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

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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 synthesizes 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.

KEYWORDS

albatrosses, at-sea threats, conservation, distributions, longline fisheries, megafauna, petrels, seabird density

1 | INTRODUCTION

Oceans face a number of threats, including overexploitation, 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, for example 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, Caldwell, & 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; Opper et al., 2018; Sequeira et al., 2018).

Although utilization distributions (i.e. probability distributions of space use; Fieberg & Kochanny, 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-Solis, & 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 multispecies 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.

2 | MATERIALS AND METHODS

2.1 | 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 standardized according to established protocols (Lascelles et al., 2016). See Appendix S1 for details on the species used here and for tracking data compilation and standardization. The steps are: (a) 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); (b) estimating utilization 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’); (c) assessing the representativeness of each data group; (d) combining data group UD and weighting them based on phenological data to produce monthly distribution maps; (e) using the outputs of (a) to weight monthly distribution maps for each life-history stage by the proportion of the total population represented; (f) aggregating monthly distribution maps in relation with 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>.

2.2 | 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 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 Agreement on the Conservation of Albatrosses and Petrels (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).

2.3 | Step 2: Estimating utilization 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 platform terminal transmitters (PTT) and global positioning system (GPS) data, and 200 km for global location sensing (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).

2.4 | 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.

2.5 | 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>.

2.6 | Step 6: Spatial and temporal aggregation of distribution grids

The resulting monthly distributions for each life-history stage were given equal weightage 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 5×5 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 5×5 degree cell coloured according to the percentage of the population using that cell during a given season or year (Appendix S6).

2.7 | Adequacy of stage replacements

To test whether our replacements adequately represent the distributions of juveniles and immatures, we quantified the similarity of UD 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 Bhattacharyya's affinity index to quantify overlap; ranging from 0 (no overlap) to 1 (identical UD), it is considered to be the most appropriate index for quantifying the degree of similarity among UD estimates (Fieberg & Kochanny, 2005).

2.8 | 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 (a) just using data from adult breeders and (b) just adult breeders and non-breeders (i.e. all adults). We used the steps described above to estimate these distributions but excluding (a) adult non-breeders, juveniles and immatures, and (b) 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 (c) 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 (a) scaled adult breeders, (b) scaled adult breeders and non-breeders and (c) 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.

3 | 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 (Figure 1). Adult non-breeders represented an average of 18% of the total number of individuals of any population (range 7%–39%; Figure 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 prelaying 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; Figure 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 (Figure 2). We visualized the distributions of several populations for which we had complete datasets (e.g. wandering albatross *Diomedea exulans* from Crozet; Figure 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 (Figure 4).

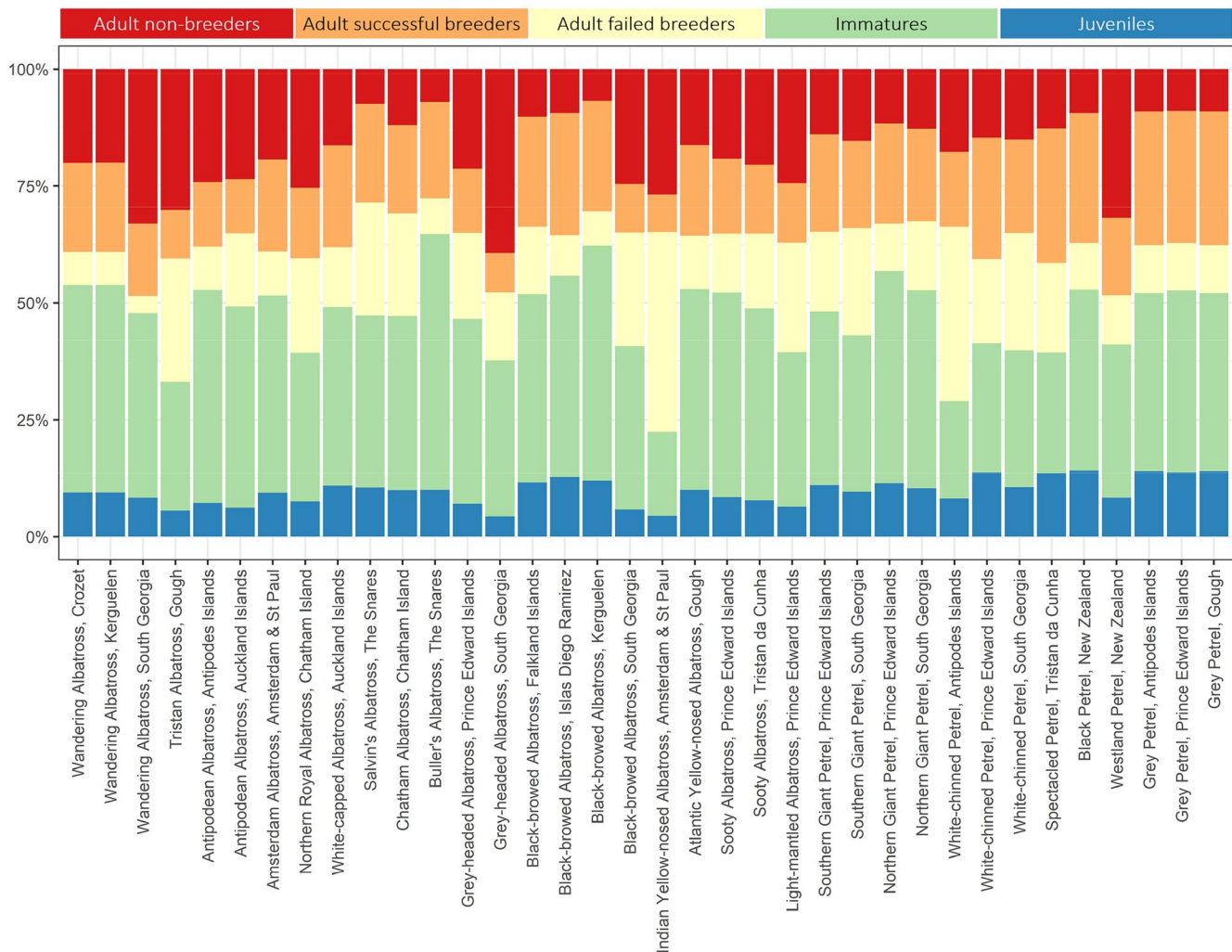


FIGURE 1 The proportion of the population represented by each major life-history stage for 22 species of albatrosses and petrels (36 populations) breeding in the Southern Ocean. Five distinct life-history stages were considered here: juveniles during their first year at sea, immatures (from second year 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)

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).

3.1 | 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 (a) adult breeders and (b) all adults, with pelagic longline fisheries resulted in an average underestimation of the total fisheries overlap by (a) 36.2% (42.4% in winter and 28.6% in summer) and (b) 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 (c) 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 (Figure 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

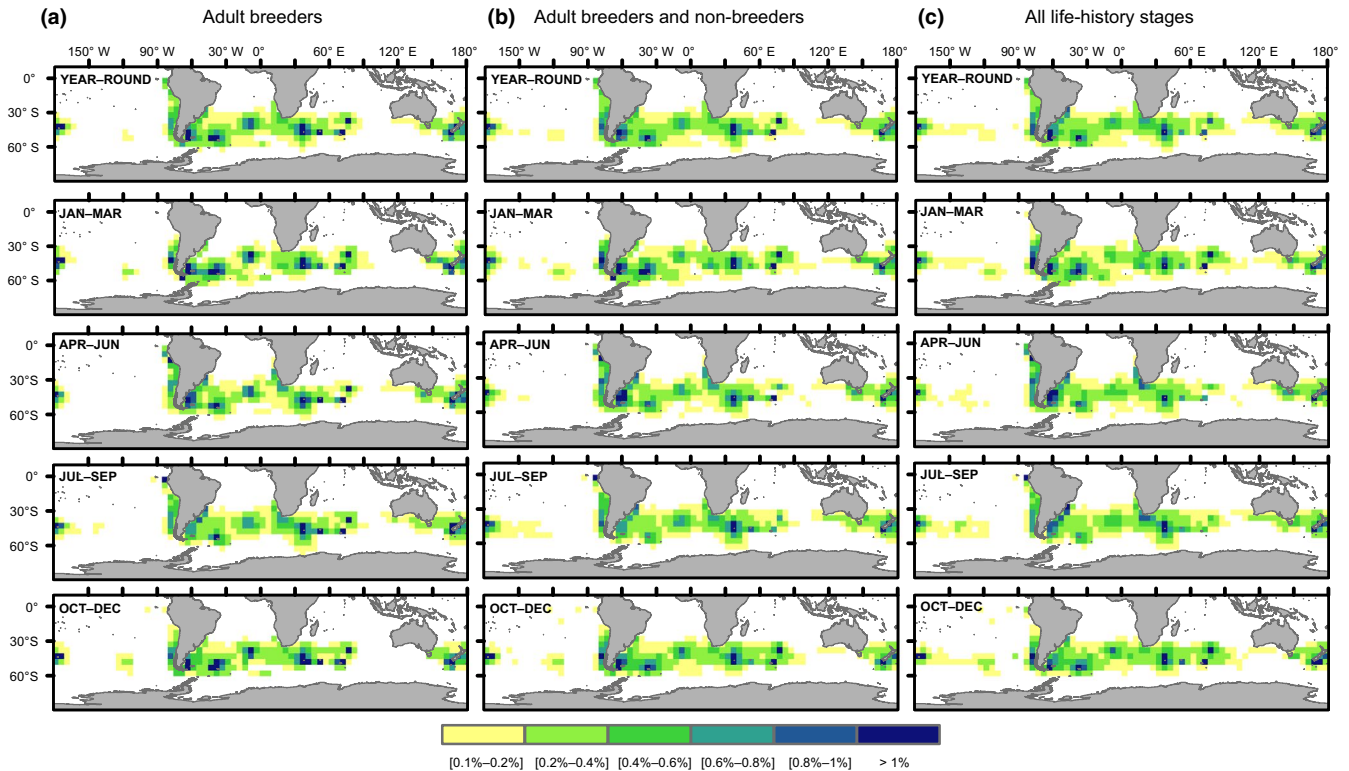


FIGURE 2 The quarterly and year-round density distributions of 22 species of albatrosses and petrels (36 populations) breeding in the Southern Ocean. Equal weightage is given to each of the 36 populations (i.e. the proportions of each population are averaged) and are illustrated as relative density. The colour gradient refers to the percentage of the population represented within each $5 \times 5^\circ$ 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)

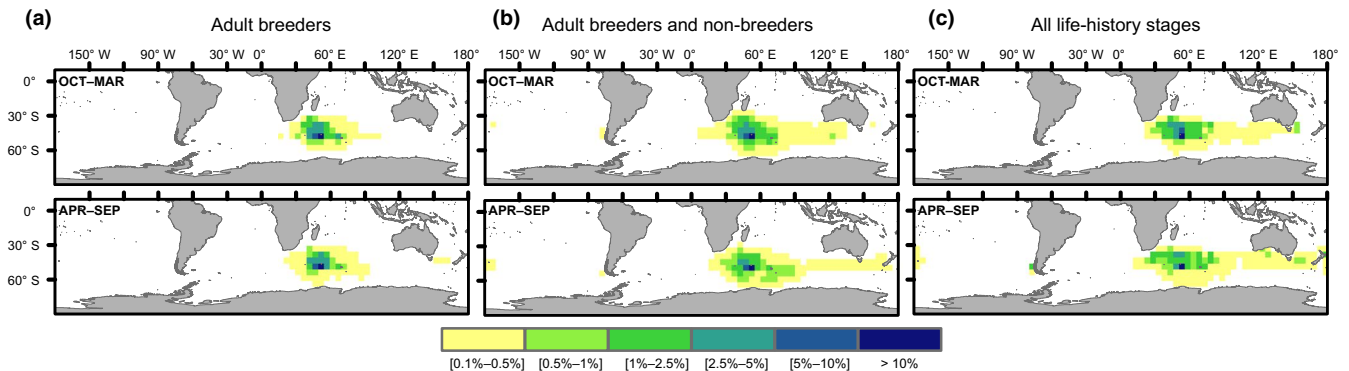


FIGURE 3 The seasonal density distributions of wandering albatrosses from Crozet. The colour gradient refers to the percentage of the population represented within each $5 \times 5^\circ$ grid. Darker shades (of blue) depict a greater density of birds. Maps are based on data for (a) adult breeders (successful 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)

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; Figure 6; Appendix S9).

4 | 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.

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 $5 \times 5^\circ$ 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)

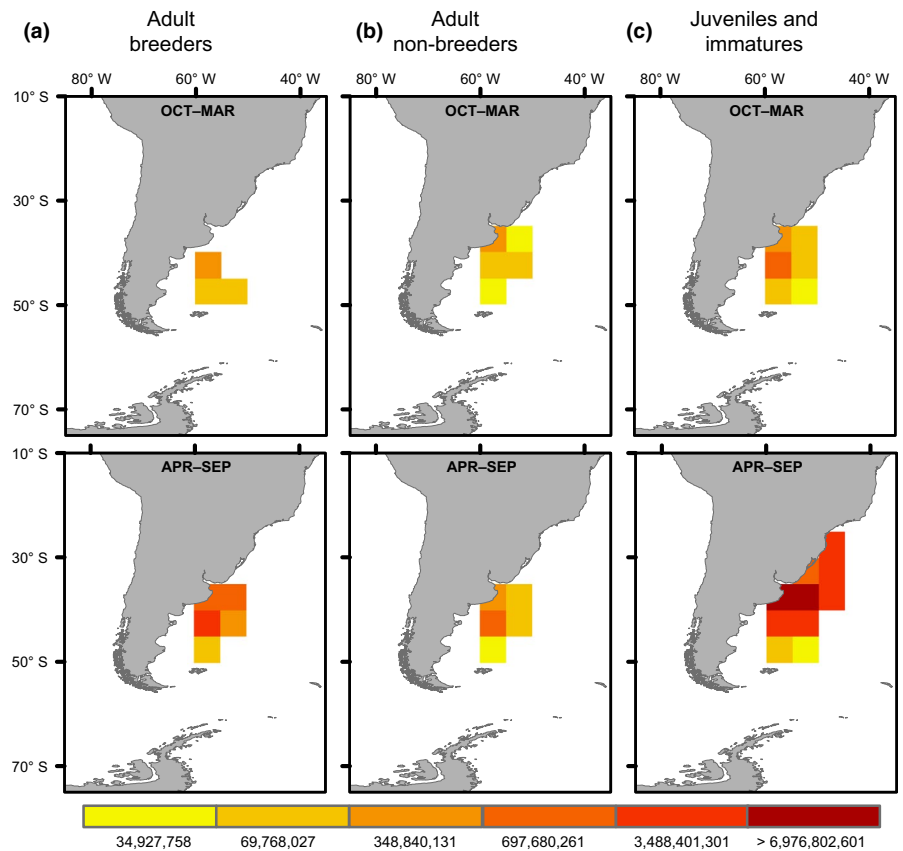
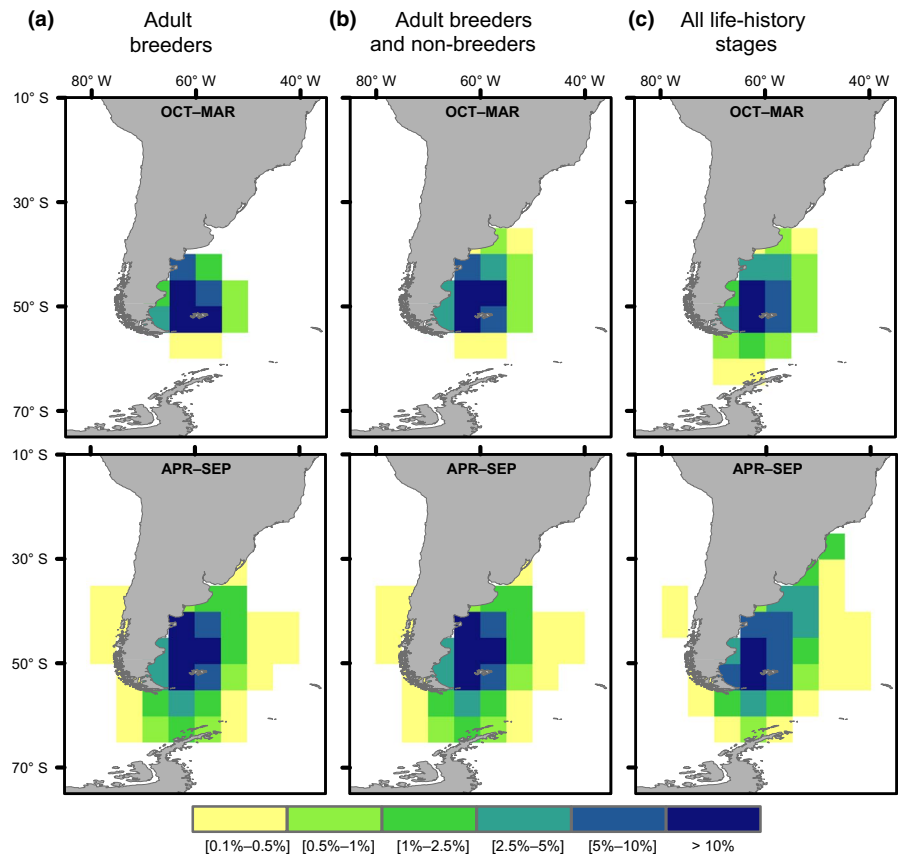


FIGURE 5 The seasonal overlap of black-browed albatrosses from Falkland Islands with pelagic longline fisheries averaged across years (2007–2016). Darker shades [of red] depict a greater overlap. The colour gradient refers to the number of individuals multiplied by number of hooks within each $5 \times 5^\circ$ 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

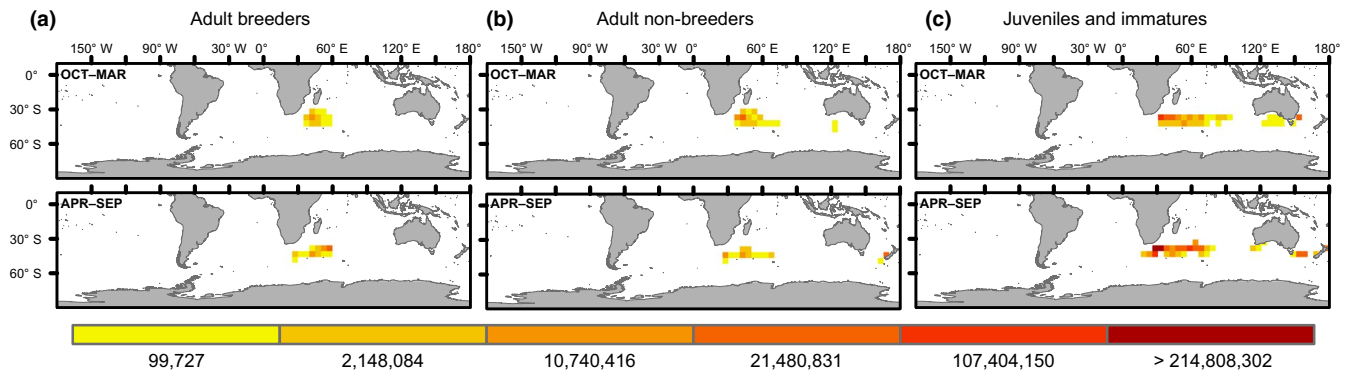


FIGURE 6 The seasonal overlap of wandering albatrosses from Crozet with pelagic longline fisheries averaged across years (2007–2016). Darker shades [of red] depict a greater overlap. The colour gradient refers to the number of individuals multiplied by number of hooks within each $5 \times 5^\circ$ grid. 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

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 standardized 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 *Phoebetria* 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 characterize the distributions of each life-history stage, we emphasize 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 emphasize 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 characterize 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 multispecies risk zones and periods.

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AUTHORS' CONTRIBUTIONS

A.P.B.C., E.J.P., S.O., T.A.C., R.A.P., A.-S.B.-L. and M.P.D. conceived the ideas and designed methodology; S.O., R.M.W., R.A.P., J.R., B.J.D., P.G.R., J.A., J.P.Y.A., E.B., L.B., L.C., P.C., J.C., L.D., G.E., A.F., J.G.-S., J.P.G., D.G., T.J.L., A.M., D.N., D.G.N., K.R.-H., C.J.R.R., P.M.S., P.S., J.-C.S., A.S., K.L.S., D.R.T., L.T., K.W., S.M.W. and H.W. provided the data; A.P.B.C. and E.J.P. analysed the data; A.P.B.C. 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.html>)), 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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