

Moult intensity in blue petrels and a key moult site off West Antarctica

PETER G. RYAN ¹, JASMINE R. LEE ² and FABRICE LE BOUARD ³

¹FitzPatrick Institute of Africa Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Rondebosch 7701, South Africa

²School of Biological Sciences, Monash University, Clayton, VIC 3800, Australia

³Centre d'Etude Biologiques de Chize, CNRS, 79360 Villiers En Bois, France
pryan31@gmail.com

Abstract: Blue petrels (*Halobaena caerulea* Gmelin) rapidly moult their flight feathers in Antarctic waters in February–April, immediately following the breeding season, yet the behaviour of moulting birds at sea has not been described. We observed large numbers of moulting blue petrels off West Antarctica from 67–71°S and 78–119°W in mid-February 2017. Most of these birds probably breed at the Diego Ramirez archipelago, southwest of Cape Horn, which is the closest colony to this area. Moulting petrels often sit on the water in dense flocks, just outside the marginal ice zone, at sea temperatures of -0.7 to 0.9°C. Wing moult is intense, with 7–8 inner primaries (62–75% of primary length and 55–69% of primary mass), their corresponding primary coverts and all greater secondary coverts being grown at the same time. Moulting petrels need a reliable food source during this energetically demanding period, so the waters off West Antarctica are probably crucial for the Diego Ramirez population, which makes up more than half of the world's blue petrels.

Received 27 March 2019, accepted 3 October 2019

Key words: Amundsen Sea, Bellinghousen Sea, Diego Ramirez, greater covert moult, *Halobaena caerulea*, primary moult

Introduction

The blue petrel (*Halobaena caerulea* Gmelin) is an abundant seabird with a circumpolar distribution that mainly forages at high latitudes in the Southern Ocean (Marchant & Higgins 1990). Some birds disperse north off the west coast of South America in winter, but elsewhere they seldom venture north of the Subtropical Front (Brown *et al.* 1986, Ryan *et al.* 1989). Almost the entire population of some 2.4 million pairs breeds from 47 to 56°S at five sub-Antarctic island groups and islands off the southern tip of South America (Dilley *et al.* 2017), with a small population recently discovered farther north on Gough Island (40°S, 10°W; Ryan *et al.* 2015). Adults breed in early summer, returning to colonies from the end of August, laying eggs in late October and fledging chicks in late January–early February (Marchant & Higgins 1990; although breeding occurs ~1 month later at Gough Island; Ryan *et al.* 2015). Moult takes place immediately after breeding, with some birds dropping up to three inner primaries even before leaving their colonies (Marchant & Higgins 1990). Wing moult is complete and rapid, with birds in fresh plumage returning to their colonies to reoccupy breeding burrows for a few days in April–June (Fugler *et al.* 1987, Marchant & Higgins 1990). Recently, leg-mounted activity loggers (wet-dry sensors) have

shown that blue petrels exhibit a marked increase in the proportion of time spent sitting on the water during moult (Cherel *et al.* 2016). Using the duration of this period of decreased flight activity as a proxy for the moult period, Cherel *et al.* (2016) inferred that blue petrel moult lasts ~10 weeks, which is shorter and thus probably more intense than that of ecologically similar prion *Pachyptila* species (Rohwer & Rohwer 2013).

Tracking studies (Navarro *et al.* 2015, Cherel *et al.* 2016), the low $\delta^{13}\text{C}$ values of blue petrel feathers (Cherel *et al.* 2002, 2006, Phillips *et al.* 2009) and the few records of moulting birds at sea (Bierman & Voous 1950, Wanless & Harris 1988) all indicate that moult occurs in Antarctic waters. Adults breeding at Kerguelen and South Georgia mainly moult at 55–65°S and between 20°W and 30°E (Cherel *et al.* 2016, R.A. Phillips, personal communication 2019) in a 'hotspot' shared with several other seabird species (Quillfeldt *et al.* 2015, Cherel *et al.* 2016). Given that the only other substantial populations in the Atlantic and Indian oceans breed at islands located between South Georgia and Kerguelen (i.e. the Prince Edward and Crozet islands), it is probable that virtually all birds from these ocean basins moult in Antarctic waters south of Africa. However, approximately half of the world's population of blue petrels breeds at the Diego Ramirez archipelago, south-west of Cape Horn (Lawton *et al.* 2006). Nothing

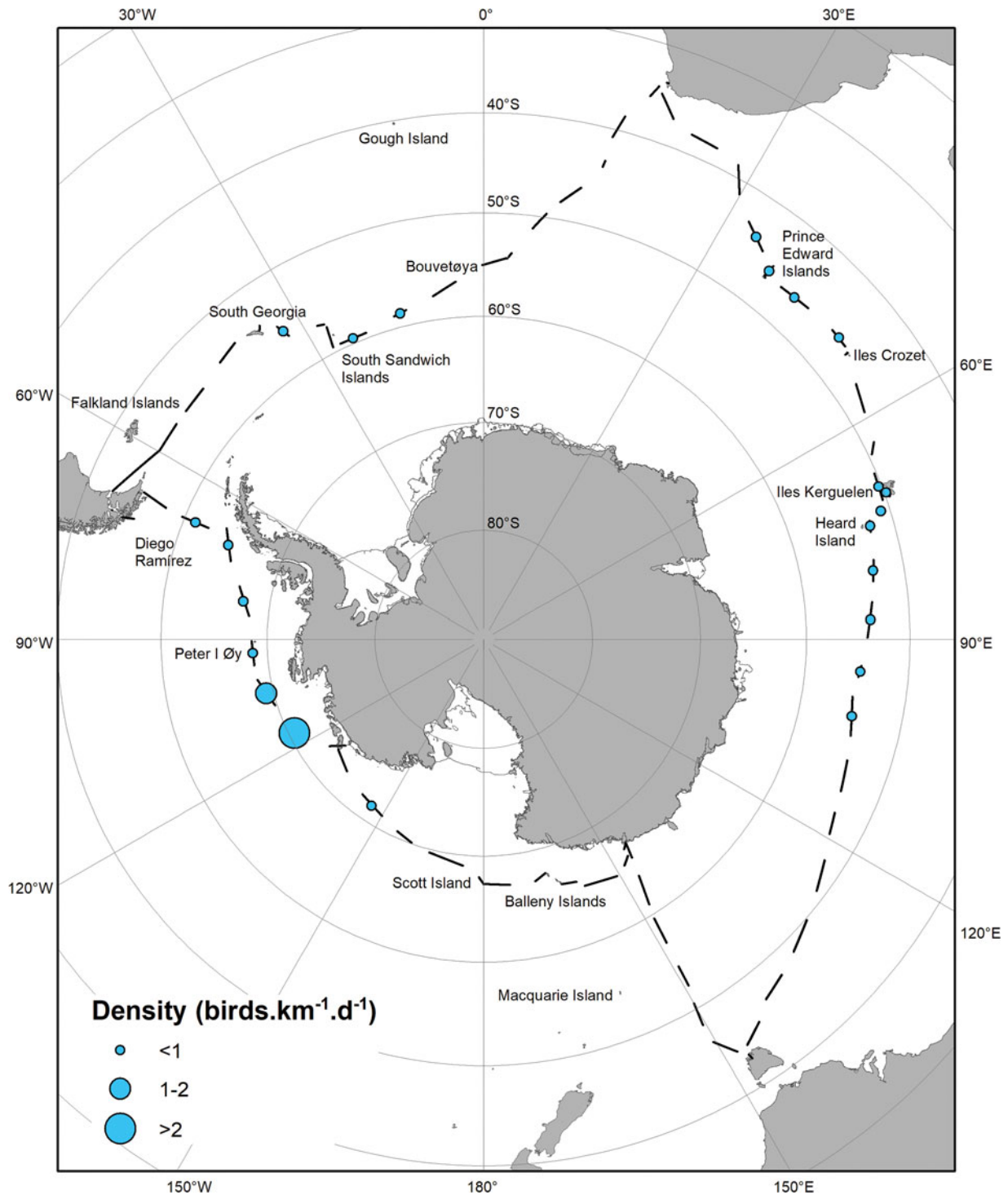


Fig. 1. Map of daily seabird transect counts during the Antarctic Circumnavigation Expedition (bold dashed line) and the average encounter rate with blue petrels (birds $\text{km}^{-1} \text{d}^{-1}$).

is known about the moulting location of birds from this colony, although Wanless & Harris (1988) noted that most blue petrels seen in early February 1987 in the western Amundsen Sea ($\sim 67^\circ\text{S}$ and $148\text{--}153^\circ\text{W}$) were in moult. We report very large concentrations of blue

petrels moulting in the Amundsen Sea and adjacent Bellinghousen Sea, most of which probably come from Diego Ramirez, as this is the closest colony to this region. Photographs of birds in flight confirm the intense nature of moult, with birds replacing seven to eight

primaries and most greater coverts at the same time. Given the increased flight costs while undergoing rapid wing moult (Hedenström & Sunada 1999) and the high energetic cost of moult in general (Lindström *et al.* 1993), blue petrels need a reliable food source during this short, intense moult period. We suggest that the nutrient-rich waters off West Antarctica are a key moult area for half of the world's blue petrels.

Study area and methods

We counted seabirds from the *Akademik Tryoshnikov* during daylight steaming throughout the Antarctic Circumnavigation Expedition (ACE) from 21 December 2016 to 19 March 2017. The expedition travelled from Cape Town to Hobart via the sub-Antarctic islands (Prince Edward Islands, Iles Crozet, Iles Kerguelen and Heard Island), then at higher latitudes from Hobart to Punta Arenas via the Balleny Islands, Scott Island, Mount Siple, Peter 1 Øy and Diego Ramirez, and then from Punta Arenas to Cape Town via South Georgia, the South Sandwiches and Bouvetøya (Fig. 1). Standard 300 m-wide transect counts of seabirds were made on the side of the bow with best visibility following Tasker *et al.* (1984). Birds following the ship were excluded from counts. Despite using the 'snapshot' approach (~1 scan per min, depending on the ship's speed) to reduce the risk of over-counting birds moving faster than the ship (Tasker *et al.* 1984), we report birds counted per kilometre of transect per day as an index of abundance rather than absolute density estimates, because blue petrels often approach vessels (Griffiths 1982), thus increasing the effective transect width to an unknown extent (cf. Ainley *et al.* 1998). However, area-based densities were estimated for birds sitting on the water because there is little risk of the ship influencing the distribution of birds in moulting flocks, which typically only fly when flushed by the ship's passage. These densities were extrapolated across the range over which we encountered moulting flocks to get a very rough idea of the numbers involved, assuming the band of birds was ~50–100 km wide. We also recorded the presence of pack ice (estimated % cover over the 10 min observation period), as well as the presence of icebergs in the general vicinity (within ~1 km of the transect). Sea temperature was recorded every minute from the ship's ferrybox (intake 5 m below the surface) and averaged per 10 min observation period.

Moult was scored from photographs of birds in flight. Birds with a mix of old and new primaries were easily distinguished, but birds completing primary moult (finishing growing P10) were difficult to differentiate from birds that had completed moult, and it was not easy to tell whether inner primaries had completed growing or

not. Images were taken with a Canon 7D mark II SLR camera equipped with a Canon 500 mm f4 telephoto lens or Canon 5D mark IV with a 100–400 mm zoom lens. Moult intensity typically is reported as the number of primaries replaced at once (Rohwer & Rohwer 2013) or the raggedness value, which is the sum of the difference between the moult score of each growing primary and a fully grown score of 5 (Haukioja 1971, Bensch & Grahn 1993). However, both of these measures ignore the large differences in primary length/mass across the wing, especially in species such as petrels that have long, pointed wings (Dawson 2005). Accordingly, moult intensity also was estimated as the proportion of total feather length and mass being grown at once. The lengths and masses of blue petrel remiges (primaries and secondaries) were measured from the wings of birds killed by brown skuas (*Catharacta antarctica* Lesson) on Marion Island. All primary and secondary feathers were collected, dried (40°C for 24 h), weighed (to the nearest 1 mg) and measured (flattened feather length).

Results

During the ACE, 30 338 seabirds from 89 species were counted on 15 452 km of transects totalling 635 h over 75 days. With 2645 birds, the blue petrel was the third most abundant species counted after short-tailed shearwater (*Ardenna tenuirostris* Temminck, $n = 6835$; Ryan *et al.* 2017) and Salvin's prion (*Pachyptila salvini* Mathews, $n = \sim 3350$), with Antarctic prions (*Pachyptila desolata* Gmelin) and slender-billed prions (*Pachyptila belcheri* Mathews) also totalling > 2000 individuals. Despite their circumpolar range, blue petrels were patchily distributed along the ACE cruise track (Fig. 1). In the Indian Ocean sector (late December–mid-January), birds were seen around their breeding islands (Prince Edwards, Crozet and Kerguelen), extending east to 55°S, 105°E. In the Pacific Ocean sector (late January–February), they were seen from 72°S, 144°W to 62°S, 68°W off West Antarctica, and in the Atlantic Ocean sector (late February–March), a few birds were observed east of South Georgia and the South Sandwich Islands (Fig. 1).

Most blue petrels were counted in the Pacific Ocean sector (96.5%), with only 3.4% in the Indian Ocean sector and 0.1% in the Atlantic Ocean sector. Off West Antarctica, 95.6% were seen from 13 to 16 February in the Amundsen and western Bellinghousen seas between 71°S, 119°W and 67°S, 78°W (Fig. 2). The average density per hour over these four days was 0.62 ± 2.21 birds km^{-2} (range 0–14.5 birds km^{-2} , $n = 47$), with an average density per 10 min observation period of 3.8 ± 12.6 birds km^{-2} (range 0–88 birds km^{-2} , $n = 280$) due to the many large flocks seen on 13 February at 70°S, 115°W and on 14 February at 69°S, 103°W. The mean density

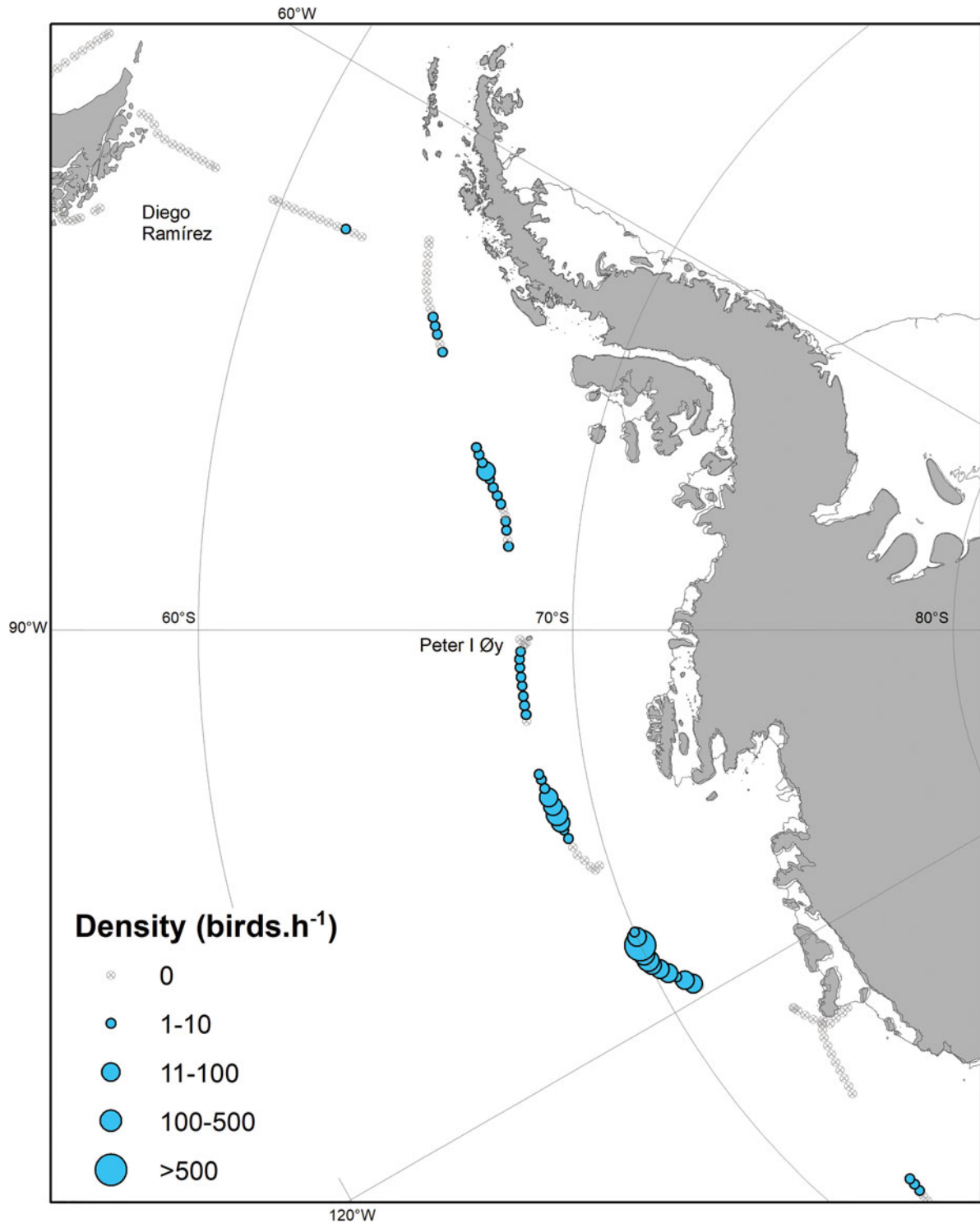


Fig. 2. Map of hourly blue petrel counts off West Antarctica from 9 to 18 February 2017.

on these two days, when 91.5% of all blue petrels were counted, was 1.16 ± 3.03 birds km^{-2} averaged hourly ($n=24$) and 7.0 ± 17.0 birds km^{-2} averaged per 10 min count ($n=144$). Crude extrapolation of the density estimates from 78–119°W gives a range of 50 000 (hourly

average density for a band 50 km wide) to 600 000 (10 min average density for a band 100 km wide) birds in this region. No blue petrels were seen north of 61.8°S as we approached the breeding colonies at Diego Ramirez and Cape Horn (Fig. 2).

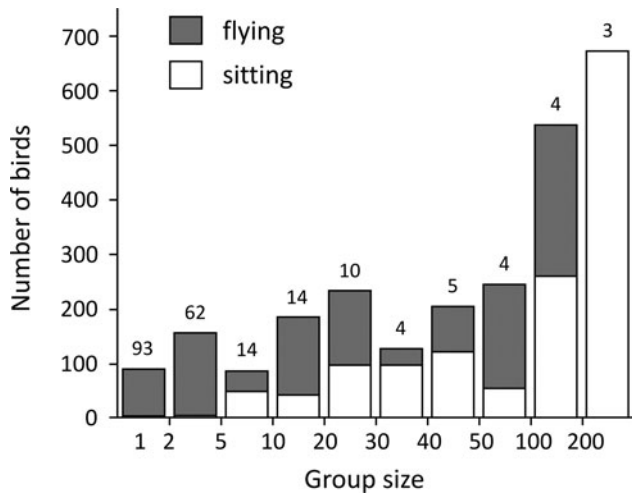


Fig. 3. Numbers of blue petrels in flocks of different sizes off West Antarctica from 9 to 18 February 2017, showing the proportion of birds sitting on the water. Numbers above each column are the number of flocks in each size group; note the uneven group size intervals.

Icebergs were regular throughout the area from 13 to 16 February (icebergs passed during 23% of 10 min count sections), but blue petrels avoided areas with pack ice (range 0–80% cover per 10 min observation period). Blue petrels were only observed in 1 out of 23 of the 10 min counts when pack ice was present (2 birds as we approached the pack off Peter 1 Øy) compared to 48% of counts without ice ($n = 257$, Fisher exact test $P = 0.002$). Sea temperature measurements over the four days ranged from -1.1 to 1.9°C , but blue petrels were

only observed from -0.7 to 0.9°C , with the largest flocks occurring at -0.3°C .

Most blue petrels off West Antarctica were encountered in large flocks of up to 300 individuals (Fig. 3). Overall, 55% of birds were sitting on the sea surface, but the proportion of sitting birds increased with group size (Fig. 3). Flocks on the water surface usually comprised only blue petrels, but they were occasionally joined by small numbers of Cape petrels (*Daption capense* L.; Fig. 4). Blue petrels often associate with prions at sea, but we only observed modest numbers of Antarctic prions and a few slender-billed prions in the eastern Bellingshausen Sea (15, 140 and 18 on 16–18 February, respectively, with 94% being Antarctic prions). Small numbers of blue petrels co-occurred with prions in nine of the 10 min count periods on 16–17 February, but there was no evidence of spatial co-occurrence on these days ($\chi^2 = 0.26$, $df = 1$, $P = 0.69$). Several small flocks of blue petrels (5–20 birds) were observed feeding, often in association with other birds (Cape and mottled petrels (*Pterodroma inexpectata* Forster) and southern fulmars (*Fulmarus glacialis* Smith)) or cetaceans (orcas (*Orcinus orca* L.) and humpback whales (*Megaptera novaeangliae* Borowski)), but there was no sign of feeding by the large flocks of birds sitting on the water.

The first blue petrels moulting wing feathers were observed on 11 January at 55°S , 96°E , towards the eastern edge of the observed range in the Indian Ocean sector. Of 22 birds seen on 11–12 January, 14 were in moult, replacing inner or central primaries. Approximately half of the birds off West Antarctica were also undergoing wing moult on 13–16 February, particularly in the large flocks



Fig. 4. Part of a large flock of blue petrels, with one Cape petrel (top left), at 70°S , 103°W off West Antarctica on 14 February 2017. Inset shows a blue petrel in flight moulting six inner primaries on its left wing, seven on its right wing, the corresponding primary coverts and all secondary greater coverts (photographs: P.G. Ryan).

Table I. The average (\pm SD) length and mass of blue petrel primary ($n = 13$) and secondary ($n = 3$) feathers.

Feather	Length (mm)	Mass (mg)
Primary 10	166.9 \pm 3.8	151.2 \pm 10.3
Primary 9	170.6 \pm 4.0	149.8 \pm 9.0
Primary 8	166.8 \pm 4.4	137.4 \pm 8.5
Primary 7	157.3 \pm 4.1	123.8 \pm 7.5
Primary 6	147.8 \pm 3.3	108.9 \pm 7.3
Primary 5	134.7 \pm 3.1	92.8 \pm 5.8
Primary 4	120.2 \pm 3.1	73.3 \pm 4.4
Primary 3	105.5 \pm 3.0	56.2 \pm 4.2
Primary 2	92.3 \pm 2.5	43.6 \pm 3.1
Primary 1	82.5 \pm 2.4	35.8 \pm 2.4
All primaries	1344.8 \pm 31.1	972.8 \pm 58.3
All secondaries	1202.0 \pm 21.7	399.7 \pm 19.9

resting on the water surface. None of the three birds seen in the Atlantic Ocean sector (5–9 March) was moulting its flight feathers.

Moult was often intense, with seven to eight primaries and their primary coverts growing on each wing, plus all of the greater secondary coverts (Fig. 4). It was possible to score the primary moults of 36 birds in one flock of ~300 birds photographed as it flushed on 14 February off West Antarctica. Of these, 16 (44%) retained 1–4 old outer primaries, at least 6 (17%) were growing the outer primary and the remainder apparently had completed the primary moult (although it was probable that some were still growing P10). It was clear that birds with as few as two old outer primaries were still growing their innermost primaries (i.e. they were shorter than the adjacent secondaries), but birds with only one old outer primary may have completed growth of the inner three to four primaries. The raggedness value of birds retaining 1–4 old primaries was 14–18, with no pattern related to moult progression. Despite the marked reduction in wing area (Fig. 4), such birds were capable of sustained flight, sometimes flying alongside the ship's bow for several minutes. Replacing 7–8 inner primaries at once is a substantial proportion of the total length (62–75%) and mass (55–69%) of the primaries (Table I). Expressed as a proportion of all remiges, these birds are simultaneously replacing 33–40% of the length and 39–49% of the flight feather mass (Table I). Replacing the corresponding primary greater coverts and all secondary greater coverts at the same time further adds to moult intensity.

Discussion

The rate of feather growth only increases slightly with body mass and feather size (Rohwer *et al.* 2009, de le Hera *et al.* 2012), which means that large birds take longer to replace their flight feathers, unless they increase the number of feathers replaced at once

(i.e. increase the intensity of moult; Bridge 2006, Rohwer & Rohwer 2013). A bird the size of a blue petrel typically grows its primaries at 4–6 mm per day (Rohwer & Rohwer 2013). If each primary was moulted sequentially, it would take at least 6 months to replace only the primaries, yet blue petrels replace all of their wing feathers in ~10 weeks between the end of the breeding season in January–February and their brief return to their colonies in April–May (Fugler *et al.* 1987, Chérel *et al.* 2016). They achieve this by having one of the most intense wing moults yet recorded (Bridge 2006).

Rohwer and Rohwer (2013) showed that moult intensity explains most of the variation in moult duration, with the average number of primaries grown at once varying from one to four among birds that retain the ability to fly while moulting. Some petrels grow four to six inner primaries at once (Bridge 2006), but blue petrels are exceptional in replacing up to eight primaries at once. Northern fulmars (*Fulmarus glacialis* L.) occasionally also have up to eight inner primaries growing at the same time, but such birds apparently lose the ability to fly (Warham 1996). The primaries are replaced in a simple descending wave, creating a very large gap in the wing area, which has a greater impact on flight ability than several smaller gaps (Hedenström & Sunada 1999). It is impressive that blue petrels with only two to three outer primaries can still fly. Although hummingbirds also achieve this feat (Chai 1997), some passerines that undergo very rapid moult become flightless (Haukioja 1971). In addition to replacing up to eight primaries at once, blue petrels also moult all of the greater secondary coverts, which facilitates the simultaneous moult of large numbers of secondaries later in the moult cycle. The greater secondary coverts are unusually long in petrels and albatrosses, and thus once grown, they reduce the wing gaps created by moulting of the secondaries.

Moulting petrels partially compensate for large moult gaps in the primaries by increasing the spread of the remaining primaries (Bridge 2006) and perhaps also the tail feathers (Fig. 4). However, it is not surprising that moulting blue petrels spend considerably more time sitting on the water (44–66%) than post-moult birds (7–19%; Chérel *et al.* 2016). Reducing wing area typically results in a reduction in the amount of time birds spend in flight (e.g. Carrascal & Polo 2006). The inverse relationship between moult duration and the amount of time moulting birds and blue petrels sit on the water presumably reflects differences in moult intensity between species (Chérel *et al.* 2016). Reduced flight ability during moult also increases the risk of predation (e.g. Lind 2001). We saw a blue petrel being closely pursued by a south polar skua (*Catharacta maccormicki* Saunders) for several minutes off West Antarctica. The outcome of this chase was not observed, but it is possible that predation risk by

skuas contributes to the flocking behaviour of moulting blue petrels.

It would be interesting to know whether blue petrels also moult their body plumage at the same time as they replace their flight feathers, because birds replacing body feathers experience higher thermal conductance due to reduced insulation (Murphy 1996). We might thus expect that body moult should not occur during wing moult, given the large amount of time moulting blue petrels spend sitting in cold water ($\sim 0^{\circ}\text{C}$). If body moult occurred gradually throughout winter, it would also spread the physiological cost of moult. However, very few blue petrels exhibit body moult in winter (Brown *et al.* 1986), whereas birds collected in January have extensive body moult coinciding with primary and secondary moult (Bierman & Voous 1950). Stable isotope ratios are similar in primary and body feathers (Cherel *et al.* 2016), suggesting that both sets of feathers moult at the same time. By comparison, prions show greater variability in the isotope signatures of body feathers than primaries, indicating that body moult is more protracted than wing moult (Cherel *et al.* 2016).

Moult is energetically demanding not only due to the costs of feather production, but also due to the necessity to maintain the tissues necessary for feather production (Lindström *et al.* 1993, Murphy 1996). Just as breeding birds can be categorized along a continuum from income to capital breeders (Jonsson 1997), the energy to support moult can derive from body stores ('capital' moulters) or from food ingested during moulting ('income' moulters). Penguins are an extreme example of the former strategy, as they fast ashore throughout most of their catastrophic moult, but many other birds also lose mass during moult, suggesting some contribution from stored energy reserves (e.g. Portugal *et al.* 2007). Adult blue petrels moult immediately after breeding, however, so they have little opportunity to accumulate energy and key nutrients prior to moulting, suggesting that they rely substantially on food obtained during moult (i.e. they are probably income moulters). As a result, they probably depend on a reliable food source to fuel their very intense moult (Cherel *et al.* 2016). Blue petrels are thought to target krill and other macrozooplankton while moulting, when foraging occurs mostly at night (Cherel *et al.* 2016), although some foraging does occur during the day (Wanless & Harris 1988, this study).

Adult blue petrels from Kerguelen and South Georgia mainly moult between $55\text{--}65^{\circ}\text{S}$ and $20^{\circ}\text{W}\text{--}30^{\circ}\text{E}$ (Cherel *et al.* 2016, R.A. Phillips, personal communication 2019), at the same time and place where slender-billed prions from the world's two largest colonies, Kerguelen and the Falklands, moult (Quillfeldt *et al.* 2015, Cherel *et al.* 2016). Large numbers of Kerguelen petrels (*Aphrodroma brevirostris* Lesson) also moult in this area

in February (P.G. Ryan, personal observation). We encountered surprisingly few blue petrels in the Atlantic Ocean sector of the ACE in early March 2017 (Fig. 1), possibly because our track was north of their main moulting area. However, we did count some 1500 slender-billed prions (72% of all birds of this species seen during the ACE), 700 Antarctic prions (26%) and 150 Kerguelen petrels (63%) between 60°S , 25°W and 54°S , 03°E from 8 to 11 March, with all of the slender-billed prions on 9–10 March between 59°S , 15°W and 57°S , 04°W . Most of the slender-billed prions, some of the Antarctic prions and a few Kerguelen petrels were in moult (some just starting inner primaries and others nearly complete with just the outer tail still growing). All of these species presumably exploit a late summer abundance of zooplankton, principally Antarctic krill (*Euphausia superba* Dana), making this region a key foraging area for moulting seabirds (Cherel *et al.* 2016).

Our observations identify the seas off West Antarctica as a second moult hotspot for blue petrels. Previous seabird studies also have reported blue petrels in the Amundsen and Bellinghousen seas in February–March (Zink 1981, Wanless & Harris 1988, Ainley *et al.* 1998, Ropert-Coudert *et al.* 2014, B. Raymond, personal communication 2019). It is difficult to estimate the numbers of petrels moulting in this region, because we do not know their latitudinal extent. The ACE cruise track was selected to be as short as possible without venturing into dense pack ice and thus mostly remained just north of the pack, where bird densities might be particularly high (e.g. Ainley *et al.* 1998, Ribic *et al.* 2011). However, we may have underestimated the western limit of the moult area, because we saw small numbers of birds on 9 February at $71\text{--}72^{\circ}\text{S}$ and $142\text{--}144^{\circ}\text{W}$, before heading farther south to the Mount Siple area (Fig. 2). Wanless & Harris (1988) observed large flocks as far west as 165°W in early February. However, even relatively conservative extrapolation over the area from 120 to 80°W suggests a population of $10^5\text{--}10^6$ blue petrels off West Antarctica in late summer (see the Results section for details). These birds almost certainly breed at Diego Ramirez, the closest colony to this moult area, which has a population of ~ 1.35 million pairs (Lawton *et al.* 2006), representing more than half the world's population (Dilley *et al.* 2017). Blue petrels breeding at the Prince Edward Islands and Iles Crozetts have not been tracked, but these islands lie between Ile Kerguelen and South Georgia (Fig. 1), and given the fact that adults return to their colonies in April–May, adults almost certainly moult south of Africa, together with birds from South Georgia and Kerguelen.

During winter, blue petrels disperse widely across the Pacific Ocean (Szijj 1967, Navarro *et al.* 2015) and more broadly across the Southern Ocean (Marchant & Higgins 1990, Cherel *et al.* 2016). By relying on a few

relatively small areas in which to moult, blue petrels are potentially susceptible to local environmental change and subsequent food chain impacts. The marine ecosystems west of the Antarctic Peninsula are experiencing some of the fastest and most extreme impacts of climate change on Earth (Meredith & King 2005, Ducklow *et al.* 2007), with changes in pack ice and krill abundance driving changes in seabird communities (Ainley *et al.* 2010, Trivelpiece *et al.* 2011). These changes may also have adverse consequences for the world's most important population of blue petrels, and trends in the breeding population on Diego Ramirez should be assessed.

Acknowledgements

We dedicate this paper to the memory of David Walton, chief scientist of the ACE cruise, who delighted in the diversity of Antarctic life. Richard Phillips, Ben Raymond and Yan Ropert-Coudert kindly provided additional information, and Giuseppe Suaria provided sea temperature data. The ACE was a research cruise of the Swiss Polar Institute, supported by funding from the ACE Foundation.

Author contributions

PGR wrote the paper, JRL prepared the maps and all authors conducted field observations and commented on the draft paper.

References

- AINLEY, D.G., JACOBS, S.S., RIBIX, C.A. & GAFNEY, I. 1998. Seabird distribution and oceanic features of the Amundsen and southern Bellingshausen seas. *Antarctic Science*, **10**, 111–123.
- AINLEY, D.G., RUSSELL, J., JENOUVRIER, S., WOHLER, E., LYVER, P.O., FRASER, W.R. & KOOYMAN, G.L. 2010. Antarctic penguin response to habitat change as Earth's troposphere reaches 2°C above preindustrial levels. *Ecological Monographs*, **80**, 49–66.
- BENSCH, S. & GRAHN, M. 1993. A new method of estimating individual speed of molt. *Condor*, **95**, 305–315.
- BIERMAN, W.H. & VOOUS, K.H. 1950. Birds observed and collected during the whaling expeditions of the 'Willem Barendsz' in the Antarctic, 1946–1947 and 1947–1948. *Ardea*, **37**(Suppl.), 1–121.
- BRIDGE, E.S. 2006. Influences of morphology and behavior on wing-molt strategies in seabirds. *Marine Ornithology*, **34**, 7–19.
- BROWN, R.S., NORMAN, F.I. & EADES, D.W. 1986. Notes on blue and Kerguelen petrels found beach-washed in Victoria, 1984. *Emu*, **86**, 228–238.
- CARRASCAL, L.M. & POLO, V. 2006. Effects of wing area reduction on winter body mass and foraging behaviour in coal tits: field and aviary experiments. *Animal Behaviour*, **72**, 663–672.
- CHAI, P. 1997. Hummingbird hovering energetics during moult of primary flight feathers. *Journal of Experimental Biology*, **200**, 1527–1536.
- CHEREL, Y., BOCHER, P., TROUVÉ, C. & WEIMERSKIRCH, H. 2002. Diet and feeding ecology of blue petrels *Halobaena caerulea* at Iles Kerguelen, Southern Indian Ocean. *Marine Ecology Progress Series*, **228**, 283–299.
- CHEREL, Y., PHILLIPS, R.A., HOBSON, K.A. & MCGILL, R.A.R. 2006. Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. *Biology Letters*, **2**, 301–303.
- CHEREL, Y., QUILLFELDT, P., DELORD, K. & WEIMERSKIRCH, H. 2016. Combination of at-sea activity, geolocation and feather stable isotopes documents where and when seabirds moult. *Frontiers in Ecology and Evolution*, **4**, 3.
- DAWSON, A. 2005. The scaling of primary flight feather length and mass in relation to wing shape, function and habitat. *Ibis*, **147**, 283–292.
- DE LA HERA, I., DESANTE, D.F. & MILÁ, B. 2012. Feather growth rate and mass in Nearctic passerines with variable migratory behavior and molt pattern. *Auk*, **129**, 222–230.
- DILLEY, B.J., DAVIES, D., CONNAN, M., SCHRAMM, M. & RYAN, P.G. 2017. The distribution and abundance of blue petrels (*Halobaena caerulea*) breeding at subantarctic Marion Island. *Emu*, **117**, 222–232.
- DUCKLOW, H.W., BAKER, K., MARTINSON, D.G., QUETIN, L.B., ROSS, R.M., SMITH, R.C., *et al.* 2007. Marine pelagic ecosystems: the West Antarctic Peninsula. *Philosophical Transactions of the Royal Society*, **B362**, 67–94.
- FUGLER, S.R., HUNTER, S., NEWTON, I.P. & STEELE, W.K. 1987. Breeding biology of blue petrels *Halobaena caerulea* at the Prince Edward Islands. *Emu*, **87**, 103–110.
- GRIFFITHS, A.M. 1982. Reactions of some seabirds to a ship in the Southern Ocean. *Ostrich*, **53**, 228–235.
- HAUKIOJA, E. 1971. Flightlessness in some moulting passerines in northern Europe. *Ornis Fennica*, **48**, 101–116.
- HEDENSTRÖM, A. & SUNADA, S. 1999. On the aerodynamics of moult gaps in birds. *Journal of Experimental Biology*, **202**, 67–76.
- JONSSÖN, K.I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*, **78**, 57–66.
- LAWTON, K., ROBERTSON, G., KIRKWOOD, R., VALENCIA, J., SCHLATTER, R. & SMITH, D. 2006. An estimate of population sizes of burrowing seabirds at the Diego Ramirez archipelago, Chile, using distance sampling and burrow-scoping. *Polar Biology*, **29**, 229–238.
- LIND, J. 2001. Escape flight in moulting tree sparrows (*Passer montanus*). *Functional Ecology*, **15**, 29–35.
- LINDSTRÖM, Å., VISSER, G.H. & DAAN, S. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. *Physiological Zoology*, **66**, 490–510.
- MARCHANT, S. & HIGGINS, P.J. 1990. *Handbook of Australian, New Zealand and Antarctic birds, Vol. 1: Ratites to ducks*. Melbourne: Oxford University Press.
- MEREDITH, M.P. & KING, J.C. 2005. Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophysical Research Letters*, **32**, 10.1029/2005GL024042.
- MURPHY, M.E. 1996. Energetics and nutrition of molt. In CAREY, C., ed. *Avian energetics and nutritional ecology*. Berlin: Springer, 158–198.
- NAVARRO, J., CARDADOR, L., BROWN, R. & PHILLIPS, R.A. 2015. Spatial distribution and ecological niches of non-breeding planktivorous petrels. *Scientific Reports*, **5**, 12164.
- PHILLIPS, R.A., BEARHOP, S., MCGILL, R.A.R. & DAWSON, D.A. 2009. Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. *Oecologia*, **160**, 795–806.
- PORTUGAL, S.J., GREEN, J.A. & BUTLER, P.J. 2007. Annual changes in body mass and resting metabolism in captive barnacle geese (*Branta leucopsis*): the importance of wing moult. *Journal of Experimental Biology*, **210**, 1391–1397.
- QUILLFELDT, P., CHEREL, Y., MASELLO, J.F., DELORD, K., MCGILL, R.A.R., FURNESS, R.W., *et al.* 2015. Half a world apart? Overlap in nonbreeding distributions of Atlantic and Indian Ocean thin-billed prions. *PLoS ONE*, **10**, e0125007.

- RIBIC, C.A., AINLEY, D.G., FORD, G., FRASER, W.R., TYNAN, C.T. & WOEHLE, E.J. 2011. Water masses, ocean fronts, and the structure of Antarctic seabird communities: putting the eastern Bellingshausen Sea in perspective. *Deep Sea Research II*, **58**, 1695–1709.
- ROHWER, V.G. & ROHWER, S. 2013. How do birds adjust the time required to replace their flight feathers? *Auk*, **130**, 699–707.
- ROHWER, S., RICKLEFS, R.E., ROHWER, V.G. & COPPLE, M.M. 2009. Allometry of the duration of flight feather molt in birds. *PLoS Biology*, **7**, e1000132.
- ROPERT-COUDERT, Y., HINDELL, M.A., PHILLIPS, R., CHARRASSIN, J.-B., TRUELLE, L. & RAYMOND, B. 2014. Biogeographic patterns of birds and mammals. In DE BROUWER, C., KOUUBI, P., GRIFFITHS, H.J., RAYMOND, B., UDEKEM D'ACOSTA, C. D., VAN DE PUTTE, A.P., *et al.* eds. *Biogeographic Atlas of the Southern Ocean*. Cambridge: Scientific Committee on Antarctic Research, 364–387.
- RYAN, P.G., AVERY, G., ROSE, B., ROSS, G.J.B., SINCLAIR, J.C. & VERNON, C.J. 1989. The Southern Ocean seabird irruption to South African waters during winter 1984. *Cormorant*, **17**, 41–55.
- RYAN, P.G., DILLEY, B.J., JONES, C. & BOND, A. 2015. Blue petrels breeding on Gough Island. *Ostrich*, **89**, 193–194.
- RYAN, P.G., LE BOUARD, F. & LEE, J. 2017. Westward range extension of short-tailed shearwaters in the Southern Ocean. *Polar Biology*, **40**, 2323–2327.
- SZIJ, L.J. 1967. Notes on the winter distribution of birds in the western Antarctic and adjacent Pacific waters. *Auk*, **84**, 366–378.
- TASKER, M.L., JONES, P.H., DIXON, T.J. & BLAKE, B.F. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. *Auk*, **101**, 567–577.
- TRIVELPIECE, W.Z., HINKE, J.T., MILLER, A.K., REISS, C.S., TRIVELPIECE, S.G. & WATTERS, G.M. 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 7625–7628.
- WANLESS, S. & HARRIS, M.P. 1988. Seabird records from the Bellingshausen, Amundsen and Ross seas. *British Antarctic Survey Bulletin*, no. 81, 87–92.
- WARHAM, J. 1996. *The behaviour, population biology and physiology of the petrels*. London: Academic Press.
- ZINK, R.M. 1981. Observations of seabirds during a cruise from Ross Island to Anvers Island, Antarctica. *Wilson Bulletin*, **93**, 1–20.