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RESEARCH ARTICLE

A comprehensive large-scale assessment of fisheries bycatch risk to threatened seabird populations

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Abstract

1. Incidental mortality (bycatch) in fisheries remains the greatest threat to many large marine vertebrates and is a major barrier to fisheries sustainability. Robust assessments of bycatch risk are crucial for informing effective mitigation strategies, but are hampered by missing information on the distributions of key life-history stages (adult breeders and non-breeders, immatures and juveniles).
2. Using a comprehensive biologging dataset (1,692 tracks, 788 individuals) spanning all major life-history stages, we assessed spatial overlap of four threatened seabird populations from South Georgia, with longline and trawl fisheries in the Southern Ocean. We generated monthly population-level distributions, weighting each life-history stage according to population age structure based on demographic models. Specifically, we determined where and when birds were at greatest potential bycatch risk, and from which fleets.
3. Overlap with both pelagic and demersal longline fisheries was highest for black-browed albatrosses, then white-chinned petrels, wandering and grey-headed albatrosses, whereas overlap with trawl fisheries was highest for white-chinned petrels.
4. Hotspots of fisheries overlap occurred in all major ocean basins, but particularly the south-east and south-west Atlantic Ocean (longline and trawl) and south-west Indian Ocean (pelagic longline). Overlap was greatest with pelagic longline fleets in May–September, when fishing effort south of 25°S is highest, and with demersal and trawl fisheries in January–June. Overlap scores were dominated by particular fleets: pelagic longline—Japan, Taiwan; demersal longline and trawl—Argentina, Namibia, Falklands, South Africa; demersal longline—Convention for Conservation of Antarctic Marine Living Resources (CCAMLR) waters, Chile, New Zealand.
5. *Synthesis and applications*. We provide a framework for calculating appropriately weighted population-level distributions from biologging data, which we

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recommend for future fisheries bycatch risk assessments. Many regions of high spatial overlap corresponded with high seabird bycatch rates recorded by onboard observers, indicating that our approach reliably mapped relative bycatch risk at large spatial scales. Implementation of effective bycatch mitigation in these high-risk regions varies considerably. Although potential bycatch risk appears to have decreased since the early 2000s, albatross and petrel populations from South Georgia and elsewhere are still declining, emphasizing the need for much improved observer coverage and monitoring of compliance with bycatch regulations.

KEYWORDS

albatross, biologging, ecological risk assessment, longline fisheries, marine megafauna, petrel, population model, trawl fisheries

1 | INTRODUCTION

Industrial fisheries have widespread impacts on marine ecosystems (Pauly, Watson, & Alder, 2005). During the past two decades, fisheries management has shifted emphasis from stock assessment to address unintended consequences of fishing, such as habitat destruction, changes to ecosystem structure and incidental mortality (bycatch) of non-target species (FAO, 2003; Zhou et al., 2010). Fisheries bycatch has been identified as the most serious threat to many large marine vertebrate species, including marine mammals, birds, turtles and fishes (Lewison et al., 2014; Phillips et al., 2016). Removal of these upper trophic-level predators has downstream effects on wider ecosystem functioning (Estes et al., 2011), and the immediate reduction of bycatch to negligible levels is crucial to halt their ongoing population declines (Lewison, Crowder, Read, & Freeman, 2004).

Large marine vertebrates such as seabirds are long-lived, with life-history traits (e.g. delayed maturity, low reproductive rates), that make them sensitive to small increases in mortality resulting from bycatch in fisheries (Lewison et al., 2004). Albatrosses and large petrels are opportunistic scavengers attracted to vessels by the availability of discards; in longline fisheries, they can be hooked and drowned during line-setting, whereas in trawl fisheries, most mortality results from strikes on warp cables (Bugoni, Mancini, Monteiro, Nascimento, & Neves, 2008, Jiménez, Abreu, Pons, Ortiz, & Domingo, 2010; Sullivan, Reid, & Bugoni, 2006). Many species are wide ranging, bringing them into contact with a broad range of fishing gears and fleets in national and international waters (Anderson et al., 2011; BirdLife, 2004; Lewison et al., 2014).

Given the vast geographical distribution of global fisheries (Kroodsma et al., 2018), bycatch reduction requires management efforts that are well targeted in space and time. However, bycatch rates vary at multiple scales, due to the distribution, type and magnitude of fishing effort, and the distributions and habitat preferences of non-target species (Lewison et al., 2014; Phillips et al., 2016). Moreover, its estimation is particularly challenging because observer data are often sparse, unrepresentative or are of insufficient quality to allow species or population identification (Anderson et al., 2011; Phillips, 2013; Tuck et al., 2011).

Spatio-temporal assessments of overlap with fisheries are used increasingly to identify high-risk areas (Roe et al., 2014), and recent developments in biologging have vastly improved our ability to map distributions of marine vertebrates in relation to fishing activities at alternative spatial scales (Cuthbert, Hilton, Ryan, & Tuck, 2005; Jiménez et al., 2016; Torres, Sagar, Thompson, & Phillips, 2013). However, many species are long-lived with age-structured populations and major gaps exist in knowledge of young age classes (juveniles, immatures) and adult non-breeders, which are challenging to track because of their smaller size or long periods spent entirely at sea (Hazen et al., 2012; Phillips, Lewis, González-Solís, & Daunt, 2017). As non-breeders can represent a large component of the total population (Arroyo et al., 2016; Saether & Bakke, 2000), neglecting them leads to biased estimates of bycatch risk. Also, due to their generally more dispersed distributions and, for juveniles, naïve foraging behaviours, these life-history stages are often at greater risk than breeding adults (Gianuca, Phillips, Townley, & Votier, 2017).

South Georgia (hereafter SG), in the south Atlantic Ocean, holds globally important populations of grey-headed (GHA, *Thalassarche chrysostoma*), black-browed (BBA, *Thalassarche melanophris*) and wandering (WA, *Diomedea exulans*) albatrosses, and white-chinned petrels (WCP, *Procellaria aequinoctialis*) (representing 12–50+ percent of each species), which have undergone major declines associated with low adult and juvenile survival since the 1980s (Croxall, Rothery, Pickering, & Prince, 1990; Pardo et al., 2017). Bycatch is suspected to be a critical factor, confirmed by direct observations on vessels (Brothers, 1991; Croxall & Prince, 1990). The adoption of mitigation measures in demersal longline and trawl fisheries around SG has reduced seabird bycatch substantially over the last 20 years (Croxall, 2008); however, the continued population

declines implicate fisheries further afield (Poncet, Wolfaardt, Black, & Browning, 2017). The SG albatross populations are three of only nine, globally, considered of the highest priority for conservation by the Agreement on the Conservation of Albatrosses and Petrels (ACAP; www.acap.aq).

Here, we used extensive biologging datasets collected over three decades from all relevant life-history stages, to calculate population-level bycatch risk. Population distributions were overlapped with the best available spatial and temporal data on fishing effort, either from logbooks or reconstructed from landings, for pelagic and demersal longline (Tuck, Polacheck, & Bulman, 2003) and trawl fisheries in which the study species (except WA) have been bycaught. We aimed to provide a holistic, population-level assessment of fisheries overlap across a 20-year period (1990–2009) and, by inference, potential bycatch risk. More specifically, we quantified overlap by (a) region, (b) fishing fleet, and (c) temporally (by year and month), which should enable better targeting of bycatch mitigation measures and monitoring of compliance across fisheries, fleets and ocean basins.

2 | MATERIALS AND METHODS

2.1 | Long-term monitoring and tracking

Demographic and tracking data were obtained from long-term (spanning five and three decades respectively) individual-based monitoring studies at Bird Island, SG (54°00'S, 38°03'W). Colonies of BBA and GHA, and all WA on the island, are monitored intensively on a daily to weekly basis, providing survival, return and breeding probability and breeding success (for detailed field protocols, see Pardo et al., 2017). Demographic data were unavailable for WCP, which are burrow-nesting and hence less tractable for individual-based monitoring.

Tracking data were collected from 1990 to 2015 using a range of devices: platform terminal transmitters (PTTs), GPS loggers and geolocators. PTTs were deployed on breeding adults and juveniles, GPS loggers on breeding adults and geolocators on non-breeding adults, immatures and juveniles. Further details on device deployment and retrieval and processing of tracks are in Appendix S1. Data were split into unique combinations of species, age class and breeding stage and utilization distributions (UDs) generated for each combination. We conducted a gap analysis to determine whether sample sizes were sufficient to represent the population. For each data combination, we iteratively resampled the relationship between number of individuals tracked and size of the core (50%) UD, fitting nonlinear models to resampled outputs. We determined the minimum sample size required as the number of individuals at which the area occupied reached a threshold asymptote value (see Appendix S3). If our observed sample size was larger than the minimum predicted, it was deemed sufficient to adequately represent space use by that group.

2.2 | Population modelling

To calculate the proportion of the population represented by different life-history stages, annual estimates of survival, recruitment, return, breeding and success probabilities were obtained for juveniles, immatures and adults using a multi-event capture–mark–recapture model (Figure 1a) (Pardo et al., 2017). These were fed into an age- and stage-structured matrix population model using a prebreeding census (Caswell, 2001) based on a six-stage life cycle (assuming minimum age at recruitment of 6 years), including four adult stages (see Pardo et al., 2017). Models were fitted with the program E-SURGE 1.9.0 (Choquet, Rouan, & Pradel, 2008). The population age structure, which indicates the proportion of birds in each breeding stage or age class, was then calculated for each year. For parsimony, ages or stages with similar foraging distributions were pooled, resulting in six distinct life-history stages: juveniles in their first year at sea (post-fledging, J1), juveniles in their second or third year (J2 + J3), immatures (IMM), successful breeders (SB), failed breeders (FB) and adult non-breeders (NB) (Figure 1). WCP are not routinely monitored, and

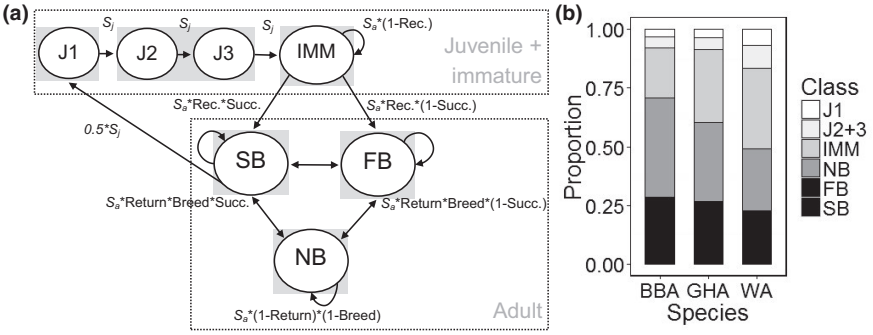

FIGURE 1 (a) Simplified life cycle diagram used to determine population structure based on an age- and stage-structured model (prebreeding census). The six life-history stages are shown by grey boxes: juveniles in their first (J1), second and third year at sea (J2 + 3), and from their fourth year up to recruitment (IMM; immatures), adult non-breeders (NB) and failed (FB) and successful breeders (SB). Rec. = recruitment, Succ. = breeding success, Return = return probability, Breed = breeding probability, S_a = adult survival, S_j = juvenile survival. Immature survival was the same as adult survival (Pardo et al., 2017). (b) Proportions of the study populations represented by each life-history stage, averaged over the study period (1990–2009)

so their population structure was based on values for BBA, given their broadly similar life histories.

2.3 | Weighting of distributions

Tracking data were assigned to each of the six life-history stages and monthly distribution grids generated, incorporating differences in breeding and migration schedules, that is, the grid was weighted by the number of days in that month represented by that stage (Figure S1 in Appendix S2). Distributions during incubation and brood were weighted by 0.5, as one pairmember remains at the breeding colony. For life-history stages for which tracking data were unavailable (e.g. immature BBA, GHA and WCP), we substituted data from the same species, but a different age class or breeding stage (Appendix S4). These substitutions were chosen a priori, based on studies of movements and distributions of different life-history stages in other seabirds (Phillips et al., 2017).

The study period was 1990–2009 (due to limitations in fishing effort data), which was sufficient to capture the precipitous declines of the three albatrosses (Pardo et al., 2017). Monthly distribution grids for each life-history stage were multiplied by the proportion of the population in each stage from the outputs of population models averaged over 5-year periods (1990–1994, 1995–1999, 2000–2004, 2005–2009) and the study duration (1990–2009), and summed to create monthly distribution grids for the whole population (Figures S1, S2–S5 in Appendix S5). Distribution grids were then resampled to a 5 × 5° resolution and overlaid on fishing effort. As we lacked sufficient tracking data for each life-history stage in multiple years, we assumed that bird distributions were consistent over the study duration.

2.4 | Fishing effort data

We collated fishing effort for pelagic and demersal longline and trawl fisheries in which at least one of the study species has been bycaught and with which they are known to interact (reviewed in Pardo et al., 2017). Effort data for pelagic longline fisheries targeting tuna and billfishes (Scombridae) were obtained from all tuna regional fisheries management organizations (RFMOs): Western and Central Pacific Fisheries Commission (WCPFC), International Commission for the Conservation of Atlantic Tunas (ICCAT), Indian Ocean Tuna Commission (IOTC) and Inter-American Tropical Tuna Commission (IATTC). For several RFMOs, effort data were provided as raised estimates (Appendix S6). Fleet-specific information was available for all RFMOs except WCPFC. Effort data for demersal longline fisheries were obtained from the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), the Falkland Islands Government and national agencies of Argentina, Australia, Chile, Namibia, New Zealand, South Africa and Uruguay. Effort data were averaged for each 5-year period and the study duration, by month and 5 × 5° cell. Effort is represented as number of hooks deployed and estimated fishing hours, for longline and trawl fisheries respectively.

2.5 | Overlap analyses

We calculated spatial overlap between birds and fisheries by multiplying the number of hooks/hours by predicted proportions of the population in each grid cell, by month (Cuthbert et al., 2005; Jiménez et al., 2016). For albatrosses, overlap was calculated for each 5-year period and over the study period, but only the study period for WCP (which lacked reliable demographic data). WA do not interact with trawl fisheries and so this overlap was not investigated. Unless otherwise specified, all analyses were conducted in R v. 3.3.1 (R Core Team, 2014).

3 | RESULTS

3.1 | Population-level distributions

Overall, 1,692 tracks were obtained from 788 individuals (Table 1). Juveniles of all species were tracked immediately post-fledging (n = 47), whereas data on immatures were available only for WA. Gap analyses revealed that sample sizes were adequate to represent home ranges for all adult species-stage combinations (Table 2; Appendix S3). Sample sizes for first-year juvenile and immature WA, but not juvenile BBA, GHA and WCP, were sufficient (Table 2). Population models revealed that only *c*. 25% of the total population constituted breeding adults and up to *c*. 50% were pre-recruits (juveniles and immatures) (Figure 1b).

Population-level distributions were mapped by month (Figures S2–S5) and year (Figure 2), revealing the importance of the south-west Atlantic Ocean for all species, especially during summer (October–May). During winter, BBA predominantly used the

TABLE 1 Sample sizes for tracking data by species, age class and breeding stage. Numbers of individuals are shown with numbers of tracks in parentheses

	Age class and breeding stage						
	Adults						
Species	Incubation	Brood	Post-brood	Non-breeding	Immatures	Juveniles	Total
BBA	61 (61)	78 (120)	20 (269)	25 (49)	–	7 (7)	178 (506)
GHA	25 (25)	63 (86)	20 (158)	55 (55)	–	5 (5)	156 (329)
WA	63 (67)	80 (95)	137 (227)	111 (151)	70 (239)	27 (27)	404 (794)
WCP	15 (15)	2 (2)	6 (19)	19 (19)	–	8 (8)	50 (63)

Abbreviations: BBA = black-browed albatross, GHA = grey-headed albatross, WA = wandering albatross, WCP = white-chinned petrel.

Benguela Upwelling (Figure 2; Figure S2; Phillips, Silk, Croxall, Afanasyev, & Bennett, 2005). GHA and WA also used the south-west Indian Ocean year-round, with seasonal use of the south-east Atlantic, Indian and Pacific Oceans, and for WA, the Chatham Rise east of New Zealand (Figure 2; Figures S3–S4; Clay et al., 2016; Clay, Pearmain, McGill, Manica, & Phillips, 2018). WCP were predominantly distributed around the Patagonian Shelf, Brazil-Falklands Confluence and Humboldt Upwelling off Chile (Figure 2; Figure S5; Phillips, Silk, Croxall, & Afanasyev, 2006).

TABLE 2 Gap analysis showing where there were sufficient (✓), insufficient (✗) and no data, for each species and life-history stage. Where there were no tracking data, appropriate data substitutions were used (Appendix S4). SB = successful breeders, FB = failed breeders, NB = adult non-breeders, JUV1 = juveniles in their first year at sea, juveniles in their second and third years at sea, IMM = immatures

Species	JUV1	JUV 2 + 3	IMM	NB	FB	SB
BBA	✗	No data	No data	✓	✓	✓
GHA	✗	No data	No data	✓	✓	✓
WA	✓	✗	✓	✓	✓	✓
WCP	✗	No data	No data	✓	✓	✓

3.2 | Spatial and temporal distribution of fishing effort

Pelagic longline effort within the distribution of the study species was highest around 30–40°S (Figure 3a), while demersal longline and trawl effort were concentrated within exclusive economic zones (EEZs) of Chile, Argentina, Namibia, South Africa, Australia and New Zealand (Figure 3a). Demersal longline effort was also high around sub-Antarctic islands within the CCAMLR region, whereas trawl effort was also concentrated around the Falklands and Uruguay. Monthly fishing effort maps are provided in Appendix S6. Effort for all fisheries within the distribution of the four species increased until the early 2000s and then decreased (Figure 3b). Pelagic longline effort peaked around 350 million hooks per year in the early 2000s, before declining to 1980s levels by 2009, and was dominated by the fleets of Taiwan and Japan (Figure 3b).

3.3 | Overlap with fisheries

3.3.1 | Temporal variation

The highest overlap for pelagic and demersal longline fisheries was with BBA followed by WCP, WA and GHA (Figure 4a). WCP overlapped most with trawl fisheries, followed by BBA and GHA. For all species, overlap with pelagic longline fisheries was greatest

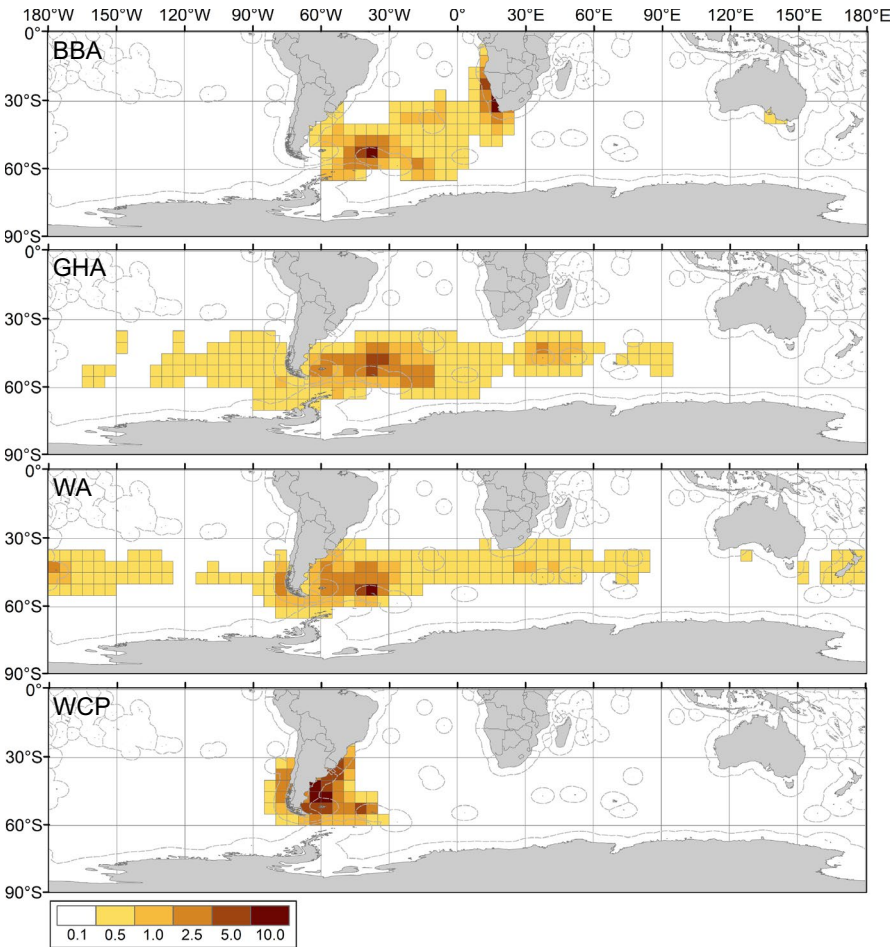

FIGURE 2 The annual population distribution of BBA, GHA, WA and WCP from South Georgia calculated from the average of monthly distributions. The colour gradient refers to the percentage of the population represented within each 5 × 5° square

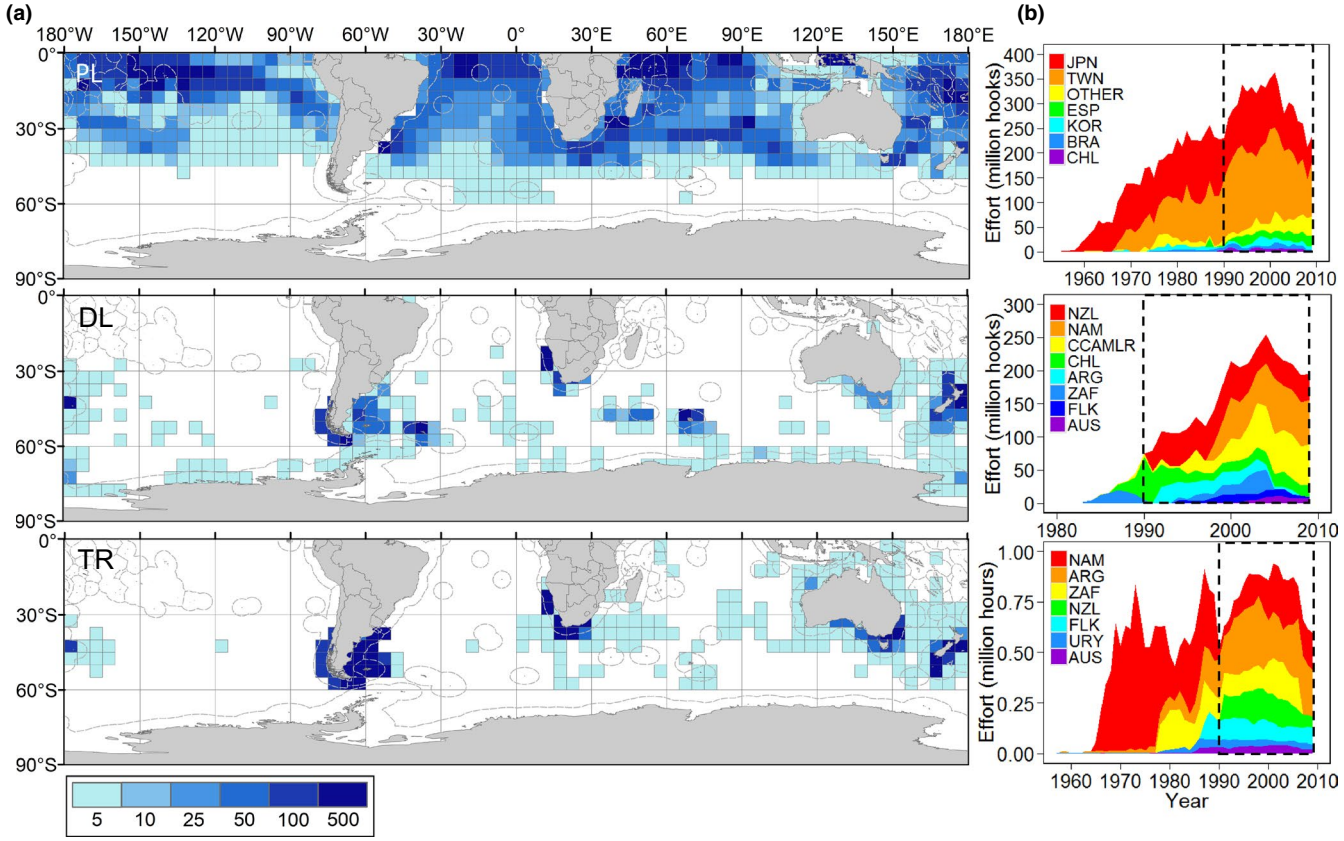

FIGURE 3 Spatial distribution and annual variation in pelagic (top row; PL) and demersal longline (middle row; DL) and trawl (bottom row; TR) fishing effort. (a) Cumulative fishing effort across the study period (1990–2009). Effort is shown per 10^6 hooks for longline and per 10^3 fishing hours for trawl fisheries. (b) Annual effort within the distribution of all four species (in 5 × 5° cells where at least one species present). Only the top six pelagic longline fleets are shown, and other fleets are pooled in the category OTHER. Colours in each plot do not always refer to the same fleet. ARG = Argentina, AUS = Australia, BRA = Brazil, CCAMLR = Convention for the Conservation of Antarctic Marine Living Resources, CHL = Chile, ESP = Spain, FKL = Falklands, KOR = South Korea, NAM = Namibia, NZL = New Zealand, TWN = Taiwan, URY = Uruguay, ZAF = South Africa. Dashed boxes indicate the duration of the study period

in May–August (representing 85%, 73%, 70% and 67% of the cumulative annual overlap of GHA, BBA, WA and WCP respectively), largely reflecting variation in fishing effort (Appendix S6). In contrast, the highest temporal overlap with demersal longline and trawl fisheries varied (Figure 4a); overlap with demersal longline and trawl effort was highest for BBA in April–July, and WCP in January–March, whereas overlap with demersal longline effort was high for WA in January–June and GHA in May–June.

Overlap with pelagic longline fisheries was highest during the 1990s and declined in the 2000s (Figure 4b; Figure S9 in Appendix S7). Although overlap with demersal longline and trawl effort declined slightly in the early 2000s, for BBA overlap in 2005–2009 remained higher than in the 1990s (Figure 4b; Figures S10 and S11 in Appendix S7).

3.3.2 | Overlap hotspots by RFMO and major fleets

The areas of greatest risk from pelagic longline fisheries for the albatrosses were in the south-east (BBA and GHA) and south-west (all species) Atlantic and south-west Indian Oceans (GHA and WA) (Figures 5 and 6; for monthly bycatch risk maps for each species and fishing gear, see Figures S13–S23 in Appendix S7). Considering the important fleets (those contributing to >10% of overlap), the overlap of albatrosses was greatest with the Japanese and Taiwanese (Figure 6, Table S3 in Appendix S7). Since the 1990s, overlap of BBA with the Japanese fleet has reduced, but has increased with the Spanish, Namibian and South African fleets (Figures S9 & S12 in Appendix S7). The albatrosses also overlapped to a lesser degree with the South Korean fleet (especially GHA in the late 1990s) (Table S3; Figure 6h,o; Figures S9e–l), and WA with the fleets of Brazil and Uruguay (the latter within the category 'OTHER') (Figure 6o), and with unspecified fleets in the south-west Pacific Ocean (WCPFC) (Figures 5, 6s, S12). There was high overlap of WCP with the fleets of Taiwan, Brazil and Uruguay (Figures 5, 6w) and within the IATTC region off Chile (OTHER) (Figures 5, 6v).

All species overlapped with demersal longline fisheries in the south-west Atlantic Ocean (Table S3; Figure 5). BBA overlapped most with demersal longline and trawl fleets off South Africa and Namibia (Figures 5, 6f,g; Figures S10 and S11 in Appendix S7). The other three species overlapped most with the demersal longline

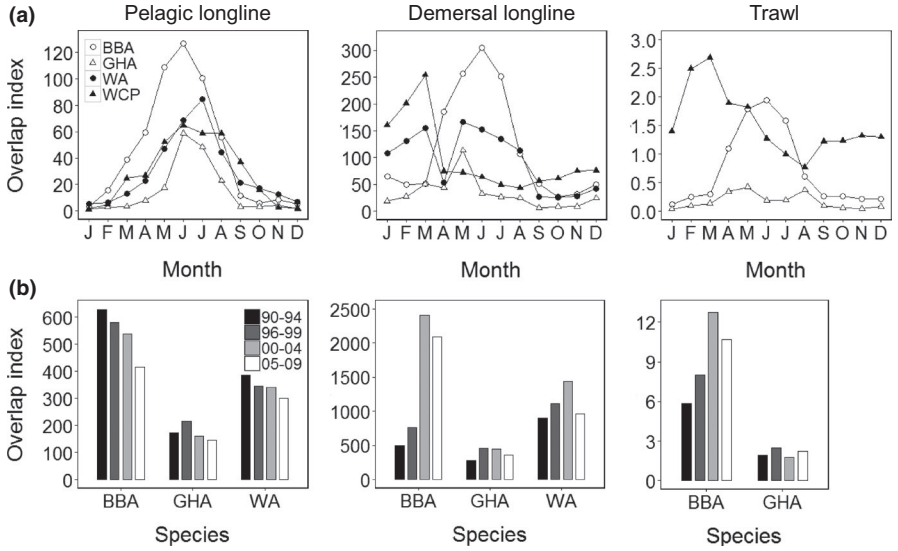

FIGURE 4 (a) Monthly and (b) yearly variation in population overlap for each species with pelagic (left column) and demersal (middle column) longline and trawl (right column) fisheries. Monthly calculations are based on the mean over the study period (1990–2009; $\times 10^3$), and yearly variation the annual sum averaged over 5-year periods

fleets of Chile (in January–March only), Argentina, Falklands and around the Prince Edward, Crozet and Kerguelen archipelagos (CCAMLR) (mainly in May–August; Figures 5 and 6m,t,z), whereas WA, and to a lesser extent GHA, overlapped with the New Zealand fleet in June–September (Figures 5 and 6t). WCP overlapped most with the trawl fleets of Argentina, Falklands and Uruguay (Figures 5 and 6aa), while for GHA, there was negligible overlap with the Argentinian and Falklands fleets (Figures 5 and 6n).

4 | DISCUSSION

Here we provide among the most comprehensive large-scale assessments of potential bycatch risk for any large marine vertebrate. We detected spatial overlap with fisheries in all major southern hemisphere ocean basins; particular hotspots were in the south-west and south-east Atlantic Ocean (all fisheries) and in the south-west Indian Ocean (pelagic longline). Overlap with pelagic longline fleets was highest in May–September and dominated by vessels from Japan and Taiwan. In contrast, overlap with trawl and demersal longline fleets was highest off South America, southern Africa and within the CCAMLR area.

This study benefited both from an extensive dataset on seabird distributions, including life-history stages that are generally under-researched, and long-term demographic studies (Croxall et al., 1990; Pardo et al., 2017). Much less is usually known about year-round distributions of juveniles and immatures, largely due to the challenges of tracking representative samples during multi-year phases of dispersal (Hazen et al., 2012). In long-lived species, non-breeders can represent a major component of the population (Saether & Bakke, 2000). With appropriate weighting for the many adult non-breeders, juveniles and immatures (based on demographic models), our population-level distributions were less centred around SG than might be expected, emphasizing the importance of these life-history stages to risk assessments. Indeed, we recommend concerted efforts that fill these data gaps for bycaught species. Although representative tracking data were available for all adult stages, for BBA, GHA and WCP, we had insufficient data for juveniles, and none for immatures, and therefore substituted data from non-breeding adults during the winter and year-round (to include prospective visits to the colony during the summer) respectively. However, our estimates of potential risk are likely to be conservative as these stages generally have a more northerly distribution and disperse more widely than adults, and may therefore encounter a greater range of fisheries (particularly pelagic longline; Thiers et al., 2014, Phillips et al., 2017).

4.1 | Overlap with pelagic longline fisheries

Pelagic longline fishing effort for high-value species such as southern bluefin *Thunnus maccoyii* and albacore tuna *T. alalunga* is concentrated below 30°S, predominantly by the fleets of Japan and Taiwan, and greatest during the austral winter (April–September, representing 80% of annual effort; Tuck et al., 2003), which was reflected in our overlap scores. Indeed, the areas of high overlap generally accord with the regions of documented bycatch of all four species, particularly in the south-west and south-east Atlantic and south-west Indian Oceans. We found particularly high overlap of WA and WCP with fishing effort in the Brazil-Falklands confluence (Jiménez et al., 2016). High bycatch rates of several species (including BBA, WA and WCP, but not GHA) were documented in the 2000s by observers on board Uruguayan (Jiménez et al., 2010) and Brazilian vessels (Bugoni et al., 2008), and on Japanese vessels under license in Uruguayan waters (Jiménez, Phillips, Brazeiro, Defeo, & Domingo, 2014). We note, however, that there has been no commercial longline effort within the Uruguayan Exclusive Economic Zone (EEZ) in recent years (since 2014; S. Jiménez, pers. commun.). High overlap was also documented with the Taiwanese fleet, for which bycatch has been reported (Yeh, Huang, Dietrich,

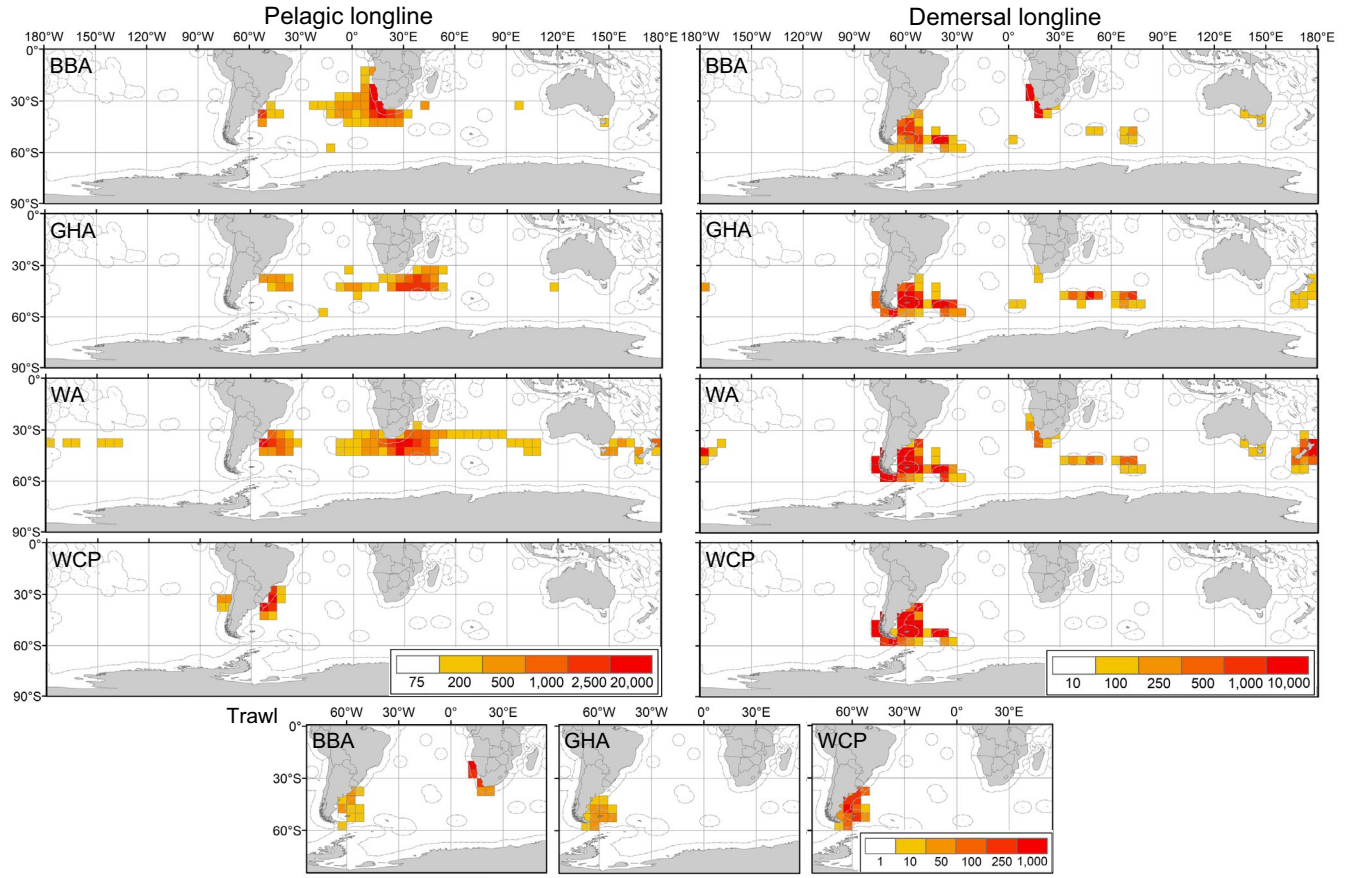

FIGURE 5 Annual overlap with pelagic and demersal longline and trawl fisheries averaged across months and years (1990–2009; $\times 10^3$) for each species

Melvin, & Katzner, 2012). However, the rates were surprisingly low compared with other flag states using similar gear (Jiménez et al., 2014; Tuck et al., 2003), suggesting under-reporting or a bias associated with the very small percentage (*c.* 1%) of Taiwanese fishing effort observed (Phillips, 2013).

In the south-east Atlantic and south-west Indian Ocean, the high overlap indices match documented bycatch by Japanese and Taiwanese fleets (Inoue, Yokawa, Minami, & Ochi, 2012a, 2012b; Yeh et al., 2012). Although fishing effort and overlap have decreased over past decades (Tuck et al., 2003; this study), surprisingly, a dramatic increase in the bycatch rate of GHA was recently reported by Japanese vessels in the south-east Atlantic south of 40°S (>350 birds caught in 2010–2015; Inoue, Yokawa, Minami, & Ochi, 2012b, Katsumata, Yokawa, & Oshima, 2017). The reasons are unclear, but may reflect previous under-reporting of bycatch or species misidentification, or a recent change in practice; regardless this is cause for serious concern. Further north, we documented high overlap between BBA and longline effort off South Africa and Namibia. Bycatch rates of many seabirds, including BBA, were formerly very high in the South African tuna longline fishery; however, these have been reduced, particularly in the foreign charter fleet (Petersen, Honig, Ryan, & Underhill, 2009). Finally, WA overlapped with pelagic longline fleets in the Tasman Sea and around the Chatham Rise, where bycatch of this species is reported by the fleets of Japan and Taiwan (Huang, 2015; Inoue, Yokawa, Minami, & Ochi, 2012a).

4.2 | Overlap with demersal longline and trawl fisheries

Overlap with demersal longline and trawl fisheries, which generally operate over continental shelf or shelf-break habitats, was highest for BBA and WCP, and with the fleets of Argentina, Falklands, Namibia and South Africa. These fleets were responsible for large mortality rates of seabirds in the 2000s (up to 10,000 in some years; e.g. Paterson et al., 2017; Sullivan et al., 2006). However, the introduction of regulations has led to substantial improvements; for example, in the South African trawl fishery, 100% observer coverage and widespread adoption of mitigation have reduced mortality of seabirds by up to 95% (Maree, Wanless, Fairweather, Sullivan, & Yates, 2014), and the closure in summer of the longline fishery for Patagonian toothfish *Dissostichus eleginoides* around SG, together with night setting, heavier line-weighting and bird-scaring lines, has reduced bycatch dramatically (Croxall, 2008). This underlines that high overlap indicates *potential* bycatch risk only; bycatch can be minimized with careful management.

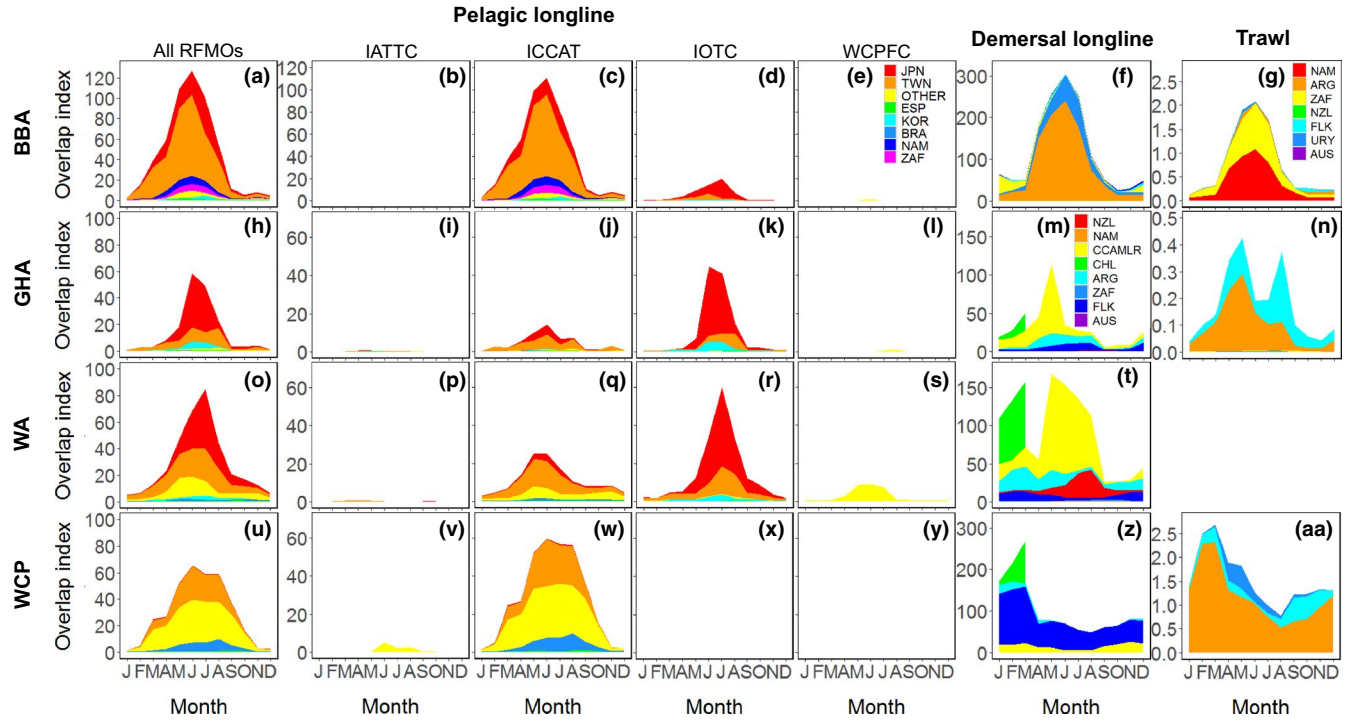

FIGURE 6 Monthly population overlap for each species, fishing gear and major fleet. Pelagic longline overlap is shown for each all regional fisheries management organization (RFMO) together and separately. Overlap values ($\times 10^3$) are averaged over the study period (1990–2009): for BBA (first row), GHA (second row), WA (third row) and WCP (fourth row). Only fleets with the eight highest overlap scores across all species are shown, and the other fleets (including all those from the WCPFC) are pooled in the category OTHER. WA are not recorded as bycatch in trawl fisheries and so overlap is not shown. Note that the colours and y-axes differ for each gear type, and gear type and species respectively.

4.3 | Bycatch risk and seabird population declines

Unsustainable levels of bycatch are implicated in declines of many pelagic seabirds (Phillips et al., 2016; Tuck et al., 2011). A recent archipelago census at SG revealed declines comparable to or greater than those in the well-studied colonies on Bird Island (Poncet et al., 2017). Both natal and breeding-site philopatry are very high in albatrosses, and declines are unlikely to be explained by the negligible proportion of birds which may emigrate to other island groups (Tickell, 2000). Demographic analyses suggest that over the past two decades, fisheries have negatively influenced vital rates of both BBA and WA (Pardo et al., 2017), which is supported by our overlap analyses. However, we found that GHA consistently had the lowest overlap scores, and hence, our results do not explain their precipitous decline (5% per annum) at SG since 2004 (Poncet et al., 2017). Their inability to buffer the effects of climate change, or predation at colonies, may also be contributing factors (Pardo et al., 2017). Nevertheless, the apparent increase in bycatch rates in the southeast Atlantic by the Japanese fleet (Katsumata et al., 2017) is a major cause for concern.

4.4 | Implications for management

Like many ecological risk assessments in fisheries, we make the assumption that the large-scale quantification of spatial overlap (i.e. encounterability; Hobday et al., 2011) provides a proxy of potential bycatch risk in the absence of effective mitigation on-board vessels (Roe et al., 2014; Tuck et al., 2011). However, overlap is scale dependent, and likely lower at finer spatial and temporal scales (Amoroso, Parma, Pitcher, McConnaughey, & Jennings, 2018; Torres et al., 2013). As our aim was to investigate overlap across all fleets for which birds interact, we were limited by the availability of effort data for most fleets at 5 x 5° and monthly resolution, which precluded fine-scale analyses. Also, we could only access data legally reported to the major RFMOs or fisheries agencies, which for some fleets are known to be incomplete or unreliable (Tuck et al., 2003). Estimates of illegal, unreported and unregulated (IUU) fishing activities (Agnew et al., 2009) were unavailable; these could represent a major problem as IUU vessels likely operate in similar areas to legal fleets (i.e. where fishing is most lucrative), and are very unlikely to use bycatch mitigation.

While we present a comprehensive assessment of spatial overlap, we acknowledge that the relationship between overlap and bycatch is complex, and capture rates can vary substantially according to operational, meteorological or behavioural factors (Brothers, 1991, Jiménez, Domingo, Abreu, & Brazeiro, 2012; Jiménez et al., 2014, Torres et al., 2013). As such, our metrics provide an estimate of potential, and not real, risk. For example, birds may differ in their attraction to or attendance at vessels (Collet, Patrick, & Weimerskirch, 2017), and catchability may vary substantially between different

vessels or fleets (Jiménez et al., 2014). Nonetheless, at broad scales, regions of high overlap (i.e. more birds or fishing activity) correspond fairly well with regions of documented bycatch. This is also supported by ring recoveries of birds killed on pelagic longlines (Jiménez et al., 2016, BAS unpubl. data). Despite these limitations, as management measures require standardization across all vessels and at-risk species, large-scale risk analyses remain a crucial tool for conservation.

Over the past two decades, reductions in fishing effort and implementation of effective mitigation with close monitoring of compliance (Anderson et al., 2011; Croxall, 2008; Phillips et al., 2016) have led to substantial reductions in seabird bycatch. However, continued population declines suggest that in many fisheries, in particular pelagic longline, the mitigation measures required by the RFMOs or national fisheries bodies are inadequate or not fully implemented. There is therefore scope to impose more stringent regulations on fleets that have not adopted best practice standards (Phillips et al., 2016). In addition, because effective implementation is dependent on close monitoring and penalties for non-compliance, fully independent observers or tamper-proof electronic monitoring systems are required on a far higher proportion of vessels in most fleets (Phillips, 2013). In the short-term, attention should be focused on addressing bycatch in regions of high overlap identified here, targeted in particular at the fleets of Taiwan and Japan; these account for a significant proportion of overlap and, like other fleets in the High Seas, are not currently required by regulatory bodies to use the bycatch mitigation measures considered to be the best practice by ACAP. We recommend that where sufficient tracking data exist, our framework be applied to other species to gain a more complete understanding of multispecies bycatch risk zones and to better identify the RFMOs and fleets involved.

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AUTHORS' CONTRIBUTIONS

R.A.P., C.S., T.A.C. and A.P.B.C. conceived the ideas and designed the methodology. R.A.P., J.P.C. and A.G.W. oversaw data collection. G.N.T., R.A.P., A.G.W., T.A.C. and G.T.C. collated or processed data; D.P. and T.A.C. analysed the data. T.A.C. led the writing of the manuscript. All authors provided intellectual input and gave the final approval for publication.

DATA AVAILABILITY STATEMENT

Seabird tracking data can be downloaded from the BirdLife International Seabird Tracking Database (http://seabirdtracking.org/mapper/contributor.php?contributor_xml:id=361; dataset ids: 438, 439, 457, 459, 460, 461, 462, 463, 473, 492, 493, 494, 495, and 1,405). See Section 22 and Appendix S1 for details on how datasets were combined. Publicly available fishing effort data were downloaded directly from IATTC (https://www.iattc.org/PublicDomainData/IATTC-Catch-by-species1.htm), ICCAT (https://www.iccat.int/en/t2ce.asp) and WCPFC (https://www.wcpfc.int/folder/public-domain-data), or are provided in Tuck et al. Dryad Digital Repository: https://doi.org/10.5061/dryad.7f63m (Tuck et al., 2015, 2015b). Trawl data for Uruguay and Namibia are available via the Dryad Digital Repository. https://doi.org/10.5061/dryad.k540b54 (Clay et al., 2019). Data from several fisheries agencies are commercially sensitive and have not been archived, but can be requested through the agency data managers: New Zealand (www.mpi.govt.nz/); Australia (www.afma.gov.au/); CCAMLR (www.ccamlr.org/), Falkland Islands (www.fis.com/falklandfish), South Africa (https://www.environment.gov.za).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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