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Satellite Tracking and Photographic-Identification as Connectivity-Based Tools Towards Conservation Planning of Pilot Whales

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ABSTRACT

Identifying biogeographical patterns and important biological (blue) corridors can greatly contribute to conservation planning. Yet, this is particularly challenging when addressing pelagic species. In this study, satellite telemetry and photographic-identification data of short-finned pilot whales (*Globicephala macrorhynchus*) were used to identify preferred areas and pathways in the Macaronesia biogeographical region, namely between Madeira and two regions in the Canary Islands, the Western (WCI, La Palma and El Hierro) and the Central (CCI, Tenerife and La Gomera). Home-range and time-varying move persistence analyses from tracking data of four whales that moved between both archipelagos over 578 days revealed preferred areas in Madeira and the WCI, new connectivity pathways and the importance of both regions for area-restricted behaviours. These findings were corroborated by a high number ($n = 71$) of photographic matches between Madeira (catalogue of 1276 individuals) and the WCI (456 individuals), compared to only four between Madeira and the CCI (717 individuals). The high linkage of the WCI with Madeira and the CCI ($n = 48$) suggests that the WCI constitute a key habitat for potential mixing of pilot whales from different groups. This study emphasizes that a combined methodological approach provides robust baseline information for pilot whales' conservation management, which could be valuable for other scenarios and species. Furthermore, shown connectivity patterns

contribute to broadening our knowledge on potential blue corridors in the eastern North Atlantic and highlight the importance of considering wide and international geographic areas for conservation planning of highly mobile marine species.

1 | Introduction

Understanding the movements and ranging patterns of highly mobile species is of paramount importance for various facets of conservation biology, including the assessment of conservation status, the optimization of protected areas or the development of dynamic management strategies (Fraser et al. 2018; Reisinger, Johnson, and Friedlaender 2022). This is highly relevant within the realm of megafauna conservation, especially of marine mammals, given that many species are threatened (Chen et al. 2022; IUCN 2022) and play pivotal roles in the structure and maintenance of their ecosystems (Moore 2008; Woodstock et al. 2023). However, acquiring comprehensive movement data on animals living in oceanic waters is challenging due to their elusive nature and the vast and complex three-dimensional environment they inhabit (Alves, Queiroz, and Jodice 2023).

Technological advancements and development of analytical tools over the past decades have significantly enhanced the ability to study the movement patterns of marine mammals (Hays et al. 2016), yet each method offers unique advantages and faces specific limitations. Photographic-identification (hereafter photo-identification), which entails cataloguing individuals based on distinctive features and marks, has been commonly used to gain insights into population dynamics (Würsig and Jefferson 1990; Friday et al. 2000). By comparing catalogues from different geographical regions, it has also provided information regarding large-scale movements of several cetacean species (Olson, Galletti, and Español-Jiménez 2020). Other methods, such as acoustic monitoring (Risch et al. 2014; Davis et al. 2020) and genetic analyses (Oremus et al. 2009; Van Cise et al. 2019), allow inferring distribution changes, and gene flow and population structure, respectively. Another cutting-edge approach to studying movement patterns and habitat use of large marine organisms over a wide scale is satellite telemetry, which involves the attachment of a device (a 'biologger' or 'tag') that stores and/or transmits positional (and in some cases environmental) data. Such devices can provide near real-time data on horizontal and/or vertical movements. This approach also allows for the collection of movement information in offshore domains that are less accessible and thus less surveyed (Block et al. 2011; Hazen et al. 2012; Hays et al. 2016).

A combination of methods can also be applied to enhance the necessary information for a better understanding of a species' spatial and temporal use (Alves, Queiroz, and Jodice 2023). The application of such techniques can contribute towards species' conservation management, especially when dealing with animals moving across borderless seas, which requires higher international efforts and proper legislation that is usually difficult to meet (McGowan et al. 2017; Fraser et al. 2018). For example, satellite telemetry and stable isotopes have been used to study baleen whales' movements in the North Atlantic (M. A. Silva et al. 2019; Pérez-Jorge et al. 2020). Baumann-Pickering et al. (2015) combined passive acoustic monitoring with satellite telemetry to distinguish signals from two delphinid species in Hawai'i, thereby enhancing long-term monitoring efforts to mitigate bycatch. Satellite telemetry has also been combined with photo-identification to identify Southern right whales *Eubalaena australis* conservation areas in sub-Antarctic remote waters (Kennedy et al. 2023). Approaches such as Biologically Important Areas (BIAs) and Important Marine Mammal Areas (IMMAs) serve as examples of combining multiple data sources, including photo-ID, telemetry, acoustics and sighting data, among others, to inform conservation management (Kratofil et al. 2023; IUCN-MMPATF 2024).

The short-finned pilot whale *Globicephala macrorhynchus*, hereafter pilot whale, is a deep-diving, highly mobile marine top predator, distributed throughout tropical and warm temperate waters (Betty et al. 2023), which exhibits a complex social and geographical ecology (Olson 2009; Mahaffy et al. 2015; Aguilar de Soto and Alves 2023). Pilot whales are typically organized in matrilineal groups with stable and long-term social bonds (Betty et al. 2023). Within-population social structure, with distinct communities and varying levels of site fidelity, may influence their movements and space-use patterns at different scales. In the Macaronesia biogeographical region (eastern North Atlantic), which is considered a hotspot for marine megafauna (Afonso et al. 2020), this species is among the most frequently sighted cetaceans (Carrillo, Pérez-Vallazza, and Álvarez-Vázquez 2010; M. A. Silva et al. 2014; Alves, Ferreira, et al. 2018). Based on photo-identification data, wide-ranging movements of 21 pilot whales with distinct residency patterns (transients—individuals photographed once; visitors—individuals that exhibited multi-year but seasonal specific presence; and residents—individuals that exhibited multi-year and year-round site fidelity) have been recorded between the archipelagos of the Azores, Madeira and Canary Islands (Alves et al. 2019). A highly resident group of animals from Madeira observed travelling to the Azores and back highlights that long-ranging movements are not limited to visitors or transients and supports the connectivity observed in the area (Alves, Alessandrini, et al. 2018). These findings, together with genetic analyses, have contributed to our knowledge that animals with different residency patterns and from different archipelagos may not be genetically isolated (Alves et al. 2013; Miralles et al. 2016). Although connectivity within the Macaronesia biogeographical region has been established, substantial information has been lacking for several areas, such as the westernmost islands, which could have resulted in skewed results (Alves et al. 2019). Therefore, comparisons with additional and updated data could be useful to improve our understanding of movement patterns and connectivity in the region and to identify additional important regions. Since climate change could contribute to dynamic shifts in behaviour, continuous monitoring of movements and habitat use is paramount.

Conservation areas for cetaceans have been identified in Macaronesia by international conservation programmes such as the Natura 2000 Network, Mission Blue ('Hope Spots') and Whale

Heritage Site ('Whale Sanctuary'). Moreover, important habitat areas have been identified for island-associated pilot whales in the Canary Islands and Madeira, specifically off the southwest of Tenerife and southeast of Madeira (Boran and Heimlich 2019; Servidio et al. 2019; Fernandez et al. 2021; Esteban, Verborgh, and Freitas 2022). All combined, it supports the idea that pilot whales exhibit spatial segregation and that there is an ecological connectivity network in Macaronesia (Alves et al. 2019). Nevertheless, additional keystone information is needed to promote the creation of a large marine protected area in the Eastern Atlantic, such as the 'Macaronesian Biodiversity and Ecological Migration Corridor for Cetaceans' (Carrillo 2007; Herrera et al. 2021). Blue corridors, as such, are marine routes designated for the safe migration, movement and protection of marine species and often connect crucial habitats across large distances, which would contribute to the conservation of several cetacean species with known connectivity patterns between Macaronesian archipelagos (Prieto et al. 2014; Steiner et al. 2015; Alves et al. 2019; Dinis et al. 2021; Ferreira et al. 2021). Crucial keystone information includes obtaining fine-scale movement/tracking data, which has provided new insights into the dynamic ecology and management of pilot whales worldwide (Kratofil et al. 2023; Thorne et al. 2017; Hill et al. 2019). Connectivity and potential biological oceanic corridors could be identified by integrating tracking data with photo-identification. Such a connectivity-based approach could provide the necessary tools for effective conservation planning (Pastor et al. 2023) in offshore Atlantic archipelagos of different countries geostrategically located between Europe and Africa.

This study aims to quantify previously unknown movement patterns and to identify connectivity and potentially unknown preferred regions and pathways of an apex pelagic predator, the short-finned pilot whale, within Macaronesia. It builds upon existing knowledge (Alves et al. 2019) by integrating information from novel fine-scale biologgers and updated long-term photo-identification data from the Canary Islands and Madeira, to explore key locations or corridors linking populations, using home-range analyses and innovative time-varying move persistence models. Such an improved and updated understanding of marine metapopulation dynamics through a multimethodological and connectivity-based approach is expected to increase knowledge and advance conservation management of an iconic species and its surrounding elements.

2 | Material and Methods

2.1 | Study Area

This study covered two archipelagos of the Macaronesia biogeographical region—Madeira (Portugal) and the Canary Islands (Spain) (Figure 1)—where pilot whales are at times abundant (Alves et al. 2015; Servidio et al. 2019; Verborgh et al. 2022). Madeira Island is mainly influenced by a branch of the Azores Current System, while the Canary Islands are mainly influenced by the Canary Current. Together with the Gulf Stream in the western North Atlantic, these Currents form the

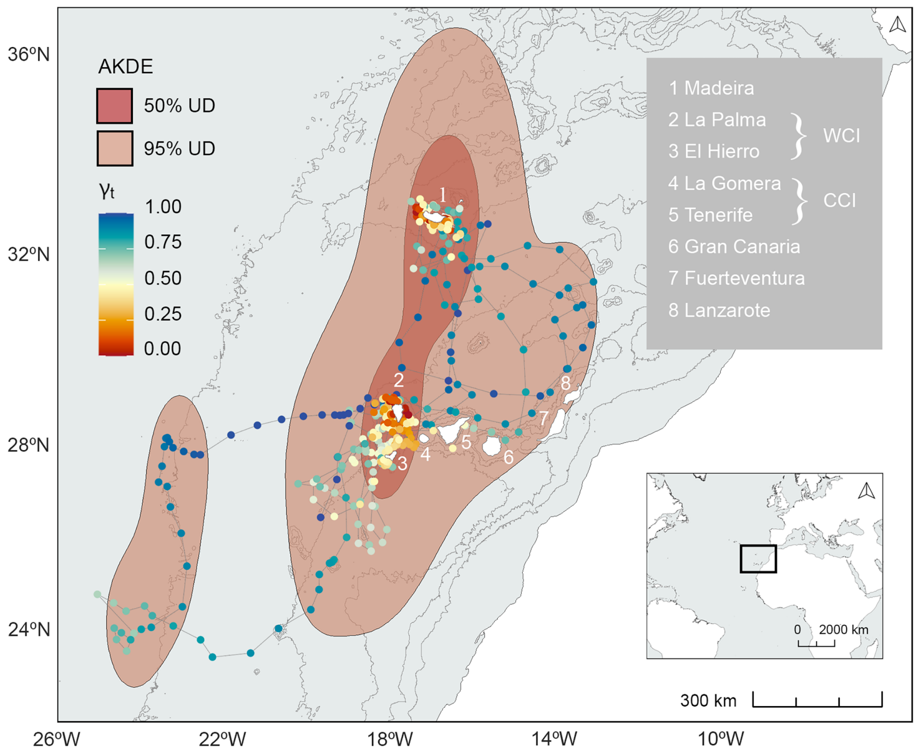

FIGURE 1 | Satellite tracks, move persistence index (γ_t) and range estimates (utilization distribution—UD) at 50% and 95% isopleths (from an autocorrelated kernel density estimation—AKDE) of four short-finned pilot whales tagged in Madeira between 2018 and 2021. Low move persistence values observed around Madeira and the Western Canary Islands indicate lower autocorrelation in speed and directionality along the trajectory (solid line between locations), while high values indicate high speed and directed travel. Isobaths refer to 1000 m depth contours. Lower right inset: The black square indicates the study area in the eastern North Atlantic. The three regions considered in this study are Madeira Island, and the Western and Central Canary Islands (WCI and CCI, respectively). Information on individual movements is available in Figures S2–S4.

boundaries of the North Atlantic Gyre (Cropper 2013; Cardoso and Caldeira 2021). Both archipelagos have an exclusively volcanic origin, where great depths are found relatively close to shore, and complex oceanographic disturbances (leeward eddies, island wakes, upwelling and downwelling) and topographic features can be observed (Caldeira et al. 2002; Benazzouz, Demarcq, and Déniz-González 2015), leading to spatio-temporal variation in the habitat use of pilot whales in these islands (Servidio et al. 2019; Fernandez et al. 2021; Esteban, Verborgh, and Freitas 2022). Surrounding waters in Madeira (mainly to the south) are utilized by resident animals throughout the year, with visits of seasonal populations that stay in the area for 1–3 seasons (Alves et al. 2013). Among the Canary Islands, which span > 500 km in a west–east orientation—about the same distance between these and Madeira Island (Figure 1), there is a non-uniform interisland distribution of pilot whales. For example, there is a higher preference among island-associated animals for the central islands of Tenerife and La Gomera, where the same individuals regularly move in-between, and for Gran Canaria to a lesser extent (Servidio 2014). In contrast, mainly transients are known to visit the eastern islands of Lanzarote and Fuerteventura, and limited data exist for the western islands of La Palma and El Hierro (Servidio et al. 2019). This non-uniform interisland distribution of pilot whales, coupled with the limited data available for the western islands, led us to focus on compiling data from three main regions, namely, Madeira Island, the Western Canary Islands—WCI (La Palma and El Hierro) and the Central Canary Islands—CCI (Tenerife and La Gomera) (Figure 1).

2.2 | Satellite Telemetry

Satellite biologgers (low impact minimally percutaneous electronic transmitter—LIMPET SPOT6 tags from Wildlife Computers) were deployed on healthy (i.e., robust and with no signs of emaciation) adult and subadult pilot whales (not accompanied by calves) between 2018 and 2021 in the southern waters of Madeira Island as part of a multi-purpose telemetry programme towards medium- and large-sized odontocetes to infer habitat use and the presence of preferred areas or corridors, led by MARE-ARDITI (Marine and Environmental Sciences Centre—Regional Agency for the Development of Research, Technology and Innovation) (MARE-Madeira 2024). A Dan-Injection CO_2 dartgun was used for tag deployment during dedicated field trips, following all legal requirements and permits according to current legislation (see Ethics Statement). Each tag is made up of an electronics unit and two 6.0-cm long medical-grade titanium darts with backward-facing 'barbs', specially designed for cetaceans (Andrews et al. 2019). SPOT tags transmit to the Argos Satellite system, and consecutive transmissions, received in a single satellite pass, are used to calculate the location of the tag and, therefore, of the animal. The tags were programmed to transmit twice daily (morning [6:00 AM to 1:00 PM] and afternoon [6:00 PM to 12:00 AM]) during the first 55 days (location uplink limit of 25 per hour), once daily (8:00 AM to 12:00 PM) between 55 and 180 days, and every 2 days after 180 days (8:00 AM to 12:00 PM). The selected hours for transmission took into account the time and coordinates of the passage of the satellites, as well as the potential regions where the tagged individuals could move (i.e., longitudinally between the Mid-Atlantic and West Africa, and latitudinally between Biscay and Cape Verde). The mask feature prevented transmissions during hours with few or no satellite passes to save battery power.

Data from individuals that moved between Madeira and the Canary Islands were used for the analyses, which were performed using the amt (Signer and Fieberg 2021) and aniMotum R packages (Jonsen et al. 2023) in the R Statistical Software v4.1.3 (R Core Team 2022). Initially, the obtained location data, which includes error ellipse information, were formatted and cleaned, removing both locations on land and locations with quality class Z. Next, a correlated random walk and move persistence model was fitted, applying a 4.0-ms^{-1} speed filter threshold and a 24-h prediction interval. Simulated paths that crossed land barriers were re-routed. Home-range estimators were used as an exploratory method to show the spatial extent of the area used by individuals during tracking periods. Home ranges at 50% and 95% isopleths were then estimated from the correlated random walk re-routed locations, employing autocorrelated kernel density estimation (AKDE). This family of estimators addresses the challenges posed by contemporary movement data, including autocorrelation, limited sample sizes, and missing or irregularly sampled data (Signer and Fieberg 2021; I. Silva et al. 2022). The time-varying move persistence approach encompasses the autocorrelation observed in speed and direction during successive horizontal displacements. An index of how an animal's movement behaviour varies in space and time is provided through the estimated persistence parameter (γ_t). It is presented along a continuous scale, ranging from 0 (reflecting low move persistence, suggesting low speed and directionality) to 1 (indicating high move persistence, reflective of high speed and directed travel) (Jonsen et al. 2019). Individual home ranges, and associated semivariograms, obtained using the ctmm R package (Fleming and Calabrese 2022), are provided in Figures S2 and S3, respectively, to aid in interpreting the pooled data. Individual move persistence over time is provided in Figure S4. Results were used to identify potentially preferred regions and biological connectivity between islands/regions.

Whenever possible, biopsy samples and photographs were collected simultaneously during the deployment of the satellite tags. The former were collected using a biopsy darting system (Mathews, Keller, and Weiner 1988) and allowed to determine the sex through molecular analysis (detailed in Alves et al. 2020). The latter were obtained using digital cameras with telephoto lenses (70–300-mm F4 and 80–200-mm F2.8, among others) to identify individuals and infer residency pattern throughout the animals' capture histories (following Alves et al. 2013, 2020).

2.3 | Photo-Identification

Photo-identification catalogues of pilot whales from the three target regions were compared to identify individual matches, thereby inferring movement patterns and potential source-destination preferences.

The catalogue of Madeira was based on photographic data collected between 2003 and 2020 from research vessels and platforms of opportunity (see Acknowledgements), comprising 1276 naturally well-marked animals (i.e., distinctive individuals) from good quality images (following Alves et al. 2013) (Table S1). These were grouped according to the number of notches in the trailing edge of the dorsal fin to facilitate comparison (Würsig and Jefferson 1990; Alves et al. 2019).

The catalogues of the Canary Islands were compiled by two sources (described in Table S1). A whale-watching company compiled one for La Palma with 335 well-marked animals from data collected between 2019 and early 2022. Additionally, Tonina Association compiled a catalogue encompassing several islands of the CCI and WCI, totalling 838 well-marked animals (see Data Availability Statement), captured between 2014 and 2021 from research vessels and whale-watching companies (see Acknowledgements).

Photographic data were collected using digital cameras equipped with telephoto lenses from vessels operating until about 7 nautical miles (~13 km) off the coast, mainly on the lee side of the islands, which coincides with high aggregation areas for the species (Servidio et al. 2019; Fernandez et al. 2021; Esteban, Verborgh, and Freitas 2022). Research surveys over the years were non-systematic, had a more or less consistent spatial extent and focused on the collection of a diverse array of data from multiple species, including pilot whales, during days of good weather and sea conditions. Effort information from whale-watching companies in Madeira is available from previous publications (Alves, Ferreira, et al. 2018; Sambolino et al. 2022) and coincides largely with the area in which research surveys took place. But this information is lacking from the Canary Islands. Little information from the remainder of the available habitat could result in bias when interpreting the results and should be considered. Simultaneously with photo-identification, biopsy samples collected during dedicated research trips in Madeira (for other purposes) allowed for molecular sexing of some individuals (detailed in Alves et al. 2020).

The compilation of each digital catalogue followed standard photo-identification procedures (Würsig and Würsig 1977), and the dorsal fin matching of each individual was based primarily on the number of unique notches on the dorsal fin and secondarily on fin shape or scars (Urian et al. 2015), as detailed in Alves et al. (2019). Comparison between catalogues was carried out visually (e.g., Wilson, Hammond, and Thompson 1999; Robbins et al. 2011) by the same person (MW), and only matches with 100% certainty by at least two researchers experienced in photo-identification were used in the present study. Analyses and visualizations were created in R Statistical Software v4.1.3 (Gu 2014; R Core Team 2022).

3 | Results

3.1 | Satellite Telemetry

Four individuals were tagged off Madeira between September 2018 and November 2021, with a mean duration of 145 days (range: 105–175, Table 1) and a combined total of 578 days, resulting in 3109 filtered locations. Tag locations are available in Figure S1. These four individuals moved to the Canary Islands, but their paths varied (Figure S2). Three individuals followed a direct path to the Canary Islands, and one made almost two full circular roundtrips before stopping at the Canary Islands.

The 50% and 95% home ranges were 127,654 km^2 (with 95% isopleths: 108,687–148,119 km^2) and 829,225 km^2 (with 95% isopleths: 708,579–959,866 km^2), respectively (Figure 1). While the 50% home range consisted of only one polygon, encompassing Madeira, the WCI and the area directly linking them, the 95% home range consisted of two polygons, with one surrounding the aforementioned regions, including the CCI and part of the eastern islands, and the other smaller region being located west-southwest of the Canary Islands. All individual home ranges (Figure S2) included Madeira in the 50% UD (utilization distribution); however, a certain amount of variation was present in the Canary Islands. The 50% UD of Tag1_Gma did not extend into the Canary Islands, compared with the UD from Tag20_Gma, which included many of the islands. The semivariograms (Figure S3) confirm the presence of range resident behaviours, combined with variation in the periods of directed movement. It is important to note that seasonal patterns may not have been fully captured due to the duration of the tags.

Considering behaviour, the lowest move persistence indexes were observed in the south, southeast and west of Madeira, and all around La Palma, with slightly higher values around El Hierro, in the Canary Islands (Figure 1). Relatively low move persistence was further observed west and southwest of La Gomera, and one individual passed by the southern region

TABLE 1 | Summary information for the four short-finned pilot whales tagged in Madeira that moved to the Canary Islands.

Tag ID	Sex	Residency pattern	Deploy date	Tag duration (days)
Tag1_Gma	F	Visitor (12 captures between 2009 and 2020 during summer–autumn)	28 September 2018	105
Tag7_Gma	F	Visitor (nine captures between 2010 and 2020 during summer–autumn)	9 November 2020	150
Tag14_Gma	—	Visitor (five captures between 2017 and 2019 during spring–summer)	25 August 2021	175
Tag20_Gma	—	—	19 November 2021	148

Note: Sex inferred through molecular sexing (F, female). Residency pattern based on photo-identification and the animal capture histories in Madeira. Tag20_Gma is an animal with no previous captures. Although this would normally result in the designation of the residency pattern 'transient', the animal was tagged in 2021. As the catalogue was only updated until 2020, it is possible there are earlier sightings of this animal in 2021. Therefore, no residency pattern was assigned to this animal.

of Tenerife, displaying moderate values. Directed movements (higher move persistence) were revealed in the remaining regions, including in offshore waters between Madeira and the Canary archipelago and southwest of the Canary Islands (Figure 1). When looking in more detail into the move persistence over time per individual, we can see that Tag1_Gma spent approximately 1.5 months (out of a total of 3.5 months) with relatively high move persistence values (Figure S4), corresponding to the movements to offshore areas and to the Canary Islands (Figure S3). Tag7_Gma displayed a short period with relatively high move persistence values (approximately half a month out of a total of 5 months), which corresponds with a more direct path taken to the Canary Islands. Intermediate values after reaching the WCI correspond with back-and-forth offshore movements. Although an increase in move persistence was observed to reach the Canary Islands in the case of Tag14_Gma, the highest relative move persistence was observed afterwards, for a short period (around 1 month out of 6 months), while travelling offshore the WCI, after which the tag stopped transmitting. Finally, Tag20_Gma spent approximately 2 months (out of a total of 5 months) with relatively high move persistence, divided over two different periods. These periods correspond with directed movement towards the Canary Islands and offshore movement after reaching the WCI.

3.2 | Photo-Identification

In total, 1276 individuals from Madeira, 717 individuals from the CCI and 456 from the WCI were used for the comparison (Table S1), resulting in a combined dataset of 2449 individuals. A total of 123 individual matches were obtained between the three regions, of which 12 were molecularly sexed (six males and six females)—indicating interregional movements of animals of both sexes. The highest number was observed between Madeira and the WCI ($n = 71$), while the lowest was observed between Madeira and the CCI ($n = 4$). Within the Canary Islands, there were 48 individual matches between the Western and Central regions (Figure 2). Considering the total number of catalogued animals per region, 5.6% of the animals catalogued in Madeira were photographed in the WCI and 0.3% in the CCI, and 15.6% from the WCI were photographed in Madeira and 10.5% in the CCI. Finally, 6.7% of the animals from the CCI were photographed in the WCI and only 0.6% in Madeira. The matches between any two regions were distinct, meaning no individuals were shared between the catalogues of the three regions. Additionally, none of the four tagged individuals were part of the observed photo-identification matches. All residency types were represented among the matches.

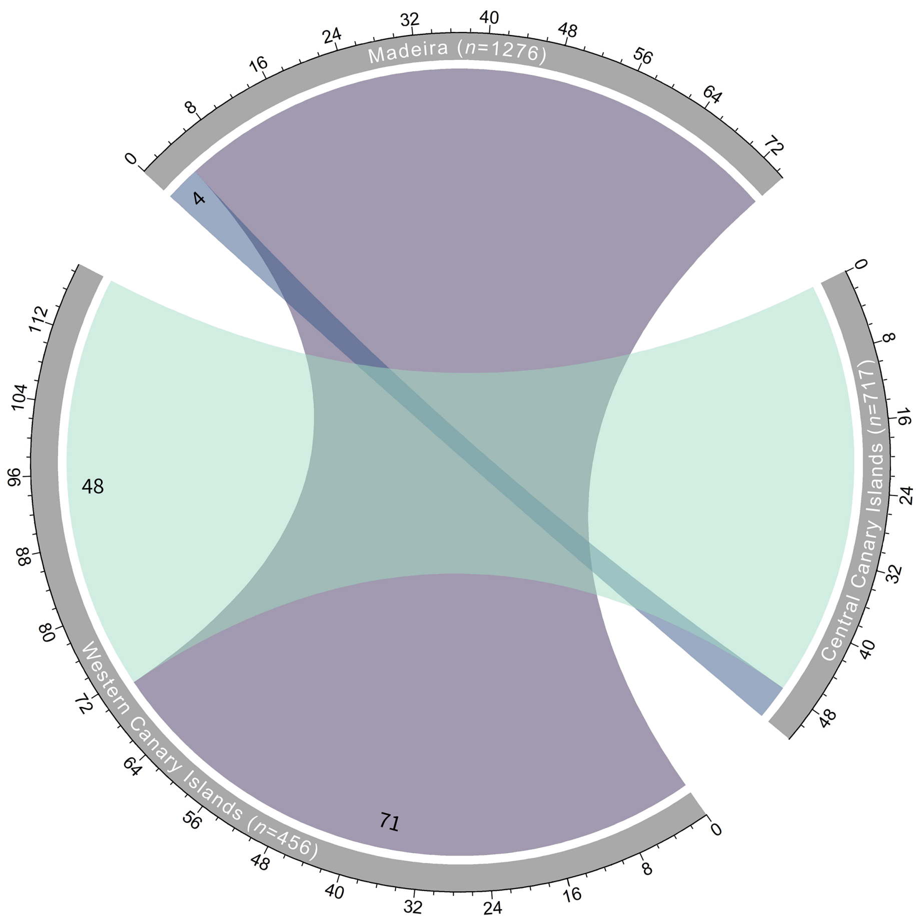

FIGURE 2 | Number of individual photo-identification matches between the three studied regions: Madeira Island, the Western Canary Islands—WCI (La Palma and El Hierro) and the Central Canary Islands—CCI (Tenerife and La Gomera). Madeira and the WCI show a higher population linkage among them than with the CCI. The number of individuals in the catalogue used for the comparison in each region is mentioned between brackets.

4 | Discussion

This study demonstrates that combining satellite telemetry and photo-identification data can yield valuable insights into the movement ecology of a top predator—such as the pilot whale—and support marine conservation management. This is especially relevant in the context of the Macaronesia region due to the novel findings presented here.

Satellite telemetry has been emphasized in the context of marine megafauna conservation, notwithstanding its specific challenges (Ogburn et al. 2017; Hays et al. 2019). In this study, telemetry-based home range analysis revealed new important regions and high population connectivity of pilot whales between Madeira and the WCI, which was corroborated by the move persistence and photo-identification analyses. Low move persistence, observed in Madeira and the WCI (especially in La Palma), may indicate area-restricted behaviours, such as foraging, resting or breeding (Kareiva and Odell 1987; Bailey et al. 2009; Jonsen et al. 2019), thus providing insights into the potential ecological significance of specific habitats. These vital activities and behaviours can indicate pivotal habitats integral to the whales' survival, which provides crucial information in the broader context of conservation planning. Notably, individual-level differences in movement paths were observed among the tagged whales when travelling between Madeira and the WCI. These differences could be due to a wide range (and combination) of factors (e.g., differential space use by animals of different social groups and residency patterns, driven intrinsically or by environmental, geographic or oceanographic conditions). Additional research would be required to understand this variability to inform conservation strategies effectively. Although the biotelemetry data were based on a low number of individuals—which is a limitation in most biotelemetry studies due to financial and ethical constraints—the mean tag duration of the four tagged animals was much higher than some other similar biologging studies in pilot whales: 145 days in our study versus, for example, around 1 month in Hawai'i (Kratofil et al. 2023), 61 days in the West Atlantic (Thorne et al. 2017) or 74 days in the Mariana Archipelago (Hill et al. 2019). Moreover, the total (of 578) satellite transmission days provided an overall robust data set to carry out movement analysis. Given the small sample size ($n = 4$), there is a possibility that some individuals contributed disproportionately to the observed patterns in the pooled AKDE home range, a known bias in kernel density estimations. Individuals Tag7_Gma and Tag20_Gma likely had an influence, as their tracks and home ranges extend more towards the WCI.

Photo-identification played a crucial role in supporting and expanding the telemetry-based insights. The high number of matches observed between the catalogues of Madeira and the WCI indicates substantial and recurrent movement patterns between these regions. However, it is important to consider that no information is available on the frequency of matches between the regions, which does not allow us to provide a precise conclusion on the strength of the connectivity. Conversely, the clear lower number of matches obtained between the WCI and CCI suggests a smaller population linkage, even though these regions are in closer proximity to each other and there is a well-known suitable habitat for pilot whales in the CCI (Servidio et al. 2019; Herrera et al. 2021). In addition, all matches between regions were unique, that is, matches between Madeira and the WCI, between Madeira and the CCI, and between the WCI and CCI were all different, not shared. This suggests that the WCI could play an important ecological role for Macaronesian pilot whales, allowing different groups to meet and mix, similar to what is suggested for the southeast of Madeira during summer–autumn (Alves et al. 2013). This can help to explain the absence of genetic differentiation in Macaronesian pilot whales (Alves et al. 2013; Miralles et al. 2016). However, an increase in the species' presence in the waters of El Hierro has been detected in recent years, which may be related to the tropicalization of the island's marine ecosystem (unpublished data). There is an oceanographic gradient in terms of sea surface temperatures (SST) between the westernmost (El Hierro) relative to the easternmost islands (Fuerteventura and Lanzarote) (approximately 1°C–2°C, occasionally 3°C) (Barton et al. 1998; Davenport et al. 2002) and is considered an entry point for species with tropical affinity into the archipelago (Espino et al. 2019). Similar patterns have been found for the island of La Palma. Although it is not possible to confirm a direct link between the findings and global warming, this study provides important baseline data that can support future research into the potential effects of climate change on pilot whale distribution in the Macaronesia region, as suggested by Sousa et al. (2023). Furthermore, it is important to consider the potential bias caused by unequal and non-systematic effort when interpreting the photo-identification results. The spatial and temporal coverage could influence the true number of matches between regions, instead of indicating a lack of matches. Although most effort occurred in high aggregation areas in the current study, additional survey effort in less covered areas could provide a more complete image.

The very few (only four) individuals identified travelling between Madeira and the CCI showcase the clearly higher population linkage that Madeira has with the WCI. One possible explanation is that individuals travelling between Madeira and the Canary Islands tend to avoid the suitable region of the southwest of Tenerife, possibly to minimize competition with the year-round core resident pilot whales (Boran and Heimlich 2019; Servidio et al. 2019). Instead, travelling towards more oligotrophic (Barton et al. 1998, Davenport et al. 2002) areas, such as the WCI, would restrict potential interactions among individuals from different groups that share similar ranges, as observed with the common bottlenose dolphin *Tursiops truncatus* (e.g., Lusseau et al. 2006). These results support the complex spatial structure of pilot whales in Macaronesia (Alves et al. 2019; Servidio et al. 2019) and emphasize the intricate web of movements among these regions. It is important to consider that the findings of this study cannot be generalized across residency types. While most tagged individuals were considered visitors, the photo-identification matches included animals from all residency types. Therefore, movements between islands are not limited to visitors, as has previously been observed (Alves, Alessandrini, et al. 2018). It would be interesting to understand if animals of different residency types use the same pathways to travel between areas or if spatial and temporal differences can be observed. Additional telemetry data of animals with different residency patterns could prove useful to answer such questions, including more detailed analyses of the photo-identification comparison. Moreover, it is important to recognize that the social structure of pilot whales, which includes strong, stable group bonds and distinct communities, may shape observed movement and space-use patterns. These spatial–social dynamics could have implications for connectivity and conservation efforts, as social groups may exhibit unique habitat preferences, core areas or migratory routes (Kratofil et al. 2023). Integrating this social aspect into conservation planning can enhance efforts to protect habitats crucial for distinct communities and to accommodate community-specific needs within the population.

This study confirms that the Macaronesia biogeographical region is a favourable habitat for the target species. Although the existence of favourable habitats has been shown for specific islands (Pérez-Vallazza et al. 2008; Alves et al. 2019; Servidio et al. 2019; Fernandez et al. 2021; Herrera et al. 2021; Esteban, Verborgh, and Freitas 2022), this study shows it for the first time in offshore waters. Moreover, it suggests a preference for a connectivity-based corridor for animals of both sexes between two distinct regions (Madeira and the WCI). However, it is important to consider the variability in routes taken by the tagged individuals and acknowledge that path data are unavailable for the matched individuals, making it plausible that a broader region encompasses important habitats. The limited sample of 12 sexed individuals further constrains our ability to draw broad conclusions on interregional connectivity for animals of both sexes. The disparity in the level of connectivity between regions, highlighted by both satellite telemetry and photo-identification, raises intriguing ecological questions as to why certain groups prefer specific habitats. Therefore, future research should aim to link this to oceanographic and biological data (e.g., Abecassis et al. 2015; Thorne et al. 2017; Tyson Moore et al. 2020) to help foster such reasons.

This study highlights the importance of transboundary conservation efforts transcending individual geopolitical boundaries, as is the case of most large marine predators. The absence of previous recognition of evident connectivity between Madeira and the WCI underscores the need for sustained and international collaborative efforts, integration of multiple approaches and adaptivity in conservation management (McGowan et al. 2017). These findings could be used to inform and optimize the management of pilot whales and other marine species in Macaronesia. However, delineation of marine protected areas, such as the proposed 'Macaronesian Biodiversity and Ecological Migration Corridor for Cetaceans' (Carrillo 2007), for large marine species, is challenging, particularly when dealing with cetaceans moving across the open ocean. The intricacy is heightened by variations observed at individual and population level scales in species' migratory routes (Agardy, di Sciara, and Christie 2011; Pendoley et al. 2014; Shuert et al. 2023), as observed in the current study. Connectivity patterns between Macaronesian archipelagos have been identified for several cetacean species (Prieto et al. 2014; Steiner et al. 2015; Alves et al. 2019; Dinis et al. 2021; Ferreira et al. 2021), requiring coordinated conservation efforts. The findings of the current study reinforce the importance of these existing efforts to safeguard against current (as outlined in McIvor et al. 2022 and Aguilar de Soto and Alves 2023) and future threats (Sousa et al. 2019), such as increased ocean temperatures, acidification and oxygen loss. To this end, specific measures have been or are being implemented. In the Madeira Archipelago, a Site of Community Importance for cetaceans was proposed in 2016, surrounding Madeira, Porto Santo and Desertas, while around the Selvagens Archipelago, located between Madeira and the Canary Islands, the largest marine reserve with full protection in Europe and the North Atlantic was created in 2021 (Alves et al. 2022). In the Canary Islands, several Sites of Community Importance (SCIs) and Special Areas of Conservation (SACs) have been designated; however, an extension of the latter into the open sea was proposed as this could prove beneficial for several endangered marine mammal species (Herrera et al. 2021). The recent delineation of an Important Marine Mammal Area (IMMA) covering both Madeira and the Canary Islands (IUCN-MMPATF 2024) could further aid in current and future conservation of Macaronesian marine mammals, including in guiding the establishment of the 'Macaronesian Biodiversity and Ecological Migration Corridor for Cetaceans', which would require governmental policies and regulations from both Spain and Portugal (Carrillo 2007; Herrera et al. 2021). Such an initiative will particularly benefit from incorporating data on connectivity and movement patterns, as shown in this study, to protect and manage cetacean populations across the region's international waters. Further research on these topics for less-studied cetacean populations within the region is also recommended to provide a more comprehensive conservation framework.

Overall, we showed that the integration of satellite telemetry and photo-identification, with additional inputs from molecular sexing, can provide robust connectivity-based tools to enrich our understanding of the movement patterns and behaviours of a large marine predator. This can be applied to other oceanic species, especially in remote areas (e.g., Kennedy et al. 2023), providing valuable insights into dynamic and spatial ecology, as well as broadening our knowledge of blue corridors. Such information can significantly contribute to planning future research endeavours and conservation strategies crossing regional boundaries, promoting the protection of a globally threatened marine biodiversity.

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Ethics Statement

Tagging and biopsy collection in Madeiran waters followed the guidelines and regulations set by the Instituto de Florestas e Conservação da Natureza—IFCN (Instituto Português—Região Autónoma da Madeira) under permits 508/2018, 02/IFCN//2019, 02/IFCN//2020, 01/IFCN//2021 and 01/IFCN/2022. The IFCN is a governmental body from an EU country that carefully follows all national and international legislation. To acquire the correct knowledge and avoid causing harm to animals, tag deployment training was provided by a consultant from an EU organization. Due to the social structure of these animals, in the field, tagged animals were selected based on age, size, absence of young individuals, apparent health, among others. Best practice guidelines were also consulted before tagging took place.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Satellite telemetry data that supports the findings of this study are openly available in Movebank at https://www.movebank.org (Whales Telemetry—MARE-ARDITI/Oceanic Observatory of Madeira). Photographic information from Madeira is openly available on the Oceanic Observatory of Madeira webpage at https://oomdata.arditi.pt/products/catalogofotoid/, while the catalogue from the Canary Islands has been made openly available in Mendeley Data at https://doi.org/10.17632/rf9csj2tcz.1.

References

Abecassis, M., J. Polovina, R. W. Baird, et al. 2015. "Characterizing a Foraging Hotspot for Short-Finned Pilot Whales and Blainville's Beaked Whales Located Off the West Side of Hawai'i Island by Using Tagging and Oceanographic Data." *PLoS ONE* 10: e0142628. https://doi.org/10.1371/journal.pone.0142628.

Afonso, P., J. Fontes, E. Giacomello, et al. 2020. "The Azores: A Mid-Atlantic Hotspot for Marine Megafauna Research and Conservation." *Frontiers in Marine Science* 6: 826. https://doi.org/10.3389/fmars.2019.00826.

Agardy, T., G. N. di Sciara, and P. Christie. 2011. "Mind the Gap: Addressing the Shortcomings of Marine Protected Areas Through Large Scale Marine Spatial Planning." *Marine Policy* 35: 226–232. https://doi.org/10.1016/j.marpol.2010.10.006.

Aguilar de Soto, N., and F. Alves. 2023. "Short-Finned Pilot Whale *Globicephala macrorhynchus* Gray, 1846." In *Handbook of the Mammals of Europe*, edited by K. Hackländer and F. E. Zachos, 1–32. Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-65038-8_101-1.

Alves, F., N. Queiroz, and P. G. R. Jodice. 2023. "Editorial: Ecological and Behavioral Traits of Apex Predators in Oceanic Insular Ecosystems: Advances and Challenges in Research and Conservation." *Frontiers in Marine Science* 10: 1252360. https://doi.org/10.3389/fmars.2023.1252360.

Alves, F., J. G. Monteiro, P. Oliveira, and J. Canning-Clode. 2022. "Portugal Leads With Europe's Largest Marine Reserve." *Nature* 601: 318. https://doi.org/10.1038/d41586-022-00093-8.

Alves, F., A. Alessandrini, M. Fernandez, K. L. Hartman, and A. Dinis. 2018. "Home Sweet Home? Wide-Ranging Movements of Socially Stable Resident Delphinids (*Globicephala macrorhynchus*)." *Scientia Insularum* 1: 37–49. https://doi.org/10.25145/j.SI.2018.01.004.

Alves, F., R. Ferreira, M. Fernandes, Z. Halicka, L. Dias, and A. Dinis. 2018. "Analysis of Occurrence Patterns and Biological Factors of Cetaceans Based on Long-Term and Fine-Scale Data From Platforms of Opportunity: Madeira Island as a Case Study." *Marine Ecology* 39: e12499. https://doi.org/10.1111/maec.12499.

Alves, F., A. Dinis, C. Nicolau, et al. 2015. "Survival and Abundance of Short-Finned Pilot Whales in the Archipelago of Madeira, NE Atlantic." *Marine Mammal Science* 31: 106–121. https://doi.org/10.1111/mms.12137.

Alves, F., S. Quérouil, A. Dinis, et al. 2013. "Population Structure of Short-Finned Pilot Whales in the Oceanic Archipelago of Madeira Based on Photo-Identification and Genetic Analyses: Implications for Conservation." *Aquatic Conservation: Marine and Freshwater Ecosystems* 23: 758–776. https://doi.org/10.1002/aqc.2332.

Alves, F., M. Dromby, V. Baptista, et al. 2020. "Ecophysiological Traits of Highly Mobile Large Marine Predators Inferred From Nucleic Acid Derived Indices." *Scientific Reports* 10: 1–10. https://doi.org/10.1038/s41598-020-61769-7.

Alves, F., A. Alessandrini, A. Servidio, et al. 2019. "Complex Biogeographical Patterns Support an Ecological Connectivity Network of a Large Marine Predator in the North-East Atlantic." *Diversity and Distributions* 25: 269–284. https://doi.org/10.1111/ddi.12848.

Andrews, R. D., R. W. Baird, J. Calambokidis, et al. 2019. "Best Practice Guidelines for Cetacean Tagging." *Journal of Cetacean Research and Management* 20: 27–66.

Bailey, H., B. R. Mate, D. M. Palacios, L. Irvine, S. J. Bograd, and D. P. Costa. 2009. "Behavioural Estimation of Blue Whale Movements in the Northeast Pacific From State-Space Model Analysis of Satellite Tracks." *Endangered Species Research* 10: 93–106. https://doi.org/10.3354/esr00239.

Barton, E. D., J. Aristegui, P. Tett, et al. 1998. "The Transition Zone of the Canary Current Upwelling Region." *Progress in Oceanography* 41: 455–504. https://doi.org/10.1016/S0079-6611(98)00023-8.

Baumann-Pickering, S., A. E. Simonis, E. M. Oleson, R. W. Baird, M. A. Roch, and S. M. Wiggins. 2015. "False Killer Whale and Short-Finned Pilot Whale Acoustic Identification." *Endangered Species Research* 28: 97–108. https://doi.org/10.3354/esr00685.

Benazzouz, A., H. Demarcq, and I. Déniz-González. 2015. "Recent Trends in Coastal Upwelling." In *Oceanographic and Biological Features in the Canary Current Large Marine Ecosystem*, edited by L. Valdés and I. Déniz-González. Paris: IOC-UNESCO Paris IOC Tech Ser No. 115:383.

Betty, E. L., E. M. J. Zwamborn, M. Weyn, E. Luck, and F. Alves. 2023. "Life History Parameters, Sociobiology, and Reproductive Strategies of Pilot Whales." In *Sex in Cetaceans: Morphology, Behavior, and the Evolution of Sexual Strategies*, edited by B. Würsig and D. N. Orbach, 327–351. Cham: Springer. https://doi.org/10.1007/978-3-031-35651-3_15.

Block, B. A., I. D. Jonsen, S. J. Jorgensen, et al. 2011. "Tracking Apex Marine Predator Movements in a Dynamic Ocean." *Nature* 475: 86–90. https://doi.org/10.1038/nature10082.

Boran, J., and S. Heimlich. 2019. "Pilot Whales: Delphinid Matriarchies in Deep Seas." In *Ethology and Behavioral Ecology of Odontocetes. Ethology and Behavioral Ecology of Marine Mammals*, edited by B. Würsig, 281–304. Cham: Springer International Publishing. https://doi.org/10.1007/978-3-030-16663-2_13.

Caldeira, R. M. A., S. Groom, P. Miller, D. Pilgrim, and N. P. Nezlin. 2002. "Sea-Surface Signatures of the Island Mass Effect Phenomena Around Madeira Island, Northeast Atlantic." *Remote Sensing of Environment* 80: 336–360.

Cardoso, C., and R. M. A. Caldeira. 2021. "Modeling the Exposure of the Macaronesia Islands (NE Atlantic) to Marine Plastic Pollution." *Frontiers in Marine Science* 8: 653502. https://doi.org/10.3389/fmars.2021.653502.

Carrillo, M. 2007. "Cetaceans in the Macaronesia Region (Eastern Central Atlantic Ocean) and Threats Faced in the Canary Islands." In *Conserving Cetaceans and Manatees in the Western African Region 2012*, edited by K. Van Waerebeek, 41–49. Bonn, Germany: CMS Secretariat.

Carrillo, M., C. Pérez-Vallazza, and R. Álvarez-Vázquez. 2010. "Cetacean Diversity and Distribution Off Tenerife (Canary Islands)." *Marine Biodiversity Records* 3: e97. https://doi.org/10.1017/s1755267210000801.

Chen, C., T. A. Jefferson, B. Chen, and Y. Wang. 2022. "Geographic Range Size, Water Temperature, and Extrinsic Threats Predict the Extinction Risk in Global Cetaceans." *Global Change Biology* 28: 6541–6555. https://doi.org/10.1111/gcb.16385.

Cropper, T. 2013. "The Weather and Climate of Macaronesia: Past, Present and Future." *Weather* 68: 300–307. https://doi.org/10.1002/wea.2155.

Davenport, R., S. Neuer, P. Helmke, J. Perez-Marrero, and O. Llinas. 2002. "Primary Productivity in the Northern Canary Islands Region as Inferred From SeaWiFS Imagery." *Deep Sea Research Part II: Topical Studies in Oceanography* 49: 3481–3496. https://doi.org/10.1016/S0967-0645(02)00095-4.

Davis, G. E., M. F. Baumgartner, P. J. Corkeron, et al. 2020. "Exploring Movement Patterns and Changing Distributions of Baleen Whales in the Western North Atlantic Using a Decade of Passive Acoustic Data." *Global Change Biology* 26: 4812–4840. https://doi.org/10.1111/gcb.15191.

Dinis, A., C. Molina, M. Tobeña, et al. 2021. "Large-Scale Movements of Common Bottlenose Dolphins in the Atlantic: Dolphins With an International Courtyard." *PeerJ* 9: e11069. https://doi.org/10.7717/peerj.11069.

Espino, F., F. Tuya, A. del Rosario, et al. 2019. "Geographical Range Extension of the Spotfin Burrfish, *Chilomycterus reticulatus* (L. 1758), in the Canary Islands: A Response to Ocean Warming?" *Diversity* 11: 1–15. https://doi.org/10.3390/d11120230.

Esteban, R., P. Verborgh, and L. Freitas. 2022. "Dynamics of Short-Finned Pilot Whales Long-Term Social Structure in Madeira." *Mammalian Biology* 102: 1315–1332. https://doi.org/10.1007/s42991-022-00280-0.

Fernandez, M., F. Alves, R. Ferreira, et al. 2021. "Modeling Fine-Scale Cetaceans' Distributions in Oceanic Islands: Madeira Archipelago as a Case Study." *Frontiers in Marine Science* 8: 688248. https://doi.org/10.3389/fmars.2021.688248.

Ferreira, R., A. Dinis, A. Badenas, et al. 2021. "Bryde's Whales in the North-East Atlantic: New Insights on Site Fidelity and Connectivity Between Oceanic Archipelagos." *Aquatic Conservation: Marine and Freshwater Ecosystems* 31: 2938–2950. https://doi.org/10.1002/aqc.3665.

Fleming, C. H., and J. M. Calabrese. 2022. "ctmm: Continuous-Time Movement Modeling." R package version 1.1.0.

Fraser, K. C., K. T. A. Davies, C. M. Davy, A. T. Ford, D. T. T. Flockhart, and E. G. Martins. 2018. "Tracking the Conservation Promise of Movement Ecology." *Frontiers in Ecology and Evolution* 6: 150. https://doi.org/10.3389/fevo.2018.00150.

Friday, N., T. D. Smith, P. T. Stevick, and J. Allen. 2000. "Measurement of Photographic Quality and Individual Distinctiveness for the Photographic Identification of Humpback Whales, *Megaptera novaeangliae*." *Marine Mammal Science* 16: 355–374. https://doi.org/10.1111/j.1748-7692.2000.tb00930.x.

Gu, Z. 2014. "Circlize Implements and Enhances Circular Visualization in R (Computer Software)." *Bioinformatics* 30: 2811–2812.

Hays, G. C., H. Bailey, S. J. Bograd, et al. 2019. "Translating Marine Animal Tracking Data Into Conservation Policy and Management." *Trends in Ecology and Evolution* 34: 459–473. https://doi.org/10.1016/j.tree.2019.01.009.

Hays, G. C., L. C. Ferreira, A. M. M. Sequeira, et al. 2016. "Key Questions in Marine Megafauna Movement Ecology." *Trends in Ecology and Evolution* 31: 463–475. https://doi.org/10.1016/j.tree.2016.02.015.

Hazen, E. L., S. M. Maxwell, H. Bailey, et al. 2012. "Ontogeny in Marine Tagging and Tracking Science: Technologies and Data Gaps." *Marine Ecology Progress Series* 457: 221–240. https://doi.org/10.3354/meps09857.

Herrera, I., M. Carrillo, M. Cosme de Esteban, and R. Haroun. 2021. "Distribution of Cetaceans in the Canary Islands (Northeast Atlantic Ocean): Implications for the Natura 2000 Network and Future Conservation Measures." *Frontiers in Marine Science* 8: 669790. https://doi.org/10.3389/fmars.2021.669790.

Hill, M. C., A. R. Bendlin, A. M. Van Cise, et al. 2019. "Short-Finned Pilot Whales (*Globicephala macrorhynchus*) of the Mariana Archipelago: Individual Affiliations, Movements, and Spatial Use." *Marine Mammal Science* 35: 797–824. https://doi.org/10.1111/mms.12567.

IUCN. 2022. "The IUCN Red List of Threatened Species." https://www.iucnredlist.org/en.

IUCN-MMPATF. 2024. "Canary and Madeira Islands IMMA Factsheet." IUCN Joint SSC/WCPA Marine Mammal Protected Areas Task Force, 2024. https://www.marinemammalhabitat.org/factsheets/canary-and-madeira-islands-imma/.

Jonsen, I. D., W. J. Grecian, L. Phillips, et al. 2023. "aniMotum, an R Package for Animal Movement Data: Rapid Quality Control, Behavioural Estimation and Simulation." *Methods in Ecology and Evolution* 14: 806–816. https://doi.org/10.1111/2041-210X.14060.

Jonsen, I. D., C. R. McMahon, T. A. Patterson, et al. 2019. "Movement Responses to Environment: Fast Inference of Variation Among Southern Elephant Seals With a Mixed Effects Model." *Ecology* 100: 1–8. https://doi.org/10.1002/ecy.2566.

Kareiva, P., and G. Odell. 1987. "Swarms of Predators Exhibit 'Preytaxis' if Individual Predators Use Area-Restricted Search." *American Naturalist* 130: 233–270. https://doi.org/10.1086/284707.

Kennedy, A. S., E. L. Carroll, A. N. Zerbini, et al. 2023. "Photo-Identification and Satellite Telemetry Connect Southern Right Whales From South Georgia Island (Islas Georgias del Sur) With Multiple Feeding and Calving Grounds in the Southwest Atlantic." *Marine Mammal Science* 40: e13089. https://doi.org/10.1111/mms.13089.

Kratofil, M. A., A. E. Harnish, S. D. Mahaffy, et al. 2023. "Biologically Important Areas II for Cetaceans Within U.S. and Adjacent Waters—Hawai'i Region." *Frontiers in Marine Science* 10: 1053581. https://doi.org/10.3389/fmars.2023.1053581.

Lusseau, D., B. Wilson, P. S. Hammond, et al. 2006. "Quantifying the Influence of Sociality on Population Structure in Bottlenose Dolphins." *Journal of Animal Ecology* 75: 14–24. https://doi.org/10.1111/j.1365-2656.2005.01013.x.

Mahaffy, S. D., R. W. Baird, D. J. Mcsweeney, D. L. Webster, and G. S. Schorr. 2015. "High Site Fidelity, Strong Associations, and Long-Term Bonds: Short-Finned Pilot Whales Off the Island of Hawai'i." *Marine Mammal Science* 31: 1427–1451. https://doi.org/10.1111/mms.12234.

MARE-Madeira. 2024. "The Marine and Environmental Sciences Centre." https://mare-madeira.pt/.

Mathews, E. A., S. Keller, and D. B. Weiner. 1988. "A Method to Collect and Process Skin Biopsies for Cell Culture From the Free-Ranging Gray Whales (*Eschrichtius robustus*)." *Marine Mammal Science* 4: 1–12.

McGowan, J., M. Beger, R. L. Lewison, et al. 2017. "Integrating Research Using Animal-Borne Telemetry With the Needs of Conservation

Management." *Journal of Applied Ecology* 54: 423–429. https://doi.org/10.1111/1365-2664.12755.

McIvor, A. J., C. T. Williams, F. Alves, A. Dinis, M. P. Pais, and J. Canning-Clode. 2022. "The Status of Marine Megafauna Research in Macaronesia: A Systematic Review." *Frontiers in Marine Science* 9: 819581. https://doi.org/10.3389/fmars.2022.819581.

Miralles, L., M. Oremus, M. A. Silva, S. Planes, and E. Garcia-Vazquez. 2016. "Interspecific Hybridization in Pilot Whales and Asymmetric Genetic Introgression in Northern *Globicephala melas* Under the Scenario of Global Warming." *PLoS ONE* 11: e0160080. https://doi.org/10.1371/journal.pone.0160080.

Moore, S. E. 2008. "Marine Mammals as Ecosystem Sentinels." *Journal of Mammalogy* 89: 534–540. https://doi.org/10.1644/07-MAMM-S-312R1.1.

Ogburn, M. B., A.-L. Harrison, F. G. Whoriskey, S. J. Cooke, J. E. Mills Flemming, and L. G. Torres. 2017. "Addressing Challenges in the Application of Animal Movement Ecology to Aquatic Conservation and Management." *Frontiers in Marine Science* 4: 70. https://doi.org/10.3389/fmars.2017.00070.

Olson, P. A. 2009. "Pilot Whales: *Globicephala melas* and *G. macrorhynchus*." In *Encyclopedia of Marine Mammals*, edited by W. F. Perrin, B. Würsig, and J. G. M. Thewissen, Second ed., 847–852. London: Academic Press. https://doi.org/10.1016/B978-0-12-373553-9.00197-8.

Olson, P. A., B. Galletti, and S. Español-Jiménez. 2020. "Using Photo-Identification to Investigate the Identity of Blue Whales at South Georgia: A Comparison of Photographs With Chile." Report—International Whaling Commission SC/68B/SH/13.

Oremus, M., R. Gales, M. L. Dalebout, et al. 2009. "Worldwide Mitochondrial DNA Diversity and Phylogeography of Pilot Whales (*Globicephala* spp.)." *Biological Journal of the Linnean Society* 98: 729–744. https://doi.org/10.1111/j.1095-8312.2009.01325.x.

Pastor, A., I. A. Catalán, J. Terrados, B. Mourre, and A. Ospina-Alvarez. 2023. "Connectivity-Based Approach to Guide Conservation and Restoration of Seagrass *Posidonia oceanica* in the NW Mediterranean." *Biological Conservation* 285: 110248. https://doi.org/10.1016/j.biocon.2023.110248.

Pendoley, K. L., G. Schofield, P. A. Whittock, D. Ierodiaconou, and G. C. Hays. 2014. "Protected Species Use of a Coastal Marine Migratory Corridor Connecting Marine Protected Areas." *Marine Biology* 161: 1455–1466. https://doi.org/10.1007/s00227-014-2433-7.

Pérez-Jorge, S., M. Tobeña, R. Prieto, et al. 2020. "Environmental Drivers of Large-Scale Movements of Baleen Whales in the Mid-North Atlantic Ocean." *Diversity and Distributions* 26: 683–698. https://doi.org/10.1111/ddi.13038.

Pérez-Vallazza, C., R. Álvarez-Vázquez, L. Cardona, C. Pintado, and J. Hernández-Brito. 2008. "Cetacean Diversity at the West Coast of La Palma Island (Canary Islands)." *Journal of the Marine Biological Association of the United Kingdom* 88: 1289–1296. https://doi.org/10.1017/S0025315408001239.

Prieto, R., M. A. Silva, G. T. Waring, and J. M. A. Gonçalves. 2014. "Sei Whale Movements and Behaviour in the North Atlantic Inferred From Satellite Telemetry." *Endangered Species Research* 26: 103–113. https://doi.org/10.3354/esr00630.

R Core Team. 2022. "R: A Language and Environment for Statistical Computing (Computer Software)." R Foundation for Statistical Computing. https://www.R-project.org/.

Reisinger, R. R., C. Johnson, and A. S. Friedlaender. 2022. "Marine Mammal Movement Ecology in a Conservation and Management Context." In *Marine Mammals: The Evolving Human Factor. Ethology and Behavioral Ecology of Marine Mammals*, edited by G. Notarbartolo di Sciara and B. Würsig, 149–192. Cham: Springer. https://doi.org/10.1007/978-3-030-98100-6_5.

Risch, D., M. Castellote, C. W. Clark, et al. 2014. "Seasonal Migrations of North Atlantic Minke Whales: Novel Insights From Large-Scale Passive Acoustic Monitoring Networks." *Movement Ecology* 2: 24. https://doi.org/10.1186/s40462-014-0024-3.

Robbins, J., L. D. Rosa, J. M. Allen, et al. 2011. "Return Movement of a Humpback Whale Between the Antarctic Peninsula and American Samoa: A Seasonal Migration Record." *Endangered Species Research* 13: 117–121. https://doi.org/10.3354/esr00328.

Sambolino, A., F. Alves, M. Fernandez, A. K. Badenas, R. Ferreira, and A. Dinis. 2022. "Spatial and Temporal Characterization of the Exposure of Island-Associated Cetacean Populations to Whale-Watching in Madeira Islands (NE Atlantic)." *Regional Studies in Marine Science* 49: 102084. https://doi.org/10.1016/j.rsma.2021.102084.

Servidio, A. 2014. "Distribution, Social Structure and Habitat Use of Short-Finned Pilot Whale, *Globicephala macrorhynchus*, in the Canary Islands." Doctoral thesis, University of St Andrews. https://hdl.handle.net/10023/6441.

Servidio, A., E. Pérez-Gil, M. Pérez-Gil, A. Cañadas, P. S. Hammond, and V. Martín. 2019. "Site Fidelity and Movement Patterns of Short-Finned Pilot Whales Within the Canary Islands: Evidence for Resident and Transient Populations." *Aquatic Conservation: Marine and Freshwater Ecosystems* 29: 227–241. https://doi.org/10.1002/aqc.3135.

Shuert, C. R., N. E. Hussey, M. Marcoux, M. P. Heide-Jørgensen, R. Dietz, and M. Auger-Méthé. 2023. "Divergent Migration Routes Reveal Contrasting Energy-Minimization Strategies to Deal With Differing Resource Predictability." *Movement Ecology* 11: 31. https://doi.org/10.1186/s40462-023-00397-y.

Signer, J., and J. R. Fieberg. 2021. "A Fresh Look at an Old Concept: Home-Range Estimation in a Tidy World." *PeerJ* 9: e11031. https://doi.org/10.7717/peerj.11031.

Silva, I., C. H. Fleming, M. J. Noonan, et al. 2022. "Autocorrelation-Informed Home Range Estimation: A Review and Practical Guide." *Methods in Ecology and Evolution* 13: 534–544. https://doi.org/10.1111/2041-210X.13786.

Silva, M. A., A. Borrell, R. Prieto, et al. 2019. "Stable Isotopes Reveal Winter Feeding in Different Habitats in Blue, Fin and Sei Whales Migrating Through the Azores." *Royal Society Open Science* 6: 181800. https://doi.org/10.1098/rsos.181800.

Silva, M. A., R. Prieto, I. Cascão, et al. 2014. "Spatial and Temporal Distribution of Cetaceans in the Mid-Atlantic Waters Around the Azores." *Marine Biology Research* 10: 123–137. https://doi.org/10.1080/17451000.2013.793814.

Sousa, A., F. Alves, A. Dinis, J. Bentz, M. J. Cruz, and J. P. Nunes. 2019. "How Vulnerable Are Cetaceans to Climate Change? Developing and Testing a New Index." *Ecological Indicators* 98: 9–18. https://doi.org/10.1016/j.ecolind.2018.10.046.

Sousa, A., M. Fernandez, F. Alves, et al. 2023. "A Novel Expert-Driven Methodology to Develop Thermal Response Curves and Project Habitat Thermal Suitability for Cetaceans Under a Changing Climate." *Science of the Total Environment* 860: 160376. https://doi.org/10.1016/j.scitotenv.2022.160376.

Steiner, L., M. Pérez-Gil, M. van der Linde, et al. 2015. "Long Distance Movements of Female/Immature Sperm Whales in the North Atlantic." In *Poster Presented at the Biennial Society for Marine Mammalogy Conference, San Francisco, USA*.

Thorne, L. H., H. J. Foley, R. W. Baird, D. L. Webster, Z. T. Swaim, and A. J. Read. 2017. "Movement and Foraging Behavior of Short-Finned Pilot Whales in the Mid-Atlantic Bight: Importance of Bathymetric Features and Implications for Management." *Marine Ecology Progress Series* 584: 245–257. https://doi.org/10.3354/meps12371.

Tyson Moore, R. B., D. C. Douglas, H. H. Nollens, L. Croft, and R. S. Wells. 2020. "Post-Release Monitoring of a Stranded and Rehabilitated Short-Finned Pilot Whale (*Globicephala macrorhynchus*) Reveals

Current-Assisted Travel." *Aquatic Mammals* 46: 200–214. https://doi.org/10.1578/AM.46.2.2020.200.

Urian, K., A. Gorgone, A. Read, et al. 2015. "Recommendations for Photo-Identification Methods Used in Capture-Recapture Models With Cetaceans." *Marine Mammal Science* 31: 298–321. https://doi.org/10.1111/mms.12141.

Van Cise, A. M., R. W. Baird, C. S. Baker, et al. 2019. "Oceanographic Barriers, Divergence, and Admixture: Phylogeography and Taxonomy of Two Putative Subspecies of Short-Finned Pilot Whale." *Molecular Ecology* 28: 2886–2902. https://doi.org/10.1111/mec.15107.

Verborgh, P., E. H. Janssen, R. Esteban, P. Gauffier, and L. Freitas. 2022. "Proposing a Framework for Monitoring Demographic Parameters in Local Cetacean Populations: The Case of Short-Finned Pilot Whales in Madeira." *Mammalian Biology* 102: 1425–1444. https://doi.org/10.1007/s42991-022-00266-y.

Wilson, B., P. S. Hammond, and P. M. Thompson. 1999. "Estimating Size and Assessing Trends in a Coastal Bottlenose Dolphin Population." *Ecological Applications* 9: 288–300. https://doi.org/10.2307/2641186.

Woodstock, M. S., J. J. Kiszka, M. R. Ramírez-León, et al. 2023. "Cetacean-Mediated Vertical Nitrogen Transport in the Oceanic Realm." *Limnology and Oceanography* 68: 2445–2460. https://doi.org/10.1002/lno.12433.

Würsig, B., and T. A. Jefferson. 1990. "Methods of Photo-Identification for Small Cetaceans." Report of the International Whaling Commission (Special Issue). p 42-43.

Würsig, B., and M. Würsig. 1977. "The Photographic Determination of Group Size, Composition, and Stability of Coastal Porpoises (*Tursiops truncatus*)." *Science* 198: 755–756. https://doi.org/10.1126/science.198.4318.755.

Supporting Information

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