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Ontogeny of movement patterns and habitat selection in juvenile albatrosses

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Optimal selection of foraging habitats is key to survival, but it remains unclear how naïve individuals are able to locate patchily-distributed resources and maximize energy gain in completely new environments. In most animals, juveniles disperse unaccompanied by their parents, and hence their movements are likely guided, at least at fine scales, by external cues. However, the extent to which environmental processes and individual learning shape habitat selection and movement strategies of juveniles remains unclear, especially in species with cryptic life-stages. Here, we use a mechanistic modelling framework – integrated step selection analysis – to examine the development of habitat preferences in a pelagic seabird with a prolonged period of immaturity, the grey-headed albatross *Thalassarche chrysostoma*. Juveniles were tracked from Bird Island, South Georgia, in two years ($n=9$ in 2018 and $n=12$ in 2019), using satellite transmitters (platform terminal transmitters), and we investigated ontogenetic changes in individual movement characteristics (step lengths and turning angles) in response to two environmental variables; tailwind support (which enables low-cost movement) and chlorophyll *a* concentration (a proxy for resources) during their first four months at sea. Naïve juveniles dispersed rapidly away from South Georgia towards the same general region (subantarctic and subtropical waters in the east Atlantic Ocean) by increasing their travel speeds and directional persistence in response to favourable wind conditions. In the first month post-fledging, juveniles also responded to local resource availability (chlorophyll *a* concentration) by reducing travel speeds in more productive regions, but thereafter engaged in comparatively slower and more sinuous movements, apparently focusing foraging effort on frontal zones. While complex movement strategies such as long-distance migrations may take several years to develop, our results indicate that dispersing juveniles are able to respond rapidly both to changes in wind and local resource availability, maximising flight and foraging efficiency.

Keywords: habitat selection, ontogeny, seabird ecology, step-selection, tracking

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Introduction

Habitat selection is the decision-making process through which animals choose resources according to their availability or accessibility (Johnson 1980). While the location of certain high-quality habitats may be predictable, food items are often patchily distributed in time and space, and a number of extrinsic and intrinsic processes (e.g. competition, predation and breeding constraints) may limit access to productive areas (Stephens and Krebs 1986, Fauchald 1999, Piatt et al. 2006, Phillips et al. 2017). Making optimal decisions about which habitats to target and how to access food patches requires individuals to recognize food, memorize profitable areas and reduce costs associated with travel between patches (Charnov 1976). Animals should ideally fine-tune their behaviour in response to fluctuating conditions, moving between food patches as they become depleted (Villard and Taylor 1994, Rebach 1996, Merkle et al. 2019, Beumer et al. 2020). As such, they should adopt specific habitat preferences and movement strategies (e.g. migration routes) that maximize individual fitness. However, it remains unclear how these vital skills develop in naïve individuals with no prior experience of their environment (Hazen et al. 2012, Kays et al. 2015, Pyke 2019).

In many animals with parental care, juveniles undergo a transition from dependence on delivered food to independent feeding (Clutton-Brock 1991). Mortality is often high during this period, which is traditionally attributed to lower foraging efficiency in young individuals because of their inexperience and physical immaturity (Lack 1954, Ashmole 1963). Young of some species benefit from extended parental support (e.g. primates, tropical passerines and frigatebirds; Clutton-Brock 1991, Russell 2000), but in others (e.g. sea turtles, procellariform seabirds and phocid seals; Shillinger et al. 2012, de Grissac et al. 2016, Orgeret et al. 2019), they are abandoned at their natal sites and, as they disperse, must acquire food in an unknown environment with no such guidance. In these instances, skills necessary for finding food may be genetically determined, such as the ability to navigate or to move efficiently by exploiting favourable winds (Vega et al. 2016, Frankish et al. 2020). It is also likely that individuals undergo a period of learning and adjustment to their environment during which external cues (physical, chemical, biological and social) play an important role in shaping initial movements (Watts 1985, Kennedy and Ward 2003, Campagna et al. 2006, Vila Pouca et al. 2020).

Quantifying the relationship between environmental conditions and early-life behaviour can be challenging as juveniles typically have lower survival rates and may be smaller than adults, and disperse to remote areas, making them difficult to observe for long periods of time (Hazen et al. 2012, Kays et al. 2015). In particular, within marine environments, juveniles of many species seemingly 'disappear' for many years before returning to their natal grounds to breed. Developments in tracking technology (miniaturisation and improvements to battery life) are progressively uncovering the movements of these cryptic life-stages, but have mainly focused on determining habitat associations or describing general movement patterns, e.g. by comparing juveniles and adults, rather than the mechanisms underpinning individual movement decisions (Andersen et al. 2013, Ketchum et al. 2013, Gutowsky et al. 2014). However, the latter may be explored by new analytical frameworks which model animal movement as a series of discrete steps, characterised by specific velocity and autocorrelation distributions, and provide tools for identifying the key extrinsic (environmental) drivers (Breed et al. 2018, Biddlecombe et al. 2020, Carter et al. 2020). In particular, integrated step-selection functions seem well-suited for investigating how strategies develop in naïve individuals, as they can be used to examine the processes influencing foraging-habitat selection (e.g. oceanography and prey availability; Roberts et al. 2021), whilst also testing for responses to conditions encountered along movement paths, such as ocean currents or wind (Avgar et al. 2016, Nourani et al. 2018).

Pelagic seabirds dispersing at sea after fledging represent exemplary study systems for researching ontogenetic changes in movements and habitat selection, as there is a prolonged period of immaturity during which naïve individuals must learn to navigate a seemingly featureless ocean in search of sparse prey patches (MacLean 1986, Weimerskirch et al. 2014). Adults are reliant on winds to cover great distances at low energetic cost (Weimerskirch et al. 2000), and generally switch from fast and directed movement (indicative of travelling) to slow and sinuous movement (indicative of searching or foraging) in response to both static topographic (e.g. continental shelf-break; Freeman et al. 2010) and dynamic oceanographic features (e.g. mesoscale fronts, eddies; Dean et al. 2013, Scales et al. 2016) which are known to concentrate prey. Tracking studies have shown that juveniles are similarly capable of very large-scale movements post-fledging and that they show a tendency to switch to more sinuous exploratory movements over time (Alderman et al. 2010, de Grissac et al. 2016, Corbeau et al. 2019). However, our understanding is still limited of how juveniles respond to changing conditions as they disperse, and how this generates overall movement patterns. Determining the main environmental cues used by juveniles may help explain the high degree of individual specialisation in movement and migration patterns observed in adults of many seabird species (Phillips et al. 2017). It would also shed light on how naïve individuals survive the initial, critical learning period; this has major implications for conservation given these life-stage can make up to 50% of seabird populations, many of which are threatened (Weimerskirch et al. 1997, Sæther and Bakke 2000, Pardo et al. 2017).

Here we use integrated step-selection analysis to investigate ontogeny of movement patterns in a very long-lived and wide-ranging seabird, the grey-headed albatross *Thalassarche chrysostoma*. Specifically, we analysed movement data from juveniles tracked from Bird Island, South Georgia, in 2018 and 2019 with the aims of determining 1) general post-fledging movements, 2) whether individuals showed a change in movement characteristics (step lengths and turning angles) during the first months at sea and 3) how they responded to local environmental conditions, specifically tailwind support (a driver of low-cost movement) and chlorophyll *a* concentration (a proxy for prey availability) and 4) if movements in response to environmental cues changed over time. Given naïve individuals have no prior experience of their environment, we hypothesized that juveniles would reduce travel costs by dispersing away from their colony via a low-cost route, i.e. using prevailing winds. Thus, we expected increased tailwind support to increase displacement rate and directional persistence, as seen in travelling adult albatrosses which use fast directed flight to efficiently cover large distances (Clay et al. 2020). Secondly, as individuals develop their foraging skills or encounter favourable habitats over time, we hypothesized that the distribution of productive resources plays an increasingly important role in determining how juveniles move irrespective of wind conditions, i.e. that there would be inverse relationships between displacement rate, directional persistence and chlorophyll *a* concentration.

Material and methods

Deployments and tracking data processing

Juvenile grey-headed albatrosses were tracked after fledging from Bird Island, South Georgia (54°00′S, 38°03′W), in May–June 2018 (n = 9) and 2019 (n = 14) using Telonics TAV-2630 satellite transmitters (Platform Terminal Transmitters, PTTs) with a duty cycle of 8-h ON and 48-h OFF for 101.1 ± 47.5 and 82.7 ± 54.3 days on average in 2018 and 2019, respectively (for details see Frankish et al. 2021). PTTs were attached to the back feathers using Tesa tape and provided locations every 40 min on average during ON periods. In all cases, the total mass of devices (40 g, including tape) was less than the 3% threshold of body mass beyond which deleterious effects are more common in pelagic seabirds (Phillips et al. 2003). All locations from PTTs in ARGOS classes A, B, 0, 1, 2 and 3 were used, but unrealistic positions requiring a sustained flight speed of over 90 km h^{-1} were removed (McConnell et al. 1992). In order to obtain regular positions required for subsequent analysis, only movements within ON periods were considered for analysis, based on locations linearly-interpolated at 40-min intervals from the PTT fixes using function 'redisltraj' from package adehabitatLT (Calenge 2006). Data from ON periods with only one or two locations were removed from the analysis because they did not enable calculation of turning angles. Interpolating movement data can obscure the exact timing of changes in behaviour; however, the sampling resolution in this study was in any case relatively coarse and unlikely to capture fine-scale movement decisions. Instead, as adult grey-headed albatrosses can cover very large distances when migrating (Clay et al. 2016), the aim was to investigate changes in behaviour at similar spatio–temporal scales (e.g. remaining within versus travelling between oceanic regions). All data manipulations and analyses were conducted in R ver. 3.6.2 (<www.r-project.org>).

Integrated step-selection models

We used integrated step-selection analysis (*i*SSA; Avgar et al. 2016), which is an ideal framework for modelling the processes influencing movement decisions of naïve animals. It tests for responses to external conditions encountered en route, thereby approximating a juvenile exploring its environment for the first time. This is distinct from various types of species distribution models, which generally examine the selection of specific habitats and assume prior knowledge of the accessible area (Carneiro et al. 2016, Clay et al. 2016, Scales et al. 2016). Instead, consecutive movements are represented by a fixed time step length and turning angle (the distance and change in travel direction between consecutive locations, respectively). In addition, environmental covariates can be extracted at the start of individual steps and included in the *i*SSA as an interaction to test for a significant effect on the response of individuals to local conditions, by comparing observed step characteristics with those of possible steps randomly sampled from analytical distributions fitted to all observed step lengths and turning angles. Here, we computed step lengths and turning angles from the tracking data using the amt package for managing and analysing animal movement data (Signer et al. 2019), and investigated the response of individuals to two environmental variables; 1) chlorophyll *a* concentration (a proxy for prey resources), and 2) tailwind support (a proxy for the cost of movement; Wakefield et al. 2009b). Although grey-headed albatrosses are known to forage in association with mesoscale oceanographic features (e.g. oceanic fronts and eddies), previous studies have found chlorophyll *a* concentration to be a better predictor of habitat use (Clay et al. 2016, Scales et al. 2016). It was not possible to include additional metrics (e.g. of frontal activity) given problems with over-parameterizing models which include three-way interactions.

Monthly remotely-sensed chlorophyll data ('chl') were obtained from the GlobColour-merged chlorophyll *a* product disseminated via the Copernicus Marine Environmental Monitoring Service (<https://resources.marine.copernicus.eu/?option=com_csw&view=details&product_id=OCEANCOLOUR_GLO_CHL_L4_REP_OBSERVATIONS_009_082>; accessed June 2020; Garnesson et al. 2019). Wind speeds (V_w) and directions were computed from hourly zonal and meridional wind speed components downloaded from the European Centre for Medium Range Weather Forecasts (ECMWF) ERA5 reanalysis dataset (<https://doi.org/10.24381/cds.adbb2d47>; accessed June 2020). These data are available at 10 m a.s.l. , but as mean recorded flight heights for grey-headed albatrosses are ~ 3.5 m a.s.l., wind speeds were reduced to this height using a logarithmic model of wind gradient (assuming a scale height of 0.03 m; Pennycuick 1982, Wakefield et al. 2009b). Tailwind support ('tailwind'), defined as the length of the wind vector in the direction of flight, was then calculated as $V_{tw} = V_w \cos\theta$, where θ is the difference between the track and wind directions (Safi et al. 2013). Both environmental variables were available at a 0.25° spatial resolution, corresponding to around 15–25 km at the latitudes used by tracked birds, and were projected using a Lambert azimuthal equal-area projection centred at 90°S and 38°W to limit distortion. Mean covariate values at each tracking location were extracted using a 1.5 km buffer with the function *gBuffer* in package raster (Hijmans et al. 2010) to account for PTT location error (CLS Argos 2008), and standardized using the function *scale* available within base R.

In order to determine how movement in response to environmental variables changed over time, we included the calendar month since fledging ('month') as a factor interacting with step lengths, turning angles and environmental covariates in four three-way interactions; 1) month × step × tailwind, 2) month × step × chl, 3) month × turn × tailwind and 4) month × turn × chl. Changes in behaviour were evaluated on a monthly scale to better capture ontogenetic processes, rather than variation driven by differences in the environments encountered by individual birds on shorter temporal scales (e.g. daily or weekly). In addition, 'month' was included as a factor rather than a continuous variable to avoid making assumptions about how individuals respond to their environment over time. As the sample size of tracked individuals reduced in number over time due to device failure or mortality, we applied the *i*SSA to the movement data from the first four post-fledging months only (Supporting information).

Juveniles tracked in 2018 and 2019 did not differ significantly in terms of their step-length distribution and only to a small extent in terms of turning-angle distribution (yearly means differed by ~ 0.02 radians), and were therefore pooled to increase monthly sample sizes (Supporting information). Individual steps were then assigned to daylight or darkness using function *crepuscule* in package maptools to determine the timing of civil twilight, when the sun is 6 degrees below the horizon (Bivand and Lewis-Koh 2017). Step lengths of birds were much shorter during darkness than daylight (9.1 ± 12.1 versus 23.7 ± 18.1 km h^{-1}) suggesting that juveniles rarely travel or search for prey during darkness (Supporting information and in line with de Grissac et al. 2017, Pajot et al. 2021); hence steps occurring during the night were excluded from the *i*SSA. A further two birds were removed from the final test dataset as observations were too few (< 26) to account for within-individual temporal autocorrelation. Finally, to control for individual variation in movement parameters, our model was fitted using mixed-effects conditional Poisson regression with stratum (sets of one observed step and 50 time-matched random steps)-specific intercepts within package glmmTMB (Brooks et al. 2017, Muff et al. 2020). This modelling framework is the likelihood equivalent of mixed-effects conditional logistic regression (the standard modelling technique used to fit *i*SSAs; Signer et al. 2019), and allows for a mixed-*i*SSA to be fitted in one straightforward step using standard statistical software. As estimating stratum-specific intercepts is not of interest in step-selection functions, they were incorporated as random intercepts with large, fixed variances and random slopes were added to control for potential individual heterogeneity in step length and turning angle distributions (Muff et al. 2020). As our sample size was relatively small and individuals were tracked for differing lengths of time (Supporting information), we did not attempt to fit a more complex random-effects structure accounting for among-individual variation in the two- and three-way interactions between movement characteristics, environmental variables and time since fledging; consequently, the *i*SSA may underestimate confidence intervals for these responses (Muff et al. 2020).

The remaining observed steps (n = 2476 total steps; n = 837 in month 1, n = 637 in month n = 2, 566 in month 3 and n = 436 in month 4) were each matched with 50 random steps, as a set of models consisting of all observed steps and varying numbers of random steps (up to 100) found that coefficients for each parameter and model cross-validation scores stabilized around 25–50 random steps (Supporting information). Random steps were generated by sampling step lengths and turning angles from statistical distributions fitted to observed steps (the Gamma and the Von Mises distributions for step length and turning angle respectively) using the function *random_steps* from the package amt (Signer et al. 2019). Resulting coefficients from fitted *i*SSAs represent likelihood-based estimates of the shape of these underlying statistical distributions and, prior to fitting, all step lengths and turning angles (observed and random) were log- and cosine-transformed, respectively, to correct for any bias introduced by the way random steps were generated (for detailed explanation see Duchesne et al. 2015, Avgar et al. 2016). All possible combinations of predictors were then computed and models ranked according to Akaike information criterion (AIC) values, where the best supported model(s) were considered to be those within 2Δ AIC of the top model (Burnham and Anderson 2004). Candidate models were excluded from this set if there were simpler nested versions with lower AIC values (Arnold 2010). To account for temporal autocorrelation among observations, we estimated confidence intervals for our best-supported models from robust standard errors calculated following the approach of Forester et al. (2009). We clustered our data based on the lag of significant temporal autocorrelation (lag = 26) and placed every other cluster per individual in a second dataset. Robust standard errors were then calculated by averaging the covariance matrices for models fitted to both subsets of data. Parameter estimates however represent fitted values from the full dataset. Model fit was assessed using *k*-fold cross-validation adapted for a case-control design, on 80% of randomly selected strata (groupings comprised of one observed and 50 random steps) to generate predictions for observed and random steps within the withheld strata 100 times (Fortin et al. 2009). This approach yields an average Spearman rank correlation (r_s) and associated 95% confidence intervals for observed (r_{obs}) and random steps (r_{rand}). Robust models are considered to have high r_{obs} relative to r_{rand}. Finally, we calculated expected average movement rates as a function of tailwind support, chlorophyll *a* concentration and month since fledging using the following equation (Fig. 3):

$$\text{Movement rate}\left(\frac{\text{metres}}{40\ \text{min}}\right) = b_2 \times \left[b_1 + \beta_{\log(\text{step})} + \left(\beta_{(1\ldots n)} \times x_{(1\ldots n)} \right) \right] \quad (1)$$

where b_1 and b_2 are the tentative shape and scale values respectively of the gamma distribution previously fitted to observed step lengths, $\beta_{\log(\text{step})}$ is the estimated coefficient for the natural logarithm of step length 'log(step)' and $\beta_{(1\ldots n)}$ are the estimated coefficients for the interactions between covariates $x_{(1\ldots n)}$ and 'log(step)' (Avgar et al. 2016, Ladle et al. 2019). Unless otherwise indicated, all means in the Results are given ± standard deviation (SD).

Results

General description of post-fledging movements

The juvenile grey-headed albatrosses fledged from Bird Island in May–June 2018 and 2019 and dispersed away from the colony at very large spatial scales, with two individuals conducting near-complete global circumnavigations within 5–7 months of fledging (Fig. 1a, b, Table 1). Initially, all individuals dispersed in a northeasterly direction towards South Africa, and by the end of the first month were an average of 4435 ± 1471 km from the natal colony. Thereafter, movements were more restricted as most individuals remained within the southeast Atlantic and southwest Indian Oceans between 10°W–81°E and 50°–27°S (4006 ± 1776 km from Bird Island). However, three juveniles travelled much further east, reaching south of Australia, the southwest Pacific Ocean and southern Chile. One individual showed a third strategy, returning west towards South Georgia in its third month at sea and remaining within 1428 ± 583 km of the islands until the PTT stopped transmitting (see the Supporting information for monthly distributions).

Changes in movement patterns and response to environmental conditions

Although there was some individual variation in monthly distributions, the best-supported *i*SSA provided strong evidence for a change in behaviour in months 2–4 relative to month 1 since fledging, indicated by the three-way interactions between month, tailwind support and step length or turning angle in the best-supported model (Table 2). Model results were robust to cross-validation as r_{obs}, the correlation of predictions for observed steps, was relatively high compared to r_{rand}, the correlation of predictions for random steps (Table 2). These models predicted that individuals moved faster and in a more directed manner during their first month at sea than during later months (positive coefficients for step length and turning angle in month 1; Fig. 2), and longer steps (~22 km h^{-1} predicted increase in travel speed from tailwind speeds of −15 to 15 m s^{-1} at low chlorophyll *a* concentrations (< 0.5 mg cm^{-3})) and lower turning angles occurred in regions of high tailwind support (Fig. 2, 3b). After arrival in the southeast Atlantic (month 1; Fig. 3a), juveniles showed a significant decrease in average travel speeds (a maximum decrease of around 8–13 km h^{-1} at high tailwind speeds (> 14 m s^{-1}) and low chlorophyll *a* concentrations (< 0.5 mg cm^{-3}), indicated by a lower step length coefficient; Fig. 2, 3b), and a progressive increase in path sinuosity (indicated by lower directional persistence; Fig. 2) in months 2–4. During month 3 and 4, individuals appeared to settle in oceanic frontal regions (between the Subtropical and Polar fronts) (Fig. 3a), and responses to tailwind support in terms

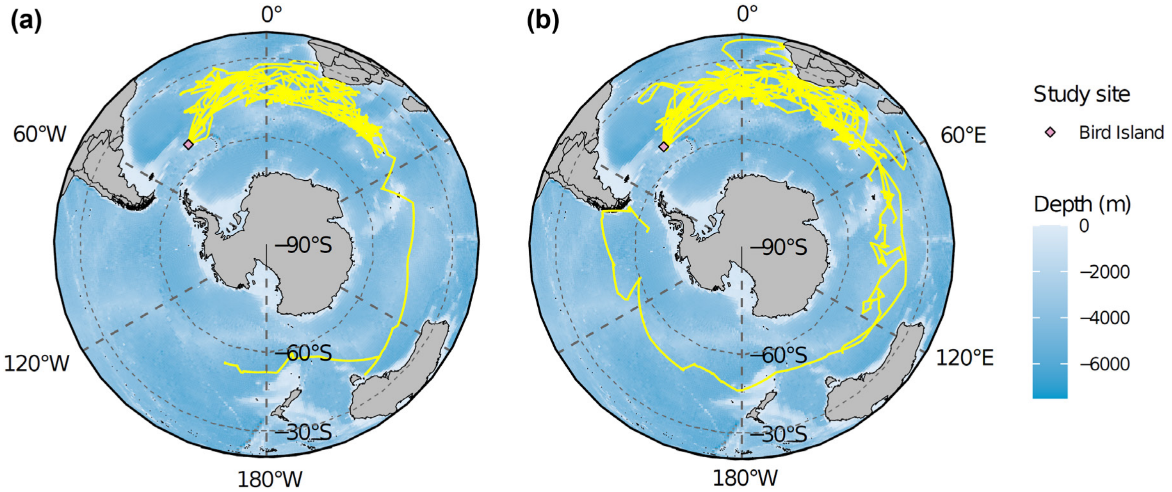

Figure 1. At-sea distribution of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in (a) 2018 (n = 9) and (b) 2019 (n = 14) using platform terminal transmitters (PTTs), and underlying bathymetry (downloaded using function *getNOAA.bathy* from R package marmap; Amante and Eakins 2009).

Table 1. Summary of post-fledging movements of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in 2018 and 2019 using platform terminal transmitters (PTTs).

Month since fledging	Sample size	Calendar month(s)	Maximum distance from Bird Island (km; mean ± standard deviation)	Range	Oceanic regions used
1	23	May–July	4435 ± 1471	48°48'W–64°45'E 56°04'–18°48'S	Southeast Atlantic and southwest Indian Oceans
2	20	June–August	5093 ± 1271	10°01'W–62°42'E 49°56'–15°69'S	Southeast Atlantic and southwest Indian Oceans
3	16	July–August	5073 ± 1265	35°32'W–96°96'E 53°29'–31°31'S	Central south Atlantic, southeast Atlantic, southwest Indian and central south Indian Oceans
4	12	August–September	6089 ± 1979	34°29'W–136°55'E 51°66'–37°49'S	Central south Atlantic, southeast Atlantic, southeast and southwest Indian Oceans
5	6	September–October	5836 ± 2520	179°57'W–164°93'E 60°50'–39°43'S	Southwest Atlantic, southeast Atlantic, southwest Indian and south Pacific Oceans
6	4	October–November	6427 ± 2928	80°92'W–142°79'E 63°91'–40°43'S	Southeast Pacific, southeast Atlantic, southeast and southwest Indian Oceans
7	1	December	9370	169°74'W–179°26'E 58°70'–41°87'S	Southwest Pacific Ocean

of turning angles were minimal relative to month 1 (Fig. 2), even though mean tailwind support was similar (~ −15 to 21 m s^{-1} in month 2 and −15 to 15 m s^{-1} in month 1, 3 and 4; Fig. 3b). The interaction of step length with tailwind support followed a similar pattern over time, but this response was only significantly different from month 1 in month 3 since fledging (Fig. 2).

Juveniles also altered their movements in response to chlorophyll *a*, as the best-supported model retained the two-way interaction between step length and chlorophyll *a* concentration (Table 2). Juveniles decreased travel speeds in response to increasing productivity regardless of time since fledging (~ 6–39 km h^{-1} predicted decrease in travel speeds across the range of chlorophyll *a* values encountered per month since fledging, Fig. 3b), as indicated by a negative interaction coefficient between step length and chlorophyll *a* concentration (Fig. 2). The best-supported model retained the two-way interaction between turning angle and chlorophyll *a* concentration, but the negative interaction coefficient between these two variables was not considered significant as the confidence intervals included 0 (Fig. 2).

Discussion

Using integrated step selection analysis (*i*SSA), we show a clear change in movement characteristics and responses to environmental conditions of juvenile albatrosses tracked over the first four months post-fledging. Juveniles engaged in fast and directed travel in response to tailwinds during their first month at sea and reduced travel speeds when they encountered more productive regions; thereafter, they switched to slower and more sinuous movements. These results provide new insights into the environmental drivers of behaviour in naïve individuals, as well as the timing and development of broad-scale movement strategies in a very wide-ranging and long-lived seabird species.

Response to winds in dispersing juveniles

The ability to use prevailing winds efficiently to reach distant locations (e.g. foraging grounds), thereby lowering travel costs, is well-established in procellariiform seabirds (Wakefield et al. 2009b), as well as in terrestrial birds (Kemp et al. 2010), and is comparable to the use of ocean currents by swimming animals during long-distance migrations (Lambardi et al. 2008). Adult procellariiform seabirds often orient favourably with respect to wind direction, and by using crosswinds or tailwinds, they benefit from increased ground speeds or reduced energy expenditure associated with flapping (Weimerskirch et al. 2000, González-Solís et al. 2009, Amelineau et al. 2014). Previous work has shown that juveniles of several seabird species are able to orient with respect to wind direction almost immediately after fledging, or learn to do so over the first few months at sea (Riotte-Lambert and Weimerskirch 2013, Collet et al. 2020, Syposz et al. 2021).

In our study, the fledgling grey-headed albatrosses were able to exploit prevailing westerlies to rapidly reach the productive frontal zones in the southeast Atlantic within their first month at sea, as they moved faster and in a more directed manner in response to increasing tailwind support. Thereafter, responses to tailwinds in terms of directional persistence were minimal, and average speeds and directional travel were reduced, suggesting juveniles had reached favourable foraging destinations, a pattern that was broadly common to all the tracked individuals. It could be argued that passive drift, as used by juvenile sea turtles in ocean currents (Scott et al. 2014), accounts for the movement patterns that we observed in the tracked albatrosses. However, the remarkably similar initial bearings and consistent reduction in travel speeds from month 2 onwards, despite the similar tailwind speeds experienced in all months, lends support to the hypothesis that migratory birds with limited post-natal care use an innate compass (Perdeck 1958, Yoda et al. 2017, Wynn et al. 2020). In this case, naïve individuals use winds to maximise travel efficiency across a comparatively unproductive oceanic

Table 2. Predictors retained in the best-supported Poisson GLMM investigating the effects of tailwind support ('tailwind'), chlorophyll *a* concentration (a proxy for prey resources; 'chl') and time (months since fledging; 'month') on the movement characteristics (step lengths; 'step', and turning angles; 'turn') of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in 2018 (n = 9) and 2019 (n = 12) using platform terminal transmitters (PTTs). Models including all possible combinations of the predictor variables were considered and ranked according to Akaike information criterion (AIC). Those reported below were within 2Δ of the best model. 'x' indicates predictor variables that were retained in top models; 'weight' the relative probability that a given model is the best model; r_{obs} and r_{rand} means and 95 confidence intervals are metrics of model performance generated using *k*-fold cross-validation adapted for case-control design.

Model	Predictors																	
no.	Step	Step:month	Step:chl	Step:chl:month	Step:tailwind	Step:tailwind:month	Turn	Turn:month	Turn:chl	Turn:chil:month	Turn:tailwind	Turn:tailwind:month	df	AIC	ΔAIC	Weight	r_{obs}	r_{rand}
1	×	×	×		×	×	×	×	×		×	×	29	28231	0.00	1.00	0.652 ± 0.047	0.005 ± 0.129

region, where locating patchy resources requires complex foraging abilities (Fauchald 1999), and quickly reach a genetically coded goal, the extensive frontal region in the southeast Atlantic where prey is largely predictable and plentiful. In terms of oceanography, this is a region of high eddy activity where the southerly Agulhas Return Current and the Antarctic Circumpolar Current interact with bathymetric features, and is an important foraging area for other pelagic seabird species (Reisinger et al. 2022). This includes non-breeding adult grey-headed albatrosses from South Georgia (mainly from June to October), and breeding birds from the Prince Edward Islands during the austral summer (Nel et al. 2001, Clay et al. 2016).

Although juveniles responded less to variation in tailwind support after reaching waters southwest and south of Africa, it is likely that wind still plays a pivotal role in behavioral decisions given its importance for dynamic soaring, the dominant flight mode in albatrosses (Richardson et al. 2018). Instead, the reduced dependence on tailwinds at the large scale could reflect the improved ability of juveniles to make informed decisions of when and where to move, resulting in the intermittent use of tailwinds to sustain shorter flight bouts in regions where foraging is optimal, similar to non-breeding adults (Mackley et al. 2010). It is likely, however, that juveniles require a long period of behavioural refinement in order to make optimal use of winds, as studies of other birds show that young can take months to years to attain the flight capabilities of adults in terms of travel speeds (wandering albatross *Diomedea exulans*; Riotte-Lambert and Weimerskirch 2013), soaring (white stork *Ciconia ciconia*; Rotics et al. 2016) or compensation for wind drift (osprey *Pandion haliaetus* and honey buzzard *Pernis apivorus*; Thorup et al. 2003).

Response to resources: evidence for innate foraging abilities and progressive development of search strategies

Contrary to our expectations, juveniles responded to resource availability immediately after fledging by reducing their displacement rates, and there was no evidence for a progression in this response over time. A similarly rapid adjustment of foraging behaviour in response to oceanographic proxies for prey availability (bathymetry and chlorophyll *a* concentration) has been shown for juvenile wandering albatrosses from the Crozet Islands (de Grissac et al. 2017). As acquiring resources is vital to survival, it could be that naïve individuals have an innate ability to interpret certain cues indicating prey availability, such as odor or water color (Nevitt 2000), or respond to the presence of foraging conspecifics (Thiebault et al. 2014).

Our analysis also provided support for a significant change in broad-scale movement strategies over time, whereby juveniles reduced travel speeds and increased sinuosity after their first month at sea. This behaviour, identified in young *Thalassarche* albatrosses and white-chinned petrels *Procellaria aequinoctialis* from the Indian Ocean (de Grissac et al. 2016), has also been demonstrated in adults when searching for

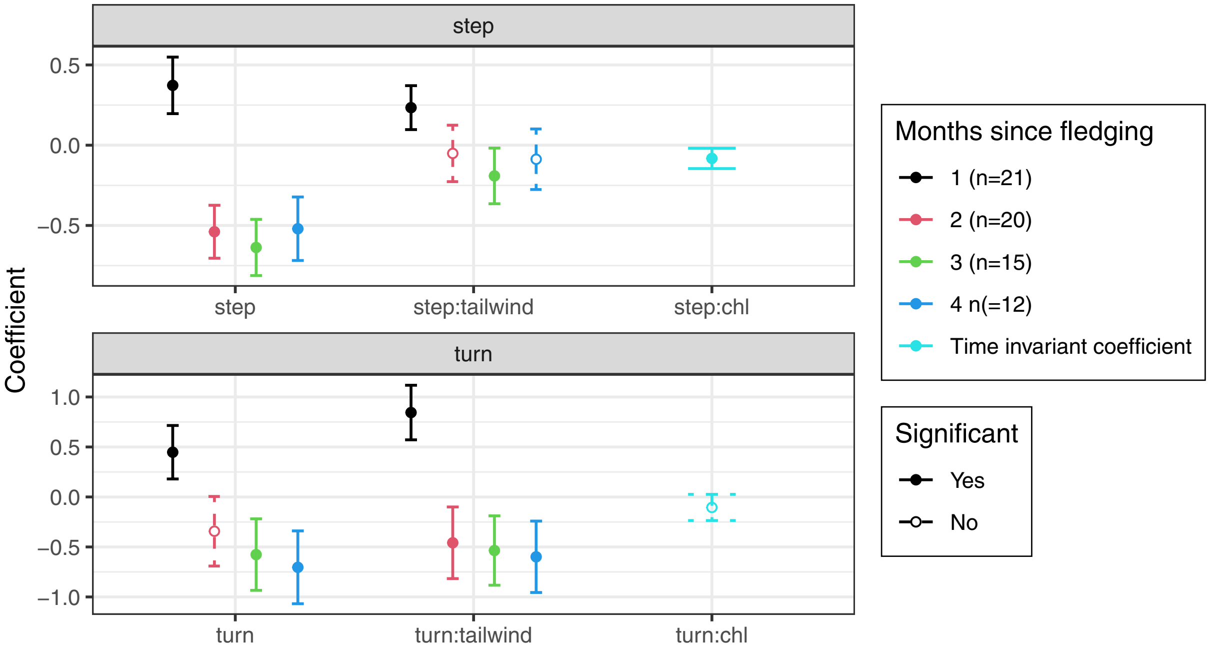

Figure 2. Predicted effects of environmental conditions (tailwind support 'tailwind' and chlorophyll *a* concentration as a proxy for prey resources 'chl') and time (months since fledging 'month') on the movement characteristics (step lengths 'step' and turning angle 'turn') of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in 2018 (n = 9) and 2019 (n = 12) using integrated step-selection analysis fitted using a Poisson GLMM. Mean coefficients (dots) were extracted from the best-supported model ranked using Akaike information criterion (AIC) and represent average population effects for the 1st month since fledging and change in average population effects for the 2nd, 3rd and 4th months relative to the first month since fledging. Confidence intervals (95%; error bars) were calculated following Forester et al. (2009) to account for temporal autocorrelation among observations. 'Time invariant coefficient' signifies there was no significant interaction of this coefficient with time. A higher coefficient value for 'step' indicates increased travel speeds, while a higher coefficient for 'turn' indicates increased directional persistence, and hence, lower turning angles. Positive coefficients for two-way interactions between movement characteristics and environmental parameters; 'tw' ('step:tw' and 'turn:tw') and 'chl' ('step:chl' and 'turn:chl'), indicate increased travels speeds and directional persistence in areas of increasing tailwind support and chlorophyll *a* concentration, respectively, while negative coefficients indicate the opposite relationship (reduced travel speeds and directional persistence in areas of increasing tailwind support and chlorophyll *a* concentrations). Coefficients for which 95% confidence intervals contained 0 are considered to have a non-significant effect on juvenile movement characteristics and are displayed with dashed lines.

food (Fauchald and Tveraa 2003, Weimerskirch et al. 2007, Louzao et al. 2011). It could indicate an improvement in the skills needed to locate prey over large spatial scales, such as flying across the wind to optimize the probability of encountering odour plumes (Nevitt et al. 2008), or to identify suitable prey whilst in flight, minimizing the high energy costs associated with unnecessary landings and take-offs (Weimerskirch et al. 2000, Clay et al. 2020). Alternatively, this behaviour may have been triggered by the arrival of juveniles at frontal regions in months 3–4 post-fledging, where area-restricted search may be required to locate prey patches and swarms at finer scales (Weimerskirch 2007). Regardless of the process underlying this behavioural transition, the development of large-scale search abilities may allow juveniles more generally to explore their surroundings, and sample a range of different oceanographic conditions before adopting optimal migration or foraging strategies in terms of preferred habitats or travel routes for instance (early-exploration-later-canalization hypothesis; Guilford et al. 2011, Votier et al. 2017, Collet et al. 2020).

Methodological limitations and future opportunities

Modelling the environmental conditions experienced by individuals can be challenging given the variable temporal and spatial scales at which remotely-sensed variables are measured (Martin 2004). While the spatial resolution of wind speed and chlorophyll *a* data used in this study were considered to provide a good representation of the local environment at the appropriate scale (0.25°), modelling foraging conditions using a single proxy for prey availability is complicated by the time lags between biophysical processes (e.g. peak in primary production) and their effects at higher trophic levels (e.g. peak in prey availability for seabird; Passuni et al. 2016). Here, we were able to detect the response of juveniles to monthly-averaged chlorophyll *a* concentrations; however, developing a global model of productivity which incorporates spatial and temporal dynamics in chlorophyll *a* variance might provide new insights into the main factors determining the timing of arrival and departure of individuals from specific foraging sites (Suryan et al. 2012). Indeed, juveniles in this study left the

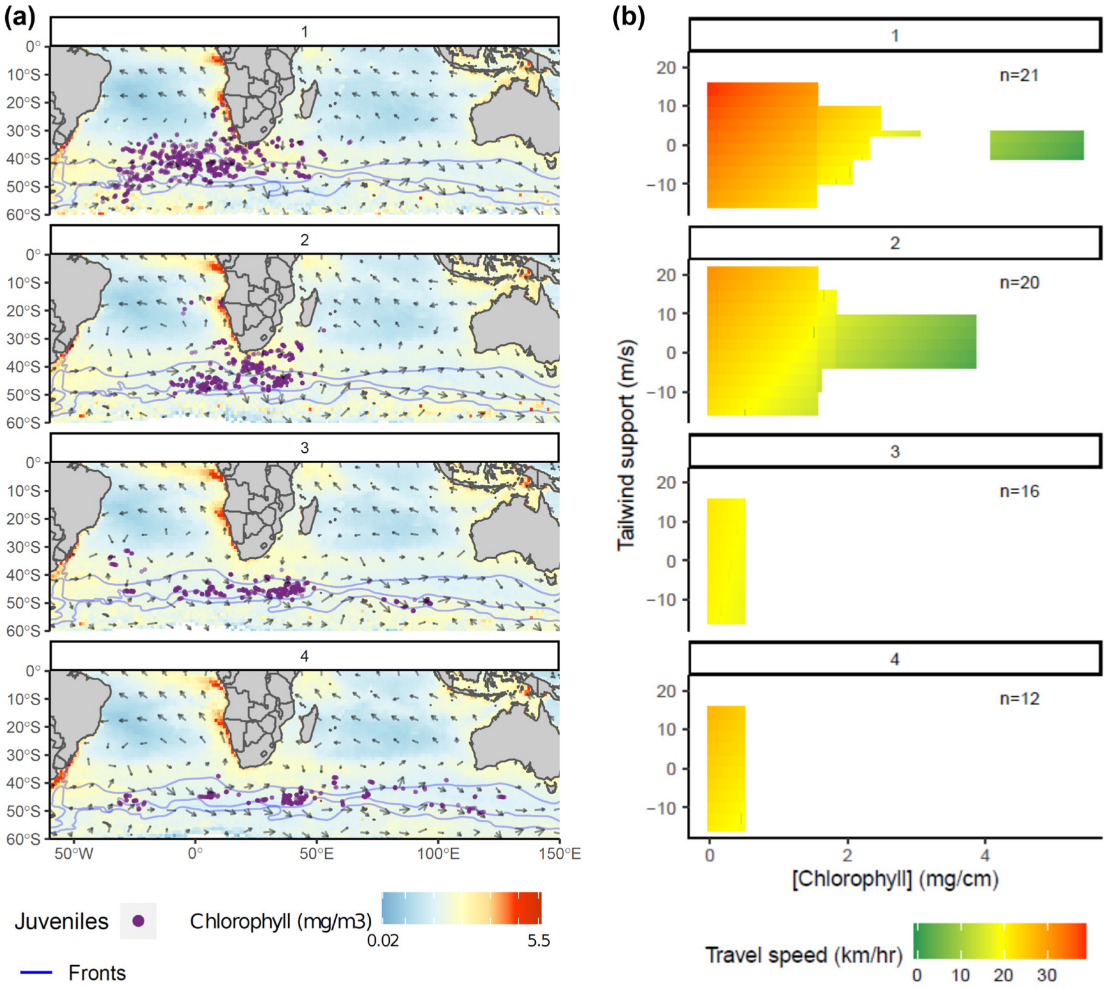

Figure 3. (a) Locations of juvenile grey-headed albatrosses tracked from Bird Island (South Georgia) in 2018 (n = 9) and 2019 (n = 12) using platform terminal transmitters during their first four months at sea (1, 2, 3, 4) in relation to chlorophyll *a* concentration, winds (speed and direction are represented by the direction and length of arrows, respectively) and three oceanic fronts (the Subtropical, Subantarctic and Antarctic Polar fronts from top to bottom; Orsi et al. 1995). The location of major fronts are shown in dark blue. (b) Predicted change in juvenile travel speeds as a function of environmental (tailwind support and chlorophyll *a* concentration) and temporal covariates (months since fledging [1, 2, 3, 4]) using integrated step-selection analysis.

productive frontal region in the southeast Atlantic after their second month at sea and it is unclear whether this decision was motivated by a seasonal depletion in resources (Koné et al. 2005), or factors such as increased intra- and inter-specific competition for prey (Abrams and Griffiths 1981).

Finally, *i*SSA provided a useful analytical framework for investigating the environmental drivers of juvenile movements, and this modelling tool could easily be adapted to answer wider questions. Although we chose to focus on two simple environmental proxies for transport costs and productivity (or prey availability), other oceanographic parameters could be included in the model, thereby improving our understanding of the time needed for naïve individuals to learn how to interpret external cues of varying complexity (e.g. mesoscale features such as ridges or seamounts which concentrate prey; Wakefield et al. 2009a). In addition, larger sample sizes, and tracks of longer duration could facilitate investigation of whether individuals vary in their responses to the environment, and hence speed of learning, which may be a key trait determining the likelihood of successfully recruiting into the breeding population (Sergio 2014). Given that mortality is relatively high in this age class (average survival rates of juveniles and adults are 0.764 ± 0.076 and 0.952 ± 0.029, respectively, at South Georgia; Pardo et al. 2017), we highly recommend further research on the role of different cues in shaping movement patterns and the behaviours enhancing survival in early life. These processes will be key to predicting and mitigating the impacts of climate change and other threats such as fisheries bycatch on the population trajectories of long-lived and wide-ranging marine species (Ong et al. 2015, Rotics et al. 2017, Sherley et al. 2017, Frankish et al. 2021).

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Author contributions

Caitlin Kim Frankish: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead). **Andrea Manica**: Formal analysis (supporting); Methodology (supporting); Supervision (equal); Writing – review and editing (supporting). **Thomas A. Clay**: Formal analysis (supporting); Methodology (supporting); Writing – review and editing (supporting). **Andrew G. Wood**: Data curation (lead); Writing – review and editing (supporting). **Richard A. Phillips**: Conceptualization (lead); Funding acquisition (lead); Investigation (supporting); Project administration (supporting); Supervision (equal); Writing – review and editing (supporting).

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 id: 1845. (Frankish et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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