



Research



Cite this article: Warwick-Evans V, Pearmain E, Phillips RA. 2026 Year-round spatial segregation and fisheries overlap of white-chinned petrels from multiple populations at South Georgia. *R. Soc. Open Sci.* **13**: 260099.

<https://doi.org/10.1098/rsos.260099>

Received: 9 February 2026

Accepted: 21 July 2026

Subject Category:

Ecology, Conservation and Global Change Biology

Subject Areas:

ecology

Keywords:

by-catch, population trends, sea-birds, spatial segregation, conservation, fisheries

Author for correspondence:

Victoria Warwick-Evans

e-mail: vicrwi@bas.ac.uk

Supplementary material is available online at
<https://doi.org/10.6084/m9.figshare.c.8641570>.

Year-round spatial segregation and fisheries overlap of white-chinned petrels from multiple populations at South Georgia

Victoria Warwick-Evans¹, Elizabeth Pearmain^{1,2} and Richard A. Phillips¹

¹Ecosystems, British Antarctic Survey, Cambridge, UK

²Department of Zoology, University of Cambridge, Downing Street, Cambridge, UK

VW, 0000-0002-0583-5504; RAP, 0000-0002-0208-1444

By-catch in fisheries is the leading cause of population decline in pelagic sea-birds. The white-chinned petrel (*Procellaria aequinoctialis*) is the most by-caught sea-bird species in the Southern Ocean, and many populations are in decline. To better understand by-catch risk, we tracked white-chinned petrels from three sites across South Georgia throughout the annual cycle. There was no spatial segregation among colonies in at-sea distributions of failed or non-breeding birds, but birds tracked during chick-rearing from the easternmost site (Cooper Island) and the centre (King Edward Point), travelled both east and west of South Georgia, whereas those tracked from the west (Bird Island) only travelled west. Consequently, white-chinned petrels from Cooper Island overlapped less with fisheries than those from the other sites. Habitat models suggest that white-chinned petrels from all sites foraged in areas with similar environmental characteristics and that suitable conditions were present both east and west of South Georgia. Thus, broad-scale areas of high by-catch risk could be identified from predicted distributions, but overlap at finer scales could be distinguished more clearly from tracking data. Although the driver of spatial segregation in foraging areas was unclear, it affects by-catch risk and has implications for conservation and management.

1. Introduction

Globally, 57% of sea-bird species are in decline and 43% are listed as globally threatened [1]. Incidental mortality (by-catch) in fisheries is the leading cause of population declines in pelagic sea-birds [1,2], and is dependent on both the spatio-temporal overlap of sea-birds with fishing fleets and the behaviour of individuals around

vessels [3–5]. Sea-bird–fishery overlap frequently occurs in productive waters with predictable prey availability, targeted by both sea-birds and fisheries [6]. Within these productive foraging areas, many species are attracted to fishing vessels by baited hooks, discards or offal, leading to mortality if birds collide with trawl warps or monitoring cables become entangled in lines or caught on hooks [3,7–9].

By-catch in fisheries can be reduced greatly by the implementation of various cost-effective mitigation measures [10,11]. The Agreement for the Conservation of Albatrosses and Petrels (ACAP) advises that the best practice is to use three mitigation measures in combination to reduce by-catch of albatrosses and petrels in long line fisheries, and to use discard management, streamer lines and prohibition of net monitoring cables to reduce by-catch in trawl fisheries [12–14]. However, many fisheries fail to implement the best practice, and most regional fisheries management organizations (RFMOs) which manage fisheries in the high seas mandate only two mitigation measures. Furthermore, many RFMOs require <5% observer coverage, resulting in under-reporting of by-catch and reducing the capacity to check or enforce compliance [15–17]. By-catch rates vary greatly by flag state or fishery as a result of different mitigation or operational measures (e.g. time of setting, line-weighting regime), and observer coverage is often low [17,18]. Standard mitigation practices include setting lines at night when visual foragers are less active, weighting hooks so they sink faster and reduce the time they are available to diving sea-birds and using streamer lines behind vessels to deter sea-birds. However, for nocturnal foragers (e.g. white-chinned petrels) night-setting may increase by-catch risk, and consequently other mitigation measures are essential.

At high latitudes in the Southern Ocean, long line and trawl fisheries are managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR), with further protection around South Georgia imposed by the Government of South Georgia and the South Sandwich Islands, which includes strict regulations and enforcement, including 100% observer coverage [19]. Consequently, sea-bird by-catch in this region is extremely low [19,20]. However, many pelagic sea-birds breeding on sub-antarctic islands frequently visit continental shelf waters or the subtropical high seas where mitigation measures are not the best practice, compliance is often poor and observer coverage is low [8,18,21,22].

The white-chinned petrel (*Procellaria aequinoctialis*), which breeds on subantarctic islands, is the most by-caught species in the Southern Ocean and is classified as vulnerable on the IUCN Red List [21,23]. White-chinned petrels are burrow-nesting, and although reliable estimates of population size and trends are challenging to acquire, there is evidence for a sustained long-term decline at Bird Island, South Georgia [24,25]. This is of major concern as >50% of the global population breeds at South Georgia [25]; however, whether the trend on Bird Island is representative of other sites in the archipelago is unknown. White-chinned petrels have huge foraging ranges in neritic and pelagic waters, and target many prey types including euphausiids, fish and squid, supplemented by bait and discards from fishing vessels [26–29]. Unlike albatrosses, white-chinned petrels show high nocturnal activity, foraging in both darkness and daylight [30,31]. It is unknown to what extent nocturnal foraging is associated with fishing vessels; it may also be an adaptation to exploit prey undergoing vertical migration [16,30–32]. Regardless, it increases the duration of interactions with long line vessels, some of which are required to set at night to reduce by-catch of albatrosses [16]. Furthermore, white-chinned petrels are able to dive deeper than albatrosses and other petrels in mixed foraging aggregations, making them particularly susceptible to by-catch on long lines as they dive down to retrieve baited hooks [30,33].

Previous tracking studies indicate that white-chinned petrels breeding at Bird Island, South Georgia overlapped with fisheries on the Patagonian Shelf throughout the annual cycle, although to a lesser extent during the chick-rearing period when foraging trips tended to be closer to their breeding sites [23,30,34]. However, the distribution and resulting overlap of white-chinned petrels breeding elsewhere on South Georgia with fisheries is unknown. It is often assumed that populations of pelagic sea-birds breeding in relative proximity compared with the scale of their at-sea ranges will forage in similar areas and consequently encounter comparable threats at sea. However, this assumption is often unverified, and there is uncertainty in extrapolating at-sea distribution and hence by-catch risk from one colony to another. Indeed, spatial segregation between neighbouring colonies of wandering albatrosses *Diomedea exulans* at South Georgia affects relative overlap with fisheries during the breeding and non-breeding seasons [22,35]. Consequently, estimates of by-catch risk for colonies where at-sea distributions are inferred may be biased, with important consequences for conservation and management [22]. This could be driven by spatial segregation between colonies, potentially as a result of density-dependent competition, habitat or prey specialization, information sharing and cultural evolution or foraging site fidelity [22,36–39].

Table 1. Summary statistics (mean $\pm$ s.d.) of foraging trips of white-chinned petrels tracked from Bird Island, Cooper Island and KEP, South Georgia, during different life-history stages. No values are provided for most metrics for failed birds as not under a central-place breeding constraint.

life-history stage	colony	year	number of birds	number of trips	foraging range (km)	total distance travelled (km)	trip duration (days)	distance travelled per day (km)
incubation	Bird Island	2023	12	15	1821 $\pm$ 574	7623 $\pm$ 2669	14.4 $\pm$ 4.2	557 $\pm$ 163
	Bird Island	2022	15	17	1698 $\pm$ 427	6320 $\pm$ 1678	10.5 $\pm$ 3.2	623 $\pm$ 121
	Cooper Island	2022	4	4	1756 $\pm$ 402	7002 $\pm$ 1268	10.75 $\pm$ 2.2	657 $\pm$ 68
	KEP	2023	11	12	1929 $\pm$ 409	7872 $\pm$ 2264	15.5 $\pm$ 6.8	554 $\pm$ 149
chick-rearing	Bird Island	2023	9	53	922 $\pm$ 758	3600 $\pm$ 3173	9.2 $\pm$ 6.7	515 $\pm$ 308
	Bird Island	2022	23	116	928 $\pm$ 746	3113 $\pm$ 2842	5.0 $\pm$ 5.0	642 $\pm$ 224
	Cooper Island	2022	5	32	863 $\pm$ 662	3437 $\pm$ 3263	8.3 $\pm$ 5.0	479 $\pm$ 295
	KEP	2023	8	56	776 $\pm$ 647	2796 $\pm$ 2568	6.9 $\pm$ 5.7	536 $\pm$ 272
failed	Bird Island	2023	3	3	NA	NA	NA	345 $\pm$ 86
	Bird Island	2022	8	9	NA	NA	NA	292 $\pm$ 59
	Cooper Island	2022	4	4	NA	NA	NA	514 $\pm$ 21
	KEP	2023	10	10	NA	NA	NA	395 $\pm$ 174

The aims of this study were to track white-chinned petrels from three breeding sites located across South Georgia to determine whether relative fisheries overlap, and hence by-catch risk from particular vessel types and flag states was driven by spatial segregation in their at-sea distributions. We also tested if differences in habitat preferences or activity budgets might drive any observed spatial segregation, and discussed the results in the context of conservation and management, particularly to allow advocacy and resources to be focused on what are likely to be the most problematic fleets.

2. Methods

2.1. Study sites and fieldwork

Within the Atlantic Ocean, white-chinned petrels only breed in two island groups in the southwest, and the population at South Georgia is far larger than at the Falkland Islands (approx. 800 000 versus approx. 200 breeding pairs [40]). White-chinned petrels are widespread across South Georgia, and densities are generally higher on the offshore islands than the mainland [25]. In this study, we tracked birds from the largest of the most eastern and western populations (Cooper Island, 54°48' S, 35°47' W and Bird Island, 54°00' S, 38°03' W), and from a small but growing population on the mainland (King Edward Point (KEP), Thatcher Peninsula, 54°17' S, 36°29' W, [figure 1](#)) from December 2021 to April 2022 or from December 2022 to October 2023 ([table 1](#)).

Study groups are referred to by site and year during the chick-rearing period (e.g. birds tracked from Bird Island in December 2021 are referred to as Bird Island 2022). Breeding adults were extracted from

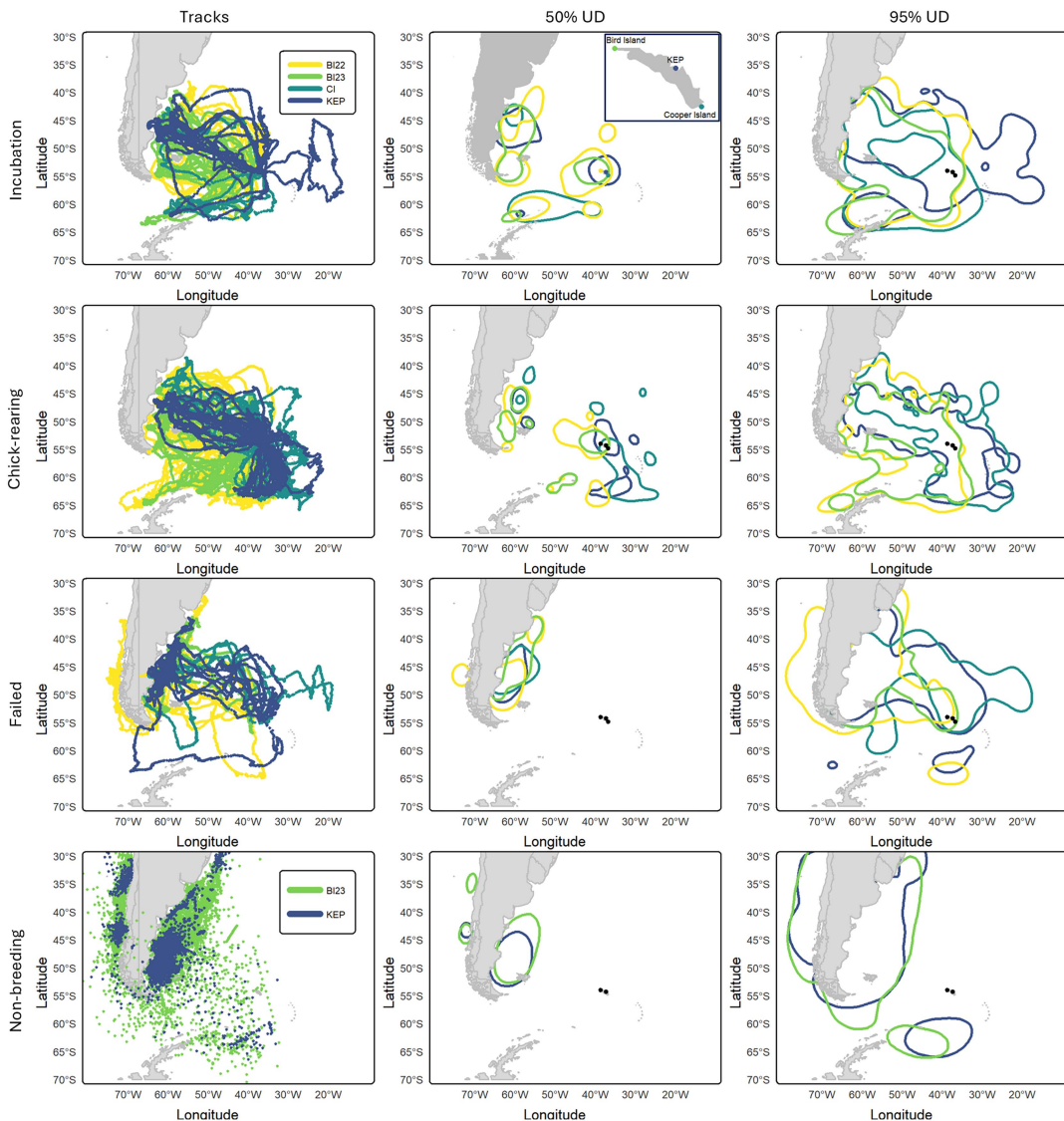


Figure 1. Tracks and UD of white-chinned petrels tracked from Bird Island (BI), Cooper Island (CI) and King Edward Point (KEP) at South Georgia in 2022 and 2023. Core foraging areas (50% UD) and home-range areas (95% UD) are shown for each population.

burrows in the mid-incubation period, and a remote-download Global Positioning System (GPS) logger or platform terminal transmitter (PTT) was taped to the mantle feathers with Tesa[®] tape, and a geolocator-immersion logger attached by a cable-tie to a plastic ring deployed on the leg. PTTs (Telonics TAV-2630, 35 g) were deployed at Cooper Island and KEP, and both PTTs and GPS (Pathtrack, <25 g) were deployed at Bird Island. GPS loggers were set to record a fix every 5 minutes, and PTTs were set to transmit every 60 seconds. The geolocator-immersion loggers (global location sensors or GLS loggers; Migrate Technology Intigeo C330) were set to mode 9: sampling of light every minute, and the maximum recorded after 5 minutes; temperature every 8 hours after continuous immersion for 20 minutes; immersion every 3 seconds, and every change of state recorded that lasted ≥ 6 seconds.

In order to track for as long as possible during breeding, and given the challenges of recapturing birds in chick-rearing, no attempt was made to retrieve PTTs and GPS loggers. As such, locations were obtained until the batteries depleted or the device was lost from the feathers. Geolocators deployed at Bird Island in 2022 and 2023, and King Edward Point in 2023, were recovered in subsequent years. As only one geolocator was recovered at Cooper Island, comparisons of movements during the non-breeding season were restricted to the GLS data from Bird Island and King Edward Point collected in 2023. All birds were of unknown sex.

2.2. Data processing

All data processing and analyses were undertaken using R 4.3.2 [41]. Raw location data were filtered to remove unrealistic fixes requiring travel speeds of $>80 \text{ km h}^{-1}$ [30,39]. The R package *crawl* was used to estimate location error from the PTT data, and to predict the most likely track using correlated random walks [42]. GPS data were subsampled to regular hourly intervals to broadly match the interval between PTT locations. The R package *track2KBA* [43] was used to split the data into individual trips, and to calculate trip summary statistics. Life-history stage was inferred from locations, trip duration and colony attendance, as birds alternate trips of >7 days at sea with long stints in the burrow during incubation, whereas—following the brood-guard period of a few days—they arrive and depart on the same night when delivering meals during chick-rearing. Birds which last returned to the colony in January–March were classed as failed breeders, whereas those that left in April were assumed to have fledged a chick, and were classed as non-breeders thereafter. We assessed effects of breeding site or year on the characteristics of the single trip per bird recorded in incubation using linear models, and of the multiple trips per bird recorded during chick-rearing using linear mixed-effects models to account for repeated measures. A bootstrapping approach to assess the representativeness of the samples from each population was undertaken using *track2KBA*.

Geolocator data were processed using *probGLS* [44]. This uses light data to estimate latitude and longitude according to day length and twilight times. A cloud of points generated for each time stamp is then refined using sea surface temperature (SST) and travel speed to weight each point and identify the most likely track. Locations without an associated SST or if the SST differed by $>3^{\circ}\text{C}$ from contemporaneous remotely sensed SST data, or where speeds were unrealistic (70 m s^{-1} or 5 m s^{-1} for periods in flight or on the water, respectively) were weighted as zero. Non-zero weighted data were linearly interpolated to provide two positions per day for each individual.

2.3. At-sea activity patterns

Immersion data were used to provide the timing and duration of flights and landings. Events were assigned to daylight or darkness according to twilight times based on the light data. The following mean activity metrics were calculated separately for the daylight and darkness periods of each foraging trip: (i) landing rate (landings per hour), (ii) proportion of time spent wet, (iii) wet bout length (minutes), and (iv) flight time (dry bout length, minutes). Separate linear models were used to assess whether activity patterns varied by breeding site or year for each life-history stage to account for repeated measures during chick-rearing, but not during the other life-history stages. During incubation, failed and non-breeding stages, linear models with activity metric as the response and colony as the predictor variable were used. During chick-rearing, linear mixed models with individual ID as random effects were used. Linear mixed models were used to test for differences in activity metrics between different life-history stages (with all breeding sites considered together). The *emmeans* package [45] was used to identify between-group differences using Tukey's *post hoc* tests.

2.4. Spatial segregation

Usage distributions (UDs) of the core foraging area (50%) were estimated for each population using *track2KBA*. We also attempted to estimate the home range area (95%); however, this did not converge for some breeding site/life-history stage combinations, likely because of small sample size or very divergent foraging routes. Consequently, groups where we were unable to calculate the 95% UD were considered unrepresentative of the population and excluded from further analyses. Population-level overlaps in UD were calculated using Bhattacharyya's Affinity (BA), and a randomization procedure was used to test for significant differences in UD following [46]. The overlap among populations was calculated with BA; each trip was then randomly assigned to a breeding site and new population-level UD and BA were calculated. This was repeated 1000 times, and the proportion of occurrences where the randomly assigned overlap was smaller than the overlap from the tracked sample provided the *p*-value. This procedure was used to test for spatial segregation between years (2022 and 2023) for birds tracked from Bird Island; as this was not significant, both years were combined in the comparisons among breeding sites.

2.5. Habitat models

To identify whether spatial segregation may be driven by variation among breeding sites in preferred foraging habitats, habitat models were developed for each life-history stage and site. Three pseudo-absences for each presence point were generated randomly within the maximum distance travelled from each colony. Environmental covariates used previously in habitat models for white-chinned petrels and considered to be proxies for prey availability [47] were extracted from the Copernicus Marine Service (table A1). Eddy kinetic energy and chlorophyll-a were $\log_{10}$ -transformed, and the standard deviation of SST was square-root-transformed to improve the spread of the data. General additive mixed models (GAMMs) with a binomial error structure and cubic spline smoothing were used to model presence-absence as a function of environmental covariates, with bird identity included as a random effect. The number of knots was limited to a maximum of six to avoid over-fitting to the data. Where collinearity between covariates was >0.6 , the covariate with the highest predictive power was included in model selection. Final models were checked for concurvity, which always remained <0.3 . Forward model selection and cross-validation among individuals were used to develop final models using area under the curve (AUC) to evaluate predictive power. AUC values of 0.5–0.7, 0.7–0.9 and >0.9 were considered to represent poor, reasonable and very good model performance, respectively [46]. Final models were used to predict the distribution of each population across the study area, using average environmental conditions for each life-history stage.

2.6. Overlap with fisheries

Fishing activity (hours fished) across the study area, based on the vessel automatic identification system (AIS) was downloaded from Global Fishing Watch for each life-history stage (incubation: 24 December–4 February, chick-rearing: 15 January–28 March, failed: 12 January–28 February and non-breeding: 1 February–30 October). Data were downloaded at a scale of 0.1° during the breeding season and 1° during the non-breeding season to account for the differing error in positions between PTT and GPS versus geolocator data. The proportion of time that all birds from each breeding site spent in each grid cell was multiplied by the number of hours fished in that cell to provide an overlap index for each life-history stage [18]. These indices were calculated for each flag state and vessel type, including drifting (pelagic) long liners, set (demersal) long liners and trawlers. Apparent fishing effort (the sum of hours fished) was also calculated for each life-history stage and year.

We also assessed the overlap of distributions predicted from habitat models with fishing activity to evaluate whether the former was an adequate substitute if the sample of tracked individuals was too small to be representative. This followed a similar approach to that used for tracking data. The predicted probability of occurrence in each cell was divided by the total value of all cells to ascertain relative importance, and this was multiplied by the number of hours fished in that cell to provide an overlap index for each life-history stage. Fishing data for this analysis were downloaded at a scale of 1° to account for error in predicted distributions. As such, relative overlap—but not absolute values—can be compared between the two approaches.

3. Results

3.1. Tracking data

Overall, 142 trips, 71 trips, 78 trips and 40 trips were obtained from 23, 12, 13 and 9 white-chinned petrels during the breeding season at Bird Island in 2022 and 2023, King Edward Point in 2023 and Cooper Island in 2022, respectively (figure 1, table 1). In addition, seven birds from King Edward Point and 27 birds from Bird Island were tracked during the non-breeding season in 2023. The mean and frequency distributions of trip duration, total travel distance and maximum range did not differ significantly between breeding sites during either incubation or chick rearing (table A2).

Based on the bootstrapping analyses, the sampled tracks from the chick-rearing period were representative of the foraging locations of the entire population (87–98% for both the 50% UD and 95% UD, table A3). However, for some of the breeding site and stage combinations, representativeness at the 95% UD could not be calculated or was very low, probably because the sample size was insufficient, particularly when birds travelled to very different locations. As such, only tracks where the representativeness

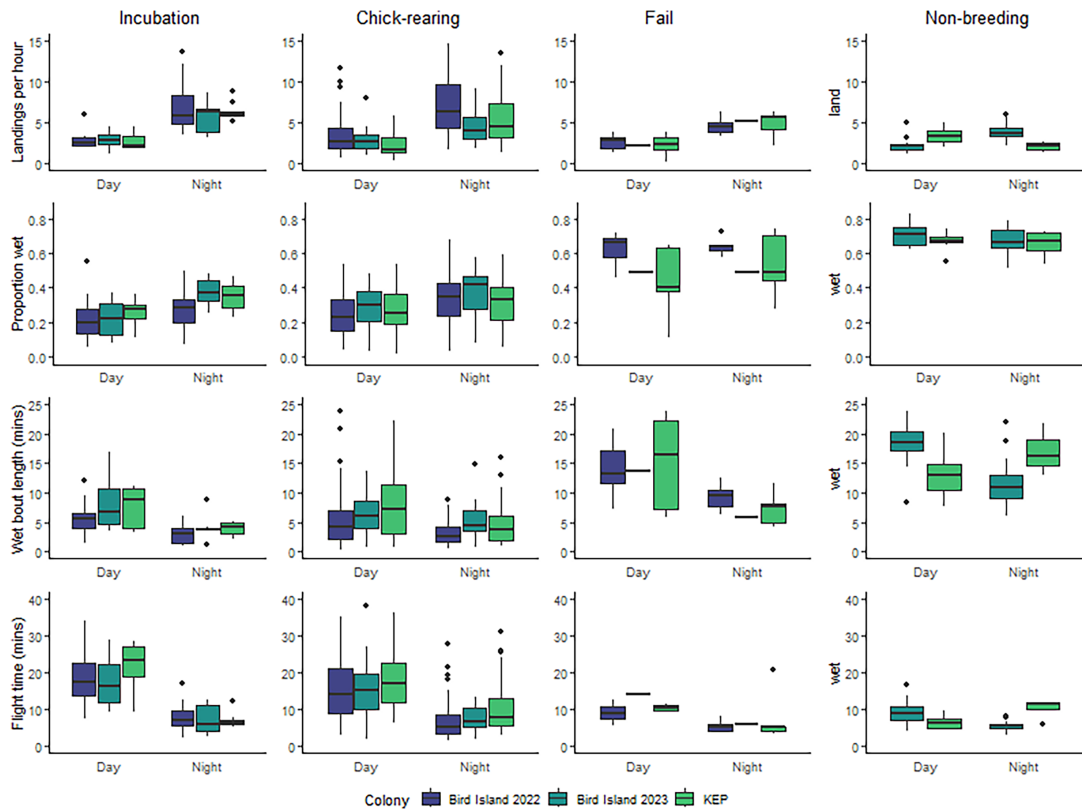


Figure 2. Activity metrics from white-chinned petrels tracked during different life-history stages at Bird Island in 2022 and 2023 and King Edward Point in 2023.

was >80% were included in the main analyses; these were from incubation at Bird Island in 2023, chick-rearing at all colonies, and for failed birds at Bird Island and King Edward Point in 2023.

3.2. Activity patterns

There were no significant differences in activity patterns for white-chinned petrels at Bird Island and KEP within each life-history stage (figure 2, table A4). However, pooling all breeding sites and years, mean values for all activity metrics with the exception of flight time at night differed significantly between life-history stages (table A5).

3.3. Distribution and spatial segregation

There was no evidence of spatial segregation between birds tracked from Bird Island in 2022 and 2023 (table A6), and so these data were pooled in analyses of spatial segregation among breeding sites. During incubation, white-chinned petrels from all colonies travelled west to the Patagonian Shelf and southwest to the Antarctic Peninsula (figure 1). Only one individual (from King Edward Point) travelled east as far as the mid-Atlantic ridge and South American-Antarctic Ridge. During chick-rearing, white-chinned petrels from all colonies used the Patagonian Shelf and travelled south to the Weddell Sea. Individuals breeding at Bird Island also visited the Antarctic Peninsula, whereas those breeding at Cooper Island and KEP travelled east to the South Sandwich Islands. During chick-rearing, the core foraging area (50% UD) and home range area (95% UD) of white-chinned petrels from different breeding sites were more segregated than expected by chance (table 2). There were insufficient tracks to evaluate this during incubation. Failed birds from all colonies travelled to the Patagonian Shelf, and some from Bird Island were tracked past Cape Horn into the Humboldt Current System. The distribution of white-chinned petrels tracked during the non-breeding season showed a similar pattern (figure 1). There was no evidence of spatial segregation between failed or non-breeding birds from different breeding sites (table 2). The proportions of locations that were on the Patagonian Shelf were 42%, 19%, 26% and 30% during incubation,

Table 2. Observed and randomized overlap (Bhattacharyya's Affinity) of usage distributions (UDs) of white-chinned petrels tracked from Bird Island, Cooper Island and King Edward Point, South Georgia, during different life-history stages. Randomized overlaps are shown as a mean $\pm$ s.d. and p represents the proportion of randomized overlaps that were smaller than the observed overlap. Maximum values for core foraging area and home-range areas are 0.50 and 0.95, respectively.

usage distribution	stage	colonies	sample overlap	randomized overlap	P
50% (core foraging area)	chick-rearing	BI-CI	0.04	0.33 ± 0.03	<0.01
		BI-KEP	0.22	0.36 ± 0.02	<0.01
		CI-KEP	0.21	0.31 ± 0.03	<0.01
	fail	BI-KEP	0.39	0.36 ± 0.04	0.70
	non-breeding	BI-KEP	0.40	0.38 ± 0.04	0.56
95% (home-range area)	chick-rearing	BI-CI	0.40	0.78 ± 0.03	<0.01
		BI-KEP	0.62	0.83 ± 0.03	<0.01
		CI-KEP	0.65	0.75 ± 0.04	0.02
	fail	BI-KEP	0.74	0.80 ± 0.04	0.12
	non-breeding	BI-KEP	0.88	0.84 ± 0.04	0.86

25%, 12%, 27% and 30% during chick-rearing and 76%, 16%, 76% and 76% for failed birds tracked from King Edward Point, Cooper Island and Bird Island in 2022 and Bird Island in 2023, respectively.

3.4. Habitat models

Habitat models for all life-history stages and breeding sites had good predictive power with AUC ranging from 0.82 to 0.97 and deviance explained ranging from 27 to 65% (table A7). For each breeding site and life-history stage, distance from the colony, depth and sea surface temperature were included in final models. Including slope or chlorophyll-*a* concentration increased the predictive power for some groups. Birds from all breeding sites preferred shelf habitats closer to breeding sites with SST $< 20^{\circ}\text{C}$ during all stages of the breeding season (figures A1–A4). Birds from some sites also had a preference for areas with medium to high chlorophyll or greater slope. During the non-breeding season, white-chinned petrels similarly favoured shelf waters with medium to high chlorophyll concentrations; however, they also favoured areas further from the colony and with SST peaking at 10°C .

Predicted distributions from the final models were similar to observed distributions (figure 3; figures A5–A7). Model predictions suggest that for birds from all sites, habitat conditions from the Patagonian Shelf to the South Sandwich Islands, Antarctic Peninsula and Weddell Sea are suitable during incubation and chick-rearing, those to the north of South Georgia and on the Patagonian Shelf are suitable for failed birds and those at the Patagonian Shelf, Humboldt Current System and the tip of the Antarctic Peninsula are suitable for birds during the non-breeding period.

3.5. Overlap with fisheries

Based on vessel AIS data, overlap of tracked white-chinned petrels from all breeding sites with fisheries occurred almost exclusively at the Patagonian Shelf break during incubation and chick-rearing, and at the Patagonian Shelf break and further onshore after birds had failed and during the non-breeding period (figure 3; figures A5–A7). The areas of highest potential overlap with fisheries based on predicted distributions were similar to those highlighted from the tracking data. However, areas of lower overlap

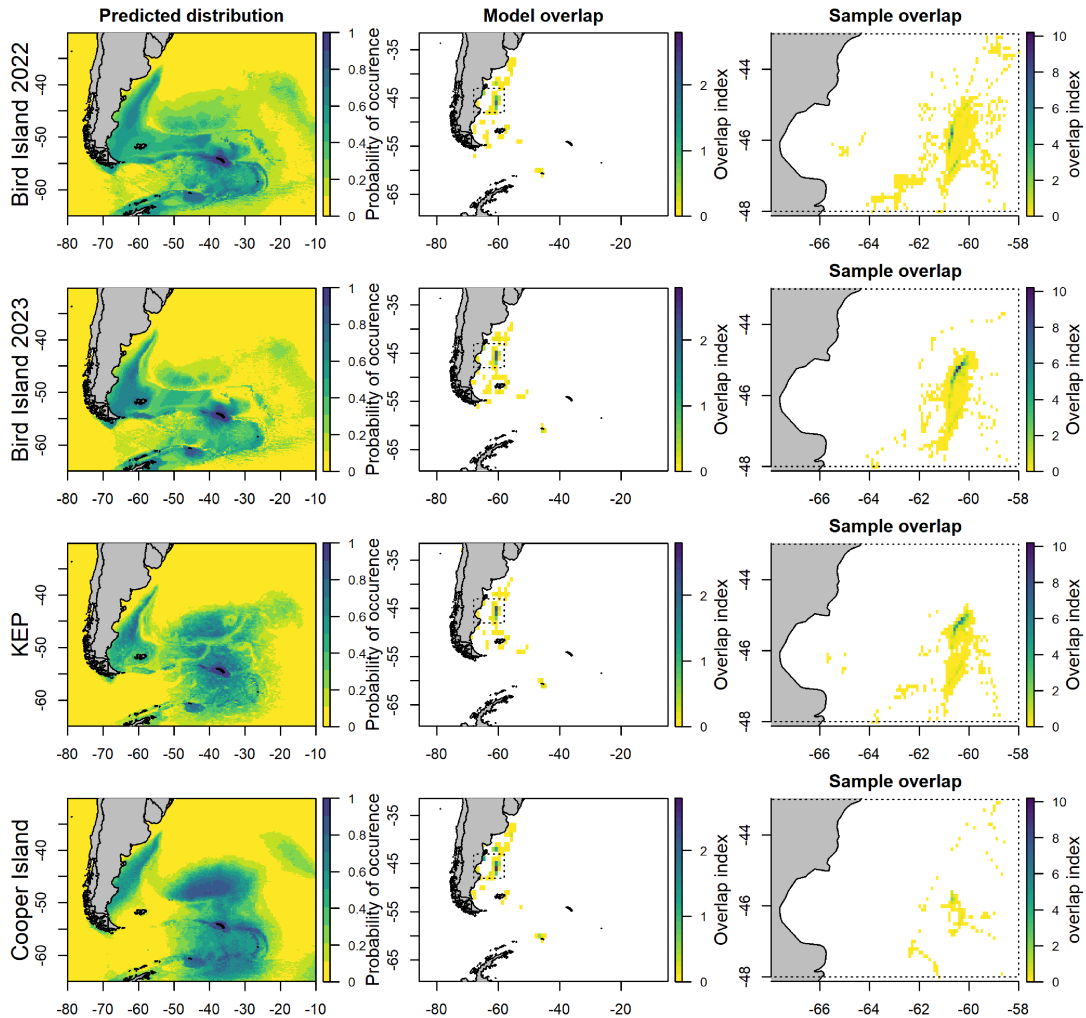


Figure 3. Predicted distributions of white-chinned petrels from Bird Island, King Edward Point and Cooper Island during the chick-rearing period, and overlap of the predicted distributions and the tracking (sample) data with fishing activity. Model predictions and overlap are at a scale of 1° , whereas sample overlap is at 0.1° , and thus values cannot be compared. The dotted line in maps based on model predictions (middle panel) relates to the area in the map of sample overlap (right panel). Appendix 1 includes similar plots for incubation, failed and non-breeding birds.

were also predicted at a much wider latitudinal scale along the Patagonian Shelf break for all life-history stages (figure 3; figures A5–A7). During chick rearing, overlap with fishing was higher for white-chinned petrels tracked from Bird Island, King Edward Point than Cooper Island (table 3). Fisheries overlap differed less between breeding sites based on predicted distributions rather than tracking data.

Birds from all breeding sites overlapped most frequently with trawlers flagged to Spain, China and Korea during all life-history stages. Additionally, failed birds and non-breeding birds had high overlap with Argentinean trawlers (figure 4). During the chick-rearing stage, white-chinned petrels from Bird Island (both years) and King Edward Point, but not Cooper Island, also overlapped with drifting (pelagic) and set (demersal) long liners flagged to China. Overlap estimated using the modelled distributions was highest with trawlers from Argentina, China and Spain during all life-history stages (figure 5). Apparent fishing effort was higher in 2023 than in 2022 for all life-history stages (table A8).

4. Discussion

Previous studies have shown variability in the distribution and activity patterns of white-chinned petrels among life-history stages and discussed the implications for overlap with fisheries [23,30–32,39]. However, ours is the first to provide comprehensive coverage of the distribution and overlap with

Table 3. Overlap of white-chinned petrels from South Georgia with fisheries calculated either as the proportion of time spent in each cell (tracking data) or relative importance (predicted distributions) of each cell multiplied by hours fished in each cell. Overlap is calculated at the scale of 0.1° for tracking data during the breeding season, and 1° for the non-breeding season and for predicted distributions. Consequently, values at different scales are not comparable.

data type	life-history stage	drifting (pelagic) long lines				set (demersal) long lines				trawlers				total			
		KEP	CI	Bi22	Bi23	KEP	CI	Bi22	Bi23	KEP	CI	Bi22	Bi23	KEP	CI	Bi22	Bi23
tracking data	incubation	NA	NA	NA	3	NA	NA	NA	1.8	NA	NA	NA	42	NA	NA	NA	46.8
	chick-rearing	3.0	0.5	2	3.5	2	0.2	0.6	2.1	64	11	52	87	69	11.7	54.6	92.6
	failed	2	NA	1.1	NA	1.5	NA	0.9	NA	44	NA	25	NA	47.5	NA	27	NA
	non-breeding	22	NA	NA	96	108	NA	NA	201	4318	NA	NA	5440	4448	NA	NA	5737
predicted distributions	incubation	0.4	0.2	0.3	0.2	0.4	0.1	0.2	0.2	7.8	4.9	4.5	4.4	8.6	5.2	5	4.8
	chick-rearing	0.2	0.4	0.3	0.3	0.3	0.3	0.3	0.5	7.9	12.5	8.2	10.2	8.4	13.2	8.8	11
	failed	0.7	1	0.8	1.8	0.7	0.9	1.7	2.2	33	35	26	62	34.4	36.9	28.5	66
	non-breeding	1.8	NA	NA	1.6	11	NA	NA	7.9	79	NA	NA	70	91.8	NA	NA	79.5

fisheries throughout the annual cycle of white-chinned petrels from multiple breeding populations in the same island group. We show that these populations are spatially segregated in terms of core foraging and home-range areas during chick-rearing, which affects the relative overlap with fishing vessels from different flag states. This may have implications for population trends across the archipelago and is an important consideration for conservation and management.

4.1. Distribution and spatial segregation

Many procellariiform sea-birds from South Georgia forage in the highly productive waters of the Patagonian Shelf and shelf break, the Antarctic Peninsula and the South Orkney Islands shelf and shelf break, where prey are abundant and highly predictable [18,48,49]. Thus, it was not surprising that white-chinned petrels from all breeding sites travelled west or southwest from South Georgia to forage in these regions during the annual cycle. During the breeding season, core foraging areas were around South Georgia, the Antarctic Peninsula, the South Scotia Ridge and the Patagonian Shelf and shelf-break. Spatial segregation in core foraging areas and home range areas among the study populations was clear during chick-rearing, and possible during incubation, though our sample size was insufficient to reach a firm conclusion. In particular, only birds breeding in the central and eastern sites at South Georgia travelled east to the South Sandwich Islands, and only those from the western site (Bird Island) travelled southwest to the Antarctic Peninsula. The core foraging areas of birds which had failed and non-breeding birds were exclusively on the Patagonian Shelf and Humboldt Current System, and were not spatially segregated, reflecting the unconstrained nature of distributions in those life-history stages.

Spatial segregation between birds from neighbouring colonies has been shown in many pelagic sea-birds and is often thought to be a mechanism to avoid density-dependent competition [37,50,51]. However, most examples are of birds with relatively small foraging ranges breeding in colonies situated close together [37,52,53], or wide-ranging species in colonies situated hundreds of kilometres apart [46,54]. By contrast, white-chinned petrels can forage >1900 km from their breeding sites, which in our study were <160 km apart, and so density-dependent competition does not appear to explain why only the breeding population at Bird Island foraged at the Antarctic Peninsula during chick-rearing, and only birds from King Edward Point and Cooper Island foraged to the east of South Georgia.

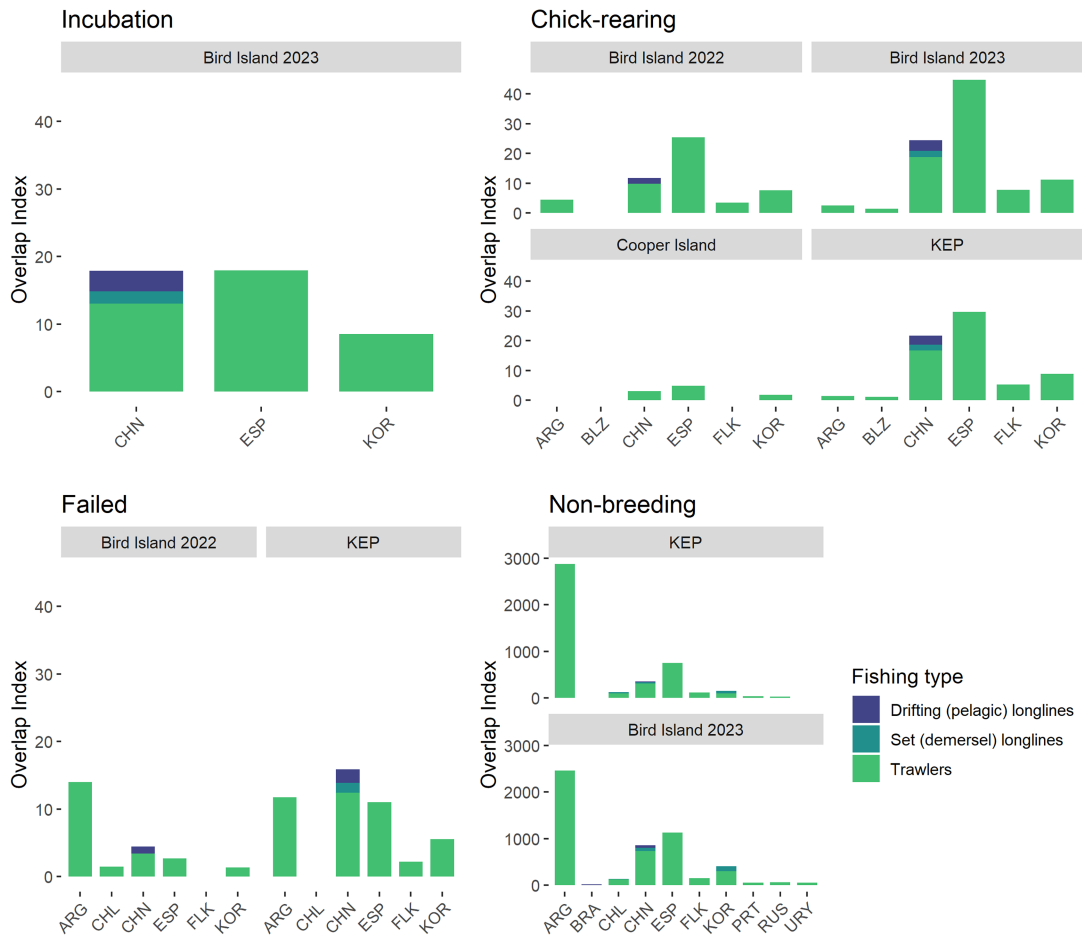


Figure 4. Overlap of white-chinned petrels tracked from Bird Island, Cooper Island and King Edward Point, South Georgia in 2022 or 2023 with vessel flag state and gear type. Colour scale represents primary fishing gear type for vessels actively fishing. Registered flag states as follows: ARG, Argentina; BLZ, Belize; BRA, Brazil; CHL, Chile; CHN, China; ESP, Spain; FLK, Falkland Islands; KOR, South Korea; PRT, Portugal; RUS, Russia; and URY, Uruguay.

Spatial segregation may occur if conspecifics prefer different habitat types or types of prey [38,55]. However, our habitat models showed similar responses to environmental covariates and predicted similar distributions of birds from all three populations. Similarly, trip characteristics and at-sea activity budgets, which can be used to infer foraging behaviour and energetic expenditure, were also similar for individuals breeding at different sites. Thus, it is unlikely that energetic constraints led to the observed spatial segregation. Wandering albatrosses (*Diomedea exulans*) from different populations at South Georgia also show spatial segregation during the breeding and non-breeding season [22,35]; individuals from Bird Island only foraged to the west, whereas those from Prion Island travelled both east and west during the breeding season. In lieu of an alternative explanation, the conclusion was that the segregation was a consequence of social learning, cultural evolution and past experience. It is equally plausible that these factors could be driving the spatial segregation observed in this study [51].

The distribution of white-chinned petrels during the chick-rearing period in our study was markedly different from previous tracking at South Georgia, which showed that birds were almost always exclusively at or south of the Antarctic Polar Front, and concentrated at the South Orkney shelf-slope and the seasonal sea-ice in the northern Weddell Sea [23,24,37]. By contrast, we found that although birds from all populations visited these areas, they also spent considerable time on the Patagonian Shelf and shelf-break. This could plausibly be explained by lower prey availability in the South Georgia or South Orkney shelf regions in January–April in our study years, and so some individuals instead targeted the Patagonian Shelf, possibly to feed on more abundant natural prey, or on discards or bait from fishing vessels (which may be more predictable).



Figure 5. Overlap of predicted distributions of white-chinned petrels tracked from Bird Island, Cooper Island and King Edward Point, South Georgia in 2022 and fishing vessels by flag state and gear type. Colour scale represents primary fishing gear type for vessels actively fishing. Registered flag states as follows: ARG, Argentina; BRA, Brazil; CHL, Chile; CHN, China; ESP, Spain; FLK, Falkland Islands; KOR, South Korea; PRT, Portugal; RUS, Russia; and URY, Uruguay.

4.2. Daily and seasonal variation in at-sea activity patterns

The differences in activity patterns observed between life-history stages and day and night were consistent with previous studies [30,31]. For example, failed and non-breeding birds spent a higher proportion of time wet, the duration of wet bouts was considerably longer, and they landed less often per day than during incubation or chick-rearing. During the non-breeding season, sea-birds are unconstrained and have low energetic demand; hence, they typically spend more time resting on the water and less time foraging than breeding birds [56]. Long periods spent on the water may indicate resting or foraging, potentially using the sit-and-wait method [30,31]. Landing rate and the proportion of time wet was higher in darkness than daylight for birds from all populations during incubation and chick-rearing, suggesting more foraging at night, as in previous studies. Although nocturnal foraging may provide benefits such as reducing competition with larger albatrosses, or access to prey undergoing vertical migration at night, it also increases the risk of by-catch in fisheries [16,30–32].

4.3. Habitat models

Our habitat models had good predictive power, and the environmental characteristics that were identified as important for each breeding population and life-history stage were broadly consistent with a previous study [47]. The areas used by the tracked white-chinned petrels were highly productive and are also targeted by other sea-birds from South Georgia [57]. Nuances of models for different breeding populations may be artefacts of the modelling process. For example, although white-chinned petrels from all breeding sites used shelf slopes, the covariate for slope was only included in models for Bird Island during incubation and Cooper Island during chick-rearing. It is likely that while this is an

important habitat characteristic, the effect is masked by other environmental covariates which have a stronger signal. The main differences in the relationship between white-chinned petrel occurrence and environmental covariates among stages are indicative of the constraint to return to the egg or chick during the breeding season, compared with the freedom during the non-breeding season that allows individuals to remain in productive areas with high prey abundance, further from the colony.

4.4. Fisheries overlap from tracks versus model predictions

The areas of high fisheries overlap identified using predicted bird distributions were very similar to those using the sample of tracked individuals. However, nuances such as variability in the level of overlap of white-chinned petrels from different populations were not apparent using the predictions, and overlaps with some fleets (e.g. Argentinian trawlers) were overestimated. The latter is likely because the predicted distributions extended further north than the tracking data. Our results suggest that although predicted distributions have value for identifying broad-scale areas of high risk where empirical data are limited in some way, the results should be interpreted with caution. The proportion of time spent on the Patagonian Shelf during different life-history stages may therefore be the simplest metric of the relative risk posed by fisheries to white-chinned petrels from South Georgia.

4.5. Overlap with fisheries

High overlap between white-chinned petrels and fisheries at the Patagonian shelf-break was not surprising as this area is well known for high levels of sea-bird-fishery interactions and by-catch [4,18,21,30,58]. Indeed, overlap of birds from all breeding sites with fisheries was in similar areas of the Patagonian Shelf and shelf-break throughout the annual cycle, although the extent differed among breeding populations and life-history stages. In particular, birds tracked from Cooper Island overlapped considerably less with all types of fisheries than those from central or west South Georgia, reflecting the lower proportion of time spent on the Patagonian Shelf. White-chinned petrels tracked from Bird Island had a lower overlap with fisheries in 2022 than 2023, despite the similarity in distributions (no significant differences in core foraging or home range areas). The lower overlap in 2022 was therefore owing to reduced fishing effort in that year.

White-chinned petrels at Bird Island were in decline at least until the late 1990s [34], but there are no data on trends elsewhere in the island group. The rate of decline of other sea-bird species varies across South Georgia [59], most likely owing to spatial segregation in at-sea distributions leading to variable rates of overlap with fisheries, and hence overall by-catch rates [22]. Based on our study, there should be more concern about fisheries interactions for white-chinned petrels breeding in the west of South Georgia; however, birds from all populations overlapped considerably with fisheries during incubation and the non-breeding season, and the species is particularly susceptible to by-catch, so there is no reason for complacency. Although burrow-nesting species are challenging to monitor, particularly in such a remote environment, another clear inference from our study is the need for a much-improved understanding of population trends and demography of white-chinned petrels, ideally at several sites at South Georgia, given it is the largest global population [25,40].

4.6. Overlap with gear types, flag states and regional fisheries management organizations

Overlap was highest with trawlers flagged to China, Spain and Korea during incubation and chick-rearing, and with Argentine trawlers for failed birds and birds during the non-breeding season. The overlap indices were considerably higher for trawlers than drifting (pelagic) or set (demersal) long liners, which were all flagged to China or Korea. Overlap with trawlers poses a significant risk to white-chinned petrels as by-catch rates from both cable strikes and net captures are high [8]. Our results contrast with previous studies which showed high overlap during 1990–2015 with pelagic long liners flagged to Taiwan, Brazil and other unspecified flag states, demersal long liners flagged to the Falklands and Chile, trawlers flagged to Argentina [18] and, using effort data from 2012–2020, with pelagic long liners flagged to Taiwan, Japan, Spain and Uruguay, demersal long liners flagged to South Korea, Chile and Argentina and trawlers flagged to Argentina, Spain and various other states [40]. Part of this reflects changes over time in distribution and magnitude of fishing effort from different flag states, and may also reflect the finer scale of our overlap analysis. Both previous studies were conducted at 5° resolution, whereas ours

was at 0.1° resolution during the breeding season and 1° resolution during the non-breeding season. Working at a finer scale allows the detection of smaller-scale differences in fisheries overlap among populations or life-history stages, but may be more susceptible to bias if the sample size is small [60]. Nevertheless, overlap of sea-birds with vessels flagged to different states affects by-catch rates owing to variability in operational practices, including implementation of mitigation measures [8,16].

When operating within an Exclusive Economic Zone (EEZ), fishing vessels are required to adhere to mitigation measures imposed by that country, whereas in Areas Beyond National Jurisdiction (ABNJ) mitigation requirements are set by the relevant RFMO, or in lieu of this by the flag state. Requirements for mitigation and observers to monitor sea-bird by-catch and ensure compliance vary greatly between EEZs, flag states and RFMOs. South of the Antarctic Polar Front, fishing is regulated by CCAMLR, which requires best-practice mitigation measures and 100% observer coverage [19]. By contrast, the International Commission for the Conservation of Atlantic Tunas regulates the pelagic long line fisheries in the South Atlantic, and only one mitigation measure is required in waters north of 25° S, two are required south of 25° S, and observer coverage is <5% [16]. Perhaps even more concerning is that no RFMO currently regulates the demersal fisheries in the southwest Atlantic [61]. However, white-chinned petrels from all breeding sites overlapped with demersal long line and trawl fisheries on the high seas. These vessels are technically under the jurisdiction of their flag states, but these rarely impose any mitigation requirement independent of those of the relevant EEZ or RFMO; it is therefore probable that these vessels do not implement any sea-bird by-catch mitigation measures and are without observers, so by-catch is unmonitored.

The data from Global Fishing Watch (GFW) are the most complete for fishing activity in this region in recent years but are not comprehensive. GFW data rely on the vessel AIS and consequently may not include fishing activity in some regions where satellite coverage is poor, small artisanal vessels are not fitted with AIS transmitters or when AIS is switched off [58,62]. Indeed, some artisanal fleets which operate on the Patagonian Shelf, and which have reported by-catch of white-chinned petrels, are not fitted with AIS transponders, and consequently will not have been included in these analyses [7,63].

4.7. Implications for management

Tracking of individuals from multiple breeding populations within an island group is rarely feasible, particularly in remote locations. However, we have shown that spatial segregation, and consequently vulnerability to fisheries by-catch of white-chinned petrels from different sites at South Georgia can have important consequences for management. We identified fishing fleets and regions where by-catch is a serious risk to white-chinned petrels and other sea-birds [18,22]. Although considerable progress has been made to reduce sea-bird by-catch by some fleets, mitigation measures in the high seas fall short of best practice (e.g. [18,19,64]). It is recommended that three mitigation measures are used, in addition to the use of hook-shielding devices and that these should extend throughout the distribution of vulnerable species [65]. Furthermore, observer coverage is poor and there is no independent monitoring of compliance [16]. Without independent observers, it is likely that mitigation measures will not be implemented and that by-catch will go unreported. As it stands, enforcement of best-practice mitigation and monitoring of sea-bird by-catch remains a major challenge [16,40]. Further engagement with RFMOs, fishing vessel operators and managers is fundamental to ensure progress in the protection of white-chinned petrels and other globally threatened sea-birds.

Ethics. All fieldwork was approved by the British Antarctic Survey Animal Welfare and Ethical Review Body and carried out under permit from the Government of South Georgia and the South Sandwich Islands.

Data accessibility. All tracking data are available from the Seabird Tracking Database (<https://www.seabirdtracking.org/>).

Supplementary material is available online [66].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. V.W.-E.: conceptualization, data curation, formal analysis, funding acquisition, methodology, project administration, writing—original draft; E.P.: data curation, methodology, writing—review and editing; R.A.P.: conceptualization, funding acquisition, methodology, project administration, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This article is a contribution to the Ecosystems CONSEC programme of the British Antarctic Survey Polar Science for a Sustainable Planet science strategy, funded by the Natural Environment Research Council. The study

was funded in part by Darwin Plus under grant no. DPLUS120 and E.P. was supported by the Natural Environment Research Council C-CLEAR doctoral training programme (grant no. NE/S007164/1).

Acknowledgements. We are grateful to all those involved in collecting the tracking data, particularly Mark Whiffin, Imogen Lloyd, George Perry, Carrie Gunn and Kelvin Floyd at Bird Island and King Edward Point and to the crew of the MV Pharos SG for logistical support.

References

- Phillips R, Fort J, Dias M. 2022 Conservation status and overview of threats to seabirds. In *Conservation of marine birds* (eds L Young, E VanderWerf), pp. 33–56. London, UK: Academic Press.
- Dias MP *et al.* 2019 Threats to seabirds: a global assessment. *Biol. Conserv.* **237**, 525–537. (doi:10.1016/j.biocon.2019.06.033)
- Jiménez S, Domingo A, Abreu M, Brazeiro A. 2011 Structure of the seabird assemblage associated with pelagic longline vessels in the southwestern Atlantic: implications for bycatch. *Endanger. Species Res.* **15**, 241–254. (doi:10.3354/esr00378)
- Jiménez S, Phillips RA, Brazeiro A, Defeo O, Domingo A. 2014 Bycatch of great albatrosses in pelagic longline fisheries in the southwest Atlantic: contributing factors and implications for management. *Biol. Conserv.* **171**, 9–20. (doi:10.1016/j.biocon.2013.12.035)
- Weimerskirch H, Capdeville D, Duhamel G. 2000 Factors affecting the number and mortality of seabirds attending trawlers and long-liners in the Kerguelen area. *Polar Biol.* **23**, 236–249. (doi:10.1007/s003000050440)
- Karpouzi VS, Watson R, Pauly D. 2007 Modelling and mapping resource overlap between seabirds and fisheries on a global scale: a preliminary assessment. *Mar. Ecol. Prog. Ser.* **343**, 87–99. (doi:10.3354/meps06860)
- Bugoni L, Mancini PL, Monteiro DS, Nascimento L, Neves TS. 2008 Seabird bycatch in the Brazilian pelagic longline fishery and a review of capture rates in the southwestern Atlantic Ocean. *Endanger. Species Res.* **5**, 137–147. (doi:10.3354/esr00115)
- Phillips R, Fox E, Crawford R, Prince S, Yates O. 2024 Incidental mortality of seabirds in trawl fisheries: a global review. *Biol. Conserv.* **296**, 110720. (doi:10.1016/j.biocon.2024.110720)
- Sullivan BJ, Reid TA, Bugoni L. 2006 Seabird mortality on factory trawlers in the Falkland Islands and beyond. *Biol. Conserv.* **131**, 495–504. (doi:10.1016/j.biocon.2006.02.007)
- Cox T, Lewison R, Žydelis R, Crowder L, Safina C, Read A. 2007 Comparing effectiveness of experimental and implemented bycatch reduction measures: the ideal and the real. *Conserv. Biol.* **21**, 1155–1164. (doi:10.1111/j.1523-1739.2007.00772.x)
- Løkkeborg S. 2011 Best practices to mitigate seabird bycatch in longline, trawl and gillnet fisheries—efficiency and practical applicability. *Mar. Ecol. Prog. Ser.* **435**, 285–303. (doi:10.3354/meps09227)
- ACAP. 2023 *ACAP review of mitigation measures and best practice advice for reducing the impact of pelagic and demersal trawl fisheries on seabirds*. Hobart, Australia: ACAP Secretariat.
- ACAP. 2024 *ACAP review of mitigation measures and best practice advice for reducing the impact of demersal longline fisheries on seabirds*. Hobart, Australia: ACAP Secretariat.
- ACAP. 2024 *ACAP review of mitigation measures and best practice advice for reducing the impact of pelagic longline fisheries on seabirds*. Hobart, Australia: ACAP Secretariat.
- Gilman EL. 2011 Bycatch governance and best practice mitigation technology in global tuna fisheries. *Mar. Policy* **35**, 590–609. (doi:10.1016/j.marpol.2011.01.021)
- Jiménez S, Domingo A, Winker H, Parker D, Gianuca D, Neves T, Coelho R, Kerwath S. 2020 Towards mitigation of seabird bycatch: large-scale effectiveness of night setting and Tori lines across multiple pelagic longline fleets. *Biol. Conserv.* **247**, 108642. (doi:10.1016/j.biocon.2020.108642)
- Phillips R. 2013 Requisite improvements to the estimation of seabird by-catch in pelagic longline fisheries. *Anim. Conserv.* **16**, 157–158. (doi:10.1111/acv.12042)
- Clay TA, Small C, Tuck GN, Pardo D, Carneiro AP, Wood AG, Croxall JP, Crossin GT, Phillips RA. 2019 A comprehensive large-scale assessment of fisheries bycatch risk to threatened seabird populations. *J. Appl. Ecol.* **56**, 1882–1893. (doi:10.1111/1365-2664.13407)
- Collins MA, Hollyman PR, Clark J, Söffker M, Yates O, Phillips RA. 2021 Mitigating the impact of longline fisheries on seabirds: lessons learned from the South Georgia Patagonian toothfish fishery (CCAMLR Subarea 48.3). *Mar. Policy* **131**, 104618. (doi:10.1016/j.marpol.2021.104618)
- Croxall JP. 2008 The role of science and advocacy in the conservation of Southern Ocean albatrosses at sea. *Bird Conserv. Int.* **18**, S13–S29. (doi:10.1017/S0959270908000300)
- Phillips RA *et al.* 2016 The conservation status and priorities for albatrosses and large petrels. *Biol. Conserv.* **201**, 169–183. (doi:10.1016/j.biocon.2016.06.017)
- Warwick-Evans V, Pearmain EJ, Thorne L, Phillips RA. 2025 Spatial segregation and bycatch risk as potential drivers of population trends of wandering albatrosses at South Georgia. *Conserv. Biol.* **40**, e70126. (doi:10.1111/cobi.70126)
- Phillips RA, Silk JR, Croxall JP, Afanasyev V. 2006 Year-round distribution of white-chinned petrels from South Georgia: relationships with oceanography and fisheries. *Biol. Conserv.* **129**, 336–347. (doi:10.1016/j.biocon.2005.10.046)
- Berrow SD, Croxall JP, Grant SD. 2000 Status of white-chinned petrels *Procellaria aequinoctialis* Linnaeus 1758, at Bird Island, South Georgia. *Antarct. Sci.* **12**, 399–405. (doi:10.1017/S0954102000000468)

25. Martin A, Poncet S, Barbraud C, Foster E, Fretwell P, Rothery P. 2009 The white-chinned petrel (*Procellaria aequinoctialis*) on South Georgia: population size, distribution and global significance. *Polar Biol.* **32**, 655–661. (doi:10.1007/s00300-008-0570-5)
26. Berrow SD, Croxall JP. 1999 The diet of white-chinned petrels *Procellaria aequinoctialis*, Linnaeus 1758, in years of contrasting prey availability at South Georgia. *Antarct. Sci.* **11**, 283–292. (doi:10.1017/S0954102099000371)
27. Gandini P, Frere E. 2006 Spatial and temporal patterns in the bycatch of seabirds in the Argentinian longline fishery. *Fish. Bull.* **104**, 482–485.
28. González-Zevallos D, Yorio P. 2006 Seabird use of discards and incidental captures at the Argentine hake trawl fishery in the Golfo San Jorge, Argentina. *Mar. Ecol. Prog. Ser.* **316**, 175–183. (doi:10.3354/meps316175)
29. Jiménez S, Xavier JC, Domingo A, Brazeiro A, Defeo O, Viera M, Lorenzo MI, Phillips RA. 2017 Inter-specific niche partitioning and overlap in albatrosses and petrels: dietary divergence and the role of fishing discards. *Mar. Biol.* **164**, 174. (doi:10.1007/s00227-017-3205-y)
30. Frankish CK, Manica A, Navarro J, Phillips RA. 2021 Movements and diving behaviour of white-chinned petrels: diurnal variation and implications for bycatch mitigation. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **31**, 1715–1729. (doi:10.1002/aqc.3573)
31. Mackley EK, Phillips RA, Silk JR, Wakefield ED, Afanasyev V, Furness RW. 2011 At-sea activity patterns of breeding and nonbreeding white-chinned petrels *Procellaria aequinoctialis* from South Georgia. *Mar. Biol.* **158**, 429–438. (doi:10.1007/s00227-010-1570-x)
32. Péron C, Delord K, Phillips RA, Charbonnier Y, Marteau C, Louzao M, Weimerskirch H. 2010 Seasonal variation in oceanographic habitat and behaviour of white-chinned petrels *Procellaria aequinoctialis* from Kerguelen Island. *Mar. Ecol. Prog. Ser.* **416**, 267–284. (doi:10.3354/meps08785)
33. Rollinson D, Dilley B, Ryan P. 2014 Diving behaviour of white-chinned petrels and its relevance for mitigating longline bycatch. *Polar Biol.* **37**, 1301–1308. (doi:10.1007/s00300-014-1521-y)
34. Berrow SD, Wood AG, Prince PA. 2000 Foraging location and range of white-chinned petrels *Procellaria aequinoctialis* breeding in the South Atlantic. *J. Avian Biol.* **31**, 303–311. (doi:10.1034/j.1600-048X.2000.310305.x)
35. Warwick-Evans V, Pearmain EJ, Phillips RA. 2026 Overlap of nonbreeding wandering albatrosses with fisheries and implications for colony-specific population trajectories at South Georgia. *Conserv. Biol.* **40**, e70260. (doi:10.1111/cobi.70260)
36. Grémillet D, Dell’Omo G, Ryan P, Peters G, Ropert-Coudert Y, Weeks S. 2004 Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. *Mar. Ecol. Prog. Ser.* **268**, 265–279. (doi:10.3354/meps268265)
37. Wakefield ED *et al.* 2017 Breeding density, fine-scale tracking and large-scale modeling reveal the regional distribution of four seabird species. *Ecol. Appl.* **27**, 2070–2091. (doi:10.1002/eap.1591)
38. Granroth-Wilding HM, Phillips RA. 2019 Segregation in space and time explains the coexistence of two sympatric sub-Antarctic petrels. *Ibis* **161**, 101–116. (doi:10.1111/ibi.12584)
39. Patterson A. 2022 Foraging range scales with colony size in high-latitude seabirds. *Curr. Biol.* **32**, 3800–3807e3. (doi:10.1016/j.cub.2022.06.084)
40. Rexer-Huber K *et al.* 2025 Metapopulation distribution shapes year-round overlap with fisheries for a circumpolar seabird. *Ecol. Appl.* **35**, e70019. (doi:10.1002/eap.70019)
41. R Core Team. 2021 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
42. Johnson D. 2013 Crawl: fit continuous-time correlated random walk models to animal movement data. R package version:1.4-1.
43. Beal M *et al.* 2021 track2KBA: an R package for identifying important sites for biodiversity from tracking data. *Methods Ecol. Evol.* **12**, 2372–2378. (doi:10.1111/2041-210X.13713)
44. Merkel B, Phillips RA, Descamps S, Yoccoz NG, Moe B, Strøm H. 2016 A probabilistic algorithm to process geolocation data. *Movem. Ecol.* **4**, 26. (doi:10.1186/s40462-016-0091-8)
45. Lenth R. 2025 Estimated marginal means, aka least-squares means. R package version 1.11.1. <https://CRAN.R-project.org/package=emmeans>. (accessed 15 July 2026).
46. Clay TA, Pearmain EJ, McGill RAR, Manica A, Phillips RA. 2018 Age-related variation in non-breeding foraging behaviour and carry-over effects on fitness in an extremely long-lived bird. *Funct. Ecol.* **32**, 1832–1846. (doi:10.1111/1365-2435.13120)
47. Bentley LK, Manica A, Dilley BJ, Ryan PG, Phillips RA. 2023 Divergent foraging habitat preferences between summer-breeding and winter-breeding *Procellaria* petrels. *Ibis* **165**, 618–628. (doi:10.1111/ibi.13152)
48. Botto F, Martinetto P, Alemany D, Díaz de Astarloa C. 2024 Food web topology associated with the Patagonian shelf-break front. In *The Patagonian shelf-break front: ecology, fisheries, wildlife conservation* (eds EM Acha, OO Iribarne, AR Piola), pp. 261–282. Cham, Switzerland: Springer.
49. Phillips R, Croxall J, Silk J, Briggs D. 2007 Foraging ecology of albatrosses and petrels from South Georgia: two decades of insights from tracking technologies. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **17**, S6–S21. (doi:10.1002/aqc.906)
50. Bolton M, Conolly G, Carroll M, Wakefield ED, Caldow R. 2019 A review of the occurrence of inter-colony segregation of seabird foraging areas and the implications for marine environmental impact assessment. *Ibis* **161**, 241–259. (doi:10.1111/ibi.12677)
51. Wakefield ED *et al.* 2013 Space partitioning without territoriality in gannets. *Science* **341**, 68–70. (doi:10.1126/science.1236077)
52. Wanless S, Harris MP. 1993 Use of mutually exclusive foraging areas by adjacent colonies of blue-eyed shags (*Phalacrocorax atriceps*) at South Georgia. *Colonial Waterbirds* **16**, 176–182. (doi:10.2307/1521435)
53. Bertrand P *et al.* 2021 Fine-scale spatial segregation in a pelagic seabird driven by differential use of tidewater glacier fronts. *Sci. Rep.* **11**, 22109. (doi:10.1038/s41598-021-01404-1)

54. Ramos R *et al.* 2013 Meta-population feeding grounds of Cory's shearwater in the subtropical Atlantic Ocean: implications for the definition of Marine Protected Areas based on tracking studies. *Divers. Distrib.* **19**, 1284–1298. (doi:10.1111/ddi.12088)
55. Vilchis LI, Ballance LT, Fiedler PC. 2006 Pelagic habitat of seabirds in the eastern tropical Pacific: effects of foraging ecology on habitat selection. *Mar. Ecol. Prog. Ser.* **315**, 279–292. (doi:10.3354/meps315279)
56. Mackley EK, Phillips RA, Silk JR, Wakefield ED, Afanasyev V, Fox JW, Furness RW. 2010 Free as a bird? Activity patterns of albatrosses during the nonbreeding period. *Mar. Ecol. Prog. Ser.* **406**, 291–303. (doi:10.3354/meps08532)
57. Wakefield ED *et al.* 2025 Seasonal resource tracking and use of sea-ice foraging habitats by albatrosses and large petrels. *Prog. Oceanogr.* **230**, 103334. (doi:10.1016/j.pocean.2024.103334)
58. Carneiro AP, Clark BL, Pearmain EJ, Clavelle T, Wood AG, Phillips RA. 2022 Fine-scale associations between wandering albatrosses and fisheries in the southwest Atlantic Ocean. *Biol. Conserv.* **276**, 109796. (doi:10.1016/j.biocon.2022.109796)
59. Mackley EK *et al.* 2025 Endurance or extinction: long-term declines in albatrosses at South Georgia highlight threats from South Atlantic fisheries and climate change. *Endanger. Species Res.* **57**, 437–451. (doi:10.3354/esr01427)
60. Torres LG, Sagar PM, Thompson DR, Phillips RA. 2013 Scale-dependence of seabird-fishery data analysis and management: reply to Croxall(2013). *Mar. Ecol. Prog. Ser.* **493**, 301–304. (doi:10.3354/meps10600)
61. Bell JB, Guijarro-García E, Kenny A. 2019 Demersal fishing in areas beyond national jurisdiction: a comparative analysis of regional fisheries management organisations. *Front. Mar. Sci.* **6**, 596. (doi:10.3389/fmars.2019.00596)
62. Orben RA *et al.* 2021 Across borders: external factors and prior behaviour influence North Pacific albatross associations with fishing vessels. *J. Appl. Ecol.* **58**, 1272–1283. (doi:10.1111/1365-2664.13849)
63. Frankish CK, Cunningham C, Manica A, Clay TA, Prince S, Phillips RA. 2021 Tracking juveniles confirms fisheries-bycatch hotspot for an endangered albatross. *Biol. Conserv.* **261**, 109288. (doi:10.1016/j.biocon.2021.109288)
64. Da Rocha N *et al.* 2021 Reduction in seabird mortality in Namibian fisheries following the introduction of bycatch regulation. *Biol. Conserv.* **253**, 108915. (doi:10.1016/j.biocon.2020.108915)
65. Bell JB *et al.* 2025 Evaluating the effectiveness of seabird bycatch mitigation measures for pelagic longlines in the South Atlantic. *Biol. Conserv.* **302**, 110981. (doi:10.1016/j.biocon.2025.110981)
66. Warwick-Evans V, Pearmain E, Phillips RA. 2026 Supplementary material from: Year-round spatial segregation and fisheries overlap of white-chinned petrels from multiple populations at South Georgia. Figshare. (doi:10.6084/m9.figshare.c.8641570)