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Snapshot chronicles: a 25-year study of *Orcinus orca* population dynamics in the Strait of Gibraltar

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Lic. Margarida Reis Perfeito

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Abstract

This study presents a comprehensive analysis of the Iberian orca (*Orcinus orca*) population in the waters of the Strait of Gibraltar, spanning a period of 25 years (1999–2023). A thorough analysis was conducted, utilising photo-identification and mark-recapture tools, with 87 distinct individuals identified from 43,522 analysed photos.

The model estimate for the overall survival rate of these orcas was 0.97. As of 2023, the population was estimated at around 39 individuals with a trend showing a decline of 0.9% over the study period. The age distribution showed a dominance of the adult class which was mostly composed of females. At least five well-defined social groups were established over the course of the study, being subject to changes over time. The best fitting model was that of preferred companions and casual acquaintances, demonstrating a social structure that is stable but shows fluidity over time, with more recent analysis (2023) showing only three clearly defined social groups.

The relationship between orcas and prey availability was complex, potentially influenced by several factors, including an increase in the number of orcas interacting with Atlantic Bluefin tuna (*Thunnus thynnus*) fisheries. Though surprisingly stable, the overall population metrics were lower than what is observed in other piscivore populations, highlighting the need for the implementation of protection measures for orcas and a better management of the tuna stocks. Although this study provides valuable insight into the population dynamic of Iberian orcas, much remains to be understood about these animals, making careful and continuous monitoring of the orca population crucial for future insights into their population dynamics and social structure.

The present thesis was partly conducted during an Erasmus+ Traineeship facilitated by the University of Vienna, which enabled the collaboration with the Spanish association *Circe (Conservación, Información y Estudio de Cetáceos)* lead by Dr Renaud de Stephanis. This partnership provided an opportunity for data collection, hands-on experience, and guidance from experts in the field. In addition, it allowed the use of photographic data collected over the years through the work of researchers and volunteers at *Circe,* which was fundamental for this research.

TABLE OF CONTENTS

1. Introduction

Orcas (*Orcinus orca*) or killer whales, as they are often called, are marine mammals of the family Delphinidae with a cosmopolitan distribution that spans all the world's oceans (Forney and Wade, 2007; Ford, 2019). While all orcas are currently classified as a single species, *O. orca* (Rice, 1998), genetic studies have revealed significant differences between populations, potentially indicating the presence of multiple species or subspecies (LeDuc et al., 2008; Morin et al., 2010, 2024). Over the last 350,000 years, *O. orca* has undergone rapid global radiation, with minimal gene flow among geographically isolated populations (Morin et al., 2015). Currently, orca populations are categorised into ecotypes, defined by physical characteristics, prey preferences, hunting strategies, vocalisation patterns, and social structures (Barret-Lennard et al., 1996; Ford et al., 1998; Baird, 2000; Pitman and Ensor, 2003). These ecotypes reflect adaptations driven by ecological pressures and cultural transmission, facilitating ecological specialisation and divergence across populations (Riesch et al., 2012).

Orcas are also known for their complex social structures, often matrilineal and forming stable multi-generation groups, particularly in fish-eating populations (Bigg et al., 1990; Baird, 2000). Cultural transmission, whereby ecological knowledge and behaviour are passed on through generations, plays a crucial role in the development and maintenance of these distinct ecotypes (Rendell and Whitehead, 2001). The transmission of learned behaviours enables the persistence of specialised foraging techniques and social structures within ecotypes, contributing to reproductive isolation and lineage divergence over time (Riesch et al., 2012; Morin et al., 2015). Genomic studies support this view, evidencing that genetic structuring among orca populations correlates with socially inherited ecological niches, where habitat, diet and social factors are key drivers of differentiation (Foote et al., 2016).

Orcas are long-lived animals, with research on the Resident Killer Whales of British Columbia showing a mean life expectancy of 46 years for females and 31 years for males, while the maximum longevity was around 80–90 years for females and 60–70 years for males (Olesiuk et al., 1990; Olesiuk et al., 2005). Interestingly, female orcas are part of a very small group of animals that undergo menopause (Dalton, 2021). On average, orca females reach menopause between ages 35 and 45, though cases of reproduction have been observed into the mid 40s (Olesiuk et al., 2005; Ward et al., 2009; Brent et al., 2015). The post-reproductive lifespan of female orcas is thought to offer evolutionary advantages, as these older females play a crucial role in the survival of their offspring through social transmission of ecological knowledge (Foster et al., 2012a; Brent et al., 2015).

The best-studied orca populations are the three sympatric ecotypes found in the Pacific Northwest: resident, transient (or Bigg's), and offshore (Ford et al. 2000). These ecotypes exhibit distinct dietary preferences, with residents feeding almost exclusively on salmon, transients preying on marine mammals, and offshores targeting sharks and other fish (Ford et al. 2000). These ecological specialisations are also manifested in their social structure, vocal behaviour, and geographic range (Ford et al. 2000). Resident killer whales, for example, form stable matrilineal groups and exhibit intricate vocalisations used for social bonding and coordination (Ford, 1989; Bigg et al., 1990; Ford et al., 2000). In contrast, transients form smaller, more fluid social groups and use less frequent vocalisations, presumably to be stealthier and avoid alerting their prey (Ford and Ellis, 1999). Offshore killer whales, due to their elusive nature, remain less understood, though they are thought to form larger groups for open-water hunting, as they have a more varied diet (Ford et al., 2000). Cultural learning appears to drive much of the observed specialisation in these ecotypes, as behaviour is transmitted vertically and horizontally within and between groups (Rendell and Whitehead, 2001; Whitehead et al., 2004). Examples of learned behaviour in orcas range from the depredation of longlines (Yano and Dahlheim, 1995), to the dead salmon-carrying trend starting in 1987 in Puget Sound (Osborne, personal observation) to the infamous interactions with sailboats around the Iberian Peninsula (Esteban et al., 2022). Remarkably, orca culture plays a role not only in social and foraging behaviour but also in shaping population structure and driving speciation (Whitehead et al., 2004; Riesch et al., 2012). The complex and stable knowledge systems in these populations, such as foraging techniques and interactions with humans, reflect the dynamic interplay between culture, ecology, and evolution (Whitehead et al., 2004).

As mentioned above, orcas are a globally distributed species with distinct ecotypes in different regions (de Bruyn et al., 2013). One notable population is the so-called "Iberian orcas", frequently seen in the Strait of Gibraltar (SoG), a complex and dynamic ecosystem connecting the Atlantic Ocean and the Mediterranean Sea, hosting a diverse range of cetacean species (de Stephanis et al., 2008).

The "Iberian orcas", a subpopulation of the North Atlantic ecotype, mostly inhabit the waters off Portugal and Spain, though, they also known to swim all the way from Moroccan waters to the North of France or even further - as one of the orcas of the Iberian population was found stranded in the Netherlands in 2022. While genetic data suggests low differentiation between them, likely due to historical gene flow, the orcas of the SoG are ecologically, reproductively, and socially distinct from the orcas found off the Canary Islands, functioning as different subpopulations (Esteban et al., 2016c). These orcas have a highly specialised diet, mainly hunting Atlantic bluefin tuna (*Thunnus thynnus*) (Guinet et al., 2007; de Stephanis et al., 2008; García-Tiscar, 2009; Esteban et al., 2014). The Atlantic bluefin tuna (ABFT) is a migrating fish, entering the Mediterranean Sea in late spring to spawn and making its way back to the Atlantic in summer (Sella, 1929; Rooker et al., 2007; Aranda et al. 2013). These migratory routes largely determine the movement patterns of the orcas on the hunt for ABFT. In spring, they are usually seen hunting in shallow waters, west of the SoG, where they prey on fish entering the Mediterranean; while in summer, they tend to stay in the central waters of the SoG hunting ABFT that are on their way back to the Atlantic Ocean (Guinet et al., 2007; de Stephanis et al., 2008; Esteban et al., 2014).

One of the ways these orcas hunt for tuna is through the endurance-exhaustion technique, where they chase tuna for up to 30 minutes at moderately high speeds until they capture them (Guinet et al., 2007). This strategy seems to be used for small- to medium-sized fish, but it is very energy demanding (Guinet et al., 2007). The orcas in this region are also known to interact with fisheries, stealing the tuna from longlines (de Stephanis et al., 2008; Guinet et al., 2007; Esteban et al., 2016a). This behaviour has positive effects on the interacting orcas as it saves energy, improving survival and breeding capacity (Esteban et al., 2016a).

ABFT populations have faced great challenges over the years, with a history of overfishing, coming close to collapsing between 2005-2007 (Fromentin and Powers, 2005; ICCAT, 2007; MacKenzie et al., 2009). Decreases in ABFT had a negative impact on the calf survival rates of Iberian orcas (Esteban et al., 2016a), a pattern also seen in other populations when their main prey is depleted. In the Pacific Ocean, for example, the fecundity rate of Southern Resident Orcas was negatively impacted by a decrease in the population of their main prey, the Chinook salmon (Ward et al., 2009). Recent observations, however, suggest that the ABFT population in the North Atlantic is recovering (Cort and Abaunza, 2019; Bjørndal, 2023), which may have a positive effect on the Iberian orca population.

The last comprehensive census of this population was carried out in 2011, estimating the population at 39 individuals (Esteban et al. 2016a), and detailed research on these orcas has faded in recent years. Additionally, the orcas of the SoG are classified as “Critically endangered” by the IUCN due to their small number of adults, low recruitment rate and dependence on an endangered species (ABFT) (Esteban et al., 2016d; Esteban and Foote, 2019), which makes it even more important to maintain research efforts.

To address knowledge gaps, this study aims to investigate the ecology of orcas in the SoG, focusing on population dynamics, social structure, and possible effects of ABFT availability. This translates into three working hypotheses: (1) The population size, survival rates and life metrics of Iberian orcas have changed over time; (2) there is a significant correlation between the ABFT availability and orca population dynamics; and (3) the orcas present a matriarchal and stable social structure that evolves over time.

Understanding the ecological role of orcas and their interaction with humans in this area is crucial for effective conservation and management strategies. As apex predators, orcas play a pivotal role in shaping marine ecosystems, and their conservation is integral to preserving marine biodiversity at all trophic levels (Kiszka et al., 2015).

2. Methodology

2.1 Sampling area

This study was performed in the waters of the Strait of Gibraltar (SoG), a 60 km long natural connection between the Mediterranean Sea and the Atlantic Ocean that features a canyon-like structure with shallow waters on the Atlantic side and deeper waters on the Mediterranean side (Fig. 1). The region is characterised by complex water exchange with less saline surface inflow of Atlantic waters and more saline deep outflow of Mediterranean Sea Water (Lacombe and Richez, 1982). Here we also find the convergence of several almost conflicting factors, including heavy marine traffic, the presence of Atlantic bluefin tuna (ABFT) (*Thunnus thynnus*) and associated human fisheries as well as various resident and transient cetacean species. One in particular - *Orcinus orca* – is the most charismatic species present in this area and the focus of this research. Most of the boat transects were performed in the areas around Barbate and Tarifa as these are the zones with the highest probability of orca presence (Fig. 2).

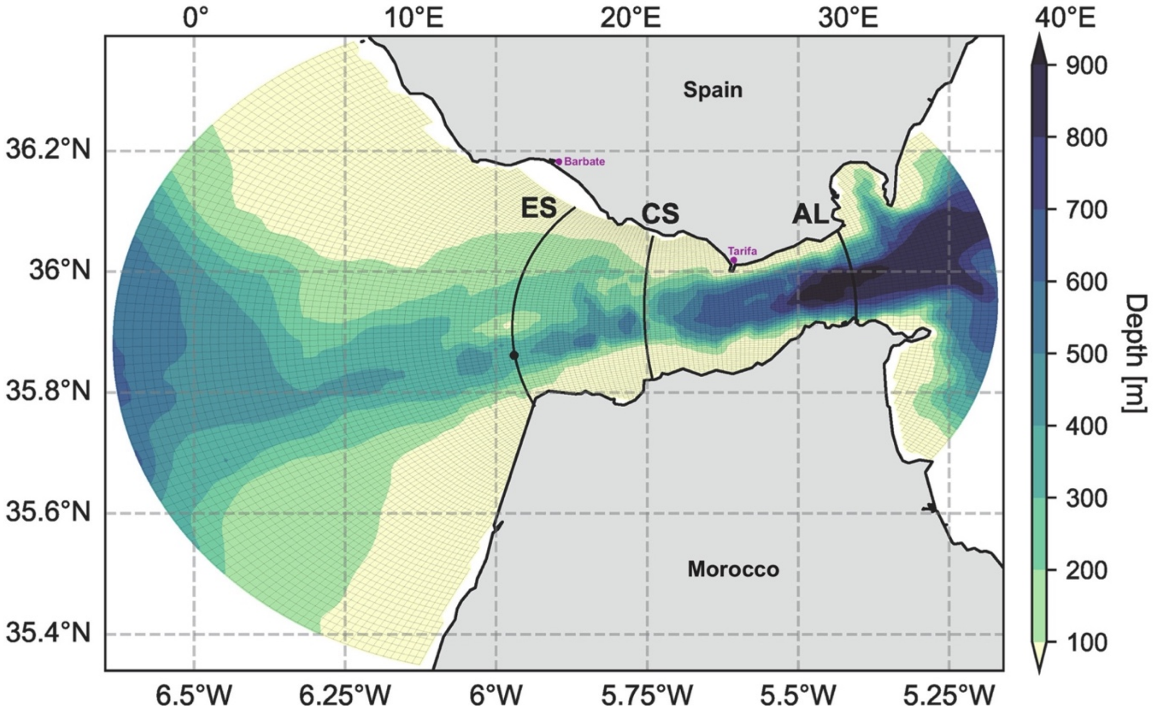

Fig. 1 – Bathymetric map of the Strait of Gibraltar. The three latitudinal sections are Espartel Sill (ES), Camarinal Sill (CS) and the entrance of the Alboran Sea (AL). The two points in dark pink represent the ports of Barbate and Tarifa. Adapted from Gonzalez et al. (2023).

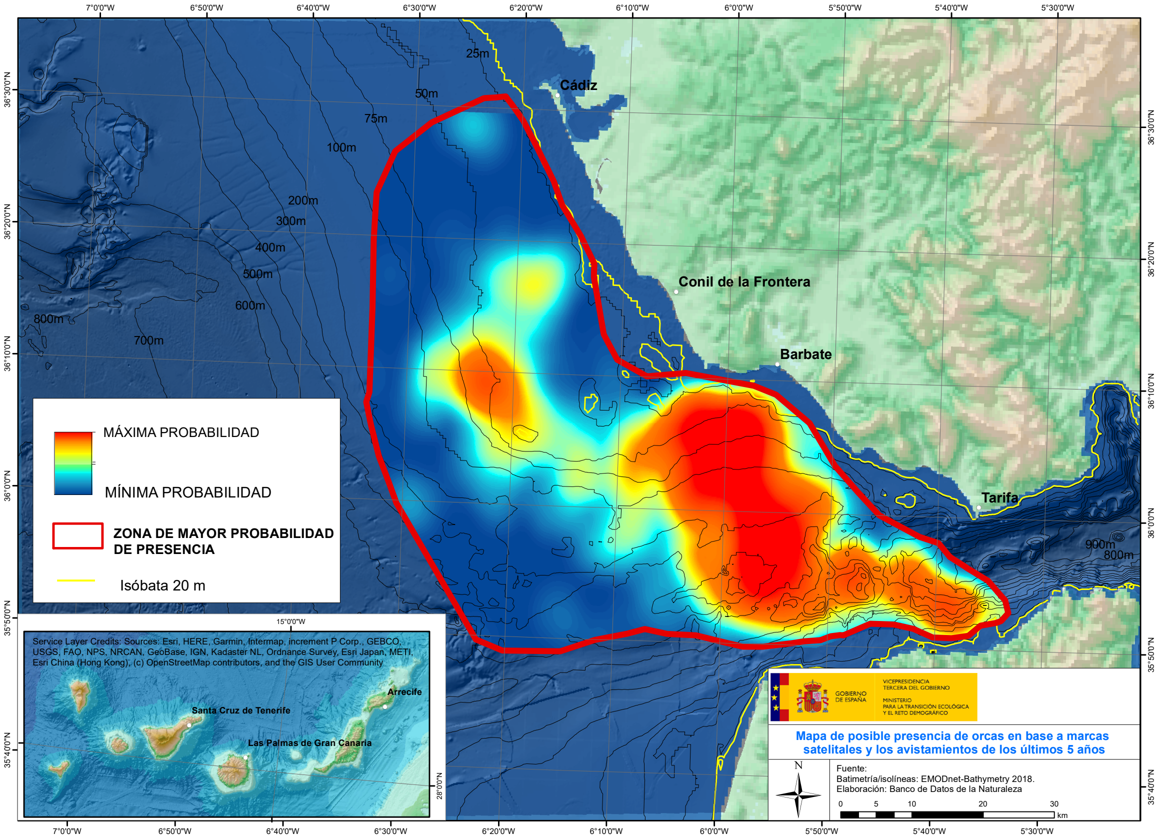

Fig. 2 – Map with presence probability of orcas in the south of Spain, based on satellite tags and sightings from the years 2018-2023. Source: Ministerio para la Transición Ecológica y el Reto Demográfico, 2023.

2.2 Photo-identification

2.2.1 Data collection for the orca population

This work is based on photo-identification, a widely non-invasive and cost-effective method that relies on the natural markings found in the animals to identify them (Bigg, 1982). This technique allows for the in-depth study of cetaceans, providing insights into group structure, site fidelity and population parameters through mark-recapture methods (Hammond, 1986).

Data were collected through footage taken aboard *Circe* research vessels as well as partnering whale watching boats. While photographing the orcas, the boat would approach as closely as possible without causing unnecessary stress to the animals. Photographs were preferably taken from the sides of the animals, either at a 270º or 90º angle (Fig. 3). The photos mostly focused on the dorsal fin (1), eye patch (2) and saddle patch (3) as these are the most relevant characteristics for photo-identification of orcas (Fig. 4). The eye patch and the saddle patch remain largely unaltered once formed, making them especially useful to identify younger or lightly marked individuals (Bigg, 1982). Both sides of each animal were documented to account for natural asymmetries.

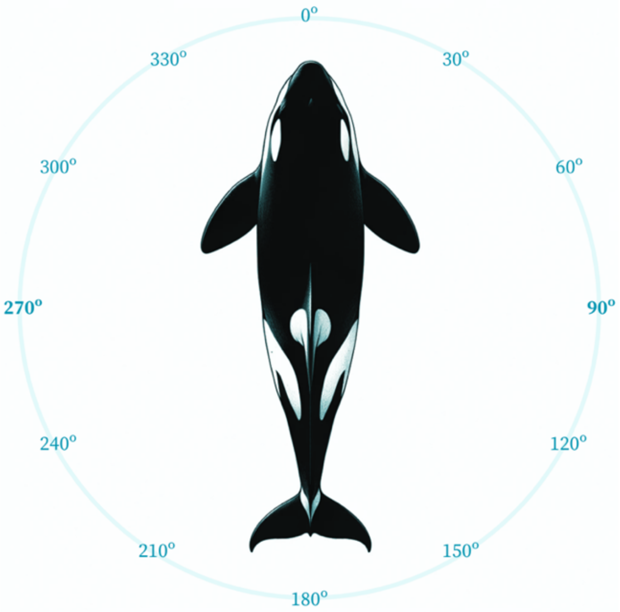

Fig. 3 – Diagram showing angles representing the position of the photographer in relation to the animal when the analysed photo was taken.

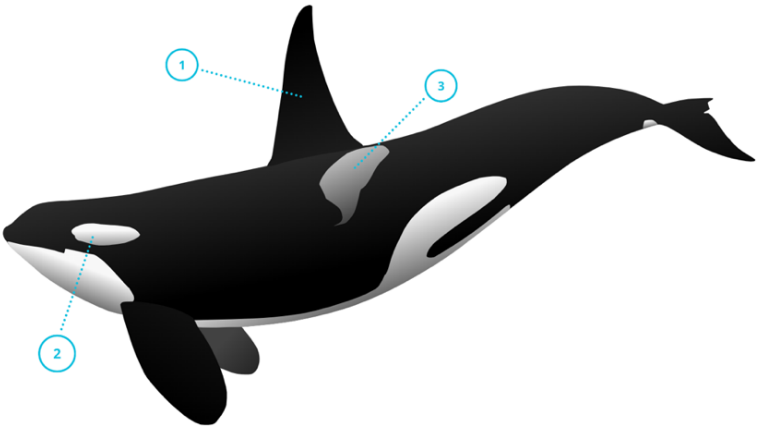

Fig. 4 – Key characteristics considered for the photoidentification of orcas: (1) dorsal fin (shape and markings) (2) eye patch (size and shape) and (3) saddle patch (shape, colouration and markings).

To make data collection as consistent as possible, the same effort was made to photograph all the individuals present, independent of their level of distinctiveness. The generated photos, together with existing pictures taken in previous years by other *Circe* collaborators, formed the main dataset used in this study, spanning 25 years of orca sightings in the Strait of Gibraltar.

During every boat survey, in addition to capturing images, the protocol included the use of a GPS tracker to register the trip transect. Most recently, this was done through the app 'bergfex' (version 4.14.2). Moreover, environmental and animal data were initially collected using paper sheets and subsequently through *Circe*'s custom forms within the 'fastfield' app (version 3.6.5) until present day.

2.2.2 Data processing – photo-analysis

The photos of each sighting day went through a filtering process to remove pictures that were not of interest - most often because they did not contain the target animal. The files were then adequately re-named, and their metadata extracted with R version 2023.12.0+369 (R Core team 2023). All the parameters used in the analysis were added to an excel file. These included the sighting identifier, picture number, camera model, date, time, angle, feature, quality, distinctiveness, fin exposition (yes/no), amount of exposed back (1 to 3), amount of exposed eyepatch (1 to 3), group (if it was possible to identify it), and status (age class of the individual). Some of these characteristics are very important for successful identification of an individual. Particularly important were the angle at which the picture was taken (Fig. 3), the quality of the picture (denoted as Q) and the distinctiveness of the individual (denoted as M) (Fig. 5A and Fig. 5B).

Fig. 5A (left) and Fig. 5B (right) – Example of Q2 pictures used in the photo-identification process. The female orca OO_008 (left) and the male OO_046 (right) both are classified as M1 in terms of distinctiveness since they are lightly marked.

The overall quality of each picture was assessed based on criteria such as focus, contrast, angle, and fin visibility. With these in mind, a scale for picture quality was created, with a range from 0 to 2 defined as follows:

- Q0, picture not useful for identification due to distance, lack of focus or being taken from an angle between 330º-30º or 150º-210º;
- Q1, picture of medium quality where the dorsal fin is either completely or partially visible;
- Q2, picture of high quality where the dorsal fin is fully visible.

Similarly, the distinctiveness of the individuals was evaluated using a scale from 0 to 3, based on the prominence of marks in individuals:

- M0, individuals with no marks;
- M1, individuals with few small marks only visible in good quality pictures;
- M2, individuals with medium-sized markings or many small markings;
- M3, individuals with very distinctive markings (deep markings or with partial/total amputation of a part).

Only images with high or medium quality were used for the identification of orcas. Once identified, each individual was assigned a unique identifier (code name) and added to the master catalogue.

2.2.3 Estimation of Population Parameters

2.2.3.1 Goodness-of-fit tests

The goodness of fit was tested using the programme U-care 3.3 (Choquet et al., 2020), which provides specialised versions of general goodness-of-fit tests to capture recapture survival models (Choquet et al., 2009). This programme makes it possible to assess different aspects of the data through specific tests. Particularly, test 3.SR evaluates transience, where transients are individuals captured only once and not seen again (Pradel et al., 1997). Test 3.SM assesses the effects of mortality and immigration, indicating changes in the population due to death or permanent departure. Test 2.CT evaluates trap dependence, where individuals show varying capture probabilities overtime (trap-shyness or trap-happiness) (Pradel et al., 1993). Lastly, test 2.CL assesses equal catchability, checking if all individuals have the same likelihood of being captured. The overall goodness-of-fit test for single state data incorporates these four specific tests to evaluate the model's assumptions comprehensively (Choquet et al., 2009).

2.2.3.2 Apparent survival rates and capture probabilities

The programme MARK 10.1 (White and Burnham, 1999) was used to estimate the apparent survival rate and capture probability from the annual mark-recapture (MR) data through a standard Cormack-Jolly-Seber (CJS) model (which is based on live recaptures). The CJS model assumes:

- equal catchability (all individuals have the same probability of capture/recapture at each time point, regardless of their capture history);
- marking does not affect survival (process of marking individuals does not affect their survival probabilities (this does not really apply since it is a sight re-sight model);
- closed population between capture occasions (no immigration or emigration occur between capture occasions; however, births and deaths can occur);
- independence of events (the capture or survival of one individual is independent of that of another) (Pollock et al., 1990; Lebreton et al., 1992).

The fundamental assumption in these types of models (mark-recapture) is that both marked and unmarked individuals experience the same survival rate for the evaluated period. Thus, the calculation of survival rate focuses on following just the marked individuals from immediately after sample i to immediately before sample $i + 1$. For this model (CJS), there is no estimation of the first year of study because its calculations are based on a comparison with the year before the one for which the parameter is being calculated.

The best of the competing models was chosen based on the lowest Akaike's Information Criterion (AIC) values. The estimated mean annual survival rates (along with their standard errors and 95% confidence intervals) were plotted using R.

2.2.3.3 Abundance estimates

The abundance estimates for the study period were computed using the Jolly-Seber model through the FSA package in R (Ogle et al., 2023), yielding annual abundance estimates for the study period, except for the first and the last year of sampling, as both are omitted in this model. As outlined by Krebs (1999), the general Jolly-Seber model operates under the assumptions of equal catchability, no loss or overlook of marks, negligible sampling time in relation to intervals between samples, and uniform survival probabilities for all individuals between sampling occasions, independent of their distinctiveness level. The best of the competing models was once again chosen based on the lowest AIC values. The resulting estimates, along with their associated 95% confidence intervals and standard errors, were visualised in R.

As is later described in the *Results* section, the last year of the study (2023) had a high number of sightings and analysed photos, which created a considerable amount of data for an abundance estimate. Since the classic Jolly-Seber model's constraints prevent it from providing an estimate for the last year of the study period, a POPAN model was employed for this purpose. The POPAN is a parametrization of the Jolly-Seber model which incorporates estimates for the probability of entrance into the population and population size (Schwarz and Arnason, 1996). The abundance estimates for the size of the Iberian orca population in 2023 was obtained using the package RMark (Laake, 2013) within the R environment.

2.2.3.4 Defining age, sex and maternal kinship and calculating life parameters

The determination of the age, sex and parental relationships between the orcas involved a combination of direct observation, photographs, and videos. For the age categories following Olesiuk et al. (1990), the classes were differentiated:

- "calf" as an individual up to one year old;
- "juvenile" as an individual of at least one year old until it reaches maturity;
- "adult" as an individual of mature size as indicated by the development of the dorsal fin in males and by either the presence of a calf or mature size without the development of a dorsal fin in females.

Female Resident Killer Whales generally have their reproductive years between ages 11 and 40, while males typically reach sexual maturity at 13-15 years of age (Olesiuk et al., 1990; Olesiuk et al., 2005). This information also served as guidance for determining age of maturity, with most orcas being classified as adults around 13 years old.

The mothers and their respective calves were identified by observing their swimming patterns on various occasions and verifying that the calves swam in echelon position (diagonally) relative to the adult female, while closely accompanying them. As menopause appears to occur between the ages of 35 and 45 (Olesiuk et al., 2005; Ward et al., 2009; Brent et al., 2015), reproductive females were defined as orcas that recently had calves or were in their reproductive years, which were conservatively set to come to an end at the age of 40 (if there were no observed births). Orcas were considered dead if they were not seen with their group for three consecutive years. The year of death was then counted as the fourth year of absence. Since it is safe to assume that any given orca would have been present for at least part of the year of its presumed death, it is still counted as part of the population for that year but as absent in all following years.

Using these definitions, the proportion of males to females and of the different age groups in the population were determined. To provide information on the general population status, the metrics birth rate, mortality rate, population growth rate, birth interval, fecundity rate and calving rate were calculated. The birth interval is defined as the space within which a female gives birth to successive viable calves while fecundity rate is the reciprocal of the birth interval (Olesiuk et al., 1990). By determining the birth intervals for all reproductive females with known calves, the overall birth interval was calculated, assuming each interval is equally representative of the population. Additionally, calving rate was determined as the number of viable calves born per reproductive female per year, calculated annually and then averaged across the study period. Viable calves were defined as offspring that made it past their first year of life, since that is when orcas have the lowest survival rate (Olesiuk et al., 1990). To calculate the overall birth, mortality and growth rates of the Iberian orca population, the following formulas were applied:

$$birth\,rate = B * (N_t * Y)^{-1}$$

$$mortality\,rate = M * (N_t * Y)^{-1}$$

$$population\,growth\,rate = (B - D) * (N_t * Y)^{-1}$$

Where, Y is the number of years of the study period, B is the number of individuals born in the Y years, D is the number of individuals dead in the Y years and N_t is the total number of individuals identified in the study period.

2.2.3.5 Interaction with fisheries

As an additional descriptor of the studied population and since these orcas have the particularity of interacting with tuna fisheries in this region to capture their preferred prey, a simple assessment of depredating versus non-depredating orcas was done. An orca was classified as depredating (DEP) when:

- seen displaying the behaviour in which they steal tuna from the fishing lines;
- seen in the zone where fishermen gather and drop their lines (often at an area called “Las Bajas”);
- not seen exclusively in spring and in areas lacking these types of fisheries (as the groups seen in this period tend to hunt by their own means).

Non-depredating individuals (NOT) were the ones that did not fit any of the definitions above. The proportions of DEP and NOT orcas were calculated, both for the overall and for the currently live population.

2.2.4 Social Structure Analysis

Throughout the study period, the number of sightings was variable between years. For the social structure analysis, the sampling periods were individual days (sightings) and only groups in which the number of pictures taken was at least double that of the estimated group size were used. According to Williams and Lusseau (2006), individuals are associated if they belong to the same group and a group is composed of animals within ten body lengths of each other engaging in similar or coordinated behaviour. In this study, individuals photographed in the same sighting were considered associated, as this generally respects the above definition. To reduce the bias that might have been caused by introducing infrequently sighted individuals, the analysed data were restricted to orcas sighted on more than three occasions (Tosh et al., 2008) and to sightings in which at least two individuals were identified. In addition, calves were excluded (i.e., individuals in their first year of life) as they can introduce bias due to the strength of mother-calf bonds (Gero et al., 2015).

As a first step in the social structure analysis, a permutation test was performed to determine whether the associations between individuals could be a result of mere chance - by comparing the observed associations with ones created randomly (Manly, 1995; Bejder et al., 1998; Whitehead, 1999). Both the Half-Weight Index (HWI) and the Simple Ratio Index (SRI) were used to ensure a comprehensive analysis (Cairns and Schwäger, 1987). The HWI describes frequency of co-occurrence, estimating the probability of two individuals being seen together, given that at least one of them has been observed. It accounts for the possibility of some individuals being missed during observations, making it a more reliable measure when observation effort is inconsistent. While the HWI is the most often used index in this type of research, it can be prone to overestimations, the reason why the SRI was also employed for comparison (Ginsberg and Young, 1992). The SRI calculates the ratio of the number of times two individuals are observed together to the total number of observations in which at least one of them was seen, offering a straightforward measure of their co-occurrence in relation to their overall visibility.

To establish the role individual orcas play in the community, the network analysis statistics were calculated based on the association matrix (Whitehead and Parijs, 2010). These are:

- strength, indicating an individual's gregariousness;
- eigenvector centrality, a measure of how well connected an individual is within the network;
- reach, describes the overall strength of associates;
- clustering coefficient, showing how well the associates of an individual are themselves associated;
- affinity, a descriptor of the weighted mean strength of associates.

To visualise the association patterns between the orcas in the population, a hierarchical cluster analysis was performed. This includes the calculation of the cophenetic correlation coefficient (CCC), a measure of how faithfully the resulting dendrogram preserves the pairwise distances between the original unmodeled data points (Rohlf and Fisher, 1968). The overall clustering analysis was controlled for modularity, ensuring that the clusters reflect meaningful social structures. Additionally, a social network diagram of the groupings between individuals without the hierarchical organization was generated for an alternate view of the social structure.

Lastly, a temporal analysis – Lagged Association Rate (LAR) – was performed to assess the stability of the associations between individuals over time. The LAR calculates the probability that if individuals are seen together at an initial time (t0) they will be seen together once more at a later time (t0+d) (Whitehead, 1995). The standard error was calculated using the Jackknife method (Efron and Gong, 1983). To identify the social structures that best fit the observed data, their mathematical models were compared based on the Akaike Information Criterion (AIC) and corrected AIC (QAICc) values, with the lowest values indicating the best fit.

All analyses related to the social structure were performed using the compiled version of SOCPROG 2.9 (Whitehead, 2009).

2.2.5 Data collection of the prey population

As previously mentioned, the main prey of the studied orca population is the Atlantic Bluefin Tuna (ABFT). To estimate the prey population in the target area, data were sourced from the publicly available statistical database of the International Commission for the Conservation of the Atlantic Tunas (IPCCAT). The ICCAT is a regional organisation responsible for the management and conservation of tuna and related species in the Atlantic Ocean and surrounding areas. Data on nominal annual catches (in tons) of ABFT were collected for the fleets of Spain, Portugal, Morocco, and Gibraltar as they all operate in zones of interest for Iberian orcas.

Though catch information is readily available in the ICCAT database, it may not accurately represent the actual ABFT stock at any given time. Therefore, to complement this analysis, estimated ABFT stock categories were created based on information gathered from the ICCAT biannual reports corresponding to the study period. These categories, ranging from -2 to +2, were defined as follows:

- critically low (-2) - stock levels are critically depleted, indicating severe overfishing and immediate action is required to prevent collapse;
- overfished (-1) - stock levels are below the target reference points or biomass thresholds, indicating overfishing but not yet critically low;
- recovering (0) - stock levels are increasing due to effective management but have not yet reached the target biomass levels. This indicates positive trends but acknowledges the stock is still rebuilding;
- conditionally healthy (+1) - stock levels are within or above the target reference points or biomass thresholds, indicating a well-managed and sustainable population;
- healthy (+2) - stock levels fluctuate due to natural variability but remain around the target levels, indicating a generally healthy stock that might have occasional declines or increases.

2.2.6 Correlation Analysis

The possible relationships between the yearly ABFT catches and both the yearly survival rate and abundance estimates for the orca population, were evaluated using the Spearman's Rank Correlation coefficient. The same method was applied to test possible relationships between the orca population's annual survival rates and abundance estimates with the ABFT stock, as represented by the categories mentioned above. Given that *O. orca* is a long-lived species, these correlation tests were reiterated for different time lags, ranging from 1 to 3 years, to assess potential delayed responses of the predator to fluctuations in prey populations. The entire analysis was carried out in R (R Core team 2023).

3. Results

3.1 Effort and identified individuals

For the period evaluated in this study there was a total of 198 sighting occasions which resulted in 43,522 photos. It is often the case that a single picture contains multiple orca individuals, which brings the number of individuals analysed to 50,445.

Notably, the number of photos analysed shows drastic fluctuations throughout the study period. The lowest values were reached between 2019 and 2020 and the highest in 2011 and 2023. Similarly, the total number of identified individuals showed some variability between the years, but the highest number was registered for the year 2023 when 33 orca individuals were identified (Fig. 6). The year 2023 also represented the biggest collection of photographic data in a single year, with 14,505 analysed pictures (from the 18,091 raw photos), highlighting a great increase in sampling effort. It should also be noted that, except for 2023, the years with the highest number of new individuals did not directly correspond to the years of the most intense research effort, hinting at a different motive behind the increase in newly identified individuals in years like 2003, 2005 and 2017.

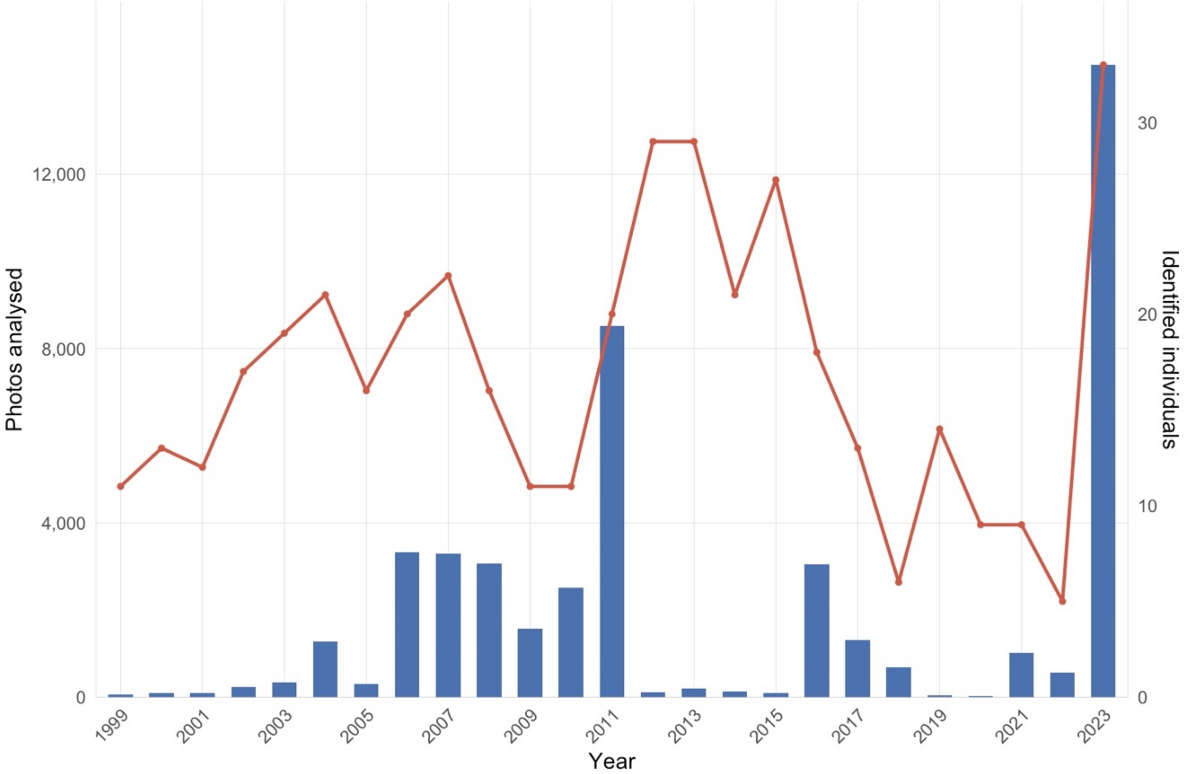

Fig. 6 – Trends in research effort (photos analysed) and identified individuals (captures) between 1999 and 2023. The blue bars represent the number of analysed pictures, serving as a proxy for research effort (left y-axis) and the orange line shows the identified individuals (right y-axis).

The number of newly identified individuals varies significantly between years while the recaptures show more consistency (Fig. 7A). The year 2023 also had the highest number of newly identified individuals. After the start of the study, all but one of the years showed a higher proportion of recaptured individuals compared to newly identified ones. This points to a persistent monitoring and identification effort within the existing orca population, as well as the effectiveness of the photo-identification method.

As might be expected, the cumulative number of identified individual orcas showed a steady upward trend over the course of the study. Despite some larger fluctuations, which were the steepest in 2023, starting from 11 individuals in 1999 all the way to 87 individuals in 2023, there was an overall consistent rise in the number of identified orca individuals (Fig. 7B).

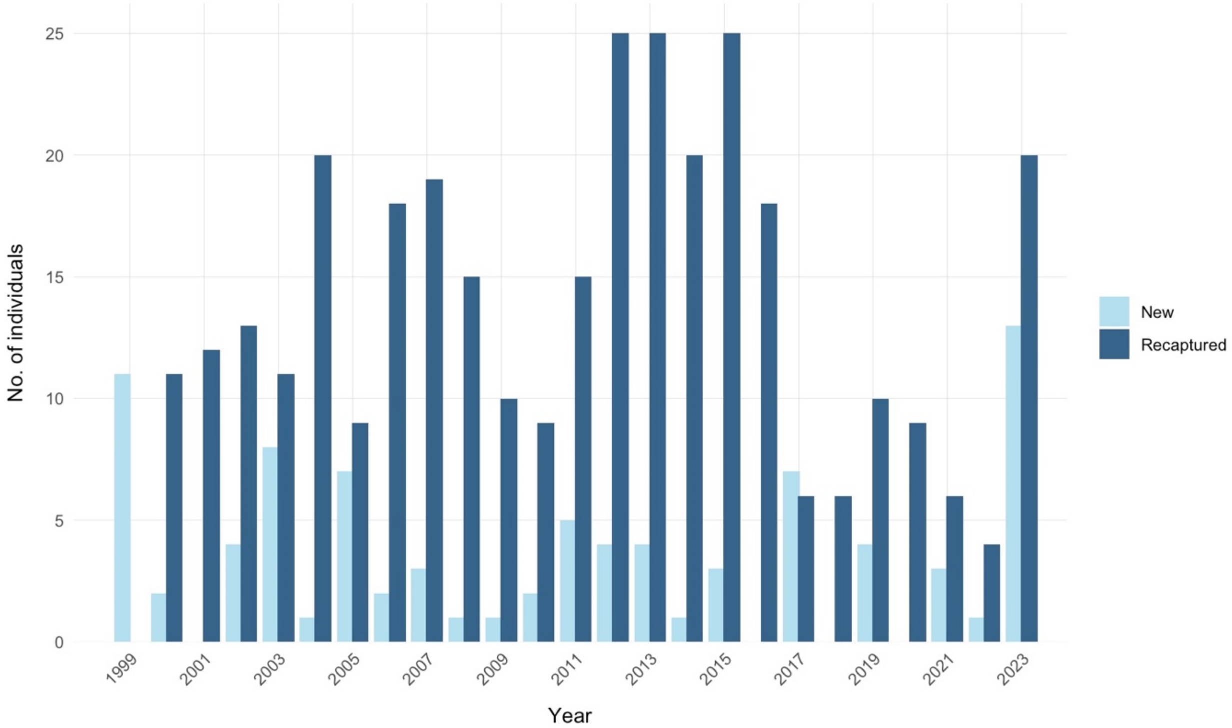

Fig. 7A – Comparison of new captures and recaptures of Iberian orcas from 1999 to 2023. The dark blue bars represent the annual number of "recaptured" individuals (orcas that had been sighted previously), while the light blue bars indicate the number of "new" captures (individuals captured for the first time) in each year.

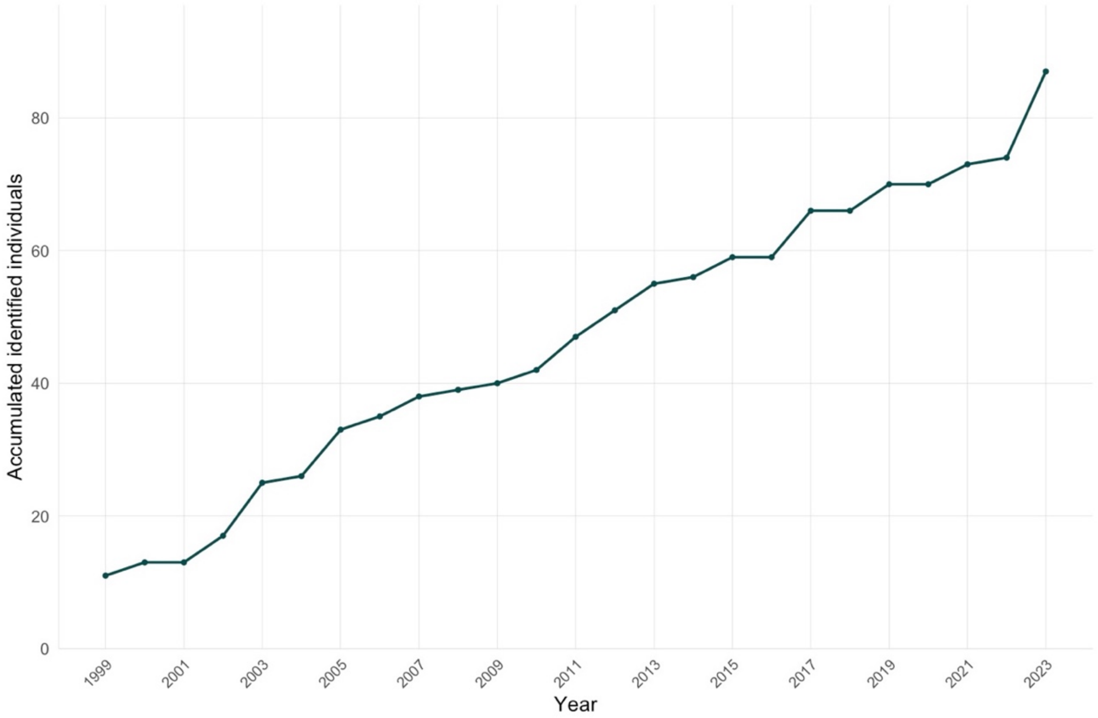

Fig. 7B – Cumulative number of identified orca individuals sighted from 1999 to 2023 in the Strait of Gibraltar.

3.2 Population status

3.2.1 Goodness of fit tests

For the series of tests performed to evaluate the goodness-of-fit of the models used, the results are as follows:

- Transience (Test 3.SR): significant transient effect was observed indicating a higher probability of individuals being observed only once.
- Mortality/emigration (Test 3.SM): there was significant in capture probabilities was detected, suggesting greater variation than expected.
- Trap-dependence (Tests 2.CT): strong negative trap dependent effect was detected indicating trap-shyness among individuals.
- Equal catchability (Test 2.CL): significant heterogeneity and capture probabilities was found suggesting variability in individual capture likelihoods.

3.2.2 Apparent survival rate

The time-dependent CJS model estimated an average survival rate (Φ) of 0.974 (95% CI: 0.970-0.978), over the 25-year study period. This means that, on average, an individual orca had a 97.4% probability of surviving from one year to the next. The corresponding capture probability (p) was 0.725 (95% CI: 0.713-0.736) which indicates a moderately high likelihood that an individual orca, if alive and present in the study area, will be re-sighted (or re-captured) during any given sampling event.

There were evident fluctuations in the yearly survival rates, with a slight declining trend that is particularly noticeable after 2015 (Fig. 8). Even so, the survival rates were generally high and rarely dropped below 0.9. There was a noticeable drop between 2015 and 2017, followed by two other substantial decreases in 2020 and 2022. The confidence intervals varied in width from year to year, indicating varying degrees of uncertainty in the survival estimates, but they were also particularly high in the mentioned years, as well as in 2018 and 2023.

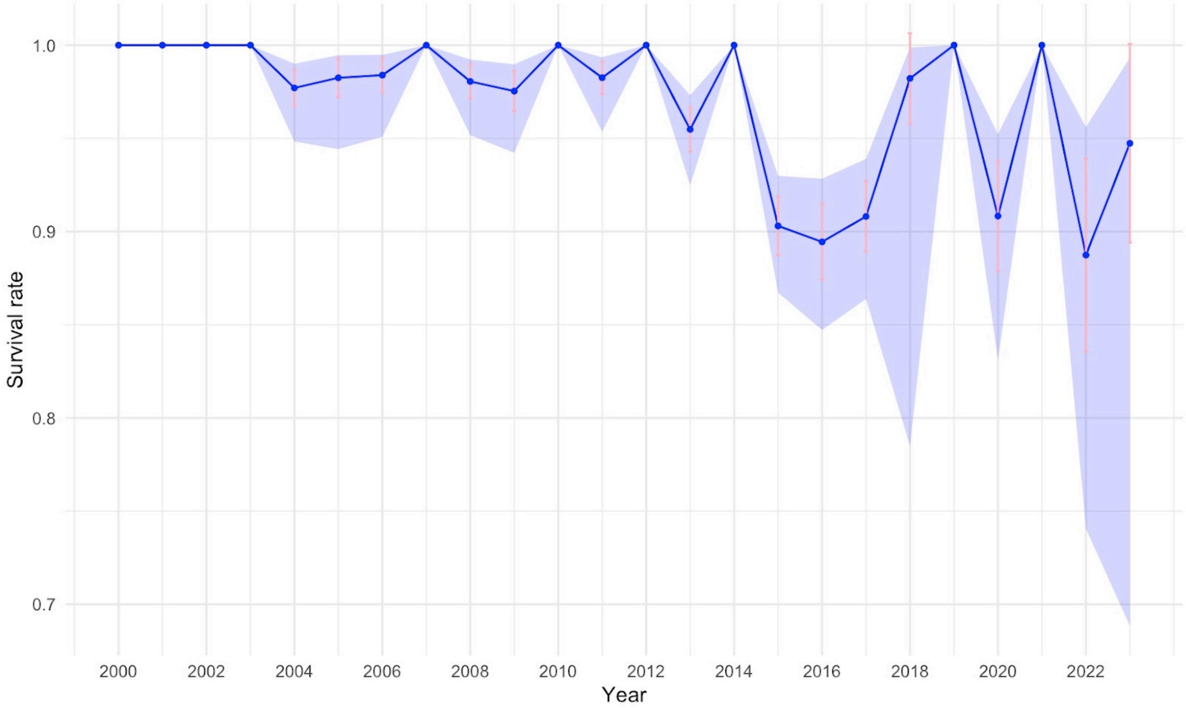

Fig. 8 – Estimated annual survival rates of the orca population between 2000 and 2023 (dark blue line). 95% confidence intervals are represented by the shaded area and standard error by the pink lines. The estimates are derived from a time dependent CJS model (Φt.pt).

3.2.3 Apparent abundance

The population size calculated for the year 2023 using the POPAN parametrization was estimated to be approximately 39 individuals (95% CI: 33-46). This is congruent with the values obtained for the estimated orca abundance in 2023 while applying the previously mentioned definition of mortality (i.e., individuals not seen in their group for three consecutive years—see *Methodology*) which was also gauged at 39 individuals.

For the yearly abundance estimates, there were notable fluctuations throughout the time series (Fig. 9). The estimates were fairly constant between 2006 and 2013, with a slight increasing trend, but showed the sharpest increase in 2017. Similarly, the increases in 2005 and 2021 were noticeable, although not as remarkable as in 2017. Conversely, lower estimates were observed in the early 2000s, 2018 and 2020. The width of the confidence intervals varies over the years but are more evident in the three peaks indicating major increases in uncertainty.

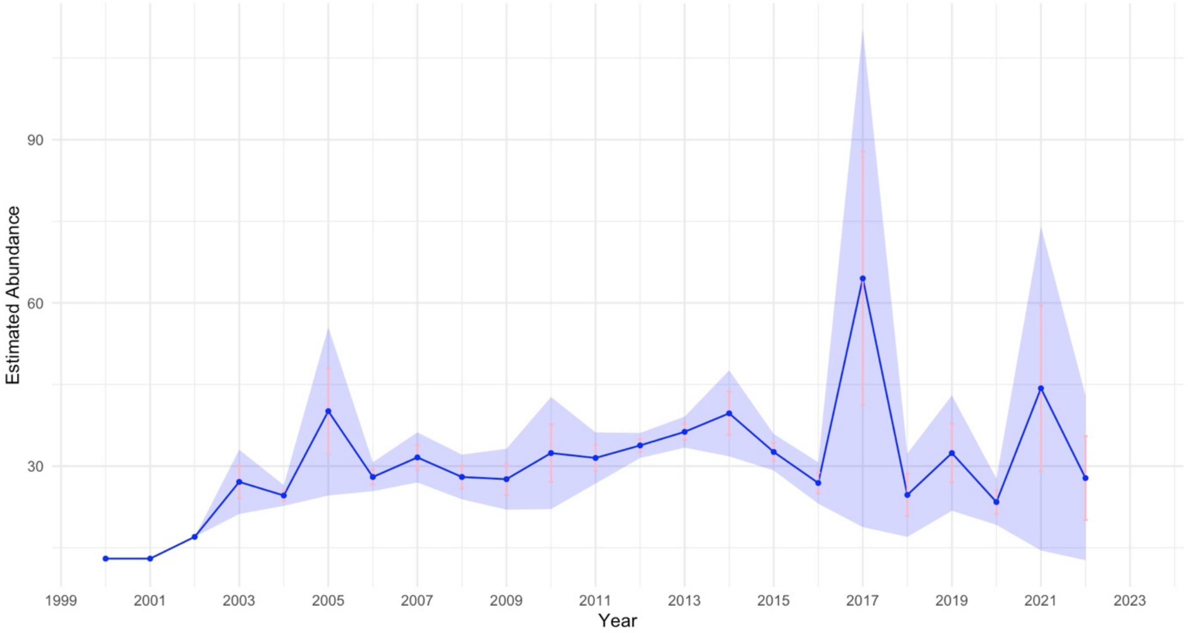

Fig. 9 – Estimated annual orca abundance using the Jolly-Seber open population model. The central dark blue line represents point estimates of population size for each year, the shaded area shows 95% confidence intervals, and the pink lines show the standard error.

3.2.4 Population metrics

The age distribution of the individuals over the years indicated a clear and constant dominance of the adult class (Fig. 10). The juveniles made up a smaller proportion of the population than adults (except for the first four years) but maintained a consistent presence over time. Among the three classes, the calves constantly had the smallest percentage despite slight yearly variations, including three years where no calves were accounted for (2002, 2019 and 2020). In contrast, the years 2011 and 2023 had the highest proportion of calves.

Overall, the chart suggests a relatively stable population structure with a dominant adult class. The average age class proportions over the years were 55.6% adults, 39.8% juveniles and 4.6 % calves. Within the adult class, females represented the majority with 61.9% while males comprised only 38.1% of the population.

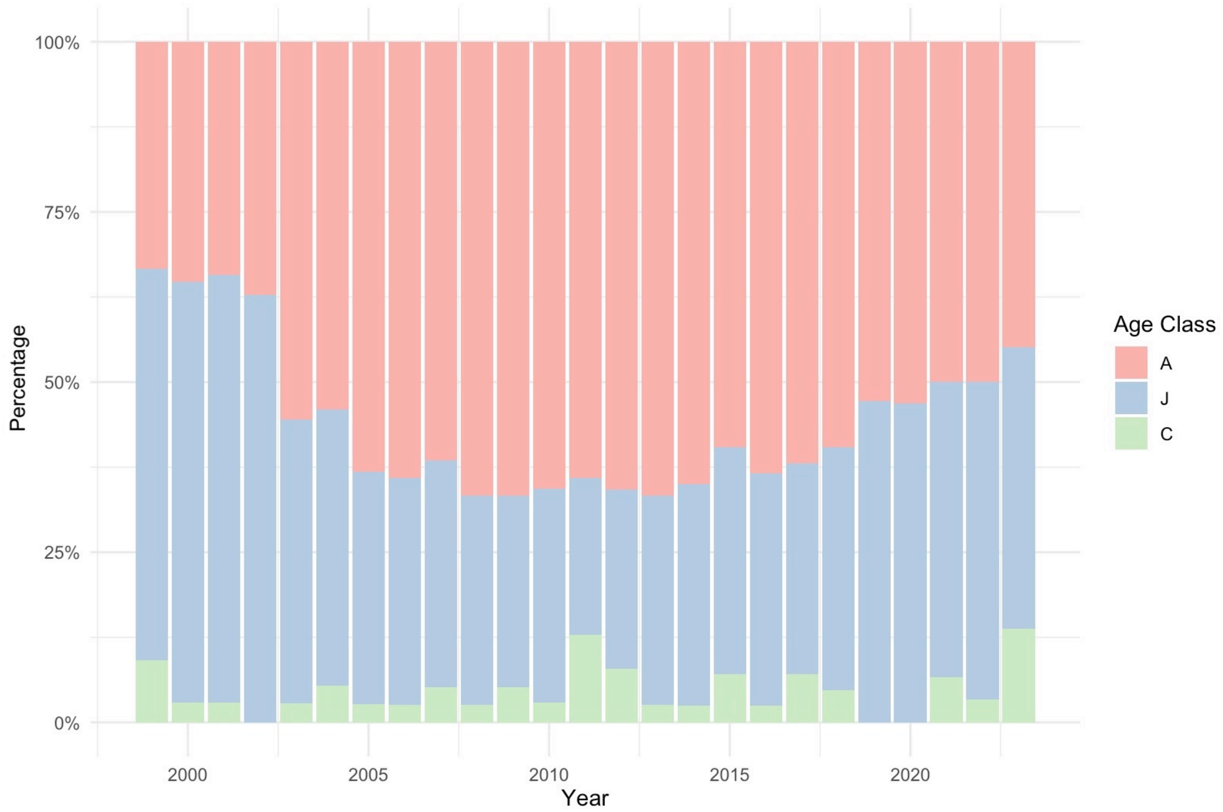

Fig. 10 – Age classes of the members of the population over the years shown in percentages. Adults (A) are shown in red, juveniles (J) in blue and calves (C) in green.

The birth and mortality rates were 0.013 (95% CI 0.009 - 0.019) and 0.022 (95% CI 0.014-0.031), respectively. With a mortality rate higher than the birth rate, the orca population showed a general declining trend during the study period, with a population growth rate of -0.009 (95% CI -0.018- -0.002) (Table 1). That is a decrease of less than 1% between 1999 and 2023, as more individuals emigrated or died than were born or immigrated into the population.

A total of 17 female orcas with known offspring were part of the dataset. Out of these, 11 had more than one viable calf and were used to calculate birth intervals, fecundity, and calving rate. These females had an average birth interval of 6.7 years (95% CI 5.15-8.25), a median birth interval of 6 years, and a fecundity rate of 0.149 (95% CI 0.114 - 0.184) (Table 1). The birth intervals for viable calves ranged from as little as 3 years in two of the females, up to 15 years in another individual.

Table 1 – Summary of the estimated population parameters for the Iberian orca population between 1999 and 2023. SE is standard error, LCI is lower confidence limit and UCI is upper confidence limit.

Life parameters	**Estimate**	**SE**	**95% LCI**	**95% UCI**
Apparent survival rate (Φ)	0.974	0.002	0.970	0.978
Capture probability (c)	0.725	0.006	0.713	0.736
Mortality rate	0.022	0.004	0.014	0.031
Birth rate	0.013	0.003	0.009	0.019
Population growth rate	-0.009	0.005	-0.021	-0.001
Avg. birth interval	6.7	0.742	5.15	8.25
Fecundity rate	0.149	0.0165	0.114	0.184
Calving rate	0.111	0.024	0.063	0.160
Avg. proportion adults	55.6%			
Avg. proportion juveniles	39.8%			
Avg. proportion calves	4.6%			
Avg. proportion of adult females	61.9%			
Avg. proportion of adult males	38.1%			

3.2.5 Interactions with fisheries

For the 87 individuals identified over the course of the study, the proportion of orcas that partake in the depredation of fishing lines was quite high, with 72.4% of orcas displaying this behaviour versus the 27.6% that hunt exclusively using other methods. Moreover, for the estimated live population (as of 2023), the values were slightly higher for the depredating orcas with 74.4% compared to the 25.6% of the non-participating orcas.

3.3 Social structure

3.3.1 Cluster analysis and network statistics

The permutation tests for both the half-weight index (HWI) and the simple ratio index (SRI) revealed the associations between individuals were significant (Appendices A1 and A2). Although both indices were used for a robust social structure analysis, only values from the HWI are presented in this study, as it is expected to better reflect the strength of social ties in this orca population.

The hierarchical cluster analysis based on the HWI revealed a strong non-random modular structure within the network. This is evidenced by a high cophenetic correlation coefficient (CCC) of 0.882 suggesting an accurate depiction of the pairwise associations in the original data in the dendrogram (Fig. 11A). Additionally, the modularity value was significant at 0.355, which indicates a well-defined community structure within the network. The maximum modularity was found at an association index (AI) threshold of 0.124, suggesting that even relatively weak associations were meaningful in forming these social clusters. Based on the dendrogram (Fig. 11A) and diagram (Fig. 11B), it is possible to infer the presence of at least five distinct social groups (pods). Pod Toñi (OO_039) is the biggest of the pods with around 21 orcas. Its namesake is a female known as the oldest orca in this subpopulation and thought to be born around 1970. The second biggest group is Pod Niebla (OO_032) with at least 14 individuals. Due to previously mentioned restrictions, this analysis was limited to 52 of the 87 orcas observed throughout the duration of the study. Conversely, the smallest group is Pod Vega (OO_052) with around 4 individuals.

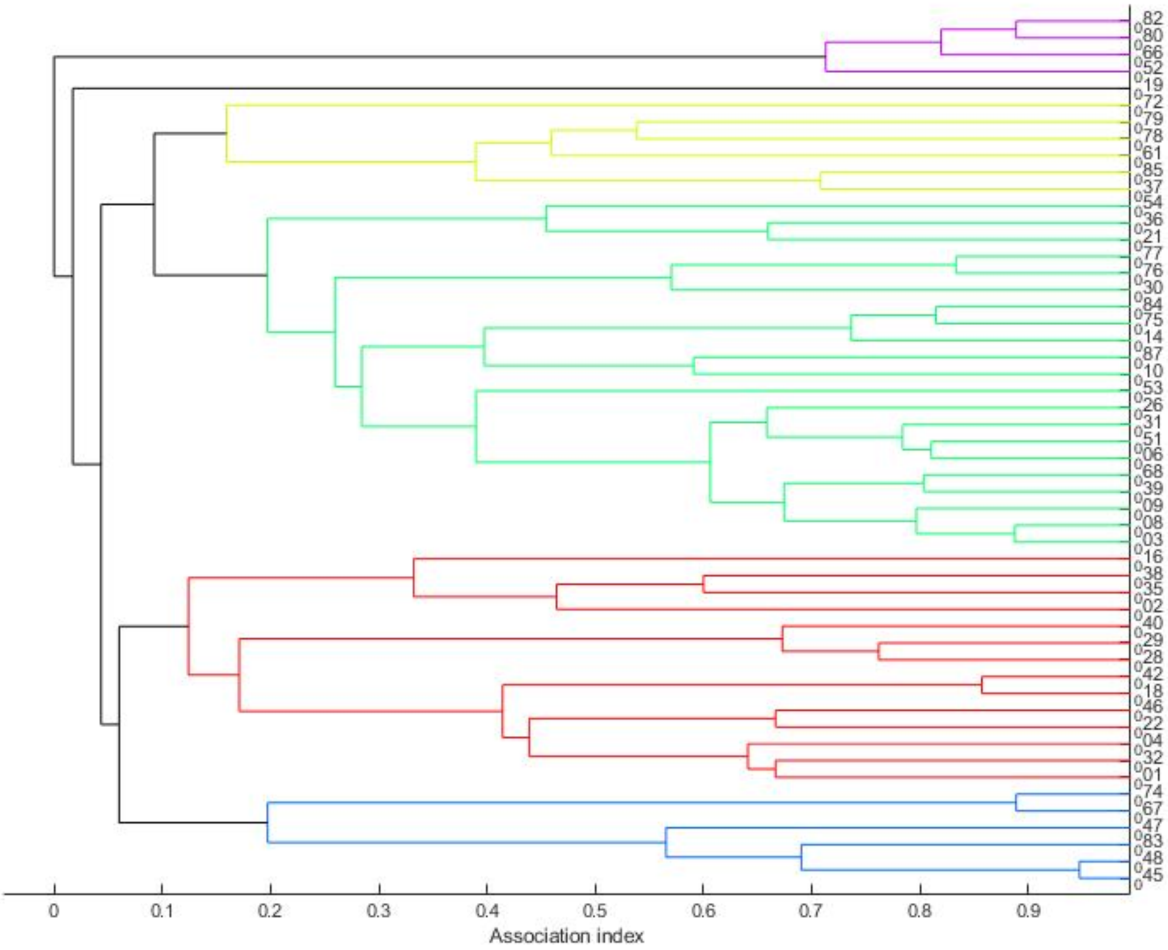

Fig. 11A – Hierarchical cluster analysis using the HWI and average linkage. The CCC of 0.882 indicates high clustering quality. Clusters are colour-coded based on a modularity score of 0.355, calculated at an AI threshold of 0.124. Individuals linked at smaller distances are more closely associated, whereas ones linked at higher distances have weaker associations. Pod Vega is shown in purple, Pod Macarra appears in yellow, Pod Toñi is shown in green, Pod Niebla is in red and Pod Sedna in blue.

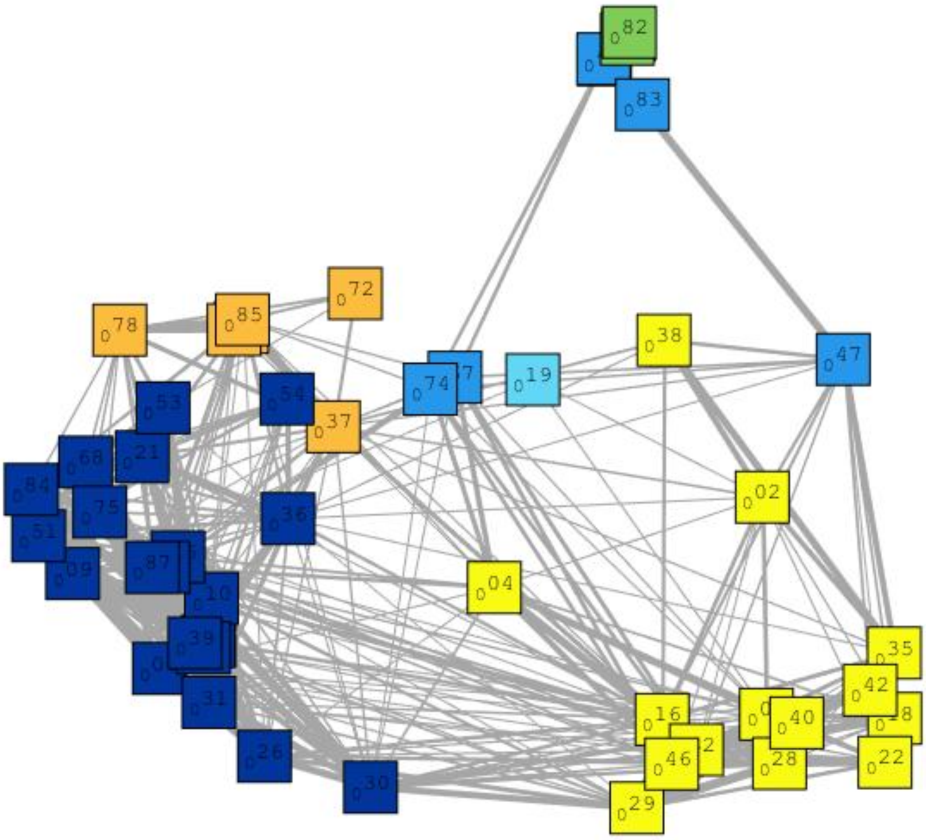

Fig. 11B – Orca network diagram using the HWI and average linkage. The CCC of 0.882 indicates high clustering quality. Clusters are colour-coded based on a modularity score of 0.355, calculated at an AI threshold of 0.124. Numbered nodes represent different orcas, and the thickness of edges reflects the strength of associations between individuals. Pod Vega is shown in green, Pod Macarra appears in orange, Pod Toñi is shown in dark blue, Pod Niebla is in yellow and Pod Sedna in median blue.

On the last year of the study (2023), the hierarchical cluster analysis based on the HWI also evidenced the presence of a strong non-random modular structure.

The high cophenetic CCC of 0.895 indicates an accurate depiction of the pairwise associations in the original data in the dendrogram (Fig. 12). Further, the modularity value was significant at 0.355, showing a clear community structure within the network. The maximum modularity was found at an association index (AI) threshold of 0.352, indicating only stronger associations were meaningful in forming social groups. The data showed three well-defined pods, composed of between 8 and 9 individuals. These are Pod Toñi, Pod Muesca and Pod Niebla. This analysis was limited to 25 of the 33 orcas observed in 2023.

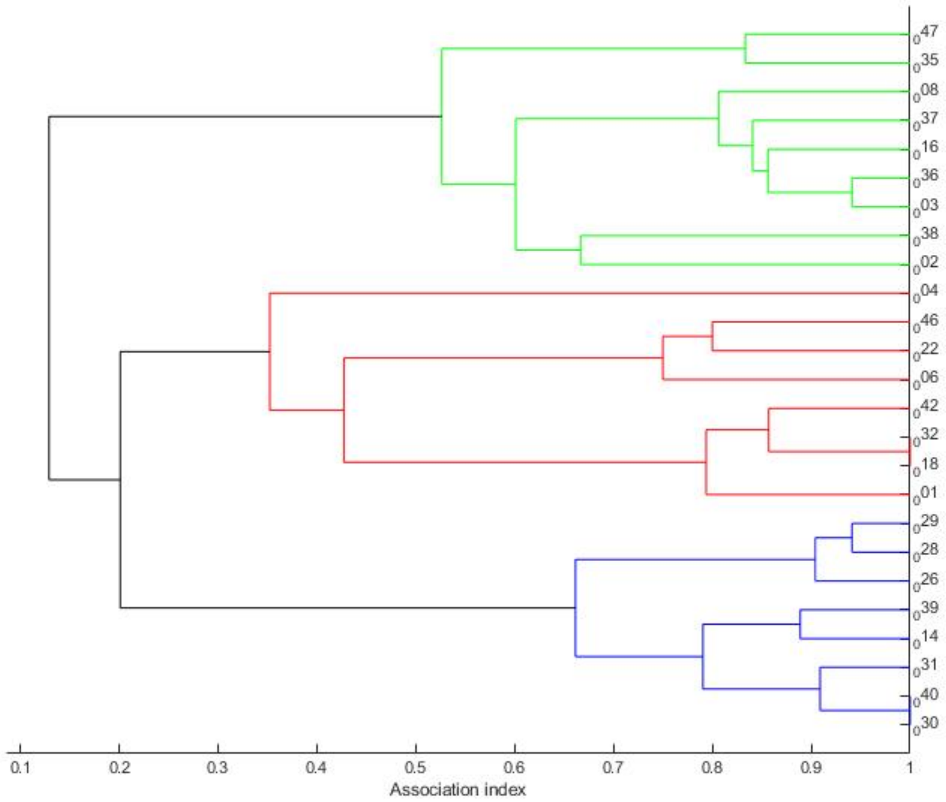

Fig. 12 – Hierarchical cluster analysis using the HWI and average linkage for the year 2023. The CCC of 0.895 indicates high-quality clustering. Clusters are colour-coded based on a modularity score of 0.359, calculated at an AI threshold of 0.352. Pod Toñi is shown in blue, Pod Muesca in green and Pod Niebla in red.

The social network analysis based on the HWI displayed several key network metrics. The overall mean strength of associations among individuals was 5.90 (SE = 2.90), indicating a moderate level of connectedness within the population. The eigenvector centrality had an overall mean of 0.11 (SE = 0.09), suggesting that most individuals held relatively peripheral positions in the network. The reach, which measures the extent of indirect connections, was relatively high with a mean of 43.12 (SE = 28.09). The clustering coefficient, representing the tendency of individuals to form tightly knit groups, was moderate at 0.34 (SE = 0.18). Additionally, the affinity, reflecting the average association strength between an individual and its associates, was 6.70 (SE = 1.86), indicating strong ties within certain groups. Correlation between strength and clustering coefficient (r = -0.334) showed a slight negative relationship between how strongly individuals are connected and the extent of their group cohesion. On the other hand, correlation between strength and affinity (r = 0.669) evidenced a positive relationship between an individual's association strength and its affinity with connected group members.

3.3.2 Lagged association rate

To evaluate changes in the social structure, the Lagged Association Rate (LAR) was calculated, as it measures the probability that two individuals seen together on one occasion will be seen together again after a given time lag (Fig. 13). The null association rate, which assumes no preferred associations among individuals, remained significantly lower than the LAR across all time lags, reinforcing the presence of non-random associations within the population. Initially, the LAR was relatively high, indicating strong associations between individuals shortly after a sighting. It then declined rapidly, suggesting a decrease in the likelihood re-sighting the same individuals together. Beyond this point, the LAR increased again, exhibiting considerable fluctuations, eventually stabilising at lower values over longer times lags. The best fitting model (*preferred companions* + *casual acquaintances*) closely followed the observed LAR (Fig. 13), particularly capturing the initial decline and the subsequent increase. This model, highlighted in Table 2, suggests observed associations rates are best explained by a combination of individuals maintaining long-term associations (preferred companions) and individuals whose associations are more transient (casual acquaintances).

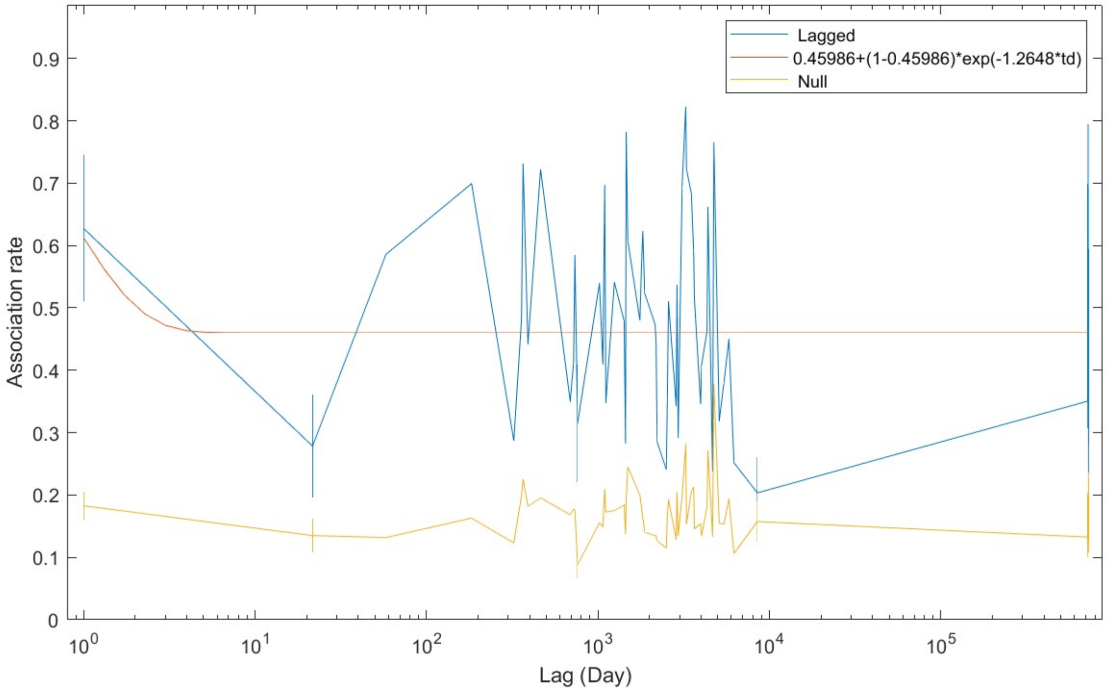

Fig. 13 – Association rate versus time lag between sightings (in days) on a logarithmic scale. Lagged association rate (blue), null association rate (yellow) and the best fitting model preferred companions + casual acquaintances (orange). Vertical lines show standard error calculated with the Jackknife method, providing an estimation of the variability in the association rate across different time lags.

Table 2 – Summary of simulated Lagged Association Rate (LAR) models. Highlighted in green is the model that best fits the observed LAR. The best fitting model is chosen based on the Quasi Akaike's Information Criterion (QAICc) since overdispersion was detected.

Model formula	**Description**	**Parameters**	**SE**	**AIC**	**QAIC**
$g(\tau) = a_1$	RD + PC	$a_1 = 0.460$	0.026	355714.020	46327.285
$g(\tau) = e^{(-a_1.\tau)}$	CA	$a_1 = 3.47e-04$	2.562e-05	2343960.876	305272.928
$g(\tau) = a_2.e^{(-a_1.\tau)}$	RD + CA	$a_1 = 3.645e-08$ $a_2 = 0.466$	1.075e-06 0.492	355678.081	46324.344
$g(\tau) = a_2.(1 - a_2).e^{(-a_1 . \tau)}$	PC + CA	a1 = 1.265 a2 = 0.460	0.75372 0.026185	355618.738	46316.615
$g(\tau) = a_2 + a_3 e^{(-a_1.\tau)}$	RD + PC + CA	$a_1 = 8.249$ $a_2 = 0.460$ $a_3 = 639.263$	11.954 0.026 2538.481	355611.510	46317.413
$g(\tau) = a_3.e^{(-a_1.\tau)} + (1 - a_3) + e^{(-a_2.\tau)}$	Two levels of CA	$a_1 = 0.502$ $a_2 = 2.644e-08$ $a_3 = 0.537$	0.051 9.965e-08 0.030	355774.871	46338.689
$g(\tau) = a_3 e^{(-*a_1.\tau)} + a_4 e^{(-*a_2.\tau)}$	RD + two levels of CA	$a_1 = 0.387$ $a_2 = 3.324e-08$ $a_3 = 0.803$ $a_4 = 0.465$	1.423 3.465e-07 1.359 0.136	367609.835	47881.793

3.4 Association between the ABFT and orca populations

The two measures used to describe the Atlantic Bluefin Tuna (ABFT) population status, though related, have some differences. ABFT catches represent actual extraction levels by fisheries, which are influenced by both stock availability and management regulations. In contrast, stock categories provide a broader assessment of the stock's overall health and sustainability.

The analysis of ABFT catches from 1999 to 2021 revealed a fluctuation in catch volumes, with a significant decline observed between 2010 and 2014 (Fig. 14). Following this last period there was a notable recovery and increase in catches, stabilising slightly over 10,000 tons by 2021. Understandably, the period of lowest catches did not coincide with the classification of ABFT stock as critically low (Fig. 15). Instead, it overlaps with stock categories indicating a status between overfished (-1) and recovering (0). The ABFT stock was at its lowest between 2005 and 2007, after which point it began improving, culminating in the classification of the stock as healthy by 2023.

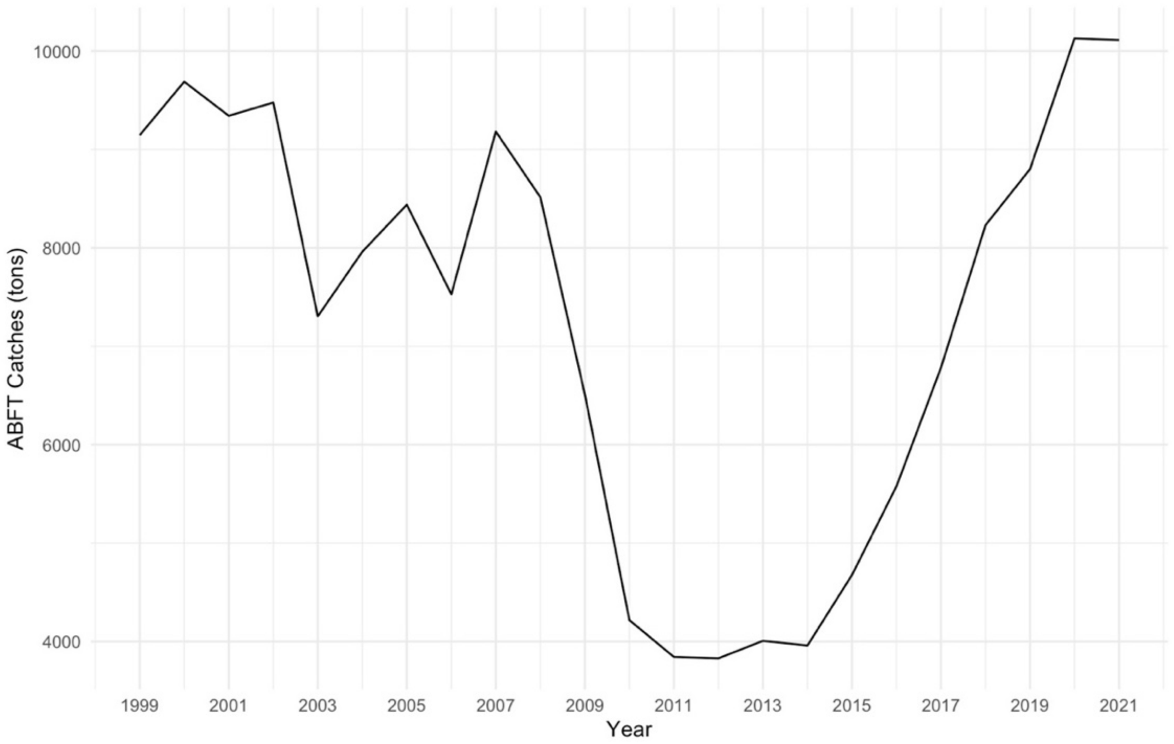

Fig. 14 – Atlantic bluefin tuna catches (in tons) for the fleets of Spain, Morocco, Portugal and Gibraltar from all fishing gears between 1999 and 2021. Source: ICCAT, 2024.

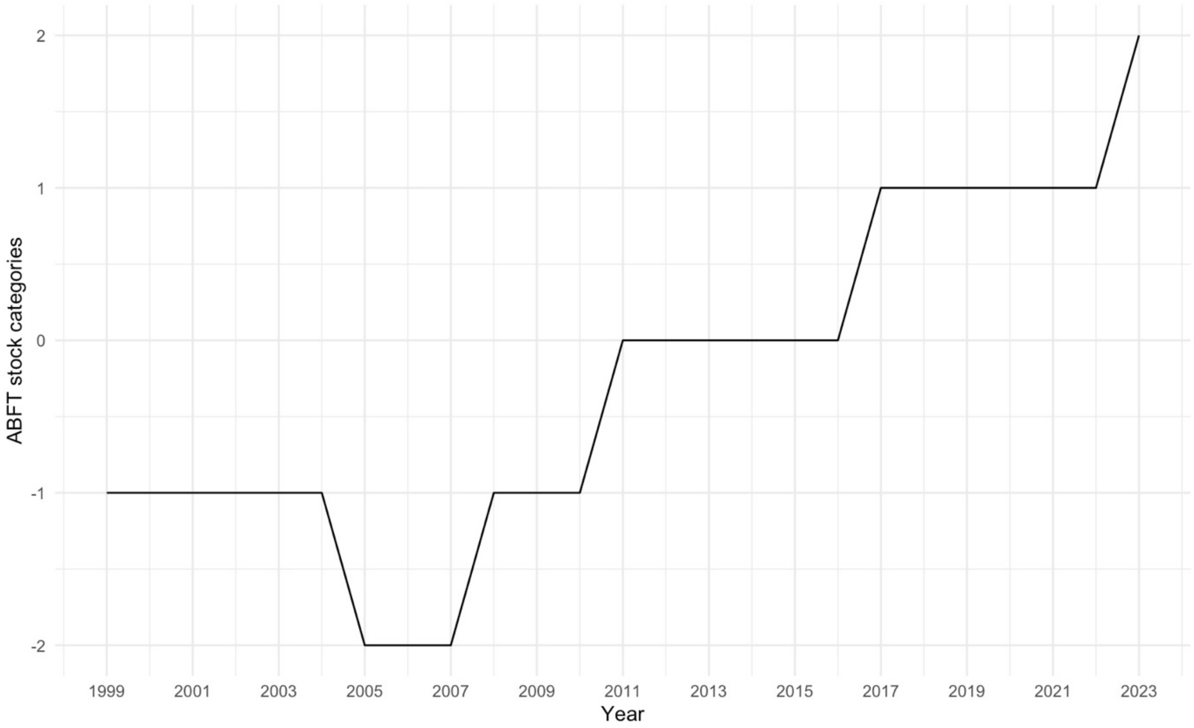

Fig. 15 – ABFT stock estimates in five categories from 1999 to 2023 based on ICCAT reports. Categories are: critically low (-2), overfished (-1), recovering (0), conditionally healthy (+1) and healthy (+2).

Spearman's rank correlation analysis (described in Table 3) showed positive, though not statistically significant, correlations between ABFT catches (Fig. 14) and orca survival rates. This correlation, although weak, peaked at a 3-year time-lag, nearing significance (ρ = 0.422, p = 0.064). Conversely, orca abundance estimates exhibited a negative correlation with ABFT catches, a relationship that increased in both magnitude and significance with increasing time-lags. The strongest negative correlation was observed at a 2-year time-lag (ρ = -0.528, p = 0.014).

There was no significant association between ABFT stock categories (Fig. 15) and orca abundance estimates. This was true for "time 0" as well as for all the time lags tested. However, a consistent weak negative correlation was observed between ABFT stock categories and orca survival rates, with the highest, though not quite significant, correlation at time-lag 0 (ρ = -0.396, p = 0.056).

Table 3 – Spearman's rank correlation coefficient (ρ) and respective p-values for survival rate and ABFT stock (SR-ABFT.S), abundance estimate and ABFT stock (AE-ABFT.S), survival rate and ABFT catches (SR-ABFT.C), and abundance estimate and ABFT catches (AE-ABFT.C) with and without time lags (0-5).

Time lag (years)	**SR – ABFT.S**		**AE – ABFT.S**		**SR – ABFT.C**		**AE – ABFT.C**	
	ρ	*P-Value*	*ρ*	*P-Value*	*ρ*	*P-Value*	*ρ*	*P-Value*
0	-0.396	0.056	-0.023	0.918	0.216	0.333	-0.435	0.043
1	-0.341	0.103	-0.0139	0.950	0.377	0.084	-0.469	0.028
2	-0.353	0.098	-0.074	0.743	0.365	0.103	-0.528	0.014
3	-0.360	0.100	-0.196	0.395	0.422	0.064	-0.290	0.214

4. Discussion

4.1 Population estimates and metrics

Over the years, there was a general increasing trend of identified orca individuals. This is expected, as there are improvements in the identification techniques as well as an accumulation of knowledge over time. This trend persists, despite fluctuations in research efforts, highlighting the effectiveness of continued research.

The fact that 2023 was the highest on record in terms of analysed pictures, and consequently identified individuals, appears to be primarily due to extensive research efforts and the availability of skilled personnel for photo-identification, with 2011 following a similar pattern (Fig.6). These were the two years in the study with the highest percentage of calves (Fig. 10), suggesting that increased research effort enhances the granularity of population analysis.

Across the 25-year span of this study, a total of 87 orcas were identified, with the current population estimated at 39 individuals (as of December of 2023). Curiously, the last complete assessment of this population, done in 2011, also resulted in a count of 39 individuals (Esteban et al., 2016a).

Other small populations include the one found off the Marion Islands, estimated to encompass around 37 individuals (Reisinger et al., 2011) and the one in the Archipelago of Crozet which had seen a reduction from 98 individuals in 1988 to only 37 individuals between 1998 and 2000 (Poncelet et al., 2010).

The overall survival rate for the studied orcas is high (0.974, 95% CI 0.970 - 0.978), consistent with the expected range of known piscivorous orca populations (Olesiuk et al., 1990; Poncelet et al., 2010; Kuningas et al., 2007). However, high survival rates are expected in long-living cetaceans such as orcas and the small size of this population means that even minor fluctuations can have significant impacts. Moreover, small populations are more vulnerable to genetic risks such as the loss of genetic diversity and inbreeding depression (Ford et al., 2018).

Looking at the reproductive patterns, a calving rate of 0.111 (95% 0.063-0.160) indicates that approximately 11% of reproductive females successfully gave birth to viable calves each year. This measure provides a snapshot of the annual reproductive success within the population and, in comparison to previous research, is much lower than depredating orcas but higher than that of the non-depredating orcas off Gibraltar (Esteban et al., 2016a). The birth interval of 6.7 years (95% CI 5.15-8.25) is long, falling on the high end of the range found in other fish-eating orca populations (Olesiuk et al., 1990; Kuningas et al., 2014) but quite similar to the value found in a previous study on the same population (Esteban et al., 2016a). Consequently, the fecundity rate, which offers a broader perspective on the reproductive potential of the population over time, is also lower than what is expected in a healthy population of such size, at 0.149 (95% CI 0.114 - 0.184). For comparison, the Southern Resident Killer Whales, which were listed as endangered in 2001 (Baird, 2001), have a fecundity rate of 0.21 and are showing little signs of recovery (Wasser et al., 2017). Some females in the present study had birth intervals as long as 15 years while others had intervals as low as 3 years. This high variation likely reflects difficulties in accurately counting calves due to their mothers' tendency to remain distant, compounded by variability in assessment efforts.

Finally, the average mortality rate was higher than the birth rate, resulting in an overall decline of approximately 0.9%. While this might hint at a vulnerable population due to its small size, it is also true that the small population makes small changes seem more impactful and that the population has remained relatively stable suggesting a degree of endurance.

Overall, these numbers define a population that is very small and, therefore, more vulnerable to any threats (Hoelzel et al., 2002) but also resilient, as it remained surprisingly stable over the course of the study. Despite this, even taking into consideration potential sources of error, the population metrics for this orca subpopulation seem to be below optimal, especially when compared to other sympatric groups (Table 4).

Table 4 – Overview of population parameters of fish-eating orca populations. Studies separated the orcas by sex — female (F) or male (M) — and, in Esteban et al. (2016a), by orcas that depredate longline fisheries (INT) and orcas that do not depredate fisheries (NOT). Adapted from Jourdain et al., 2019.

Area and source	**Study period**	**Survival rate**	**Birth interval**	**Fecundity rate**	**Calving rate**
Gibraltar (Esteban et al., 2016a)	1999-2011	INT: 0.991 (SE = 0.014) NOT: 0.901 (SE = 0.067)	INT: 7	INT: 0.14	INT: 0.219 (SE = 0.034) NOT: 0.020 (SE = 0.013)

Norway (Kuningas et al., 2014)	1986-2003	F: 0.977 (SE = 0.009) M: 0.971 (SE = 0.008)	5.06 (SE = 0.722)	0.197 (SE = 0.065)	-
Pacific Northeast (Olesiuk et al., 2005)	1973-1995	F: 0.984 (SE = 0.004) M: 0.959 (SE = 0.008)	4.88 (SE=0.793)	0.205	-
	1996-2004	F: 0.971 (SE = 0.007) M: 0.909 (SE = 0.017)	5.53 (SE = 1.103	0.180	-
Crozet Archipelago (Poncelet et al,. 2010)	1977	F: 0.942 (95%CI 0.844- 0.980) M: 0.935 (95%CI 0.817-0.979)	-	-	-
	2002	F: 0.901 (95%CI 0.742-0.966) M: 0.895 (95%CI 0.746-0.961)	-	-	-

Previous studies found a significant correlation between the main prey of orcas and their survival, fecundity rates and even social structure (Ward et al., 2009; Esteban et al., 2016a; Jordaan et al., 2023). However, the findings from the present study revealed a more complex relationship between ABFT availability and orca population dynamics. A weak, non-significant positive correlation between ABFT catches and orca survival rates, peaking with a 3-year lag, suggests a possible delayed effect of prey availability. However, the absence of statistical significance requires a careful interpretation. Unexpectedly, the only statistically significant finding was a negative correlation between ABFT catches and orca abundance with a 2-year lag. This counterintuitive result, coupled with a weak negative correlation between ABFT stock categories and orca survival rates suggests that orca population dynamics might be influenced by broader ecosystem trends rather than prey availability alone. In addition, discrepancies between reported ABFT catches (Fig.14) and ABFT stock categories (Fig.15) indicate potential issues with accurately reflecting true ABFT availability. These factors likely contribute to the complexity seen in the correlation analysis.

Interestingly, younger age classes within the orca population appear to respond more directly to changes in ABFT availability (Appendices B1 and B2). This may indicate that the correlation between prey availability and survival is more evident in younger orcas, who are more vulnerable and reliant on stable prey sources, whereas adults have more complex survival dynamics.

In the Marion Island orca population, survival correlated positively with social structure and the previous year's fishing effort, but not with direct prey counts or environmental proxies of prey availability (Jordaan et al., 2023). This suggests that orca survival may be more closely linked to the presence of fishing activity than to the actual abundance of prey, evidencing the role of artificial provisioning. In the Strait of Gibraltar, an increase in the percentage of orcas engaging in the depredation of fishing lines—a behaviour known to be advantageous in terms of energy conservation and access to larger prey (Guinet et al., 2007; Esteban et al., 2016) —was observed. This behaviour is likely spread through both vertical and horizontal knowledge transfer (Thornton and Clutton-Brock, 2011; Abramson et al., 2013; Esteban et al., 2016b) and its increased prevalence may be one of the factors responsible for the apparent complexity of orca responses to ABFT availability. It may also explain the resilience of this population despite less-than-optimal life metrics and their small population size.

4.2 Social structure and network metrics

Overall, this orca population has a complex but well-defined social structure. The analysis showed at least five clearly defined pods, consistent with a previous study on these orcas (Esteban et al., 2016b) and research on other populations (Bigg et al., 1990; Tosh et al., 2008; Beck et al., 2012). Pod Vega (OO_052) was both the smallest and the most differentiated group and did not seem to associate with any of the other pods. This is consistent with previous research showing marked differences in the associations between Pod Vega and the other four pods present at the time (Esteban et al., 2016c).

The emergence of Pod Muesca, noted in the 2023 social structure (Fig.12), primarily resulted from the fission of Pod Toñi, with the addition of a few individuals from Pods Macarra and Sedna. Such fission events are quite common orca societies and are thought to occur following the death of the oldest female in a pod (Ford et al., 2000). As of 2023, there remain no living members of Pod Vega, and most individuals from Pods Macarra and Sedna have also disappeared. This explains the altered groupings observed in 2023 which closely align with the social structure derived from the last five years of the study (Appendix C), showing three larger, well-defined groups, and a smaller group, possibly indicating a fourth pod.

Throughout the study, all orcas in Pod Toñi, Pod Macarra and Pod Muesca have been seen depredating fishing lines around the Strait of Gibraltar, whereas none in Pod Vega exhibited this behaviour. Pod Niebla and Pod Sedna contained a mixture of depredating and non-depredating individuals. Additionally, in terms of interactions with sailboats, all three pods seen in 2023 (Fig. 12) contain individuals associated with this behaviour—the so-called 'Gladis'. This is consistent with past research evidencing the plasticity in the sociality and foraging behaviour of these orcas (Esteban et al., 2016b).

Regarding the network metrics, an average strength (5.90) suggests that most individuals maintain moderately strong connections with their peers, with some variability. The low mean eigenvector centrality (0.11) implies that most individuals have low influence within the network, but there are likely a few key orcas who are more central and may play crucial roles in maintaining social cohesion. A mean reach of 43.12 means that nearly half of the potential associations within the network are strong. However, a high standard error (28.09) indicates considerable variation in the extent of connections within the network, evidencing the presence of certain orcas who act as "bridges" between different pods or subgroups. A clustering coefficient of 0.34, with significant variability (SE 0.18), points to a tendency in individuals forming smaller groups. The affinity score (6.70) implies that orcas in this population tend to associate with others who have similar social habits or preferences. Additionally, the negative correlation between strength and clustering coefficient demonstrates that individuals with stronger associations tend to be less embedded in tightly knit groups. The positive correlation between strength and affinity shows that individuals who have strong associations also tend to associate with others who have similar social preference, reinforcing the idea of selective social bonding within the population.

The lagged association rate showed that the animals of this study tend to form short-term associations, with the best fitting model indicating a combination of preferred companions and casual acquaintances (Fig.13). The persistence of some association probabilities even at long time lags, implies long-term memory or intermittent long-term associations in the population. These results align with the multifaceted and adaptive nature of orca social structures, where stable, preferred relationships—consistent with the stable matrilineal societies for which they are known (Parsons et al., 2009; Esteban et al., 2016b) — coexist with more flexible, casual associations, reflecting the sophisticated nature of their social lives. Orcas are indeed known to show social and behavioural plasticity and adapt to local ecological conditions (Beck et al., 2012). They exhibit a more connected network when food availability is high (Foster et al., 2012b), which is likely an example of the adaptive responses to the challenges of the environment, including the need for efficient foraging, reproductive success, and social learning opportunities (Hoelzel et al., 1991; Baird and Whitehead, 2000; Beck et al., 2012; Brakes et al., 2019).

4.3 Study limitations

This study acknowledges several limitations, including disparities in data collection and identification methods across different years, which likely influenced the population models. One significant factor affecting the robustness of the survival rate estimates is the variability in capture probability (Appendix D). The fluctuating capture probability values, potentially due to inconsistent research efforts, could have increased the uncertainty in some years and contributed to the wide confidence intervals observed, particularly 2016, 2020 and 2022. These periods, while appearing to suggest an increase in mortality, might instead reflect lower research efforts rather than true changes in population dynamics. This is also seen in the abundance estimates, where some data points with wide confidence intervals could be artifacts caused by low data quality or quantity.

Additionally, the goodness of fit tests uncovered evidence of transience and trap-dependence effects, indicating challenges in accurately modelling this population. These limitations underscore the complexities inherent to orca population modelling and the need for caution in interpreting the derived parameters.

Estimates such as birth, death, fecundity, and calving rates have an inherent uncertainty as they rely on approximations for ages of birth, death, maturation, and female senescence. Mortality, in particular, can be difficult to determine as, unless orcas are found stranded, date of death is not obvious. A similar issue can arise in determining births.

Lastly, it is important to mention that, though the descriptors used for ABFT are the best information currently available, they are based on different criteria. While stock categories provide a broad measure of ABFT health, they may not directly reflect immediate prey availability for orcas. In contrast, stock categories, though a more direct reflection of ABFT availability, are much less detailed and precise. Discrepancies in these measurements may also arise from fluctuations in fishing effort, reporting inconsistencies or mismatches between stock recovery measures and local prey availability for orcas. ABFT is a dynamic population inhabiting a wide area subject to various pressures and that makes it difficult to assess with accuracy.

4.4 Further research

The observed increase in the percentage of orcas depredating ABFT fisheries raises important questions about knowledge transfer, in the form of learned behaviours and their transmission, as well as the adaptability of orcas. An interesting hypothesis is that this behaviour may have contributed to the stability of this small population of orcas, despite fluctuations in ABFT availability and other environmental stressors. Additionally, since social structure in these orcas has been shown to be shaped by maternal kinship as well as foraging behaviour (Esteban et al., 2016b), interesting dynamics may arise from this strategy. A more detailed assessment of this behaviour—and one that considers different categories (e.g., age, sex, hunting technique) —could provide valuable insights into these animals' adaptive capacities.

Another critical area of concern is the high levels of pollutants in the waters inhabited by these cetaceans. Research suggests that environmental contaminants, particularly polychlorinated biphenyls (PCBs), are associated with immunosuppression in marine species, potentially increasing their susceptibility to disease (Beineke et al., 2005; Schwacke at al., 2012; Desforges et al., 2016). PCBs have also been linked to other health issues in cetaceans, such as anaemia and hypothyroidism (Schwacke et al. 2012).

In the Strait of Gibraltar, epizootic events caused significant declines in the resident population of long-finned pilot whales (*Globicephala melas*) (Verborgh et al., 2019; Pons et al., 2022). The frequency of these events might be related to anthropogenic actions such as organochlorine contamination (Pons et al., 2022). While the orca population seems to have so far remained unaffected by these outbreaks, the high concentrations of PCBs found in the orcas of this region, which exceed known toxicity thresholds (Jepson et al., 2016), warrant continued concern. The persistence of PCBs, despite being banned in most of the world several decades ago, is both due to their environmental stability and biomagnification. Due do their long life spans and position at a high trophic level as apex predators, orcas are particularly affected by persistent organic pollutants through bioaccumulation (Hickie et al., 2007). Long-term models predict that PCB-mediated effects on reproduction and immune function will place over half of the world's orca populations at risk of collapse within the next century (Desforges et al., 2018).

Technological advancements in photo-identification could significantly enhance the accuracy and efficiency of future research efforts, particularly in tracking long-term population trends and social structures. Overlap between human activities and orcas is unavoidable, especially in the Strait of Gibraltar. Examples of this overlap are the depredation of fisheries (Esteban et al., 2016a), whale watching activities (Ouled-Cheikh et al., 2023) and the more recent interactions with sailboats (Esteban et al., 2022). The latter has led to a surge in public interest in orcas, but it has also generated a negative sentiment toward them. Thus, it is essential to maintain consistent data collection for this population to understand its fluctuations, social structure alterations, and to predict potential declines.

5. Conclusion

The Iberian orca population currently comprises approximately 39 individuals, organised into at least three pods. As expected, while their social structure is relatively stable, there is some degree of plasticity within it. The overall trend over the study period shows a decline of around 0.9%, a figure that is not necessarily a reason for concern. Even so, other life metrics are far from optimal, especially when compared to similar orca populations, which could be reason of concern in such a small population. Despite this, the population appeared generally stable with no major declining trends, which may be the result of adaptive strategies—most notably, the depredation of fishing lines. There was an increase in the proportion of orcas depredating fisheries in the Strait of Gibraltar compared to previous years and that is expected to have a positive impact on their survival.

Interestingly, the response in the Iberian orcas to fluctuations in their main prey, the Atlantic bluefin tuna (ABFT), appears more complex than initially thought. No strong positive correlations were found between orca survival/abundance and ABFT availability, and the significant correlation observed was negative, potentially indicating the involvement of other influencing factors.

These findings highlight the need for continued monitoring of this population, as well as the implementation of more robust protection measures, including better management of the ABFT stocks, reductions in pollution, and marine traffic regulation. This is especially necessary in areas such as the Strait of Gibraltar where orcas are highly exposed to human activities. The orca subpopulation in the Strait of Gibraltar was previously classified as “Critically endangered” by the IUCN and the same issues remain pressing today, underscoring the need for swift implementation of proposed conservation plans. As bureaucratic processes and human conflict continue to stall progress, the path to welfare for this orca population remains distant.

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7. Appendix

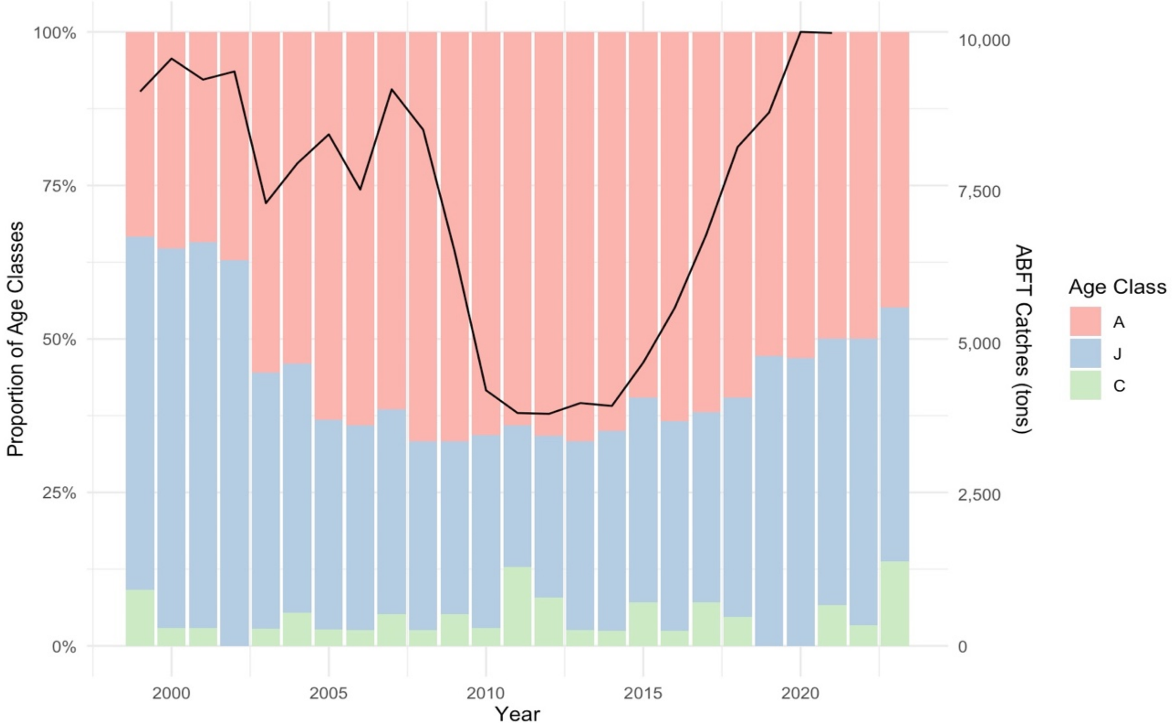
Appendix A1 – Results from the permutations test using the half-weight index (HWI).

Test Statistic	Real Value	Mean (Random)	Count (Real>Random)	P(1-sided)
Mean	0.11575	0.11575	942/1000	-
s.d.	0.18528	0.18509	999/1000	0.001
CV	1.60068	1.59909	999/1000	0.001
Prop. non-zero elements	0.49548	0.49548	465/1000	0.465
Mean non-zero elements	0.23362	0.23361	943/1000	0.057
s.d. non-zero elements	0.20434	0.204	1000/1000	0.000
CV non-zero elements	0.87468	0.87324	999/1000	0.001

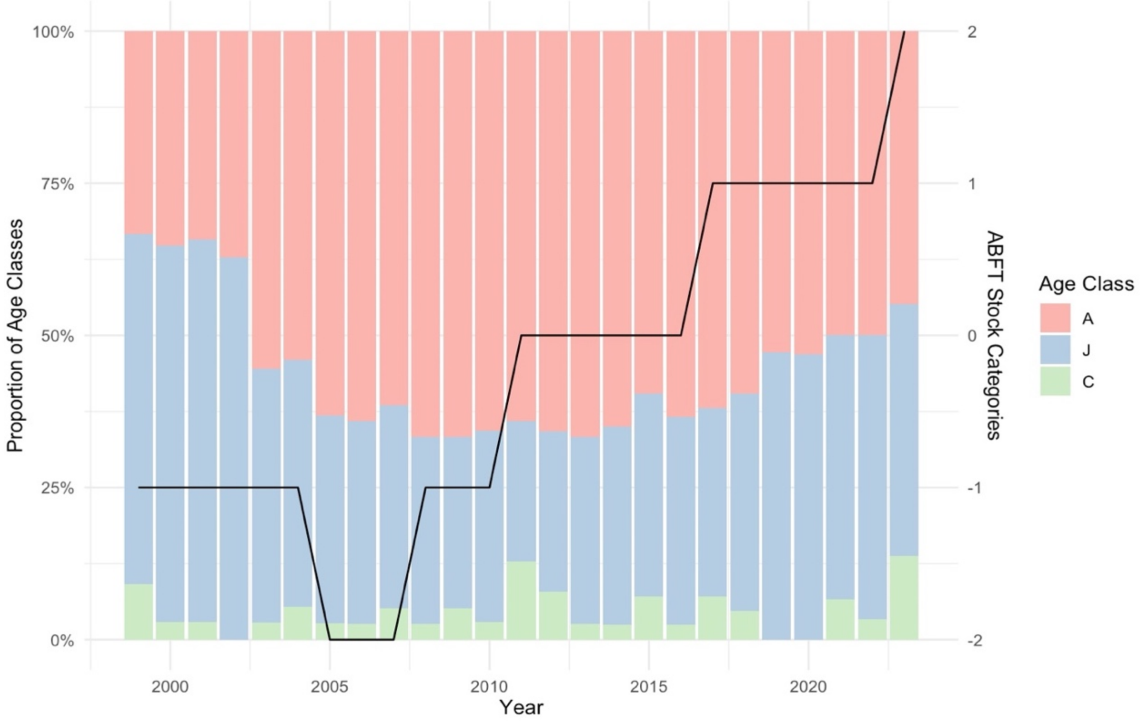
Appendix A2 – Results from the permutations test using the simple ratio index (SRI).

Test Statistic	Real Value	Mean (Random)	Count (Real>Random)	P(1-sided)
Mean	0.07477	0.07475	1000/1000	-
s.d.	0.13658	0.13639	999/1000	0.001
CV	1.82678	1.82467	1000/1000	0.000
Prop. non-zero elements	0.49548	0.49548	494/1000	0.494
Mean non-zero elements	0.1509	0.15086	999/1000	0.001
s.d. non-zero elements	0.16176	0.16145	1000/1000	0.000
CV non-zero elements	1.072	1.07022	1000/1000	0.000

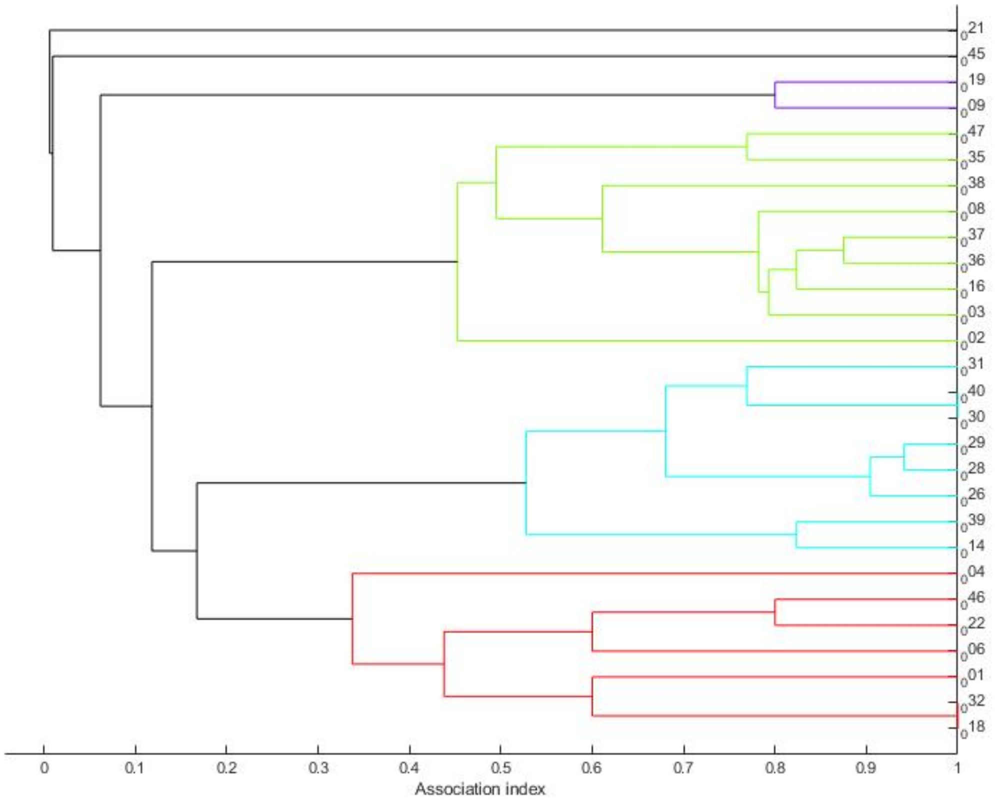
Appendix B1 – Age class proportions over the years—with A, J and C representing the adults, juveniles, and calves, respectively—along with the Atlantic bluefin tuna (ABFT) catches in tons (sourced from the ICCAT).



Appendix B2 – Age class proportions over the years—with A, J and C representing the adults, juveniles, and calves, respectively—along with the Atlantic bluefin tuna (ABFT) stock categories which are based on the ICCAT annual assessments of the ABFT.



Appendix C – Hierarchical cluster analysis using the HWI and average linkage for 2019-2023. Clusters are colour-coded based on a modularity with Pod Toñi shown in light blue, Pod Muesca in light green and Pod Niebla in red.



Appendix D – Capture probability obtained from the CJS model run in MARK.

Zusammenfassung

Diese Studie präsentiert eine umfassende Analyse der Iberischen Orcas (*Orcinus orca*) in den Gewässern der Straße von Gibraltar über einen Zeitraum von 25 Jahren (1999–2023). Es wurde eine gründliche Analyse durchgeführt, bei der Foto-Identifikation und Rückfangmethode verwendet wurden. Dabei wurden 87 verschiedene Individuen aus 43.522 analysierten Fotos identifiziert.

Das Modell schätzt die Gesamtüberlebensrate dieser Orcas auf 0,97. Im Jahr 2023 wurde die Population auf etwa 39 Individuen geschätzt, mit einem Trend, der über den Studienzeitraum einen Rückgang von 0,9% zeigt. Die Altersverteilung zeigt eine Dominanz der erwachsenen Klasse, die hauptsächlich aus Weibchen besteht. Im Verlauf der Studie wurden mindestens fünf gut definierte Sozialgruppen identifiziert, die im Laufe der Zeit Veränderungen unterworfen waren. Das am besten passende Modell ist das von bevorzugten Gefährten und gelegentlichen Bekannten, was eine soziale Struktur demonstriert, die stabil ist, aber im Laufe der Zeit Fluidität zeigt, wobei die neuere Analyse (2023) nur drei klar definierte Sozialgruppen zeigt.

Die Beziehung zwischen Orcas und der Verfügbarkeit von Beute war komplex und möglicherweise durch mehrere Faktoren beeinflusst, einschließlich eines Anstiegs der Anzahl von Orcas, die mit Fischereien auf den Roten Thunfisch (*Thunnus thynnus*) interagieren. Obwohl überraschend stabil, waren die Gesamtdaten der Population niedriger als die in anderen Fischfresser-Populationen beobachteten, was die Notwendigkeit von Schutzmaßnahmen für Orcas und einer besseren Bewirtschaftung der Thunfischbestände hervorhebt. Obwohl diese Studie wertvolle Einblicke in die Populationsdynamik der Iberischen Orcas bietet, bleibt noch viel über diese Tiere zu verstehen, was eine sorgfältige und kontinuierliche Überwachung der Orca-Population für zukünftige Erkenntnisse unerlässlich macht.