Agreement on the Conservation of Albatrosses and Petrels

Fifth Meeting of the Population and Conservation Status Working Group

Florianópolis, Brazil, 9 - 10 May 2019

Mapping the global distribution of seabird populations: a framework for integrating biologging, demographic and phenological datasets

Ana P. B. Carneiro, Elizabeth J. Pearmain, Steffen Oppel, Thomas A. Clay, Richard A. Phillips, Anne-Sophie Bonnet-Lebrun, Edward Abraham, Yvan Richard, Jonathan Handley, Ross M. Wanless, Cleo Small, Ben J. Dilley, Peter G. Ryan, Javier Arata, Elizabeth Bell, Leandro Bugoni, Letizia Campioni, Paulo Catry, Richard Cuthbert, Lorna Deppe, Graeme Elliott, Amanda Freeman, Jacob Gonzalez-Solis, Jose Pedro Granadeiro, David Grémillet, Todd J. Landers, Azwianewi Makhado, Deon Nel, David G. Nicholls, Christopher Robertson, Paul Sagar, Paul Scofield, Jean-Claude Stahl, Andrew Stanworth, Kim L. Stevens, Philip N. Trathan, David Thompson, Leigh Torres, Kath Walker, Susan M. Waugh, Henri Weimerskirch, Maria P. Dias

Password protect this document, with only the summary made publicly available: **Y**

If Yes - Allow protected access to this document in other fora (e.g. RFMO meetings): **N**

SUMMARY

The identification of geographic areas and periods when the densities of animals are highest across their annual cycles is a crucial step in conservation planning, including for the designation of protected areas and regulation of potentially detrimental human activities. Many species of marine megafauna are declining, however for the majority, the methods used to identify these important sites and times are usually biased towards adults, neglecting the distribution of other life-history stages even though they can represent a substantial proportion of the total population. Here we develop a methodological framework for estimating population-level density distributions at quarterly and annual resolutions, incorporating tracking data for all major life-history stages (adult breeders, adult non-breeders, juveniles and immatures). We incorporate demographic information (adult and juvenile survival, breeding frequency and success, age at first breeding) and phenological data (average timing of breeding and migration) to appropriately weight distribution grids according to the proportion of the population represented by each life-history stage. We demonstrate the utility of this framework by applying it to 21 species (including 28 populations) of albatrosses and petrels. The resulting distribution grids accounting for all major life-history stages highlight that omitting juveniles, immatures and adult non-breeders leads to spatial biases, particularly as these classes may account for 55-75% of all individuals for many species. As such, ignoring the distributions of pre-breeders and adult non-breeders is likely to bias estimates of overlap with threats, and potentially lead to suboptimal targeting of resources directed at management and conservation. Our framework synthesizes and improves on previous approaches to estimate seabird densities at sea, and provides a standard and replicable methodology that can be easily updated as new tracking and demographic data become available.

1. INTRODUCTION

Understanding how marine megafauna overlap and interact with threats in space and time is crucial to their conservation. Biologging technology has greatly improved our knowledge of how animals interact with their environment and facilitated a better understanding of the spatio-temporal distribution of marine megafauna (Hays et al., 2016; Oppel et al., 2018; Sequeira et al., 2018). In the past, the distribution of marine megafauna was mapped based on presence-absence data or static range maps, which simplistically assumed homogeneous distribution within the species range (Williams et al., 2014). However, many marine animals show a distinctly non-homogenous distribution throughout their range, and the identification of areas with highest densities of individuals is potentially paramount for conservation planning (Dias et al., 2017; Hays et al., 2019; Johnston et al., 2015; Nur et al., 2011). This is particularly relevant for seabirds, which comprise the most mobile marine species that can show high spatial aggregations at sea (Burger et al., 2004; Clua and Grosvalet, 2001; Duffy, 1989).

Although utilization distributions (i.e. probability distributions of space use; Fieberg et al., 2005) based on seabird tracking data can identify areas most frequently used and improve spatial priority-setting compared to range maps, studies using this approach generally cannot extrapolate densities at the population level due to common biases in data collection. Most tracking studies have focused on breeding adults, neglecting the distribution of non-breeding individuals even though they represent a large proportion of the total population (Péron and Grémillet, 2013; Weimerskirch et al., 2014). Young age classes and adult non-breeders are generally under-represented in tracking studies because they spend extensive periods at sea and are therefore more difficult to track (Gutowsky et al., 2014; Phillips et al., 2017). Due to their more dispersed distributions, these life-history stages may be more susceptible to anthropogenic threats (Gianuca et al., 2017; Lewison et al., 2012; Pardo et al., 2017; Riotte-

Lambert and Weimerskirch, 2013). Thus, current approaches to estimate the distribution of seabirds are frequently unable to include certain key life-history stages (e.g. Augé et al., 2018; Block et al., 2011), and may therefore underestimate the potential risk from threats such as bycatch in fisheries. Assessing the potential impact of threats at the population level, however, requires reliable estimates of the density distribution of all life-history stages of a given species (Clay et al., in press).

Several recent studies investigating overlap of seabirds with fisheries have incorporated data from different life-history stages (e.g. Carneiro et al., 2017; Clay et al., in press; Tuck et al., 2015, 2011). By using detailed information on migratory and breeding schedules, demographic parameters from population models and extensive tracking datasets, Clay et al., (in press) were able to compare population-level distributions of four seabird species from South Georgia with industrial fisheries in the Southern Ocean. Here, we expand the approaches of Carneiro et al., (2017) and Clay et al., (in press) to provide a coherent framework to estimate the density distribution of seabird species at a quarterly and annual resolution. This framework can be used to improve the assessment of threats to seabird species by much better representing the distribution and abundance of all life-history stages that may be affected. We demonstrate this framework for 21 seabird species of global conservation concern for which tracking data for two or more of the major life-history stages were available. Although our approach requires both demographic and tracking data, the resulting density distribution maps can be readily updated whenever new information becomes available.

2. METHODS

2.1. Study species

Currently, 21 of the 31 species listed under Agreement for the Conservation of Albatrosses and Petrels (ACAP, see https://www.acap.aq/en/acap-species for a complete list) are threatened with extinction (BirdLife International, 2018). Most ACAP species are bycaught in large numbers in fisheries, emphasizing the need to map their at-sea distributions. We considered all ACAP species that breed in the Southern Ocean in the analyses, except for the pink-footed shearwater (*Ardenna creatopus*), southern royal (*Diomedea epomophora*), Indian yellow-nosed (*Thalassarche carteri*), Campbell (*T. impavida*) and shy (*T. cauta*) albatrosses for which insufficient tracking data were available to confidently map their distributions.

2.2. Framework

Our framework constitutes ten steps: 1) data compilation (tracking, phenology and demography); 2) cleaning and standardisation of tracking data; 3) estimating utilisation distributions (UDs) for each species, breeding site, device type, age and stage of the annual cycle (hereafter referred to as 'data group'); 4) applying a land mask to UDs; 5) assessing representativeness for each data group; 6) combining UDs into monthly distribution grids based on the duration of each stage in each month according to phenological data (i.e. related to the timing of key events such as breeding and migration schedule); 7) estimating the proportion of the population in each life-history stage using age- and stage-structured Leslie-Lefkovitch matrix models; 8) estimating the abundance of birds of a given life-history stage in each monthly grid cell based on the distribution grids and the proportion of the total population in each life-history stage derived from demographic models; 9) converting the monthly distribution grids into quarterly or yearly distribution grids, and summing the distributions of each life-history stages into a single population-level distribution; and finally, 10) aggregating abundance estimates to the relevant spatial resolution.

2.3. Tracking data compilation and standardization

We compiled tracking data deposited in the Seabird Tracking Database (http://seabirdtracking.org/) for ACAP species, which includes data from the three most commonly used tracking devices: Global Positioning Systems (GPS), Platform Terminal Transmitters (PTT) and Global Location Sensors (GLS loggers or geolocators). All tracking data were split into data groups, which consisted of unique combinations of species, breeding site (using the same definition as in ACAP breeding site database; Phillips et al., 2016), device type (GPS, PTT or GLS), age and stage of the annual cycle. Adult non-breeding data were further split into year quarters: Quarter 1 (Q1, Jan–Mar), Quarter 2 (Q2, Apr–Jun), Quarter 3 (Q3, Jul–Sep) and Quarter 4 (Q4, Oct–Dec) to facilitate temporal integration with other data. Juvenile (first year at sea after fledging) and immature (from the beginning of second year at sea until recruitment into the breeding population) data, when available, were split into seasonal combinations (summer: combination of Q4 and Q1, and winter: combination of Q2 and Q3) instead of year quarters to increase data coverage, resulting in two data groups each for juveniles and for immatures. We assumed that seabird distributions were consistent between years, and data were aggregated over all available years; however, we recognise that weather patterns can influence location on an inter-annual basis, so results will be more robust where extensive tracking data exist across multiple years.

2.4. Kernel and bootstrap analysis of tracking data

For each data group, we estimated kernel UDs using the adehabitatHR package (Calenge, 2006) in R. Given the wide-ranging foraging distributions of our focal species, a fixed smoothing parameter (*h*) of 50 km was used for PTT and GPS data, and 200 km for GLS data. When tracking data were available from several breeding sites within an island or island group, UDs were combined by weighting the percentage of the total population involved (based on population estimates, i.e. number of annual breeding pairs, from ACAP species assessments and other sources). Tracking data from breeding sites were assumed to represent the distributions of the wider island or island-group population. Utilization distributions during pre-laying, incubation and brood-guard were multiplied by 0.5 as one member of each pair is at the breeding colony (i.e. not at sea) at any one time (during the pre-laying phase, females are generally away for longer periods while males tend to guard the nest; Carneiro et al., 2016; Hedd et al., 2014; Quillfeldt et al., 2014). The final UDs were cropped by a land mass polygon so that they only included marine areas. We assessed representativeness of each dataset following the bootstrapping methods described in Lascelles et al., (2016) and Oppel et al., (2018). Preference was given to GPS and PTT data; UDs derived from GLS data were only used when GPS and PTT data were not available. If a data group included either fewer than 5 individuals or representativeness was lower than 70%, we combined GPS and PTT with GLS data to increase sample sizes by weighting the UDs by the proportion of all individuals represented by each sample. A grid cell size of 10 km was used for all device types to enable UDs to be combined. In cases where no tracking data were available for a particular stage, the distribution was estimated based on a substitute life-history stage according to a set of rules detailed in Annex 2. At least one data group was required for both the breeding (e.g. incubation, brood-guard, etc.) and non-breeding periods to create distribution maps.

2.5. Incorporating phenological data

Phenological data obtained from the literature or provided by researchers were used to calculate monthly distributions for each life-history stage. Each month was represented by the duration of each stage of the annual cycle for each life-history stage (i.e. a weighted average of the bird distribution during the stages associated with its respective month). Utilization distributions were assigned to four distinct life-history stages: juvenile birds, immature birds, adult breeding birds and adult non-breeding birds (the latter including deferring breeders and sabbaticals but not failed breeders).

2.6. Using demographic data to estimate age and life-history structure of populations

An age- and stage-structured Leslie-Lefkovitch matrix model was used to calculate the proportion of the population represented by different life-history stages in a given year (Caswell, 2001). For each species, estimates of juvenile (average annual survival over the period from fledging until recruitment) and adult annual survival, breeding frequency (annual or biennial), breeding success and age at first breeding were obtained from the literature (see Table 1). These parameters were used in population models from which a stable-stage distribution was extracted to estimate the proportion of the population in each life-history stage (see Table 1). To convert these proportions into numbers of birds, we used population estimates from ACAP species assessments and other sources (Table 1) for each island or island group. The number of non-breeding birds (juveniles, immatures and non-breeding adults) was extrapolated from the proportion of the total population estimated to be represented by these classes, and the number of annual breeding pairs. Where no demographic estimates were available, we substituted with the proportions from another island or island group or species with similar attributes. The proportion of breeders that were successful was the product of the number of adult breeders (from the demographic models) and the breeding success; the remainder were considered to be failed breeders. For populations with breeding seasons spanning slightly more than one year (e.g. wandering Albatross, *Diomedea exulans*), we considered adults to be non-breeders for the short time between completion of a full year as a successful breeder, and fledging of the chick, in order to simplify the analysis and enable the same framework to be used for all species regardless of breeding-season duration. Monthly distribution grids for each life-history stage were multiplied by the total number of birds of a given population in each life-history stage based on the outputs of the demographic models.

2.7. Aggregation of distribution grids

The resulting monthly distributions for each life-history stage were given equal weight in generating quarterly and yearly distribution grids for each of the islands and island groups. In order to standardise the results, distribution grids were aggregated into a coarse 5 x 5 degree resolution. We chose this relatively coarse spatial resolution to enable a comparison of overlap with fishing effort data, which are often reported at this spatial resolution to many fisheries management organizations (Tuck et al., 2003). However, we note that the spatial resolution of the calculated distribution grids should always relate to the spatial scale of interest (e.g. the threat). Here we present quarterly and annual at-sea distributions, with each 5 x 5 degree cell coloured according to the percentage of the population contained within that cell. The total proportion of the population represented does not always scale to 1 as for some quarters, one member of each pair may spend extensive periods at the colony (during the pre-laying, incubation and brood-guard periods). All analyses were carried out in R software (R Core Team, 2018).

3. RESULTS

We modelled the distribution of 21 species of albatrosses and petrels. The distributions of more than half of those species (n = 13, 52%) were based on tracking data from islands and island groups accounting for more than 50% of their global populations. The species for which the greatest number of individuals were tracked were wandering and black-browed albatrosses *Thalassarche melanophris* (over 1,000 individuals each). The analyses of tracking data representativeness showed that sample sizes were adequate for the majority of adult breeding datasets, except for the pre-egg stage where data from only four out of 28 populations were representative (see Appendix 2). Juvenile and immature data were lacking or not representative for most populations; consequently, adult distributions were used as replacements for 68% of populations (Appendix 2). Demographic parameter estimates for annual juvenile and adult survival were missing for some species (see Table 1).

Population models showed that adult breeders always represented less than 50% of the total number of individuals of any species (mean: 31%, range 22–43%), and that pre-breeding birds (juveniles and immatures) accounted for over 50% of the population in 12 (43%) out of 28 populations, and over 40% in 24 (86%) of those populations (Fig. 1, Table 1). When all life-history stages were incorporated, the population-level distributions were generally less centred on breeding sites than if only adult breeders were considered. For example, the use of the Benguela Current during Quarter 1 and 4 by black-browed albatrosses from South Georgia is only highlighted when using the framework presented here, i.e., by including data on failed breeders, adult non-breeders (i.e. differing breeders), juveniles and immatures (Fig. 2). Similarly, the distribution of adult breeders of the biennially breeding wandering albatross from Crozet shows the year-round use of only the western Indian Ocean from Antarctic to subtropical waters (Fig. 3). However, if adult non-breeders (i.e. sabbaticals) and pre-breeders are taken into account, areas around the southern and eastern coast of Australia and off eastern New Zealand and Chile are also highlighted (Fig. 3). For wandering albatross, even when including data on adult non-breeders as well as breeders, the lack of data from pre-breeders reduces the importance of areas used in Australia (including the Tasman Sea) throughout the year, Chile during Quarters 2 and 3, and New Zealand in Quarter 3 (Fig. 3). Species-specific density distributions at quarterly and annual resolutions according to the framework presented here are available for all populations in Annex 2.

Combining the year-round population-level distributions of all species highlighted the importance of neritic areas such as the Patagonian Shelf, south Brazil Shelf, New Zealand Shelf and Chatham Rise, as well as the Humboldt Current, for albatrosses and petrels breeding in the Southern Ocean (Fig. 4). The main breeding sites for these species including the Falkland Islands (Islas Malvinas), South Georgia (Islas Georgias de Sur), Gough and Tristan da Cunha, Prince Edward Islands, Crozet, Kerguelen, Amsterdam and St Paul, and New Zealand subantarctic islands were used year-round, but more intensely during Quarters 4 and 1, corresponding to the austral spring and summer when most species are breeding. In Quarters 2 and 3 seabird distributions were generally more dispersed, with much greater use of the Benguela Current and the southeast Australian Shelf (Fig. 5).

4. DISCUSSION

This study presents a detailed framework and analytical tools which allow estimation of seabird density distributions at different spatial and temporal resolutions, incorporating all major life-history stages. By incorporating demographic parameters and counts of breeding adults, our approach allows the abundance of non-breeding individuals to be estimated. These often constitute >50% of all individuals of a population. Our approach incorporates phenological data for each life-history stage to facilitate temporally flexible estimates of the distribution of highly mobile species such as seabirds, and allows rapid updates of the at-sea distributions as new data become available.

Although the framework was developed for albatrosses and petrels, it can easily be modified for use with other groups and taxa for which some information on all key life-history stages is available. The resulting density distributions better reflect spatial patterns of entire populations throughout the year, and therefore will improve assessments of overlap with threats and spatial prioritisation of management actions. Our results confirmed that multiple threatened albatrosses and petrels target key areas (Patagonian Shelf, south Brazil Shelf, New Zealand Shelf and Chatham Rise, Humboldt Current) where local physical features or processes increase primary production; these same areas have previously been highlighted as important for the conservation of seabirds in general (Croxall and Wood, 2002; Delord et al., 2014; Dias et al., 2017; Lascelles et al., 2016).

This is the most comprehensive, multi-species tracking study of seabirds to date. While others have attempted to map the year-round movements and distributions of adult seabirds at global, national or regional scales (Augé et al., 2018; BirdLife International, 2004; Block et al., 2011; Raymond et al., 2015), relatively few have considered more than one life-history stage (but see Weimerskirch et al 2014, Carneiro et al., 2017; Tuck et al. 2011; Clay et al., in press). There are still major data gaps in our knowledge of the distribution of younger age classes (juveniles and immatures) and adult non-breeders for many seabirds (Phillips et al., 2017). However, several studies have found differences between the distributions of juveniles and immatures, and those of adults (de Grissac et al., 2016; Fayet et al., 2015; Gutowsky et al., 2014; Riotte-Lambert and Weimerskirch, 2013; Thiers et al., 2014; Votier et al., 2011). Our results reveal that omitting non-breeding adults from calculation of density distributions leads to an underestimation of the importance of oceanic areas which are mostly used by those life-history stages. The use of the Benguela Current by black-browed albatrosses during spring and summer, for example, is probably a result of incorporating failed and non-breeders (deferring breeding), which leave the colony much earlier than successful breeders (Phillips et al., 2005). A similar temporal pattern of movements is also seen in other seabirds (Bogdanova et al., 2011; Carneiro et al., 2016; Catry et al., 2013; Clay et al., 2016). Earlier in the season, however, non-breeders often attend the colony and their distribution is similar to that of breeding birds (Phillips et al., 2005, 2017). Hence the importance of including tracking data on juveniles, immatures and non-breeding adults depends on which period is of interest in the annual cycle, as they are often necessary for generating an at-sea distribution that adequately represents the total population. Moreover, without these data, critical marine areas may not feature in the annual population-level distributions.

For near-obligate biennial breeders such as the great albatrosses *Diomedea* spp., sooty albatrosses *Phoebetria* spp. and grey-headed albatross *Thalassarche chrysostoma*, a proportion of individuals spend the sabbatical period entirely at sea, and so segregation between different life-history stages is likely to be higher than in annual breeders. Extensive dispersal capabilities, including multiple circumpolar migrations in a single sabbatical year, may further increase segregation as many oceanic regions are available to non-breeding birds (Clay et al., 2016; Croxall et al., 2005; de Grissac et al., 2016; Weimerskirch et al., 2015). Also, the post-fledging movements of juvenile birds generally take them away from their natal colonies to reduce competition with breeding adults, which are present around the colony throughout the year (Gutowsky et al., 2014; Weimerskirch et al., 2006). All these factors contribute to the much broader dispersion of wandering albatrosses in all seasons highlighted by our framework by accounting for all life-history stages.

The bias in the population-level density distributions caused by omitting non-breeding life-history stages has important implications for management and conservation, especially as mortality of young age classes can reduce recruitment below the minimum level needed to maintain population stability (Fayet et al., 2015; Gianuca et al., 2017). Our framework provides a pragmatic approach to overcome this problem, but requires juvenile and immature tracking data. Currently, very few tracking data are available for these age classes and we had no option but to substitute distributions of other life-history stages for many populations. The replacements we used were based on general a priori assumptions of seabird movements during these stages. In the Southern Hemisphere, after leaving the natal colony, the juveniles of several species of albatrosses and petrels disperse more widely and more to the north of the species range, often to less productive waters than adults (Riotte-Lambert and Weimerskirch, 2013; Weimerskirch et al., 2014). Therefore, when not available, the juvenile distribution was replaced by the distribution of adults during the non-breeding season. In this season, birds are away from the colony and not constrained by central-place foraging, so their distribution is more similar to that of juveniles. Although there is segregation between adult breeders, non-breeders and pre-breeders in some species, this is not universal (Clay et al., 2018; Péron and Grémillet, 2013). For immatures, we therefore used the annual distribution of adults as surrogate, given that older immatures also visit the colony and can have similar attendance patterns and distributions to breeders, at least in the early-mid breeding season (de Grissac et al., 2017; Fayet et al., 2015; Jaeger et al., 2014; Weimerskirch, 2018). While our approach facilitates a rapid update of estimated distributions when new data become available, the data already in-hand provide a reasonable extrapolation that improves greatly upon estimates based solely on the distribution of breeding adults.

The importance of accounting for demographic variation among species and the correct weighting of the distribution maps by the number of individuals in each life-history stage also proved essential for assessment of the density of birds in different oceanographic regions over the annual cycle. This is especially true for albatrosses and petrels where pre-breeders and adult non-breeders can represent more than half of the total population (de Grissac et al., 2016; Gutowsky et al., 2014; Pardo et al., 2017; Clay et al., in press, this study). Since these life-history stages may have different distributions and vulnerability to certain threats, non-breeders may be exposed to different sources of mortality. Density distribution maps should be combined with cumulative threat layers in risk-mapping exercises for examining the vulnerability of each species and life-history stage. This would allow inferences to be drawn on whether some species or life-history stages are inherently more vulnerable to specific threats, or whether higher mortality is a result of different distributions (Gianuca et al., 2017).

Our results emphasize the urgent need to collect data on little-known life-history stages such as juveniles and immatures, and at colonies holding an important percentage of the global population. The lack of tracking data for juveniles, immatures and adult non-breeders is likely to bias estimates of overlap with threats and therefore potentially result in ineffective targeting of often-limited resources available for management, monitoring and conservation. Ideally, only a dataset consisting of large numbers of individuals of both sexes, collected in multiple years, and covering all major life-history stages can provide an unbiased assessment of the most important areas used by a species across all seasons (Delord et al., 2014; Clay et al., in press). Notwithstanding these potential limitations for some of the species, our framework and extensive multi-species analysis represents a major improvement on previous assessments.

5. REFERENCES

Augé, A.A., Dias, M.P., Lascelles, B., Baylis, A.M.M., Black, A., Boersma, P.D., Catry, P., Crofts, S., Galimberti, F., Granadeiro, J.P., Hedd, A., Ludynia, K., Masello, J.F., Montevecchi, W., Phillips, R.A., Pütz, K., Quillfeldt, P., Rebstock, G.A., Sanvito, S., Staniland, I.J., Stanworth, A., Thompson, D., Tierney, M., Trathan, P.N., Croxall, J.P., 2018. Framework for mapping key areas for marine megafauna to inform Marine Spatial Planning: the Falkland Islands case study. Mar. Policy 92, 61–72. https://doi.org/10.1016/j.marpol.2018.02.017

BirdLife International, 2018. IUCN Red List for birds.

BirdLife International, 2004. Tracking Ocean Wanderers: the global distribution of albatrosses and petrels. BirdLife International, Cambridge.

Block, B.A., Jonsen, I.D., Jorgensen, S.J., Winship, A.J., Shaffer, S.A., Bograd, S.J., Hazen, E.L., Foley, D.G., Breed, G.A., Harrison, A.-L., Ganong, J.E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B.R., Shillinger, G.L., Schaefer, K.M., Benson, S.R., Weise, M.J., Henry, R.W., Costa, D.P., 2011. Tracking apex marine predator movements in a dynamic ocean. Nature 475, 86–90. https://doi.org/10.1038/nature10082

Bogdanova, M.I., Daunt, F., Newell, M., Phillips, R.A., Harris, M.P., Wanless, S., 2011. Seasonal interactions in the black-legged kittiwake, Rissa tridactyla: links between breeding performance and winter distribution. Proc. R. Soc. Lond. B Biol. Sci. rspb20102601. https://doi.org/10.1098/rspb.2010.2601

Burger, A.E., Hitchcock, C.L., Davoren, G.K., 2004. Spatial aggregations of seabirds and their prey on the continental shelf off SW Vancouver Island. Mar. Ecol. Prog. Ser. 283, 279–292.

Calenge, C., 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecol. Model. 197, 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Carneiro, A.P.B., Manica, A., Clay, T.A., Silk, J.R.D., King, M., Phillips, R.A., 2016. Consistency in migration strategies and habitat preferences of brown skuas over two winters, a decade apart. Mar. Ecol. Prog. Ser. 553, 267–281. https://doi.org/10.3354/meps11781

Carneiro, A.P.B., Mulligan, B., Beare, D., Small, C., 2017. Albatross and petrel distribution in the Atlantic Ocean and overlap with ICCAT longline effort. Collect Vol Sci Pap ICCAT 73, 3285–3314.

Caswell, H., 2001. Matrix population models: construction, analysis, and interpretation, 2nd ed. Sinauer Associates, Sunderland, Massachusetts.

Catry, P., Dias, M.P., Phillips, R.A., Granadeiro, J.P., 2013. Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. Ecology 94, 1230–1235. https://doi.org/10.1890/12-2177.1

Clay, T.A., Manica, A., Ryan, P.G., Silk, J.R.D., Croxall, J.P., Ireland, L., Phillips, R.A., 2016. Proximate drivers of spatial segregation in non-breeding albatrosses. Sci. Rep. 6, 29932. https://doi.org/10.1038/srep29932

Clay, T.A., Pearmain, E.J., McGill, R.A.R., Manica, A., Phillips, R.A., 2018. Age-related variation in non-breeding foraging behaviour and carry-over effects on fitness in an extremely long-lived bird. Funct. Ecol. 32, 1832–1846. https://doi.org/10.1111/1365-2435.13120

Clua, É., Grosvalet, F., 2001. Mixed-species feeding aggregation of dolphins, large tunasand seabirds in the Azores. Aquat. Living Resour. 14, 11–18. https://doi.org/10.1016/S0990-7440(00)01097-4

Croxall, J.P., Silk, J.R.D., Phillips, R.A., Afanasyev, V., Briggs, D.R., 2005. Global Circumnavigations: tracking year-round ranges of nonbreeding albatrosses. Science 307, 249–250. https://doi.org/10.1126/science.1106042

Croxall, J.P., Wood, A.G., 2002. The importance of the Patagonian Shelf for top predator species breeding at South Georgia. Aquat. Conserv. Mar. Freshw. Ecosyst. 12, 101–118. https://doi.org/10.1002/aqc.480

de Grissac, S., Bartumeus, F., Cox, S.L., Weimerskirch, H., 2017. Early-life foraging: behavioral responses of newly fledged albatrosses to environmental conditions. Ecol. Evol. 7, 6766–6778. https://doi.org/10.1002/ece3.3210

de Grissac, S., Börger, L., Guitteaud, A., Weimerskirch, H., 2016. Contrasting movement strategies among juvenile albatrosses and petrels. Sci. Rep. 6. https://doi.org/10.1038/srep26103

Delord, K., Barbraud, C., Bost, C.-A., Deceuninck, B., Lefebvre, T., Lutz, R., Micol, T., Phillips, R.A., Trathan, P.N., Weimerskirch, H., 2014. Areas of importance for seabirds tracked from French southern territories, and recommendations for conservation. Mar. Policy 48, 1–13. https://doi.org/10.1016/j.marpol.2014.02.019

Dias, M.P., Oppel, S., Bond, A.L., Carneiro, A.P.B., Cuthbert, R.J., González-Solís, J., Wanless, R.M., Glass, T., Lascelles, B., Small, C., Phillips, R.A., Ryan, P.G., 2017. Using globally threatened pelagic birds to identify priority sites for marine conservation in the South Atlantic Ocean. Biol. Conserv. 211, 76–84. https://doi.org/10.1016/j.biocon.2017.05.009

Duffy, D.C., 1989. Seabird Foraging Aggregations: A Comparison of Two Southern Upwellings. Colon. Waterbirds 12, 164–175. https://doi.org/10.2307/1521337

Fayet, A.L., Freeman, R., Shoji, A., Padget, O., Perrins, C.M., Guilford, T., 2015. Lower foraging efficiency in immatures drives spatial segregation with breeding adults in a long-lived pelagic seabird. Anim. Behav. 110, 79–89. https://doi.org/10.1016/j.anbehav.2015.09.008

Fieberg, J., Kochanny, C.O., Lanham, 2005. Quantifying home-range overlap: the importance of the utilization distribution. J. Wildl. Manag. 69, 1346–1359. https://doi.org/10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2

Gianuca, D., Phillips, R.A., Townley, S., Votier, S.C., 2017. Global patterns of sex- and age-specific variation in seabird bycatch. Biol. Conserv. 205, 60–76. https://doi.org/10.1016/j.biocon.2016.11.028

Gutowsky, S.E., Tremblay, Y., Kappes, M.A., Flint, E.N., Klavitter, J., Laniawe, L., Costa, D.P., Naughton, M.B., Romano, M.D., Shaffer, S.A., 2014. Divergent post-breeding distribution and habitat associations of fledgling and adult Black-footed Albatrosses Phoebastria nigripes in the North Pacific. Ibis 156, 60–72. https://doi.org/10.1111/ibi.12119

Hays, G.C., Bailey, H., Bograd, S.J., Bowen, W.D., Campagna, C., Carmichael, R.H., Casale, P., Chiaradia, A., Costa, D.P., Cuevas, E., Bruyn, P.J.N. de, Dias, M.P., Duarte, C.M., Dunn, D.C., Dutton, P.H., Esteban, N., Friedlaender, A., Goetz, K.T., Godley, B.J., Halpin, P.N., Hamann, M., Hammerschlag, N., Harcourt, R., Harrison, A.-L., Hazen, E.L., Heupel, M.R., Hoyt, E., Humphries, N.E., Kot, C.Y., Lea, J.S.E., Marsh, H., Maxwell, S.M., McMahon, C.R., Sciara, G.N. di, Palacios, D.M., Phillips, R.A., Righton, D., Schofield, G., Seminoff, J.A., Simpfendorfer, C.A., Sims, D.W., Takahashi, A., Tetley, M.J., Thums, M., Trathan, P.N., Villegas-Amtmann, S., Wells, R.S., Whiting, S.D., Wildermann, N.E., Sequeira, A.M.M., 2019. Translating Marine Animal Tracking Data into Conservation Policy and Management. Trends Ecol. Evol. 0. https://doi.org/10.1016/j.tree.2019.01.009

Hays, G.C., Ferreira, L.C., Sequeira, A.M.M., Meekan, M.G., Duarte, C.M., Bailey, H., Bailleul, F., Bowen, W.D., Caley, M.J., Costa, D.P., Eguíluz, V.M., Fossette, S., Friedlaender, A.S., Gales, N., Gleiss, A.C., Gunn, J., Harcourt, R., Hazen, E.L., Heithaus, M.R., Heupel, M., Holland, K., Horning, M., Jonsen, I., Kooyman, G.L., Lowe, C.G., Madsen, P.T., Marsh, H., Phillips, R.A., Righton, D., Ropert-Coudert, Y., Sato, K., Shaffer, S.A., Simpfendorfer, C.A., Sims, D.W., Skomal, G., Takahashi, A., Trathan, P.N., Wikelski, M., Womble, J.N., Thums, M., 2016. Key Questions in Marine Megafauna Movement Ecology. Trends Ecol. Evol. 31, 463–475. https://doi.org/10.1016/j.tree.2016.02.015

Hedd, A., Montevecchi, W.A., Phillips, R.A., Fifield, D.A., 2014. Seasonal sexual segregation by monomorphic Sooty Shearwaters Puffinus griseus reflects different reproductive roles during the pre-laying period. PLOS ONE 9, e85572. https://doi.org/10.1371/journal.pone.0085572

Jaeger, A., Goutte, A., Lecomte, V.J., Richard, P., Chastel, O., Barbraud, C., Weimerskirch, H., Cherel, Y., 2014. Age, sex, and breeding status shape a complex foraging pattern in an extremely long-lived seabird. Ecology 95, 2324–2333. https://doi.org/10.1890/13-1376.1

Johnston, A., Fink, D., Reynolds, M.D., Hochachka, W.M., Sullivan, B.L., Bruns, N.E., Hallstein, E., Merrifield, M.S., Matsumoto, S., Kelling, S., 2015. Abundance models improve spatial and temporal prioritization of conservation resources. Ecol. Appl. 25, 1749–1756. https://doi.org/10.1890/14-1826.1

Lascelles, B.G., Taylor, P.R., Miller, M.G.R., Dias, M.P., Oppel, S., Torres, L., Hedd, A., Corre, M.L., Phillips, R.A., Shaffer, S.A., Weimerskirch, H., Small, C., 2016. Applying global criteria to tracking data to define important areas for marine conservation. Divers. Distrib. 22, 422–431. https://doi.org/10.1111/ddi.12411

Lewison, R., Oro, D., Godley, B.J., Underhill, L., Bearhop, S., Wilson, R.P., Ainley, D., Arcos, J.M., Boersma, P.D., Borboroglu, P.G., Boulinier, T., Frederiksen, M., Genovart, M., González-Solís, J., Green, J.A., Grémillet, D., Hamer, K.C., Hilton, G.M., Hyrenbach, K.D., Martínez-Abraín, A., Montevecchi, W.A., Phillips, R.A., Ryan, P.G., Sagar, P., Sydeman, W.J., Wanless, S., Watanuki, Y., Weimerskirch, H., Yorio, P., 2012.

Research priorities for seabirds: improving conservation and management in the 21st century. Endanger. Species Res. 17, 93–121. https://doi.org/10.3354/esr00419

Nur, N., Jahncke, J., Herzog, M.P., Howar, J., Hyrenbach, K.D., Zamon, J.E., Ainley, D.G., Wiens, J.A., Morgan, K., Ballance, L.T., Stralberg, D., 2011. Where the wild things are: predicting hotspots of seabird aggregations in the California Current System. Ecol. Appl. 21, 2241–2257. https://doi.org/10.1890/10-1460.1

Oppel, S., Bolton, M., Carneiro, A.P.B., Dias, M.P., Green, J.A., Masello, J.F., Phillips, R.A., Owen, E., Quillfeldt, P., Beard, A., Bertrand, S., Blackburn, J., Boersma, P.D., Borges, A., Broderick, A.C., Catry, P., Cleasby, I., Clingham, E., Creuwels, J., Crofts, S., Cuthbert, R.J., Dallmeijer, H., Davies, D., Davies, R., Dilley, B.J., Dinis, H.A., Dossa, J., Dunn, M.J., Efe, M.A., Fayet, A.L., Figueiredo, L., Frederico, A.P., Gjerdrum, C., Godley, B.J., Granadeiro, J.P., Guilford, T., Hamer, K.C., Hazin, C., Hedd, A., Henry, L., Hernández-Montero, M., Hinke, J., Kokubun, N., Leat, E., Tranquilla, L.M., Metzger, B., Militão, T., Montrond, G., Mullié, W., Padget, O., Pearmain, E.J., Pollet, I.L., Pütz, K., Quintana, F., Ratcliffe, N., Ronconi, R.A., Ryan, P.G., Saldanha, S., Shoji, A., Sim, J., Small, C., Soanes, L., Takahashi, A., Trathan, P., Trivelpiece, W., Veen, J., Wakefield, E., Weber, N., Weber, S., Zango, L., Daunt, F., Ito, M., Harris, M.P., Newell, M.A., Wanless, S., González-Solís, J., Croxall, J., 2018. Spatial scales of marine conservation management for breeding seabirds. Mar. Policy 98, 37–46. https://doi.org/10.1016/j.marpol.2018.08.024

Pardo, D., Forcada, J., Wood, A.G., Tuck, G.N., Ireland, L., Pradel, R., Croxall, J.P., Phillips, R.A., 2017. Additive effects of climate and fisheries drive ongoing declines in multiple albatross species. Proc. Natl. Acad. Sci. 114, E10829–E10837. https://doi.org/10.1073/pnas.1618819114

Péron, C., Grémillet, D., 2013. Tracking through Life Stages: Adult, Immature and Juvenile Autumn Migration in a Long-Lived Seabird. PLOS ONE 8, e72713. https://doi.org/10.1371/journal.pone.0072713

Phillips, R.A., Lewis, S., González-Solís, J., Daunt, F., 2017. Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. Mar. Ecol. Prog. Ser. 578, 117–150. https://doi.org/10.3354/meps12217

Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V., Bennett, V.J., 2005. Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. Ecology 86, 2386–2396. https://doi.org/10.1890/04-1885

Quillfeldt, P., Phillips, R.A., Marx, M., Masello, J.F., 2014. Colony attendance and at-sea distribution of thin-billed prions during the early breeding season. J. Avian Biol. 45, 315–324. https://doi.org/10.1111/jav.00307

Raymond, B., Lea, M.-A., Patterson, T., Andrews-Goff, V., Sharples, R., Charrassin, J.-B., Cottin, M., Emmerson, L., Gales, N., Gales, R., Goldsworthy, S.D., Harcourt, R., Kato, A., Kirkwood, R., Lawton, K., Ropert-Coudert, Y., Southwell, C., Hoff, J. van den, Wienecke, B., Woehler, E.J., Wotherspoon, S., Hindell, M.A., 2015. Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. Ecography 38, 121–129. https://doi.org/10.1111/ecog.01021

Riotte-Lambert, L., Weimerskirch, H., 2013. Do naive juvenile seabirds forage differently from adults? Proc. R. Soc. B Biol. Sci. 280. https://doi.org/10.1098/rspb.2013.1434

Sequeira, A.M.M., Rodríguez, J.P., Eguíluz, V.M., Harcourt, R., Hindell, M., Sims, D.W., Duarte, C.M., Costa, D.P., Fernández-Gracia, J., Ferreira, L.C., Hays, G.C., Heupel, M.R., Meekan, M.G., Aven, A., Bailleul, F., Baylis, A.M.M., Berumen, M.L., Braun, C.D., Burns, J., Caley, M.J., Campbell, R., Carmichael, R.H., Clua, E., Einoder, L.D., Friedlaender, A., Goebel, M.E., Goldsworthy, S.D., Guinet, C., Gunn, J., Hamer, D., Hammerschlag, N., Hammill, M., Hückstädt, L.A., Humphries, N.E., Lea, M.-A., Lowther, A., Mackay, A., McHuron, E., McKenzie, J., McLeay, L., McMahon, C.R., Mengersen, K., Muelbert, M.M.C., Pagano, A.M., Page, B., Queiroz, N., Robinson, P.W., Shaffer, S.A., Shivji, M., Skomal, G.B., Thorrold, S.R., Villegas-Amtmann, S., Weise, M., Wells, R., Wetherbee, B., Wiebkin, A., Wienecke, B., Thums, M., 2018. Convergence of marine megafauna movement patterns in coastal and open oceans. Proc. Natl. Acad. Sci. 115, 3072–3077. https://doi.org/10.1073/pnas.1716137115

Thiers, L., Delord, K., Barbraud, C., Phillips, R.A., Pinaud, D., Weimerskirch, H., 2014. Foraging zones of the two sibling species of giant petrels in the Indian Ocean throughout the annual cycle: implication for their conservation. Mar. Ecol. Prog. Ser. 499, 233–248. https://doi.org/10.3354/meps10620

Tuck, G.N., Phillips, R.A., Small, C., Thomson, R.B., Klaer, N.L., Taylor, F., Wanless, R.M., Arrizabalaga, H., 2011. An assessment of seabird–fishery interactions in the Atlantic Ocean. ICES J. Mar. Sci. 68, 1628–1637. https://doi.org/10.1093/icesjms/fsr118

Tuck, G.N., Polacheck, T., Bulman, C.M., 2003. Spatio-temporal trends of longline fishing effort in the Southern Ocean and implications for seabird bycatch. Biol. Conserv. 114, 1–27. https://doi.org/10.1016/S0006-3207(02)00378-6

Tuck, G.N., Thomson, R.B., Barbraud, C., Delord, K., Louzao, M., Herrera, M., Weimerskirch, H., 2015. An integrated assessment model of seabird population dynamics: can individual heterogeneity in susceptibility to fishing explain abundance trends in Crozet wandering albatross? J. Appl. Ecol. 52, 950–959. https://doi.org/10.1111/1365-2664.12462

Votier, S.C., Grecian, W.J., Patrick, S., Newton, J., 2011. Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. Mar. Biol. 158, 355–362. https://doi.org/10.1007/s00227-010-1563-9

Weimerskirch, H., 2018. Linking demographic processes and foraging ecology in wandering albatross—Conservation implications. J. Anim. Ecol. 87, 945–955. https://doi.org/10.1111/1365-2656.12817

Weimerskirch, H., Åkesson, S., Pinaud, D., 2006. Postnatal dispersal of wandering albatrosses Diomedea exulans: implications for the conservation of the species. J. Avian Biol. 37, 23–28. https://doi.org/10.1111/j.2006.0908-8857.03675.x

Weimerskirch, H., Cherel, Y., Delord, K., Jaeger, A., Patrick, S.C., Riotte-Lambert, L., 2014. Lifetime foraging patterns of the wandering albatross: Life on the move! J. Exp. Mar. Biol. Ecol., Charismatic marine mega-fauna 450, 68–78. https://doi.org/10.1016/j.jembe.2013.10.021

Weimerskirch, H., Delord, K., Guitteaud, A., Phillips, R.A., Pinet, P., 2015. Extreme variation in migration strategies between and within wandering albatross populations during their sabbatical year, and their fitness consequences. Sci. Rep. 5. https://doi.org/10.1038/srep08853

Williams, R., Grand, J., Hooker, S.K., Buckland, S.T., Reeves, R.R., Rojas-Bracho, L., Sandilands, D., Kaschner, K., 2014. Prioritizing global marine mammal habitats using density maps in place of range maps. Ecography 37, 212–220. https://doi.org/10.1111/j.1600-0587.2013.00479.x

ANNEX 1: TABLES AND FIGURES

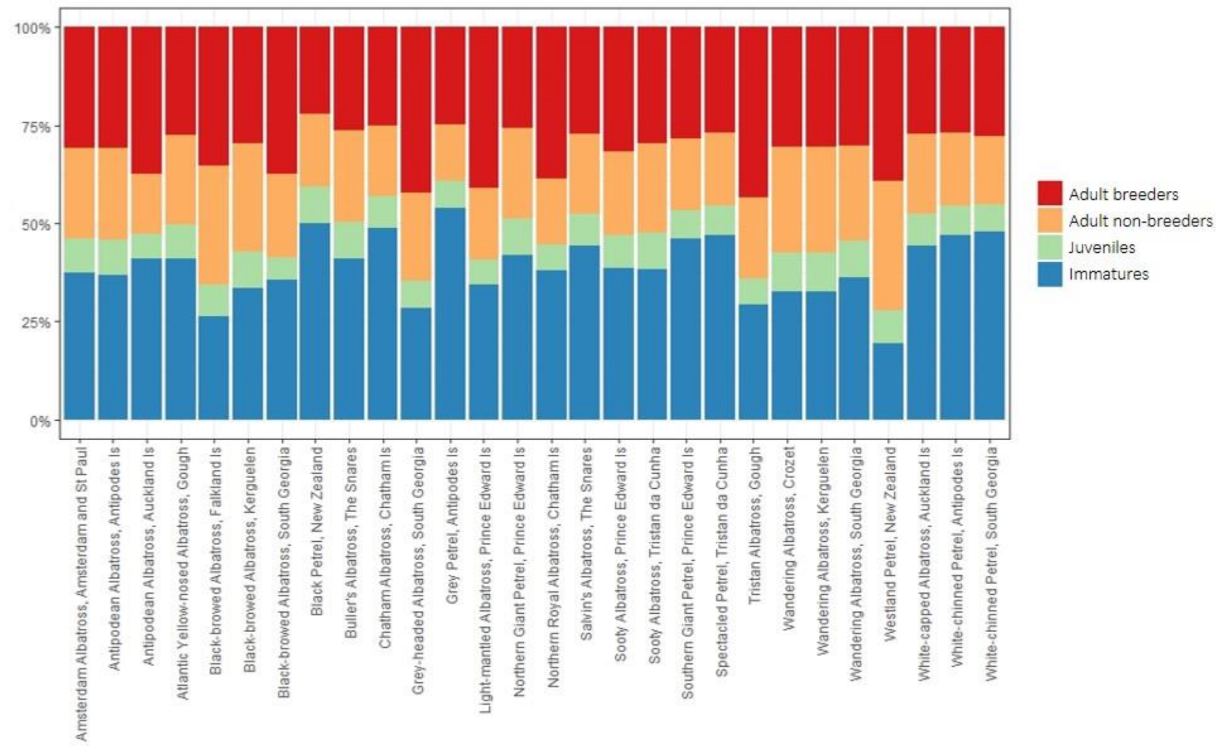

Figure 1. The proportion of the population represented by each major life-history stage for 21 species of albatrosses and petrels (28 populations) breeding in the southern ocean. Four distinct life-history stages were considered here: juveniles during their first year at sea, immatures (from second year at sea until recruitment into the breeding population; both combined also referred to as ‘pre-breeders’), adult breeders and adult non-breeders.

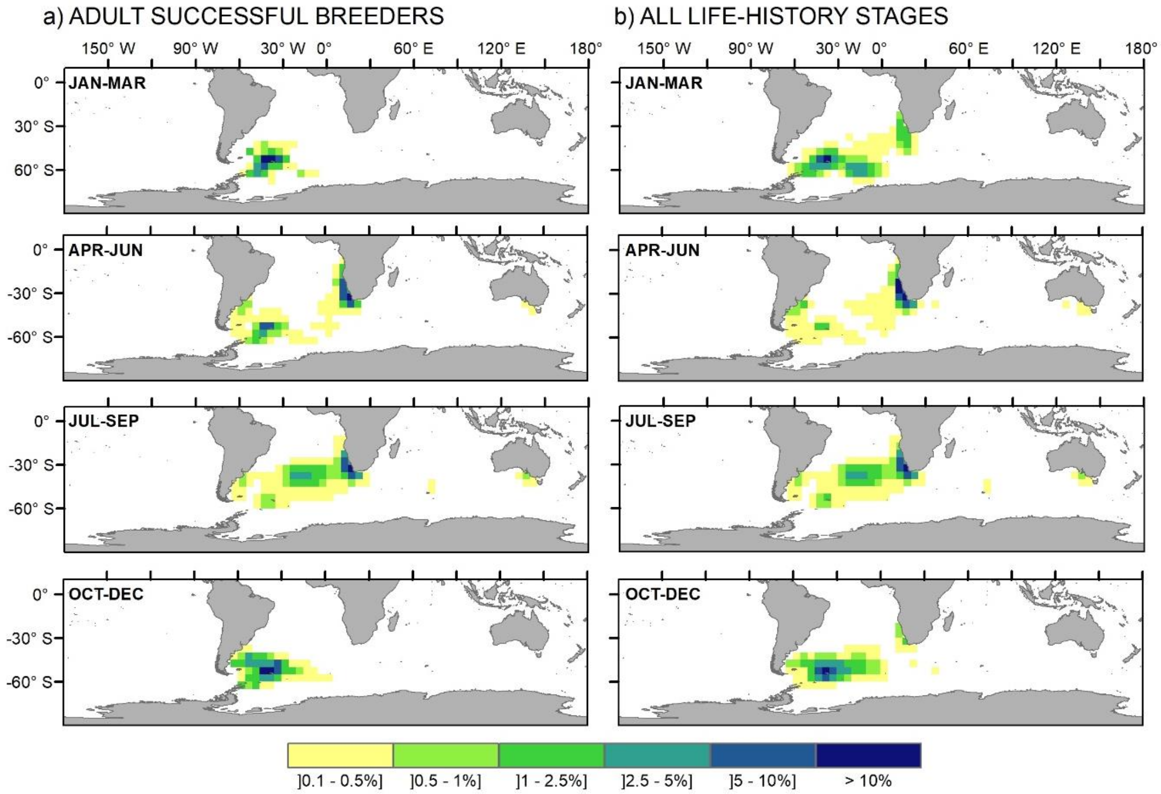

Figure 2: The quarterly density distributions of black-browed albatrosses from South Georgia (Islas Georgias del Sur). The colour gradient refers to the percentage of the population represented within each 5 x 5° grid. Darker shades (of blue) depict a greater density of birds. a) Density distribution grids based solely on adult successful breeders (i.e. including pre-egg, incubation, brood-guard, post-guard and non-breeding stages). Density is represented as percentage of the total number of adult successful breeders at-sea in each quarter; b) population-level density distributions created using this framework (incorporating information on adult successful and failed breeders, adult non-breeders, juveniles and immatures). Density is represented as percentage of the total population in each quarter.

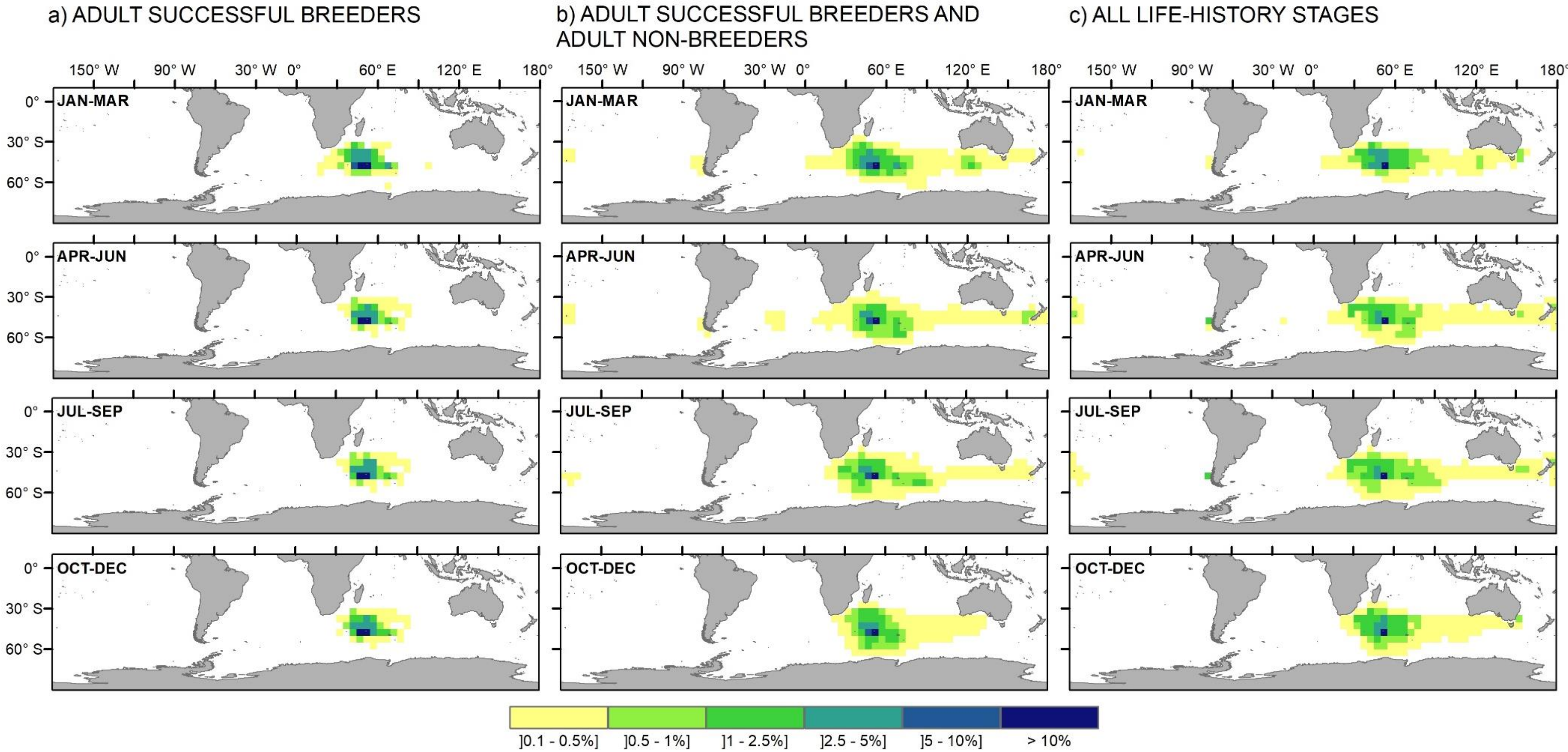

Figure 3. The quarterly density distributions of wandering albatrosses from Crozet. The colour gradient refers to the percentage of the population represented within each 5 x 5° grid. Darker shades (of blue) depict a greater density of birds. a) Density distribution grids based only on adult successful breeders (i.e. using distributions of adults during the pre-egg, incubation, brood-guard, and post-guard stages); b) density distribution grids based on data for adult successful breeders and adult non-breeders; c) density distributions are the result of applying the framework presented here, which includes information for adult breeders, adult non-breeders, juveniles and immatures weighted according to the demographic models.

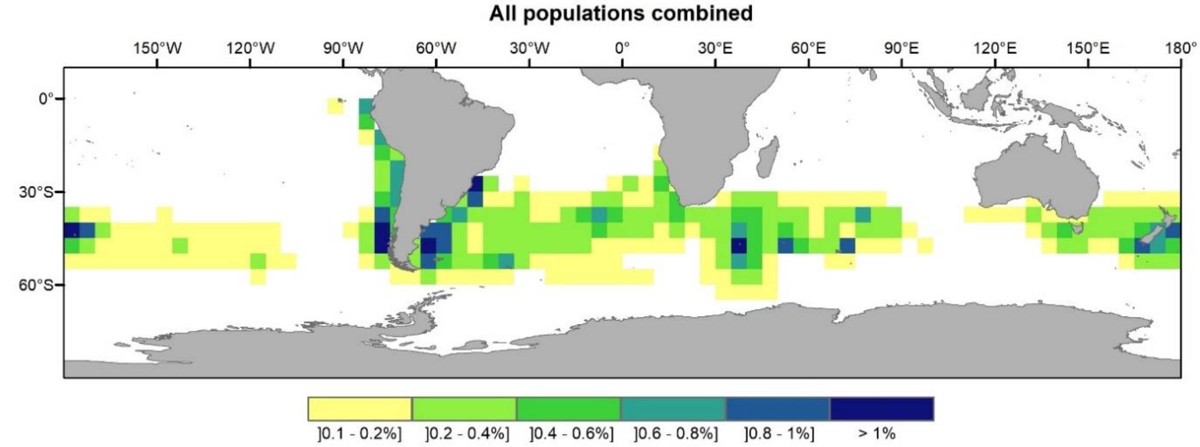

Figure 4. The annual density distribution of 21 species of albatrosses and petrels (28 populations) breeding in the southern ocean based on tracking, phenology and demography data. Equal weight is given to each of the 28 populations (i.e. the proportions of each population are averaged) and are illustrated as relative density. The colour gradient refers to the percentage of the population represented within each 5 x 5° grid. Darker shades (of blue) depict a greater density of birds.

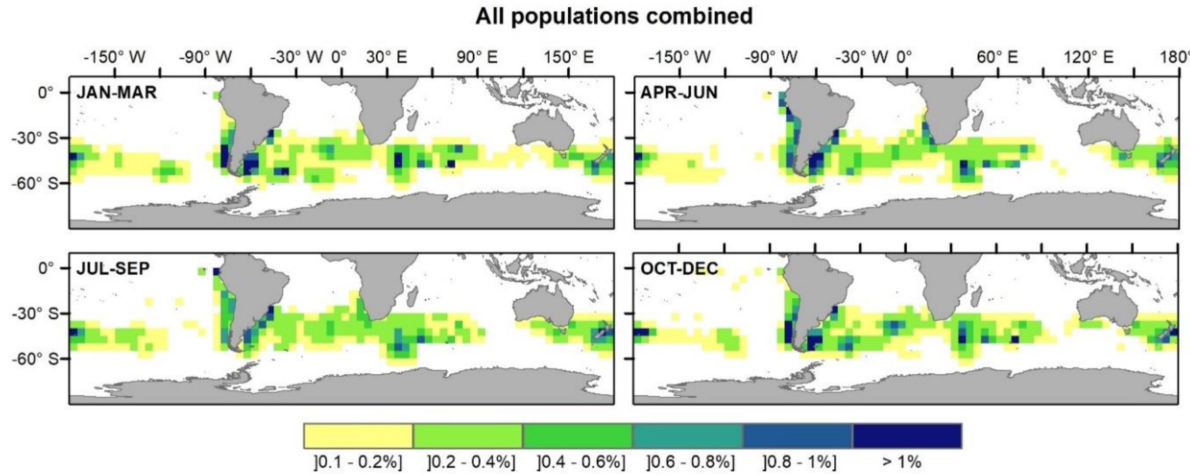

Figure 5. The quarterly density distribution of 21 species of albatrosses and petrels (28 populations) breeding in the southern ocean based on tracking, phenology and demography data. Equal weight is given to each of the 28 populations (i.e. the proportions of each population are averaged) and are illustrated as relative density. The colour gradient refers to the percentage of the population represented within each 5 x 5° grid. Darker shades (of blue) depict a greater density of birds.

Table 1. Population numbers (i.e. estimates of annual breeding pairs), demographic estimates of annual juvenile and adult survival, breeding frequency (annual or biennial) and success and age at first breeding for the species and island groups from which tracking data were available for the analyses. These parameters were input in a stage-structured Leslie-Lefkovitch matrix model to estimate the number of birds in each life-history stage (juvenile, immature, adult breeders, adult non-breeders). Note that data were only considered when at least 5 individuals were tracked during at least one breeding and one non-breeding stage, and data met representativeness criteria (see text for details).

Common name	Island Group	N. breeding pairs	Ann juv. survival	Ann adult survival	A or B	Breeding success	Age 1st breeding	Reference	Adult breeders	Adult non-breeders	Juveniles	Immatures
Amsterdam Albatross	Amsterdam and St Paul	40-50	0.936	0.971	B	0.677	9.4	1, 2	52	39	15	63
Antipodean Albatross	Antipodes Islands	3,945	0.880	0.880	B	0.600	12.0	3, 4	12,572	9,470	3,630	14,990
	Auckland Islands	5,817	0.880	0.889	B	0.253	12.4	5, 6	10,530	4,331	1,769	11,590
Atlantic Yellow-nosed Albatross	Gough	5,300	0.835	0.920	A	0.630	10.5	7, 8	10,600	8,764	3,331	15,864
Black Petrel	New Zealand	1,358	0.792	0.900	A	0.770	6.0	9, 10	3,300	2,787	1,351	7,484
Black-browed Albatross	Falkland Islands	399,416	0.653 [a]	0.942	A	0.620	7.5	11, 12, 13	798,832	688,467	182,768	600,772
	South Georgia	74,296	0.653	0.875	A	0.300	12.1	13, 14	148,592	83,289	22,624	141,519
	Kerguelen	3,215	0.776	0.910	A	0.725	10.0	13, 15, 16	6,430	6,043	2,028	7,287
Buller's Albatross	The Snares	8,713	0.910	0.950	A	0.727	12.0	13, 17	17,426	15,524	6,100	27,093
Chatham Albatross	Chatham Island	5,247	0.828	0.887	A	0.463	8.0	18, 19	9,150	6,598	2,890	17,794
Grey Petrel	Antipodes Islands	53,000	0.923 [b]	0.940	A	0.458 [c]	7.0	13, 20	106,000	62,272	29,360	232,157
Grey-headed Albatross	South Georgia	47,674	0.764	0.952	B	0.365	14.2	13, 14, 21	95,348	50,401	15,682	64,260
Light-mantled Albatross	Prince Edward Islands	657	0.876	0.959	B	0.352	11.0	13, 18	1,314	583	206	1,103
Northern Giant Petrel	Prince Edward Islands	464	0.880 [d]	0.880	A	0.741	10.0	13	928	830	334	1,507
Northern Royal Albatross	Chatham Island	5,800	0.876	0.960	B	0.427	9.0	13, 18	11,600	5,125	1,959	11,482
Salvin's Albatross	The Snares	1,195	0.939	0.967	A	0.467	9.0	13, 18, 22	2,390	1,802	714	3,918
Sooty Albatross	Prince Edward Islands	2,493	0.883 [e]	0.898 [e]	B	0.540	12.0	13	4,986	3,336	1,314	6,058
	Tristan da Cunha	8,458	0.883 [e]	0.898 [e]	B	0.480	12.0	13, 8	16,916	13,178	5,232	22,010
Southern Giant Petrel	Prince Edward Islands	2,343	0.840 [d]	0.840	A	0.461	8.0	13	4,686	3,031	1,183	7,661

Common name	Island Group	N. breeding pairs	Ann juv. survival	Ann adult survival	A or B	Breeding success	Age 1st breeding	Reference	Adult breeders	Adult non-breeders	Juveniles	Immatures
Spectacled Petrel	Tristan da Cunha	30,000	0.840	0.970	A	0.600	5.0	23	20,000	13,743	5,591	34,696
Tristan Albatross	Gough	1,800	0.762	0.910	B	0.230	10.0	7, 8, 24	3,526	1,694	535	2,395
Wandering Albatross	South Georgia	1,858	0.680	0.879	B	0.808	9.8	13, 14	2,840	2,290	870	3,396
	Crozet	1,815	0.825	0.945	B	0.730	10.0	13, 25, 26	3,716	3,292	1,176	3,985
	Kerguelen	1,184	0.825 [e]	0.931 [e]	B	0.736 [e]	10 [e]	26	2,374	2,103	751	2,546
Westland Petrel	New Zealand	4,000	0.875	0.936	B	0.607	7.7	13, 27	8,000	6,682	1,740	3,925
White-capped Albatross	Auckland Islands	97,089	0.834	0.960	A	0.63	9.0	13, 18, 28	194,178	146,380	57,986	318,352
White-chinned Petrel	South Georgia	773,150	0.653	0.875	A	0.444	6.0	13, 29	1,546,300	958,386	386,327	2,665,822
	Antipodes Islands	58,725	0.923 [d]	0.94	A	0.514 [e]	6.5	20	117,450	80,704	32,835	203,750

[a] Values are from Black-browed Albatross at Kerguelen. [b] Values are from Black Petrel at Great Barrier Island. [c] Values are from Macquarie Island. [d] Replaced with adult annual survival of the same species at same island group. [e] Values are from the same species at Crozet.

[1] Jaeger et al., (2018). [2] Rivalan et al., (2010). [3] Edwards et al., (2017). [4] Elliot and Walker, (2017). [5] Francis et al., (2015). [6] Elliot et al., (2016). [7] Cuthbert et al., (2003). [8] Cuthbert et al., (2014). [9] Bell et al., (2011). [10] Bell et al., (2007). [11] Campioni et al., (2017). [12] Catry et al., (2011). [13] ACAP, 2018. [14,15] Pardo et al., (2017a, 2017b). [16] Nevoux et al., (2010). [17] Francis and Sagar, (2012). [18] Abraham et al., (2016). [19] Fraser et al., (2011). [20] Richard et al., (2017). [21] Clay et al., (2016). [22] Sagar et al., (2011). [23] Ryan et al., (2006). [24] Wanless et al., (2009). [25] Barbraud and Weimerskirch, (2012). [26] Delord et al., (2014). [27] Waugh et al., (2015). [28] Francis, (2012). [29] Clay et al., (in press).

ANNEX 2: APPENDIX

Data replacements

Adult breeding birds were further split into two status classes: successful and failed breeders. As very few tracks were available for failed breeders, we assumed that their distribution equalled the distribution of adult successful breeders until half-way through the breeding season, and that after this date, failed breeders used the same areas as adult non-breeders. This assumption may have some inaccuracies if birds fail earlier or later during the breeding season, and the framework can be refined with more information on how the accumulation curve of failed breeders throughout the breeding season is, to better reflect which proportion of birds moves from the breeders to non-breeders distributions during each month. The distribution of adult breeders started from the beginning of the breeding season and spanned over breeding and non-breeding periods, including the pre-laying, incubation, brood-guard, post-guard, and non-breeding phases. When tracking data were not available for the pre-laying phase we used incubation data as a replacement. For some species, brood-guard and post-guard were combined into a chick-rearing stage or into a “breeding” stage (also representing the pre-laying and incubation). Adult non-breeders assumed the non-breeding distribution only. Adult non-breeding data were further split into year quarters according to the dates of the locations to facilitate temporal integration with other data, resulting in four different data groups: Quarter 1 (Q1): Jan-Mar, Quarter 2 (Q2): Apr-Jun, Quarter 3 (Q3): Jul-Sep, Quarter 4(Q4): Oct-Dec).

Juvenile and immature data, when available, were split into seasonal combinations (summer: combination of Q4 and Q1, and winter: combination of Q2 and Q3), resulting in two data groups each for juveniles and for immatures. It was not possible to split juvenile and immature data into year quarters because of the poor coverage of the data. In the southern hemisphere, after leaving the natal colony, several species of albatrosses and petrels disperse more widely to the north of the species range spending more time in subtropical waters when compared with adults which are more likely to stay in subantarctic waters (de Grissac et al., 2016; Gianuca et al., 2017; Riotte-Lambert and Weimerskirch, 2013; Weimerskirch, 2018; Weimerskirch et al., 2014). With time, immatures start to behave more similarly to breeding adults, visiting the colony for the first time and then visiting the colony regularly before starting to breed (Fayet et al., 2015; Jaeger et al., 2014; Votier et al., 2011; Weimerskirch, 2018). Therefore, when not available, the juvenile distribution was replaced by the winter distribution of adults (non-breeding Q2 and Q3), when birds are away from the colony and not constrained by central place foraging, which is likely to be similar to the distribution of juveniles (Weimerskirch et al., 2006). For immatures, the annual distribution of adults was used as immatures also visit the breeding grounds and have similar strategies to those of breeders.

The replacements were only conducted in cases where sufficient tracking data for a given life-history stage were unavailable, and were based on general assumptions and expert opinion of movements during these stages.

Table A1. Sample sizes (number of birds) for tracking data by species, island or island group and stage of the annual cycle. Values in italics (never reached asymptote) and bold (not tested because of different smoothing factors) are those that may not have been representative of the tracked population. Where there were no tracking data or when data was not representative, appropriate data substitutions were used.

	Pre-egg	Incubation	Brood-guard	Post-guard	Non-breeding	Juvenile	Immature
Amsterdam Albatross							
Amsterdam and St Paul	No data	29	17	10	14	11	*5*
Antipodean Albatross							
Antipodes Islands	6	36	23	13	**59**	*3*[1]	
Auckland Islands	8	18	9	7	**91**	No data	No data
Atlantic Yellow-nosed							
Gough	No data	42	**24**	20	37	No data	No data
Black Petrel							
New Zealand	No data	40	31	15	*12*	No data	No data
Black-browed Albatross							
Falkland Islands	22	109	246	30[2]	33	No data	No data
Kerguelen	No data	8	24[3]		123	No data	No data
South Georgia	23	63	78	24	25	*11*	No data
Buller's Albatross							
The Snares	No data	27	85	13	30	No data	No data
Chatham Albatross							
Chatham Island		29[4]			15	No data	No data
Grey Petrel							
Antipodes Islands		18[4]			*18*	No data	No data
Grey-headed Albatross							
South Georgia	No data	30	86	38	22	*5*	No data
Light-mantled Albatross							
Prince Edward Islands		*8*[4]			*6*	No data	No data
Northern Giant-petrel							
Prince Edward Islands	No data	*14*	16[3]		16	No data	No data
Northern Royal Albatross							
Chatham Island	No data	9	*4*[4]		**9**	No data	No data
Salvin's Albatross							
The Snares		22[4]			22	No data	No data
Sooty Albatross							
Tristan da Cunha	No data	**19**	12	10	*13*	No data	No data
Prince Edward Islands		10[4]			*10*	No data	No data
Southern Giant-petrel							
Prince Edward Islands	No data	*8*	7[3]		8	No data	No data
Spectacled Petrel							
Tristan da Cunha		*8*[4]			10	No data	No data
Tristan Albatross							
Gough	No data	35	9	12	26	*5*	No data

	Pre-egg	Incubation	Brood-guard	Post-guard	Non-breeding	Juvenile	Immature
Wandering Albatross							
Crozet	No data	319	79	30	95	*13*	11
Kerguelen	No data	14	12	7	23	*11*	10
South Georgia	No data	65	72	145	91	**39**	21
Westland Petrel							
New Zealand		8[4]		12	*8*	No data	No data
White-capped Albatross							
Auckland Islands	No data	27	52	60	24	No data	No data
White-chinned Petrel							
Antipodes Islands		13[4]			*14*	No data	No data
South Georgia	No data	16	*6[4]*		10	*13*	No data

[1] Breeding-stage from the original dataset classified as juvenile/immature. [2] Breeding-stage from the original dataset classified both as post-guard and breeding. [3] Breeding-stage from the original dataset classified as chick-rearing. [4] Breeding-stage from the original dataset classified as breeding

Table A2: Number of individuals per year-quarter and year-round. The population represented varies between quarters because one member of each pair is at the colony at any one time during the pre-laying, incubation and brood-guard stages, and this at-colony bird is not represented in our distributions.

Common name	Island or Island Group	Quarter 1 (Jan-Mar)	Quarter 2 (Apr-Jun)	Quarter 3 (Jul-Sep)	Quarter 4 (Oct-Dec)	Year-round
Amsterdam Albatross	Amsterdam and St Paul	152	148	170	169	160
Antipodean Albatross	Antipodes Islands	34,356	37,643	40,691	40,660	38,338
Antipodean Albatross	Auckland Islands	22,862	26,698	28,195	27,061	26,204
Atlantic Yellow-nosed Albatross	Gough	38,489	38,612	36,849	33,862	36,953
Black Petrel	New Zealand	12,062	14,247	12,070	10,214	12,148
Black-browed Albatross	Falkland Islands	2,251,021	2,278,562	2,216,613	1,875,717	2,155,478
Black-browed Albatross	Kerguelen	21,304	21,937	21,586	18,427	20,814
Black-browed Albatross	South Georgia	374,650	402,509	400,171	324,453	375,446
Buller's Albatross	The Snares	57,037	63,829	65,823	66,187	63,219
Chatham Albatross	Chatham Island	36,825	37,171	34,732	32,766	35,374
Grey Petrel	Antipodes Islands	401,761	392,775	428,608	428,437	412,895
Grey-headed Albatross	South Georgia	214,506	225,212	221,837	177,687	209,810
Light-mantled Albatross	Prince Edward Islands	3,065	3,179	3,206	2,571	3,005
Northern Giant Petrel	Prince Edward Islands	3,594	3,585	3,293	3,400	3,468
Northern Royal Albatross	Chatham Island	25,876	30,232	30,095	24,941	27,786
Salvin's Albatross	The Snares	8,799	8,834	8,102	7,893	8,407
Sooty Albatross	Tristan da Cunha	57,202	57,172	55,586	48,792	54,688
Sooty Albatross	Prince Edward Islands	15,615	15,681	15,181	13,177	14,913
Southern Giant Petrel	Prince Edward Islands	16,496	16,489	16,029	14,489	15,876
Spectacled Petrel	Tristan da Cunha	74,200	74,292	71,370	64,391	71,063
Tristan Albatross	Gough	6,390	8,146	8,152	7,367	7,514
Wandering Albatross	Crozet	10,264	11,707	12,112	11,604	11,422
Wandering Albatross	Kerguelen	6,595	7,481	7,737	7,428	7,310
Wandering Albatross	South Georgia	7,961	9,191	9,357	8,833	8,835
Westland Petrel	New Zealand	20,524	17,921	18,358	20,272	19,269
White-capped Albatross	Auckland Islands	661,192	713,981	715,359	637,355	681,972
White-chinned Petrel	Antipodes Islands	415,760	436,632	435,511	399,485	421,847
White-chinned Petrel	South Georgia	5,355,169	5,502,009	5,515,191	4,894,489	5,316,714

Figure A1-A28: Annual population-level density distributions for 21 species of albatrosses and petrels (28 populations) breeding in the Southern Ocean based on tracking, phenology and demography data. The colour gradient refers to the percentage of the population represented within each 5 x 5° grid. Darker shades (of blue) depict a greater density of birds. For details on the number of individuals, see Table A2.

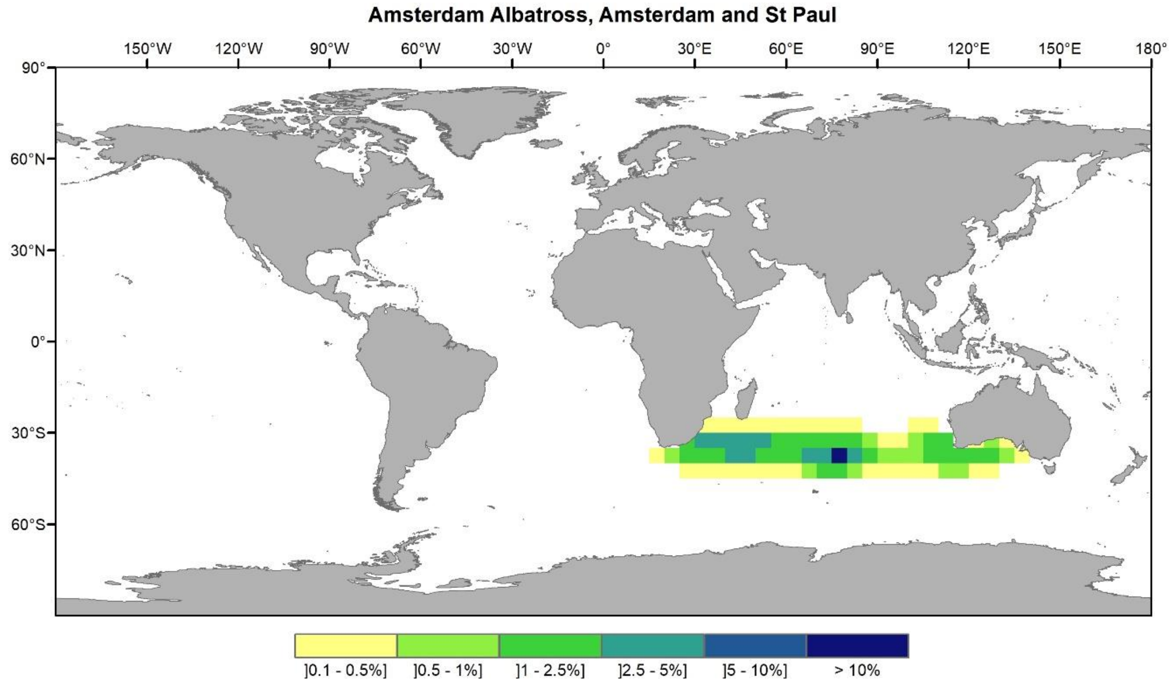

Figure A1: Amsterdam Albatross, Amsterdam and St Paul

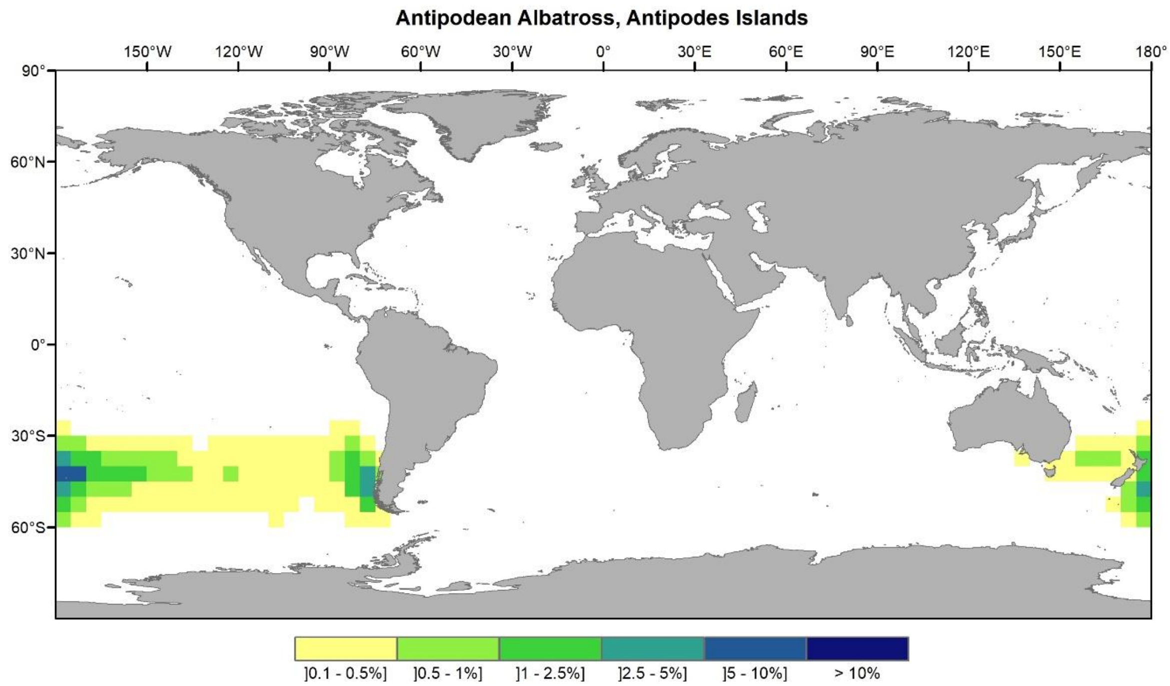

Figure A2: Antipodean Albatross, Antipodes Island

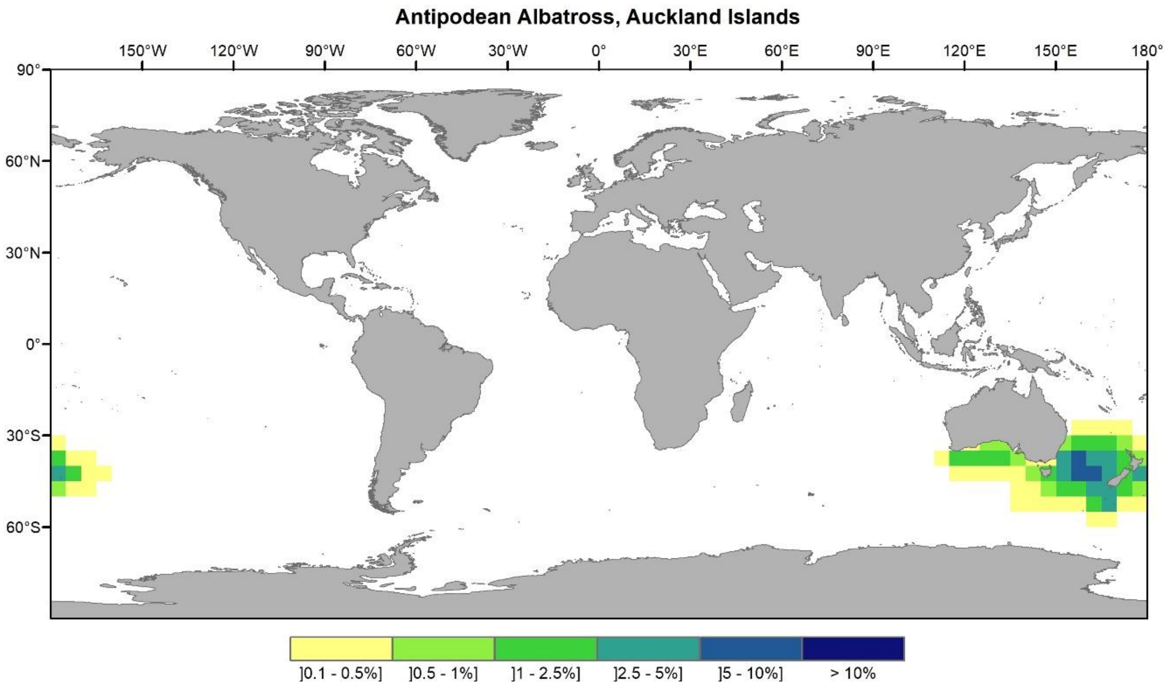

Figure A3: Antipodean Albatross, Auckland Islands

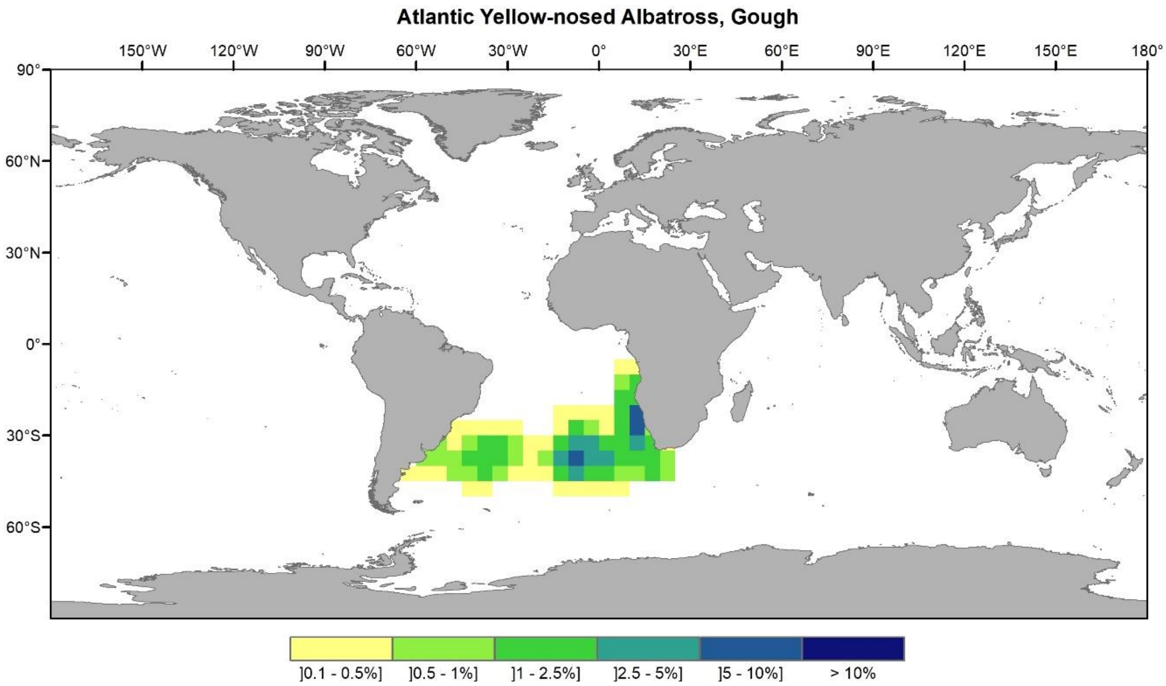

Figure A4: Atlantic Yellow-nosed Albatross, Gough

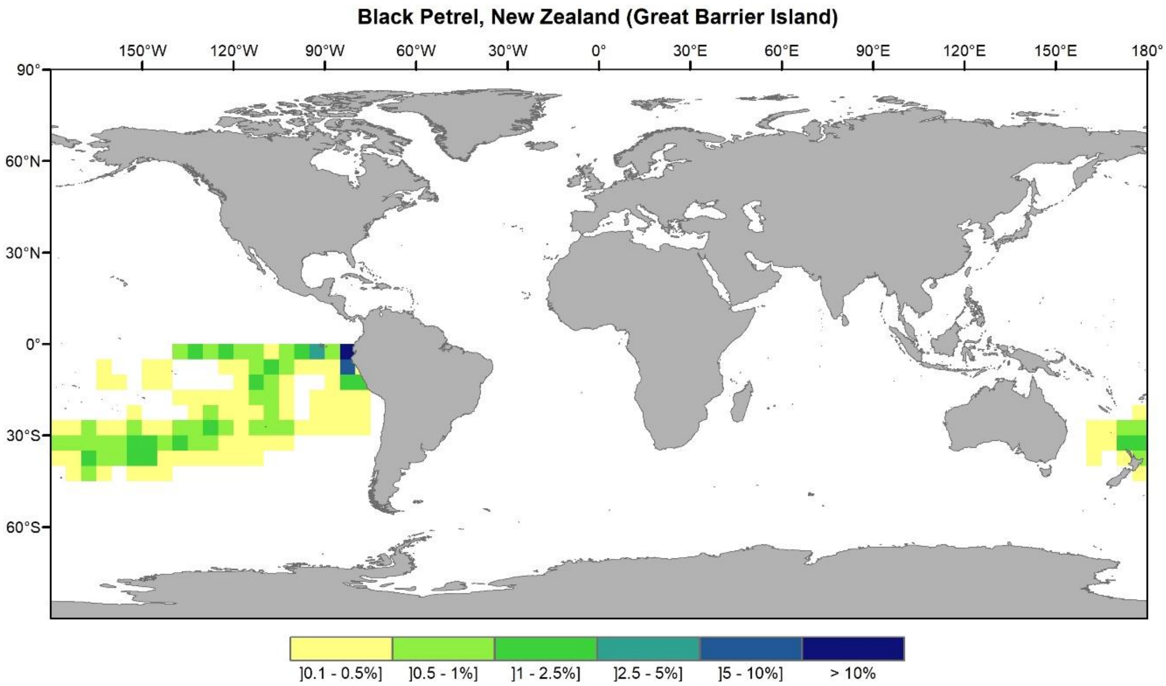

Figure A5: Black Petrel, New Zealand (Great Barrier Island)

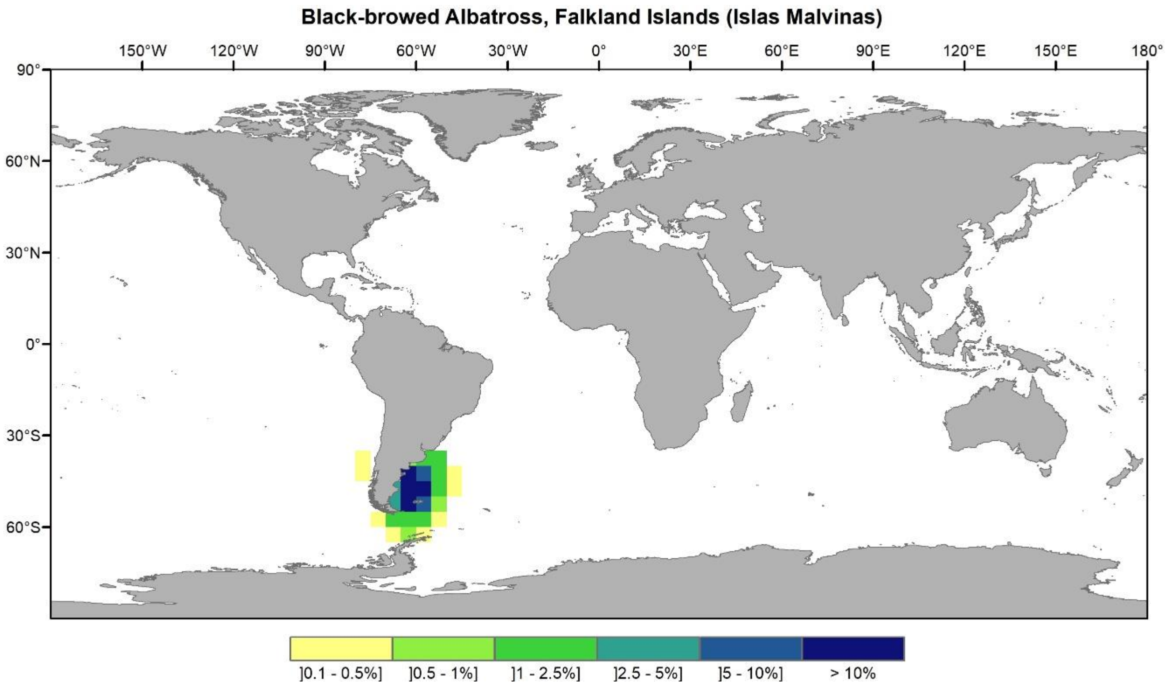

Figure A6: Black-browed Albatross, Falkland Islands (Islas Malvinas)

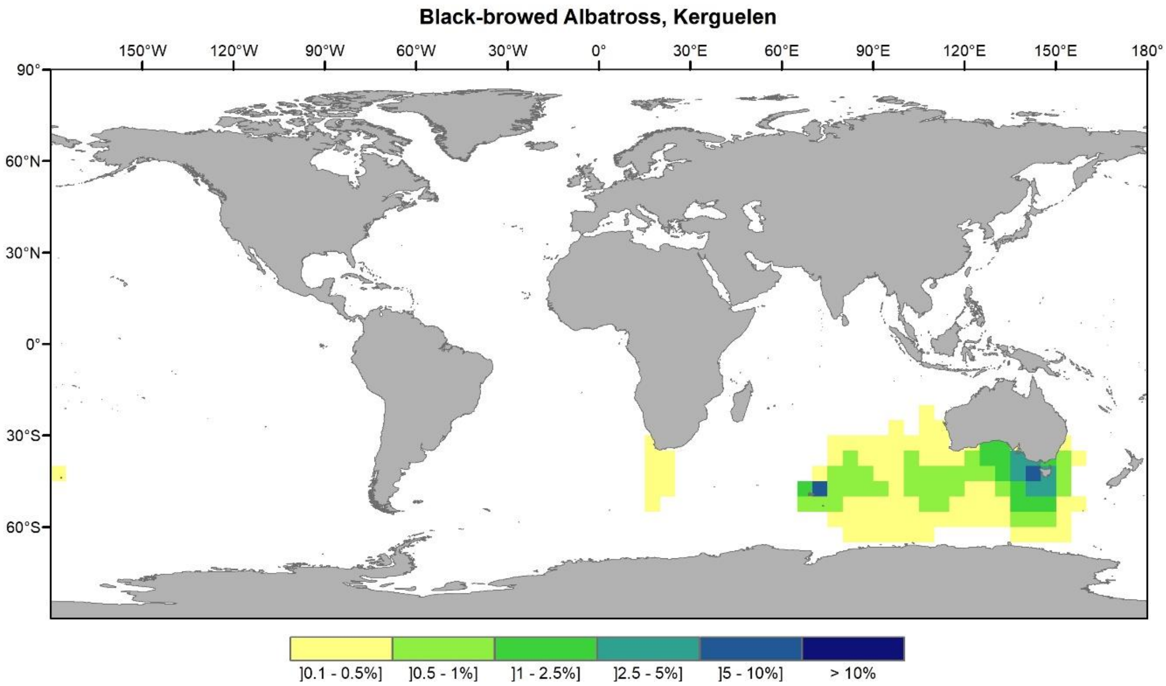

Figure A7: Black-browed Albatross, Kerguelen

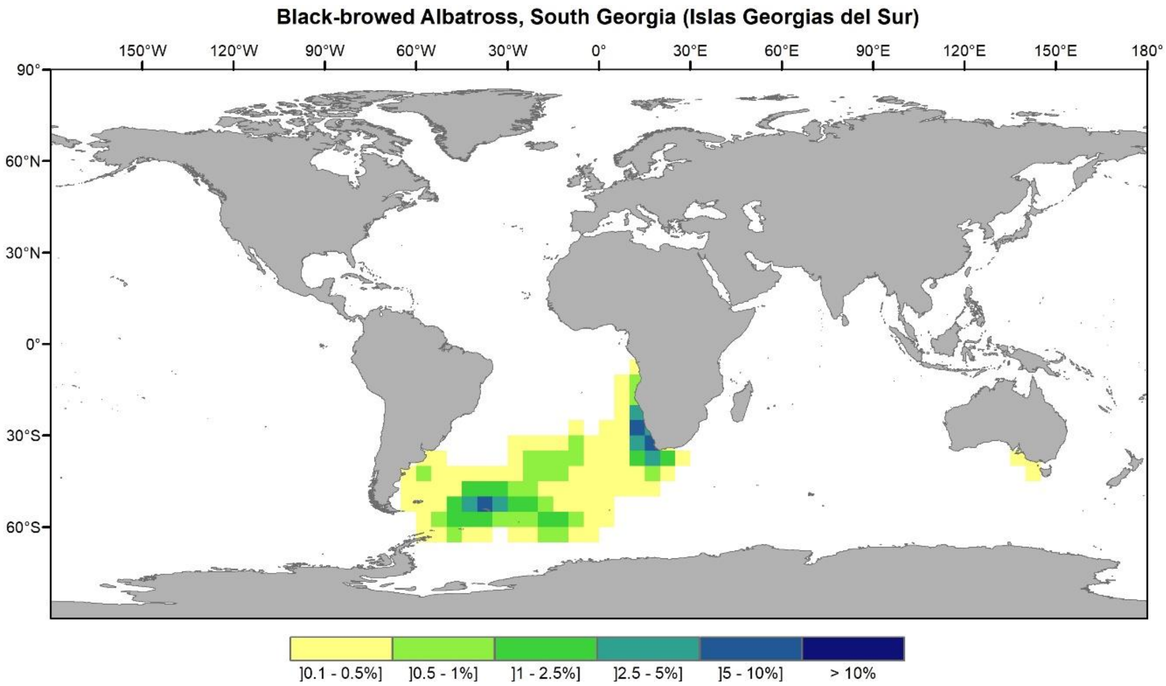

Figure A8: Black-browed Albatross, South Georgia (Islas Georgias del Sur)

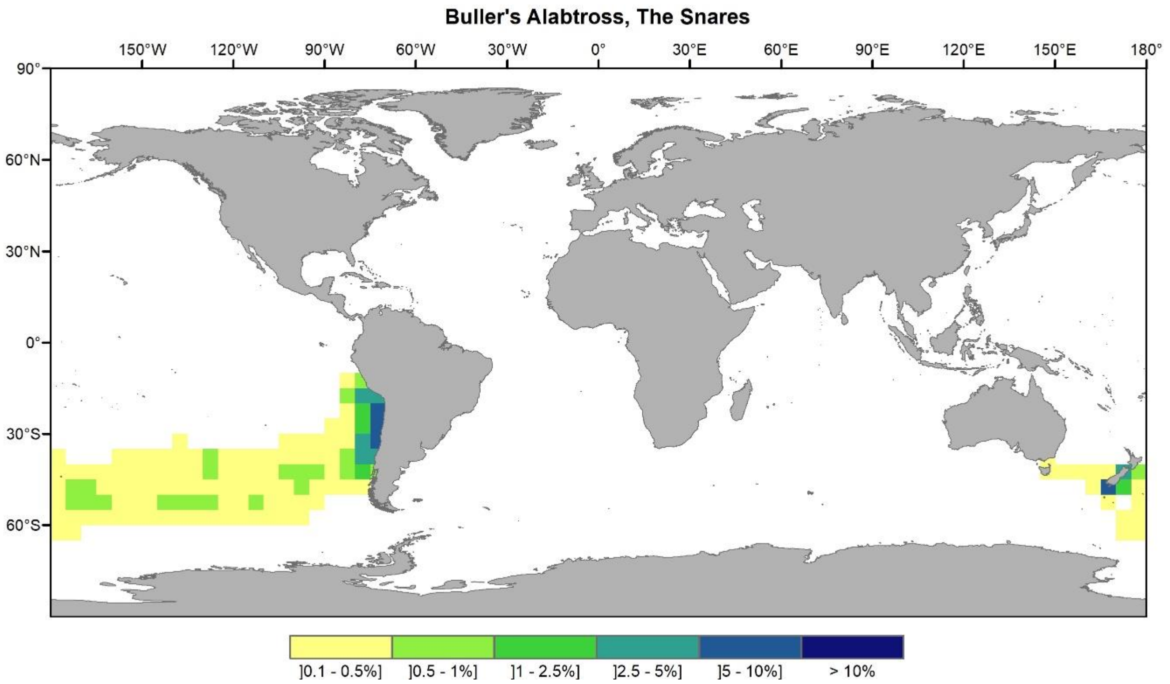

Figure A9: Buller’s Albatross, The Snares

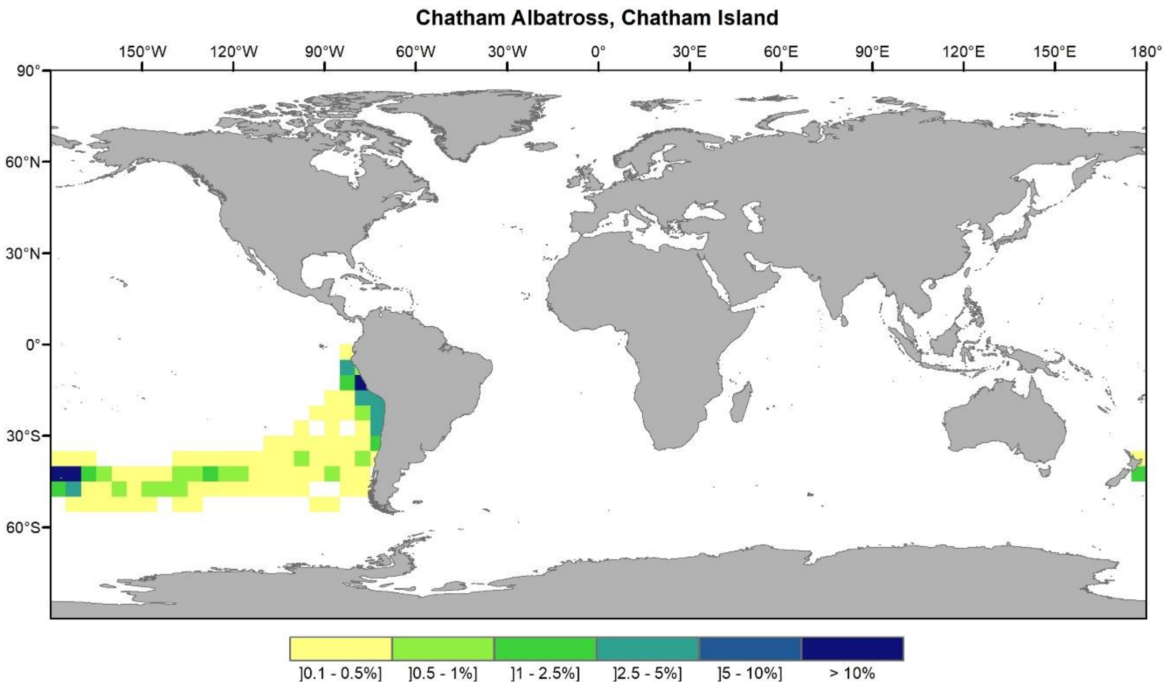

Figure A10: Chatham Albatross, Chatham Island

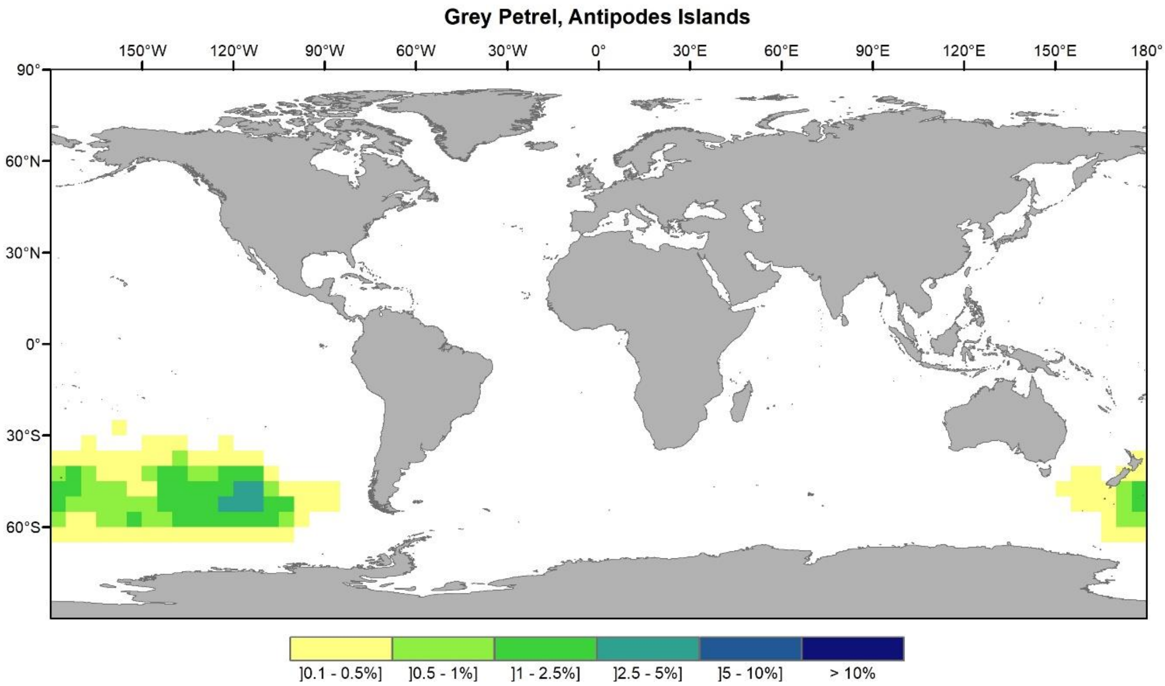

Figure A11: Grey Petrel, Antipodes Islands

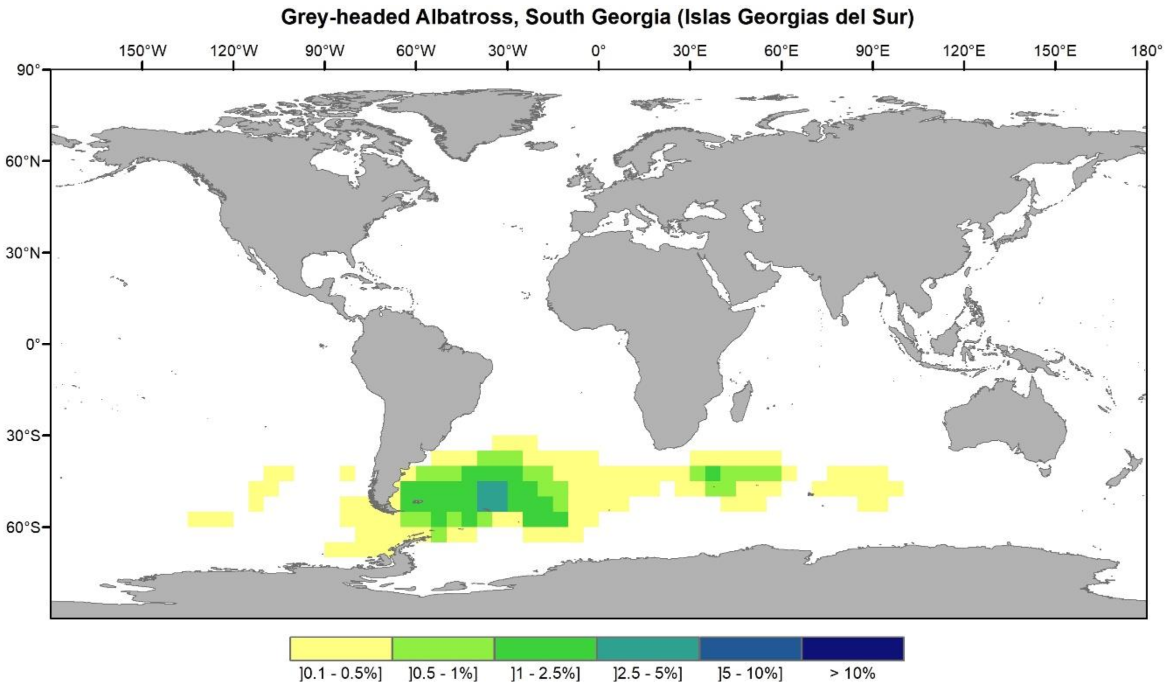

Figure A12: Grey-headed Albatross, South Georgia (Islas Georgias del Sur)

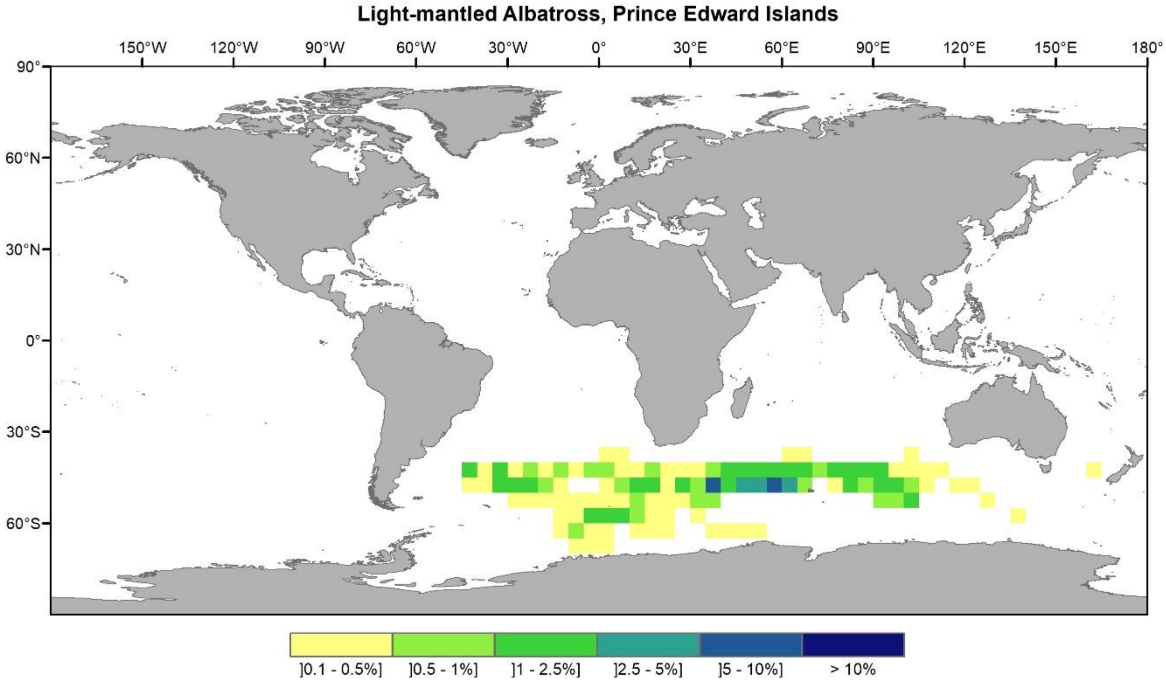

Figure A13: Light-mantled Albatross, Prince Edward Islands

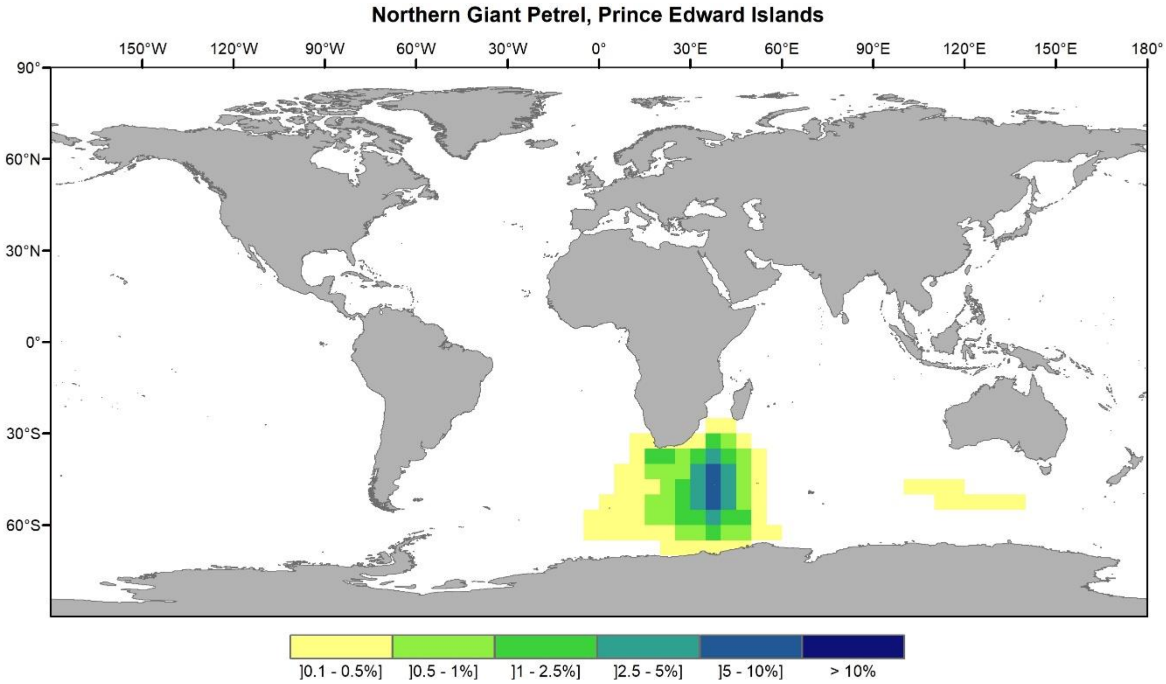

Figure A14: Northern Giant Petrel, Prince Edward Islands

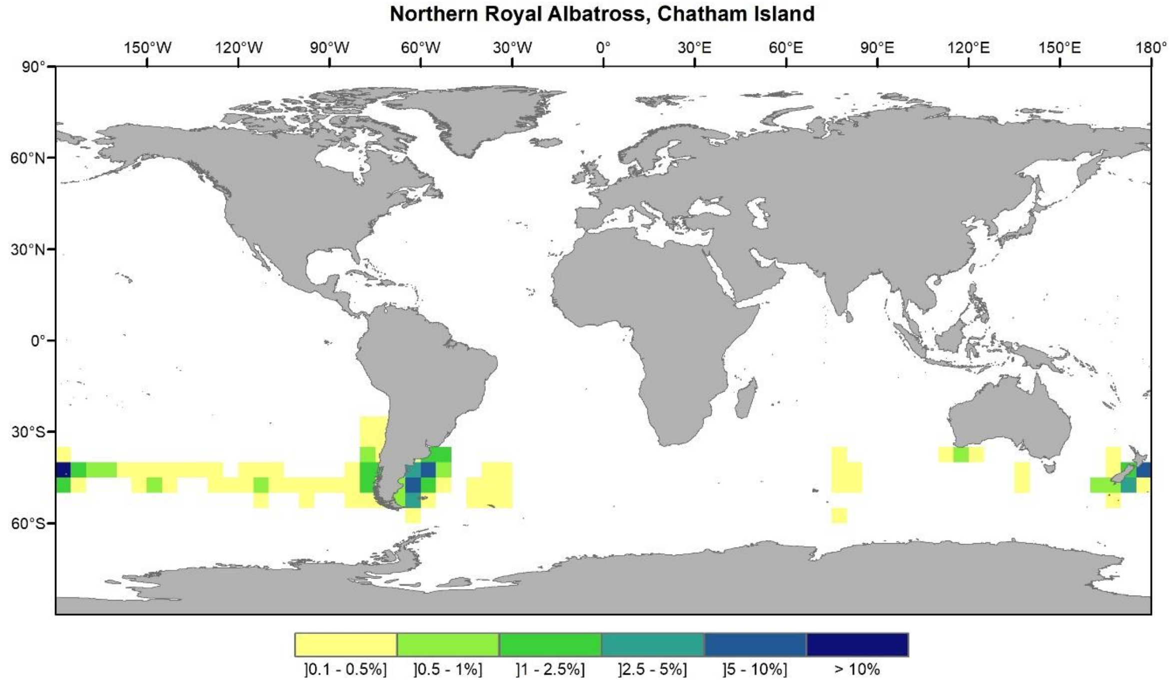

Figure A15: Northern Royal Albatross, Chatham Island

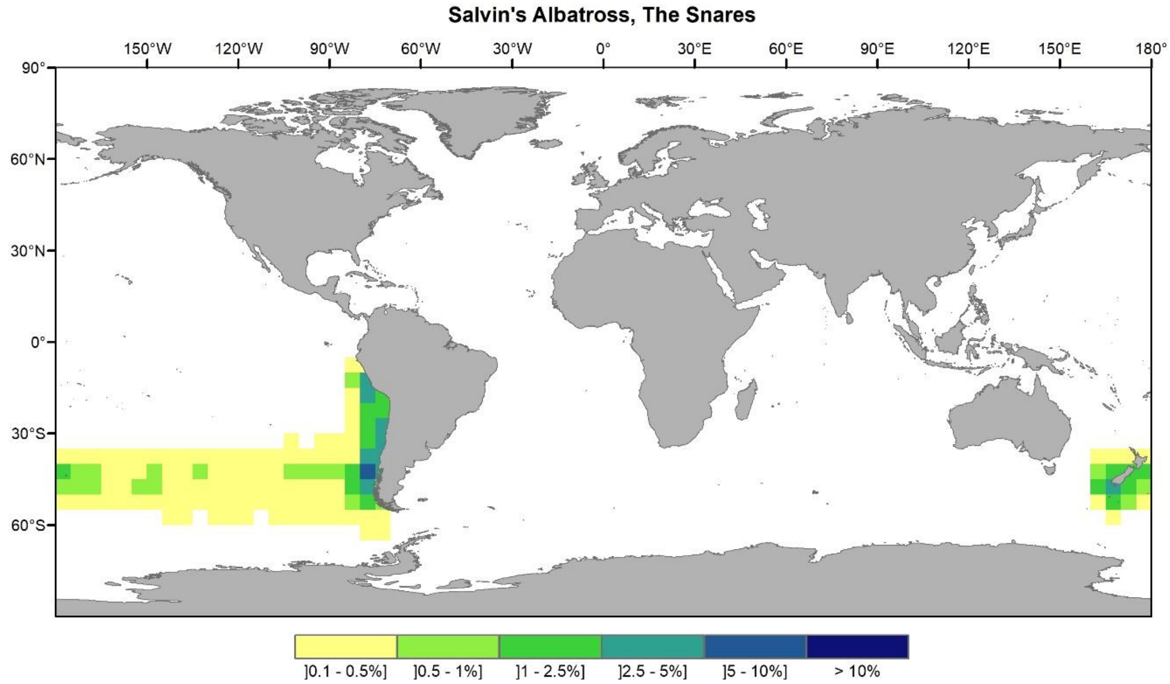

Figure A16: Salvin’s Albatross, The Snares

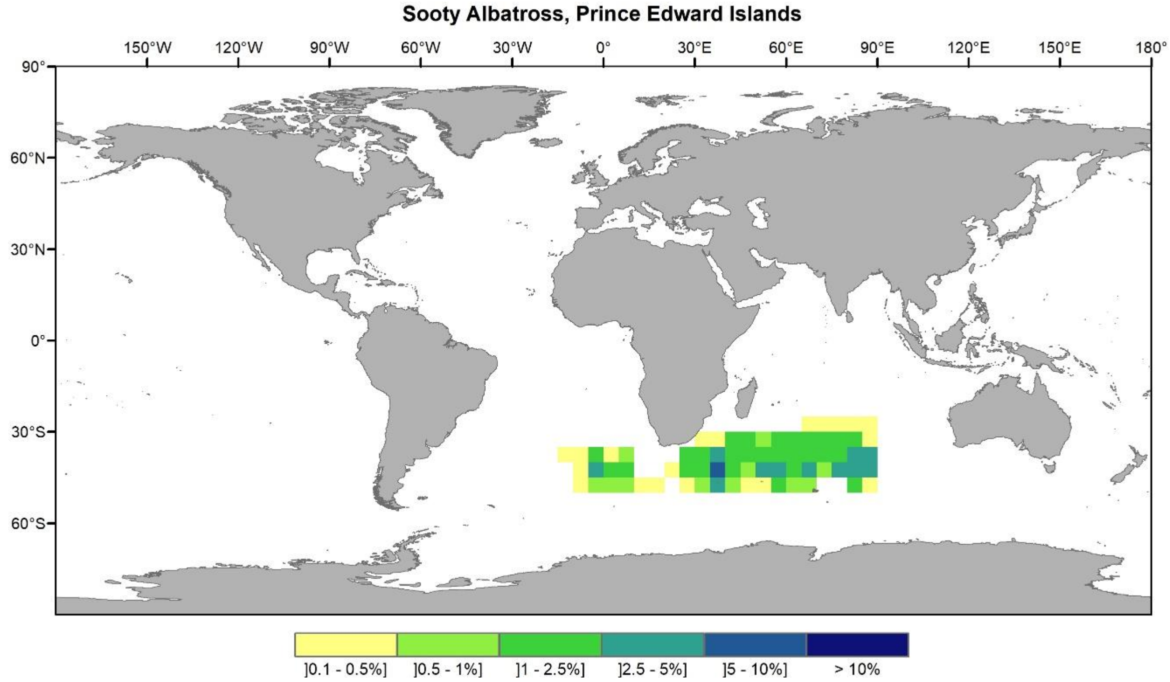

Figure A17: Sooty Albatross, Prince Edward Islands

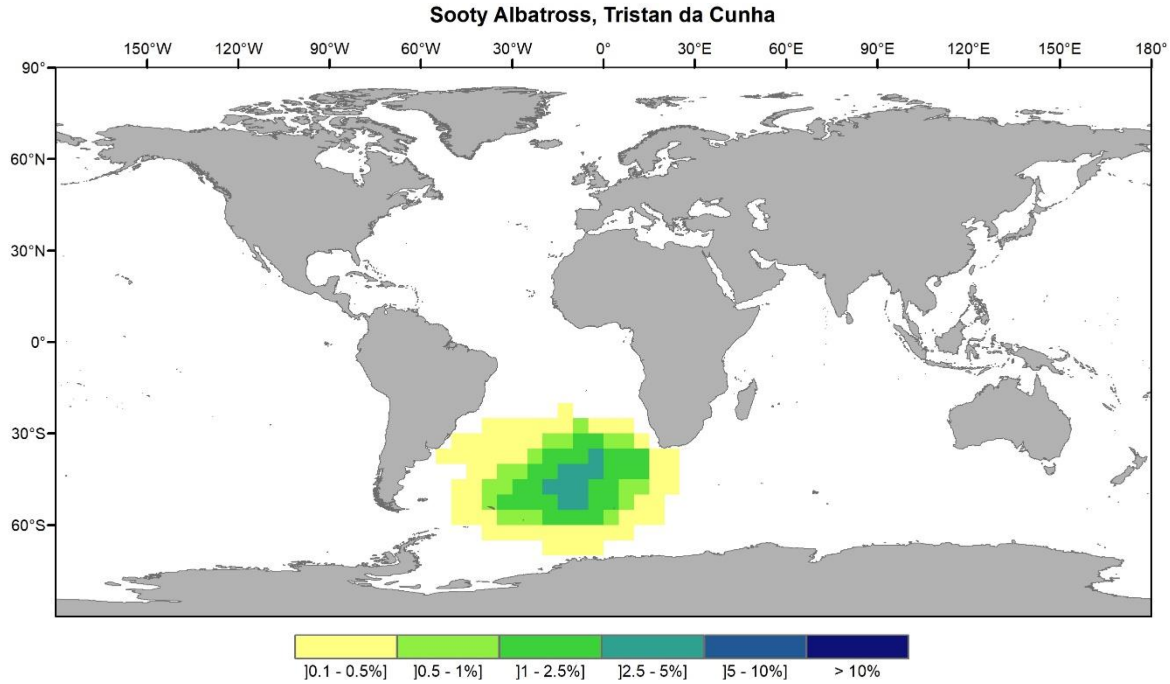

Figure A18: Sooty Albatross, Tristan da Cunha

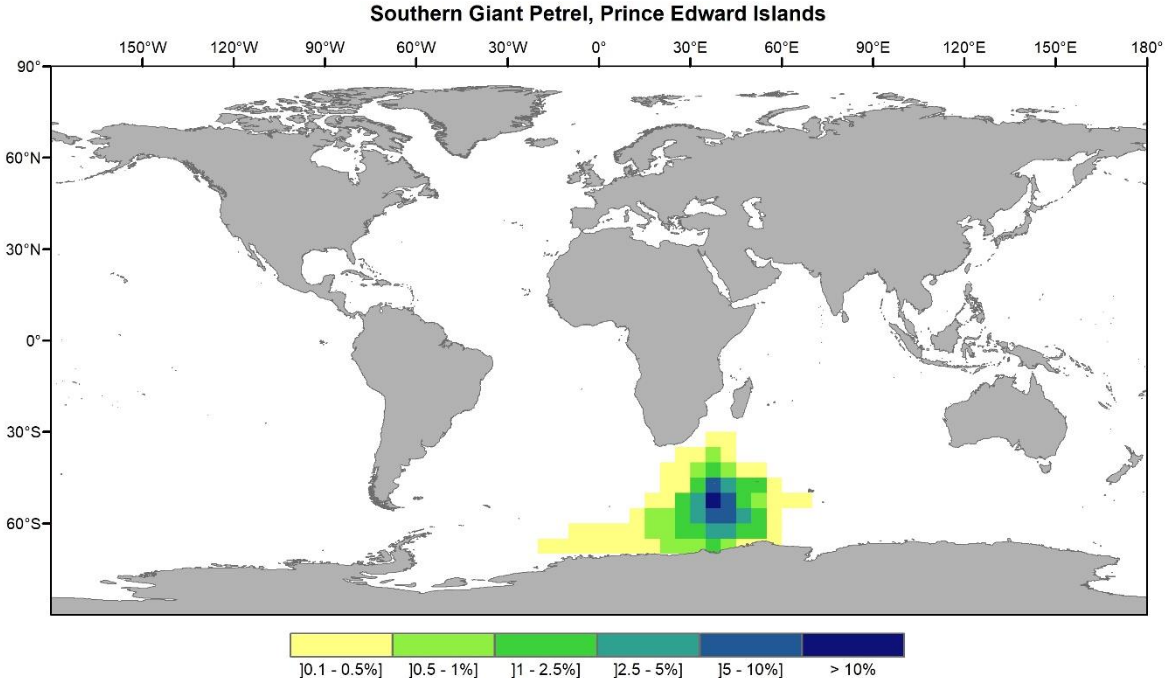

Figure A19: Southern Giant Petrel, Prince Edward Islands

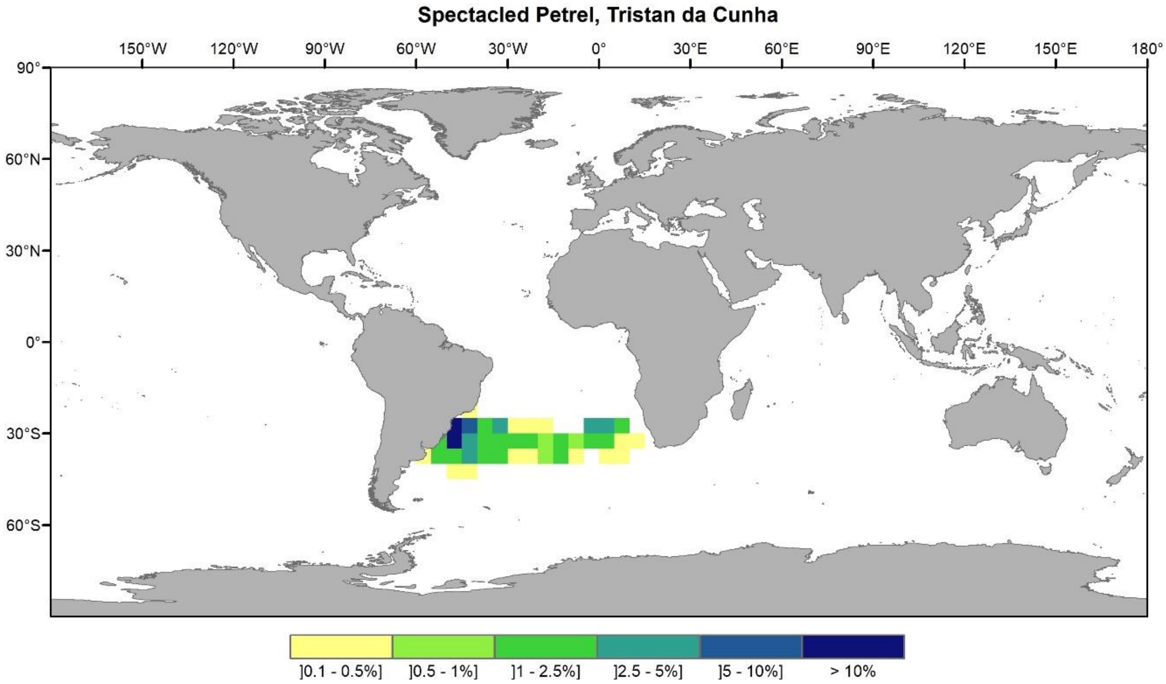

Figure A20: Spectacled Petrel, Tristan da Cunha

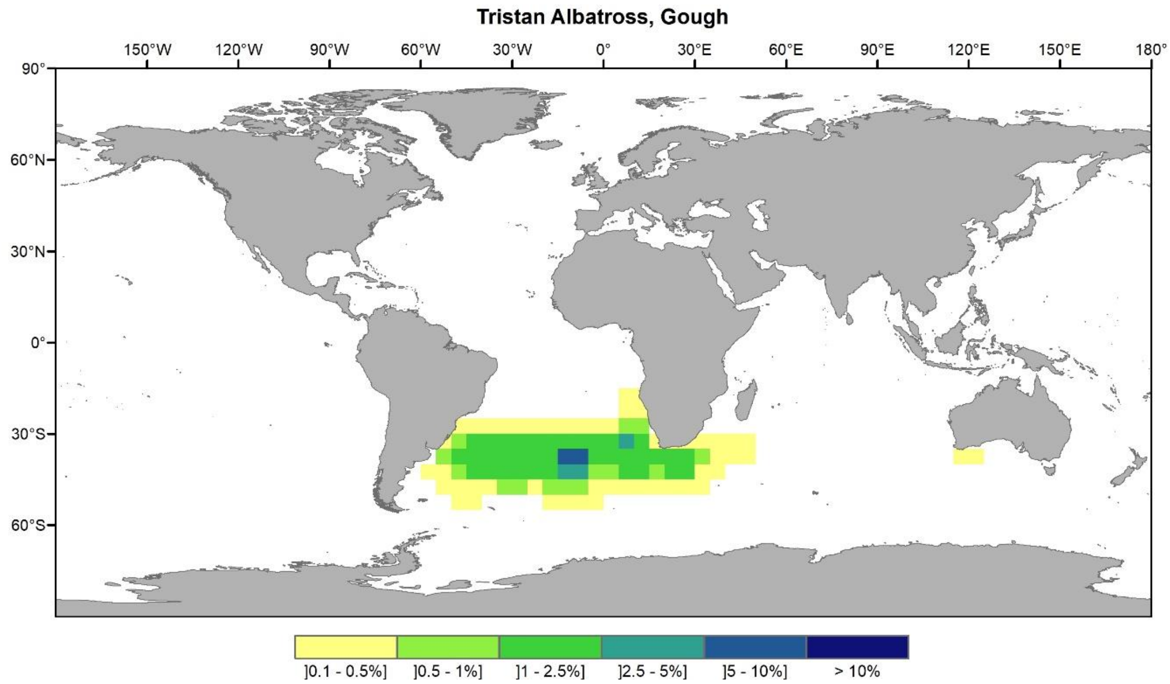

Figure A21: Tristan Albatross, Gough

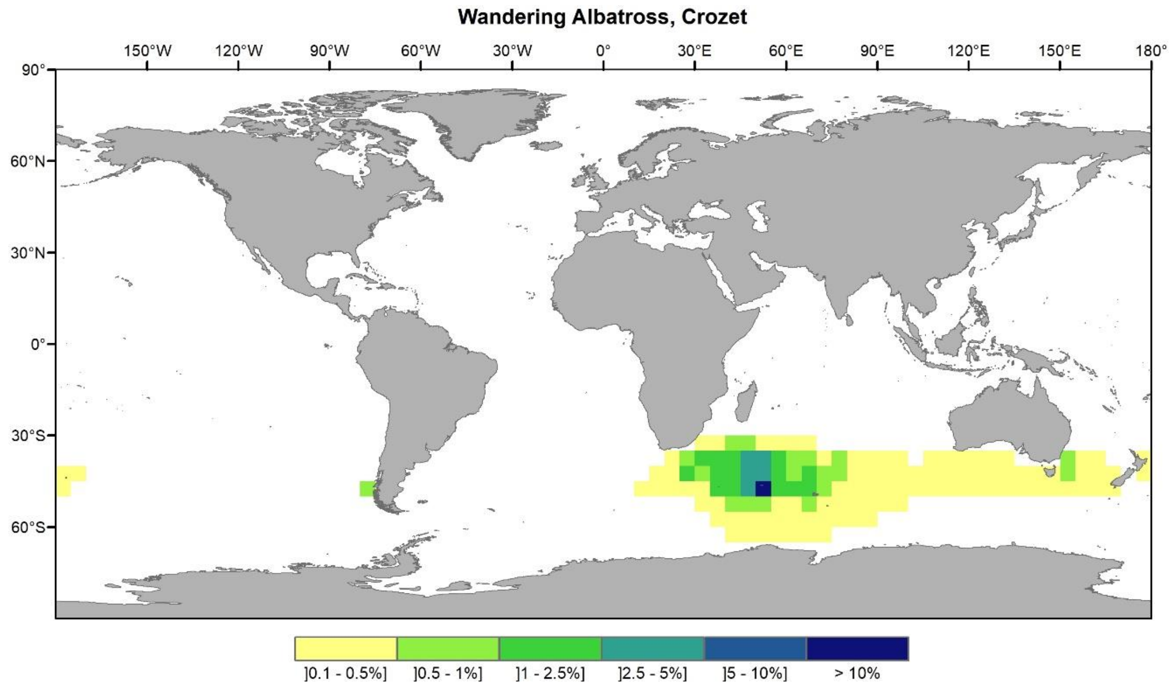

Figure A22: Wandering Albatross, Crozet

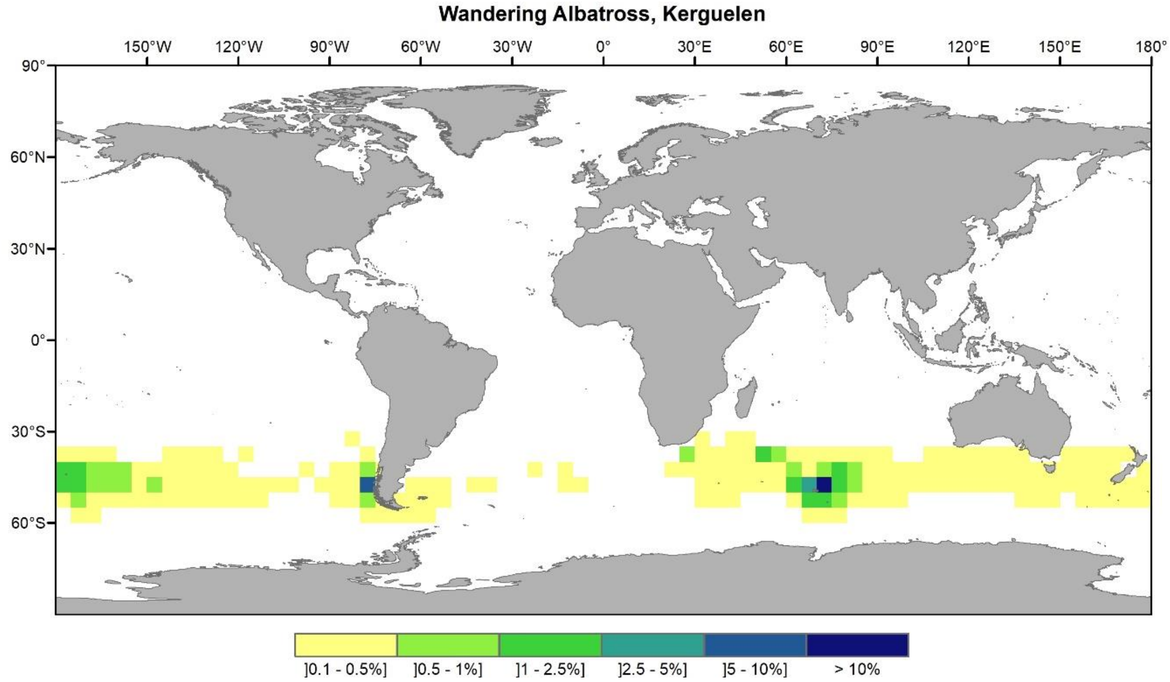

Figure A23: Wandering Albatross, Kerguelen

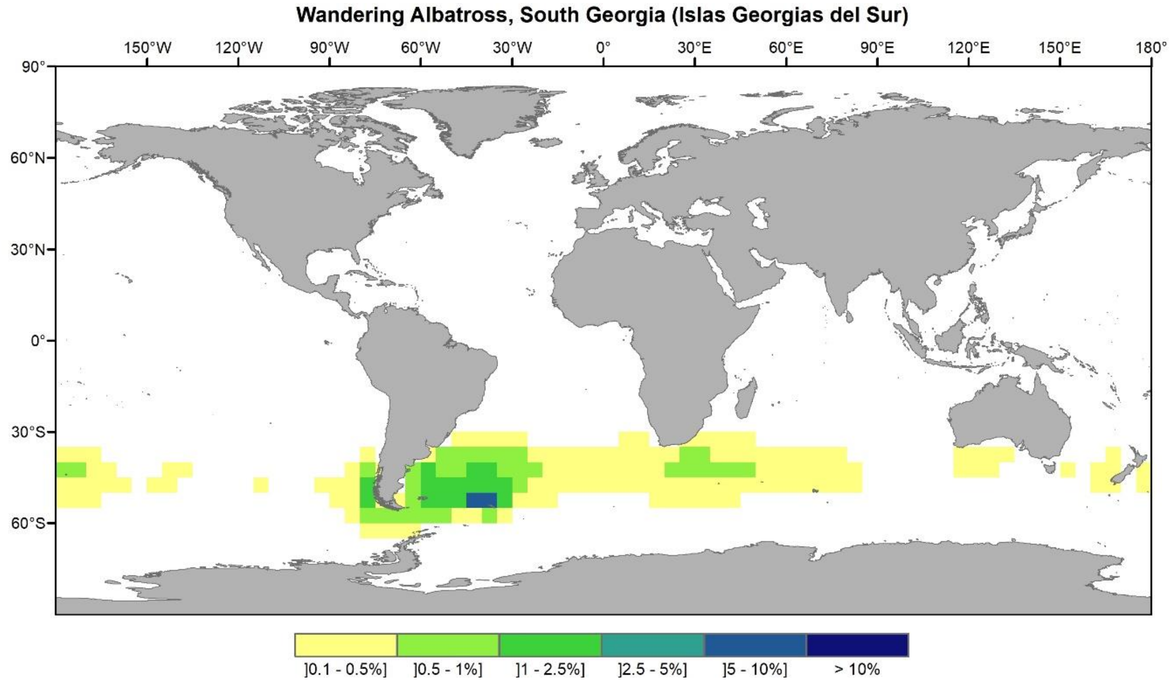

Figure A24: Wandering Albatross, South Georgia (Islas Georgias del Sur)

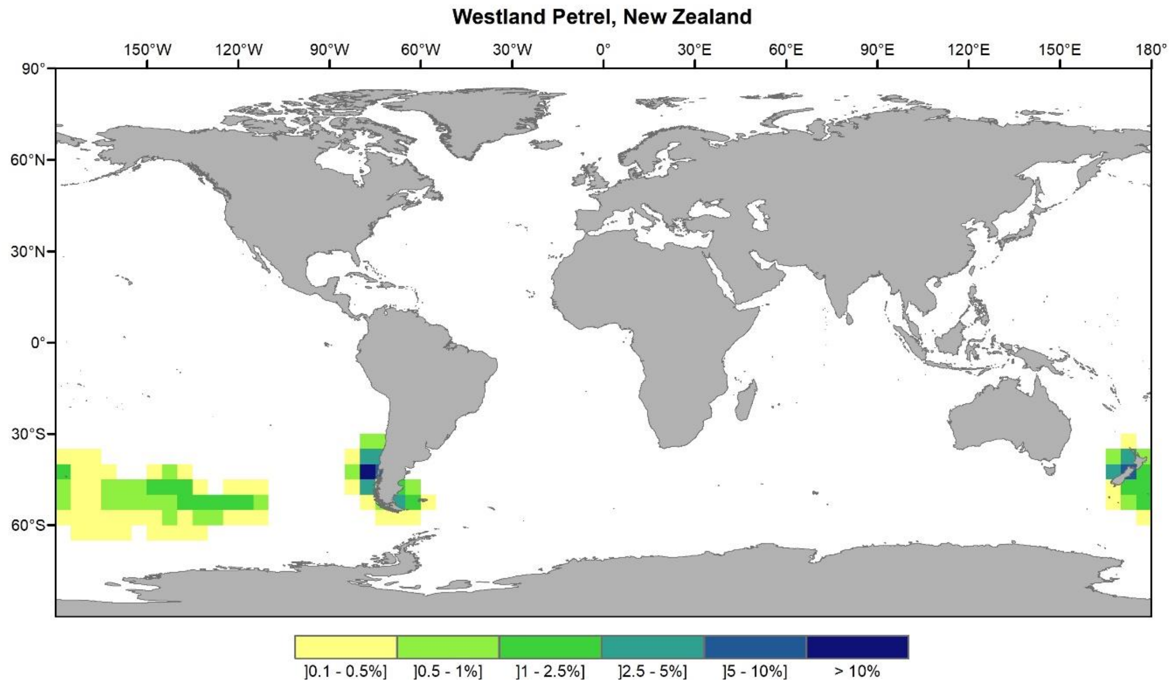

Figure A25: Westland petrel, New Zealand

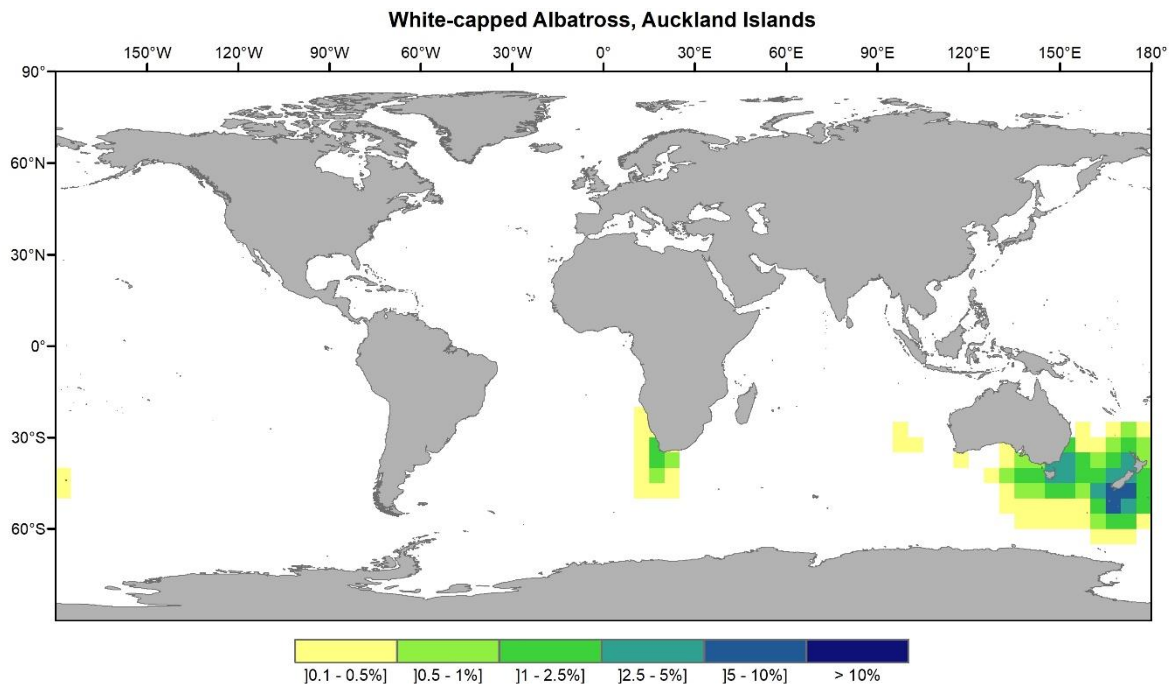

Figure A26: White-capped Albatross, Auckland Islands

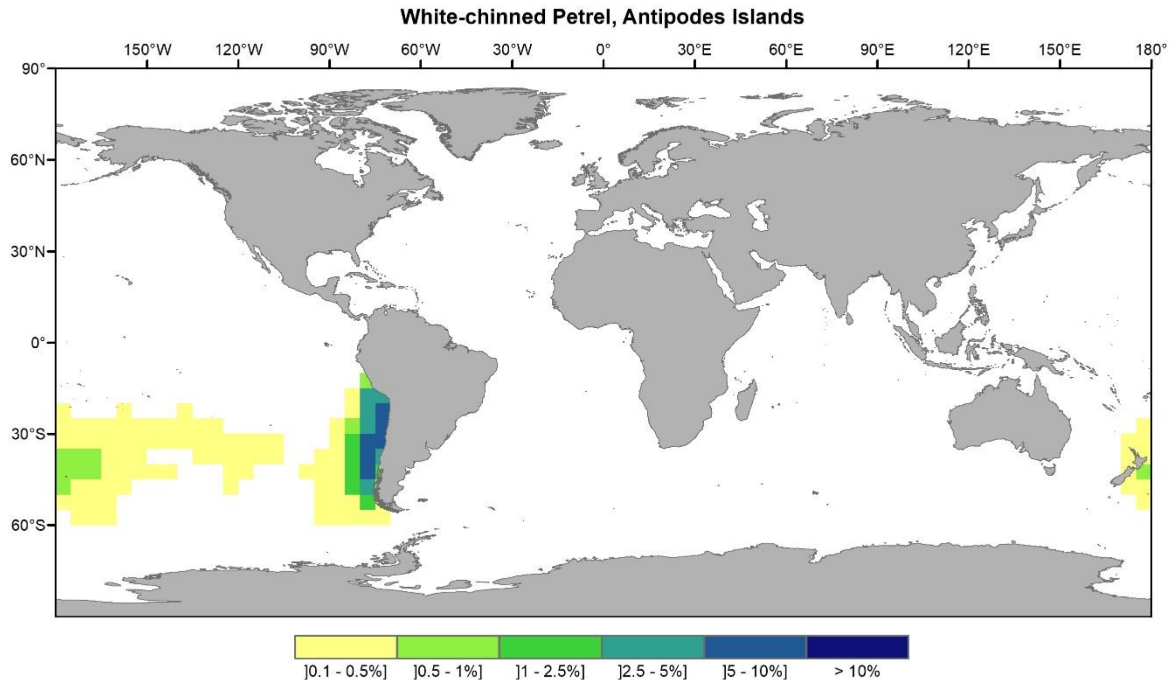

Figure A27: White-chinned Petrel, Antipodes Islands

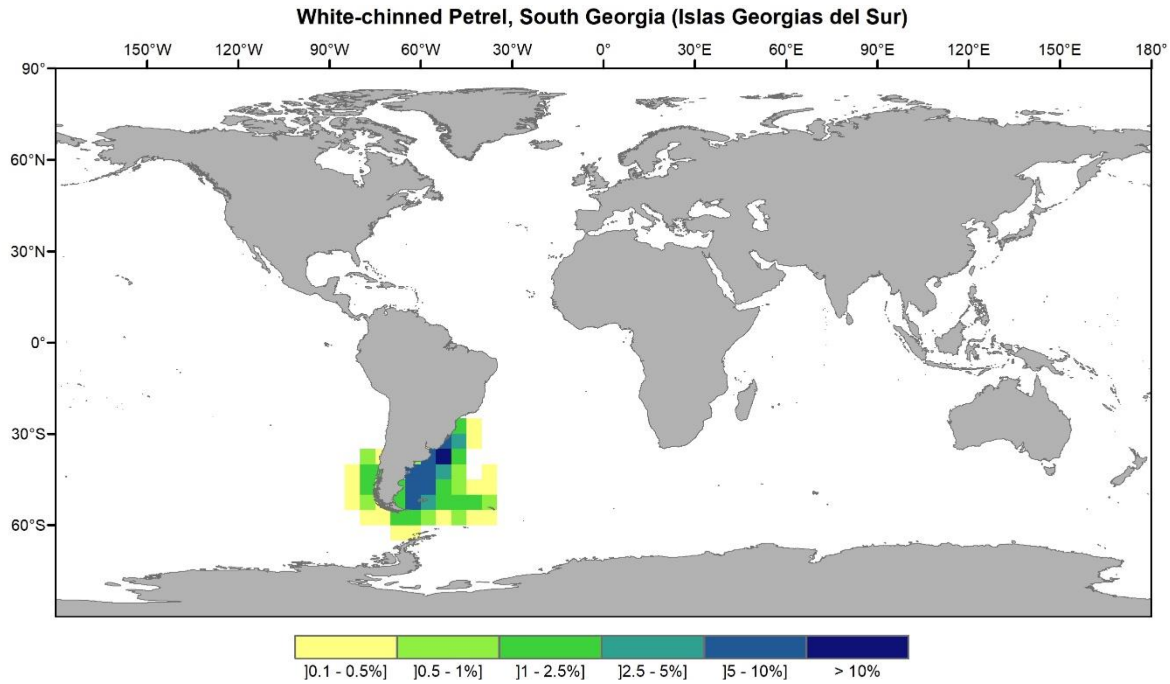

Figure A28: White-chinned Petrel, South Georgia (Islas Georgias del Sur)

Figures A29-A56: Quarterly population-level density distributions for 21 species of albatrosses and petrels (28 populations) breeding in the Southern Ocean based on tracking, phenology and demography data. The colour gradient refers to the percentage of the population represented within each 5 x 5° grid. Darker shades (of blue) depict a greater density of birds. For details on the number of individuals, see Table A2.

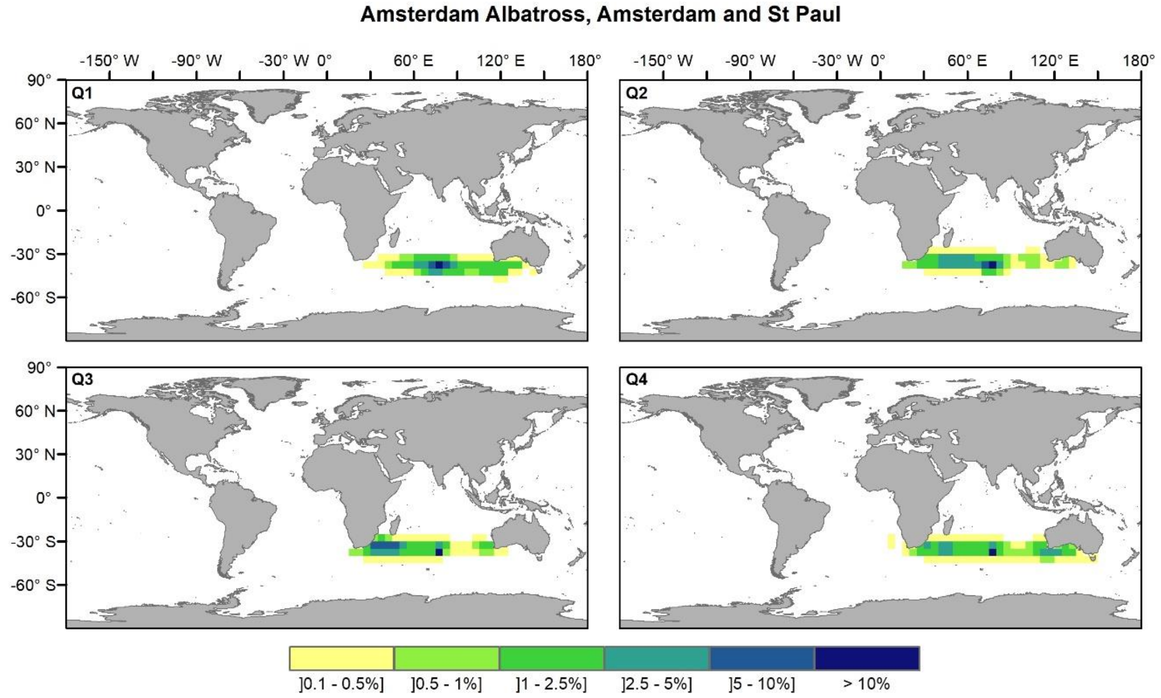

Figure A29: Amsterdam Albatross, Amsterdam and St Paul

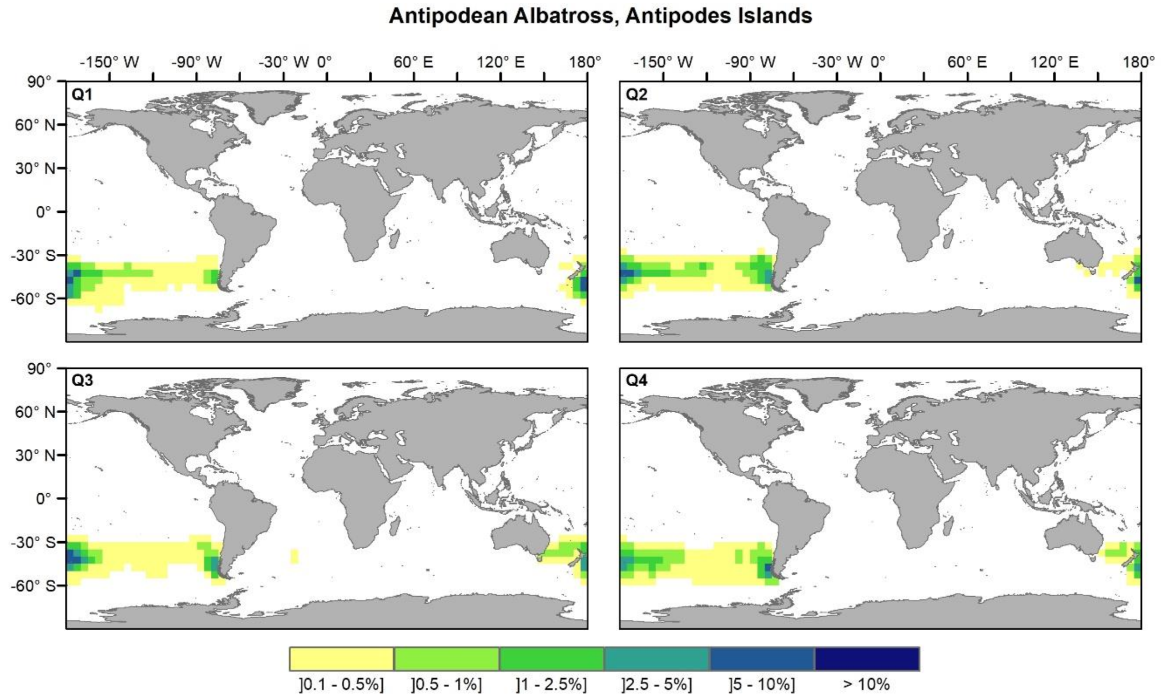

Figure A30: Antipodean Albatross, Antipodes Island

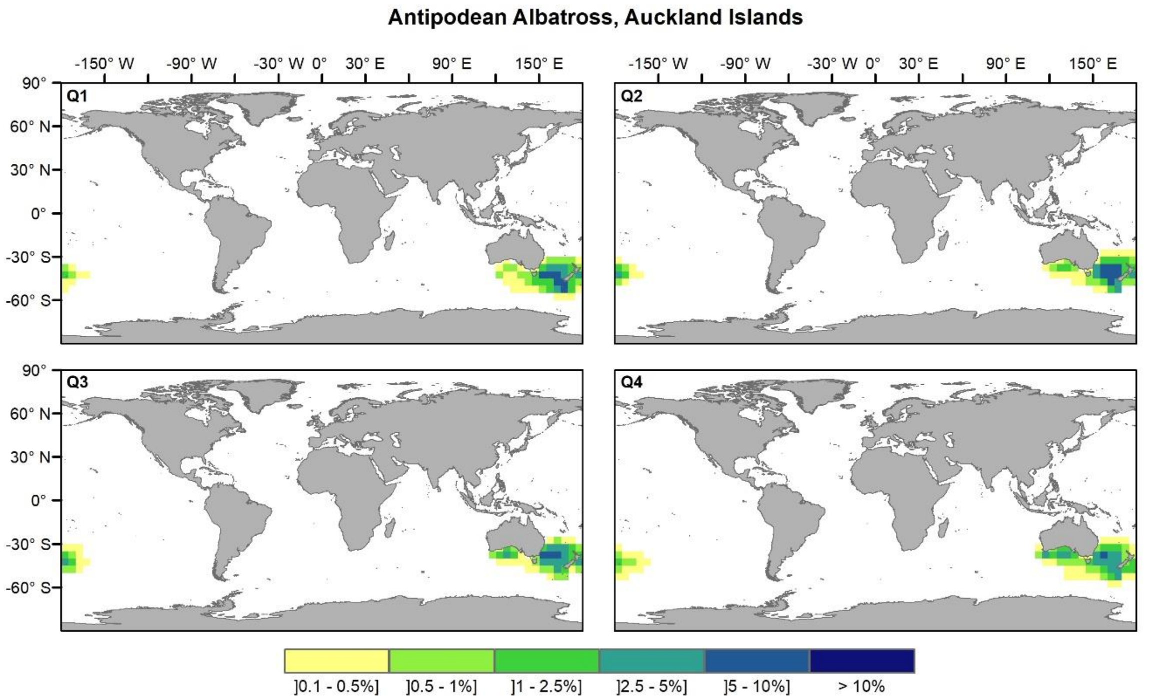

Figure A31: Antipodean Albatross, Auckland Islands

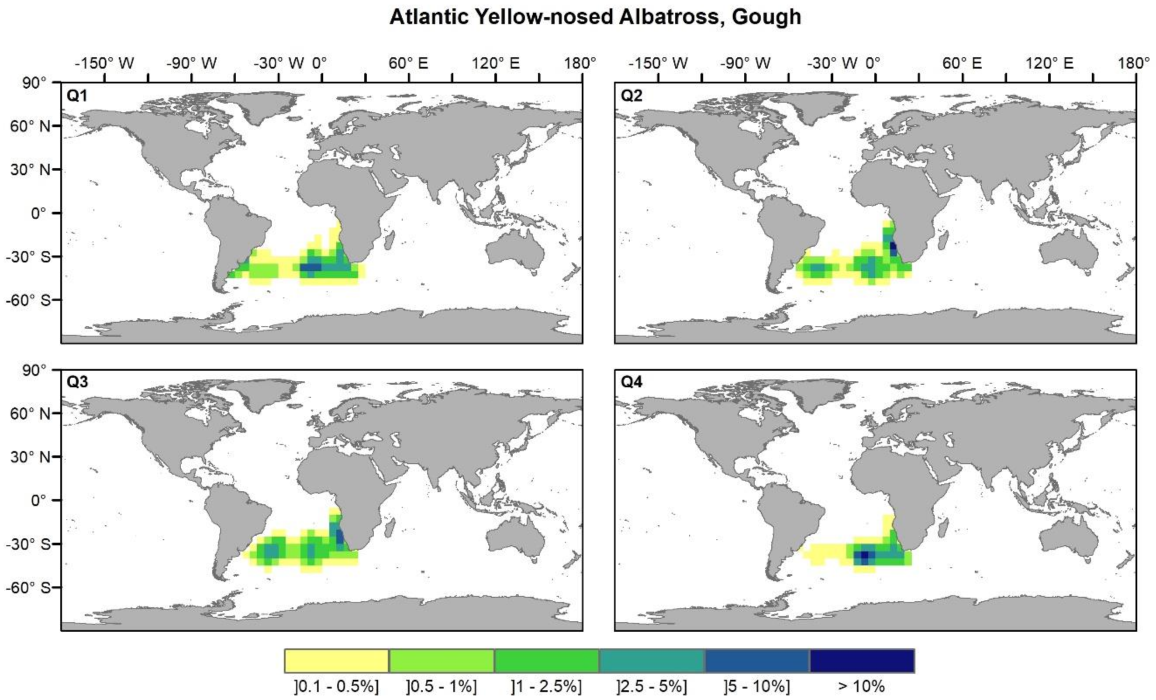

Figure A32: Atlantic Yellow-nosed Albatross, Gough

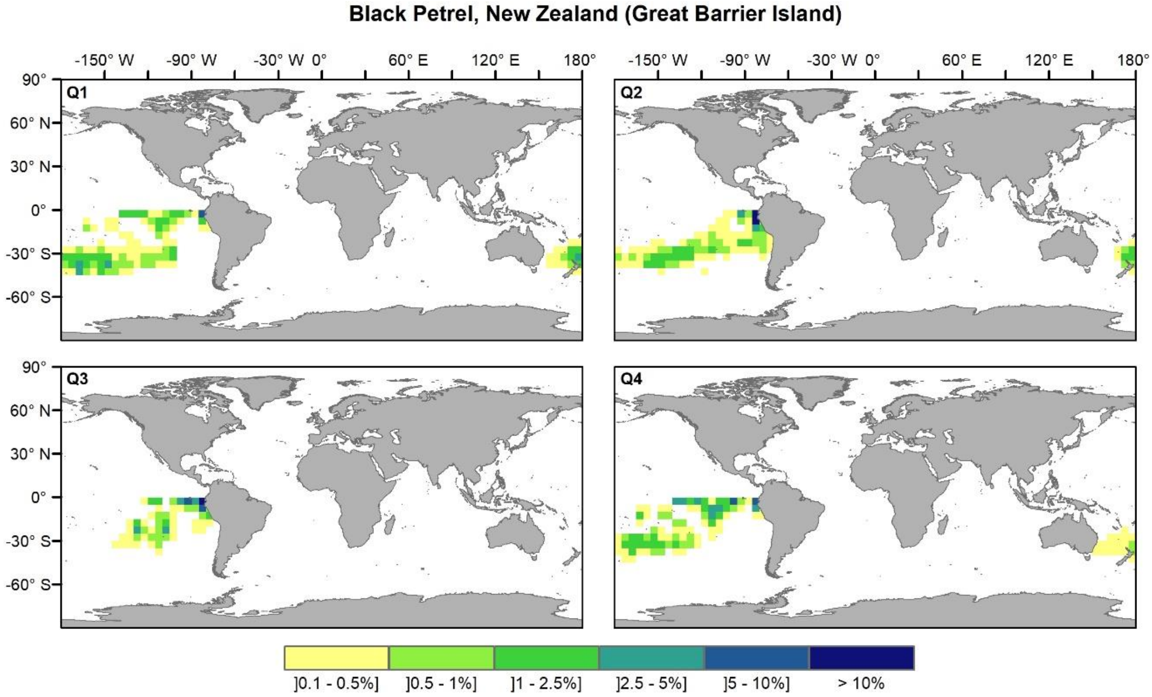

Figure A33: Black Petrel, New Zealand (Great Barrier Island)

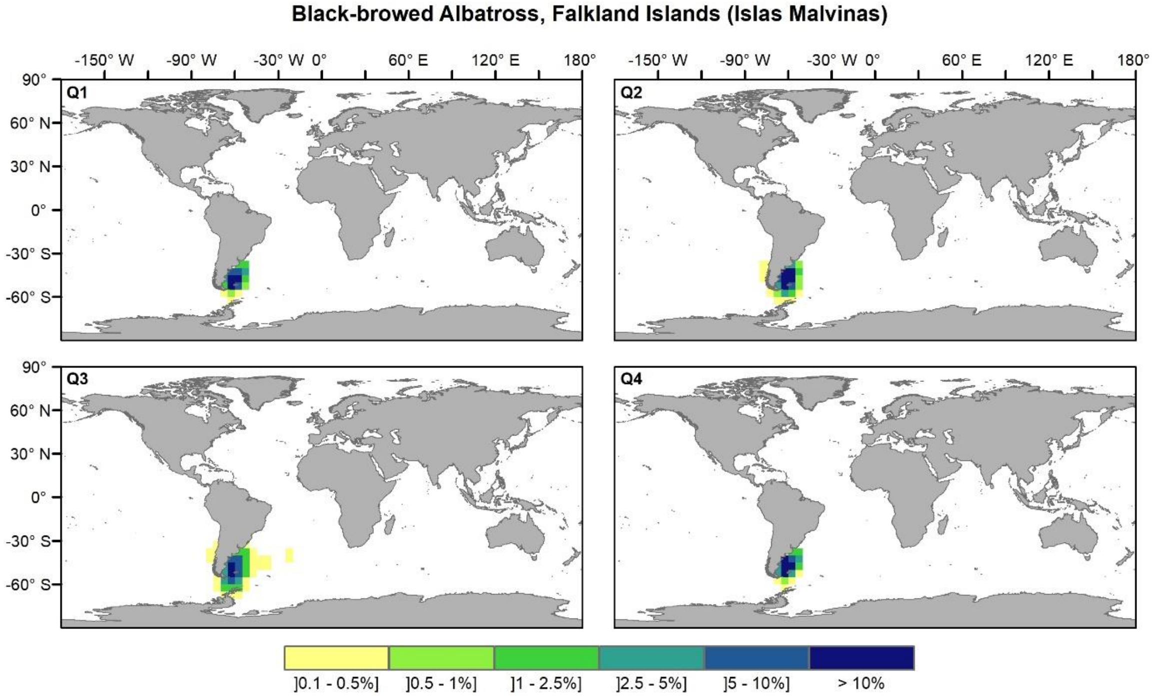

Figure A34: Black-browed Albatross, Falkland Islands (Islas Malvinas)

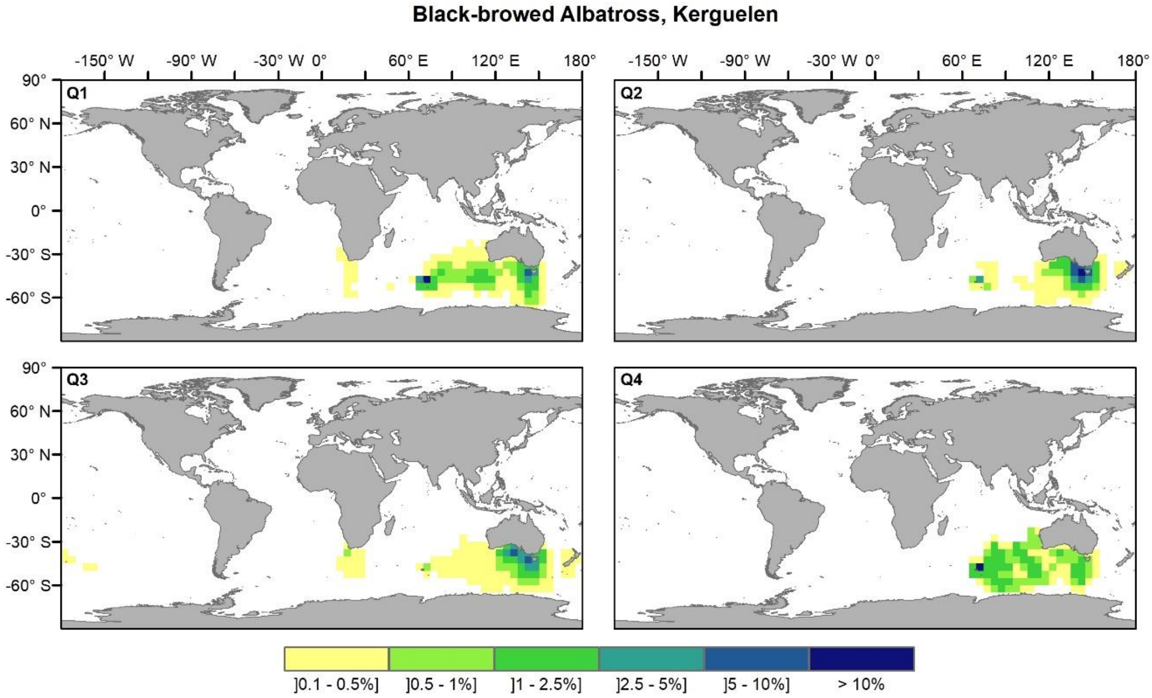

Figure A35: Black-browed Albatross, Kerguelen

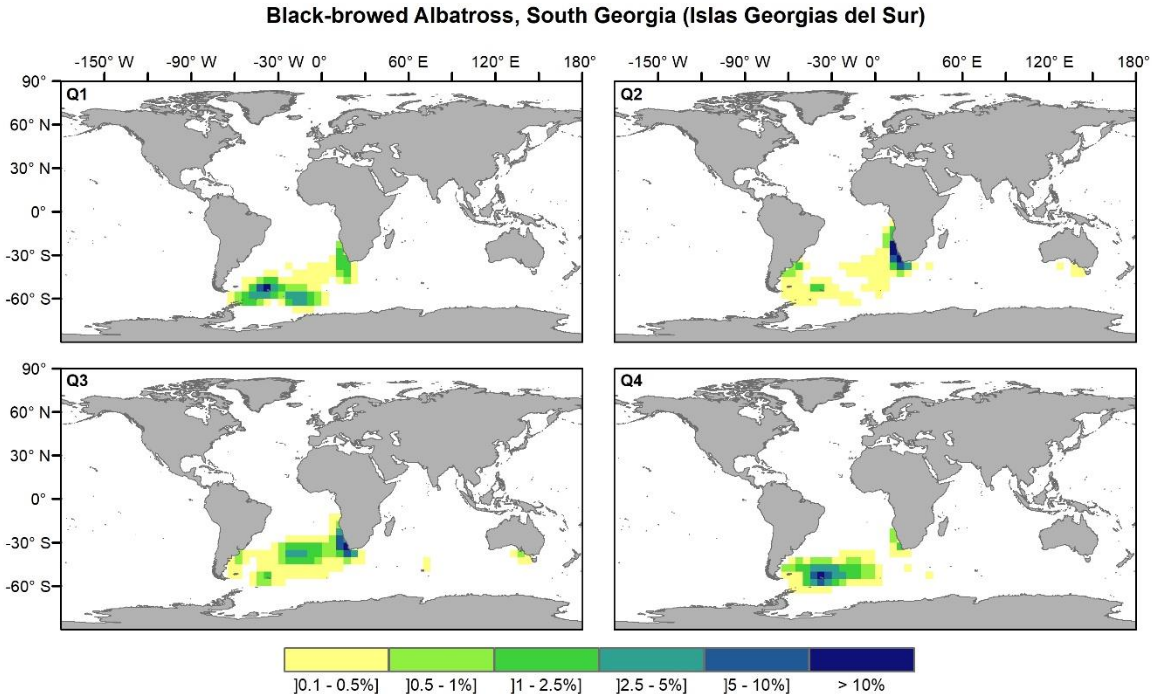

Figure A36: Black-browed Albatross, South Georgia (Islas Georgias del Sur)

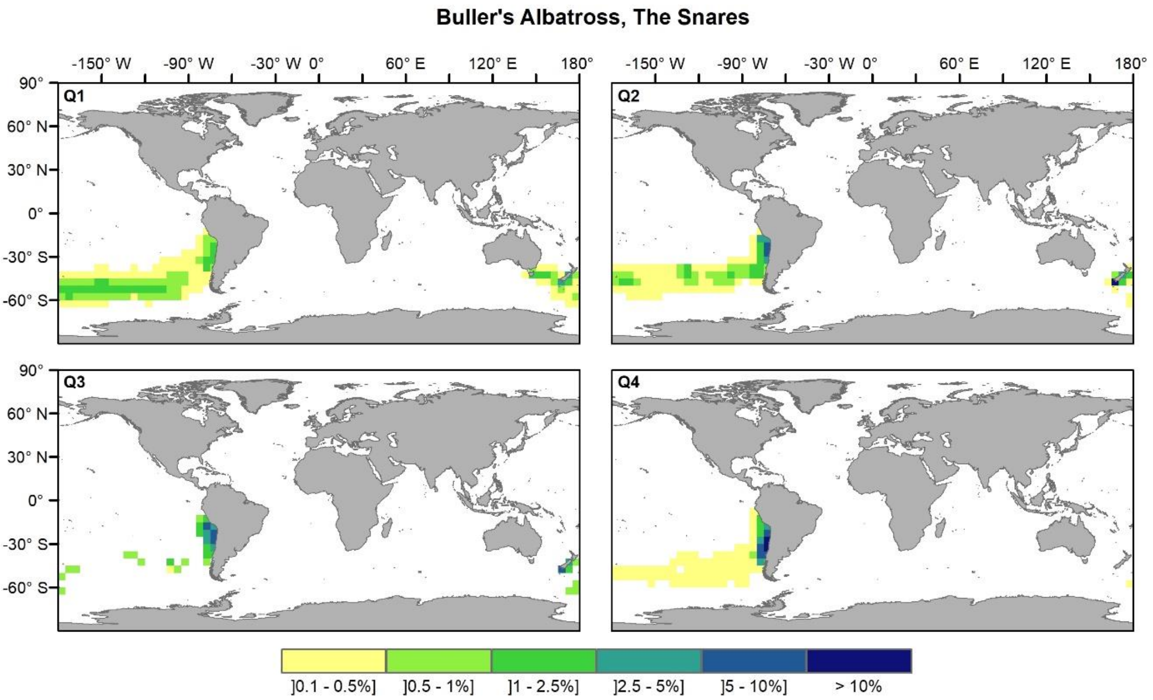

Figure A37: Buller's Albatross, The Snares

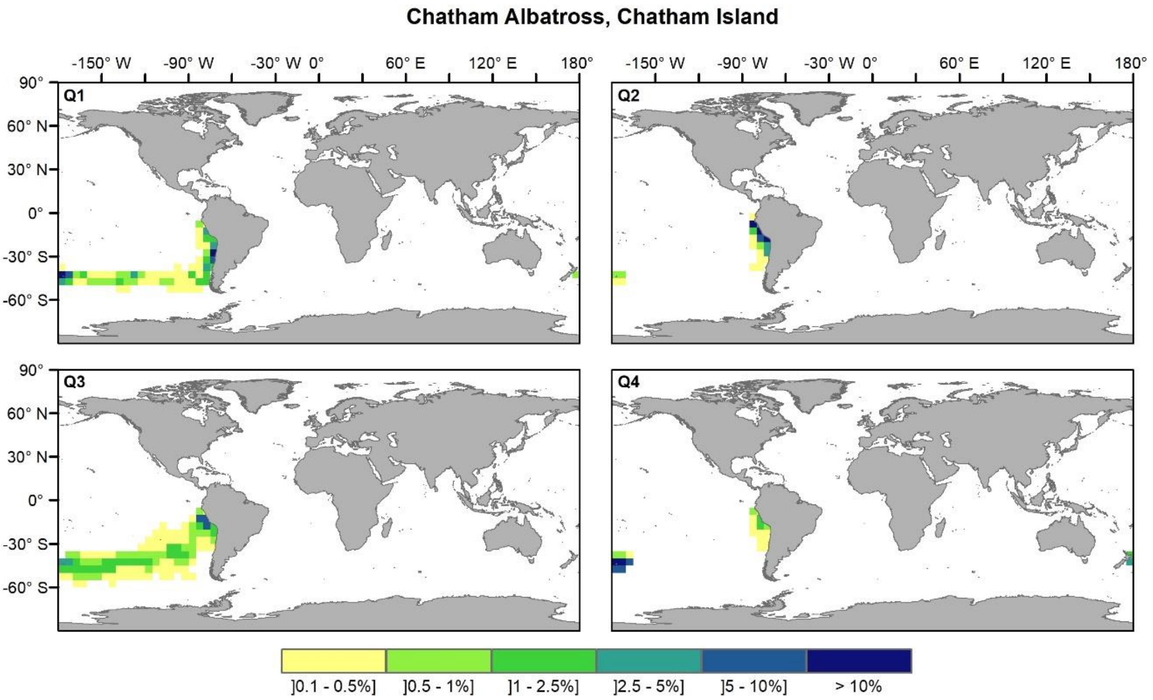

Figure A38: Chatham Albatross, Chatham Island

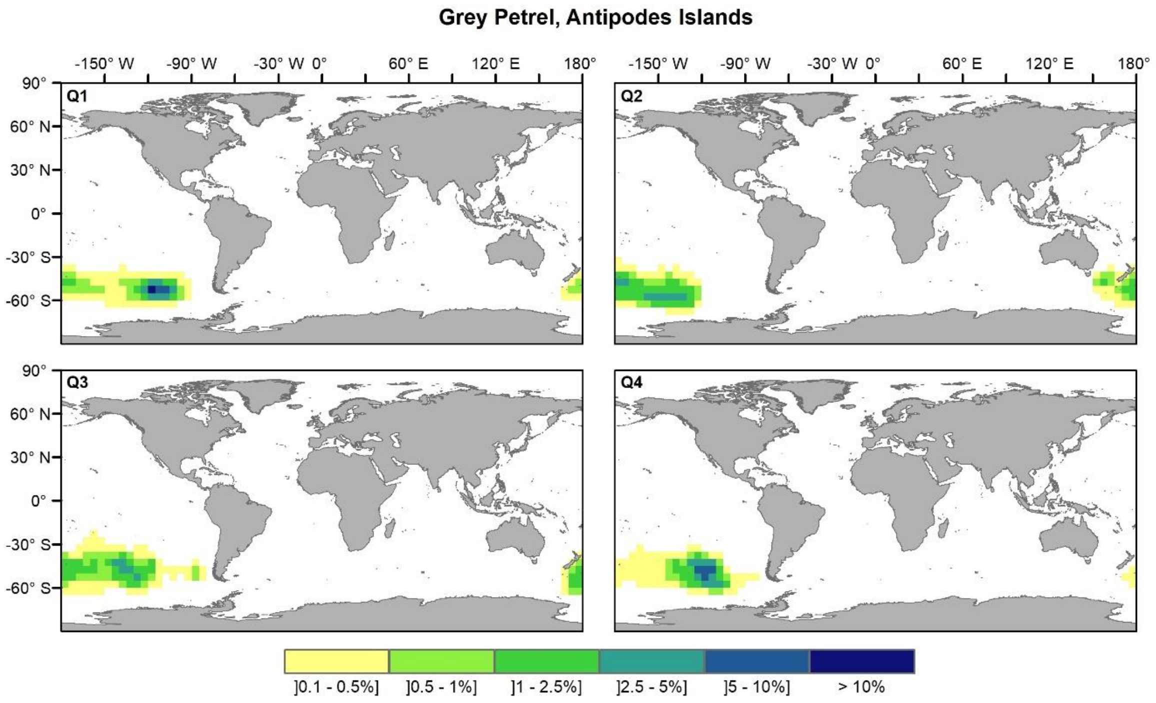

Figure A39: Grey Petrel, Antipodes Islands

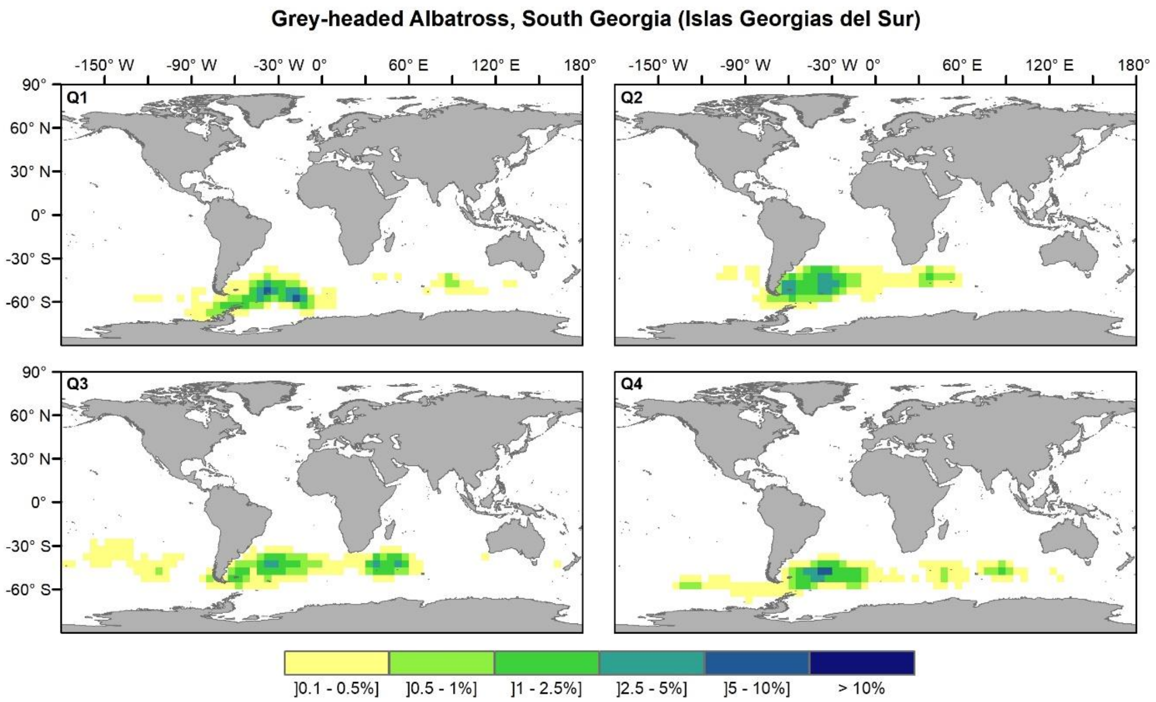

Figure A40: Grey-headed Albatross, South Georgia (Islas Georgias del Sur)

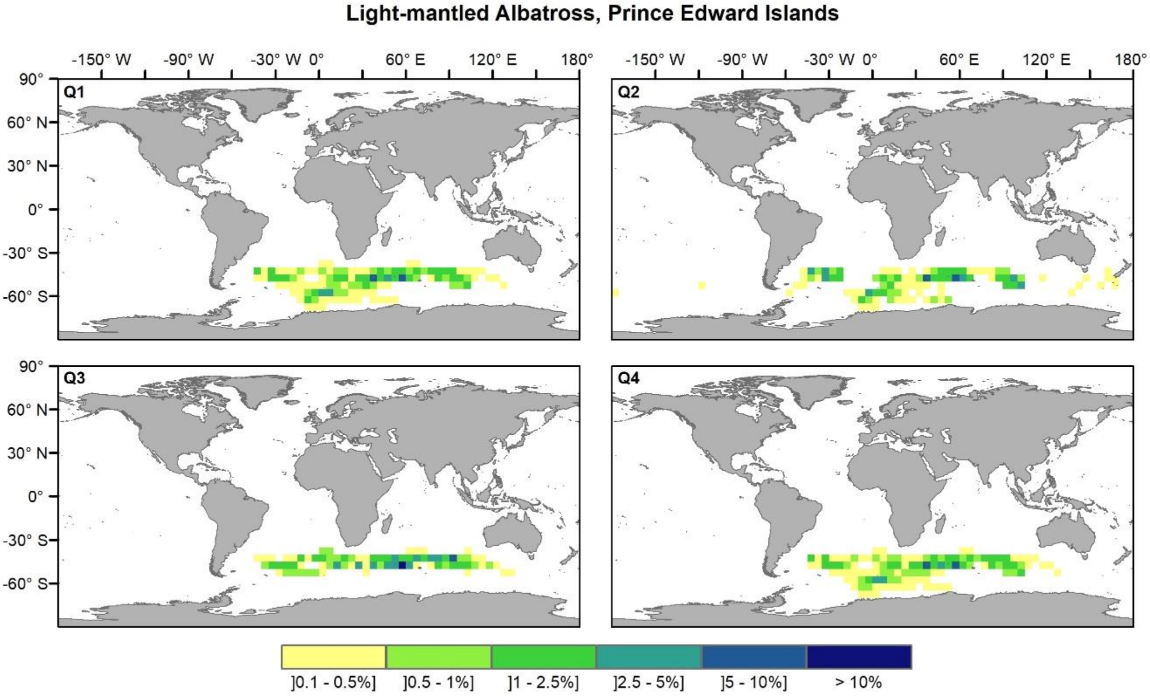

Figure A41: Light-mantled Albatross, Prince Edward Islands

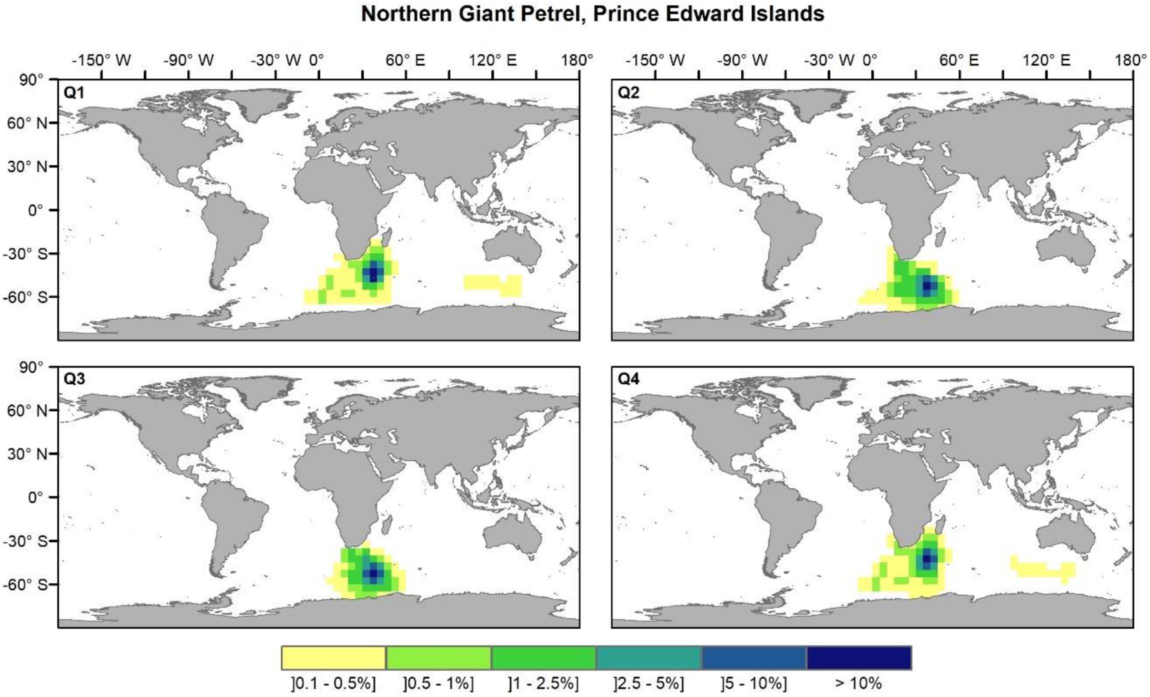

Figure A42: Northern Giant Petrel, Prince Edward Islands

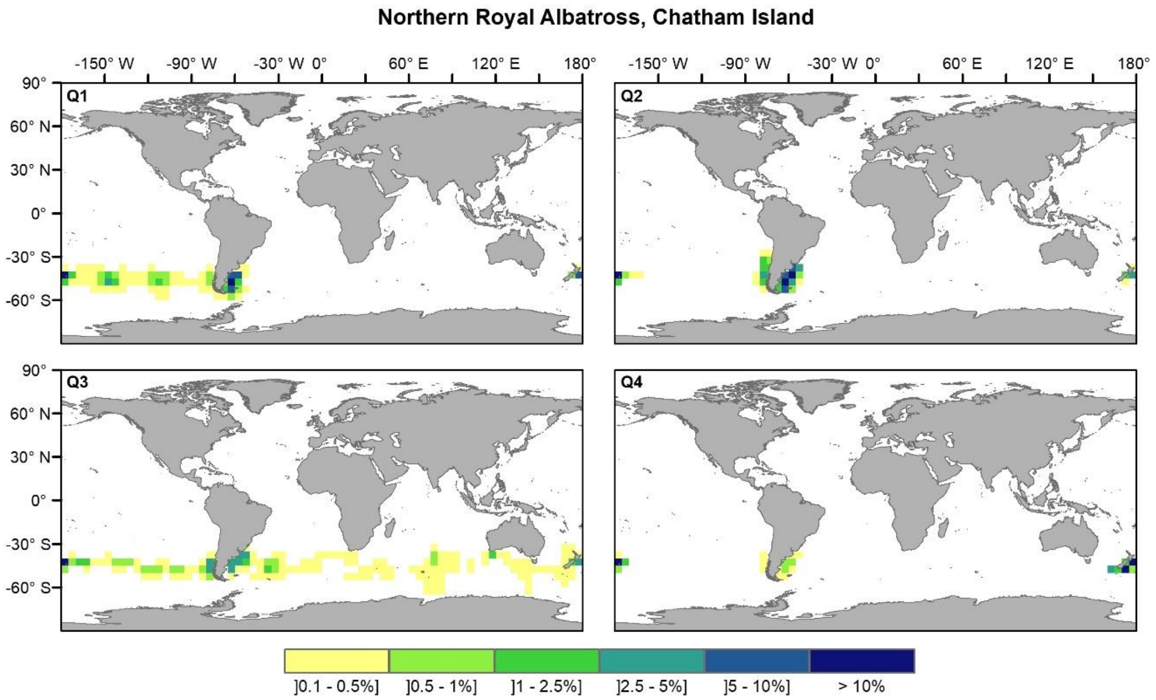

Figure A43: Northern Royal Albatross, Chatham Island

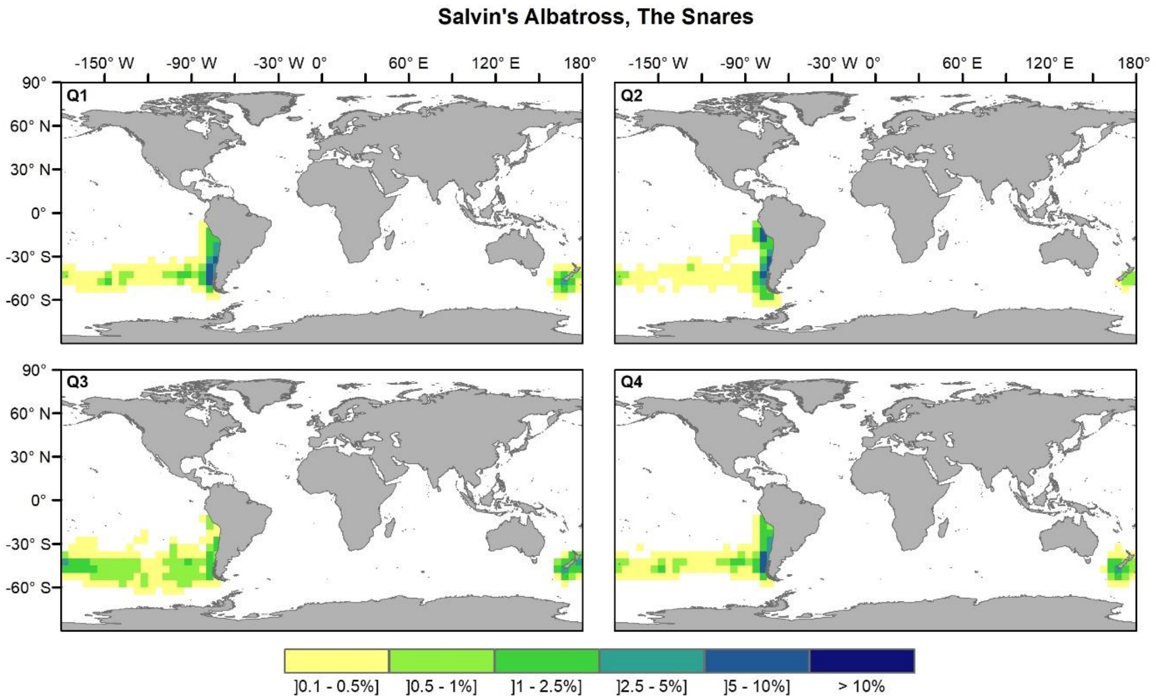

Figure A44: Salvin's Albatross, The Snares

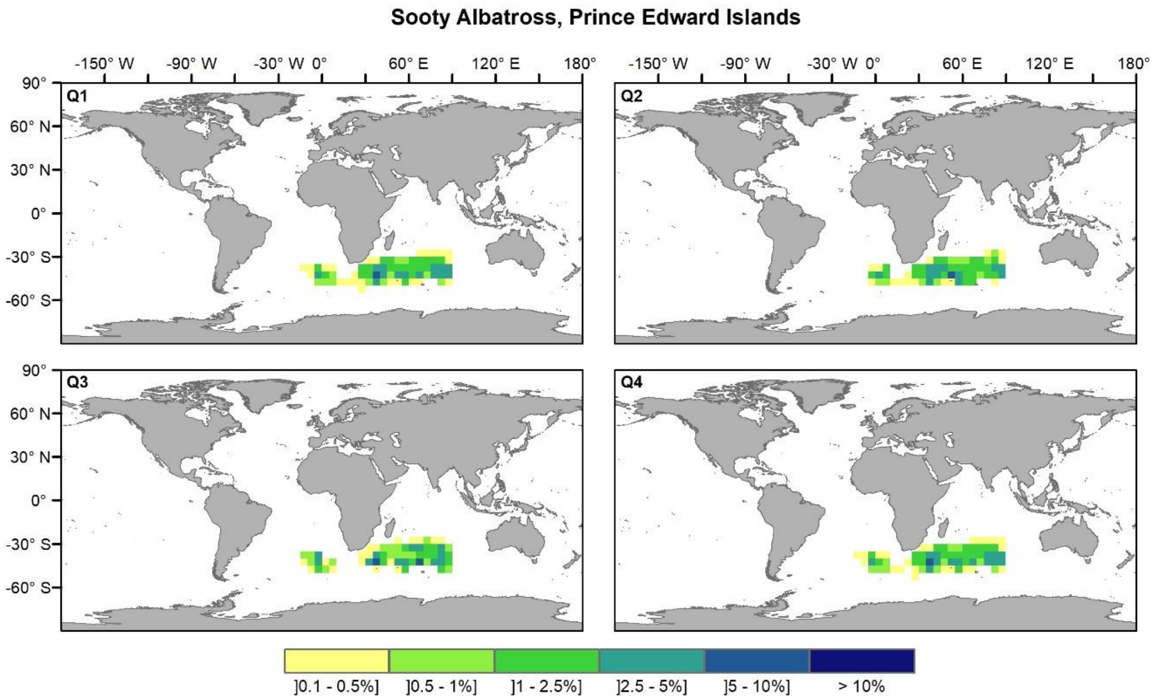

Figure A45: Sooty Albatross, Prince Edward Islands

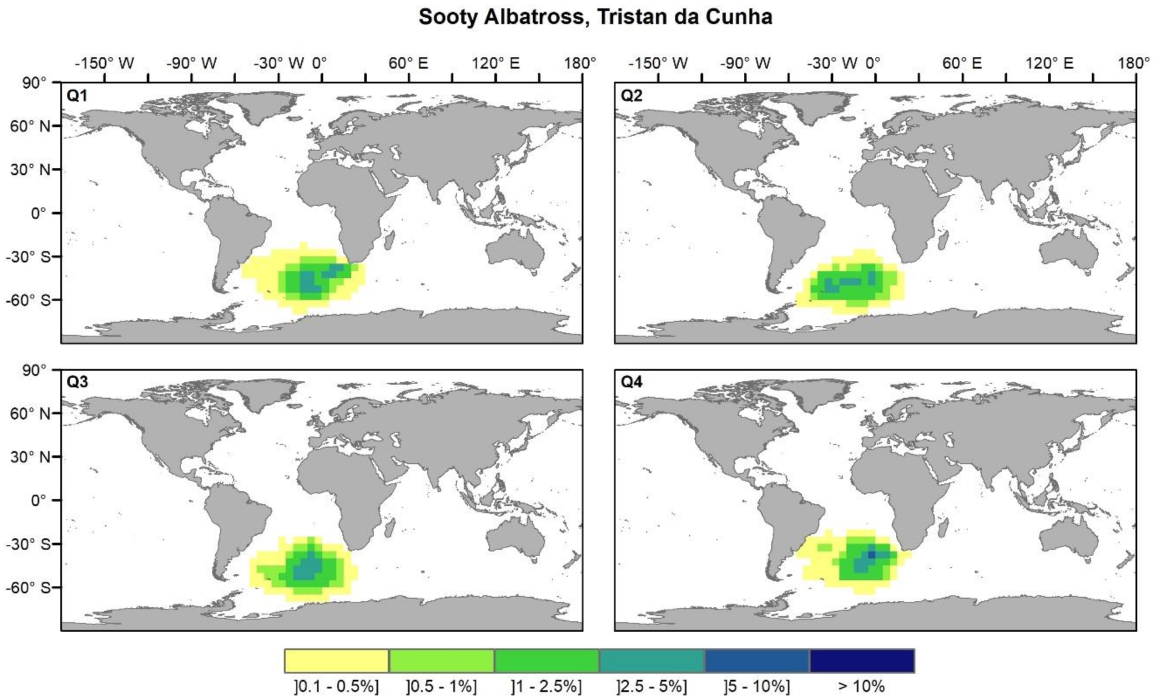

Figure A46: Sooty Albatross, Tristan da Cunha

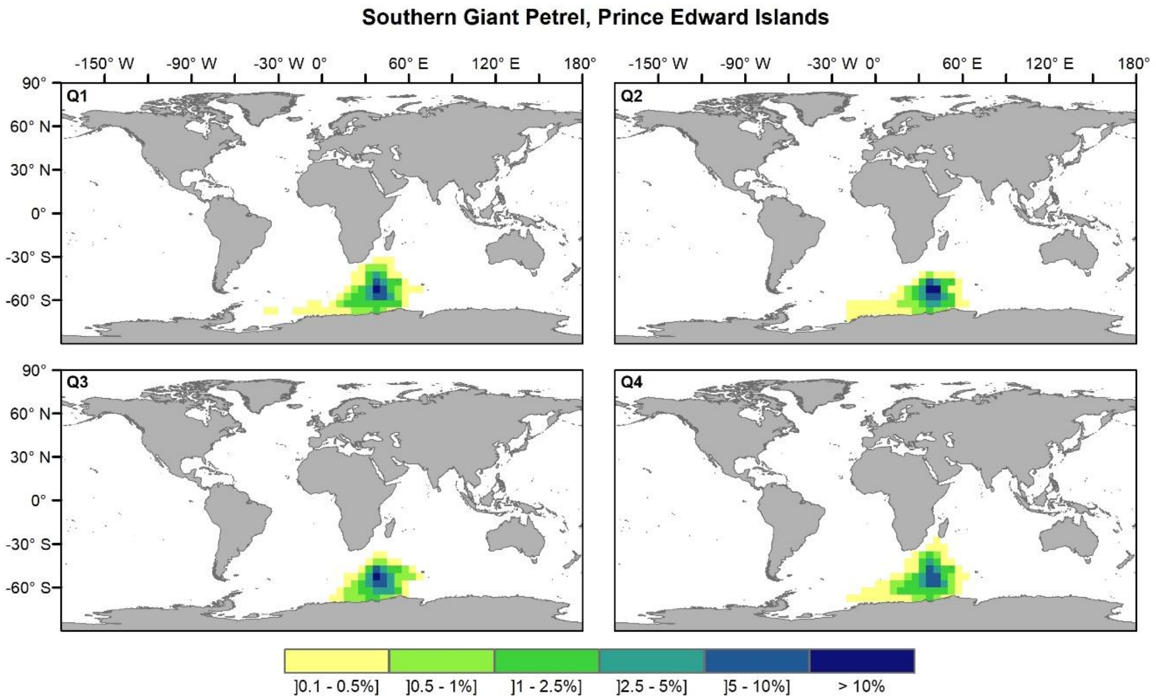

Figure A47: Southern Giant Petrel, Prince Edward Islands

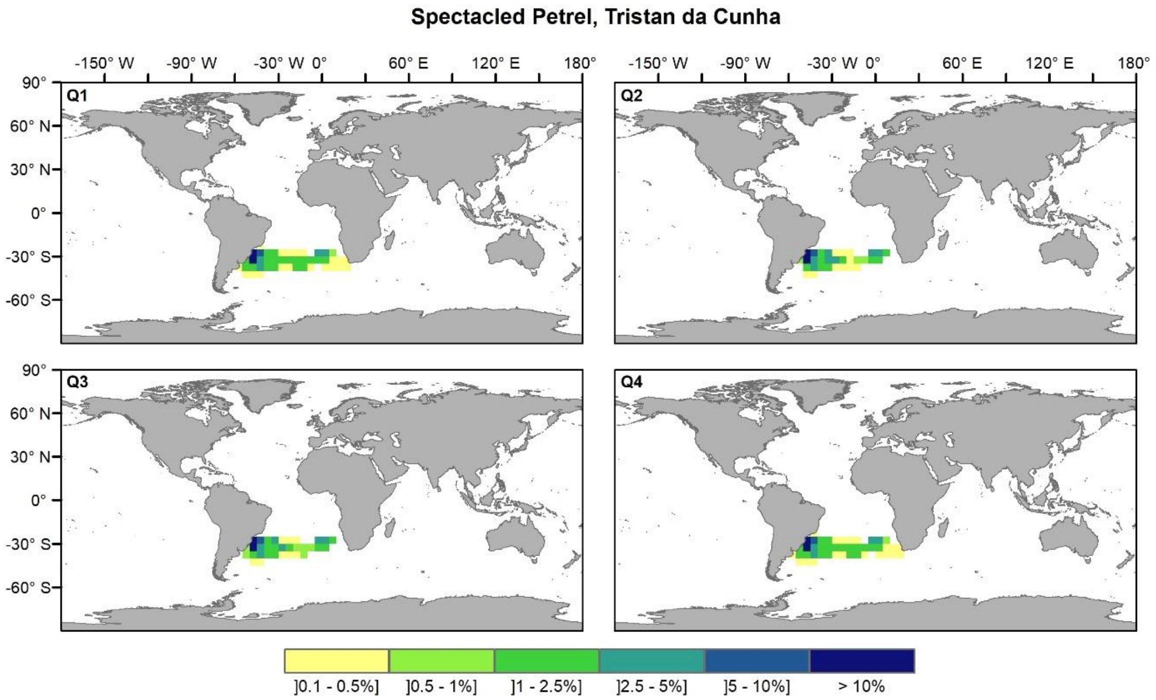

Figure A48: Spectacled Petrel, Tristan da Cunha

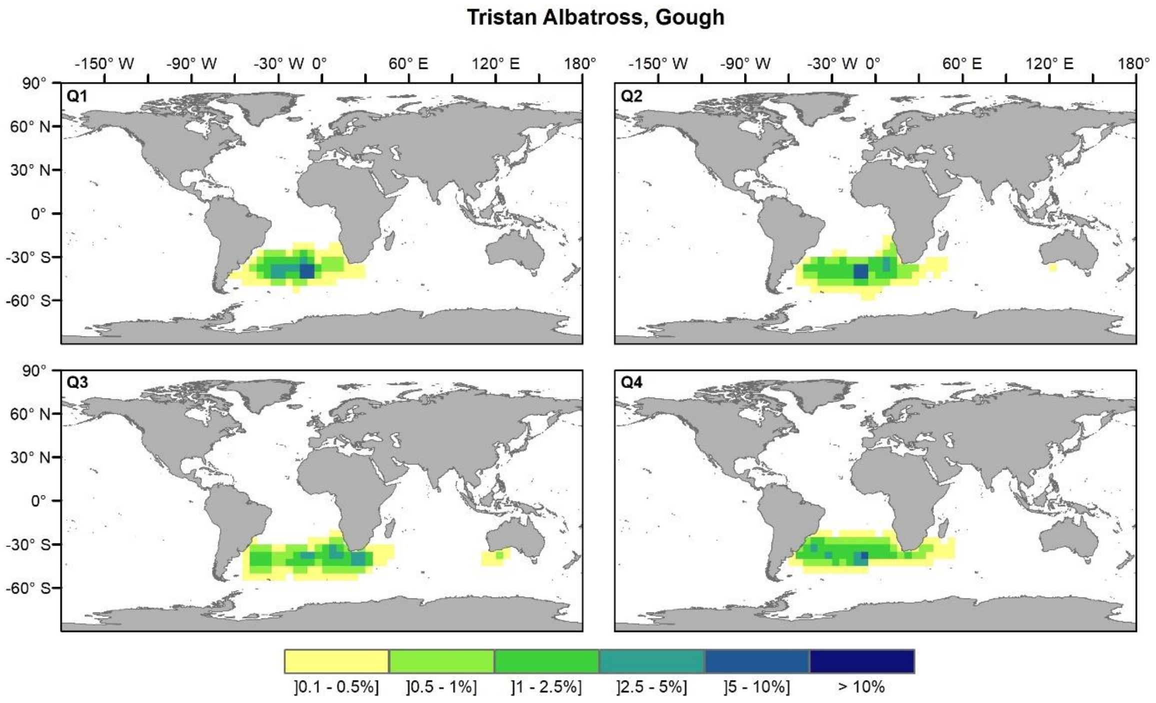

Figure A49: Tristan Albatross, Gough

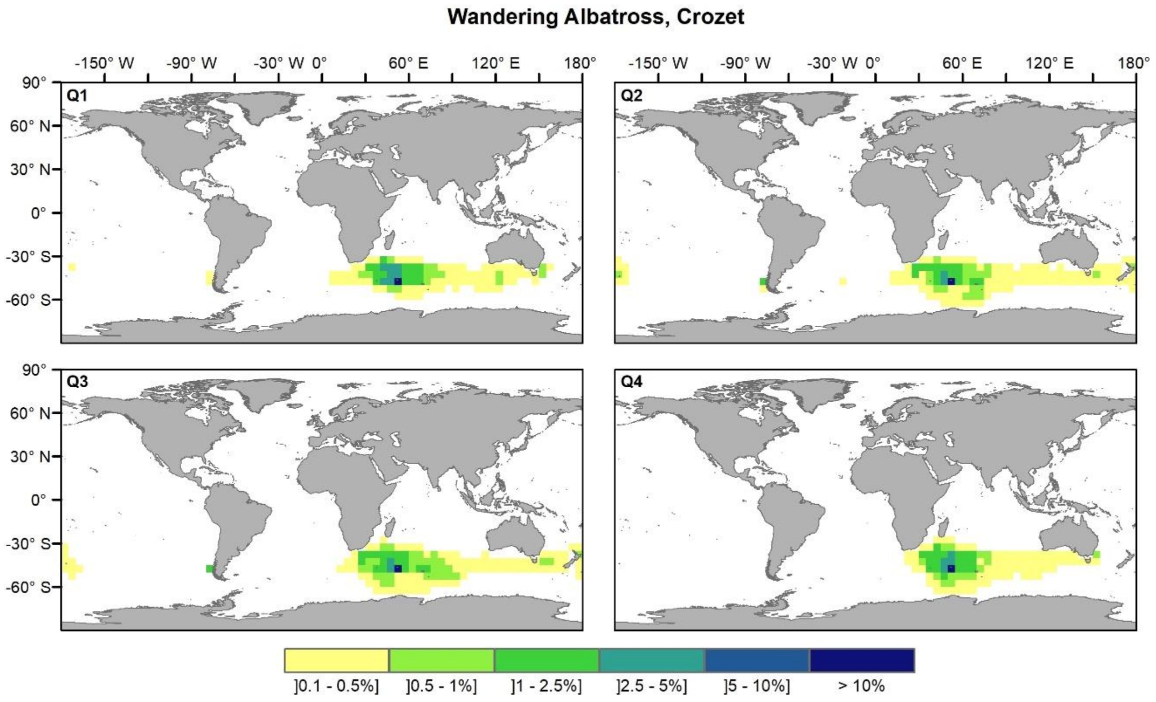

Figure A50: Wandering Albatross, Crozet

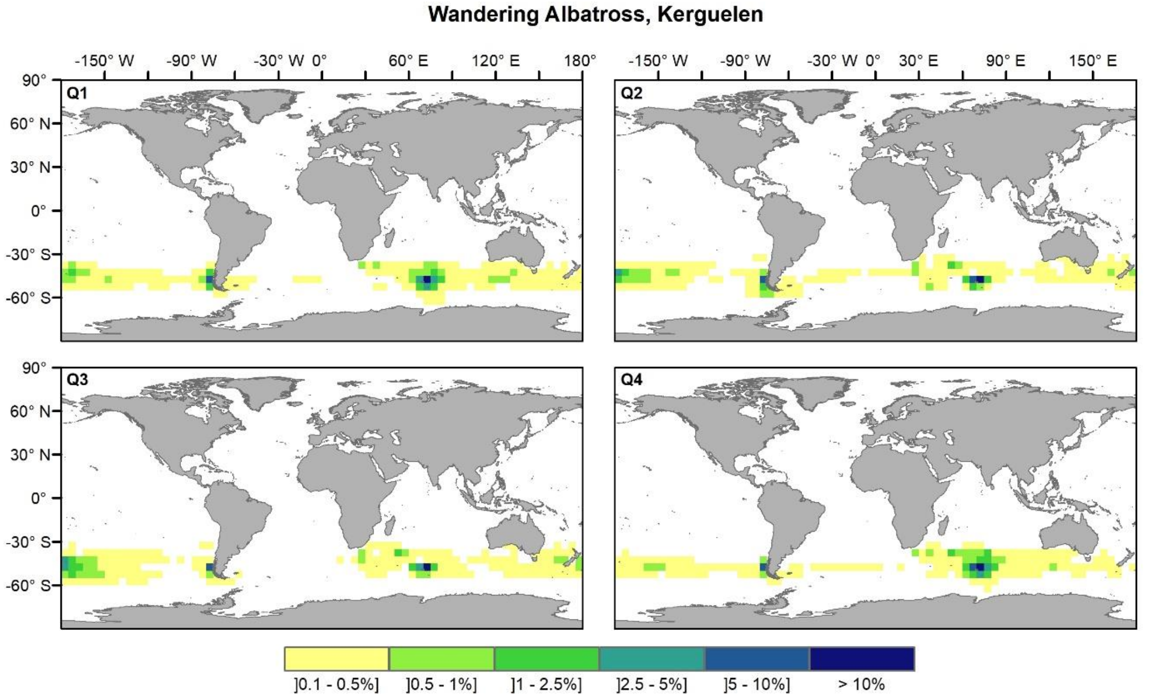

Figure A51: Wandering Albatross, Kerguelen

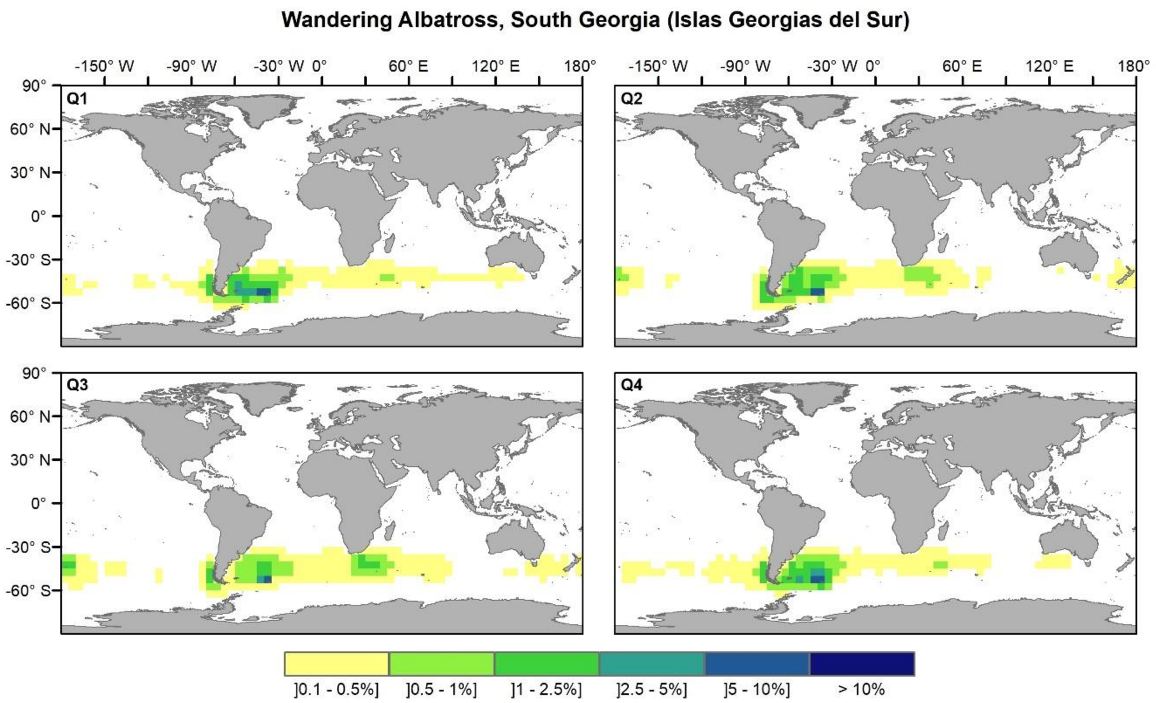

Figure A52: Wandering Albatross, South Georgia (Islas Georgias del Sur)

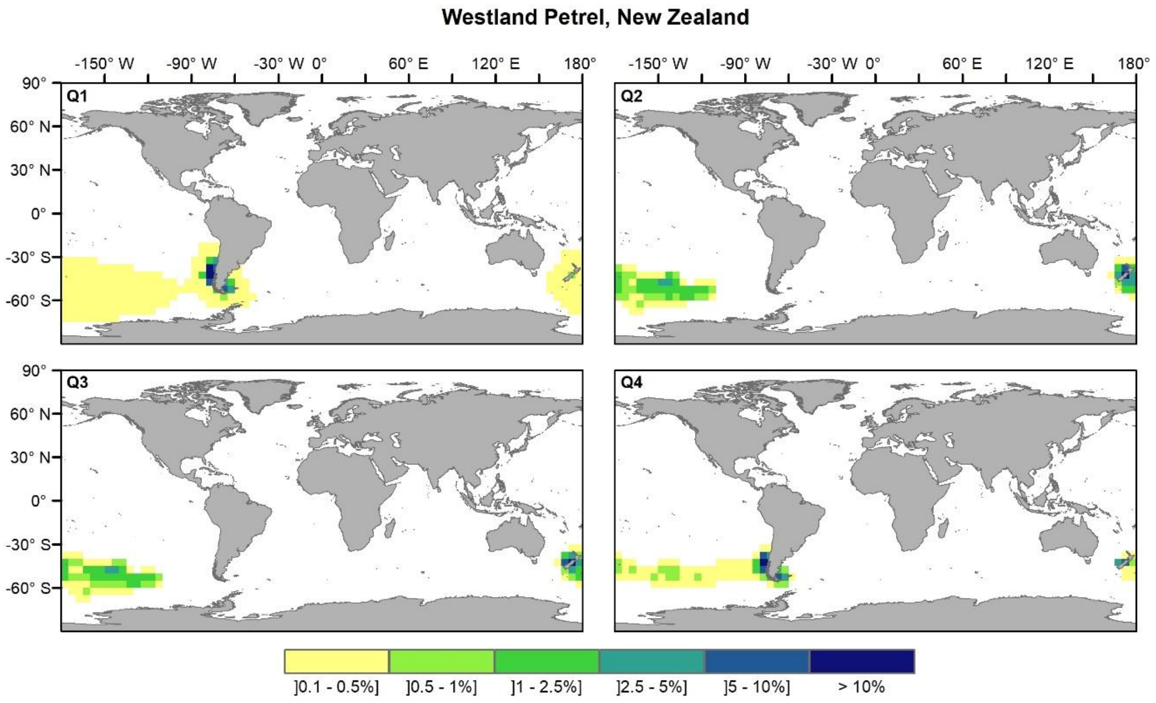

Figure A53: Westland petrel, New Zealand

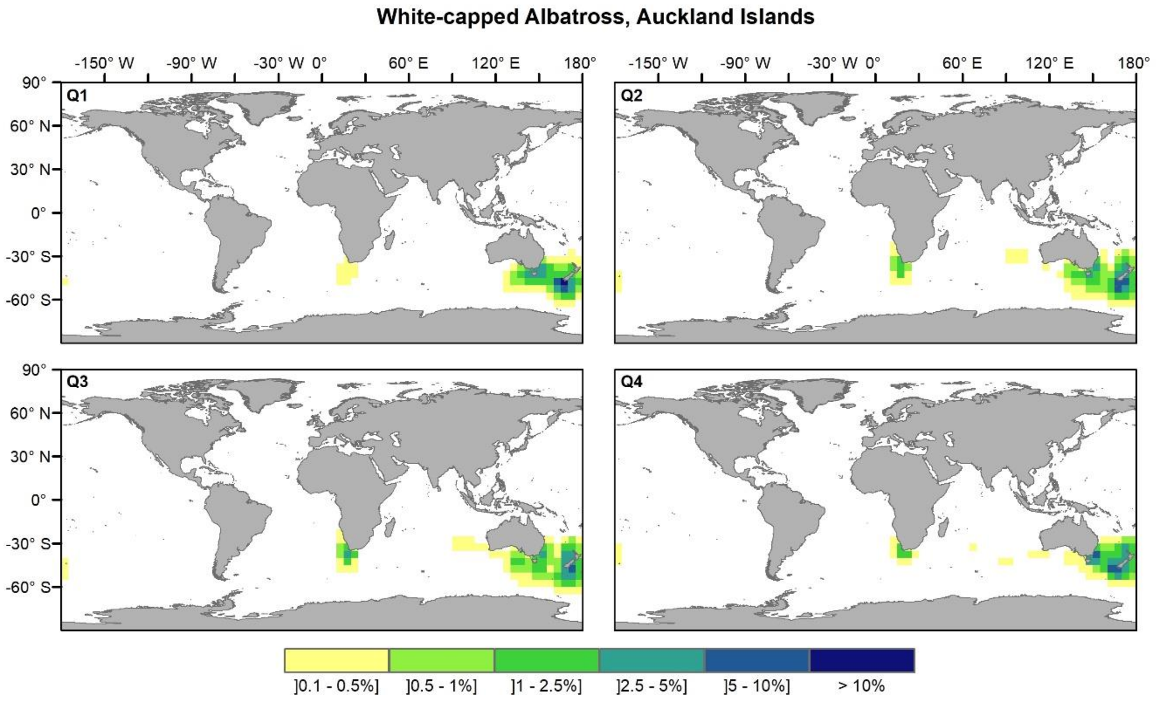

Figure A54: White-capped Albatross, Auckland Islands

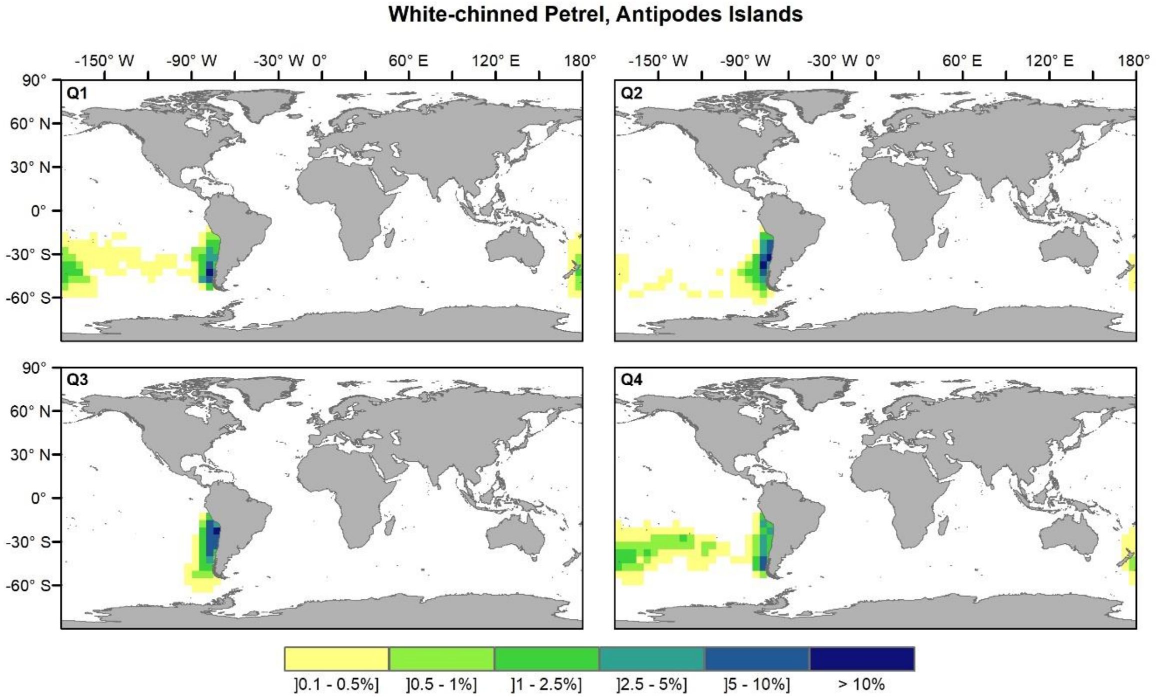

Figure A55: White-chinned Petrel, Antipodes Islands

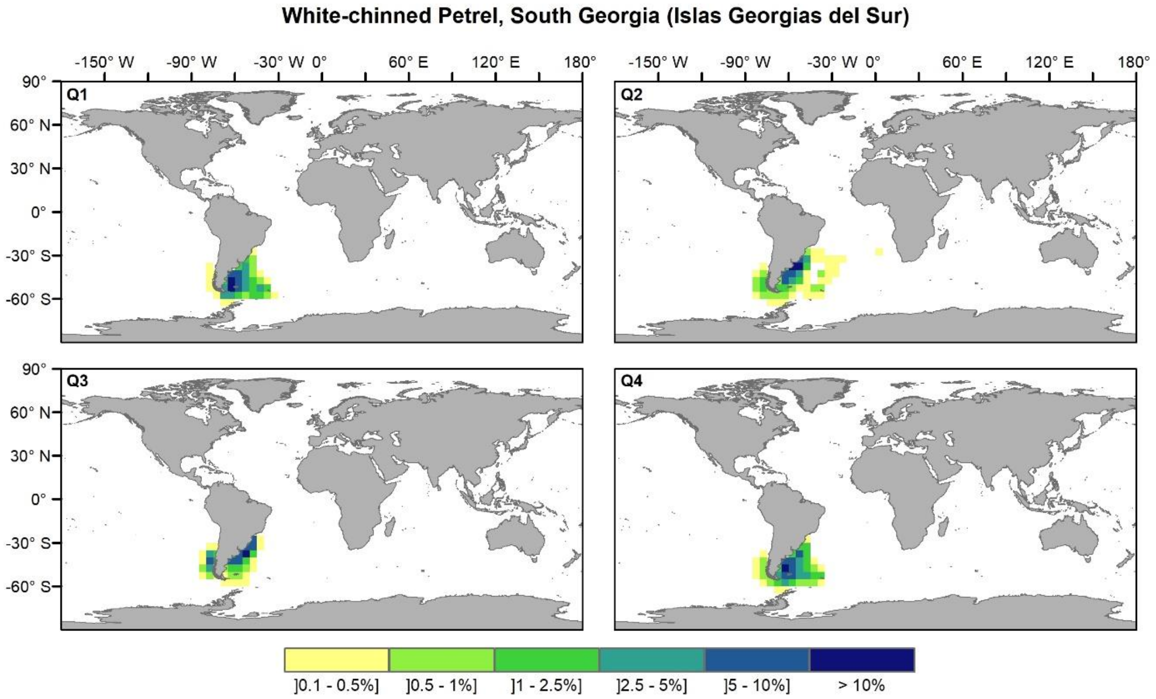

Figure A56: White-chinned Petrel (Islas Georgias del Sur)