Universidade de Évora - Instituto de Investigação e Formação Avançada

Programa de Doutoramento em Biologia

Tese de Doutoramento

Dynamic ecological patterns of insular short-finned pilot whales

Mieke Mariette J Weyn

Orientador(es) | Catarina Sofia Mateus
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‘Ocean’ (Alex, 13 months)

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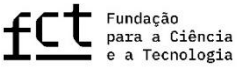

ABSTRACT

Effective conservation of highly mobile species, such as cetaceans, depends on understanding the spatial and temporal dynamics of habitat use, movements, and connectivity, particularly in insular systems. This thesis advances that understanding for Atlantic Naisa short-finned pilot whales inhabiting Macaronesia by integrating satellite telemetry, long-term photographic-identification data, and ecological modelling, complemented by sex-specific social analyses based on genetically sexed individuals which provide behavioral context for interpreting dispersal and philopatry. At a regional scale, marked connectivity was observed between Madeira and the western Canary Islands based on photo-identification and telemetry data. Preferred areas and movement pathways were identified, highlighting the potential importance of the western Canary Islands as a mixing area and the existence of a potential biological corridor. Specifically, in Madeira, biotelemetry and movement modelling showed that short-finned pilot whales use island-associated waters in a strongly structured way. Madeira functions as an important seasonal aggregation area, with critical near-shore habitat southeast of Madeira Island used by individuals differing in site fidelity, consistent with condition-dependent tactics in a partial-migration system. At the oceanic basin scale, crossmatching of large long-term photo-identification catalogues from the eastern and western North Atlantic found no conclusive evidence of current trans-Atlantic movements, suggesting that such interchange is either rare or difficult to detect with currently available datasets. Finally, sex-specific social analyses showed that both females and males form long-term, non-random associations, with females more strongly anchored to clusters and males contributing disproportionately to occasional inter-cluster links. Overall, this thesis shows that the dynamic ecology of short-finned pilot whales in Macaronesia is characterized by a combination of seasonal residency, recurrent inter-archipelago movements between preferred/important areas - emphasizing the need for international collaboration - and sex-specific social organization. This integrated perspective helps refine current understanding of the species and provides a stronger ecological basis for conservation planning.

Keywords: *Globicephala macrorhynchus* - Movement patterns - Home range - Biotelemetry - Photographic-identification - Social structure

RESUMO

Padrões ecológicos dinâmicos de baleias-piloto-tropicais insulares

A conservação eficaz de espécies altamente móveis depende da compreensão das dinâmicas espaciais e temporais da utilização do habitat, dos movimentos e da conectividade, particularmente em sistemas insulares. Esta tese aprofunda esse conhecimento relativamente às baleias-piloto-tropicais (*Globicephala macrorhynchus*) na Macaronésia, integrando telemetria por satélite, foto-identificação e modelação ecológica, complementados por análises sociais específicas por sexo, baseadas em indivíduos geneticamente sexados, que fornecem contexto comportamental para interpretar dispersão e filopatria.

À escala regional, os dados de foto-identificação e telemetria revelaram conectividade significativa entre a Madeira e as ilhas oeste das Canárias. Foram identificadas áreas preferenciais e corredores de movimentação, evidenciando a potencial importância destas ilhas oeste como área de mistura e a existência de um possível corredor biológico. Na Madeira, a biotelemetria e a modelação de movimentos demonstraram que as baleias-piloto-tropicais utilizam as águas associadas à ilha de forma estruturada. A Madeira funciona como uma importante área de agregação sazonal, com habitat costeiro crítico (a sudeste da ilha), utilizado por indivíduos com diferentes níveis de fidelidade, consistente com táticas dependentes da condição num sistema de migração parcial.

À escala da bacia oceânica, a comparação entre catálogos de foto-identificação do Atlântico Norte oriental e ocidental não encontrou evidência conclusiva de movimentos transatlânticos atuais, sugerindo que tal intercâmbio é raro ou difícil de detetar com os dados disponíveis. Por fim, as análises sociais revelaram que tanto fêmeas como machos formam associações duradouros e não aleatórias, com as fêmeas mais fortemente associadas a grupos e os machos a contribuírem desproporcionadamente para ligações ocasionais entre grupos.

No geral, esta tese demonstra que a ecologia dinâmica desta espécie é caracterizada por uma combinação de residência sazonal, movimentos recorrentes entre arquipélagos e organização social específica por sexo. Esta perspetiva integrada contribui para incrementar o conhecimento sobre esta espécie e fornece uma base ecológica mais robusta para a sua conservação.

Palavras-chave: *Globicephala macrorhynchus* - Padrões de movimento - Área de utilização - Biotelemetria -Foto-identificação - Estrutura social

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Cetaceans in marine ecosystems and conservation relevance

Cetaceans are top predators that occupy upper trophic levels and play important roles in the structure and functioning of marine ecosystems (Bowen, 1997; Heithaus et al., 2008). Changes in the abundance of these species can trigger cascading effects throughout the broader ecosystem, disrupting food webs and altering community dynamics (Figure 1.1) (Baum and Worm, 2009; Estes et al., 2004; Kiszka et al., 2022). They are indicators of ecosystem health, and as large consumers, they can influence trophic interactions, nutrient cycling, and the distribution of energy across broad spatial scales (Bossart, 2011; Gilbert et al., 2023; Plön et al., 2024; Roman et al., 2025). Their occurrence, movements, and space use can therefore provide insight into ecosystem processes and habitat relationships that are otherwise difficult to observe directly, especially in pelagic systems (Hazen et al., 2019; Zacharias and Roff, 2001). Despite their ecological importance, many marine mammal species are increasingly threatened by human pressures, such as vessel traffic, underwater noise, fisheries interactions, prey alteration, pollution, and climate-driven environmental change (Avila et al., 2018; Plön et al., 2024). As cetaceans have slow life histories (i.e., long-lived, low reproductive rates), they are particularly vulnerable (Avila et al., 2018; Davidson et al., 2012). In this context, understanding the dynamic ecology of cetaceans is central to conservation, because it can help identify ecologically important areas, evaluate connectivity between them, and assess the extent to which essential areas overlap with anthropogenic pressures, among others (Lascelles et al., 2014; Reisinger et al., 2022; Sequeira et al., 2025).

1.2 Dynamic ecology of cetaceans

Cetacean ecology is inherently dynamic because key aspects vary across spatial and temporal scales within marine environments which are themselves heterogeneous, fluid, and temporally variable (Mann and Lazier, 2005). Understanding cetacean ecology, therefore, requires more than static descriptions of where animals occur. It also requires attention to how individuals and groups use space through time, how areas are connected by movement, and how the same areas serve different ecological roles and may vary across various timescales (i.e., diel, seasonal, and interannually) (Becker et al., 2022; Dunn et al., 2019).

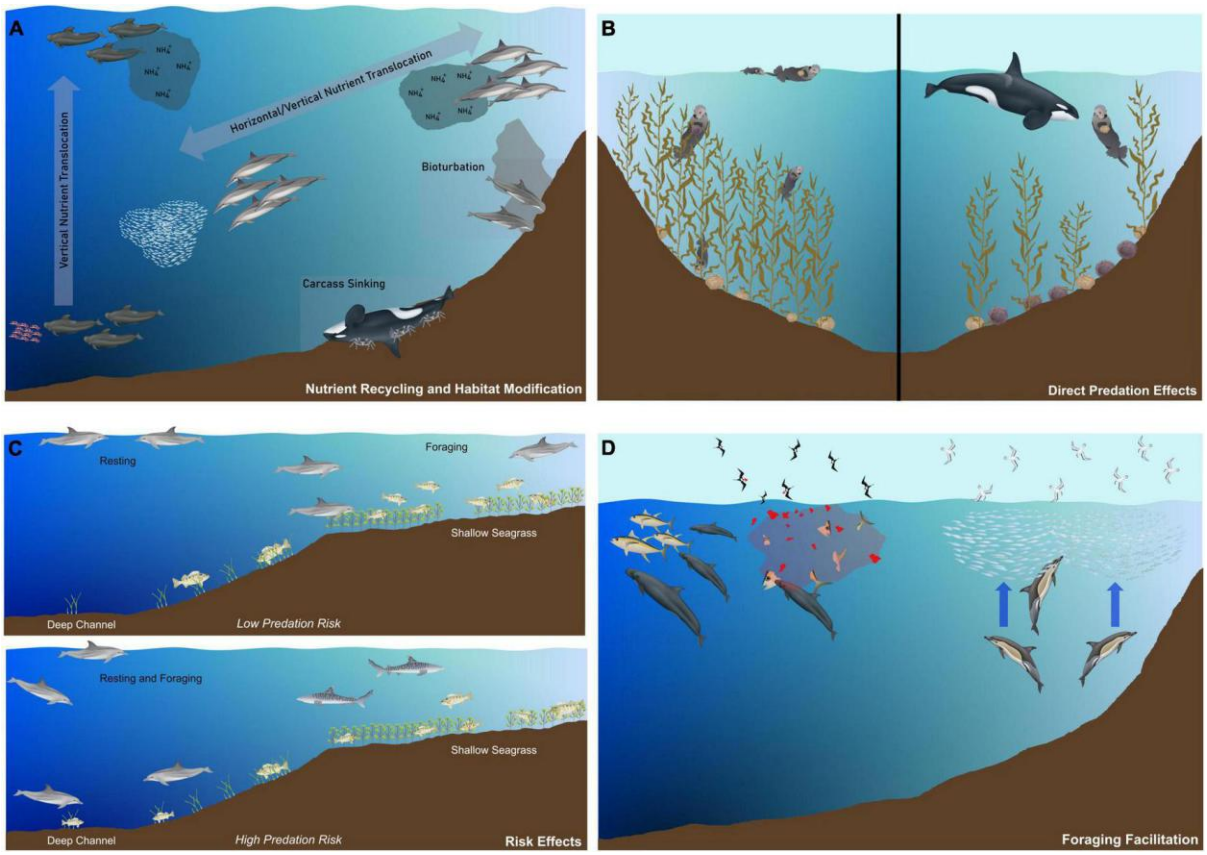

Figure 1.1: Conceptual model showing the different ecological roles small odontocetes can have in aquatic (primarily marine) food webs. A) Nutrient translocation and habitat modification through vertical and horizontal transport, and bioturbation. B) Mediation of the consumptive effects of other predators in the ecosystem. C) Changes in foraging behavior and habitat use in response to predation risk. D) Facilitation of foraging opportunities for other predators by altering prey availability. **Image: Kiszka et al. (2022)**.

In this thesis, dynamic ecology refers to how cetaceans use space through time, including variation in habitat use, movement, site fidelity, residency, and social organization, and how these are shaped by environmental heterogeneity, oceanographic variability, prey accessibility, intrinsic state, and socially mediated behavior. This is especially relevant in marine systems, where the same area may not serve a constant ecological function over time; repeated occurrence in an area, for example, does not necessarily imply year-round residency, continuous use, or a single ecological role. Instead, habitats may be used intermittently, by different individuals, or for different purposes such as foraging, resting, socializing, nursing, or transit (Ferreira et al., 2022; Mayaud et al., 2025; Tyne et al., 2015).

Movement is a particularly dynamic component of cetacean ecology, because it mediates how individuals respond to environmental heterogeneity, locate and exploit resources, connect

habitats, and adjust their behavior through time (Shaw, 2020). Rather than representing a fixed property of a species, movement may vary within individuals, among individuals, and among populations, and can be expressed as localized foraging movements, repeated area use, dispersive movements, seasonal migrations, or wider-ranging nomadic behavior (Heape, 1931; Mueller and Fagan, 2008; Nathan et al., 2008; Shaw, 2020). In this sense, movement provides an important process through which habitat use, site fidelity, and residency can be interpreted.

Literature suggests that distribution, habitat use, and movement often reflect the heterogeneous nature of marine environments. Across spatial and temporal scales, these patterns may be associated with broadscale environmental gradients and water-mass characteristics, as well as with finer-scale dynamic oceanographic and topographic features, such as fronts, eddies, shelf breaks, slopes, and submarine canyons, which can influence prey availability and accessibility, thereby creating recurrent but shifting opportunities for foraging and other essential activities (Abecassis et al., 2015; Braun et al., 2023; Scales et al., 2014). These patterns may also be modified by biotic interactions, such as predation and competition, as well as by anthropogenic disturbance, which can alter behavior and spatial use over ecologically meaningful scales (Erbe et al., 2019; Matthews et al., 2020).

In many species, movement and spatial use may also be shaped by social factors (Bräger and Bräger, 2019). This is especially relevant in some strongly structured larger odontocete populations, such as sperm whales (*Physeter macrocephalus*) and resident killer whales (*Orcinus orca*) (Engelhaupt et al., 2009; Hauser et al., 2007). Long-term associations, kinship, philopatry, fission-fusion dynamics, and sex-specific dispersal can influence how individuals move, which habitats they use, and how connectivity is expressed at the population level (Möller, 2012; Rendell et al., 2019; Weiss et al., 2021). Examples from killer whales, sperm whales, pilot whales (*Globicephala* spp.), common dolphins (*Delphinus delphis*), and bottlenose dolphins (*Tursiops truncatus*) also show that sex, age, reproductive state, and social roles can all contribute to observed variation in movement and space use (Gowans et al., 2007; Heithaus and Dill, 2002; Jefferson et al., 2015). These components should therefore also be taken into account when trying to understand spatial use through time.

Studies focusing on the dynamic ecology of species have already informed conservation and management in several important ways. Recurrent seasonal habitat use has been translated into spatial protection. For North Atlantic right whales (*Eubalaena glacialis*), U.S. critical habitat designations explicitly recognize separate feeding grounds in the Northeast and nursery/calving

grounds in the Southeast, illustrating how recurring seasonal habitat use can underpin formal conservation measures (NMFS, 2016). Moreover, dynamic ecological studies have been crucial for evaluating whether existing static protection is actually effective. At Banks Peninsula, seasonal shifts in Hector's dolphin (*Cephalorhynchus hectori*) distribution showed that sanctuary design needed to account for both temporal and spatial variation in habitat use (Rayment et al., 2010). Likewise, telemetry of southern right whales (*Eubalaena australis*) in Aotearoa/New Zealand identified previously unknown important areas outside existing protected zones and revealed high whale–vessel overlap within some MPAs, demonstrating that static boundaries may fail to capture the full space use of highly mobile species (Zhang et al., 2024). Finally, these products have enabled more responsive dynamic management approaches. Dynamic strategies that respond to changing whale habitat conditions can outperform fixed seasonal measures, especially during anomalous ocean conditions such as marine heatwaves (Barlow and Torres, 2021; Hausner et al., 2021). Habitat-based predictions of blue whale (*Balaenoptera musculus*) distribution, for example, were translated into the WhaleWatch system, a dynamic management tool developed to forecast whale density in the California Current and support efforts to reduce ship-strike risk around shipping lanes (Hazen et al., 2017).

Overall, these examples highlight that cetacean ecology is fundamentally dynamic, and that conservation measures based solely on static patterns of occurrence may fail to capture the full ecological importance of habitats and their connections. Understanding how habitat use, movement, and connectivity vary through time is therefore central to both ecological interpretation and effective management.

Insular regions may be particularly informative for understanding the dynamic ecology of highly mobile cetaceans, as their distinctive topography and oceanography provide an important setting for investigating how habitat use, residency, and movement pathways interact across spatial and temporal scales. In this context, the work presented in this thesis was conducted in Macaronesia, an insular region of the eastern North Atlantic.

1.3 Insular environments – Macaronesia

The Macaronesia biogeographic region is a group of volcanic archipelagos in the eastern North Atlantic that has traditionally included the Azores, Madeira, the Canary Islands and Cabo Verde (Sjögren, 2000). However, in the marine context, that definition has been increasingly

reconsidered, because the northern archipelagos are temperate to subtropical and interconnected by oceanographic processes, whereas Cabo Verde has a more tropical ecological affinity and distinct marine biogeographic relationships (Freitas et al., 2019). In this thesis, the definition of Macaronesia follows the proposal of Spalding et al. (2007), which groups Madeira, the Azores, Selvagens and the Canary Islands as a single ecoregion (Ferreira et al., 2022; Sousa et al., 2021) (Figure 1.2). The Webbnesia ecoregion, as proposed by Freitas et al. (2019), leaves out the Azores.

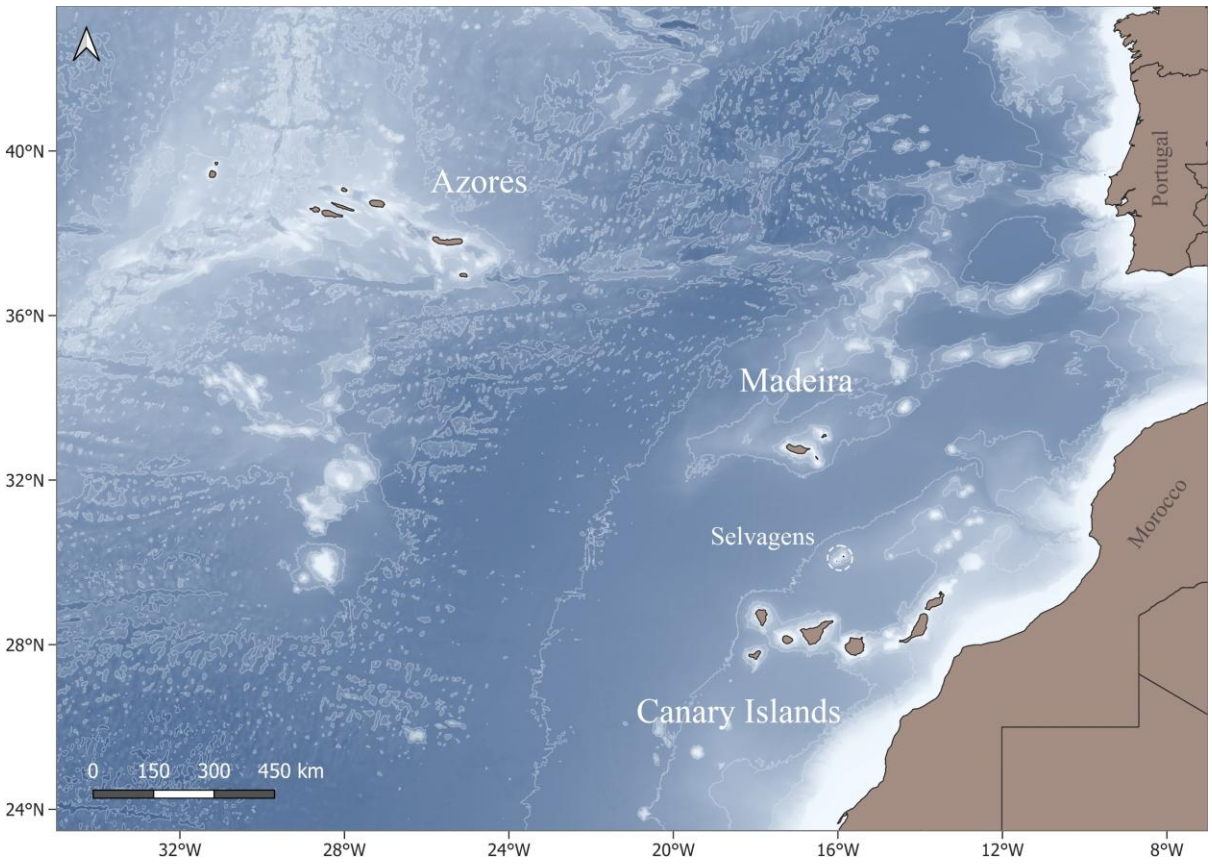

Figure 1.2: The Macaronesia region, located in the eastern North Atlantic. In the context of this thesis, Macaronesia encompasses Madeira (including Selvagens), the Canary Islands, and the Azores.

Macaronesia is largely influenced by the wind-driven North Atlantic subtropical gyre (Frazão et al., 2022). Within this system, the Azores constitutes the most remote oceanic archipelago in the North Atlantic and represents a mid-Atlantic biogeographic crossroad linking the eastern and western Atlantic margins (Afonso et al., 2020). The archipelago consists of nine volcanic islands and is oceanographically influenced by the Azores Current-Azores Front system, which forms the northeastern boundary of the subtropical gyre and separates cooler, more productive temperate waters to the north from warmer, more oligotrophic subtropical waters to the south (Frazão et al., 2022). At a more regional scale, the Azores are also under the persistent influence

of the Azores High, which promotes Ekman transport and contributes to the convergence of mesoscale features around the archipelago. In this setting, the western and central island groups are more strongly affected by Gulf Stream-derived meanders and filaments, whereas the eastern island group is more influenced by westward-propagating eddies pinching off from the Azores Current (Caldeira and Reis, 2017).

The Azores Current continues eastward towards Madeira and the Canary Islands, which form the eastern boundary region of the North Atlantic subtropical gyre. The Azores Current flows north of Madeira, and a branch enters the Canary Basin and feeds the Canary Current (New et al., 2001). The interaction with persistent northeasterly trade winds and steep island topography generates a pronounced "island mass effect" around Madeira (which consists of one main island and two sub-archipelagos). This is expressed through warm leeward wakes, frontal structures, eddies, and localized vertical motions (Caldeira et al., 2002; Caldeira and Sangrà, 2012), with the area between Madeira and the Desertas Islands described as particularly dynamic with localized upwelling. The broader thermal response around Madeira is asymmetric, with cyclonic anomalies and associated upwelling near the west flank and anticyclonic anomalies, downwelling, and a deeper mixed layer near the east flank (Alves et al., 2021), highlighting the region's dynamic nature at different scales. Within the Canary Islands, which are comprised of eight islands, the western side is characterized by deep, relatively sheltered coastal waters where circulation and retention processes may enhance productivity and prey availability near shore (Arístegui et al., 1997; Hernández-León et al., 2007). By contrast, the eastern islands have wider continental shelves and more exposed waters, possibly reducing prey predictability (Servidio et al., 2019). The Canary Islands are also influenced by nutrient-rich filaments originating from the Northwestern African upwelling system, which reach the archipelago and transport food sources for marine mammals (Landeira et al., 2017).

Together, this shows that Macaronesia is not a collection of isolated islands, but a physically structured oceanic region where the convergence of oceanographic currents and atmospheric processes create a highly dynamic environment. In ecological terms, these processes create a heterogeneous oceanographic and topographic setting in which prey fields are patchy and temporally variable, and where the distribution of top predators is therefore expected to be structured.

Macaronesia supports remarkably high cetacean diversity, with up to 30 recorded species (Afonso et al., 2020; Cartagena-Matos et al., 2021; Freitas et al., 2012; Herrera et al., 2021), making these archipelagos among the most diverse regions for cetaceans in Europe. Beyond the taxonomic richness, the region provides valuable opportunities to investigate the dynamic ecology of cetaceans, including patterns of habitat use, movements, residency, connectivity, as well as social structure (Dinis et al., 2021; Ferreira et al., 2022; McIvor et al., 2022; Prieto et al., 2014). In particular, insular environments enable the study of offshore and deep-diving taxa through near-shore operations (e.g., whale-watching, scientific field excursions), as deep bathymetry and steep slopes are often found close to land (Geldmacher et al., 2000). Within this context, the next section introduces Atlantic Naisa short-finned pilot whales as the focal species for which dynamic ecological patterns are examined in an insular environment.

1.4 Atlantic Naisa short-finned pilot whales in Macaronesia

The short-finned pilot whale (*Globicephala macrorhynchus*) is an oceanic delphinid and one of the two currently recognized species in the genus *Globicephala*, together with the long-finned pilot whale (*G. melas*) (Olson, 2018). Genomic studies indicate that short-finned pilot whales comprise three major types (Figure 1.3), associated with distinct oceanic regions: The Atlantic Ocean (Atlantic Naisa) type, the western/central Pacific and Indian Ocean (Pacific Naisa) type, and the eastern Pacific and northern Japan (Shiho) type (Van Cise et al., 2019). Mitochondrial differentiation further suggests two putative subspecies separated by the East Pacific Barrier, although these entities have not yet been universally adopted in formal taxonomy and additional sampling is still needed to resolve the species' taxonomic delimitation fully (Van Cise et al., 2019). In the North Atlantic, short-finned pilot whales belong to the Atlantic Ocean or Atlantic Naisa type. In this basin, their distribution partially overlaps that of long-finned pilot whales, and recurrent hybridization between the two species has been documented in the northeast Atlantic (Miralles et al., 2013, 2016).

Globally, the species is distributed throughout tropical and warm-temperate waters, covering a broad circumglobal belt (Betty et al., 2023; Paula A. Olson, 2009; Oremus et al., 2009). More generally, short-finned pilot whales are closely associated with shelf breaks, continental slopes, submarine canyons, and other areas where topography may enhance prey accessibility (Thorne et al., 2017; Wells et al., 2013). In the eastern North Atlantic, the species is especially common in Macaronesia, particularly around Madeira and the Canary Islands (Alves et al., 2019; Servidio et al., 2019).

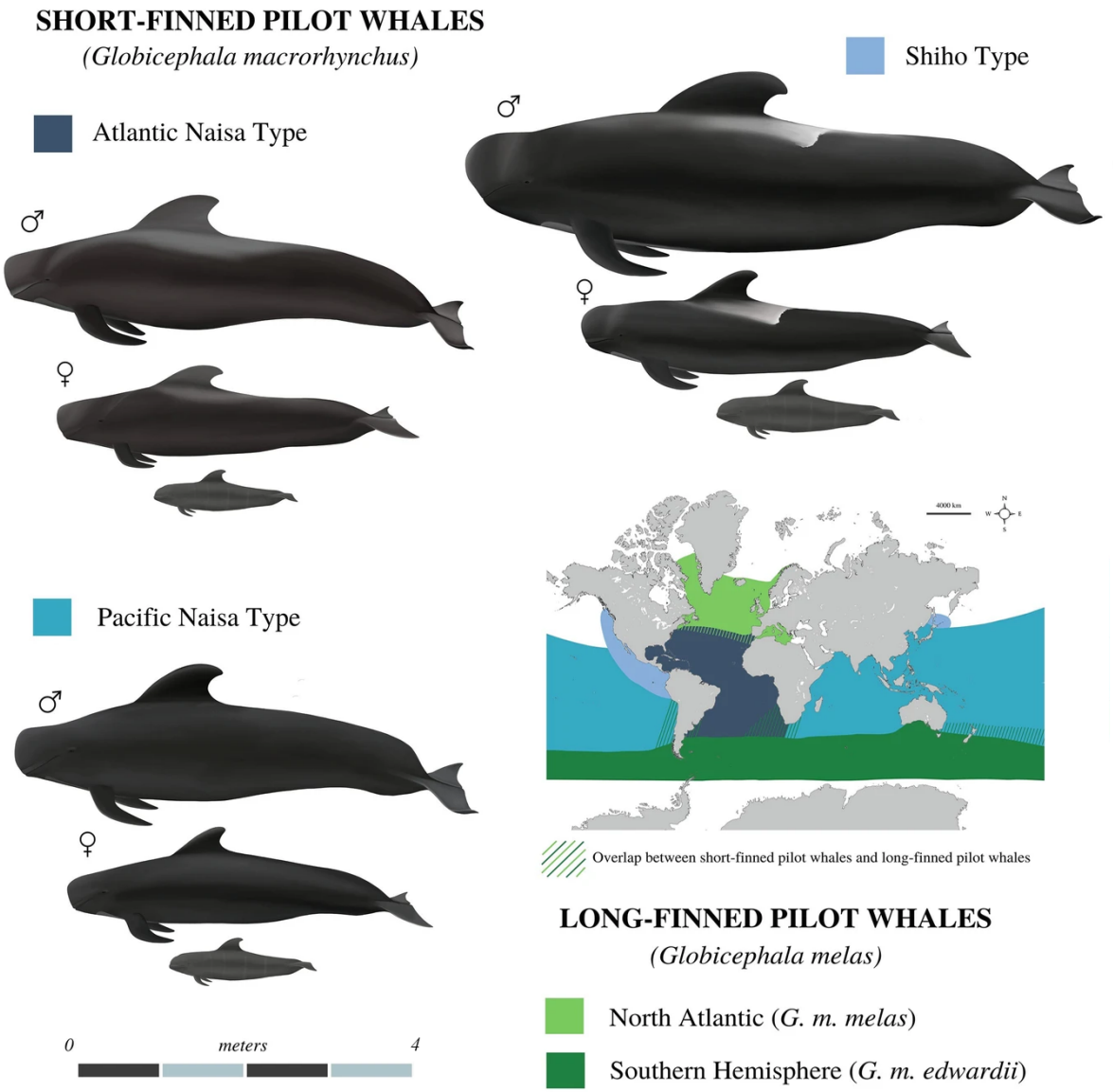

Figure 1.3: Global short-finned pilot whale (*G. macrorhynchus*) types, showing sexually dimorphic characteristics. Long-finned pilot whale (*Globicephala melas*) subspecies mentioned with the global distribution of both species provided in the map (bottom right). Original illustration by Emma Luck. **Image: Adapted from Betty et al.** (2023).

Within Macaronesia, the distribution of short-finned pilot whales is not uniform. Instead, occurrence is patchy and appears to track local bathymetry and other features likely to influence prey aggregation and habitat use (Fernandez et al., 2021; Servidio et al., 2019). In the Canary Islands, the species has been reported year-round, but with greater densities concentrated in patchy areas, mainly on the leeward side of the main islands (Servidio et al., 2019). Spatial modelling in the Canary Islands has further indicated habitat preferences in waters around 1,000–1,500 m depth, with higher densities between Tenerife and La Gomera, a region long recognized as particularly important for this species (Servidio et al., 2019). Around Madeira,

multiple studies similarly indicate that short-finned pilot whale occurrence is spatially (and temporally) structured rather than uniform. Long-term photo-identification and abundance studies have shown regular use of the southern and eastern waters, which was supported by fine-scale habitat modelling revealing highly suitable areas particularly in the southeast, with depth and slope among the main environmental predictors of suitability (Alves et al., 2015; Fernandez et al., 2021; Freitas et al., 2026). Additionally, a preference was detected for warmer waters (18-24ºC) and low Chl-a values. In the Azores, short-finned pilot whales were mainly found in waters deeper than 1000m, with a higher sighting rate in Summer, though fine-scale spatial and oceanographic descriptions are limited in this region (Gonzalez Garcia, 2019; Negulescu, 2020; Silva et al., 2014; Tobeña et al., 2016). Overall, it has been suggested that the species uses these preferred areas for vital functions such as resting, feeding, breeding and calving.

Within Macaronesia, short-finned pilot whales display complex movement patterns that extend beyond a single island. Comparing long-term photo-identification catalogues across the Azores, Madeira and the Canary Islands, Alves et al. (2019) documented inter-archipelago movements (between Madeira and both the Azores and the Canary Islands) and estimated heterogeneous transition probabilities within and between areas, supporting the interpretation of an ecological connectivity network across the region (Figure 1.4). In addition, differences in residency times among archipelagos suggest that these areas may not play equivalent ecological roles and are consistent with a spatially structured system that nonetheless remains connected through seasonal inflows from more offshore waters (Alves et al., 2019; Servidio et al., 2019).

Animals with different residency patterns have been identified in Macaronesia, although the terminology and criteria used to describe them differ slightly among archipelagos. In Madeira, Alves et al. (2013b) reported marked variability in site fidelity and distinguished residents (captured ≥5 times in at least 3 years and 3 seasons, i.e. spring, summer, autumn and winter), transients (sighted only once), and visitors (individuals that fell between these thresholds). Later work in the same archipelago focused more specifically on “core resident” animals (Esteban et al., 2022). In the Canary Islands, Servidio et al. (2019) applied a more detailed classification comprising core residents, residents, occasional individuals, and transients. Although these categories are not directly equivalent among studies, the broader conclusion is consistent: short-finned pilot whales in Macaronesia are not ecologically uniform but differ

substantially in the degree and duration of repeated area use (Alves et al., 2013b, 2019; Esteban et al., 2022; Servidio et al., 2019).

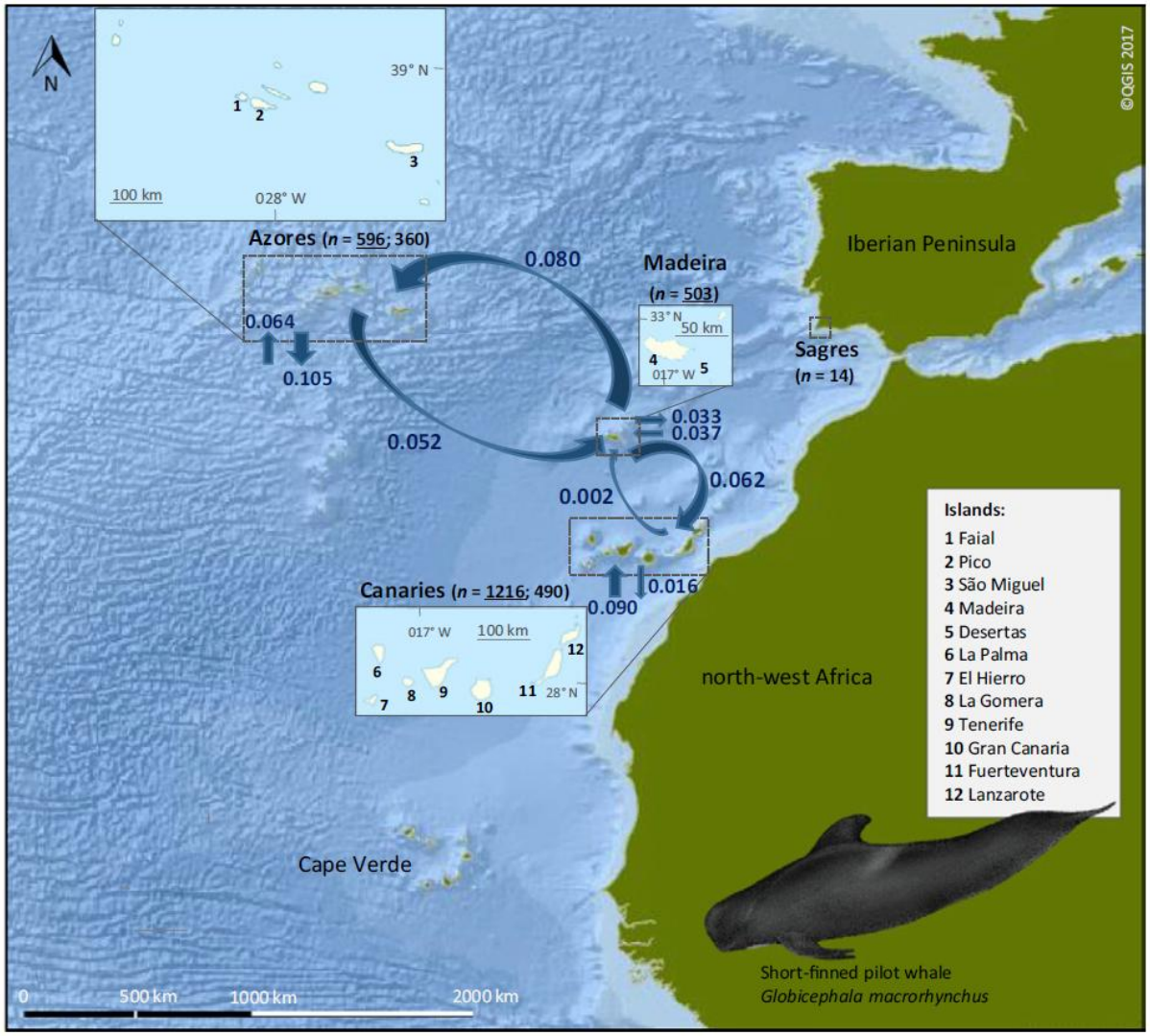

Figure 1.4: Study area showing the four regions (Azores, Madeira, the Canary Islands and Sagres) from which photographic and sighting data of short-finned pilot whales were obtained. The n (underlined) indicates the number of well-marked catalogued individuals used to estimate residency and transition probabilities, while the nonunderlined indicates the number of additional well-marked whales used to help analyze movement patterns. The arrow width and values illustrate heterogeneous transition probabilities. No matches were found between Sagres and any other area. **Image: Alves et al. (2019)**.

Macaronesian short-finned pilot whales are strongly socially structured (Alves et al., 2013b; Boran and Heimlich, 2019; Esteban et al., 2022; Heimlich-Boran, 1993; Servidio, 2014). Off Madeira, it is suggested that island-associated whales form several matrilineal groups, with an estimated mean group size of about 15 individuals, and genetic relatedness has been shown to be higher within groups than between groups (Alves et al., 2013b). Long-term photo-

identification analyses showed that social clusters are formed by preferred companions, that individuals maintain stable cluster membership over long time spans, and that clusters have highly overlapping distribution areas, indicating that social preferences rather than simple spatial segregation play a key role in structuring this population (Alves et al., 2013b; Esteban et al., 2022). It is suggested that males reproduce when groups meet and mix, then return to their social unit, reinforcing the view that movement, sociality, and dispersal are tightly linked. However, sex-resolved social and genetic analyses would be required to better understand the species' sex-specific social structure. Dedicated social analyses are also available for the Canary Islands, particularly off Tenerife, where long-term association patterns and hierarchical social structuring have been described (Heimlich-Boran, 1993; Servidio, 2014). Comparable work from the Azores remains limited (Negulescu et al., 2020). Nevertheless, the detection of a resident social unit in Madeira travelling towards the Azores and back to Madeira indicates that short-finned pilot whales maintain long-term relationships over hundreds of kilometers (Alves et al., 2018a).

Short-finned pilot whales in the Macaronesia region are thought to mainly feed on cephalopods, however, data regarding the diet of the species in the region is sparse (Aguilar de Soto and Alves, 2023; Fernández et al., 2009; Hernández-García and Martín, 1994; Luna et al., 2024). Tagging studies with biologgers off Tenerife and Madeira show that the species forages at considerable depth, with dives approaching or exceeding 1,000 m (Aguilar de Soto et al., 2008; Alves et al., 2013a). Recent work in Webbnesia suggests that trophic ecology is not uniform across archipelagos. Stable-isotope analyses identified significant differences between Tenerife and Madeira in trophic niche and inferred foraging habitat, with Tenerife whales suggesting prey from higher trophic levels and greater prey diversity, and Madeira whales indicating reliance on prey from more diverse habitats; overall, the results were consistent with an important benthic or benthopelagic component in the region (Escánez et al., 2024). Complementing this, blubber fatty-acid profiles indicated partially distinct trophic niches between highly island-associated whales from both archipelagos. Animals from Madeira showed a more pelagic dietary signature, and individuals from southwest Tenerife appeared to forage closer to the seafloor within a more restricted feeding area, while less island-linked individuals may forage across both archipelagos or wider areas (Íñiguez et al., 2025b). Together, these studies suggest that prey use and inferred foraging habitat vary within Macaronesia, which may help explain heterogeneity in site fidelity and space use across the region. Finally, it has been observed that social calls are produced during deep foraging dives,

indicating that social coordination remains relevant for Macaronesian short-finned pilot whales, even during subsurface feeding (Jensen et al., 2011).

Overall, current understanding of short-finned pilot whale dynamic ecology in Macaronesia is derived largely from nearshore effort, particularly photographic-identification and occurrence datasets (Alves et al., 2013b; Freitas et al., 2026; Servidio et al., 2019; Silva et al., 2014). Although such data can provide valuable insights into seasonal occurrence and site-fidelity patterns within surveyed areas (Alves et al., 2013b; Alves et al., 2015; Servidio et al., 2019), they often offer limited inference on the behavioral processes underlying recurrent habitat use and on the environmental conditions associated with these behaviors. In addition, while photo-identification can reveal inter-archipelago movements (Alves et al., 2018a, 2019), it provides only limited information on space use in offshore pelagic regions away from land, where animals may use recurrent movement pathways, or exploit offshore prey fields associated with bathymetric features such as seamounts. Addressing these limitations requires complementary approaches such as biotelemetry, which has so far only been used sparsely in the region (Aguilar de Soto et al., 2008; Alves et al., 2013a).

From a conservation perspective, short-finned pilot whales are currently classified by the IUCN (International Union for Conservation of Nature) as Least Concern, both at the global and European level (Gauffier et al., 2023; Minton et al., 2018), but this should not be interpreted as the absence of regionally relevant pressures. In Macaronesia, the best documented threats are vessel related. In the Canary Islands, short-finned pilot whales have been recorded among cetaceans killed by vessel collisions (Carrillo, 2010). Studies off Tenerife also showed that whale-watching vessel noise can reduce resting and nursing behavior in short-finned pilot whales, particularly in mother–calf pairs, and subsequent work further indicated that behavioral responses depend on vessel source level and cumulative underwater noise (Arranz et al., 2021, 2024). Around Madeira, long-term analyses revealed substantial and spatially uneven exposure of island-associated pilot whales to whale-watching activity (Figure 1.5) (Sambolino et al., 2022). Climate change represents an additional concern, as a trait-based assessment ranked the archipelago-associated units in Madeira and the Canary Islands among the most climate-vulnerable cetacean units in Macaronesia (Sousa et al., 2021). Emerging contaminants are also increasingly being documented, including phthalates and organic UV filters detected in pilot whale blubber off Madeira (Íñiguez et al., 2025a; Sambolino et al., 2024). Taken together, these findings suggest that, despite the current global status, Atlantic Naisa short-finned pilot whales in Macaronesia may be sensitive to cumulative, region-specific pressures and therefore merit

continued monitoring and precautionary regional management. This also has relevance for the broader ecosystem, as conservation efforts targeting marine megafauna also often benefit lower trophic levels (Hooker and Gerber, 2004).

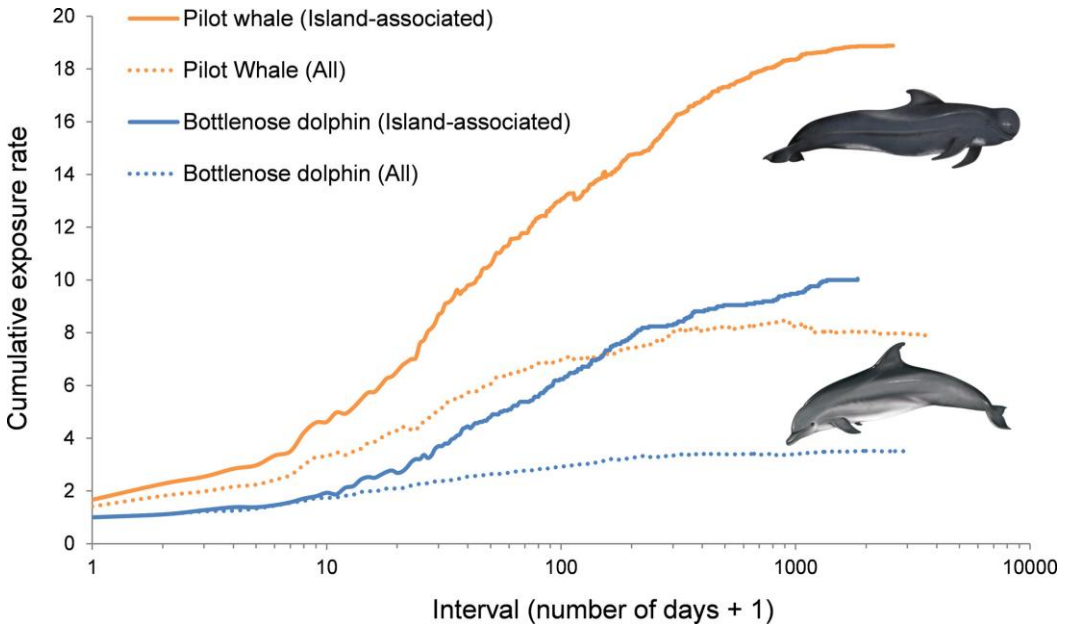

Figure 1.5: Cumulative exposure rates of individual bottlenose dolphins (*Tursiops truncatus*) and pilot whales (*Globicephala macrorhynchus*) to whale-watching boats off the south coast of Madeira Island. Rates represent the ratio of recaptures to recaptured individuals within each interval across the study period (2003–2016). Increasing the interval time increases the number of recaptures per individuals if the same individuals keep coming back to the study area. Comparison between all the individuals and the island-associated ones is shown. X–axis is log-scaled. Illustrations by E. Berninsone. ©ARDITI. **Image: Sambolino et al. (2022)**

Taken together, the available literature shows that Atlantic Naisa short-finned pilot whales in Macaronesia are characterized by complex ecological patterns across multiple spatial and temporal scales. This body of work provides an important foundation for understanding the species in the region, while also highlighting that several aspects of its dynamic ecology, relevant for conservation and management purposes, remain incompletely resolved.

1.5 Aims and structure of the thesis

The present thesis aims to advance the understanding of the dynamic ecology of Atlantic Naisa short-finned pilot whales in insular habitats, with Macaronesia as a case study, across different spatial and temporal scales, by addressing critical gaps and adding valuable information to

existing knowledge through integrated approaches and both classical and state-of-the-art methodologies.

The first chapter (**Chapter 1**) provides a general introduction to the main themes of this research (dynamic ecology and insular environments) and provides background information regarding the focal species in the broader study region (short-finned pilot whales in Macaronesia). It provides the foundation upon which the aims and research presented in the following chapters are built.

The subsequent chapters (**Chapters 2-5**) consist of research studies and focus on:

i) Assessing spatial connectivity and habitat use of short-finned pilot whales within the Macaronesia region, specifically between Madeira and the Canary Islands. By combining satellite telemetry data with photographic-identification, key areas of use and movement pathways between archipelagos are assessed, contributing to the identification of biologically important blue corridors and providing information relevant to the conservation planning of a highly mobile pelagic species. (**Chapter 2**). This chapter is already published in a peer-reviewed journal (detailed at the beginning of Chapter 2).

ii) Examining the spatial and temporal dynamics of short-finned pilot whales with particular attention to island-associated habitat use and site fidelity. Using biotelemetry and ecological modelling, the study aims to assess behavioral states, residency range behavior, and environmental drivers shaping movement strategies around Madeira (**Chapter 3**). This chapter is currently submitted to a peer-reviewed journal (detailed at the beginning of Chapter 3).

iii) Investigating potential large-scale basin-wide movements in the North Atlantic by using long-term photo-identification data through manual and algorithm-based comparison to evaluate potential connectivity between eastern and western North Atlantic regions (**Chapter 4**).

iv) Exploring ecological dynamics expressed through social organization and temporal association patterns, which underpin spatial residency, connectivity, and dispersal in insular systems. It focuses on examining sex-specific social structure, within- and between-cluster associations, and the temporal stability of social relationships in Atlantic Naisa short-finned pilot whales, using long-term photographic-identification data from genetically sexed individuals (**Chapter 5**). This chapter is currently submitted to a peer-reviewed journal (detailed at the beginning of Chapter 5).

Finally, **Chapter 6** provides a general discussion and synthesis of the main findings across the thesis. The chapter also discusses implications for conservation and management, highlights methodological strengths and limitations, and identifies priorities for future research.

1.6 Related Scientific Publications co-authored during the PhD

Peer-reviewed journal articles

Escánez, A., Marrero-Pérez, J., Dromby, M., Pimentel-González, A., Dias, E., García-Pastor, E.M., **Weyn, M.**, Ferreira, R., Montañés-Pérez, A., Fernandez, M., Dinis, A., Alves, F., 2024. Isotope-based inferences of the trophic niche of short-finned pilot whales in the Webbnesia. Mar. Environ. Res. 201, 106700. https://doi.org/10.1016/j.marenvres.2024.106700

Sambolino, A., Alves, F., Rodriguez, M., **Weyn, M.**, Ferreira, R., Correia, A.M., Rosso, M., Kaufmann, M., Cordeiro, N., Dinis, A., 2024. Phthalates and fatty acid markers in free-ranging cetaceans from an insular oceanic region: Ecological niches as drivers of contamination. Environ. Pollut. 360, 124693. https://doi.org/10.1016/j.envpol.2024.124693

Íñiguez, E., Sambolino, A., Escánez Pérez, A., Marrero Pérez, J., Reis, D.B., Pimentel, A., **Weyn, M.**, Fernandez, M., Cordeiro, N., Pérez Pérez, J.A., Dinis, A., Rodríguez González, C., Alves, F., 2025. Intraspecific variation in the feeding habits of short-finned pilot whales based on blubber fatty acid profiles. Mar. Environ. Res. 204, 106974. https://doi.org/10.1016/j.marenvres.2025.106974

Peer-reviewed book chapters

Betty, E.L., Zwamborn, E.M.J., **Weyn, M.**, Luck, E., Alves, F., 2023. Life history parameters, sociobiology, and reproductive strategies of pilot whales, in: Würsig, B., Orbach, D.N. (Eds.), Sex in Cetaceans: Morphology, Behavior, and the Evolution of Sexual Strategies. Springer, Cham, pp. 327–351. https://doi.org/10.1007/978-3-031-35651-3_15

Communications at international conferences

Alves, F., Rosso, M., Ferreira, R., Sambolino, A., Correia, A.M., **Weyn, M.**, Fernandez, M., Dinis, A., (2021, 18-22 October). Short-finned pilot whales movements in the Eastern North Atlantic: preliminary insights from satellite biologgers. [Poster communication]. 7th Biologging Conference, Honolulu, Hawaii.

Alves, F., Ferreira, R., Sambolino, A., **Weyn, M.**, McIvor, A., Steiner, L., Sanchez, A., Hartman, K., Marrero-Pérez, J., Fusar, F., Martín, V., Aguilar de Soto, N., Fernandez, M., Dinis, A., (2022, 5-7 April). Connectivity patterns of cetaceans in the oceanic islands system of Macaronesia inferred from photo-ID and biotelemetry: How much do we know? [Oral communication]. 33th European Cetacean Society Conference, Ashdod, Israel (Online)

Weyn, M., Sanchez, A., Gonzalez-Pimentel, A., Marrero-Pérez, J., Ferreira, R., Sambolino, A., Dinis, A., Mateus, C., Fernandez, M., Alves, F., (2022, 5-7 April). A potential inter-archipelago biological corridor for short-finned pilot whales in Macaronesia, using photo-identification and satellite-linked biologgers. [Poster communication]. 33th European Cetacean Society Conference, Ashdod, Israel (Online)

Alves, F., **Weyn, M.**, Ferreira, R., Sambolino, A., Badenas, A., Correia, A.M., Gil, A., Valente, R., Mora, A., Fernandez, M., Rosso, A., Sousa-Pinto, I., Dinis, A., (2022, 1-5 August). Habitat-specific use by short-finned pilot whales in Macaronesia revealed through satellite-linked biologgers. [Poster communication]. 24th Biennial Conference on the Biology of Marine Mammals, Palm Beach, Florida.

Sambolino, A., Dinis, A., **Weyn, M.**, Ferreira, R., Valente, R., Gil, A., Correia, A.M., Rosso, M., Sousa Pinto, I., Alves, F., Kaufmann, M., Cordeiro, N., (2022, 5-7 April). Fatty acids composition in blubber tissue of two Odontocete species (*Tursiops truncatus* and *Globicephala macrorhynchus*) in NE Atlantic. [Poster communication]. 33th European Cetacean Society Conference, Ashdod, Israel (Online)

Weyn, M., Fernandez, M., Ferreira, R., Mateus, C., Alves, F., (2023, 18-20 April). Stability and fluidity of short-finned pilot whale social groups of known sex off Madeira Island. [Poster communication]. 34th European Cetacean Society Conference, O Grove, Spain.

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Fernandez, M., **Weyn, M.** & Alves, F., (2024, 15-19 July). Evaluating residency patterns of short-finned pilot whales using integrated step selection analysis [Poster communication]. ISEC2024 International Statistical Ecology Conference, Swansea, Wales.

Sambolino, A., Alves, F., Rodriguez, M., **Weyn, M.**, Ferreira, R., Correia, A.M., Rosso, M., Kaufmann, M., Cordeiro, N. & Dinis, A. (2024, 5-9 May). Unveiling Contaminant Exposure Patterns in Cetaceans from Madeira Island: Insights into Phthalates and Fatty Acid Markers [Poster communication]. SETAC - Society of Environmental Toxicology and Chemistry - Europe 34th Annual Meeting, Sevila, Spain.

Weyn, M., Mora, A.S., Pimentel-Gonzalez, A., Marrero-Pérez, J., Ferreira, R., Sambolino, A., Dinis, A., Mateus, C., Fernandez, M. & Alves, F. (2024, 8-12 April). Integrating satellite tracking and photographic-identification to understand connectivity between Madeira and the Canary Islands and support conservation planning [Poster communication]. 35th European Cetacean Society Conference, Catania, Italy.

Alves, F., Marrero-Pérez, J., Sambolino, A., Hartman, K., van der Harst, P., Ferreira, R., Pimentel-González, A., Iñiguez, E., **Weyn, M.**, Escánez, A., Dinis, A., & Fernandez, M. (2025, May 12-16). Body condition, movements and trophic ecology of short-finned pilot whales (*Globicephala macrorhynchus*) in Macaronesia [Oral communication]. Workshop "Pilot whales (*Globicephala* spp.) in the North Atlantic: review of current knowledge, research gaps, and potential to create a North Atlantic pilot whale research network", 36th European Cetacean Society Conference, São Miguel, Azores.

Alves, R., Alessandrini, A., **Weyn, M.**, Ferreira, R., Fernandez, M., Alves, F., Olio, M., & Cheeseman, T. (2025, May 12-16). Evaluating false-negative detection in dorsal fin catalogues using Happywhale's photo-identification algorithm [Poster communication]. 36th European Cetacean Society Conference, São Miguel, Azores.

Fernandez, M., **Weyn, M.**, Ferreira, R., Rosso, M., Correia, M., Hartman, K., Van der Harst, P., Dinis, A., & Alves, F. (2025, May 12-16). From points to paths: discrete-continuous analysis of short-finned pilot whale residency and movements using satellite telemetry data [Poster communication]. 36th European Cetacean Society Conference, São Miguel, Azores.

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CHAPTER 2

SATELLITE TRACKING AND PHOTOGRAPHIC-IDENTIFICATION AS CONNECTIVITY-BASED TOOLS TOWARDS CONSERVATION PLANNING OF PILOT WHALES

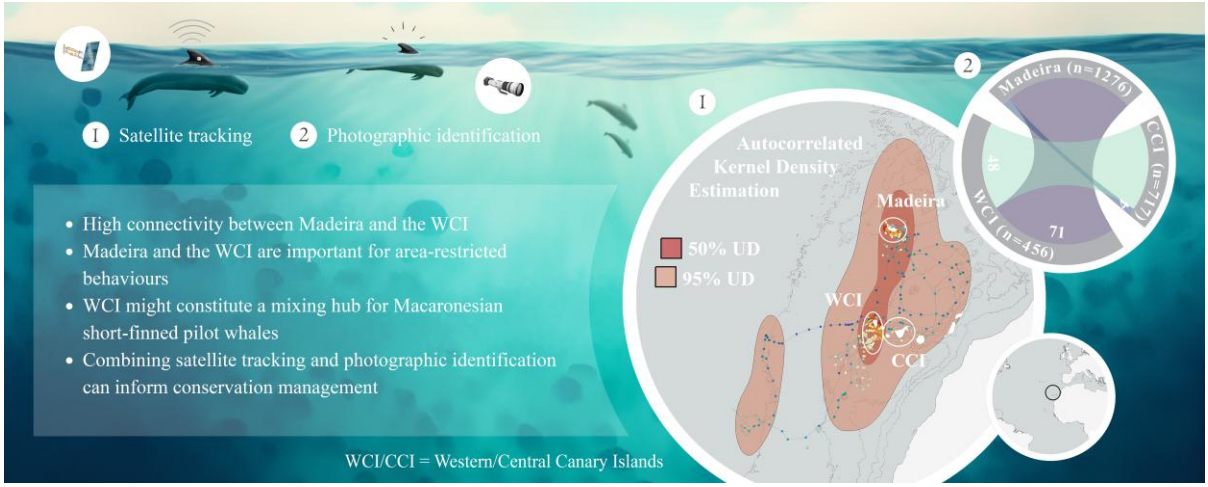

Figure 2.1: Graphical abstract of Chapter 2

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2.1 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 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 behaviors. 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.

2.2 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 et al. 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 et al. 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 & 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 et al. 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 transmits radio signals, from which the animal's location is subsequently estimated based on the Doppler shift. 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 et al. 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 (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 & 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 et al. 2010, Silva et al. 2014, Alves et al. 2018b). 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 multiyear 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 traveling 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 et al. 2018a). 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 behavior, continuous monitoring of movements and habitat use is paramount.

Conservation areas for cetaceans have been identified in Macaronesia by international conservation programs 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 & Heimlich 2019, Servidio et al. 2019, Fernandez et al. 2021, Esteban et al. 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 geo-strategically 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 multi-methodological and connectivity-based approach is expected to increase knowledge and advance conservation management of an iconic species and its surrounding elements.

2.3 Materials and Methods

2.3.1 Study area

This study covered two archipelagos of the Macaronesia biogeographical region - Madeira (Portugal) and the Canary Islands (Spain) (Figure 2.2) - 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 boundaries of the North Atlantic Gyre (Cropper 2013, Cardoso & 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 et al. 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 et al. 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 2.2), there is a non-uniform inter-island 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 exists for the western islands of La Palma and El Hierro (Servidio et al. 2019). This non-uniform inter-island 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 2.2).

2.3.2 SATELLITE TELEMETRY

Satellite-linked 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 program 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 CO2 dartgun was used for tag deployment during dedicated field trips, following all legal requirements and permits according to current legislation (see Ethical approval). Each tag is made up of an electronics unit and two 6.7 cm long medical-grade titanium darts, each with six backward-facing ‘barbs’, specially designed for cetaceans (Andrews et al. 2019). Pressure was adjusted according to deployment distance. 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 in two blocks daily (morning (6am to 1pm) and afternoon (6pm to 12 midnight)) during the first 55 days (location uplink limit of 25 per hour), once daily (8am to 12 midday) between 55-180 days, and every 2 days after 180 days (8am to 12 midday). 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 & 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 24h 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 rerouted 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 & Fieberg 2021, 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 behavior 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 & Calabrese 2022), are provided in Figure S2.2 and S2.3, respectively, in the Supplementary Material, to aid in interpreting the pooled data. Individual move persistence over time is provided in Figure S2.4 in the Supplementary Material. 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-linked tags. The former were collected using a biopsy darting system (Mathews et al. 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).

2.3.3 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 well-marked animals (i.e., distinctive individuals) from good quality images (following Alves et al. 2013) (Table S1 in Supplementary Material). These were grouped according to the number of notches in the trailing edge of the dorsal fin to facilitate comparison (Würsig & Jefferson 1990, Alves et al. 2019).

The catalogues of the Canary Islands were compiled by two sources (described in Table S2.1 in Supplementary Material). 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, totaling 838 well-marked animals (see Data availability), 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 (~13km) 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 et al. 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 et al. 2018b; 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 & 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., Robbins et al. 2011, Wilson et al. 1999) 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 visualisations were created in R Statistical Software v4.1.3 (Gu 2014, R Core Team 2022).

2.4 Results

2.4.1 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 2.1) and a combined total of 578 days, resulting in 3109 filtered locations. Tag locations are available in Figure S2.1 in the Supplementary Material. These four individuals moved to the Canary Islands, but their paths varied (Figure S2.2 in Supplementary Material). 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 km2 (with 95% isopleths: 108 687-148 119 km2) and 829 225 km2 (with 95% isopleths: 708 579-959 866 km2), respectively (Figure 2.2). 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 S2.2 in Supplementary Material) included Madeira in the 50% UD; 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 S2.3 in Supplementary Material) confirm the presence of range resident behaviors, 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.

Table 2.1: Summary information for the four short-finned pilot whales tagged in Madeira that moved to the Canary Islands. 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.

Tag ID	Sex	Residency Pattern	Deploy date	Tag Duration (days)
Tag1_Gma	F	Visitor (12 captures between 2009 and 2020 during summer-autumn)	28/09/2018	105
Tag7_Gma	F	Visitor (9 captures between 2010 and 2020 during summer-autumn)	09/11/2020	150
Tag14_Gma	-	Visitor (5 captures between 2017 and 2019 during spring-summer)	25/08/2021	175
Tag20_Gma	-	-	19/11/2021	148

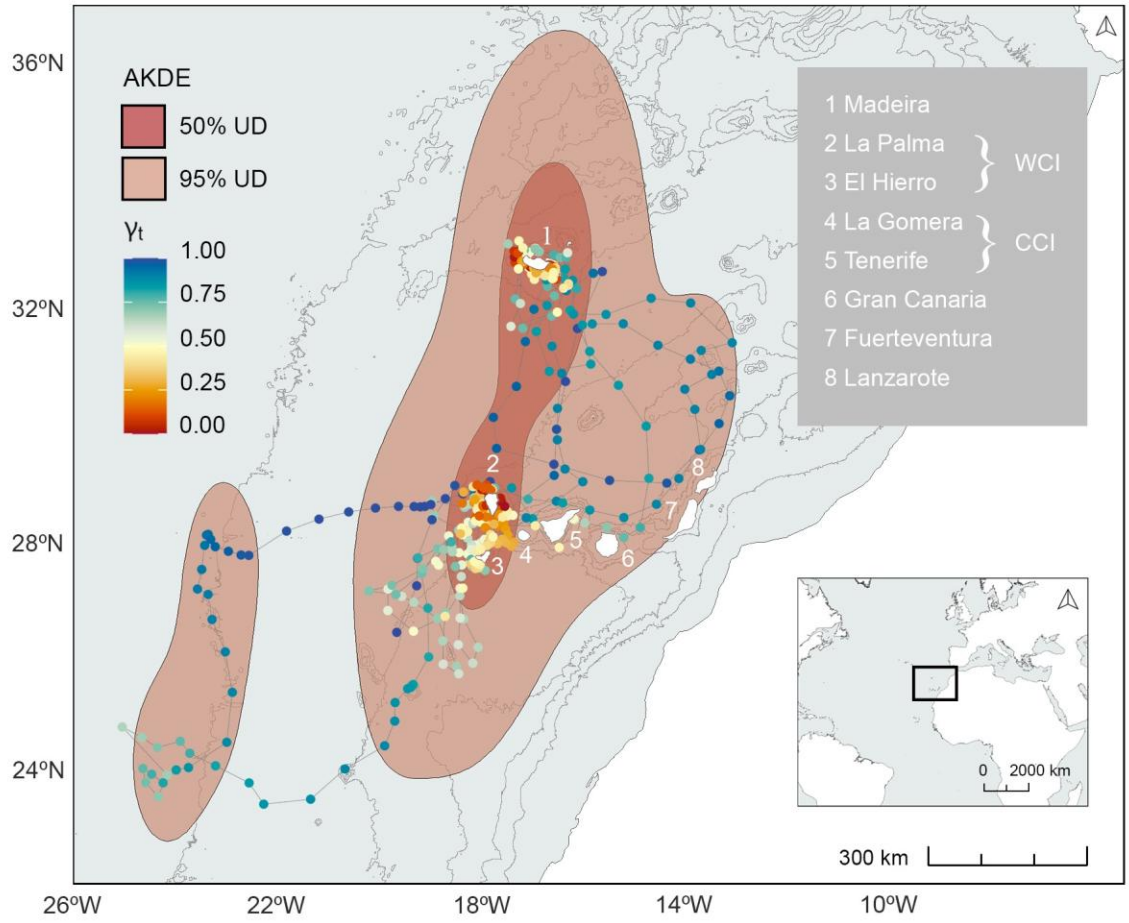

Figure 2.2: Satellite tracks, move persistence index (γ_t) and range estimates (Utilization distribution – UD) at 50% and 95% isopleths (from an Autocorrelated Kernel Density Estimation – AKDE) of four short-finned pilot whales tagged in Madeira between 2018 and 2021. Low move persistence values observed 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. 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 the Supplementary Material (Figures S2.2-S2.4).

Considering behavior, 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 2.2). Relatively low move persistence was further observed west and southwest of La Gomera, and one individual passed by the southern region 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 2.2). When looking into 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 S2.4 in the Supplementary Material), corresponding to the movements to offshore areas and to the Canary Islands (Figure S2.3 in Supplementary Material). Tag7_Gma displayed a short period with relatively high move persistence values (approximately half a month out of a total of five months), which corresponds with a more direct path taken to the Canary Islands. Intermediate values after reaching the Western Canary Islands 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 one month out of six months), while traveling offshore the Western Canary Islands, after which the tag stopped transmitting. Finally, Tag20_Gma spent approximately two months (out of a total of five 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 Western Canary Islands.

2.4.2 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 in Supplementary Material), 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 (6 males and 6 females) – indicating inter-regional 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 2.3). 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.

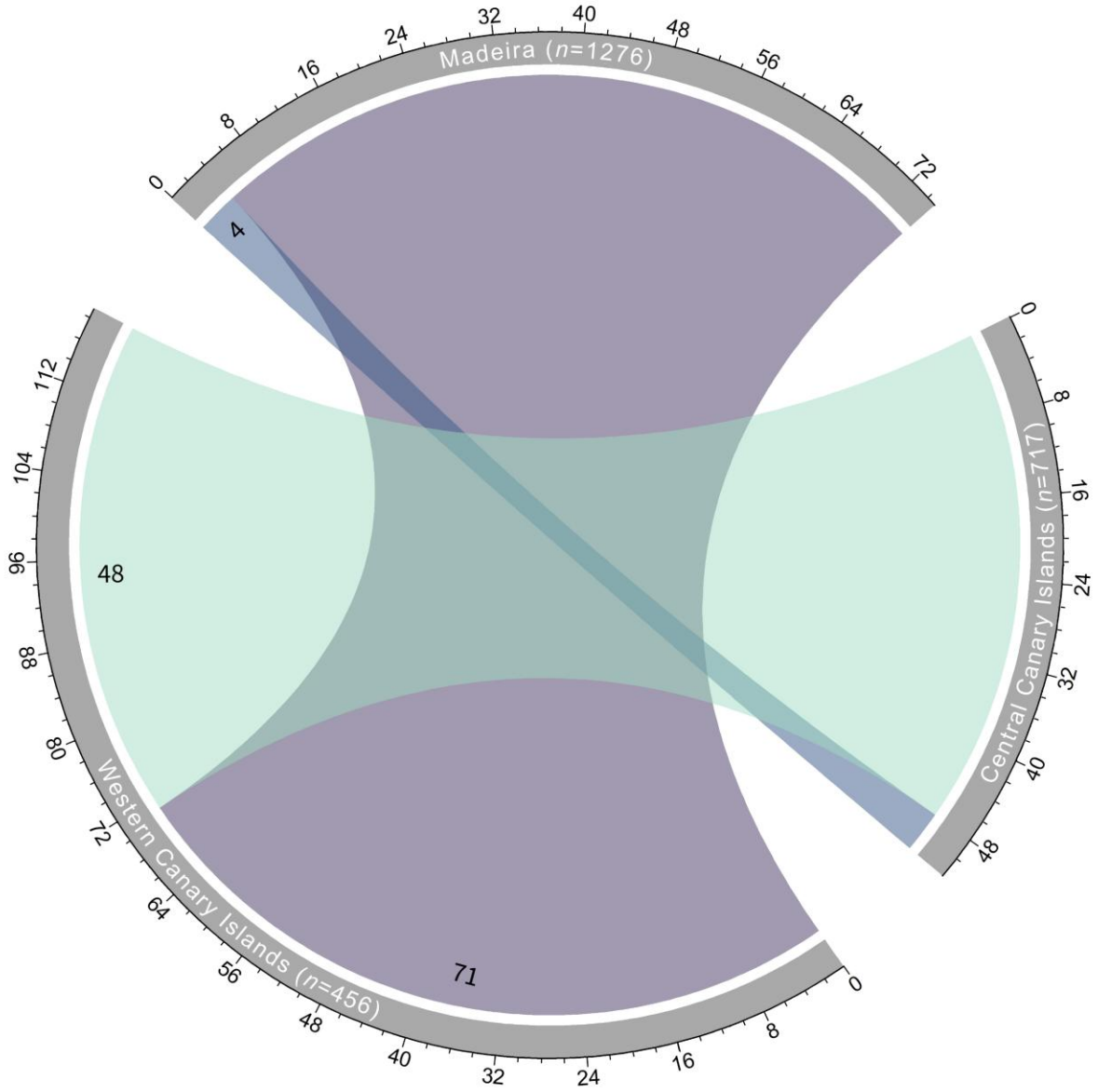

Figure 2.3: Number of individual photo-identification matches between the three studied regions: Madeira Island, the Western Canary Islands - WCI (La Palma and El Hierro), and the Central Canary Islands - CCI (Tenerife and La Gomera). Madeira and the WCI show a higher population linkage among them than with the CCI. The number of individuals in the catalogue used for the comparison in each region is mentioned between brackets.

2.5 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 behaviors, such as foraging, resting, or breeding (Kareiva & 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 behaviors 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 Western Canary Islands. 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 vs. for example around one 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 Western Canary Islands.

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 indicate 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, i.e. 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 1-2 ºC, occasionally 3 ºC) (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 & 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 emphasise 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 et al. 2018a). 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 et al. 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 is 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 inter-regional 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 optimise 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 et al. 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 & 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 behaviors 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.

2.6 Ethics and integrity statements

2.6.1 Data availability

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 http://doi.org/10.17632/rf9csj2tcz.1

2.6.2 Ethics and permit approval 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.

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2.8 Supplementary Materials

Table S 2.1: Summary of the photo-identification catalogues of short-finned pilot whales used for the comparison in the three covered regions in this study: the Madeira Island, the Western Canary Islands - WCI (La Palma (LP) and El Hierro (EH)), and the Central Canary Islands - CCI (Tenerife (TF) and La Gomera (LG)). Overlap between the catalogues of OceanExplorer and Tonina Association was taken into consideration in the total number for comparison.

Region	**Source**	**Island and period**	**Number of animals**	**Total number for comparison**
Madeira Island	MARE-ARDITI	Madeira: Jun. 2003 - Dec. 2020	1276	1276
Western Canary Islands	OceanExplorer	LP: Dec. 2019 - Sep. 2022	335	456
	Tonina Association	LP: Dec. 2019 - Feb. 2021 EH: Oct. 2014 - Oct. 2019	51 137	
Central Canary Islands	Tonina Association	TF and LG: Aug. 2014 - Sep. 2021	717	717

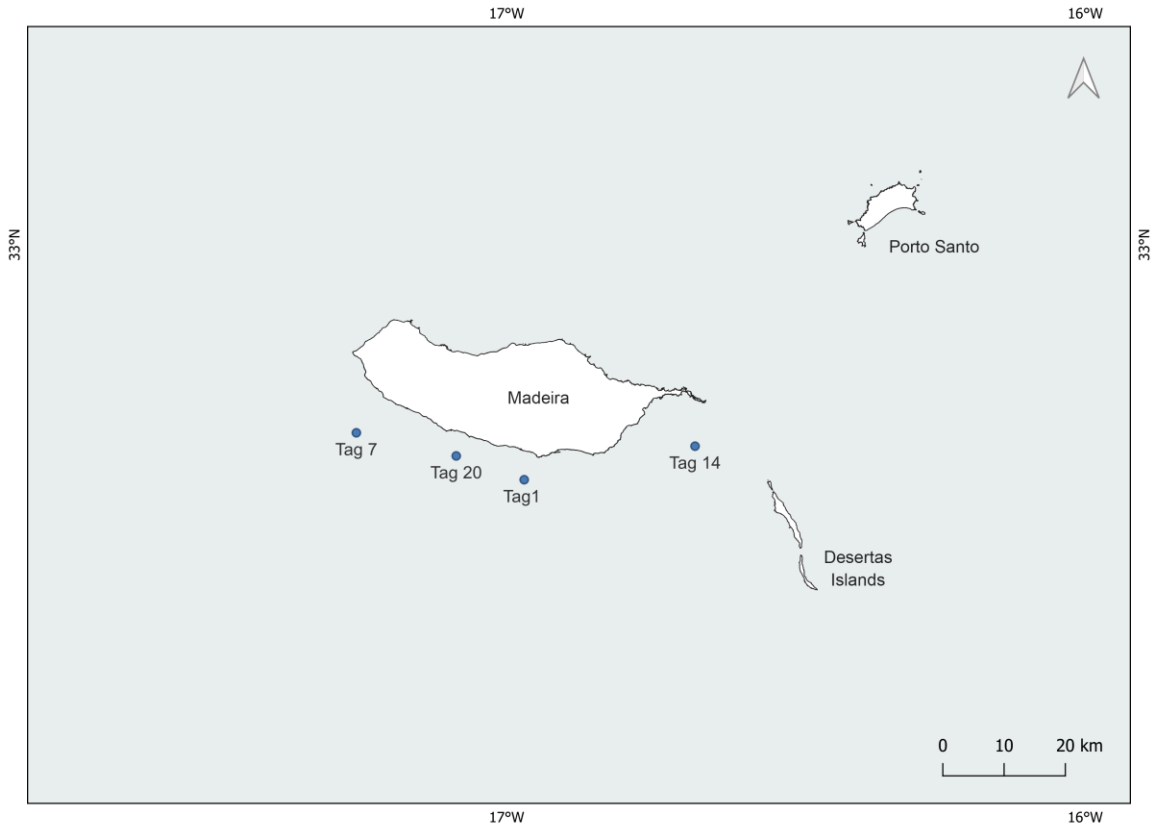


Figure S 2.1: Map showing the tag locations of four short-finned pilot whales tagged in Madeira between 2018 and 2021.

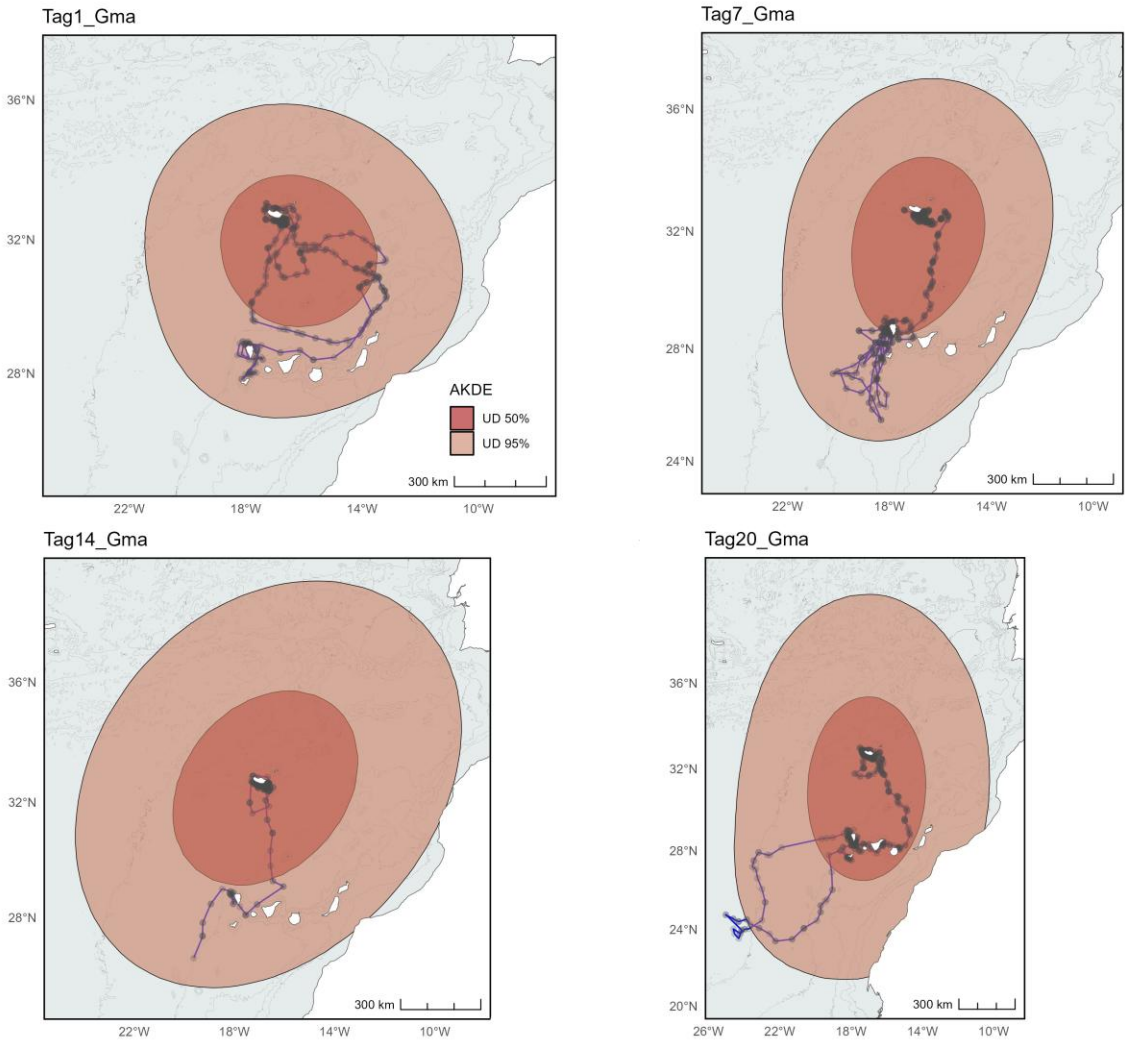
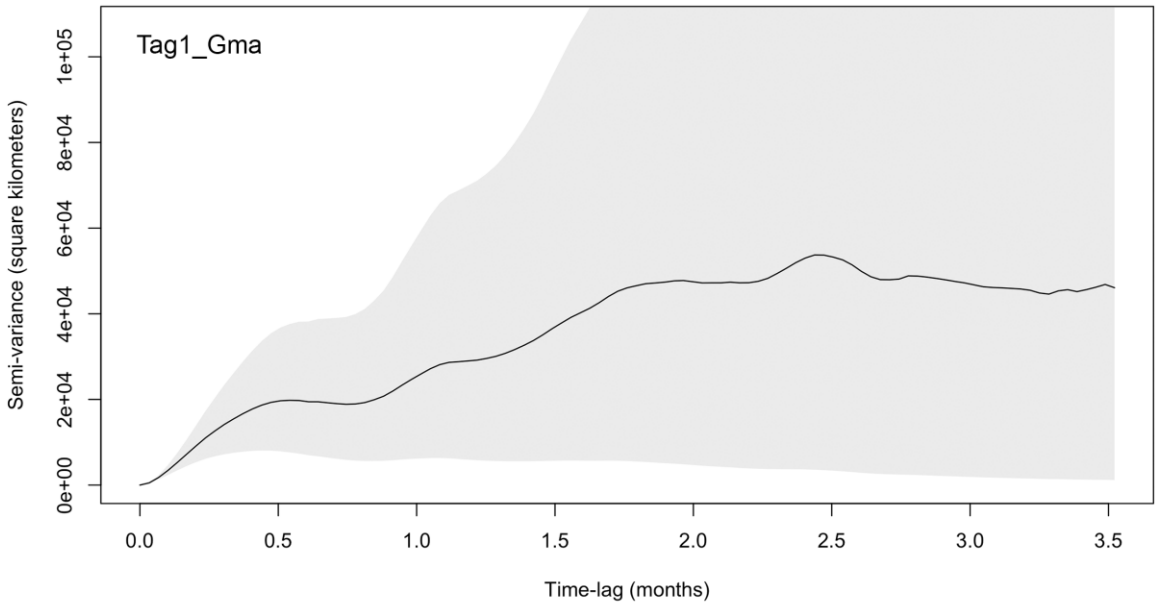
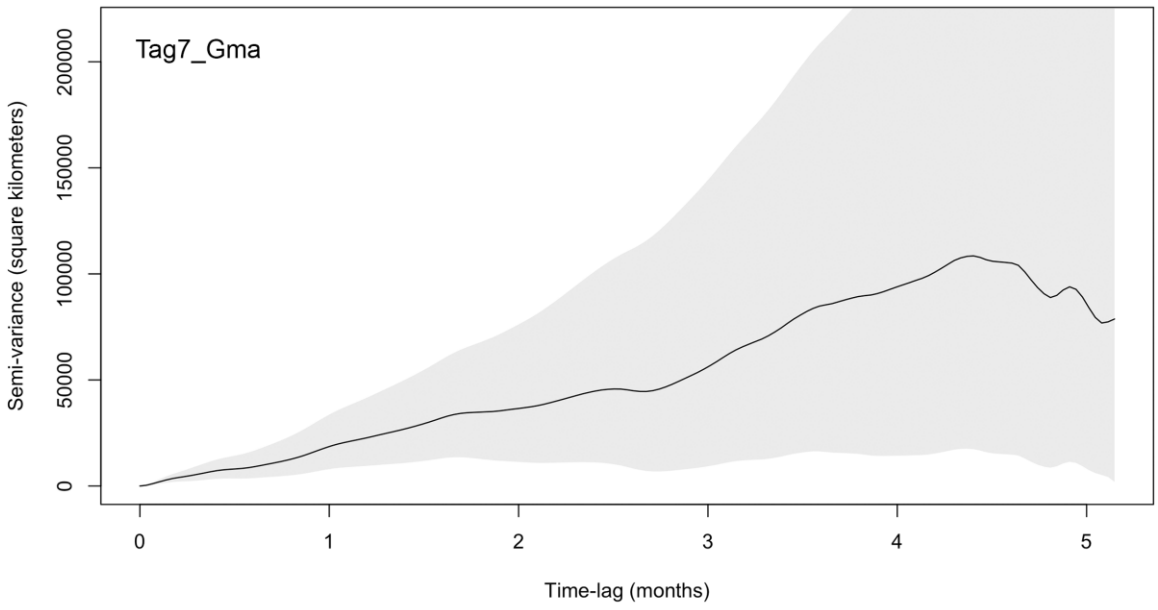


Figure S 2.2: Individual tracks (blue) and home range estimates (Utilization distribution – UD) at 50% and 95% isopleths (from an Autocorrelated Kernel Density Estimation – AKDE) of four short-finned pilot whales tagged in Madeira between 2018 and 2021.


Tag1_Gma
Semi-variance (square kilometers)
0e+00
2e+04
4e+04
6e+04
8e+04
1e+05
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Time-lag (months)


Tag7_Gma
Semi-variance (square kilometers)
0
50000
100000
150000
200000
0
1
2
3
4
5
Time-lag (months)

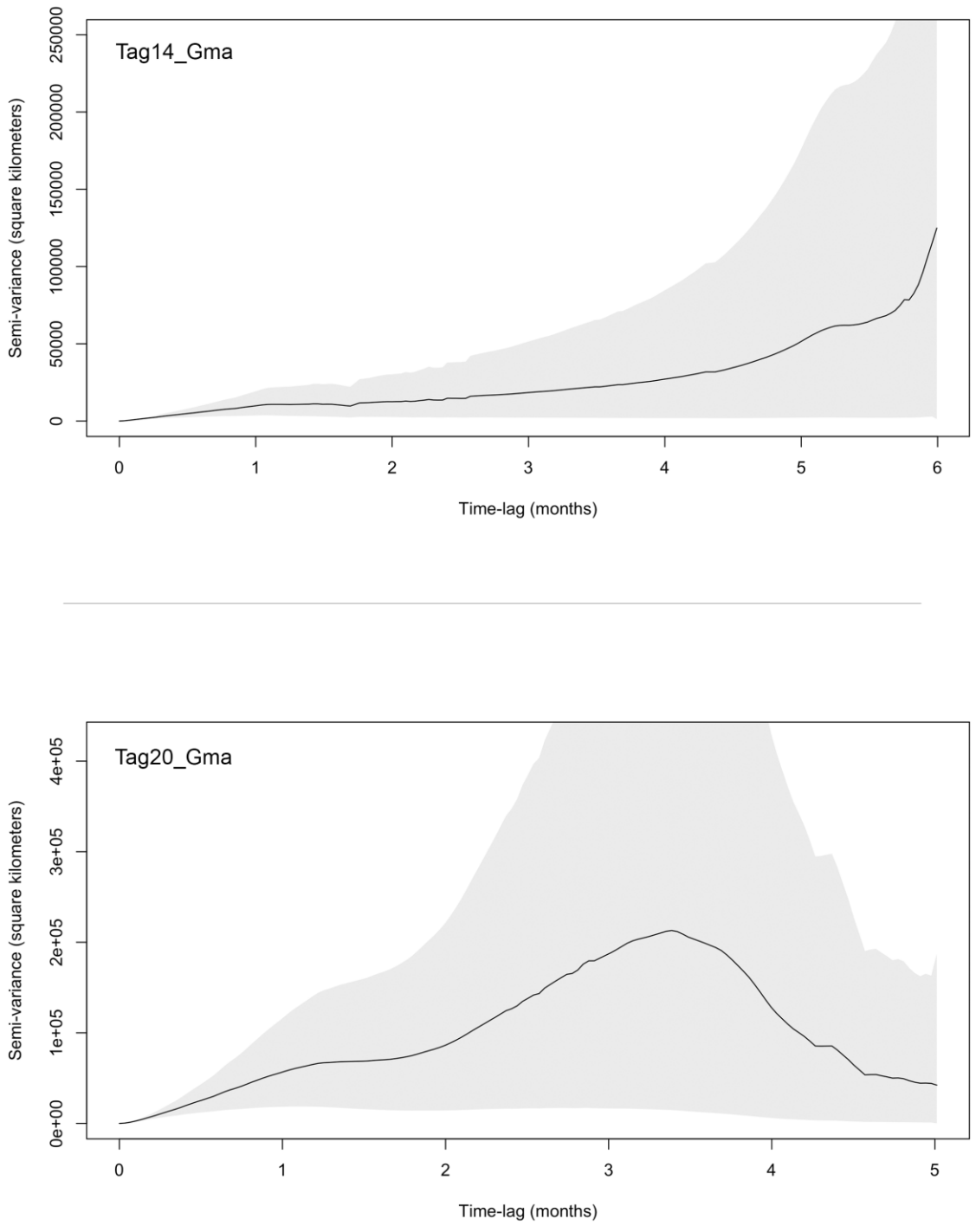
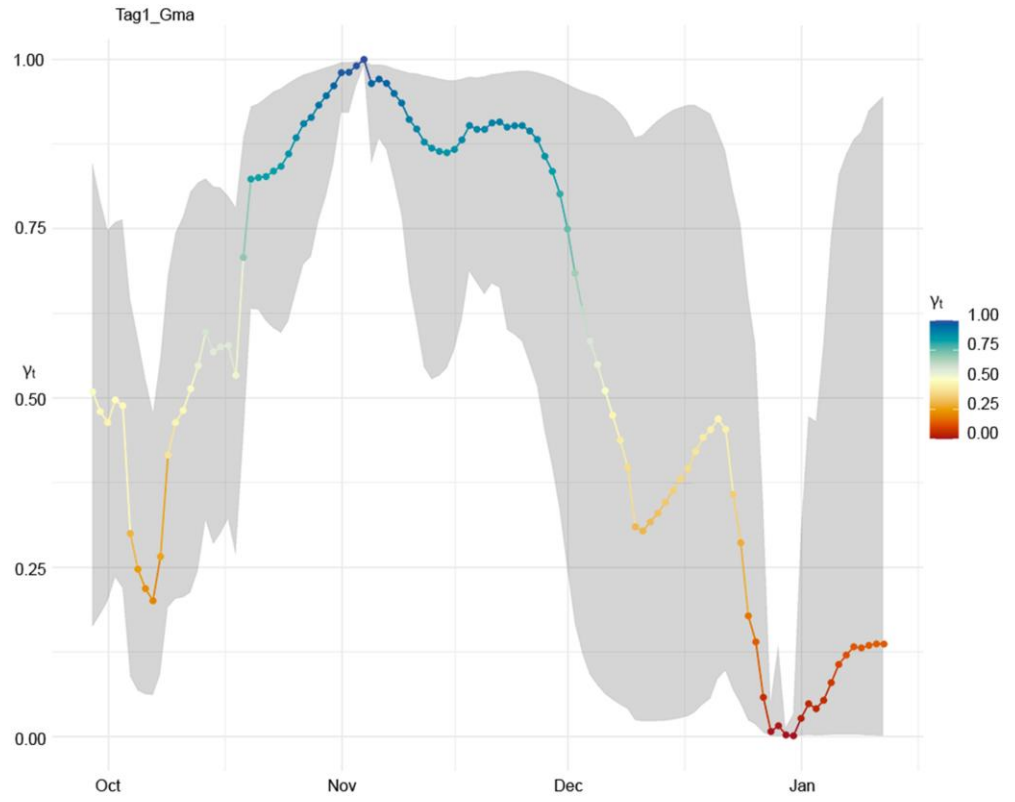
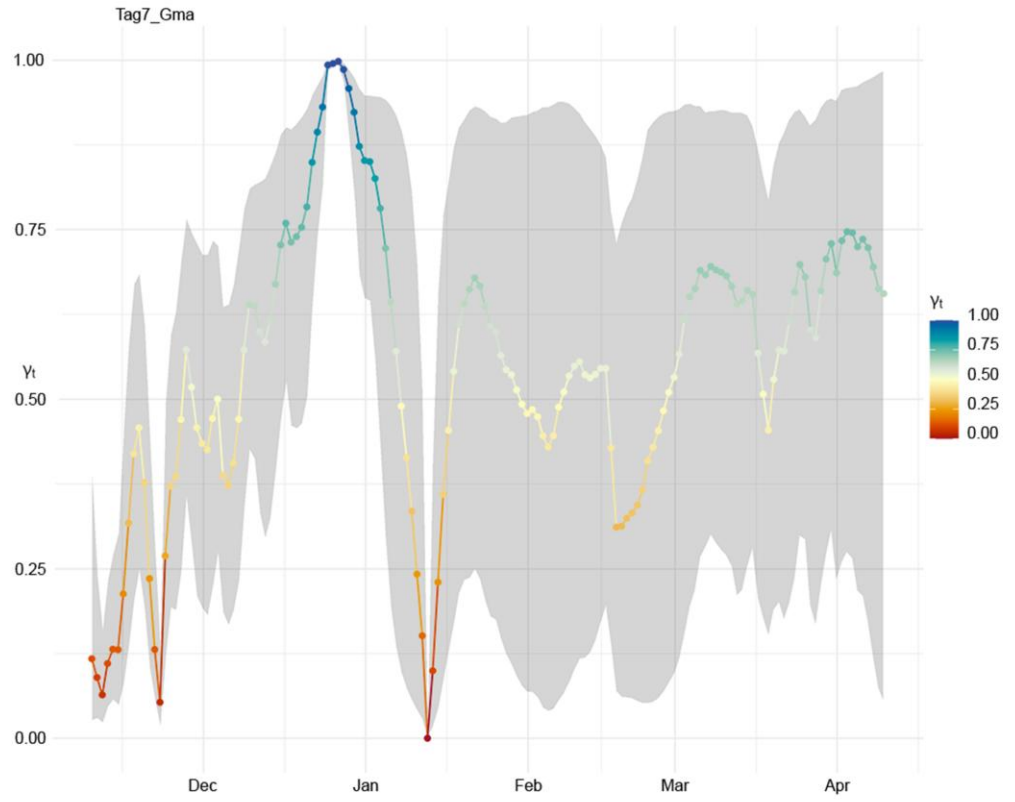


Figure S 2.3: Semivariograms of four short-finned pilot whales tagged in Madeira between 2018 and 2021.


Tag1_Gma
1.00
0.75
Yt
0.50
0.25
0.00
Oct
Nov
Dec
Jan
Yt
1.00
0.75
0.50
0.25
0.00


Tag7_Gma
1.00
0.75
Yt
0.50
0.25
0.00
Dec
Jan
Feb
Mar
Apr
Yt
1.00
0.75
0.50
0.25
0.00

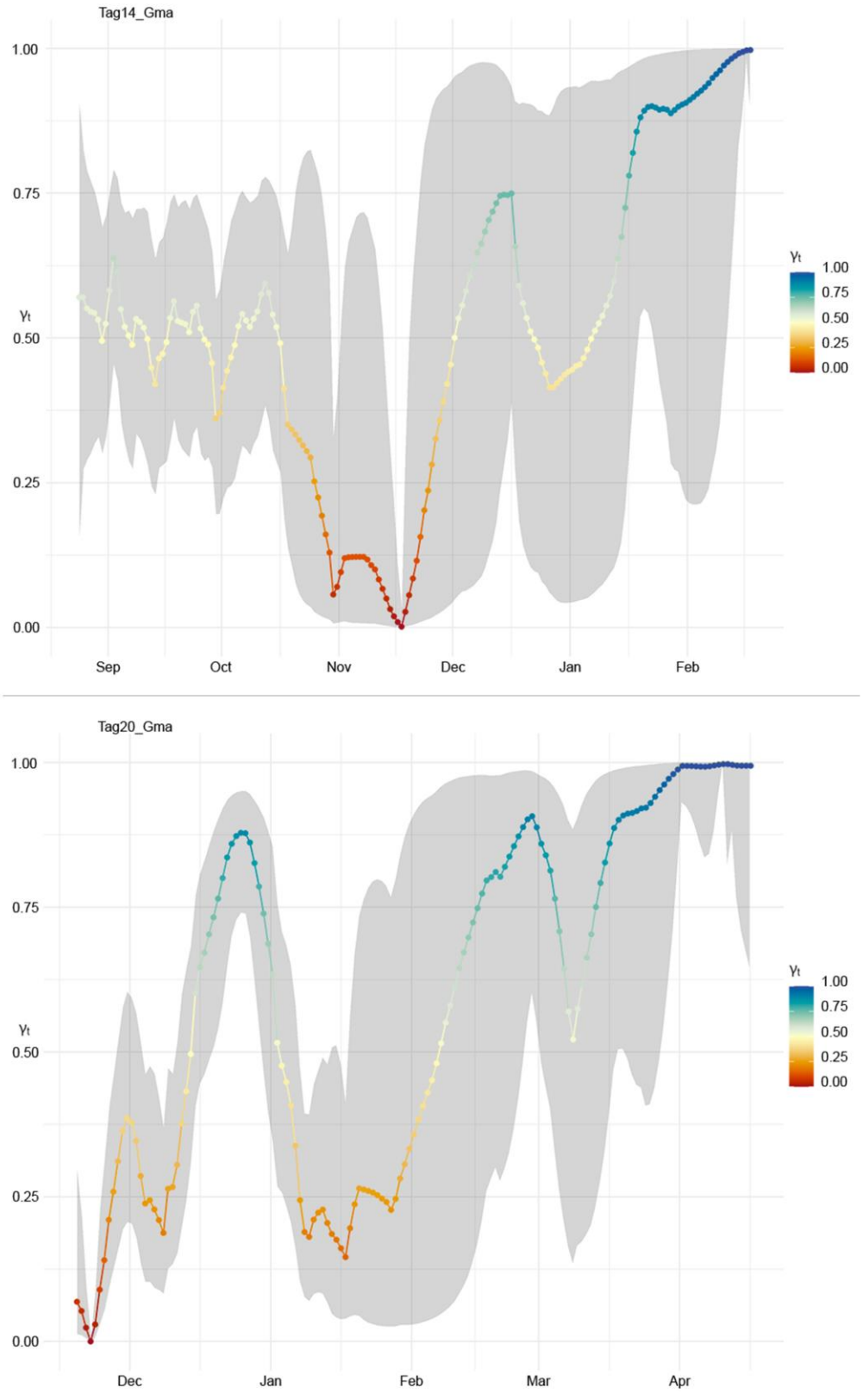


Figure S 2.4: Individual move persistence (γ_t) and associated uncertainty plotted over time, of four short-finned pilot whales tagged in Madeira between 2018 and 2021.

CHAPTER 3

OCEANIC ISLANDS AS SEASONAL AGGREGATION SITES: PARTIAL MIGRATION AND RESTRICTED HOME RANGES STRATEGY IN SHORT-FINNED PILOT WHALES

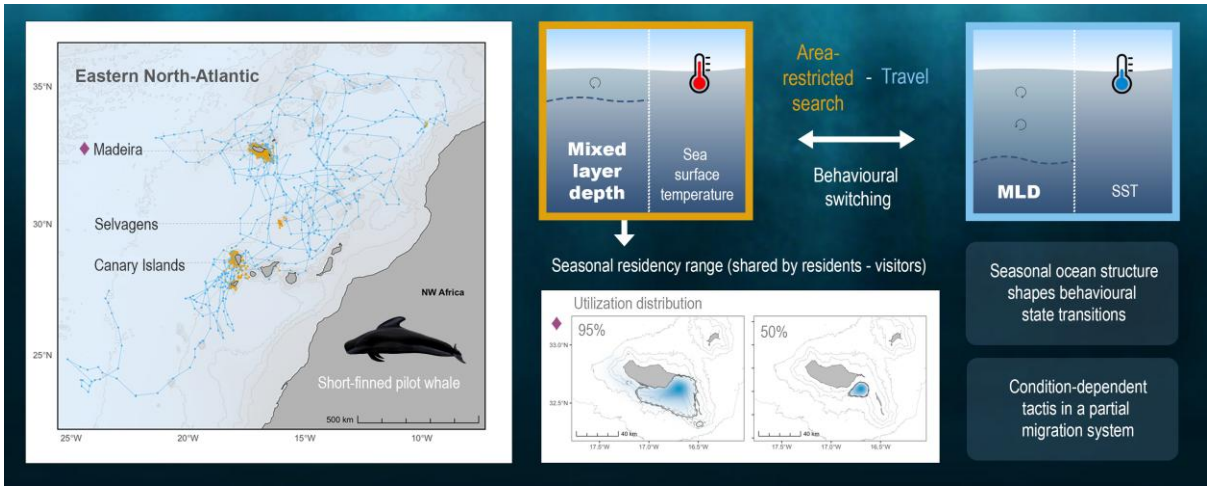


Figure 3.1: Graphical abstract of Chapter 3

This Chapter has been **submitted** to the journal *Movement Ecology* on 18 Feb 2026 as:

Fernandez, M., Weyn, M., Ferreira, R., Rosso, M., Correia, A. M., Hartman, K., Van der Harst, P., De la Fuente, J., Arbelo, M., Fernandez A., Caldeira, R., Dinis, A., Mateus, C.S., Alves, F. Oceanic Islands as Seasonal Aggregation Sites: Partial Migration and Restricted Home Ranges in Short-Finned Pilot Whales.

3.1 Abstract

Oceanic islands can serve as predictable, high-value habitat patches in otherwise resource-sparse pelagic environments, potentially favoring different residency strategies. However, the processes linking seasonal ocean structures to individual movements and population-level aggregation in deep-diving predators remain poorly understood. We employed biotelemetry and movement models that explicitly account for location uncertainty and temporal irregularity to investigate the spatial and temporal dynamics of short-finned pilot whales (*Globicephala macrorhynchus*) in the eastern North Atlantic. Sixteen biologgers deployed off Madeira Island between 2018 and 2024, transmitting data for periods ranging from 13 to 180 days (mean = 85), revealed movements across an area of 1,170,790 km² over a span of 1362 days. Using a multiple-imputation hidden Markov model, we identified two distinct behavioral states: area-restricted search (ARS), which is concentrated around islands, and travelling, which occurs during offshore exploration. The mixed layer depth was the strongest among the dynamic covariates considered for the state transitions. Whales were more likely to remain in or switch to ARS under shallow, stratified conditions and to switch to travelling under deeper, mixed conditions, with inter-individual variation. The autocorrelated kernel density estimation indicated seasonal range residency around Madeira (mean 53 consecutive days; max 120), producing a constrained population range (95% UD 1,450 km²; 50% UD 193 km²), located approximately at 10 km offshore. Integrating telemetry with long-term photo-identification showed that individuals spanning resident-to-visitor fidelity classes congregated within the same seasonal residency range, consistent with condition-dependent tactics in a partial-migration system. These findings show how seasonal ocean structure can structure switching between movement states in highly mobile marine predators, providing a mechanistic link between environmental variability and partial migration-like tactics.

3.2 Introduction

Animals inhabiting spatially extensive and heterogeneous environments must balance the benefits of remaining in profitable habitat patches with those of dispersal and exploration. This trade-off can generate a range of movement strategies, including residency, migration, and partial migration, in which individuals within the same population adopt different movement tactics depending on environmental conditions, individual state, or social context (Dingle & Drake 2007; Kokko & Lundberg 2001; Shaw & Couzin 2011). Understanding the mechanisms

that drive transitions between restricted space use and directed movement is a challenge in movement ecology, as these transitions can shape population structure, connectivity, and the spatio-temporal emergence of aggregation sites (Nathan et al., 2008; Shaw & Couzin 2011). In highly mobile species, such transitions can also influence ecological connectivity by linking distant regions through recurrent patterns of movement and aggregation.

Pelagic ecosystems present a challenging context for animal movement, as resources are often sparse, patchy, and temporally variable. Nevertheless, fixed physical features such as continental shelves, seamounts, and island slopes can increase habitat complexity and alter prey availability relative to the surrounding open ocean (Abecassis et al. 2015; Braun et al. 2022). In marine systems, these fixed features can generate predictable spatial structure in predator movements by interacting with oceanographic processes that influence prey distribution across depth layers, particularly for deep-diving species (Braun et al. 2022). As a consequence, highly mobile marine predators often exhibit movement trajectories characterized by alternating phases of spatial restriction and directed displacement, rather than continuous or homogeneous space use (Block et al. 2011). Oceanic islands provide a particularly informative setting for investigating these dynamics. Although embedded within generally oligotrophic pelagic regions, island-associated bathymetry and circulation can locally modify physical conditions, producing persistent or seasonally predictable oceanographic features (Barton et al. 2000). For deep-diving predators, these conditions may improve the accessibility of prey across different depths, leading to a consistent use or extended occupation of habitats near islands. This is supported by observations that several odontocete species exhibit strong associations with islands, often evidenced by long-term site fidelity or repeated seasonal visits (Alves et al. 2013; Hartman et al. 2015; Mahaffy et al. 2015).

Despite this growing evidence for island-associated space use, most existing studies rely on photo-identification (based on natural markings) or broad-scale distributional data. While these approaches are powerful for documenting long-term site fidelity and population structure (Whitehead 2001), they do not resolve individual movement trajectories or the timing of transitions between restricted and directed movement. Biotelemetry has become increasingly common in marine mammal research (Hussey et al. 2015, Hays et al. 2016), including for odontocetes associated with island and archipelago systems. In these settings, telemetry studies have often focused on broad-scale space use, habitat associations, and inter-island connectivity (e.g., Baird et al. 2010; Abecassis et al. 2015; Hill et al. 2019), whereas the temporal structure of behavioral switching has been less frequently explicitly addressed. For short-finned pilot

whales (*Globicephala macrorhynchus*), satellite tracking has revealed extensive movements among oceanic archipelagos and strong island associations (Hill et al. 2019; Weyn et al. 2025), yet the timing and drivers of transitions between restricted space use and directed travel remain poorly understood. In particular, whether such transitions are synchronized across individuals, seasonally structured, or linked to dynamic oceanographic conditions has received limited attention.

Recent advances in biotelemetry and movement modelling now provide the tools needed to overcome these limitations (Williams et al. 2020). High-resolution tracking data allows individual movement trajectories to be reconstructed across broad spatial and temporal scales, while statistical movement models enable inference about behavioral states and transitions that are not directly observable (Nathan et al. 2008). In particular, state-space and hidden Markov modelling frameworks have been widely adopted to distinguish periods of area-restricted movement from directed travel, offering insight into how animals dynamically adjust their movement behavior in response to changing environmental conditions (Morales et al. 2004; McClintock 2017). In marine systems, explicitly accounting for location uncertainty and irregular sampling is essential, as satellite telemetry data often violates the assumptions of regularly spaced and error-free observations (Johnson et al. 2008; McClintock & Michelot 2018).

These approaches also allow movement behavior to be interpreted within a broader ecological and evolutionary context. Partial migration theory predicts that individuals within the same population may adopt different movement tactics, or switch between residency and dispersal across time, depending on environmental conditions and individual state (Lundberg 1987; Kokko & Lundberg 2001). Rather than producing fixed resident and migratory classes, such systems can generate dynamic patterns of space use and seasonal aggregation, even when individuals differ in their long-term movement histories (Chapman et al. 2011; Shaw & Couzin 2011). Identifying when and where these aggregation phases occur, and the conditions under which individuals transition into and out of them, is therefore key to understanding population connectivity and habitat dependence in highly mobile species.

Short-finned pilot whales provide an ideal case study for examining these processes in pelagic environments. Across multiple oceanic archipelagos, including Madeira, the Canary Islands, Hawai‘i, and the Mariana Archipelago, this species has been shown to combine strong island associations with long-distance movements, suggesting a mixture of restricted and exploratory

movement tactics within the same population (Alves et al. 2013; Mahaffy et al. 2015; Hill et al. 2019; Servidio et al. 2019; Esteban et al. 2022). For deep-diving predators, these island-associated features may be particularly important because vertical foraging behavior interacts with spatially structured oceanography across depth layers. By increasing prey accessibility throughout the water column, island-modified circulation and stratification can support repeated exploitation of localized prey fields, potentially promoting seasonal residency or prolonged spatial restriction despite the capacity for long-distance movement (Braun et al. 2022).

More broadly, restricted space use and long-term residency have been documented across a range of cetacean species, spanning both coastal and pelagic systems. Bottlenose dolphins (*Tursiops truncatus*), for example, often exhibit strong site fidelity and relatively small home ranges in productive coastal habitats, with substantial individual variation in movement behavior (Wilson et al. 1997; Dinis et al. 2016, 2021). In oceanic environments, female sperm whales (*Physeter macrocephalus*) can maintain long-term residency within discrete regions despite extensive vertical movements and male dispersal, indicating that restricted horizontal space use can coexist with high mobility (Whitehead 2001). Similarly, deep-diving odontocetes such as Cuvier's beaked whales (*Ziphius cavirostris*) have been shown to repeatedly use spatially constrained offshore habitats over extended periods (Foley et al. 2021).

Together, these examples indicate that residency and restricted space use are not confined to coastal species or shelf systems, but can also arise in pelagic predators occupying heterogeneous ocean environments. However, it remains unclear whether such patterns reflect static residency, seasonal range restriction, or condition-dependent transitions driven by dynamic oceanographic processes.

Here, we combine satellite biotelemetry, movement models that explicitly account for location uncertainty and temporal irregularity, and long-term photo-identification data to investigate the spatio-temporal movement dynamics of short-finned pilot whales in the eastern North Atlantic. Specifically, we aim to (i) identify behavioral states associated with restricted and directed movement, (ii) quantify the timing, duration, and spatial extent of seasonal range residency around an oceanic island system, and (iii) evaluate how dynamic oceanographic conditions influence transitions between these movement states. By linking individual-level movement behavior with population-level patterns of space use, this study provides a mechanistic

framework for understanding how predictable aggregation dynamics can emerge in pelagic environments and how partial migration-like strategies arise in highly mobile marine predators.

3.3 Material and Methods

3.3.1 Study area

Although the biologgers were deployed off Madeira Island (Portugal) (see "Data collection and preparation"), the extensive movements of the tagged whales covered a wide portion of the Macaronesia biogeographical region, especially the Webbnesia marine ecoregion that includes Madeira, Selvagens (Portugal), and Canary Islands (Spain) (Freitas et al., 2019). Located in the eastern North Atlantic, these subtropical archipelagos of volcanic origin are surrounded by depths of around 4500 m and share similar environmental characteristics, such as oligotrophic waters, surface temperatures ranging between 15 and 27◦C, a salinity range of 36.5–37.1 PSU, and the presence of submarine canyons (Spalding et al., 2007; Kim et al., 2008). These geographical features, coupled with physical disturbances such as upwellings and eddies, create favorable feeding grounds for deep-diving cetaceans (Carracedo and Troll, 2021; Cartagena-Matos et al., 2021; Fernandez et al., 2021), including the short-finned pilot whale (Boran and Heimlich, 2019; Aguilar de Soto and Alves, 2023). Inter-archipelago movements and lack of genetic population differentiation have been described for this species in Macaronesia, as well as groups exhibiting distinct residency patterns, especially in Madeira and the Canary Islands, where there are estimates of a few hundred island-associated whales (Alves et al., 2013, 2015, 2019; Miralles et al., 2016; Servidio et al., 2019; Esteban et al., 2022; Verborgh et al., 2022; Weyn et al., 2025).

3.3.2 Data collection and preparation

Between 2018 and 2024, we deployed 16 low-impact, minimally percutaneous LIMPET SPOT6 satellite-linked transmitters (Wildlife Computers) on apparently healthy adult and subadult short-finned pilot whales in the southern waters of Madeira. Tagged individuals showed no signs of emaciation and were not accompanied by calves at the time of deployment. Tags were attached during dedicated research surveys using a Dan-Inject CO_2-powered dart gun, under appropriate legal permits (see Ethics Statement). Each device consisted of an electronic unit secured with two 6.7-cm titanium darts designed for cetaceans (Andrews et al., 2019), and transmitted geolocation data via the Argos satellite system. Transmission schedules were duty-cycled to balance data acquisition and battery life: tags transmitted in two blocks

daily during the first 55 days, once daily between days 55 and 180, and every two days thereafter.

The obtained datasets were filtered to remove potential errors and unreliable Argos location data using visual exploration and the *sdafilter* function from the *argosfilter* R **packag**e (Freitas, 2022). After the cleaning process, the data were split into sub-tracks to avoid gaps exceeding 72 hours, which could introduce high uncertainty into the posterior analysis.

Simultaneously with the satellite telemetry, biopsy samples and photographs were collected from the targeted animals. The biopsies were collected using a remote darting system (Mathews et al., 1988), following legal permits (see Ethics Statement), to determine sex through molecular analysis (as detailed in Ferreira et al., 2025). The photographs were obtained with digital cameras and zoom lenses and used to identify individuals and infer long-term site-fidelity patterns across the animals' capture histories (see Photo-ID site fidelity classifications).

3.3.3 Behavioral states

A widely used method for inferring behavior from tracking data is the discrete-time hidden Markov model (HMM). This type of time-series model consists of two components: an observable series and an underlying, non-observable state sequence. Typically, HMMs used for studying animal movement rely on two data variables—step length and turning angle—to infer behavioral states (Jonsen et al., 2005; Morales et al., 2004). These states are generally considered proxies for animal behavior, which can be characterized as (1) area-restricted-search-type (ARS) movements ("encamped" or "foraging"), with low values of step length and high turning angles (indicating many reversals), and (2) travelling-type movements ("exploratory" or "transit"), with high values of step length and low turning angles (indicating directed movement). While these methods are relatively easy to implement through several R packages, such as *moveHMM* (Michelot et al., 2016) or *momentuHMM* (McClintock and Michelot, 2018), they require data streams without errors and at regular temporal intervals (McClintock, 2017).

Given the nature of Argos data (with satellite coverage gaps) and the pilot whales' diving behavior (with periods of absence at the surface), the deployed tags had limited exposure to available satellites, resulting in measurement errors and temporal irregularities in the location data. This violates the assumption of regular time intervals and that there are no errors, which is needed to build animal movement HMMs. To address this limitation, we used a multiple-imputation approach (McClintock, 2017). This two-step method enables the inclusion of

measurement error and irregular temporal data, including missing observations, in animal movement HMMs. First, we employed a single-state movement model to accommodate the location measurement error and temporally irregular data. For this purpose, we fitted a continuous-time correlated random walk model to animal telemetry data, as implemented in the *crawl* R package (Johnson et al., 2018). Subsequently, a two-state HMM was fitted to the temporally regularized data streams using the *momentuHMM* R package. To perform these steps, we started with the *crawlWrap* function from *momentuHMM* to fit a continuous-time correlated random walk and then predicted temporally regular tracks at 24-hour intervals. Afterwards, a series of HMMs were fitted to 10 imputed datasets through the *MIfitHMM* function. Based on the ten model fits, we derived pooled estimates, standard errors, and confidence intervals utilizing standard multiple imputation formulas (McClintock & Michelot, 2018). Data streams or covariates that exhibit spatial dependency—such as step length, turning angle, sea surface temperature, and mixed layer depth—are expected to vary across the ten realizations of the position process. Consequently, the pooled inferences drawn from the fitted Hidden Markov Models (HMMs) encapsulate the inherent uncertainty related to location.

We used a gamma distribution for the step length and a wrapped Cauchy distribution for the turning angle. Initial values for the optimizer were selected based on data visualization, following the rationale by Michelot & Langrock (2023). Two states were defined according to these parameters: (1) an ARS state with short step lengths and high turning angles, and (2) a transit state with long step lengths and low turning angles. To control label switching in the models when using a multiple imputation approach, we added parameter constraints through the use of the userBounds and workBounds arguments in *MIfitHMM*. For the step length, we constrained the standard deviation to a maximum of 40,000 m and the mean value to a maximum of 432,000 m (based on a maximum constant speed of 5m/s over 24 hours). We used the workBounds to constrain the step length of the different behavioral states, such that $432{,}000 \geq b_2 \geq b_1 \geq 0$, meaning that the length of the steps for travelling behavior must always be greater than or equal to that in ARS. We applied a similar approach for the angle, setting the natural bounds to $\{-\pi, \pi\}$, and $\rho_2 \leq 0.95$, to avoid problems with sparse datasets. To ensure the travelling state always has higher directional persistence than the ARS, we constrained $\rho_1 \leq \rho_2$ using workBounds, which, in summary, means $0 \leq \rho_1 \leq \rho_2 \leq 0.95$. A very weakly informative prior, based on a normal distribution, was used to facilitate model convergence.

Finally, the hidden process model was run to better understand the effects of two environmental covariates on the transition probabilities: sea surface temperature (SST) and mixed layer depth

(MLD). While static environmental covariates, such as depth, slope, and proximity to islands or seamounts, clearly affect whale behavior, here we focused on the dynamic factors that trigger transitions between the two distinct behavioral states. Therefore, among the available dynamic covariates, we selected these two based on previous studies, in which MLD and SST were found to be highly relevant for various distributional and ecological aspects of the target species (Heimlich-Boran 1993, Fernandez et al. 2021, Freitas et al. 2026). The variables were obtained from the GLOBAL_MULTIYEAR_PHY_001_030 product from the Marine Copernicus services at a spatial resolution of 8 km and a daily temporal resolution.

3.3.4 Range residency

For the estimation of home range, which quantifies the spatial extent and intensity of landscape utilization by individual animals (Signer & Fieberg, 2021), we adopted the framework proposed by Fleming et al. (2015). This framework elucidates the long-term behavior of movement processes that exhibit restricted spatial use, thereby aligning with Burt's classical definition of home range. Estimating the range distribution of an animal involves predicting where it is likely to travel over a long period, assuming that its movement behaviors remain consistent. In contrast, estimating "occurrence" focuses on determining where the animal travelled during the observation period (Fleming et al., 2016). Therefore, when calculating the range distribution, we can estimate the area used by the individuals (or populations), rather than only the area used during the tagging duration.

After identifying distinct behavioral states, we focused on characterizing the home range of pilot whales in the vicinity of Madeira Island, where the ARS state was the most prevalent throughout the study area. The range distribution was calculated using an autocorrelated kernel density estimator (AKDE) to account for the autocorrelation in tracking data (Noonan et al. 2019). The AKDE and its associated corrections have outperformed traditional home range estimators across various species, degrees of autocorrelation, and sample sizes (Noonan et al., 2019). We used the *ctmm* package (Calabrese et al. 2016) and the described workflow to fit and adjust the models. First, we plotted the locations of each individual and built semi-variograms (an unbiased way to visualize the autocorrelation structure) to identify range residency behaviors. When a non-stationary behavior was identified (e.g., migration), the data were subsetted following the recommendations of Fleming & Calabrese (2023). Afterwards, a continuous-time stochastic process model (Calabrese et al., 2016) with a location-error model was fitted to each individual movement using a perturbative Hybrid REML (Fleming et al., 2019) approach and selected based on AIC methods. An optimally weighted area-corrected

AKDE (wAKDE) was used to correct for unrepresentative temporal sampling (Fleming et al., 2018). The AKDE 95% and 50% values were calculated for individuals who exhibited a range residency behavior for more than 20 days. We used a hierarchical model to calculate the debiased mean of the calculated home ranges, as implemented in the *meta* function of the *ctmm* (Fleming et al. 2022). Using the *pkde* function from the *ctmm* package, we calculated a population kernel density. This function performs hierarchical kernel density estimation with bias correction, placing density kernels at each sampled time point with a bandwidth optimized to estimate the population range. The goal of this approach is to infer the range of an entire population (in this case, the residency range around Madeira) based on data collected from a subset of individuals. Since estimates of the population range (or population kernel density estimation) can be sensitive to sampling bias (Fleming 2022), we employed a funnel plot to examine potential biases. To assess potential non-independence, social cluster membership was examined.

3.3.5 Photo-ID site fidelity classifications

Photographs of the tagged animals were compared with a long-term digital photo-identification catalog that has been maintained since 2003. This catalog includes 1,472 distinctively marked pilot whales, based on high-quality images collected from research surveys and platforms of opportunity, such as whale-watching vessels, in the southern region of Madeira. The catalog follows the methods outlined by Alves et al. (2013) and documents year-round efforts (for more details, see Alves et al., 2018; Sambolino et al., 2022). The compilation of the catalogue and comparison of photographs followed standard photo-identification procedures (Alves et al., 2013; Urian et al., 2015; Würsig & Würsig, 1977).

The establishment of the long-term site fidelity classifications was based on the data set of individual-specific encounter histories – taking seasonality, years, and the general frequency of captures into account (adapted from Alves et al., 2020):

Residents: Individuals that exhibit multi-year and year-round site fidelity, photographed in at least four different years and across all four seasons. They are typically seen consistently throughout the study period or since their initial capture.

Extended visitors: Individuals with a multi-year presence limited to specific seasons, observed between July and March, covering three consecutive seasons.

Regular visitors: Individuals that show multi-year presence restricted to July through December, encompassing two consecutive seasons.

Occasional visitors/Transients: Individuals photographed only once or within a few days, not associated with catalogued animals, to prevent misclassification of new or non-catalogued residents and visitors.

3.4 Results

Sixteen tags successfully transmitted between 13 and 180 days (mean = 85, Table 3.1). The tagged animals exhibited extensive movement across an area of 1,170,790 km², spanning from 33°N (north of Madeira) to 23.5°N (south of the Canary Islands) and extending from offshore regions to the African coastline (Fig. 3.2). Two pairs of individuals had overlapping tracking periods but in both cases, the trajectories diverged following deployment, providing no evidence of sustained co-movement during the periods of overlap. Although different animals demonstrated distinct movement patterns (see Fig. S3.1), several common trends emerged regarding the timing of their behaviors and site fidelity classifications.

Table 3.1: Summary information for the 16 satellite-linked tags deployed on short-finned pilot whales (*Globicephala macrorhynchus*) on the southern coast of Madeira Island. Sex inferred through molecular analysis (F – female, M - male). Site fidelity classification based on photo-identification (photo-ID) and the animal capture histories in Madeira between 2003-2024. "-" means not applicable (with no skin sample or photo-ID).

Tag ID	Deployment date	Duration (days)	Sex (Molecular)	site fidelity classification (Photo-ID)
Tag1-Gma	28/09/2018	105	F	Regular Visitor (15 captures over 9 years between 2009-2023 in Summer-Autumn)
Tag2-Gma	29/09/2018	28	M	Resident (25 captures over 8 years between 2014-2024 in all seasons)
Tag4-Gma	30/05/2019	16	M	Resident (64 captures over 10 years between 2015-2024 in all seasons)
Tag5-Gma	26/01/2020	21	-	Occasional visitor/Transient (2 captures over 2 years between 2019 and 2020 in Winter)
Tag6-Gma	28/10/2020	13	M	Resident (54 captures over 8 years between 2015-2024 in all seasons)

Tag7-Gma	09/11/2020	150	F	Regular Visitor (18 captures over 8 years between 2010-2023 in Summer-Autumn)
Tag8-Gma	12/02/2021	53	F	Resident (9 captures over 7 years between 2016-2022 in Autumn-Spring)
Tag10-Gma	13/04/2021	127	F	Resident (58 captures over 14 years between 2007-2023 in all seasons)
Tag14-Gma	24/08/2021	175	-	Regular Visitor (8 captures over 3 years between 2017-2021 in Summer-Autumn)
Tag15-Gma	25/08/2021	73	M	Extended visitor (31 captures over 7 years between 2015-2023 in Summer-Winter)
Tag17-Gma	11/10/2021	180	F	Occasional visitor/Transient (2 captures in Summer-Autumn 2021)
Tag20-Gma	05/11/2021	148	-	Regular Visitor (13 captures over 4 years between 2018-2023 in Summer-Autumn)
Tag23-Gma	03/11/2022	31	F	Regular Visitor (48 captures over 13 years between 2007-2023 in Summer-Autumn)
Tag24-Gma	22/11/2022	16	M	Extended visitor (25 captures over 10 years between 2010-2022 in Summer-Winter)
Tag27-Gma	03/04/2024	48	-	-
Tag28-Gma	09/07/2024	178	-	Regular Visitor (8 captures over 5 years between 2018-2024 in Summer-Autumn)

3.4.1 Behavioral states

The two behavioral states were clearly identified by the models (Fig. S3.2): ARS - non-directed movement with short step lengths (19,379±13,992m per day), and travelling - a highly directed movement with larger step lengths (69,558±32,435m per day). The results showed that the ARS state was predominantly concentrated around island regions, particularly in Madeira (84% of all ARS states) and, to a lesser extent, in the western Canary Islands (La Palma and El Hierro, with 14% of all ARS states). Additionally, ARS states were observed near the Selvagens Islands. Transit states were observed throughout the area, primarily when the animals were exploring offshore areas or travelling between islands (Fig. 3.2).

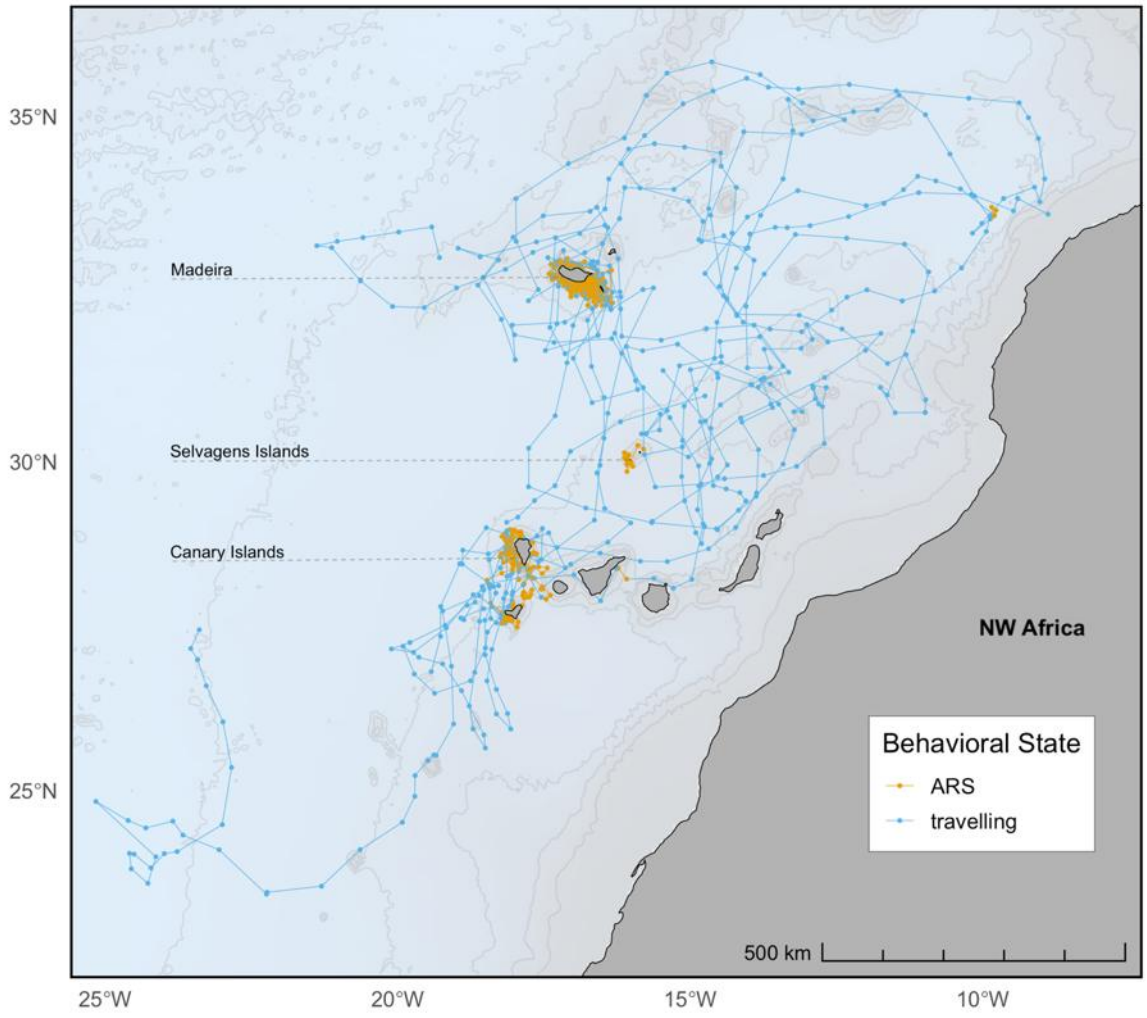


Figure 3.2: Movements of 16 short-finned pilot whales (*Globicephala macrorhynchus*) in Macaronesia. The map shows discrete time-steps of 24h (represented as dots) resulting from the error correction models (single-state movement model) and the results of a two-state Hidden Markov Model (the states are represented in different colors). The two states are: (1) area-restricted-search-type (ARS) movements ("encamped" or "foraging") and travelling-type movements ("exploratory" or "transit"). Isolines correspond to 1000 m depth.

The examination of the two covariates, MLD and SST, showed clear effects on the transition probabilities of animal behaviors (Fig. S3.3, S.4). The MLD demonstrated a markedly clearer and stronger influence compared to SST. Specifically, the likelihood of an animal transitioning from ARS behavior (state 1) to travelling behavior (state 2) increased as the MLD deepened beyond 50 meters. Although SST exhibited some influence - warmer waters exceeding 21°C tended to slightly favor the ARS behavioral state - its effect was comparatively minor. This indicates that the likelihood of exhibiting ARS behavior rises in the presence of stratified and

warmer waters, whereas animals are more inclined to shift to travelling behavior when these conditions are absent (Fig. 3.3).

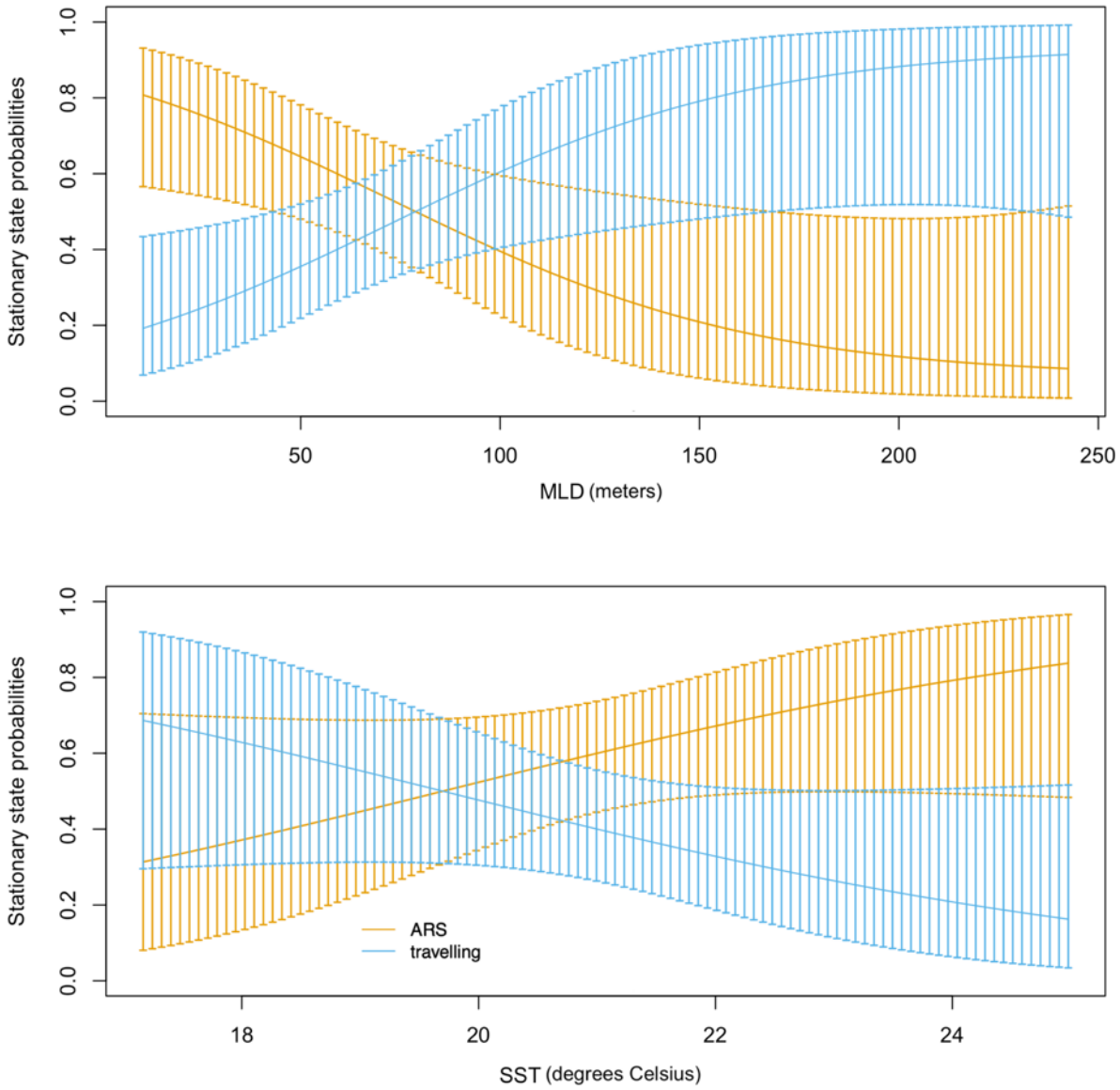


Figure 3.3: Stationary state probabilities resulting from the Hidden Markov Model for 16 short-finned pilot whales in Macaronesia. Two models are presented, one using the mixed layer depth (MLD, at the top) and sea surface temperature (SST, at the bottom) as covariates. The two states defined are: (1) area-restricted-search-type (ARS) movements ("encamped" or "foraging") and travelling-type movements ("exploratory" or "transit").

3.4.2 Range residency

Ten animals exhibited range residency behavior around Madeira, based on semivariogram analysis, with a mean of 53 (SD±37) and a maximum of 120 consecutive days. This behavior was observed across all months but showed a marked concentration from October to December.

Animals classified by photo-identification as residents and visitors (namely, extended and regular visitors), and including one as an occasional visitor/transient (Tag17), displayed both residency range and travelling behaviors. The Tag10, classified as resident (Table 3.1), spent 96 days in the range residency state (76% of the time the tag remained attached) and the rest of the time performing exploratory movements outside the residency area. Others, such as Tag28, classified as a regular visitor, spent 120 days in residency range behavior (67% of the time) before moving afterwards to the Canary Islands (see Fig. S3.1).

Eight individuals exhibited range residency behavior for more than 20 days (Table 3.2) and, therefore, were retained for the AKDE analysis. Both the 95% and 50% utilization distribution (UD) areas were located on the south coast of Madeira, with an emphasis on the southeast area (Fig. 3.4). The 95% UD ranged from over 3000 km2 (for Tag2 and Tag20 - the two animals with lower residency days) to a minimum of 1039 km2. A similar pattern emerges from the 50% UD, with values ranging from over 800 km² (for the same two animals) to a minimum of 171 km2 (Table 3.2). The debiased population-mean value for the 95% UD was 1819 km2 (CI: 1248-2549) and 350 km2 (CI: 206-553) for the 50% UD (Fig. 3.5). In the funnel plot, we identified two individuals, Tag2 and Tag20, with higher confidence intervals (and correspondingly higher AKDE values) who were tracked for less than one month (Fig. S3.5). This short tracking period may have introduced biases in this particular analysis. Therefore, we used the remaining six tracked individuals to estimate the population range. The 95% UD was estimated as 1450km2 (CI: 1198- 1726) and the 50% as 193 km2 (CI: 159 - 230) (Fig. 3.5). Mean depth values within the 95% UD were 1544 m (SD: ± 942), while the 50% UD, as expected, exhibited more restricted bathymetric characteristics at 1560 m (SD: ± 378), as denoted by the lower standard deviation values. The centroid of the 50% UD was located approximately 10 km from the coastline, with distances ranging from a minimum of 3 km to a maximum of 19 km to the shore.

Among the tagged individuals for which association information was available, three social clusters each contained two tagged individuals, whereas the remaining assessed individuals were the only tagged members of their respective clusters. Of the six individuals contributing to the adopted population home-range estimate, only Tag8 and Tag10 belonged to the same social cluster. These were two weakly connected females within the same resident cluster. The other co-clustered tagged individuals did not contribute to the adopted estimate: Tag4 and Tag6 did not exhibit range residency, Tag2 was excluded from the final population estimate because

of its short residency period and associated uncertainty, and Tag24 was not retained for the home-range analysis.

Table 3.2: Summary for the 10 short-finned pilot whales that exhibited range residency behavior around Madeira Island, with information on the range distribution (mean and confidence intervals [CI] from an autocorrelated kernel density estimator [AKDE]) for the eight tags that transmitted for more than 20 days. "Res." refers to consecutive days of range residency behavior (with indication of the start and end month).

Tag ID	Res. (days)	Start (month)	End (month)	Mean AKDE 95 (km^2)	CI AKDE 95 (km^2)	Mean AKDE 50 (km^2)	CI AKDE 50 (km^2)
Tag1-Gma	14	9	10	-	-	-	-
Tag2-Gma	28	9	10	3979	2293-6123	771	444-1186
Tag7-Gma	42	11	12	1902	1366-2526	344	247-456
Tag8-Gma	45	2	3	1526	1190-1903	244	190-304
Tag10-Gma	96	5	8	1323	1071-1602	154	124-186
Tag14-Gma	87	8	11	1038	840-1255	171	139-207
Tag15-Gma	67	8	11	1136	907-1391	222	177-272
Tag17-Gma	12	10	10	-	-	-	-
Tag20-Gma	23	11	12	3237	1976-4804	811	496-1205
Tag28-Gma	120	7	11	1215	990-1464	193	157-232

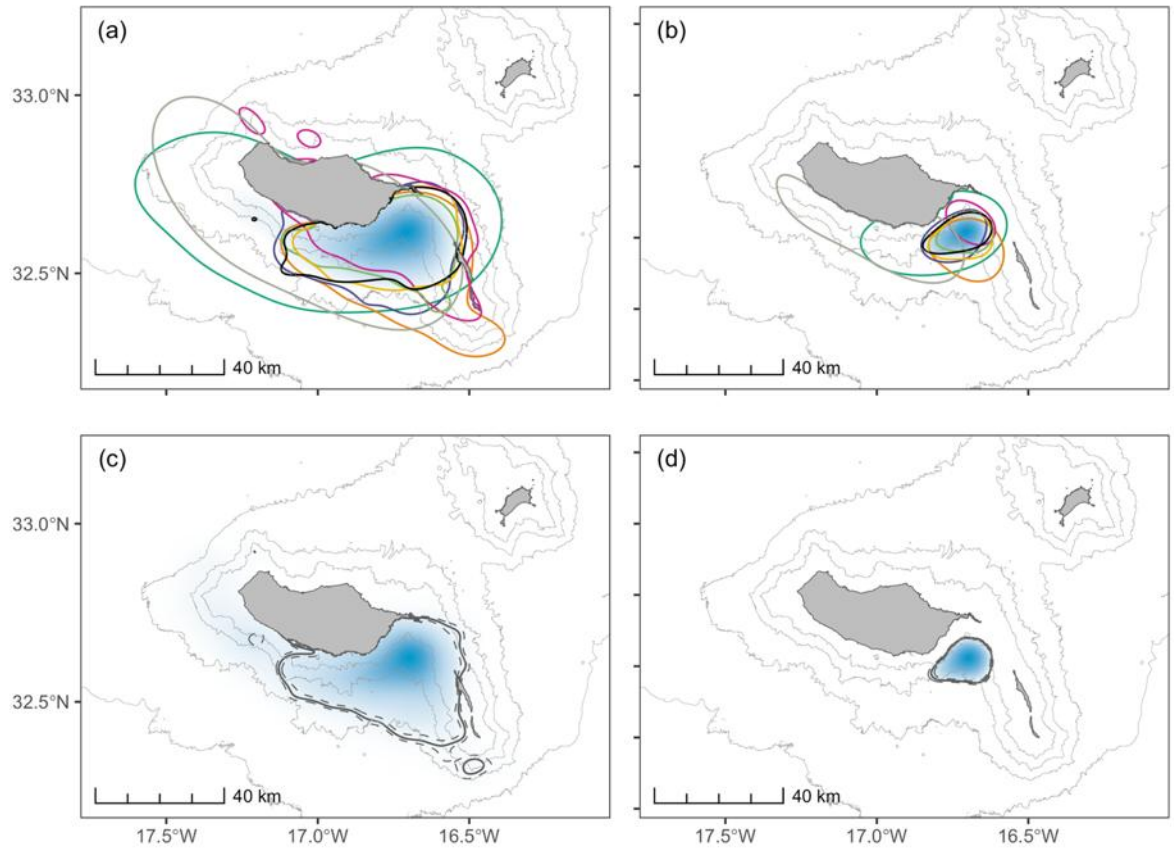


Figure 3.4: Resulting maps showing the home range of short-finned pilot whales around Madeira Island. a, b) autocorrelated kernel density (AKDE) estimator for eight individuals (one color per individual) at the 95% and 50% levels (respectively). c, d) population kernel density results at the 95% and 50% levels (respectively). The main island depicted in the figure is Madeira, with Porto Santo at the Northeast and the Desertas islands at the Southeast.

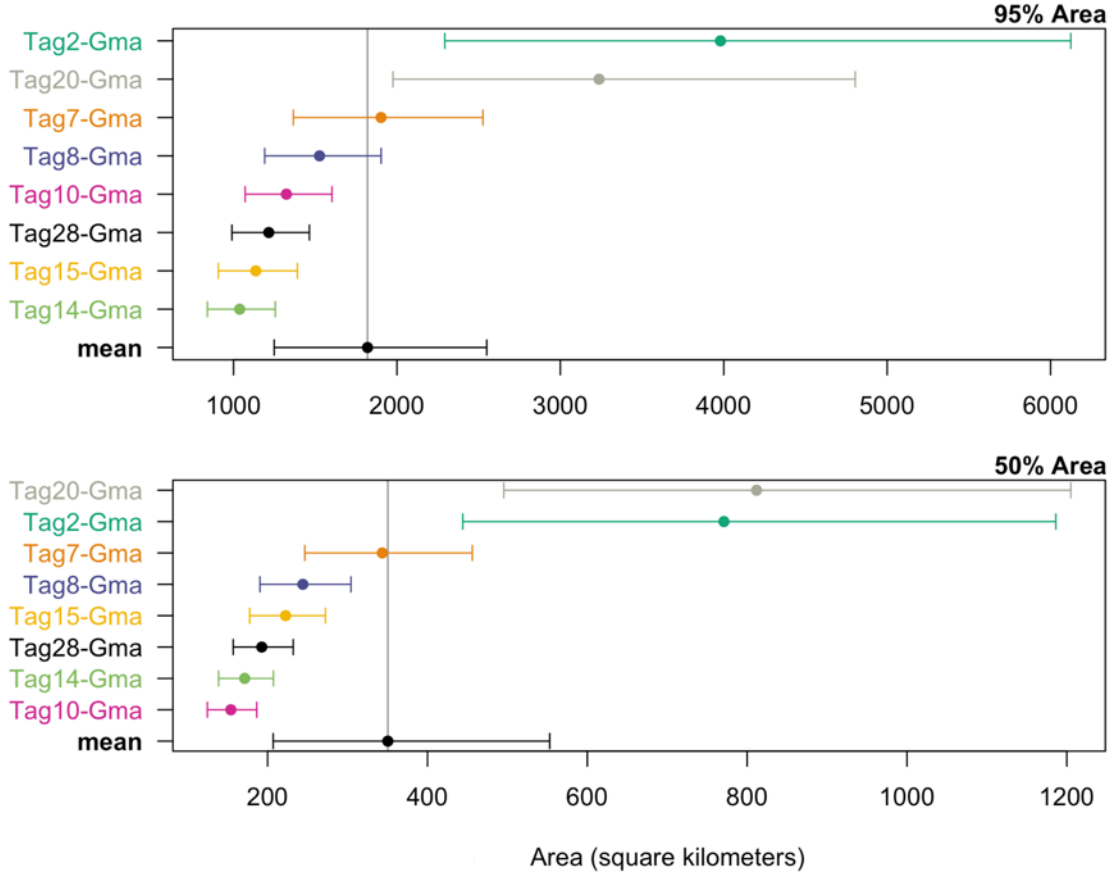


Figure 3.5: Debiased population mean estimates of home-range areas for eight short-finned pilot whales at the 95% (top) and 50% levels (bottom). Two individuals (Tag 20 and Tag 2) have higher utilization distribution values and wider confidence intervals, potentially due to fewer available sampling points for home-range estimation. Mean home ranges (grey vertical lines) were 1,820 km² and 350 km² for the 95% and 50% levels, respectively.

3.5 Discussion

This study examined the spatio-temporal structure of movement in a deep-diving cetacean inhabiting an oceanic island system, with the aim of understanding how transitions between restricted and directed movement relate to seasonal environmental variability. By integrating satellite biotelemetry, movement models that account for location uncertainty and irregular sampling, and long-term photo-identification data, we characterized when and where short-finned pilot whales exhibited periods of constrained and spatially restricted residency-type behavior near islands, and how these periods varied across individuals and seasons. Rather than indicating fixed resident or migratory strategies, the results point to temporally structured shifts in movement behavior that occur within a broader context of large-scale mobility.

3.5.1 BEHAVIORAL STATES

Across the study period, ARS behavior was most frequently observed in the vicinity of oceanic islands, particularly around Madeira, but was also recorded near other bathymetric features, including the western Canary Islands and the Selvagens Islands, where some individuals spent several days. Travelling behavior, in contrast, occurred primarily in offshore areas and during movements between island systems, consistent with the existence of a corridor between Madeira and the western Canary Islands (Weyn et al., 2025). Similar spatial patterns have been described previously for short-finned pilot whales for oceanic habitats, where individuals repeatedly use near-island waters while retaining the capacity for long-distance movements (Mahaffy et al. 2015; Abecassis et al. 2015; Alves et al., 2019; Hill et al. 2019; Weyn et al. 2025).

The distribution of behavioral states was not static through time. Most travelling movements occurred during periods associated with deeper mixed layers and cooler surface conditions, whereas stratified periods were associated with a higher probability of remaining in, or transitioning into, ARS. Among the environmental covariates considered, mixed layer depth showed the strongest association with behavioral state transitions, while sea surface temperature had a weaker effect. Because MLD reflects the seasonal structure of the upper ocean, distinguishing mixed from stratified conditions (Kara et al. 2003), this result suggests that seasonal changes in ocean structure are linked to the timing of shifts between restricted and directed movement.

At the same time, confidence intervals around the estimated transition probabilities were relatively wide, suggesting a potential inter-individual variability in behavioral responses to environmental conditions. Some individuals exhibited ARS behavior even during periods characterized by deeper mixed layers, suggesting that seasonal environmental structure does not impose a uniform response across the population. This variability is consistent with previous evidence of persistent island association in a subset of individuals around Madeira (Alves et al. 2013; Esteban et al. 2022), and indicates that movement decisions are likely influenced by a combination of environmental context and individual-specific factors rather than by environmental conditions alone.

Seasonal patterns in behavioral switching are consistent with known dynamics of the upper ocean in the temperate North Atlantic, where winter cooling and wind forcing deepen the mixed layer, followed by progressive shoaling during spring and summer as surface heating increases

and stratification develops (Kara et al. 2003). Around islands, wind exposure, bathymetry, and island–wake dynamics can locally influence how this seasonal cycle is expressed, often leading to spatial heterogeneity in mixed layer structure, with shallower mixed layers in leeward regions (Barton et al. 2000).

Changes in mixed layer depth are likely to influence prey accessibility indirectly, by modifying the vertical structure of the upper ocean and the organization of mesopelagic prey layers. During periods of deep mixing, the redistribution of biomass across depth can weaken vertical gradients and reduce the vertical compression of prey fields, potentially decreasing their predictability in space and time. Conversely, stratified conditions may favor the persistence of vertically structured prey layers. Recent work has shown that deep convective mixing can redistribute mesopelagic biomass and alter the expression of diel vertical migration, with implications for predator–prey interactions in the upper ocean (Bloom et al., 2025). For deep-diving odontocetes such as short-finned pilot whales, which exploit mesopelagic prey and adjust their diving behavior across diel cycles—showing shallower dives and a higher frequency of feeding attempts at night (Aguilar Soto et al. 2008)—such changes may translate into more accessible foraging opportunities during stratified periods.

The higher probability of transitioning to the ARS state during stratified and warmer periods was also reflected in the residency-range analysis, with most tagged individuals exhibiting spatially restricted behavior during the same months. Several individuals left the area toward the end of the stratified season after prolonged residency, including Tag14 (87 consecutive days) and Tag28 (120 consecutive days), both of which departed by late November. This seasonal pattern is consistent with previous studies showing increased abundance or higher habitat suitability for short-finned pilot whales during warmer months in Madeira (Alves et al. 2015; Fernandez et al. 2021), as well as an influx of visitors and mixed groups during this period, facilitating social interactions and breeding among individuals with different residency patterns (Alves et al. 2013).

Similar seasonal aggregation dynamics have been reported in other oceanic island systems. In the Canary Islands, larger group sizes have been associated with warmer conditions (Heimlich-Boran 1993), and a substantial proportion of transient and occasional individuals enter the archipelago during these months, mixing with resident animals and producing larger, mixed-sex groups (Servidio et al. 2019). In Hawai‘i, all neonate sightings occurred between July and November, indicating a similar seasonal concentration of reproductive activity (Mahaffy et al.

2015). Taken together, these observations suggest that warm, stratified periods coincide with predictable phases of spatial restriction and aggregation around islands, during which individuals with different long-term site fidelity classifications converge on the same areas for extended periods. Rather than reflecting fixed residency or migration strategies, these patterns are consistent with temporally structured movement tactics in which restricted space use emerges seasonally within a broader context of large-scale mobility.

3.5.2 HOME RANGES

During periods of range residency around Madeira, short-finned pilot whales exhibited a spatially constrained pattern of space use. At the population level, the estimated utilization distribution encompassed approximately 1,450 km² (95% UD), with a core area of 193 km² (50% UD) located close to the coastline (approximately 10 km offshore). Home range estimates are generally intended to characterize the spatial extent of routine activities during residency phases, consistent with the classical definition of a home range as the area used by an animal for its normal activities, excluding infrequent exploratory movements (Burt 1943). Because the individuals in this study also undertook long-distance movements outside this area, the estimated values should be interpreted as seasonal home ranges during residency episodes around Madeira, rather than as lifetime home ranges.

The existence of a highly island-associated component of the short-finned pilot whale population in Madeira has been previously documented using long-term photo-identification and related approaches (Alves et al. 2013, 2019; Esteban et al. 2022; Betty et al. 2023). However, photo-identification datasets typically reflect where observation effort is concentrated, and estimates of space use can be strongly influenced by heterogeneous spatial coverage and sampling design (Fieberg et al. 2007; Kie et al. 2010). This is particularly relevant in oceanic island systems, where surveys often focus on nearshore waters and conditions can constrain effort. For this reason, earlier work could robustly identify island association and site fidelity, but had more limited capacity to characterize the spatial distribution and extent of the residency area. Telemetry studies have started to address these constraints. For short-finned pilot whales, Abecassis et al. (2015) used satellite telemetry to relate whale locations to environmental conditions in Hawai‘i, and Hill et al. (2019) combined satellite tracking with social information in the Mariana Archipelago, including kernel-based estimates of space use. Nevertheless, differences in study objectives, spatial scale, tracking duration, and estimators mean that reported UD areas across studies should not be treated as directly comparable

biological quantities (Signer & Fieberg 2021). Instead, they reflect different aspects of space use under different behavioral contexts and sampling regimes.

A key consideration is that many conventional home-range estimators assume location independence, whereas telemetry data are inherently autocorrelated in time (Fleming et al. 2015; Signer & Fieberg 2021). For this reason, we used autocorrelated kernel density estimation within a continuous-time movement modelling framework, and applied weighted corrections for irregular sampling (Fleming et al. 2015; Fleming et al. 2018; Silva et al. 2022). This approach is particularly appropriate when the goal is to quantify the spatial extent of restricted space use while acknowledging autocorrelation and uncertainty, rather than simply mapping the footprint of observed locations.

Two individuals (Tag2 and Tag20) had notably wider confidence intervals and larger AKDE values, and both were tracked for relatively short periods (less than one month). This pattern is consistent with the expectation that limited observation duration can increase uncertainty and inflate apparent area estimates. For this reason, we treated these individuals cautiously and estimated the population range using the remaining six individuals with more stable residency signals. The other six individuals showed home ranges primarily concentrated in the same area, with a much more defined core range and lower CI. Of the six individuals contributing to the population-level home-range estimate, only one pair (Tag8 and Tag10) belonged to the same social cluster, suggesting that the pooled estimate was unlikely to be dominated by repeated sampling of a single social group. However, because social association structure was not incorporated into the home-range estimation, some residual non-independence cannot be excluded. Overall, these results provide quantitative support for a temporally bounded phase of restricted space use near Madeira. Rather than implying permanent spatial confinement, the estimated residency range represents a seasonal concentration of space use embedded within broader patterns of inter-island and offshore movement.

3.5.3 Ecological implications

Oceanic environments generally offer limited optimal sites, such as productive island slopes or seamounts, for large pelagic predators like deep-diving cetaceans. Thus, securing and maintaining access to such locations through residency can, under certain conditions, outweigh the advantages of dispersal (Kokko & Lundberg, 2001). The constrained population home-range estimates observed during residency phases indicate repeated use of the same areas, consistent with site fidelity at seasonal timescales. The observed prolonged site tenacity (up to

120 consecutive days) suggests that residency behavior may be associated with ecological benefits, potentially related to foraging opportunities, resting, socializing, breeding, or calving. The adoption of this behavior even by individuals classified as 'extended' or 'regular visitors' (i.e. with a marked seasonal presence) indicates that the advantages of remaining in these areas during specific seasons may offset the potential costs associated with local competition (Kokko & Lundberg, 2001).

The co-occurrence of individuals exhibiting different residency patterns within the same areas during specific seasons suggests a dynamic population structure. Such seasonal mixing may facilitate gene flow, but also highlights that the decision to remain resident versus migrating or transiting is likely condition-dependent, influenced by factors such as age, reproductive state, social context, or fine-scale environmental conditions, rather than representing a fixed trait expressed consistently by all individuals (Griswold et al., 2010).

This temporal pattern of residency behavior, strongly associated with shallow mixed layer depth and more weakly associated with sea surface temperature, is consistent with a movement strategy analogous to partial migration (Lundberg, 1987). Under this framework, individuals within a population adopt different movement tactics, adjusting their space use in response to seasonal environmental variation (Kokko & Lundberg, 2001; Shaw & Couzin, 2011). The higher probability of transit behavior during cooler periods may reflect movements towards alternative foraging areas or broader exploratory behavior when local conditions are less favorable, consistent with theoretical models in which migration functions as a response to temporarily suboptimal conditions (Kokko & Lundberg, 2001). The coexistence of long-term residents and temporary visitors adopting residency behavior during favorable periods suggests that southeastern Madeiran waters constitute an important seasonal area within the broader spatial range of the eastern North Atlantic population (Alves et al., 2013).

3.5.4 Conservation implications

The existence of a partial migration system with a pronounced seasonal component in spatially restricted areas close to oceanic islands has important implications for conservation. Periods of prolonged residency bring short-finned pilot whales into repeated and sustained spatial overlap with human activities concentrated in nearshore waters. In island systems, these areas are often subject to high levels of vessel traffic, making anthropogenic disturbance a central concern for island-associated populations of deep-diving cetaceans.

Marine traffic represents a major potential source of disturbance for short-finned pilot whales through both acoustic and physical interactions (Servidio et al., 2019). Activities such as commercial shipping, ferry routes, recreational boating, fishing operations, and whale-watching can increase exposure to noise, alter behavior, and elevate the risk of close encounters. Such disturbances have been documented across a range of cetacean species and are expected to intensify as global marine traffic continues to increase (Nowacek et al. 2001). In oceanic island settings, the spatial concentration of these activities within relatively narrow coastal zones further increases the likelihood of overlap during periods of seasonal residency.

Whale watching represents a particularly relevant pressure in this context. It is a significant and growing component of marine ecotourism on many oceanic islands, including Madeira and the Canary Islands, and can provide important economic benefits when appropriately regulated (Hoyt 2005; Ferdin et al. 2022). However, the predictable aggregation of pilot whales in accessible coastal waters for extended periods also increases their exposure to repeated interactions. The presence of potentially sensitive social contexts, such as calving, nursing, and socializing, may further heighten susceptibility to disturbance (Cunha et al. 2017; Sambolino et al. 2022; Servidio et al. 2019). These findings highlight the importance of considering seasonality when evaluating the intensity and potential impacts of whale-watching activities in island-associated habitats.

From a management perspective, the results suggest that temporal variation in whale distribution and behavior should be considered when assessing carrying capacity within residency areas. Adjusting the number, frequency, or spatial distribution of vessel activities during periods of peak aggregation may reduce cumulative disturbance without necessitating permanent spatial restrictions. Such seasonally informed approaches may be particularly relevant in systems where residency is temporally bounded rather than continuous.

In summary, this study provides new insight into the spatio-temporal dynamics of short-finned pilot whale residency around oceanic islands in Macaronesia. By identifying periods of predictable spatial restriction linked to seasonal oceanographic conditions, it highlights when and where overlap with human activities is most likely to occur. While our analysis focused on mixed layer depth and sea surface temperature as key environmental correlates, other factors—including fine-scale bathymetry, prey distribution, and additional oceanographic features—are likely to further influence movement behavior. Lunar illumination, for example, can influence pilot whale diving behavior and fine-scale habitat use (Owen et al. 2019). Future work

integrating prey-field observations, higher-resolution environmental data, and long-term telemetry with photo-identification and genetic studies would help refine the understanding of population connectivity, social structure, and resilience to both environmental variability and anthropogenic pressure.

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3.8 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, 01/IFCN/2022, and 02/IFCN/2024 – FAU MAD. 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 class, size, absence of young individuals, and apparent health, among others. Best practice guidelines were also consulted before tagging took place.

3.9 Author contributions

Marc Fernandez and Mieke Weyn contributed equally to this work. They conceived the study and designed the methodology; collected and analyzed the data; and led the writing of the manuscript. Filipe Alves contributed to the conception of the study, participated in data collection, contributed to funding acquisition, and to the writing of the manuscript. Rita Ferreira, Massimiliano Rosso, Ana Mafalda Correia, and Ana Dinis contributed to fieldwork and manuscript revision. Karin Hartman, Pieter van der Harst, Jesus De la Fuente, Manuel Arbelo, Antonio Fernandez, and Rui Caldeira contributed to funding acquisition and manuscript revision. Catarina Sofia Mateus contributed to manuscript revision. All authors approved the final version of the manuscript.

3.10 Data availability

The datasets supporting the conclusions of this article are available in the Movebank repository under the study Whales Telemetry – MARE-ARDITI / Oceanic Observatory of Madeira (Movebank Study ID: 886013997).

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3.12 SUPPLEMENTARY MATERIALS

Figure S 3.1: Movement tracks of 16 satellite-tagged short-finned pilot whales (*Globicephala macrorhynchus*) near Madeira Island (eastern North Atlantic). Each panel displays the track for an individual tagged whale, including the tag identifier (top left) and the deployment-detachment month and duration of transmissions in days ("n", bottom left). Blue lines (with a time gradient display from dark to light, deployment to detachment, respectively) indicate the movement path of each whale during the tracking period. Site fidelity classification based on photo-identification: R= Resident, EV = Extended visitor, RV = Regular visitor, OV = Occasional visitor/Transient.

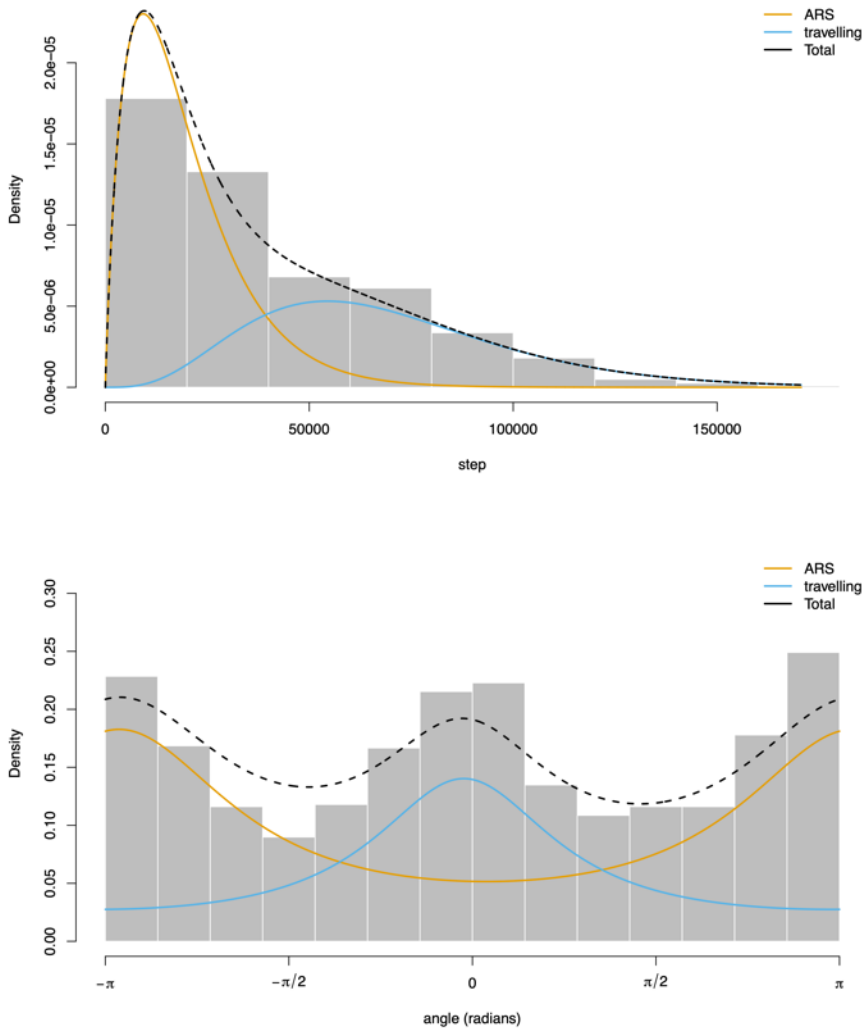

Figure S 3.2: Step length (in meters) and turning angle from the modelled states using a Hidden Markov model for behavioral selection. The top graph represents the density of the observed and modelled step lengths. The bottom graph represents the density of the observed and modelled turning angles. The two states are: (1) area-restricted-search-type (ARS) movements (smaller step lengths and directional movement) and travelling-type movements (larger step lengths and non-directional movement).

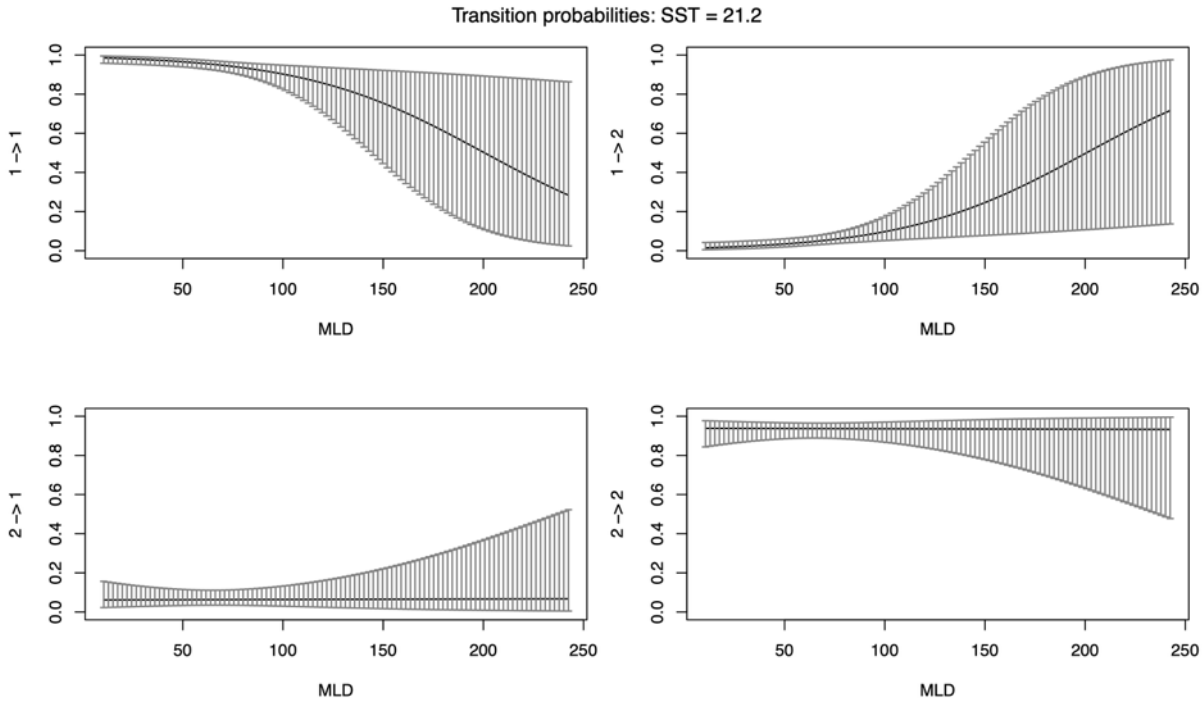

Figure S 3.3: Modelled transition probabilities for the two states (state 1 is ARS and state 2 is travelling behavior) in relation to the mixed layer depth (MLD). Vertical lines represent the 95% confidence intervals.

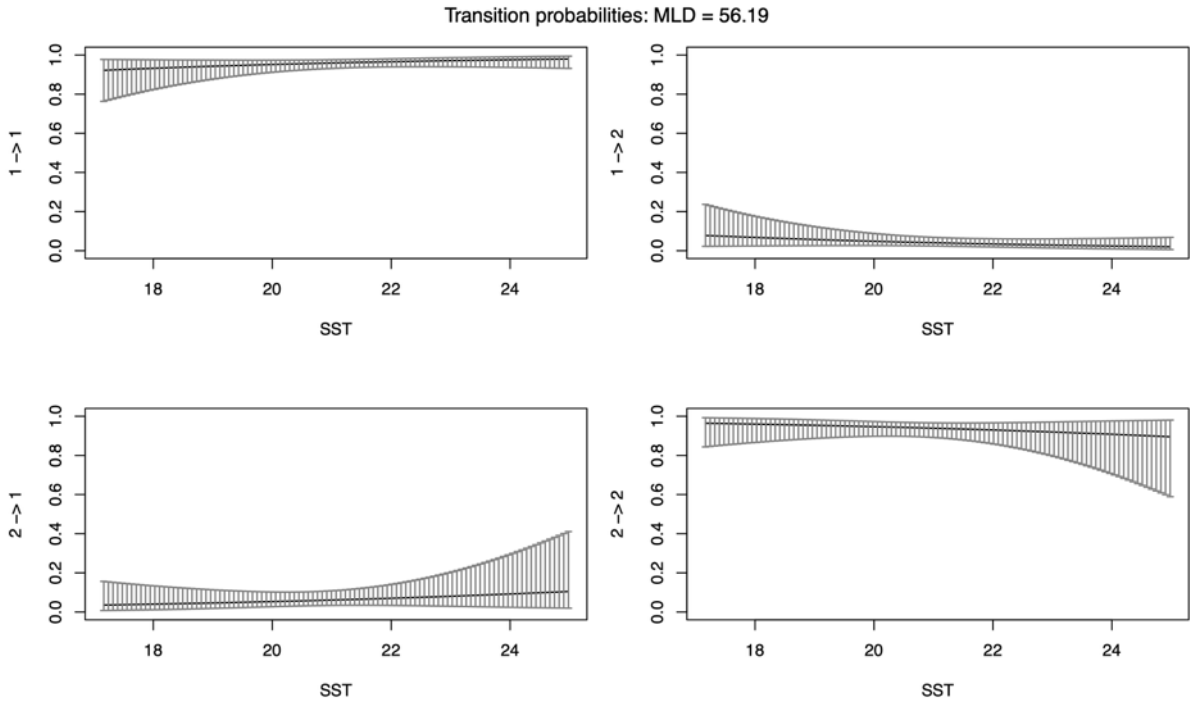

Figure S 3.4: Modelled transition probabilities for the two states (state 1 is ARS and state 2 is travelling behavior) in relation to the sea surface temperature (SST). Vertical lines represent the 95% confidence intervals.

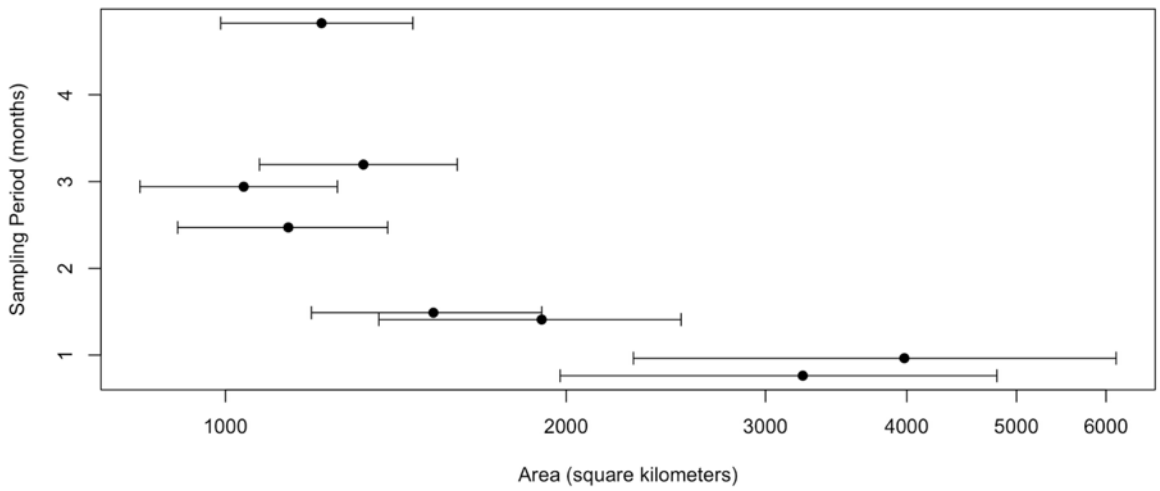

Figure S 3.5: Funnel plot showing the relation between the sampling period and the estimated AKDE. The tags with higher confidence intervals (and correspondingly higher AKDE values) are Tag2 and Tag20, which have less than one month of data.

CHAPTER 4

ABSENCE OF DIRECT PHOTO-IDENTIFICATION EVIDENCE FOR TRANS-ATLANTIC MOVEMENTS IN SHORT-FINNED PILOT WHALES

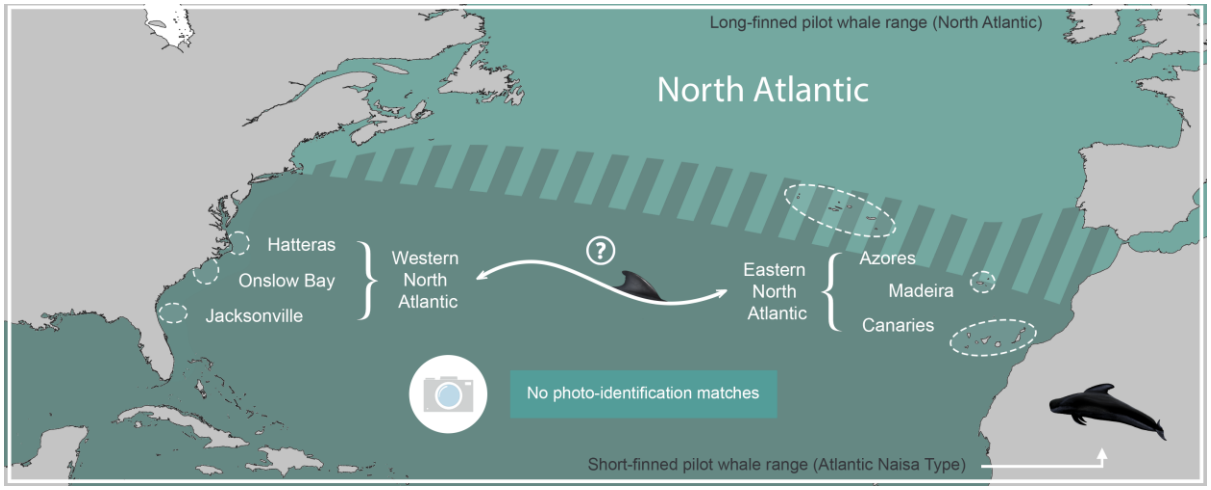

Figure 4.1: Graphical abstract of Chapter 4

This Chapter is formatted as paper, but will not be submitted for publication

4.1 Abstract

Understanding basin-wide connectivity is essential for conservation and management of highly mobile species, yet trans-Atlantic movements remain poorly documented in toothed whales. Here, we investigated potential connectivity of Atlantic Naisa short-finned pilot whales (*Globicephala macrorhynchus*) between Macaronesia (eastern North Atlantic, ENA) and the western North Atlantic (WNA) by cross-matching long-term photo-identification catalogues. Manual comparison and algorithm-assisted dorsal-fin matching (Happywhale and FinFindR) were applied to large catalogues spanning multiple years and regions. No conclusive matches were found between the ENA and WNA datasets. Although non-detections cannot exclude rare interchange, the results suggest that trans-Atlantic movements, if they occur, are uncommon or difficult to detect with currently available photo-identification resources. The absence of matches is discussed in relation to North Atlantic oceanography, the species' ecology and future research priorities.

4.2 Introduction

Understanding the extent of species' movement patterns is crucial for guiding conservation efforts as it offers insights into the scale of population connectivity, important migration corridors, and key habitats (Allen and Singh, 2016; Hays et al., 2019). It contributes to our knowledge of species' ecological needs and movement drivers, which is important for effective management of highly mobile species (Kot et al., 2023; Ogburn et al., 2017). Although documenting wide-ranging movements of marine mammals, particularly cetaceans, is often challenging due to their elusive nature and limited survey coverage across the open ocean, international collaborations and the integration of complementary approaches such as genetics, photographic identification (photo-identification hereafter), and biotelemetry have provided critical, multi-scale evidence of movement and connectivity (Bräger and Bräger, 2019; Castelblanco-Martínez et al., 2019; Dunn et al., 2019).

In the North Atlantic, individual basin-wide movements have been mainly documented in baleen whales (mysticetes), especially in humpback whales (*Megaptera novaeangliae*), blue whales (*Balaenoptera musculus*), and fin whales (*Balaenoptera physalus*) where long-term photo-identification and telemetry have revealed migrations spanning thousands of kilometers and, in some cases, trans-oceanic crossings (Jones et al., 2025; Pérez-Jorge et al., 2020). By contrast, evidence of North Atlantic basin-wide movements in toothed whales (odontocetes)

remains comparatively sparse. An exception is the sperm whale (*Physeter macrocephalus*), for which long-ranging longitudinal and latitudinal displacements throughout the North Atlantic have been documented (Lydersen et al., 2025; Mullin et al., 2022). Direct evidence for other odontocetes comes mainly from limited photo-identification and telemetry studies, namely on killer whales (*Orcinus orca)* and Atlantic white-sided dolphins (*Leucopleurus acutus*) (De Clerck et al., 2025; Mrusczok et al., 2022). In this context, genetics can provide an important complementary line of evidence on broad-scale structure, potential connectivity, and movements, although genetic patterns integrate over longer timescales and do not directly quantify individual interchange (Lowe & Allendorf, 2010). This is illustrated in long-finned pilot whales (*Globicephala melas*), for which genetic markers have revealed large-scale population structure in Atlantic waters (Monteiro et al., 2015).

The short-finned pilot whale (*Globicephala macrorhynchus*) can be found in tropical and warm-temperate waters worldwide, including up to around 40ºN in the North Atlantic, occurring on both sides of this oceanic basin (Aguilar de Soto & Alves, 2023; Olson, 2009). In the western North Atlantic (WNA), regional genetic studies suggest low differentiation and substantial connectivity between the eastern Caribbean and the southeastern USA (Hanson, 2022), while in the eastern North Atlantic (ENA), a lack of genetic differentiation is suggested among different archipelagos of Macaronesia (Alves et al., 2013; Miralles et al., 2016). On a North Atlantic basin-wide scale, Van Cise et al. (2019) performed phylogeographic analyses, and although the study was not particularly designed to test fine-scale east-west differentiation in the North Atlantic, samples from both sides were grouped within the same Atlantic lineage (often termed the Atlantic Naisa type, but note that no subspecies are currently formally recognized), suggesting no clear genetic differentiation on that scale. While this pattern is consistent with broad-scale affinity and may reflect past or recent connectivity, it does not in itself demonstrate current-day interchange between the ENA and WNA. Regional studies demonstrate extensive, wide-ranging movements (at the scale of hundreds of kilometers) and individual heterogeneity in movement behavior based on photo-identification and telemetry studies, yet direct evidence of ENA and WNA interchange has not been documented (Alves et al., 2018, 2019; Thorne et al., 2017; Tyson Moore et al., 2020; Wells et al., 2013; Weyn et al., 2025).

Accordingly, the current study investigates direct basin-wide movements in Atlantic Naisa short-finned pilot whales by cross-matching collaboratively compiled long-term photo-identification catalogues from the ENA and WNA using manual and algorithm-assisted dorsal-

fin matching. This approach could reveal whether individuals are shared between regions and thus whether current connectivity exists, while also guiding future research priorities and the management of the species in the North Atlantic.

4.3 Materials and Methods

To identify individual matches, photo-identification catalogues from three Macaronesian archipelagos (Madeira, the Canary Islands, and the Azores) in the ENA were compared with a compiled catalogue from the WNA, spanning several broader regions, as detailed below (Figure 4.2). Different workflows were applied across catalogue pairs due to access to updated photo-identification datasets over time and the release of emerging comparison-based methodologies.

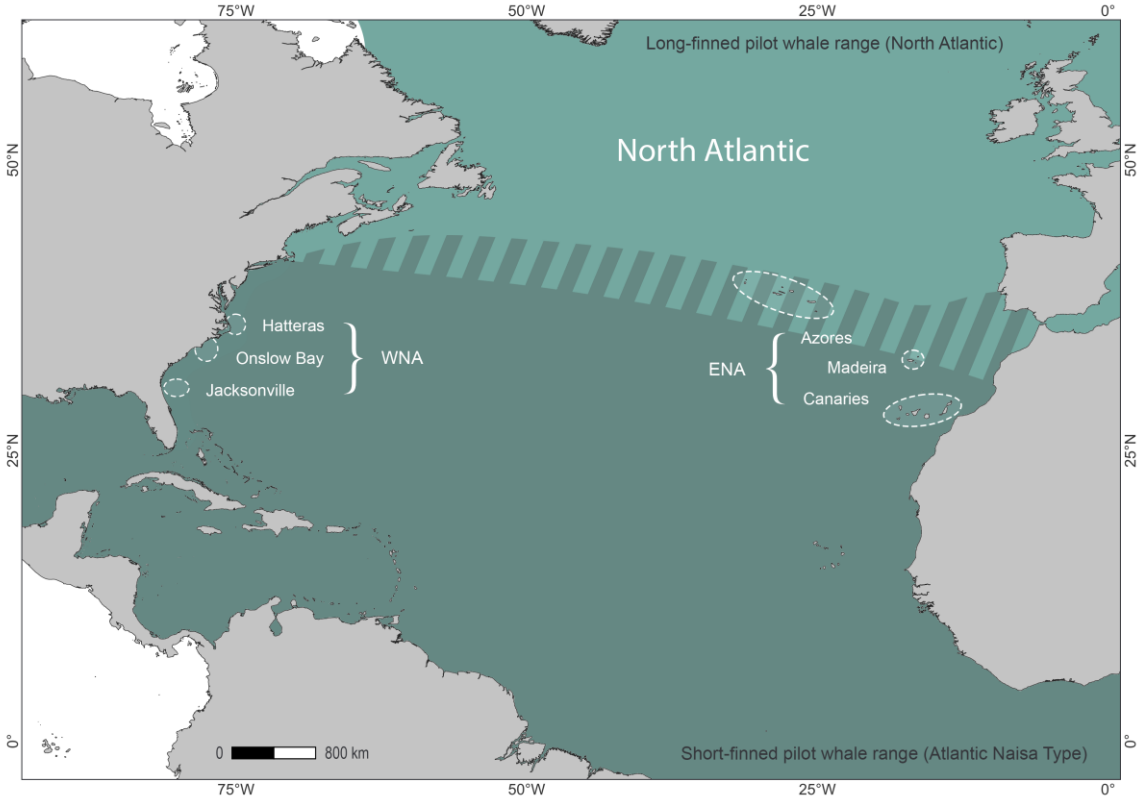

Figure 4.2: Broader regions from which short-finned pilot whale photo-identification catalogues were used for comparison purposes are highlighted by dotted lines. For the western North Atlantic (WNA), this includes Hatteras, Onslow Bay and Jacksonville, while for the eastern North Atlantic (ENA), this includes the Azores, Madeira, and the Canary Islands. Approximate ranges of North Atlantic long-finned pilot whales (*Globicephala melas*) and Atlantic Naisa type short-finned pilot whales (*G. macrorhynchus*) are shown for context, including where both overlap (diagonal lines). **Image: Adapted from Betty et al. (2023)**.

In general, only high-quality images of well-marked dorsal fins were included in the comparison datasets (following Alves et al., 2013), though very distinctive fins of lesser quality were also included where appropriate. Very poorly marked individuals (often including calves) and low-quality images were excluded, as they had a low probability of producing reliable matches and reduced certainty in match confirmation.

4.3.1 Comparison between Madeira and the WNA

A preliminary exploratory comparison between Madeira and the WNA was conducted manually in 2022, using photo-identification data compiled through 2020 (Table 4.1).

Table 4.1: Data summary of the preliminary manual short-finned pilot whale photo-identification catalogue comparison between Madeira and the western North Atlantic (WNA). Period = Year range covered by the images included in the catalogue; Total ind. (images) = Total number of individuals (and images) in the catalogue; Comparison ind. (images) = Total number of individuals (and images) used for comparison purposes. In the case of Madeira, only transient individuals (sighted only once) were used, as they were hypothesized to be more likely to cross vast areas.

Region (source)	**Area**	**Period**	**Total ind. (images)**	**Comparison ind. (images)**
WNA (Duke University)	Hatteras, North Carolina	2006-2020	1359 (1401)	802 (804)
Madeira (MARE-Madeira)	Madeira	2003-2020	1276 (1731)	191 (221[a])

[a] Only transient individuals (sighted only once) were used, as they were hypothesized to be more likely to cross vast areas.

Subsequently, in 2025 and 2026, improved photo-identification algorithms facilitated a more robust comparison of a more comprehensive dataset using Happywhale (Cheeseman et al., 2022), which implements the model developed by Patton et al. (2023), thereby increasing speed and reducing manual effort. The Happywhale photo-identification catalogue of Madeira consisted of photographic data collected from research vessels and platforms of opportunity along the south coast of Madeira between 2003 and 2024, comprising 1517 well-marked animals (2087 images) (as described in Alves et al., 2019; Weyn et al., 2025; Table 4.2). For the WNA, Duke University compiled photographic information from three locations (Hatteras, North Carolina, Onslow Bay, North Carolina, and Jacksonville, Florida; detailed in Table 4.2)

along the east coast of the USA between 2006 and 2023 collected during research trips, totaling 1483 individuals (1567 images). Because this dataset combined three regional catalogues, some overlap of individuals was possible. Comparisons in 2018 identified four matches between the Hatteras and Onslow Bay catalogues, whereas overlap between Hatteras and Jacksonville was not assessed. However, because the objective of the present study was to detect cross-regional matches between the ENA and WNA, overlap within the WNA dataset itself was not quantified further. For each individual, all suggested candidate matches provided by Happywhale were assessed by a photo-identification specialist with expertise in this program, and any potential matches were independently reviewed by at least three experienced photo-identification researchers.

Table 4.2: Summary of the short-finned pilot whale photo-identification catalogues that were used for comparison purposes between Madeira and the western North Atlantic (WNA), using Happywhale. Period = Year range covered by the images included in the catalogue; Total individuals = Total number of individuals in the catalogue on Happywhale; Total images = Total number of images in the catalogue on Happywhale. Uncertain numbers caused by potential individual overlap in the compiled information are indicated by an asterisk (*).

Region (source)	**Areas**	**Period**	**Total individuals**	**Total images**
WNA (Duke University)	East coast of the USA	2006-2023	1483*	1567
	* Hatteras	2006-2023	1393	1454
	* Onslow	2007-2017	23	26
	* Jacksonville	2009-2023	67	87
Madeira (MARE-Madeira)	Madeira	2003-2024	1517	2087

4.3.2 Comparison between the WNA and the Canary Islands and Azores

Comparisons between the WNA and the Canary Islands and the Azores catalogues were performed using FinFindR (Thompson et al., 2022). Photographic information for the WNA was compiled by Duke University, as described above, though the dataset for the FinFindR comparison was limited to data collected between 2006 and 2020, and consisted of data from

Hatteras, totaling 1359 well-marked individuals (1401 images). The Canary Islands catalogue was compiled by the Tonina Association and included images collected from research vessels and platforms of opportunity between 2004 and 2021, encompassing different regions in the Canary Islands, and totaling 1038 individuals (1038 images) (see Table 4.3). The Azores catalogue comprised 1023 individuals (1023 images) collected mainly in the south of Faial, Pico and São Miguel Islands (central and east groups), from 1999 to 2015, during dedicated and opportunistic (whale-watching) surveys (especially from the online MONICET platform) as described in Alves et al. (2019). As both the Canary Islands and Azores catalogues included information from different regions and/or sources, some overlap of individuals is possible, but this was also not quantified. Prior to analysis in FinFindR, images were manually cropped for optimal use. Dorsal fin contours generated in FinFindR were then visually checked and, where necessary, adjusted. Only images producing a reliable fin contour were used for matching. The top 20 candidate matches for each individual were visually assessed, and any potential matches were reviewed by experienced researchers.

Table 4.3: Summary of the short-finned pilot whale photo-identification catalogues, that were used for comparison purposes between the western and eastern North Atlantic (WNA and ENA, respectively), using FinFindR. Period = Year range covered by the images included in the catalogue; Total ind. (images) = Total number of individuals (and images) in the catalogue; Comparison ind. (images) = Total number of individuals (and images) used for comparison purposes. Uncertain numbers caused by potential individual overlap in the compiled information are indicated by an asterisk (*).

Region (source)		**Areas**	**Period**	**Total ind. (images)**	**Comparison ind.(images)**
WNA (Duke University)		Hatteras, North Carolina	2006-2020	1359 (1401)	802 (804)
ENA	Canary Islands (Tonina Association)	Tenerife, La Gomera, La Palma, El Hierro, Lanzarote, Fuerteventura	2004-2021	1038* (1038)	890* (890)
	Azores (Monicet)[a]	São Miguel, Faial, Pico	1999-2015	1023* (1023)	578* (578)

[a] Detailed catalogue composition described in Alves et al. (2019).

4.4 Results

The number of individuals used in the pairwise photo-identification catalogue comparisons are detailed in Tables 4.1-4.3.

The photo-identification catalogue comparisons did not result in any conclusive matches. Although Happywhale detected several strong potential matches between Madeira and the WNA (Figure S4.1), none could be confirmed with certainty.

4.5 Discussion

To our knowledge, this study represents the first photo-identification study that investigates basin-wide movements of Atlantic Naisa short-finned pilot whales across the North Atlantic using long-term catalogues spanning multiple regions. Negative results are inherently difficult to interpret, as non-detection does not necessarily imply absence of interchange. Nevertheless, the absence of matches is informative because the analysis covered a large spatiotemporal dataset, i.e., long-term catalogues across multiple regions. The results are briefly discussed in the context of North Atlantic oceanography, the species' physiology, habitat use, foraging ecology, and social structure, and future research priorities are highlighted.

The ENA and WNA are connected through the wind-driven North Atlantic subtropical gyre. Along the western boundary, the Florida Current/Gulf Stream transports surface waters rapidly northward and then eastward. Downstream, the Azores Current originates as a branch of the Gulf Stream near the Grand Banks and crosses the Mid-Atlantic Ridge toward the eastern basin, placing the Azores within a dynamic confluence zone. Farther east, the Azores Current passes north of Madeira and helps feed the southward Canary Current (Caldeira and Reis, 2017; Cropper, 2013; Frazão et al., 2022; Knoll et al., 2002). Short-finned pilot whale movements are known to be linked to these oceanographic features, especially in the WNA. Current-assisted travel along the Loop Current and Gulf Stream system has been documented (Tyson Moore et al., 2020), and some animals followed Gulf Stream meanders to move vast distances (> 1000 kilometers) offshore the continental shelf of the east coast of the USA (Thorne et al., 2017). However, none of these movements continued directionally toward the opposite side of the North Atlantic. Physiologically, basin-wide displacements could be feasible, as telemetry studies have documented movements spanning hundreds to thousands of kilometers over relatively short timespans, including extensive movements along the continental shelf, and between US waters and the Caribbean in the WNA (Tyson Moore et al., 2020; Wells et al.,

2013), and recurrent movements between different archipelagos in the ENA (Alves et al., 2018, 2019; Weyn et al., 2025). Though physiologically feasible, it is likely that oceanographic features and mesoscale variability in the North Atlantic structure and influence trans-Atlantic movements, but their role in facilitating or constraining basin-wide movements remains unclear.

Atlantic Naisa short-finned pilot whales typically use preferred/foraging habitats associated with steep bathymetry (e.g., (island) slopes and canyons) and mesoscale oceanographic features (e.g., fronts and (leeward) eddies) that can enhance prey availability and accessibility (Fernandez et al., 2021; Servidio et al., 2019; Shearer et al., 2022; Silva et al., 2014; Thorne et al., 2017). In the WNA, for example, Thorne et al. (2017) showed that area-restricted search (ARS) behavior was highest near the shelf break and in submarine canyons, consistent with reliance on bathymetric gradients for foraging opportunities. In the Webbnesia region (Canary Islands and Madeira, ENA), ARS movement (potentially related to foraging, resting, socializing, breeding, or calving) was concentrated around islands and other bottom-related features, with ARS generally favored under more stratified (shallower mixed layer) conditions, which can develop leeward of islands (unpublished data, see Chapter 2). In the Azores, movement data indicate that some island-associated short-finned pilot whales also range offshore towards the Mid-Atlantic Ridge (Movebank Study ID: 4044018643; https://www.movebank.org/), suggesting that some island-associated populations may in some regions combine insular habitat use with broader offshore movements. Although differences and specializations exist in the foraging strategies of the species on both sides of the Atlantic, to a certain degree, the species is also described as being able to strategically adapt its foraging strategies to local habitat features (Aguilar de Soto et al., 2008; Quick et al., 2017; Shearer et al., 2022). Such plasticity, together with diet variability (Aguilar de Soto and Alves, 2023), is compatible with long-distance movements. Nevertheless, trans-Atlantic crossings would require extended travel through areas where preferred habitat and prey-aggregating features may be less common, thereby reducing the ecological likelihood of basin-wide transitions. Transatlantic movements have been observed in Atlantic bluefin tuna, basking sharks, and other cetacean species, indicating that trans-Atlantic crossings are ecologically possible (Block et al., 2001; Gore et al., 2008; Mullin et al., 2022). It remains unclear why this has not yet been documented in short-finned pilot whales.

Under ongoing climate change, warming is expected to alter stratification, circulation and prey fields, and small cetaceans in the North Atlantic, including short-finned pilot whales, are

projected to undergo a broad poleward redistribution (Chandelier and Kiszka, 2026; Sousa et al., 2021), suggesting that the likelihood and potential routes of future interchange may shift as habitat suitability changes.

As a final note, social structure may shape the mode of long-distance movements. Short-finned pilot whales form stable social units with long-lasting, non-random associations in both sexes (Alves et al., 2013; Esteban et al., 2022), and inter-archipelago movements within Macaronesia (e.g., Madeira–Azores) have been documented and appear to involve at least subsets of associated individuals, including animals with strong site fidelity (Alves et al., 2013, 2018). Traveling with familiar associates may be advantageous through coordinated foraging, kin coordination and predator defense (Rendell et al., 2019; Wright et al., 2016). Any basin-scale interchange may therefore depend more on how often groups range into offshore oceanic habitat, which could be more likely in less-studied and more difficult to document transient/pelagic populations (described in Alves et al., 2013), rather than on the solitary dispersal capabilities of individuals.

Future directions

Although no direct movements were detected in the current study, conclusions must remain cautious, as it may reflect low detectability or rare interchange rather than proof of no connectivity. This caution is particularly relevant because, as outlined in the introduction, broad-scale phylogeographic analyses in the Atlantic suggest no clear genetic differentiation at the lineage level (Van Cise et al., 2019). However, the eastern North Atlantic was represented by very few samples. This very limited regional representation substantially restricts the power of the study to assess fine-scale differentiation between the eastern and western North Atlantic. Moreover, closer inspection of the mitogenome phylogeny indicates some internal structuring within the Atlantic clade. All Tenerife samples had haplotypes unique to Tenerife, and these samples fell on one side of an internal Atlantic split, together with two haplotypes detected in the Caribbean. Northwestern Atlantic haplotypes fell on the other side of this split, together with two additional Caribbean haplotypes, one of which was found in both the Caribbean and the northwestern Atlantic (Van Cise et al., 2019). Several demographic and evolutionary processes could produce such a pattern, including very recent isolation or divergence accompanied by incomplete lineage sorting, as well as a longer period of east–west differentiation followed by more recent immigration from the eastern Atlantic into the Caribbean. In line with this uncertainty, the study highlights a need for additional genetic data,

expanded analyses, and broader sampling to properly delimit an Atlantic Ocean subspecies. This suggests that the current data are insufficient to firmly exclude subtle east-west differentiation in the North Atlantic. Therefore, future genetic studies could (i) integrate demographic inference approaches (e.g., Carroll et al., 2019) to test for past and/or ongoing gene flow between populations (Hoelzel et al., 2026), which may provide an indirect proxy for connectivity, and (ii) employ more comprehensive genomic data (e.g., whole-genome sequencing), along with broader geographic sampling across the Atlantic (particularly from Africa and South America), to robustly assess fine-scale genetic differentiation.

Interpretation of the absence of photographic matches should also consider the relative population size and spatial coverage of the catalogues. The best abundance estimate for short-finned pilot whales in U.S. Atlantic waters from Florida north (extending out only to 200 nautical miles offshore), is approximately 19,000 individuals, although this estimate excludes the Gulf of Mexico, Puerto Rico, and other areas of the wider western North Atlantic (Hayes et al., 2024). The total western North Atlantic population may therefore be considerably larger, meaning that the photographic catalogue represents only a small proportion of the animals potentially occurring in the region. No directly comparable abundance estimate exists for the entire eastern North Atlantic study area. Available estimates cover particular archipelagos, survey areas, seasons, methodological approaches, and population components. Recent coordinated line-transect surveys conducted in 2017–2018 produced a model-based estimate of 3,204 individuals for the surveyed waters of the Canary Islands (95% CI: 2,128–5,926) and 223 individuals in the surveyed Madeira waters (95% CI: 156-369) (Esteban et al., 2026). The number of well-marked individuals included in the eastern North Atlantic comparisons was comparable to, and in some regions exceeded, the available regional abundance estimates. This suggests that the catalogues provided substantial coverage of the whales using these regions over time. However, because the abundance estimates refer to defined areas and survey periods, whereas the catalogues accumulated individuals over up to two decades, the exact proportion of the wider eastern North Atlantic population represented in the comparisons could not be quantified reliably. Future studies could apply approaches such as those described by Baird et al. (2009) and Aschettino et al. (2012) to estimate movement rates between areas or populations that are consistent with the absence of photographic matches.

The absence of matches cannot be interpreted as definitive evidence that trans-Atlantic movements do not occur. Additional good-quality photographic information and catalogue integration on reliable photo-identification platforms (e.g., Happywhale), especially from the

Azores - due to its central location in the North Atlantic, could increase the likelihood of detecting rare individual interchange, if present. In parallel, long-duration satellite biotelemetry data could further help quantify how tracks relate to fronts and eddies and elucidate potential movements between the ENA and WNA. Additional information on basin-wide movements and connectivity will be important for guiding the conservation and management of the species in the North Atlantic.

4.6 Acknowledgements

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4.8 Data availability

The majority of the photographic information from Madeira can be found on the Oceanic Observatory of Madeira webpage (https://oomdata.arditi.pt/products/catalogofotoid/), as well as Happywhale (https://happywhale.com/org/1681). The catalogue from the Canary Islands containing the majority of the images analyzed in the current study has been made available on a public repository (Weyn, 2024). The Azores data are currently not publicly available. The three WNA photo-identification catalogues included in this project, from Hatteras North Carolina, Onslow Bay, North Carolina and Jacksonville, Florida are also available on Happywhale.

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4.10 SUPPLEMENTARY MATERIALS

A) Gma0924 (2020) and Gma_8-070_HAT (2015)

B) Gma1104 (2017) and Gma_7-140_HAT (2013)

C) Gma1710 (2023) and Gma_7-483_HAT (2018).

Figure S 4.1: Three potential matches resulting from the photo-identification catalogue comparison between Madeira (eastern North Atlantic (ENA)) and the western North Atlantic (WNA), performed using Happywhale, with none being confirmed. The image from Madeira is shown on the left, while the image from the WNA is on the right.

CHAPTER 5

SEX-SPECIFIC LONG-TERM SOCIAL ASSOCIATIONS IN ATLANTIC NAISA SHORT-FINNED PILOT WHALES

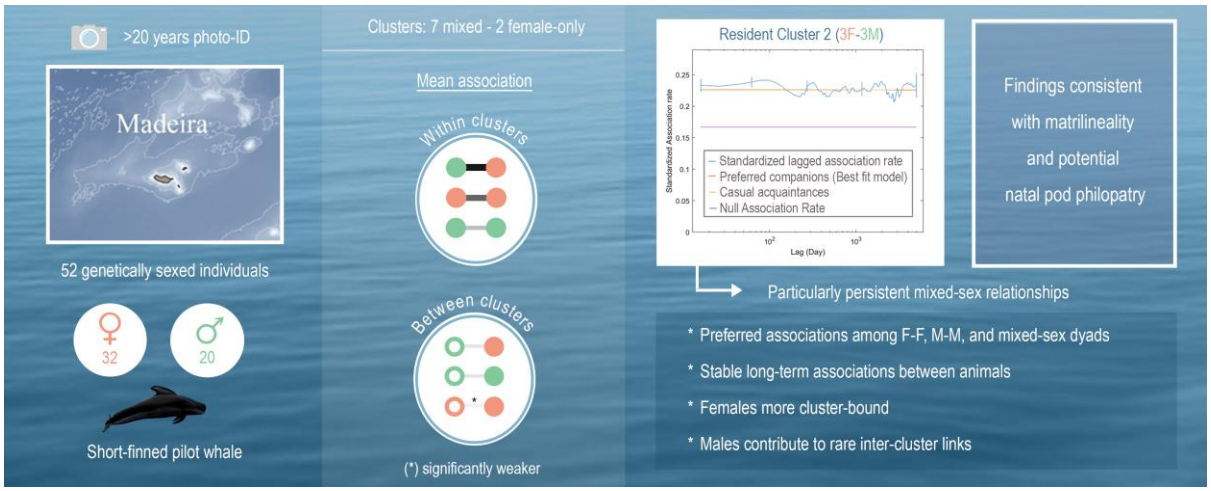

Figure 5.1: Graphical abstract of Chapter 5

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Weyn, M., Alessandrini, A., Alves, R., Ferreira, R., Dinis, A., Mateus, C. S., Fernandez, M., Alves, F. Sex-specific long-term social associations in Atlantic Naisa short-finned pilot whales.

5.1 Abstract

Among mammals, short-finned pilot whales *Globicephala macrorhynchus* exhibit complex social organization with stable units and indications of natal philopatry in both sexes. Clarifying such philopatry requires a combination of genetic and temporal analyses of individual association patterns, which remains preliminary for the Atlantic Naisa type. To address this knowledge gap, this study examined sex-specific association patterns, within- and between-cluster social structure, and temporal stability, using >20 years of photo-identification data (restricted to high or full coverage encounters) from 52 genetically sexed individuals (32 females, 20 males) in Madeira Island. Hierarchical cluster analyses revealed seven mixed-sex and two female-only clusters, with stronger associations within than between clusters. Within clusters, mixed-sex dyads had the highest association indices, followed by female-female dyads and male-male dyads, whereas between clusters, associations were uniformly weak, particularly for female-female dyads. Permutation tests showed preferred, persistent associations among female-female, male-male and mixed-sex dyads. Temporal analyses supported long-term stability of associations for both sexes, with particularly persistent mixed-sex relationships in a resident cluster. These findings are consistent with male natal philopatry but are not conclusive. Although kinship was not confirmed, the combination of strong temporal associations and within-cluster cohesion, low female-mediated connectivity, and male-involving inter-cluster links, supports a predominantly matrilineal social structure with males remaining socially embedded while mediating occasional connections between groups. This study provides the first detailed sex-specific description of social structure in Atlantic Naisa short-finned pilot whales and forms a basis for future genetic analyses to fully determine the extent of natal philopatry and matrilineal organization.

5.2 Introduction

Social structure is a defining feature of animal societies, shaping how individuals forage, reproduce, care for offspring, and respond to ecological pressures such as predation and resource distribution (Clutton-Brock, 2021). Among mammals, social organization ranges from largely solitary or loosely associated individuals to stable, long-term units that may persist across generations (Kappeler, 2019; Prox and Farine, 2020), with variation in the fitness consequences of group living among species and populations (Connor, 2002; East and Hofer, 2010).

Key mechanisms shaping social organization are dispersal and natal social philopatry (hereafter natal philopatry), defined as the tendency of individuals to remain in, or return to, their natal social unit (Clutton-Brock and Lukas, 2012). These processes influence gene flow, mating patterns, local competition, and the emergence of kin-structured societies (Clutton-Brock and Lukas, 2012). Dispersal strategies vary widely across taxa and are often sex- and age-biased, reflecting trade-offs among access to resources, mating opportunities, inbreeding avoidance, and costs of competition with relatives (Gamelon et al., 2025; Greenwood, 1980; Pusey, 1987). These dynamics are particularly relevant in species with long lifespans and enduring social bonds, such as in cetaceans, where natal philopatry can produce stable social units and long-term association structure (Badenas et al., 2022; Wright et al., 2023).

Considerable variation exists in both the extent of natal philopatry and the individuals that retain natal affiliations in cetaceans, at intra- and interspecific levels. In large-sized toothed whales, natal philopatry is typically sex-biased (Rendell et al., 2019). Females frequently remain in their natal groups, forming stable matrilineal social units structured around maternal kin, whereas males disperse, presumably to reduce kin competition and avoid inbreeding (Baird and Whitehead, 2000; Christal et al., 1998; Desportes et al., 1992). Although sex-biased dispersal is common, some species diverge from this pattern, displaying natal philopatry in both sexes, which is rare in vertebrates (de Stephanis et al., 2008; Martien et al., 2019; Ralls and Mesnick, 2019; Wright et al., 2016). Male natal philopatry may enhance inclusive fitness through kin cooperation, territorial or predator defense, and increased foraging efficiency (Boran and Heimlich, 2019; Rendell et al., 2019; Wright et al., 2016). To mitigate fitness risks related to philopatry, some species and populations display natal group exogamy, in which males mate with unrelated females from other groups, outside of their social group, before returning (Amos et al., 1993; Martien et al., 2019; Pilot et al., 2010).

Although both species of pilot whales - the long-finned *Globicephala melas* and the short-finned *G. macrorhynchus* - exhibit multilevel and highly cohesive social structures, their mating strategies are not yet fully understood (Aguilar de Soto and Alves, 2023; Betty et al., 2023). This is especially relevant for the latter species, for which mitogenomic analysis suggests the existence of three types associated with distinct oceanic regions, though no subspecies are currently formally recognized (Van Cise et al., 2019): i) Atlantic Ocean (more similar to the Naisa form), ii) western/central Pacific and Indian Ocean (Naisa), and iii) eastern Pacific Ocean and northern Japan (Shiho). Across these regions, studies have identified stable social units and/or long-lasting, non-random social relationships in short-finned pilot whales

(Alves et al., 2013; Esteban et al., 2022; Heimlich-Boran, 1993; Mahaffy et al., 2015; Riou et al., 2024; Servidio, 2014). Repeated co-occurrence of individuals across multiple years also suggests persistent social affiliations in the Mariana Archipelago, although low recaptures precluded formal quantification of association strength (Hill et al., 2019). In some populations, mating outside the natal social unit has been suggested, either through extra-pod mating during inter-pod associations, as observed in Hawai‘i and Macaronesia (Madeira and the Canary Islands) (Alves et al., 2013; Heimlich-Boran, 1993; Servidio, 2014; Van Cise et al., 2017) or through male movement among breeding schools, as suggested in Japan (Kasuya and Marsh, 1984).

These findings were mainly inferred either from genetics on free-ranging or stranded animals - which enables sex confirmation and kinship inference but often does not resolve the temporal dynamics of individual associations - and/or from long-term photo-identification studies - which provide a longitudinal perspective but do not allow for robust sex-specific inference without genetics. Combining both approaches can therefore provide a stronger framework for a detailed quantification of sex-specific associations. However, explicit quantitative analyses of sex-specific association dynamics remain uncommon, particularly those based on molecularly sexed individuals. For the Pacific Naisa type in Hawai‘i, long-term photo-identification has been complemented by extensive genetic sampling to examine how social structure aligns with kinship and to test for sex-biased dispersal (Mahaffy et al., 2015; Van Cise et al., 2017). Together, these studies show the value of combining these methodologies, but they did not systematically quantify association strength and temporal stability across sex-dyad categories. In the Atlantic Naisa context, encompassing short-finned pilot whales from tropical and warm-temperate Atlantic waters, including Macaronesia, sex- and age-class association analyses have been conducted (Heimlich-Boran, 1993; Servidio, 2014), but relied largely on morphological characteristics for sex assignment, which can be biased, especially for subadult animals. Additionally, in the North Atlantic, some social structure studies did not incorporate sex into their analyses (Riou et al., 2024), while other studies that included genetically sexed individuals i) lacked sex-specific association inference (Alves et al., 2013), ii) comprised a small number of genetically sexed animals (<5) (Esteban et al., 2022), or iii) addressed sex-specific analyses only preliminarily (Betty et al., 2023).

To address this knowledge gap, this study examines the sex-specific social structure and group fidelity of Atlantic Naisa short-finned pilot whales. To do so, a comprehensive social analysis based on longitudinal photo-identification data and genetically sexed short-finned pilot whales

from a well-studied population in Madeira is used. Building on the dataset used in Betty et al. (2023), the present study leverages a more substantial baseline, now spanning over two decades of photo-identification and incorporating a higher number of genetically sexed individuals. This allows an in-depth analysis of whether adult males and females exhibit long-term, stable associations with their social cluster, which may provide support for the natal philopatry hypothesis for Atlantic Naisa short-finned pilot whales. By resolving these dynamics at a sex-specific level, this study provides the behavioral groundwork necessary for future investigations integrating genetic analyses to robustly test natal philopatry.

5.3 Materials and Methods

5.3.1 Study area and target species

Located in the Macaronesia biogeographic region, the archipelago of Madeira (32º N 017º W, Portugal) is characterized by deep waters close to the shoreline. The region's habitat diversity is shaped by a combination of complex oceanographic processes, including leeward eddies, island wakes, and upwelling and downwelling patterns (Benazzouz et al., 2015; Caldeira et al., 2002). These features contribute to a unique environment, supporting a wide range of marine life and predators (McIvor et al., 2022), including the short-finned pilot whale, for which a few hundred island-associated individuals have been estimated (Alves et al., 2015; Verborgh et al., 2022), with a more recent one estimating 223 individuals in the surveyed Madeira waters (95% CI: 156-369) (Esteban et al., 2026). A certain degree of social philopatry has been suggested for this population, based on findings that individuals with different residency patterns may not be genetically isolated and that small groups are composed of related individuals (Alves et al., 2013). Those groups are predominantly composed of mixed sex and age, with stable, long-lasting relationships characterized by preferred companions (Alves et al., 2013; Esteban et al., 2022), and some animals are known to move to the neighboring Azores and Canary Islands and back (Alves et al., 2019; Weyn et al., 2025).

In this study, a group refers to a naturally occurring aggregation of short-finned pilot whales observed together in the field, and a cluster to a set of identified individuals assigned analytically on the basis of repeated and comparatively strong associations across encounters, A pod generally implies a stable social unit, often with assumed or demonstrated genetic relatedness; because relatedness was not assessed in this study, this term was avoided except when referring to terminology used in previous studies.

5.3.2 PHOTO-IDENTIFICATION

The photo-identification catalogue used in this study contains good-quality photographic and encounter information from 1472 well-marked short-finned pilot whales photographed between 2003 and 2024, obtained during year-round dedicated surveys and from opportunistic sources, such as whale watching operators. Effort information is available from previous publications (Alves et al., 2018; Sambolino et al., 2022). Photographic data were gathered using digital cameras equipped with telephoto lenses from vessels operating up to approximately seven nautical miles (~13 km) off the coast, with a focus on the lee side of Madeira Island, as this coincides with high aggregation areas for the species (Esteban et al., 2022; Fernandez et al., 2021; Freitas et al., 2026). Individuals were considered to belong to the same group on a single day if they were observed within a 250m radius of each other and exhibiting similar behavior (Heimlich-Boran, 1993).

The compilation of the catalogue followed standard photo-identification procedures (Würsig and Würsig, 1977), based on the unique pattern of markings on the leading and trailing edges of the dorsal fin, as well as overall shape, coloration, and scarring. Pictures of both sides were collected, distinctiveness and picture quality were assigned visually (following Alves et al., 2013), and individuals were grouped based on the number of notches on the trailing edge of the dorsal fin (Alves et al., 2019; Würsig and Jefferson, 1990). Collected pictures up until (and including) 2020 were compared with the catalogue visually by a specialist, while pictures from 2021-2024 were compared using the Happywhale platform (Cheeseman et al., 2022), using the model developed by Patton et al. (2023), to increase the speed and reduce the workload.

5.3.3 RESIDENCY PATTERN

A residency pattern was attributed to individuals based on their photographic capture histories, considering seasonality, years, capture frequency, and the subdivision into clusters (see 5.3.5). A capture was defined as an individual identification from a photographic encounter. Residents are individuals that exhibit multiyear and year-round site fidelity, i.e., photographed in at least four years and in all four seasons. These animals were typically photographed throughout the entire study period or at regular intervals since their initial capture. Extended Visitor and Regular Visitors exhibit a multi-year presence, albeit seasonal-specific, between July and March (covering three consecutive seasons) and between July and December (covering two consecutive seasons), respectively. Occasional Visitors/Transients were photographed once

(i.e., not previously catalogued) or within a few days apart and not mixed with catalogued animals (to avoid erroneous classification of new/non-catalogued resident or visitor animals).

5.3.4 Biopsy collection

During dedicated research trips, biopsy samples were collected using a biopsy darting system (Mathews et al., 1988) and immediately stored in liquid nitrogen. No animals with young individuals in the vicinity were targeted, nor were juveniles themselves, to minimize any potential impact. Molecular analyses of these samples allowed for the genetic sexing of 52 individuals (as detailed in Ferreira et al., 2025). To ensure accuracy, this study did not include any individuals whose sex was visually determined (e.g., dorsal fin shape and/or association with calves).

5.3.5 Social analysis and dataset

Social analyses were restricted to genetically sexed individuals, thus social groups presented here represent subsets rather than complete social groups. Due to the nature of whale watching data, which comprises a large proportion of the dataset, it is possible to capture the same group multiple times a day. When this was the case, individuals were merged into one encounter to ensure independent evidence of association and to avoid autocorrelation (Bejder et al., 1998). To improve accuracy, only encounters with high or full coverage were considered. Therefore, a selection was made of all encounters where the proportion of photographically captured individuals per encounter was ≥0.8 (Alves et al., 2013). Additionally, only encounters with >1 sexed individual present and individuals with ≥4 captures were considered for all analyses, except for the temporal (SLAR) analyses, which used all data regardless of capture frequency. This threshold was chosen to balance precision and retain sufficient information. Such reasoning is because individuals with few captures (i.e., <4 times) provide only limited information on association strength and can introduce noise (Whitehead, 2008a), while employing higher thresholds might improve metric precision but reduce sample size. Additionally, the dataset was restricted to distinctive (i.e., well-marked) individuals (as defined in Alves et al., 2013).

Overall, the final dataset for the social analyses comprised 46 distinctive, genetically sexed individuals from groups with high or full coverage, including >1 sexed individual and ≥4 captures; except for the temporal analysis, which used the 52 biopsied individuals. All analyses were performed using the compiled version of SOCPROG v2.9 (Whitehead, 2009).

5.3.5.1 Associations patterns

The association strength between sexed individuals was investigated by calculating association indices. The sampling period was defined as one day, and associations as individuals grouped during the sampling period. To quantify the association strength between short-finned pilot whales, the half-weight association index (HWI) was used (Cairns and Schwager, 1987) as it minimizes potential bias associated with missing identifications (Whitehead, 2008b). This index takes a value between 0, meaning the individuals were never associated, and 1, indicating they were always photographed together. Additionally, mean and maximum association were also calculated to provide further insight into the frequency and strength of associations among individuals. The variation in the social system, or social differentiation, defined as the coefficient of variation of the true association indices, was estimated using the maximum likelihood method. Values <0.3 suggest a homogeneous society, values >0.5 indicate a well-differentiated society, and values >2.0 correspond to extremely well-differentiated societies (Whitehead, 2009). Furthermore, the correlation coefficient between the true and calculated association indices was determined using the maximum likelihood method. This coefficient indicates the power of the analysis to detect the true social system. A value of 1.0 indicates a perfect representation, while 0.0 indicates no informative value. Values close to 0.4 are considered to give a "somewhat representative" indication, and 0.8 a "good representation" (Whitehead, 2008a, 2008b, 2009). The standard errors for both indexes were calculated from 1000 bootstrap iterations. A Mantel test was carried out to assess overall differences in association between and within sex classes (Schnell et al., 1985).

5.3.5.2 Preferred associations

Permutation tests were performed to identify preferred associations (Bejder et al., 1998; Whitehead, 1999) between all individuals, and between and within sex classes. The null hypothesis was that individuals associate with the same probability with all other individuals, given their availability. Significantly higher observed coefficients of variation (CV) of the pairwise association indices compared to the permuted datasets were used as indications of preferred companions. The number of permutations was increased until the p-values stabilized (Bejder et al., 1998; Whitehead, 1999), using 1000 trial flips per permutation (Whitehead, 2009).

5.3.5.3 Hierarchical cluster analysis

A hierarchical cluster analysis was performed to classify and quantitatively illustrate relationships between the sexed individuals. The cophenetic correlation coefficient (CCC),

which ranges from 0 to 1 and indicates how well the dendrogram matches the association index matrix, was obtained and used to decide which linkage method would provide the best representation of the data (Whitehead, 2009). A CCC >0.8 indicates that the dendrogram is a good match and represents the population well (Whitehead, 2008a).

Modularity was used as a measure to assess how well the population could be divided into social units (Newman, 2004; Whitehead, 2008a). It can be described as the difference between the proportion of the total association within clusters and the expected proportion, given the summed associations of the different individuals. Modularities >0.3 are usually considered to indicate a useful division of the data (Newman, 2004). The threshold for defining clusters was chosen as the association index that produced the maximum modularity (Q) while accounting for differences in individual gregariousness (Whitehead, 2008b). A Mantel test was performed to assess differences in association strength between and within clusters, and a Kruskal-Wallis nonparametric test to investigate if association strength differed by residency pattern.

A resident cluster previously analyzed in Alves et al. (2013) (R4) and identified in the current analysis (under R2) was analyzed in more detail, as it contained animals of both sexes (three females - three males) and had the highest number of captures between 2003 and 2024. Additionally, two female-only clusters, although not observed throughout the entire study period, were assessed to investigate female-female associations.

Kruskal-Wallis nonparametric tests followed by Dunn post hoc tests were performed in the R Statistical Software v4.1.3 (R Core Team, 2022) to assess whether dyad type associations (female-female (F-F), male-male (M-M), mixed sex) differed within and between clusters.

5.3.5.4 Network analyses

A social network diagram was generated using NetDraw 2.176 (Borgatti, 2002) to qualitatively illustrate the social structure (Whitehead, 2008a). Clusters identified through hierarchical cluster analysis were used to assign individuals to discrete social clusters. Nodes represent individuals, colored according to their social cluster, while the thickness and color of connecting lines denote the strength of association between dyads. Sex was incorporated as an additional attribute for each individual and visualized through node shapes. A spring-embedding algorithm using squared distances was used to construct the network diagram.

5.3.5.5 Temporal analysis

To investigate long-term temporal stability in the association patterns, standardized lagged association rates (SLARs) were calculated for all sexed individuals, regardless of capture frequency (Alves et al., 2013). The method calculates the probability that, given an association between two individuals at a particular time, following a defined interval, the second individual will be a randomly chosen associate of the first (Whitehead, 2009). Standardized rates were used because it is highly likely that not all true associates of an individual were recorded during the sampling period. The moving average was chosen to balance smoothing and precision, and standard errors (SE) were estimated using the jackknife method (Whitehead, 2009). A moving average of 8000 was used for the temporal analyses of all sexed individuals, while for Resident cluster 2, a moving average of 4000 was used. Four mathematical models representing different social association patterns were fitted to the data simultaneously, along with a null association rate. The first model (preferred companions) posits that certain pairs of individuals exhibit a consistent preference for association over time. The second model (casual acquaintances) describes interactions involving casual acquaintances, who may associate for a period, subsequently disassociate, and potentially reassociate later. The third model (casual acquaintances + preferred companions) indicates preferred companions and casual acquaintances. The final model (two levels of casual acquaintances) suggests distinct levels of disassociation. The model with the lowest Quasi Akaike Information Criteria (QAIC) was selected as the best-fitting model (Whitehead, 2008a). The fit of the other models was also assessed by comparing the differences (Δ) in QAIC between each model and the best-fitting model. A ΔQAIC <2 indicates substantial support for the model; if between 4 and 7, it has less support; and if >10, there is no support (Burnham and Anderson, 2002).

A separate SLAR was also created for the individuals from the resident group previously identified in Alves et al. (2013) and also in the current study, for all individuals and within and between sex classes. Additionally, a SLAR was created for two female-only clusters. Although they have fewer photographic captures and were not photographed throughout the entire study period, they provide information on temporal association trends in females.

5.4 Results

5.4.1 Association patterns

The dataset consisted of 437 encounters, with 27 females (F) and 19 males (M). In brief, most individuals showed a high number of captures, i.e., 18 individuals (39%) had between 11 and 30 photographic captures and 15 individuals (33%) had between 31 and 96, and only three

individuals (7%) had <6 captures (Figure S5.1). Due to restricting the analyses to individuals with ≥4 captures, only three residency patterns were identified, as follows: Residents: 43%, of which 50% F and 50% M; Extended Visitors: 20%, of which 33% F and 67% M; Regular Visitors: 37%, of which 82% F and 18% M.

A social differentiation estimate of 1.373 (SE = 0.014) and a correlation coefficient of 0.416 (SE = 0.009) were obtained, reflecting a well-differentiated society and a moderately accurate representation of the social system. The mean association index among sexed individuals was low (0.042 ± 0.016) (Figure S5.2.A). Analysis of dyadic associations revealed that the majority (79%) were never recorded as being associated with each other during the study period. Despite the generally low average association, some individuals demonstrated notably stronger social connections. The average maximum association index was 0.639 ± 0.197 (range = 0.11 - 0.92; Figure S5.2.B). Notably, 26% of the individuals exhibited a maximum association index >0.8.

Association rates did not differ significantly between and within sex classes (Mantel test: p>0.2). However, within-sex associations (mean HWI = 0.046 ± 0.029) were slightly higher than mixed-sex associations (mean HWI = 0.037 ± 0.031) (Table S5.1). Female-female pairs showed the highest mean association values (0.048 ± 0.034), with some dyads exhibiting particularly strong bonds (average maximum = 0.510 ± 0.249). Male-male associations were weaker (mean = 0.043 ± 0.021, average maximum = 0.452 ± 0.205). Mixed-sex associations (F-M: mean HWI = 0.037 ± 0.038; M-F: mean HWI = 0.037 ± 0.018) were lower on average and more variable, with a few stronger dyads (F-M: average maximum = 0.356 ± 0.341; M-F: average maximum = 0.578 ± 0.242; Table S5.1).

5.4.2 Preferred companions

Significantly high CV (observed = 3.223, random = 3.064, p<0.001) of all association indices indicate that tested individuals are not associated at random but instead have long-term preferred companions (Table 5.1). Across all sex categories, the CV of the observed HWI was consistently higher than that of the randomized data, with significant p-values in every case, indicating the presence of preferred companions among both same-sex and mixed-sex pairs. Notably, mixed-sex dyads showed the largest deviations from random values, suggesting the clearest signs of strongly preferred partners.

Table 5.1: Permutation test results for preferred associations within and between sexed short-finned pilot whales off Madeira, photographed between 2003 and 2024. CV= Coefficient of variation, HWI = half-weight association index, F = female, M = male.

	CV of observed HWI mean	CV of random HWI mean	p-value
F-F	3.08963	3.04819	0.001
M-M	2.96749	2.89047	0.003
F-M	3.61159	3.49524	<0.001
M-F	3.61159	3.5318	0.001
All individuals	3.30222	3.12128	0.001

5.4.3 HIERARCHICAL CLUSTER ANALYSIS

The average-linkage method was used as it represented the highest CCC (= 0.986), suggesting that the dendrogram matches the matrix of association indices very well. The existence of preferred companions, along with the high cophenetic correlation coefficient, provides robust support for the use of a cluster diagram.

A maximum modularity of 0.796 was obtained at an association index of 0.039. The cluster diagram based on genetically sexed individuals divided them into nine clusters (four Resident, three Regular Visitor and two Extended Visitor clusters) (Figure 5.2). Of these, seven consisted of mixed sexes, while the other two consisted of females only. The smallest cluster contained three members, while the largest contained six.

A positive matrix correlation coefficient (r = 0.831) indicates the existence of significant differences in association strength within and between clusters. Association levels within clusters were significantly higher than those among clusters (mean: 0.402 ± 0.155 and 0.004 ± 0.004, respectively, p<0.001; Table S5.2). Mixed-sex clusters spanned a slightly wider range of mean and maximum association values (mean = 0.239-0.656, mean maximum = 0.460-0.853) compared to female-only clusters (mean = 0.245-0.510, mean maximum = 0.533-0.728). Mean and mean maximum association did not differ significantly among residency patterns (Kruskal-Wallis, p = 0.801 and p = 0.607, respectively).

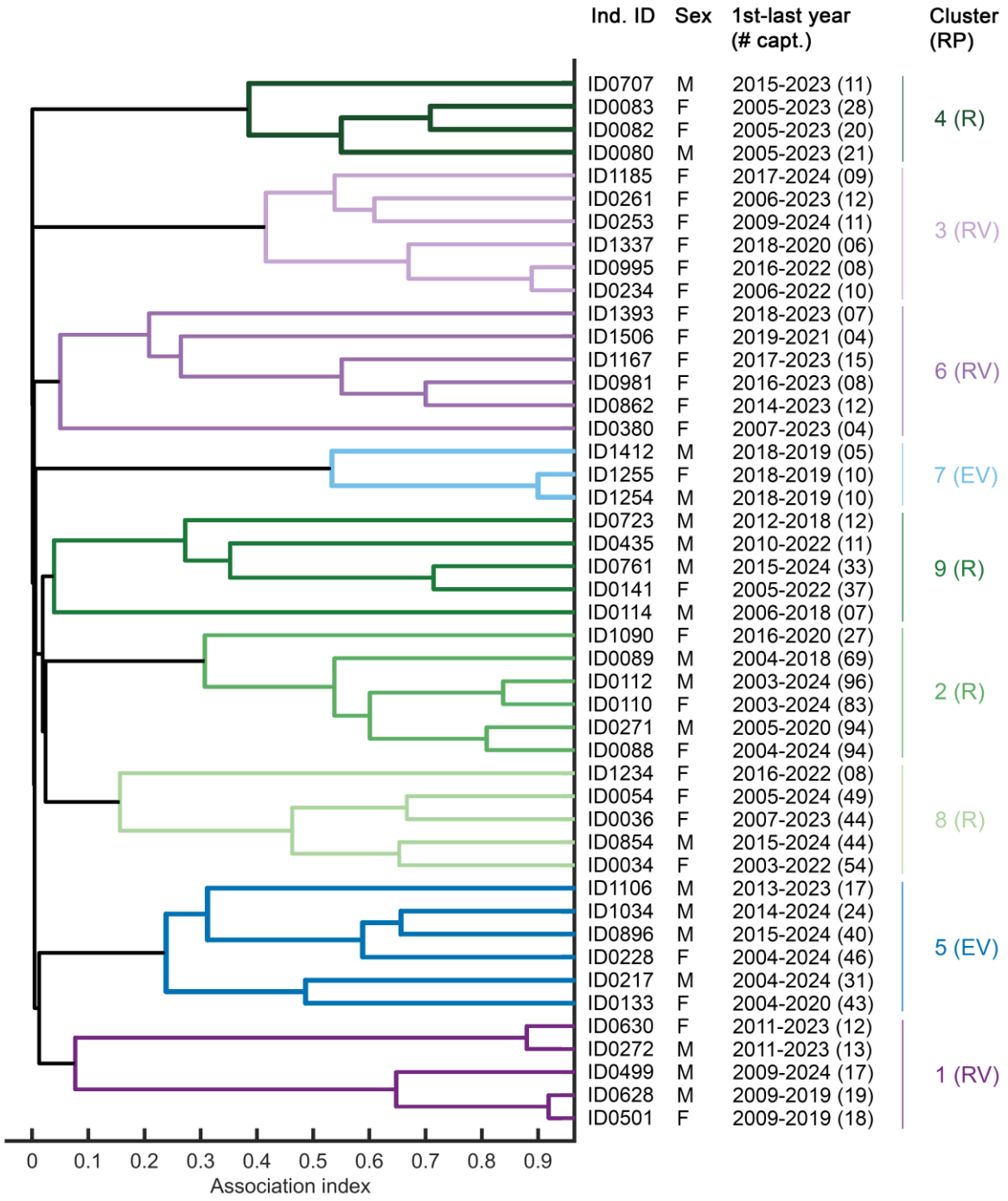

Figure 5.2: Cluster diagram of sexed short-finned pilot whales off Madeira, based on individuals with ≥ 4 photographic captures between 2003 and 2024. Individual identification (Ind. ID), the sex (F = female; M = male), the first and last year the animal was photographed (number of captures), and the number of the cluster (with assigned residency pattern (RP)) are provided on the right. Clusters in shades of green indicate Residents (R), in blue indicate Extended Visitors (EV), and in purple indicate Regular Visitors (RV).

Within clusters, no significant differences in mean and mean maximum association across dyad types (F-F, M-M, mixed) were observed (Kruskal-Wallis, $p = 0.281$ and $p = 0.151$, respectively), though M-M dyads showed the lowest values compared to F-F (intermediate) and mixed-sex dyads (highest values) (Table S5.3). Between clusters, mean associations were significantly lower for F-F dyads compared to both mixed-sex and M-M dyads (Kruskal-Wallis, $p = 0.007$; Dunn's test for multiple comparison: $p<0.05$). Mean maximum associations across dyad types were also significantly different (Kruskal-Wallis, $p = 0.043$); however, no individual pairwise comparison was significant under Bonferroni correction. Nevertheless, the Dunn post-hoc tests revealed trends toward lower mean maximum associations in F-F dyads, compared to both M-M (Dunn's test for multiple comparison: $p = 0.073$) and mixed-sex dyads (Dunn's test for multiple comparison: $p = 0.108$).

Resident cluster 2 was analyzed in more detail as it consists of six individuals with an equal sex distribution (three females and three males) and contains animals observed throughout the entire study period, with a high number of captures (mean = 86). The cluster has a relatively high mean and mean maximum association rate, with some dyads displaying very strong associations (mean = 0.516 ± 0.112, average maximum = 0.704 ± 0.197; Table S5.2). Two individuals from this group (ID0088 and ID0271) were photographed between 2004 and 2020, displaying an association rate of 0.809. Similarly, individuals ID0110 and ID0112 displayed a very high association rate of 0.880 and were repeatedly photographed together throughout the entire study period (2003 to 2024).

5.4.4 Temporal analysis

The dataset consisted of 959 encounters, with 32 females and 20 males. Based on the lowest QAIC, the model that best fit the SLAR data for all sexed individuals was the *casual acquaintances* model, although the *casual acquaintances + preferred companions* model also showed substantial support (Table 5.2, Figure 5.3.A). Associations declined only gradually over increasing time lags, while remaining consistently well above the null association rate.

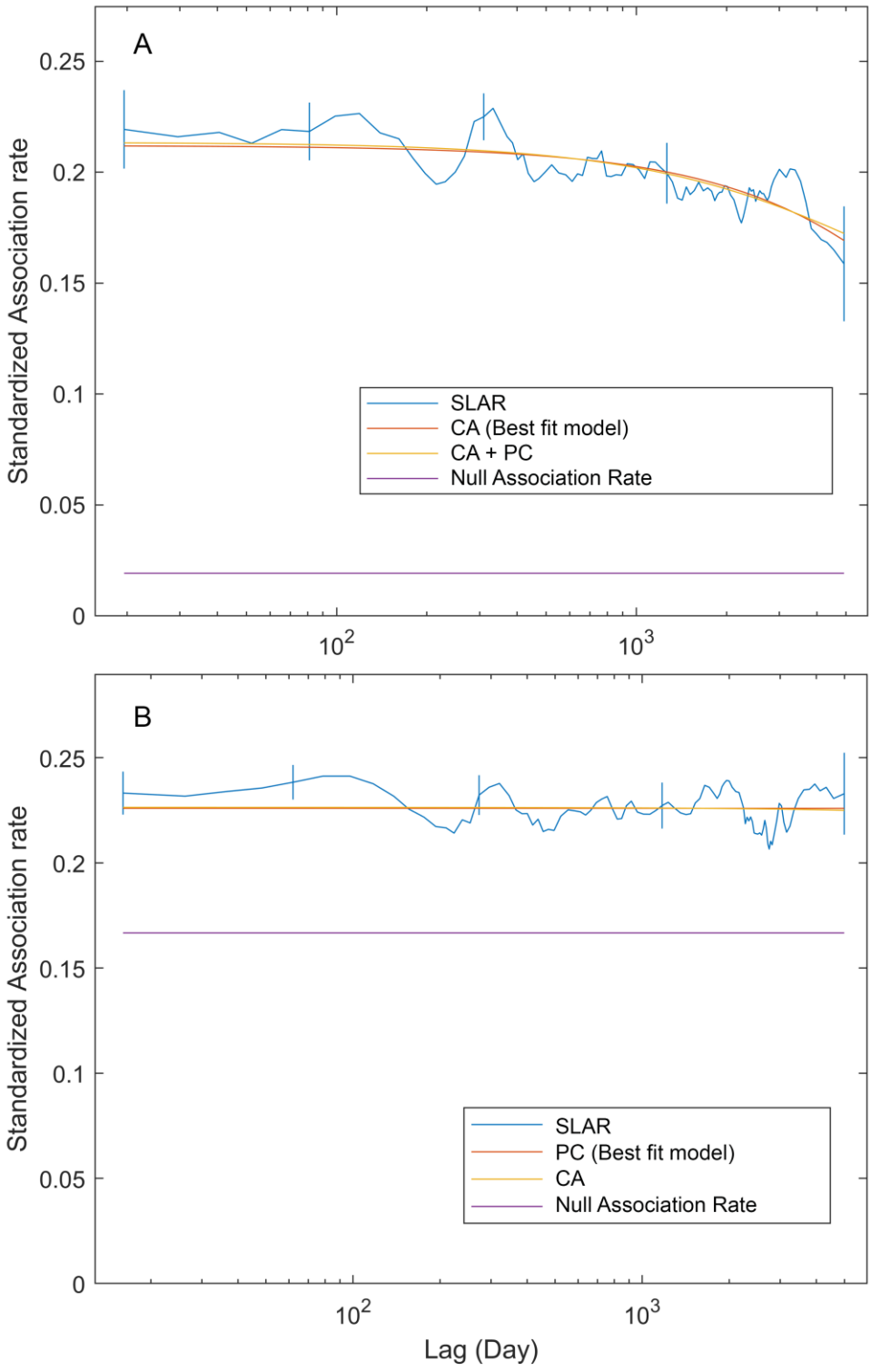

Figure 5.3: Standardized lagged association rate (SLAR) for A) all 52 sexed short-finned pilot whales, and B) Resident cluster 2 (consisting of three females and three males), photographed in Madeira between 2003 and 2024, calculated using a moving average of 8000 and 4000, respectively, with standard error bars produced through jackknifing. The null association rate, best-fitting model, and model with substantial support are shown. PC = preferred companions, CA = casual acquaintances.

Associations in Resident cluster 2 remained stable over time, with the best-fitting model being the *preferred companions* model; however, the *casual acquaintances* model also showed substantial support (Table 5.2, Figure 5.3.B). Temporal analyses by sex class are available in the supplementary information (Table S5.4, Figure S5.3). They indicate that, in this cluster, mixed-sex dyads and males among each other show long-term associations with preferred companions (although some support exists for casual acquaintances), while females among each other are characterized by casual acquaintances. As the results are based on limited information (3F, 3M), these should be interpreted cautiously.

Table 5.2: Models fitted to the standardized lagged association rate (SLAR) for all sexed short-finned pilot whales off Madeira, and the Resident cluster 2, photographed between 2003 and 2024. PC = preferred companions, CA = casual acquaintances. QAIC = Quasi-likelihood Information Criterion, the smallest value indicates the best-fitting model. ΔQAIC = The difference in the QAIC of the model in question and the best-fitting model; which when <2 can also provide substantial support (both models in bold).

SLAR	Model	Model formula	QAIC	ΔQAIC
All	PC	0.1976	210605.72	174.83
	CA	**$0.212\ e^{(-4.5716e-05 \times td)}$**	**210430.89**	**-**
	PC + CA	**$0.14323 + 0.070206\ e^{(-0.00017805 \times td)}$**	**210431.86**	**0.97**
	Two levels of CA	$8.1068\ e^{(-7.7482 \times td)} + 0.21196\ e^{(-4.5633e-05\ td)}$	210434.85	3.96
Cluster 2 (R)	**PC**	**0.22593**	**152652.56**	**-**
	CA	**$0.22638\ e^{(-1.2412e-06 \times td)}$**	**152654.46**	**1.90**
	PC + CA	$0.22592 + 0.031841\ e^{(-2.057 \times td)}$	152656.53	3.97
	Two levels of CA	$8.0898\ e^{(-7.7031 \times td)} + 0.22635\ e^{(-1.1852e-06 \times td)}$	152658.43	5.87

Results regarding the female-only clusters (Table S5.5, Figure S5.4) indicate that females form long-term preferred companionships, though the analysis also showed substantial support for the *casual acquaintances* model. Because these results are based on fewer captures, they also require some caution in interpretation.

5.4.5 SOCIAL NETWORK ANALYSIS

The 46 sexed individuals formed a single social network (Figure 5.4). Two clusters had limited links to the main network. One resident cluster was connected to the main social network solely through a single individual. This male was associated with two females of another resident cluster. The other cluster (Regular Visitor) with few connections linked to the main network through two females who were associated with two males from a resident cluster (different from the resident clusters mentioned before). Several other clusters maintained numerous connections across multiple clusters. Association strength was strongest between individuals within the same cluster, while connections between clusters were weak.

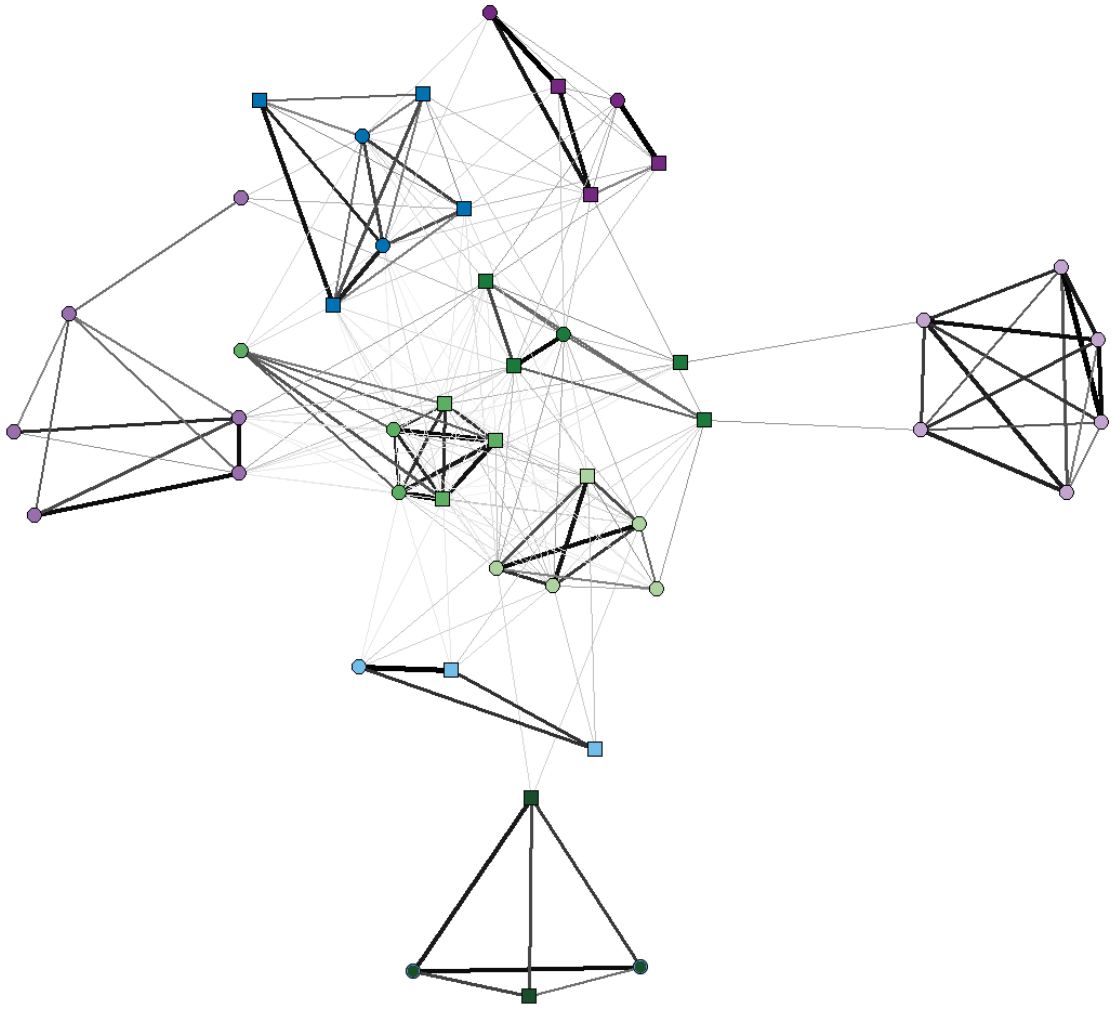

Figure 5.4: Social network of 46 genetically sexed short-finned pilot whales photographed off Madeira between 2003 and 2024. Nodes represent individual whales, colored according to their residency pattern (green = Residents, blue = Extended Visitors, purple = Regular Visitors) and

clusters (different shades) as defined by hierarchical cluster analysis using the half-weight association index. Node shape indicates sex (squares = males; circles = females). Edges are colored (and scaled in width) according to association strength (light grey/thin = weaker, black/thick = stronger).

5.5 Discussion

This study provides the most comprehensive examination of social structure and temporal association stability in genetically sexed Atlantic Naisa short-finned pilot whales, complementing previous studies (Alves et al., 2013; Boran and Heimlich, 2019; Esteban et al., 2022; Hartny-Mills, 2015; Heimlich-Boran, 1993; Servidio, 2014; Servidio et al., 2019). By restricting analyses to individuals of known sex inferred from molecular analysis, the study provides insights into how (sub)adult males and females partake in groups and how their associations persist through time. Due to not capturing the complete group composition, this approach requires caution in interpretation. However, the study enables discussion of sex-specific association patterns and potential philopatry in both sexes, contributing to a still not well-studied topic in short-finned pilot whales.

Overall patterns among sexed individuals were indicative of the social structure documented in short-finned pilot whale studies worldwide (Hartny-Mills, 2015; Mahaffy et al., 2015; Servidio, 2014), as well as in the local population. In the latter, weak associations were common, yet particularly strong connections were established among individuals within clusters (Alves et al., 2013; Esteban et al., 2022). This was visually detectable in the network analyses, which revealed a single, cohesive social network in which all clusters were interconnected through both sexes, albeit through weak ties. Although satellite clusters were described for this target population by Alves et al. (2013), none were detected in the current study. The structure is consistent with a community composed of stable groups that occasionally interact or join larger aggregations but maintain strong internal cohesion, as previously suggested for short-finned pilot whales (Alves et al., 2013; Boran and Heimlich, 2019).

This is also supported by the significant differences in association strength within and between clusters, as observed in other regions (Mahaffy et al., 2015; Servidio, 2014). Across all sex dyads, association indices were substantially higher within clusters than between clusters, confirming that meaningful and persistent social relationships are primarily maintained at the

group level. Clusters varied in the density and strength of their inter-cluster links, indicating that some groups engage more frequently with the broader population than others. However, the network diagram and overall study should be interpreted in the context of sampling constraints. The mean group size in Madeira is approximately 15 individuals, and many group members were never biopsied and, consequently, are not represented in this analysis, although they may form key connections (Alves et al., 2013). This is particularly relevant for clusters (especially one resident cluster) that appear to connect to the rest of the network through only one or two sexed individuals. Although less-connected clusters (which included resident individuals) have been documented elsewhere (Mahaffy et al., 2015), previous work in Madeira suggests that most resident clusters maintain substantial inter-connections in the main network (Alves et al., 2013; Esteban et al., 2022), and some of the apparent sparsity of inter-cluster links in the current study likely reflects sampling incompleteness rather than strict biological segregation.

General findings aligned with those from Servidio (2014), in that association patterns differed between and within sex classes (though significantly in the case of Servidio, 2014), and that within-sex associations tended to be stronger than mixed-sex associations overall. However, breaking these patterns down by sex dyad and cluster membership revealed a more nuanced picture. Within clusters, mean and mean maximum association indices among sex dyads tended to be lowest for male-male dyads, intermediate for female-female dyads, and highest for mixed-sex dyads. Although no significant differences were observed, the lowest male-male associations may indicate that males form more variable bonds with other males within their group. These findings partly contradict results from Heimlich-Boran (1993), who observed the strongest associations among adult males, both within and among pods. However, methodological differences, including demographic classification (sex and age classes vs sex only), sex assignment (photogrammetry/field-based inference vs genetic sexing), and the resolution of between-unit relationships (linked and unlinked pods vs a single pooled between-cluster category), as well as differences in analytical workflow (e.g., the association index used and network inference framework) may confound direct comparison between studies. Mixed-sex dyads being strongest within clusters indicate that males form strong associations within their groups, some of which potentially reflect persistent mother-offspring relationships.

Between clusters, females rarely formed strong ties, while males were more likely to participate in occasional but stronger inter-cluster relationships, either with other males or females. This pattern is consistent with the idea that females are more philopatric and cluster-bound, which

may confer advantages such as cooperative foraging, alloparental care, and communal defense (Rendell et al., 2019), while males may mediate connectivity between social units, for example, through temporary associations with individuals from other pods for mating or social purposes, as also observed in long-finned pilot whales (de Stephanis et al., 2008; Rendell et al., 2019). This male inter-pod connectivity may help offset potential fitness costs of philopatry, including increased kin competition and elevated inbreeding risk (Ford et al., 2018; Martien et al., 2019). Larger groups of short-finned pilot whales are observed in the warm-temperate water of the eastern North Atlantic in the warmer months of the year, potentially reflecting such aggregations of smaller groups (Alves et al., 2013; Heimlich-Boran, 1993). The relatively strong within-cluster associations involving females, combined with their weak links across clusters, indicate that groups may be structured along matrilineal lines. This aligns with previous research, which has shown that short-finned pilot whale populations exhibit higher relatedness within groups than between groups (Alves et al., 2013; Van Cise et al., 2017).

Permutation tests indicated significant preferred and persistent associations not only among females and among males, but also among mixed-sex dyads. These results imply that long-term, non-random social bonds are maintained across sex classes within the subset of the population, and support that mixed-sex dyads form part of the core social structure rather than being restricted to transient affiliations.

Most clusters obtained through the hierarchical cluster analyses contained both females and males, as similarly described by Alves et al. (2013), Servidio (2014), and de Stephanis et al. (2008), among others, for both species of pilot whales. However, two female-only clusters were also observed. Groups without adult males have been previously documented in short-finned pilot whales (Heimlich-Boran, 1993; Mahaffy et al., 2015; Servidio, 2014), and may reflect female-bias observed in adult short-finned pilot whale groups (Olson, 2009), or represent groups from which males have dispersed, groups in which males are temporarily absent, or genuinely female-centered groups. However, in the current study, the absence of males in certain clusters does not necessarily imply that groups are biologically male-free. It could also reflect sampling incompleteness (e.g. males in those groups not biopsied or not meeting inclusion criteria). Although male-only or strongly male-biased groups have been described in some regions (Baird, 2016; Heimlich-Boran, 1993; Mahaffy et al., 2015), no such groups were identified in the current study or observed in the field during two decades of intensive fieldwork off Madeira (Betty et al., 2023), suggesting potential regional variation in male social strategies. Both female-only and mixed clusters exhibited mean and maximum within-cluster

association values within comparable ranges, suggesting that the presence or absence of males within a cluster does not substantially alter internal association patterns.

At the cluster level, mean association varied considerably but did not differ significantly among residency pattern categories. This suggests that, within the limits of the study, there is no clear evidence that residency pattern strongly structures association strength. However, given the small number of clusters per category (particularly in EV) and the uneven sampling effort, these results should be interpreted with caution and may not exclude more subtle differences among residency categories.

Standardized lagged association rates (SLAR) provided indications of long-term stability of both females and males in clusters, consistent with findings for the larger population (Alves et al., 2013; Esteban et al., 2022). The overall SLAR began to decline after approximately three years, consistent with previous findings for Madeira (Alves et al., 2013), and was best described by a casual acquaintances model, indicating gradual disassociations over time. This contrasts with Esteban et al. (2022), who found an exponential decline for all core resident short-finned pilot whales off Madeira, but aligns with patterns reported by Mahaffy et al. (2015) and Servidio (2014). A gradual decline in SLAR can be attributed to environmental variability, changes in social status, or demographic events, such as mortality and the departure of individuals from the natal group, which occurs when groups become too large, making it difficult to maintain associations between all individuals or increasing competition (Ménard, 2017). This can cause splitting of clusters and has been indicated in several pilot whale studies (Augusto et al., 2017; Esteban et al., 2022).

Markedly strong and stable long-term associations were observed in the more thoroughly examined Resident cluster 2, particularly between animals of different sexes. This resident cluster, consisting of six individuals in the current study, includes five of the individuals from the R4 pod analyzed in Alves et al. (2013), which was composed of nine individuals, and now has much more temporal capture information available. The preferred companion model was the best fit for the entire cluster (consistent with Alves et al., 2013) and for all sex-class combinations, except female-female pairs, which were best described by a casual acquaintances model. This may reflect under-sampling of some of the strongest female associations (e.g. between adult females and their female offspring), or genuinely more labile female-female relationships within this cluster compared to male-female or male-male ties. In Madeira, Alves et al. (2013) found that genetic relatedness was higher within groups than

between them, and that individuals who associated more had a higher tendency of being genetically related, a pattern also observed in Hawai‘i (Van Cise et al., 2017). However, it is essential to note that social associations alone do not necessarily prove kinship (Hill et al., 2019; Oremus et al., 2013). In the Mariana Archipelago, Hill et al. (2019) reported that short-finned pilot whales with shared mitochondrial haplotypes were frequently observed together across multiple years, but additional genetic analyses were still required to determine whether these associations reflected true kinship, as multiple matrilines may associate without being closely related (Oremus, 2008; Oremus et al., 2013). Moreover, individuals with differing haplotypes may occur in the same social clusters, further highlighting that association does not always indicate close genetic ties. Thus, while the strong mixed-sex associations in Resident cluster 2 cannot be taken as direct evidence of kinship, their high association indices and long-term stability over the timespan of the study (over two decades in one case), together with previous evidence for elevated within-group relatedness in Madeira, suggest potential familial bonds, including mother-son or close kin dyads, and could be consistent with male natal philopatry in at least some groups. This would add to previous suggestions for natal philopatry in Atlantic Naisa short-finned pilot whales from Madeira (Alves et al., 2013; Esteban et al., 2022) and aligns with hypotheses raised in other regions (Heimlich-Boran, 1993; Hill et al., 2019).

Aside from long-term associations between individuals of different sexes, stable and long-term associations were also identified between individuals of the same sex. Servidio (2014) obtained SLARs for the most frequently photographed short-finned pilot whales in La Gomera and Tenerife (Canary Islands) and likewise found that associations within animals of the same sex as well as between animals of different sexes were temporarily consistent. Long-term female stability has also been observed in other pilot whale and cetacean studies, such as sperm whales and killer whales (Boran and Heimlich, 2019; Heimlich-Boran, 1986; Rendell et al., 2019; Whitehead and Weilgart, 1999).

Although analyses were restricted to a subset of the population, the convergence of sex-specific association patterns within and between clusters, the temporal (SLAR) analyses, and the detailed example of Resident cluster 2 point to a social system in which both females and males maintain long-term and non-random associations within groups. Overall, the study supports stable group-level social organization and highlights sex-specific contributions to cohesion and connectivity in Atlantic Naisa short-finned pilot whales.

5.6 Conclusion

Using long-term photo-identification data restricted to genetically sexed short-finned pilot whales off Madeira Island, this study provides a sex-resolved description of social structure in the Atlantic Naisa type. The results demonstrate that both sexes form long-term, non-random associations, including highly stable mixed-sex dyads that persist over decades in a resident cluster. Females are more strongly anchored to their own clusters, which, in conjunction with previous genetic work (Alves et al., 2013), is consistent with matrilineally structured social groups, characterized by female philopatry. Males are disproportionately involved in the rare but stronger inter-cluster links, either with other males or with females, contributing to occasional connectivity between groups. The persistence of strong male-female associations within a resident cluster suggests that at least some adult males remain socially embedded within their social groups, which is consistent with the possibility of male natal philopatry.

Yet, definitive tests of natal philopatry and matrilineal structure will require integrating the behavioral patterns described here with expanded genetic sampling and explicit kinship inference using nuclear markers such as microsatellites and/or SNPs (e.g. Barrett-Lennard, 2000; Martien et al., 2019), to determine whether documented persistent associations reflect kinship, broader familial networks, or socially maintained bonds that are only partly shaped by relatedness.

This study also highlights the limitations inherent to working with a subset of sexed individuals, as incomplete representation of group membership may obscure additional social connections. Nonetheless, the consistency of association patterns across hierarchical clustering, network analyses, and temporal models supports the interpretation that the observed stability reflects genuine social bonds rather than sampling artefacts.

5.7 Ethics and permit approval statement

Biopsy collection in Madeiran waters followed the guidelines and regulations set by the Instituto de Florestas e Conservação da Natureza (Instituto Português – Região Autónoma da Madeira) under permits 508/2018, 02/IFCN//2019, 02/IFCN//2020, 01/IFCN//2021, and 01/IFCN/2022.

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5.11 Supplementary Materials

Figures

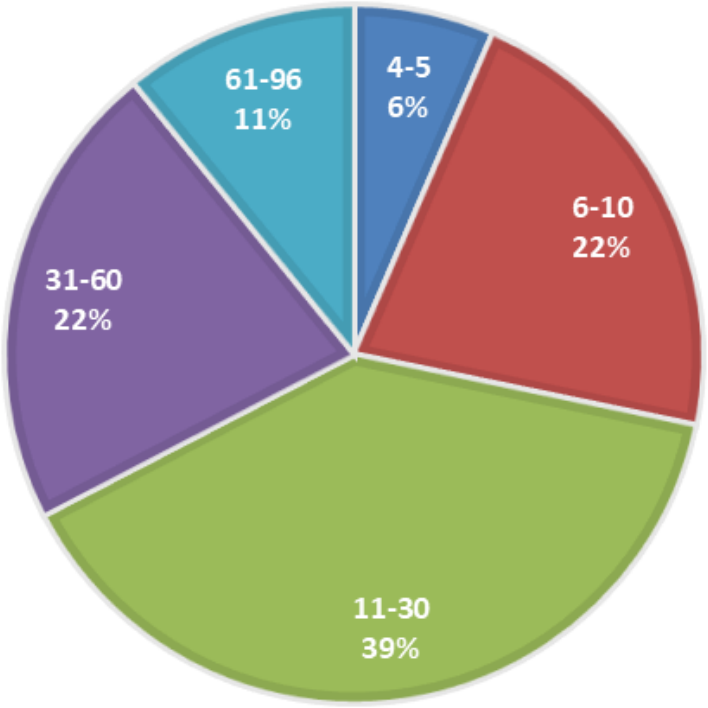

Figure S 5.1: Proportion (%) of genetically sexed short-finned pilot whales by number of photographic captures (in classes: 4-5, 6-10 captures, etc.) for sexed short-finned pilot whales photographed off Madeira between 2003 and 2024 in the current study.

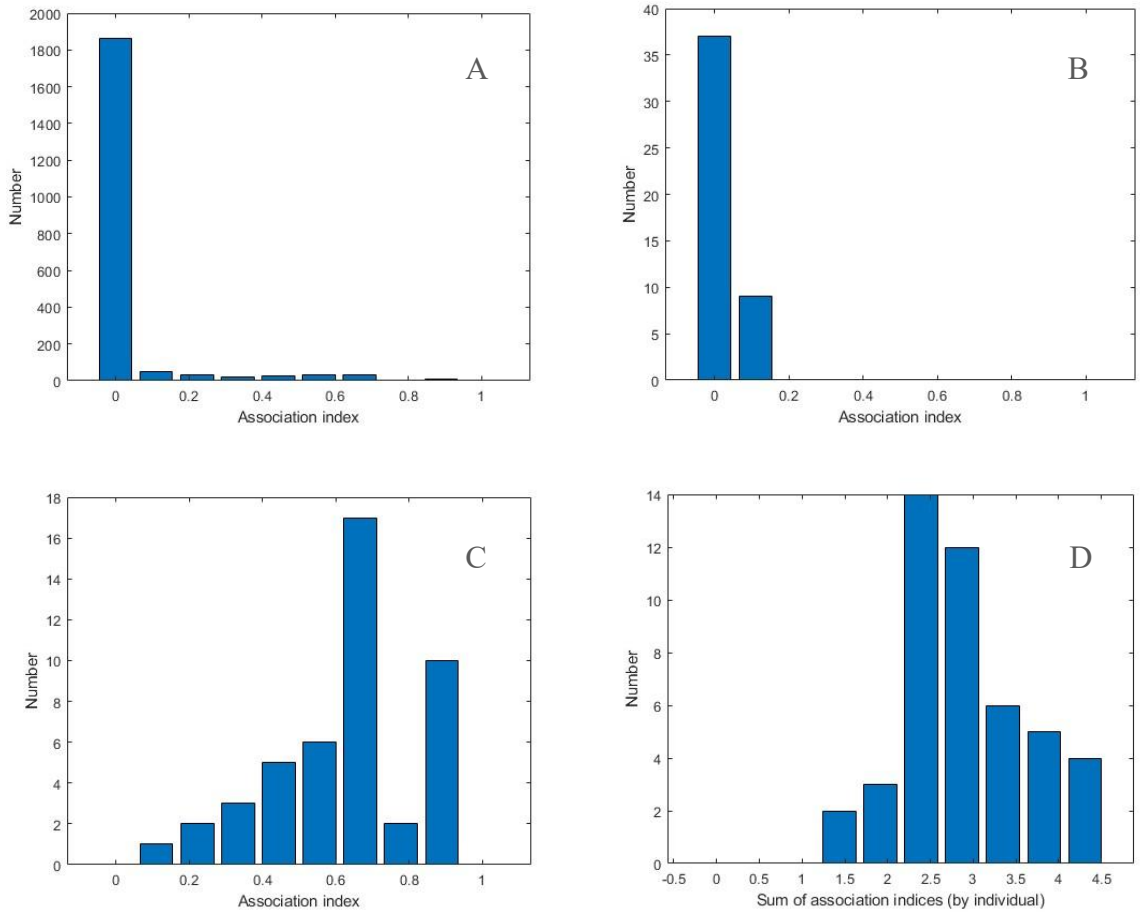

Figure S 5.2: Histograms of association indices for short-finned pilot whales in Madeira, photographed between 2003 and 2024. The plots represent the distribution of A) half-weight association indices (HWI), B) mean HWI, C) maximum HWI, and D) the sum of HWI. In panel A, the y-axis represents the number of dyad entries (non-diagonal association-matrix values), while in panel B-D, the y-axis represents the number of individuals.

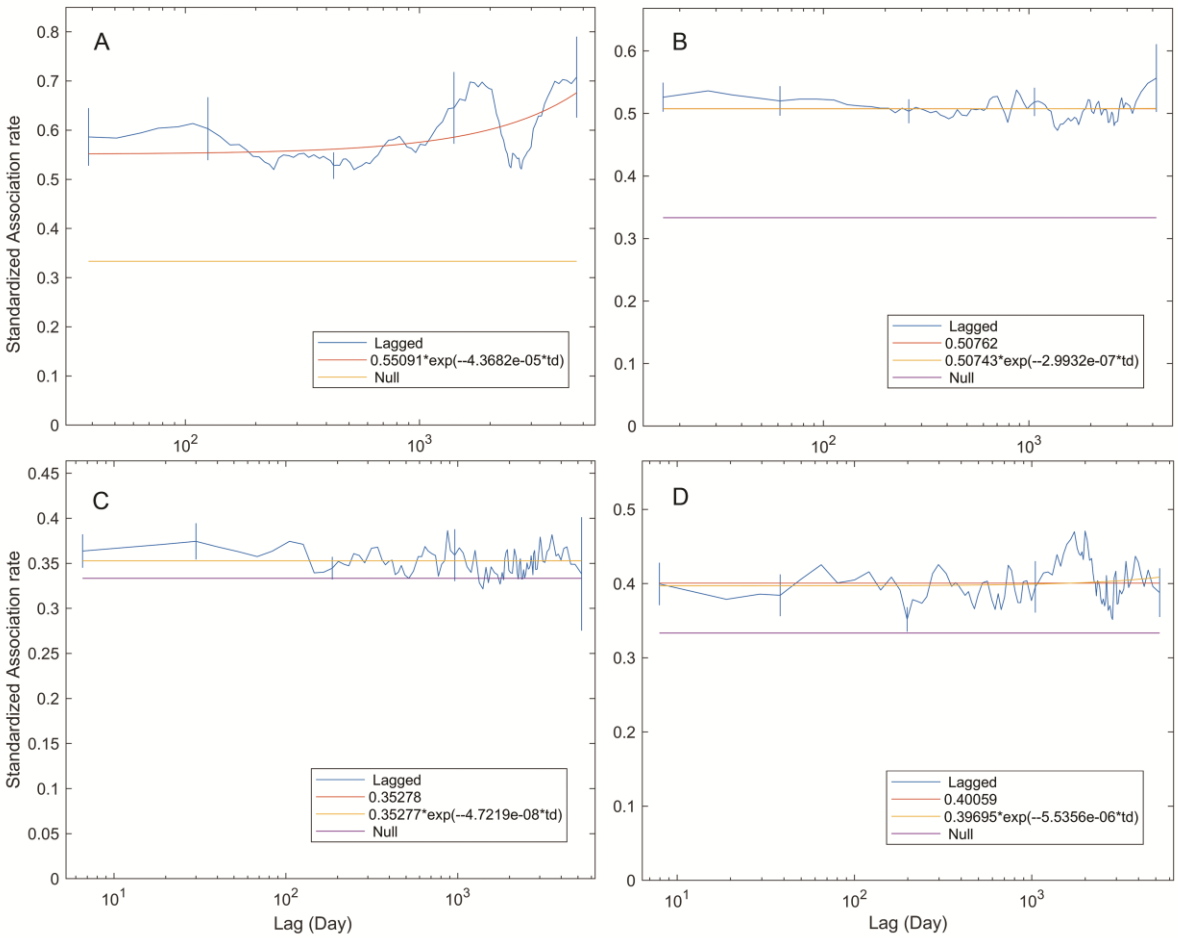

Figure S 5.3: Standardized lagged association rates (SLARs) for associations between sexed short-finned pilot whales in Resident cluster 2 (consisting of three females and three males), photographed between 2003 and 2024, calculated using a moving average of 400 with standard error bars produced through jackknifing. The null association rate and the best fit models are shown. Female-female (A) has *casual acquaintances* as best fit model, while male-male (B), female-male (C), and male-female (D) have *preferred companions* as best fit model, with some support for *casual acquaintances*.

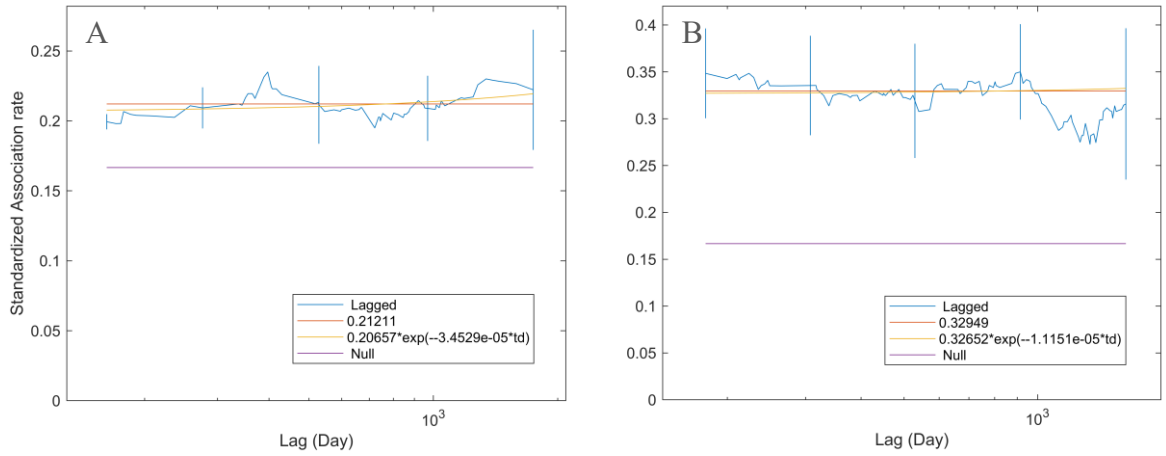

Figure S 5.4: Standardized lagged association rates (SLARs) for associations between female short-finned pilot whales in Regular Visitor cluster 3 (A) and 6 (B) (both consisting of six females; photographed in Madeira between 2006 and 2024, and 2007 and 2023, respectively), calculated using a moving average of 300 and 150 respectively, with standard error bars produced through jackknifing. The null association rate and the best fit models are shown (*preferred companions* and *casual acquaintances* in both cases).

Tables

Table S 5.1: Summary of within- and between-sex association indices for 46 sexed short-finned pilot whales of Madeira, photographed between 2003 and 2024. HWI = half-weight index, max. assoc. = maximum association, SD = standard deviation, F = female, M = male.

Class	Mean HWI (SD)	Sum of Assoc. (SD)	Mean max. Assoc. (SD)
F	0.043 (0.016)	2.945 (0.712)	0.657 (0.187)
M	0.039 (0.016)	2.773 (0.721)	0.613 (0.212)
F-F	0.048 (0.034)	2.248 (0.876)	0.510 (0.249)
M-M	0.043 (0.021)	1.781 (0.379)	0.452 (0.205)
F-M	0.037 (0.038)	0.698 (0.716)	0.356 (0.341)
M-F	0.037 (0.018)	0.991 (0.488)	0.578 (0.242)
Within	0.046 (0.029)	2.055 (0.745)	0.486 (0.231)
Between	0.037 (0.031)	0.819 (0.642)	0.448 (0.321)
Overall	0.042 (0.016)	2.874 (0.713)	0.639(0.197)

Table S 5.2: Summary of association index information within clusters (as defined by maximum modularity) for sexed short-finned pilot whales photographed off Madeira between 2003 and 2024. RP = residency pattern, HWI = half-weight Index, max. assoc. = maximum association, SD = standard deviation, F = female, M = male, R = Resident, EV = Extended Visitor, RV = Regular Visitor, NA = not applicable.

Cluster (RP)	Mean Assoc. HWI (SD)	Sum of Assoc. (SD)	Mean max. Assoc. (SD)	Nº animals (F-M)	Mean # captures
1 (RV)	0.355 (0.074)	2.422 (0.297)	0.853 (0.106)	5 (2-3)	22.8
2 (R)	0.516 (0.112)	3.579 (0.558)	0.704 (0.197)	6 (3-3)	86.0
3 (RV)	0.510 (0.064)	3.551 (0.318)	0.728 (0.131)	6 (6-0)	12.7
4 (R)	0.494 (0.086)	2.483 (0.258)	0.623 (0.117)	4 (2-2)	32.8
5 (EV)	0.344 (0.084)	2.721 (0.419)	0.552 (0.100)	6 (2-4)	50.3
6 (RV)	0.245 (0.120)	2.226 (0.602)	0.533 (0.197)	6 (6-0)	21.7
7 (EV)	0.656 (0.106)	2.311 (0.212)	0.778 (0.212)	3 (2-1)	11.7
8 (R)	0.380 (0.127)	2.518 (0.508)	0.582 (0.175)	5 (4-1)	49.0
9 (R)	0.239 (0.127)	1.957 (0.509)	0.461 (0.261)	5 (1-4)	37.6
Within	0.402 (0.155)	2.692 (0.692)	0.639 (0.197)	NA	NA
Between	0.004 (0.004)	0.183 (0.152)	0.046 (0.033)	NA	NA
Overall	0.042 (0.016)	2.874 (0.713)	0.639 (0.197)	NA	NA

Table S 5.3: Mean and mean maximum association values for sex-dyads between and within clusters, calculated for sexed short-finned pilot whales photographed off Madeira between 2003 and 2024. The * indicates that significant differences were obtained based on a Kruskal-Wallis and Dunn post-hoc test. SD = standard deviation, F = female, M = male.

Cluster relation	Dyad type	Mean Association (SD)	Mean max. Assoc. (SD)
Within	F-F	0.381 (0.241)	0.547 (0.219)
Within	M-M	0.326 (0.228)	0.475 (0.184)
Within	Mixed	0.443 (0.254)	0.592 (0.240)
Between	F-F	0.003 (0.010) *	0.023 (0.024)
Between	M-M	0.006 (0.015)	0.041 (0.027)
Between	Mixed	0.005 (0.015)	0.40 .033)

Table S 5.4: Models fitted to the standardized lagged association rate (SLAR) for Resident cluster 2 (consisting of three females and three males) photographed between 2003 and 2024 off Madeira, calculated using a moving average of 400. PC = preferred companions, CA = casual acquaintances. QAIC = Quasi-likelihood Information Criterion, the smallest value indicates the best fit (in bold). ΔQAIC = The difference in the QAIC of the model in question and the best fitting model. A ΔQAIC <2 indicates substantial support of a model (also in bold). F = female, M = male.

SLAR	Model	Model formula	QAIC	ΔQAIC
F-F	PC	0.59053	7109.08	27.25
	CA	**0.55091 $e^{(4.3682e-05 \times td)}$**	**7081.83**	-
	PC + CA	0.59066 - 0.074539 $e^{(-0.89923 \times td)}$	7113.00	31.17
	Two levels of CA	0.80002 $e^{(-0.52808 \times td)}$ + 0.5501 $e^{(4.4139e-05 \times td)}$	7391.61	309.78
M-M	PC	**0.50762**	**21144.36**	-
	CA	**0.50743 $e^{(2.9932e-07 \times td)}$**	**21146.36**	2.00
	PC + CA	0.50755 + 19.7494 $e^{(-6.1028 \times td)}$	21148.14	3.77
	Two levels of CA	0.24419 $e^{(-1.736 \times td)}$ + 0.50715 $e^{(5.451e-07 \times td)}$	21150.14	5.78
F-M	PC	**0.35278**	**39428.62**	-
	CA	**0.35277 $e^{(4.7219e-08 \times td)}$**	**39430.62**	2.00
	PC + CA	0.35273 + 0.023361 $e^{(-0.42471 \times td)}$	39432.52	3.90
	Two levels of CA	0.021665 $e^{(-0.36865 \times td)}$ + 0.35258 $e^{(2.5115e-07 \times td)}$	39434.52	5.90
M-F	PC	**0.40059**	**36012.33**	-
	CA	**0.39695 $e^{(5.5356e-06 \times td)}$**	**36013.34**	1.01
	PC + CA	0.40065 - 335.77 $e^{(-10.0093 \times td)}$	36016.25	3.92
	Two levels of CA	0.96152 $e^{(-0.39999 \times td)}$ + 0.39597 $e^{(6.4873e-06 \times td)}$	37804.91	1792.58

Table S 5.5: Models fitted to the standardized lagged association rate (SLAR) for Regular Visitor (RV) clusters 3 and 6 (both consisting of six females; photographed between 2006 and 2024, and 2007 and 2023, respectively) off Madeira, calculated using a moving average of 300 and 150 respectively. PC = preferred companions, CA = casual acquaintances. QAIC = Quasi-likelihood Information Criterion, the smallest value indicates the best fit (in bold). ΔQAIC = The difference in the QAIC of the model in question and the best fitting model. A ΔQAIC <2 indicates substantial support of a model (also in bold).

SLAR	Model	Model formula	QAIC	ΔQAIC
RV 3	PC	**0.21211**	**1500.65**	-
	CA	**0.20657 $e^{(3.4529e-05 \times td)}$**	**1502.40**	1.75
	PC + CA	$0.21207 + 0.58822\ e^{(-0.67392 \times td)}$	1504.69	4.04
	Two levels of CA	$-13.9964\ e^{(-0.83433 \times td)} + 0.20725\ e^{(3.2406e-05 \times td)}$	1506.28	5.63
RV 6	PC	**0.32949**	**654.0751**	-
	CA	**0.32652 $e^{(1.1151e-05 \times td)}$**	**656.0639**	1.99
	PC + CA	$0.33069 - 0.10563\ e^{(-0.17306 \times td)}$	657.8740	3.80
	Two levels of CA	$-0.12739\ e^{(-0.32489 \times td)} + 0.32915\ e^{(4.6693e-06 \times td)}$	659.9167	6.84

CHAPTER 6

GENERAL DISCUSSION AND FUTURE STEPS

6.1 General discussion

Understanding the dynamic ecology of highly mobile cetaceans is essential for conservation, because movement, spatial use, and connectivity determine how populations interact with heterogeneous environments and with anthropogenic pressures. This is especially relevant in insular systems, where productive habitats may be spatially restricted, seasonally variable, and linked by movements across broad seascapes (De Falco et al., 2022). Within this context, the present thesis examined the dynamic ecology of Atlantic Naisa short-finned pilot whales (*Globicephala macrorhynchus*) in Macaronesia across multiple spatial and temporal scales, with the aim of improving understanding of space use, movement strategies, connectivity and social structure relevant to conservation and management, and guiding future research priorities.

This thesis contributes to this purpose in several ways. First, it provides an important advance to our understanding of previously observed connectivity in Macaronesia. Recurrent movements had been identified between Madeira and the Canary Islands based on long-term photo-identification catalogue comparisons (Alves et al., 2018, 2019). However, the few inter-archipelago movements previously known involved only 12 individuals (Alves et al., 2019). Chapter 2 builds on this previous knowledge by adding, for the first time on this side of the Atlantic, telemetry information, and using updated catalogue comparisons, thereby improving the spatial and temporal resolution. The number of matches documented between these two archipelagos based on photo-identification was increased to 75 (71 between Madeira and the western Canary Islands, and 4 between Madeira and the central Canary Islands), which is at least six times more than previously documented (Alves et al., 2019), showing that these movements are much more frequent than initially expected. It also showed that regional connectivity appears to be structured through preferred areas, with particularly strong linkage between Madeira and the western Canary Islands. Interestingly, a much stronger linkage was also observed between Madeira and the western Canary Islands than between Madeira and the central Canary Islands, highlighting that the western Canary Islands might function as a mixing region for Macaronesian short-finned pilot whales, and inter- and intra-archipelago differences in spatial use in Macaronesia. This is interesting and reinforces findings that, in island systems, distance alone does not predict connectivity well. Local habitat and environmental influences, social structure or learned movement traditions may also strongly shape which islands are linked and which are not (Courtin et al., 2023). Additionally, trophic niche and foraging habitat seems to differ between Madeira and different islands of the Canary Islands (Escánez et al.,

2024; Íñiguez et al., 2025; Sambolino et al., 2024), which could influence spatial use, and competition with strongly resident populations may deter animals from certain regions. The exact reasons for the strong linkage between the western Canary Islands and Madeira remain poorly understood but should be a topic of future studies (See Future steps).

Using telemetry data, the thesis also showed, for the first time, that short-finned pilot whales in Macaronesia used offshore waters between Madeira and the Canary Islands. Such information is difficult to obtain for cetaceans because movement studies at sea remain technically and logistically challenging and, for small cetaceans in particular, tag deployment is constrained by attachment, welfare and cost considerations (Balmer et al., 2023; Nowacek et al., 2016). Yet, telemetry is especially valuable because it can reveal movement pathways, habitat use and ecological connectivity that are otherwise hard to document, and has repeatedly informed conservation planning in marine systems (Hays et al., 2019; Kot et al., 2023; Ogburn et al., 2017), including in pilot whales (Stepanuk et al., 2018; Thorne et al., 2017).

In Chapter 2, move-persistence analyses based on telemetry data of four individuals indicated that offshore waters were associated mainly with directed travel, suggesting that these waters functioned primarily as transit space. However, the exact route followed varied among individuals. Three tagged individuals travelled relatively directly towards the Canary Islands, while one individual made almost two full roundtrips before stopping in the archipelago, indicating that individuals can use the offshore region variably. The pooled 50% utilization distribution included not only Madeira and the western Canary Islands, but also the area directly linking them, indicating that the offshore zone formed part of the main used space rather than lying outside it. The use of recurrent pathways therefore suggests the presence of a blue corridor between the two archipelagos. These areas are important because, for highly mobile marine vertebrates, conservation depends not only on protecting core habitats but also on retaining the routes that connect breeding, resting and foraging areas (Gardner et al., 2024).

In general, the findings of Chapter 2 are important because they moved beyond merely demonstrating that inter-archipelago movements occur. They helped to identify where movements are concentrated and which regions may function as key pathways and habitats, which is highly relevant for conservation purposes and lacking in Macaronesia (McIvor et al., 2022). Such an approach can also be applied to other cetacean species for which such information is lacking in the region (McIvor et al., 2022) or extended to other insular regions worldwide to guide conservation efforts.

Second, it improves understanding of behavioral dynamics. While Chapter 2 added valuable information on preferred areas, broad-scale space use, inter-island movements, and offshore pathways in Macaronesia, it did not explicitly examine the timing and drivers of behavioral transitions between restricted space use (in preferred areas) and directed travel (between archipelagos), questions that are especially well suited to hidden Markov approaches applied to telemetry data (McClintock, 2017; Saldanha et al., 2023). Nor did it investigate whether these transitions were synchronized across individuals, seasonally structured, or linked to dynamic oceanographic conditions. This information is ecologically important to assess overlap with pressures such as whale-watching in the region (Sambolino et al., 2022). Chapter 3 addressed this gap by focusing on behavioral states, seasonal range residency and dynamic oceanographic conditions around Madeira, using an expanded telemetry dataset relative to Chapter 2. By applying a multiple-imputation hidden Markov model, two behavioral states were identified: area-restricted search (ARS), concentrated mainly around islands, and travelling, expressed primarily during offshore exploration and movements between island systems.

Results from Chapter 3 showed that behavioral switching was associated most strongly with mixed layer depth, with whales more likely to remain in or switch to ARS under shallow and warm, stratified conditions and more likely to switch to travelling under deeper, mixed conditions. This suggests that seasonal oceanographic structure and variability may be an important driver of the observed pattern in Macaronesia, most likely through effects on prey accessibility rather than through productivity alone (Braun et al., 2023). Local differences in environmental variability across island systems may contribute to observed contrasts in how island-associated space use is expressed, as island systems can differ in whether they favor highly localized, spatially restricted populations or broader spatial exchange (Abecassis et al., 2015; Alves et al., 2019; Mahaffy et al., 2015; Van Cise et al., 2017).

Ten tagged individuals showed range-residency behavior around Madeira, with a mean of 53 consecutive days and a maximum of 120 days, and these residency episodes were concentrated particularly from October to December. Interestingly, this behavior was shown not only by whales classified as long-term residents from photo-identification, but also by regular visitors, extended visitors, and even one occasional visitor/transient. This is an important finding, because it shows that seasonal restriction of space use around Madeira is not confined to a single fixed fidelity category. Instead, whales spanning different site-fidelity classes appear to converge on the same relatively constrained area under favorable conditions, showing that this

is an important seasonal area within the broader spatial range of the species. The resulting pattern is therefore more consistent with condition-dependent tactics in a partial-migration-like system (Chapman et al., 2011), in which individuals adjust their space use in response to seasonal environmental variation (Kokko and Lundberg, 2001; Shaw and Couzin, 2013). The observed directional movements to the Canary Islands during cooler periods may reflect movements towards alternative foraging areas when local conditions are less favorable, consistent with theoretical models in which migration functions as a response to temporarily suboptimal conditions (Kokko and Lundberg, 2001). The results show that southeastern Madeiran waters constitute an important seasonal area within the broader spatial range of the eastern North Atlantic population (Alves et al., 2013, 2018, 2019).

Similar combinations of broad movement capacity and prolonged spatial restriction have been described in other cetaceans and regions, including female sperm whales (*Physeter macrocephalus)* and Cuvier's beaked whales (*Ziphius cavirostris)*, indicating that restricted space use in pelagic predators is not unusual when profitable or predictable habitat patches are available (Foley et al., 2021; Whitehead, 2001).

Third, it contributes to our understanding of movements and connectivity on a basin-wide scale. Such information is important because it helps determine whether conservation and population assessments should be considered at ocean-basin rather than regional scales, particularly for highly mobile species that cross local, national, and international jurisdictions (Dunn et al., 2019; Kot et al., 2023). However, although inter-archipelago movements were detected, this was not the case on a basin-wide scale in the North Atlantic. In Chapter 4, an extensive photo-identification catalogue comparison was conducted between the eastern and western North Atlantic, but this did not yield conclusive evidence for present-day interchange. Although this is a negative result, it is informative, showing that regional large-scale movements between archipelagos should not simply be extrapolated to a basin-wide scale.

This distinction is important because other types of evidence may otherwise be overinterpreted. Broad-scale phylogeographic work suggests that eastern and western North Atlantic short-finned pilot whales belong to the same Atlantic lineage, but such evidence integrates over much longer timescales and does not directly demonstrate current east-west interchange (Van Cise et al., 2019). Likewise, the existence of currents such as the Gulf Stream and Azores Current, together with the known long-distance movement capacity of the species, shows that trans-

Atlantic movement is physically possible, but not that it is necessarily common in present-day ecological terms (Alves et al., 2019; Tyson Moore et al., 2020; Wells et al., 2013).

The absence of matches should not be treated as evidence that trans-Atlantic movements never occur. Instead, it could mean that interchange is uncommon or difficult to detect with the applied method. Different approaches to better resolve connectivity between the eastern and western North Atlantic are discussed in 'Future steps' section.

Fourth, it addressed a different but complementary dimension of dynamic ecology, that is, social structure, which in many cetacean species may also shape movement and space use. This is especially relevant in odontocetes, several of which form stable, socially differentiated societies or dynamic fission–fusion networks (Rendell et al., 2019; Weiss et al., 2021). Long-term associations, kinship, philopatry, fission–fusion dynamics, and sex-biased dispersal can influence how individuals move, which habitats they use, and how spatial structure is expressed at the population level (Ball et al., 2017; Rendell et al., 2019; Tsai and Mann, 2013).

Previous work in Madeira has shown that short-finned pilot whales form stable social clusters, that association strength is higher within than between groups, and that relatedness tends to be higher within than between groups (Alves et al., 2013; Esteban et al., 2022). Similar conclusions about stable social units and long-term bonds had also been reached in Hawai'i, Tenerife, and other regions (Heimlich-Boran, 1993; Mahaffy et al., 2015; Servidio, 2014). What remained missing was a much more explicit sex-specific analysis based on genetically sexed individuals, together with long-term temporal assessment of these associations, especially for Atlantic Naisa short-finned pilot whales. Results from Chapter 5 showed that both sexes participate in long-term, non-random associations, with very strong stable temporal associations described for two potential mother-offspring pairs. Differences in how males and females contribute to cluster cohesion and weaker inter-cluster links were observed. Female-mediated links between clusters were weak, whereas males were more often involved in occasional inter-cluster links. Whether these sex-specific differences have consequences for broader spatial organization in this system should be explored in the future.

Overall, results support a social system that is predominantly matrilineal and that is consistent with male natal philopatry. However, such interpretation should remain cautious, as kinship between individuals was not confirmed, and strong or repeated associations do not necessarily imply close relatedness in pilot whales and cetaceans in general (Gerber et al., 2021; Hartman et al., 2023). Future studies are required to understand these processes better (See Future steps).

Even though short-finned pilot whales are listed as Least Concern by IUCN (Gauffier et al., 2023; Minton et al., 2018), Chapters 2 and 3 of this thesis show that conservation and management of this species, or at least the areas it uses, could be highly relevant due to the specificity and complexity of spatial use compared to other cetacean species in the region, especially in Madeira (Freitas et al., 2026). In the Canary Islands, their distribution broadly seems to overlap with other cetacean species in specific near-island areas, which makes protection of these preferred areas relevant for cetaceans in general (Herrera et al., 2021; Servidio et al., 2019)

Management efforts should address both recurrent island-associated use areas and broader inter-archipelago connectivity pathways. Seasonal residency around Madeira lasted up to a maximum of 120 consecutive days within a constrained range located southeast, approximately 10 km offshore. More broadly, this area lies within a high-use marine traffic zone in South Madeira, where vessel traffic and cetacean use were identified as forming a potential conflict area, and where short-finned pilot whales appeared to be of particular concern because much of their representative patch overlapped that zone (Cunha et al., 2017). A recent study focusing specifically on whale-watching also showed that the residency range partially overlaps with whale-watching effort in Madeira, which is concentrated mainly within about 10 km of the south coast, with core encounter areas off Funchal, an average of 6.5 vessels per day in that area, and peaks of 14 vessels in August (Sambolino et al., 2022). Island-associated pilot whales were exposed to high levels year-round, suggesting sustained overlap with tourism pressure is a realistic conservation concern, especially during periods of seasonal residency (Sambolino et al., 2022). This highlights the need to account for seasonality when assessing and managing vessel-related pressures, including both whale-watching and broader marine traffic, in island-associated habitats worldwide.

Current protection only partially matches the species' dynamic ecology. For a species with this combination of recurrent seasonal aggregation in specific areas and long-distance movement, a layered and dynamic conservation strategy would be beneficial in Macaronesia, rather than reliance on a single static approach (Conners et al., 2022). Static protection could be justified for predictable core-use areas such as southeastern Madeira and the main island-associated sectors of the Canary Islands, because highly mobile species can still benefit from protection of recurrent foraging, social, and potentially reproductive habitat, as well as the prey fields and oceanographic features that support those functions (Conners et al., 2022). In that regard, some efforts have already been made. In Madeira, a Site of Community Interest was approved in

2016 and encompasses the archipelago's coastal waters to a depth of 2500m for cetaceans within the exclusive economic zone (EEZ). Around the Selvagens Archipelago, an area also visited and used by short-finned pilot whales (Chapter 2), the largest marine reserve in Europe and the North Atlantic with full protection 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 (Herrera et al., 2021). Additionally, the importance of Madeira and the Canaries for marine mammals has recently been acknowledged with the delineation of an Important Marine Mammal Area (IMMA), which are increasingly being used in environment assessments and conservation, policy and management initiatives (IUCN-MMPATF, 2024; Tetley et al., 2022). These are valid and important efforts towards the conservation of cetacean species in the region, though some approaches lack the inclusion of multiple cetacean species, do not reflect true spatial and temporal use, or don't provide legal protection in themselves, offering limited effective protection (Allan et al., 2021; Conners et al., 2022; Herrera et al., 2021; Lascelles et al., 2014; Tetley et al., 2022).

Cetacean management and conservation efforts also do not cover the blue corridor that was detected, although the area is used by several cetacean species (Correia et al., 2020; Valente et al., 2019). The observed core areas, together with the blue corridor, could, for example, be linked within a dynamic conservation or corridor network (e.g., MPA network) which could also benefit other species that use the area (Dunn et al., 2019; Maxwell et al., 2015; Podda and Porporato, 2023). In that regard, the findings of Chapter 2 and 3 could help guide the establishment of the "Macaronesian Biodiversity and Ecological Migration Corridor for Cetaceans", between Madeira and the Canary Islands, which would cover several cetacean species (Carrillo, 2007; Herrera et al., 2021). In reality, this is complex, as migratory marine species regularly cross multiple jurisdictions and often require coordinated international management, in this case between Portugal and Spain, and potentially also adjacent Northwest African jurisdictions, as indicated by the telemetry data from Chapter 3 (Dunn et al., 2019; Maxwell et al., 2015).

On a broader basin-wide scale, the absence of evidence for current trans-Atlantic interchange does not, on its own, justify splitting the Atlantic population into separate management stocks (Martien et al., 2019a). In cetaceans, management units are generally delimited using multiple, converging lines of evidence rather than a single negative result, because the absence of detected exchange may reflect limited sampling, overlap, or detection power rather than true demographic independence (Martien et al., 2019a). This is, for example, the case in western

North Atlantic bottlenose dolphins (*Tursiops truncatus truncatus*), for which stock boundaries have been inferred from combinations of morphology, genetics, photo-identification, telemetry, and spatial distribution data (Hayes et al., 2021). Comparable multi-source approaches have also been used to delineate management units in harbor porpoises (*Phocoena phocoena*), combining genetics, morphology, acoustics, and satellite tracking (Sveegaard et al., 2015). By contrast, the results of Chapter 4 indicate that current evidence is still insufficient to determine whether eastern and western North Atlantic short-finned pilot whales should be managed separately. Instead, the results of Chapter 4 highlight the need for additional research to better understand if trans-Atlantic movements occur and whether management would be recommended (See 'Future steps').

This thesis additionally highlights the importance of integrating complementary techniques to study movements and understand spatial use and temporal variation in a highly mobile marine mammal. Chapters 2, 3, and 4 show that accessible photo-identification data obtained from platforms of opportunity, such as whale-watching operations, are invaluable for initial assessments of movements and potential connectivity. Although such data lack the fine-scale resolution of telemetry and do not directly reveal the pathways used between areas, the long time periods they can cover add a crucial temporal dimension that telemetry often lacks due to limited tag longevity, bandwidth, and continuity. By contrast, telemetry, particularly when integrated with dynamic analytical approaches such as ecological modelling, provides the fine-scale spatial and behavioral information needed to identify pathways, characterize habitat use, and support conservation planning (Hays et al., 2019; Nowacek et al., 2016; Ogburn et al., 2017).

To conclude, the present thesis advances understanding on the dynamic ecology of Atlantic Naisa short-finned pilot whales in Macaronesia and helps identify priorities for future conservation, management, and research. Taken together, the findings suggest that Macaronesia should be viewed as a dynamic insular system and that short-finned pilot whales within it should be understood as a highly mobile species whose ecology is expressed across multiple spatial and temporal scales, from seasonal, repeated and restricted island-associated use, to broader regional movements. The social analyses add a complementary perspective by showing that these ecological patterns are expressed within a socially sex-specific structured population. Indirectly, conservation efforts focusing on marine megafauna will also be relevant to the broader ecosystem through benefits to lower trophic levels (Hooker and Gerber, 2004).

6.2 FUTURE STEPS

A recurring message of this thesis is that no single method can fully capture the dynamic ecology of a highly mobile pelagic odontocete. Continued integration of distinct and complementary methods, such as photo-identification, biotelemetry, ecological modelling, genetics, and social analyses, among others, would therefore be the most effective way to understand the dynamic ecology of short-finned pilot whales, and specifically in the case of Macaronesia, to identify management and conservation priorities. This is also relevant in the context of climate change, because dynamic shifts in behavior, habitat use, and regional movements may occur as environmental conditions change (Sousa et al., 2019, 2023). The same integrated approach is likely to be useful for other cetacean species and marine megafauna that use island systems in a temporally variable way. Below, several priorities for future research, management, and conservation are outlined.

Maintain and expand integrative, collaborative monitoring across methods and regions

Continuing the effort to collect additional **photo-identification** data and integrating these on reliable platforms (e.g., Happywhale) would be advised (Cheeseman et al., 2022). Obtaining this information from all islands in Macaronesia (especially from the Azores) and running broad-scale comparisons including all regions could drastically improve our understanding of island-specific movements and connectivity across Macaronesia. Additionally, incorporating photo-identification information from Cabo Verde would also be important. As no such information was available from this region at the time of Alves et al. (2019), no assessment was possible. Nevertheless, in this thesis, movements ranging about half-way between the Canary Islands and Cabo Verde were detected, which suggests that comparisons with Cabo Verde should be explored. If photo-identification data would still be lacking to date, local research teams could be trained to collect such data. Expanding good-quality photo-identification data from the western North Atlantic would also remain relevant to further assess potential basin-wide movements.

Additionally, in this thesis, no analyses were performed based on the photo-identification capture histories. However, compiling this information for the different regions and sharing it between research groups could 1) help better understand seasonality, and 2) allow assessing whether inter-archipelago movements tend to involve subsets or entire groups of associated individuals, though it is likely these movements entail social units based on the social structure of the species (Chapter 5; Alves et al., 2013; Esteban et al., 2022).

Apart from photo-identification data, additional studies should focus on **biotelemetry** data, as it is particularly relevant for guiding management and conservation efforts (Hays et al., 2019). Expanding this approach across archipelagos (including Cabo Verde) would be advised. This approach should ideally also take into account seasonality (with tags deployed during different seasons) and residency (targeting animals with different residency patterns), as aside from obtaining fine-scale info on spatial use and movements, it could aid in understanding whether animals with different residency patterns use the same areas and pathways, show the same timing of movements and respond similarly to dynamic environmental conditions. Such efforts on both sides of the North Atlantic might also provide information regarding basin-wide movements, if detected. Additionally, tagging multiple animals within a group could provide fine-scale information on whether they use space continuously together.

Finally, linking long-duration satellite telemetry data to additional static and dynamic **environmental variables and prey-related processes** would be important, as it could help understand behavior and the drivers of observed spatial use and movements in Macaronesia. This is especially relevant to understand the seasonal range residency around Madeira and the strong linkage between the western Canary Islands and Madeira (Chapter 2 and 3).While this thesis focused on mixed layer depth and sea surface temperature as key environmental correlates, other factors that should be explored include fine-scale bathymetry, prey distribution (using eDNA or echosounder acoustic profiles), and other oceanographic features relevant to deep-diving species (Abecassis et al., 2015; Braun et al., 2022). Using techniques such as echosounders could also help better understand the foraging ecology of the species. It may also be valuable to integrate fine-scale and coarse-scale tracking data in more complex movement analyses, for example through hierarchical hidden Markov model frameworks that can accommodate processes operating at different temporal scales (Glennie et al., 2023). In addition, social-structure-related or other individual-level factors could be incorporated and explored through mixed hidden Markov models, for example by treating effects such as residency pattern as random effects (McClintock, 2021). On a broader scale, information regarding environmental drivers, prey species and foraging ecology could also help clarify the potential of basin-wide movements in the North Atlantic.

Genetic approaches to assess natal pod philopatry and basin-scale connectivity inference

Chapter 5 provides the first detailed sex-specific description of social structure in Atlantic Naisa short-finned pilot whales and shows patterns that are consistent with, but do not prove,

male natal philopatry and a predominantly matrilineal system. A major next step is therefore to integrate long-term association data with genetic approaches. This would require additional genetic sampling and explicit kinship inference using nuclear markers such as microsatellites and/or SNPs (e.g., Barrett-Lennard, 2000; Martien et al., 2019b), to determine whether documented persistent associations reflect kinship, broader familial networks, or socially maintained bonds that are only partly shaped by relatedness. This will strengthen inferences about how social structure could contribute to spatial use, dispersal, and broader movement patterns in Macaronesia in the future. This is relevant not only for pilot whales, but also for other odontocetes in which movement and space use may be shaped by stable social units.

In the context of Chapter 4, to help distinguish between true rarity of basin-wide interchange and low detectability due to incomplete spatial coverage, future genetic studies could integrate demographic inference to test for past and/or ongoing gene flow (e.g., Carroll et al., 2019) and employ more comprehensive genomic approaches such as whole-genome sequencing, which has recently proved useful for detecting trans-oceanic kinship in cetaceans (Hoelzel et al., 2026). Wider Atlantic sampling would also be recommended, especially from Africa and South America. This would allow us to better understand differentiation in the Atlantic Ocean and potential connectivity between regions. More broadly, similar genomic approaches could improve understanding of population structure and large-scale movements in other cetacean species for which direct evidence of interchange remains limited.

Investigate the impact of vessel-related threats

From a conservation perspective, a better understanding of vessel-related threats acting in the different preferred and seasonal areas across Macaronesia would be valuable. This is especially the case for the area southeast of Madeira where short-finned pilot whales repeatedly use near-island waters that overlap with intense human activity (Cunha et al., 2017; Erbe et al., 2019; Sambolino et al., 2022). A recent study from Tenerife showed that the behavior of short-finned pilot whales changes in response to vessel noise, and that cumulative exposure from multiple vessels matters (Arranz et al., 2021, 2024). More broadly, Aguilar de Soto and Alves (2023) highlight that vessel-related threats to this species are not limited to acoustic disturbance, but also include risks associated with whale-watching pressure, masking of communication, and collisions with small vessels and potentially fast ferries.

In Madeira, spatial overlap with whale-watching has been observed, and stress responses reported in pilot whales followed by whale watching boats (Freitas et al., 2004; Sambolino et

al., 2022). Although marine traffic impacts on cetaceans in Madeira have previously been assessed (Cunha et al., 2017), the study lacked a specific focus on short-finned pilot whales. Given the likely growth of vessel activity in the region since earlier assessments, an updated understanding of the impacts in the region would be beneficial in guiding management and conservation, and is important not only for pilot whales, but also for other cetaceans in Macaronesia that repeatedly use near-island habitats and may be exposed to the same local pressures. Future research should therefore assess how vessel traffic, noise, and collision risk vary across preferred areas and seasons, and whether particular classes of vessels, routes, or cumulative exposure levels are associated with changes in behavior, area use, nursing, resting, or group cohesion. Such work would provide a stronger basis for temporally and spatially explicit management in island-associated habitats and aligns with the broader recommendation of Aguilar de Soto and Alves (2023) that management should increasingly account for overlap between short-finned pilot whales' preferred habitats and human activities. More broadly, future assessments should also consider climate-related shifts in prey and distribution, and emerging offshore pressures where relevant, as these have also been identified as future management concerns for the species in European waters (Aguilar de Soto & Alves, 2023).

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