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A framework for mapping the distribution of seabirds by integrating tracking, demography and phenology

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BirdLife International, UK

Abstract

1. The identification of geographic areas where the densities of animals are highest across their annual cycles is a crucial step in conservation planning. In marine environments, however, it can be particularly difficult to map the distribution of species, and the methods used 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.
2. Here we develop a methodological framework for estimating population-level density distributions of seabirds, integrating tracking data across the main life-history stages (adult breeders and non-breeders, juveniles and immatures). We incorporate demographic information (adult and juvenile/immature survival, breeding frequency and success, age at first breeding) and phenological data (average timing of breeding and migration) to weight distribution maps according to the proportion of the population represented by each life-history stage.
3. We demonstrate the utility of this framework by applying it to 22 species of albatrosses and petrels that are of conservation concern due to interactions with fisheries. Because juveniles, immatures and non-breeding adults account for 47–81% of all individuals of the populations analysed, ignoring the distributions of birds in these stages leads to biased estimates of overlap with threats, and may misdirect management and conservation efforts. Population-level distribution maps using only adult

distributions underestimated exposure to longline fishing effort by 18–42%, compared with overlap scores based on data from all life-history stages.

4. Synthesis and applications. Our framework synthesises and improves on previous approaches to estimate seabird densities at sea, is applicable for data-poor situations, and provides a standard and repeatable method that can be easily updated as new tracking and demographic data become available. We provide scripts in the R language and a Shiny app to facilitate future applications of our approach. We recommend that where sufficient tracking data are available, this framework be used to assess overlap of seabirds with at-sea threats such as overharvesting, fisheries bycatch, shipping, offshore industry and pollutants. Based on such an analysis, conservation interventions could be directed towards areas where they have the greatest impact on populations.

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A framework for mapping the distribution of seabirds by integrating tracking, demography and phenology

Ana P. B. Carneiro¹, Elizabeth J. Pearmain¹, Steffen Oppel², Thomas A. Clay³, Richard A. Phillips⁴, Anne-Sophie Bonnet-Lebrun⁴, Ross M. Wanless^{5,6}, Edward Abraham⁷, Yvan Richard⁷, Joel Rice⁸, Jonathan Handley¹, Tammy E. Davies¹, Ben J. Dilley⁶, Peter G. Ryan⁶, Cleo Small², Javier Arata⁹, John P. Y. Arnould¹⁰, Elizabeth Bell¹¹, Leandro Bugoni¹², Letizia Campioni¹³, Paulo Catry¹³, Jaimie Cleeland², Lorna Deppe¹⁴, Graeme Elliott¹⁵, Amanda Freeman¹⁶, Jacob González-Solís¹⁷, José Pedro Granadeiro¹⁸, David Grémillet^{19,6}, Todd J. Landers^{20,21}, Azwianewi Makhado^{6,22}, Deon Nel²³, David G. Nicholls²⁴, Kalinka Rexer-Huber²⁵, Christopher J. R. Robertson²⁶, Paul M. Sagar²⁷, Paul Scofield²⁸, Jean-Claude Stahl²⁹, Andrew Stanworth³⁰, Kim L. Stevens⁶, Philip N. Trathan⁴, David R. Thompson²⁷, Leigh Torres³¹, Kath Walker¹⁵, Susan M. Waugh²⁹, Henri Weimerskirch³², Maria P. Dias^{1,13}

¹BirdLife International, UK; ²Royal Society for the Protection of Birds, UK; ³School of Environmental Sciences, University of Liverpool, UK; ⁴British Antarctic Survey, Natural Environment Research Council, UK; ⁵Institute of Marine Affairs and Resources Management, National Taiwan Ocean University, Taiwan; ⁶FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence, University of Cape Town, South Africa; ⁷Dragonfly Data Science, New Zealand; ⁸Rice Marine Analytics, USA; ⁹Centro FONDAP de Investigación en Dinámica de Ecosistemas Marinos de Altas Latitudes, Chile; ¹⁰School of Life and Environmental Sciences, Deakin University, Australia; ¹¹Wildlife Management International Ltd., New Zealand; ¹²Universidade Federal do Rio Grande - FURG, Brazil; ¹³MARE - Marine and Environmental Sciences Centre, ISPA - Instituto Universitário, Portugal; ¹⁴The Hutton's Shearwater Charitable Trust, New Zealand; ¹⁵Albatross Research, New Zealand; ¹⁶Nature North, Australia; ¹⁷Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, Spain; ¹⁸CESAM Departamento de Biologia Animal, Universidade de Lisboa, Portugal; ¹⁹CEFE, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, France; ²⁰Auckland Council,

Research and Evaluation Unit (RIMU), New Zealand; ²¹School of Biological Sciences, University of Auckland, New Zealand; ²²Department of Environmental Affairs, Oceans & Coasts Branch, South Africa; ²³Global Resilience Partnership, Stockholm Resilience Centre, Stockholm University, Sweden; ²⁴Chisholm Institute, Australia; ²⁵Department of Zoology, University of Otago, New Zealand; ²⁶Wild Press, New Zealand; ²⁷National Institute of Water and Atmospheric Research, New Zealand; ²⁸Canterbury Museum, New Zealand; ²⁹Museum of New Zealand Te Papa Tongarewa, New Zealand; ³⁰Falklands Conservation, Falkland Islands; ³¹Department of Fisheries and Wildlife, Oregon State University, Oregon; ³²Centre d'Etude Biologique de Chizé, CNRS, France

Correspondence: Ana P. B. Carneiro. Email: ana.carneiro@birdlife.org

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INTRODUCTION

Oceans face a number of threats, including over-exploitation, habitat destruction and the introduction of alien species (Halpern et al., 2008; Jones et al., 2018). Fisheries are one of the oldest, most widespread and principal threats to marine ecosystems (Crowder & Norse, 2008; Jennings, Reynolds, & Mills, 1998), and are responsible for the decline of many populations of marine megafauna (seabirds, marine turtles, marine mammals, sharks and rays) through direct competition (Cury et al., 2011; Grémillet et al., 2018), deliberate capture for food (Grémillet, Péron, Provost, & Lescroel, 2015) and incidental capture (bycatch) (Lewison et al., 2014; Scales et al., 2018). Furthermore, marine megafauna populations are also exposed to other anthropogenic threats, including climate change (Fuentes et al., 2015; McCauley et al., 2015) and pollution e.g. marine pollutants, oil spills, and plastics (Rigét, Bignert, Braune, Stow, & Wilson, 2010; Thompson et al., 2004; Votier et al., 2005). Many megafauna species such as pelagic seabirds, have wide at-sea distributions, are near the apex of the food chain and are often easier to monitor than lower trophic-level organisms, and so are considered to be useful indicators for the general health of the marine environment (Durant et al., 2009; Parsons et al., 2008).

Understanding how marine megafauna overlap and interact with threats in space and time is crucial for their conservation. Historically, the spatial distribution of pelagic seabirds was mapped based on static range maps or presence-absence data, both of which have implicit spatial biases. Most analyses based on range maps simplistically assume homogeneous distribution within the species range (Williams et al., 2014); however, most marine animals have distinctly heterogeneous distributions. Indeed, the identification of areas with highest densities of individuals is paramount for conservation planning (Hays et al., 2019; Johnston et al., 2015), and is particularly relevant for seabirds, which can have large ranges but often aggregate in particular areas (Oppel et al., 2018). The predominant

methods for estimating presence-absence and densities of animals at sea have been through ship-based surveys and electronic devices attached to individual animals (Eguchi, Gerrodette, Pitman, Seminoff, & Dutton, 2007; Tremblay et al., 2009). Ship-based surveys can provide a good overview of the space use of a species representing all life-history stages combined; however, they are often restricted to the surveyed area and cannot adequately describe the at-sea distribution of seabirds from a particular breeding location because the observed individuals are of unknown provenance (Mott & Clarke, 2018; Sansom, Wilson, Caldow, & Bolton, 2018). Tracking data have therefore proved vital in complementing traditional surveys and overcoming several of these limitations, improving our knowledge of how animals interact with their environment and facilitating a better understanding of the spatio-temporal distribution of seabirds and overlap with marine threats (Hays et al., 2016; Oppel et al., 2018; Sequeira et al., 2018).

Although utilisation distributions (i.e. probability distributions of space use; Fieberg, Kochanny, & Lanham, 2005) based on tracking data can improve spatial priority-setting compared to presence-absence data, range maps and ship-based surveys, studies using this approach generally cannot extrapolate densities to the population level due to common biases in data collection. Tracking devices often have to be recovered to retrieve the data, so data collection has generally focussed on life-history stages or periods of the annual cycle (such as adult breeders during the breeding season) for which deployment and retrieval are most straightforward (Hays et al., 2016; Hazen et al., 2012). As a result, juveniles, immatures and non-breeding adults are generally under-represented because they spend extensive periods at sea and return to colonies only for short periods (Gutowsky et al., 2014; Phillips, Lewis, González-Solís, & Daunt, 2017). However, for long-lived species such as most seabirds, non-breeding individuals represent typically a large proportion of the total population (Saether & Bakke, 2000). As non-breeding individuals generally disperse more widely they may encounter a greater number of threats (Weimerskirch, Åkesson, & Pinaud, 2006). As such, evaluations of risk posed by spatially heterogeneous threats (such as bycatch in fisheries or exposure to pollutants) based solely on data from breeding adults are likely to bias or underestimate risk.

Previous studies have incorporated data from multiple life-history stages to investigate overlap of seabirds with fisheries (e.g. BirdLife International, 2004; Clay et al., 2019; Tuck et al., 2011, 2015). By using detailed information on migratory and breeding schedules, demographic parameters from population models and extensive tracking datasets, Clay et al., (2019) were able to compare population-level distributions of four seabird species from South Georgia with industrial fisheries in the Southern Ocean. Their methodology, however, is not widely applicable to data-poor situations where less information is available on demographic parameters and tracking data are often not available for all life-history stages. In this study, we simplify the approach of Clay et al., (2019) to provide a coherent and generalizable framework to estimate the density distribution of seabird species at sea, including for data-poor situations, through combining tracking data, outputs from demographic models and information on the timings of major events in the annual cycle (i.e. phenology). Our approach is broadly applicable to other species and sites, and can be used to assess the potential exposure of seabirds to a variety of threats by adequately representing the distribution and abundance of all life-history stages that may be affected. Here, we expand on Clay et al., (2019) by providing all the details of the analytical steps of the framework as R scripts and a Shiny app, and by presenting the results of the application of this framework to 22 seabird species of global conservation concern, to identify multi-species hotspots of use at a global scale. Lastly, as many of these species are by-caught in pelagic longline fisheries, we use overlap with fisheries as a relevant case study for examining how disregarding the distribution of particular life-history stages can lead to biases in threat assessment.

MATERIALS AND METHODS

Overview of the framework for estimating density maps

Our framework consists of six steps, which require data on phenology and demography, and tracking data that have been cleaned and standardised according to established protocols (Lascelles et al.,

2016). See Appendix S1 for details on the species used here and for tracking data compilation and standardisation. The steps are: 1) estimating the proportion of the population in each life-history stage using age- and stage-structured population matrix models (Abraham, Yvan, & Clements, 2016; Caswell, 2001); 2) estimating utilisation distributions (UDs) from tracking data for each species, breeding site, device type, age class and stage of the annual cycle (hereafter referred to as 'data group'); 3) assessing the representativeness of each data group; 4) combining data group UD and weighting them based on phenological data to produce monthly distribution maps; 5) using the outputs of 1) to weight monthly distribution maps for each life-history stage by the proportion of the total population represented; 6) aggregating monthly distribution maps in time and space to the spatio-temporal resolution of management interest. All analyses were carried out in R software version 3.3.2 (R Core Team, 2016), and R scripts to replicate the analyses are provided via <https://github.com/anacarneiro/DensityMaps>.

Step 1: Using demographic data to estimate life-history structure of populations

For each population (i.e. each species at each island or island group), estimates of annual survival (juvenile/immature and adult), breeding frequency (approximate proportion of the adult population breeding each year), breeding success and age at first breeding were obtained from the literature (Appendix S2). We used these parameters to construct an age- and stage-structured Leslie-Lefkovich matrix population model. We calculated the age- and stable-stage distributions, which we used to estimate the proportion of the population represented by each life-history stage in a given year (Abraham et al., 2016; Caswell, 2001). The model was based on a three-stage life cycle comprising juveniles (first year at sea after fledging), immatures (from the beginning of second year at sea until recruitment into the breeding population), and adults (Appendix S3). Estimates of breeding frequency were used to split adults into breeding and non-breeding birds (those not attempting to breed in a given year), and estimates of breeding success were used to further split successful and failed

breeders (Appendix S3). To convert these proportions into numbers of birds, we used estimates of the annual breeding population (number of breeding pairs) for each island or island group (using the same definition as in ACAP breeding site database; Phillips et al., 2016) from ACAP species assessments and other sources (Appendix S2). The number of non-breeding birds (juveniles, immatures and non-breeding adults) was extrapolated from the number of breeding pairs given the proportion of the total population estimated to be represented by breeding adults (Appendix S3).

Step 2: Estimating utilisation distributions with tracking data

For each data group, we estimated kernel UD_s using the *adehabitatHR* package (Calenge, 2006; Appendix S4). 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 (BirdLife International, 2004). Tracking data from breeding sites were assumed to represent the distributions of the wider island or island-group ('population'), but if data from several sites within an island or island-group were available we combined those and weighted them in proportion to the total number of individuals at each site (Appendix S4).

Step 3: Assessing the representativeness of each data group

We assessed representativeness (i.e. whether the tracked sample encapsulate the variation in the wider population) of each data group following the bootstrapping methods described in Lascelles et al., (2016) and Oppel et al., (2018). Briefly, for an increasing number of individuals, we took a random subset, calculated the 50% UD and quantified the proportion of the remaining data that fell within this area (Lascelles et al., 2016). Preference was given to GPS and PTT data; UD_s 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 UD_s by the proportion of all individuals represented by

each sample. Juvenile and immature data, when available, were used regardless of their representativeness. A grid cell size of 10×10 km was used for all device types to enable UD's to be combined.

Steps 4-5: Estimating temporal changes in distribution by incorporating phenology

We used phenological data obtained from the literature or provided by researchers to calculate monthly distributions for each life-history stage. Monthly distributions were calculated for the five distinct life-history stages: juveniles, immatures, successful and failed adult breeders (during the breeding and non-breeding seasons) and non-breeders (adults skipping breeding for the year; during the breeding and non-breeding seasons). A UD for each life-history stage and month was calculated by combining the UD's estimated from the relevant data groups according to phenology (Appendix S5). The UD's for each data group were weighted by the average number of days spent in the respective stage of the annual cycle in that month, which was calculated using average start dates and durations of each stage. The resulting monthly distribution maps for each life-history stage were multiplied by the total number of birds in each life-history stage based on the outputs of the demographic models for a given population.

When tracking data were not available to create monthly distribution maps, we used stage replacements (Appendix S5). The potential bias generated by these replacements was investigated (see 'adequacy of stage replacements' below). 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. To explore the use of phenological metadata to create the monthly distributions, we have created an interactive app in R Shiny, which is available at <https://github.com/lizziepear/seabird-phenology>.

Step 6: Spatial and temporal aggregation of distribution grids

The resulting monthly distributions for each life-history stage were given equal weight in generating seasonal and yearly distribution maps for each of the islands and island groups (other temporal

combinations derived from the monthly distribution maps can be generated). We aggregated distribution maps to a 5x5 degree resolution to overlay with logbook fishing effort data (below), but aggregation to a finer resolution is also feasible within our framework. We note that the spatial resolution of the calculated distribution maps should relate to the spatial scale of interest (e.g. threat, extent of management area) and to the resolution of the tracking data. Here we present seasonal and annual at-sea distributions as maps, with each 5x5 degree cell coloured according to the percentage of the population using that cell during a given season or year (Appendix S6).

Adequacy of stage replacements

To test whether our replacements adequately represent the distributions of juveniles and immatures, we quantified the similarity of UD_s between the results of our framework and maps using stage replacements (i.e. adult distribution replacing juvenile and immature distributions – see Appendix S5). For these comparisons, we only considered populations and year-quarters where tracking data from juveniles and immatures were available ($n = 36$). Our expectation was that if the degree of overlap between distributions using real data and using stage replacements was high, then these replacements are adequate. We used the Bhattacharyya's affinity index to quantify overlap; ranging from 0 (no overlap) to 1 (identical UD_s), it is considered to be the most appropriate index for quantifying the degree of similarity among UD estimates (Fieberg et al., 2005).

Testing the framework – assessment of overlap with pelagic longline fisheries

Fishing effort data were collated for all tuna Regional Fisheries Management Organizations which includes the Western and Central Pacific Fisheries Commission, the Commission for the Conservation of Southern Bluefin Tuna, the International Commission for the Conservation of Atlantic Tunas, Indian Ocean Tuna Commission and Inter-American Tropical Tuna Commission. Fishing effort data

(represented by the number of hooks set) were averaged for the 10 most recent years (2007–2016, based on data availability), for each season and 5×5 degree cell.

To understand the potential management and conservation implications of accounting for all life-history stages in density distribution maps, we compared metrics of overlap of pelagic longline fisheries with seabird distributions estimated using the framework presented here (i.e. all life-history stages) against overlaps with distributions estimated based on 1) just using data from adult breeders and 2) just adult breeders and non-breeders (i.e. all adults). We used the steps described above to estimate these distributions but excluding 1) adult non-breeders, juveniles and immatures, and 2) juveniles and immatures, when aggregating distribution maps. To enable comparisons between distributions featuring differing numbers of life-history stages (e.g. just adult breeders vs all life-history stages), all maps were scaled to the estimated number of birds comprising the whole population. Furthermore, we conducted another test to determine how fisheries overlap varies if 3) stage replacements are used for juvenile and immature data. Overlap was compared between population-level distributions based on real juvenile and immature data and those using replacements. We focused our comparisons on the populations and year-quarters for which we had a good representation of all life-history stages.

Overlap between birds and pelagic longline fisheries was calculated from quarterly seabird distributions and fishing effort raster maps by multiplying the number of hooks set for each 5×5 degree cell by the number of individuals using the same cell. Prior to the overlap we excluded cells which contained less than 0.1% of the total for each life-history stage and year quarter, to avoid the confounding effect of high overlaps resulting from cells with a very small number of birds but with a very high pelagic longline fishing effort. Average relative differences in overlap score between the full framework and 1) scaled adult breeders, 2) scaled adult breeders and non-breeders, and 3) stage replacements were calculated per quarter and averaged per season (summer being an average of quarters 1 and 4, and winter the average of quarters 2 and 3) for comparisons.

RESULTS

Population models revealed that adult breeders generally represented less than 50% of the total number of individuals of any population (mean: 35%, range 19–53%). Juveniles and immatures accounted for more than 50% of the population in 16 (44%) out of 36 populations, and more than 40% in 29 (81%) populations (Fig. 1). Adult non-breeders represented an average of 18% of the total number of individuals of any population (range 7–39%; Fig. 1).

We estimated the distribution of 22 species of albatrosses and petrels, 68% ($n = 15$) of which were from populations which cumulatively represented >50% of their species' global population numbers (Appendix S2). In total, the analyses included 4,281 tracked individuals from 18 breeding sites and 15 islands or island groups (Appendix S7). The analyses of tracking data representativeness showed that sample sizes were adequate for the majority of adult breeding datasets, except for the pre-laying stage where data from only seven out of 36 populations were available (Appendix S7). Adult distributions during the non-breeding season were available for all 36 populations, most of which (33 out of 36) were representative (Appendix S7). Juvenile and immature data were lacking for several populations; consequently, adult distributions were used as replacements for 55% of populations.

When all life-history stages were incorporated, the combined population-level distributions of all species were generally less centred on breeding sites than if only adult breeders were considered (particularly obvious in the Atlantic; Fig. 2). The inclusion of adult non-breeders in distributions better documented the importance of the Humboldt Current throughout the year. There was also greater importance of the south Brazilian Shelf and the Benguela Current when juveniles and immatures were taken into account (Fig. 2). We visualised the distributions of several populations for which we had complete datasets (e.g. wandering albatross [*Diomedea exulans*] from Crozet; Fig. 3) and for these, the importance of several regions, such as waters off Australia, New Zealand and Chile, only became clear when including adult non-breeders (20% of the population), juveniles (9% of the population) and

immatures (44% of the population) in the distribution map. Similarly, the importance of south Brazilian waters for black-browed albatrosses (*Thalassarche melanophris*) from the Falkland Islands was only evident when taking into account the juveniles (12% of the population) and immatures (40% of the population) in distribution maps, as adults rarely forage that far north (Fig. 4).

Although the inclusion of juveniles and immatures in the distribution maps revealed important areas for certain populations that are not captured by other life-history data combinations, our assessment of the validity of stage replacements for juvenile and immature data showed them to be, in many cases, adequate in the absence of those datasets. Spatial overlap between the distributions including juvenile and immature data compared with those using the distribution of adults was always relatively high (Bhattacharyya's affinity index > 0.60, mean 0.91). However, we were only able to test for the adequacy of stage replacements in a limited sample of quarterly distributions for which we had either juvenile or immature tracking data available (36 out of 144 quarterly population-level maps).

Overlap of seabirds with pelagic longline fisheries

Population-level density distribution maps using only adult distributions suggested substantially lower exposure to longline fishing effort than the overlap estimated with our framework. The comparisons of the overlap between the distributions of all life-history stages with 1) adult breeders and 2) all adults, with pelagic longline fisheries resulted in an average underestimation of the total fisheries overlap by 1) 36.2% (42.4% in winter and 28.6% in summer) and 2) 28.3% (36.3% in winter and 18.3% in summer), respectively (Appendix S8). Finally, when comparing fisheries overlap between real population-level distributions using juvenile and immature data, and those using 3) stage replacements, the latter underestimated fisheries overlap by an average of 17.9% (29.1% in winter and 4% in summer; Appendix S8).

For example, areas such as the south Brazilian coast used by juvenile and immature black-browed albatrosses during winter also have a high concentration of fishing effort; as a result, exposure risk for

these life-history stages is higher than for adults (Fig. 5; Appendix S9). Including the juvenile and immature distribution increased the exposure by an average of 1.4 million hooks compared to the baseline assumption that the entire population would use only the areas frequented by adult birds. Similarly, when considering juvenile and immature distributions, the wandering albatross population from Crozet encounters 2.4 and 5.7 times as many hooks on average during summer and winter, respectively, than when population-level distributions were based on adult data only (1.7 and 10.7 million hooks more; Fig. 6; Appendix S9).

DISCUSSION

This study presents a detailed framework which allows the estimation of seabird density distributions at different spatial and temporal resolutions across the main life-history stages. By incorporating demographic parameters and counts of breeding adults, our approach allows the abundance of non-breeding individuals to be estimated. We demonstrate that these life-history stages constitute >50% of all individuals within a population, and so neglecting them likely biases estimation of threats to species with age- and stage-structured populations (Clay et al., 2019; Saether & Bakke, 2000).

Because our framework is based on standardised data derived from the Seabird Tracking Database and provides R codes, at-sea distributions can be rapidly updated when new data become available.

We apply our framework to albatross and petrel populations, yet many marine megafauna share similar life-history traits (i.e. they are generally long-lived with delayed reproduction, and may not breed every year) resulting in populations which are age- and stage-structured, with different life-history stages often having different movement strategies (e.g. juveniles are often more dispersive than adults; Hays & Hawkes, 2018; Hays & Scott, 2013). This framework can therefore easily be modified for use with other groups, which have similar life histories, and for which some information on all key life-history stages is available.

Our results showed that some important areas for albatrosses and petrels were omitted when not accounting for all life-history stages in the distributions. The appropriate weighting of the distributions by the number of individuals in each life-history stage resulted in population-level distributions that were much less centred on breeding colonies than when only adult breeders were considered. For example, the importance of the south Brazil shelf for several populations was only highlighted when all life-history stages were included. Similarly, the importance of other areas such as the coast of Uruguay, the Tasman Sea between Australia and New Zealand, and the Benguela Current off South Africa was greater when non-breeding adults, juveniles and immatures were included in distribution maps. For example, use of the south Brazil shelf by black-browed albatrosses during mid-autumn and winter is only shown when incorporating juveniles and immatures in distribution maps (Bugoni & Furness, 2009; Bugoni, Mancini, Monteiro, Nascimento, & Neves, 2008). Indeed, 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 & Weimerskirch, 2013; Weimerskirch et al., 2014). Similarly, the often substantial individual variability among juvenile and immature birds can be difficult to capture with limited tracking effort (Clay, 2017), but as immatures age, their distributions become increasingly similar to those of adults (de Grissac, Börger, Guitteaud, & Weimerskirch, 2016; Weimerskirch, 2018). Accounting for all life-history stages in distribution maps may be even more relevant for near-obligate biennial breeders such as the great *Diomedea* spp., sooty *Phoebastria* spp. and grey-headed *Thalassarche chrysostoma* albatrosses because a proportion of individuals spend the non-breeding (sabbatical) period entirely at sea, and so segregation between different life-history stages is likely to be higher than in annual breeders. 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). Therefore, the resulting density distributions from our framework will better reflect spatial patterns of entire populations throughout the year.

While the aim of our study was not to characterise the distributions of each life-history stage, we emphasise that ignoring those classes when assessing overlap with threats is likely to bias estimates of the risks. Using fisheries bycatch as an example, we showed that the overlap between seabird distributions and pelagic longline fishing effort resulted in substantially lower estimated risk when more dispersive life-history stages (immatures, juveniles and adult non-breeders) were not included. For instance, the increased overlap between black-browed albatrosses and pelagic longline fishing effort corroborates the high capture rates in the south Brazil shelf area reported by on-board observers (Bugoni et al., 2008; Jiménez, Domingo, & Brazeiro, 2009; Jiménez et al., 2016). We noted a similar pattern in wandering albatrosses, whereby juvenile, immature and non-breeding adults (especially females) generally favour lower latitudes and are much more likely to encounter longline tuna vessels (Riotte-Lambert & Weimerskirch, 2013; Weimerskirch et al., 2014). We acknowledge that the spatio-temporal resolution of our results is relatively coarse and provides an estimate of potential, not real, risk. Several studies focusing on fisheries bycatch, however, have found a relationship between indices of seabird-fisheries overlap and bycatch rates or hotspots (Clay et al., 2019; Jiménez et al., 2016), suggesting that our analysis nevertheless provide a crucial tool for conservation.

Our approach highlights the need to better understand the distribution of immature and juvenile birds. However, we recognize that the availability of such data is often limited. Our study also showed that adult non-breeding distribution can approximate juvenile and immature distribution and improve maps which do not consider these life-history stages. However, replacements tended to underestimate overlap with threats compared to maps using data from all life-history stages.

Furthermore, the validity of assuming non-breeding distributions as a replacement for juvenile and immature phases is likely species-specific. The use of stage replacements may be more appropriate when segregation between life-history stages is low (Clay, Pearmain, McGill, Manica, & Phillips, 2018; Péron & Grémillet, 2013). However, using stage replacements when the distribution differs markedly among stages (Campioni, Granadeiro, & Catry, 2017; de Grissac et al., 2016) may omit critical marine areas. While our framework aims to make the most use of existing datasets, we emphasise that

population-level distributions will be most accurate when tracking data from all major life-history stages are available. As such, we recommend researchers and conservation practitioners fill data gaps to gain a better understanding of the space use and threats faced by neglected life-history stages.

Additionally, we used average values for demographic and phenological parameters from the literature. For populations with wide confidence intervals in demographic parameters, we recommend analyses of the sensitivity of results to changes in poorly-known parameters and consideration of this uncertainty when planning conservation interventions (e.g. lower survival of juveniles may underestimate their use of certain areas). We also recommend future studies to adapt our simple demographic model in cases where more detailed demographic, phenological, or spatial distribution data are available. For example, sex-specific differences in at-sea distributions are apparent in many seabirds, resulting in biased bycatch rates (Gianuca, Phillips, Townley, & Votier, 2017; Jiménez et al., 2016). If data exist to characterise sex-specific survival and spatial distribution, then our basic model could be expanded readily to incorporate such differences and improve the assessment of risk exposure.

This study highlights the value of combining tracking and phenology data with demographic models and provides a generalizable framework for estimating the density of seabirds at sea. It is likely that many as-yet unidentified hotspots of threats to marine megafauna may be found when explicitly incorporating all life-history stages. We recommend use of our distribution maps to improve and enforce bycatch mitigation measures in those areas where large proportions of threatened seabird populations occur. We also recommend this framework be applied to other marine megafauna, different threats or other spatial scales (i.e. using high resolution fisheries data) to gain a more complete understanding of multi-species risk zones and periods.

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AUTHORS' CONTRIBUTIONS

APBC, EJP, SO, TAC, RAP, ASBL and MPD conceived the ideas and designed methodology; SO, RMW, RAP, JR, BJD, PGR, JA, JPYA, EB, LB, LC, PC, JC, LD, GE, AF, JGS, JPG, DG, TJL, AM, DN, DGN, KRH, CR, PMS, PS, JCS, AS, KLS, DT, LT, KW, SMW and HW provided the data; APBC and EJP analysed the data; APBC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Seabird tracking data can be downloaded from the BirdLife International Seabird Tracking Database (<http://seabirdtracking.org/mapper/>; dataset ids: 418, 419, 420, 421, 422, 423, 424, 425, 426, 427, 429, 430, 431, 432, 433, 434, 435, 436, 437, 438, 439, 444, 448, 457, 459, 460, 461, 462, 463, 465, 469, 470, 471, 472, 473, 474, 475, 476, 477, 478, 479, 483, 484, 487, 488, 489, 490, 491, 492, 493, 494, 495, 532, 533, 554, 556, 600, 602, 603, 604, 606, 618, 619, 620, 621, 627, 631, 632, 634, 635, 636, 640, 643, 644, 648, 649, 650, 651, 652, 653, 654, 657, 658, 659, 666, 683, 685, 700, 833, 834,

835, 850, 858, 901, 949, 951, 957, 968, 1103, 1104, 1129, 1133, 1134, 1135, 1136, 1137, 1138, 1288, 1290, 1293, 1295, 1296, 1297, 1298, 1299, 1300, 1301, 1302, 1303, 1304, 1305, 1306, 1307, 1308, 1309, 1310, 1311, 1312, 1313, 1314, 1317, 1318, 1319, 1320, 1321, 1322, 1324, 1325, 1382, 1383, 1384, 1386, 1387, 1388, 1389, 1390, 1391, 1394, 1395, 1405, 1412, 1447, 1448, 1449, 1450, 1451).

Publicly available fishing effort data were provided by Joel Rice who collated the information directly from IATTC (<https://www.iattc.org/PublicDomainData/PublicLLTunaBillfish.zip>), ICCAT (the Task II catch and effort database available on the ICCAT website (<https://www.iccat.int/en/accesingdb.htm>), WCPFC (<https://www.wcpfc.int/public-domain>), CCSBT (<https://www.ccsbt.org/en/content/sbt-data>) and IOTC (<http://www.iotc.org/documents/ce-longline>). Data were cleaned and filtered for double reporting (i.e. reporting to both CCSBT and IOTC) and highly irregular effort (i.e. millions of hooks with zero reported catch). Annual and quarterly population-level density distributions maps are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.z612jm685> (Carneiro et al., 2019).

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FIGURE 1 The proportion of the population represented by each major life-history stage for 22 species of albatrosses and petrels (36 populations) breeding in the Southern Ocean. Five 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), adult breeders (further split into successful and failed breeders) and adult non-breeders (birds not attempting to breed in a given year)

FIGURE 2 The quarterly and year-round density distributions of 22 species of albatrosses and petrels (36 populations) breeding in the Southern Ocean. Equal weight is given to each of the 36 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 5x5° grid. Darker shades (of blue) depict a greater density of birds. Density distribution maps are based on data for a) adult breeders (successful and failed breeders), b) adult breeders and non-breeders (the latter representing birds not attempting to breed this year), and c) all life-history stages (which includes information for adult breeders and non-breeders, juveniles and immatures)

FIGURE 3 The seasonal density distributions of wandering albatrosses from Crozet. The colour gradient refers to the percentage of the population represented within each 5x5° grid. Darker shades (of blue) depict a greater density of birds. Maps are based on data for a) adult breeders (successful and failed breeders), b) adult breeders and non-breeders (the latter representing birds not attempting to breed this year), and c) all life-history stages (which includes information for adult breeders and non-breeders, juveniles and immatures)

FIGURE 4 The seasonal density distributions of black-browed albatrosses from Falkland Islands. The colour gradient refers to the percentage of the population represented within each 5x5° grid. Darker

shades (of blue) depict a greater density of birds. Maps are based on data for a) adult breeders (successful and failed breeders), b) adult breeders and non-breeders (the latter representing birds not attempting to breed this year), and c) all life-history stages (which includes information for adult breeders and non-breeders, juveniles and immatures)

FIGURE 5 The seasonal overlap of black-browed albatrosses from Falkland Islands with pelagic longline fisheries averaged across years (2007-2016). Darker shades [of red] depict a greater overlap. The colour gradient refers to the number of individuals multiplied by number of hooks within each 5x5° grid. Maps are based on data for a) adult breeders (successful and failed breeders; during the breeding and non-breeding seasons), b) adult non-breeders (birds not attempting to breed this year), and c) juveniles and immatures

FIGURE 6 The seasonal overlap of wandering albatrosses from Crozet with pelagic longline fisheries averaged across years (2007-2016). Darker shades [of red] depict a greater overlap. The colour gradient refers to the number of individuals multiplied by number of hooks within each 5x5° grid. Maps are based on data for a) adult breeders (successful and failed breeders; during the breeding and non-breeding seasons), b) adult non-breeders (birds not attempting to breed this year), and c) juveniles and immatures

FIGURE 1

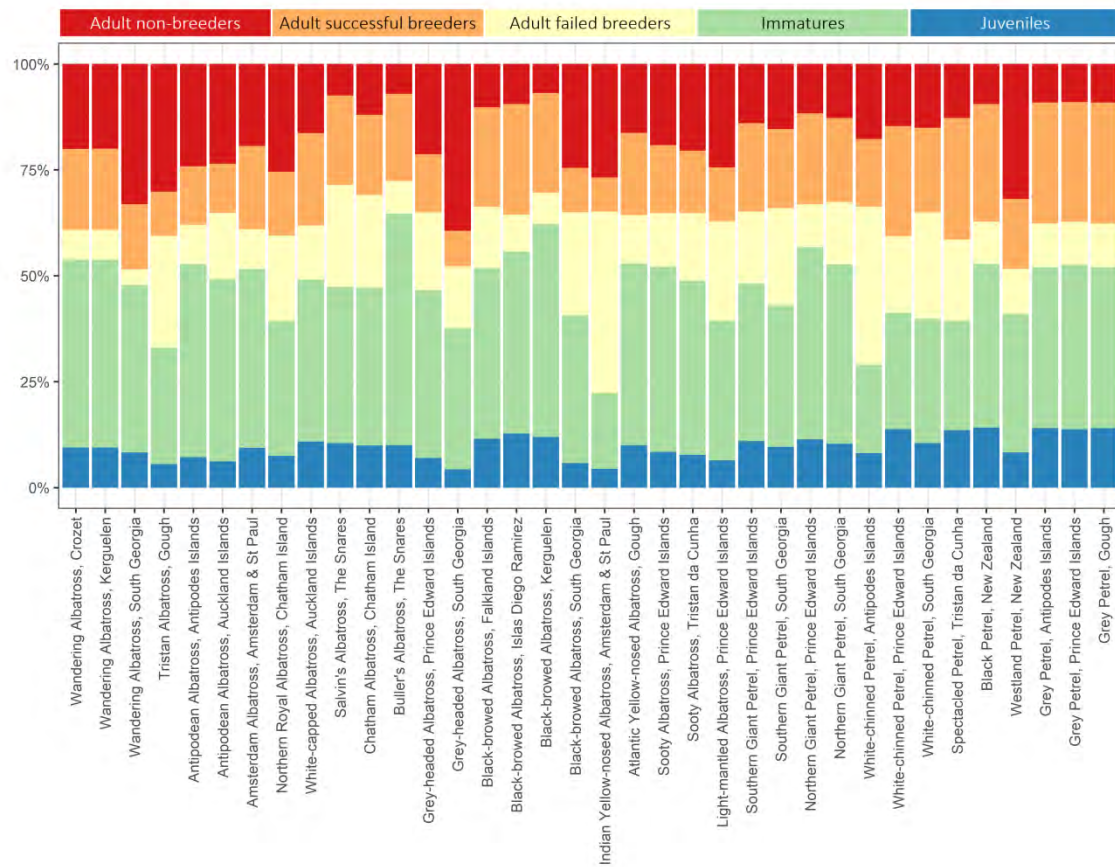


FIGURE 2

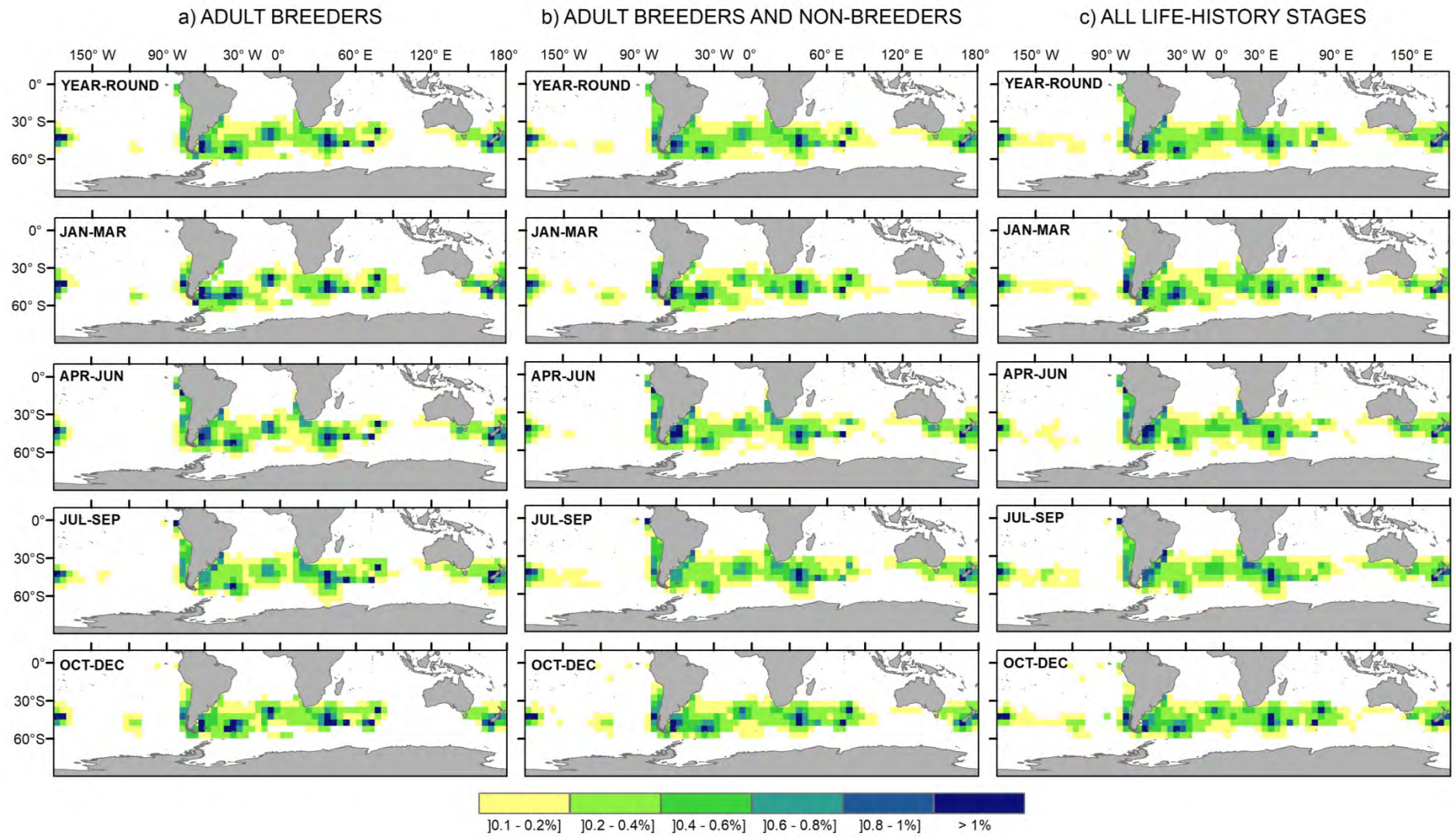


FIGURE 3

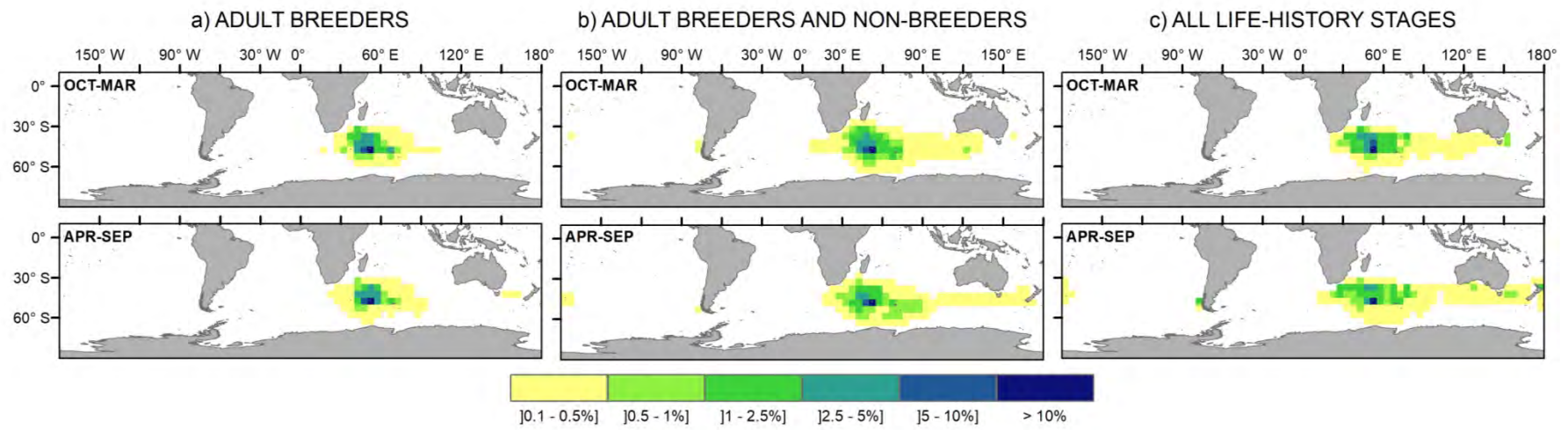


FIGURE 4

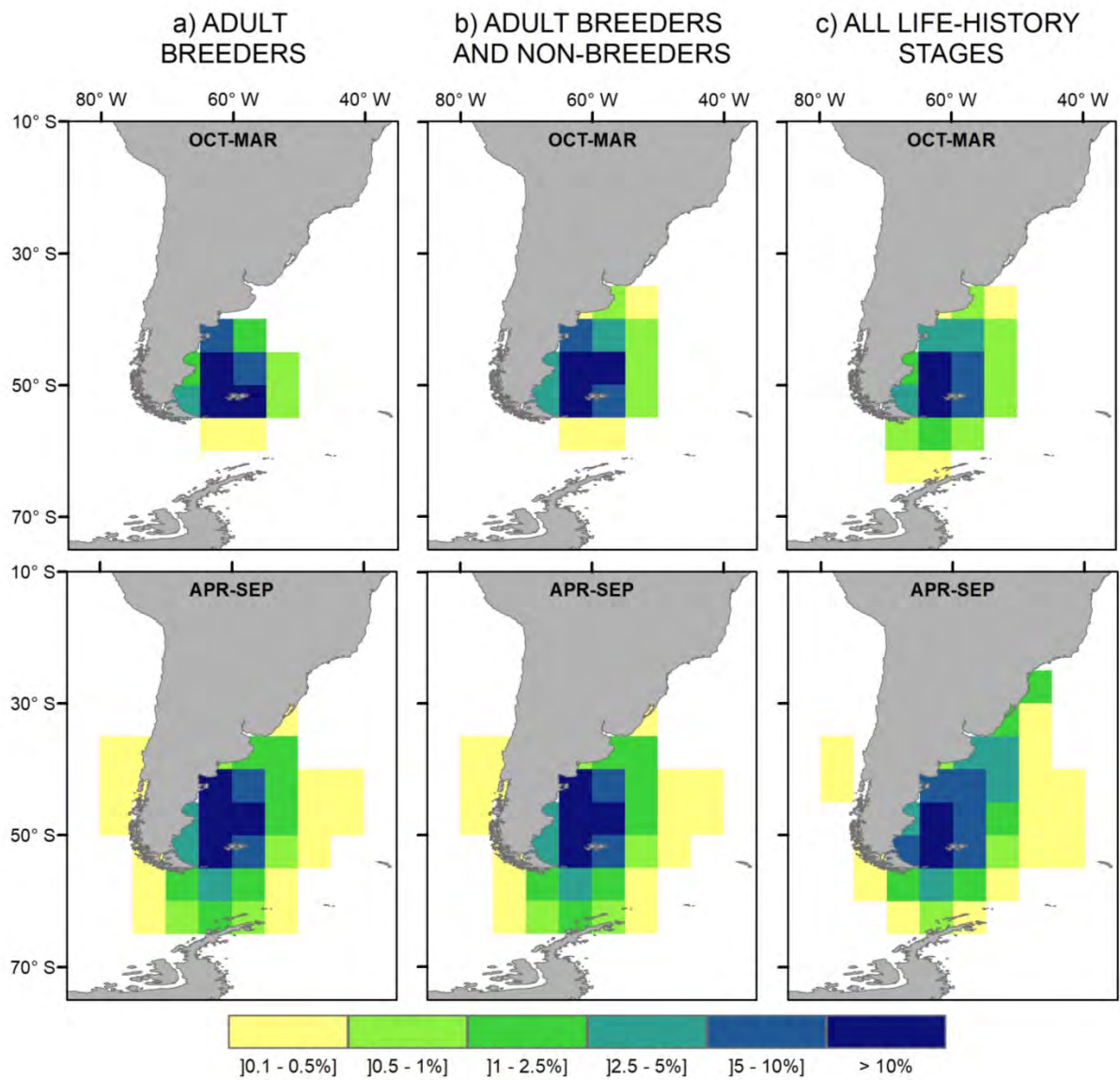


FIGURE 5

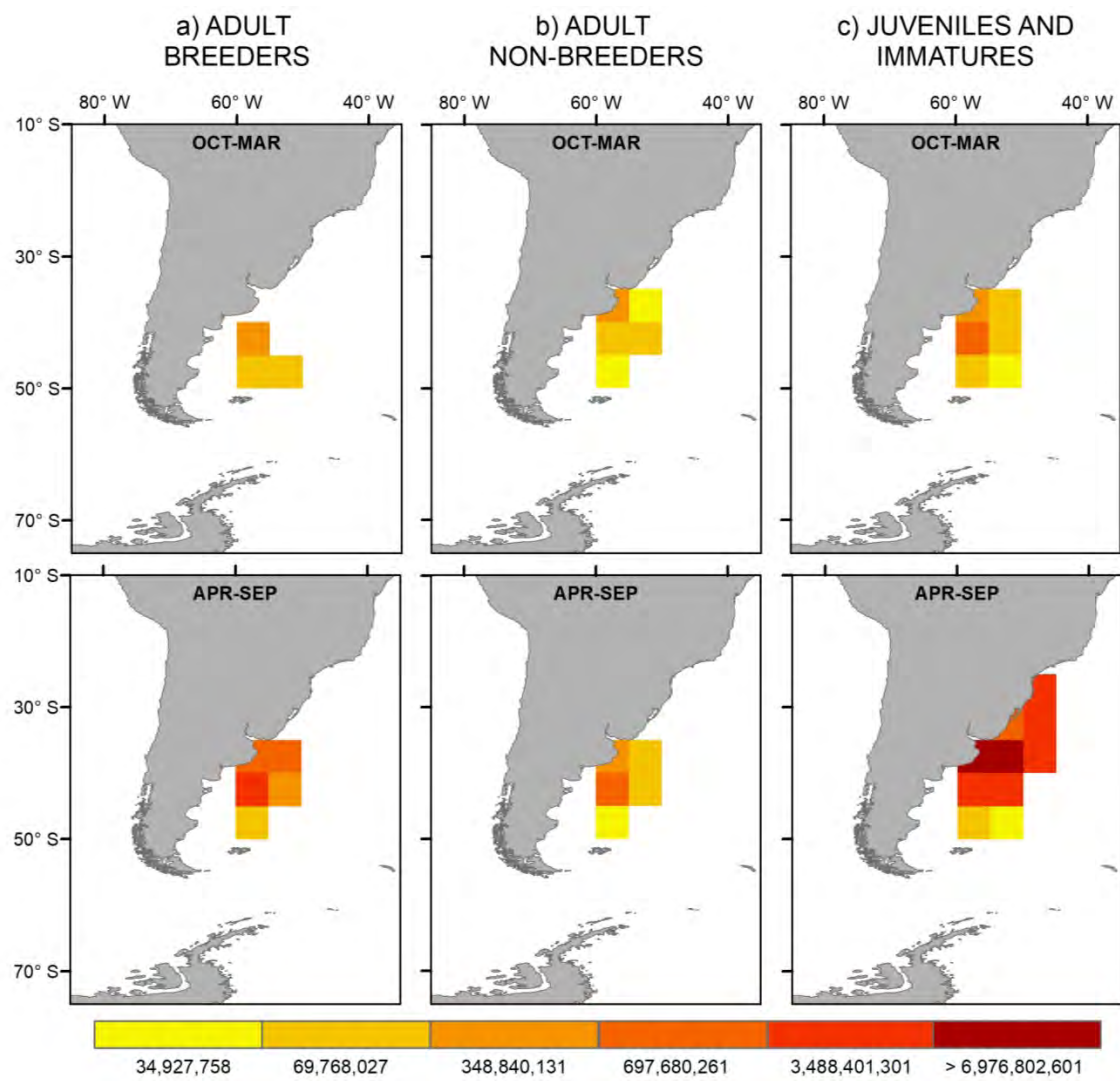
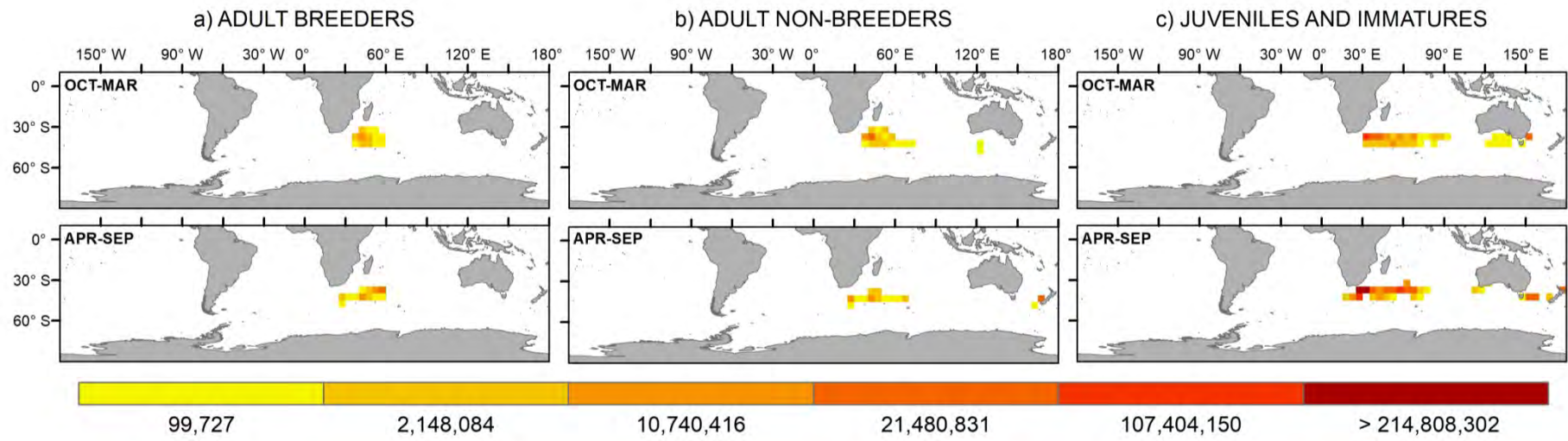


FIGURE 6



SUPPORTING INFORMATION

Appendix S1

A framework for mapping the distribution of Southern Ocean seabirds across life-history stages, by integrating tracking, demography and phenology

More details can be found at <https://github.com/anacarneiro/DensityMaps>

Study species

We apply this framework to 22 of the species listed under the Agreement for the Conservation of Albatrosses and Petrels (ACAP, see <https://www.acap.aq/en/acap-species> for a complete list). These species represent iconic megafauna that have an important role in ecosystem functioning (Lewison et al., 2014), and are of global conservation concern due to interactions with fisheries (Dias et al., 2019; Phillips et al., 2016). Currently, 21 of the 31 species listed under ACAP are threatened with extinction (BirdLife International, 2018), emphasizing the need to map their at-sea distributions. We considered all ACAP species that breed in the Southern Ocean, except for the pink-footed shearwater (*Ardenna creatopus*), southern royal (Diomedea epomophora), Campbell (Thalassarche impavida) and shy (T. cauta) albatrosses for which insufficient tracking data were available in the Seabird Tracking Database (<http://seabirdtracking.org/>) to confidently map their distributions.

Tracking data compilation and standardization

We compiled tracking data deposited in the Seabird Tracking Database (<http://seabirdtracking.org/>) for our 22 focal 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 or geolocators). A basic speed filter was applied for PTT data in order to remove erroneous positions with speeds > 90 km/h (McConnell, Chambers, & Fedak, 1992). GLS data are expected to be cleaned prior to uploading in the Seabird Tracking Database, not requiring additional cleaning. PTT and GPS data were linearly interpolated (i.e. rediscritization every hour) to obtain regular positions. Re-sampling was not conducted for GLS data since the locations of tracked birds collected using this type of device are available at regular intervals (approximately 12-hour). All positions within 5 km (for GPS data) and 15 km (for PTT data) of the colony were excluded.

All tracking data were split into data groups (by pooling all data for each combination of species, breeding site, device type, age class and stage of the annual cycle). The classification of tracking data into age and stage of the annual cycle followed the classification provided by data owners when uploading data into the Seabird Tracking Database, with the exception of adult non-breeding, juvenile and immature data. Adult non-breeding distribution data were further split into year quarters for analysis: quarter 1 (Q1, Jan–Mar), quarter 2 (Q2, Apr–Jun), quarter 3 (Q3, Jul–Sep) and quarter 4 (Q4, Oct–Dec); juvenile and immature data were split into summer (both Q4 and Q1) and winter (both Q2 and Q3) periods instead of year quarters to increase data coverage. We assumed that seabird distributions were largely consistent between years (Croxall, Silk, Phillips, Afanasyev, & Briggs, 2005; Guilford et al., 2011; Phillips, Silk, Croxall, Afanasyev, & Bennett, 2005), and data were aggregated over all available years. We recognise that distributions may change between years, and results will be more robust where tracking data exist across multiple years, but annual shifts in distribution are fairly small compared to the transoceanic range of all species considered here (Phillips, Lewis, González-Solís, & Daunt, 2017).

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SUPPORTING INFORMATION

Appendix S2

A framework for mapping the distribution of Southern Ocean seabirds across life-history stages, by integrating tracking, demography and phenology

More details can be found at <https://github.com/anacarneiro/DensityMaps>

TABLE S1 Population estimates (i.e. annual breeding pairs), % of all sites (i.e. percentage in relation to global estimates), demographic estimates of juvenile/immature (average annual survival from fledging to average age of 1st breeding) and adult annual survival, breeding frequency and success and age at first breeding for the populations from which tracking data were available for the analysis. Where no estimates were available for particular demographic parameters from a given population or age class, we used parameters from another location or another species with similar life-history attributes. For some species, no estimates of juvenile survival existed, and we estimated juvenile survival from adult survival, using age effect: juvenile survival = adult survival multiplied by the average ratio of juvenile to adult survival calculated from all available data for the relevant genus (*Procellaria*, *Thalassarche*, or both). Species in bold were representative of island or island group(s) holding >50% of the global population estimates.

Population (reference)	Annual pairs	% all sites	Juv/Imm survival	Adult survival	Br frequency	Br success	Age 1st br
Wandering albatross							
Crozet (1, 2, 3, 4, 5, 6)	1,815	23.1	0.889	0.945 ^a	0.566 ^b	0.730	10.0
Kerguelen (1, 2, 3)	1,184	14.7	0.889 ^c	0.945 ^c	0.566 ^c	0.730 ^c	10.0 ^c
South Georgia (1, 7)	1,858	17.6	0.819	0.879	0.365 ^b	0.808	9.8
Tristan albatross							
Gough (1, 8, 9)	1,650	100.0	0.836	0.910	0.550	0.283	10.1
Antipodean albatross							
Antipodes Islands (1, 10, 11, 12)	3,945	54.4	0.894	0.918	0.489	0.600	12.0
Auckland Islands (1, 11, 13, 14)	5,817	45.6	0.880	0.889	0.536	0.427	12.4
Amsterdam albatross							
Amsterdam (1, 15, 16, 17)	51	100.0	0.936	0.971	0.600	0.677	9.4
Northern royal albatross							
Chatham Island (1, 11)	5,800	99.5	0.876	0.960	0.581	0.427	9.0
White-capped albatross							
Auckland Islands (1, 11, 18)	97,089	99.9	0.834	0.960	0.680	0.630	9.0
Salvin's albatross							
The Snares (1, 11, 19)	1,195	3.7	0.837	0.967	0.859	0.467	9.0
Chatham albatross							
Chatham Island (1, 11, 20)	5,245	100.0	0.828	0.887	0.773	0.463	8.0
Buller's albatross							
The Snares (1, 21, 22)	8,704	28.6	0.910	0.950	0.800	0.727	12.0
Grey-headed albatross							
Prince Edward Islands (1, 11, 23)	9,500	10.8	0.883 ^d	0.949 ^d	0.601 ^d	0.427 ^d	12.0 ^d
South Georgia (1, 7)	47,674	49.8	0.912	0.952	0.368 ^b	0.365	14.2

Cont.

Population (reference)	Annual pairs	% all sites	Juv/Imm survival	Adult survival	Br frequency	Br success	Age 1st br
Black-browed albatross							
Falkland Islands ^(1, 7, 24, 25, 26)	399,416	66.6	0.862 ^e	0.942	0.787 ^{b,f}	0.620	7.5
Islas Diego Ramirez ^(1, 7, 24, 25, 27)	55,000	9.2	0.862 ^g	0.942 ^g	0.787 ^g	0.750	7.5 ^g
Kerguelen ^(1, 5, 7, 28, 29)	3,215	0.5	0.843	0.910	0.818 ^{b,h}	0.763	9.7
South Georgia ^(1, 7)	74,296	12.4	0.820	0.875	0.586 ^b	0.300	12.1
Atlantic yellow-nosed albatross							
Gough ^(1, 31, 33, 34)	5,300	15.9	0.836	0.920	0.655	0.630	10.5
Indian yellow-nosed albatross							
Amsterdam and St Paul ^(1, 15, 17, 31, 32)	22,000	65.0	0.794	0.902	0.655 ⁱ	0.159	9.0
Sooty albatross							
Prince Edward Islands ^(1, 34, 35, 36)	2,493	18.8	0.842 ^e	0.920	0.600	0.560	11.8
Tristan da Cunha ^(1, 33, 34, 35)	8,188	61.7	0.842 ^e	0.920	0.600	0.480	11.8
Light-mantled albatross							
Prince Edward Islands ^(1, 11)	657	3.2	0.876	0.959 ^j	0.597 ^j	0.352 ^j	11.0 ^j
Southern giant petrel							
Prince Edward Islands ^(1, 23, 35, 37, 38)	2,800	4.7	0.795 ^k	0.890 ^l	0.730	0.550	8.0
South Georgia ^(1, 35, 39, 40)	5,500	11.0	0.821 ^k	0.920	0.730	0.449	8.0
Northern giant petrel							
Prince Edward Islands ^(1, 23, 32, 35, 37, 41)	750	3.9	0.795 ^k	0.890	0.730 ^m	0.680	10.0
South Georgia ^(1, 32, 35, 39, 40)	4,310	36.5	0.813 ^k	0.910	0.730 ^m	0.573	10.0
White-chinned petrel							
Antipodes Islands ^(1, 7, 35, 37, 42, 43)	40,000	3.0	0.819 ^k	0.940	0.750	0.300 ⁿ	6.5
Prince Edward Islands ^(1, 35, 44, 45, 46, 47)	36,000	2.7	0.700 ^o	0.895 ^o	0.750	0.590	6.1 ^o
South Georgia ^(1, 7, 35, 43)	773,150	58.8	0.820 ⁿ	0.875 ⁿ	0.750	0.444	6.0
Spectacled petrel							
Tristan da Cunha ^(1, 34, 35, 48, 49)	30,000	100.0	0.840	0.970	0.790 ^p	0.600 ^q	5.0 ^q
Black petrel							
Great Barrier Island ^(1, 49, 50, 51, 52)	2,427	94.3	0.792	0.903	0.800	0.735	6.6
Westland petrel							
New Zealand ^(1, 53)	4,000	100.0	0.875 ^r	0.936	0.460	0.607	7.7 ^s
Grey petrel							
Antipodes Islands ^(1, 35, 52, 55)	53,000	NA	0.819 ^t	0.940 ^u	0.810	0.735 ^v	7.0 ^u
Prince Edward Islands ^(1, 35, 52, 55, 56)	5,000	NA	0.819 ^t	0.940 ^u	0.810	0.735 ^v	7.0 ^u
Gough ^(1, 35, 52, 55, 56)	15,000	NA	0.819 ^t	0.940 ^u	0.810	0.735 ^v	7.0 ^u

^a Average between males: 0.947 and females: 0.942; ^b Product of return and breeding probabilities; ^c Replaced from Crozet; ^d Replaced from grey-headed albatross at New Zealand; ^e AGE EFFECT - *Thalassarche*; ^f Breeding probability from Falkland Islands and return probability replaced from South Georgia; ^g Replaced from Falkland Islands; ^h Breeding probability from Kerguelen and return probability replaced from South Georgia; ⁱ Replaced from Atlantic yellow-nosed albatross at Gough; ^j Replaced from light-mantled albatross at New Zealand; ^k AGE EFFECT - *Procellaria* and *Thalassarche*; ^l Replaced from northern giant petrel at New Zealand; ^m Replaced from southern giant petrel; ⁿ Replaced from black-browed albatross at South Georgia; ^o Replaced from white-chinned petrel at Crozet; ^p Average of other *Procellaria* species; ^q Replaced from white-chinned petrel at Marion; ^r From fledging to first return; ^s Age of first return used as proxy for age of first breeding; ^t AGE EFFECT - *Procellaria*; ^u Replaced from grey petrel at Crozet; ^v Replaced from black petrel at New Zealand.

¹ ACAP; ² Delord et al., (2013); ³ Fayet et al., (2015); ⁴ Barbraud & Weimerskirch, (2012); ⁵ Pardo, Barbraud, Authier, & Weimerskirch, (2013); ⁶ Barbraud & Weimerskirch, (2012); ⁷ Pardo et al., (2017); ⁸ Davies, Dilley, Bond, Cuthbert, & Ryan,

(2015); ⁹ Wanless et al., (2009); ¹⁰ Elliott & Walker, (2017); ¹¹ Abraham, Yvan, & Clements, (2016); ¹² Edwards, Robers, Walker, & Elliott, (2017); ¹³ Elliott, Walker, Parker, & Rexer-Huber, (2016); ¹⁴ Francis, Elliott, & Walker, (2015); ¹⁵ Heerah et al., (2019); ¹⁶ Rivalan, Barbraud, Inchausti, & Weimerskirch, (2010); ¹⁷ Jaeger et al., (2018); ¹⁸ Francis, (2012); ¹⁹ Sagar, (2011); ²⁰ Fraser, Henderson, Robertson, & Scofield, (2011); ²¹ Sagar, (2014); ²² Francis & Sagar, (2012); ²³ Ryan, Jones, Dyer, Upfold, & Crawford, (2009); ²⁴ Catry, Forcada, & Almeida, (2011); ²⁵ Campioni, Granadeiro, & Catry, (2017); ²⁶ Catry unpub. data; ²⁷ Robertson et al., (2014); ²⁸ Nevoux, Weimerskirch, & Barbraud, (2010); ²⁹ Pardo, Jenouvrier, Weimerskirch, & Barbraud, (2017); ³⁰ Rolland, Barbraud, & Weimerskirch, (2009); ³¹ Cuthbert, Ryan, Cooper, & Hilton, (2003); ³² NZ birds online; ³³ Cuthbert, Cooper, & Ryan, (2014); ³⁴ Ryan pers. comm; ³⁵ Dobson & Jouventin, (2007); ³⁶ Schoombie, Crawford, Makhado, Dyer, & Ryan, (2016); ³⁷ Richard, Abraham, & Berkenbusch, (2017); ³⁸ Ryan et al., (2003); ³⁹ Gianuca et al., (n.d.); ⁴⁰ Brown, Techow, Wood, & Phillips, (2015); ⁴¹ Jones, Risi, Cleeland, & Ryan, (2019); ⁴² Thompson pers. comm.; ⁴³ Clay et al., (2019); ⁴⁴ Ryan, Dilley, & Jones, (2012); ⁴⁵ Rollinson, Dilley, Davies, & Ryan, (2018); ⁴⁶ Barbraud, Marteau, Ridoux, Delord, & Weimerskirch, (2008); ⁴⁷ Dilley et al., (2018); ⁴⁸ Ryan, Dorse, & Hilton, (2006); ⁴⁹ Francis & Bell, (2010); ⁵⁰ Bell et al., (2018); ⁵¹ Bell, Sim, & Scofield, (2011); ⁵² Bell, Mischler, MacArthur, Sim, & Scofield, (2016); ⁵³ Waugh et al., (2015); ⁵⁴ Bell, (2013); ⁵⁵ Barbraud, Delord, Marteau, & Weimerskirch, (2009); ⁵⁶ Dilley pers. comm.

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SUPPORTING INFORMATION

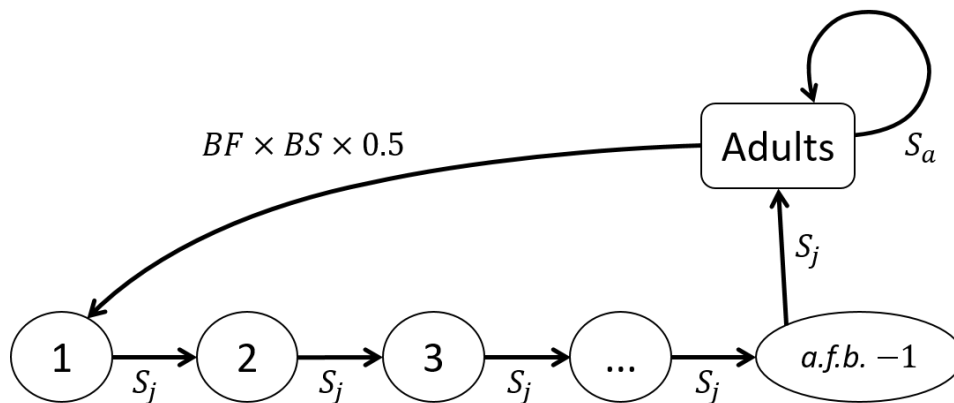
Appendix S3

A framework for mapping the distribution of Southern Ocean seabirds across life-history stages, by integrating tracking, demography and phenology

More details can be found at <https://github.com/anacarneiro/DensityMaps>

Demography analysis

Figure S1. State transitions in the general seabird age-structured Leslie-Lefkovitch matrix model used to model a population of females in order to estimate the proportion of each population in each life-history stage, following Abraham et al., (2016). The model has one adult state and one state for each immature year class until recruitment into the breeding population. Each year, a proportion S_a of adult birds and S_j of immature birds survive. All immatures are assumed to recruit into the breeding population at age $a.f.b.$, the average age at first breeding. For each adult female in the population, $BF \times BS \times 0.5$ first-year female immatures are produced each year, where BF is the breeding frequency (the approximate proportion of the adult population attempting to breed in any given year), BS is the breeding success (the proportion of breeding attempts resulting in a fledged chick) and the sex ratio is assumed to be even (0.5).



Demography modelling

For each population (each species at each island group), we constructed a matrix model (see Fig. S1) with number of age classes = $a.f.b$ and used the function `stable.stage` from the R package `popbio` to calculate the stable stage distribution (R Core Team, 2016; Stubben & Milligan, 2007). The immature age classes were split into “juveniles” (first year fledglings) and “immatures” (sum of all year classes from 2 to recruitment, Fig. S1) in order to create the density distribution maps using juvenile and immature spatial data. The proportion of adults was split into a proportion of adults breeding each year (breeders) and a proportion of adults skipping breeding each year (adult non-breeders) using breeding frequency BF , where breeders = adults $\times BF$ and non – breeders = adults $\times (1 - BF)$. The proportion of breeders was further split into successful and fail breeders using breeding success BS , where successful breeders = breeders $\times BS$ and fail breeders = breeders $\times (1 - BS)$. For more details, please see the R scripts available on GitHub.

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SUPPORTING INFORMATION

Appendix S4

A framework for mapping the distribution of Southern Ocean seabirds across life-history stages, by integrating tracking, demography and phenology

More details can be found at <https://github.com/anacarneiro/DensityMaps>

Kernel analysis

Utilization distributions (UDs) using kernel analysis in the *adehabitatHR* package (Calenge, 2006) were estimated for each data group 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, age and stage of the annual cycle. Tracking data derived from GPS and PTT were combined before the kernel analysis. To control for differences in the number of trips or years of tracking per individual, UD were generated for each bird and then averaged so that each individual had equal weighting (Carneiro et al., 2016; Clay et al., 2016, 2019). A fixed smoothing parameter (h) of 50 km was used for PTT and GPS data, and 200 km for GLS data (BirdLife International, 2004). Tracking data for black-browed and white-capped albatrosses were available for several breeding sites within the same island or island group, therefore, the final UD represented the combination of sites based on the percentage of the total population involved. For the incubation period, the final UD for black-browed albatross was the combination of UD created for Saunders Island, New Island and Steeple Jason, representing each 6%, 7% and 87% of the Falkland Islands (Islas Malvinas) population, while during the brood-guard stage, data was available for New Island (8%) and Steeple Jason (92%) and for Saunders Island (45%) and New Island (55%) for the non-breeding distribution. For the white-capped albatross UD for both brood-guard and post-guard were the combination of UD from Auckland Island (5%) and Disappointment Island (95%). The UD created for each data group were used as surrogates for the population-level distributions (i.e. island or island groups when using the same definition as ACAP). The final UD were cropped by a land mass polygon so that they only included marine areas.

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SUPPORTING INFORMATION

Appendix S5

A framework for mapping the distribution of Southern Ocean seabirds across life-history stages, by integrating tracking, demography and phenology

More details can be found at <https://github.com/anacarneiro/DensityMaps> and <https://github.com/lizziepear/seabird-phenology>

Estimating temporal changes in distribution by incorporating phenology

The distribution of successful 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. 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 at any given time during those stages (Carneiro et al., 2016; Hedd, Montevecchi, Phillips, & Fifield, 2014). When tracking data were not available for the pre-laying phase we used incubation data as a replacement.

For non-breeding adults we considered the non-breeding (sabbatical) distribution during both the breeding and non-breeding seasons. As very few tracks were available for failed breeders, we gave this life-history stage the distribution of successful breeders until half-way through the breeding season, after which they took the distribution of adult non-breeders. This approach accounts for the tendency in many populations for failed breeders to leave the colonies much earlier than successful breeders (Phillips, Lewis, González-Solís, & Daunt, 2017). For populations with breeding seasons spanning slightly longer than one year (e.g. wandering albatross, *Diomedea exulans*), we truncated the post-brood period for successful breeders, removing the short time between completion of a full year since the start of pre-laying and fledging of the chick. Curtailing the breeding season to a single year enables the same framework to be used for all species regardless of breeding-season duration.

The distributions of juveniles and immatures were estimated from UD's based on a seasonal combination of tracking data. In several cases, when tracking data were not available for juvenile and immature birds, the juvenile distribution was replaced by the distribution of adults during the non-breeding season, when birds are away from the colony and not constrained by central place foraging, which in many species is likely to be broadly similar to the distribution of juveniles (Clay et al., 2019; Weimerskirch, Åkesson, & Pinaud, 2006). For immatures, unavailable data were substituted with the annual distribution of non-breeding adults as immatures (particularly the older ones) tend to visit the breeding grounds and may have similar strategies to those of breeders, at least during certain periods of the breeding season (Campioni, Dias, Granadeiro, & Catry, 2019; Fayet et al., 2015; Jaeger et al., 2014; Weimerskirch, 2018).

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SUPPORTING INFORMATION

Appendix S6

A framework for mapping the distribution of Southern Ocean seabirds across life-history stages, by integrating tracking, demography and phenology

More details can be found at <https://github.com/anacarneiro/DensityMaps>

Seabird density distributions at quarterly and annual resolutions

Figures S1-S36. Annual population-level density distributions for 22 species of albatrosses and petrels (36 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 5x5° grid. Darker shades (of blue) depict a greater density of birds. For details on the number of individuals, see Appendix S6 Table S1.

Figures S37-S72. Quarterly population-level density distributions for 22 species of albatrosses and petrels (36 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 Appendix S6 Table S1.

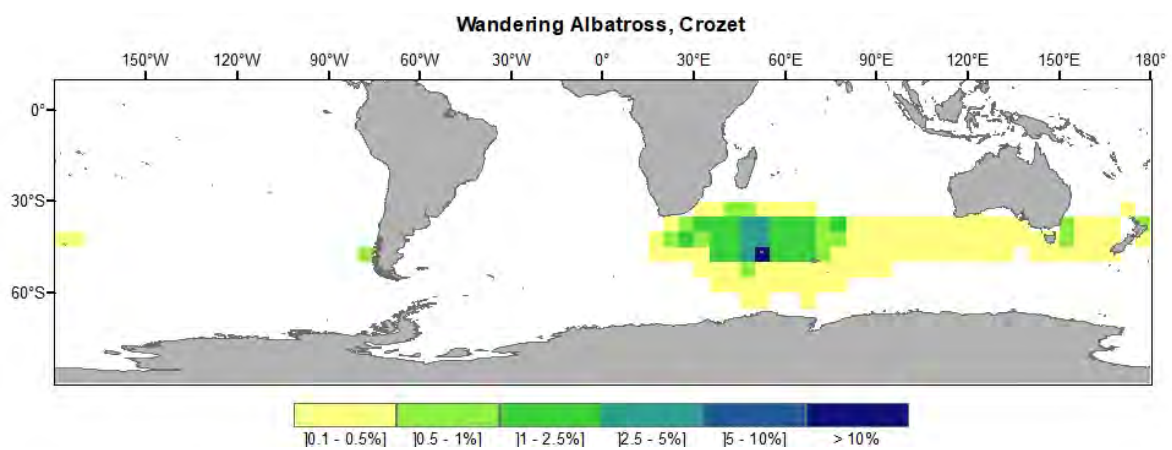


Figure S1. Wandering Albatross, Crozet

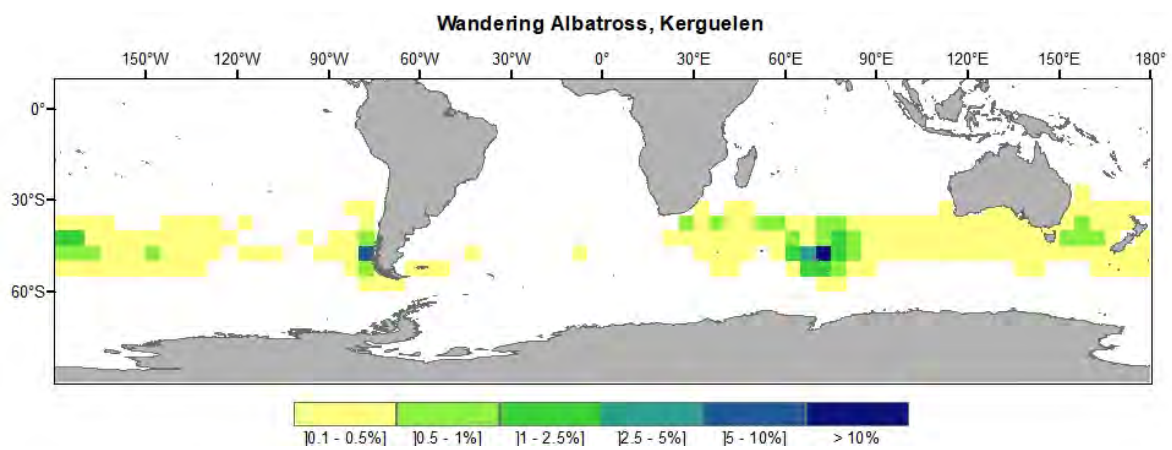


Figure S2. Wandering Albatross, Kerguelen

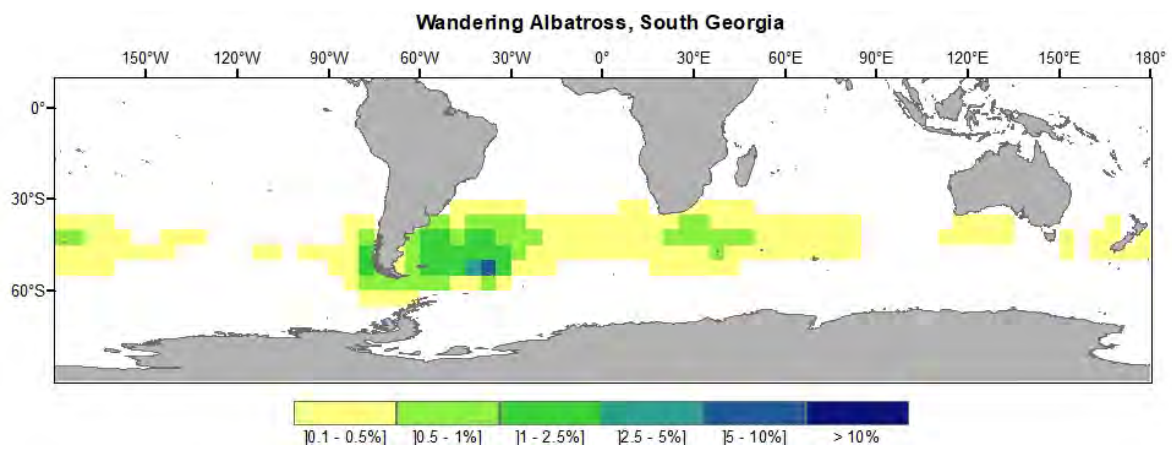


Figure S3. Wandering Albatross, South Georgia

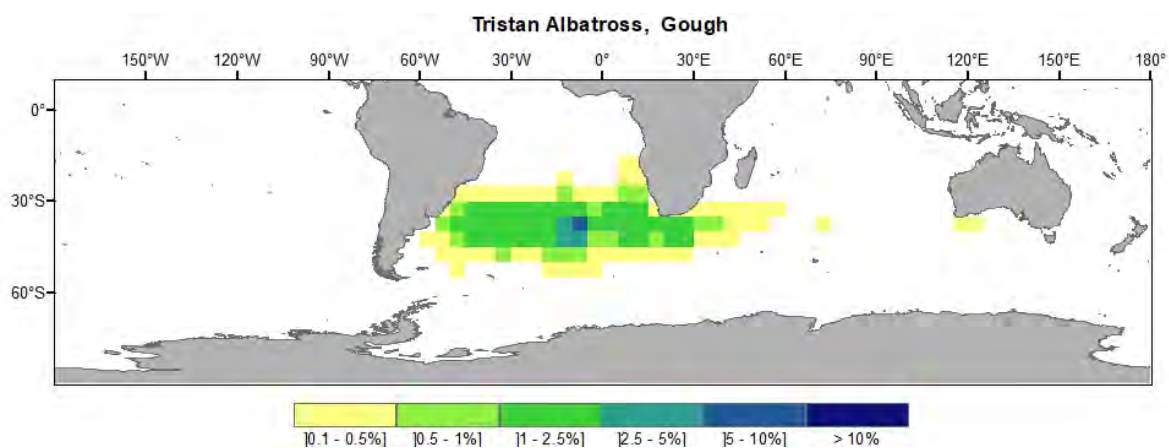


Figure S4. Tristan Albatross, Gough

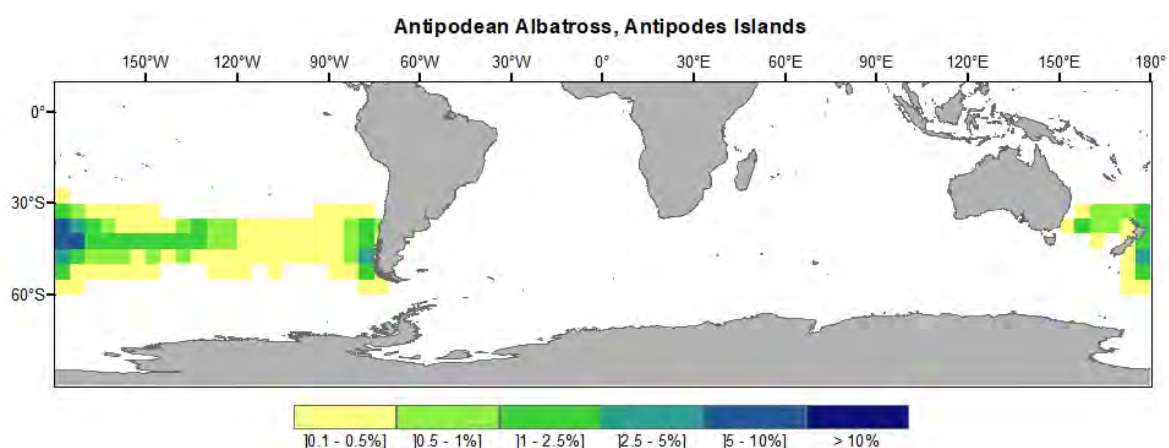


Figure S5. Antipodean Albatross, Antipodes Islands

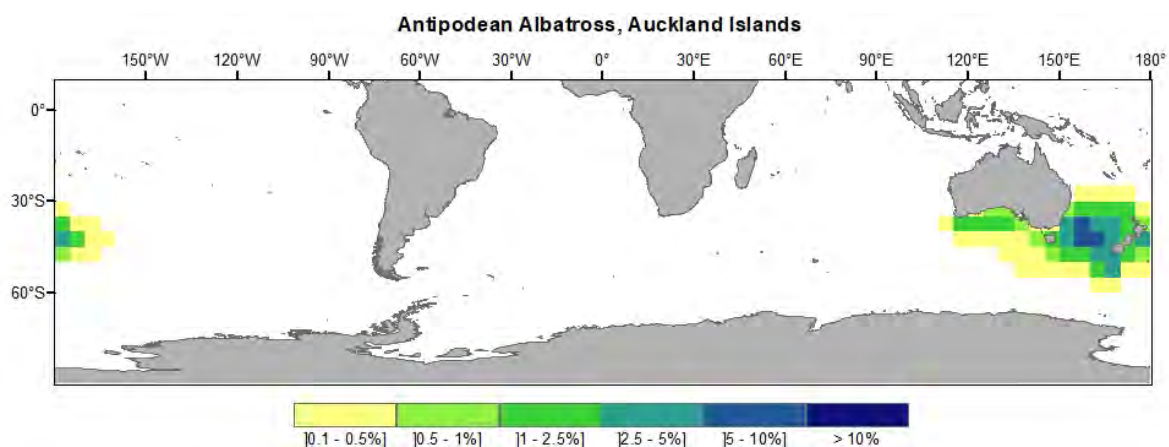


Figure S6. Antipodean Albatross, Auckland Islands

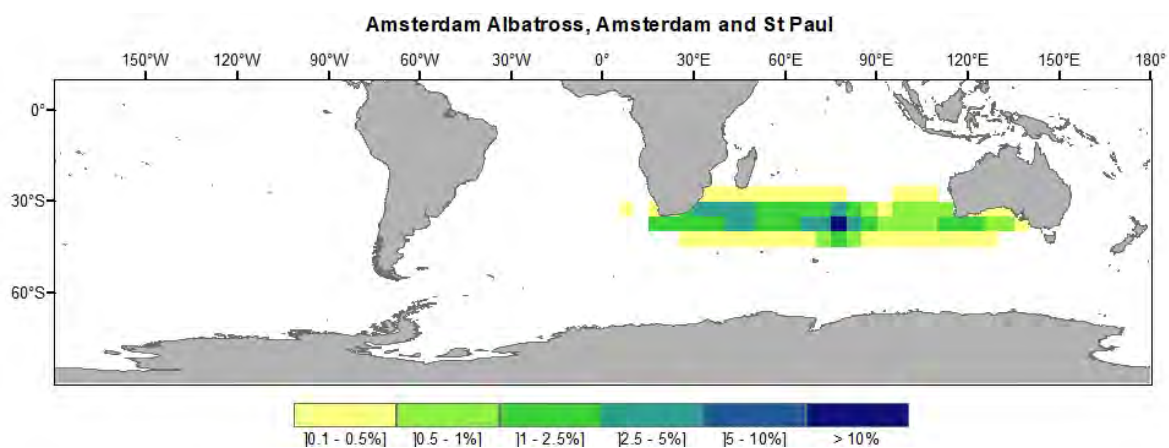


Figure S7. Amsterdam Albatross, Amsterdam and St Paul

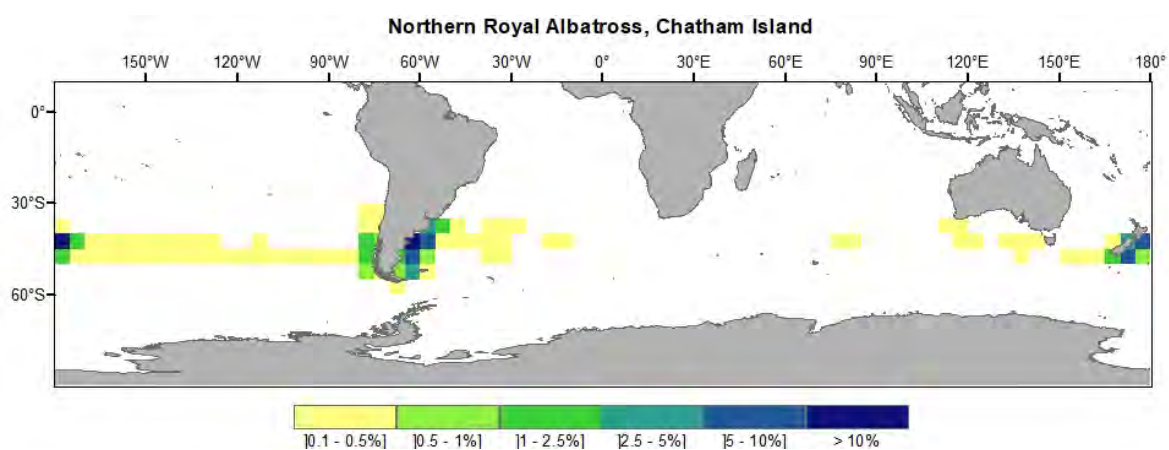


Figure S8. Northern Royal Albatross, Chatham Island

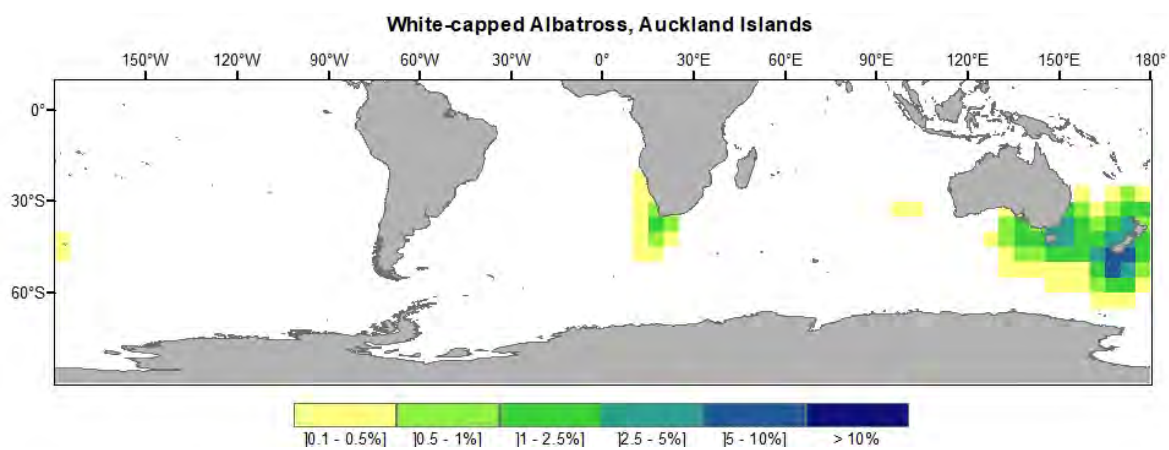


Figure S9. White-capped Albatross, Auckland Islands

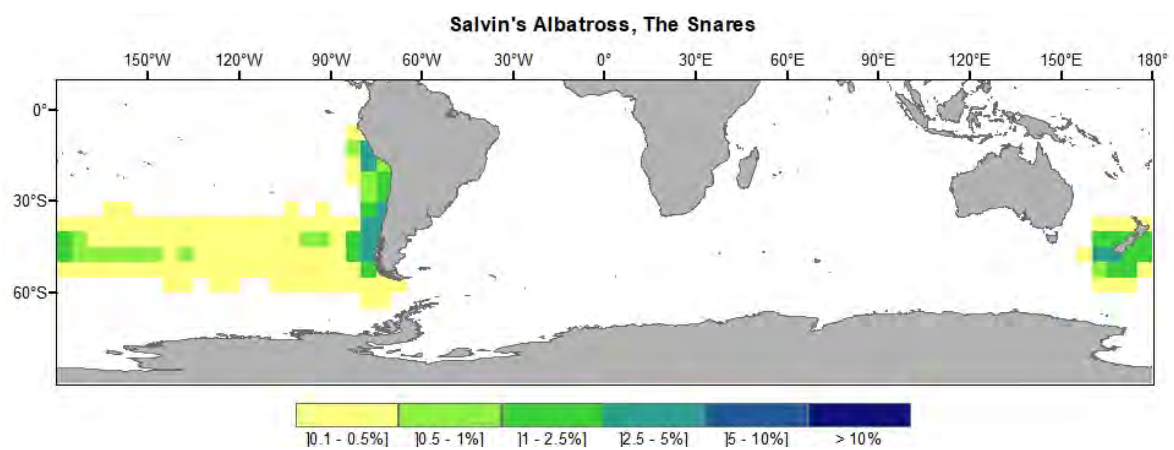


Figure S10. Salvin's Albatross, The Snares

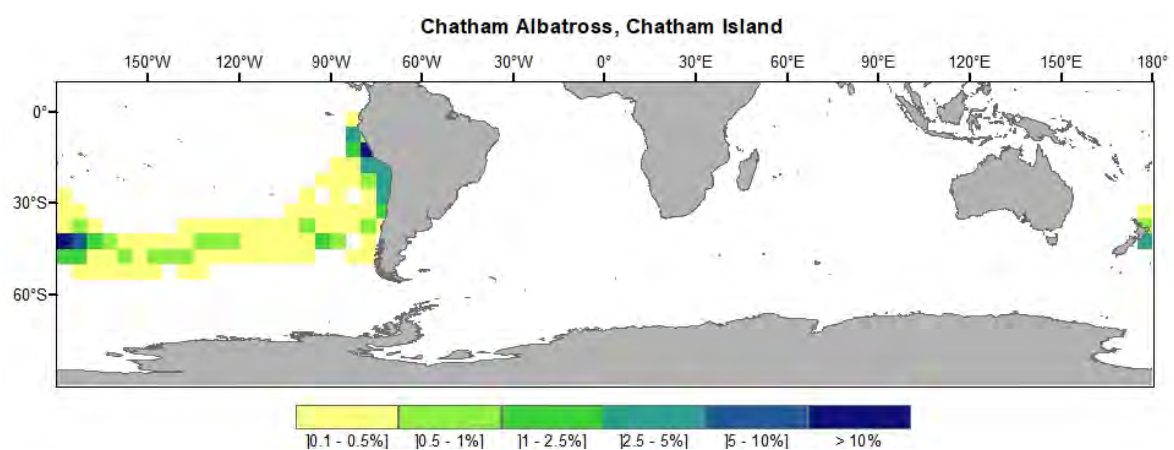


Figure S11. Chatham Albatross, Chatham Island

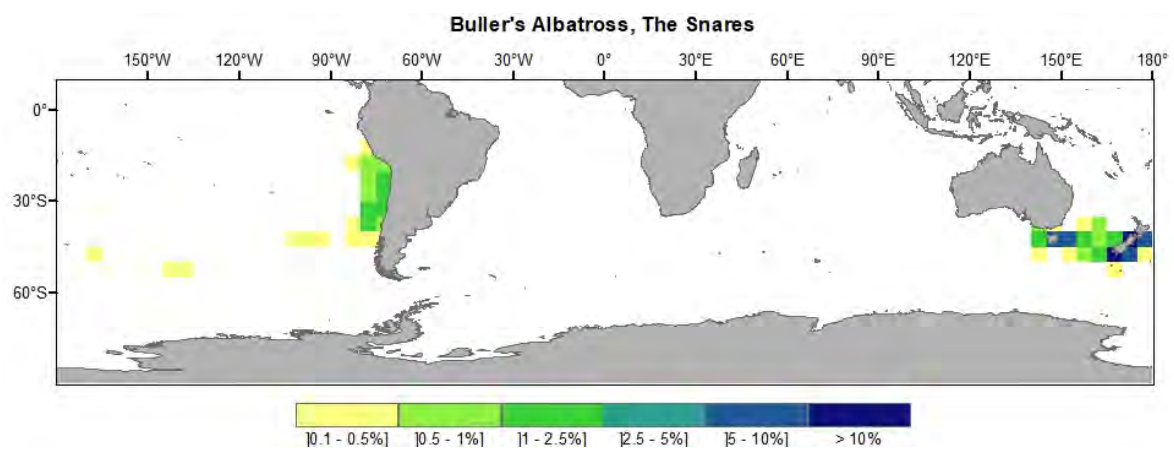


Figure S12. Buller's Albatross, The Snares

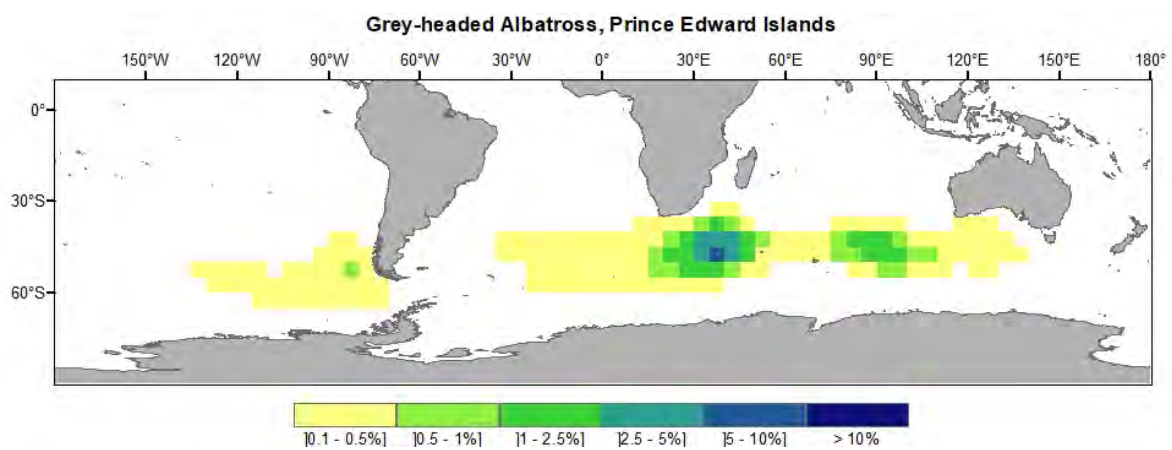


Figure S13. Grey-headed Albatross, Prince Edward Islands

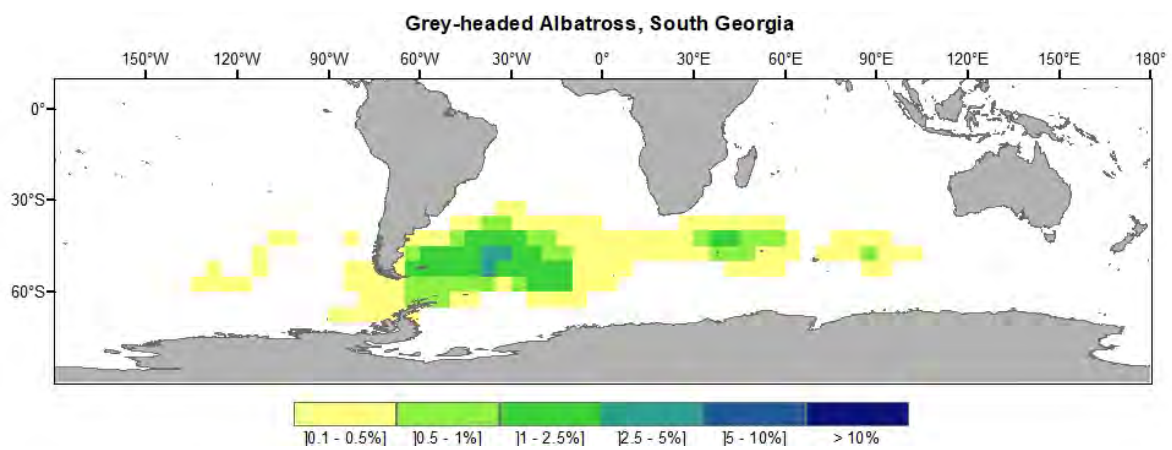


Figure S14. Grey-headed Albatross, South Georgia

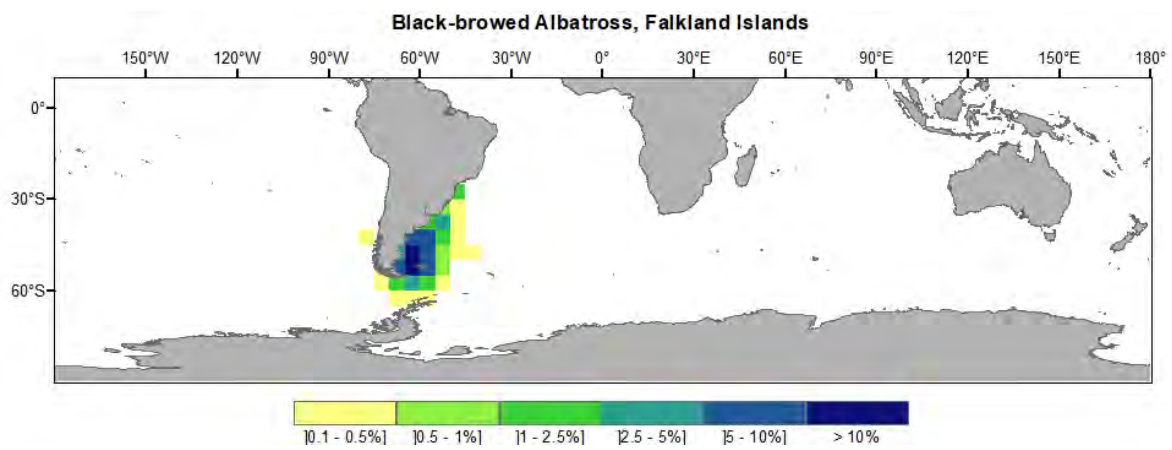


Figure S15. Black-browed Albatross, Falkland Islands

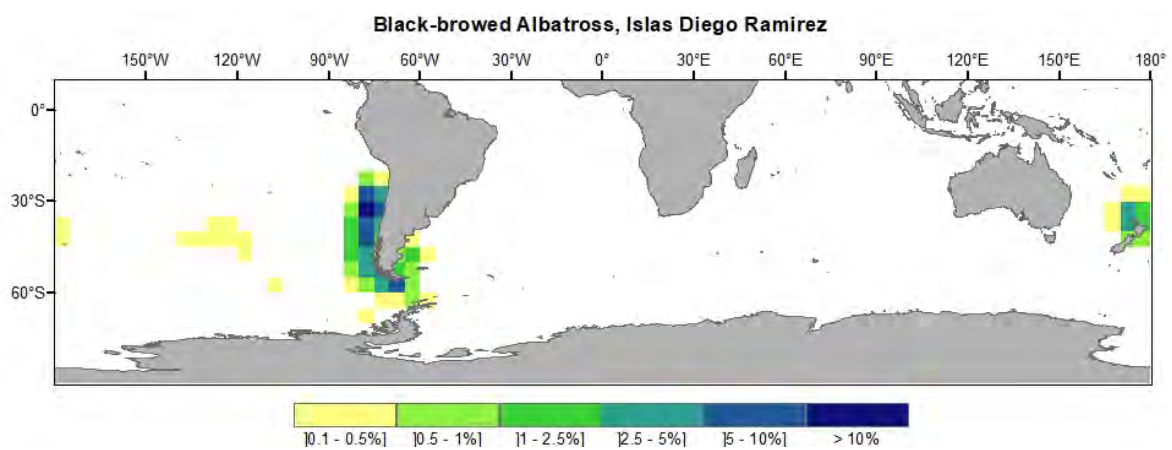


Figure S16. Black-browed Albatross, Isla Diego Ramirez

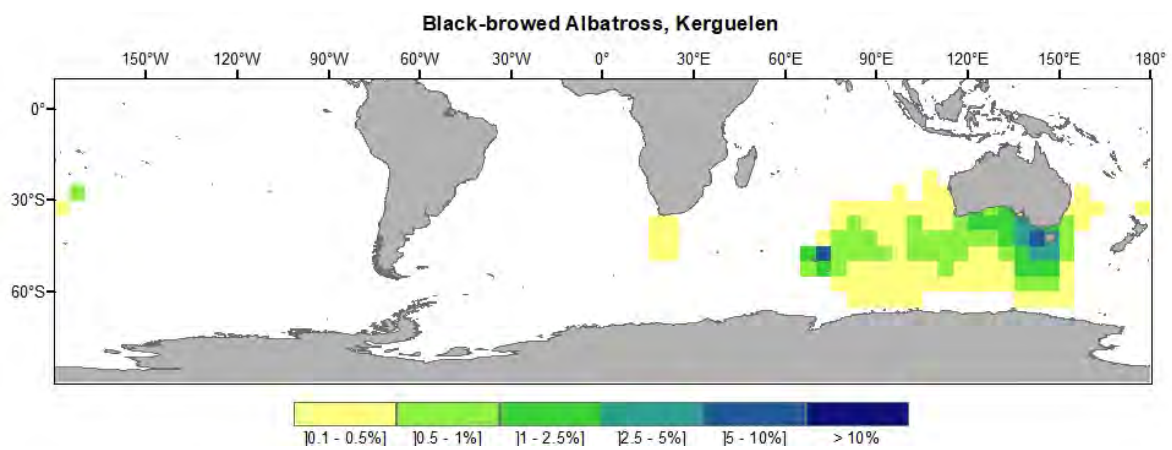


Figure S17. Black-browed Albatross, Kerguelen

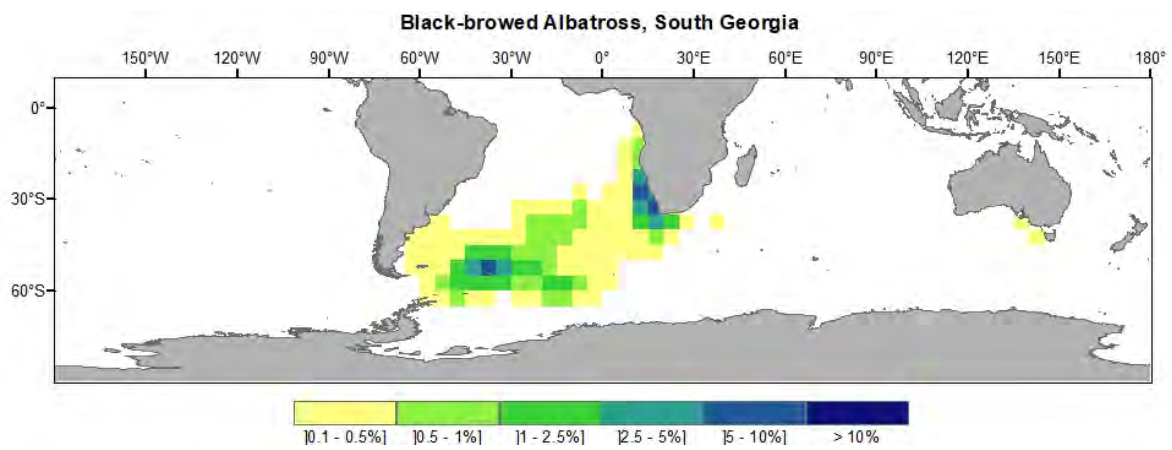


Figure S18. Black-browed Albatross, South Georgia

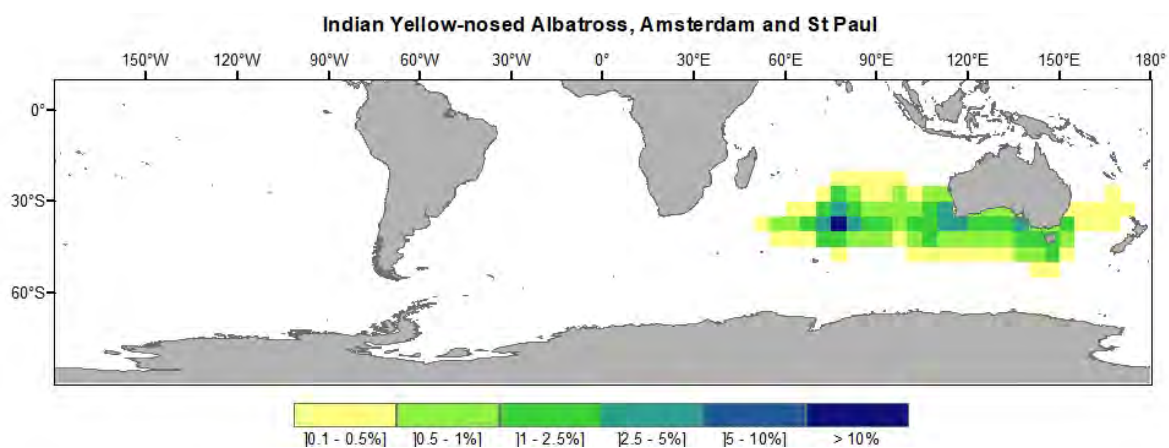


Figure S19. Indian Yellow-nosed Albatross, Amsterdam and St Paul

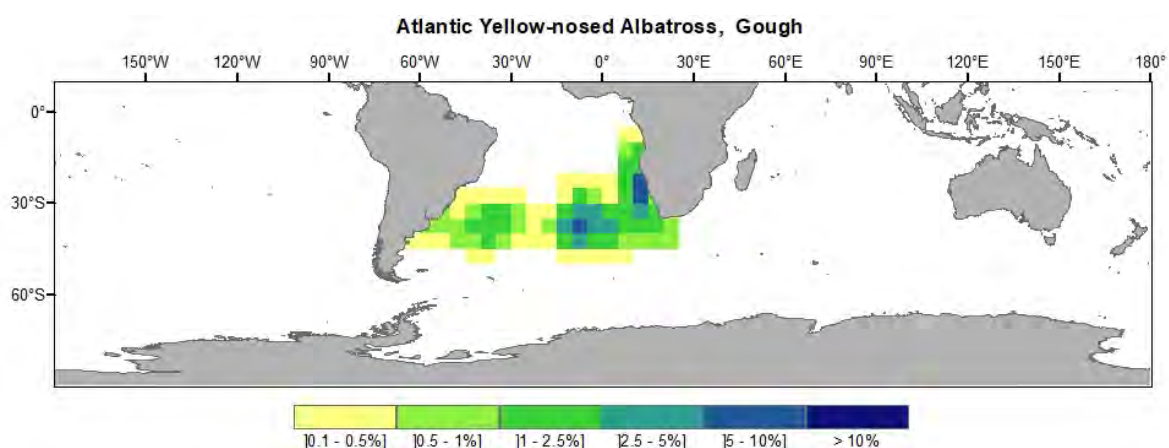


Figure S20. Atlantic Yellow-nosed Albatross, Gough

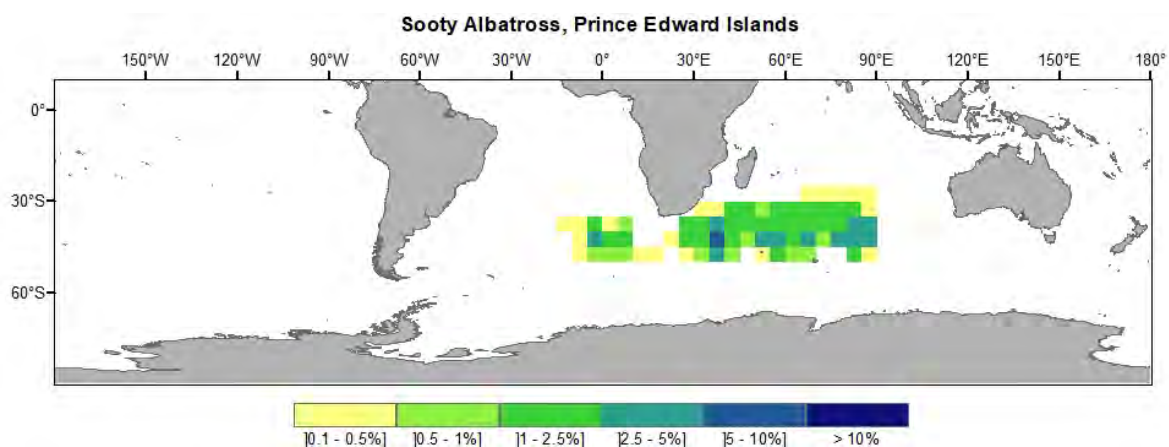


Figure S21. Sooty Albatross, Prince Edward Islands

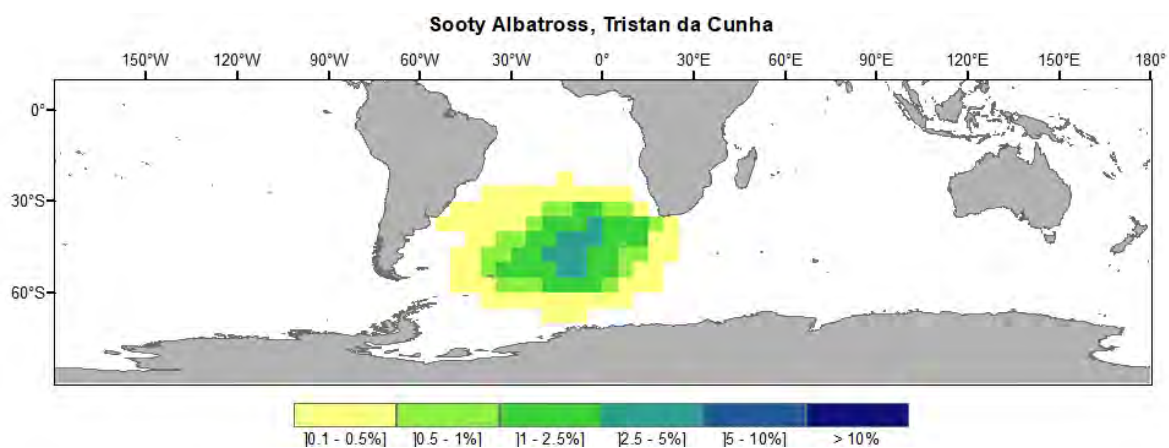


Figure S22. Sooty Albatross, Tristan da Cunha

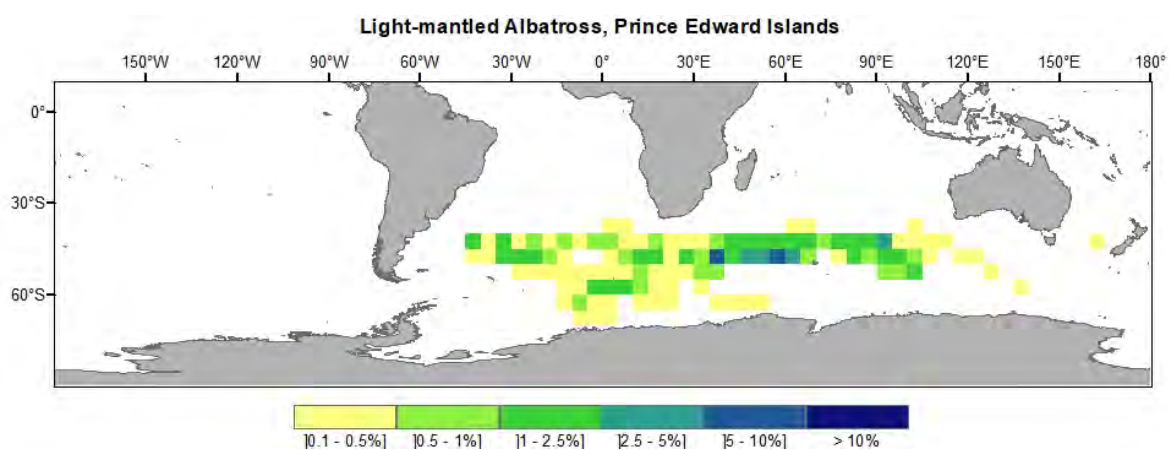


Figure S23. Light-mantled Albatross, Prince Edward Islands

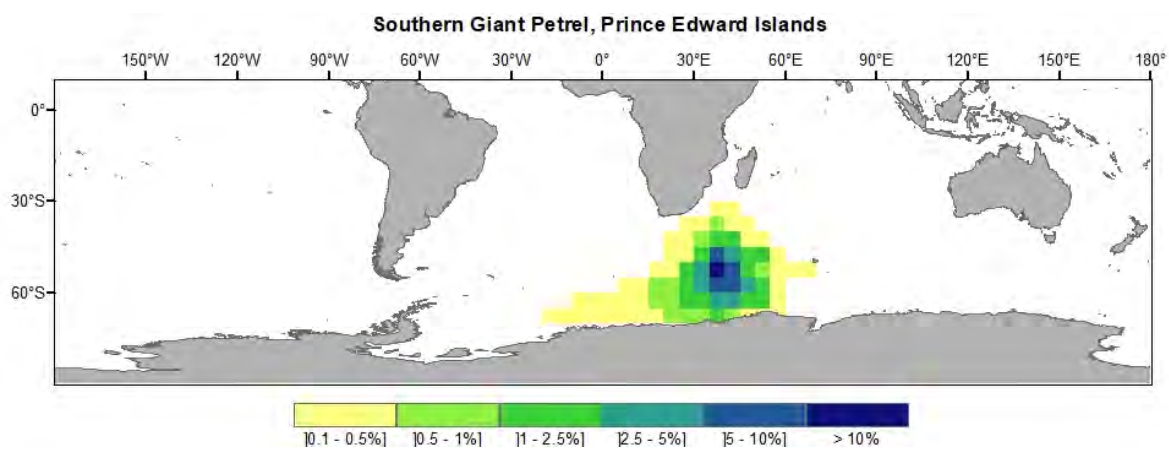


Figure S24. Southern Giant Petrel, Prince Edward Islands

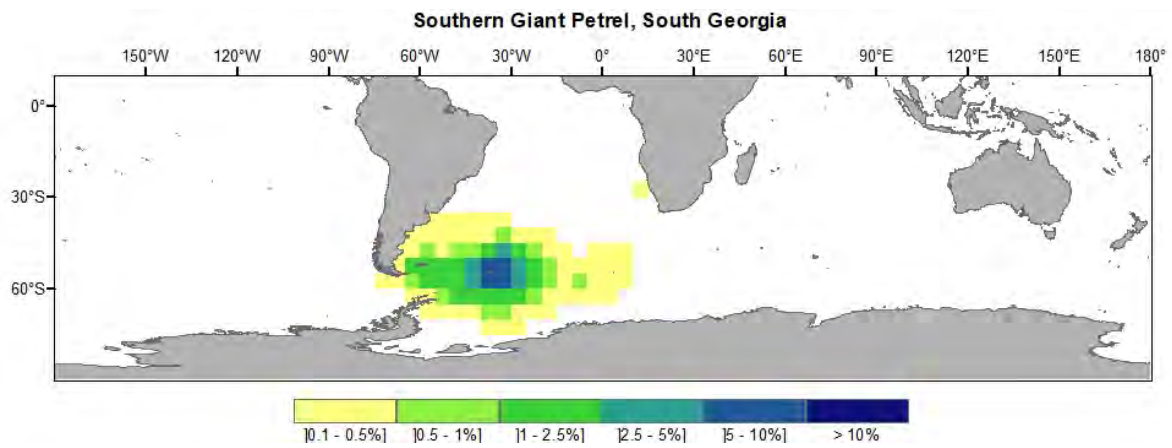


Figure S25. Southern Giant Petrel, South Georgia

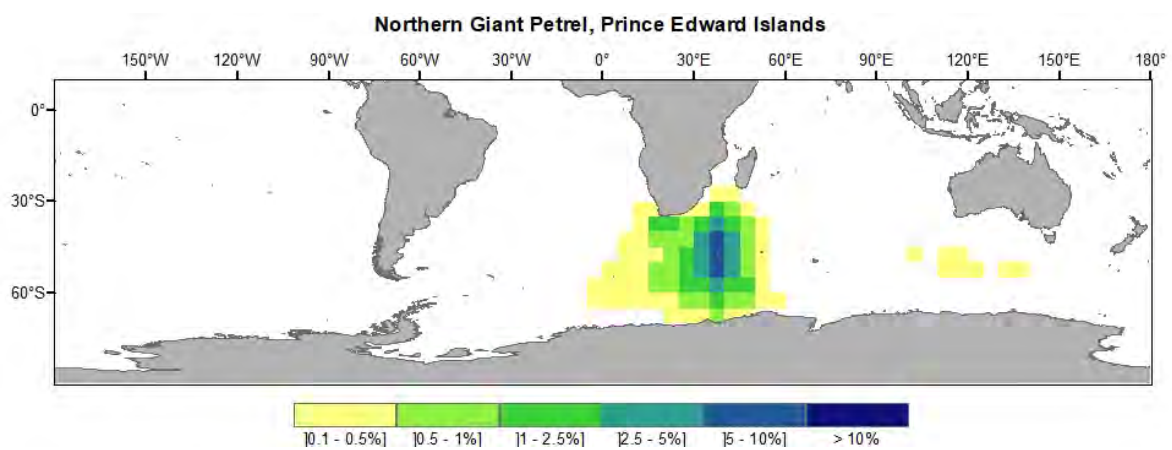


Figure S26. Northern Giant Petrel, Prince Edward Islands

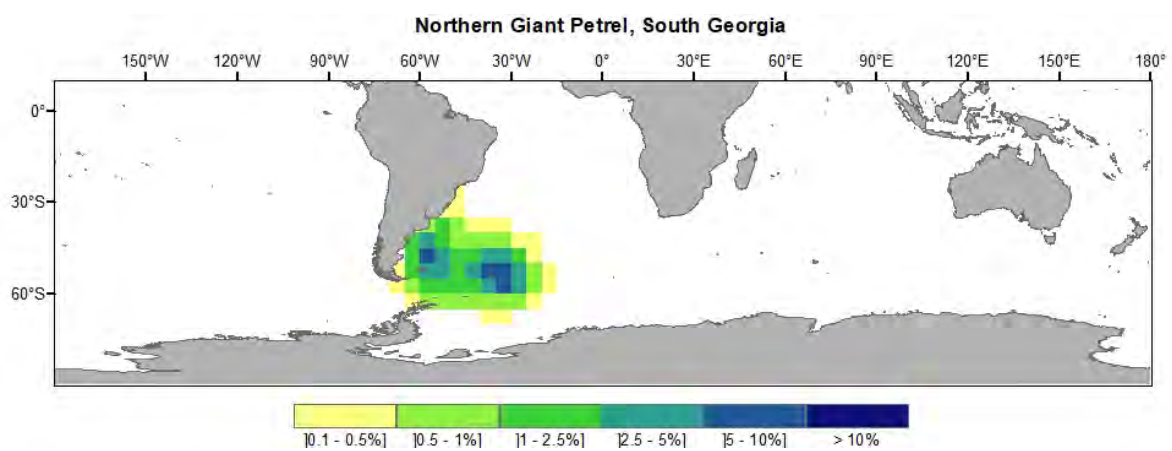


Figure S27. Northern Giant Petrel, South Georgia

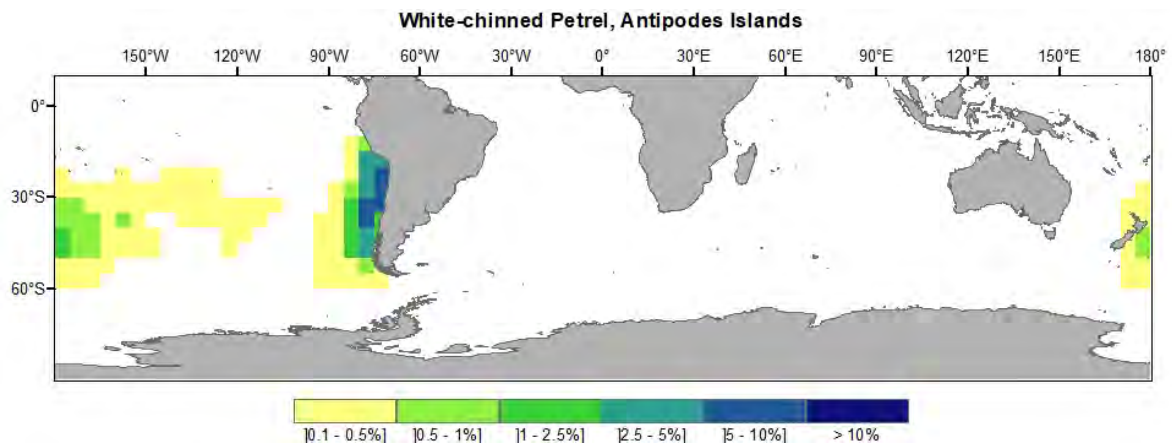


Figure S28. White-chinned Petrel, Antipodes Islands

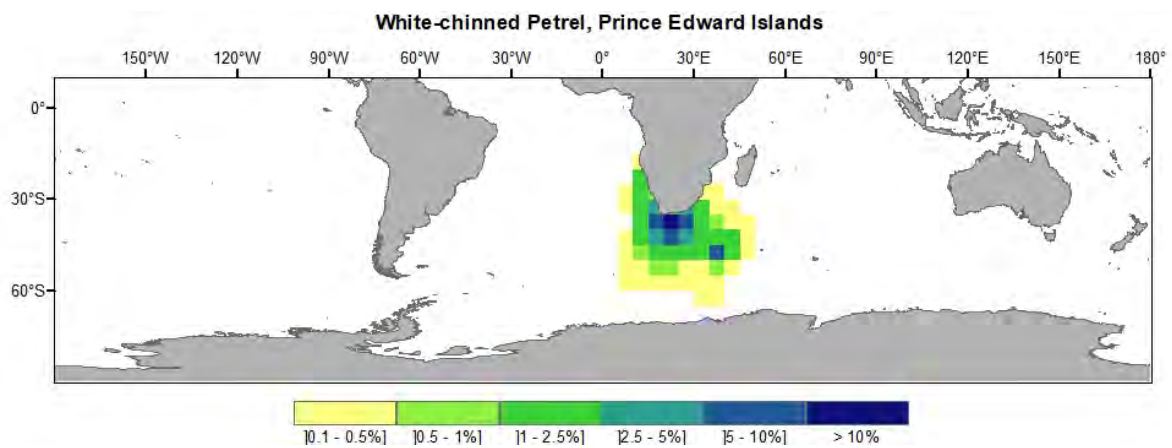


Figure S29. White-chinned Petrel, Prince Edward Islands

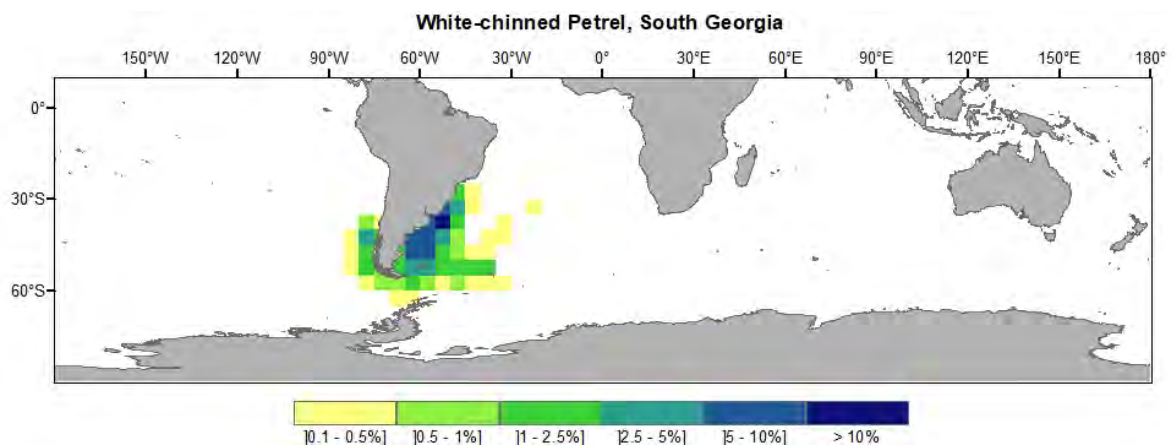


Figure S30. White-chinned Petrel, South Georgia

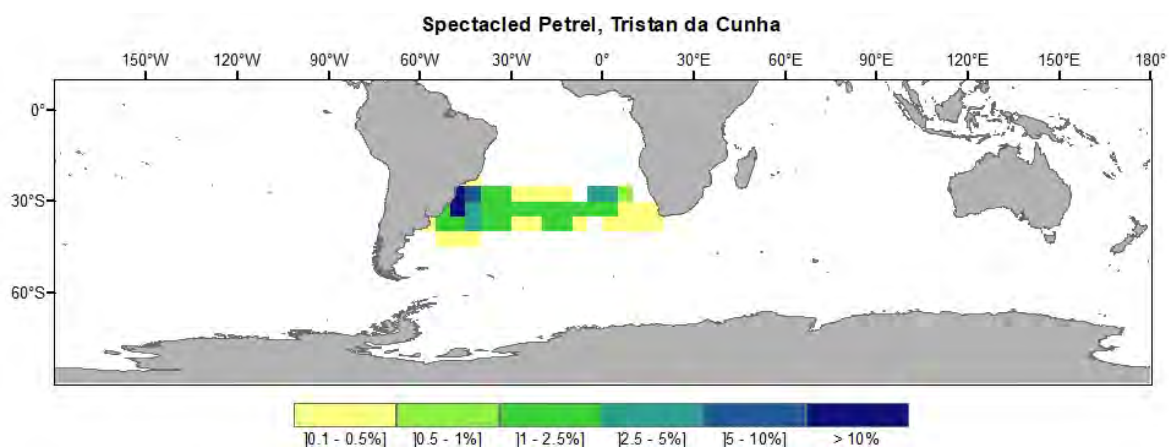


Figure S31. Spectacled Petrel, Tristan da Cunha

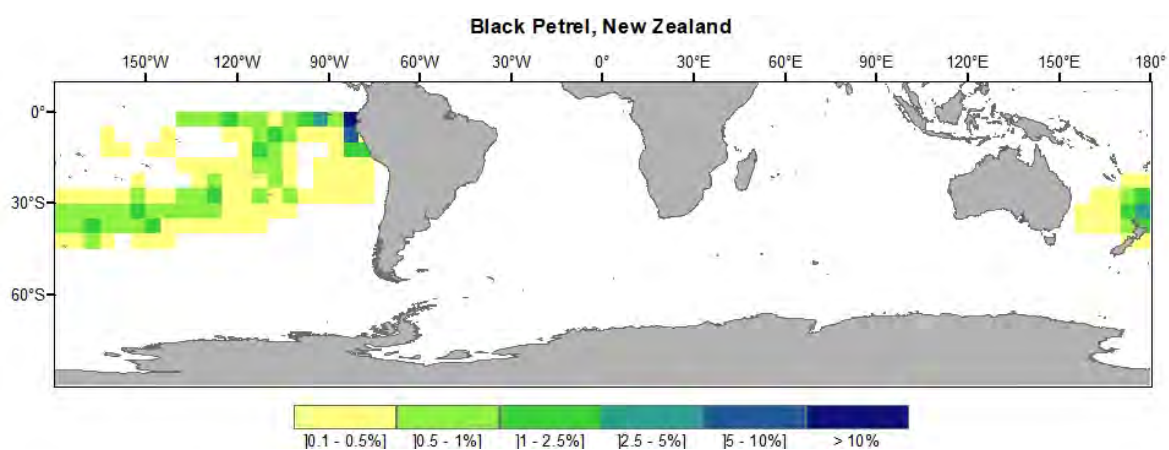


Figure S32. Black Petrel, New Zealand

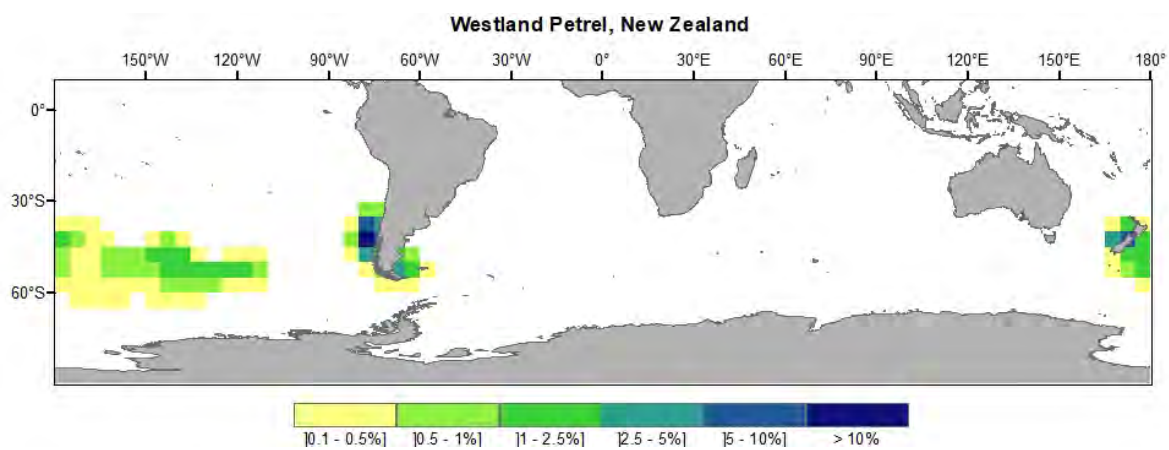


Figure S33. Westland Petrel, New Zealand

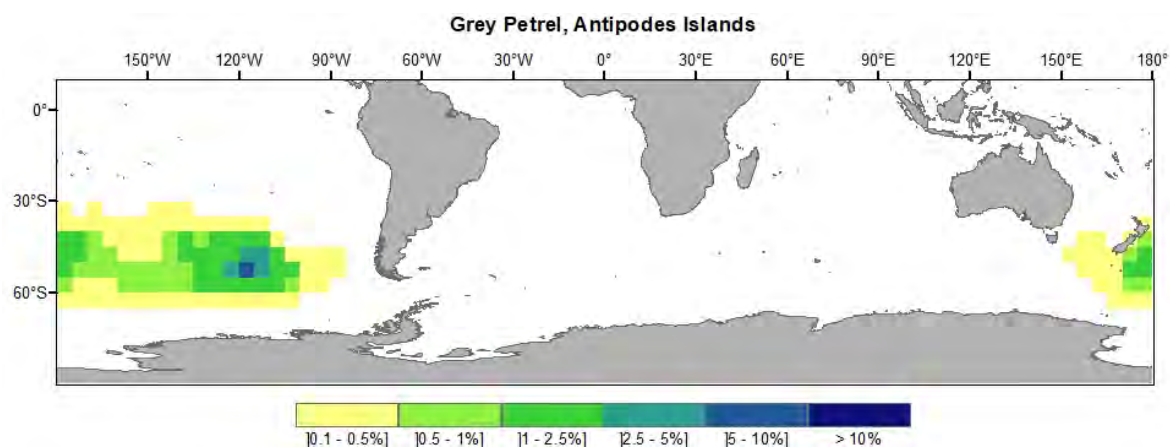


Figure S34. Grey Petrel, Antipodes Islands

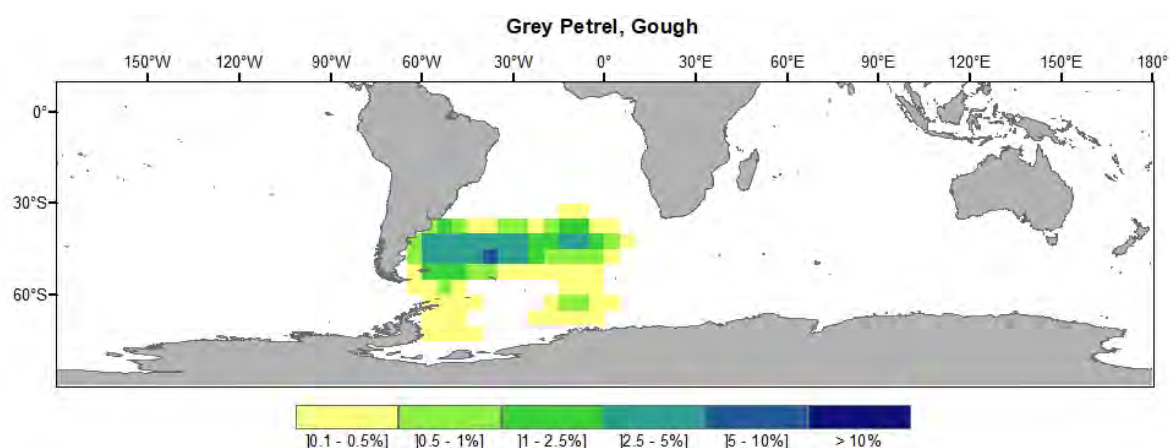


Figure S35. Grey Petrel, Gough

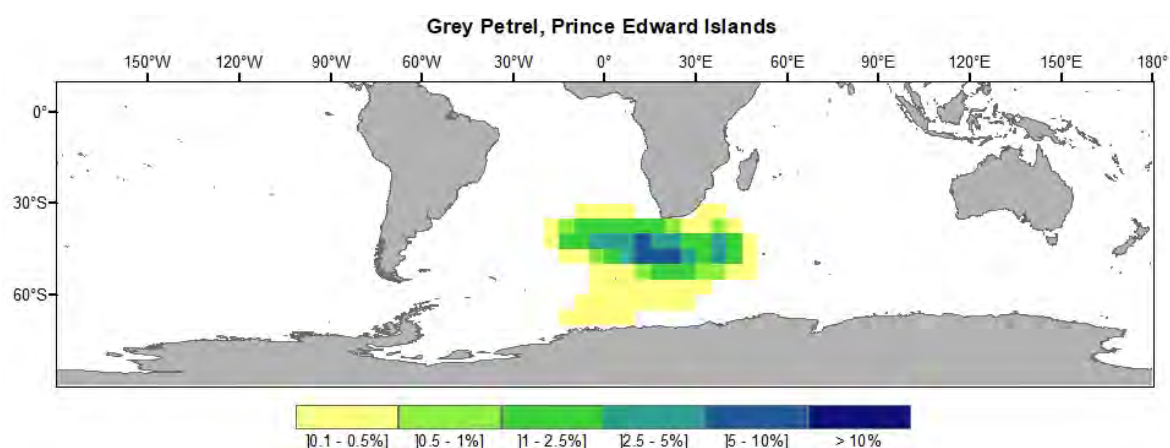


Figure S36. Grey Petrel, Prince Edward Islands

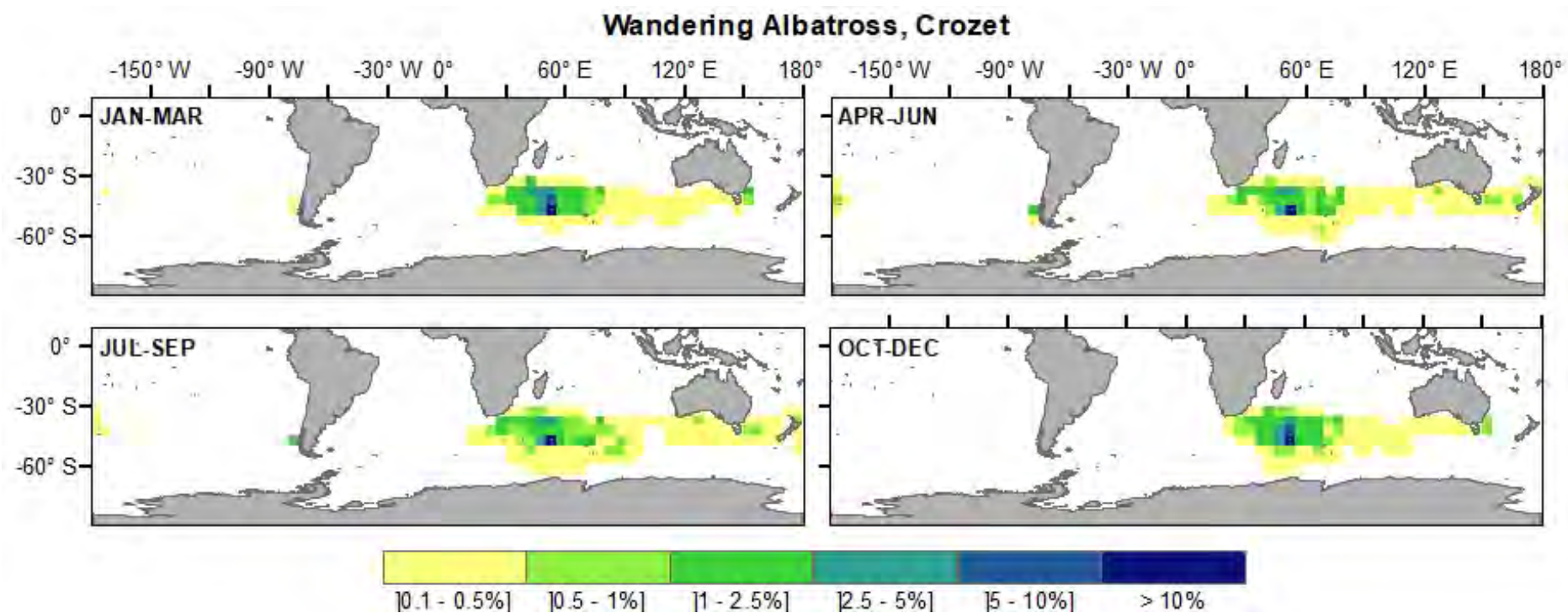


Figure S37. Wandering Albatross, Crozet

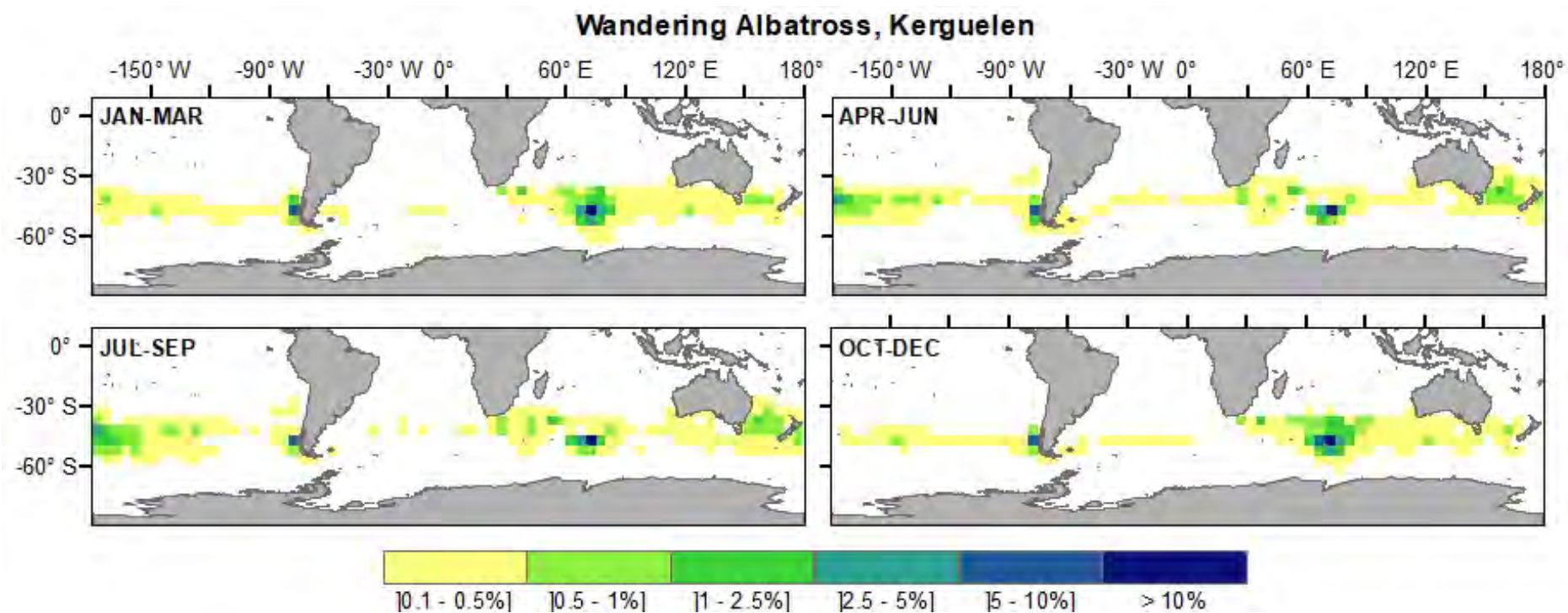


Figure S38. Wandering Albatross, Kerguelen

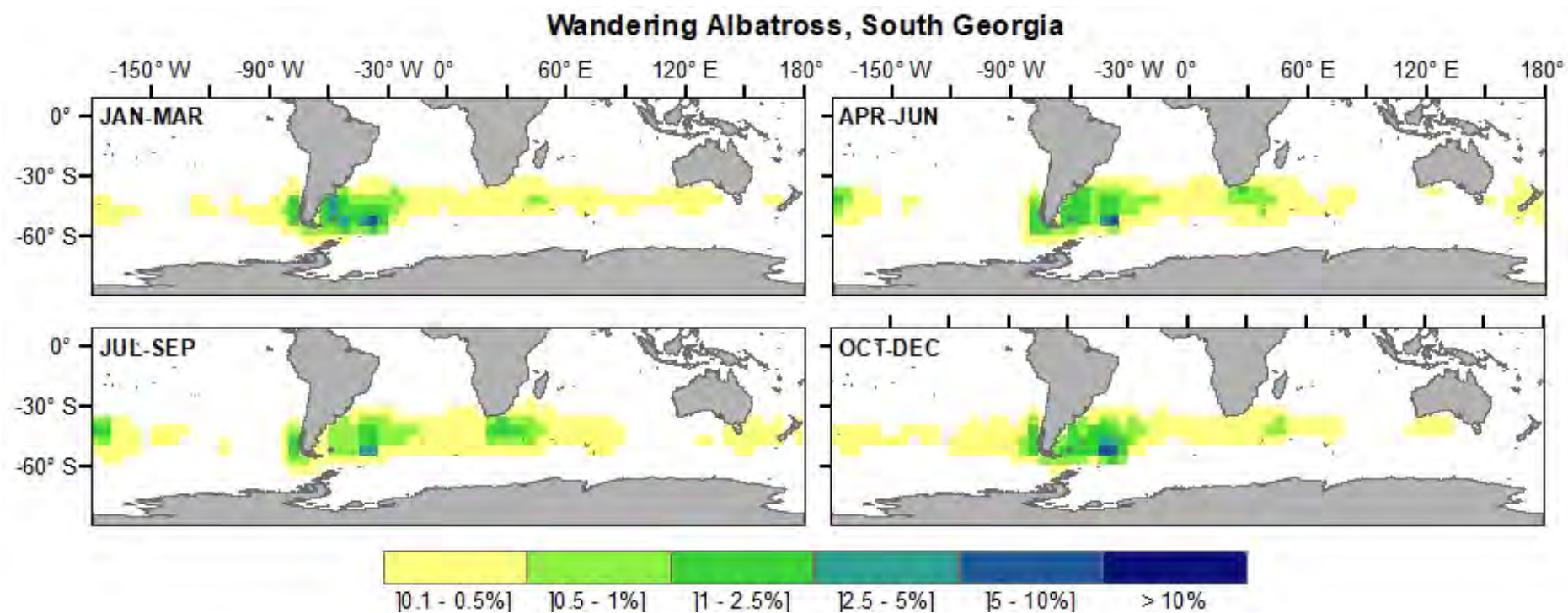


Figure S39. Wandering Albatross, South Georgia

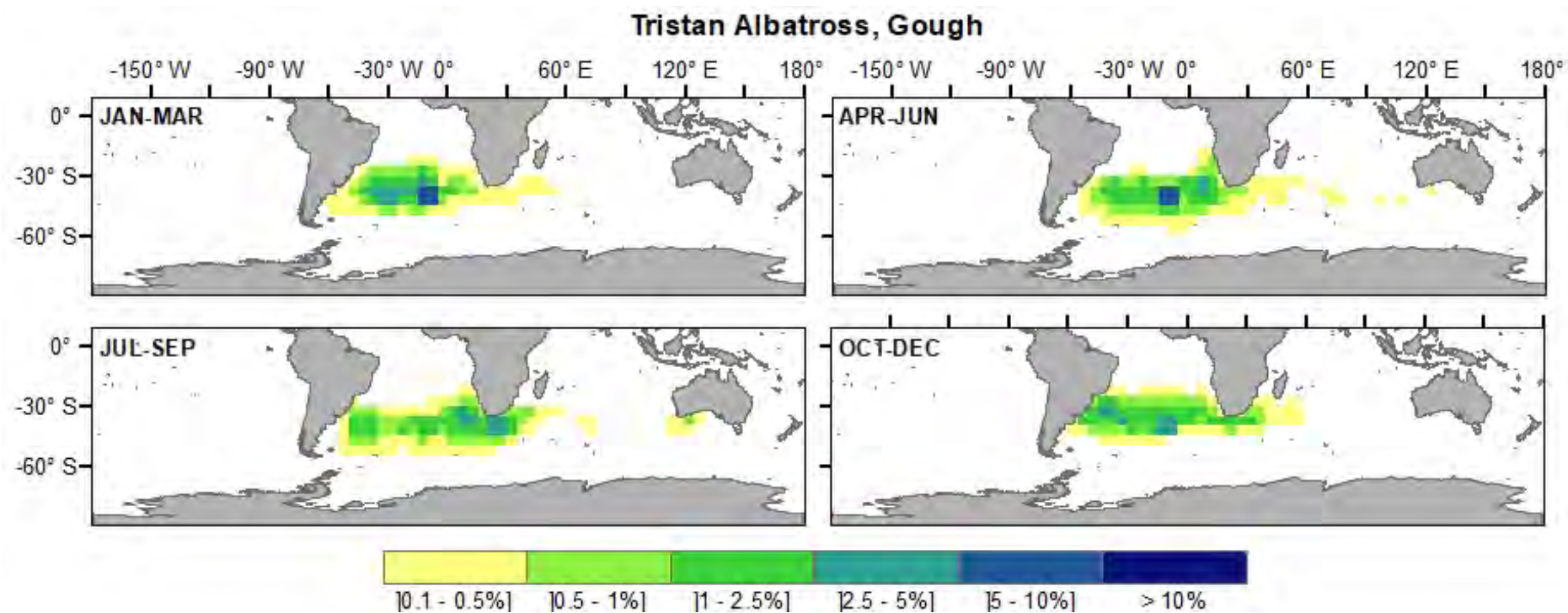


Figure S40. Tristan Albatross, Gough

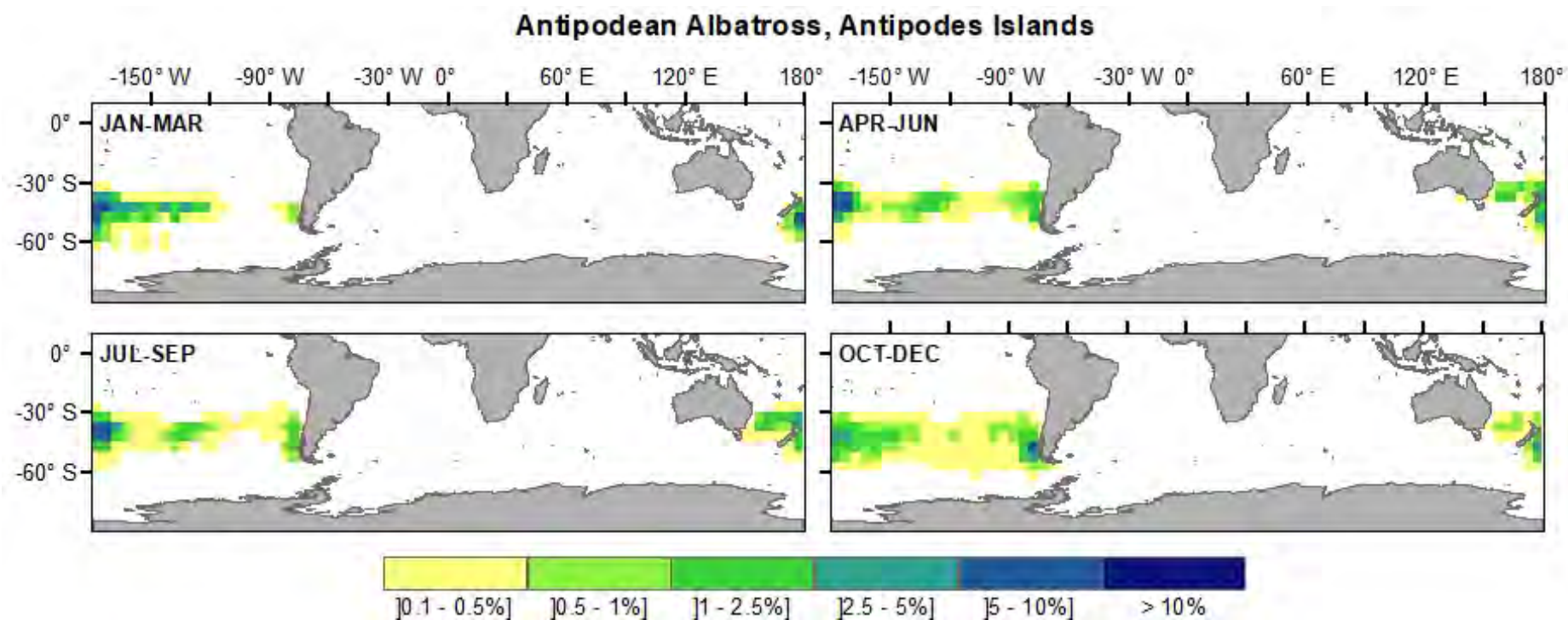


Figure S41. Antipodean Albatross, Antipodes Islands

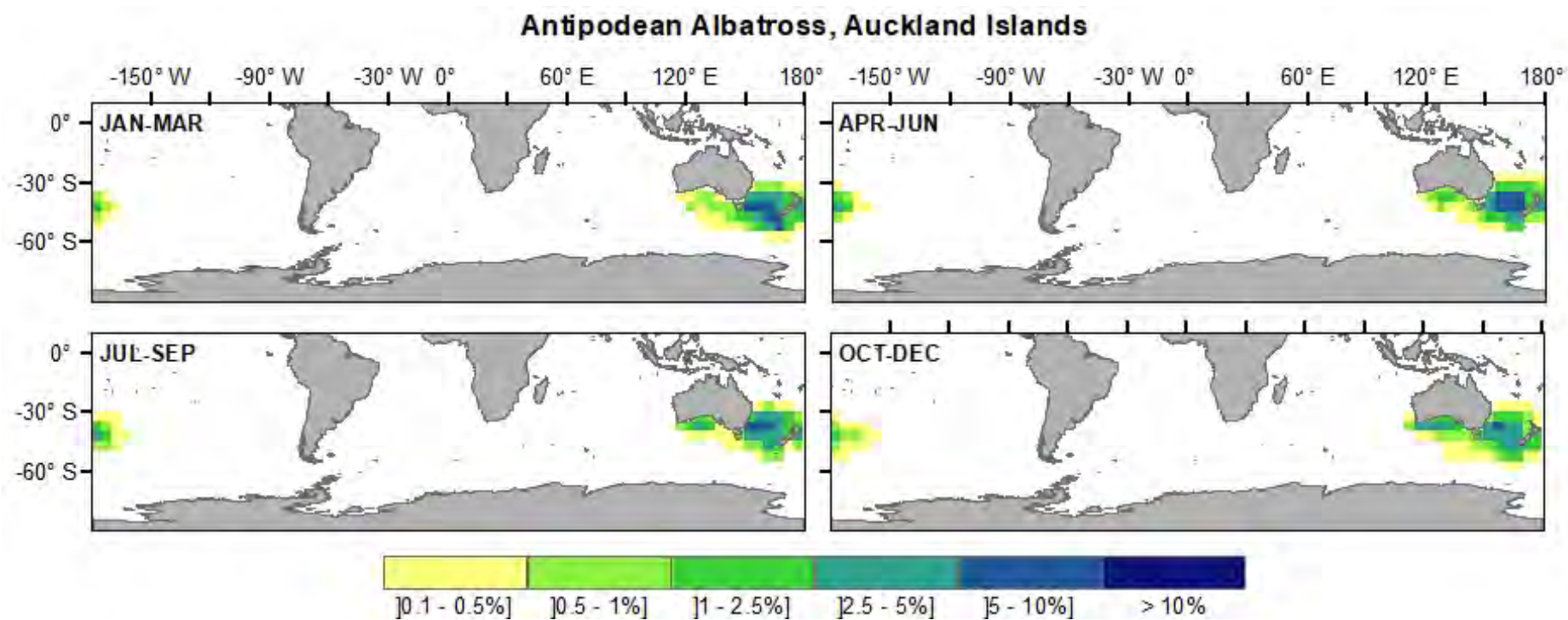


Figure S42. Antipodean Albatross, Auckland Islands

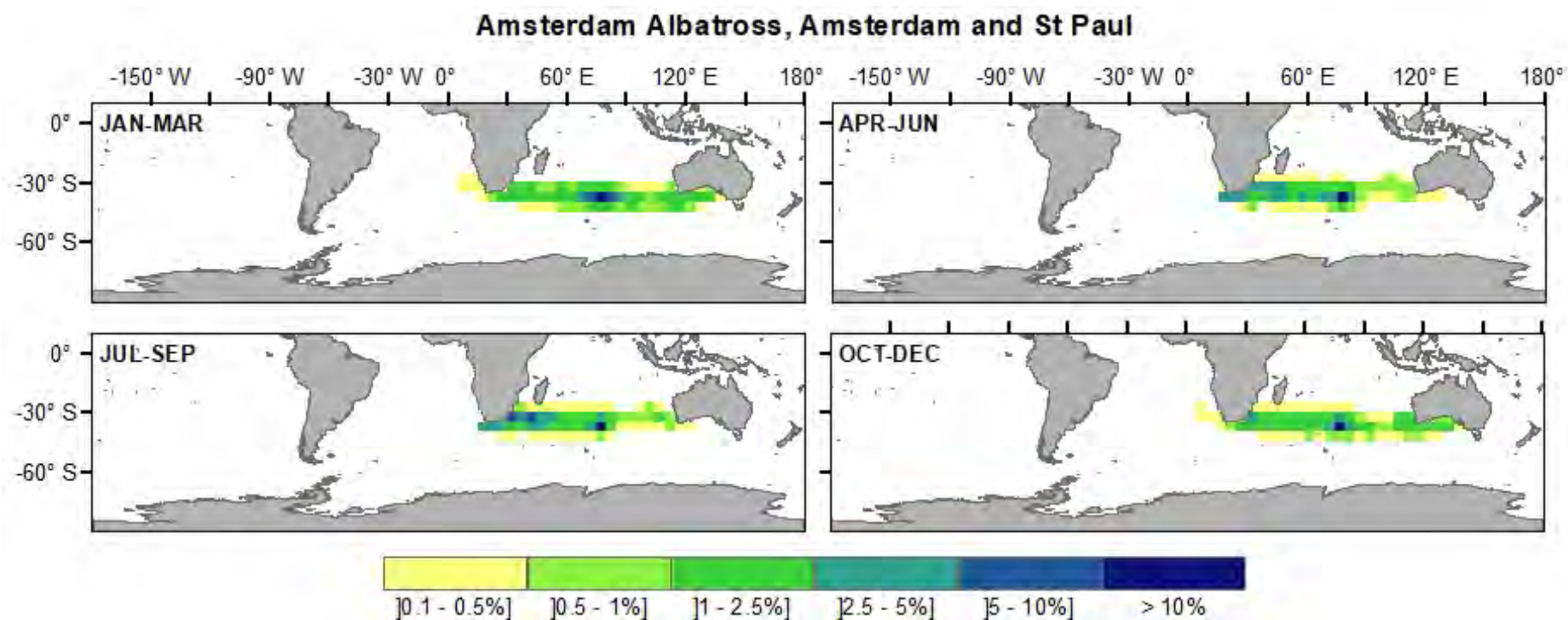


Figure S43. Amsterdam Albatross, Amsterdam and St Paul

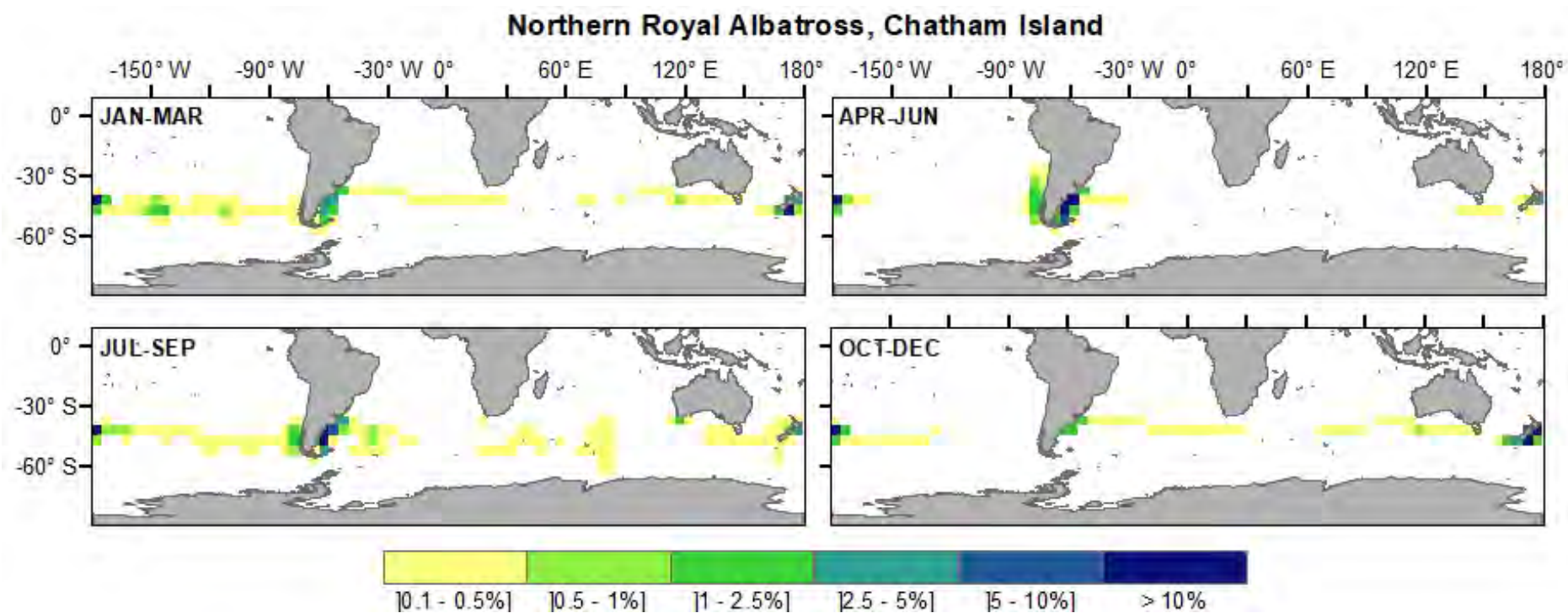


Figure S44. Northern Royal Albatross, Chatham Island

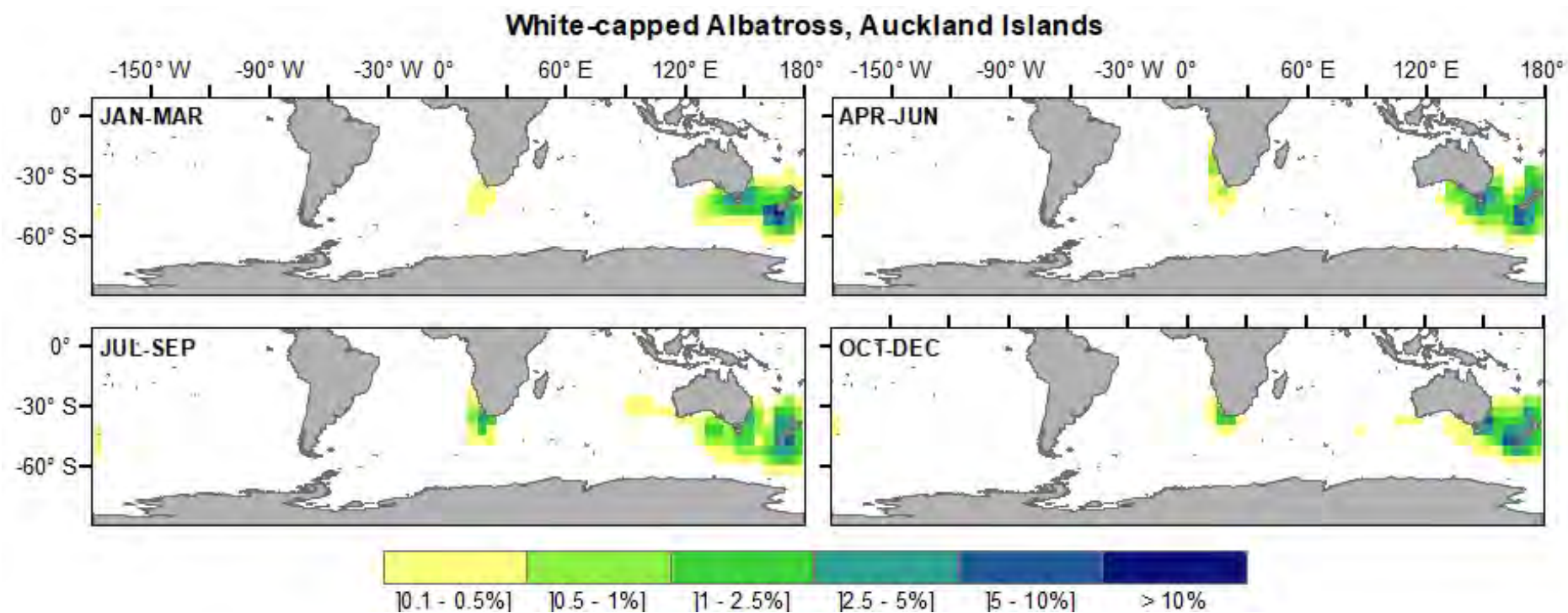


Figure S45. White-capped Albatross, Auckland Islands

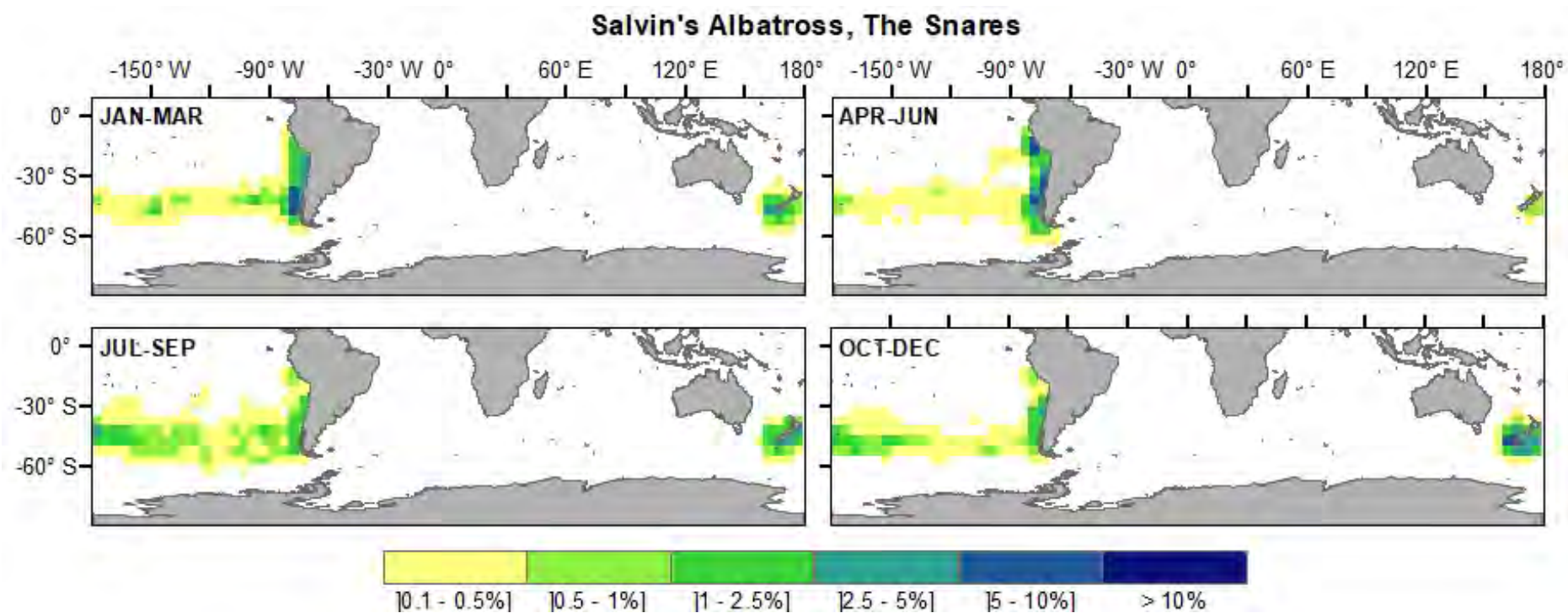


Figure S46. Salvin's Albatross, The Snares

Chatham Albatross, Chatham Island

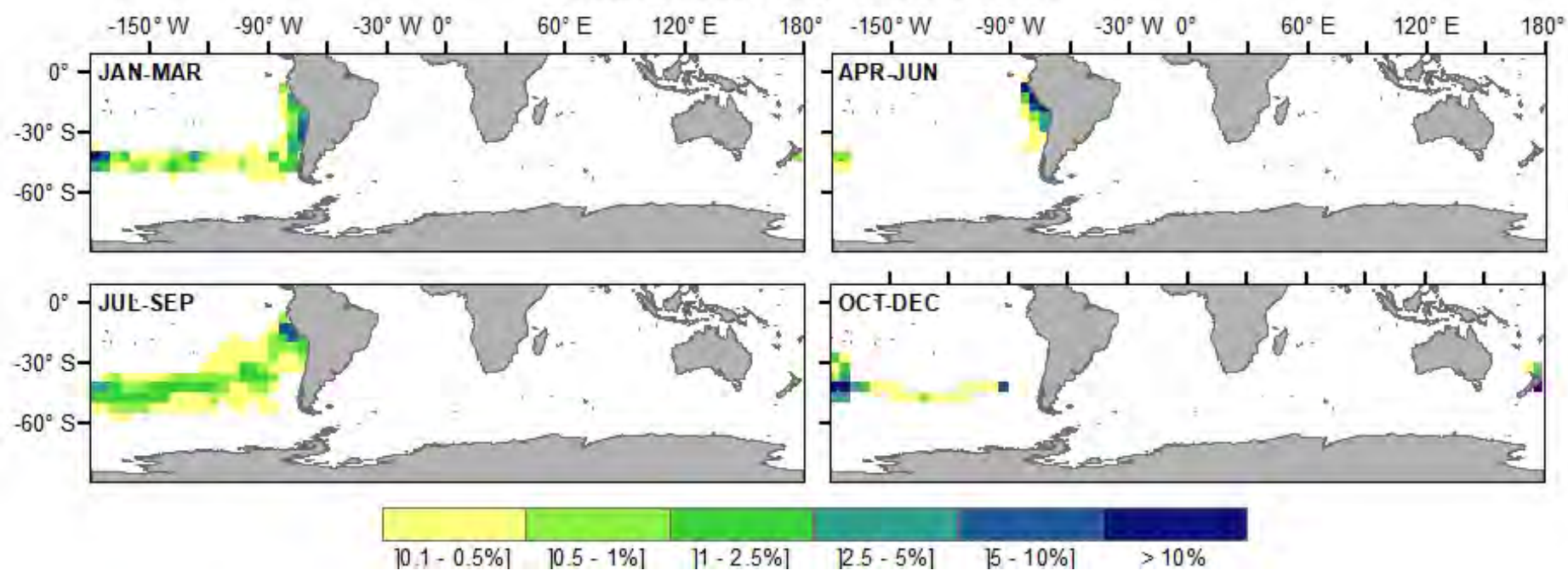


Figure S47. Chatham Albatross, Chatham Island

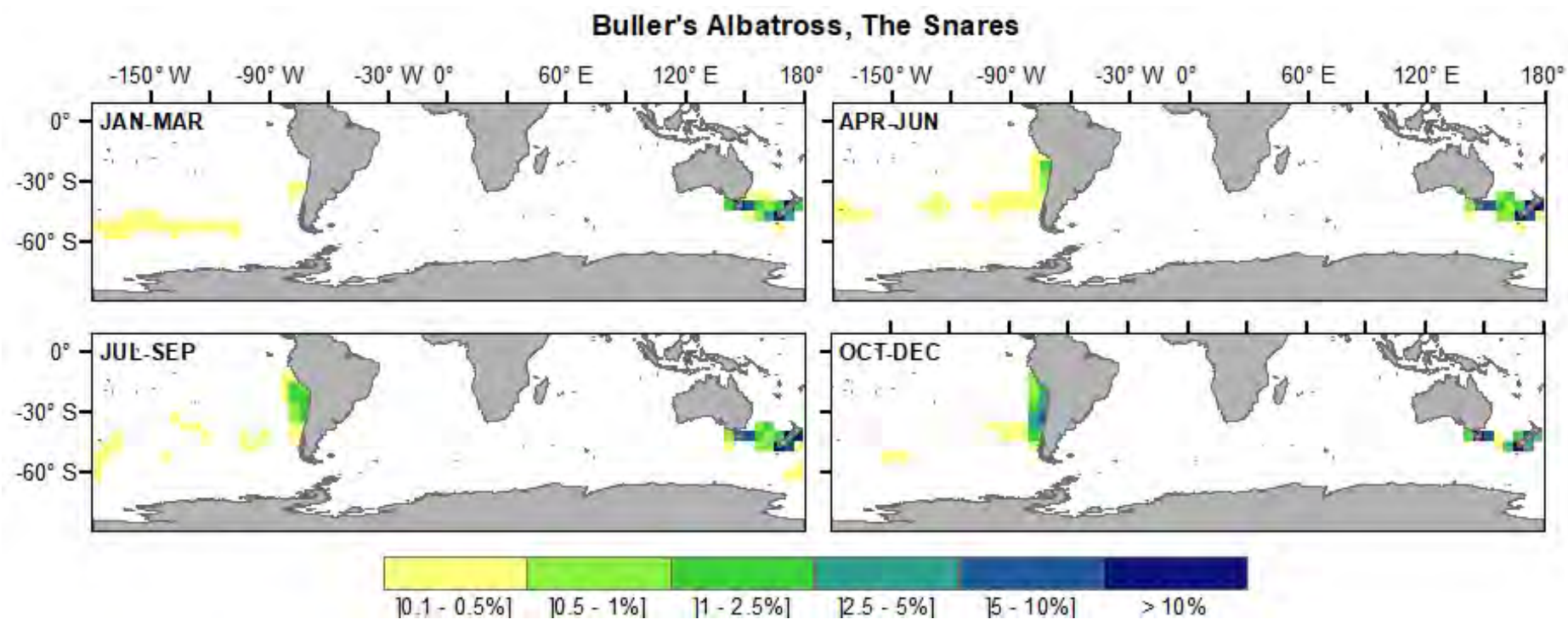


Figure S48. Buller's Albatross, The Snares

Grey-headed Albatross, Prince Edward Islands

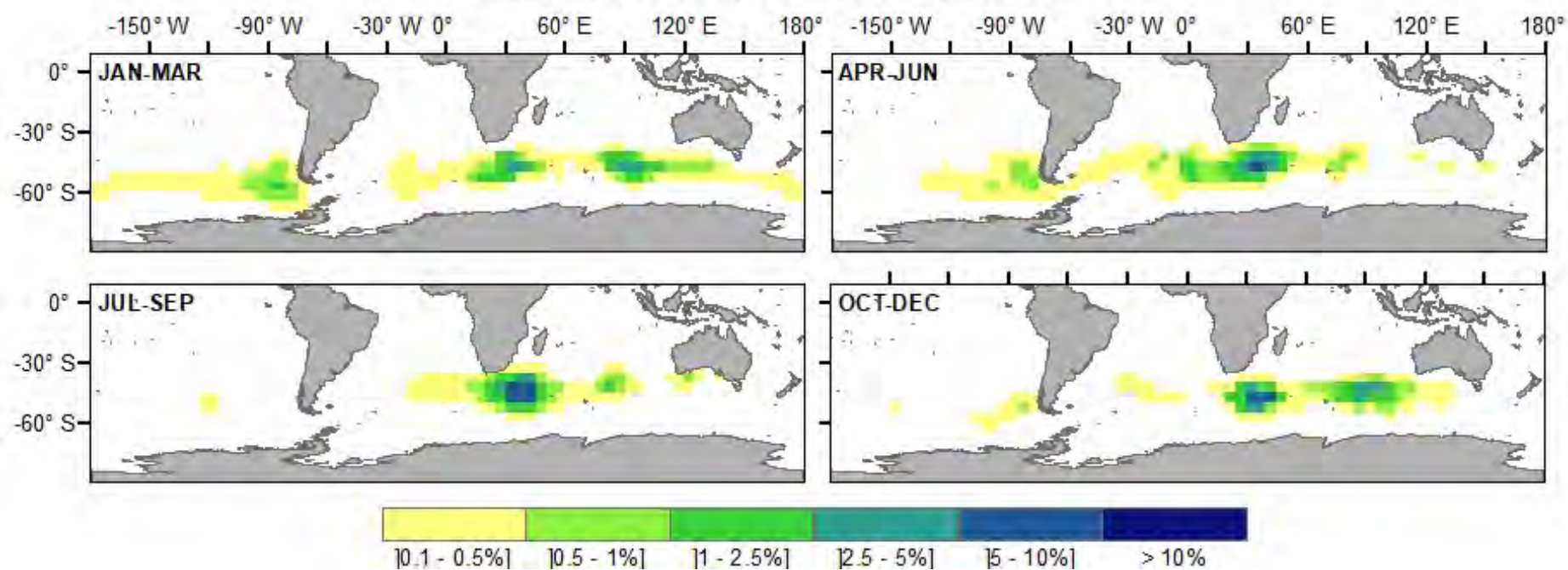


Figure S49. Grey-headed Albatross, Prince Edward Islands

Grey-headed Albatross, South Georgia

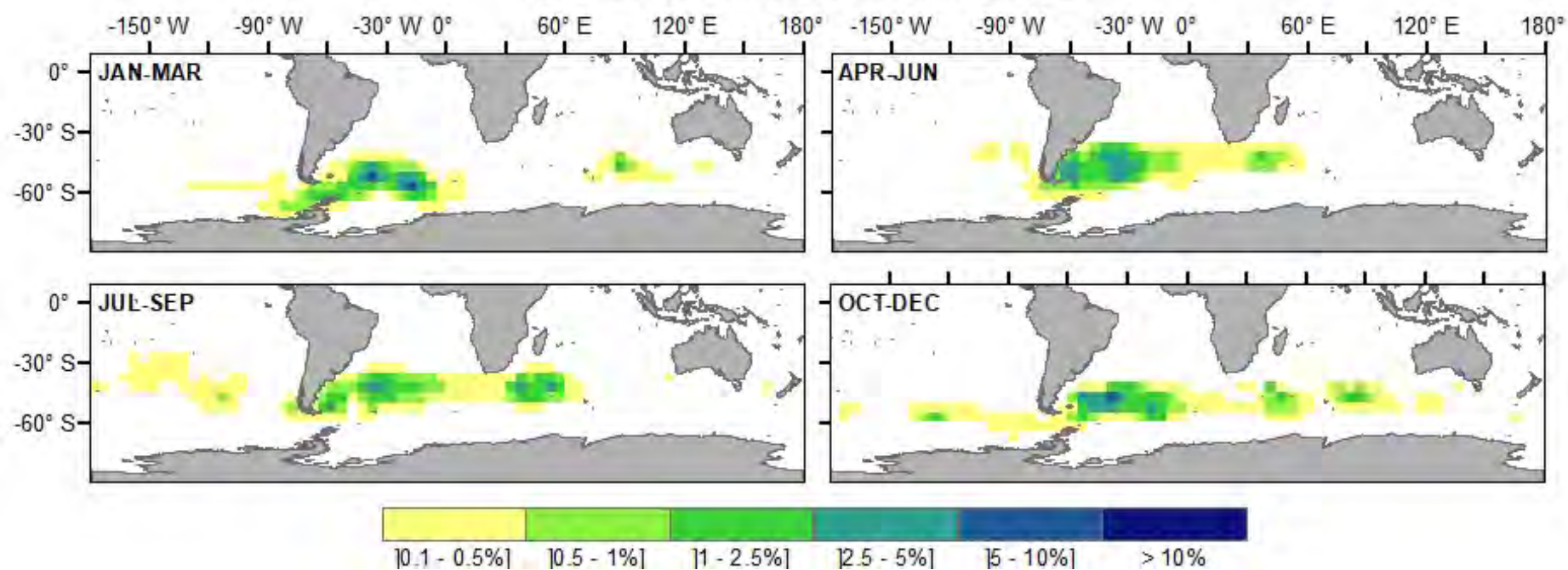


Figure S50. Grey-headed Albatross, South Georgia

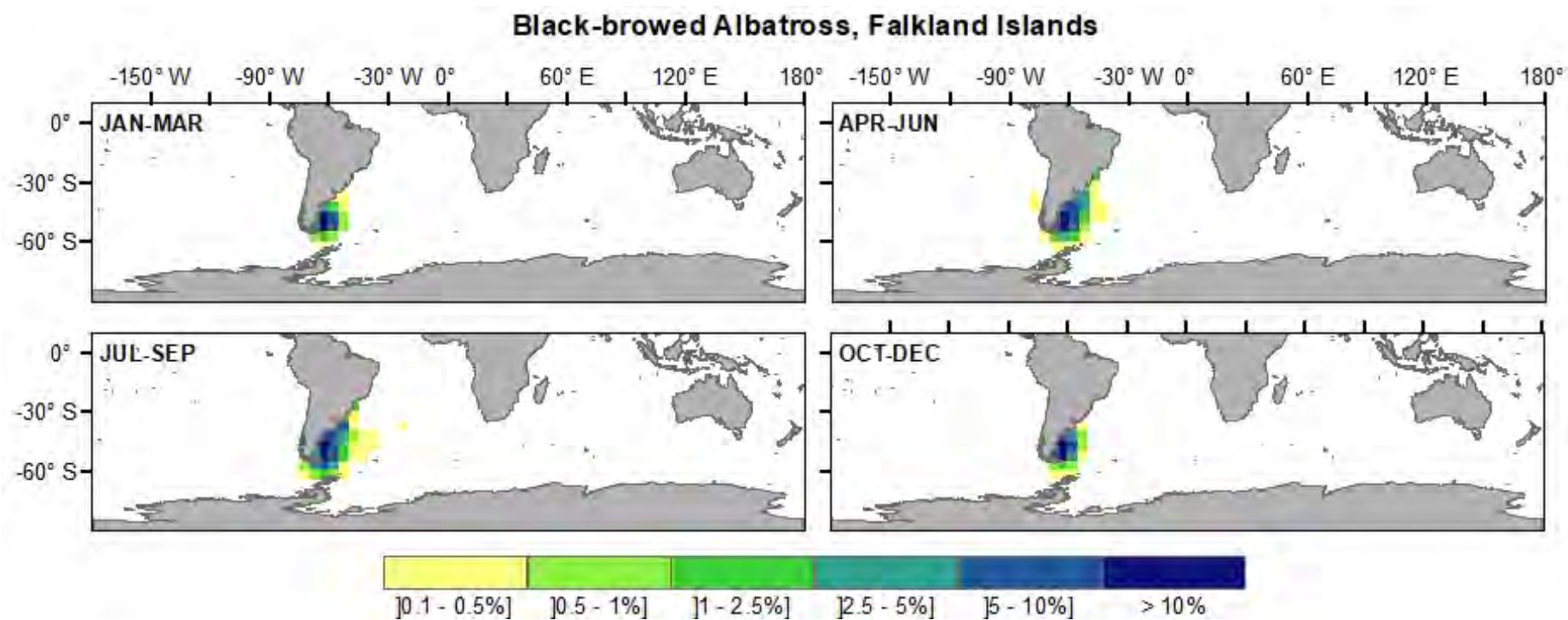


Figure S51. Black-browed Albatross, Falkland Islands

Black-browed Albatross, Islas Diego Ramirez

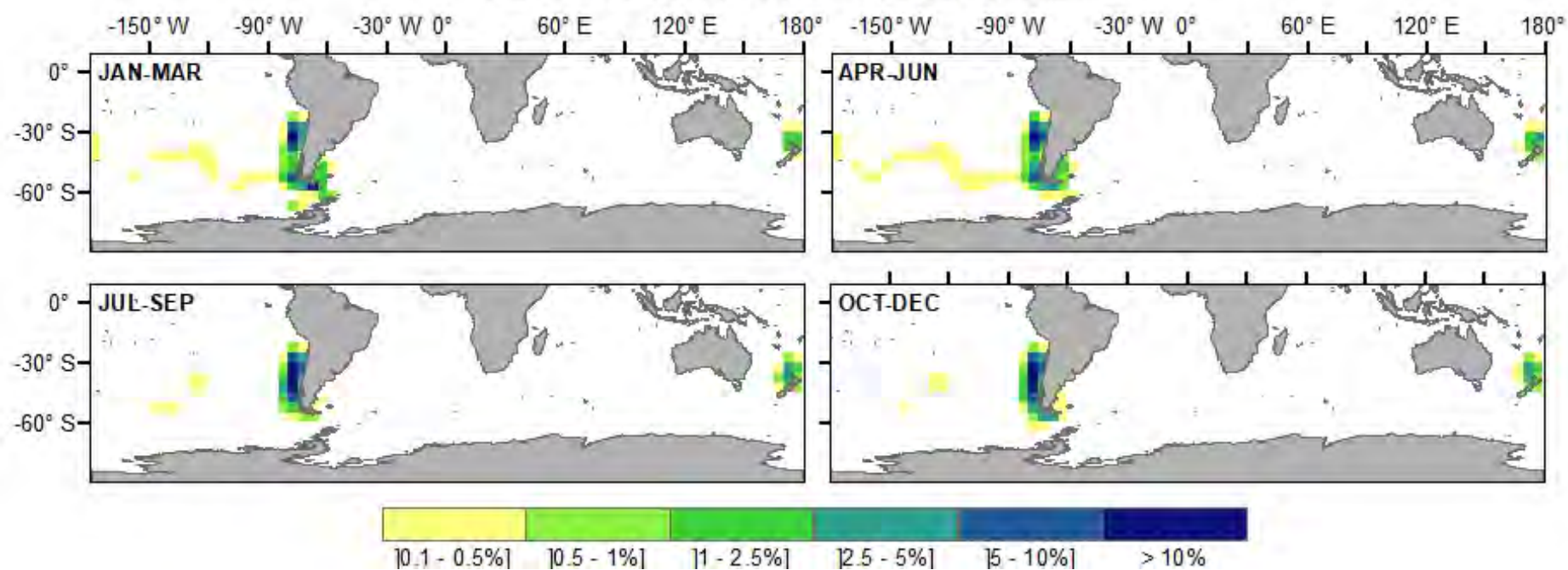


Figure S52. Black-browed Albatross, Islas Diego Ramirez

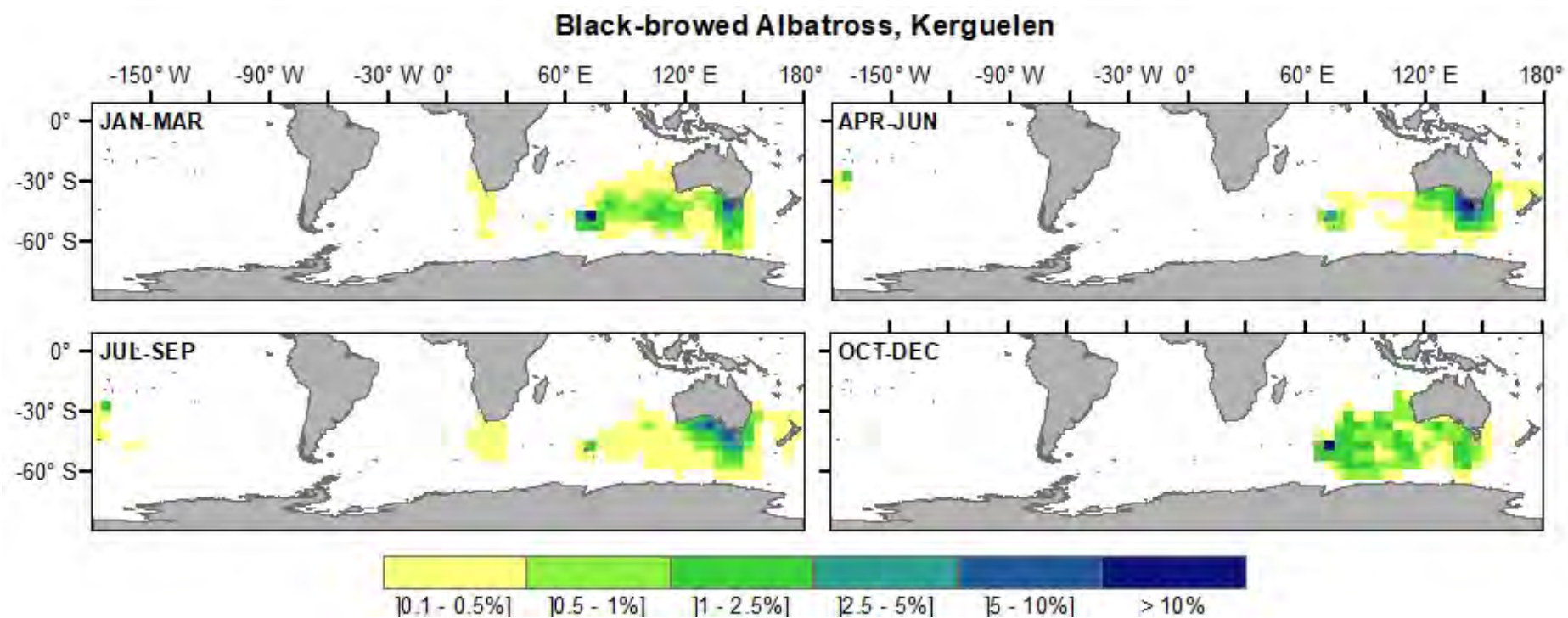


Figure S53. Black-browed Albatross, Kerguelen

Black-browed Albatross, South Georgia

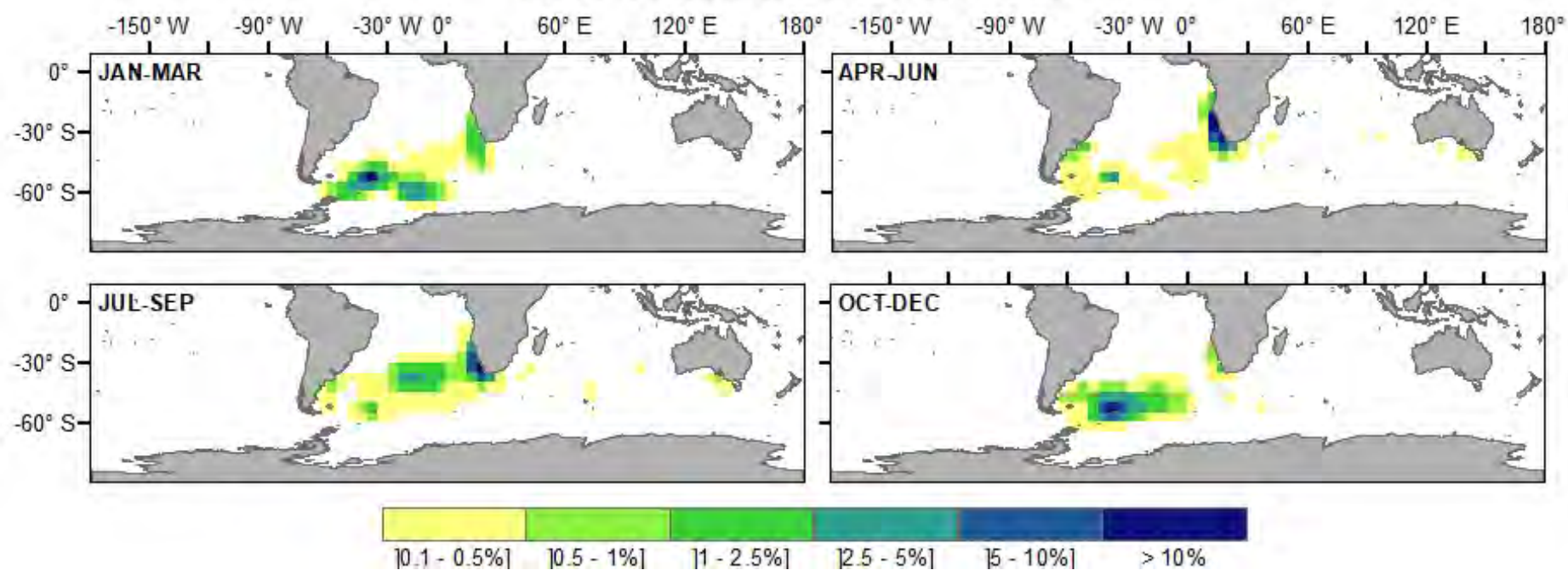


Figure S54. Black-browed Albatross, South Georgia

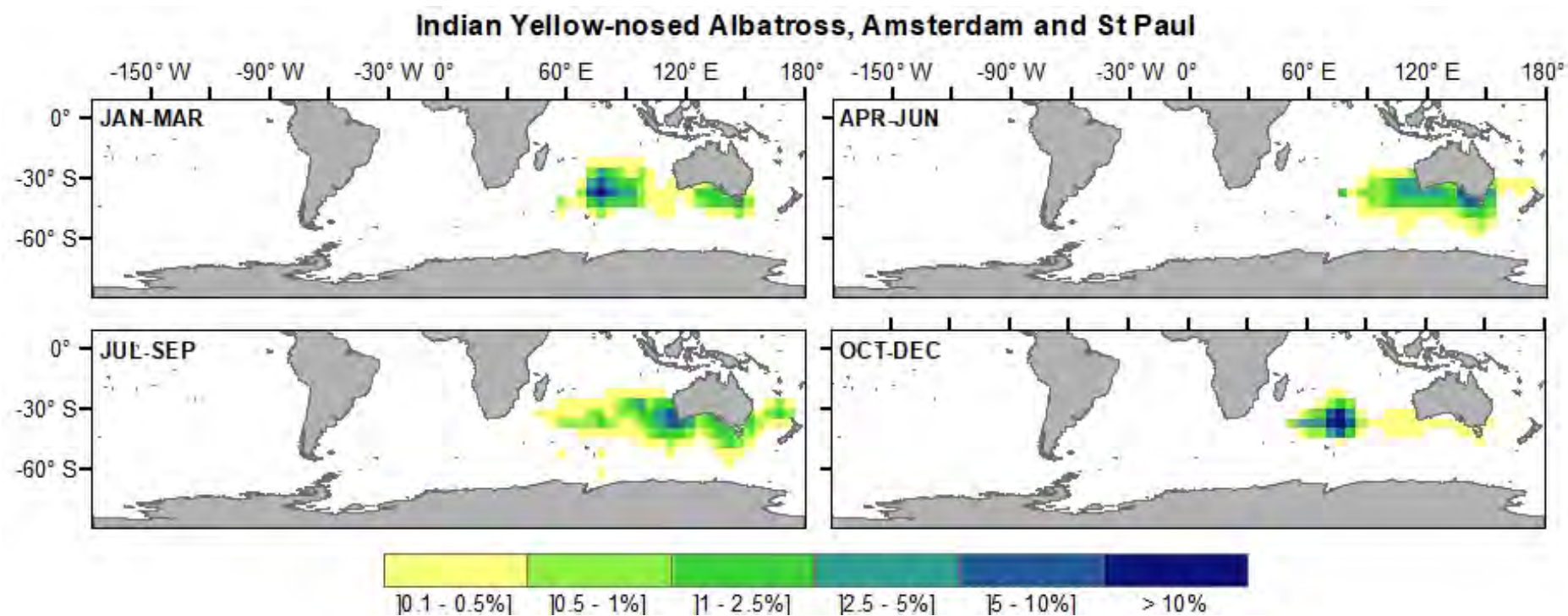


Figure S55. Indian Yellow-nosed Albatross, Amsterdam and St Paul

Atlantic Yellow-nosed Albatross, Gough

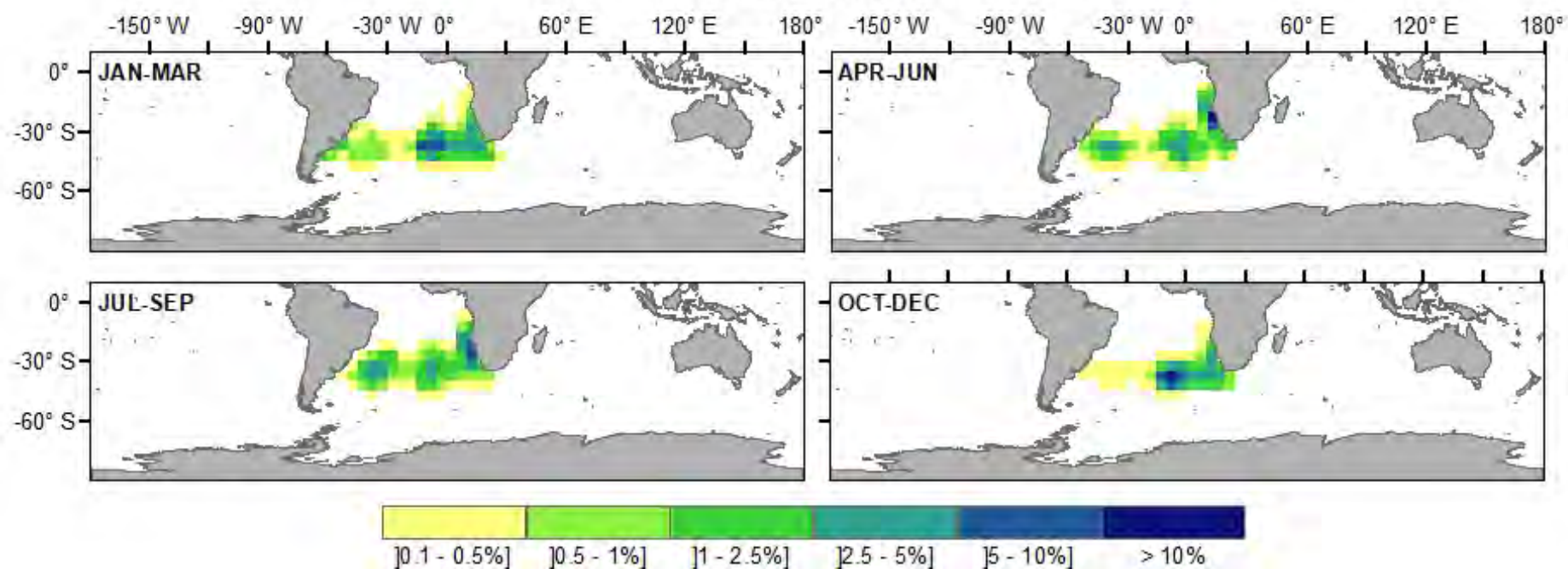


Figure S56. Atlantic Yellow-nosed Albatross, Gough

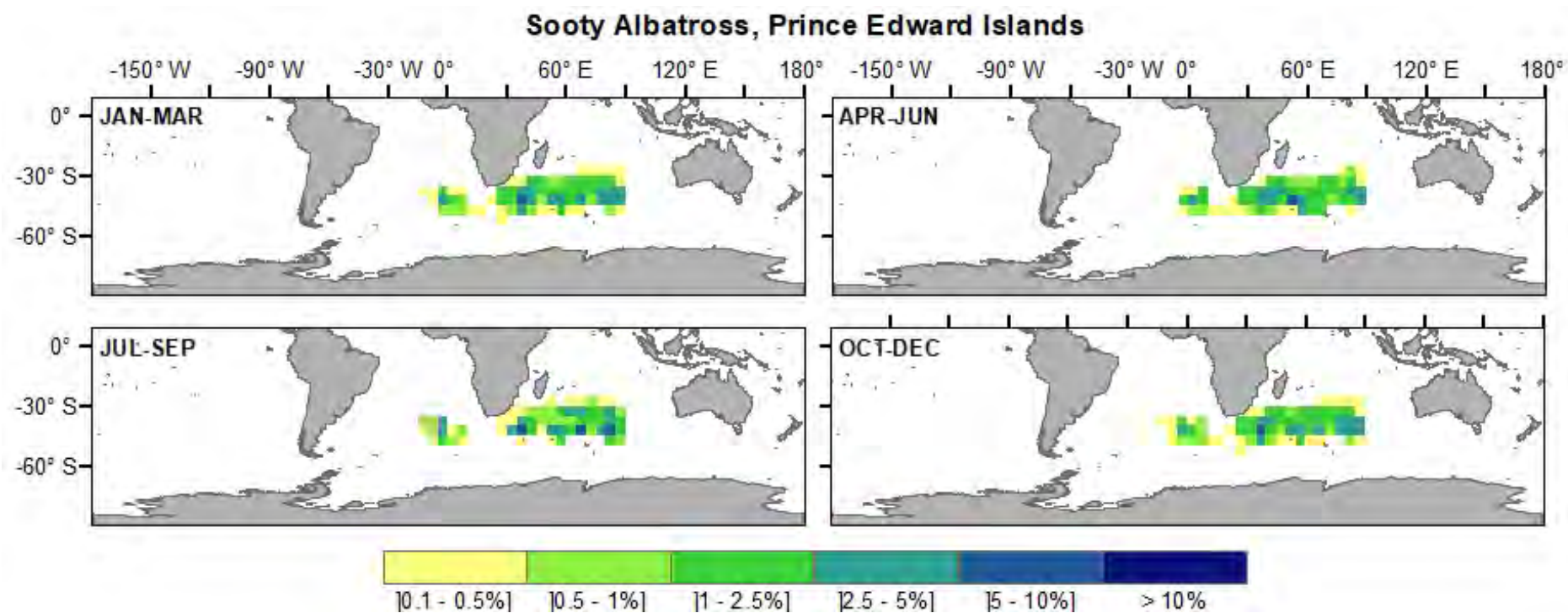


Figure S57. Sooty Albatross, Prince Edward Islands

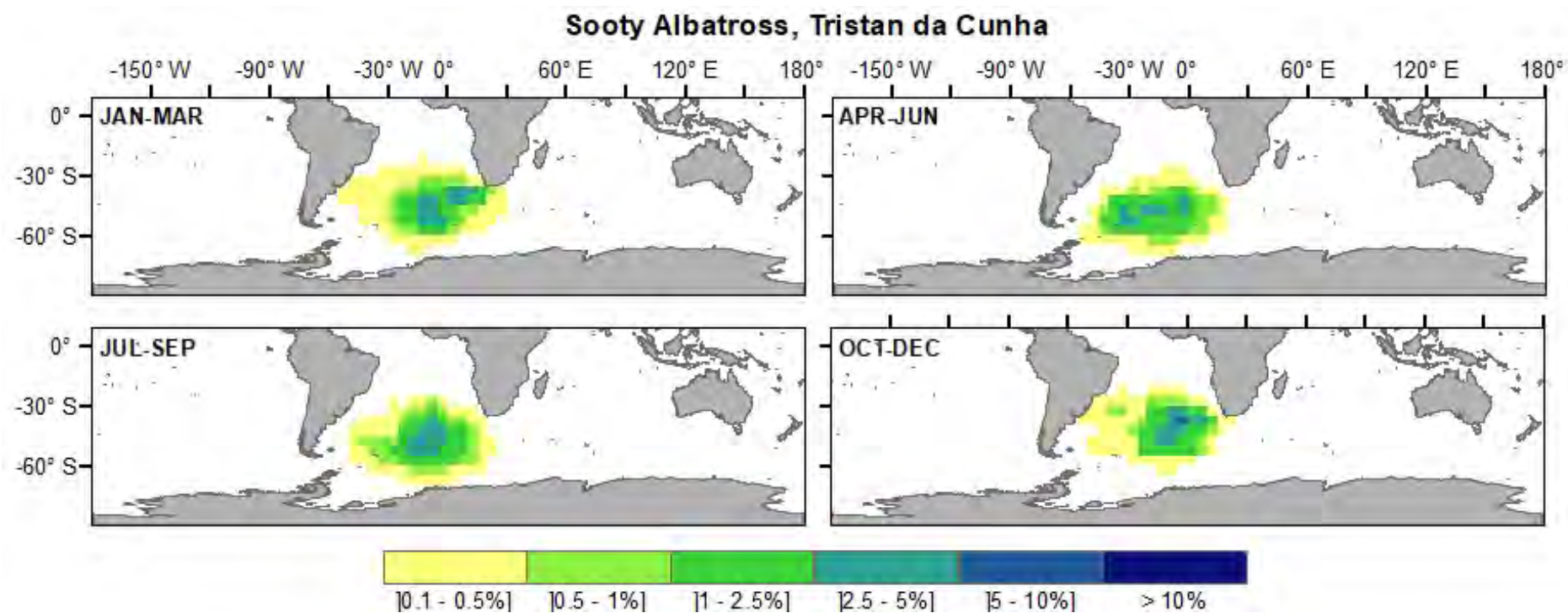


Figure S58. Sooty Albatross, Tristan da Cunha

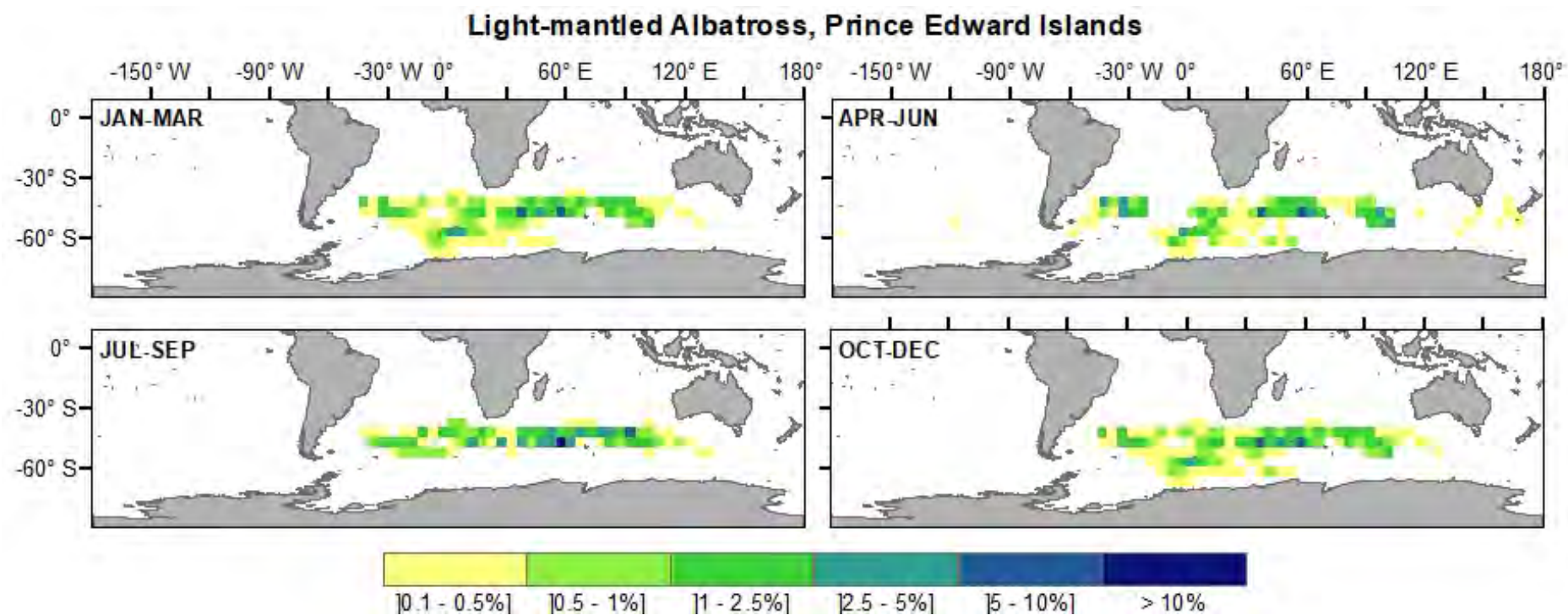


Figure S59. Light-mantled Albatross, Prince Edward Islands

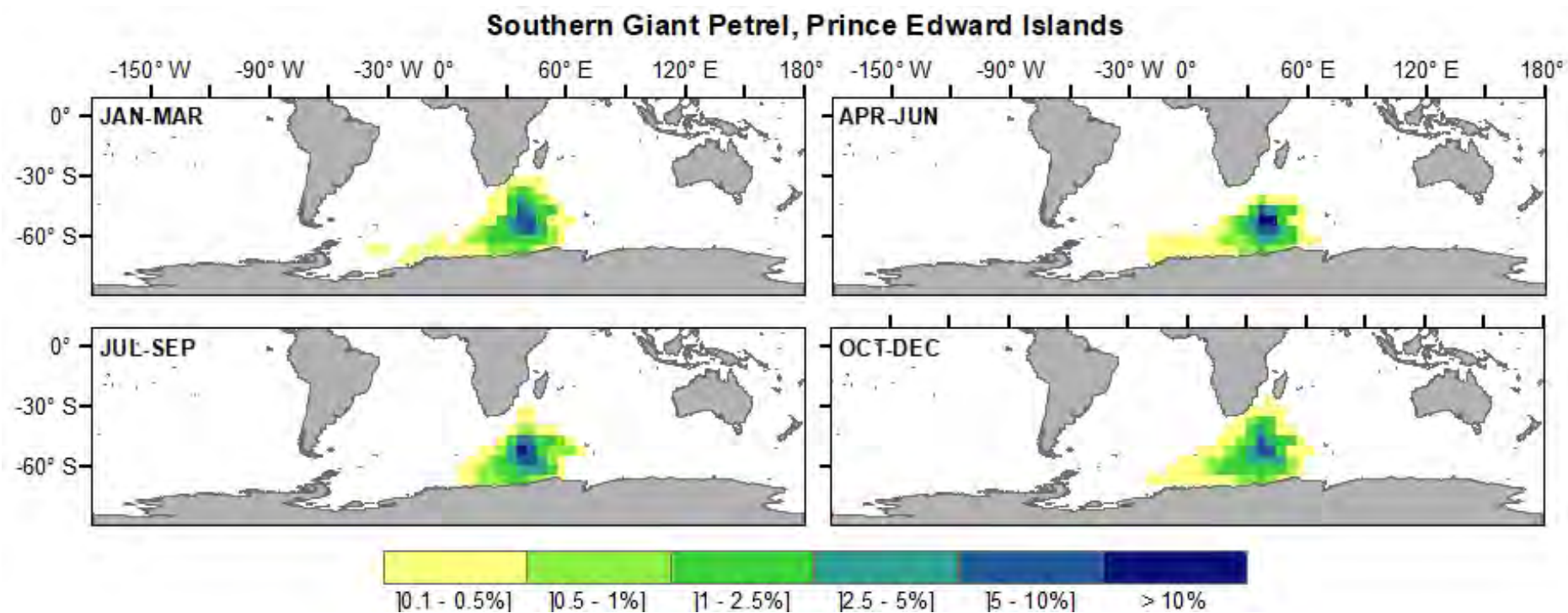


Figure S60. Southern Giant Petrel, Prince Edward Islands

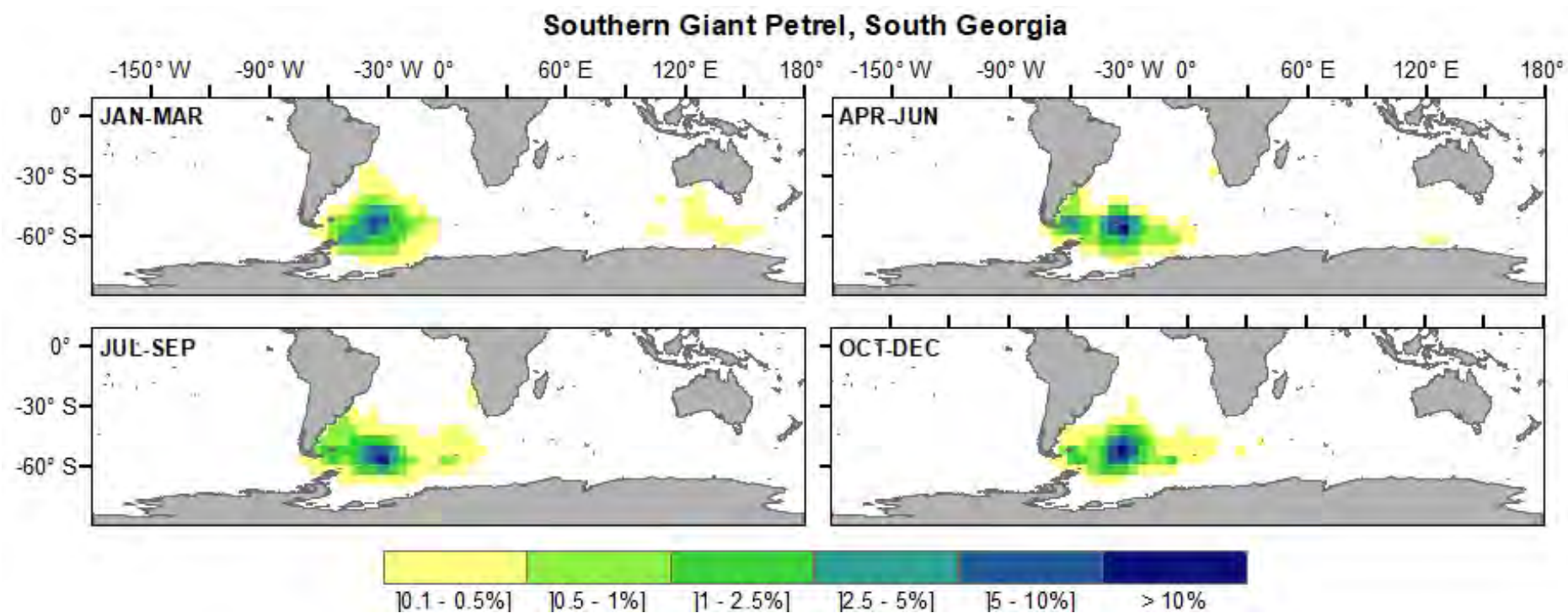


Figure S61. Southern Giant Petrel, South Georgia

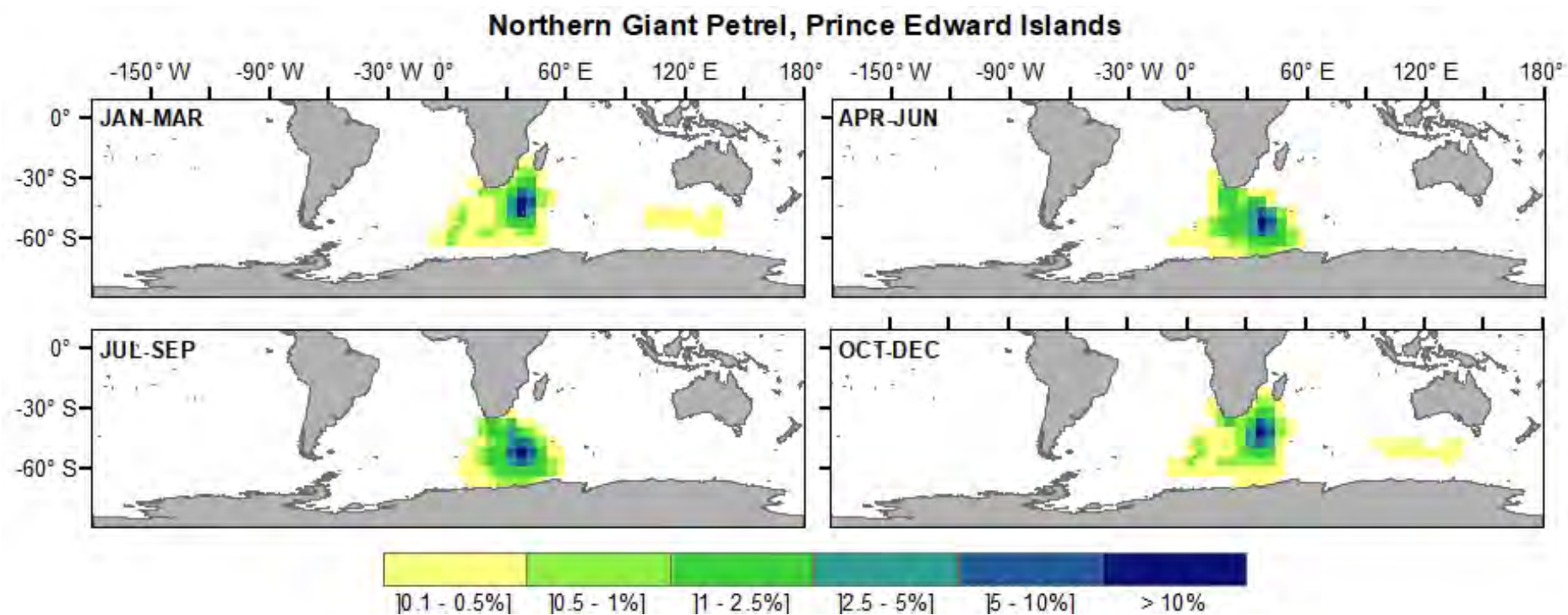


Figure S62. Northern Giant Petrel, Prince Edward Islands

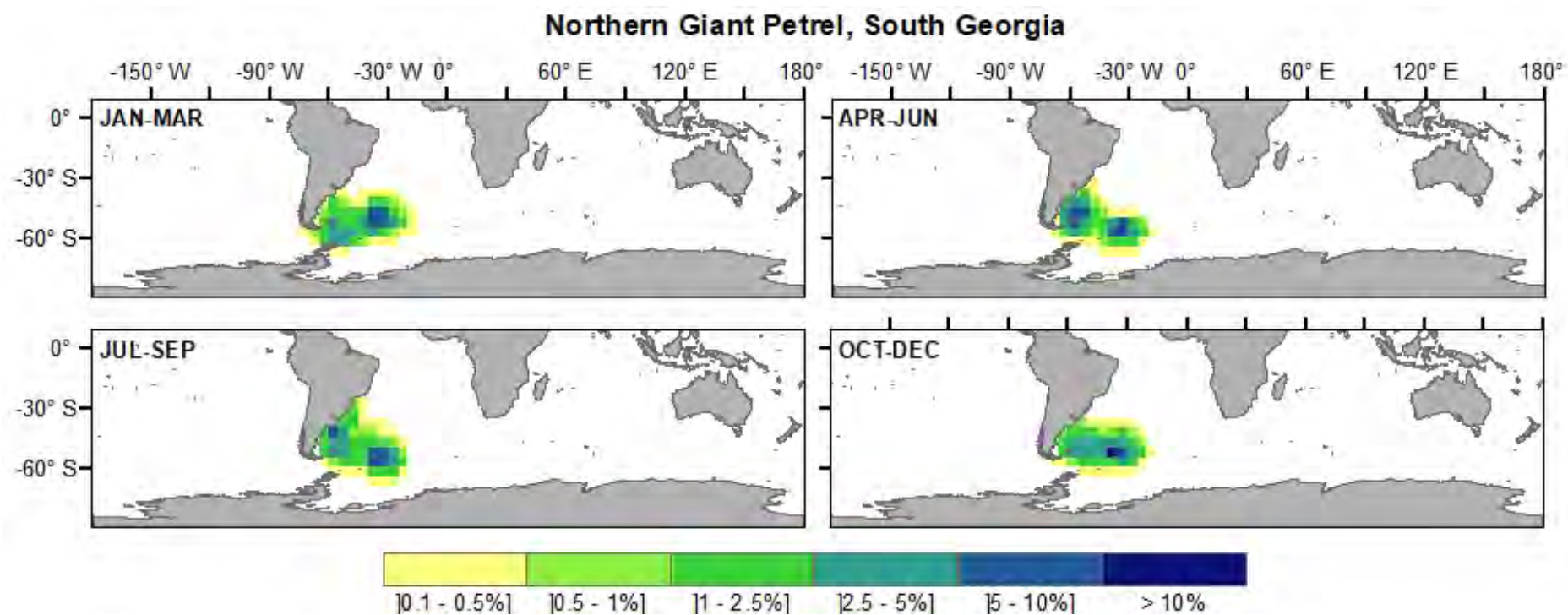


Figure S63. Northern Giant Petrel, South Georgia

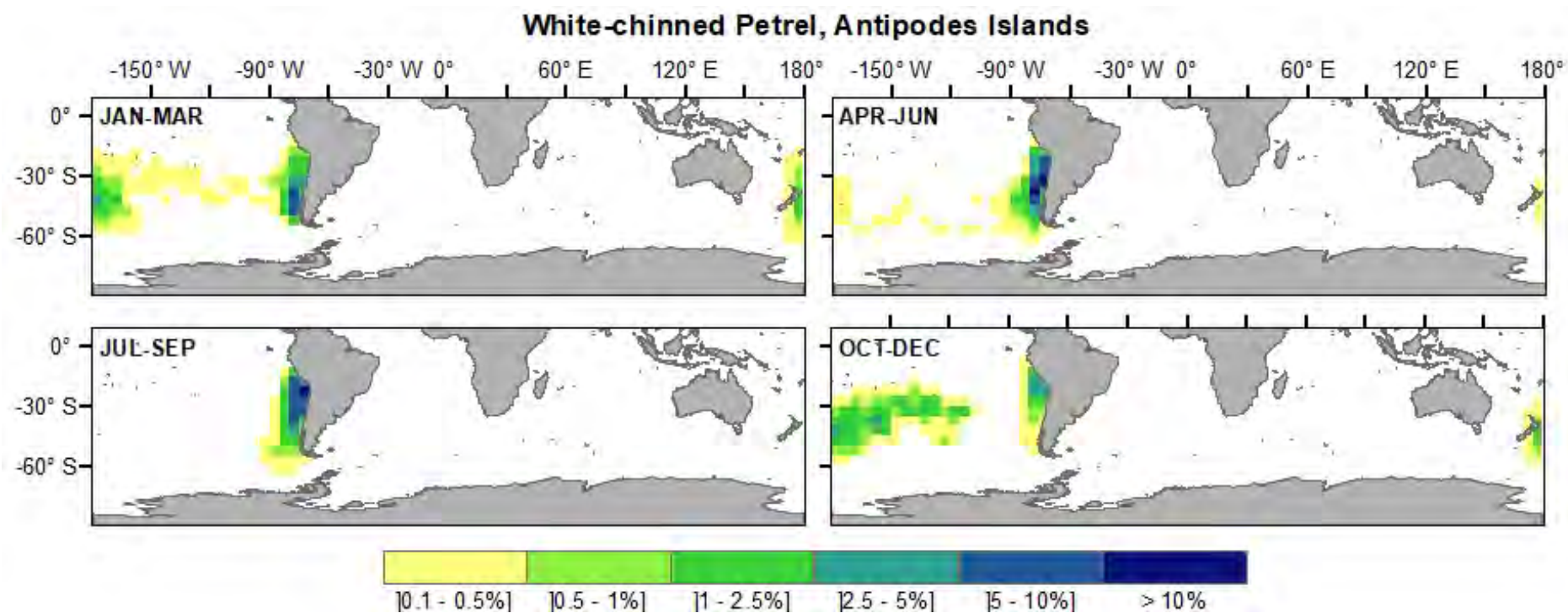


Figure S64. White-chinned Petrel, Antipodes Islands

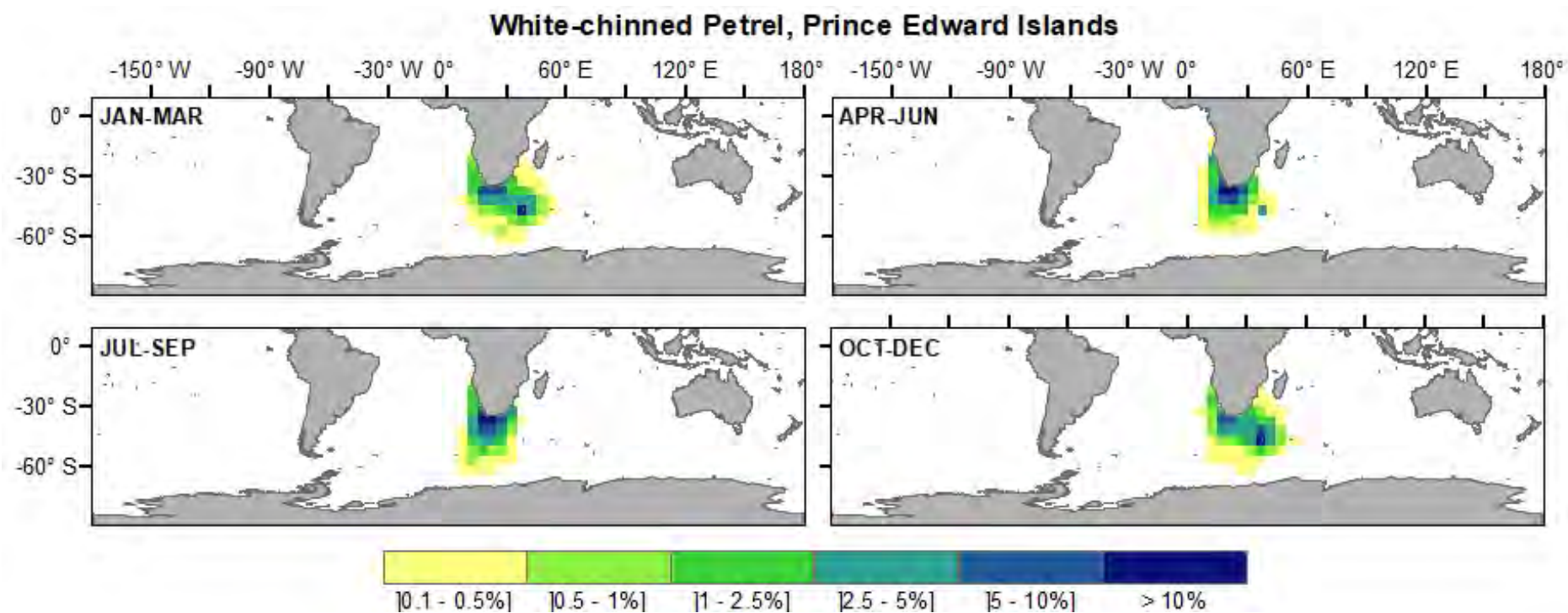


Figure S65. White-chinned Petrel, Prince Edward Islands

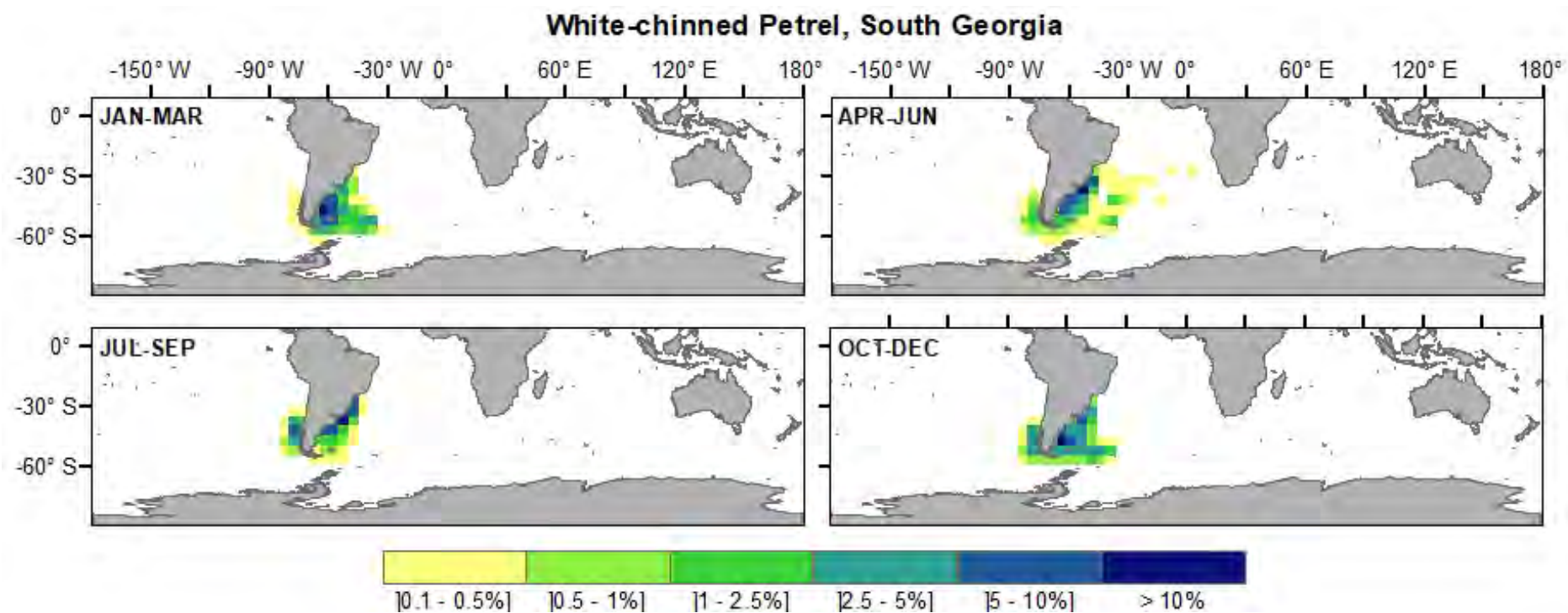


Figure S66. White-chinned Petrel, South Georgia

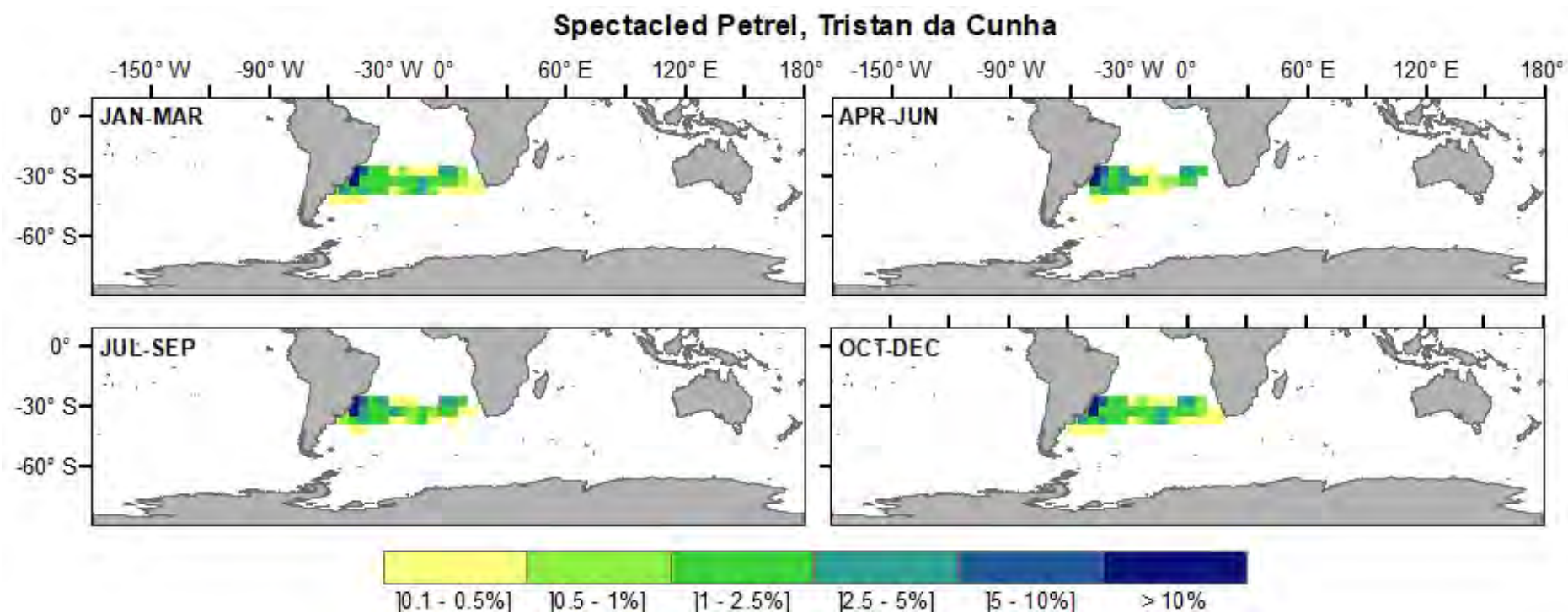


Figure S67. Spectacled Petrel, Tristan da Cunha

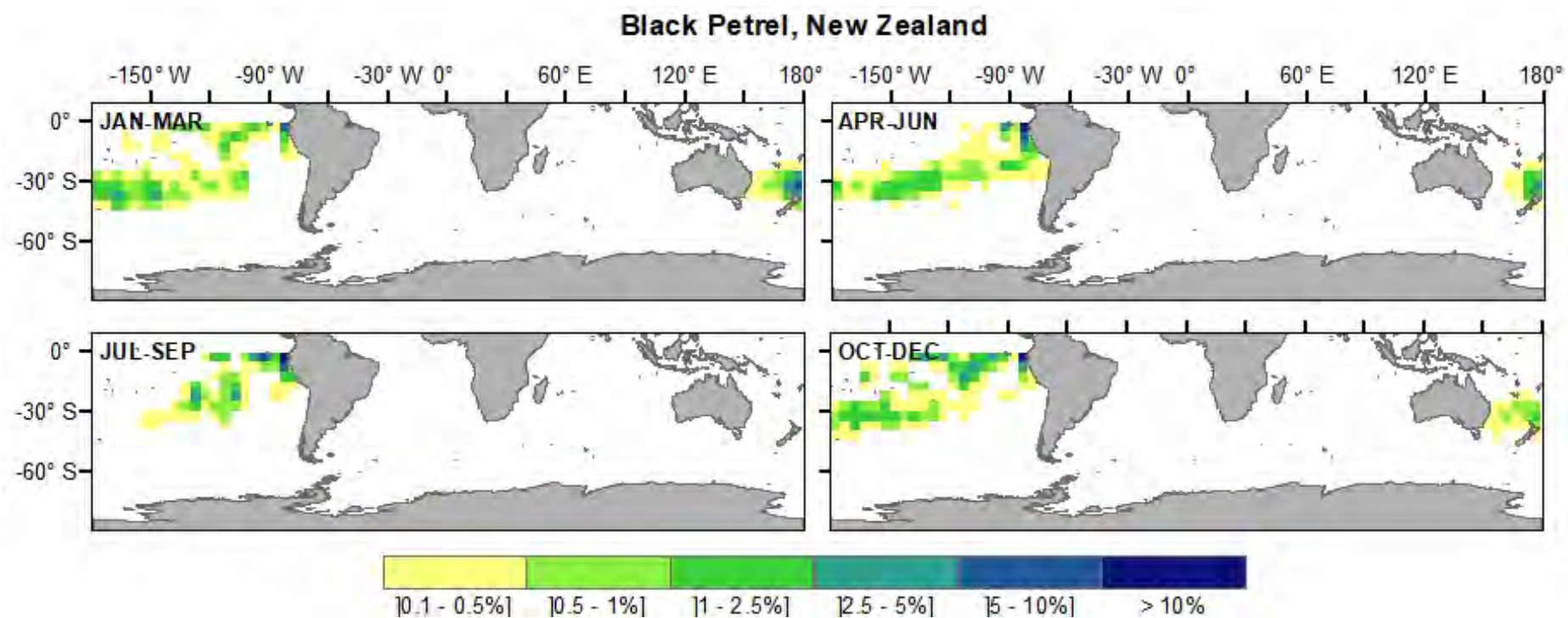


Figure S68. Black Petrel, New Zealand

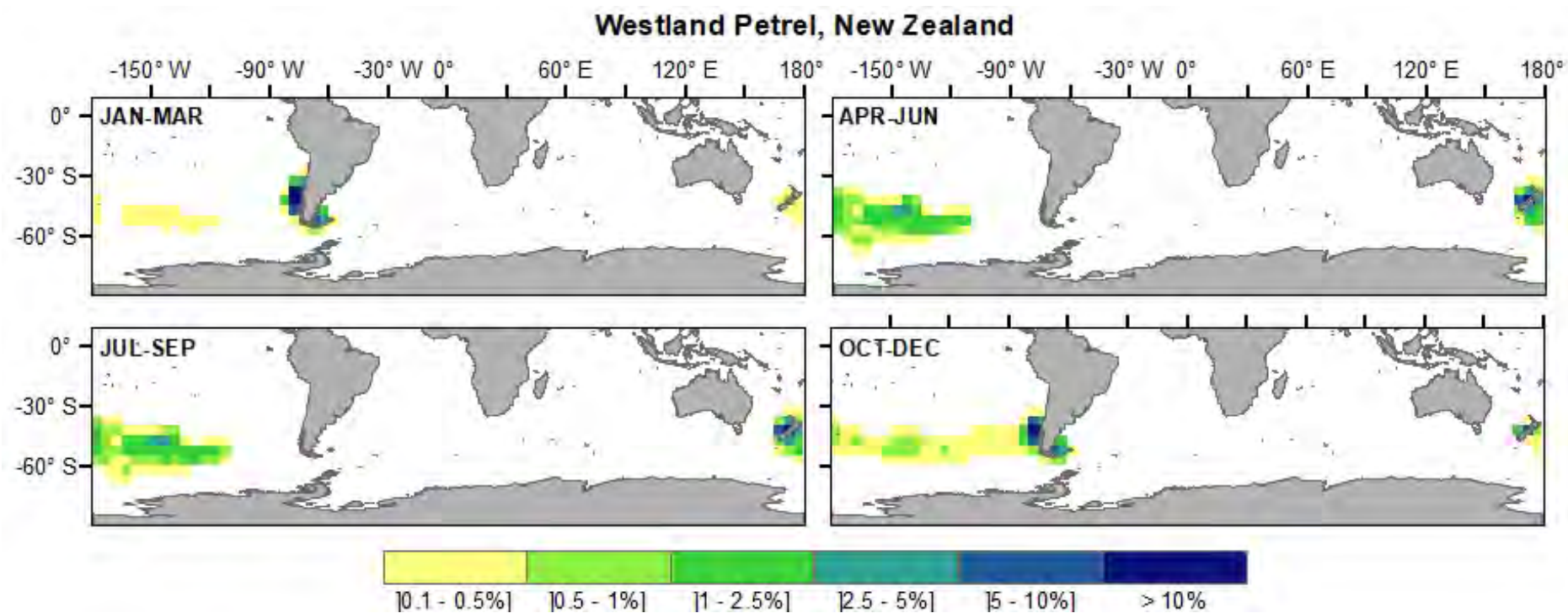


Figure S69. Westland Petrel, New Zealand

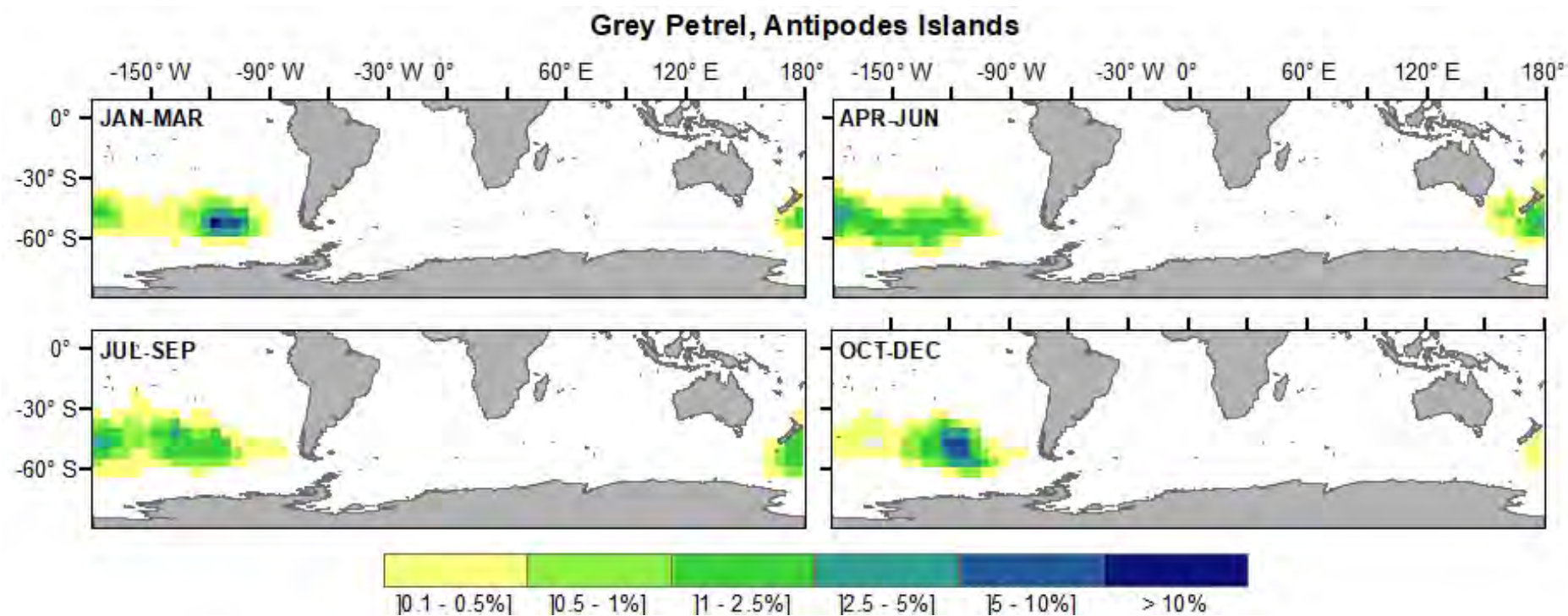


Figure S70. Grey Petrel, Antipodes Islands

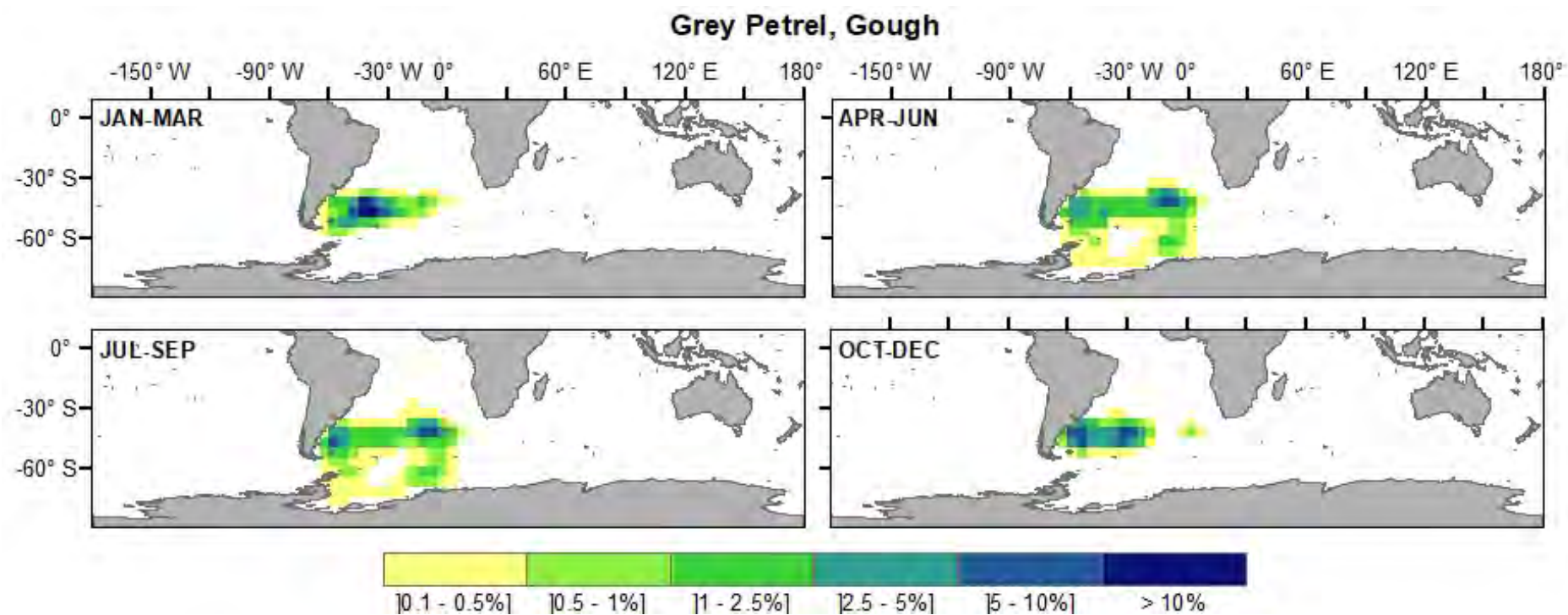


Figure S71. Grey Petrel, Gough

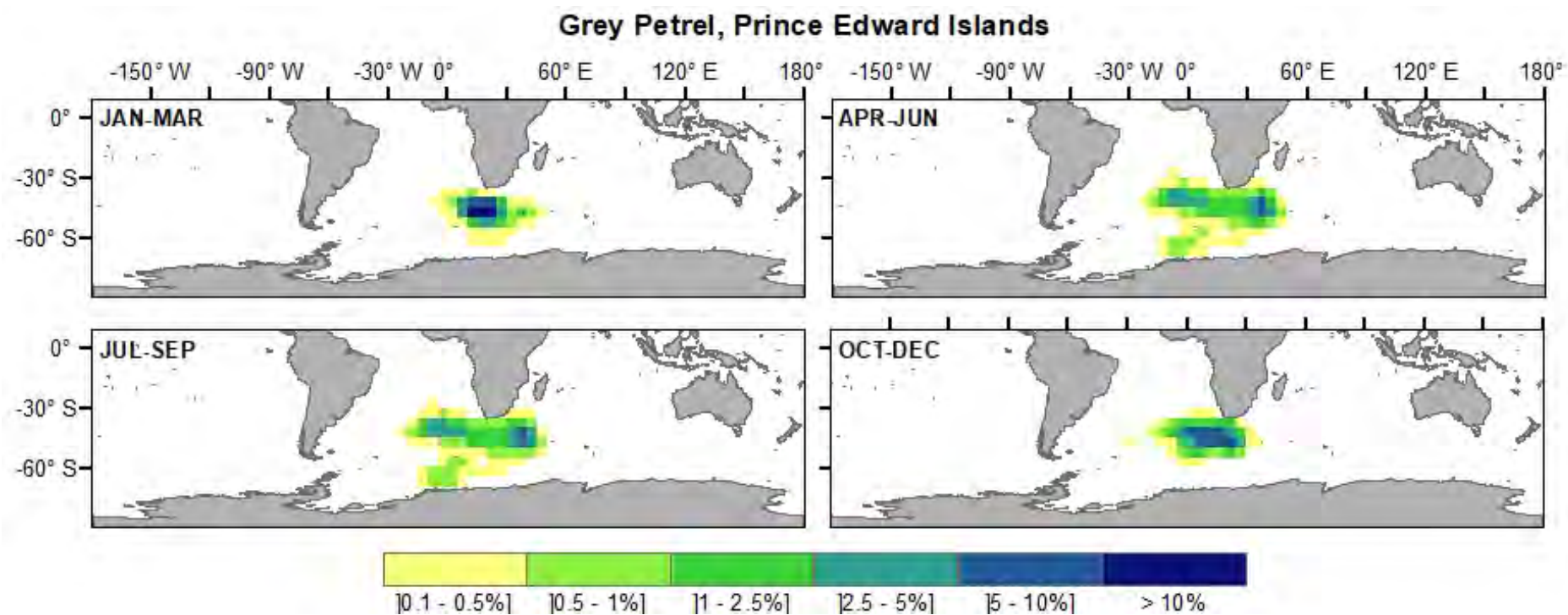


Figure S72. Grey Petrel, Prince Edward Islands

TABLE S1 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
Wandering Albatross	Crozet	12,001	13,418	13,813	13,310	13,135
Wandering Albatross	Kerguelen	7,896	8,763	9,020	8,727	8,601
Wandering Albatross	South Georgia	17,630	19,236	19,447	18,767	18,770
Tristan Albatross	Gough	7,310	8,953	8,956	8,228	8,362
Antipodean Albatross	Antipodes Islands	30,162	32,242	34,135	34,124	32,666
Antipodean Albatross	Auckland Islands	36,749	41,028	42,704	41,427	40,477
Amsterdam Albatross	Amsterdam and St Paul	318	310	352	351	333
Northern Royal Albatross	Chatham Island	27,267	33,201	33,103	26,281	29,963
White-capped Albatross	Auckland Islands	505,226	558,546	559,380	481,533	526,171
Salvin's Albatross	The Snares	5,259	5,286	4,571	4,343	4,865
Chatham Albatross	Chatham Island	26,005	26,227	23,753	20,965	24,238
Buller's Albatross	The Snares	50,023	56,830	58,873	58,970	56,174
Grey-headed Albatross	Prince Edward Islands	57,719	59,046	56,352	49,577	55,674
Grey-headed Albatross	South Georgia	403,862	414,774	411,548	366,685	399,217
Black-browed Albatross	Falkland Islands	2,123,81	2,106,62	2,046,84	1,731,98	2,002,31
Black-browed Albatross	Islas Diego Ramirez	9	9	5	3	9
Black-browed Albatross	Kerguelen	320,553	319,009	307,744	261,490	302,199
Black-browed Albatross	South Georgia	20,337	21,088	20,744	17,468	19,909
Black-browed Albatross	South Georgia	405,932	434,256	431,685	355,783	406,914
Indian Yellow-nosed Albatross	Amsterdam and St Paul	86,547	86,994	79,897	65,954	79,848
Atlantic Yellow-nosed Albatross	Gough	34,345	34,461	32,680	29,668	32,789
Sooty Albatross	Prince Edward Islands	17,276	17,345	16,830	14,837	16,572
Sooty Albatross	Tristan da Cunha	54,919	54,889	53,304	46,509	52,405
Light-mantled Albatross	Prince Edward Islands	3,490	3,603	3,634	2,997	3,431
Southern Giant Petrel	Prince Edward Islands	14,731	14,723	14,171	12,332	13,989
Southern Giant Petrel	South Georgia	24,788	26,257	26,280	22,327	24,913
Northern Giant Petrel	Prince Edward Islands	4,748	4,736	4,264	4,434	4,545
Northern Giant Petrel	South Georgia	24,813	24,796	24,192	20,634	23,609
White-chinned Petrel	Antipodes Islands	137,537	150,905	150,529	126,452	141,356
White-chinned Petrel	Prince Edward Islands	162,890	164,819	164,417	137,978	157,526
White-chinned Petrel	South Georgia	3,224,44	3,391,26	3,398,13	2,763,29	3,194,28
White-chinned Petrel	South Georgia	3	8	3	5	5
Spectacled Petrel	Tristan da Cunha	125,370	125,681	116,915	95,978	115,986
Black Petrel	New Zealand	10,342	12,241	10,446	8,718	10,437
Westland Petrel	New Zealand	29,959	26,813	27,370	29,709	28,463
Grey Petrel	Antipodes Islands	245,388	236,514	271,997	271,943	256,460
Grey Petrel	Prince Edward Islands	24,800	22,671	25,998	25,992	24,865
Grey Petrel	Gough	70,443	69,813	76,980	77,017	73,563

SUPPORTING INFORMATION

Appendix S7

A framework for mapping the distribution of Southern Ocean seabirds across life-history stages, by integrating tracking, demography and phenology

More details can be found at <https://github.com/anacarneiro/DensityMaps>

Sample sizes

TABLE S1 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 were not representative, appropriate data substitutions were used.

Common name	Island or Island Group	Pre-egg	Incubation	Brood-guard	Post-guard	Non-breeding	Juvenile	Immature
Wandering Albatross	Crozet	No data	319	79	30	95	13	11
Wandering Albatross	Kerguelen	No data	14	12	7	23	<i>11</i>	10
Wandering Albatross	South Georgia	No data	65	72	145	91	39	21
Tristan Albatross	Gough	No data	35	66	12	26	16	No data
Antipodean Albatross	Antipodes Islands	6	36	23	13	59		<i>3</i> ¹
Antipodean Albatross	Auckland Islands	8	18	9	7	91	No data	No data
Amsterdam Albatross	Amsterdam and St Paul	No data	29	17	10	14	11	8
Northern Royal Albatross	Chatham Island	No data	9		<i>4</i> ²	9		<i>2</i> ¹
White-capped Albatross	Auckland Islands	No data	27	52	60	24	No data	No data
Salvin's Albatross	The Snares			<i>22</i> ²		22	No data	No data
Chatham Albatross	Chatham Island			<i>29</i> ²		15		<i>2</i> ¹
Buller's Albatross	The Snares	No data	27	85	13	30		<i>6</i> ¹
Grey-headed Albatross	Prince Edward Islands	No data	27	11	<i>40</i> ³	25	No data	No data

Grey-headed Albatross	South Georgia	No data	30	86	38	22	15	No data
Black-browed Albatross	Falkland Islands	22	109	246	30 ⁴	33	3	76
Black-browed Albatross	Islas Diego Ramirez	No data	24	20	12	5	No data	No data
Black-browed Albatross	Kerguelen	No data	8		24 ³	123	2	No data
Black-browed Albatross	South Georgia	23	63	78	24	25	11	No data

Cont.

Common name	Island or Island Group	Pre-egg	Incubation	Brood-guard	Post-guard	Non-breeding	Juvenile	Immature
Indian Yellow-nosed Albatross	Amsterdam and St Paul	No data	45	16	10 ⁵	17	4	No data
Atlantic Yellow-nosed Albatross	Gough	No data	42	39	20	37	1	No data
Sooty Albatross	Prince Edward Islands			10 ²		10	No data	No data
Sooty Albatross	Tristan da Cunha	No data	19	12	10	13	No data	No data
Light-mantled Albatross	Prince Edward Islands			8 ²		6	No data	No data
Southern Giant Petrel	Prince Edward Islands	No data	8		7 ⁵	8	No data	No data
Southern Giant Petrel	South Georgia	No data	11	17	16	36	No data	No data
Northern Giant Petrel	Prince Edward Islands	No data	14		16 ⁵	16	No data	No data
Northern Giant Petrel	South Georgia	No data	18	26	21	27	No data	No data
White-chinned Petrel	Antipodes Islands			13 ²		14	No data	No data
White-chinned Petrel	Prince Edward Islands	No data	9		11 ⁵	7	No data	3
White-chinned Petrel	South Georgia	No data	16		22 ⁶	10	13	No data
Spectacled Petrel	Tristan da Cunha			8 ²		10	No data	No data
Black Petrel	New Zealand (Great Barrier Island)	No data	40	31	15	12	No data	No data
Westland Petrel	New Zealand	14	42	32 ⁵	12	8	No data	No data
Grey Petrel	Antipodes Islands			18 ²		18	No data	No data
Grey Petrel	Prince Edward Islands	7	8		9 ⁵	8	No data	No data
Grey Petrel	Gough	15	15		15 ⁵	15	No data	No data

¹ Breeding-stage from the original dataset classified as juvenile/immature

² Breeding-stage from the original dataset classified as breeding

³ Combination of breeding, incubation and brood-guard

⁴ Combination of post-guard and breeding data

⁵ Breeding-stage from the original dataset classified as chick-rearing

⁶ Combination of breeding and incubation

SUPPORTING INFORMATION

Appendix S8

A framework for mapping the distribution of Southern Ocean seabirds across life-history stages, by integrating tracking, demography and phenology

More details can be found at <https://github.com/anacarneiro/DensityMaps>

TABLE S1 Average relative differences ($\pm$ standard error) in overlap score between the full framework (i.e. all life-history stages) and 1) scaled adult breeders, 2) scaled adult breeders and non-breeders, and 3) stage replacements calculated per quarter and averaged per season (summer being an average of quarters 1 and 4, and winter the average of quarters 2 and 3). Negative numbers represent underestimation of overlap score when using 1), 2) and 3) compared to the full framework.

	Summer	Winter	Year-round
Scaled adult breeders	$-28.6 \pm 14.0 \%$	$-42.4 \pm 8.6 \%$	$-36.2 \pm 7.8 \%$
Scaled adult breeders and non-breeders	$-18.3 \pm 9.8 \%$	$-36.3 \pm 10.5 \%$	$-28.3 \pm 7.3 \%$
Stage replacements	$-4.0 \pm 18.3 \%$	$-29.1 \pm 15.0 \%$	$-17.9 \pm 11.7 \%$
Sample size*	16	20	36

*Results only include populations and year-quarters for which we had a good representation of all life-history stages.