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Site fidelity and residency patterns of rough-toothed dolphins (*Steno bredanensis*) in Madeira Island, using photo-identification data

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Master’s in Marine and Coastal Systems

Work performed under the supervision of:

Annalisa Sambolino,
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UNIVERSIDADE DO ALGARVE
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2025

Declaration of Work (Declaração de autoria do trabalho)

Declaro ser a autora deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída**.**

Statement of authorship

I declare to be the author of this work, which is original and unpublished. Authors and works consulted are duly cited in the text and included in the reference list.

Claire Raffaelli

Dedication and Acknowledgments

I sincerely thank all the whale-watching companies involved in the data collection process, in particular Lobosonda, H2O-Madeira, Ventura | nature emotions and Seaborn, for their collaboration, availability, and logistical support throughout the study. Their willingness to share valuable sighting information and facilitate access to the field was instrumental in the acquisition of high-quality data over an extended period.

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Abstract

The rough-toothed dolphin (*Steno bredanensis*) is a poorly understood odontocete species with a scattered global distribution, particularly in oceanic and insular habitats. In the Eastern North Atlantic, including the waters surrounding Madeira, their habitat use and movement patterns remain largely unknown. This study presents the first long-term assessment of site fidelity and residency of rough-toothed dolphins in Madeira using photo-identification data. A total of 637 distinct individuals were identified, during 160 days of sampling occasions, between 2016 and 2024, based on distinctive dorsal fin markings (3-4) and high image quality (2-4). Using Lagged Identification Rates, residency modeling, and site fidelity indices, temporal patterns of occurrence and return were analyzed. The discovery curve did not reach an asymptote, and 62.5% of individuals were seen only once, suggesting an open population. The best-fit residency model estimated that at any given time, ~28 individuals are present, with an average stay of 6.7 days and absence of ~1700 days, indicating transient usage of the area. However, a subset of individuals exhibited recurrent visitation patterns. The cluster analysis of site fidelity indices revealed two distinct patterns: a larger group with intra- and interannual fidelity characterized by short-term, periodic visits; and a smaller group with inter-annual fidelity and longer presence spans. These findings point to ecological heterogeneity within the population, potentially driven by individual preferences, social structure, or environmental factors. Despite these variations, the overall metrics point to a limited and discontinuous use of the region. In conclusion, rough-toothed dolphins show generally low site fidelity to Madeira, as evidenced by short residence durations, long absences, and low re-sighting rates. These results align with their presumed ecological preference for wide-ranging movements in oceanic habitats. Understanding this spatio-temporal variability is crucial to inform conservation efforts, particularly in dynamic and low-density contexts typical of pelagic cetaceans.

Keywords: Habitat use, Eastern North Atlantic, Photo-identification, Lagged Identification Rates, Standardized Site Fidelity

Resumo

O presente estudo investiga, pela primeira vez de forma exaustiva e a longo prazo, a fidelidade ao local e os padrões de residência do golfinho-de-dentes-rugosos (*Steno bredanensis*) nas águas do sul da Ilha da Madeira, com base em dados de fotoidentificação recolhidos entre 2013 e 2024. Esta espécie, apesar da sua ampla distribuição em águas tropicais e subtropicais, permanece pouco conhecida, particularmente em regiões oceânicas como a Macaronésia (Jefferson, 2009; Kiszka et al., 2019). O estudo baseou-se em 341 dias de amostragem, totalizando 22312 fotografias processadas, das quais foi possivel identificar 637 indivíduos distintos, através das marcas únicas na barbatana dorsal e da qualidade das imagens (Würsig & Jefferson, 1990).

Após uma filtragem rigorosa (na qual foram avaliadas a qualidade da imagem e a distintividade dos individuos), foram utilizadas 1092 capturas de 637 indivíduos, distribuídas por 160 dias de amostragem efetiva entre 2016 e 2024. Como a curva de descoberta não atingiu um platô, e 62.5 % dos indivíduos foram registados apenas uma vez, os autores concluem que se trata de uma população aberta (Whitehead, 2001).

As taxas de reidentificação defasada (Lagged Identification Rates) permitiram modelar a fidelidade ao local. O modelo mais adequado, que inclui emigração e reimigração, estimou que, em média, 28 indivíduos (SE = 4.9) estavam presentes simultaneamente na zona durante o verão (julho–agosto), com uma duração média de permanência de 6,4 dias (SE = 2.3), seguida de uma ausência média de 625.6 dias (SE = 323.2). Estes resultados revelam uma utilização essencialmente transitória da região e indicam uma fidelidade geralmente baixa.

Os índices de fidelidade ao local, calculados segundo Tschopp et al. (2018), baseiam-se em três indicadores: frequência de ocorrência (*IO*), permanência (*IT*) e periodicidade (*It*). O índice IH4 (Índice de Fidelidade Harmónica padronizada) apresentou uma média muito baixa (0.0057 ± 0.0008), indicando uma fidelidade ao local muito limitada. Uma análise de agrupamento (clustering) com base em quatro índices (IA2, IH2, IH3 e IH4) revelou dois grupos distintos. O método agrupamento por K-means foi o mais eficaz (silhueta média = 0.691; WSS = 1.0).

O grupo 1 (n = 174) incluía indivíduos com fidelidade intra-anual: as suas visitas eram mais frequentes, mas de curta duração (*It* = 0.3123; *IT* = 0.0662). O grupo 2 (n = 65) reunia indivíduos com fidelidade interanual, caracterizada por estadias mais prolongadas mas mais espaçadas no tempo (*It* = 0.0014; *IT* = 0.584). Todas as diferenças entre grupos foram estatisticamente significativas ($p < 0,05$), confirmando comportamentos ecológicos distintos.

Foi observado um forte padrão sazonal, com picos de deteção em julho ($\bar{x}$ = 40.0) e agosto ($\bar{x}$ = 48.6), coincidindo com condições oceanográficas favoráveis, associadas ao efeito de massa insular (Island Mass Effect), que aumenta a produtividade local (Caldeira et al., 2002; Gove et al., 2016). A espécie é também conhecida por preferir temperaturas da água superiores a 21 °C, comuns nesta região durante o verão (Fernandez et al., 2021).

Apesar da fidelidade global ser reduzida, a estrutura em dois grupos sugere a existência de estratégias ecológicas divergentes dentro da população. O grupo 1 poderá refletir uma utilização sazonal e oportunista da região (alimentação, socialização), enquanto o grupo 2 incluiria indivíduos com maior familiaridade com a zona, possivelmente relacionada com dinâmicas sociais. Padrões semelhantes foram observados no México (Pouey-Santalou et al., 2024) e na Polinésia Francesa (Gannier & West, 2005).

Comparando com outras espécies de cetáceos na Madeira, como os golfinhos-roazes (*Tursiops truncatus*) ou as baleias-de-Bryde (*Balaenoptera brydei*), esta espécie apresenta comportamentos semelhantes de baixa fidelidade, embora alguns indivíduos destas espécies demonstrem fidelidade marcada (Dinis et al., 2016; Ferreira et al., 2021). Estes resultados sugerem que *Steno bredanensis* utiliza a zona da Madeira de forma oportunista, em consonância com a sua tendência ecológica para elevada mobilidade (Baird et al., 2008; Lodi et al., 1992).

Contudo, a sua presença regular no verão sublinha a importância ecológica da região, como potencial área de passagem, descanso ou procura alimentar. A heterogeneidade intra-populacional aqui detetada é crucial para estratégias de conservação, uma vez que as ameaças humanas (tráfego marítimo, poluição, interações com a pesca) podem afetar de forma diferenciada os indivíduos consoante a sua estratégia de deslocação (Mintzer et al., 2018; Kiszka et al., 2019).

Assim, é recomendada uma abordagem interdisciplinar (ex. genética, telemetria e acústica passiva) e de escala regional, para melhor compreender as ligações entre arquipélagos e reforçar as políticas de conservação à escala macaronésica (Weyn et al., 2025). A combinação de dados de fotoidentificação com modelos estatísticos robustos (LIR, clustering) demonstrou ser eficaz no estudo de espécies altamente móveis.

Em conclusão, os golfinhos-de-dentes-rugosos manifestam uma fidelidade ao local geralmente reduzida na Madeira, com uma utilização sazonal e oportunista, embora uma minoria da população revele padrões de presença mais regulares. Estes resultados enriquecem a nossa compreensão da ecologia espacial desta espécie no Atlântico Nordeste e apelam a uma conservação baseada em dados de longo prazo e numa abordagem coordenada à escala dos arquipélagos.

Palavras-chave: Uso do habitat; Atlântico Nordeste; Foto-identificação; Taxas de Reidentificação defasada; Fidelidade ao local

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Abbreviation list

AHC – Agglomerative Hierarchical Clustering

CITES – Convention on International Trade in Endangered Species

CV – Coefficient of Variation

DHC – Divisive Hierarchical Clustering

EM – Expectation-Maximisation

GMM – Gaussian Mixture Model

IA – Arithmetic Index

IH – Harmonic Index

IME – Island Mass Effect

IUCN – International Union for Conservation of Nature

LIR – Lagged Identification Rates

PCA – Principal Component Analysis

QAIC – Quasi-Akaike Information Criterion

SD – Standard Deviation

SE – Standard Error

SSFI – Standardized Site Fidelity Index

WSS – Within-Cluster Sum of Squares

1. Introduction

As apex predators and key components of marine ecosystems, cetaceans play a fundamental role in maintaining trophic balance and ecosystem functioning (Camphuysen, 2006, Rupil et al., 2022). Nevertheless, they are increasingly exposed to a wide range of large-scale anthropogenic pressures (Bridge et al., 2023), including maritime traffic (Pennino et al., 2017; Sambolino et al., 2022), whale-watching (Ferreira et al., 2008), plastic and chemical pollution (Schwacke et al., 2012; Sambolino et al., 2024), bycatch (Miyazaki, 1994; Lewison et al., 2004; Marçalo et al., 2024), or underwater noise (Richardson et al., 2013; Papale et al., 2015), which are disrupting their populations worldwide.

Understanding their spatial dynamics is, therefore, of strong ecological interest, as it provides critical information to assess exposure to threats, ecosystem health, resilience, and for the management of marine biodiversity. Within this context, site fidelity defined as the tendency of individuals to return to previously occupied areas, represents a key aspect of habitat use and movement ecology (Greenwood, 1980; Switzer, 1993; Gerber 2019). It is shaped by environmental factors such as resource availability, predation risk, and the spatiotemporal distribution of conspecifics (Switzer, 1993; Nathan et al., 2008), as well as individual traits including age, prior reproductive success, and knowledge of alternative sites (Switzer, 1993). For simplicity, site fidelity is defined with respect to the location where an individual was initially identified or marked (Bose et al., 2017). It is commonly assessed using artificial (e.g. rings, tags) or natural markings (e.g. skin patterns, dorsal fin notches) that allow individual recognition upon return to the study area (Lewis et al., 1996; Simões-Lopes & Fabian, 1999; Hoffman & Forcada, 2012).

The photo-identification, based on distinctive dorsal fin markings, offers a non-invasive and effective method for studying cetaceans in open-ocean environments, where is usually challenging to obtain data due to high costs and logical constraints (Auger-Méthé & Whitehead, 2007; Badenas et al., 2022; Alves et al., 2023). Although satellite telemetry (Abecassis et al., 2015), passive acoustics (Gotz et al., 2005), and/or genetics (Palsbøll et al., 1997; Alves et al., 2013) provide valuable insights, each method has constraints regarding invasiveness, identification accuracy, or feasibility. Therefore, the capture-recapture methodology (based on individual photographic identifications), making use of likelihood techniques, such as Lagged Identification Rates (Whitehead, 2001) or site fidelity indexes (Tschopp et al., 2018), offers a robust framework to investigate spatial use, residency patterns, and social dynamics. The photo-identification provides crucial information on site fidelity, as it allows individuals to be monitored over time using capture-recapture methods in a given area (Würsig & Jefferson, 1990). By identifying the same individuals in the same areas over time, it is possible to determine whether dolphins return regularly to certain sites or whether they are just transiting (Urian et al., 2015). Additionally, photo-identification data can be used to study the social structures of dolphin populations. By analyzing associations between individuals observed together, it is possible to infer social relationships and group dynamics within the population (Alves et al., 2013).

In the Macaronesian region (Eastern North Atlantic), several studies have revealed heterogeneous site fidelity patterns across odontocete species (Cartagena-Matos et al., 2021; McIvor et al., 2022). For example, a highly resident population of Risso's dolphins have been described in the Azores (Hartman et al., 2008), island-associated short-finned pilot whales have been identified in Madeira and the Canaries (Alves et al., 2013; Servidio et al., 2019; Esteban et al., 2022; Verborgh et al., 2022) and common bottlenose dolphins in Madeira (Dinis et al., 2016) and the Azores (Silva et al., 2008). In contrast, other species like the sperm whales or groups/populations of pilot whales and bottlenose dolphins demonstrate more transient, wide-ranging movement patterns (Alves et al., 2019; Dinis et al., 2021; Ferreira et al., 2022). However, for delphinids that range across open oceanic environments, empirical data on site fidelity and movement patterns still remain scarce or is only available for a very limited number of species, reducing the capacity to identify critical habitats and inform effective conservation strategies (Pouey-Santalou et al., 2024).

The rough-toothed dolphin (*Steno bredanensis*, Cuvier in Lesson, 1828) is primarily an oceanic species (i.e. mainly over bathymetries of > 1000m; Ritter et al., 2002; Baird et al., 2008) distributed worldwide in tropical and subtropical regions (Lodi, 1992; Jefferson, 2009; West et al., 2011; Kiszka et al., 2019). Despite their wide distribution, the species remains poorly documented in oceanic zones, and knowledge on its spatial and social ecology remains limited. In the Madeira Archipelago, scientific literature on its ecology and behaviour is scarce. It is known to be among the 10 most sighted odontocete species, and to use the Madeiran waters for travelling, feeding, resting and socializing, in groups with a mean of 21 individuals (SD = 13, range = 1-60, n = 42) (Alves et al., 2018), and mainly during July and October (Fernandez et al., 2021). The gap is critical, as understanding spatial behaviour in these environments is essential to assess habitat use, identify critical areas and implement effective conservation strategies. Studies from regions such as Hawaii, Mexico and Brazil, show that the site fidelity and social structure of this species can be highly variable, ranging from stable coastal associations (Baird et al., 2008; Pouey-Santalou et al., 2024) to solitary and highly mobile behaviour (Lodi et al., 1992). This variability underscores the need for region-specific ecological studies.

In this context, the present study aims to fill knowledge gaps on the rough-toothed dolphin spatial ecology in the Eastern North Atlantic by exploring the site fidelity and residency patterns around Madeira Island. To that, it will make use of a long-term photo-identification dataset to feed capture-recapture models. Moreover, it aims to contribute with broader information about this species at a Macaronesian level towards efforts to protect cetacean diversity at a larger scale.

2. Materials & Methods

2.1. Data collection

Photo-identification data were collected over a 12-year period (2013–2024) during research surveys for multiple purposes (i.e. photo-identification, biopsying, tagging, or acoustics, throughout several scientific projects; see ‘Acknowledgments’) by MARE-Madeira/ARDITI’s Rigid Inflatable Boats, and during platforms of opportunity, namely, on commercial whale-watching trips operated by local ecotourism companies (Lobosonda, H2O-Madeira, Ventura | nature emotions and Seaborn), mainly in the southern waters of Madeira Island.

The protocol was based on photo-identification standardized procedures, focusing on the natural markings of the dorsal fin for individual identification (Würsig & Jefferson, 1990). It is important to note that whale-watching companies focus on encounters with cetaceans for tourism purposes, regardless of the species encountered. These companies were making use of trained observers, who scanned the horizon using powerfull binoculars from land, and communicated sightings via radio to facilitate the encounters. When the target species was encountered, the dolphins were approached, and photos of the left and right sides of each individual dorsal fin were taken whenever possible, in order to improve the accuracy of identification.

All platforms used covered offshore and inshore zones or varying sectors within the south of Madeira depending on weather conditions and recent cetacean tips (i.e. from other companies or look-out posts). On some days, two sampling outings were conducted, depending on sea conditions and logistical feasibility. However, for subsequent analyses, these multiple observations on the same day were merged into a single sampling occasion to ensure uniform temporal resolution. The sighting data collection protocol followed the methodology described by Alves et al. (2018), ensuring consistency with established procedures. Although photo-identification was collected year-round, the seasonal pattern is not related to search efforts due to uncontrolled variables, such as the number of photographers, availability of cameras, weather conditions, and the number of trips or encounters.

2.2. Study area

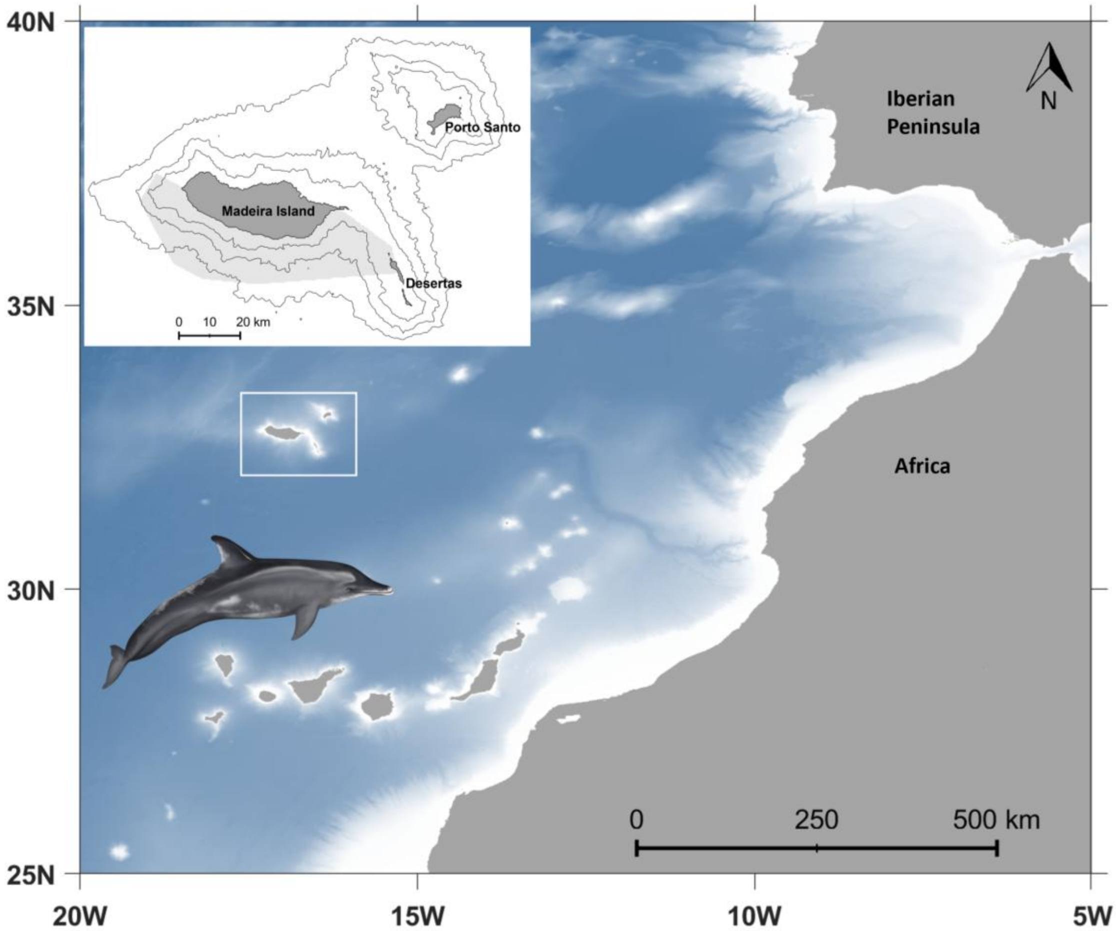

Figure 1. Map showing the data collection area (shaded zone) based on Fernandez et al. (2021), reflecting multi-species whale watching operations, not exclusively focused on the rough-toothed dolphin species.

Madeira Island, situated in the Eastern North Atlantic and part of the Macaronesia biogeographic region, is distinguished by its complex oceanographic and geomorphological features. The steep coastal profile and narrow continental shelf (***Figure 1***) give way to deep submarine canyons exceeding 1500 m nearshore, creating hydrodynamic conditions that modulate ocean currents and facilitate localized nutrient upwelling (Geldmacher et al., 2006). Although the surrounding waters are predominantly oligotrophic, episodic nutrient inputs from upwelling and Mediterranean inflows (Iorga & Lozier, 1999; Lemos & Pires, 2004; Sangil et al., 2018) enhance biological productivity, supporting a diversity of marine megafauna (Alves et al., 2018; McIvor et al., 2022). These canyons act as topographic conduits, concentrating nutrients and fostering trophic cascades that sustain higher trophic levels and attract open-ocean mobile predators such as rough-toothed dolphins.

The proximity of the island to other Macaronesian archipelagos, promotes ecological connectivity, particularly with the Canaries and Azores influencing cetacean movements and population structure across the region (Kim et al., 2008; Alves et al., 2019; Ferreira et al., 2021; Weyn et al. 2025). This interplay between geographic, oceanographic, and ecological factors positions Madeira as a critical habitat for cetaceans within the Eastern North Atlantic, offering a unique natural setting to investigate the spatial ecology and habitat use of mobile open-ocean marine predators within a dynamic marine ecosystem.

2.3. Photo-identification

Photo-identification is a widely used non-invasive method for studying animal populations. It is based on the recognition of individuals on the distinctive and lasting traits of their dorsal fin, such as notches, scars and pigmentation patterns (Hammond & Donovan, 1990; Auger-Méthé & Whitehead, 2007; Cheney et al., 2013). By avoiding physical contact or capture, it reduces stress and behavioural perturbations (Hammond & Donovan, 1990). In fact, photos are taken from boats at a distance, reducing interference with natural behaviours. Long-term monitoring of individual dolphins is carried out using this technique, providing valuable insights into site fidelity, movement patterns, and social dynamics over time, as well as seasonal migration tracking and changes in group composition or social bonds (Auger-Méthé & Whitehead, 2007; Badenas et al., 2022; Cheeseman et al., 2023).

Following the methodology of Alves et al. (2013), the procedure was applied as described, where, succinctly, the method of processing the photos involves cropping the dorsal fin, enhancing contrast to highlight key features, and using the unique notches on the edges of the fin as the main identifiers for matching images from the left and right sides. In the absence of distinctive notches, secondary features such as scars and fin shape are used to identify individuals. All matches were double-checked by an experienced researcher to ensure accuracy. Photos were evaluated on two separate 4-point scales: one assessing image quality (1 = poor, 4 = excellent), based on focus, clarity, and framing (***Figure 2; top***); and another assessing individual distinctiveness (1 = low, 4 = high), based on the visibility of identifying features

(***Figure 2; bottom***). For the analysis, only photos with a quality rating of 2 or higher and a distinctiveness rating of 3 or 4 were selected, thus filtering all the data qualitatively over a period of 9 years, between July 2016 and October 2024.

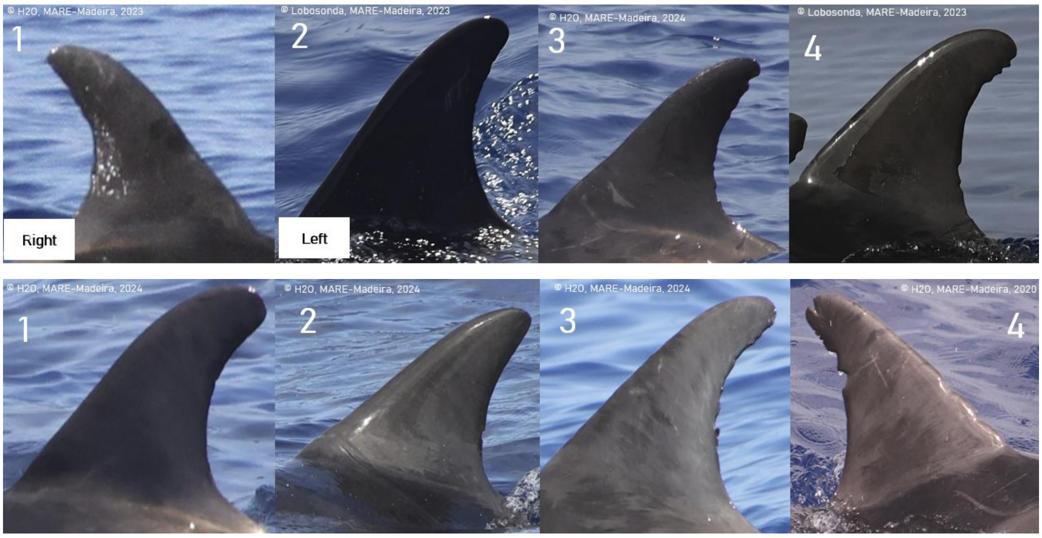

Figure 2. Examples of dorsal fins of rough-toothed dolphins illustrating (***top***) photo quality (1–4) and (***bottom***) individual distinctiveness (1–4).

The Happywhale platform was used to identify individuals and find matches. It automatically compares photos using a similarity score, facilitating the recognition of known individuals and the detection of new ones (Cheeseman et al., 2017). After the automated comparison, the program displays a set of possible matches ranked by similarity. However, the final decision always rests with the researcher, who must manually validate, accept, or reject the suggested matches to ensure the reliability of the identification process. This manual validation step is especially important when image quality (e.g. angle, lighting, visible markings) is suboptimal. In this study, the use of Happywhale enabled efficient sorting and cross-referencing of dorsal fin images against a large dataset, significantly improving the accuracy and speed of individual identification.

The resulting dataset of individual captures was analyzed to determine the number of individuals captured only once, as well as those that had multiple recaptures. Recaptured individuals were categorized based on the timing of their recaptures, distinguishing between intra-annual recaptured individuals (i.e. individuals with recaptures within the same year) and inter-annual recaptured individuals (i.e. individuals with at least one recapture in a different year). Then, the capture frequency was calculated, based on the percentages of individuals captured once, and those with intra- or interannual recaptures. Simultaneously, the cumulative number of new identifications of individuals was calculated, and compared with the cumulative number of identifications of individuals, and illustrated as a discovery curve. If the curve levels off, it suggests that all individuals in the population have been identified. However, if the curve continues to increase without stabilizing, it implies that new individuals are still being added to the catalogue.

2.4. Site fidelity

2.4.1. Lagged Identification Rates

Modelling tools can be used to assess the residence duration of individuals in a specific area. These include the Lagged Identification Rates (LIR), which estimate the probability of re-sighting an individual after a certain period. LIRs were calculated by comparing initial captures with subsequent recaptures of the same individuals over varying time intervals (days, months, years). Based on Whitehead (2001), LIRs were compared with those expected from exponential residency models and fitted using maximum likelihood methods (***Table 1***).

Table 1. Models that can be fitted to lagged identification rates (see the SOCPROG manual; Whitehead, 2015).

Equation	**Explanation**
$B = \frac{1}{a_1}$	(1) *Closed*
$D = \left(\frac{1}{a_1}\right) \times \exp\left(-\frac{t_d}{a_2}\right)$	(2) *Emigration/mortality*
$F = \dfrac{\frac{1}{a_1} \times \left(\frac{1}{a_3} + \frac{1}{a_2} \times \exp\left(-\left(\frac{1}{a_3} + \frac{1}{a_2}\right) \times t_d\right)\right)}{\frac{1}{a_3} + \frac{1}{a_2}}$	(3) *Emigration + reimmigration*
$H = \dfrac{\exp(-a_4 \times t_d)}{a_1} \times \left(\dfrac{\frac{1}{a_3} + \frac{1}{a_2} \times \exp\left(-\left(\frac{1}{a_3} + \frac{1}{a_2}\right) \times t_d\right)}{\frac{1}{a_3} + \frac{1}{a_2}}\right)$	(4) *Emigration + reimmigration + mortality*

where $a_1 = N$; a_2 = mean time in study area; a_3 = mean time out of study area; a_4 = mortality rate; t_d = time lag

The model with the lowest Quasi-Akaike Information Criterion (QAIC) was selected as the best fit to the data (Whitehead, 2009). The Standard Error (SE) was estimated using a bootstrap method.

The methods used for this analysis were performed using SOCPROG 2.10 MATLAB2023b (Whitehead, 2009). Based on the SOCPROG manual (Whitehead, 2015) and the collaboration with Hal Whitehead (see 'Acknowledgments'), the Excel input file is built in 2 columns: the first with the date of each identification, converted into a number (to avoid any reading problems) and the second column associated with the IDs of each individual, converted into hexadecimal to avoid the '999' reading limit (i.e. 3 characters for the ID of an individual). Therefore, it is possible to have several lines with the same date, associated with different individuals, and also to have several different dates with the same individual in the case of recaptured individuals. The outputs are shown in the next section (in Sec. 3.2).

2.4.2. Site Fidelity Indexes

The Site Fidelity Indexes, were applied to quantify population-level site fidelity. Based on capture-recapture data, these indexes are ranged from 0 (indicating no site fidelity) to 1 (indicating a fully resident population). Among the most common indicators are *Occurrence*, *Permanence* and *Periodicity* (Simões-Lopes & Fabian, 1999; Morteo et al. 2012) and were used to calculate the site fidelity indexes (Tschopp et al., 2018). Given the opportunistic and systematic nature of the data, the day was used as the sampling occasion time unit, as using months would combine several sampling occasions into a single occasion, which would significantly reduce the amount of usable data. In addition, as mentioned previously (in section 2.1), multiple observations on the same day are merged into a single sampling occasion in order to ensure uniformity without losing data.

Firstly, the *Occurrence* IO_i indicator represents the frequency at which an individual was recaptured throughout the entire sampling period.

$$IO_i = \frac{\sum_{j=1}^{T} C_{ij} - 1}{T - 1} \tag{5}$$

where C_{ij} is the constant of capture presented as a binary value indicating capture (1) or absence (0) for an individual i, during a sampling occasion j, and T is the total number of sampling occasions, given in time unit (i.e. days, months). Total occurrence would be 0 for an individual seen once, and 1 for an individual seen in all surveys.

Secondly, the *Permanence* IT_i indicator measures the proportion of time spent in the study area, calculated by dividing the interval, between the first capture and the last recapture (F_i) by the total sampling period (F). As defined by Tschopp et al. (2018), F_i was calculated as $F_i = (\max\{t_j : C_{ij} = 1\} - \min\{t_j : C_{ij} = 1\})$, where t_j is the sampling time of occasion j in a given time unit (i.e. days, months). Therefore, F could be evaluated as $F = t_T - t_1$, which is the time between the first and the last sampling occasion, in the same unit of time as F_i. Note that T, the sampling occasions, and F, the total sampling period, do not refer to the same parameter. The variable T represents the number of days or months in which there is an observation, whereas F represents the difference between the first observation and the last in the entire study period, including days or months in which there are no observations. Similarly with F_i, where the number of days or months between the last and first capture of an individual is counted, also including days with no sightings. Thus, an individual i observed only once t_j, had a value $F_i = 0$, and consequently $IT_i = 0$, which was considered to be transient.

$$IT_i = \frac{F_i}{F} \tag{6}$$

Finally, the *Periodicity* It_i indicator quantifies the frequency of recaptures of an individual, determined by the inverse of the average time between two consecutive recaptures. The parameters C_{ij} and F_i have been previously defined in Eq. (5) and (6). Non-recaptured individuals had a default value $It_i = 0$, as they had a value $F_i = 0$, and as mentioned above, they were automatically considered as transients.

$$It_i = \left(\frac{F_i}{\sum_{j=1}^{T} C_{ij} - 1} \right)^{-1} \tag{7}$$

Based on the combinations of *IO*, *IT* and *It*, eight individual site fidelity indexes were constructed using the methods described by Tschopp et al. (2018). Four of these indices were calculated as arithmetic means structure (IA1-IA4) and the four as harmonic means structure (IH1-IH4). These indexes, as shown in ***Table 2***, and whose values range from 0 (without fidelity) to 1 (maximum fidelity), summarize individual behaviour while ensuring comparability with other similar studies.

Table 2. Site Fidelity Indexes from Tschopp et al. (2018) using *Occurrence* (*IO*), *Permanence* (*IT*) and *Periodicity* (*It*) indicators.

Indexes with an arithmetic mean structure (IA)	**Indexes with a harmonic mean structure (IH)**
$\text{IA1} = \frac{1}{3}(IO + IT + It)$	$\text{IH1} = \frac{3}{\frac{1}{IO} + \frac{1}{IT} + \frac{1}{It}}$
$\text{IA2} = \frac{1}{2}(IO + IT)$	$\text{IH2} = \frac{2}{\frac{1}{IO} + \frac{1}{IT}}$
$\text{IA3} = \frac{1}{2}(IO + It)$	$\text{IH3} = \frac{2}{\frac{1}{IO} + \frac{1}{It}}$
$\text{IA4} = \frac{1}{2}(IT + It)$	$\text{IH4} = \frac{2}{\frac{1}{IT} + \frac{1}{It}}$

The IH4 site fidelity index, developed by Tschopp et al. (2018), also referred to as Standardized Site Fidelity Index (SSFI; Ferreira et al., 2022) was used as a standardized metric of site fidelity, due to its robust performance under conditions of imperfect detection and non-constant sampling efforts (Cantor et al., 2019, Bolaños et al., 2021; Verborgh et al., 2022).

$$\text{IH4} = \frac{2}{\frac{1}{IT} + \frac{1}{It}} \tag{8}$$

2.4.3. Clustering

The data were standardized and Pearson correlation matrix (Pearson, 1896) was calculated to assess the degree of pairwise independence between the different indexes, previously defined (in Sec. 2.4.2). When a pair of variables were significantly correlated (|r| ≥ 0.7), the variables were discarded to avoid redundancy and improve the robustness of the statistical analyses. The pair of indices with the lowest overall correlation with the other variables was selected. In these statistical analyses, individuals observed only once (non-recaptured) were not included in the following clustering method.

Then, groupings based on site fidelity were performed using the clustering method and the selected indexes derived from the eight metrics (in Sec. 2.4.2). Based on the work of Verborgh et al. (2022), four clustering methods were used: K-means, Divisive Hierarchical Clustering (DHC), Agglomerative Hierarchical Clustering (AHC) and Gaussian Mixture Model, for which the number of components is estimated automatically. They were compared in order to choose the one with the better clustering. All clustering methods aim to group observations into mutually exclusive clusters with high within-group similarity and high between-group dissimilarity.

In K-means clustering, each cluster is defined by the mean of its assigned observations (*kmeans()* function on R). Hierarchical clustering includes agglomerative (AHC), which builds clusters bottom-up (*stats* packages and *hclust()* function on R), and divisive (DHC), which splits clusters top-down (*cluster* package and *diana()* function on R). DHC is often preferred for identifying broad clustering patterns (Legendre & Legendre, 2012). Gaussian Mixture Models (GMMs) are model-based clustering methods that use a combination of normal distributions to assign individuals to clusters probabilistically, accounting for uncertainty in classification (McLachlan & Basford, 1988). Each cluster is characterized by its mean, covariance, and weight, estimated via the Expectation-Maximisation (EM) algorithm. This approach is well-suited for data with overlapping or non-spherical clusters. In this study, GMMs were implemented using the *Mclust* package and function on R (Scrucca et al., 2016), with both three- and six-cluster models (GMM3 and GMM6) tested for comparison.

For K-means, DHC and AHC, the optimal number of clusters *k* was defined using the average silhouette method (Rousseeuw, 1987), which simultaneously assesses cohesion within clusters and separation between them. In the case of the K-means method, 25 initial configurations were tested to ensure the stability of the final result.

Hence, the silhouette width and Within-Cluster Sum of Squares (WSS) are commonly used metrics to evaluate clustering methods performance. Silhouette width assesses both cohesion and separation by measuring how similar an observation is to its own cluster compared to others, with values closer to 1 indicating better-defined clusters. WSS quantifies the compactness of clusters by summing the squared distances between each point and its cluster centroid; lower values indicate tighter groupings. Together, these metrics help compare clustering methods by balancing internal consistency and inter-cluster distinctiveness.

The resulting classification was then represented in a two-dimensional space using Principal Component Analysis (PCA), using *factoextra* packages on R, to illustrate the distribution of individuals along the axes that maximize the variance explained by the selected indexes.

In order to assess the significant differences between the identified groups, pairwise comparisons were performed using the non-parametric Mann-Whitney U test (also known as the Wilcoxon rank-sum test), which determines whether two independent samples originate from the same distribution without assuming normality (Mann & Whitney, 1947). The test was applied to the selected fidelity indexes using the *rstatix* package in R. These analyses can allow to identify distinct profiles ranging from occasional visitors, characterized by low site fidelity, to regular residents with high site fidelity. The group representing the population with regular visitors has individuals who are detected more frequently (higher IO_i), present over a longer period (higher IT_i) and with a more regular presence over time (higher It_i periodicity).

Analyses were carried out in RStudio (v2025.05.0+496), employing the open-access R code developed by Verborgh et al. (2022).

3. Results

3.1. Photo-identification data overview

Following 341 sampling occasions between 2013 and 2024, including all data, with a total of 22312 photos processed. In this database, the photos are classified as *Poor* (11.1 %), *Fair* (51.4 %), *Good* (29 %) and *Excellent* (8.5 %) with a total of 2249 photos for photo quality criterion. While the majority of the photos showed acceptable quality, a relatively small proportion actually satisfied the most stringent standards required for optimum identification of the individuals. In addition, they are also classed as *Low distinctive* (6.6 %), *Sightly distinctive* (27.8 %) *Distinctive* (45.8 %) and *High distinctive* (19.8 %) with a total of 995 individuals for distinctiveness criterion, indicating that a significant proportion of individuals have sufficiently marked features to allow for reliable long-term identification.

However, after filtering the data, using only image quality between 2-4 and distinctiveness between 3-4, and merging the multiple sampling occasions in a single day, we obtain 160 days of sampling occasions over a 9-year period, between 2016 and 2024 (***Table S1***), with a total of 1092 captures and 637 individuals identified (***Table 3***). From 2013 to 2015, the data were not selected, due to a lack of data quality according to the two criteria.

Table 3. Total number of captures of individuals and percentages of their respective categories for photographic quality and distinctiveness.

Captures (total number)	**1092**
Fair (2)	49.7 %
Good (3)	37.3 %
Excellent (4)	13.0 %
Individuals (total number)	**637**
Distinctive (3)	69.7 %
High distinctive (4)	30.3 %

Over this 9-year period, the number of captures tends to increase steadily (***Figure 3***), with the highest numbers observed in 2020 (n = 147), 2023 (n = 237) and 2024 (n = 218). Since 2016, the annual proportion of new identifications in relation to the total number of individuals (n = 637) is approximately constant, with an exceptional value in 2024 (~19%; ***Table S2***) as a result of the large number of new individuals identified (n = 124). In addition, regarding the annual rate of new identifications in relation to the number of identifications (discovery curve slope; ***Figure 4***), the slope values are relatively stable (slope ~0.8; ***Table S2***). Nevertheless, a flattening period (***Figure 4***) is observed (slope = 0.31; ***Table S2***), when the number of captures recorded is very high (n = 237; ***Table S2***) for a lower number of new individuals (n = 74; ***Table S2***). The discovery curve did not reach an asymptote, which indicates the process of individual identification is not yet complete, implying that the entire population has not yet been fully identified.

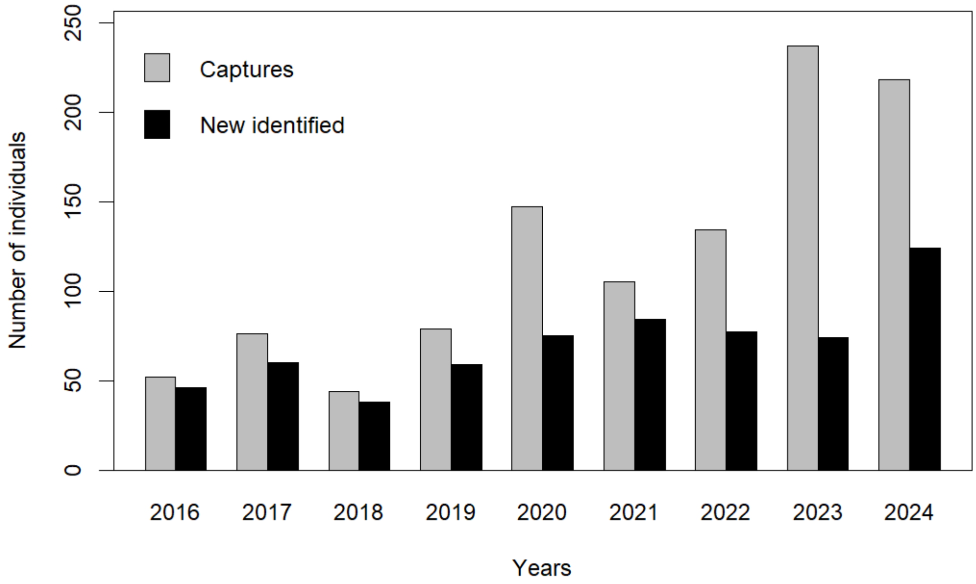

Figure 3. Number of total captures of rough-toothed dolphins and new identified individuals per year, from 2016 to 2024 in Madeira.

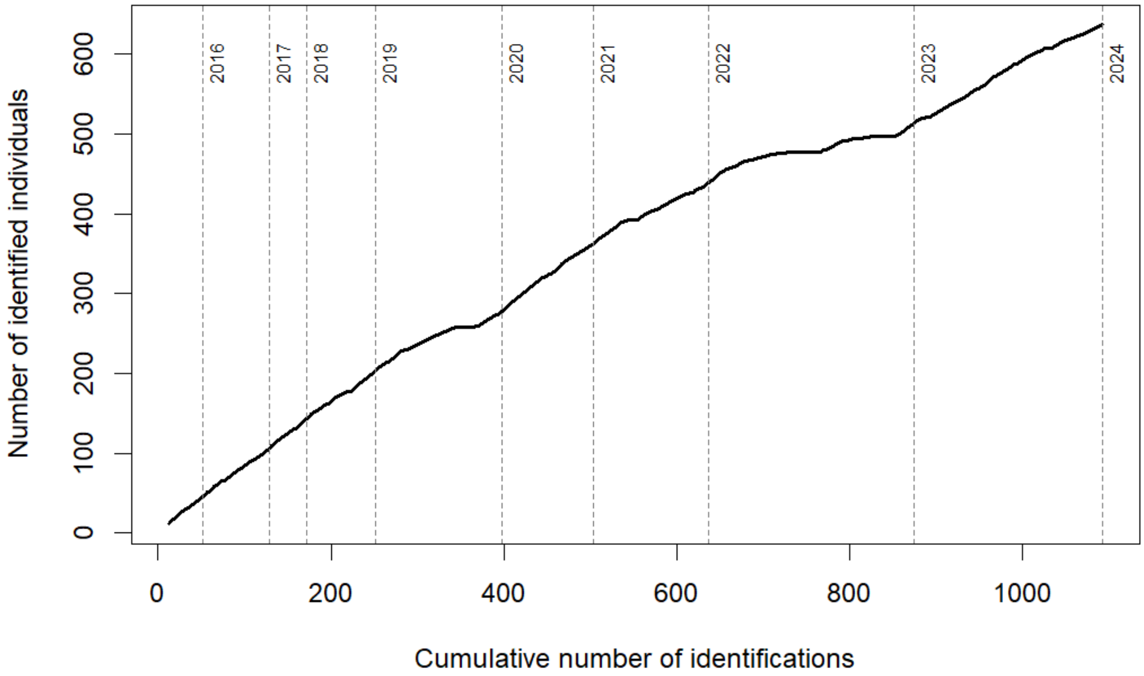

Figure 4. Discovery curve for rough-toothed dolphins in Madeira, based on the cumulative number of new identifications in relation to the cumulative number of identifications from 2016 to 2024.

Among the 637 identified individuals, 398 (62.5 %) have been captured only once, while 239 (37.5 %) were recaptured at least once (***Table 4***). One individual has been recaptured up to 10 times throughout the study period (***Figure 5***). All recaptures, with a nearly even distribution between interannual (n = 127, 53.1 %) and intra-annual (n = 112, 46.9 %). The interannual intervals, reflecting long-term site fidelity (or at least seasonal; see the seasonal pattern below), have a median of 2 years, a standard deviation (SD) of 0.44 years and vary from 2 to 4 years. Most individuals (88.2 %) were observed over only 2 years, while 8.7 % were recorded over 3 years and only 3.1 % over 4 years.

Table 4. Total number and percentages of catalogued individuals in Madeira.

Total number of catalogued individuals	Individuals captured once	Resighting rate	Individuals with recaptures		
			Total	Interannual	Intra-annual
637	398	37.52 %	239	127	112

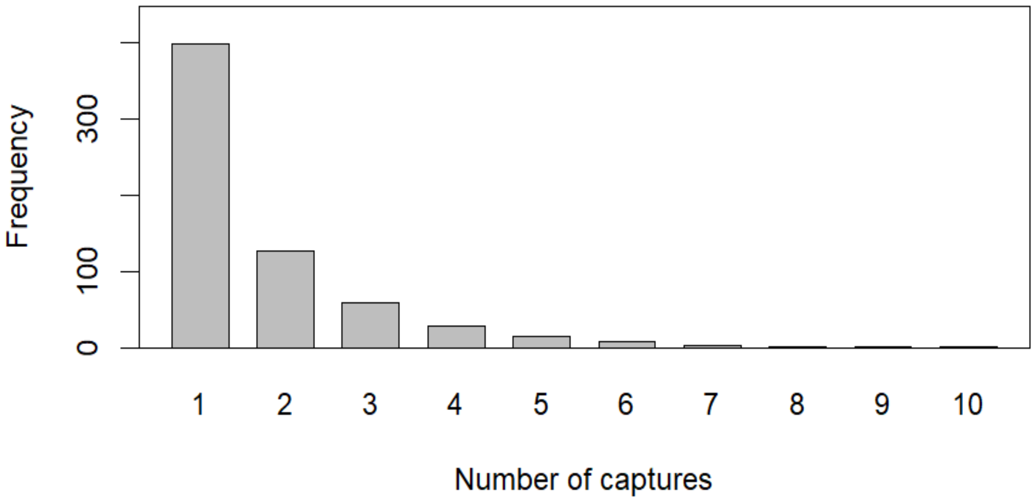

Figure 5. Capture frequency histogram for rough-toothed dolphins (n = 637) from 2016 to 2024. More than half of the individuals (n = 398) were captured only once.

Alongside the increasing number of captures described previously, a distinct seasonal pattern is observed over the 9 years (***Figure 6***). In July, the average number of captures is high ($\bar{x}$ = 40.00; SD = 45.17), despite a coefficient of variation (CV) at 102.7 %, indicating strong fluctuations from one year to the next and resulting in a limited predictability. The average for August is slightly higher ($\bar{x}$ =48.56; SD = 34.68) with more moderate variability (CV at 71.4%), suggesting greater consistency in capture success. By contrast, September shows a significantly lower average ($\bar{x}$ = 20.67 SD = 15.02), while variability remains high (CV at 72.7%). Overall, the month of August shows the most potential in terms of yield and stability, while July has high potential but is highly irregular, and September demonstrates lower activity with significant variability.

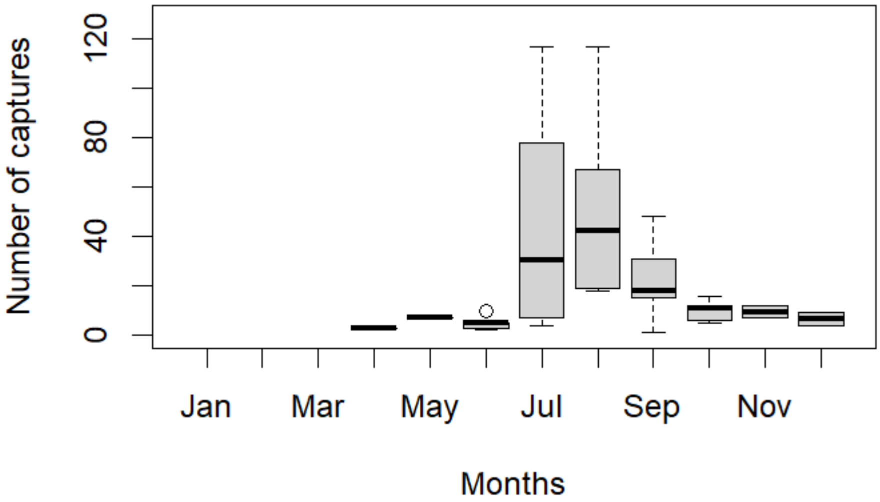

Figure 6. Seasonal pattern of monthly capture frequency of rough-toothed dolphins from 2016 to 2024.

3.2. Site fidelity and residency pattern

3.2.1. Modelled residency pattern

Due to overdispersion (variance inflation factor $c > 3$), only the months with the most consistent number of identifications were used for the analysis, in this case, July and August between 2016 and 2024 (***Figure 6***). In contrast, the month of September was removed from the analysis. The C*losed* model (***Table*** 1; Eq. 1) has the lowest QAIC (47.2; ***Table 5***), while the variance inflation factor is excessively high (61.46; ***Table 5***).

Therefore, the model incorporating *Emigration, reimmigration* (***Table 1***; Eq. 3) best fitted the LIR for Madeira during the summer season (July and August), with an average of a_1 = 28 individuals (SE = 4.9) present in the area at any given time (July and August). Individuals were estimated to remain in the area for a_2 = 6.4 days (SE = 2.3) before leaving for approximately a_3 = 625.6 days (SE = 323.2). This analysis was obtained for a dataset of 637 individuals based on 160 sampling occasions (as a day), with 1092 captures, between 2016 and 2024. This model showed a good fit to the empirical LIR curve (χ^2 = 8.046, df = 7, P = 0.3285; c = 1.15; ***Figure*** *7*). It was selected as the best-supported model because it had the lowest quasi-Akaike information criterion (QAIC = 1983.7) among the candidate models, with a total of four parameters (***Table 5***). This model was fitted using maximum likelihood methods and accounted for potential overdispersion, as described in the methods. Nevertheless, the second-best fitting model, *Emigration, reimmigration and mortality* (a_4 = -0.00069) (***Table*** 1; Eq. 4), also showed good support, given that the QAIC difference was close for the best model (***Table 5***).

Table 5. Models fitted to LIR for rough-toothed dolphins in Madeira from 2016 to 2024. Comparison between four models with performance metrics (QAIC and Summed log likelihood).

Models	**No. of parameters**	**QAIC**	**Summed log likelihood**	**Variance inflation factor**
Closed	1	47.2	-1450.9	61.46
Emigration/mortality	2	2581.0	-1289.5	5.91
Emigration + reimmigration	3	**1983.7**	-1137.8	1.15
Emigration + reimmigration + mortality	4	2276.3	-1135.1	0.51

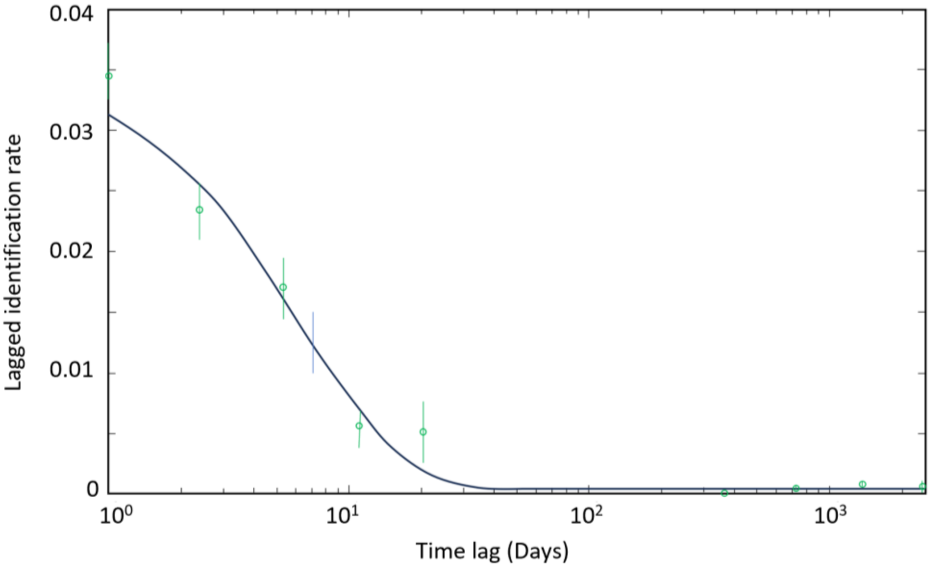

Figure 7. Lagged Identification Rates for rough-toothed dolphins in Madeira during peak season (July–August) modelled by the best-fitting model (Eq. 3) with 1000 bootstraps and standard errors (from SOCPROG).

3.2.2. Site fidelity structure

As previously mentioned (in Sec. 3.1), the photo-identification database resulted in 637 photo-identified individuals for 160 days of sampling occasions (*T*), within a sampling period of 3024 days (*F*) with a non-constant effort. The mean time between each sampling occasion was 19 days, with a range of 1-294 days, which highlights the heterogeneous disparity of sampling occasions over the 9-year study period. Among the 398 individuals captured only once, the site fidelity is 0, automatically categorizing them as transients. However, the recaptured individuals (n = 239) generally show a low site fidelity (based on IH4), with values very close to 0 (0.0057, 95% CI 1.7398–2.0756) and ranging from 0.0006 to 0.0393 (***Table 6***). Most individuals do not consistently return to the same area over time. The parameters IO_i, IT_i and It_i also show the same trend (***Table 6***), reflecting considerable variability in observation frequency, temporal span, and temporal aggregation among individuals.

Table 6. Descriptive statistics of indicators (IO_i, IT_i, It_i) and the site fidelity index (IH4) for recaptured individuals: median, mean, minimum, and maximum values and standard deviation.

	IO_i	IT_i	It_i	**IH4**
Median	0.0063	0.1121	0.0086	0.0028
Mean	0.0119	0.2000	0.2278	0.0057
Min, Max	0.0063, 0.0566	0.0003, 0.9831	0.0003, 1	0.0006, 0.0393
SD	0.0083	0.2507	0.3415	0.0065

The Pearson pair-wise correlation test with the 8 site fidelity indexes shows that IA2, IH2 and IH3 have the lowest correlation, with a coefficient below the critical redundancy threshold ($|r| < 0.7$) (***Table** 7*). In addition, for clustering, IH4 was retained instead of IH1 because, although both are strongly correlated ($|r| = 0.96$), IH4 shows generally lower correlations with the other variables, thereby reducing redundancy in the dataset. According to Tschopp et al. (2018), it is the index that showed the best performance across all scenarios studied. In contrast, IA1, IA3, and IA4 were not retained because they were highly intercorrelated ($|r| \geq 0.7$), indicating redundancy among them.

As a result, these variables were selected for further clustering analyses, as it allows for the complementary examination of two distinct dimensions of spatio-temporal fidelity without statistical interference between the variables.

Table 7. Pearson correlation matrix by pair of site fidelity indexes: arithmetic mean structure (IA1-IA4) and harmonic mean structure (IH1-IH4). Values in bold have |r| ≥ 0.7.

	IA1	**IA2**	**IA3**	**IA4**	**IH1**	**IH2**	**IH3**	**IH4**
IA1	**1**							
IA2	0.24	**1**						
IA3	**0.70**	-0.52	**1**					
IA4	**1.00**	0.24	**0.70**	**1**				
IH1	-0.56	-0.20	-0.33	-0.57	**1**			
IH2	-0.17	0.52	-0.51	-0.19	0.49	**1**		
IH3	0.19	-0.55	0.59	0.18	0.27	-0.28	**1**	
IH4	-0.59	-0.24	-0.33	-0.61	**0.96**	0.36	0.21	**1**

Beforehand, the Silhouette method provided an optimal number of clusters k = 2 for K-means (***Figure 8***) as well as DHC and AHC (***Figure S2a; S3a***), with the four selected indexes IA2, IH2, IH3 and IH4. Based on the comparison of different clustering methods, the results (***Table 8***) show that the K-means method obtains both the best silhouette score (0.691) and the lowest WSS value (1.0), indicating a well-defined cluster structure. In contrast, the three- and six-cluster GMM methods have very low silhouette width (-0.080: GMM3; 0.213: GMM6) and also relatively high WSS (483.6: GMM3). Although AHC and DHC obtain relatively the same average silhouette width score as K-means, they have significantly higher WSS (107.5 and 172.9) respectively, indicating less intra-cluster density, i.e. a dispersion of the points in relation to the centroids of each cluster. As a result, the K-means method is selected as the most effective for ensuring better clustering (***Figure 8***).

Table 8. Comparison of clustering performance metrics (Average Silhouette Width and WSS) between K-means, DHC, AHC and two GMM (3 clusters and 6 clusters).

	K-means	**DHC**	**AHC**	**GMM3**	**GMM6**
WSS	**1.0**	107.5	172.9	483.6	37.0
Average silhouette width	**0.691**	0.691	0.691	-0.080	0.213

Thus, the K-means clustering resulted in two groups with contrasting spatio-temporal profiles (***Figure 8***). The first group, cluster 1, includes 174 individuals, while cluster 2 has 65. This structure reflects a differentiation of individuals according to their fidelity to the area. The clustering revealed a clear differentiation in fidelity patterns: the 112 individuals with intra-annual fidelity were grouped together in cluster 1, while inter-annual fidelity was more evenly distributed between the two groups, with 62 individuals in cluster 1 and 65 in cluster 2. Additionally, the robustness of the clustering was supported by the Mann-Whitney U test (***Table 9****)*. The IA2 and IH2 indices showed highly significant differences between the two groups (U = 0 and U = 1520, respectively, $p < 0.05$), with higher values observed in cluster 2, indicating greater site fidelity in that group. Similarly, the IH3 and IH4 indices also showed significant differences (U = 10532 and U = 7838, respectively, $p < 0.05$), reinforcing the distinction in long-term residency patterns between the clusters. These results confirm that individuals in cluster 2 exhibit stronger and more consistent site fidelity behaviour compared to those in cluster 1.

Table 9. Results of Mann-Whitney tests between the two clusters for IA2, IH2, IH3 and IH4.

Tests	**Parameters**	**IA2**	**IH2**	**IH3**	**IH4**
Mann-Whitney	U	0	1520	10532	7838
	p-value	< 0.05	< 0.05	< 0.05	< 0.05

The individuals in cluster 1, exhibited higher periodicity *(It* mean = 0.3123, 95% CI 0.2574–0.3672) but lower permanence (*IT* mean = 0.0662, 95% CI 0.0526–0.0798) compared to cluster 2 (It mean = 0.0014, 95% CI 0.0012–0.0016; IT mean = 0.5584, 95% CI 0.5149–0.6019), suggesting that individuals in cluster 1 returned more frequently but for shorter periods.

Likewise, IA2 and IA3, which reflect the contribution of periodicity and occurrence in the arithmetic structure, were markedly higher in cluster 2 (IA2 = 0.2858, 95% CI 0.2635–0.3080; IA3 = 0.0073, 95% CI 0.0059–0.0087), while cluster 1 showed higher IA3 values (0.1619, 95% CI 0.1345–0.1893), indicating more regular presence within a season.

Similarly, harmonic mean indices (IH1–IH4) were generally lower in cluster 2, particularly IH4 (0.0028, 95% CI 0.0022–0.0034 *vs*. 0.0068, 95% CI 0051–0.0091), reinforcing the idea that cluster 1 individuals exhibit more temporally structured patterns, consistent with intra-annual fidelity. This distinction is also supported by higher values for *Months*, *Years*, and *Seasons* variables in cluster 2 (*Months* = 1.9077, 95% CI 1.73977–2.07563; *Years* = 2.2769, 95% CI 2.1340–2.4198; *Seasons* = 1.4154, 95% CI 1.2920–1.5388), suggesting broader temporal dispersion of inter-annual individuals, compared to cluster 1 (*Months* = 1.4828, 95% CI 1.3998–1.5658; *Years* = 1.3621, 95% CI 1.2882–1.436; *Seasons* = 1.1609, 95% CI 1.1060–1.2156) (***Figure 9; Figure S1***).

Overall, these results confirm that the clustering process effectively separated intra-annual from inter-annual patterns of site fidelity, based on meaningful differences in both arithmetic and harmonic summaries of occurrence, permanence, and periodicity.

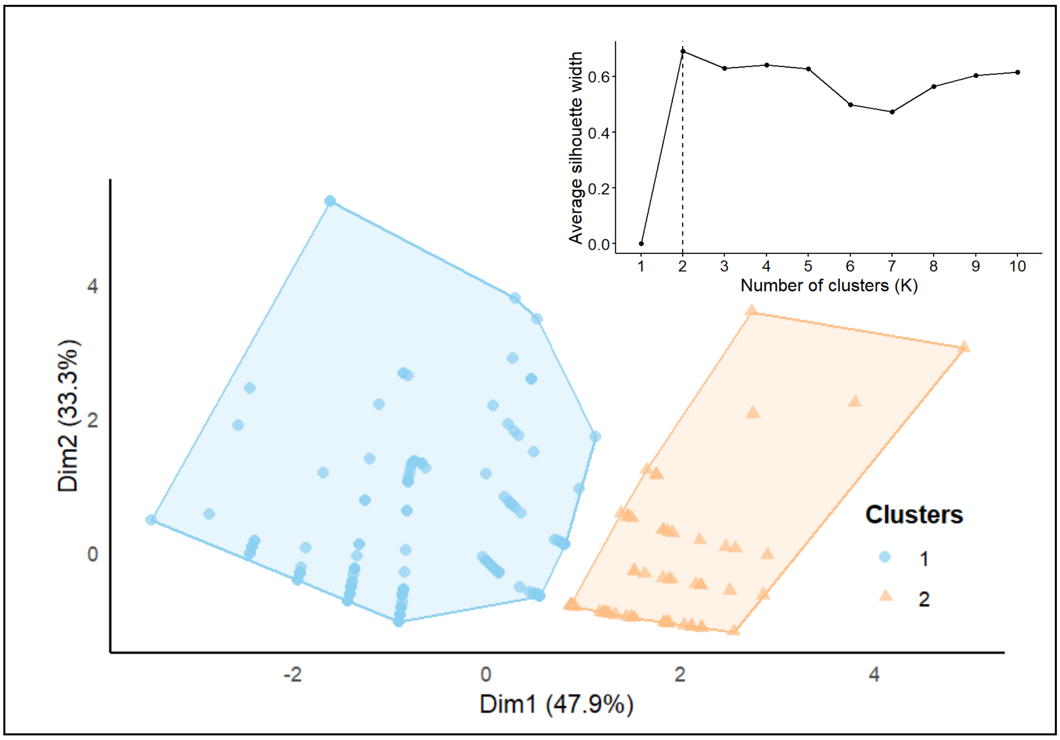

Figure 8. Top left plot shows the Silhouette results with the optimal number of clusters with dashed lines (k = 2) of rough-toothed dolphin in Madeira based on the K-means method. The main plot shows the two clusters illustrated on two first dimensions of a Principal Component Analysis (PCA) based on four selected site fidelity indexes: IA2, IH2, IH3 and IH4.

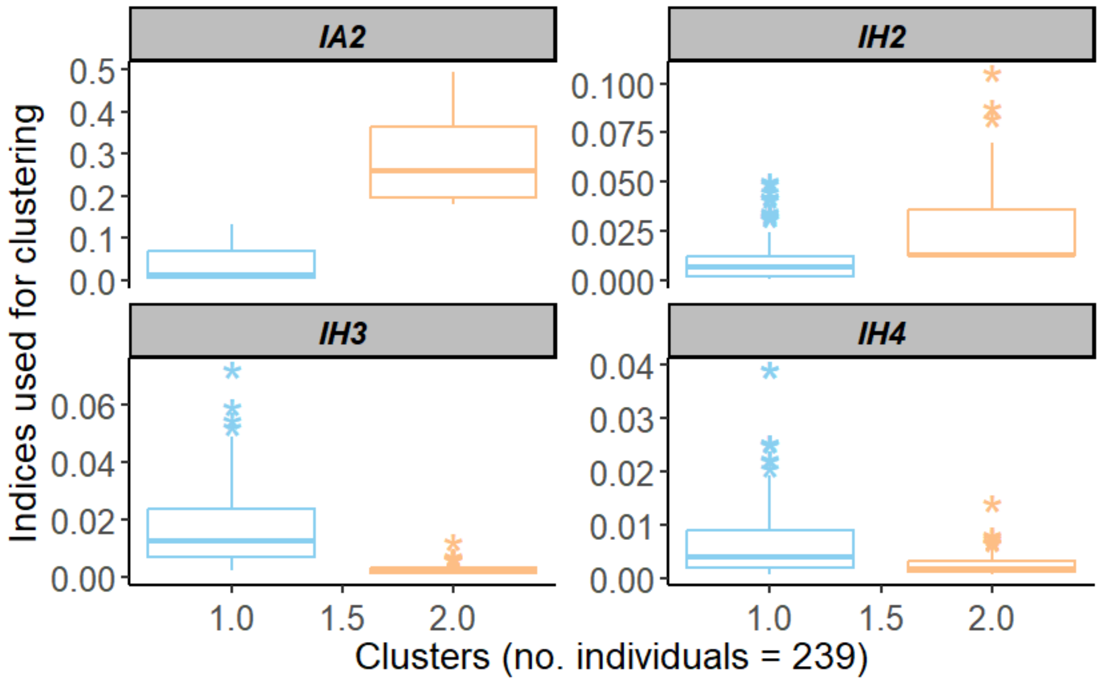

Figure 9. Boxplots of the four selected site fidelity indexes IA2, IH2, IH3 and IH4 according to the 2 clusters.

4. Discussion

This study presents the first photo-identification-based study of site fidelity in rough-toothed dolphins around Madeira Island, a region where this species remains largely understudied. The photo-identification approach used, based on both dedicated and opportunistic data, revealed certain limitations. While a low proportion of high-quality photographs was initially considered a key constraint, this issue was largely mitigated by the exclusion of poor-quality images from the analyses. Moreover, whale-watching operators generally used good photographic equipment, and their imagery was often comparable in quality to that of researchers. Therefore, image quality is unlikely to have been the main limitation. A more significant source of potential bias arises from the heterogeneous nature of sampling effort across time, locations, platforms, and observers. This variability, which is inherent to the combination of dedicated surveys and opportunistic data, likely led to unequal capture probabilities among individuals and may have affected the detection of recaptures and estimates of site fidelity. Similar challenges have been acknowledged in previous studies (e.g. Alves et al., 2019). The fact likelihood techniques to estimate parameters of movement models were used (following Whitehead, 2001), allowed dealing with the effort associated in collecting the individual identifications that had been neither randomly nor systematically distributed in space-time. Moreover, the high distinctiveness of individuals used (i.e. restricted to well-marked animals) allowed for reliable identification, highlighting the robustness of photo-identification methods. However, beyond marking patterns, interindividual behavioural differences, such as the shy–bold continuum, can also influence detectability. Bold individuals displaying novelty-seeking behaviour may approach boats more frequently or tolerate human presence, making them easier to photograph than shyer individuals, as observed in bottlenose dolphins (López B. D., 2020). The progressive increase in capture numbers (see 'Supplementary data, ***Table S2.***'), especially in recent years, reflects not only increasing survey effort but also potentially enhanced detectability or shifts in the species' spatial behaviour. The discovery curve, which shows no sign of plateauing, confirms that a substantial portion of the population remains undocumented, a trend also observed by Pouey-Santalou et al. (2024) off Guerrero in the southwest Pacific coast of Mexico. These patterns underscore the need for continued sampling to achieve more representative coverage and improve estimates of fidelity, social structure, and demographic trends.

Regarding site fidelity patterns, all analytical approaches converge on the same finding: the majority of individuals exhibit little to no fidelity to the study area. Recaptures are infrequent, and the temporal dispersion between sightings is broad. The standardized site fidelity index (IH4), along with its components (*ITi, Iti*), shows low values, pointing to episodic and irregular usage of the area over time. This is supported by the LIR analysis, which indicates extremely short residence durations and long absences from the study area. Applied to the more stable months of July and August, the LIR reveals that Madeira is used opportunistically, likely in response to seasonal ecological conditions. The strong agreement between the LIR and the fidelity indexes reinforces the empirical observation that Madeira does not function as a permanent habitat for rough-toothed dolphins but rather as a temporary or transit area, roamed predominantly in the summer season, where individuals have been observed engaging in behaviours such as traveling, feeding, resting and socializing, as reported for cetaceans in general in this region (Alves et al., 2018). For this species, the average group size has been reported to be around 21 individuals (Alves et al., 2018).

Despite their low values, the site fidelity indexes which exhibit low inter-correlations were used in a cluster analysis to identify potential groupings based on different site fidelity patterns. Unlike Verborgh et al. (2022), a Pearson correlation threshold of 0.7 was used in this study. This choice was made because of the low amplitude and proximity of the observed values, justifying the use of a stricter threshold to better distinguish between correlated indexes. This analysis aims to highlights the existence of contrasting space-use strategies among rough-toothed dolphin individuals. Our results reveal a differentiation between the two groups identified on the basis of spatio-temporal site fidelity indexes. Individuals in group 1, which includes all individuals with intra-annual and some interannual fidelity, show high periodicity but low permanence (*It* high, *IT* low), reflecting a regular presence but over short periods, often on a seasonal scale. By contrast, group 2, composed exclusively of individuals with interannual fidelity, shows marked permanence but almost no periodicitysuggesting that the individuals are considered as sporadic visitors and visit the island multiple years but at least once per year. This opposition is reinforced by the higher values of the arithmetic indices (IA2 and IA4) in the interannual individuals, highlighting the relative importance of permanence in their fidelity structure, whereas the intra-annuals stand out with higher values of IA3 and the harmonic indices (IH3, IH4), reflecting a more regular and recurring temporal structure. Finally, the differences observed for the temporal variables (*Months*, *Years*, *Seasons*) confirm that the interannual individuals from group 2, are part of a more extensive and less structured temporal dynamic, whereas the intra-annual and interannual individuals from group 1, show a marked seasonal fidelity. These results suggest the existence of two complementary fidelity strategies in the population, possibly linked to distinct ecological and social behaviours or environmental pressures.

However, these results must be interpreted with caution, as the absolute values of the site fidelity indexes remain low overall, often close to zero. This suggests that, although statistical differences are observed between clusters, the overall intensity of fidelity behaviour remains low. Thus, the contrasts described reflect relative trends between groups rather than marked or systematic fidelity at the individual level. This distinction between clusters should therefore be considered as a hypothesis of behavioural structuring, rather than a robust confirmation of differentiated strategies, requiring further validation (for example via long-term monitoring or complementary approaches). The coexistence of these two profiles within a single population highlights the importance of accounting for intra-population heterogeneity when analyzing habitat-use dynamics. It also underlines the relevance of clustering-based approaches for detecting fine-scale behavioural patterns that may be overlooked by global analyses. These behavioural differences may also have important conservation implications, as resident individuals could be more vulnerable to persistent local disturbances, whereas more mobile individuals may be affected by threats operating at broader spatial scales.

Although rough-toothed dolphins exhibited low site fidelity in the Madeira region according to our photo-identification data, their regular presence during the summer months can be explained by favourable environmental conditions during this period. According to the work of

Fernandez et al. (2021), this species shows a temporal distribution that is limited to warm water conditions (over 21-22°C), which is the case on the South Coast of Madeira during the summer months (July - September) (Caldeira et al., 2002; Alves et al., 2021). This confirms the seasonal pattern of rough-toothed dolphins in our captures. The ecosystems adjacent to oceanic islands like Madeira are highly dynamic and constitute biodiversity hotspots that strongly influence surrounding pelagic habitats (Fernandez et al., 2021). The insular topography and local oceanographic features such as the Azores Current, upwelling filaments from the North African coast, and the formation of mesoscale eddies generate an Island Mass Effect (IME) that locally enhances productivity (Caldeira et al., 2002; Gove et al., 2016). This process promotes phytoplankton blooms that support intermediate trophic levels, such as pelagic fish and cephalopods, ultimately attracting delphinids (Correia et al., 2015). The rough-toothed dolphin also tends to frequent areas with moderate to steep slopes (usually associated with seamounts and oceanic islands), often near underwater structures like seamounts and island canyons, indicating that both thermal and topographical factors contribute to defining an ecological niche closely associated with complex island habitats (Alves et al., 2021; Fernandez et al., 2021). The distribution of this species is therefore strongly influenced by seasonal availability of resources and habitat features, which may explain its restricted temporal occurrence around Madeira during the warmest months (Caldeira et al., 2014; Alves et al., 2021; Fernandez et al., 2021). These seasonal patterns in Madeira reflect similar ecological dynamics reported in other regions. For instance, Pouey-Santalou et al. (2024) documented predominantly transient individuals off the Pacific coast of Mexico, with some showing seasonal return, suggesting behavioural heterogeneity and opportunistic habitat use. This contrasts with tropical environments such as Tahiti and Moorea in French Polynesia, where this species is observed year-round, indicating stronger site fidelity (Gannier & West, 2005). Within the Macaronesian region, the species is present year-round in the Canary Islands (Ritter, 2002; Sànchez, 2016), but remains primarily seasonal in Madeira and rare in the Azores (Alves et al., 2018; Moura et al., 2017; Steiner, 1995), further reinforcing the interpretation that the species uses Madeira opportunistically during ecologically favourable summer conditions.

Comparing these results with studies on other cetaceans around Madeira helps better understand the ecology of the rough-toothed dolphin and the challenges for conservation. For example, Dinis et al. (2017) and Badenas et al. (2022) showed strong site fidelity in some adult females of Blainville’s beaked whale (*Mesoplodon densirostris*), demonstrating that with sufficient photographic sampling effort, even cryptic species can exhibit spatial fidelity. In contrast, the low site fidelity in rough-toothed dolphins suggests higher mobility and a wider habitat for this top marine predator, emphasizing the need to collect more data to clarify movement patterns. Similarly, Dinis et al. (2016) found that bottlenose dolphins (*Tursiops truncatus*) around Madeira form a largely open population, with only 4.3% of individuals classified as residents. This finding is reinforced by Dinis et al. (2021), who reported resightings of some individuals across multiple archipelagos in Macaronesia, suggesting that these dolphins undertake wide-ranging movements and likely inhabit a broad ecological region extending throughout and possibly beyond Macaronesia. This pattern mirrors the low re-sighting rate and high mobility observed in rough-toothed dolphins, implying similar opportunistic and pelagic ecological niches. Ferreira et al. (2021) reported high variability of site fidelity in Bryde's whales (*Balaenoptera brydei*) in Madeira, with some individuals resighted up to 12 years apart and others seen only once. This reflects complex migratory movements and regional connectivity between Madeira and the Canary Islands (Weyn et al., 2025), highlighting the importance of regional conservation measures addressing both residency habitats and migratory corridors, especially in light of anthropogenic threats like ship strikes. Likewise, Ferreira et al. (2022) revealed that roughly a quarter of sperm whale individuals (*Physeter macrocephalus*) show interannual site fidelity in Macaronesia (Madeira and the Azores), while most are highly mobile and spend significant time outside surveyed zones. This pelagic mobility parallels that observed in the rough-toothed dolphin, further underscoring the need for extensive inter-regional and coordinated data collection to unravel spatial dynamics across archipelagos.

Site fidelity varies widely across cetacean species and reflects their ecological strategies. However, for many pelagic species around Madeira, high mobility and opportunistic habitat use challenge the identification of critical habitats and the implementation of effective conservation measures. It is crucial to note that the rough-toothed dolphin is globally exposed to several anthropogenic threats, particularly opportunistic bycatch (Kiszka et al., 2019). The species frequently interacts with fisheries, particularly longlines, resulting in injury, mortality and sometimes retaliation by fishermen (Baird et al., 2008; Mintzer et al., 2018). Despite its listing in Appendix II of CITES (Convention on International Trade in Endangered Species) and its current classification as Least Concern by the IUCN (International Union for Conservation of Nature) (Kiszka et al., 2019), increasing anthropogenic pressures (e.g., maritime traffic, fishery interaction, whale-watching pressure, climate change) highlight the need for an inter-regional, multispecies, and multi-method approach.

Expanding research geographically to include the broader Macaronesian region and integrating tools such as passive acoustics, genetics, and satellite telemetry will improve understanding of movement ecology, social structure, and connectivity (e.g. Weyn et al., 2025).

For the rough-toothed dolphin, in Macaronesia, higher dedicated efforts are critical to validate ecological patterns seen here, identify key habitats, and design targeted conservation plans. Moreover, considering alternative hypotheses for low site fidelity, including predation risk, anthropogenic disturbance, and prey variability, will deepen understanding of their spatial ecology and inform adaptive management strategies. In summary, this study highlights the importance of long-term, comprehensive data collection and comparative research to support the conservation of this species and other oceanic cetaceans in the Macaronesian archipelagos.

Rough-toothed dolphin exemplifies the adaptive ecological strategies of oceanic cetaceans, whose protection requires dynamic, transboundary approaches that reflect their mobility and ecological flexibility.

5. Conclusion

In conclusion, this study aimed to assess, for the first time, the site fidelity of the rough-toothed dolphin (*Steno bredanensis*) around the island of Madeira using photo-identification. Despite heterogeneous sampling and generally low index values, the results reveal opportunistic and seasonal use of Madeiran waters, mainly in summer, probably linked to favourable environmental conditions. Two fidelity profiles were identified, suggesting behavioural heterogeneity within the population. Although these observations should be interpreted with caution, they demonstrate the value of sophisticated analytical approaches for detecting complex spatial dynamics. These results highlight the need to expand research to the whole of Macaronesia and to integrate complementary tools (genetics, acoustics, telemetry) in order to better understand habitat use strategies and guide conservation actions for this mobile species that is sensitive to anthropogenic pressures.

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Supplementary data

Table S1. Sampling occasions (in days) for each year of study (from 2013 to 2024): total efforts (n = 341) and efforts after filtering data (n = 160).

	2013	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**	**2020**	**2021**	**2022**	**2023**	**2024**	**n**
Total sampling occasions	4	3	1	11	26	13	18	34	25	56	79	71	341
Sampling occasions after filtering	0	0	0	8	18	7	11	17	12	17	26	44	160

Table S2. Summary of the number of identifications and new identifications; annual proportion of new identifications relative to the total number of identifications (n = 637); annual rate of new identifications relative to the number of identifications (slope discovery curve ***Figure 4***) for the period 2016 to 2024.

	2016	**2017**	**2018**	**2019**	**2020**	**2021**	**2022**	**2023**	**2024**	**n**
Number of new identifications	46	60	38	59	75	84	77	74	124	637
Number of identification	52	76	44	79	147	105	134	237	218	1092
Proportion (%)	7.2	9.4	6.0	9.3	11.8	13.2	12.0	11.6	19.5	100
Annual rate (slope)	0.885	0.789	0.863	0.747	0.510	0.800	0.575	0.312	0.569	

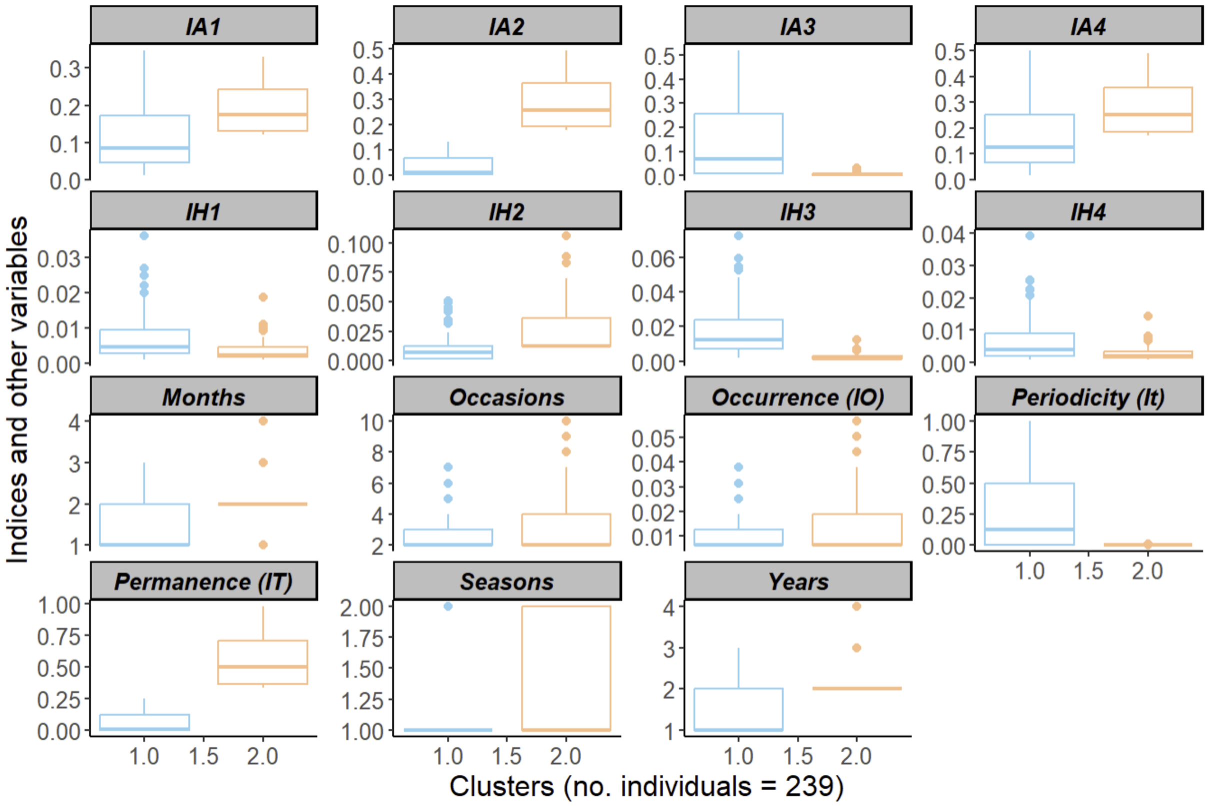

Figure S1. Boxplots of the indicators *IO*, *IT*, *It*, *Months*, *Years*, *Seasons* and indexes [IA1-IA4, IH1-IH4] according to the 2 clusters.

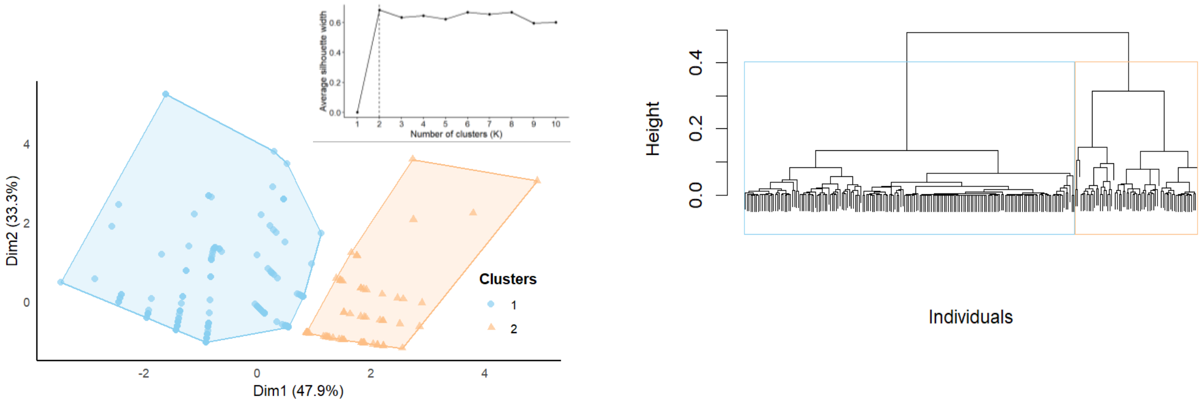

Figure S2a. The left graph shows the silhouette method and the two clusters of divisive hierarchical clustering (DHC) represented in the two first dimensions of a Principal Component Analysis. ***S2b.*** The right graph shows the DHC dendrogram with two clusters of rough-toothed dolphins in Madeira based on individual data from four Site Fidelity Indices (IA2, IH2, IH3 and IH4).

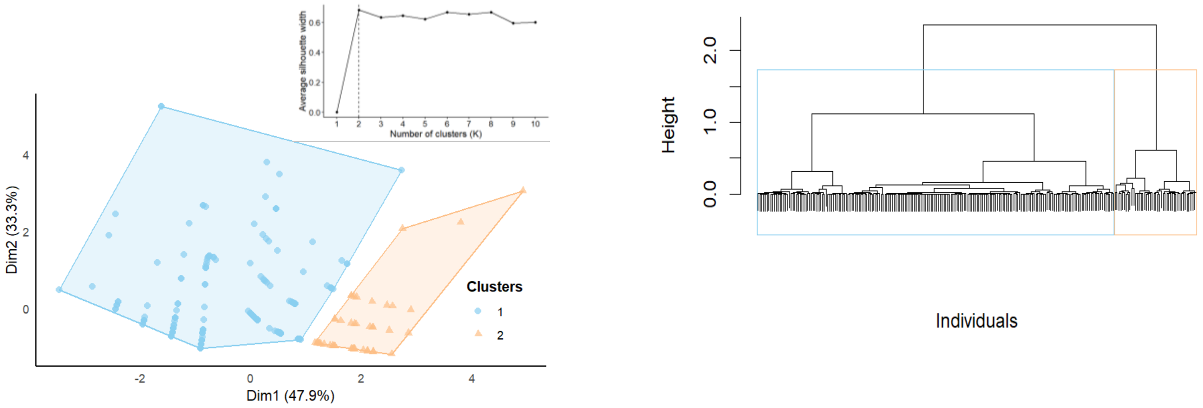

Figure S3a. The left graph shows the silhouette method and the two clusters of divisive agglomerative clustering AHC represented in the two first dimensions of a Principal Component Analysis. ***S3b.*** The right graph shows the (AHC) dendrogram with two clusters of rough-toothed dolphins in Madeira based on individual data from four Site Fidelity Indices (IA2, IH2, IH3 and IH4).

Figure S4. Graph of the Gaussian mixture model showing the best number of cluster, i.e. three (left) and six (right) clusters for comparison with the other methodologies of rough-toothed dolphins in Madeira, represented in the two first dimensions of a Principal Component Analysis based on individual data from four Site Fidelity Indices (IA2, IH2, IH3 and IH4).