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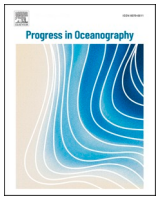

Mesoscale eddies in the Southern Ocean influence foraging trip behaviour of multiple penguin species

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ABSTRACT

Mesoscale eddies are rotating vortices of water that perturb the local physical, chemical, and biological environment. In the Southern Ocean, penguins inhabit regions characterised by intense eddy activity, which can offer foraging opportunities. To better understand relationships between penguins and eddies, we collated tracking data for five species (emperor, king, chinstrap, Adélie, and macaroni penguins), totalling 3189 individuals from 59 colonies. Data were subset by colony and breeding stage to create 74 case studies. We then fitted Hidden Markov Models to penguin tracks to identify Area-Restricted-Search (ARS) behaviour (a proxy for foraging) and used Generalised Additive Mixed Models to relate behaviour to the presence of eddies. In 28 case studies, penguins displayed a pronounced increase in ARS within specific parts of eddies. All five species exhibited an association between ARS and eddies in several case studies, though substantial regional differences in association strength were observed. In life history periods when penguins experienced central place constraints, ARS was more frequently associated with eddies. By studying five extensive case studies in greater detail, we found that eddies possibly influenced trip trajectories by aggregating prey at submesoscale filaments around their peripheries, by interacting with the distribution of sea ice, and potentially by transporting key prey species in their interiors. In these case studies, eddy maturity, amplitude, and intensity also differed between eddies collocated with ARS and the background eddy field. When eddy abundance varied, foraging trip durations also varied, though with opposing trends depending on the colony and breeding stage. Eddy activity is projected to increase in the Southern Ocean, which in isolation would have mixed impacts on penguins, though the negative impacts of broad-scale changes in prey availability and sea ice concentration are likely to outweigh any impacts of changing eddy fields.

1. Introduction

Mesoscale eddies are rotating oceanic parcels of water, 10s to 100s of kilometres in diameter, that typically persist for weeks to months (Dong et al., 2025). They often form by shearing off current meanders before propagating across the ocean, carrying with them trapped parcels of water (Rhines et al., 2019). As they traverse away from the waters where they originated, eddies can be characterised by local anomalies in environmental properties such as sea-surface height (SSH) and temperature (SST), which allow them to be detected by satellite observations (Pegliasco et al., 2022).

Eddies are classified as either anticyclonic or cyclonic depending on their rotational direction. In general, anticyclones feature positive SSH anomalies and warmer SSTs at their cores, whereas cyclonic cores possess negative SSH anomalies and cooler SSTs (Hausmann and Czaja, 2012). Furthermore, anticyclonic cores are characterised by deep thermocline perturbations while cyclonic cores exhibit shallow thermocline perturbations (Hausmann et al., 2017). Submesoscale filaments are also generated at eddy boundaries but propagate outwards towards peripheries in anticyclones and inwards towards cores in cyclones, leading to opposing patterns of submesoscale activity (Shi et al., 2024). These physical traits impact the biological component of the environment and light availability within eddies.

Several processes associated with eddies also influence oceanic biogeochemistry and productivity (McGillicuddy, 2016). Eddy stirring occurs when eddies advect parcels of water around their periphery, which contributes towards phytoplankton patchiness (Martin, 2003). Eddies also trap water within their interiors, retaining the original chemical properties and biological communities of the water mass from where they formed as they propagate across ocean basins and frontal boundaries (Bernard et al., 2007; Venkatachalam et al., 2017; Della Penna et al., 2022). Further, eddies can impact local productivity by modulating vertical velocities and stratification, with considerable regional variation in these processes (Gaube et al., 2014). Where anticyclones and cyclones meet, submesoscale frontal structures form that enhance productivity and aggregate nekton in otherwise unproductive regions (Guidi et al., 2012; Harrison et al., 2013; Sabarros et al., 2009). Enhanced mesopelagic micronekton abundance has been detected in anticyclone cores, possibly because deep mixed layer perturbations result in vertically-integrated chlorophyll-α being elevated compared to ambient waters (Della Penna and Gaube, 2020). That said, only about 6 % of eddies demonstrate an oasis effect on forage fauna, most of which are high in amplitude (Receveur et al., 2024).

Both eddies and marine predators exhibit complex behaviours, and relationships between them are far from universal. Associations have been made between anticyclone cores and higher predators such as tuna and other bony fish (Godø et al., 2012; Arostegui et al., 2022; Xing et al., 2023), sharks (Gaube et al., 2018; Braun et al., 2019), seals (Keates et al., 2022), and turtles (Gaube et al., 2017; Chambault et al., 2019), theorised to arise due to enhanced biomass at depth or eddy trapping. Meanwhile, preferences for cyclone cores have been observed in cetaceans (Davis et al., 2002; Riekkola et al., 2025), tuna (Tew Kai and Marsac, 2010), seals (Bailleul et al., 2010; Dragon et al., 2010), and seabirds (Haney, 1986), generally attributed to upwelling processes and shallow thermocline perturbations. Aggregation of near-surface prey in submesoscale fronts at eddy peripheries and eddy-eddy confluence zones is also theorised to explain foraging around eddy edges in cetaceans (Davis et al., 2002; Riekkola et al., 2025), tuna (Tew Kai and Marsac, 2010), seabirds (Nel et al., 2001; Tew Kai and Marsac, 2010; Yoda et al., 2014), and seals (Keates et al., 2022). Relationships between predators and eddies likely depend on the diet and ecology of the species, as well as local oceanographic conditions.

Penguins exhibit interspecific variation in foraging behaviour such as dive depths and distances reached from colonies (Ainley and Wilson, 2023). Many penguin species breed on subantarctic islands, which are situated in a region associated with high eddy activity where most eddies form from instabilities in the Antarctic Circumpolar Current (ACC) and in boundary currents north of the ACC (Frenger et al., 2015). Additionally, a few species breed south of the Southern Boundary of the ACC, where sea ice dynamics interplay with eddy activity. In areas of highly concentrated sea ice, eddies have a lower amplitude and density, but in the marginal ice zone, eddy activity is enhanced, particularly in cyclones (Auger et al., 2023). Eddies also contribute towards spatial heterogeneity of sea ice in the marginal ice zone, creating variability in sea ice thickness by influencing local salinity and temperature (Martínez-Moreno et al., 2025). Depending on the local currents and sea ice concentrations, some penguin colonies may encounter eddies more often than others.

Studies have highlighted the importance of eddies around individual penguin colonies. King penguins (*Aptenodytes patagonicus*) at the Crozet

Archipelago and South Georgia undertake foraging trips during which they search extensively within anticyclonic peripheries and anticyclone-cyclone confluences, possibly due to near-surface prey aggregations formed by submesoscale filaments in these zones (Cotté et al., 2007; Scheffer et al., 2010). During the post-guard stage, when king penguins are less restricted to the waters around their colony, individuals from Marion Island appear to bypass a nearby energetic eddy field and feed further west (Pistorius et al., 2017). Macaroni penguins *(Eudyptes chrysolophus)* and eastern rockhopper penguins (*E. filholhi*) from Marion Island and macaroni penguins from the Crozet Archipelago also forage in eddy peripheries and at eddy-eddy confluences, which has again been associated with submesoscale filaments (Bon et al., 2015; Whitehead et al., 2016). On the Pointe Géologie Archipelago near the Antarctic continent, Adélie penguins (*Pygoscelis adeliae*) forage at the edge of eddies, where iron-rich glacial meltwater is advected towards the shelf-break and stimulates productivity (Cottin et al., 2012). In waters near the Antarctic Peninsula, the presence of an eddy within a submarine canyon enhances availability and delivery rates of krill to Adélie and gentoo penguin (*P. papua*) foraging areas (Hudson et al., 2022). It appears that eddies can create foraging opportunities for penguins through several mechanisms. The relative importance of mechanisms may also vary throughout the breeding cycle in any one area. During breeding stages with stricter constraints, penguins are limited in how far they can travel (Clarke et al., 2006; Riaz et al., 2020), restricting their ability to explore more distant off-shelf waters that might host predictable hotspots of prey.

If differences exist in the usage of eddies amongst penguin colonies or breeding stages, this could create winners and losers under a changing climate. In recent decades, eddy kinetic energy has increased in the Southern Ocean because of increasing wind stress (Hogg et al. 2015; Martínez-Moreno et al., 2021). This supports the 'eddy saturation' hypothesis that stronger wind forcing results in greater eddy activity, with little change in ACC transport (Straub, 1993; Rintoul, 2018). Additional increases in ACC eddy activity are also projected to occur in climate models due to intensifying westerly winds (Beech et al., 2022). South of the ACC, eddy activity is expected to increase due to intensification of the Antarctic Slope Current and contracting sea ice extent which typically limits the abundance of eddies (Beech et al., 2025). These changes to Southern Ocean eddy activity could therefore benefit predators if eddies indeed aggregate their prey.

In this study, we aim to better understand the role mesoscale eddies play in influencing penguin movement along foraging trips. We concentrate on species that primarily reside in the Southern Ocean (waters south of the Subantarctic Front). By collating telemetry data from five penguin species and analysing them with the same methods, we investigate for the first time whether the effects of eddies are ubiquitous across species. We also study how the use of eddies varies amongst penguins from different colonies throughout their breeding cycle. Around each colony, we assess whether behaviour indicative of foraging is associated with the rotational direction or different zones of eddies using a modelling framework that explicitly accounts for central place foraging behaviour. Furthermore, we look at five data-rich case studies in greater detail, relating eddy maturity, amplitude and intensity to movement behaviour and identifying potential mechanisms that cause this link. We hypothesise that individuals from subantarctic colonies will exhibit a greater affinity for eddies than those from high-latitude Antarctic colonies due to the greater abundance and energy of eddies around the ACC. We also hypothesise that breeding constraints will impact whether penguins rely on eddies, as stricter constraints could either force penguins to forage within eddies rather than at further, more predictable prey hotspots, or limit the accessibility of nearby eddy fields. In this study, we define mesoscale processes as those occurring at scales of 10s to 100s of kilometres lasting for weeks to months, and submesoscale processes as those operating at scales of 1 to 10 km and persisting for hours to days.

2. Methods

2.1. Tracking data

We collated tracking data for five penguin species across their respective geographic ranges: Adélie, macaroni, king, chinstrap (*Pygoscelis antarcticus*), and emperor (*Aptenodytes forsteri*) penguins (Table S1-S3; Fig. S1-S5). 1728 of the tracks in this study were sourced from the Retrospective Analysis of Antarctic Tracking Data project (RAATD). RAATD consolidated tracking data for 17 Southern Ocean predator species; a standardised open-access dataset resulted after processing and state-space-modelling of the data (Ropert-Coudert et al., 2020). We opted not to include RAATD data collected from light level geolocator (GLS) devices because the instantaneous location error radius of these tags, which can range on average 186–400 km (Bennett et al., 2025), is often greater than the scale of mesoscale processes, and thus would generate mismatch.

To improve the representativeness of this study, we supplemented these data by identifying additional telemetry datasets from the literature and from repositories such as BirdLife International's Seabird Tracking Database (https://www.seabirdtracking.org), MoveBank (https://www.movebank.org), and the Global Biodiversity Information Facility (https://www.gbif.org). Where possible, we obtained raw data provided by the original devices to standardise track processing and state-space-modelling across studies. Each dataset was formatted to have a uniform record structure, quality controlled to remove erroneous tracks, and state-space-modelled with the R package *aniMotum* v1.2–12 (Jonsen et al., 2023). Further information on each dataset, the standardisation process, speed filters (Table S4), and the state-space-modelling procedure can be found in the supplementary information. Including RAATD, data were collated from 3189 individuals from 59 colonies (Fig. 1). Since animals from various colonies exhibit different foraging behaviours, i.e. duration, range and depth, throughout the breeding cycle due to central place foraging constraints (Charrassin et al., 1998; Ainley and Wilson, 2023), data were divided into 82 case studies by colony and breeding stage (Fig. S6-S10) before further analysis. Any case study containing fewer than three individuals was not retained for the modelling process. A schematic (Fig. 2) summarises the following methods applied to each case study.

2.2. Environmental variables

Eddy locations were sourced using two different eddy detection products. Most case studies used the altimetric Mesoscale Eddy Trajectory Atlas v3.2 (META3.2) Delayed Time (SSALTO/DUACS; https://doi.org/10.24400/527896/a01-2022.005.220209). META3.2 locates global daily positions of eddies with a lifespan over 10 days. Coordinates of eddy centres are available along with the corresponding speed radius, which is the radius of the best fitting circular contour with a maximum circum-average geostrophic speed. Speed radii in the Southern Ocean are on average ~ 40 km (Frenger et al., 2013). Eddy centres were mapped for each day and a buffer equal to double the speed radius was applied to each centre to capture the periphery of the eddy following Gaube *et al.* (Gaube et al., 2017). Then, the relative distance to the centre was calculated as the Haversine distance from each cell to the eddy centre divided by the corresponding speed radius to derive eddy cores and peripheries (Fig. 3). Where a cell was within 2 radii of multiple eddies, the smallest relative distance was prioritised.

Other environmental variables that may influence foraging behaviour and eddy availability were also accounted for, namely depth, sea ice concentration, and current velocity. These were all sourced from the Global Ocean Physics Reanalysis Model (GLORYS, Copernicus Marine Environmental Monitoring Service; https://doi.org/10.48670/moi-00021). GLORYS is a data-assimilating eddy-resolving oceanographic reanalysis model, which uses remote sensing and *in situ* platforms to calibrate outputs (Lellouche et al., 2021). All variables had a 0.083° (~9km) spatial

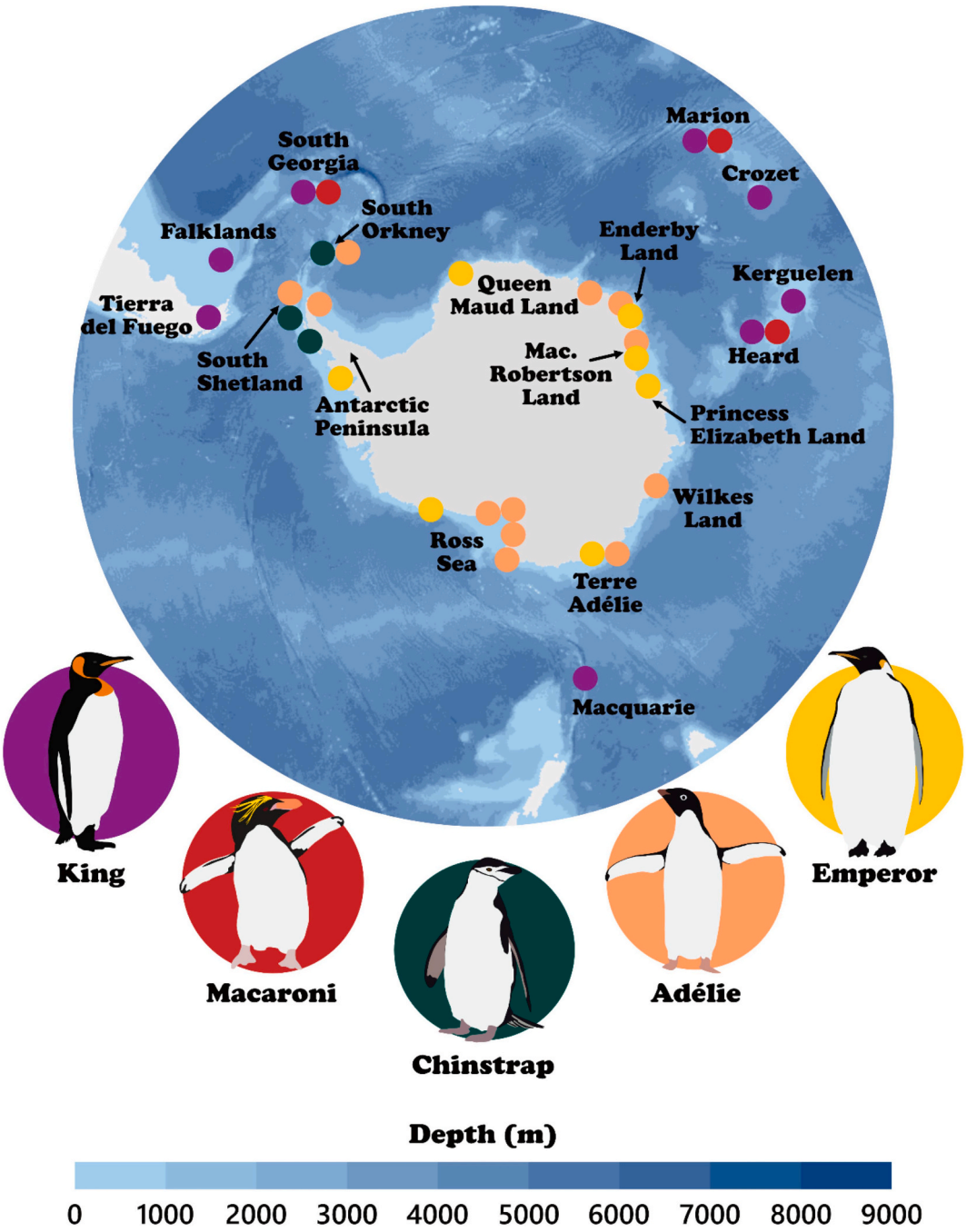

Fig. 1. Locations of tracked colonies for all five species and names of regions referred to in this manuscript. Colonies are represented by coloured circles, with each colour corresponding to a species. Background shading denotes bathymetry, with darker shading representing deeper waters. Where applicable, multiple colonies of a species from one island group are represented by a single circle, as in Table S2. To see the locations of both tracked and untracked colonies for each species, refer to Fig. S1 to S5.

resolution, and all dynamic variables were sourced at a daily temporal resolution.

A major limitation of META3.2 is that eddies cannot be identified underneath sea ice because the DUACS Absolute Dynamic Topography product that it is built on does not record observations in sea ice concentrations above ~ 10 %. Where sea ice concentrations above 10 % were present within the case study area, we used an eddy detection algorithm developed by Auger et al. (2023) for a Sea Level Anomaly product that uses specific processing in leads within the sea ice to obtain values in ice-covered regions (Veillard et al., 2024). This product only covers the period 2013–2021 and has a temporal resolution of three days. Different temporal resolutions will inevitably introduce some sampling heterogeneity, and case studies using the sea ice eddy product will experience some spatial mismatch as locations were matched with the eddy position the preceding or following day when no contemporaneous position was available.

For case studies that fell outside the timeframe of this product, we removed any locations falling within sea ice concentrations above 10 %. Eight of the 82 case studies were disregarded because over 50 % of locations were recorded in sea ice concentrations above 10 % and data were not recorded within the timeframe of the sea ice eddy product, leaving 74 case studies for further analysis. The 10 retained case studies where sea ice locations were removed (Table S5) used tracks of Adélie (n = 7) or emperor penguins (n = 3) located in the Ross Sea (n = 2),

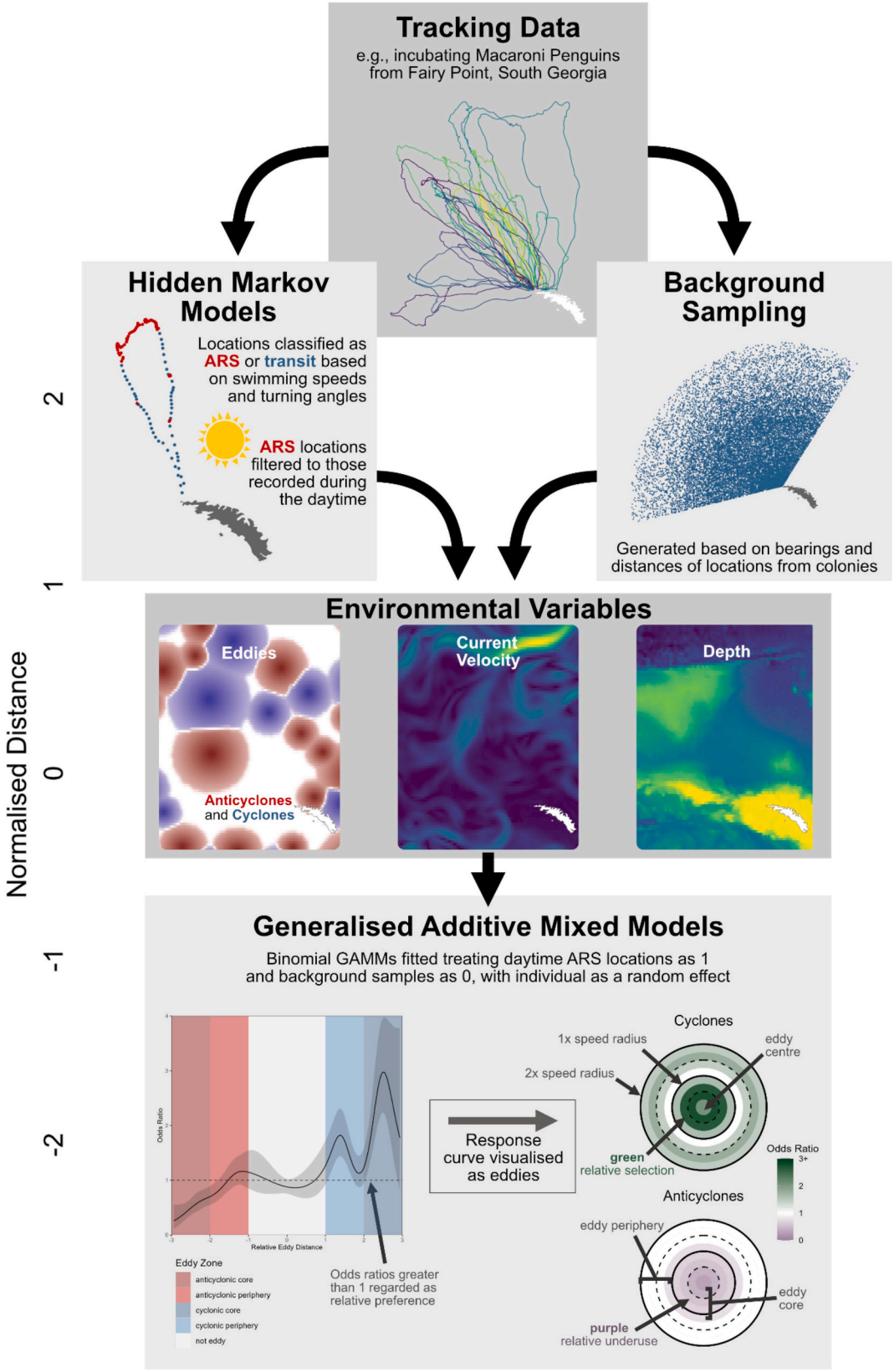

Fig. 2. An overview of the modelling process for each case study, using incubating Macaroni Penguins from Fairy Point, South Georgia as an example.

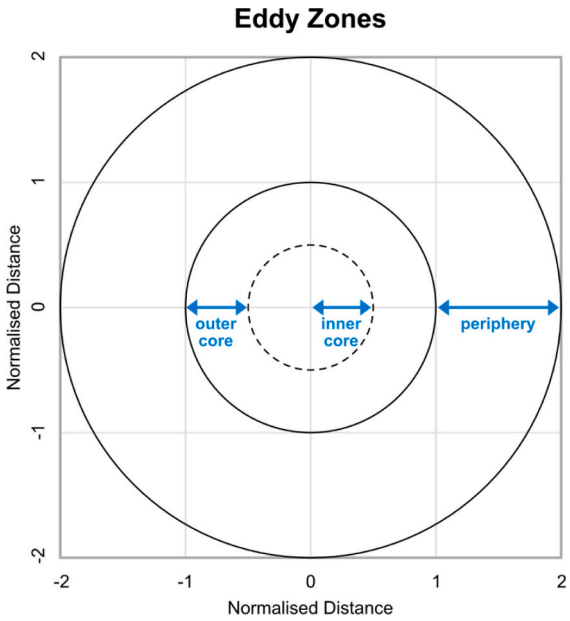

Fig. 3. Schematic representation of the eddy zones referred to in this manuscript. The normalised distance represents the distance to the eddy centre divided by the radius of that eddy.
Adapted from (Gaube et al., 2017).

Antarctic Peninsula (n = 1), or East Antarctica (n = 7), and removed locations were all below 60°S (mean: 66.96°S +/- 2.85°, range: 75.56°S to 60.09°S). Removing pack ice locations could bias these case studies as a greater proportion of locations will likely be within eddies due to the greater density of eddies outside of the sea ice, but without this step, models would miss key interactions with eddies beneath the ice.

2.3. Hidden Markov models

To identify potential foraging behaviour, Hidden Markov Models (HMMs) were fitted to tracks using the *hmmTMB* R package v1.1.0 (Michelot, 2025), applying a separate model to each case study. These models divided tracks into two distinct hidden behavioural states, transit and area-restricted-search (ARS), using observed properties of the original track. Here, we used the observed turning angle and the swimming speed relative to currents, which was defined as:

$$\sqrt{(u_p - u_c)^2 + (v_p - v_c)^2}$$

where u_p (eastwards) and v_p (northwards) are the velocity parameters of penguin movements, and u_c and v_c are the same for the currents. Transit was associated with faster swimming speeds and more directed movements, and *vice versa* for ARS (Fig. S11 and S12). Using swimming speed rather than step length allows for ARS within currents to be identified, as fast-moving currents are common in the Southern Ocean. ARS does not always represent foraging, as socialising and resting behaviours (e.g. on overnight trips) may also be interpreted as ARS with these definitions (Saldanha et al., 2023).

For each HMM, we used a Gamma distribution for swimming speeds and a Von Mises distribution for turning angles. To ensure that initial parameters were not biased, random values were selected between appropriate estimates as the initial parameters for each hidden state over 25 iterations (Table S6). The best initial parameters were then taken from the HMM with the maximum log-likelihood. Hidden states of tracks were predicted using the Viterbi algorithm for quality control. Each trip was checked to eliminate trips where ARS was assigned only to artificial looping movement created during state-space modelling or where trips were composed entirely of one hidden state. To evaluate whether ARS locations produced from GPS locations alone correlate with greater foraging behaviour, we compared dive behaviour and accelerometry-derived states with predicted hidden state assignments where possible (Fig. S13).

2.4. Background sampling

To quantify the relative use of eddies for ARS, the background availability of eddies and other variables were sampled. During breeding stages when penguins did not return to the colony, background locations (pseudo-absences) were sampled within a minimum convex polygon fit to tracks (Fig. S14). During stages when penguins returned to the colony, demonstrating central place foraging, a custom approach was created (Fig. S15). First, the maximum distance to the colony of any track location was calculated and a buffer was fitted around the colony with a radius of equal value, to exclude inaccessible waters during that breeding stage. Then, the maximum and minimum bearings of track locations from the colony were obtained and used to segment the buffer into a slice, to exclude waters that might not be used due to segregation from neighbouring colonies (Bolton et al., 2019). The number of points sampled at different distances to the colony was varied relative to the number of track locations recorded at each distance to avoid oversampling distant waters, where occurrence was sporadic, or nearby shelf seas, which penguins transited through to reach foraging grounds. Such weighting is important to account for the non-random distribution of environmental variables such as depth and eddy activity with increasing distance to the colony (Benhamou and Courbin, 2023).

For all breeding stages, the number of background samples was equal to the number of state-space-modelled track locations if over 20,000 or fixed at 20,000 if fewer track locations were recorded (Barbet-Massin et al., 2012). Each background sample was associated with a date corresponding to the distribution of dates of the tracking data to limit bias arising from temporal dynamics, particularly in the seasonal sea ice zones. Every background sample was also associated with an individual ID code corresponding to the tracking data to maintain a similar ratio of presences to background samples across individuals for statistical modelling.

2.5. Generalised additive mixed models

The relative use of eddies for ARS compared to background availability was then estimated using Generalised Additive Mixed Models (GAMMs). GAMMs were fitted using the *gamm4* R package v0.2–7 (Wood and Scheipl, 2017) with a binomial error distribution and a logit link function, treating ARS locations as a value of 1 and background samples as a value of 0, and individual as a random effect. For king and macaroni penguins, eddies, current velocity, and depth were fixed effects, while sea ice concentration was additionally included to model emperor, Adélie, and chinstrap penguin behaviour. All fixed effects were standardised before fitting GAMMs. Prior to modelling, ARS locations with an error radius greater than 5 km were also removed to reduce mismatch with eddies. Following removal of erroneous locations, mean positional error was 1.859 km, compared with the average Southern Ocean eddy radius of ~ 40 km (Frenger et al., 2013). Additionally, penguins are visual predators that primarily forage between dawn and dusk, and often rest on sea ice at night (Scheffer et al., 2010; Takahashi et al., 2018). While they can forage at depths where there is little, if any, light, they avoid foraging when they cannot detect the presence of predators (Ainley and Wilson, 2023). Therefore, nighttime ARS positions are less likely to represent foraging behaviour, so points were limited to those recorded between dawn and dusk according to the date and coordinates of each location using the *suncalc* R package v0.5.1 (Thieurmel and Elmarhraoui, 2019).

Since spatiotemporal autocorrelation of tracking data violates the assumption of independence in GAMMs, remaining ARS locations were checked for autocorrelation of step lengths and turning angles using the

acf function in R (Boyce et al., 2010). Tracks were considered autocorrelated when the absolute autocorrelation exceeded the 95 % confidence bounds. In these cases, data were progressively temporally thinned to increasingly course intervals (1 h, 2 h, 3 h, etc.) until autocorrelation was no longer detectably greater than 0. The inclusion of individual as a random effect also accounts for individual dependence structures in the data (Chambault et al., 2021). Fitted GAMMs were then checked using autocorrelation functions applied to the residuals of each model to ensure that the data were sufficiently decorrelated.

To investigate the effects of eddies on ARS, smooth estimates and 95 % confidence intervals were obtained from GAMMs and transformed with an exponential function to produce odds ratios. Odds ratios above 1 represent greater usage during daytime ARS than background availability, and values below 1 represent lesser usage during daytime ARS. When 95 % confidence intervals overlapped 1, the estimated odds ratio was relabelled to 1 to indicate no detectable relationship. To assess the predictive skill of GAMMs, we used a five-fold leave-individual-out cross-validation (Roberts et al., 2017). In this method, we iteratively isolated data from 80 % of individuals, trained GAMMs on these data, and tested their predictive accuracy on the remaining 20 % of individuals with the continuous Boyce index (CBI), averaging scores across the five iterations.

Eddy usage by penguins from each case study was then classified as either specialised, possible use, or unspecialised based on GAMM outputs. Case studies were defined as specialised if: (1) the GAMM offered greater explanatory power than a model without the eddy smooth term, should the Akaike Information Criterion (AIC) of the full model be less than that of the simpler model by 2 or more, (2) the estimated odds ratios of the smooth indicated elevated ARS within any eddy zone, and (3) the average CBI score was above 0.4. If the first two of these criteria were met but the CBI score was below 0.4, we classified this case study as possible use because low CBI scores suggest observed relationships might not be generalisable to the whole population, or that additional variables might better explain ARS distribution. Unspecialised case studies were those where either penguins did not encounter eddies, where the eddy smooth term did not detect elevated ARS within any eddy zone, or where the inclusion of the eddy smooth term did not offer improved explanatory power. Fisher's exact tests were used to compare differences in the proportions of case studies that were specialised among different species, regions and breeding stage constraints. This is a non-parametric test designed to assess association between two binary variables, especially for contingency tables with small sample sizes. Wilcoxon rank sum tests and ANOVAs were used to compare interannual differences in foraging metrics such as trip length and duration to relate these to eddy fields. A Wilcoxon rank sum test can assess whether a particular year is distinct from all other years, while ANOVAs can inform whether metrics across all years are substantially variable.

2.6. Example case studies

To explore how eddy mechanisms might influence ARS along foraging trips, we further analysed five of the most data-rich case studies where a relationship was found between the relative eddy distance and ARS. We compared how eddy maturity (number of days since the first observation scaled by the lifespan of the eddy), amplitude (difference between the sea surface height at the centre and the edge of the eddy), and intensity (amplitude divided by radius) differed between ARS and background locations within eddies.

We also investigated potential mechanisms that explain the links between ARS and eddies in these case studies. This involved the sourcing of two additional environmental variables. Daily finite-size Lyapunov exponents (FSLE) representative of submesoscale Lagrangian coherent structures (d'Ovidio et al., 2004) were sourced from AVISO (https://doi.org/10.24400/527896/a01-2022.002) at a 0.04° resolution. FSLE uses satellite altimetry to identify trajectory separation in water parcels, assuming that faster separating waters are representative of filaments and fronts. Some FSLE ridges are false positives of submesoscale activity and the relatively coarse resolution of altimetry data causes some filaments being missed, but several studies have found FSLE to generally correspond well to the locations of Lagrangian coherent structures (Karrasch and Haller, 2013; Prants, 2025).

The other additional variable was a modelled micronekton biomass product sourced at a daily 0.083° resolution (Copernicus Marine Environmental Monitoring Service; https://doi.org/10.48670/moi-00020). These outputs were produced by the spatial ecosystem and population dynamics model (SEAPODYM) that incorporates current trajectories, food availability, predator presence, and environmental conditions to predict distributions of micronekton, the prey of penguins (Lehodey et al., 2008).

Generalised linear mixed effects models were used for comparisons of ARS and background samples with eddy characteristics and auxiliary environmental variables, fitted in the *lme4* R package v1-1.37 (Bates et al., 2015) using a binomial (eddy maturity) or Gamma (all other variables) error distribution and individual ID as a random effect.

3. Results

3.1. Variation in eddy specialisation

Of the 74 case studies, 28 (37.9 %) were classified as specialised, displaying elevated ARS within one or more eddy zones (eddy cores and/or peripheries; Fig. 3), and a further 15 (20.3 %) were classified as possible use, where a relationship was detected but could not be generalised to all individuals. Variation in the importance of eddies was also investigated between species, regions, and breeding stage constraints (Fig. 4). No detectable differences were found between different species ($p = 0.54$), despite eddy usage being classified as specialised for between 16.7 % (chinstrap penguin) to 66.7 % (emperor penguin) of case studies per species.

There was considerable regional variation in the influence of eddies on ARS ($p = 0.0273$). Nine of the 23 case studies (39.1 %) at the subantarctic islands of Marion Island, the Crozet Archipelago, the Kerguelen Isles, Heard Island, Macquarie Island, and South Georgia were classified as specialised, and a further six (26.1 %) displayed possible use. A similar frequent usage of eddies was observed around the island groups of the Falkland Islands (50 % specialised, 50 % possible use) and the South Orkney Islands (30 % specialised, 50 % possible use). Around the Antarctic continent at the Antarctic Peninsula, Queen Maud Land, East Antarctica, Terre Adélie, and the Ross Sea, 11 of 23 case studies (47.8 %) were classified as specialised and another three (13 %) displayed possible use. At Tierra del Fuego, no penguins from either case study encountered eddies, while at the South Shetland Islands, only three of the 14 case studies (21.4 %) were classified as specialised.

Among breeding stages, variation was observed associated with foraging constraints ($p = 0.0306$). 21 of 50 case studies (42 %) with central place foraging constraints were classified as specialised and 13 (26 %) as possible use. When penguins were not under central place constraints, only seven of the 24 case studies (29.1 %) were classified as specialised, and another two (8.3 %) showed possible use.

3.2. Example case studies

Chick-rearing macaroni penguins from Fairy Point, South Georgia ($n = 48$; Fig. 5) displayed a preference for the boundaries of both kinds of eddy ($\chi^2 = 58.8$, $p < 0.001$, $CBI = 0.874$). The only detectable difference regarding eddy maturity, amplitude, and intensity was a greater incidence of ARS within more mature anticyclones ($z = 2.448$, $p = 0.014$). Across multiple years, ARS was observed around the peripheries of cyclones (1999), anticyclones (2004), and the confluence zones of anticyclone-cyclone pairs (2003 and 2005), all of which were associated with submesoscale filaments (Fig. S16). Lower mean FSLE values, indicative of greater submesoscale activity, were recorded at ARS

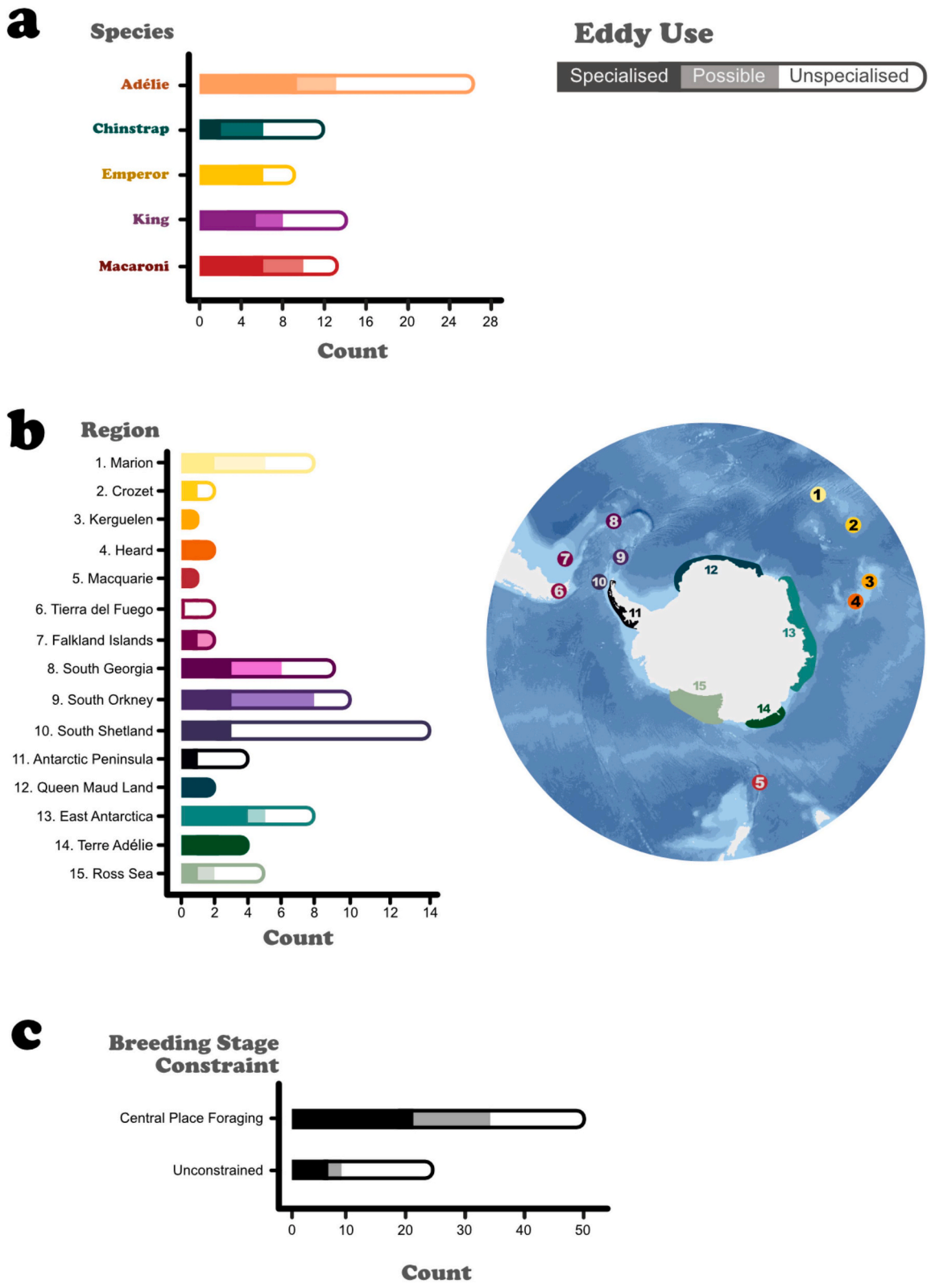

Fig. 4. Variation of eddy usage by (a) species, (b) region, and (c) breeding stage constraints. Lengths of bars correspond to the number of case studies, with the dark filled section of the bar indicating how many of those case studies were classified as specialised and the lighter filled section denoting how many studies were classified as possible use. For the regional comparison, case studies from Enderby Land, Mac. Robertson Land, Princess Elizabeth Land, and Wilkes Land were combined into the East Antarctica region due to proximity and small sample sizes of case studies. Central place foraging breeding stages were those when penguins returned to the colony within days to weeks, covering incubation and chick-rearing for all species, and pre-moult for macaroni penguins. All other stages were defined as unconstrained. The status of each case study is available in Table S2.

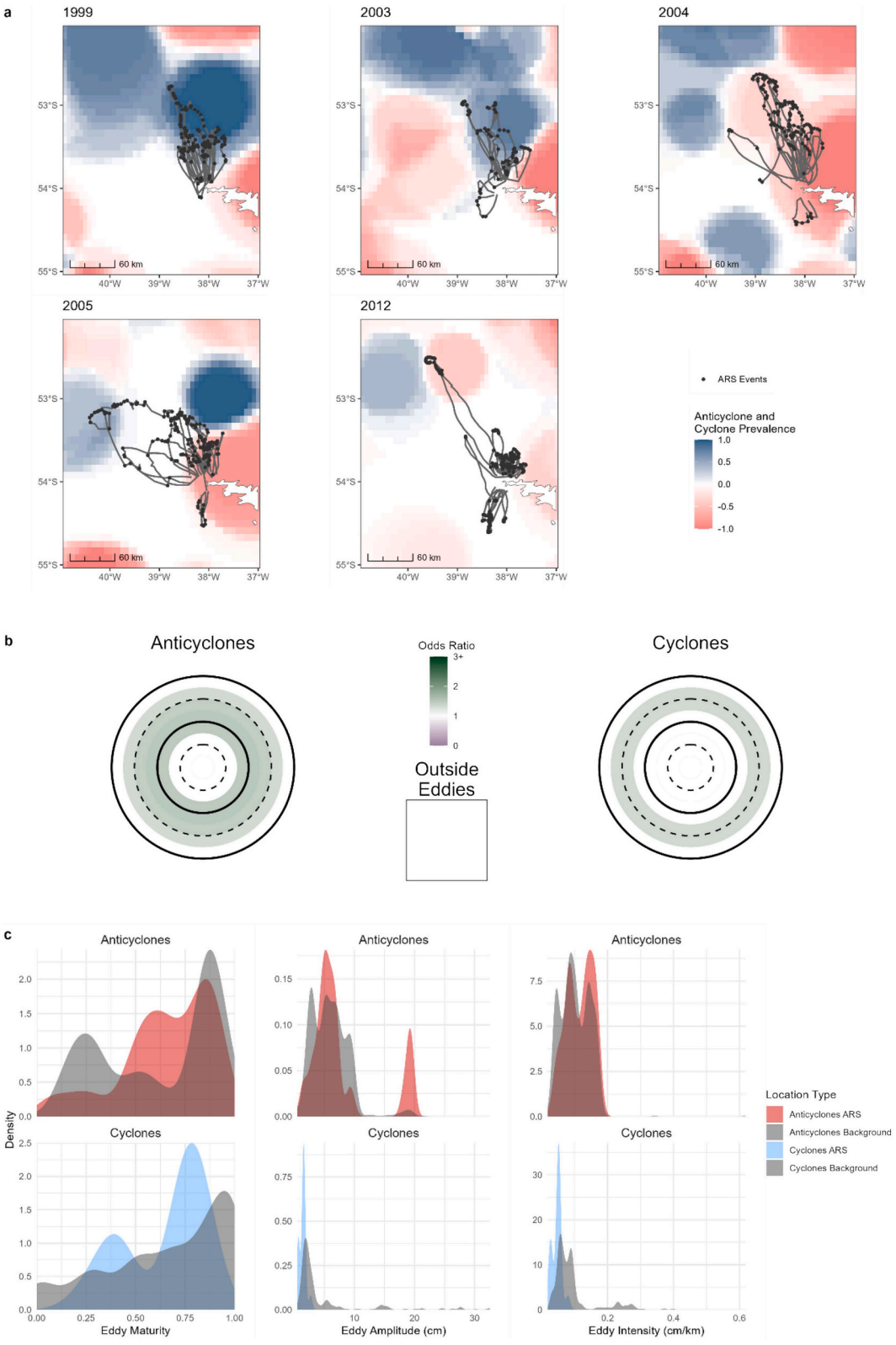

Fig. 5. (a) Tracks of chick-rearing macaroni penguins from Fairy Point, South Georgia in different years, with ARS events marked as black dots. The prevalence of eddies denotes the proportion of dates on which tracks were recorded where a given cell was a cyclone (blue) or anticyclone (red). This proportion is negative for anticyclones. (b) Odds ratios taken from GAMMs with values above 1 (green) indicating relative preference during ARS. The colour of the square indicates the odds ratio for locations outside of eddies. Solid circles denote boundaries equivalent to 1x or 2x the speed radius, while broken circles denote 0.5x and 1.5x the speed radius. (c) Comparison of eddy maturity, amplitude, and intensity at ARS (blue/red) and background locations (grey) recorded within eddies. The mean error of ARS locations was 0.12 km, and the average eddy radius was 51.46 km.

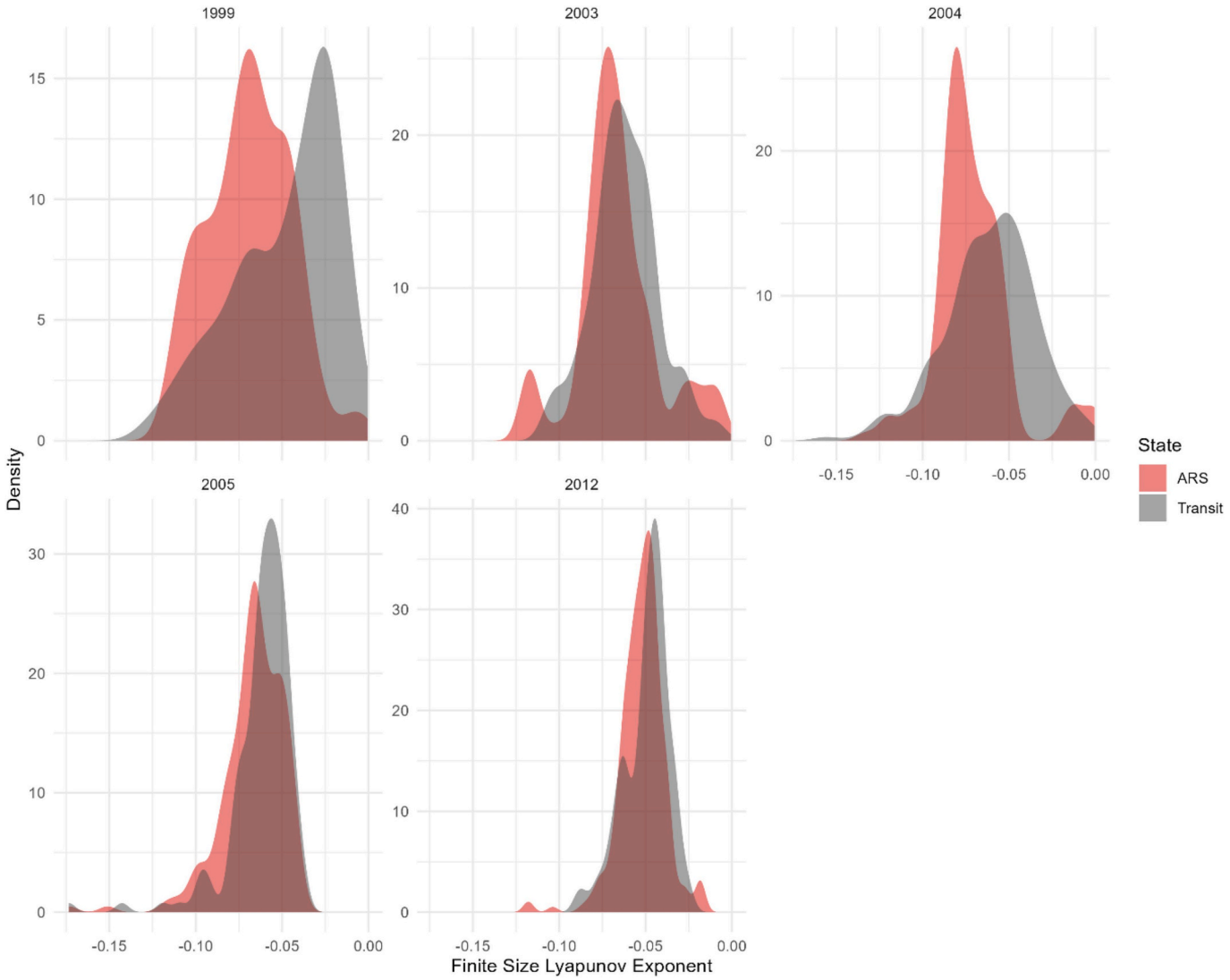

Fig. 6. Finite-size Lyapunov Exponent (FSLE) values at ARS (red) and transit (grey) locations of chick-rearing macaroni penguins from Fairy Point, South Georgia in different years. Panels represent individual years, and shaded curves show the probability density of FSLE values for each behavioural state. More negative FSLE values are indicative of greater submesoscale activity.

(−0.0612) than transit (−0.0523) locations ($t = 9.701$, $p < 0.001$), with the most notable differences in 1999 and 2004 (Fig. 6). In 2012, few eddies were detected near the colony, coinciding with short foraging trips with a median maximum distance from the colony of 35.4 km, substantially smaller than the median maximum distance of 93 km across all other years ($W = 71$, $p < 0.001$).

During incubation, macaroni penguins from Fairy Point ($n = 23$; Fig. 7) exhibited elevated ARS in the peripheries and cores of cyclones to the northwest of the colony ($\chi^2 = 153.3$, $p < 0.001$, CBI = 0.659). Cyclones containing ARS locations were on average greater in both amplitude ($z = 82.67$, $p < 0.001$) and intensity ($z = 2.21$, $p = 0.027$). ARS events again were associated with greater submesoscale activity (Fig. S17), and mean FSLE values were lower in ARS (−0.0839) than transit (−0.0764) locations ($t = 7.084$, $p < 0.001$) in all years (Fig. 8). Across 2000, 2002, and 2012, foraging trips were on average 931 km in length and took 11.6 days. However, in 2001, penguins did not encounter eddies as frequently on their outbound journeys despite following a similar initial trajectory, undertaking trips that were on average 1380 km long and lasted for 19.05 days. This represents a substantial increase in both trip length ($W = 68$, $p = 0.012$) and duration ($W = 69.5$, $p = 0.012$).

Incubating Adélie penguins from Pointe Géologie, Terre Adélie ($n = 325$; Fig. 9) showed an affinity for anticyclonic peripheries and cyclonic cores ($\chi^2 = 918.4$, $p < 0.001$, CBI = 0.92). Neither eddy amplitude nor intensity showed any clear relationship with ARS. In most years, penguins generally headed north of the colony before following eddy-eddy confluences eastwards at the northern edges of cyclones and the southern edges of anticyclones. Some tracks also ventured northwest, tracking the northern edge of anticyclones. In 2020, most tracks seem to aggregate within a persistent cyclone core. Foraging trips also appeared to target the marginal ice zone and hyposaline meltwaters (Fig. S18) associated with these same eddy zones. Indeed, ARS locations were consistently around the sea ice edge, regardless of whether most transit locations were within or outside the sea ice (Fig. 10), and a substantial difference was found between the two behavioural states ($t = 21.28$, $p < 0.001$).

Fledgling emperor penguins from Amanda Bay, Princess Elizabeth Land ($n = 22$; Fig. 11) ventured on trips reaching at least 985 km from the natal colony, exhibiting more ARS around anticyclones, with the strongest associations around peripheries ($\chi^2 = 212.6$, $p < 0.001$, CBI = 0.854). Eddies containing ARS locations in anticyclones were typically in those that were more mature ($z = 5.9$, $p < 0.001$), but lesser in

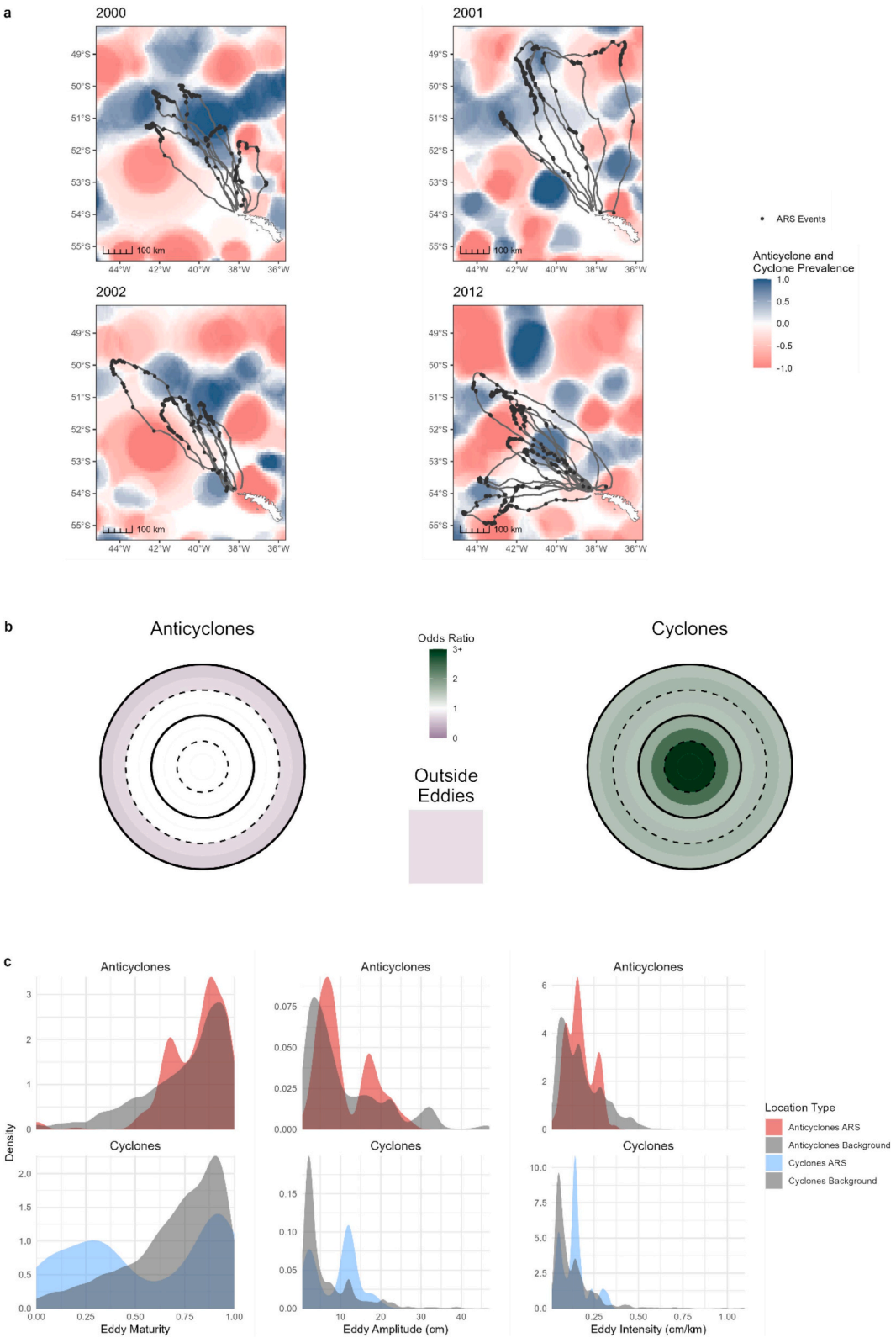

Fig. 7. (a) Tracks of incubating macaroni penguins from Fairy Point, South Georgia in different years, with ARS events marked as black dots. The prevalence of eddies denotes the proportion of dates on which tracks were recorded where a given cell was a cyclone (blue) or anticyclone (red). This proportion is negative for anticyclones. (b) Odds ratios taken from GAMMs with values above 1 (green) indicating relative preference during ARS. The colour of the square indicates the odds ratio for locations outside of eddies. Solid circles denote boundaries equivalent to 1x or 2x the speed radius, while broken circles denote 0.5x and 1.5x the speed radius. (c) Comparison of eddy maturity, amplitude, and intensity at ARS (blue/red) and background locations (grey) recorded within eddies. Mean error of ARS locations was 0.22 km, and the average eddy radius was 53.85 km.

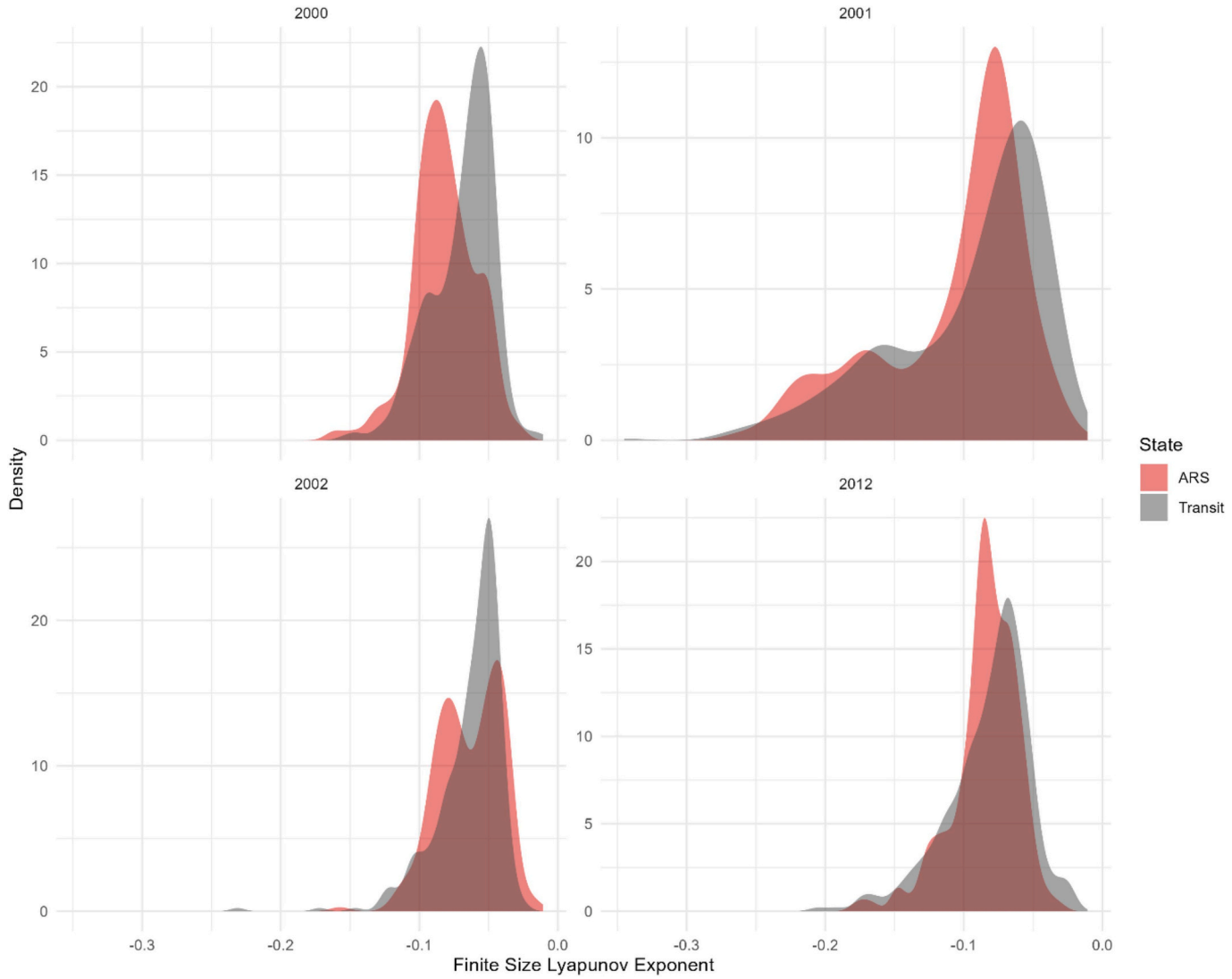

Fig. 8. Finite-size Lyapunov Exponent (FSLE) values at ARS (red) and transit (grey) locations of incubating macaroni penguins from Fairy Point, South Georgia in different years. Panels represent individual years, and shaded curves show the probability density of FSLE values for each behavioural state. More negative FSLE values are indicative of greater submesoscale activity.

amplitude (z = -2.72, p = 0.007) and intensity (z = -2.44, p = 0.015). Anticyclones encountered by these fledglings contained elevated densities of modelled migratory micronekton, peaking around the speed contour at 4.78 g m^{-2}, far greater than the normal range of 1.4–2.1 g m^{-2} found in cyclones and waters outside of eddies (Fig. S19).

Chick-rearing king penguins from Ratmanoff, Kerguelen (n = 29; Fig. 12) appeared to prefer the outer cores of anticyclones around the speed contour and the inner cores of cyclones ($\chi^2 = 44.9$, $p < 0.001$, CBI = 0.61). ARS locations were found in both cyclones (z = 2.41, p = 0.023) and anticyclones (z = 2.15, p = 0.031) with an average greater amplitude than the background eddy field. In all years, ARS events were observed at eddy-eddy confluences, many of which coincided with areas of submesoscale filament activity (Fig. S20). This is supported by the lesser mean FSLE values in ARS (−0.0428) than transit (−0.0354) locations (t = 11.968, $p < 0.001$), and these differences were most notable in 2013 and 2015 (Fig. 13). ARS within cyclones was most apparent in 2015, 2016, and 2019, when cyclones persisted near the colony. Maximum distances travelled from the colony were highly variable (F = 3.035, p = 0.0338), ranging from an average of 212 km in 2019 to 397 km in 2015.

Similar plots to those presented here can be found for each of the 74 case studies in Supplementary Data 1.

4. Discussion

We found that eddies were associated with elevated ARS, likely indicative of foraging, for penguins from many colonies across all five studied species. Eddies were common drivers of ARS in most regions, with the exceptions of Tierra del Fuego and the South Shetland Islands. Central place foraging constraints were linked with greater associations between eddies and ARS, with fewer relative associations when constraints were removed. Preferred zones and types of eddies were varied, though some similar preferences were observed at multiple colonies. When eddy fields varied between years, responses of penguins were also variable depending on the location and breeding stage.

4.1. Variation in eddy specialisation

Geographically, eddies often influenced ARS around subantarctic islands and mainland Antarctica. However, in Tierra del Fuego, neither incubating (n = 13) nor chick-rearing (n = 15) king penguins encountered eddies. Here, individuals remained exclusively in the Strait of Magellan rather than exploring nearby eddy-rich oceanic waters, suggesting that the Strait might offer a closer, more reliable supply of prey (Pütz et al., 2021). This is also a newly established small colony, so

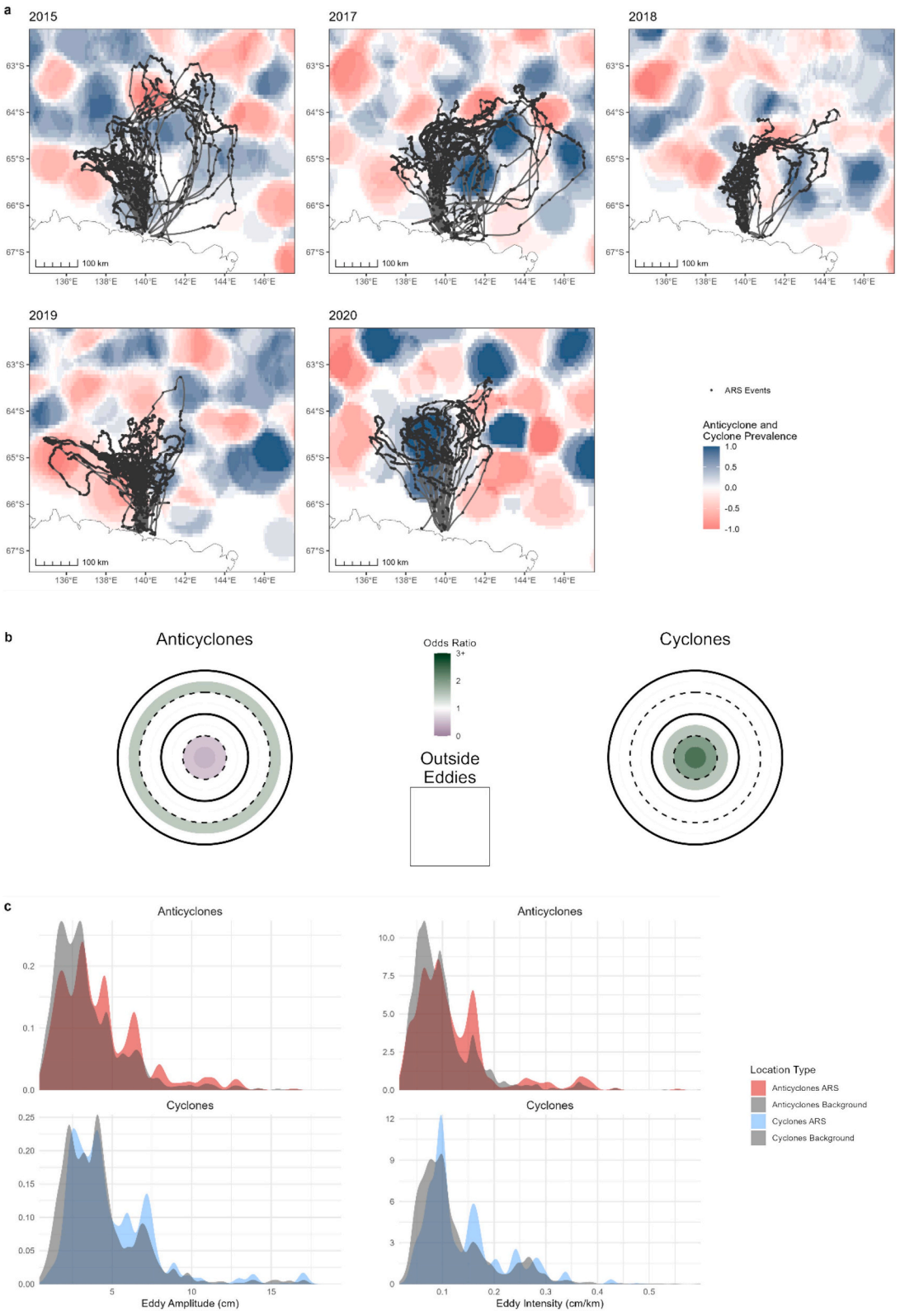

Fig. 9. (a) Tracks of incubating Adélie penguins from Pointe Géologie, Terre Adélie in different years, with ARS events marked as black dots. The prevalence of eddies denotes the proportion of dates on which tracks were recorded where a given cell was a cyclone (blue) or anticyclone (red). This proportion is negative for anticyclones. (b) Odds ratios taken from GAMMs with values above 1 (green) indicating relative preference during ARS. The colour of the square indicates the odds ratio for locations outside of eddies. Solid circles denote boundaries equivalent to 1x or 2x the speed radius, while broken circles denote 0.5x and 1.5x the speed radius. (c) Comparison of eddy amplitude and intensity at ARS (blue/red) and background locations (grey) recorded within eddies. Eddy maturity was not available in the sea ice eddy product hence it was not included here. The mean error of ARS locations was 1.41 km, and the average eddy radius was 35.7 km.

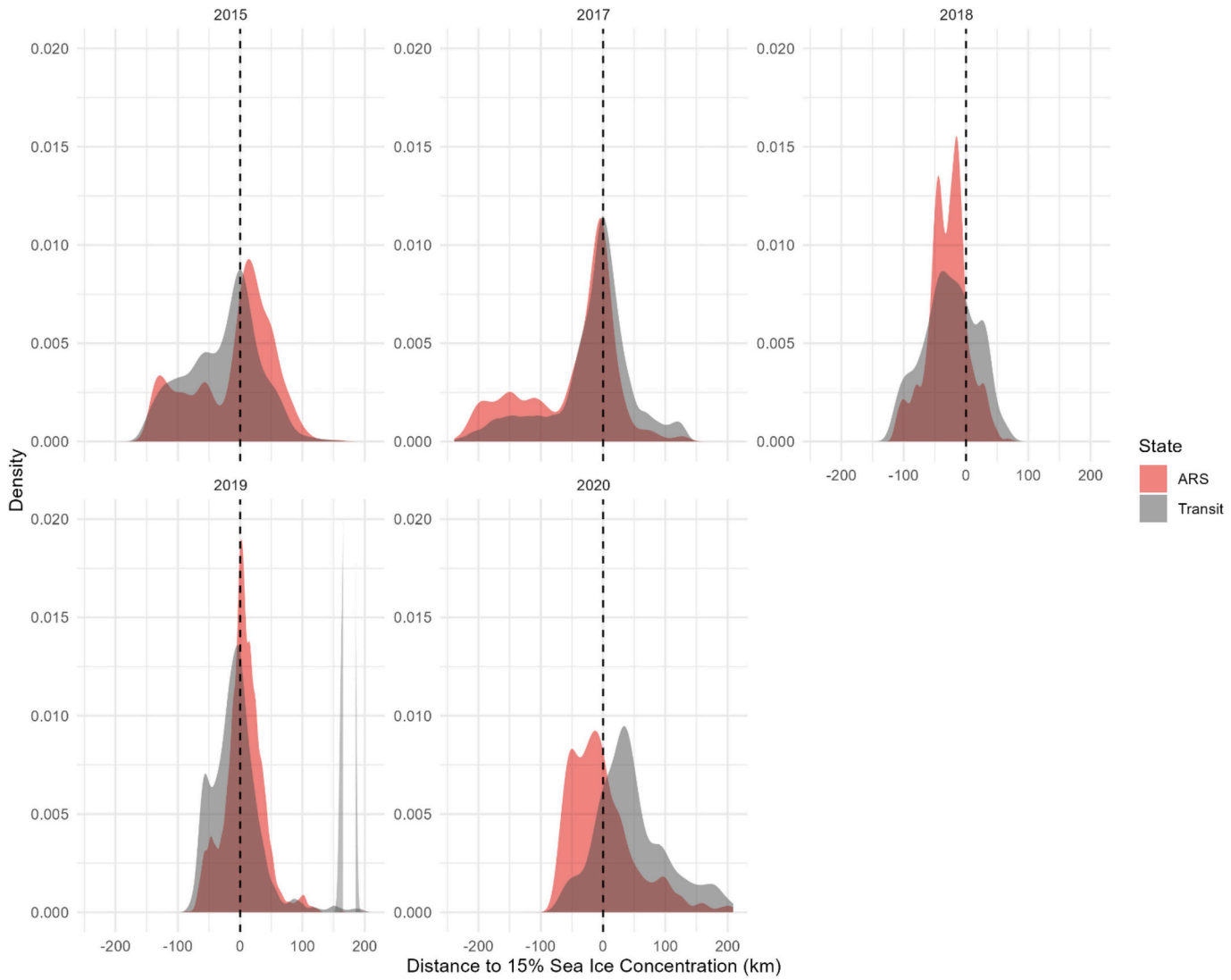

Fig. 10. Distance to the ice edge (defined as distance to the nearest 15 % sea ice concentration) values at ARS (red) and transit (grey) locations of incubating Adélie penguins from Pointe Géologie, Terre Adélie in different years. Panels represent individual years, and shaded curves show the probability density of distance to ice edge values for each behavioural state. The dashed line at a distance of 0 denotes the position of the ice edge. Negative values are within the sea ice zone at sea ice concentrations greater than 15 %, while positive values are from beyond the sea ice edge at sea ice concentrations lesser than 15 %.

reduced competition might enable all adults to forage locally (Gherardi-Fuentes et al., 2019). At the South Shetland Islands, most of the studied colonies were located on the southern coast of the islands. Eddies were sparse in the Bransfield Strait south of the islands, and Adélie and chinstrap penguins here instead forage around nearby canyons and seamounts (Kokubun et al., 2015; Machado-Gaye et al., 2024). When accessible, prey hotspots formed by bathymetric features or predictable currents may be preferred to ephemeral eddy-related aggregations. It is this geographic variability that drives interspecific variation in eddy use, as emperor and macaroni penguins had the highest proportionate use but were the only two species to not feature case studies in the South Shetland Islands or Tierra del Fuego.

Reduced influence of eddies when penguins were not under central place constraints could stem from several causes. Despite no preference for any specific eddy zone being detected, many of these unconstrained trips often exhibited extended periods of ARS within eddies. However, at this time, trips cover 100s to 1000s of kilometres and the type or zone of eddy that is most profitable may change regionally. Therefore, it could be that penguins do still forage within eddies, but within different zones in different regions. Alternatively, the removal of a central place constraint could allow penguins to reach more predictable and reliable hotspots created by bathymetric features or persistent ACC fronts. This has been observed in post-guard king penguins from Marion Island (n = 5), which bypassed a productive eddy field and targeted prey-rich waters south of the Polar Front instead (Pistorius et al., 2017). It could also be that since penguins do not return to land to rest at this time, there are more periods of rest in these tracks that were mislabelled as ARS.

4.2. *Eddy mechanisms that influence ARS*

Among the case studies explored in detail here, multiple mechanisms associated with eddies seemed to influence penguin behaviour. Eddy boundaries, anticyclone-cyclone confluences, and cyclonic cores appeared important for macaroni penguins from South Georgia and king penguins from Kerguelen. At South Georgia, krill patchiness is a better predictor of macaroni penguin fledgling success than density, suggesting that small-scale prey aggregations are more beneficial than abundant but uniformly distributed prey (Trathan et al., 2022). Similarly, it is thought that shallow and dense aggregations of prey near Kerguelen enable high prey capture rates in king penguins, particularly around fronts (Scheffer et al., 2016). Near-surface aggregations of krill and other nekton are denser in submesoscale filaments that form in the eddy

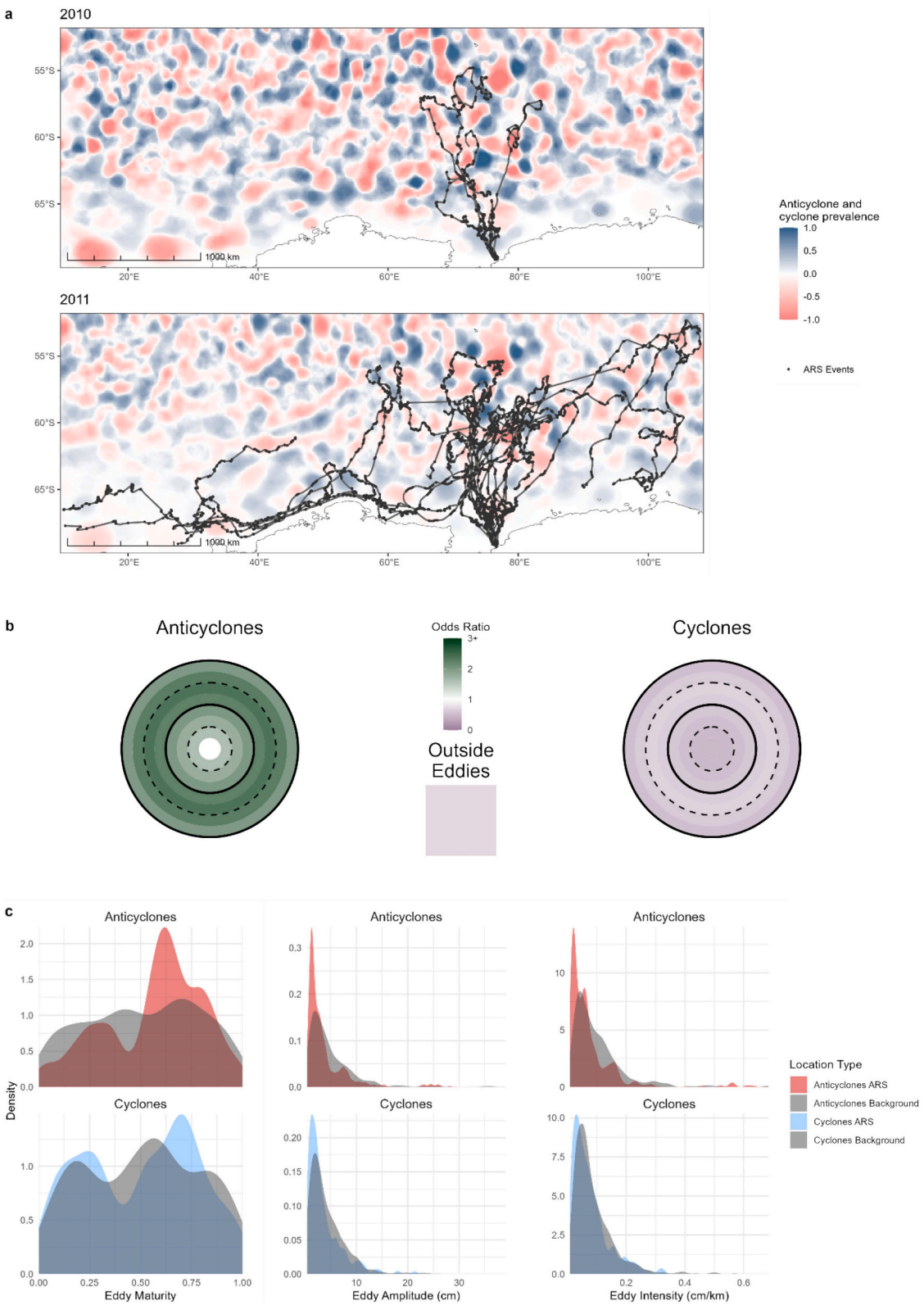

Fig. 11. (a) Tracks of fledgling emperor penguins from Amanda Bay, Princess Elizabeth Land in different years, with ARS events marked as black dots. The prevalence of eddies denotes the proportion of dates on which tracks were recorded where a given cell was a cyclone (blue) or anticyclone (red). This proportion is negative for anticyclones. (b) Odds ratios taken from GAMMs with values above 1 (green) indicating relative preference during ARS. The colour of the square indicates the odds ratio for locations outside of eddies. Solid circles denote boundaries equivalent to 1x or 2x the speed radius, while broken circles denote 0.5x and 1.5x the speed radius. (c) Comparison of eddy maturity, amplitude, and intensity at ARS (blue/red) and background locations (grey) recorded within eddies. Mean error of ARS locations was 2.58 km, and the average eddy radius was 50.99 km.

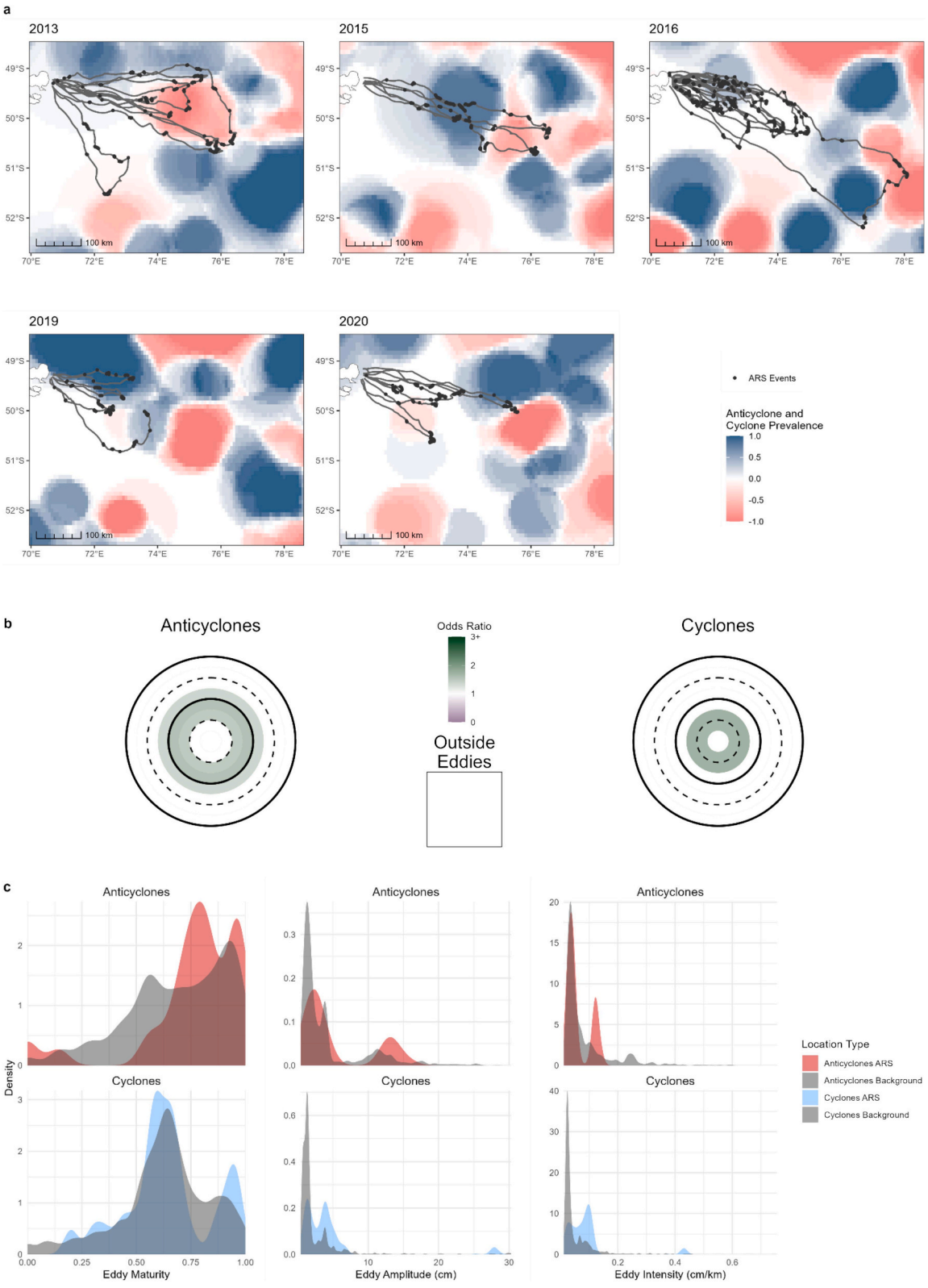

Fig. 12. (a) Tracks of chick-rearing king penguins from Ratmanoff, Kerguelen in different years, with ARS events marked as black dots. The prevalence of eddies denotes the proportion of dates on which tracks were recorded where a given cell was a cyclone (blue) or anticyclone (red). This proportion is negative for anticyclones. (b) Odds ratios taken from GAMMs with values above 1 (green) indicating relative preference during ARS. The colour of the square indicates the odds ratio for locations outside of eddies. Solid circles denote boundaries equivalent to 1x or 2x the speed radius, while broken circles denote 0.5x and 1.5x the speed radius. (c) Comparison of eddy maturity, amplitude, and intensity at ARS (blue/red) and background locations (grey) recorded within eddies. The mean error of ARS locations was 0.3 km, and the average eddy radius was 50.97 km.

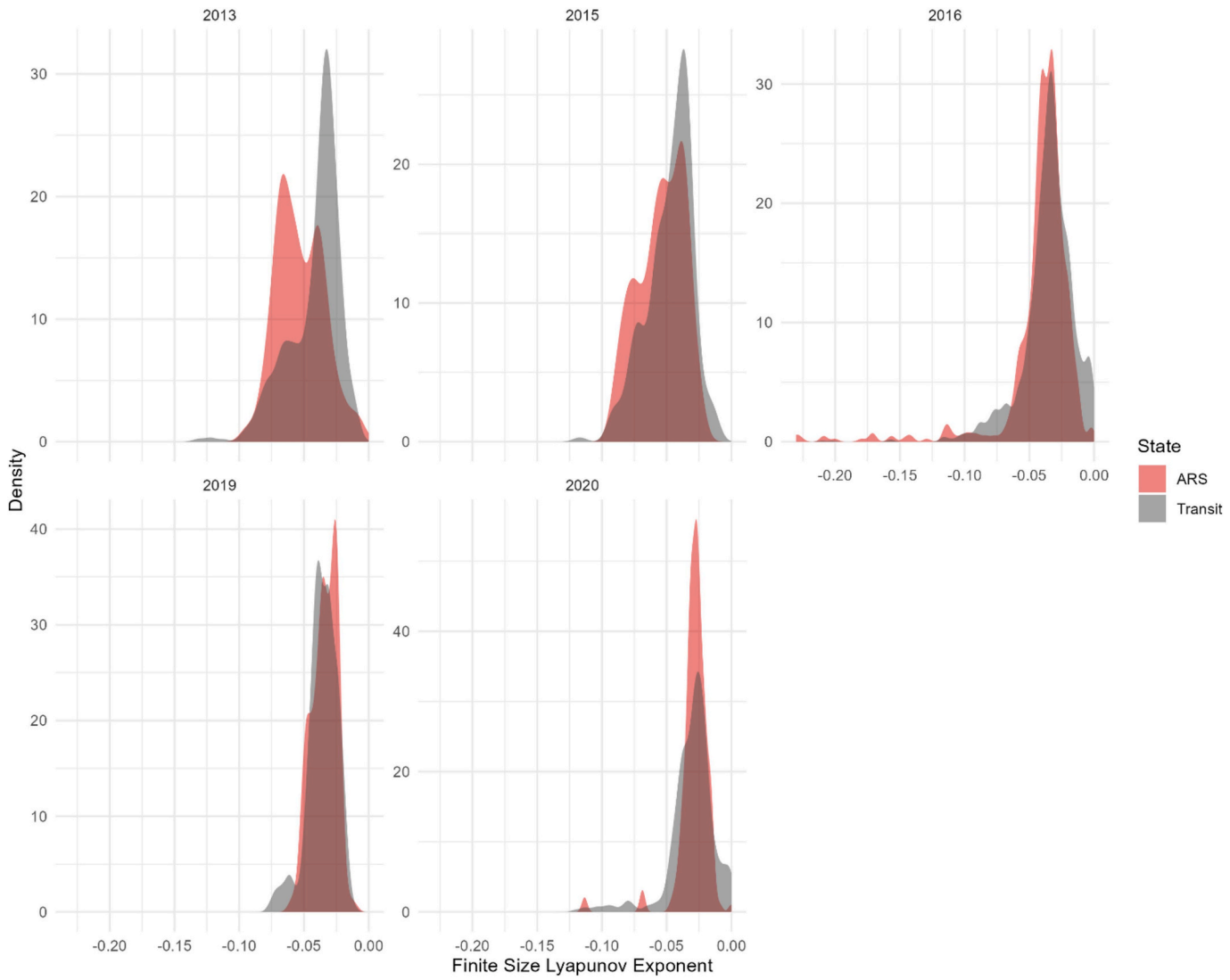

Fig. 13. Finite-size Lyapunov Exponent (FSLE) values at ARS (red) and transit (grey) locations of chick-rearing king penguins from Ratmanoff, Kerguelen in different years. Panels represent individual years, and shaded curves show the probability density of FSLE values for each behavioural state. More negative FSLE values are indicative of greater submesoscale activity.

zones associated with elevated ARS in these case studies (Sabarros et al., 2009; Veatch et al., 2025), and penguins from other colonies also target filaments (Cotté et al., 2007; Scheffer et al., 2010; Bon et al., 2015; Whitehead et al., 2016; Veatch et al., 2025). This is further supported by the association of ARS locations with lower FSLE values, representative of submesoscale processes. It is telling that in the case studies where central place foraging constraints were relaxed, ARS locations were generally in eddies with greater amplitude, since elevated submesoscale activity is associated with mesoscale eddies with greater amplitudes (McWilliams, 2016). Therefore, the aggregative effects of submesoscale filaments associated with eddies may be one of the key processes through which eddies influence the trip trajectories of penguins.

In the seasonal sea-ice zone around Antarctica, Adélie penguins from Terre Adélie exhibited elevated ARS at anticyclonic peripheries and cyclonic cores. In most years, penguins appeared to track the southern edges of anticyclones which typically coincided with the ice edge, a feature that penguins from this colony target (Michelot et al., 2020). Advection of ice floes within eddy peripheries into warmer anticyclone waters leads to enhanced melting, and so the sea ice edge is often modulated by the southern edge of anticyclones (Huot et al., 2022; Gupta et al., 2024). Meltwater at the ice edge intensifies water column stratification, which confines phytoplankton in the photic zone and stimulates productivity (Lester et al., 2021). This may explain why Adélie penguins appear also to target lower salinity values synonymous with meltwater. ARS within cyclonic cores was also observed in multiple years, but was most pronounced in 2020, when local sea ice concentrations were lower than in other years. In these conditions, cyclones can host elevated concentrations of sea ice through physical aggregation in submesoscale filaments and freezing of seawater (Manucharyan and Thompson, 2017; Huot et al., 2022). Adélie penguins and their primary prey, silverfish, are associated with sea ice (Vacchi et al., 2012; Michelot et al., 2021), so perhaps cyclones act as oases in warmer years. Eddy amplitude and intensity did not appear to impact ARS, possibly because eddies simply modulated the location of sea ice.

Fledgling emperor penguins from Amanda Bay displayed more ARS in more mature anticyclones with lesser amplitude and intensity that contained elevated nekton biomass. These preferred properties are characteristic of late-stage mature anticyclones (Durgadoo et al., 2011). Most ARS within anticyclones was located over and around the southern Kerguelen Plateau, where southern elephant seals (*Mirounga leonina*) have been shown to hunt more extensively within long-lived anticyclones (Green et al., 2020). In this region, many anticyclones form in the destabilised flow of the ACC to the north of the area that fledglings ventured to (Bestley et al., 2020). As fledglings, emperor penguins are

thought to consume myctophids (Wienecke et al., 2010; Thiebot et al., 2013), which generally spawn in subantarctic waters and are subsequently transported into Antarctic waters by anticyclones that form around the ACC (Saunders et al., 2017). Therefore, it is plausible that more mature anticyclones propagating southwards from the Polar Front might offer a greater abundance of myctophid prey.

4.3. Impacts of changing eddy fields

Regular movements of penguins towards eddy hotspots suggest that penguins adapt locally to foraging within eddy fields. This raises a key question as to whether penguins target distinct eddies or whether they follow a simpler foraging strategy wherein birds head in a learned trajectory towards eddy fields until they encounter prey aggregations (Trathan et al., 2006). Multi-year case studies support this simple foraging hypothesis. At these colonies, penguins travel in a consistent trajectory from year to year, returning after foraging extensively. During incubation, macaroni penguins from South Georgia continued on the same heading despite encountering no eddies on their early outbound journeys, which resulted in much longer trip durations and lengths. Penguins use memory and, more locally, temperature and olfactory cues to seek out prey (Culik, 2001; Trathan et al., 2008; Wright et al., 2011). They may well detect environmental changes only once within or close to an eddy.

In a future Southern Ocean characterised by greater eddy abundance (Beech et al., 2022; Beech et al., 2025), penguins in most regions should encounter eddies more frequently on foraging trips. King penguins from Kerguelen and incubating macaroni penguins from South Georgia appeared to make shorter foraging trips when they encountered eddies early on outbound trips. At these colonies, shorter trips are linked with increased body mass gain and heavier fledgling weights (Scheffer et al., 2016; Horswill et al., 2017; Brisson-Curadeau et al., 2024). This could lead to improved demographic rates and population dynamics (Horswill et al., 2014; Horswill et al., 2016), though only if large-scale prey abundance does not decline with climate change. Average eddy amplitude is also expected to increase (Beech et al., 2025), which could lead to more submesoscale activity and benefit penguins targeting submesoscale filaments. Conversely, eddy lifespans are projected to decline wherever background circulation intensifies (Beech et al., 2025), which might detract from the potential benefits of transport within eddies.

Increased eddy activity did not relate to shorter foraging trips in every case study. Chick-rearing macaroni penguins from South Georgia made the shortest trips in 2012, a year characterised by relatively few eddies near the colony. Despite possible positive effects of eddies, eddies near the colony could also disperse prey away from the shelf through eddy trapping or stirring (Matis et al., 2014). Fledgling weights were lightest in 1999 and 2004, when eddies were abundant, but heavier in 2003, 2005, and 2012, years when eddies were either abundant or virtually absent (Fig. S21). The two years with lighter fledgling weights were also years of reduced krill density around South Georgia (Fielding et al., 2014), and both featured FSLE values in ARS locations that were most distinct from those of transit locations, suggesting that submesoscale activity around eddies might have provided some accessible prey in an otherwise resource-poor year. While eddies might aggregate local patches of prey that facilitate breeding success, if regional prey abundance falls too low, even these submesoscale patches may be of insufficient density for chick provisioning. Warming has caused wide-scale shifts in key prey species for penguins such as krill and silverfish (Atkinson et al., 2019; Corso et al., 2022), and eddies are unlikely to be able to compensate for these broader distributional changes.

It is also possible that the abundance and intensity of eddies is irrelevant if other environmental variables are more important. For example, Adélie penguins at Terre Adélie favour sea ice concentrations between 20–30 % (Michelot et al., 2021) and eddies merely modulate the distribution of sea ice and associated meltwater. Antarctic sea ice extent has already declined substantially (Ionita, 2024) and could decrease by as much as 40 % by 2100 (Holmes et al., 2022). Should sea ice disappear near this colony, it is unknown whether eddies would offer any meaningful advantages to penguins. While eddies may well influence foraging trip trajectories, increasing eddy activity might not always benefit penguins in the face of other environmental changes.

A future application of these findings could be to incorporate eddy fields into predictive models of predator foraging trajectories as eddy fields change. Such models typically use eddy kinetic energy as a proxy for eddies (Klaassen et al., 2026), but our findings show that the eddy polarity, zone, amplitude, intensity, and maturity can all factor into how likely an animal is to exhibit ARS within a given eddy. Additionally, we found that the preference for eddies can vary temporally with different behavioural restrictions and environmental conditions. To properly incorporate mesoscale features into predictive models, researchers should use a more comprehensive representation of eddies and consider interactions with other environmental predictors.

4.4. Caveats

There are some caveats to these methods. First is the small sample size of some case studies. The number of tracked individuals for each case study ranged from three to 325, and 17 of the 74 case studies featured five or fewer individuals (Table S2). In addition, 41 case studies featured data from just one deployment period. Our results highlight that interannual variability is common in both eddy fields and penguin behaviour, thus studying more individuals over more years and different life-history periods would paint a fuller picture.

Additionally, the circular shape of eddy boundaries constructed through buffering the eddy centre by double the speed radius does not perfectly represent the asymmetric surface shape of many eddies (Chen et al., 2019). The exact eddy zone may therefore have been mislabelled in some instances and some non-eddy waters may have been included within buffers. This also introduces smoothing of sharp physical gradients seen around eddy boundaries. However, this method allowed for identification of eddy peripheries beyond the speed contour and was more computationally feasible for constructing a circumpolar daily raster product. Further, it has been shown that a radius approach is a reasonable proxy for subsurface anomalies within Southern Ocean eddies (Frenger et al., 2015), where penguins exploit prey resources at depth.

Furthermore, eddies in the datasets we used are detected from coarse (0.25° or 25 km) altimetric products and are biased towards larger, higher-amplitude surface features, so many submesoscale or subsurface eddies are likely not considered here (Amores et al., 2018; Chen et al., 2021). This is especially relevant in Antarctic marginal seas, where the baroclinic Rossby deformation radius is ~ 2–5 km, and locally relevant mesoscale eddies (defined as those with radii exceeding this radius) are underestimated by the products used here (Liu et al., 2025; Han et al., 2026). However, since finer resolution (2 km) altimetry products suitable for capturing these eddies only have a temporal coverage dating back to 2023 (Fu et al., 2024), these were not suitable for the temporal range of our data (1993–2024). It is also expected that some eddies were not identified in ice-covered regions, even with the sea ice eddy product, due to incomplete sampling coverage. It is therefore possible that the true influence of eddies is underestimated in some regions, particularly around Antarctica.

Fitting Hidden Markov Models to tracking data without any secondary data sources could also introduce some uncertainty around odds ratios. While ARS likely represents foraging behaviour in many cases, other behaviours such as resting or socialising can also be classified as ARS since seabirds also exhibit slower, less directed movements during these behaviours (Diop et al., 2018). However, daytime ARS did correspond to increased diving and foraging behaviour in four case studies with available time-depth-recorder or accelerometry data (Fig. S13). Future work could build on this methodology by incorporating accelerometry or time-depth-recorder data into movement models to identify

foraging behaviour with greater confidence (Bestley et al., 2016). Nonetheless, using HMMs limits the interpretation of colocation with eddies as evidence of habitat preference during periods when penguins are simply transiting through waters at fast speeds.

5. Conclusion

Using a multi-species synthesis of telemetry data from over 3000 individual penguins from 59 colonies, we found that penguins frequently displayed elevated ARS in association with eddies. However, this association was weaker in certain regions and when penguins were not restricted to central place foraging around colonies. There were multiple mechanisms through which eddies might influence ARS, all of which could influence the accessibility and abundance of prey species. When eddy fields varied across years, trip durations and distances also varied, but with variable directional responses among case studies. Eddy maturity, amplitude, and intensity also interplayed with the relative occurrence of ARS, indicative of the different mechanisms at play. Increasing eddy activity projected across the Southern Ocean may have mixed implications in different regions, and broader climate-associated changes in sea ice or prey distribution are likely more dominant drivers of population trends. Our findings emphasise the role that mesoscale features play in dictating the distribution of Southern Ocean predators. Predictive models of movement trajectories should comprehensively incorporate these processes into modelling frameworks to achieve greater accuracy. Future work could retrospectively assess how changing eddy fields are linked with foraging and breeding success to quantify whether eddy intensification has any notable influence on population dynamics.

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CRediT authorship contribution statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Two supplementary data files are provided for the manuscript. In the first, the results for each of the 74 case studies are visualised. The second contains information on the tracking data obtained for this study, the spatial coverage of the study, methods for processing tracking data, breeding stage dates, hidden markov model outputs, background sampling methods, and additional visualisations of the in-depth case studies presented in the main manuscript.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2026.103798.

Data availability

The tracking data presented here are from a collection of studies carried out by the co-authors independently. Approximately half of the tracking data were sourced from the Retrospective Analysis of Antarctic Tracking Data (RAATD). RAATD is openly accessibly at https://doi.org/10.4225/15/5afcb927e8162. Sources of the remaining tracking data (including links where applicable) are listed in Table S3 in Supplementary Data 2, and we encourage users to contact the respective data owners should they wish to use the data for research purposes.

Eddy locations were sourced from the Mesoscale Eddy Trajectory Atlas v3.2 (SSALTO/DUACS), available at https://doi.org/10.24400/527896/a01-2022.005.220209. Other environmental variables were sourced from the Global Ocean Physics Reanalysis Model (Copernicus Marine Environmental Monitoring Service), available at https://doi.org/10.48670/moi-00021.

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