



## Variation among species and populations in bill shape and size in three planktivorous petrels

Maria Laranjeiro, Marc Farré, Richard Phillips, Petra Quillfeldt, Francesco Bonadonna, Charlene Gémard, Maximiliano Daigre, Cristián Suazo, Christophe Barbraud, Joan Navarro

### ► To cite this version:

Maria Laranjeiro, Marc Farré, Richard Phillips, Petra Quillfeldt, Francesco Bonadonna, et al.. Variation among species and populations in bill shape and size in three planktivorous petrels. *Marine Biology*, 2022, 169 (2), pp.24. 10.1007/s00227-021-04014-7 . hal-03652996

**HAL Id: hal-03652996**

**<https://hal.science/hal-03652996>**

Submitted on 8 Aug 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

**Variation among species and populations in bill shape and size in three planktivorous petrels**

Maria I. Laranjeiro<sup>1,2,\*</sup>, Marc Farré<sup>1,3</sup>, Richard A. Phillips<sup>4</sup>, Petra Quillfeldt<sup>5</sup>, Francesco Bonadonna<sup>6</sup>, Charlene Gémard<sup>6</sup>, Maximiliano Daigre<sup>7</sup>, Cristian G. Suazo<sup>5</sup> & Joan Navarro<sup>1</sup>

<sup>1</sup>Institut de Ciències del Mar (ICM-CSIC), Passeig Marítim de la Barceloneta 37-49, 08003 Barcelona, Spain.

<sup>2</sup>University of Coimbra, MARE – Marine and Environmental Sciences Centre, Department of Life Sciences, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal.

<sup>3</sup>Instituto Español de Oceanografía, Centre Oceanogràfic de les Balears, Moll de Ponent, s/n, 07015, Palma, Spain.

<sup>4</sup>British Antarctic Survey, Natural Environment Research Council, High Cross, Cambridge, United Kingdom.

<sup>5</sup>Department of Animal Ecology and Systematics, Justus Liebig University Giessen, Heinrich-Buff-Ring 26, 35392 Giessen, Germany.

<sup>6</sup>CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France.

<sup>7</sup>Facultad de Ciencias de la Vida, Universidad Andrés Bello, Santiago, Chile.

\*Corresponding author: Maria Inês Laranjeiro

E-mail address: [mariaines.santos@outlook.pt](mailto:mariaines.santos@outlook.pt)

ORCID: 0000-0001-9884-4743

## Abstract

Morphological variation in biological structures may be driven by genetic and environmental factors, such as inter and intraspecific competition for resources. In seabirds, although the bill is also involved in vocalization, olfaction, sexual selection and defence, the main drivers of high morphological plasticity in bill size and shape appear to relate primarily to diet and thus to niche differentiation. Here, we combined geometric morphometrics and comparisons of linear measurements as a precise tool for measuring shape variation in anatomical features, to investigate the differences among species and populations (island groups) in bill shape of three abundant planktivorous petrels (Antarctic prion *Pachyptila desolata*, blue petrel *Halobaena caerulea* and thin-billed prion *Pachyptila belcheri*). Fieldwork was carried out in South Georgia (54°0'S, 38°3'W), Falkland Islands (51°42'S, 57°51'W), Diego Ramírez Islands (56°31'S, 68°44'W) and Kerguelen Islands (49°20'S, 69°20'E), across 2010-2021. As expected, the bills of Antarctic prions were more robust and shorter, appropriate for filtering large amounts of small prey. Blue petrels and thin-billed prions had narrower and longer bills, effective for catching and tearing large single prey. Also, Antarctic prions and blue petrels from Kerguelen had longer and narrower bills than conspecifics from other colonies, which could potentially be explained by geographic variation in diet. In conclusion, prey availability and diversity appear to be important factors influencing variation in bill morphology. This study highlights the utility of geometric morphometrics for investigating bill shape variation in seabirds. Nevertheless, further studies are needed to better understand selective pressures leading to morphological displacement of biological structures.

## Introduction

Morphological variation is known to be shaped by abiotic and biotic conditions, and their interaction. For instance, genes provide the potential for a particular phenotype, but environmental factors determine how this potential is expressed through selective pressures (Grant and Grant 1989; Aldrich and James 1991). In seabirds, selective pressures can be related to environmental conditions, predation, disease, and interspecific and intraspecific competition for resources such as food or nest sites (Buckley and Buckley 1980; Warham 1996). Suitable breeding sites are limited in number and hence multiple species of seabirds often breed in sympatry (Warham 1996; Brooke 2004). As seabirds are often very abundant, and foraging ranges subject to the central-place constraint during breeding (i.e., the need to return to incubate eggs or feed chicks), interspecific and intraspecific competition around colonies is particularly intense (Lewis et al. 2001; Phillips et al. 2005; Wakefield et al. 2014). Seabirds have therefore evolved diverse ecological strategies which allow coexistence, including segregation of foraging areas, behaviour or diet (Quillfeldt et al. 2013; Navarro et al. 2013; Corman et al. 2016), as well as allochrony to reduce overlap in the periods of higher demand for prey, including chick-rearing and moulting (Cherel et al. 2016; Jones et al. 2020). Selective pressures differ between regions and thus morphological variation might reflect adaption to local conditions in different populations (i.e., breeding at different island groups) of the same species (Mayr and Diamond 2001; Bull et al. 2004; Bull 2006).

Common examples of variation among birds in specific morphological traits include the shape and size of feeding structures such as the bill. This is widely established, for example, in different species of Darwin's finches (Coerebinae), in which bill morphology is associated with interspecific variability in foraging strategies (Boag and

Grant 1981; Kleindorfer et al. 2006; Foster et al. 2008). Similar patterns occur in boobies (*Sula* spp.) in the Pacific, and little penguins (*Eudyptula minor*) in south Australia, in which wing and bill size differ between colonies in relation to prey selection and competition with sympatric species, and with variation in environmental conditions, respectively (Colombelli-Négrel 2016; Van Oordt et al. 2018). In seabirds, the bill is of great ecological and biological importance since it provides essential functions related to food intake, vocalization, sexual selection or defensive and territorial behaviour (Warham 1996; Nebel 2005; Gémard et al. 2019). Given its versatile role, the bill is subject to strong selective forces and it shows wide morphological plasticity and divergence (Schluter 2000; Van Oordt et al. 2018). Many studies have pointed out the association between bill shape and size, and diet and niche differentiation (Nebel et al. 2005; Bull 2006; Trallero et al. 2019), presumably driven by interspecific competition and natural selection (Grémillet et al. 2004; Navarro et al. 2013; Corman et al. 2016).

In spite of sometimes wide geographic separation between colonies, breeding populations of seabirds often show limited genetic structure (Moum and Árnason 2001; Wojczulanis-Jakubas et al. 2014). This applies to Antarctic prions (*Pachyptila desolata*) and blue petrels (*Halobaena caerulea*) breeding at South Georgia and Kerguelen Islands, even though the island groups are far apart and the populations exploit different trophic niches (Quillfeldt et al. 2017). Therefore, morphological variation among individuals and populations in the bill might be related to environmental factors such as relative availability of different prey (Croxall and Prince 1980). Based on previous studies, the diet of Antarctic prions at South Georgia is composed mainly of small copepods and Antarctic krill *Euphausia superba*, followed by the amphipod *Themisto gaudichaudii*, small fish and cephalopods (Prince 1980; Croxall et al. 1997; Reid et al.

1997). At Kerguelen, although crustaceans are also important, Antarctic prion prey mainly on *T. gaudichaudii*, and only rarely on Antarctic krill and copepods (Cherel et al. 2002b). Blue petrels at South Georgia feed mostly on crustaceans and small myctophids, whereas conspecifics from Kerguelen also catch larger fish such as *Paradiplospinus gracilis* and consume substantial numbers of cephalopods (Prince 1980; Cherel et al. 2002a). The targeting of distinct prey could therefore drive morphological differences between these colonies. Cherel et al. (2002b) suggested that while other crustaceans can be caught individually, large numbers of small copepods might be ingested at once by Antarctic prions through filter feeding. Moreover, Prince (1980) suggested that long and narrow bills in blue petrels could be indicative of surface dipping, and tearing of large single prey. Accordingly, the bill, as the anatomical structure most directly related to diet, might be the key to detecting phenotypical variation within these genetically similar populations.

Geometric morphometric analyses represents a precise tool for measuring shape variation in anatomical features (Adams et al. 2013), providing insights into relationships between morphological structures and ecological strategies (Adams 1999; Zelditch et al. 2004; Farré et al. 2016b), including in seabirds (Foster et al. 2008; Navarro et al. 2009; Berns and Adams 2010; Trallero et al. 2019). With this approach, it is possible to accurately compare biological form in statistical terms, while accounting for the non-shape variation (size, orientation, deformation etc.) (Adams et al. 2004; Zelditch et al. 2004). In a previous study (Trallero et al. 2019), we quantified differences among species and sexes in bill morphology of Antarctic prions, blue petrels, and two species of diving petrels (*Pelecanoides* spp.) all breeding at South Georgia, South Atlantic. Here, we extend this by investigating the differences in bill shape among populations of three abundant planktivorous petrels (Antarctic prion, blue

petrel and thin-billed prion *Pachyptila belcheri*) which have circumpolar distributions in the Southern Ocean. Although diet proportions are similar in terms of prey classes, the three species differs in terms of the main crustacean species consumed (Prince 1980; Cherel et al. 2002a,b) which might explain the striking spatial and ecological segregation among species and populations (Quillfeldt et al. 2013, 2015; Navarro et al. 2013, 2015). Hence, our initial hypothesis was that these differences in foraging ecology would be reflected in bill-character displacement. While species differences have been described with traditional methods, geometric morphometric analyses can reveal subtler contrasts and offers a precise tool to analyse less obvious differences, as may be found between populations.

## **Material and Methods**

### *Study species*

The work focused on three monogamous, small-bodied procellariiform species: Antarctic prion, blue petrel and thin-billed prion. All can feed 100s or 1000s of km from the colony and spend most of their time at sea (Quillfeldt et al. 2013, 2014). They breed in burrows or rock crevices in dense colonies and show the typical procellariiform pattern of single-egg clutch and slow chick development (Warham 1996; Brooke 2004). Both the Antarctic prion and blue petrel feed mainly on crustaceans, and small fish (myctophids) (Table 1), but the particular prey species vary, presumably related to relative availability in the environment (Ainley et al. 1992). Similarly, thin-billed prions prey mostly on crustaceans (amphipods and krill), myctophid fish and squid (Table 1).

### *Study sites*

Fieldwork was conducted in breeding colonies at four sub-Antarctic island groups >1000 km apart (Fig. 1): Bird Island, South Georgia (54°0'S, 38°3'W), New Island, Falkland Islands (Malvinas) (51°42'S, 57°51'W), Gonzalo Island, Diego Ramírez Islands (56°31'S, 68°44'W) and Île Verte, Kerguelen Islands (49°20'S, 69°20'E). Antarctic krill are particularly abundant around and to the south of South Georgia (Atkinson et al. 2001). Prey availability for seabirds is high in the waters surrounding the Falkland Islands, which are characterised by low temperatures, strong winds and turbulent waters (Armstrong and Forbes 1997). At Diego Ramírez, temperatures are low and there are strong westerly winds and high annual rainfall (Schlatter & Riveros, 1997). The Kerguelen Islands are also in a region characterized by low temperatures and high winds, with strong upwellings (Zhou et al. 2014). Estimated breeding populations in each island group are as follows: Antarctic prion, South Georgia (22 million pairs); blue petrel, South Georgia (70 000 pairs); Antarctic prion, Kerguelen (2-3 million pairs); blue petrel, Kerguelen (100-200,000 pairs); thin-billed prion, New Island, Falkland Islands (Malvinas) (2 million pairs); blue petrel, Diego Ramírez (1.35 million pairs) (Prince and Croxall 1983; Weimerskirch et al. 1989; Schlatter and Riveros 1997; Catry et al. 2003; Barbraud and Delord 2006; Lawton et al. 2006).

#### *Sampling and morphological data acquisition*

During the breeding period, a total of 60 Antarctic prions and 29 blue petrels were sampled at Bird Island (November 2010 – February 2011); 54 Antarctic prions and 37 blue petrels at Île Verte (December 2018 – January 2019), 29 blue petrels at Gonzalo Island (November 2020 – January 2021) and 27 thin-billed prions at New Island (February 2019). For each individual, digital pictures were taken of the right profile and dorsal view of the bill using a compact digital camera in a consistent orientation: the bill



was supported using a wooden board with a ruler underneath for scale, and the camera lens was always perpendicular to the bill surface. Any pictures that were not standardized in this way were excluded from morphological analyses. In addition, three biometric measurements were taken in the field: maximum bill depth, bill depth at nares and culmen length as shown in Trallero et al. (2019). All measurements were made using digital callipers ( $\pm 0.1$  mm) (Fig. 2).

### *Bill shape analysis*

Characterization and assessment of variability in bill shape were performed using geometric morphometric methods (Rohlf and Marcus 1993; Zelditch et al. 2004). A total of 10 landmarks (fixed homologous points) in dorsal pictures (Tokita et al. 2017; Trallero et al. 2019) and 11 landmarks and 3 semilandmarks (mobile non-homologous points) in profile pictures (Navarro et al. 2009; Militão et al. 2014; Trallero et al. 2019) were used to define the overall shape of bill and nares (Fig. 2, Table 2). Landmarks and semilandmarks coordinates were digitized and transformed into geometric data using the tpsDig2 v.2.31 (Rohlf 2017), creating a metric map for each individual. A Generalized Procrustes Analysis (GPA) was then applied, using tpsRelw v.1.70 (Rohlf 2019). GPA compares all the landmark configurations removing distortions not related to shape, translating all configurations to a common centroid position, scaling them to the unit centroid size and rotating them to minimise the distances between corresponding landmarks (Adams et al. 2004; Zelditch et al. 2004). Next, a consensus configuration was obtained by averaging the spatial coordinates of all landmarks using a thin-plate spline procedure. The comparison of each configuration with this consensus form allows the shape deformation variables (relative warps, RWs) to be extracted for each individual. Each RW represents a specific set of morphological characteristics, and

their comparison allows the potential variation in shape of analysed objects to be visualised (Rohlf and Marcus 1993; Zelditch et al. 2004). Thus, the values of RWs were plotted spatially (generating a morphospace) to compare individuals according to morphological features and axis orientation. Only the first two RWs were used to create morphospaces as they represented a sufficiently high percentage of total morphological variance (Table 3), for the profile (60.27%) and dorsal (72.07%) perspectives, respectively (Farré et al. 2016a; Trallero et al. 2019). The morphospaces were built using PAST v.3.26 (Paleontological Statistics software package, Hammer et al. 2001).

#### *Statistical analysis*

Bill size (maximum bill depth, bill depth at nares and culmen length) and shape (using the RW1 and RW2 values of the profile and dorsal views) were compared among species and populations using Kruskal-Wallis and Mann-Whitney U tests, with species and island group as fixed factors. Sex was not included as a factor because it was unknown for the samples from some sites. Moreover, the study species are considered to be sexually monomorphic (Warham 1990), the differences between sexes in bill size and shape of Antarctic prions and blue petrels are very slight (Trallero et al. 2019), there are no significant sex differences in foraging strategies (Quillfeldt et al. 2008; Phillips et al. 2011; Cherel et al. 2014), and we had no reason to expect biased sex ratios during sampling. Data were tested for normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test). These analyses were performed using R 3.5.0 (R Core Team 2018).

## **Results**

### *Interspecific differences in bill morphology*

There were significant differences in bill size (all measurements) and shape of both profile and dorsal views among the three species (Tables 4 and 5). This included clear interspecific differences in profile shape (Fig. 3). Species segregated along the horizontal axis (RW1, representing 39.12% of the total morphological variability) separating individuals by shape of nares, length of *culminicorn* and size of *maxillary unguis* (Fig. 3): specimens with more triangular nares, longer *culminicorn* and smaller *maxillary* and *mandibular unguis* showed positive values (Antarctic prions); specimens with more rectangular nares, shorter *culminicorn* and proportionally bigger *maxillary* and *mandibular unguis* (blue petrels) showed negative values; and thin-billed prions showed intermediate (near to zero) values. The vertical axis (RW2, 21.15% of the total morphological variation) differentiated individuals by bill depth, and shape of *maxillary unguis* (Fig. 3): most of the blue petrels and Antarctic prions had deeper bill and sharper *maxillary unguis*, with higher values and located towards the positive extreme, and those with less deep bills and more rounded *maxillary unguis* showed lower values in the negative extreme (thin-billed prions).

Differences in bill shape among species were also observed in the dorsal perspective (Fig. 4), although less so than in the profile view. The horizontal axis (RW1) explained a high proportion of the total morphological variability (45.52%), grouping individuals by width and length of bill, length of nares and length of *maxillary unguis* (Fig. 4): birds with wider and shorter bills, shorter nares and shorter *maxillary unguis* tended to the positive extreme (Antarctic prions), and those with narrower and longer bills, longer nares and longer *maxillary unguis* to the negative extreme (blue petrels and thin-billed prions). The vertical axis (RW2, 26.55% of the total morphological variability) differentiated specimens by width of bill basis, shape of *culminicorn* and size of *maxillary unguis* (Fig. 4): birds with wider bill basis, longer and narrower *culminicorn*

and smaller *maxillary unguis* were positioned towards the positive extreme (most Antarctic prions) and those with narrower bill basis, shorter and wider *culminicorn* and bigger *maxillary unguis* had more negative RW2 values (mostly blue petrels). Thin-billed prions showed intermediate (near to zero) values.

#### *Differences in bill morphology between populations*

There were significant differences in bill size and in both profile and dorsal-view bill shape between populations of Antarctic prions and blue petrels at different island groups (Tables 4 and 5). Antarctic prions and blue petrels from South Georgia had a bigger maximum bill depth than those breeding at Kerguelen (Tables 4 and 5), and blue petrels from Diego Ramírez had bigger maximum bill depth than those from South Georgia and Kerguelen (Tables 4 and 5). Antarctic prions from South Georgia had longer culmens than at Kerguelen, and blue petrels at Diego Ramírez had shorter culmens than at South Georgia and Kerguelen (Tables 4 and 5). In profile view, there were differences among populations of the sympatric species (blue petrel and Antarctic prion) (Fig. 3). Between-population morphological variation was significant in both axes (Tables 4 and 5). Antarctic prions from Kerguelen had more rectangular nares, shorter *culminicorn* and a bigger *maxillary* and *mandibular unguis* than at South Georgia (lower RW1 values, Fig. 3). Blue petrels from Kerguelen (higher RW1 values) had slightly more triangular nares, longer *culminicorn* and smaller *maxillary* and *mandibular unguis* than at South Georgia and Diego Ramírez (Fig. 3). Also, both Antarctic prions and blue petrels from South Georgia had deeper bills and sharper *maxillary unguis* (higher RW2 values) than birds from other conspecific populations (Fig. 3).

Dorsal shape variability between populations was more apparent for Antarctic prions than blue petrels. Most birds from South Georgia and Diego Ramírez (blue petrel only)

had wider and shorter bills, as well as shorter nares and *maxillary unguis*, than conspecifics at Kerguelen (higher RW1 values, Fig. 4). Most Antarctic prions and blue petrels from Kerguelen had wider bills at the base, longer and narrower *culminicorn* and smaller *maxillary unguis* (higher RW2 values, Fig. 4) than conspecifics at Diego Ramírez (blue petrels) and South Georgia.

## Discussion

Using geometric morphometrics, we found significant differences among species and populations (island groups) in bill morphology of three planktivorous petrels. Specifically, Antarctic prions have more robust and shorter bills with shorter nares, while both blue petrels and thin-billed prions have slenderer and elongated bills, with longer nares. The Antarctic prions from Kerguelen have longer and narrower bills, and longer nares, than conspecifics from South Georgia. Overall, blue petrels from South Georgia and Diego Ramírez Islands had wider and shorter bills, with shorter nares, than conspecifics from Kerguelen Islands.

As the main function of the bill in seabirds is for foraging, niche differentiation could presumably be the main driver of the interspecific and between-population segregation in bill shape found in the present study. Antarctic prions have smaller but more robust bills than blue petrels and thin-billed prions. Antarctic prions feed mainly on crustaceans, including small copepods (see diet review in Table 1) and use a hydroplaning, surface-filtration technique to capture very large numbers of these abundant but small prey (Croxall and Prince 1980; Harper 1987; Warham 1990). These strategies consist of sitting on the water, or swimming with the head below the surface and filtering seawater through the palatal lamellae (a specialized adaptation for filter-feeding on small copepods) that line the interior edge of the upper mandible (Prince 1980; Warham 1990). We hypothesise that a wide and deep bill is particularly adapted

to this feeding strategy because it allows filtering of a greater volume of water, thus maximizing the number of small copepods that can be ingested at one time. Blue petrels and thin-billed prions, on the other hand, have narrower and longer bills that lack palatal lamellae. Although they also feed mostly on crustaceans, copepods are rare or absent, and they consume a higher percentage of small fish and squid; this applies particularly to thin-billed prions during incubation (Quillfeldt et al. 2010), compared with Antarctic prions (Table 1). The foraging strategy of blue petrels mainly involves dipping while in flight and selection of single, large prey items (Croxall and Prince 1980; Prince 1980). Their long and narrow bills are more well adapted for quick movements and catching, and may thus allow them to seize and tear quicker, more slippery and larger prey (fish or squid) that cannot be ingested whole (Harper 1987; Warham 1990).

The morphological segregation of bill morphology observed between populations from Kerguelen and South Georgia might be also related to prey selection. At South Georgia, Antarctic prions consume on large numbers of small copepods, along with Antarctic krill (Table 1), and the short but deeper bills are potentially better adapted for filter-feeding (Croxall and Prince 1980; Prince 1980; Warham 1990; Cherel et al. 2002b). In contrast, the diet of Antarctic prions at Kerguelen is mainly composed of hyperiid amphipods, primarily *T. gaudichaudii*, which are larger than copepods and are caught mostly in pelagic waters (Table 1). This would explain why the bills of Antarctic prions at Kerguelen are longer and narrower, thus more adapted for the capture of single prey items. Blue petrels from South Georgia feed mainly on Antarctic krill and small myctophids (length range:  $\approx 35$ -55 mm, Cherel et al. 2002a; Table 1). At Kerguelen, besides crustaceans and myctophids, the diet of blue petrels also includes a high percentage of larger prey such as squid, and fish *P. gracilis* (mean length:  $\approx 283$  mm, Cherel et al. 2002a) (Table 1). Hence, the long and narrow bills of blue petrels at this

site are also consistent with the requirement to seize and tear larger individual prey items. Although there are no published studies of the diet of blue petrels at Diego Ramírez, stomachs of adults contained lots of crustaceans (Euphausiids and Amphipods), followed by remains of small fish and cephalopod beaks (Suazo, unpubl. data). Therefore, we predict according to the similarity in bill morphology that their diet is more similar to conspecifics from South Georgia, rather than Kerguelen.

In conclusion, our results reveal key interspecific and geographic differences in bill shape and size of four small petrels, which seem likely to reflect variation in prey selection and foraging style. Our study also highlights the usefulness of geometric morphometric methods for investigating the bill morphology of seabirds. Further studies linking bill shape and foraging strategies are needed to better identify the main ecological drivers that lead to morphological displacement of biological structures in seabirds.

### **Compliance with Ethical Standards**

Conflicts of interest/Competing interests: The authors declare that they have no conflicts of interest.

Ethics approval: Work on South Georgia was approved by the Animal Welfare and Ethical Review Body (AWERB) of the British Antarctic Survey and was carried out under permit from the Government of South Georgia and the Sandwich Islands. Work on New Island was approved by the Falkland Islands Government (Environmental Office). Kerguelen data were supported by the French Polar Institute Paul Emile Victor. Work on Diego Ramírez Islands was supported by Armada de Chile (Chilean Navy, 3rd Naval Zone).

### **Acknowledgments**

We are grateful to Julia Slezacek, Ruth Brown and Jaume Forcada for their help during the fieldwork.

**Declarations**

**Funding**

M.I.L. was funded with an Erasmus+ internship of the European Union. MF was supported by the project CLIFISH (CTM2015-66400-C3-3-R, MINECO/FEDER) co-funded by the Ministerio de Economía y Competitividad of the Spanish government and by the European Regional Development Fund (ERDF). JN was supported by the Spanish National Program Ramón y Cajal (RYC-2015-17809). JN was funded with the Collaborative Gearing Scheme of the NERC Antarctic Funding Initiative. PQ was supported by the Deutsche Forschungsgemeinschaft (DFG) in the framework of the priority programme SPP1154 “Antarctic Research with comparative investigations in Arctic ice areas”. Kerguelen data were supported by the French Polar Institute Paul Emile Victor (IPEV, program no. 354 to FB). Work on Diego Ramírez Islands was supported by Armada de Chile (Chilean Navy, 3rd Naval Zone).

**Availability of data and material:** Not applicable

**Code availability:** Not applicable

**Consent to participate:** Not applicable

**Consent for publication:** Not applicable



## References

- Adams DC (1999) Methods for shape analysis of landmark data from articulated structures. *Evol Ecol Res* 1:959–970.
- Adams DC, Rohlf FJ, Slice DE (2004) Geometric morphometrics: Ten years of progress following the ‘revolution.’ *Ital J Zool* 71:5–16. doi: 10.1080/11250000409356545
- Adams DC, Rohlf FJ, Slice DE (2013) A field comes of age: Geometric morphometrics in the 21st century. *Hystrix* 24:7–14. doi: 10.4404/hystrix-24.1-6283
- Ainley DG, Ribic CA, Fraser WR (1992) Does prey preference affect habitat choice in Antarctic seabirds? *Mar Ecol Prog Ser* 90:207–221. doi: 10.3354/meps090207
- Aldrich J, James F (1991) Ecogeographic Variation In The American Robin (*Turdus Migratorius*). *Auk Ornithol Adv* 108:230–249. doi: 10.1093/auk/108.2.230
- Armstrong P, Forbes V (1997) The Falkland Islands and their Adjacent Maritime Area. Maritime Briefing
- Atkinson A, Whitehouse MJ, Priddle J, Cripps GC, Ward P, Brandon MA (2001) South Georgia, Antarctica: A productive, cold water, pelagic ecosystem. *Mar Ecol Prog Ser* 216:279–308. doi: 10.3354/meps216279
- Barbraud C, Delord K (2006) Population census of blue petrels *Halobaena caerulea* at Mayes Island, Iles Kerguelen. *Antarct Sci* 18:199–204. doi: 10.1017/S095410200600023X
- Berns CM, Adams DC (2010) Bill Shape and Sexual Shape Dimorphism between two Species of Temperate Hummingbirds: Black-Chinned Hummingbird (*Archilochus alexandri*) and Ruby-Throated Hummingbird (*A. colubris*). *Auk* 127:626–635. doi: 10.1525/auk.2010.09213
- Boag PT, Grant PR (1981) Intense natural selection in a population of Darwin’s finches (geospizinae) in the Galápagos. *Science* (80- ) 214:82–85. doi: 10.1126/science.214.4516.82
- Brooke M (2004) Albatrosses and petrels across the world. Oxford University Press
- Buckley FG, Buckley PA (1980) Habitat Selection and Marine Birds. In: Behavior of Marine

Animals. Plenum Press, New York, pp 69–112

Bull LS (2006) Geographical variation in the morphology of the Wedge-tailed Shearwater (*Puffinus pacificus*). *Emu* 106:233–243. doi: 10.1071/MU05050

Bull LS, Haywood J, Pledger S (2004) Components of phenotypic variation in the morphometrics of shearwater (*Puffinus*) species. *Ibis* (Lond 1859) 146:38–45. doi: 10.1111/j.1474-919X.2004.00209.x

Catry P, Campos A, Segurado P, Silva M, Strange I (2003) Population census and nesting habitat selection of thin-billed prion *Pachyptila belcheri* on New Island, Falkland Islands. *Polar Biol* 26:202–207. doi: 10.1007/s00300-002-0465-9

Cherel Y, Bocher P, Trouvé C, Weimerskirch H (2002a) Diet and feeding ecology of blue petrels *Halobaena caerulea* at Iles Kerguelen, Southern Indian Ocean. *Mar Ecol Prog Ser* 228:283–299. doi: 10.3354/meps228283

Cherel Y, Bocher P, De Broyer C, Hobson KA (2002b) Food and feeding ecology of the sympatric thin-billed *Pachyptila belcheri* and Antarctic *P. desolata* prions at Iles Kerguelen, Southern Indian Ocean. *Mar Ecol Prog Ser* 228:263–281. doi: 10.3354/meps228263

Cherel Y, Connan M, Jaeger A, Richard P (2014) Seabird year-round and historical feeding ecology: Blood and feather  $\delta^{13}\text{C}$  and  $^{15}\text{N}$  values document foraging plasticity of small sympatric petrels. *Mar Ecol Prog Ser* 505:267–280. doi: 10.3354/meps10795

Cherel Y, Quillfeldt P, Delord K, Weimerskirch H (2016) Combination of At-Sea Activity, Geolocation and Feather Stable Isotopes Documents Where and When Seabirds Molt. *Front Ecol Evol*. doi: 10.3389/fevo.2016.00003

Colombelli-Négrel D (2016) Both natural selection and isolation by distance explain phenotypic divergence in bill size and body mass between South Australian little penguin colonies. *Ecol Evol* 6:7965–7975. doi: 10.1002/ece3.2516

Corman AM, Mendel B, Voigt CC, Garthe S (2016) Varying foraging patterns in response to competition? A multicolony approach in a generalist seabird. *Ecol Evol* 6:974–986. doi: 10.1002/ece3.1884

420 Croxall JP, Prince PA (1980) Food, feeding ecology and ecological segregation of seabirds at  
 421 South Georgia. *Environment* 103:103–131.

422 Croxall JP, Prince PA, Reid K (1997) Dietary segregation of krill-eating South Georgia  
 423 seabirds. *J Zool* 242:531–556. doi: 10.1111/j.1469-7998.1997.tb03854.x

424 Farré M, Tuset VM, Cartes JE, Massutí E, Lombarte A (2016a) Depth-related trends in  
 425 morphological and functional diversity of demersal fish assemblages in the western  
 426 Mediterranean Sea. *Prog Oceanogr* 147:22–37. doi: 10.1016/j.pocean.2016.07.006

427 Farré M, Tuset VM, Maynou F, Recasens L, Lombarte A (2016b) Selection of landmarks and  
 428 semilandmarks in fishes for geometric morphometric analyses: a comparative study based  
 429 on analytical methods. *Sci Mar* 80:175–186. doi: 10.3989/scimar.04280.15a

430 Foster DJ, Podos J, Hendry AP (2008) A geometric morphometric appraisal of beak shape in  
 431 Darwin’s finches. *J Evol Biol* 21:263–275. doi: 10.1111/j.1420-9101.2007.01449.x

432 Gémard C, Aubin T, Bonadonna F (2019) Males’ calls carry information about individual  
 433 identity and morphological characteristics of the caller in burrowing petrels. *J Avian Biol.*  
 434 doi: 10.1111/jav.02270

435 Grant BR, Grant PR (1989) *Evolutionary Dynamics of a Natural Population: The Large Cactus*  
 436 *Finch of the Galápagos*, The Univer. Library of Congress Cataloging-in-Publication Data,  
 437 Chicago

438 Grémillet D, Omo GD, Ryan PG, Peters G, Ropert-coudert Y, Weeks SJ (2004) GPS tracking of  
 439 Cape gannets and intra-specific competition: a case study based on GPS tracking of Cape  
 440 gannets from neighbouring colonies. *Mar Ecol Prog Ser* 268:265–279.

441 Hammer Ø, Harper DAT, Ryan PD (2001) Past: Paleontological statistics software package for  
 442 education and data analysis. *Palaeontol Electron* 4:1–9.

443 Harper PC (1987) Feeding behaviour and other notes on 20 species of Procellariiformes at sea.  
 444 *Notornis* 34:169–192.

445 Jones CW, Phillips RA, Grecian WJ, Ryan PG (2020) Ecological segregation of two  
 446 superabundant, morphologically similar, sister seabird taxa breeding in sympatry. *Mar*  
 447 *Biol* 167:45. doi: 10.1007/s00227-020-3645-7

- Kleindorfer S, Chapman TW, Winkler H, Sulloway FJ (2006) Adaptive divergence in contiguous populations of Darwin's Small Ground Finch (*Geospiza fuliginosa*). *Evol Ecol Res* 8:357–372.
- 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 Biol* 29:229–238. doi: 10.1007/s00300-005-0043-z
- Lewis S, Sherratt TN, Hamer KC, Wanless S (2001) Evidence of intra-specific competition for food in a pelagic seabird. *Nature* 412:816–819. doi: 10.1038/35090566
- Mayr E, Diamond J (2001) *The Birds of Northern Melanesia: Speciation, Evology and Biogeography*. Oxford University Press U.K.
- Militão T, Gómez-Díaz E, Kaliontzopoulou A, González-Solís J (2014) Comparing multiple criteria for species identification in two recently diverged seabirds. *PLoS One* 9:1–27. doi: 10.1371/journal.pone.0115650
- Moum T, Árnason E (2001) Genetic diversity and population history of two related seabird species based on mitochondrial DNA control region sequences. *Mol Ecol* 10:2463–2478. doi: 10.1046/j.0962-1083.2001.01375.x
- Navarro J, Kaliontzopoulou A, González-Solís J (2009) Sexual dimorphism in bill morphology and feeding ecology in Cory's shearwater (*Calonectris diomedea*). *Zoology* 112:128–138. doi: 10.1016/j.zool.2008.05.001
- Navarro J, Votier SC, Aguzzi J, Chiesa JJ, Forero MG, Phillips RA (2013) Ecological Segregation in Space, Time and Trophic Niche of Sympatric Planktivorous Petrels. *PLoS One* 8:e62897. doi: 10.1371/journal.pone.0062897
- Navarro J, Cardador L, Brown R, Phillips RA (2015) Spatial distribution and ecological niches of non-breeding planktivorous petrels. *Sci Rep* 5:12164. doi: 10.1038/srep12164
- Nebel S (2005) Latitudinal clines in bill length and sex ratio in a migratory shorebird: A case of resource partitioning? *Acta Oecologica* 28:33–38. doi: 10.1016/j.actao.2005.02.002
- Nebel S, Jackson DL, Elnor RW (2005) Functional association of bill morphology and foraging

behaviour in calidrid sandpipers. *Anim Biol* 55:235–243. doi: 10.1163/1570756054472818

Phillips RA, Silk JRD, Croxall JP (2005) Foraging and provisioning strategies of the light-mantled sooty albatross at South Georgia: Competition and co-existence with sympatric pelagic predators. *Mar Ecol Prog Ser* 285:259–270. doi: 10.3354/meps285259

Phillips RA, McGill RAR, Dawson DA, Bearhop S (2011) Sexual segregation in distribution, diet and trophic level of seabirds: Insights from stable isotope analysis. *Mar Biol* 158:2199–2208. doi: 10.1007/s00227-011-1725-4

Prince PA (1980) The food and feeding ecology of Blue petrel (*Halobaena caerulea*) and Dove prion (*Pachyptila desolata*). *J Zool* 190:59–76. doi: 10.1111/j.1469-7998.1980.tb01423.x

Prince PA, Croxall JP (1983) Birds of South Georgia: new records and re-evaluations of status. *Br Antarct Surv Bull* 59:15–27.

Quillfeldt P, McGill RAR, Masello JF, Weiss F, Strange IJ, Brickle P, Furness RW (2008) Stable isotope analysis reveals sexual and environmental variability and individual consistency in foraging of thin-billed prions. *Mar Ecol Prog Ser* 373:137–148. doi: 10.3354/meps07751

Quillfeldt P, Michalik A, Veit-Köhler G, Strange IJ, Masello JF (2010) Inter-annual changes in diet and foraging trip lengths in a small pelagic seabird, the thin-billed prion *Pachyptila belcheri*. *Mar Biol* 157:2043–2050. doi: 10.1007/s00227-010-1472-y

Quillfeldt P, Masello JF, Navarro J, Phillips RA (2013) Year-round distribution suggests spatial segregation of two small petrel species in the South Atlantic. *J Biogeogr* 40:430–441. doi: 10.1111/jbi.12008

Quillfeldt P, Phillips RA, Marx M, Masello JF (2014) Colony attendance and at-sea distribution of thin-billed prions during the early breeding season. *J Avian Biol* 45:315–324. doi: 10.1111/jav.00307

Quillfeldt P, Cherel Y, Delord K, Weimerkirch H (2015) Cool, cold or colder? Spatial segregation of prions and blue petrels is explained by differences in preferred sea surface temperatures. *Biol Lett* 11:20141090. doi: 10.1098/rsbl.2014.1090

Quillfeldt P, Moodley Y, Weimerskirch H, Cherel Y, Delord K, Phillips RA, Navarro J,

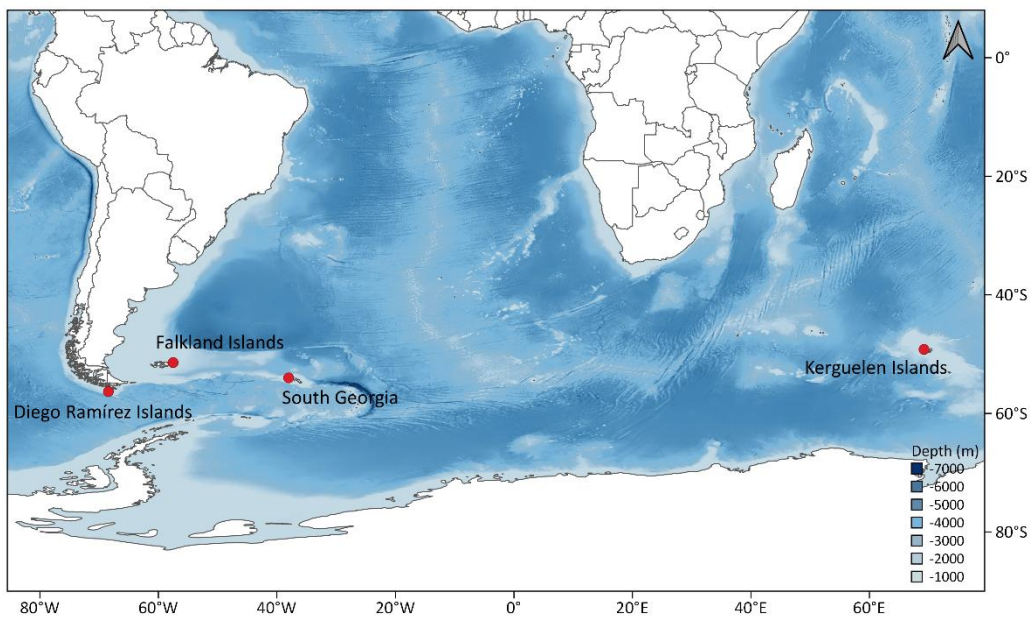
- Calderón L, Masello JF (2017) Does genetic structure reflect differences in non-breeding movements? A case study in small, highly mobile seabirds. *BMC Evol Biol* 17:160. doi: 10.1186/s12862-017-1008-x
- R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.r-project.org/>.
- Reid K, Croxall JP, Edwards TM (1997) Interannual variation in the diet of the antarctic prion *Pachyptila desolata* at South Georgia. *Emu* 97:126–132. doi: 10.1071/MU97016
- Rohlf FJ (2017) tpsDig2 2.31 relative warps software.
- Rohlf FJ (2019) tpsRelw 1.70 Relative Warps.
- Rohlf JF, Marcus LF (1993) A revolution morphometrics. *Trends Ecol Evol* 8:129–132. doi: 10.1016/0169-5347(93)90024-J
- Schlatter RP, Riveros GM (1997) Natural history of the Diego Ramirez Archipelago, Chile. *Sep Client Ina* 47:87–112.
- Schluter (2000) Ecological Character Displacement in Adaptive Radiation. *Am Nat* 156:S4–S16. doi: 10.2307/3079223
- Tokita M, Yano W, James HF, Abzhanov A (2017) Cranial shape evolution in adaptive radiations of birds: Comparative morphometrics of Darwin’s finches and Hawaiian honeycreepers. *Philos Trans R Soc B Biol Sci*. doi: 10.1098/rstb.2015.0481
- Trallero L, Farré M, Phillips RA, Navarro J (2019) Geometric morphometrics reveal interspecific and sexual differences in bill morphology in four sympatric planktivorous petrels. *J Zool* 307:167–177. doi: 10.1111/jzo.12631
- Van Oordt F, Torres-Mura JC, Hertel F (2018) Ecomorphology and foraging behaviour of Pacific boobies. *Ibis (Lond 1859)* 160:313–326. doi: 10.1111/ibi.12545
- Wakefield ED, Phillips RA, Matthiopoulos J (2014) Habitat-mediated population limitation in a colonial central-place forager: The sky is not the limit for the black-browed albatross. *Proc R Soc B Biol Sci*. doi: 10.1098/rspb.2013.2883
- Warham J (1990) The petrels: their ecology and breeding systems. A & C Black, London
- Warham J (1996) The Behaviour, Population Biology and Physiology of the Petrels. London

532 Weimerskirch H, Zotier R, Jouventin P (1989) The avifauna of the kerguelen islands. *Emu*  
533 89:15–29. doi: 10.1071/MU9890015

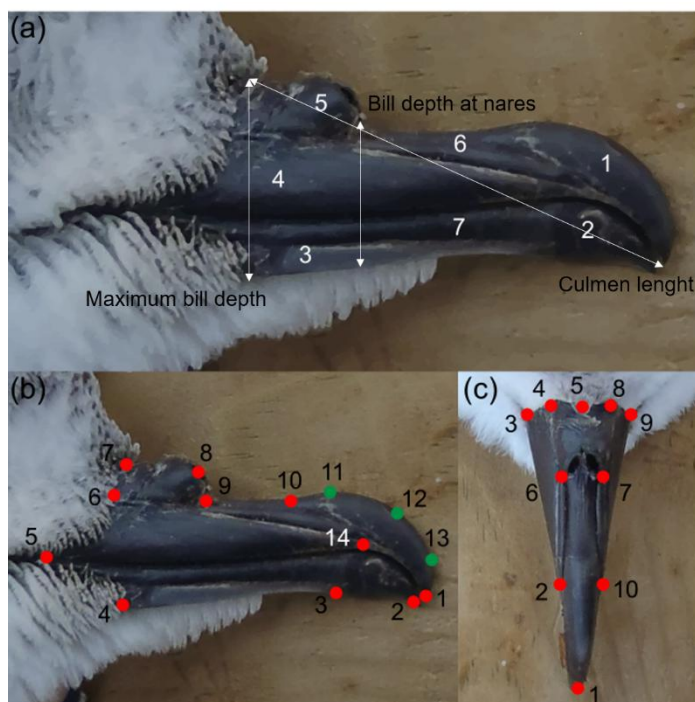
534 Wojczulanis-Jakubas K, Kilikowska A, Harding AMA, Jakubas D, Karnovsky NJ, Steen H,  
535 Strøm H, Welcker J, Gavrilov M, Lifjeld JT, Johnsen A (2014) Weak population genetic  
536 differentiation in the most numerous Arctic seabird, the little auk. *Polar Biol* 37:621–630.  
537 doi: 10.1007/s00300-014-1462-5

538 Zelditch ML, Swidersky DL, Sheeds HD, Fink WL (2004) Geometric morphometrics for  
539 biologists: a primer. London: Elsevier Academic Press

540 Zhou M, Zhu Y, D&apos;Ovidio F, Park Y-H, Durand I, Kestenare E, Sanial V, Van-Beek  
541 P, Queguiner B, Carlotti F, Blain S (2014) Surface currents and upwelling in Kerguelen  
542 Plateau regions. *Biogeosciences Discuss* 11:6845–6876. doi: 10.5194/bgd-11-6845-2014  
543



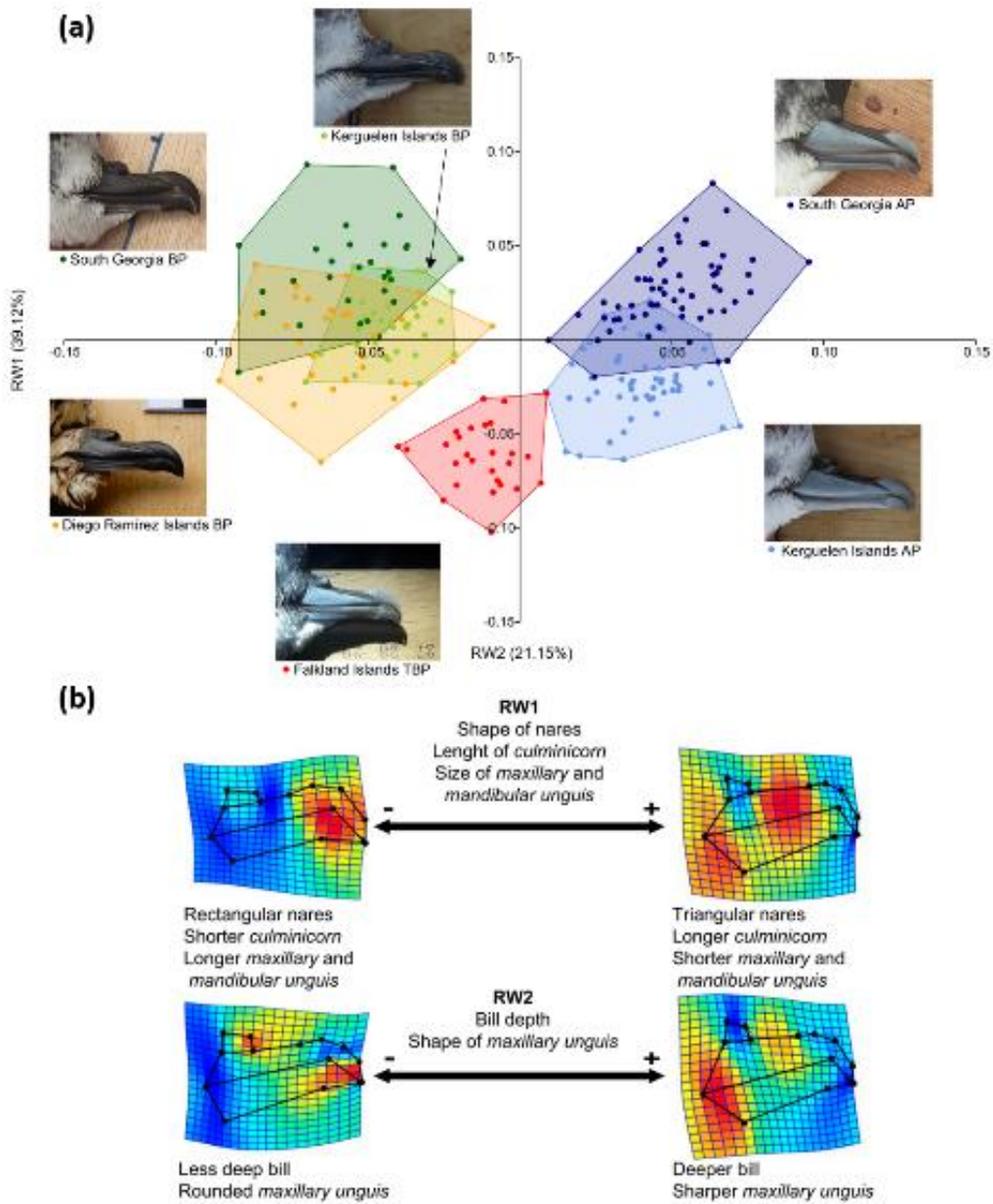
**Fig. 1** Location of the different breeding colonies of Antarctic prions, thin-billed prions and blue petrels sampled in this study



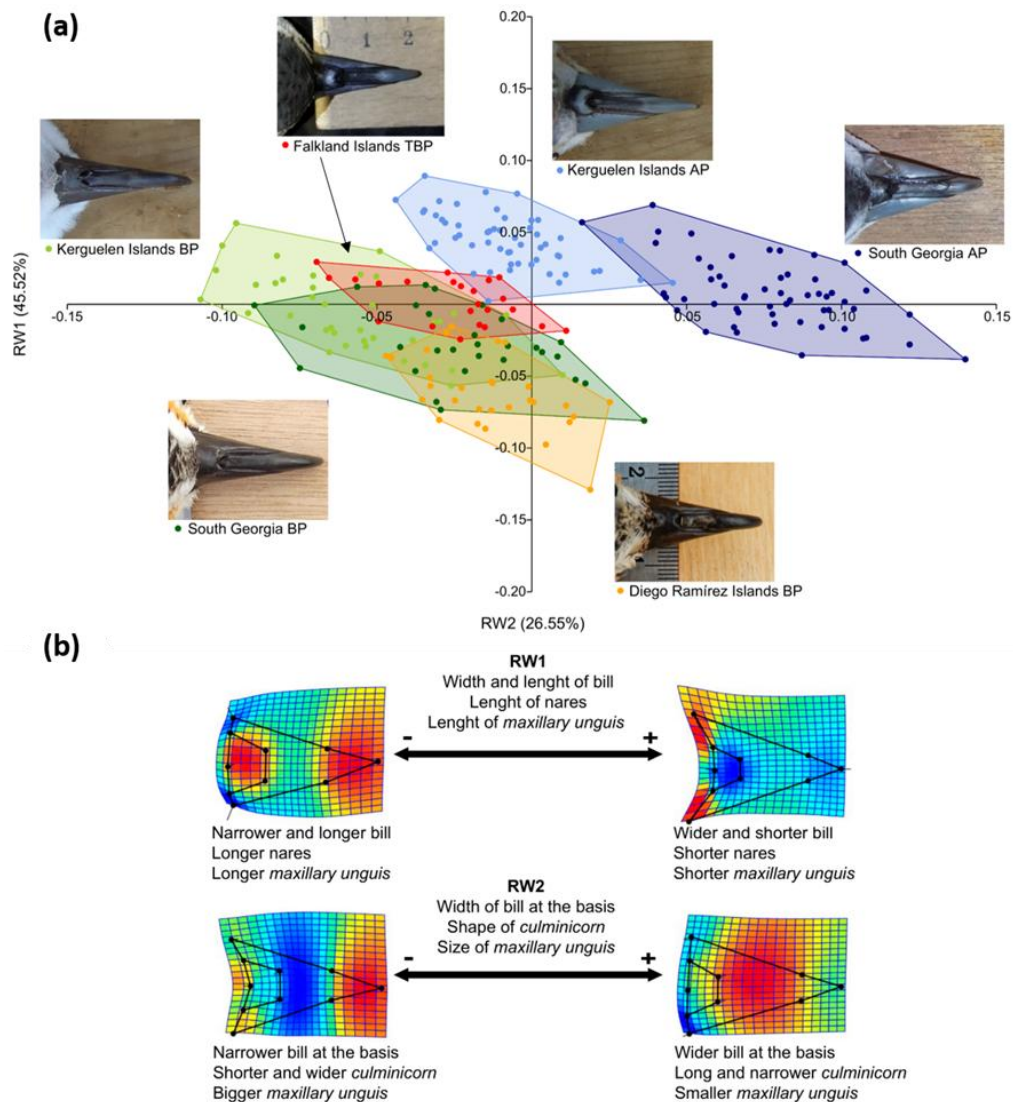
**Fig. 2** (a) Bill morphology and measurements: 1 = *superior unguicorn-maxillary unguis*, 2 = *inferior unguicorn-mandibular unguis*, 3 = *ramicorn*, 4 = *latericorn*, 5 = *nares*, 6 = *culminicorn* and 7 = *tomia-cutting edges*. Landmarks (red dots) and semilandmarks (green dots) used to



559 describe the shape of (b) the profile, and (c) the dorsal view of the bill. All pictures are of a blue  
 560 petrel



561 **Fig. 3** (a) Morphospace of the shape of the right profile of the bills of Antarctic prions (AP)  
 562 from South Georgia and Kerguelen Islands, blue petrels (BP) from South Georgia, Kerguelen  
 563 and Diego Ramírez Islands, and thin-billed prions (TBP) from Falkland Islands. (b)  
 564 Descriptions of the meaning of the relative warps (RW1 and RW2), corresponding to the  
 565 horizontal and vertical axes of profile morphospace (red/orange and blue/green indicate higher  
 566 and lower shape variation, respectively)



**Fig. 4** (a) Morphospace of the shape of the dorsal view of the bills of Antarctic prions (AP) from South Georgia and Kerguelen Islands, blue petrels (BP) from South Georgia, Kerguelen and Diego Ramírez Islands, and thin-billed prions (TBP) from Falkland Islands. (b) Descriptions of the meaning of the relative warps (RW1 and RW2), corresponding to the horizontal and vertical axes of dorsal morphospace (red/orange and blue/green indicate higher and lower shape variation, respectively)

574 **Tables**

575 **Table 1.** Review of the diet of Antarctic prions and blue petrels breeding in South Georgia and the Kerguelen Islands, and thin-billed prions breeding in the Falkland Islands.

576 There are no published studies of the diet of blue petrels at the Diego Ramírez Islands.

Species	Colony	Type of prey	Average frequency of occurrence (%)	Prey preferences	References
Antarctic prion	South Georgia	Cephalopod	11.1	Myctophidae <i>Euphausia superba</i> , Amphipoda ( <i>Themisto gaudichaudii</i> ), Copepoda	Prince (1980); Croxall <i>et al.</i> (1997); Reid, Croxall & Edwards (1997)
		Fish	28.2		
		Crustacean	96.8		
	Kerguelen Islands	Cephalopod	15.4	<i>Oegopsida sp.</i>	Cherel <i>et al.</i> (2002a)
		Fish	31.7	Myctophidae	
		Crustacean	100	Amphipoda ( <i>T. gaudichaudii</i> )	
Blue petrel	South Georgia	Cephalopod	6.4	Myctophidae <i>E. superba</i>	Prince (1980)
		Fish	83.3		
		Crustacean	97.4		
	Kerguelen Islands	Cephalopod	14.3	<i>Oegopsida sp.</i>	Cherel <i>et al.</i> (2002b)
		Fish	81.0	Myctophidae, <i>Paradiplospinus gracilis</i>	
		Crustacean	100	Amphipoda ( <i>T. gaudichaudii</i> ), <i>Thysanoessa sp.</i>	
Thin-billed prion	Falkland Islands	Cephalopod	55.9	Squid ( <i>Gonatus antarcticus</i> )	Quillfeldt <i>et al.</i> (2010)
		Fish	12.5		
		Crustacean	68.6	Euphausiids, Amphipoda ( <i>T. gaudichaudii</i> )	

577

**Table 2.** Description of the landmarks and semilandmarks used to define the shape of the profile and dorsal views of the bills of Antarctic prions, thin-billed prions and blue petrels (following Trallero *et al.*,

Profile		Dorsal	
Landmark	Description	Landmark	Description
1	Upper jaw, most distal tip of maxilla ( <i>maxillary unguis</i> )	1	Upper jaw, most distal tip of maxilla ( <i>maxillary unguis</i> )
2	Lower jaw, most distal tip of the mandibular zone ( <i>mandibular unguis</i> )	2	Articulation between the upper and lower <i>ramicorn</i> (right side)
3	Anterior tip of the inferior <i>ramicorn</i> at the conjuncture with the inferior <i>unguicorn</i>	3	The most distal tip of the <i>latericorn</i> (right side)
4	Posterior tip of the lower <i>ramicorn</i>	4	Lower and posterior border of the nare, at the junction with the posterior point of the <i>latericorn</i> joint (right

2019).

			side)
5	Posterior tip of the <i>latericorn</i>	5	Upper and posterior border of the nare
6	Lower and posterior border of the nares, at the junction with the posterior point of the <i>latericorn</i> joint	6	Point of maximum curvature at the rostral end of the right nare
7	Upper and posterior border of the nares	7	Point of maximum curvature at the rostral end of the left nare
8	Point of maximum curvature of the superior and anterior border of the nare	8	Lower and posterior border of the nare, at the junction with the posterior point of the <i>latericorn</i> joint (left side)
9	Lower and anterior border, in the joint with the <i>latericorn</i>	9	The most distal tip of the <i>latericorn</i> (left side)
10	Articulation between the upper anterior border of the <i>culminicorn</i> and the posterior superior border of the maxillary zone	10	Articulation between the upper and lower <i>ramicorn</i> (left side)
14	Articulation between the upper and lower <i>ramicorn</i>		
Semilandmark			
11, 12, 13	Curvature of the maxillary nail, between landmarks 1 and 10		

**Table 3.** Percentage explained for the first five relative warps (RW) in both dorsal and profile perspectives.

	RW1	RW2	RW3	RW4	RW5
Dorsal					
Percentage (%)	45.52	26.55	9.24	6.75	2.96
Cumulative percentage (%)	45.52	72.07	81.31	88.07	91.02
Profile					
Percentage (%)	39.12	21.15	10.73	6.46	4.11
Cumulative percentage (%)	39.12	60.27	71.00	77.46	81.57

584 **Table 4.** Comparison of bill size and shape variation measurements between Antarctic prions, thin-billed prions and blue petrels breeding at different island groups. Values  
585 are mean  $\pm$  standard deviation (sample size). Values with the same subscript indicate no significant difference between species (letters) or colonies (numbers) based on Mann-  
586 Whitney tests.

	<b>Antarctic prion</b>		<b>Blue petrel</b>			<b>Thin-billed prion</b>
	<b>Kerguelen Islands</b>	<b>South Georgia</b>	<b>Kerguelen Islands</b>	<b>South Georgia</b>	<b>Diego Ramírez Islands</b>	<b>Falkland Islands</b>
Maximum bill depth	8.44 $\pm$ 0.39 (20) <sub>A1</sub>	12.42 $\pm$ 1.04 (53) <sub>A2</sub>	9.45 $\pm$ 0.40 (14) <sub>B3</sub>	10.12 $\pm$ 0.64 (27) <sub>B4</sub>	10.93 $\pm$ 0.46 (29) <sub>B5</sub>	7.41 $\pm$ 0.35 (17) <sub>C6</sub>
Bill depth at nares		9.13 $\pm$ 0.90 (53) <sub>A1</sub>		7.51 $\pm$ 0.47 (28) <sub>B2</sub>	7.39 $\pm$ 0.47 (29) <sub>B2</sub>	
Culmen length	26.91 $\pm$ 1.01 (20) <sub>A1</sub>	28.19 $\pm$ 1.16 (53) <sub>A2</sub>	26.08 $\pm$ 1.06 (14) <sub>B3</sub>	26.32 $\pm$ 1.10 (28) <sub>B1,3</sub>	25.21 $\pm$ 0.99 (29) <sub>B4</sub>	25.10 $\pm$ 0.97 (17) <sub>C4</sub>
Dorsal						
RW1	-0.01 $\pm$ 0.02 (54) <sub>A1</sub>	0.08 $\pm$ 0.02 (55) <sub>A2</sub>	-0.06 $\pm$ 0.03 (37) <sub>B3</sub>	-0.02 $\pm$ 0.03 (29) <sub>B4</sub>	-0.01 $\pm$ 0.02 (29) <sub>B1,4</sub>	-0.03 $\pm$ 0.02 (23) <sub>B4</sub>
RW2	0.04 $\pm$ 0.02 (54) <sub>A1</sub>	0.01 $\pm$ 0.02 (55) <sub>A2</sub>	-0.01 $\pm$ 0.03 (37) <sub>B3</sub>	-0.03 $\pm$ 0.02 (29) <sub>B4</sub>	-0.06 $\pm$ 0.02 (29) <sub>B5</sub>	0.003 $\pm$ 0.016 (23) <sub>C2,3</sub>
Profile						
RW1	0.04 $\pm$ 0.01 (54) <sub>A1</sub>	0.05 $\pm$ 0.02 (60) <sub>A2</sub>	-0.04 $\pm$ 0.01 (35) <sub>B3</sub>	-0.06 $\pm$ 0.02 (29) <sub>B4</sub>	-0.06 $\pm$ 0.02 (29) <sub>B4</sub>	-0.01 $\pm$ 0.01 (27) <sub>C5</sub>
RW2	-0.02 $\pm$ 0.02 (54) <sub>A1</sub>	0.03 $\pm$ 0.02 (60) <sub>A2</sub>	0.01 $\pm$ 0.02 (35) <sub>B3</sub>	0.04 $\pm$ 0.02 (29) <sub>B4</sub>	-0.001 $\pm$ 0.024 (29) <sub>B3</sub>	-0.06 $\pm$ 0.02 (27) <sub>C5</sub>

587

**Table 5.** Summary of the Kruskal-Wallis tests examining variation in bill size and morphology (dorsal and profile) between Antarctic prions, thin-billed prions and blue petrels breeding at different island groups.

	<b>Species</b>		<b>Colony</b>		<b>Species*colony</b>	
	H	<i>p</i>	H	<i>p</i>	H	<i>p</i>
Maximum bill depth	58.2	<0.001	103.8	<0.001	138.0	<0.001
Bill depth at nares	70.2	<0.001	26.2	<0.001	96.4	<0.001
Culmen length	79.4	<0.001	68.0	<0.001	96.4	<0.001
Dorsal-RW1	93.8	<0.001	70.7	<0.001	160.2	<0.001
Dorsal-RW2	101.0	<0.001	92.2	<0.001	152.4	<0.001
Profile-RW1	189.3	<0.001	56.2	<0.001	195.9	<0.001
Profile-RW2	70.7	<0.001	139.4	<0.001	157.3	<0.001