Global Ecology and Biogeography

WILEY

Global Ecology and Biogeography — A Journal of Macroecology

RESEARCH ARTICLE OPEN ACCESS

Global Marine Flyways Identified for Long-Distance Migrating Seabirds From Tracking Data

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Received: 30 March 2024 | **Revised:** 3 January 2025 | **Accepted:** 23 January 2025

Handling Editor: Manuel Steinbauer

Funding: This work was supported by the Global Ocean Biodiversity Initiative (GOBI) with a grant from the International Climate Initiative (IKI). The German Federal Ministry for the Environment, Nature Conservation, and Nuclear Safety (BMU) supports GOBI on the basis of a decision adopted by the German Bundestag.

Keywords: biologging | conservation | ecological connectivity | flyways | migration | seabirds

ABSTRACT

Aim: To identify the broad-scale oceanic migration routes ('marine flyways') used by multiple pelagic, long-distance migratory seabirds based on a global compilation of tracking data.
Location: Global.
Time Period: 1989–2023.
Major Taxa Studied: Seabirds (Families: Phaethontidae, Hydrobatidae, Diomedeidae, Procellariidae, Laridae and Stercorariidae).
Methods: We collated a comprehensive global tracking dataset that included the migratory routes of 48 pelagic and long-distance migrating seabird species across the Atlantic, Indian, Pacific and Southern Oceans. We grouped individuals that followed similar routes, independent of species or timings of migration, using a dynamic time warping clustering approach. We visualised the

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routes of each cluster using a line density analysis and used knowledge of seabird spatial ecology to combine the clusters to identify the broad-scale flyways followed by most pelagic migratory seabirds tracked to-date at an ocean-basin scale.
Results: Six marine flyways were identified across the world's oceans: the Atlantic Ocean Flyway, North Indian Ocean Flyway, East Indian Ocean Flyway, West Pacific Ocean Flyway, Pacific Ocean Flyway and Southern Ocean Flyway. Generally, the flyways were used bidirectionally, and individuals either followed sections of a flyway, a complete flyway, or their movements linked two or more flyways. Transhemispheric figure-of-eight routes in the Atlantic and Pacific oceans, and a circumnavigation flyway in the Southern Ocean correspond with major wind-driven ocean currents.
Main Conclusions: The marine flyways identified demonstrate that pelagic seabirds have similar and repeatable migration routes across ocean-basin scales. Our study highlights the need to account for connectivity in seabird conservation and provides a framework for international cooperation.

1 | Introduction

Migratory species often travel thousands of kilometres between breeding and non-breeding areas, visiting a variety of distant ecosystems and jurisdictions on a seasonal and predictable basis (e.g., Block et al. 2005; James, Myers, and Ottensmeyer 2005; Jetz et al. 2022). As a result of these vast movements, migratory species are vulnerable to a wide range of threats, often experiencing different anthropogenic stressors across their extensive ranges and at different stages in their life histories (Kirby et al. 2008; Nemes et al. 2023; Seidler et al. 2015). Consequently, the decline of migratory species is of global conservation concern (UNEP-WCMC 2024). Although the major threats to migratory species are well-known, effective implementation of management measures to address population declines of migrants requires an understanding of migration patterns to coordinate action at national and international scales (Conners et al. 2022; Oppel et al. 2018; Runge et al. 2015).

Groups of migratory bird species generally travel using long, predictable routes known as flyways, which we define here as the broadly consistent and repeatable migratory routes of multiple populations and species between their breeding and non-breeding areas, including any stop-over locations. Four major flyway systems are generally recognised: the Americas Flyway, the African-Eurasian Flyway, the Central Asian Flyway and the East-Asian-Australasian Flyway (Boere and Stroud 2006). Within these major flyway systems, a number of flyway subdivisions are recognised (Figure S1), which simplify complex migratory pathways and represent the broad, major routes used by land and waterbirds. The flyways concept is intended to highlight the shared responsibilities of countries for conserving migratory species based on the simplified representations of migratory patterns (Boere and Stroud 2006; Kirby 2010) and thus provides a useful framework that can help forge international collaboration. multilateral environmental agreements (MEAs), such as the Convention on the Conservation of Migratory Species of Wild Animals (CMS) and it's daughter agreements, including the African-Eurasian Migratory Waterbird Agreement (AEWA), have been created because many species undertake broad migratory movements, requiring international coordination and support for effective conservation across their range (Mikander 2016; UNEP/CMS 2010).

Seabirds are one of the most-threatened groups of vertebrates in the world, with 111 of the 365 (30.4%) recognised species considered globally threatened (classified as Critically Endangered, Endangered or Vulnerable on the IUCN Red List), and 56% with declining population trends (BirdLife International 2024; Dias et al. 2019). Seabirds face threats on land and at sea, and as such their conservation requires a holistic approach that considers their entire range, annual cycles, and any cumulative effects of these threats (Busch and Garthe 2018; Maxwell et al. 2013; Phillips, Fort, and Dias 2023). Approximately 76% of seabirds are classified as ‘full-migrants’, meaning a substantial proportion of the population makes regular or seasonal cyclical movements beyond the breeding range, with predictable timing and destinations (BirdLife International 2024). Migratory seabirds can be further classified by their foraging habitat: coastal or pelagic. Many coastal migratory seabird species travel migration routes that are entirely coastal or terrestrial, that are already encompassed within the existing flyways (e.g., Lesser Black-backed Gulls *Larus fuscus* (Bustnes et al. 2013), Caspian Tern *Hydroprogne caspia* (Rueda-Uribe et al. 2021), Thayer's Gull *Larus glaucoides thayeri* (Gutowsky et al. 2020)). However, 58.6% of seabirds are classified as pelagic, meaning they primarily use deep marine waters (typically > 200 m in depth), or neritic, continental shelf waters (Dias et al. 2019), with these species spending much of their lives beyond national jurisdictions (Beal et al. 2021). Key oceanic migratory routes have been identified for individual species, such as the figure-of-eight migration paths in the Pacific and Atlantic oceans, or the circumnavigations of the Southern Ocean (Croxall et al. 2005; Egevang et al. 2010; Shaffer et al. 2006), but these routes are currently outside of any existing flyways classifications.

Rapid technological advances over the last four decades have revolutionised our understanding of animal movement (Wilmers et al. 2015). Tracking technology has revealed details of seabird distribution and behaviour at sea, including: foraging strategies, behavioural consistency or plasticity, overlap with threats, spatial segregation, and influence of environmental variables, and has enabled modelling of the impacts of future climate change (Amélineau et al. 2021; Bonnet-Lebrun et al. 2021; Dias et al. 2011; Franklin et al. 2022; Gee et al. 2024; González-Solís et al. 2009; Morten et al. 2023; Suryan et al. 2007). Tracking data have also been used to identify the main migratory routes followed by individual seabird species (e.g., Felicísimo, Muñoz, and González-Solís 2008; Weimerskirch et al. 2015), but comprehensive, multi-species migratory routes have not yet been identified.

Here, we aim to identify marine flyways, defined here as: the broad oceanic routes used by multiple pelagic, seabird populations and species—by applying a novel approach onto tracking data of long-distance migrations from six families. Like the existing flyways, marine flyways provide a useful and pragmatic framework for the conservation of pelagic seabirds by directing and prioritising coordinated management actions at an ocean-basin scale that acknowledges cumulative impacts of threats, and through highlighting broad movement patterns and shared responsibility, facilitates the incorporation of migratory connectivity into policy (Dunn et al. 2019; Harrison et al. 2018).

2 | Methods

2.1 | Summary

To delineate the marine flyways, we collated and standardised seabird tracking data for pelagic, long-distance migratory species according to previously developed protocols (Carneiro et al. 2020). We assigned the annual life cycle stage to each location, and only those recorded during migration were used in our analyses. We processed and filtered tracking data to exclude individuals that did not meet a set of criteria (outlined below). Individuals were then grouped based on the shape of the migratory route, irrespective of species identity or the timing of migration. We estimated line densities for each cluster of individuals and the results were smoothed and combined where appropriate to delineate a network of marine flyways. Each of these steps is described in detail below (Figure S2).

2.2 | Study Taxa and Regions

We focused on pelagic seabirds that are long-distance migrants, defined as species that travelled > 2000 km from their breeding colony, remained at this minimum displacement for at least 30 days, and took routes that were primarily oceanic and in the High Seas, that is, areas beyond national jurisdiction, to minimise overlap with existing coastal and terrestrial flyways. As our aim was to describe new, unrecognised oceanic flyways to complement the existing coastal and terrestrial flyways, we explicitly excluded seabird species that follow mostly coastal routes already defined for waterbirds (e.g., Northern Gannet *Morus bassanus* using the East Atlantic Flyway, Pink-footed Shearwater *Ardenna creatopus* using the Pacific Americas Flyway). Our dataset included individuals from six seabird families (Phaethontidae, Hydrobatidae, Diomedeidae, Procellariidae, Laridae and Stercorariidae), which migrated within four ocean basins (Atlantic, Indian, Pacific and Southern oceans). Tracks from migrants that breed or partially migrate within the Arctic Ocean were classified as within either the Atlantic or the Pacific Ocean, as appropriate. Each individual track was assigned to one of the four ocean basins considered, based on the majority of locations.

2.3 | Tracking Data Collation and Filtering

Seabird tracking locations were collated via BirdLife International's Seabird Tracking Database (STDB; BirdLife International 2014) or were contributed directly by individual researchers (Table S1). Candidate species with available tracking data were searched using Google Scholar and the terms: ('*seabird*') AND ('*migration*' or *long distance*) AND (GLS or GPS or PTT or ARGOS or *biologging* or *tracking*) from October 2022 to 2023, and relevant datasets were requested via the STDB. Following this initial data compilation, we identified gaps in terms of underrepresented geographic regions or seabird families and made additional requests for newly published datasets until July 2023. In total, data were obtained for 3996 birds from 51 species at 64 colonies in 27 countries or jurisdictions, tracked during 1989 to 2023, and were derived from global positioning system (GPS) loggers, platform terminal transmitters (PTTs) and global location sensor (GLS) loggers (Table S1; Figure S3).

We processed and standardised tracking data from seabirds. This involved the removal of data from individuals with limited samples (fewer than 40 locations in total), classified as juvenile or immature, or with unknown colony origins. Tracking locations were labelled with the annual life-cycle stage, and only locations recorded during migration were used to delineate the marine flyways. Any individuals that remained resident year-round around the breeding colony were removed. Further details of tracking data processing and standardisation and of methods to assign annual life cycle stage can be found in Appendix S1 of Supporting Information. Data from three species were removed as no individual met the criteria, leading to a final dataset of 48 species used in further analysis (Table 1).

2.4 | Marine Flyways Delineation

A Lambert azimuthal equal-area projection was used, with the centroid of each ocean polygon as the centre point (Atlantic: [−0.726, −29.624], Indian: [−30.475, 78.619], Pacific: [−6.0644, −154.943], Southern: [−90, 0]). Where an individual moved between ocean basins, tracks were analysed only for the main ocean basin where migration occurred (where more than 50% of the locations were recorded).

Outbound and return migrations were analysed separately to account for individuals that use different routes to and from their colonies. Based on published literature, which indicated only one flyway in the Southern Ocean used by several species (e.g., Croxall et al. 2005; Delord et al. 2014), the following steps to group individuals were performed in the Atlantic, Indian and Pacific Oceans only. To identify unique flyways, we first applied a cluster analysis to group individual outbound and return migrations based on the similarity of their migratory path, independent of the timing of migration, or of population/species (Harrison et al. in prep). We used a dynamic time warp (DTW) cluster analysis for identifying similarities in time series data. We generated a list of each longitudinal and latitudinal locations in chronological order for each individual. We ran the DTW cluster analysis over the series of longitudinal/latitudinal lists for every individual's outbound and return track within each ocean. We created a dissimilarity matrix and the DTW machine learning algorithm iteratively matched locations with the least cost in time series order (i.e., the minimum geographic distance between each tracked location of two individuals). We manually selected the number of cluster groups and produced a dendrogram that detailed the

TABLE 1 | Species using each flyway and the clusters within them.

Ocean basin	Flyway (clusters)	Study species	Other species (Reference)
Atlantic	Atlantic Ocean Flyway (Cluster A, B, C)	DIOMEDEIDAE **Black-browed Albatross *Thalassarche melanophris*** (B) HYDROBATIDAE Leach's Storm Petrel *Hydrobates leucorhous* (A[f]) LARIDAE **Arctic Tern *Sterna paradisaea*** (A, B, C) Sabine's Gull *Xena sabini* (A, B[f]) PROCELLARIIDAE Broad-billed Prion *Pachyptila vittata*—removed during filtering Bulwer's Petrel *Bulweria bulwerii* (A) Cape Verde Shearwater *Calonectris edwardsii* (A, B, C) Cory's Shearwater *Calonectris borealis* (A, B, C) Great Shearwater *Aredenna gravis* (A, B, C) MacGillivray's Prion *Pachyptila macgillivrayi*—removed during filtering Manx Shearwater *Puffinus puffinus* (A, B, C) Scopoli's Shearwater *Calonectris diomedea* (A[e,f]) Slender-billed Prion *Pachyptila belcheri* (B, C) **Sooty Shearwater *Ardenna grisea*** (A) Spectacled Petrel *Procellaria conspicillata* (B, C[a]) **White-chinned Petrel *Procellaria aequinoctialis*** (B, C) STERCORARIIDAE **Brown Skua *Catharacta antarctica*** (B[a]) Long-tailed Skua *Stercorarius longcaudus* (A[f], B[f]) **South Polar Skua Catharacta maccormicki** (A, B, C)	DIOMEDEIDAE Atlantic yellow-nosed Albatross *Thalassarche chlororhynchos* (Agreement on the Conservation of Albatrosses and Petrels 2009) Tristan Albatross *Diomedea dabbenena* (Reid et al. 2013) HYDROBATIDAE Band-rumped Storm-petrel *Hydrobates castro* (BirdLife International 2014) LARIDAE Common Tern *Sterna hirundo* (Neves et al. 2015) PROCELLARIIDAE Desertas Petrel *Pterodroma deserta* (Ramírez et al. 2016) Trindade Petrel *Pterodroma arminjoniana* (Leal and Bugoni 2021) Zino's Petrel *Pterodroma madeira* (Ramos et al. 2017) STERCORARIIDAE Arctic Skua *Stercorarius parasiticus* (O'Hanlon et al. 2024)
Indian	North Indian Ocean Flyway (one cluster)	PHAETHONTIDAE Red-tailed Tropicbird *Phaethon rubricauda* PROCELLARIIDAE Trindade Petrel *Pterodroma arminjoniana*	LARIDAE Arctic Tern *Sterna paradisaea* (Fijn et al. 2013) Brown Noddy *Anous stolidus* (Lebarbenchon et al. 2023) Lesser Noddy *Anous tenuirostris* (Lebarbenchon et al. 2023) PHAETHONTIDAE White-tailed Tropicbird *Phaethon lepturus* (Trevail et al. 2023) PROCELLARIIDAE Mascarene Petrel *Pseudobulweria aterrima* (BirdLife International 2014) Tropical Shearwater *Puffinus bailloni* (Trevail et al. 2023)

(Continues)

TABLE 1 | (Continued)

Ocean basin	Flyway (clusters)	Study species	Other species (Reference)
Indian	East Indian Ocean Flyway (one cluster)	PHAETHONTIDAE Red-tailed Tropicbird *Phaethon rubicauda* PROCELLARIIDAE Barau's Petrel *Pterodroma baraui* Trindade Petrel *Pterodroma arminjoniana* Wedge-tailed Shearwater *Ardenna pacifica*	LARIDAE Sooty Tern *Onychoprion fuscatus* (Jaeger et al. 2017)
Pacific	Pacific Ocean Flyway (Clusters A, B, C)	DIOMEDEIDAE Antipodean Albatross *Diomedea antipodensis* (C) Black-footed Albatross *Thalassarche melanophris* (A[c], B[c]) Buller's Albatross *Thalassarche bulleri* (C) Laysan Albatross *Phoebastria immutabilis* (A[c], B[c]) Northern Royal Albatross *Diomedea sanfordi* (C) Salvin's Albatross *Thalassarche salvini* (C) LARIDAE **Arctic Tern *Sterna paradisaea*** (B) PROCELLARIIDAE Black/Parkinson's Petrel *Procellaria parkinsoni* (A[b]) Black-winged Petrel *Pterodroma nigripennis* (A, B) Buller's Shearwater *Ardenna bulleri* (A, B) Chatham Petrel *Pterodroma axillaris* (A[b]) Cook's Petrel *Pterodroma cookii* (A[b], B, C) Grey Petrel *Procellaria cinerea* (C) Juan Fernandez Petrel *Pterodroma externa* (B) Little Shearwater *Puffinus assimilis* (C) Magenta Petrel *Pterodroma magenta* (C) Mottled Petrel *Pterodroma inexpectata* (A) Murphy's Petrel *Pterodroma ultima*(B) Pycroft's Petrel *Pteroddroma solandri* (A[d], B[d]) Soft-plumaged Petrel *Pterodroma mollis* (C) **Sooty Shearwater *Ardenna grisea*** (A) Westland Petrel *Procellaria westlandica* (C) **White-chinned Petrel *Procellaria aequinoctialis* (C)** White-winged Petrel *Pterodroma leucoptera* (A, B) STERCORARIIDAE **Brown Skua *Catharacta antarctica*** (C) **South Polar Skua *Catharacta maccormicki*** (A, B)	DIOMEDEIDAE Chatham Albatross *Thalassarche eremita* (Deppe 2012) Campbell Albatross *Thalassarche impavida* (Thompson et al. 2021) PROCELLARIIDAE Stejnegner's Petrel *Pterodroma longirostris*[g] (Clay and Brooke 2024) White-necked Petrel *Pterodroma cervicalis* (BirdLife International 2014)

(Continues)

TABLE 1 | (Continued)

Ocean basin	Flyway (clusters)	Study species	Other species (Reference)
Pacific	West Pacific Ocean Flyway (one cluster)	PROCELLARIIDAE Providence Petrel *Pterodroma solandri* Streaked Shearwater *Calonectris leucomelas* STERCORARIIDAE **South Polar Skua *Catharacta maccormicki***	PROCELLARIIDAE Flesh-footed Shearwater *Ardenna carneipes* (Rayner et al. 2011) Short-tailed Shearwater *Ardenna tenuirostris* (Carey et al. 2014) Wedge-tailed Shearwater *Ardenna pacifica* (Weimerskirch et al. 2020)
Southern	Southern Ocean Flyway	DIOMEDEIDAE **Black-browed Albatross *Thalassarche melanophris*** Grey-headed Albatross *Thalassarche chrysostoma* Wandering Albatross *Diomedea exulans* PROCELLARIIDAE Antarctic Prion *Pachyptila desolata* Blue Petrel *Halobaena caerulea* Slender-billed Prion *Pachyptila belcheri* White-headed Petrel *Pterodroma leucoptera*–removed during filtering	DIOMEDEIDAE Amsterdam Albatross *Diomedea amsterdamensis* (Thiebot et al. 2014) Campbell Albatross *Thalassarche impavida* (Thompson et al. 2021) Indian Yellow-nosed Albatross *Thalassarche carteri* (Delord, Barbraud, Bost, Cherel et al. 2014) Light-mantled Albatross *Phoebetria palpebrata* (Mackley et al. 2010) Sooty Albatross *Phoebetria fusca* (Schoombie et al. 2022) White-capped Albatross *Thalassarche steadi* (BirdLife International 2014) LARIDAE Arctic Tern *Sterna paradisaea* (Redfern and Bevan 2020) PROCELLARIIDAE Antarctic Petrel *Thalassoica antarctica* (Descamps et al. 2016) Common Diving Petrel *Pelecanoides urinatrix* (Fromant et al. 2022) MacGillivray's Prion *Pachyptila macgillivrayi* (Delord et al. 2022) Northern Giant Petrel *Macronectes halli* (Thiers et al. 2014) Snow Petrel *Pagodroma nivea* (Delord et al. 2016) Southern Fulmar *Fulmarus glacialoides* (Delord et al. 2016) Southern Giant Petrel *Macronectes giganteus* (Thiers et al. 2014) South Georgian Diving Petrel *Pelecanoides georgicus* (Fromant et al. 2022) Whenua Hou Diving Petrel *Pelecanoides whenuahouensis* (Fischer et al. 2021)

Note: Study species from multiple ocean basins are **shown in bold**. Underlined species (in column 'Other species') use additional flyways to those assigned during analysis, but tracking data of these additional flyway routes were not available to this analysis. Other long-distance pelagic migratory species identified as using the flyways through tracking data from a literature review are shown in the final column, including new tracking studies not available at the time of the analysis.

[a]Section: between eastern South America and South Africa.
[b]Section: between NZ and Ecuador.
[c]Section: Northern hemisphere only.
[d]Section: bottom circle of 8.
[e]Section: East Atlantic only.
[f]Section: more East Atlantic Flyway (coastal).
[g]Data not included in analysis.

similarity of their migratory routes (based on DTW distances) for every outbound and return migration. We did so using the R package *dtwclust* (Sardá-Espinosa 2019), function 'tsclust' (time series clustering), with a distance setting of 'dtw', and cluster setting of 'hierarchical'. In each ocean, this resulted in two to five cluster groups. Clustering individuals by the similarity of their migratory route meant that species and populations were separated where their routes differed, and consequently a different number of individuals were assigned to each cluster. Grouping by the similarity of migration routes (i.e., using DTW distances) mitigated biases from population and sample sizes. We performed the following analytical steps on each cluster, independently of the sample sizes, thereby minimising any species or population with a higher sample size weighting the final flyway locations.

We visualised the resulting clusters (2, 3, 4 or 5) within the Atlantic, Indian and Pacific oceans, and for all individuals within the Southern Ocean, using the 'line density' tool in ArcGIS Pro (version 2.7.0). Line density calculates the density of linear features (in this case migratory tracks) within a circular area surrounding a raster cell. We divided the sum of the distances of all seabird movements (D, km) within a raster cell by the circular area of the search radius to generate the line density (Equation 1). We used a search radius of 400 km around the raster cell to account for the approximately ±200 km accuracy of light-level geolocators (Phillips et al. 2004).

$$\frac{D_1 + D_2 + \ldots D_x}{\pi(400)^2} \quad (1)$$

We derived major flyways from clusters using a semi-quantitative approach to incorporate knowledge of seabird migration and to ensure the outputs align with their broad intention. First, for parsimony, we visually selected the minimum number of clusters in each ocean basin based on the differentiation of distinct movement patterns. We identified a total of four clusters in the Pacific Ocean, three clusters in the Atlantic Ocean, and two clusters in the Indian Ocean through the line density estimation outputs, plus the one estimation for the Southern Ocean, and exported these results to R.

We used the R package *terra* (Hijmans 2023) for all raster calculations. We extracted raster layers of the following percentiles for each of the line density estimations: 0.025, 0.050, 0.100, 0.250, 0.500, 0.750, 0.900. We saved raster layers as polygons and smoothed each percentile for every cluster separately. For ocean basins with multiple clusters, we combined those that were clearly linked through full migratory journeys (i.e., differing outbound and inbound paths to the colony) to create one flyway, which highlighted the overall movement patterns at an ocean-basin scale and is in line with the intention of the flyways to illustrate broad-scale movements. The clusters represent distinct, but not independent, sections of the flyway, as some, but not all individuals, will follow the entire ocean-basin scale flyway.

We removed any small separate polygons or small holes within the larger polygon using the R package *smoothr* (method 'ksmooth', smoothness level 7.5; Strimas-Mackey 2023). We selected contour percentiles to best represent the broad-scale routes of migrating seabirds within each ocean basin based on seabird spatial ecology from expert knowledge.

We formed the final flyways in each ocean from the most appropriate percentile group that best illustrated the full continuity of movement patterns, without losing definition. Larger percentiles showed regions with a greater density of locations. To illustrate the location of predominant outbound and inbound movements, the mean latitude of locations recorded during the outbound and return migratory flights in the East Indian Flyway were calculated separately and used to determine the most commonly used route through the flyway. In the North Indian Flyway, the mean longitude of locations recorded during the outbound and return migratory flights were compared to determine the most commonly used route through the flyway. In the West Pacific Flyway, where locations crossed the international dateline, the circular mean was calculated for northbound and southbound journeys separately and compared to determine the general route through the flyway. In all other flyways, due to the complexity of the routes followed by migrating seabirds, the directions travelled were visually determined from tracks and through knowledge on seabird movements from the literature.

We then overlaid the resulting marine flyways with countries national waters (Exclusive Economic Zones [EEZ; https://www.marineregions.org/downloads.php]), and areas of competence of the tuna Regional Fisheries Management Organisations (http://fao.org/geonetwork/) to provide further information relevant to supporting the application of the marine flyways concept.

All data were analysed in R (version 4.2.2), unless otherwise stated. Scripts and the polygons of the clusters that form the final flyway in each ocean basin are available at Dryad: https://doi.org/10.5061/dryad.59zw3r2jc.

3 | Results

Six marine flyways were identified in the four ocean basins: Atlantic Ocean Flyway, North Indian Ocean Flyway, East Indian Ocean Flyway, West Pacific Ocean Flyway, Pacific Ocean Flyway, Southern Ocean Flyway (Figure 1). Flyways comprised 10 different clusters (or segments) that were spatially combined where appropriate, as explained below.

3.1 | Atlantic Ocean

Within the Atlantic Ocean there were three clusters of migratory routes identified from tracking data from 504 individual seabirds of 17 species (Figure 2). When combined, these formed a single figure-of-eight flyway that aligns with the known seabird movements across this ocean. The Atlantic Ocean Flyway has two loops, one in each hemisphere, and reaches high latitudes in both the north and south Atlantic Ocean. Seabirds from breeding colonies on the east coast of the Americas, from western Europe and the Mediterranean,

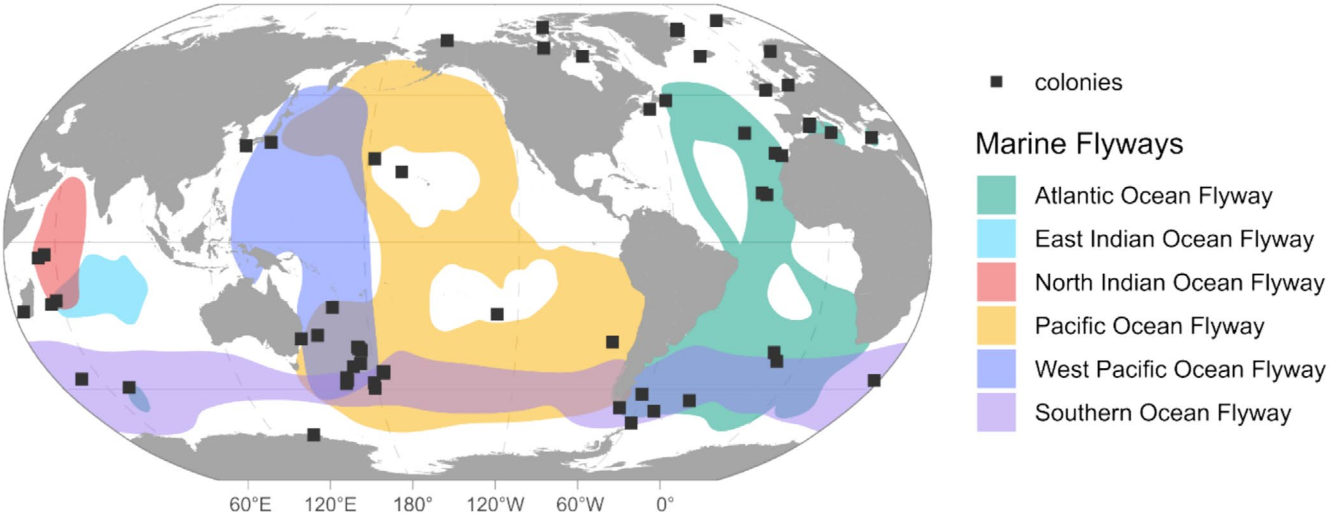

FIGURE 1 | The six marine flyways identified across four ocean basins from analysis of tracking data for 48 pelagic seabird species breeding at the 64 colonies indicated by the black squares. Map shown in Robinson projection centred at 140°W. Equal area projections for each Marine Flyway are found in Figures 2–5.

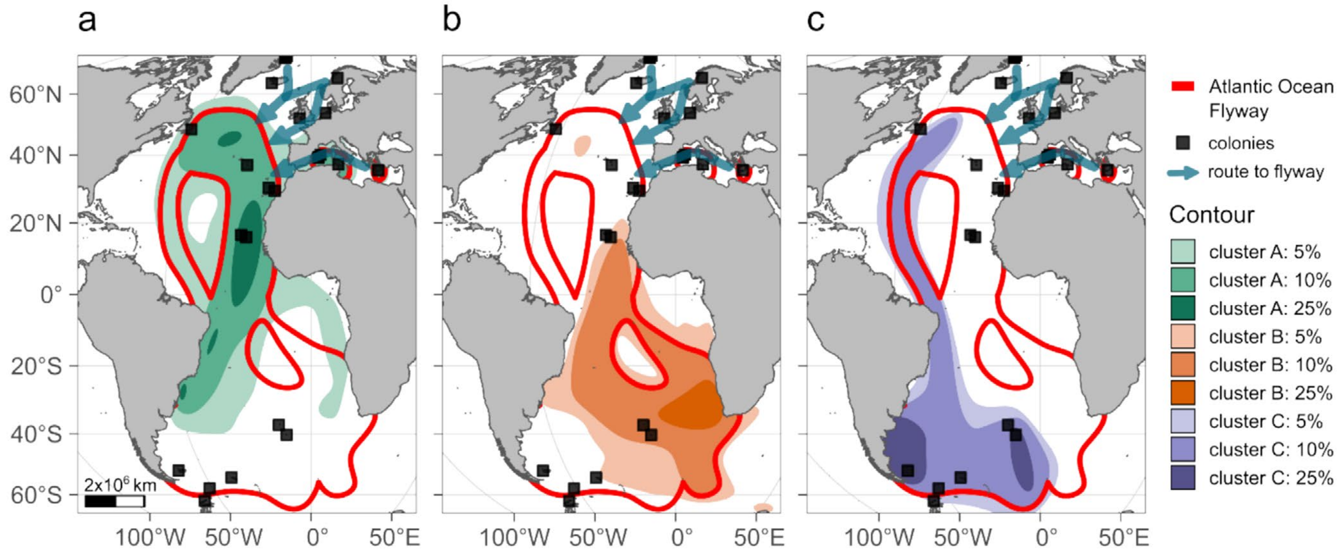

FIGURE 2 | Three key migratory route clusters in the Atlantic Ocean that were identified using tracking data from pelagic seabirds (a–c). Tracking data were from the colonies shown (black squares). The combined 10% cluster groups form the Atlantic Ocean Flyway (red outline). Map shown in Mollweide projection centred at 0°longitude.

from the west coast of Africa and from subantarctic islands migrate along the Atlantic Ocean Flyway. In addition to the species analysed in this study, at least another eight species use this flyway (Table 1). Out of the 27 species using this flyway (study species and references, Table 1), nine are globally threatened with extinction.

One cluster (Cluster A) extended from the central to eastern Atlantic in the Northern Hemisphere and crossed into the western Atlantic to the south of the Equator (Figure 2a). Seabirds migrated towards and away from the central north Atlantic via Western Europe and along the Brazilian coastline (Figure S4). This route was used by 12 of the 17 species for which migration tracks were available in the Atlantic Ocean (Table 1).

A second cluster (Cluster B) formed a loop from the Canary Current off north-west Africa to the west, towards Brazil and then extended east towards the Benguela Current and the coastal waters of South Africa, Namibia and Angola (Figure 2b). Seabirds migrated both clockwise and anticlockwise in this section of the flyway (Figure S4), and it was used by 13 of the 17 migrant species in the Atlantic Ocean (Table 1).

In the west Atlantic Ocean, a third cluster (Cluster C) was a predominantly coastal route, where migrating seabirds travelled along the eastern coast of the Americas between Argentina and Canada (Figure 2c). Migrants travelled northwards and southwards in the Southern Hemisphere, but generally only northward in the Northern Hemisphere (Figure S4). In total, nine of the 17 species analysed in the Atlantic Ocean followed this route (Table 1).

The 10% contour (*c.* 55,000,000 km^2 in extent) of the complete Atlantic Ocean Flyway (which consists of the three clusters) formed the major figure-of-eight route across the ocean basin (Figure 2), known to be travelled by the Arctic Tern (e.g., Egevang et al. 2010; and Figure S5) and South Polar Skua (Kopp et al. 2011). The flyway encompasses key migratory routes such as the bidirectional travel between Brazil and the North African coastline, longitudinal movements between Argentina and the Benguela Current, and the coastal route linking the central North Atlantic Ocean and southern South America. An additional migratory route along the west coast of Africa was highlighted by the 5% contour (combined cluster area *c.* 79,600,000 km^2), which was part of the existing East Atlantic Flyway. Key regions within the Atlantic Ocean Flyway are within the 25% contour (combined cluster group area *c.* 9,600,000 km^2) including the Canary, Benguela and Falklands/Malvinas currents. The Atlantic Ocean Flyway overlapped with the EEZ's of 25 countries (Table S2) and is also connected to an additional six northern hemisphere countries that fall beyond the defined flyway boundary (indicated in Figure 2; Table S1).

3.2 | Indian Ocean

Within the Indian Ocean there were two clear clusters, which formed the North Indian Ocean Flyway and East Indian Ocean Flyway (Figure 3), identified from tracking data of four species ($n = 152$ individuals) from colonies in the west Indian Ocean (Table S1). The Indian Ocean flyways identified are also used by seven other species (Table 1). Seabirds generally migrated to non-breeding areas either north into the Arabian Sea or east towards Indonesia and Australia (Figure S4). Some tracking locations fell outside of the flyway contours (e.g., five individuals travelled to the Bay of Bengal; Figure S3A), but this was not a major migratory route used by tracked seabirds.

In the East Indian Ocean Flyway (Figure 3a), seabirds generally travelled east at lower latitudes towards the non-breeding areas than during the return journey (mean ± SD: −20.1° S ± 7.6 and −16.0° S ± 8.5, respectively). All four species from the two southern colonies analysed in the Indian Ocean used this flyway (Table 1). The broad area of this flyway (25% contour) was *c.* 7,200,000 km^2, and the key migratory route area was 2,600,000 km^2 (50% contour). The East Indian Ocean Flyway overlapped with the EEZs of three countries (Table S2), and 40% (2 out of 5 species, Table 1) of the species using this flyway are globally threatened with extinction. In the North Indian Ocean Flyway (Figure 3b), seabirds migrated at similar longitudes during both the outward northbound migration and return southbound migration (mean ± SD: 61.6° E ± 6.3 and 62.0° W ± 6.8, respectively). Two of the four species analysed, which bred at four colonies in the southwest Indian Ocean, used this flyway (Table 1). The broad area of this flyway (25% contour) was *c.* 8,200,000 km^2, and the area around the key migration routes (50% contour) was 2,600,000 km^2. The North Indian Ocean Flyway overlapped with the EEZs of seven countries (Table S2), and 25% (2 out of 8 species, Table 1) of the species using this flyway are globally threatened with extinction.

3.3 | Pacific Ocean

We identified four clusters in the Pacific Ocean from our analyses of tracking data of 527 individuals from 28 species (Figure 4). Three clusters in the central and eastern Pacific were combined in a single figure-of-eight flyway: the Pacific Ocean Flyway (Figure 4a–c) as they were connected through multiple species migration patterns (e.g., Sooty Shearwater; Shaffer et al. 2006). Seabirds migrated both clockwise and anticlockwise throughout this flyway and joined from breeding colonies in the east Pacific (Alaska, Canada and Chile), central North Pacific (Hawaiian islands), Japan, Australia, Aotearoa New Zealand and subantarctic islands (Figure S4).

All the three clusters that formed the Pacific Ocean Flyway included a key migratory route that connected Aotearoa New Zealand and its offshore islands to Chile at latitudes below 25° S (Cluster C; Figure 4a–c). Multiple species (12 of 28 species in the Pacific) followed this longitudinal migration, which either formed a section of a migratory route (Figure 4a,b), or was the

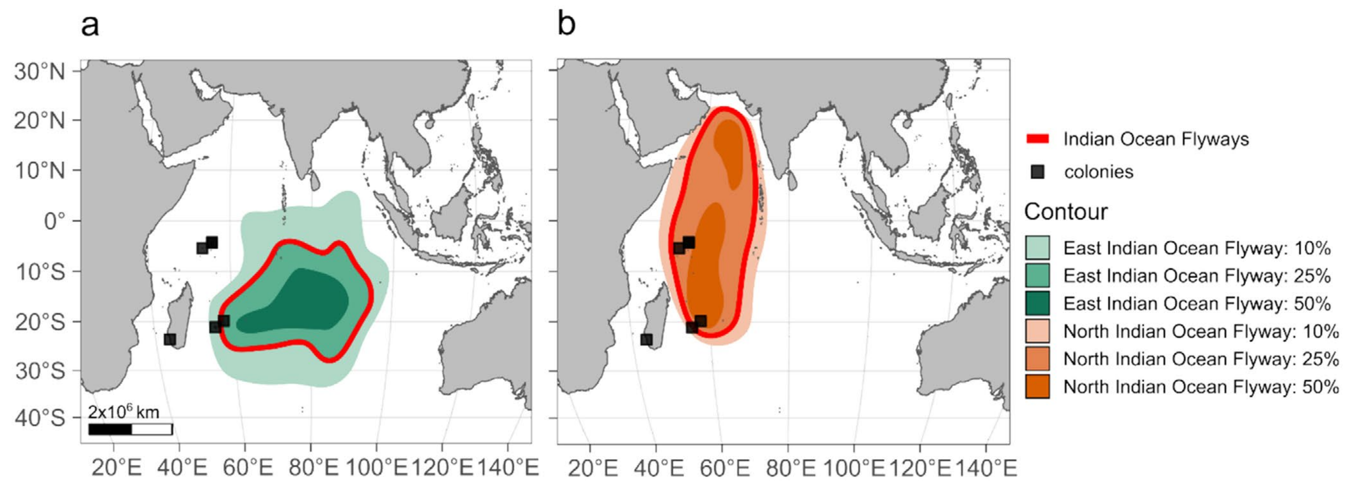

FIGURE 3 | Two key migratory route clusters in the Indian Ocean that were identified from pelagic seabird tracking data. Tracking data were from the colonies shown (black squares). Each 25% contour cluster group is identified as a separate flyway in the Indian Ocean: the East Indian Ocean Flyway (a) and the North Indian Ocean Flyway (b). Map shown in Mollweide projection centred at 78°E.

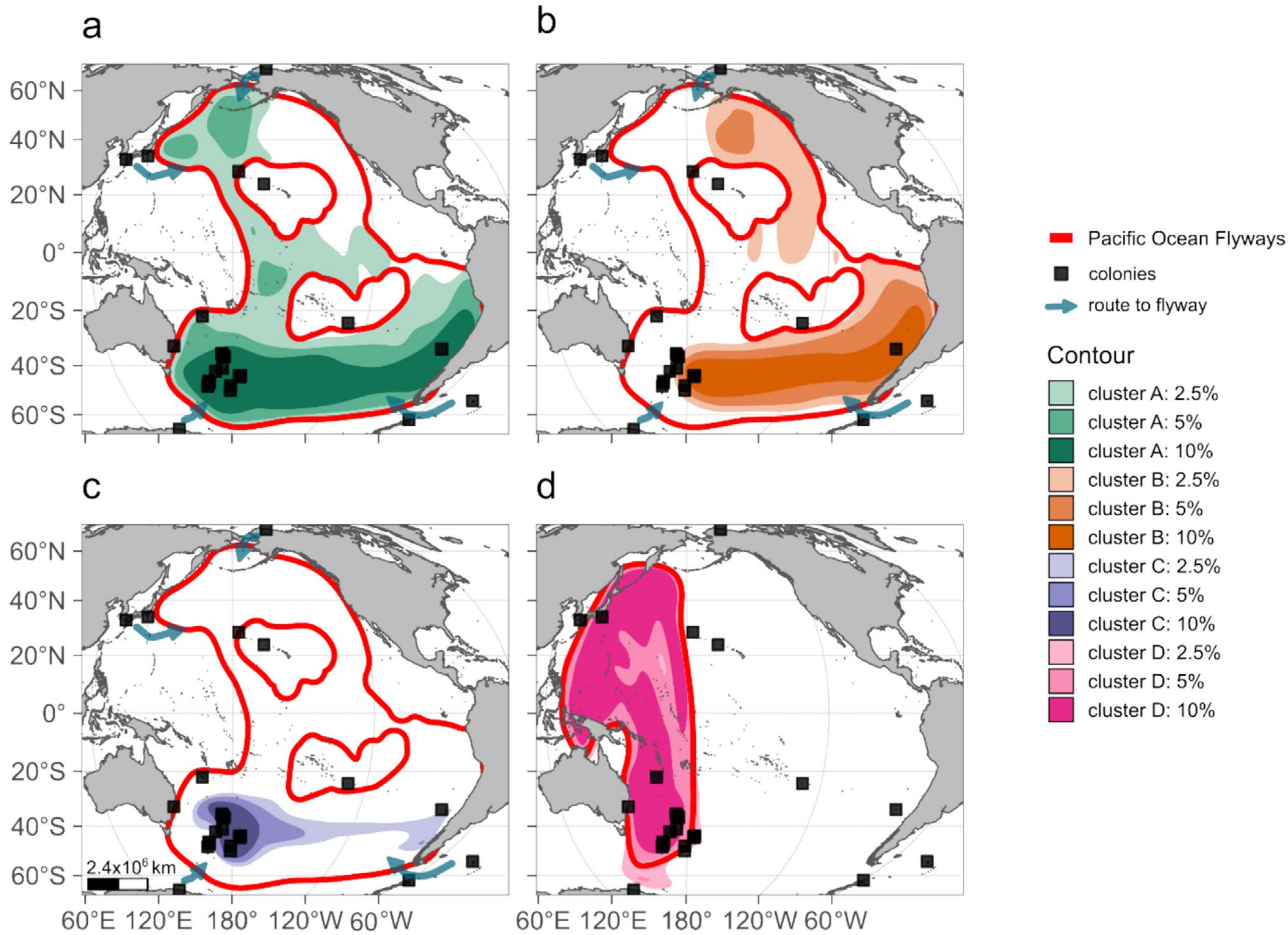

FIGURE 4 | Four key migratory route clusters within the Pacific Ocean that were identified from pelagic seabird tracking data. Tracking data were from the colonies shown (black squares). The Pacific Ocean Flyway comprises of the combined 2.5% contours of clusters (a–c). The West Pacific Ocean Flyway is identified from the 5% contour of a separate cluster group (d). Map shown in Mollweide projection centred at 179°E.

complete migration route (Figure 4c). The other two clusters that were combined in the Pacific Ocean Flyway encompassed the route through the centre of the Pacific (Cluster A; Figure 4a), and along the eastern Pacific (Cluster B), connecting the coastline of the Americas (Figure 4b). The central cluster (A) connected the Northern and Southern hemispheres through the High Seas and national waters of small island states and the eastern cluster (B) spanned the coastal waters from Canada to Chile.

The 2.5% contour (area *c.* 100,000,000 km^2) of the complete Pacific Ocean Flyway (consisting of the three Clustered groups A–C) formed the major figure-of-eight route across the ocean basin and included key migratory routes in the 5% and 10% contours (area *c.* 49,900,000 km^2 and *c.* 25,400,000 km^2, respectively). The Pacific Ocean Flyway overlapped with the EEZs of 17 countries (Table S2), and 56.7% (17 out of 30 species, Table 1) of the species using this flyway are globally threatened with extinction.

The West Pacific Ocean Flyway (three species; Figure 4d) represents a separate movement path to the Pacific Ocean Flyway and encompassed a clockwise travel direction by migrating seabirds from the north to south via an oceanic route (mean longitude 155.5° W), and south to north along a more coastal route (mean longitude 153.5° W) (Figure S4). The largest area of this flyway was *c.* 44,600,000 km^2 (5% contour), and the narrower routes that were more commonly used during migration covered an area of *c.* 30,400,000 km^2 (10% contour) in the west Pacific Ocean. The West Pacific Ocean Flyway overlapped with the EEZs of 36 countries (Table S2), and 16.7% (1 out of 6 species, Table 1) of the species using this flyway are globally threatened with extinction.

3.4 | Southern Ocean

Circumpolar movements around the Antarctic continent were represented in the Southern Ocean Flyway (Figure 5), which was delineated from the tracking data of 88 individuals across six species (Table 1). Generally, migration was clockwise from west to east (Figure S4). As in the other marine flyways, some birds migrated over shorter sections and returned via other ocean basins, and others followed the full flyway route. The greatest latitudinal range of the flyway loop was 30° S to 65° S at 30° E to 80° E. The full Southern Ocean Flyway covered an area of *c.* 57,400,000 km^2 (10% contour), and the key areas (25% contour) were *c.* 19,800,000 km^2. The Southern Ocean Flyway overlapped with the EEZs of 9 countries (Table S2) and 39.1%

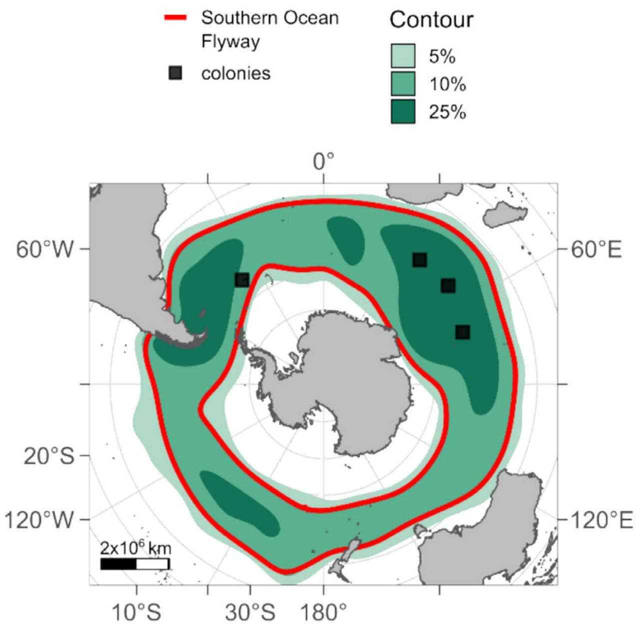

FIGURE 5 | The Southern Ocean Flyway (red outline) delineated from the tracking data of six pelagic seabird species. Tracking data were from the colonies shown (black squares). The 10% contour delineates the flyway. Map shown in Lambert Azimuthal equal-area projection centred at 90°S.

(9 out of 23 species, Table 1) of the species using this flyway are globally threatened with extinction.

4 | Discussion

Our large global tracking data compilation and novel approach revealed six marine flyways, representing the major migration routes of migratory pelagic seabirds. These marine flyways complement the four recognised terrestrial and coastal flyway systems for terrestrial and freshwater species, which encompass migration routes of coastal seabirds, and feeding areas around many breeding colonies (Figure S6). The six marine flyways cover extensive areas of the global ocean, and although very broad, serve to illustrate the vast movements and connectivity performed by seabird populations and species during their annual cycle, mirroring the terrestrial and coastal flyways.

The marine flyways are used bidirectionally and throughout the year, depending on breeding site and phenologies (Figure S4). Some migration routes only follow sections of a flyway, for example, multiple species breeding in Aotearoa New Zealand and its surrounding islands, including the Endangered Antipodean Albatross *Diomedea antipodensis*, migrate to the Humboldt Current staying within the southern portion of the Pacific Ocean Flyway (below 25° S) and often returning via a very southern flight path around 60° S. Cape Verde Shearwater *Calonectris edwardsii* (Near Threatened) use the central part of the Atlantic Ocean Flyway when migrating to Brazilian waters. In other species, some individuals follow a flyway in its entirety (e.g., Endangered Grey-headed Albatross *Thalassarche chrysostoma* in the Southern Ocean Flyway; Clay et al. 2016). Other species or individuals use multiple flyways, including Arctic Terns *Sterna paradisaea* (Least Concern) migrating along the Atlantic Ocean Flyway and into parts of the Indian Ocean Flyway and Southern Ocean Flyway (Fijn et al. 2013). Individuals from the same breeding colony can use two different flyways, such as South Polar Skuas *Stercorarius maccormicki* (Least Concern) that breed on King George Island, Antarctica, where some individuals migrate into the Pacific Ocean Flyway, and others into the Atlantic Ocean Flyway (Kopp et al. 2011).

The east–west movements between Aotearoa New Zealand and Chilean waters were apparent in all three clusters that formed the Pacific Ocean Flyway, highlighting its importance for migratory seabirds. Aotearoa New Zealand and offshore islands host large and diverse seabird communities, including 38% of the study species and 27% of colonies used to delineate the marine flyways in this study. Different individuals from this region followed each of the four clusters within the Pacific Ocean, while others are known to follow the Southern Ocean Flyway (Fischer et al. 2021).

Seabird migrations are strongly affected by wind patterns and the surface ocean currents that they drive (Thorne et al. 2023). Individuals may delay departure for migration in response to wind conditions (Thiebot et al. 2020) and adjust routes to minimise energetic costs by using tail or rear quarter winds to assist flight and avoid head winds (Powers et al. 2022). The marine flyways identified here follow the major prevailing winds. For example, the Atlantic Ocean Flyway and Pacific Ocean Flyway figure-of-eight routes correspond with the circular patterns of ocean circulation seen in each hemisphere, and the west to east movements in the Southern Ocean Flyway also correspond with ocean circulation patterns. Ocean currents have also been shown to drive the migration of other marine species, including sea turtles (Luschi, Hays, and Papi 2003), eels (Fukuda et al. 2022), and passive drifters such as many species of fish during their egg or larval stages and other plankton (Treml et al. 2008).

The broad delineation of the marine flyways encompasses variation in migration strategies that can be influenced seasonally according to wind conditions, breeding success, colony locations and the timing of migrations (Amélineau et al. 2024). For example, shearwaters migrating in the Pacific Ocean Flyway travel to the North Pacific via a range of routes within the defined flyway. Failed breeders migrate into the central South Pacific and forage in the region until after the equinox, then continue migratory flights towards Japan and waters northwest of Hawaii. Sooty Shearwaters *Ardenna grisea* that spend the non-breeding season off the west coast of North America fly east towards Chilean waters and travel north towards Hawaii, before shifting eastwards to benefit from westerly winds in the upper North Pacific to reach Canada and USA. Further investigation into how seabirds use the marine flyways at different times of year is necessary and would elucidate the spatial and temporal use of the flyways. This seasonality information could then inform relevant spatial and temporal management measures, such as seasonal fisheries closures. Future predicted changes to winds, ocean currents and sea surface temperatures due to climate change will affect migrating seabirds, potentially reducing the extent of suitable habitat and availability of food sources during the non-breeding season (e.g., Legrand et al. 2016), and leading to changes in the timing of migration (Lewin et al. 2024) or the migratory strategies (Cherel et al. 2014; Quillfeldt et al. 2010).

The intention of the flyways approach is to illustrate broad-scale movements of multiple species rather than individual or species-specific details. The process for their delineation aligns with their broad intention, including the location accuracy of GLS devices (*c.* 200 km; Phillips et al. 2004), the smoothing of polygons, and semi-quantitative approach to inform their final delineation, recognising that a smaller number of flyways are better suited to communicating broad-scale connectivity at regional and international levels (rather than multiple, overlapping clusters or flyways). Given the broad-scale approach, extensive literature review and underlying ocean circulation patterns, we do not anticipate that including additional species would change the general delineation of the marine flyways. However, additional species, including species that migrate but did not meet our long-distance criteria, may highlight the use of certain sections of the flyway. As with the existing flyways, some species will use part of the overall flyway (e.g., Eurasian curlew *Numenius arquata arquata* uses part of the East Atlantic Flyway; Pederson et al. 2022). Studies focusing on migratory seabirds in the Indian Ocean would be welcome, in particular for the Eastern section, for which our dataset was relatively small. Some potential segments are absent from the identified flyways, including routes along the east coast of North America, and from Western Australia and the west Indian Ocean into the Bay of Bengal (e.g., Fayet et al. 2020; Jaeger et al. 2017; Lebarbenchon et al. 2023; Nisbet et al. 2011; Surman, Nicholson, and Phillips 2018). The absence is, in part, due to selecting species that migrate primarily outside of national waters to avoid overlap with the four recognised terrestrial flyway systems and also because there are fewer species tracked in these regions (Carneiro et al. 2024). Additionally, we focused on tracking locations during migratory flights because the pathways from breeding colonies, such as those from Europe into the Atlantic Ocean Flyway, are encompassed within the existing flyways delineated for landbirds and waterbirds (Figures S1 and S6).

We only used tracking data from adult birds because relatively few juvenile and immature birds have so far been tracked (Carneiro et al. 2020). Compared with adults, immatures and juveniles may undertake less direct routes that include longer stopovers (Campioni et al. 2020; Péron and Grémillet 2013). As with adults, juvenile and immature movements will be influenced by the wind conditions, so the major routes overall are likely to be similar. The availability of seabird tracking data is constantly increasing, and it would be worthwhile to repeat this analysis in several years with additional (likely smaller-sized) species and immature and juvenile birds.

We did not collate population data for this study, but population size estimates are a key consideration when identifying important areas for seabirds at-sea, such as Key Biodiversity Areas (KBAs), to determine if a site meets relevant population criteria (Beal et al. 2021; Ramos et al. 2013). Using the marine flyways to highlight a network of important areas for migratory seabirds, through a combination of existing site data and identifying further sites is a valuable next step.

4.1 | Ocean-Basin Scale Conservation

By highlighting migratory connectivity at an ocean-basin scale, the marine flyways identified here provide the impetus for coordination and collaborative seabird conservation efforts, building on the conservation successes and mobilisation of international finances that have arisen through the application of the flyways concept for land and waterbirds (e.g., Boere and Piersma 2012; Oppel et al. 2023; UNEP/CMS Secreteriat 2014). The advantages of delineating marine flyways are: (1) the identification and protection of a global network of important areas for the persistence of species within a flyway, that is, KBAs (IUCN 2016) encompassing sites across the full lifecycle of a species (i.e., breeding, foraging, stopover sites and non-breeding). Many sites have already been identified, and can be considered a priority network of sites for each flyway that can form the basis for conservation action, research and monitoring, (2) the identification and mitigation of major and emerging threats to seabirds, both at key sites (e.g., invasive species eradications at colonies) and at broader-scales, in particular those found along the routes and that may pose important cumulative impacts to the same populations (e.g., fisheries-bycatch, offshore windfarms or marine pollution). In fact, 69% of the species using the marine flyways identified in this study (listed in Table 1) face at least one marine threat (based on data published in a global review; Dias et al. 2019), and almost 40% are currently classified as threatened with extinction (BirdLife International 2024). Compiling available information on species sensitivities to threats in each flyway would be a valuable first step to facilitate the development of targeted policy and conservation interventions and (3) the easier identification of inter-governmental partnerships and other stakeholder collaborations across countries within the same flyway (Table S2). Demonstrating shared ownership of migratory seabirds facilitates stakeholder engagement and allows effective partnerships to form that can lead to coordinated conservation action at a manageable scale, with broader-scale outcomes, and (4) the identification of research and capacity needs, and opportunities for each flyway, to support the implementation of coordinated decision making, including via MEAs. The marine flyways are particularly relevant to the CMS, and its daughter agreements (AEWA and the Agreement on the Conservation of Albatrosses and Petrels; ACAP), but are also pertinent to the connectivity elements of the Kunming-Montreal Biodiversity Framework of the Convention of Biological Diversity (recognised in Goal A, Milestone A.1., Target 1, 2, 3), and the forthcoming United Nations Convention on the Law of the Sea on the Conservation and Sustainable Use of Marine Biological Diversity of Areas beyond National Jurisdiction ('the High Seas Treaty'), which will create a governance framework for the protection of areas beyond national jurisdiction, addressing a critical need for migratory species conservation. The marine flyways are also relevant for facilitating collaboration via regional organisations, such as Regional Seas Conventions (including linking to international agreements), and Regional Fisheries Management Organisations (RFMOs); for example, the overlap of the Pacific Ocean Flyway with two tuna RFMOs (Western & Central Pacific Fisheries Commission [WCPFC] and Inter-American Tropical Tuna Commission [IATTC]) shows the need for collaboration and coordination between these organisations to help mitigate bycatch, which is a major threat to seabirds

(Figure S7). A challenge of working within these international and regional frameworks is that they are only binding to their contracting parties, and the lack of some key countries to participate in these fora hampers international conservation efforts. For example, not all range states of migratory seabirds are Party to ACAP (there are 13 Parties to the Agreement, but a further 12 range states [including the EU] that are non-Party). However, the emerging formalising of synergies and partnerships across biodiversity-related MEAs (CMS Resolution 11.10) presents an opportunity to engage with a greater number of countries, including non-Party range states, and build synergies to enhance conservation of migratory marine species.

5 | Conclusions

The six marine flyways that we identified encompass the major documented migration routes of pelagic seabirds in the Atlantic, Indian, Pacific and Southern oceans. They illustrate the migration routes shared by pelagic seabirds at ocean-basin scales and highlight the need to account for ecological connectivity in seabird conservation. Further investigations are warranted to understand how the marine flyways are used by seabirds at different times of the year, and to identify areas and periods that are commonly used by multiple species and populations within the flyways, and areas where seabirds are at the highest risk of threats. The marine flyways can highlight the collective responsibilities of nations and governance bodies to establish mechanisms for coordinated conservation action. The flyways have relevant policy linkages across a range of MEAs bringing the potential to strengthen collaboration across a greater number of Parties and to progress conservation of migratory marine species, including the protection of important sites on the High Seas.

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Acknowledgements

We are grateful to Olivia Crowe, Nina Mikander, Norman Ratcliffe for providing comments on earlier versions of this manuscript. This work was supported by the Global Ocean Biodiversity Initiative (GOBI) with a grant from the International Climate Initiative (IKI). The German Federal Ministry for the Environment, Nature Conservation, and Nuclear Safety (BMU) supports GOBI on the basis of a decision adopted by the German Bundestag. Additional acknowledgements and funding sources associated with the datasets used for these analyses are acknowledged in Appendix S2 in Supporting Information.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data used in analyses are available on request from the Seabird Tracking Database (https://data.seabirdtracking.org/; 90%), from other repositories (2%) or directly from data owners (8%), and where the data can be obtained is detailed in the Supporting Information. Code and a filtered and anonymized tracking dataset for the Indian Ocean to facilitate reproducing the workflow; in addition to intermediate outputs, including polygons of the clusters that form the final flyway in each ocean basin are available in a repository at Dryad accessible at the following link: https://doi.org/10.5061/dryad.59zw3r2jc.

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Supporting Information

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