmale :Month3	-0.628	0.28	-2.23	0.578
sexmale :Month4	-0.417	0.281	-1.49	**0.016**
sexmale :Month5	-0.238	0.28	-0.85	**0.002**
sexmale :Month6	0.262	0.28	0.93	**0.000**
sexmale :Month7	0.468	0.28	1.66	**0.000**
sexmale :Month8	0.634	0.28	2.24	**0.005**
sexmale :Month9	0.241	0.30	0.80	**0.004**

Table S4 At-sea activity (mean ± SD) during the inter-breeding and moulting periods of MacGillivray's prions from Saint Paul Island in 2018

Parameter - Daily time spent on water	
Inter-breeding period	
Daytime (%)	29.68 ± 13.8
Darkness (%)	27.14 ± 13.1
Moulting period	
Daytime (%)	32.04 ± 13.3
Darkness (%)	30.23 ± 11.3
Non-Moulting period	
Daytime (%)	19.31 ± 10.9
Darkness (%)	13.59 ± 11.8

Table S5. Moon and at-sea activity (mean ± SD proportion of daily time on water) during

the inter-breeding period of MacGillivray's prions from Saint Paul Island in 2018

	Daytime	Darkness
Overall	29.68 ± 13.81	27.14 ± 13.08
New moon days	35.02 ± 12.06	30.43 ± 11.59
Waxing moon days	30.71 ± 12.79	27.13 ± 12.42
Full-moon days	26.30 ± 14.74	26.61 ± 14.45
Waning moon days	32.47 ± 11.69	29.53 ± 11.94
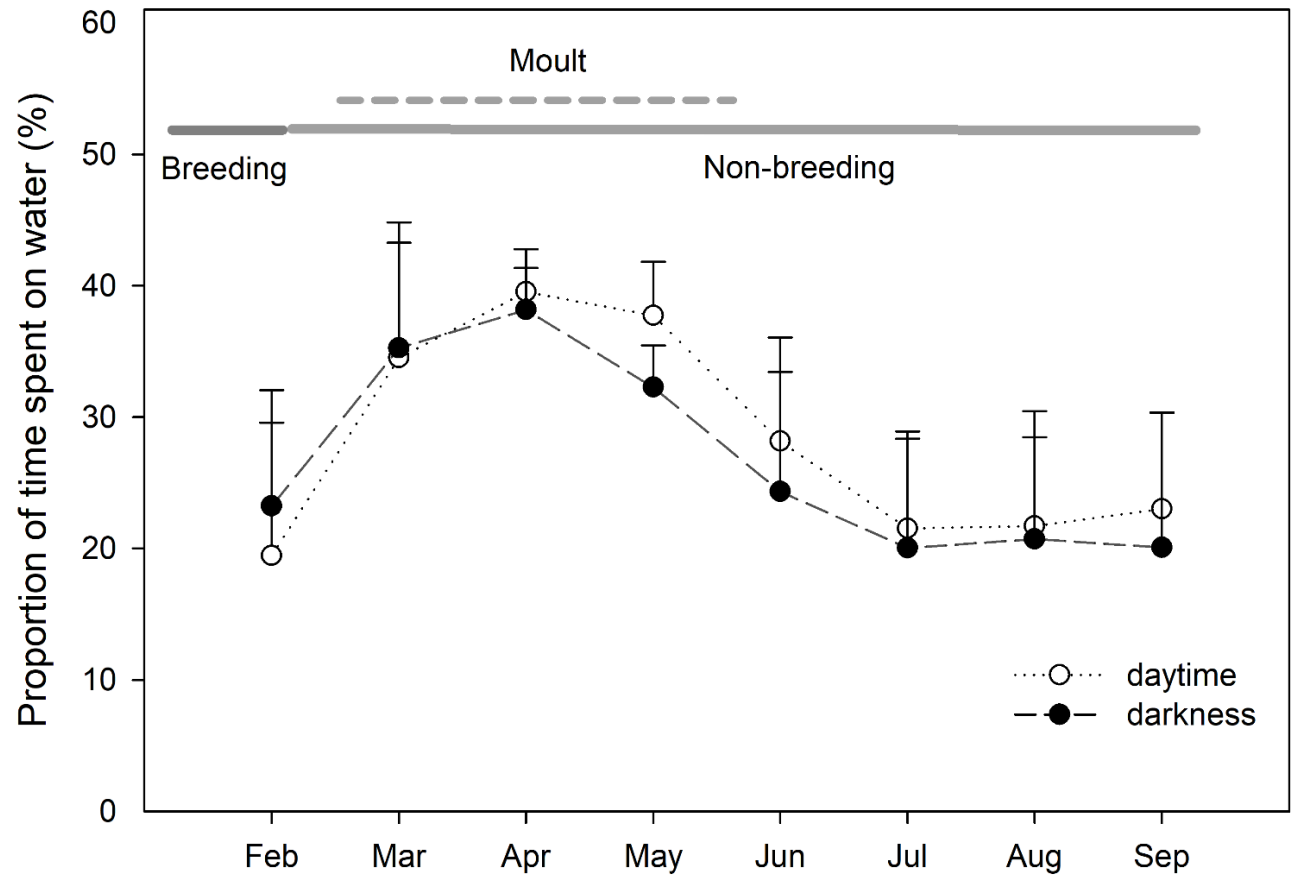
Figure S1 Daily activity pattern calculated from GLS for adults of MacGillivray's prion; proportion of time spent on water (wet) during the inter-breeding period. Birds were equipped with miniaturized saltwater immersion geolocators. Values are means ± SD
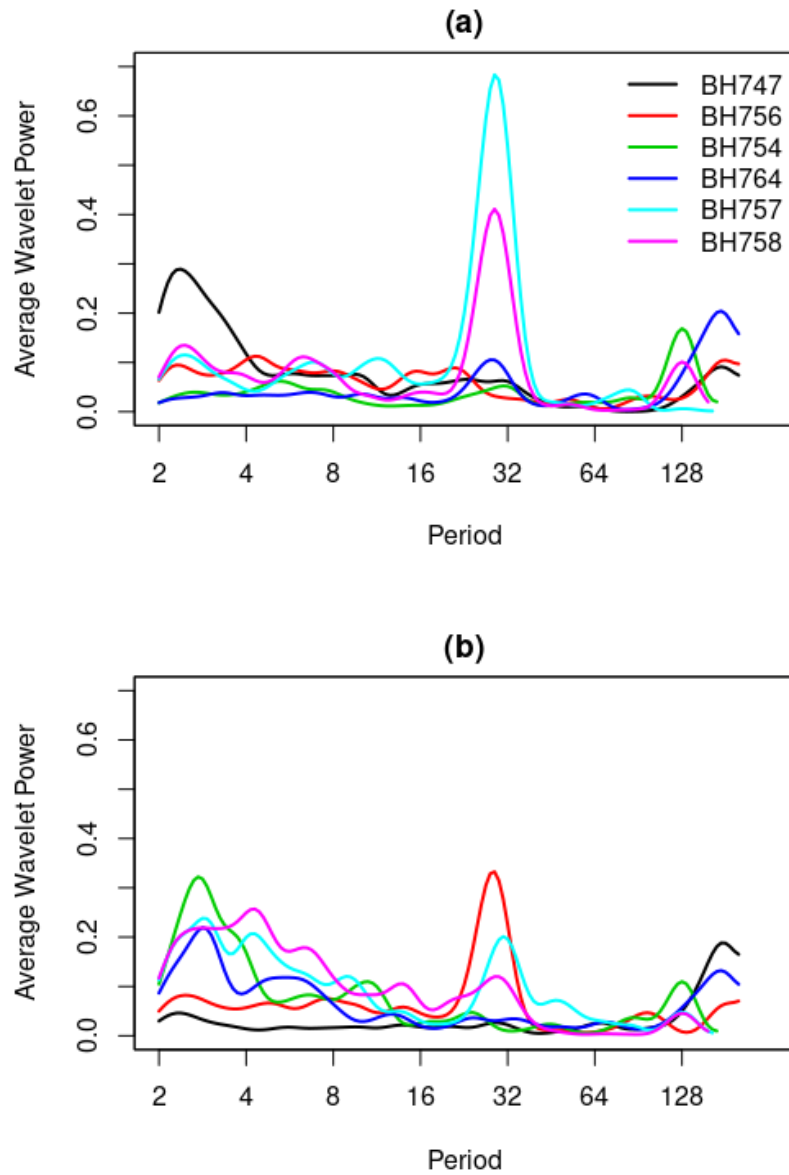
Figure S2 Averaged wavelet power across time of at-sea activity time series computed for all individuals both during daytime (a) and nighttime (b). The horizontal axis shows the Fourier periods
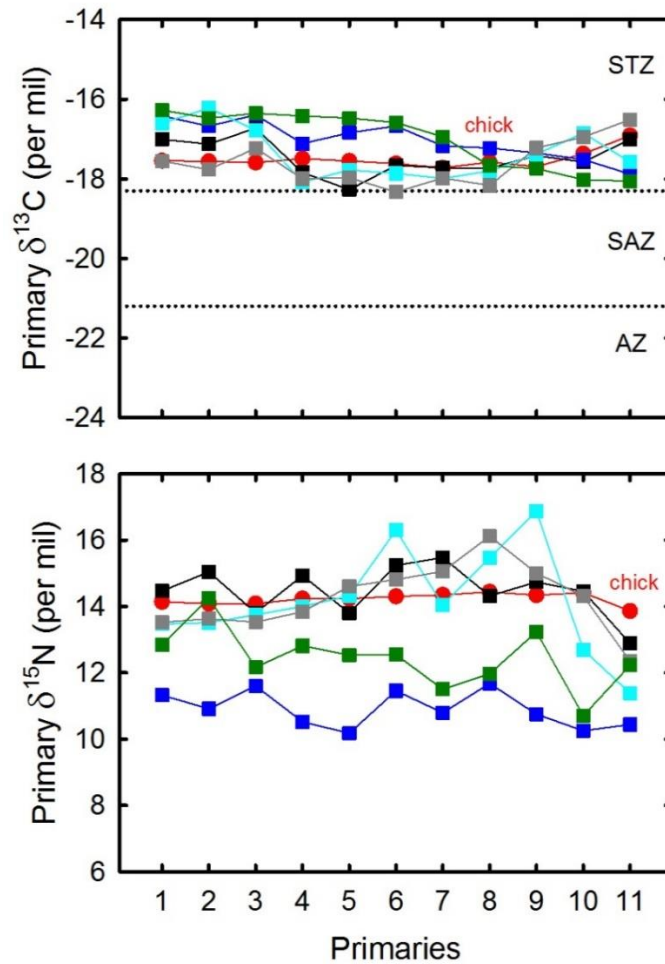
Figure S3 Primary feather δ^{13}C (upper panel) and δ^{15}N (lower panel) values of one chick (red) and five adults (light and dark blue, green, grey and black) of MacGillivray's prions. Each colour indicates an individual. Feathers were collected from dead birds. Numbering refers to the tip of each of the ten primaries from the innermost (P1) to the outermost (P10) feather; eleven refers to the base of P10 and hence to the very end of primary moult. Lower and upper control lines refer to the feather estimated δ^{13}C location of the Polar Front and Subtropical Front, respectively (Jaeger et al. 2010). Abbreviations: AZ, Antarctic Zone; SAZ, sub-Antarctic Zone; STZ, Subtropical Zone
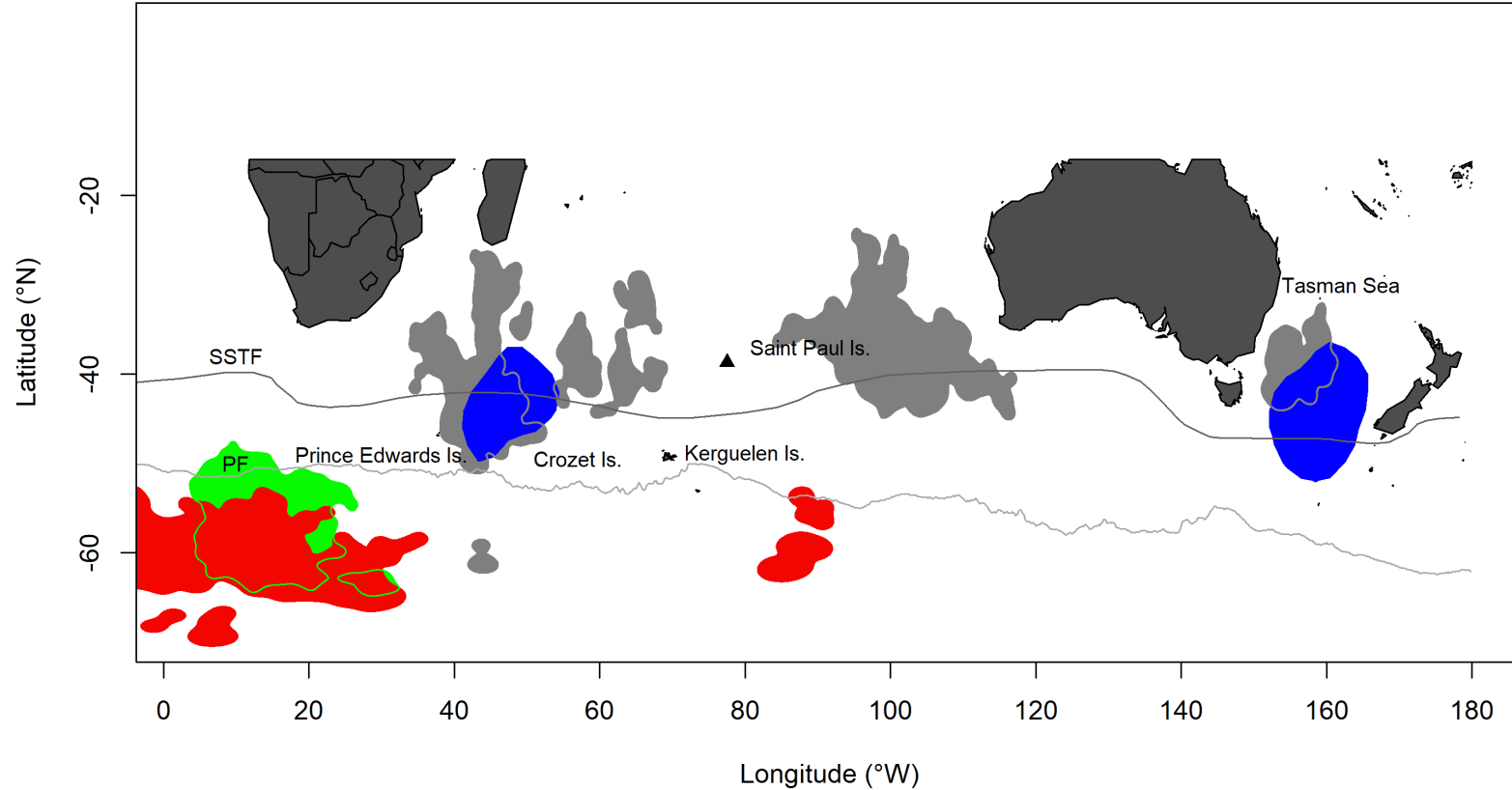
Figure S4 Density contours resulting from kernel estimation of geolocation data of MacGillivray's (this study, blue), Antarctic (grey) and slender-billed prions (green), and blue petrels (red) during moult of flight feathers (Cherel et al. 2016). Contours show the 75% location densities of the core molt area (i.e., according to the 75% on water moult activity criterion calculated using the 50% on water moult activity criterion). Oceanographic frontal structures shown are: the South Subtropical Front (dark grey line) and Polar Front (grey line) (Belkin and Gordon 1996; Sokolov and Rintoul 2009)