





Environmental drivers of movement in a threatened seabird: insights from a mechanistic model and implications for conservation

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Abstract

Aim: Determining the drivers of movement of different life-history stages is crucial for understanding age-related changes in survival rates and, for marine top predators, the link between fisheries overlap and incidental mortality (bycatch), which is driving population declines in many taxa. Here, we combine individual tracking data and a movement model to investigate the environmental drivers and conservation implications of divergent movement patterns in juveniles (fledglings) and adults of a threatened seabird, the white-chinned petrel (*Procellaria aequinoctialis*).

Location: South-west Atlantic Ocean.

Methods: We compare the spatial distributions and movement characteristics of juvenile, breeding and non-breeding adult petrels, and apply a mechanistic movement model to investigate the extent to which chlorophyll a concentrations (a proxy for food resources) and ocean surface winds drive their divergent distribution patterns. We also consider the conservation implications by determining the relative overlap of each life-history stage with fishing intensity and reported fishing effort (proxies for bycatch risk).

Results: Naïve individuals fledged with similar flight capabilities (based on distances travelled, flight speeds and track sinuosity) to adults but differed in their trajectories. Comparison of simulations from the mechanistic model with real tracks showed that juvenile movements are best predicted by prevailing wind patterns, whereas adults are attracted to food resources on the Patagonian Shelf. The juveniles initially dispersed to less productive oceanic waters than those used by adults, and overlapped less with fishing activity; however, as they moved westwards towards South America, bycatch risk increased substantially.

Main conclusions: The use of a mechanistic framework provided insights into the ontogeny of movement strategies within the context of learned versus innate behaviour and demonstrated that divergent movement patterns of adults and juveniles can have important implications for the conservation of threatened seabirds.

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KEYWORDS

fisheries bycatch mitigation, juvenile, mechanistic movement model, ontogeny, seabirds, tracking

1 | INTRODUCTION

Determining the processes that influence the capacity and motivation for movement within and among species constitutes a primary goal for ecologists, given the far-reaching consequences for individual fitness, population dynamics and conservation (Arjo, Huenefeld, & Nolte, 2007; Munday, 2001; Ribera, Foster, & Vogler, 2003). In most animals, the mechanisms shaping the initial movements of juveniles away from their natal grounds and subsequent habitat use are poorly known, yet this period represents a critical life-history stage when mortality is high (Gaillard, Festa-Bianchet, & Yoccoz, 1998; Owen & Black, 1989; Victor, 1986). Naïve individuals need to acquire foraging, navigation and other skills, and are physically immature, yet must learn how to survive in an unknown and often hostile environment (Avens, 2004; Gyuris, 1994; Riotte-Lambert & Weimerskirch, 2013). In addition, young animals may differ from older life stages in terms of their morphology, nutrient requirements or competitive abilities, and, consequently, may exploit distinct habitats (Simonović, Garner, Eastwood, Kováč, & Copp, 1999; Stamps, 1983; Stockhoff, 1993). Understanding these age-related behavioural differences is a priority for research and conservation, especially in species that undertake large-scale dispersive movements (Arthur, Boyle, & Limpus, 2008; Graham, Grubbs, Holland, & Popp, 2006; Hazen et al., 2012).

Recent advances in tracking technologies have facilitated studies that shed light on the initial movement patterns of both terrestrial and marine species (Hazen et al., 2012; Kays, Crofoot, Jetz, & Wikelski, 2015). Tag miniaturization means devices can be attached to smaller, and hence younger individuals, and improved data storage and transmission capabilities have provided increasing coverage of the “lost-years” for long-lived animals (Ciucci, Reggioni, Maiorano, & Boitani, 2009; Fedak, 2002; Mansfield, Wyneken, Porter, & Luo, 2014; Shillinger, Bailey, Bograd, Hazen, & Hamann, 2012). Juveniles sometimes follow directed movement paths with low among-individual variation, suggesting innate navigation capabilities (Avens, 2004; Putman et al., 2014). In contrast, other species exhibit high individual variability in displacement patterns, with idiosyncratic paths indicative of a period of learning or exploration (de Grissac, Börger, Guitteaud, & Weimerskirch, 2016; Ferrer, 2008; Guilford et al., 2011). In both instances, decisions made by young age classes of when and where to move are strongly linked to external cues, yet few studies have explored the environmental drivers of juvenile movements, and most were correlative (Igulu et al., 2014; Riotte-Lambert & Weimerskirch, 2013; Werner, Mittelbach, & Hall, 1981). A mechanistic approach may offer a useful framework for testing hypotheses about the ecological drivers shaping the distribution of different life-history

stages (Merkle et al., 2019; Moorcroft, Lewis, & Crabtree, 2006; Somveille, Rodrigues, & Manica, 2015).

Compared to the terrestrial realm, there are relatively few barriers to movement in the marine environment (Alderman, Gales, Hobday, & Candy, 2010; Caizergues & Ellison, 2002; Long, Diefenbach, Wallingford, & Rosenberry, 2010; Mansfield et al., 2014). In particular, pelagic seabirds often conduct extremely large-scale movements due to their ability to exploit wind gradients, leading to very low flight costs (de Grissac et al., 2016; Weimerskirch, Akesson, & Pinaud, 2006; Weimerskirch, Guionnet, Martin, Shaffer, & Costa, 2000). They are fascinating models for studying juvenile movement patterns, as juveniles are abandoned by their parents at fledging; naïve individuals must thus learn how to forage and navigate effectively in a seemingly featureless ocean in which resources are patchily distributed (Ashmole, 1963; MacLean, 1986). Tracking studies indicate that juveniles of some species disperse away from their colony with similar movement capabilities and using broadly the same routes as adults, which generally target seasonally productive foraging habitats (Mendes, Prudor, & Weimerskirch, 2017; Péron & Grémillet, 2013; Yoda, Kohno, & Naito, 2004). Recent research suggests that in pelagic seabirds, juveniles may have an innate ability to make favourable use of winds (Riotte-Lambert & Weimerskirch, 2013; Weimerskirch et al., 2006). However, they may still differ from adults in terms of speed, sinuosity, direction, distance travelled or habitat use, suggesting that contrasting drivers underpin age-specific movement patterns (Hatch, Gill, & Mulcahy, 2011; Ismar et al., 2010; Kooyman & Ponganis, 2007; Thiers et al., 2014; Trebilco, Gales, Baker, Terauds, & Sumner, 2008). As individuals of all ages must acquire resources from their environment in order to survive, the availability and accessibility of productive foraging habitats may place important constraints on movement, with major implications for mortality rates of different life-history stages (Alderman et al., 2010; Clay et al., 2019; Wakefield, Phillips, & Matthiopoulos, 2009).

The white-chinned petrel (*Procellaria aequinoctialis*) is a wide-ranging, pelagic seabird, listed as Vulnerable on the IUCN Red List (Phillips et al., 2016). While the year-round adult distribution has been investigated, less is known about the foraging behaviour of juveniles, despite the priority for conservation given ongoing population declines at most breeding sites (Phillips et al., 2016). Thirteen juveniles tracked from Kerguelen and Crozet Islands (southern Indian Ocean) travelled similar distances away from their natal sites as migrating adults, but settled in separate areas (de Grissac et al., 2016). Such results underline that juveniles may face differential mortality pressures, particularly relating to incidental mortality (bycatch) in demersal and pelagic longline fisheries, which represents the greatest at-sea threat to many seabirds (Carneiro et al., 2020; Clay et al., 2019; Dias et al., 2019). Nonetheless, the environmental drivers of

movements of juvenile white-chinned petrels and their overlap with fisheries have not been quantified.

Here, we analysed movement data from juvenile and adult white-chinned petrels tracked from South Georgia, south-west Atlantic Ocean, which is the largest global population and is declining (Berrow et al. 2000a). Our principal aims were to (a) investigate initial dispersal patterns of juveniles during the post-fledging period; (b) apply a mechanistic movement model to identify the potential drivers of movement patterns of different life-history stages; and (c) determine relative overlap with longline fisheries of juveniles and adults, and the implications for conservation using vessel tracking data from the open-source, high-resolution Global Fishing Watch dataset (Global Fishing Watch [GFW], 2019) and fishing effort for tuna and other billfishes reported to the International Commission for the Conservation of Atlantic Tunas (ICCAT). South Georgia lies in the path of prevailing westerly winds, and thus, the main wintering site for this population, the Patagonian Shelf, is directly accessed by flying into headwinds, which is energetically costly (Phillips, Silk, Croxall, & Afanasyev, 2006; Weimerskirch et al., 2000). This study system therefore offers an ideal opportunity to investigate the relative influence of different environmental factors on long-distance movement in birds: attraction to foraging resources and the effect of wind on energetic costs of movement (Somveille et al., 2015; Vansteelandt, Shamoun-Baranes, van Manen, van Diermen, & Bouten, 2017). We hypothesize that wind speed and direction is more likely to determine the trajectories of naïve individuals with no prior flight or foraging experience, whereas experienced adults should migrate directly towards known foraging areas.

2 | METHODS

2.1 | Deployments and tracking data processing

All birds were tracked from Bird Island (54°00'S, 38°03'W), South Georgia, during the 2014/15 breeding season and subsequent winter. Telonics TAV-2630 satellite transmitters (Platform Terminal Transmitters, PTTs) with a duty cycle of 8-hr ON and 44-h OFF were deployed on 13 white-chinned petrel chicks on 15 April 2015 to track at-sea movements in the few months post-fledging. These provided locations on average every hour during ON periods. Fifteen breeding adults were fitted with i-gotU GPS loggers (Mobile Action Technology Inc., New Taipei City, Taiwan) during incubation in December 2014 and devices retrieved on subsequent nest visits during daytime. GPS loggers were set to record every 30 min. Three GPS devices were not retrieved because the nest failed or the chick hatched by the time the bird returned. Both PTTs and GPS loggers were attached with Tesa® tape to back feathers. Sixteen birds (including nine of those that had been tracked with GPS) were equipped with an Intigeo C250 geolocator (global location sensor or GLS logger; Migrate Technology Lt, Cambridge, UK) between 15 December 2014 and 13 January 2015 to track movements during the subsequent non-breeding period. Geolocators were attached by

cable tie to a plastic leg ring, and all devices were retrieved in the following austral breeding season (14 December 2015 to 7 January 2016). The loggers measured light in the range of 1.1 to 74418 lux (maximum recorded at 5-min intervals), temperature every 20 min of continuous wet (maximum, minimum and mean saved every 4 hr) and tested for saltwater immersion every 6 s. The immersion data were used for generating the speed parameters used in the processing of tracks from non-breeding adults (see below, Table S1.1). In all cases, the total mass of devices including attachments was less than the 3% threshold of body mass beyond which deleterious effects are more common in pelagic seabirds (Phillips, Xavier, & Croxall, 2003).

Platform Terminal Transmitters and GPS tracks were processed using an iterative forward/backward-averaging filter (McConnell, Chambers, & Fedak, 1992) to remove any locations, which required sustained flight speeds above 80 km/hr (Berrow, Wood, & Prince, 2000). Data from GPS loggers and PTTs (during the ON periods only) were interpolated at hourly intervals to obtain regular positions, as this time step represented the coarsest tracking interval across datasets. GPS tracks from breeding adults were resampled to the same duty cycle as the tracks from juveniles in order to compare movement parameters between these life-history stages using an equivalent sampling regime.

Locations were estimated for adults tracked during the non-breeding period using the raw light intensities from the geolocators processed according to Merkel et al. (2016, see Appendix S1 for details). GLS data were not interpolated, as the estimated locations correspond to local midday and midnight. Juvenile tracks were resampled to 12-hr intervals to allow for comparisons of their movement parameters with those of the non-breeding adults. GLS locations were cropped to the juvenile departure dates from the colony to allow for the comparison of utilization distribution and overlap with fishing effort.

2.2 | Comparing movements and distributions between life-history stages

We compared the spatial distributions and movement characteristics (maximum range and average longitude; metrics #1 and #2 below) of juveniles and non-breeding adults at large spatial scales based on the twice-daily fixes from the PTTs and geolocators, and the movement characteristics (speed and track sinuosity; metrics #3 and #4 below) at small spatial scales based on the hourly interpolated PTT fixes and the GPS data from incubating adults, respectively (see above). The movement metrics were those commonly used for analyses of animal trajectories (Calenge, Dray, & Royer-Carenzi, 2009): (a) maximum range (maximum distance from the colony in km, calculated using function "spDistsN1" in package "sp"); (b) longitude averaged over weekly time periods for juveniles, and for the first eight weeks, post-departure, of non-breeding adults (corresponding to the maximum duration of a juvenile track; 57 days); (c) speed (in km/hr); and (d) track sinuosity (calculated as follows: $S = 1 - D_a/D_b$, with D_a the beeline distance between the first and last location of every "ON"

portion of the trip and D_b , the real distance travelled between the two locations). Speed and track sinuosity were also averaged over a weekly time period for juveniles to examine changes over time, as with metrics #1 and #2. Speed was square-root-transformed to improve data spread.

Linear mixed-effects models were run with each movement metric as the response variable and individual ID as a random effect, testing for differences between life-history stages as a function of time. For models with maximum range and longitude, the covariates included life-history stage (a factor with two levels; non-breeding adult *NB*, and juvenile *JUV*), weeks since departure from the colony (*WEEK*; factor with eight levels; 1–8) and their interaction. For models with speed and sinuosity, covariates included life-history stage (a factor with two levels; incubating *INC* adults, and juvenile *JUV*). Weekly differences were further investigated in juveniles only, where *WEEK* was again included as a factor with eight levels (1–8), to test whether juveniles showed signs of learning in terms of their flight abilities. For each model set, all possible combinations of predictors were computed and models were ranked according to Akaike information criterion (AICc) values, where the most supported model(s) were considered to be those within 2Δ AICc of the top model (Burnham & Anderson, 2004). Candidate models were excluded from this set if there were simpler nested versions with lower Δ AICc values (Arnold, 2010).

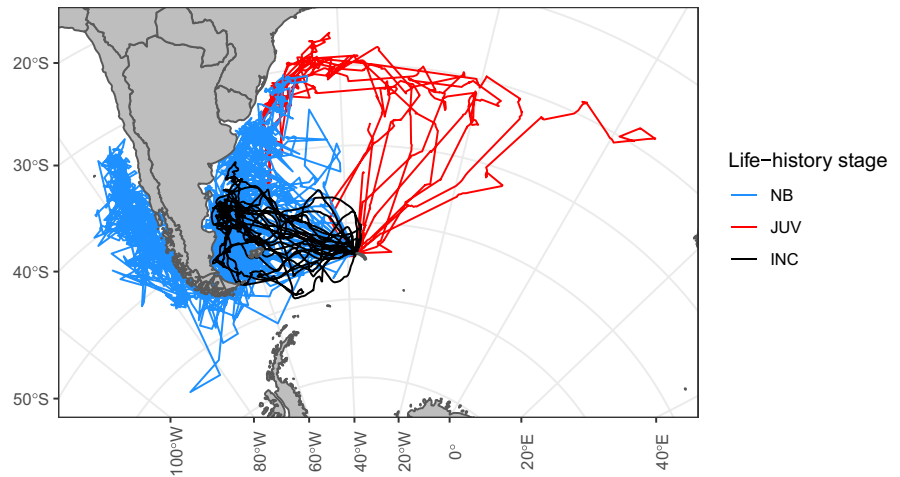
To determine whether juvenile and non-breeding adult white-chinned petrels differed in their weekly spatial distributions, we calculated utilization distribution (UD) kernels using the R package “adehabitatHR” (Calenge, 2006). We first carried out a resampling procedure to determine whether sample sizes were large enough to represent population-level space use (Tables S2.1 and Tables S2.2, and Figure S2.1; Clay et al., 2019). This was not the case, and therefore the subsequent analysis represents the utilization hotspots of the sampled individuals rather than the population. Plots of the increase in kernel area with isopleth level for each individual, stage and week, indicated that the 61% isopleth was the most appropriate for weekly cross-stage comparisons of core area, and the 95% isopleth best-represented the general use area (Figure S2.2 and Table S2.3; Vander Wal & Rodgers, 2012). To control for differences in individual track duration, separate UDs were generated weekly for each bird and then weighted by the proportion of locations from each bird with respect to the total number for all birds for a given stage-week combination. Weighted individual UDs were then summed to create weekly UDs for each life-history stage. A grid size of 5 km and a smoothing parameter of 185 km were chosen to account for geolocator error and applied to all datasets in this comparison to control for differences in location error from each type of device (Merkel et al., 2016). We then compared observed vs. randomized overlap in core and general use area between stages for each week using Bhattacharyya's affinity (BA) and previously established methods (Breed, Bowen, McMillan, & Leonard, 2006; see Appendix S2c for details).

2.3 | Mechanistic movement model

A two-parameter mechanistic model was used to investigate the potential drivers of juvenile and non-breeding adult movements (Revell & Somveille, 2017). This model simulates the movements of a bird away from a given location and through a potential landscape defined by two environmental factors: (a) attraction to chlorophyll a concentration (a proxy for food resources) and (b) the effect of wind (i.e. assistance). Both variables were modelled as described in Revell and Somveille (2017) at a monthly and 0.25° resolution. Remotely sensed chlorophyll data were obtained from NASA (https://neo.sci.gsfc.nasa.gov/view.php?datasetId=MY1DMM_CHLORA; Hu, Lee, & Franz, 2012) and zonal and meridional wind speed components from NOAA (<https://www.ncei.noaa.gov/thredds/catalog/uv/monthly/catalog.html>; Zhang, Bates, & Reynolds, 2006). These two datasets were averaged over the period from 2003 to 2015 to represent long-term conditions (i.e. a climatology) in the study area. We chose to use climatologies both to minimize gaps in measurements due to cloud cover, and because we hypothesize that differences in movement strategies of adults and juveniles are linked to longer term (i.e. evolutionary) environmental processes (Suryan, Santora, & Sydeman, 2012; Weimerskirch et al., 2000; Woodward & Gregg, 1998). As the NOAA dataset ends in 2011, the last four years (2011–2015) of monthly wind data were downloaded from Copernicus at the same spatial resolution for the two datasets (derived from SCATterometer [ASCAT] scatterometer onboard METOP-A and METOP-B satellites—WIND_GLO_WIND_L4_REP_OBSERVATIONS_012_003, <https://resources.marine.copernicus.eu/>; Bentamy & Fillon, 2012). Wind speed and direction were compared between the NOAA and ASCAT datasets in years when both were available (2008–2011); differences were found to be minimal and did not influence model simulation outcomes (Appendix S3). All environmental datasets were accessed in December 2019.

Within this potential landscape, the model framework assumes that birds are inherently attracted to resources, and we ran a range of scenarios varying the importance of the wind component relative to this attraction, characterized by the parameter a . Low values of a correspond to scenarios in which the effect of wind on movement patterns is minimal, and thus attraction to resources dominates, whereas progressively higher values of a reflect an increased role of wind on bird trajectories (Revell & Somveille, 2017). An initial search of the parameter space of a revealed that there was no further variation in results below $a = 0.005$ and above $a = 0.2$, and we interpreted these extreme values as scenarios in which effects of resource attraction and wind-assisted movement dominated, respectively. Simulations were then run for values of a as multiples of 0.015 from 0.005 to 0.2, to investigate a broad range of scenarios (84 simulations in total). Another unknown parameter kT , representing the degree of randomness in the movement decisions, was set to a low value (0.05; Revell & Somveille, 2017). All simulations began at Bird Island and were set to run for 3 months starting from April, the only month in which both non-breeding adults (6/16 birds) and juveniles (6/13 birds) departed from the colony in our study. Simulations

FIGURE 1 Distribution of adult (incubating, INC; and non-breeding, NB) and juvenile (JUV) white-chinned petrels *Procellaria aequinoctialis* tracked from Bird Island (South Georgia) during the 2014/15 breeding season and subsequent winter. Incubating ($n = 12$) and non-breeding ($n = 16$) adults were tracked using global positioning system (GPS) loggers and global location sensors (GLS), respectively, and juveniles ($n = 13$) using Platform Terminal Transmitters (PTT)



were run 6 times for each value of a to capture the behaviour of both life-history stages.

The similarity between the resulting simulated and observed (the 6 juvenile and 6 non-breeding adults which departed the colony in April) tracks was investigated using dynamic time warping (DTW), as this measure allows for the comparison of trajectories that may vary in time or speed (Cleasby et al., 2019; Ranacher & Tzavella, 2014). Pairwise DTW measures were computed for all tracks (simulated and observed), and the resulting distance matrix was examined using hierarchical clustering with a “ward-D2” linkage, which minimizes within-cluster variance. Tracks were clustered to investigate which scenario of simulated tracks most closely aligned with observed adult and juvenile tracks using an increasing number of groups (k) ranging in value between 2 and 5, at which points the tracks pertaining to a particular group (simulated, juvenile or non-breeding adult) were clustered separately.

2.4 | Juvenile and non-breeding adult distributions and overlap with fisheries

We analysed overlap by week of the distribution of juveniles and non-breeding adults with longline fishing effort based on vessel movements to investigate potential difference in susceptibility to bycatch. Weekly core UD_s were generated for each bird, resampled to a $0.1 \times 0.1^\circ$ resolution, and overlaid on a $0.1 \times 0.1^\circ$ grid of weekly fishing effort. Summed fishing effort per week for pelagic and demersal longline fisheries was collated from the Global Fishing Watch dataset (Global Fishing Watch [GFW], 2019, Option = “drifting longline”). GFW provides information on daily fishing effort (hours) of vessels transmitting their location using an automatic identification system (AIS). As AIS is fitted to only 50–75% of active vessels that are over 24 m in length (Kroodsmas et al., 2018; McCauley et al., 2016; Sala et al., 2018; Shepperson et al., 2018), we determined whether the GFW dataset accurately captured longline fishing effort of all important fleets within the study area (south Atlantic Ocean) and period (April–July 2015) by contrasting the overlap of bird distributions with pelagic longline fishing effort using both AIS data

(from GFW) and log-book effort data reported to the International Commission for the Conservation of Atlantic Tunas (ICCAT Task II Effort; <https://www.iccat.int/en/accessingdb.html> [accessed April 2020]). As effort data from ICCAT were available at monthly, $5 \times 5^\circ$ resolution, monthly core UD_s were generated for each bird for April and May (when sample sizes were high for juveniles), and resampled to a $5 \times 5^\circ$ resolution. Fishing intensity grids were obtained at the same spatial–temporal resolution for GFW data by summing $0.1 \times 0.1^\circ$ fishing effort (hours fishing) that fell within each $5 \times 5^\circ$ grid cell and daily effort for April and May of 2015 (Queiroz et al., 2019). Comparable effort data are not made available publicly for demersal fleets operating within EEZs (see data availability statement; Clay et al., 2019).

Linear mixed-effect models were run to test for differences over time in overlap of juveniles and non-breeding adults with GFW fishing activity. The overlap score (hours/week) was modelled as the response variable with individual ID as a random effect, and life-history stage (factor with two levels: non-breeding adult NB and juvenile JUV), and weeks since departure from the colony (*Week*; factor with eight levels; 1–8) were included as covariates. The overlap score was square-root-transformed to improve data spread. Model selection was conducted using the approach detailed in Section 2.2.

Unless otherwise indicated, all means in the Results are given \pm standard error (SE).

3 | RESULTS

3.1 | Distribution and movement characteristics of juveniles and adults

The juvenile white-chinned petrels fledged in April–May 2015 and dispersed in a northerly direction from South Georgia over a wide area of the south Atlantic Ocean (53.7°W – 4.7°E). Individuals were tracked for periods of 1–57 days, with the last transmissions received by the ARGOS system in July 2015 (Figure 1). The non-breeding adults tracked using geolocators began migration between late January and early May 2015 and spent the non-breeding period

on the Patagonian Shelf and shelf-slope from Tierra Del Fuego to south-eastern Brazil, the western Argentine Basin or the Humboldt Upwelling region off southern Chile. Adults tracked during incubation in December 2014 to January 2015 also travelled to the Patagonian Shelf, but foraged along the eastern coast of Argentina over what seems a more restricted area (the different accuracy of GPS and GLS data prevents a robust comparison) than that used by non-breeding adults (Figure 1 and see Tables S4.1 and S4.2 for complete tracking metadata).

Movement parameters of juvenile and non-breeding adults differed in the weeks following departure from the colony (Table 1a and Table S5.1 for full model selection and Figures 2a,b); these differences (522 km maximum range and 20° longitude, on average) were far greater than would be expected just from location error associated with the different types of tracking device (~185 km for geolocators; Merkel et al., 2016). There was strong weekly variability in the maximum ranges reached by individuals of both stages (Figure 2a), but overall maximum ranges increased during their first two weeks post-departure (juveniles: 1457 ± 105 and 2772 ± 118 km in weeks 1 and 2, respectively; non-breeding adults: 935 ± 87 and 1618 ± 87 km in weeks 1 and 2, respectively) and then plateaued, after which further displacement away from the colony was minimal (<82 km and < 433 km per week for juveniles and non-breeders, respectively). Average weekly longitudes also differed substantially between life-history stages; non-breeding adults travelled progressively west (reaching $64.2 \pm 1.9^\circ\text{W}$ in week 8), whereas juveniles initially travelled east and only in their second week post-fledging changed direction to head progressively west towards the South

American continent (to $47.4 \pm 3.1^\circ\text{W}$ in week 7, Figure 2b). Both the core and general use areas of the tracked juveniles differed significantly from those of non-breeding adults (Figure 3 and Table 2), although there was some overlap from the fourth week onwards, as juveniles moved towards waters off south-east Brazil and Uruguay (Table 2).

There was little evidence of an effect of life-history stage or number of weeks post-departure on the flight metrics of incubating adults and juveniles (Table 1a and Table S5.1 for full model selection and Figure 4a-d). While the two models for flight speed—with and without the covariate life-history stage—were both supported ($< 2 \Delta\text{AICc}$), the former predicted that juveniles flew only slightly faster (by approximately 3.7 km/hr) than incubating adults (Table 1 and Figure 4b). Track sinuosity was also similar between life-history stages (0.22 ± 0.01 , Table 1a and Figure 4a), and there was no effect of the number of weeks since fledging on the average speed and sinuosity of juveniles (Table 1a and Figures 4c,d).

3.2 | Mechanistic movement model

Hierarchical clustering of pairwise DTW distances provided strong evidence that, when compared to the simulated tracks, the observed tracks of juveniles were strongly influenced by wind, whereas those of non-breeding adults were influenced to a much greater extent by attraction to resources (see full hierarchical clustering results in Figure S6.1). Initially, the analysis grouped 60 simulated tracks into one cluster, and 24 simulated tracks and all

TABLE 1 Predictors retained in best supported linear mixed-effect models investigating differences in (a) movement metrics of adult (non-breeding, NB and incubating, INC) and juvenile (JUV) white-chinned petrels *Procellaria aequinoctialis*, and (b) overlap of the core distribution of NB and JUV birds with demersal and pelagic longline fishing effort

Life-history stages considered	Metrics	Predictor variables				df	AICc	ΔAICc	AICcw
		Intercept	Life-history stage	Week	Life-history stage: Week				
(a) Movement metrics									
NB vs. JUV	Maximum range (km)	x	x	x	x	18	2417	0.000	1.000
NB vs. JUV	Longitude (°)	x	x	x	x	18	1107	0.000	1.000
INC vs. JUV	Speed (km.hr ⁻¹)	x	x	NA	NA	4	901.5	0.000	0.654
		x		NA	NA	3	902.8	1.272	0.346
INC vs. JUV	Sinuosity	x		NA	NA	3	2.082	0.000	0.857
JUV	Speed (km.hr ⁻¹)	x	NA		NA	3	158.4	0.000	1.000
JUV	Sinuosity	x	NA		NA	3	-25.54	0.000	1.000
(b) Overlap metric									
NB vs. JUV	Overlap score (hours.week ⁻¹)	x	x	x	x	18	901.4	0.000	1.000

All birds were tracked from Bird Island (South Georgia) during the 2014/15 breeding season and subsequent winter. Models including all possible combinations of the predictor variables were considered and ranked according to Akaike information criterion (AICc). Those reported above were within 2Δ of the best model. "Life-history stages considered" indicates the life-history stages compared for a given movement metric; "x" predictor variables retained in the best models; "NA" variables that were not modelled; "df" the degrees of freedom; "Week" the weeks following departure from the colony; and "AICcw" the AICc weight, the relative probability that a given model is the best model. See Table S5.1 for all combinations of predictors considered for model selection.

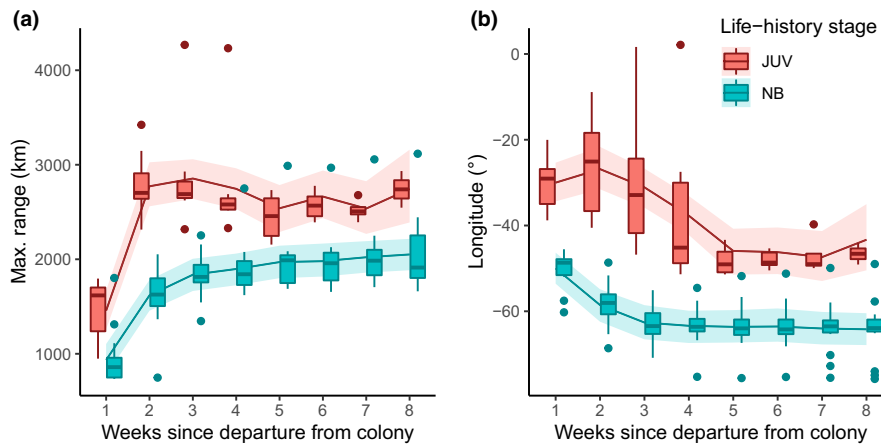


FIGURE 2 Predicted average population values for (a) maximum range from the colony and (b) longitude using fitted linear mixed models for juvenile (JUV) and non-breeding adult (NB) white-chinned petrels *Procellaria aequinoctialis* in the first eight weeks of departure from Bird Island (South Georgia) during the 2014/15 breeding season and subsequent winter. Lines and shading represent the model predictions and 95% confidence intervals for each life-history stage-week combination, respectively. Boxplots represent the spread of the observed data

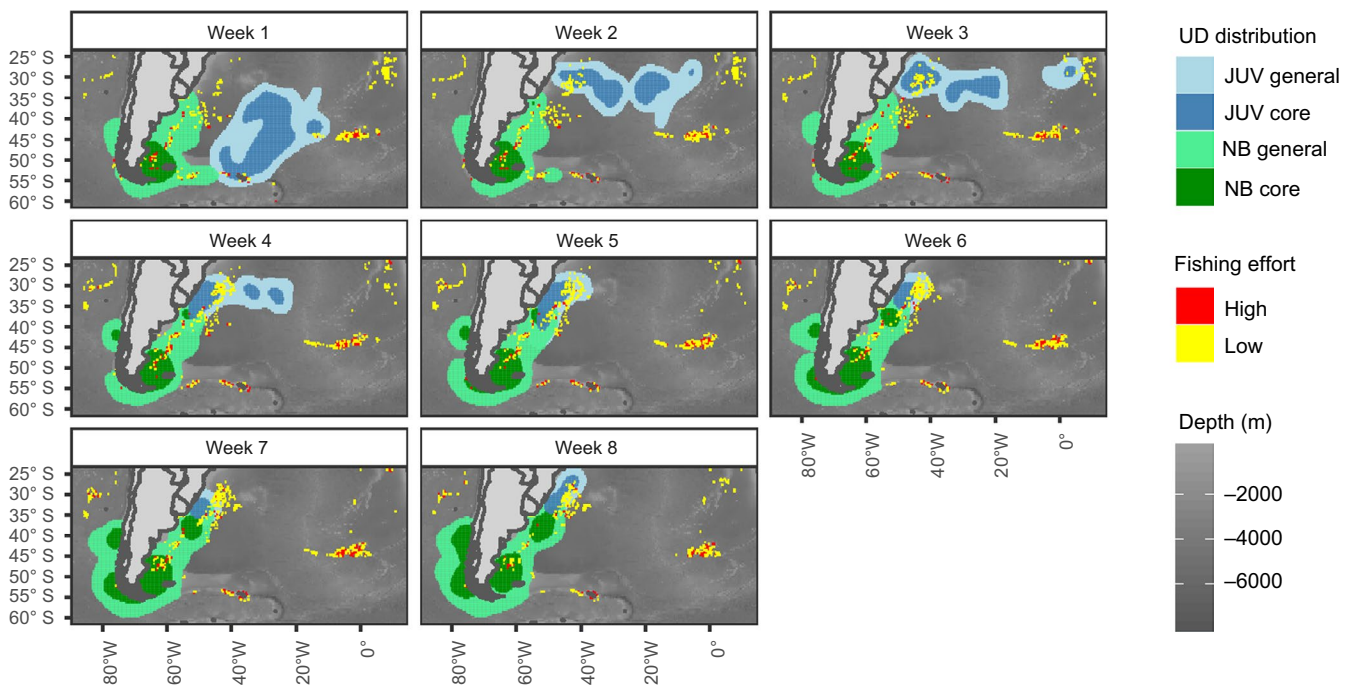


FIGURE 3 Weekly core (61%) and general (95%) utilization distributions of temporally overlapping juvenile (JUV) and non-breeding adult (NB) white-chinned petrels *Procellaria aequinoctialis* in relation to pelagic and demersal longline fishing during the first eight weeks post-fledging from Bird Island (South Georgia). Birds were tracked from Bird Island during the 2014/15 breeding season and subsequent winter. High and low levels of fishing effort are here determined according to the 75% quantile of overall fishing effort (hours/week); low effort <6.8 hours/week and high effort >6.8 hours/week based on the Global Fishing Watch (GFW) dataset

observed tracks (6 juvenile and 6 non-breeding adults) into a second cluster ($k = 2$). Increasing k to 3, however, separated the second cluster into two more groups: the first (Cluster 2; Figure 5d) containing all observed juvenile tracks and 18 simulated tracks, and the second (Cluster 3; Figure 5d) containing all observed non-breeding adult tracks and 6 simulated tracks. Increasing the number of clusters first separated all but one of the non-breeding adult tracks from the simulated tracks with a low a value ($k = 4$) and then

the juvenile tracks from the simulated tracks with a high a value ($k = 5$).

For $k = 3$, all simulated tracks from Cluster 2 corresponded to simulations run with higher values of a (0.11–0.2), suggesting that the routes taken by the tracked juveniles were strongly influenced by prevailing wind speed and direction in the south Atlantic Ocean (Figure 5b). Indeed, simulated and observed tracks in Cluster 2 indicated that routes of white-chinned petrels departing from South

TABLE 2 Observed and randomized overlap (Bhattacharyya's affinity index) of utilization distributions (UD) between juvenile (JUV) and non-breeding adult (NB) white-chinned petrels *Procellaria aequinoctialis* tracked over the first eight weeks since their departure from Bird Island (South Georgia) during the 2014/15 breeding season and subsequent winter

Sample size		WEEK	Core use area (61%)			General use area (95%)		
JUV	NB		Observed	Randomized	<i>p</i>	Observed	Randomized	<i>p</i>
11	16	1	0.00	0.76 ± 0.06	<0.001	0.00	0.73 ± 0.06	<.001
8	16	2	0.00	0.76 ± 0.08	<0.001	0.00	0.71 ± 0.07	<.001
8	16	3	0.00	0.76 ± 0.10	<0.001	0.00	0.71 ± 0.07	<.001
8	16	4	0.01	0.71 ± 0.12	0.001	0.10	0.77 ± 0.09	<.001
7	16	5	0.08	0.64 ± 0.13	<0.001	0.22	0.77 ± 0.09	<.001
6	16	6	0.00	0.54 ± 0.16	<0.001	0.09	0.72 ± 0.10	<.001
4	16	7	0.03	0.43 ± 0.24	0.012	0.21	0.65 ± 0.13	<.001
2	16	8	0.04	0.27 ± 0.22	0.037	0.13	0.48 ± 0.14	<.001

Randomized overlaps are shown as mean ± SD, and *p* represents the proportion of randomized overlaps that were smaller than the observed.

Georgia followed the prevailing westerly winds in a north-easterly direction until birds reached 30°S. North of 30°S, the prevailing winds are easterlies, and the birds changed direction accordingly, travelling west until they reached the nearest productivity hotspot located off the coast of Uruguay and south-east Brazil.

For $k = 3$, all simulated tracks in Cluster 3 corresponded to simulations run with the lowest a value possible (0.005), suggesting that dispersal patterns of non-breeding adults from the colony were driven by attraction to resources (Figure 5c). Simulated and observed birds from Cluster 3 followed slightly different trajectories, but they both dispersed towards the Patagonian Shelf. This is the closest area

to South Georgia with consistently high chlorophyll concentrations, particularly during the austral winter. Adults travelled into, rather than with the prevailing westerly winds to reach this region.

Finally, for $k = 3$, all tracks grouped within Cluster 1 corresponded to simulations run with intermediate values of a (0.02–0.185; Figure 5d), equating to a scenario in which movements are moderately influenced by wind relative to the attraction to resources. Simulated tracks were in a north-easterly direction until 30–45°S, at which point they turned directly east towards the productivity hotspot located off the coast of Namibia (Figure 5a). It is worth noting that one juvenile which departed from the colony in May also

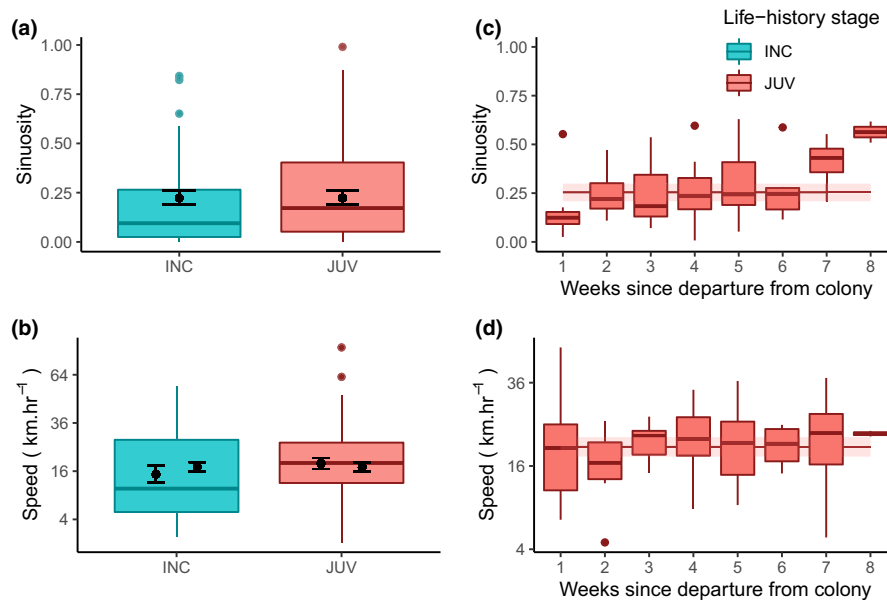


FIGURE 4 (a, b) Predicted average population values for sinuosity and speed using fitted linear mixed models for juveniles (JUV) and incubating adult (INC) white-chinned petrels *Procellaria aequinoctialis*. Dots and error bars represent the model predicted value and 95% confidence intervals for each life-history stage. Numbered dots and error bars in (b) represent the model predicted values and 95% confidence intervals for the top two models predicting speed. (c, d) Weekly predicted values are shown for juveniles only in the first eight weeks of dispersal from their natal colony. Lines and shading represent the model predicted value and 95% confidence intervals for each week, respectively. Boxplots represent the spread of the observed data in all plots. Values of transformed response variables are back-transformed on the y-axis (b–d) but the scale of the transformation is retained

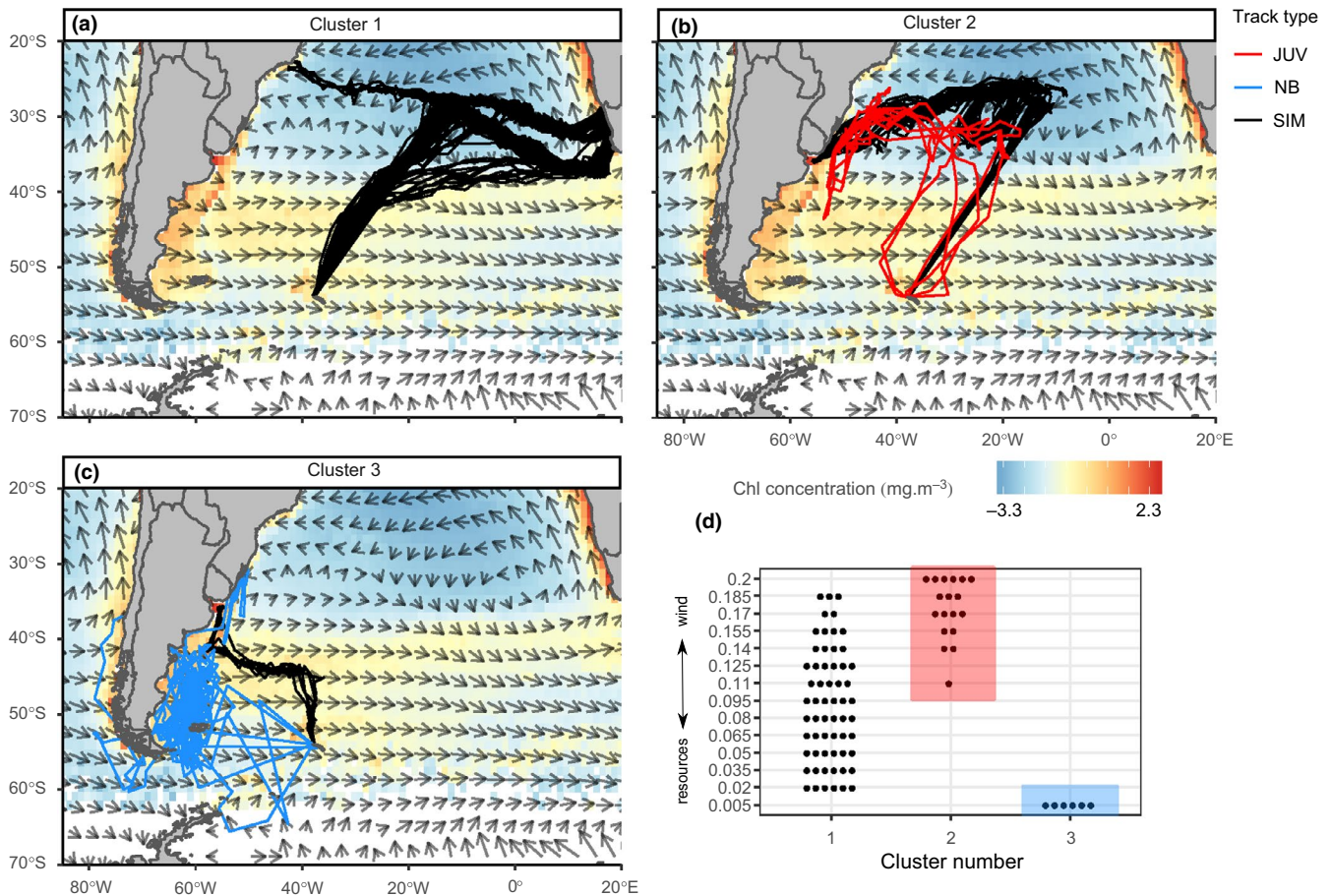


FIGURE 5 (a–c) Hierarchical clustering of observed (JUV = juvenile; NB = non-breeding adults) and model-simulated (SIM) tracks in relation to chlorophyll concentration and wind speed and direction. Results are shown for clustering of tracks into three groups ($k = 3$). Birds were tracked from Bird Island (South Georgia) in the 2014/15 breeding season and subsequent winter. Wind direction and speed are represented by the direction and length of arrows, respectively, and chlorophyll concentration is log-transformed. (d) The number of simulated tracks (represented by black dots) present in each cluster for a given value of α , and red- and blue-shaded boxes highlight the groups in which simulated tracks clustered with observed juvenile and non-breeding adult tracks, respectively

headed in this direction before the transmitter ran out, suggesting that heading towards the African coast may be a rare strategy conducted by a minority of individuals. Two simulated tracks went west instead, but towards more northerly locations along the South American coast, which would explain why they did not group into Cluster 2 for $k = 3$.

3.3 | Spatial overlap with longline fishing vessel activity

As a result of differences in their at-sea distributions, non-breeding adults and juveniles varied in the location and extent of their overlap with demersal and pelagic longline fishing activity (Figures 3, 6 & 7 and Table 1b and Table S5.1 for full model selection). On average, there was less longline fishing activity (by c. 130 hr, from vessels with active AIS) in the $0.1 \times 0.1^\circ$ grid cells used by juveniles than those used by non-breeding adults (Figure 6a), mainly because juveniles spent the first few weeks post-fledging in areas of the south Atlantic Ocean where few vessels operate (Figure 3). Although overlap scores

were lower for juveniles, they nevertheless overlapped with fishing vessels with active AIS from the first week after fledging from South Georgia. In addition, average scores increased over the study period, from a low of 0.03 hr in week 2 to a high of 9.55 hr in week 8, as individuals reached the coastal waters of Uruguay and south-east Brazil (Figures 3 and 6). In this region, however, there are likely to be a large proportion of vessels operating without active AIS, as coarser-scale analyses using ICCAT effort data revealed substantial overlap of juveniles with the fleets of Taiwan and Brazil, while overlap was negligible using GFW effort data (Figure 7).

The main areas of fisheries overlap were around South Georgia, along the coast from Argentina to south-east Brazil, around Tristan da Cunha, and off Namibia (Figures 3 and 7). Overlap of juveniles with longline vessels fitted with AIS was dominated by Spain (weeks 2–4 and 6–8), and, to lesser extents, Uruguay, Portugal, St. Helena and Ascension Islands and Taiwan (Figure 6b). Overlap with Taiwan may be underestimated, however, particularly in May, as revealed by the coarser-scale analysis of log-book data reported to ICCAT (Figure 7). Individuals also overlapped with Brazilian fleets in the same month, but to a lesser extent (Figure 7). Non-breeding adults

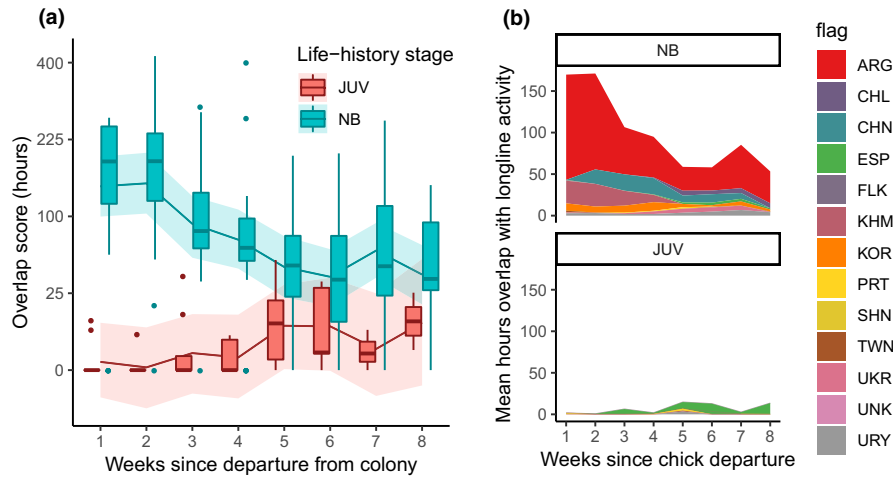


FIGURE 6 (a) Predicted average population values for overlap scores of the core use areas of juvenile (JUV) and non-breeding (NB) adult white-chinned petrels *Procellaria aequinoctialis* with pelagic and demersal longline fishing activity (obtained from Global Fishing Watch) using fitted linear mixed models over the first eight weeks of the dispersal of juveniles from their natal colony and the average corresponding temporal distribution for non-breeding adults. Lines and shading represent the model predicted value and 95% confidence intervals for each stage-week combination, respectively. Boxplots represent the spread of the observed data. (b) Mean fleet-specific overlap. ARG, Argentina; CHL = Chile; CHN, China; ESP, Spain; FLK, Falkland Islands; KHM, Cambodia; KOR, South Korea; PRT, Portugal; SHN, Saint Helena; TWN, Taiwan; UKR, Ukraine; UNK, Unknown; and URY, Uruguay

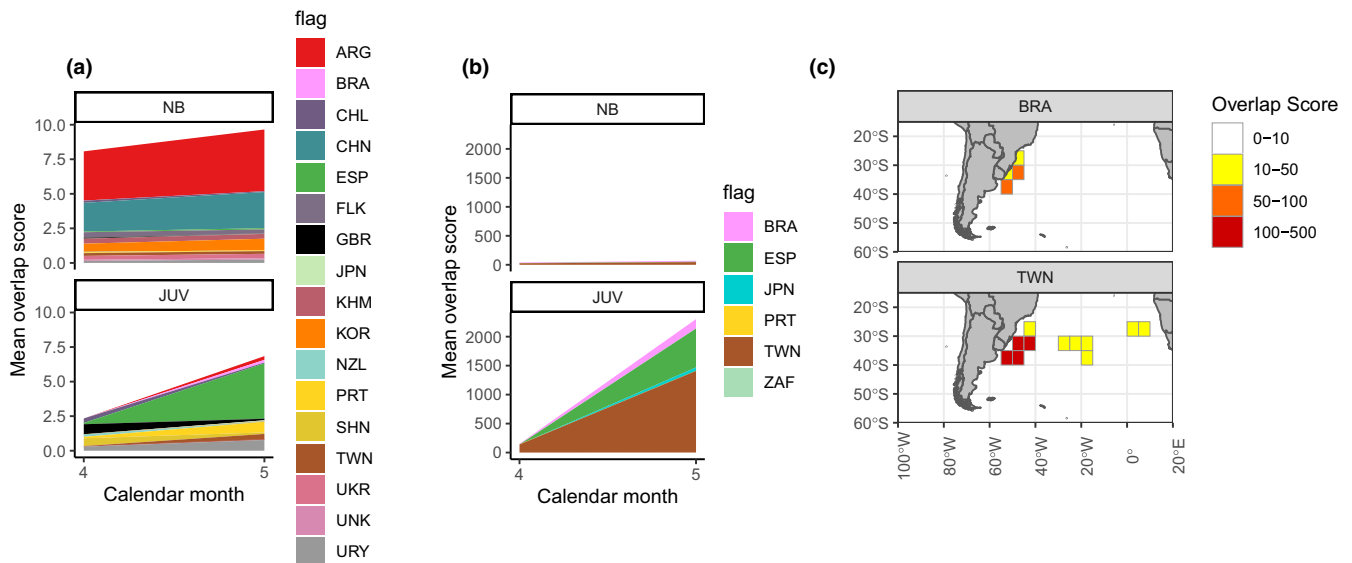


FIGURE 7 Mean individual overlap of the core use areas of juvenile (JUV) and non-breeding adult (NB) white-chinned petrels *Procellaria aequinoctialis* tracked from Bird Island (South Georgia) in the 2014/15 breeding season and subsequent winter with (a) longline effort (pelagic and demersal) as recorded in the Global Fishing Watch dataset (overlap score = hours $\times 10^3$), and (b) pelagic longline effort as reported to ICCAT (overlap score = hooks $\times 10^3$) for April and May 2015 (calendar months 4 and 5, respectively). (c) Overlap of the core use areas of juvenile white-chinned petrels with Brazilian and Taiwanese pelagic longline effort as reported to ICCAT in May 2015. Overlap score = hooks $\times 10^3$. ARG = Argentina; CHL = Chile; CHN = China; ESP = Spain; FLK = Falkland Islands; KHM = Cambodia; KOR = South Korea; PRT = Portugal; SHN = Saint Helena; TWN = Taiwan; UKR = Ukraine; UNK = Unknown and URY = Uruguay

overlapped more with longline fishing vessels with active AIS because they migrated to the productive Patagonian Shelf, where fishing activity was much more concentrated (Figure 3). Overlap was high from Tierra Del Fuego to south-east Brazil, and dominated by the fleets of Argentina (weeks 1–8), followed by Cambodia, China, South Korea, and, to a lesser extent, Uruguay, Chile, Ukraine, Spain, Taiwan, Portugal and the Falkland Islands (Figure 6b).

4 | DISCUSSION

Through combining individual tracking data and a mechanistic model, we found that juveniles and adults differed in their movement patterns and that movements were best explained by different processes: wind-assisted movement in juveniles and attraction to productive regions, irrespective of wind conditions, in adults. While

our study used tracking devices with different degrees of spatial error, by resampling locations to the same interval and smoothing spatial distributions to the same extent, we are confident the results represent true differences in behaviour between life-history stages. These results provide considerable insight into the ontogeny of movement strategies in the context of learned versus innate behaviour. Moreover, the divergent movement patterns of adults and juveniles have important implications for the conservation of this threatened seabird species.

4.1 | Ontogeny of movement strategies: learned vs. innate behaviour

The capacity for long-distance movement is widespread in the animal kingdom, and movement strategies are commonly thought to develop through a combination of learning (social or individual) or genetic programming in young life-history stages (Putman et al., 2014; Weinrich, 2008). In many species of birds (terrestrial and marine), young individuals may follow one or both of their parents on their first foraging flight or migration, allowing them to learn a migration route and the location of feeding areas, or to develop their foraging skills (Guo, Cao, Peng, Zhao, & Tang, 2010; Harding, Van Pelt, Liffjeld, & Mehlum, 2004; Regehr, Smith, Arquilla, & Cooke, 2001). In contrast, juvenile white-chinned petrels fledge independently from their parents and, as our study showed, rapidly flew large distances from the colony. Remarkably, their flight speeds and sinuosity were similar to those of breeding adults, suggesting comparable flight capability. Young individuals of other petrel and albatross species also disperse rapidly away from their natal colony, suggesting an innate ability to orientate with respect to wind direction, and fly with a high level of efficiency immediately after fledging (Alderman et al., 2010; de Grissac et al., 2016; Riotte-Lambert & Weimerskirch, 2013). This is not typical of other seabird taxa, however, which instead show progressive improvements in their flight performance with the number of days since fledging (Corbeau, Prudor, Kato, & Weimerskirch, 2019; Mendez, Prudor, & Weimerskirch, 2019; Yoda et al., 2004).

Navigating across the seemingly featureless pelagic ocean seems challenging, but innate flight skills may allow juveniles to search for patchily distributed resources across large spatial scales, similarly to adults (Adams, Brown, & Nagy, 1986; Alerstam, Hedenström, & Åkesson, 2003; Warham, 1990; Weimerskirch et al., 2000). Indeed, when the juvenile tracks were compared to model simulations, the best match was with environmental scenarios dominated by wind, suggesting movements of juveniles are strongly influenced by prevailing wind patterns in the south Atlantic. As the model assumes some inherent attraction to resources (Revell & Somveille 2017), even for wind-dominated scenarios, we were unable to simulate a scenario whereby there was full passive drift (like sea turtles with ocean currents; e.g. Scott, Marsh, & Hays, 2014). However, as prevailing winds at 40–60°S are westerly, we presume that under a full-drift scenario, birds would be carried eastwards such that they would very likely arrive in the Indian Ocean. None of the tracked

birds did this, but instead made directed movements northwards for >2,000 km before, for the most part, following trade winds westwards. While the cues used by juvenile seabirds to navigate are poorly known, we suggest that this initial direction is highly likely to be innate as it was followed by all our tracked juveniles. The same mechanism likely explains the initial bearings of juvenile white-chinned petrels, Indian yellow-nosed albatrosses *Thalassarche carteri* and black-browed albatrosses *T. melanophris* fledged from Kerguelen, Amsterdam or Crozet Islands, which make directed movements towards the productive coasts of South Africa or Australia (de Grissac et al., 2016). Ultimately, as juveniles in our study eventually reached a productive hotspot off the coast of Uruguay and south-east Brazil after several weeks of travel, wind-assisted movement may thus represent a low-energy strategy that minimizes costs of searching for prey if lacking prior knowledge of the environment.

Juveniles travelled along different routes to migrating adults; indeed, the routes taken by tracked adults towards the productive South American coast best matched resource-dominated scenarios, indicating that they migrate directly towards productive foraging habitats (Phillips, Silk, Croxall, & Afanasyev, 2006), based on prior knowledge of their environment (memory). In contrast, juveniles initially travelled across less productive waters in the first few weeks post-fledging, which presumably reduces competition with older birds while they refine their foraging skills (similar to northern and southern giant petrels, *Macronectes halli* and *M. giganteus*; de Grissac et al., 2016; Thiers et al. 2014). Although the tracking period only lasted eight weeks, the juvenile white-chinned petrels eventually reached a foraging area on the Patagonian Shelf just north of that used by non-breeding adults and presumably move progressively south into the latter over the following months or years. A similar ontogenetic shift in habitat use, often associated with changes in morphology, energetic demands or competitive abilities, has been recorded in a wide range of taxa, including seabirds, and may have far-reaching consequences in terms of the mortality risk of different age classes (Field, Bradshaw, Burton, Summer, & Hindell, 2005; Garcia-Berthou, 1999; Phillips, Lewis, González-Solís, & Daunt, 2017). Adult seabirds typically show very high fidelity to their main non-breeding areas, even if individuals show smaller-scale differences in migration routes, staging areas, etc., from year to year (Phillips et al. 2017). Hence, the juvenile phase seems to be critical in the development of a migration strategy that in most pelagic seabirds will persist through their life.

Finally, while the environmental variables considered here (particularly wind) vary substantially over small temporal scales (Desbiolles et al., 2017; Rivas, Dogliotti, & Gagliardini, 2006), simulated tracks generated using 12-year averages of resource availability and wind components matched observed tracks closely. This suggests that birds track environmental processes over longer time periods (both as a result of memory and innate mechanisms). Over the last decade, there has been little variation between years in ocean winds (Marcos, González-Reviriego, Torralba, Soret, & Doblás-Reyes, 2019); however, westerlies are gradually strengthening and shifting poleward, which may affect

initial juvenile dispersal in the future (Toggweiler, 2009). As for productivity, chlorophyll *a* concentration has generally increased over the Patagonian Shelf, presumably increasing attraction to this region associated with higher resource availability (Dunstan et al., 2018).

4.2 | Consequences of movement patterns for overlap with threats at sea

White-chinned petrels are one of the most common bycaught seabirds in longline fisheries, because they are numerous, compete aggressively for bait, offal and discards, can dive to >10 m, and occur in productive shelf habitats where fisheries are often concentrated (Barnes, Ryan, & Boix-Hinzen, 1997; Cherel, Weimerskirch, & Duhamel, 1996; Weimerskirch, Catard, Prince, Cherel, & Croxall, 1999). Adults from South Georgia winter on the Patagonian Shelf and off southern Chile, both areas of high demersal and pelagic longline fishing effort (Phillips et al., 2006). Overlap of core use areas of non-breeding adults with longline fishing activity (based on satellite AIS data) was therefore predictably high in our study, and many of the fleets have previously reported bycatch of white-chinned petrels (Argentina, Taiwan, Uruguay and Chile; Favero et al. 2013, Jiménez et al. 2009, Yeh et al. 2013 and Moreno et al. 2006, respectively), suggesting a good correspondence between overlap and bycatch rates. Our analysis did not indicate overlap between the non-breeding adults and Brazilian longline fleets—which have reported bycatch of white-chinned petrels (Bugoni et al. 2008), probably because many of those vessels are not fitted with AIS transponders, indicating a current limitation of the Global Fishing Watch dataset. Overlap with this fleet was also low when using effort data available from ICCAT, underlining potential gaps in reporting to RFMOs at a regional level. However, we revealed some overlap with longline vessels from Cambodia, China and South Korea, from which there are no published reports of seabird bycatch. Overlap indices are scale-dependent, and by studying overlap at fine spatial and temporal scales, our study highlighted new fleets for which bycatch may be a major concern, emphasizing the pressing need for much more comprehensive monitoring of seabird bycatch rates and uptake of mitigation (Phillips, 2013; Torres, Sagar, Thompson, & Phillips, 2013).

In contrast to adults, juveniles overlapped to a lesser extent with longline vessels fitted with active AIS. A low level of overlap occurred from the first week from fledging; however, it then increased over the following months as juveniles shifted distribution west towards the coast of South America. This has important implications for the dynamics and potential recovery of this threatened population. The naïve behaviour of juvenile seabirds is considered to render them more susceptible to bycatch than more experienced adult life stages (Gianuca, Phillips, Townley, & Votier, 2017). For the first two months, the juvenile white-chinned petrels mostly overlapped with pelagic longline fleets from a variety of flag states operating under the jurisdiction of ICCAT; south of 25°S, these are required to use

at least two of three mitigation measures: night setting, bird-scaring (Tori or streamer) lines and line weighting (Gilman, 2011; ICCAT, 2009). However, 95% of these vessels lack independent monitoring, observer coverage is poor, and, as a result, these measures are not implemented consistently (Brothers & Robertson, 2019; Gilman, 2011). It is thus likely that incidental mortality of juveniles occurs, which may be a major contributing factor to the population decline recorded at South Georgia (Berrow, Croxall, & Grant, 2000).

5 | CONCLUSION

Here, we demonstrated that a mechanistic movement model can be used to better understand the environmental drivers of divergent movement strategies within seabird populations. Moreover, due to their focus on underlying processes, mechanistic frameworks offer promising applications for predicting how individuals may be exposed to and respond to changes in their environment (Bocedi, Zurell, Reineking, & Travis, 2014; Evans et al., 2019; Leroux et al., 2013). It is also important that scientists continue tracking individuals across life-history stages to understand variation in the drivers of habitat use among and within species, and any consequences for susceptibility of each age class to different threats (Carneiro et al., 2020; Clay et al., 2019; Hazen et al., 2012). In the context of mitigating fisheries bycatch in seabirds, the development of exciting new bio-logging tools (e.g. loggers which detect ship radar; Weimerskirch, Filippi, Collet, Waugh, & Patrick, 2018) are paving the way for an increased understanding of marine predator–fisheries interactions at fine spatial–temporal scales, and will be crucial in setting future management priorities.

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PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13130>.

DATA AVAILABILITY STATEMENT

The datasets supporting the conclusions of this article are available for download from the BirdLife International Seabird Tracking Database (http://seabirdtracking.org/mapper/contributor.php?contributor_id=361); dataset ids: 1386, 1389 and 1500.

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BIOSKETCH

CKF is a PhD student at the British Antarctic Survey (Ecosystems Team) and the University of Cambridge (Evolutionary Ecology Group). She is interested in understanding the drivers of variation in movement in seabirds and the implications for fisheries bycatch mitigation.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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