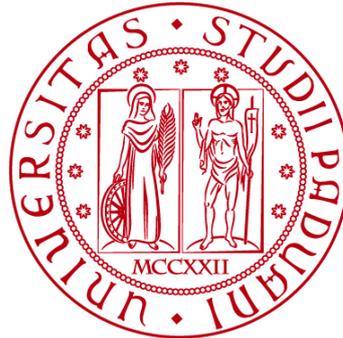


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TESI DI LAUREA

Study of the movement of *Argyrosomus regius* (Pisces, Teleostei) along the South-West coast of Portugal using network analysis

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INTRODUCTION

1) AGGREGATIONS IN THE MARINE REALM

a. General definitions and relevance for conservation

Aggregation of individuals during some phases of their life cycle is a well-established process in the animal world (Lilly *et al.*, 2020; Villegas-Ríos, Jacoby and Mourier, 2022). Research has shown that in the marine environment, many different species of elasmobranchs, marine mammals, and teleosts interact and can create long-lasting associations (Croft *et al.*, 2005; Papastamatiou *et al.*, 2020; Villegas-Ríos, Jacoby and Mourier, 2022). The possibility to find mates, escape from predators, improve strategies to find food, and initiate migrations are all aspects of the life history of marine organisms that are influenced by social processes (Ritz *et al.*, 2011; Villegas-Ríos, Jacoby and Mourier, 2022). Individual phenotypic attributes (sex, size, age, familiarity) affect how they interact with other conspecifics (Wilson, Croft and Krause, 2014; Ward, Kent and Webster, 2020; McInturf *et al.*, 2023). These attributes may lead individuals of populations to preferentially associate or, on the contrary, avoid, possibly leading to some spatial segregation between subpopulations inhabiting the same geographical area (Mourier, Vercelloni and Planes, 2012; Armansin *et al.*, 2016; Schilds *et al.*, 2019; Papastamatiou *et al.*, 2020). Therefore, the social connectivity between individuals may influence the transfer of information, the spread of diseases, and also the gene flow among subpopulations (Perryman *et al.*, 2022; Villegas-Ríos, Jacoby and Mourier, 2022), which in turn affects the entire population structure and dynamics within the ecosystem (Mourier, Vercelloni and Planes, 2012; Wilson, Croft and Krause, 2014; Perryman *et al.*, 2022; Villegas-Ríos, Jacoby and Mourier, 2022). Anthropogenic stressors (e.g., illegal fisheries, un-regulated dive tourism, pollution, noise) may disproportionately impact some individuals or groups of individuals more than others if they display a different use of the space, which will affect the entire population (Perryman *et al.*, 2022; Villegas-Ríos, Jacoby and Mourier, 2022). Understanding the social dynamics within populations is essential, as they might shape how the population is distributed over space and time. This information is of crucial relevance for marine spatial planning and the conservation of marine species (Wilson, Croft and Krause, 2014; Papastamatiou *et al.*, 2020; Perryman *et al.*, 2022; Villegas-Ríos, Jacoby and Mourier, 2022).

b. Drivers and factors that shape aggregations

Among the marine realm, the drivers that trigger associations among organisms and shape the community structure when they are formed are heterogeneous. Individuals may choose to aggregate to find food, to reproduce, to reduce the risk of predation, to reduce the risk of aggressions by conspecifics, or to save energy while moving (e.g. fish school) (Ritz *et al.*, 2011; Ward, Kent and Webster, 2020). When these aggregations occur, they can display different structures, depending on the species in question, the individual's phenotype, and the trade-off between different biotic (e.g. competitions for resources or predator defence) and abiotic contexts (favourable water temperature and availability of food) (Ritz *et al.*, 2011; Wilson, Croft and Krause, 2014; Ward, Kent and Webster, 2020; Anderson *et al.*, 2021; Weiss, Ellis and Croft, 2021; Villegas-Ríos, Jacoby and Mourier, 2022; McInturf *et al.*, 2023). When a group of individuals of the same species co-occur together at the same time, they may display preferred interactions or not. If the individuals do not show any preference for other conspecifics, we refer to these groups simply as "aggregations" (Ritz *et al.*, 2011; Armansin *et al.*, 2016; Findlay *et al.*, 2016; Schilds *et al.*, 2019; Lilly *et al.*, 2020). On the other end, if some individuals co-occur frequently and maintain these cohesions, those kinds of associations are referred to as "social groups" (Ritz *et al.*, 2011; Armansin *et al.*, 2016; Findlay *et al.*, 2016; Schilds *et al.*, 2019; Lilly *et al.*, 2020). Social groups are formed because individuals gain reciprocal advantages in collaborating, for example, for foraging or predator avoidance, and these associations should occur regardless of other environmental stimuli (Ritz *et al.*, 2011; Mourier, Vercelloni and Planes, 2012; McInturf *et al.*, 2023). Individuals can associate because they share similar physical phenotypic attributes (e.g. sex and size) or because they have a similar behavioural phenotype compared to other members of the same population (Wilson, Croft and Krause, 2014; Ward, Kent and Webster, 2020; Weiss, Ellis and Croft, 2021).

c. Examples of aggregations across elasmobranchs, marine mammals, and teleosts.

Elasmobranch aggregations are widely reported in the marine literature (Mourier, Vercelloni and Planes, 2012; Armansin *et al.*, 2016; Lédée *et al.*, 2016; Schilds *et al.*, 2019; Lédée *et al.*, 2021a; Perryman *et al.*, 2022). Sharks and rays display a wide variety of behaviour that can go from solitary migrations among white sharks (*Carcharodon carcharias*) (Findlay *et al.*, 2016; Schilds *et al.*, 2019; Anderson *et al.*, 2021) to more reef-associated species, like the blacktip reef sharks (*Carcharhinus melanopterus*) (Mourier, Vercelloni

and Planes, 2012) or ambush predators, like the spotted wobbegong (*Orectolobus maculatus*) (Armansin *et al.*, 2016). Within these associations, elasmobranchs can interact with other individuals with which they share common features. Elasmobranchs associate with individuals of a similar size or sex because they are likely to have similar dietary needs or because they can protect themselves from aggressions from larger individuals (Findlay *et al.*, 2016). For example, a previously believed unique population of blacktip reef sharks has been shown to be composed of four distinct communities (Mourier, Vercelloni and Planes, 2012). Individuals within communities display tighter associations within the community rather than between. The community had a heterogeneous demographic structure, but it has been shown that within the communities, individuals of similar sex and size tend to associate more frequently with each other (Mourier, Vercelloni and Planes, 2012). Overall, the study demonstrated that individuals associate in distinct communities due to active choice rather than passive encounters, and food availability has been hypothesised to be the primary driver of associations in the area (Mourier, Vercelloni and Planes, 2012). White sharks exhibit a more solitary life history but are known to form aggregations at feeding sites, mainly driven by food availability and favourable water temperature (Anderson *et al.*, 2021). A study on adult white sharks in South Africa showed that individuals show non-random co-occurrences during these aggregations, and some communities can be formed. In this case, the pattern of aggregations is sex-dependent, with males reducing their abundance and their associations at the feeding site when females peak their abundance (Schilds *et al.*, 2019). It has been hypothesised that females, being larger than males, could outcompete them in the exploitation of resources, leading males to use the area at a different time of the year (Schilds *et al.*, 2019). Aggregations at these "feeding events" may benefit juveniles by facilitating the transfer of knowledge about prey locations and feeding strategies from older sharks to younger ones (Anderson *et al.*, 2021). Associations in communities may not be ideal for small ambush predators, like wobbegong, in which large groups can increase the cost associated with feeding (Armansin *et al.*, 2016). Despite that, there is evidence of non-random and repeated associations in these populations that can last in time. In this case, the persistence of some associations may reduce the occurrences of aggressive competition with neighbouring sharks. Moreover, in periods with high shark density, individuals tend to re-establish bonds with others they are already familiar with. The authors hypothesise that this probably occurs because keeping interactions with familiar individuals is comparatively less costly than establishing new relationships with each aggregation event (Armansin *et al.*, 2016).

Among cetaceans, toothed whale social systems are more heterogeneous and can be more structured than baleen whales (Rendell *et al.*, 2019). Toothed whale social networks are characterised by dense connections across the entire population and quick fission-fusion dynamics (groups of individuals frequently breaking up and reforming, depending on the context (Ritz *et al.*, 2011; Weiss, Ellis and Croft, 2021). The drivers of associations and factors that shape the community structure could differ depending on the species and the environment (Weiss, Ellis and Croft, 2021). In the case of toothed whales, size does not have an evident role in shaping social communities within the same species. Where sexual dimorphism is evident, males are usually larger than females, and thus, they may pose a risk of harassment for females, leading to sexual segregation. However, this is not always the case. For example, in bottlenose whales (*Hyperoodon ampullatus*), even though males are 13% larger than females, there is no evidence of sexual segregation, as males do not manifest aggressive behaviour towards females (Weiss, Ellis and Croft, 2021). On the contrary, species mating systems have been highlighted as potentially leading to sexual segregation. In the case of Indo-Pacific Bottlenose dolphins (*Tursiops aduncus*), males form small groups to cooperate and monopolise females, which, on the other end, associate together and tend to actively avoid males to reduce the risk of harassment (Galezo, Krzyszczyk and Mann, 2018; Weiss, Ellis and Croft, 2021). Individual behavioural phenotypes also play an interesting role in population structure. In Moreton Bay bottlenose dolphins (*T. aduncus*), individuals with a higher tendency to interact with trawl fishery formed a different community compared to individuals who do not display the same behaviour (Weiss, Ellis and Croft, 2021). Maintaining social interactions is an expense of energy; therefore, keeping social bonds with individuals who share a similar behaviour is advantageous as it facilitates cooperation for feeding and transmission of information within groups that share similar foraging methods (Methion and Díaz López, 2020).

Fewer studies have focused on teleost social systems than marine mammals or elasmobranchs, especially in their natural environment (Wilson, Croft and Krause, 2014; Lilly *et al.*, 2020; Villegas-Ríos, Jacoby and Mourier, 2022). Initially, those studies mainly focused on the behavioural ecology of smaller fishes that could be reared in laboratory conditions or observed in manipulative field experiments (Wilson, Croft and Krause, 2014; Lilly *et al.*, 2020; Villegas-Ríos, Jacoby and Mourier, 2022). In fish that move in groups, the maintenance of cohesion and coordination among individuals is essential, as this behaviour improves shoal movements and reduces energy expenditure (Aivaz and Ruckstuhl, 2011; Ward, Kent and Webster, 2020). Laboratory

experiments on the zebrafish (*Danio rerio*) showed that groups of similar-sized individuals have a higher degree of synchronicity compared with groups of odd-sized individuals (Aivaz and Ruckstuhl, 2011). Moving with individuals of similar size facilitates coordination and enhances the confusion effect under the threat of predators (Jordan *et al.*, 2010; Ritz *et al.*, 2011; Ward, Kent and Webster, 2020). Moreover, similar-sized fish tend to associate with each other to reduce the risk of aggression from larger individuals and to exploit food resources that would otherwise be consumed by higher-ranking individuals in hierarchical groups (Jordan *et al.*, 2010; Ward, Kent and Webster, 2020). Like sharks, fish can also choose to associate with individuals with which they are familiar. Grouping with familiar individuals reduces the risk of aggression and competition, allowing the individual to save more energy for other activities, such as searching for food or mating (Jordan *et al.*, 2010; Ritz *et al.*, 2011; Ward, Kent and Webster, 2020). In laboratory and manipulative field experiments, solitary individuals of humpback damselfish (*Dascyllus aruanus*) received significantly less hostility when re-joining a familiar group compared to a new one (Jordan *et al.*, 2010). The role of sex presents more nuances, and so it is more complex to analyse. Similarly to some marine mammals, when sexual dimorphism is evident, like in guppies (*Poecilia reticulata*), females tend to shoal in the same groups to reduce the risk of harassment by males (Ward, Kent and Webster, 2020). Despite the absence of sexual dimorphism, males and females of common minnows (*Phoxinus phoxinus*) use different parts of their habitats, even outside of the breeding seasons, leading to social sexual segregation (Ward, Kent and Webster, 2020). Sub-adult three-spine sticklebacks (*Gasterosteus aculeatus*), on the other hand, usually associate with individuals of the other sex under low-predation risk, but this behaviour changes under threat of predations, possibly to reduce the cost of behavioural asynchronicity derived from grouping with individuals of the opposite sex (Rystrom *et al.*, 2018; Ward, Kent and Webster, 2020).

2) HOW TO STUDY MARINE MOVEMENTS AND AGGREGATIONS

The intrinsic nature of the aquatic environment has always caused difficulties in studying the movements and associations of marine organisms (Hussey *et al.*, 2015; Weiss, Ellis and Croft, 2021; Grémillet, Chevallier and Guinet, 2022; McInturf *et al.*, 2023). To study animal movements, direct observations from vessels, or even from land, have been the most frequent solutions (Grémillet, Chevallier and Guinet, 2022). Later, advances in technology allowed the use of underwater cameras that could be manoeuvred by divers or even remotely sometimes (Grémillet, Chevallier and Guinet,

2022). A recent and powerful tool in marine conservation and spatial ecology is the discovery of eDNA to study animal movements and dispersal in the water (Grémillet, Chevallier and Guinet, 2022). Despite the variety of the methodologies mentioned above, more than half of the studies on animal movements are based on electronic tracking data (e.g. satellite transmitters, GPS) and bio-logging (Grémillet, Chevallier and Guinet, 2022). Fine-scale and three-dimensional data on animal movements are some of the advantages provided by these new methodologies compared to simple positioning information (Grémillet, Chevallier and Guinet, 2022).

Aquatic telemetry requires the use of electronic tools (named "transmitters" or "tags") that are attached to marine animals (either externally or internally) and are capable of transmitting signals to different types of receiver stations (Hussey *et al.*, 2015; Matley *et al.*, 2022). Acoustic and satellite telemetry are the two most frequently used methods (Hussey *et al.*, 2015). Acoustic tags emit encoded signals detected by receivers deployed at sea, anchored on the sea bottom, or in specific vessels. In contrast, satellite tags transmit the information to orbiting satellites, which then relay the information to land-based receivers (Hussey *et al.*, 2015; Matley *et al.*, 2022). Acoustic receivers have a maximum detection range of 1km, constraining their use mainly in coastal and estuarine regions, where receivers can be deployed and retrieved to download the movement data. Satellite tags are usually bigger and therefore limited to larger aquatic animals, but they may transmit information on the depth, temperature, and location of animals that travel many kilometres, especially those far from the coast, where acoustic receivers are harder to deploy and service (Hussey *et al.*, 2015; Matley *et al.*, 2022).

Network Analysis is a well-established method that has been proven very useful in studying social and spatial patterns within animal populations (Jacoby and Freeman, 2016; Lilly *et al.*, 2020; Villegas-Ríos, Jacoby and Mourier, 2022). This type of analysis relies on graph theory, a branch of mathematics that allows the quantification of pairwise relationships between objects in the form of a network. In this context, the objects are called "nodes" or "vertex," and their relationships are called "edges" (Jacoby and Freeman, 2016). Acoustic telemetry can detect animals in their environment through correlative measures (e.g., presence/absence data) (Jacoby and Freeman, 2016). This information can then be converted into a quantitative measure such as the "strength" of social bonds (edges) between individuals (nodes) (Farine and Whitehead, 2015; Psorakis *et al.*, 2015; Lilly *et al.*, 2020), or the "degree" of connectivity/movements (edges) between geographical locations (nodes) (Jacoby *et al.*, 2012; Jacoby and Freeman, 2016). The possibility of

adopting node-based or network-based metrics helps explore the role of nodes within the network or understand the broader structural properties of the network itself (Farine and Whitehead, 2015; Jacoby and Freeman, 2016).

3) ARGYROSOMUS REGIUS MIGRATIONS

The Meagre (*Argyrosomus regius* – Asso 1801) is one of the largest members of the Sciaenidae family (Prista, 2013). It may attain over 180cm in total length and around 50 kg of weight (Prista, 2013). It has fast growth and high fecundity (Haffray *et al.*, 2012; Prista, 2013), making it a valuable species for small-scale commercial fisheries and aquaculture (Prista, 2013). It is a coastal and semi-pelagic species, with a geographical distribution extending along the eastern Atlantic Ocean from Norway until the Gulf of Guinea, the Mediterranean Sea, the Black Sea, and the Gulf of Suez (González-Quirós *et al.*, 2011; Haffray *et al.*, 2012). This species is known to form spawning aggregations in estuarine and brackish water at six main sites: the Gironde (France), Tejo (Portugal) and Guadalquivir (Spain) along the European Atlantic coast, the Banc d'Arguin (Mauritania) in the African Atlantic Coast; the Nile (Egypt) and the Menderes (Turkey) deltas in the Mediterranean Sea (González-Quirós *et al.*, 2011; Haffray *et al.*, 2012). Reproduction occurs mainly at these sites as they accomplish the fundamental requirements for larval recruitment and juvenile growth (Haffray *et al.*, 2012). Meagre forms spawning aggregations (González-Quirós *et al.*, 2011), which can be defined as “transient” (Domeier, 2012) as they occur during a specific portion of the year, usually from March to August, considering the population spawning in the Guadalquivir estuary (González-Quirós *et al.*, 2011; Morales-Nin *et al.*, 2012). During these aggregations, males produce species-specific sounds for their courtships with females (Lagardère and Mariani, 2006). The seasonal pattern of transient spawning aggregations makes them highly predictable and, therefore, vulnerable to unregulated fishing (Domeier, 2012; Molloy, Côté and Reynolds, 2012). Furthermore, transient spawning aggregations may represent the total reproductive effort of the individuals involved (Domeier, 2012; Molloy, Côté and Reynolds, 2012). These features, together with their life-history traits: late first reproduction (seven years old) and long generational interval (> 40 years), make this species particularly vulnerable to overexploitation (González-Quirós *et al.*, 2011; Haffray *et al.*, 2012; Prista, 2013). Genetic studies on meagre have shown high genetic differentiation between the Atlantic and European populations (Haffray *et al.*, 2012; Almeida *et al.*, 2022; Abecasis *et al.*, 2024a), and, more recently, within the Atlantic populations, clearly divided into four distinct subpopulations, depending on

the spawning site: Gironde, France; Tejo, Portugal; Guadalquivir, Spain; Banc D'Arguin, Mauritania (Almeida *et al.*, 2022; Abecasis *et al.*, 2024a).

A general pattern of seasonal movements can be hypothesised concerning the population inhabiting the Iberian Peninsula Atlantic coast based on results from recent studies (González-Quirós *et al.*, 2011; Gandra *et al.*, 2024). Adult meagre approach coastal and shallow waters during spring, thanks to favourable water temperatures (>20 °C) to spawn near the Guadalquivir estuary (González-Quirós *et al.*, 2011; Morales-Nin *et al.*, 2012; Winkler *et al.*, 2023). There are still uncertainties around the precise spawning mechanism, and it has also been hypothesised that meagre spawning aggregations could occur outside estuarine waters (Abecasis *et al.*, 2024b). After spawning, individuals leave the spawning areas and start migrating along the coast. Favourable water temperatures could likely trigger the migration during the summer months and the possibility of reaching highly productive areas along the Vicentine coast (SW Portugal) (Garel *et al.*, 2024). Once there, individuals cross the St. Vincent cape (Sagres, Portugal), and there is evidence of fish aggregations along the Southwestern Portuguese coast (Sudoeste Alentejano and Vicentina Coast Natural Park). At this point, as highlighted in the previous studies using satellite telemetry, some fish keep the migrations until Lisbon and slightly beyond. In contrast, some of these individuals seem to migrate back and possibly spend the overwintering months in the Gulf of Cadiz (Gandra *et al.*, 2024).

4) AIM OF THE THESIS

With the current study, we aimed to complement results from (Gandra *et al.*, 2024) using a network analysis technique applied to the acoustic telemetry data coming from adult meagre tagged in Southern Portugal. Network analysis will allow us to display: 1) which locations along the southwest coast of Portugal display a higher rate of movement compared to others, possibly representing critical habitats during the migration; 2) which locations show high residency of adult meagre throughout the study period; 3) whether the aggregations observed at some locations are significantly different from what could be expected from random, which may indicate a prerequisite for more complex interactions, as observed in other marine taxa.

MATERIAL AND METHODS

1) GENERAL INFORMATION

a. Fish capture and tagging

Between 20/09/2018 and 30/07/2021, a total of 39 individuals were captured and tagged using acoustic transmitters (Innovasea® V16-5x model; 162 dB power output, 60s to 120s nominal delay and expected lifetime of 1292 days). The average size of the individuals was 128.6 +/- 12.64 cm, with the largest individual being 142 cm total length (TL) and the smallest 70 cm TL. All the individuals were caught in a tuna trap, a large, uncovered pound net off Fuzeta, on the southern coast of Portugal. The exceptions were two individuals captured and tagged in the Tejo estuary near Lisbon (Portugal) using a rod and reel. After capture, individuals were placed in an inverted position on a soft stretcher, and a continuous seawater flow through their mouths and gills was provided to reduce stress. A small incision on their ventral region was performed, and an acoustic transmitter was implanted in the abdominal cavity. The incision was closed after the insertion of the tag using absorbable sutures (BBraun, Novosyn). Tag performance tests performed before the study showed a detection range of around 800m. The capture and the tagging of the individuals were authorised by the ICNF (Instituto de Conservação da Natureza e Florestas) permits 560/2018/CAPT and 143/2019/CAPT for the capture, tag and release of wild fish and DGAV (Direção Geral de Alimentação e Veterinária) permit 0421/000/000/2018 (29/08/2018) to perform experiments with live animals.

b. Acoustic receiver deployments

Acoustic receivers (model VR2W - Innovasea, Canada) were used to monitor the presence of the tagged individuals. The study area extended from the Gibraltar Strait until the Tejo (Lisbon, Portugal) estuary, encompassing 128 receiver stations. Due to the large extension of the geographic region, the receiver stations were grouped into 12 receiver arrays to facilitate the subsequent network analysis. The arrays are named APPA (5 stations), Arrabida (28 stations), Guadalquivir (4 stations), Guadiana (4 stations), Lagos (1 station), Sado (2 stations), Sagres (25 stations), Sines (6 stations), Tejo (27 stations), Tuna-Trap (21 stations), West-Coast North (2 stations) and West-Coast South (3 stations). The acoustic receivers were deployed thanks to the collaboration of several projects, and acoustic detections were managed and downloaded from the European Telemetry Network (ETN) database.

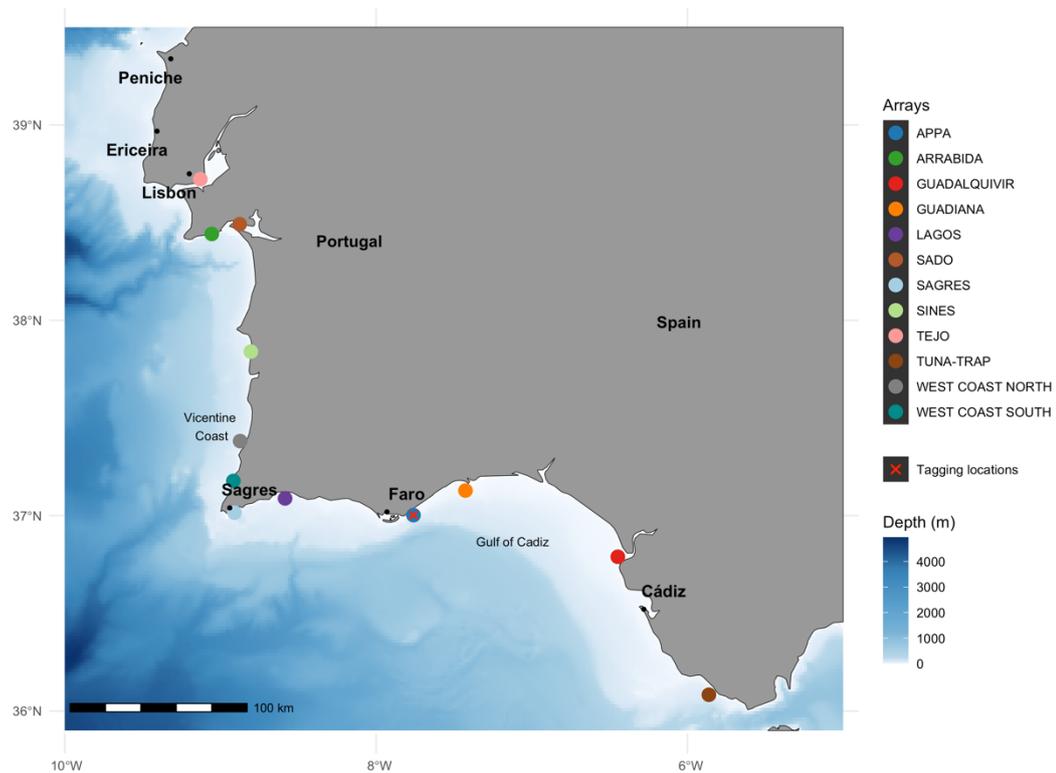


Figure 1- Study area (SW, Iberian Peninsula) and locations of the arrays used in the study. The red cross represents the tagging locations of all but two individuals that were tagged in the Tejo estuary.

2) SPATIAL NETWORK ANALYSIS

The spatial network analysis was conducted using R Statistical Software (v4.3.2; R Core Team 2023). Network and data visualisations were made using R packages *ggplot2*, *ggraphs*, *sf*, *marmap* and *ggOceanmaps* (Pante, Simon-Bouhet and Irisson, 2023; Pebesma *et al.*, 2024; Pedersen and RStudio, 2024; Wickham *et al.*, 2024; Vihtakari, Bivand and Wickham, 2024).

a. Residency index

To investigate the space use patterns of the meagre, residency indexes were estimated (Kraft *et al.*, 2023). The total number of unique days each fish was detected at each array was counted (Dd). We measured the monitoring interval (Dt) for each individual by considering how many days the array was available, ranging from the day of tag deployment (or receiver deployment if later) until the date of expected tag death (or receiver retrieval if earlier). This led to a unique monitoring interval for each combination of ID and array. The deployment period of the West-Coast North array was estimated considering the day of the first and last detections at one of its stations (Tel_036), as the data on the actual deployment period of this array were not available. For the

array of Guadalquivir, Guadiana, Tejo, and Tuna-Trap, there were discontinuities in the availability at sea of the stations composing the array. In this case, we have considered the actual period in which the array was available, manually removing days with no stations at sea for that array. The following formula has been applied:

$$I_r = \frac{Dd}{Dt}$$

The resulting value can range from 0 (no residency) to 1 (full residency) and expresses the proportion of times (in days) in which fish have been detected at the array level out of all the availability periods of the array. For each individual, we obtained the residency index at each array where the individual was detected. We then averaged the indexes of every individual at the array level to obtain an estimate of the average proportion of time fish spent at each array.

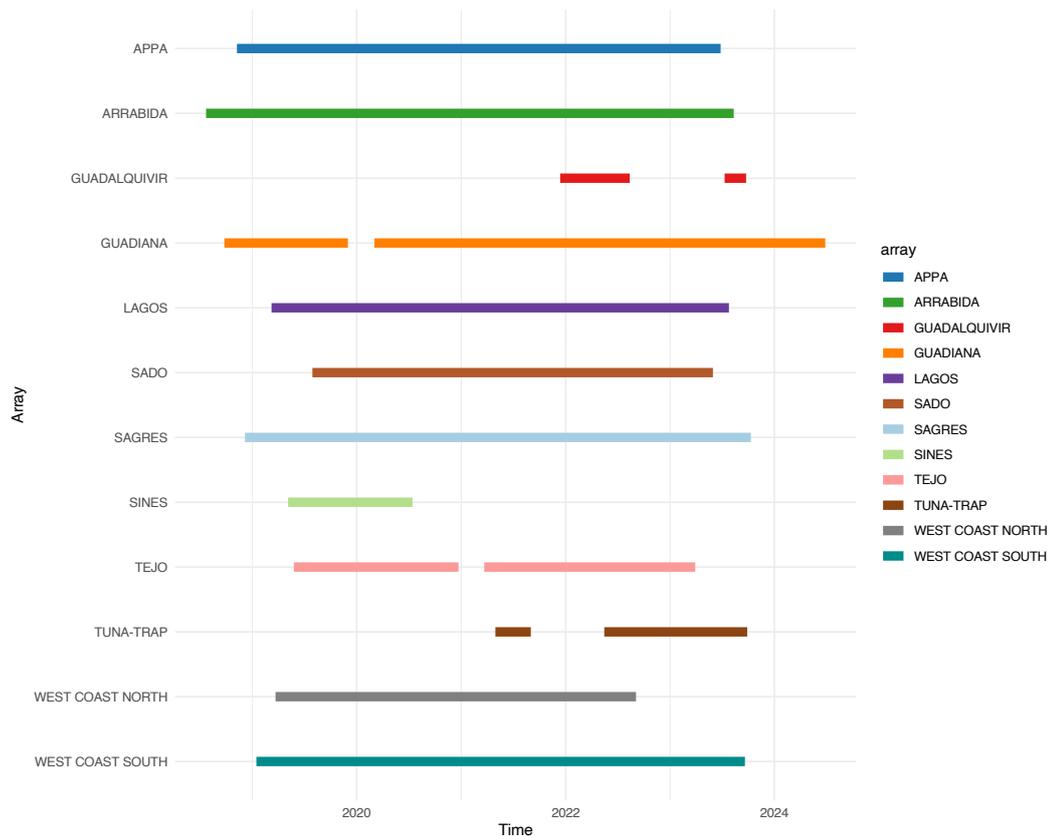


Figure 2 –Availability of the arrays in the study. Coloured lines represent the deployment period of the arrays considering the deployment of its single receiver stations.

b. Movement network

We followed procedures from the available literature to generate a movement matrix that was then used to obtain the spatial network (Jacoby *et al.*, 2012; Lea *et al.*, 2016; Perryman *et al.*, 2022). We counted the number of transitions the fish performed by looking at when they were detected at a new array throughout the study period. This procedure was applied without a temporal threshold to have a picture of the overall movement pattern that the individual follows moving along the coast. Each detection at a new array was considered a transition from the array where the individual was previously detected. This transition was counted as 1 in an $N \times N$ movement matrix, in which N represents the arrays in the study. After that, each cell in the movement matrix contained the number of transitions leaving from the $N^{th}(row)$ array and arriving at $N^{th}(column)$ array. The previous method provides the Absolute Movements of the individuals (Jacoby *et al.*, 2012). To obtain the Relative Movements, we divided each absolute movement by the total number of transitions measured in the matrix. The Relative Movements represent the proportion of transitions between two arrays relative to the total transitions in the network (Jacoby *et al.*, 2012). We obtained the spatial network from the relative movement matrix through the function "*graph_from_adjacency_matrix*" from the *igraph* package (Csárdi *et al.*, 2024). The graphical representation of the spatial network is composed of 1) nodes, represented by each array in the study; coordinates of the single stations have been averaged to generate one set of coordinates for each array; 2) edges are the observed connections between arrays and 3) edge weights are represented as the relative transitions (fish movements) between the arrays.

c. Null Models

In the spatial network analysis context, we wanted to test whether fish were migrating homogeneously between arrays along the coast or whether they utilised some areas more than what would be expected if movements occurred at random (Jacoby *et al.*, 2012). To verify that, we used the Coefficient of Variation (CV) of the transition counts in the movement matrix, which is the most common test statistic in social network analysis (Farine and Whitehead, 2015). This measure was obtained by dividing the relative movements matrix's standard deviation (σ) by its mean value (μ) (Farine and Whitehead, 2015). The logic behind this is that an observed CV higher than a random distribution of CVs obtained from permutations implies that some edge weights between nodes are higher than what would be expected if nodes were connected from random movements. Nodes in a spatial network represent locations in the physical space. Therefore, it would not be wise to

randomly re-allocate single transitions among all the nodes, as this could create connections that are very unlikely to be observed. For these reasons, a random movement network must preserve some structure of the observed spatial arrangement in the movement network (Jacoby *et al.*, 2012). To do that, we opted for randomising the single transitions only among nodes already connected between edges without creating new edges between arrays. We generated 10.000 random movement matrix, in which each node maintained its original edge, but edge weights resulted from random re-allocations of the single transitions in the movement matrix. For each random matrix, the CV was measured to generate a distribution of random CVs. The p-value was calculated by dividing the number of times the observed CV was smaller than the set of random CVs by the total number of permutations (Farine and Whitehead, 2015). A threshold of 97.5% has been chosen for a CV that is significantly higher than random (Lilly *et al.*, 2020).

d. Network metrics and node metrics

Network-level metrics give a broad view of the network structure and of the pattern of connectivity within the observed network. The number of nodes, the number of edges, and the edge density (the observed number of edges out of all the possible edges) belong to this category (Farine and Whitehead, 2015; Ospina-Alvarez *et al.*, 2020; Setyawan *et al.*, 2024). Node-level metrics are influenced by the degree (number of connections) that a node has in the network, and they are used to describe the role that each node has in the network and how it is connected to other nodes (Farine and Whitehead, 2015; Ospina-Alvarez *et al.*, 2020; Setyawan *et al.*, 2024). We used two node-level metrics to assess the role of the nodes in the network: Betweenness-centrality and Eigen-vector centrality. Betweenness is the number of times a node is included in the shortest path generated by every combination of two other nodes. Nodes with high betweenness are frequently involved as passages between distinct areas of the network, acting like a bridge between different groups of nodes (Farine and Whitehead, 2015; Ospina-Alvarez *et al.*, 2020). Betweenness centrality was calculated using an R function that considers edge weights as distances or costs. To convert edge weights into distances, we divided each edge weight by the average weight value (Farine and Whitehead, 2015; Ospina-Alvarez *et al.*, 2020; Setyawan *et al.*, 2024). Eigen-vector centrality indicates the level of connection of a node to other well-connected nodes. Nodes with high Eigen-centrality usually have either 1) a high number of connections (high degree) with other nodes or 2) strong connections with highly central nodes (Farine and Whitehead, 2015; Ospina-Alvarez *et al.*, 2020). In spatial network analysis, nodes with high Eigen-

centrality represent strategic areas that are well-connected to many other locations in the network and where individuals frequently return (Jacoby *et al.*, 2012). All the previous metrics were measured using the appropriate function from the package *igraph* (Csárdi *et al.*, 2024).

e. Community detections algorithm

There are situations in network analysis where networks display nodes that are highly connected within smaller sub-groups rather than showing a homogenous distribution of edges. These sub-groups are defined as communities within the network and can be identified using appropriate community detection algorithms (Ospina-Alvarez *et al.*, 2020). The modularity of a network is a measure that aims to evaluate if a community algorithm has identified communities that will divide the network into discrete modules (Finn *et al.*, 2014; Farine and Whitehead, 2015; Ospina-Alvarez *et al.*, 2020; Setyawan *et al.*, 2024). We used the "*cluster_optimal*" community detection algorithm to detect communities in this movement network (Setyawan *et al.*, 2024). The algorithm calculates the optimal community structure by maximising the modularity measure across all the possible partitions. The algorithm can be used for both directed and undirected networks, but in the case of directed networks it does not consider the directionality of the edge in the analysis (Pastor-Rollan *et al.*, 2024). The "*cluster_Infomap*" community detection algorithm is also feasible for spatial networks as it excels in identifying flow patterns in directed spatial networks, aiming to detect clusters of nodes with stronger connections between them (Pastor-Rollan *et al.*, 2024). Both community detection algorithms were estimated using the appropriate function from the *igraph* package (Csárdi *et al.*, 2024). The clusters obtained were then tested using the "*dCommSignif*" function from the *dnet* package (Fang and Gough, 2014). For each node in a community, the function measures the degree of connections within the community and compares it with the degree of connections outside the community. It then performs a two-sample Wilcoxon signed-rank test to evaluate whether the internal degree is significantly higher than the external degree (Fang and Gough, 2014). If the test returns a p-value less than 0.05, the community can be considered statistically significant, indicating that the algorithm has detected a "real" community with more internal connections than external ones (Finn *et al.*, 2014).

3) SOCIAL NETWORK ANALYSIS

The social network analysis was carried out using R Statistical Software (v4.3.2; R Core Team 2023). Network and data visualizations were made using R packages *ggplot2* and *ggraphs* (Pedersen and RStudio, 2024; Wickham *et al.*, 2024).

a. Definition of the study period

For the social network analysis, we needed acoustic detections to be normalised. For this reason, in the definition of the study period, we used a time interval in which all the individuals had an equal probability of being detected to avoid biased results for the social evaluations of co-occurrences. After visual observations of the dataset, we used the study interval from 28/09/2019 until 04/04/2022 (when the first tag stopped emitting signals). The detections of all the individuals tagged after 28/09/2019 were removed. By doing this, the detection for the social network analysis comes only from individuals tagged before 28/09/2019 and with the same probability of being detected from that date until 04/04/2022.

b. The Gambit of the Group Data

Our social network analysis aimed to evaluate where and when the individuals aggregated during the migrations along the South-West Coast of the Iberian Peninsula and whether these co-occurrences can be considered random. The definition of co-occurrence is based on the "Gambit of the Group assumption", which posits that individuals have the possibility to associate if they are found to be in enough spatial and temporal proximity to one another (Farine and Whitehead, 2015; Psorakis *et al.*, 2015; Lilly *et al.*, 2020; Anderson *et al.*, 2021). The approach mentioned above requires the definition of a temporal threshold within which, if at least two individuals are detected, we can assume they are co-occurring. This time interval is defined as the sampling period (Farine and Whitehead, 2015; Psorakis *et al.*, 2015; Lilly *et al.*, 2020; Anderson *et al.*, 2021). However, we point out that co-occurrence does not necessarily imply social interactions (Mourier, Vercelloni and Planes, 2012; Schilds *et al.*, 2019). We opted for a sampling period of one hour, as we considered it a reasonable time for individuals to co-occur in the same area, considering the spatial scale of our study. The same sampling period was used for another study on meagre (Gandra *et al.*, 2024) and a social network analysis on white sharks (Anderson *et al.*, 2021). Therefore, we considered all the detections of an individual occurring during the same hour at the same arrays as one single detection. Grouping of individuals in time and space was carried out using functions "*group_times*" and "*group_space*" from the

package *spatsoc* (Robitaille, Webber and Vander Wal, 2019). Animals were considered to co-occur in space and time if they were detected at the same array within the same hour. Co-occurring animals were allocated into the same group, and this information was used to generate a group-by-individual matrix using the function "get_gbi" from *spatsoc* (Robitaille, Webber and Vander Wal, 2019). The matrix of co-occurrences was used to measure the Simple Ratio Index (SRI) using the "get_network" functions from the package *asnipe* (Farine, 2013).

$$\text{SRI} = \frac{x}{x + y_{ab} + y_a + y_b}$$

The SRI represents the strength of the connections between individuals in an $N \times N$ adjacency matrix, in which N represents the number of individuals. It can range from 0 to 1, where 1 indicates individuals' high tendency to co-occur, and 0 indicates that individuals were never detected together during the same sampling period throughout the study. The number of sampling periods, where co-occurrences are scaled between 0 (individuals that were never observed together) and 1 (individuals that were always detected together), is represented by x . Y_{ab} is the total of sampling periods in which both meagre A and meagre B were detected, but at different sites, Y_a is the total of sampling period where only individual A was detected and Y_b is the total of sampling period where only individual B was detected (Farine and Whitehead, 2015; Psorakis *et al.*, 2015; Lilly *et al.*, 2020). We opted for the SRI over other indices (e.g., Half Weight Index) because the intrinsic features of acoustic data make them solid enough to hold the required assumptions to use these indices: the associations that are detected must be symmetric and accurate, the probability to detect one individual is the same regardless it is associated or not and, when one individual is detected during the observation period, one should be able to detect all individuals that it is associated with that time (Stehfest *et al.*, 2013; Lilly *et al.*, 2020; Anderson *et al.*, 2021). We obtained the social network from the adjacency matrix using the function "graph_from_adjacency_matrix" from the package *igraph* (Csárdi *et al.*, 2024). In the context of a social network, 1) individuals represent the network's nodes; 2) the edge between two individuals means that they were detected together at least within one sampling period, and thus they form a dyad; 3) social network's edges are unidirectional, and their strength is represented by the SRI (Farine and Whitehead, 2015).

c. Null Models

To test if the individuals aggregate more or less than what would be expected by chance, we need to compare a reliable test statistic that represents the observed network with the same test statistic from a set of permuted networks (Farine and Whitehead, 2015; Farine, 2017). The most applied test statistic for this type of analysis is the Coefficient of Variation (CV) of the SRI (Mourier, Vercelloni and Planes, 2012; Farine and Whitehead, 2015; Lilly *et al.*, 2020). This is a very powerful test statistic as it is independent of the size and can be used to compare different types of datasets. The p-value is measured by dividing the number of times the observed CV is smaller than the set of random CVs by the number of permutations (Farine and Whitehead, 2015). Pre-network, or data-stream, randomisations are usually preferred over network permutations (node-level permutations or edge-permutations), as they preserve some features of the original dataset, like the number of times individuals were seen and the number and size of groups (Farine, 2013, 2017; Farine and Whitehead, 2015). The package *asnipe* was used with the default "*network_permutation*" function. We opted for swapping individuals between different groups (the randomisations are applied on the group-by-individual matrix) within the same day and array of detections to preserve some aspects of the original dataset (Farine, 2013, 2017; Farine and Whitehead, 2015). The number of permutations was increased by 10.000 iterations over each run until the p-value stabilised at 60.000 iterations (Stehfest *et al.*, 2013; Lilly *et al.*, 2020). This process allowed us to generate a set of random association matrices, and then the random CVs were compared with the observed CV. The Null Hypothesis tested was that "individuals encounter each other with a random pattern"; thus, the observed CV should not significantly differ from the random ones under the Null Hypothesis. If the observed CV is greater than 97.5% (p-value < 0.025) of the random CVs, we can reject the Null Hypothesis and assume that our network displays co-occurrences that are "unlikely" to be observed by random chance (Mourier, Vercelloni and Planes, 2012; Farine and Whitehead, 2015; Farine, 2017; Lilly *et al.*, 2020).

d. Node-level metrics

To describe the role of the individuals involved in the social network analysis, we used the same centrality metrics applied for the spatial network, as they reflect the same features of the arrays also for the individual. Again, in this context, high Betweenness centrality represents those fish that connect distinct groups of individuals, acting as a bridge in the social network. Eigencentrality highlights those individuals with many connections with other

relevant fish in the network, possibly representing social hubs, which facilitate the transfer of information or diseases in the populations (Farine and Whitehead, 2015; Ospina-Alvarez *et al.*, 2020). Network metrics have been measured with the package *igraph* (Csárdi *et al.*, 2024).

e. Community detection algorithm

To detect communities in a social network, a study on tropical fish compared several algorithms, and three of them, Louvain (or Multilevel), Fast-Greedy, and Walk-Trap, yielded similar results and displayed comparable efficiency (Finn *et al.*, 2014). Additionally, undirected methods such as the Louvain or Fast-Greedy algorithms are particularly well-suited for analysing networks where the interactions between nodes lack inherent directionality, such as in social networks (Pastor-Rollan *et al.*, 2024). The Edge-Betweenness algorithm was also tested, as it should be well suited for identifying regions of the network that are sparser and attempting to include them in communities (Pastor-Rollan *et al.*, 2024). Applying multiple community detection algorithms and comparing their results is recommended before determining the most suitable one (Hernández-García *et al.*, 2024). Given each algorithm's strengths and limitations, our analysis includes all four algorithms (Louvain, Fast-Greedy, Walk-Trap, and Edge-Betweenness) to examine the network's community structure comprehensively. The communities were measured using the *igraph* package (Csárdi *et al.*, 2024). The significance of a community was assessed using the function "*dCommSignif*" from the package *dnet* (Fang and Gough, 2014). Like the spatial network, a p-value below 0.05 indicates a significant community (Finn *et al.*, 2014).

f. Mantel test

The Mantel test is a statistical test that detects whether there are correlations between two dissimilarity matrices (Farine and Whitehead, 2015). This type of test has been largely applied in many other Animal Network Analyses (Stehfest *et al.*, 2013; Anderson *et al.*, 2021; Winter *et al.*, 2021) to assess correlations between the association matrix (based on the SRI) and a matrix derived from different attributes of the individuals (e.g. sex, size or genetic relatedness) (Farine and Whitehead, 2015). The current analysis aimed to test if the presence of an edge between two individuals was positively correlated to the specific period in which the individual was tagged. The chosen explanatory periods were day, month, season, year, and whether the individuals were tagged within or outside the spawning season (considering a spawning period lasting from March until August (González-Quirós *et al.*, 2011)). Additionally, the same test was applied to detect

potential correlations between the presence of an edge between individuals and their body size (Stehfest *et al.*, 2013; Anderson *et al.*, 2021; Winter *et al.*, 2021). In this case, individuals were allocated to three different size classes defined by the mean length (128cm) and SD (12cm): small: <116cm (< mean – SD), medium: 116 – 141cm (mean +/- SD) and large: > 141cm (>mean + SD) (Winter *et al.*, 2021). Dissimilarity matrices were created, with cells filled either with 0 (if the individual has not been tagged in the same period/does not belong to the same size class) or 1 (if the individual has been tagged in the same period/belongs to the same size class (Farine and Whitehead, 2015)). The association matrix was converted into a binary matrix, as we were only interested in the presence of an edge. Pearson's product-moment correlation was used to test the correlation between the binary matrix obtained from the association coefficient and the dissimilarity matrix based on the explanatory variables (Farine and Whitehead, 2015). Significant correlations were considered when the p-value was lower than a threshold of 0.05 (Farine and Whitehead, 2015). The test was performed with 10.000 permutations using the function "*mantel*" from the *vegan* package (Oksanen *et al.*, 2024).

g. Assortativity analysis

Assortativity analysis aims to evaluate whether individuals who share some features (for example, sex, size, or also habitat preferences) have a higher tendency to be connected between them compared to other individuals in the network (Farine and Whitehead, 2015; Perryman *et al.*, 2022; Shizuka *et al.*, 2022). In our network, we wanted to test whether individuals who display a higher residency index in one area also have a higher tendency to be associated. To do that, we measured the observed weighted assortative coefficient (r_w^d) which depends on the spatial community membership of each individual (Perryman *et al.*, 2022). We allocated the arrays into the three spatial communities identified by the "*cluster_optimal*" algorithm, regardless of their significance, as they were the most representative of the actual spatial division of the study area: community 1, representing the arrays of Lagos, APPA, Guadiana, Guadalquivir, and Tuna-Trap; community 2 is represented by the array of Sagres, West-Coast South and West-Coast North and community 3 represented by Sines, Arrabida, and Tejo (Sado has been excluded as none of the fish were detected there). Given their locations, we referred to community 1 as the South Coast community and community 2 as the South-West community. The spatial membership of an individual to one of the three communities was determined based on the array where they exhibited the highest residency index. The goal was to determine whether individuals within the same spatial community aggregated more frequently with others from the

same community compared to those from different communities. To test our hypothesis, we used the “*assortment.discrete*” function, which returns: 1) the weighted assortativity coefficient (r_w^d), a value that quantifies the degree to which nodes having the same discrete attribute (e.g., membership in the same community) tend to be connected; 2) the standard error associated with the assortativity coefficient, 3) and a mixing matrix, which shows the distribution of the edges by category (in our study, the spatial membership). The function mentioned above belongs to the *assortnet* package (Farine, 2023). To test the significance of the assortment, we generated a permutation test by randomly shuffling the community membership among the individuals involved in the social network and measuring the assortativity coefficient from each permutation. A total of 10.000 permutations were applied (Perryman *et al.*, 2022). The p-value was calculated by dividing the number of times the observed assortativity coefficient (r_w^d) was smaller than the set of random coefficients by the number of permutations. The observed coefficient is considered significant if it is greater than 97.5% of the random coefficients.

RESULTS

1) PASSIVE ACOUSTIC TRACKING

Overall, the detection data was composed of 155.552 data points, corresponding to detections coming from 38 unique individuals as corvina #04 (23799) was re-captured a few months after its tagging, and its detection data were not considered. The resulting information consisted of Tag-metadata (Tag-ID, Individual Length (cm), Date of tagging and Date in which tags stopped emitting signals, day of the first and last detections, and an overall number of detections for each ID) and Receiver-metadata (date-time include the time of each detection in YY-MM-DD: HH-MM-SS, receiver-ID, Tag-ID, station name, acoustic project code, coordinates of the station and array at which the station belong). The first detections occurred on 07/12/2018, whereas the last were on 14/10/2023, leading the overall study period to spread across almost six years, or a total of 1092 unique days of detections. Of the 128 receiver stations available during the study period, we had detections from 106 unique stations. The only array from which we have no detections is the array of Sado, as receiver stations Sado 2 and Sado 4 never detected individuals while they were deployed.

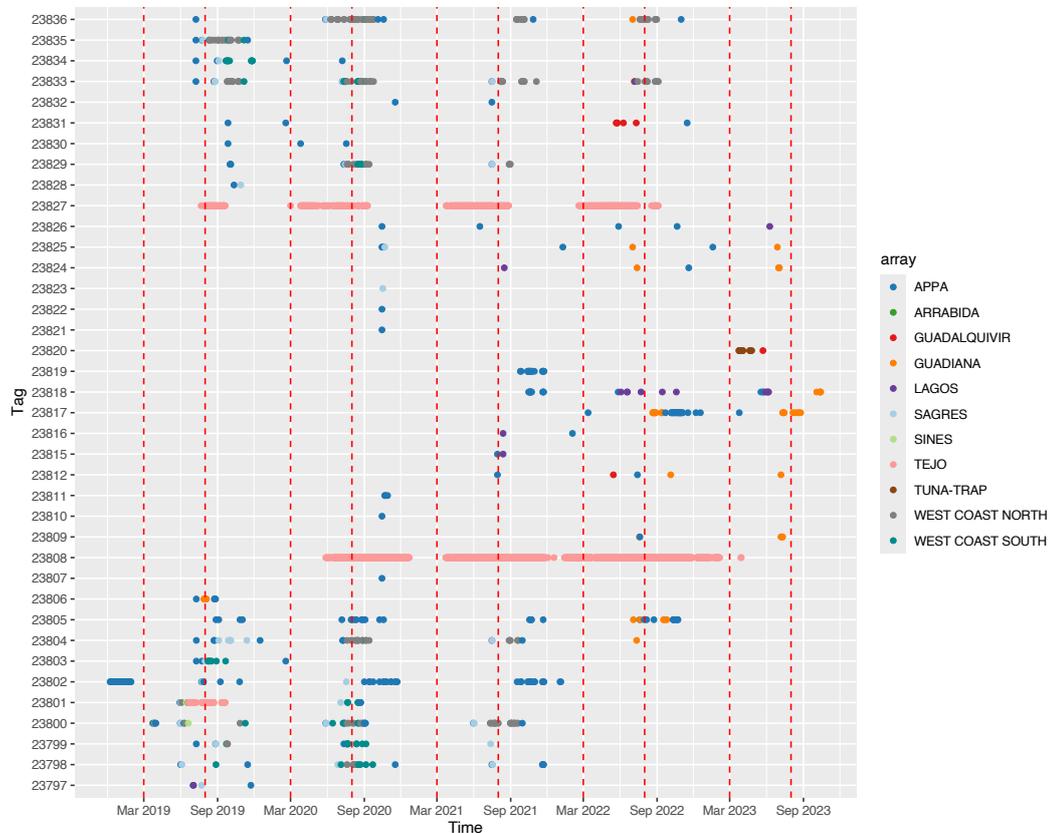


Figure 3 – Coloured dots represent unique days of detection of an individual at that array. Red vertical dotted lines represent the start and end of the spawning season, ranging from March until August.

2) SPATIAL NETWORK ANALYSIS

a. Residency index measurements

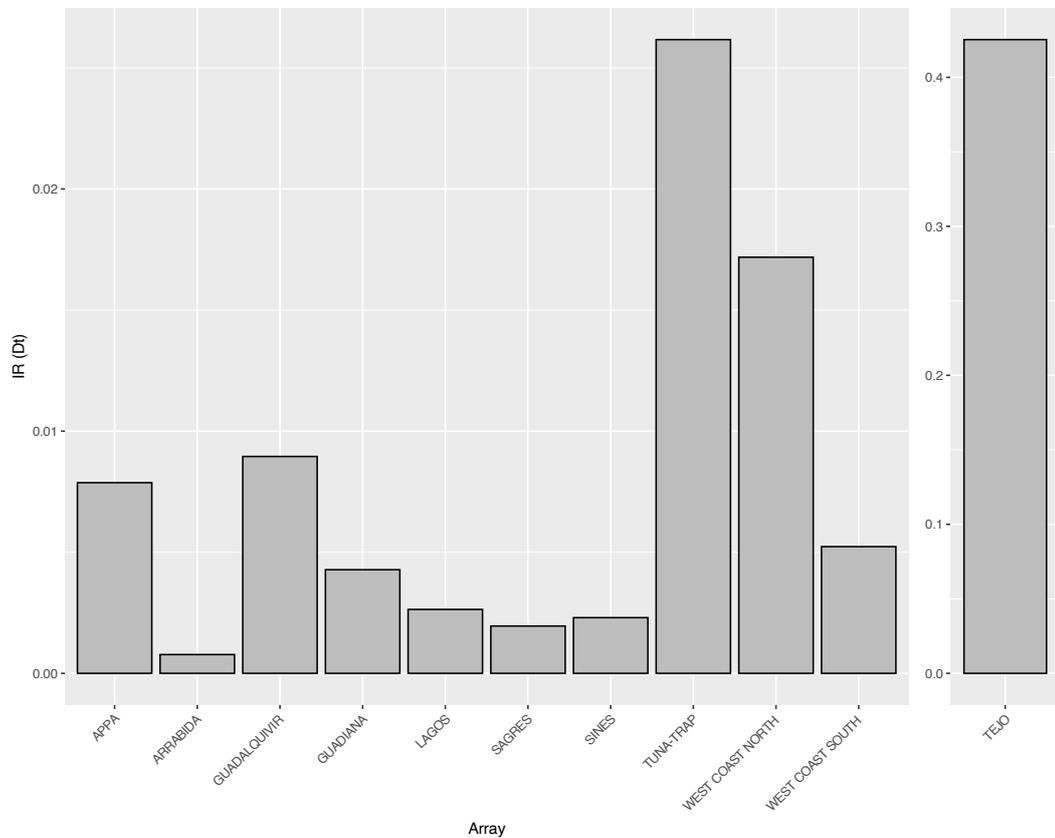


Figure 3 - Average residency index of each array for the entire study period.

Tejo displayed the highest residency index among all the arrays (0.425). Other than Tejo, the arrays of Tuna-Trap and West-Coast-North display a high residency index (0.026 and 0.017, respectively) compared to the other arrays (Figure 3).

b. Observed movement network

The overall movement network of the 38 detected individuals was composed of 12 nodes (the array stations) and 29 edges, corresponding to the observed connections between arrays, with a resulting edge density of 21.96%. The edges were composed of a total of 162 measured transitions between arrays, of which 89 (54,93%) involve the arrays of Sagres, West-Coast North and West-Coast South (Figure 5). With respect to the season, 103 transitions were observed during summer and 42 during fall (Figure 6).

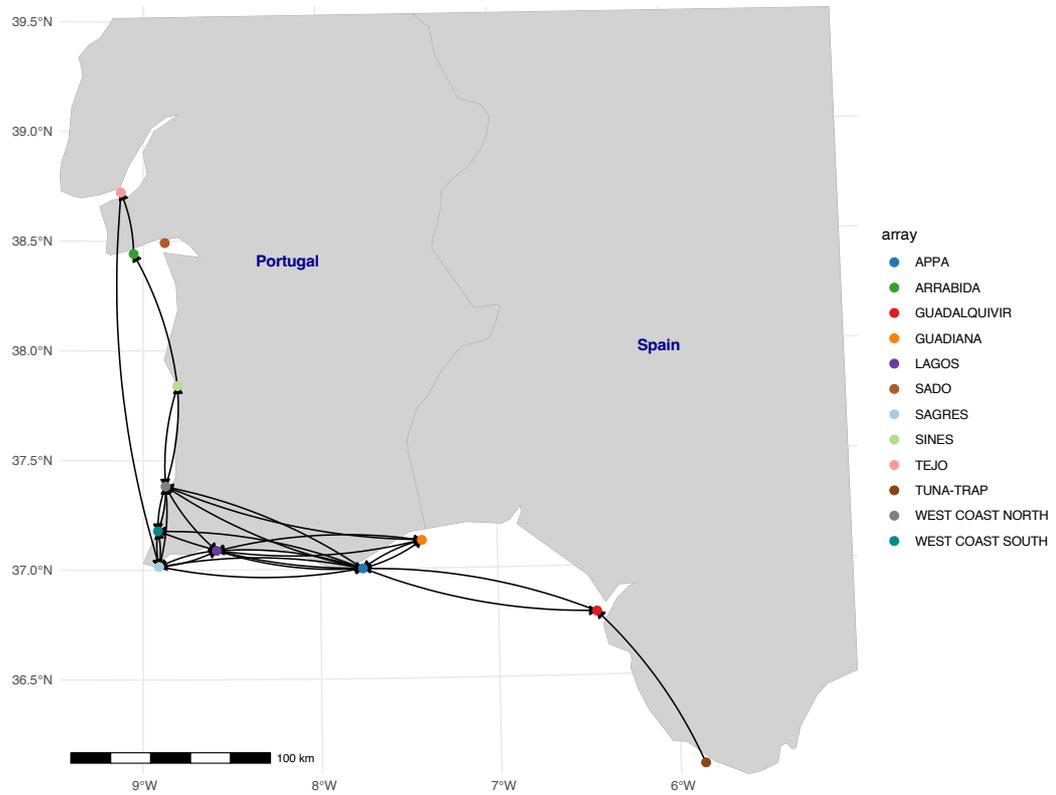


Figure 4 - Movement network showing the array location along the Portuguese coast and the connectivity between the different arrays.

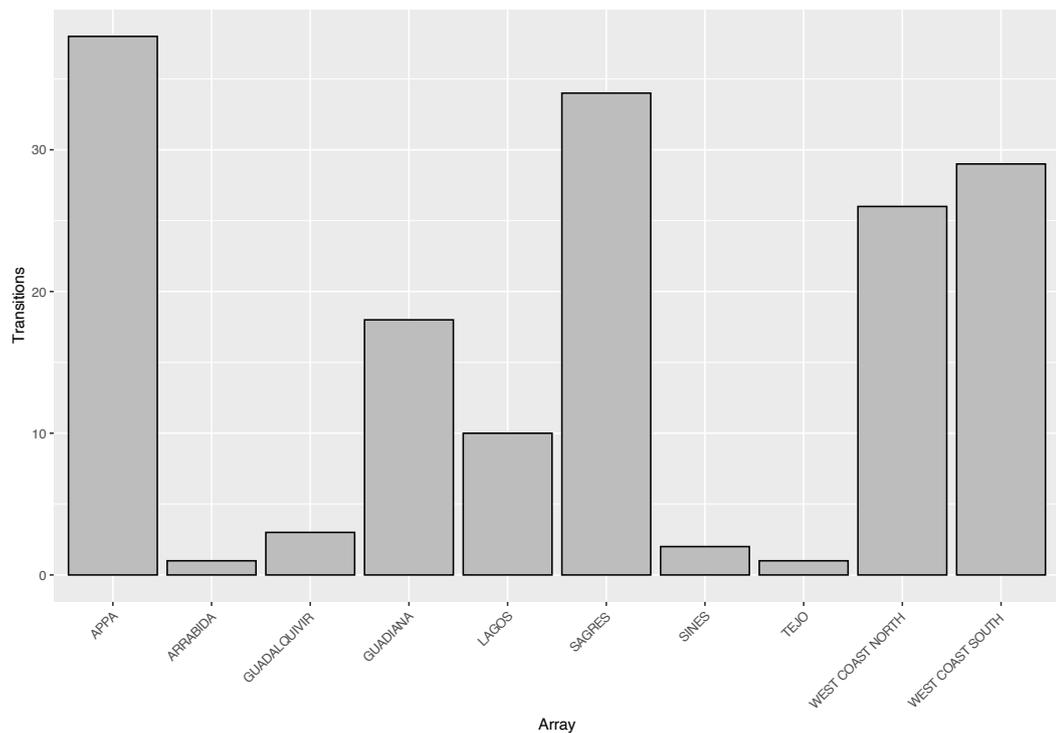


Figure 5 – Number of transitions occurring at each array

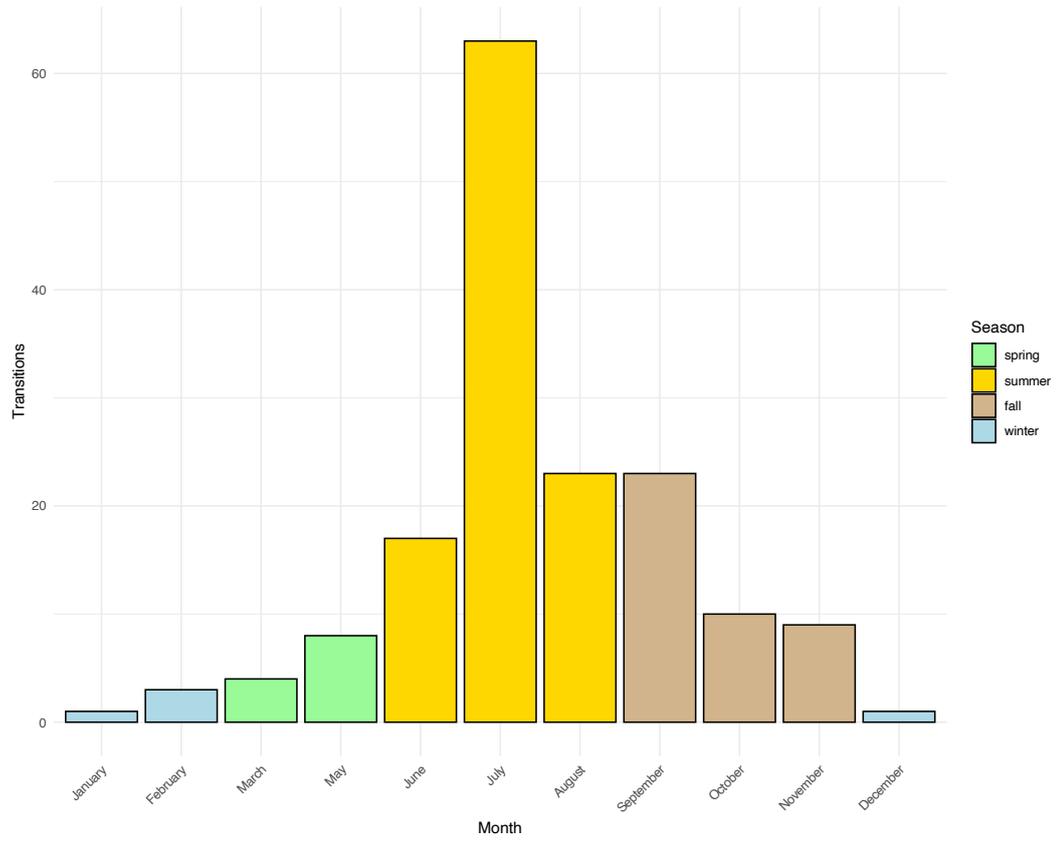


Figure 6 – Number of transitions for each month of the year.

c. Null models

The randomisation test suggests strong evidence that the observed CV (2.65) was significantly higher than what would be expected if movements between arrays occurred randomly (p-value = 0). This indicates that certain arrays played a more relevant role than others during the migrations of meagre along the coast (Figure 7).

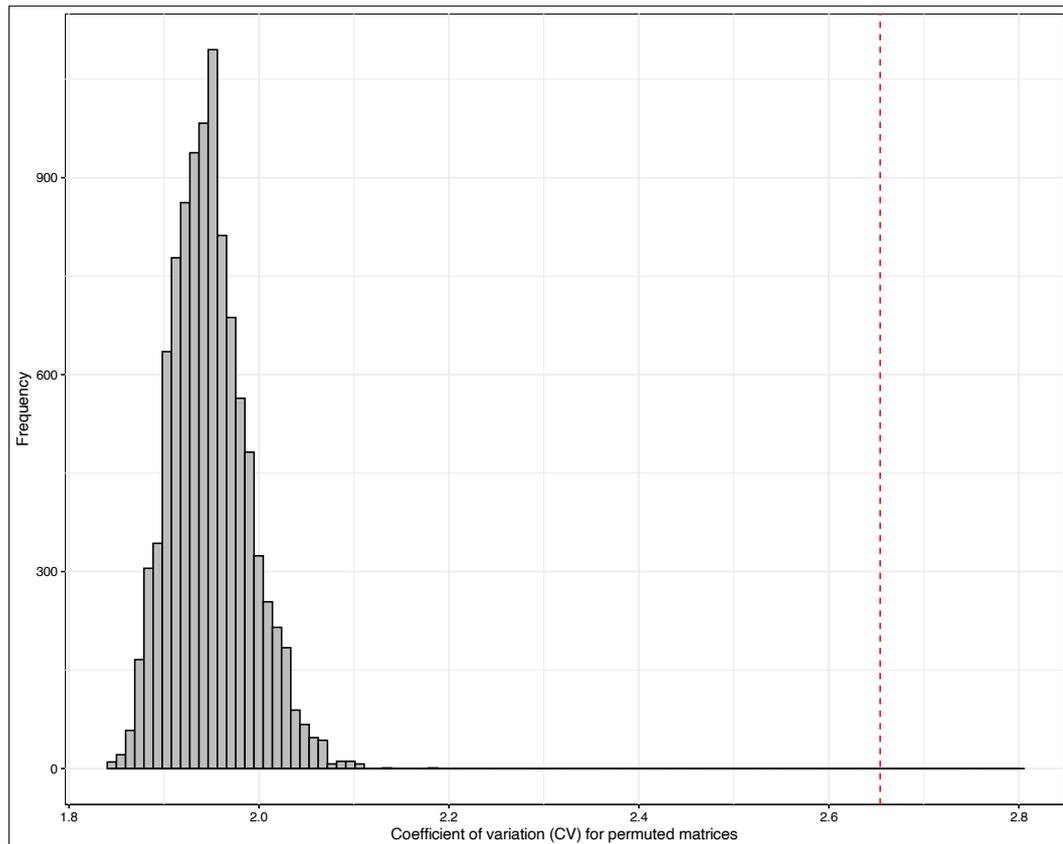


Figure 7 - Distribution of the random CVs obtained after the 10.000 permutations of the observed transition in the movement matrix. The observed CV is 2.65 (red vertical line).

d. Movement metrics

The arrays of APPA, Sagres and West-Coast North displayed the highest betweenness centrality (Table 1, Figure 8). This means that these nodes were frequently involved in the transitions of meagre between two distinct locations along their path. These nodes likely represent a “corridor” during the migrations from the southern coast towards the western coast of Portugal. The two main arrays of the West Coast (West-Coast North and South), Sagres and APPA, show a higher Eigen-Vector centrality (Table 1, Figure 9). These nodes can be considered the “core” of the movement network, meaning they are not only well-connected themselves but also connected to other highly connected nodes. This makes them relevant locations for meagre to access, and from where they can easily reach other favourable areas.

Table 1 – Values of Betweenness centrality and Eigen-centrality of the arrays in the movement network.

Arrays	Betweenness-centrality	Eigen-centrality
APPA	0.418	0.969
ARRABIDA	0.082	$2.086 * 10^{-3}$
GUADALQUIVIR	0.082	0.068
GUADIANA	0	0.561
LAGOS	0	0.318
SADO	0	$9.751 * 10^{-17}$
SAGRES	0.363	1
SINES	0.154	0.059
TEJO	0.073	$7.3 * 10^{-5}$
TUNA-TRAP	0	$9.751 * 10^{-17}$
WEST COAST NORTH	0.273	0.852
WEST COAST SOUTH	0	0.952

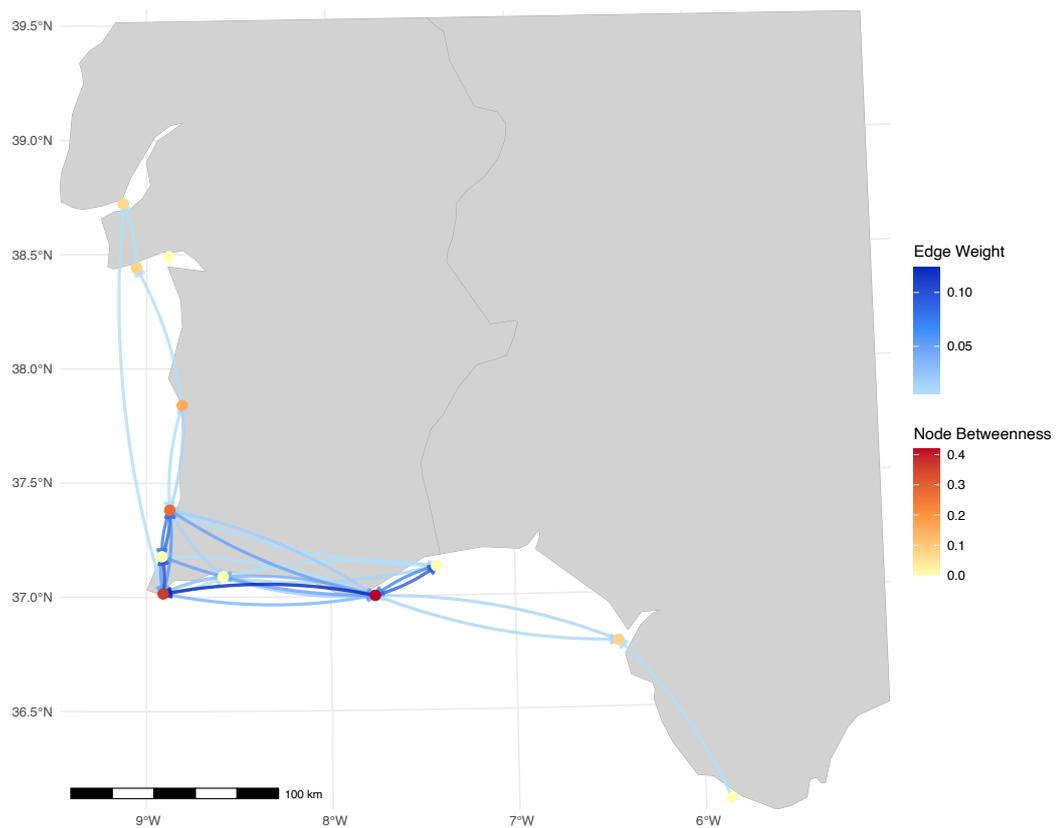


Figure 8 - Movement network displaying Betweenness-centrality. The node's colour intensity is proportional to the magnitude of the Betweenness-centrality.

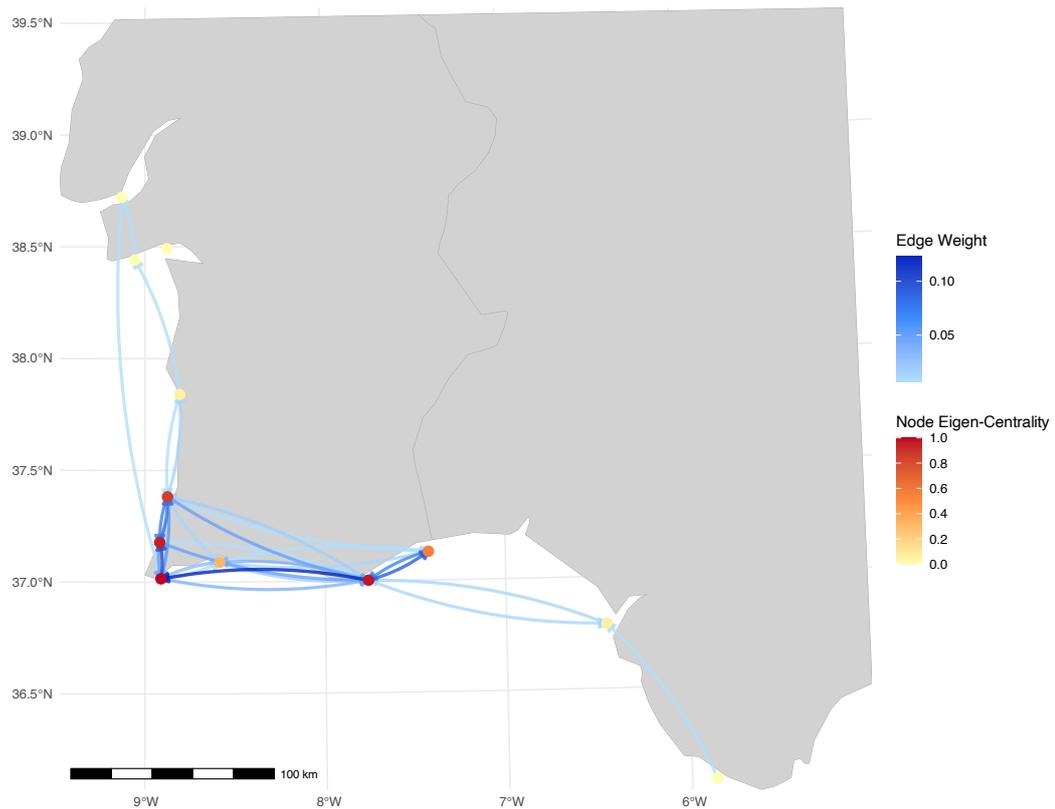


Figure 9 - Movement network displaying Eigen-centrality. The node's colour intensity is proportional to the magnitude of the Eigen-centrality.

e. Community detection algorithm

The Optimal community detection algorithm identified three distinct communities and yielded a modularity score of 0.15. Sado, not being connected to any nodes, was not included in any of the communities. The three major communities have a p-value > 0.05 (Appa, Guadiana, Guadalquivir and Tuna-Trap = 0.243 – Sagres, West-Coast South and West-Coast North = 0.658 – Sines, Arrabida and Tejo = 0.814) (Figure 10). The Infomap algorithm identified no communities in the movement network (modularity = 0). However, the unique cluster had a significant p-value ($2.52 * 10^{-5}$), implying an overall homogeneous distribution of the edges in the movement network (Figure 11).

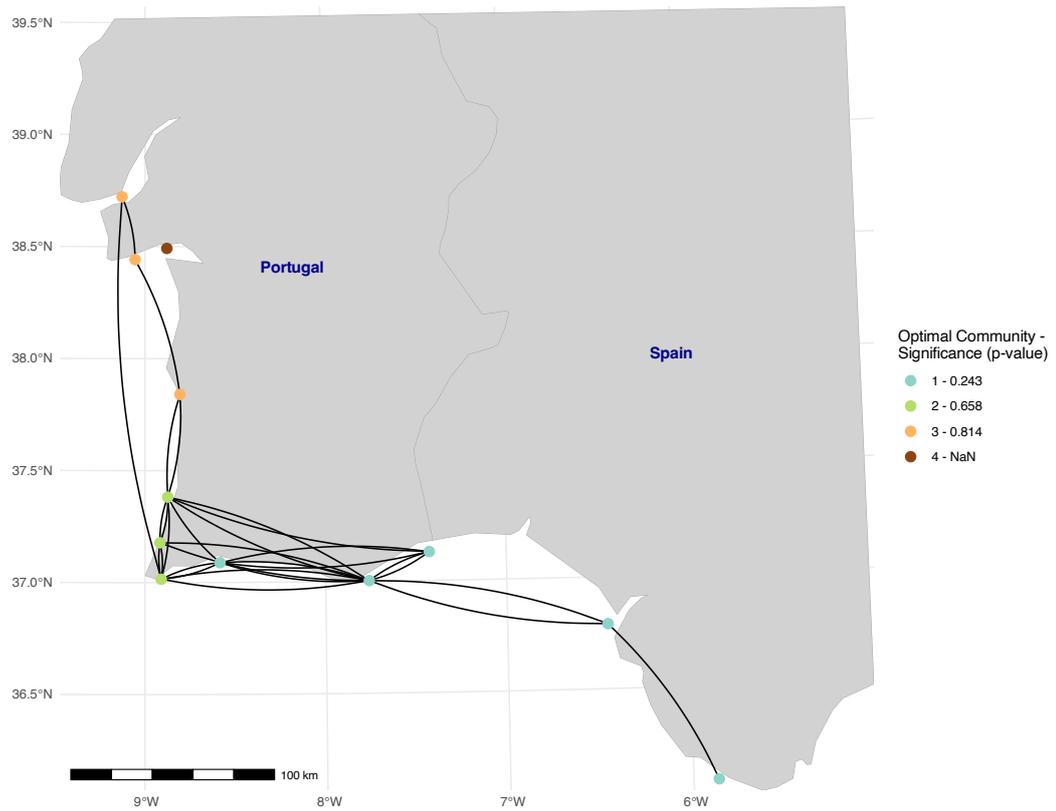


Figure 10 – Movement network with the three communities identified by the Optimal algorithm

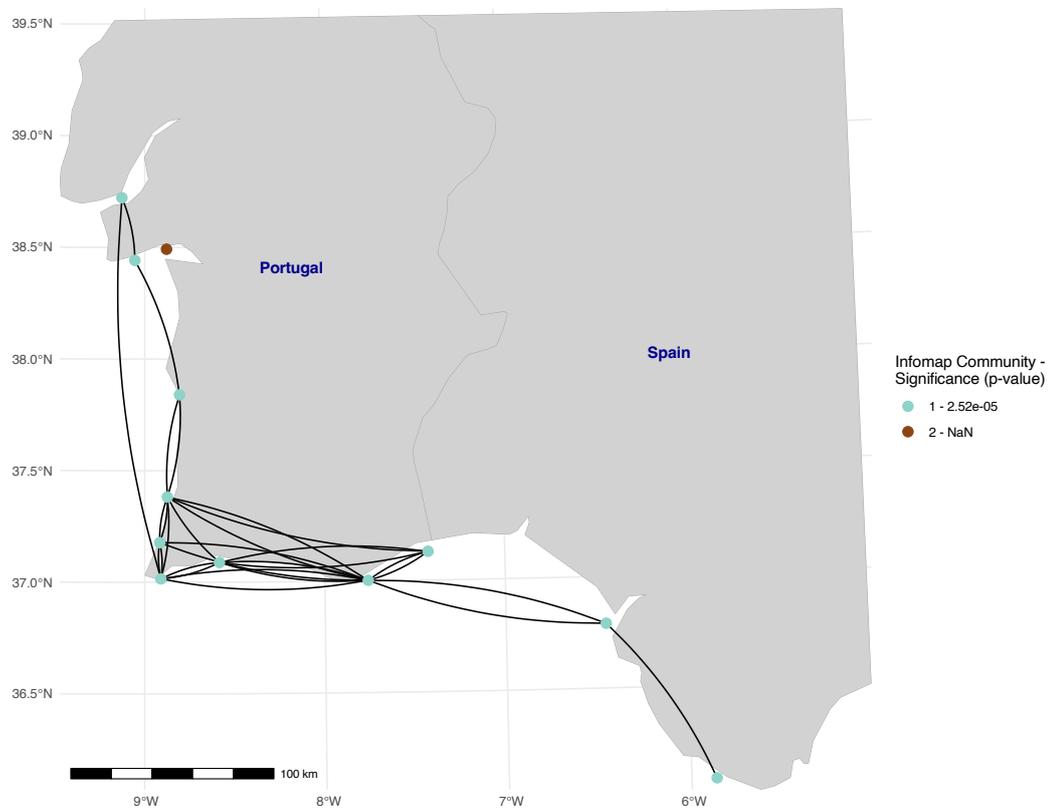


Figure 11 – Movement network with the unique community identified by the Infomap algorithm

3) SOCIAL NETWORK ANALYSIS

a. Selection of the study period

The normalized study period consisted of 391 unique days, with detections spread across almost three years. The final period encompassed 19 individuals for the Social Network Analysis. The number of unique days of detections for each individual ranged between 1 and 272 (for ID 23827, which remained within Tejo for the entire study period and, therefore, kept being detected by the receivers placed in the estuary).

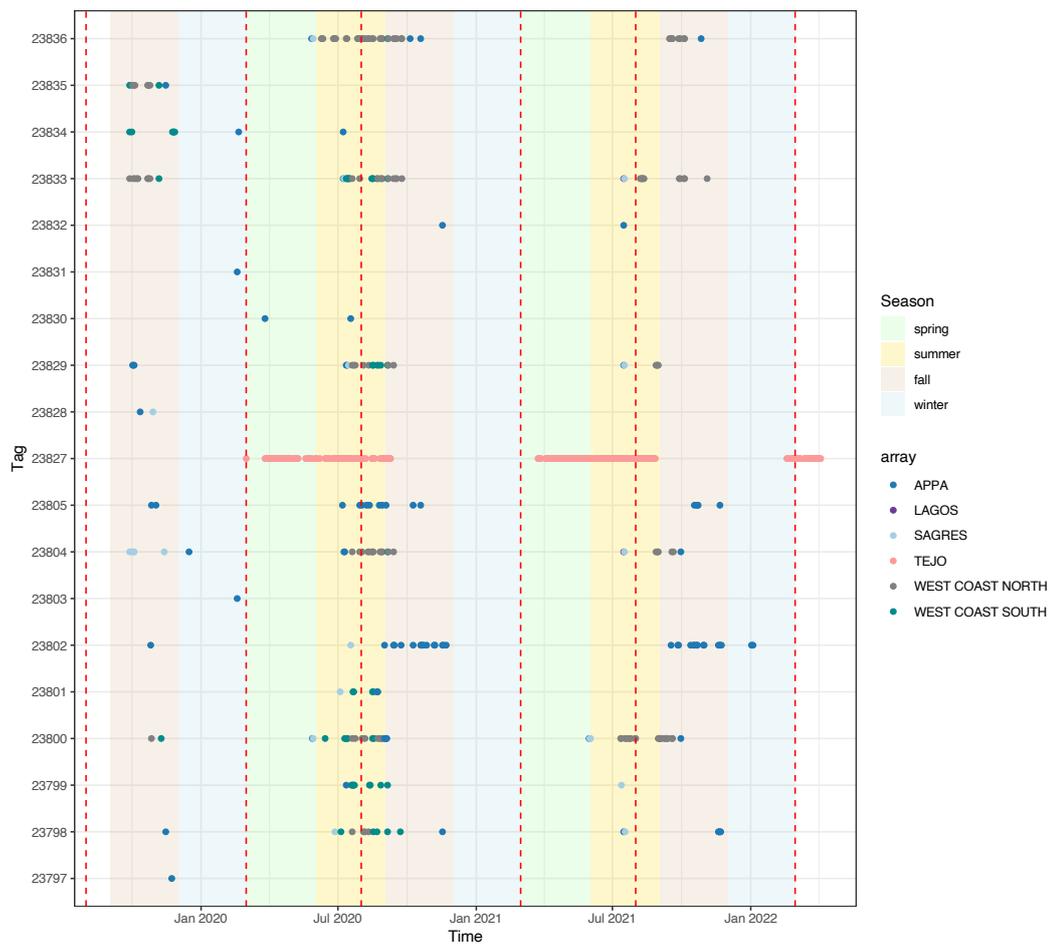


Figure 12 – Abacus plot showing the daily detection of the 19 individuals involved in the social network analysis. The Date ranges from 28/09/2019 until 04/04/2022. Red dashed lines represent the length of the spawning season, lasting from the beginning of March until the beginning of August (González-Quirós et al., 2011).

b. General stats about the social network analysis

Of all the 171 possible dyads that could have been observed throughout the study period, only 31 dyads (from 13 individuals) have occurred (SRI > 0), with a resulting edge density of 18.13%. The total number of co-occurrences of at least 2 individuals during the whole study period is 146, of which 88 (60.27%) were registered only in West-Coast North (Figure 13, 14, 15). 83 co-occurrences were registered in the Summer and 63 during the Fall Seasons, with no co-occurrences detected outside of these seasons (Figure 13). The largest co-occurrences (6, 4 and 3 unique individuals) occurred between West-Coast North and West-Coast South (Figure 15).

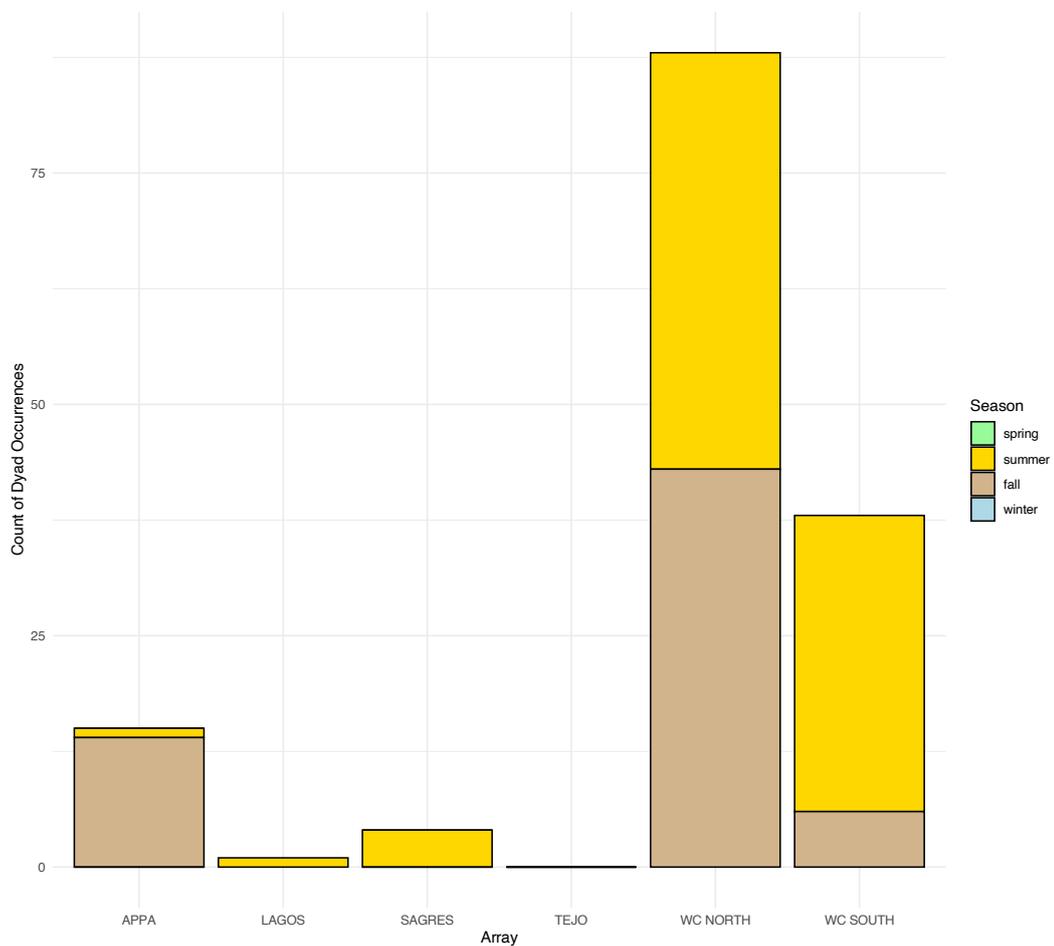


Figure 13 –Number of co-occurrences detected at each of the 6 arrays that yielded detections during the study period. Colours represent the season in which the co-occurrences happened.

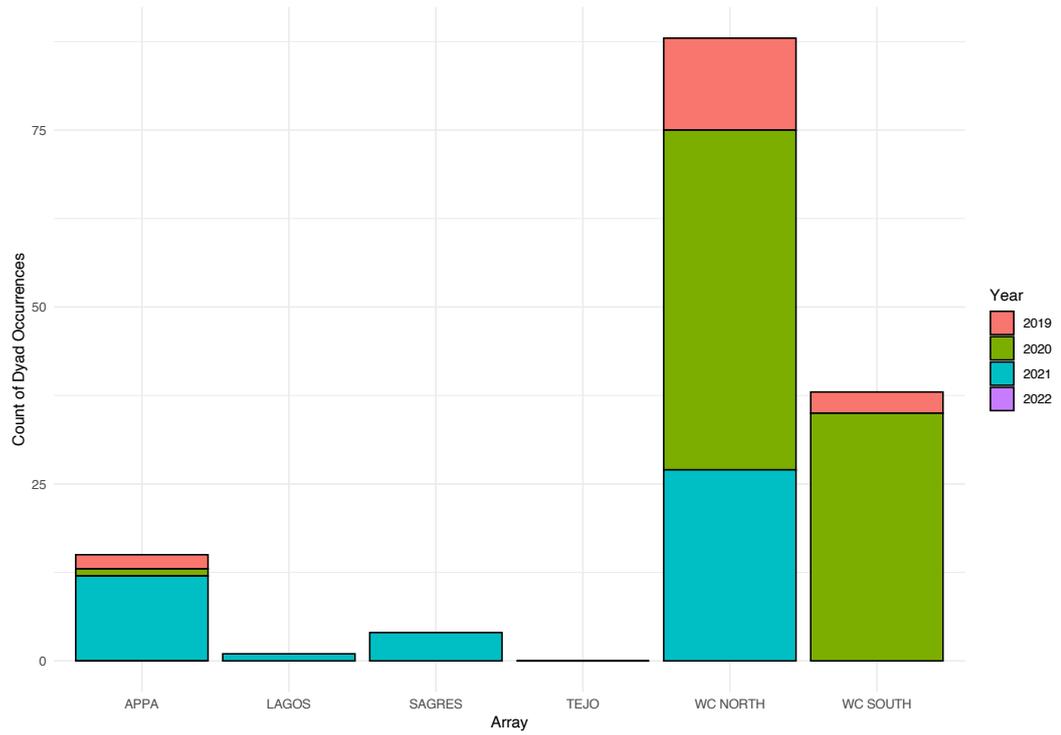


Figure 14 - Number of co-occurrences detected at each of the 6 arrays that yielded detections during the study period. Colours represent the year in which the co-occurrences took place.

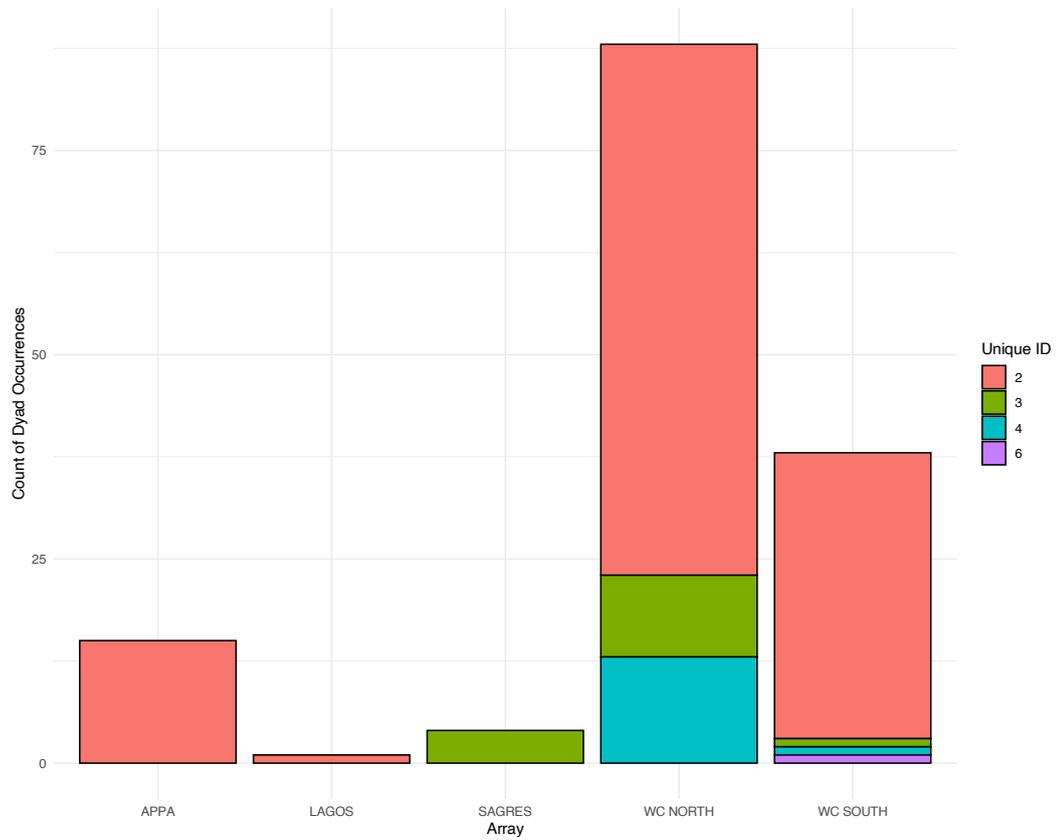


Figure 15 - Number of co-occurrences detected at each of the 6 arrays that yield detections during the study period. Colours represent the number of unique_ID detected during the same one-hour interval at the array.

c. Results of the permutation tests

The mean observed SRI was 0.0089 +/- 0.0298, and the resulting Coefficient of Variation of the observed indices was not significantly higher than the Coefficient of Variation from the random distributions (Permutations test: CV = 3.32, CVr = 3.25, p-value = 0.034, two-tailed test) (Figure 16).

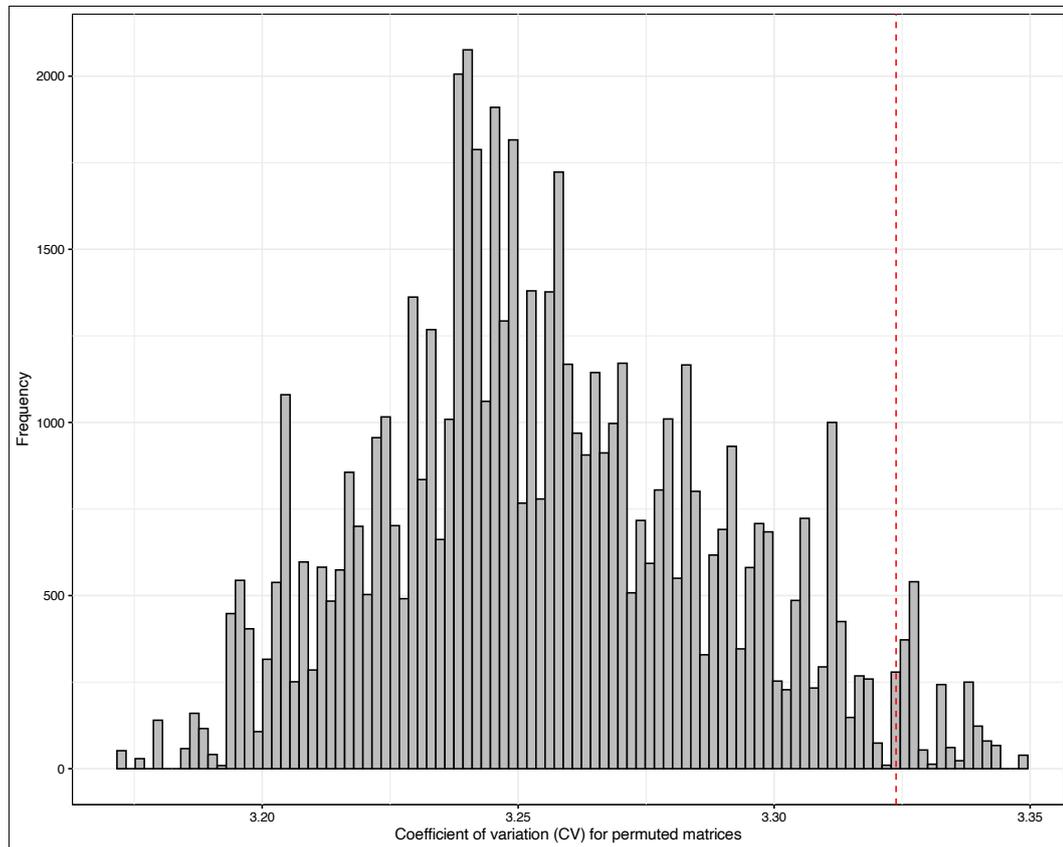


Figure 16 – Distribution of the Coefficient of Variation from the randomization test. The vertical red line represents the observed CV (3.32).

d. Results of the metrics.

Overall, individual 23829 displayed the highest betweenness centrality metrics ($be = 0.23$), followed by 23798 ($be = 0.13$) (Figure 17, Table 2). IDs 23829, 23833, 23804, 23800 and 23836 displayed the highest values of Eigen-Vector centrality (Figure 18, Table 2).

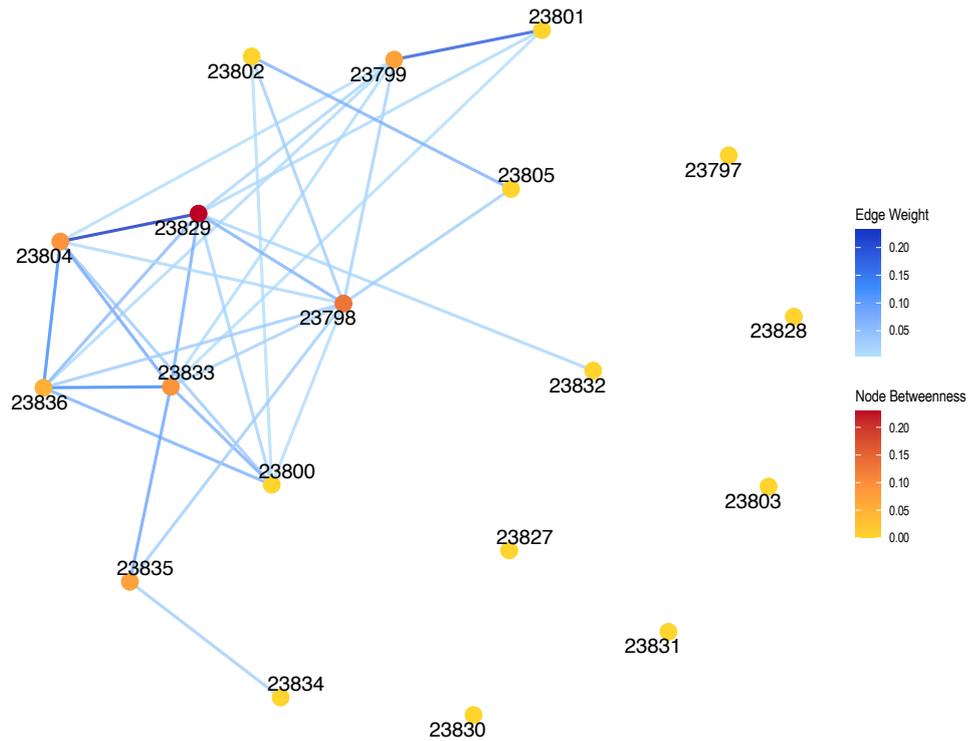


Figure 17 - Social network of the 19 individuals involved in the analysis. The node's colour intensity is proportional to the magnitude of the Betweenness-centrality.

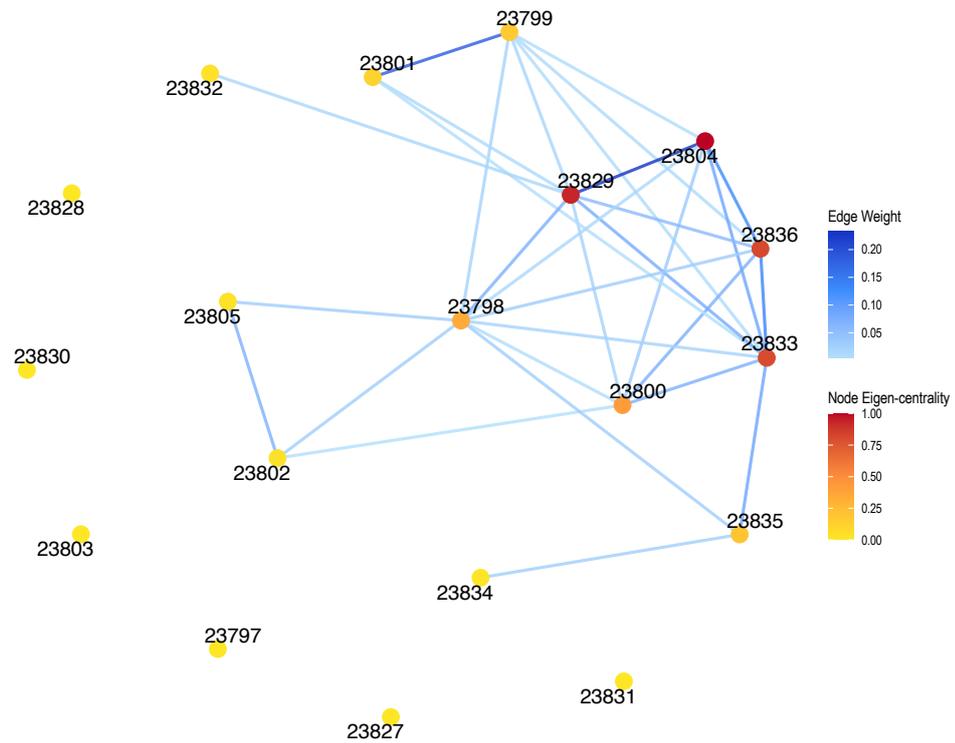


Figure 18 - Social network of the 19 individuals involved in the analysis. The node's colour intensity is proportional to the magnitude of the Eigen-centrality.

Table 2 – Table displaying the node metrics for each individual ID

ID	Betweenness-Centrality	Eigen-Centrality
23797	0	$1.75 \cdot 10^{-17}$
23798	0.13	0.338
23799	0.072	0.17
23800	0	0.423
23801	0	0.167
23802	0	0.033
23803	0	$1.75 \cdot 10^{-17}$
23804	0.092	1
23805	0	0.029
23827	0	$1.75 \cdot 10^{-17}$
23828	0	$1.75 \cdot 10^{-17}$
23829	0.229	0.932
23830	0	$1.75 \cdot 10^{-17}$
23831	0	$1.75 \cdot 10^{-17}$
23832	0	0.037

23833	0.092	0.8
23834	0	0.013
23835	0.072	0.199
23836	0.052	0.808

e. Results of the Mantel tests

The Mantel test for the correlations between the tagging period and the presence of an edge between individuals did not identify any significant relationships. The observed correlations (Mantel-Statistic r) were weak, and the p -values were largely non-significant. The Mantel test for the association matrix and size classes provided a weak ($r = 0.269$) and non-significant (p -value = 0.052) relationships (Table 3).

Table 3- results of the Mantel test performed with Pearson's product-moment correlations method.

Test-Type	Explanatory	Mantel-Statistic r	Significance
Pearson	Day	0.086	0.161
Pearson	Month	0.009	0.508
Pearson	Season	0.009	0.501
Pearson	Year	-0.071	0.774
Pearson	Spawning	0.009	0.503
Pearson	Size	0.269	0.052

f. Community detections algorithms

All three of the community detection algorithms produced similar modularity scores (Fast-Greedy algorithm $Q = 0.299$; Louvain algorithm $Q = 0.287$; Walk-Trap algorithm $Q = 0.251$). However, none of them was able to divide the social networks into real communities, as the detected p -values were all above the significance level of 0.05 (Figure 19, 20, 21). On the other hand, although the Edge-betweenness algorithm did not find any communities and grouped all the individuals connected by edges in a unique cluster, the resulting module yielded a significant p -value of 3.87×10^{-6} (Figure 22).

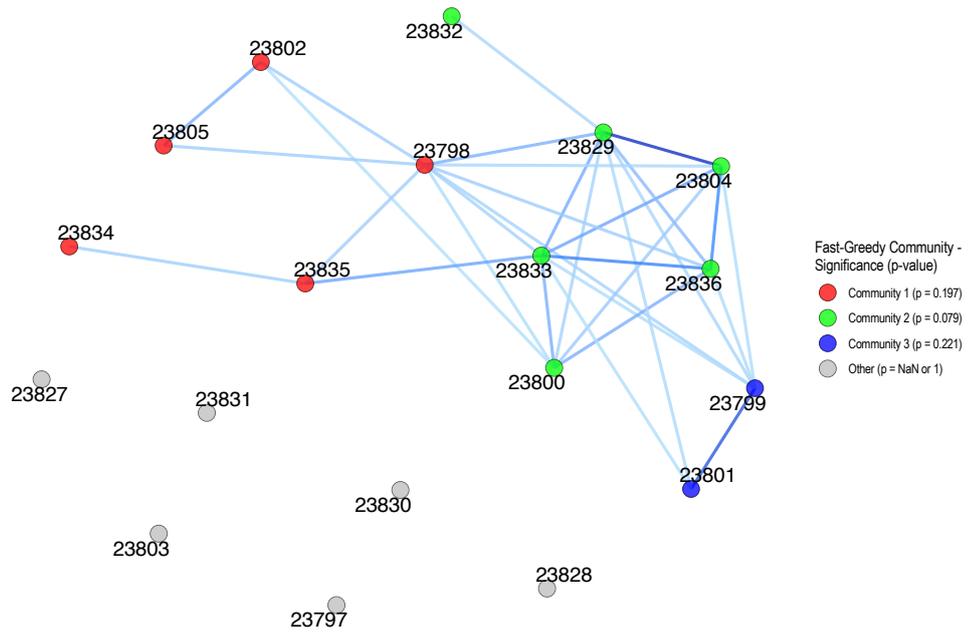


Figure 19 - social network showing the communities identified by the Fast-Greedy algorithm

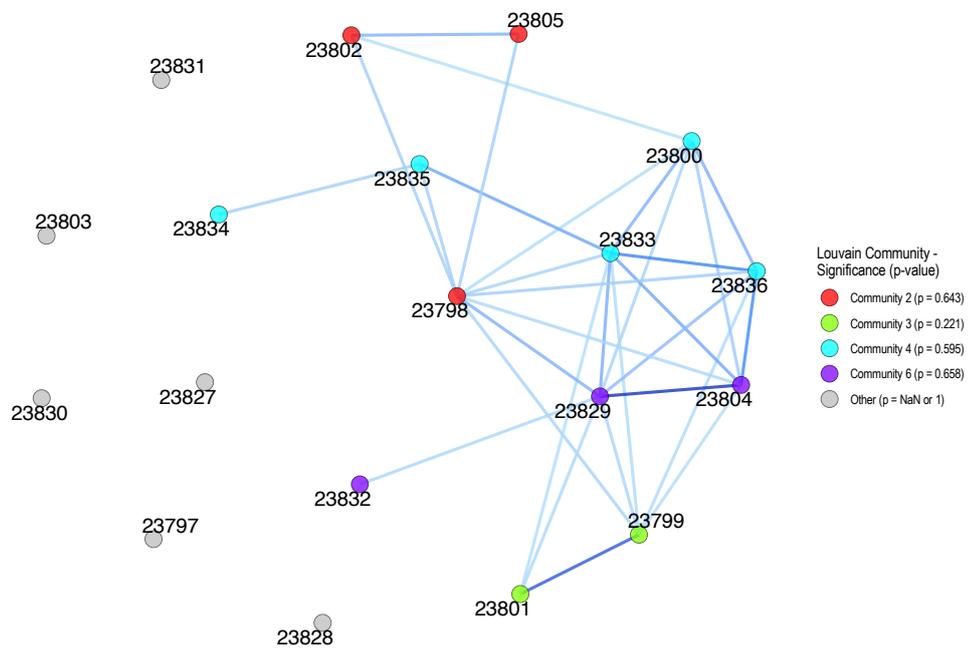


Figure 20 – social network showing the communities identified by the Louvain algorithm

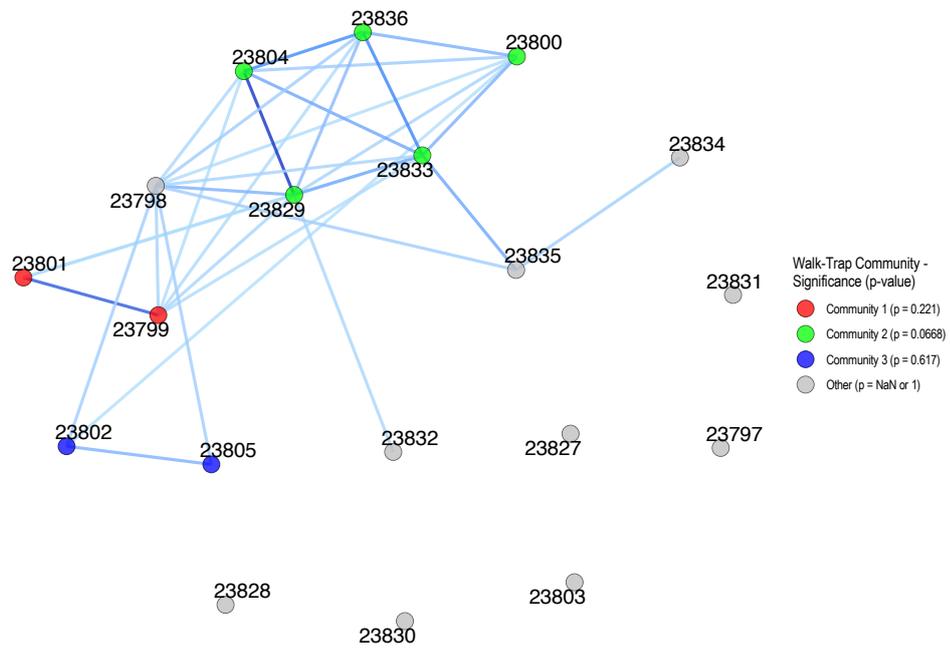


Figure 21 – social network showing the communities identified by the Walk-Trap algorithm

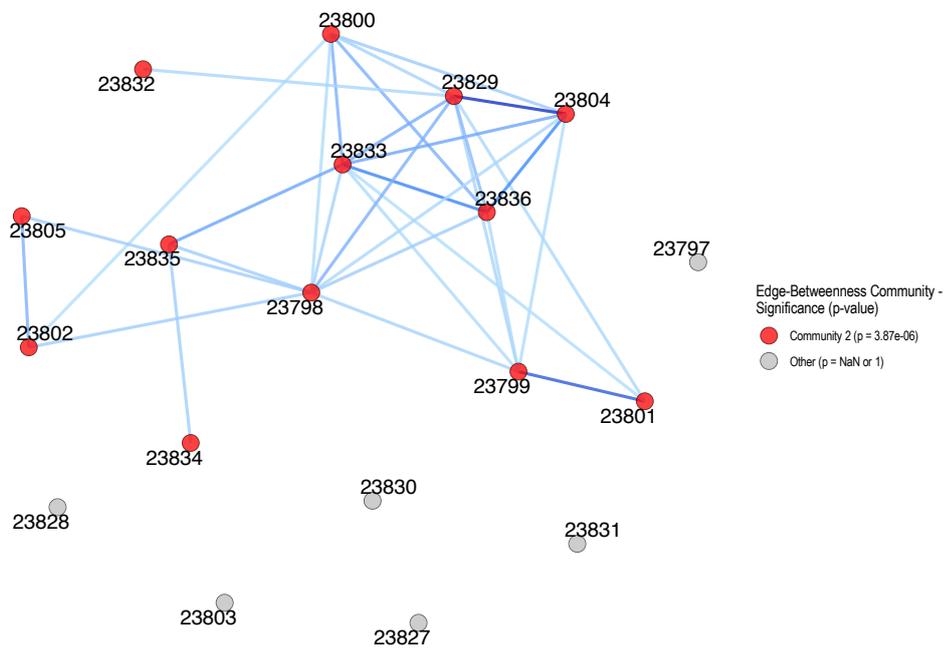


Figure 22 – social network showing the communities identified by the Edge-Betweenness algorithm

g. Assortativity analysis

The weighted assortative mixing (r_w^d) analysis showed that 78.37% of the edges in the social network occurred among individuals with had their highest residency index in the spatial community of the West Coast (composed of Sagres, West-Coast South, and West-Coast North). Additionally, 87% of all the edges in the network connect with the spatial community of the West Coast, which agrees with the results of the Eigen-centrality metrics that see individuals belonging to this community having high centrality. The overall assortative coefficient was 0.26 ± 0.25 , suggesting that there was a weak tendency for individuals to connect with individuals of the same spatial community. The p-value, obtained after 10.000 permutations was 0.216, indicating that individuals were not aggregating significantly more with others in the same spatial community.

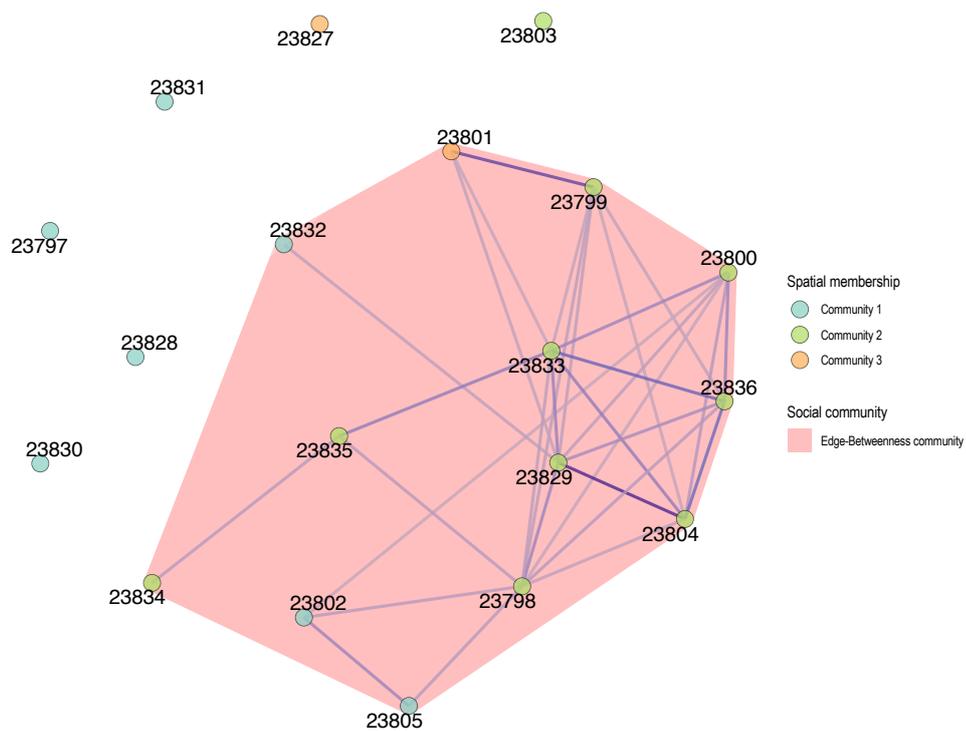


Figure 22 - Social network plot showing the output from the community detection analysis using the edge-betweenness algorithm. Individuals are coloured according to the spatial community in which they display the highest residency index: Tuna-trap, Guadalquivir, Guadiana, Appa, and Lagos in light blue; Sagres, West-Coast South, and West-Coast North in pale green; Sines, Arrabida, and Tejo in pale orange.

DISCUSSION

1) SUMMARY OF THE MAIN RESULTS

The current study relied on 155,552 acoustic detections from 38 unique IDs to study meagre migrations along the South-West Coast of the Iberian Peninsula. The two arrays of Tuna-Trap and West-Coast North displayed the highest residency index, excluding Tejo, meaning that fish spent a significant proportion of time there and didn't use these locations just as passage points. Nevertheless, we point out that the deployment period of the West-Coast North array was nearly double that of the Tuna-Trap array (1261 and 624 days, respectively), which might have slightly inflated the residency index of the latter. Moreover, the high residency observed at Tuna-Trap is attributed to detections from a single ID (23820), recorded in that array for 14 unique days between March and April 2023. One possible explanation for this high number of detections might be that this particular individual might have been captured by the tuna trap at that location. Conversely, the residency index of West-Coast North was derived from nine distinct individuals detected at that location across the entire study period. Combined with the fact that West-Coast North displayed the highest number of co-occurrences and the fourth Eigen-centrality metric, despite the array being composed of only two receiver stations, it may indicate the animal's strong site fidelity for this area. The high residency obtained from Tejo occurred for two main reasons. Firstly, the two individuals (ID 23808 and 23827) tagged there were not detected at any other array during the study period, and probably remained within or near the estuary for most of the time. Secondly, the receiver stations within the estuary of Tejo have a heterogeneous distribution, allowing good coverage across the estuary. The fact that these two individuals were the smallest among all the others (70cm TL and 100cm TL, respectively) aligns with information from other studies, which suggest that immature and pre-adult meagre (70-110cm TL) tend to remain in estuarine and shallow waters before reaching sexual maturity (González-Quirós *et al.*, 2011; Morales-Nin *et al.*, 2012). A total of 162 transitions between arrays were detected throughout the study period, mainly involving the arrays of APPA, Sagres, West-Coast North and West-Coast South. Coupled with the high Eigen-centrality centrality of these arrays, this information suggests these areas are involved in frequent movements between the two Portuguese coasts. Our community analysis aimed to determine if fish movements segmented the spatial network into sub-groups of densely connected nodes. Although the “*cluster_optimal*” algorithm produced a positive modularity score of 0.15, none of the three identified communities had statistically significant p-values. These results suggest that

nodes within the community were not significantly more connected than outside of the community but moving any nodes to a new community would reduce the modularity of the entire network (Finn *et al.*, 2014). The “*cluster_infomap*” algorithm, being appropriate for sparse networks, includes all the nodes within the same community, possibly indicating that no nodes were tight enough to represent a “real” community. We highlight that some direct transitions observed between arrays far from each other (such as Tejo to Sagres or APPA to West-Coast North) may have occurred because some receivers in between might have “missed” the passage of adult meagre during their migrations. Given some limitations of aquatic telemetry (Lédée *et al.*, 2021b; Setyawan *et al.*, 2024), the possibility of integrating biotelemetry techniques with other approaches, like oceanographic modelling and molecular technique, is recommended to obtain a complete picture of aquatic megafauna migration in their natural environment (Abecasis *et al.*, 2024a).

The present study observed 146 co-occurrence events among at least two individuals. These aggregation events occurred between 13 distinct individuals, mainly located between West-Coast North and West-Coast South and occurred primarily in summer-autumn months. The observed Coefficient of Variations (3.32) from the social network analysis was non-significant (p-value = 0.034) across the entire social network study period; thus, we cannot claim that the observed number of co-occurrences were significantly different from what would be expected if fish aggregated with a random pattern. Our Mantel test analysis detected a weak (0.269) and non-significant (p-value = 0.052) correlation between the presence of an edge in the adjacency matrix and the size class of the fish. None of the five Mantel tests for the tagging period yielded a significant p-value. Three out of four community detection algorithms identified at least two communities, despite none of them providing a significant p-value. Like our spatial network, also for the social network community analysis the only significant p-value was obtained when the algorithm groups all the individuals with at least one edge within the same cluster.

2) SIGNIFICANCE OF THE RESULTS FOR ARGYROSOMUS REGIUS MIGRATIONS

The results of the current analysis are in agreement with those of Gandra *et al.*, (2024) and underscore the critical role of the Southwest coast of Portugal (Sudoeste Alentejano and Vicentina Coast Natural Park) as a potential feeding ground during the migrations of adult meagre. This region exhibited the highest number of fish detected within the same one-hour interval as in September 2020, six unique individuals were detected in the West-Coast South, and we had multiple occurrences of four and three individuals simultaneously detected between Sagres, West-Coast South, and West-Coast North. The Marine Protected Area (MPA) in this region, combined with localised upwelling and a heterogeneous habitat, provides robust support for extensive marine biodiversity (Vargas *et al.*, 2003; Gandra *et al.*, 2024; Garel *et al.*, 2024). Adult meagre migrates along the coast during the summer and the fall seasons, with the highest number of co-occurrences and transitions observed during these periods. This agrees with previous studies that observed meagre preferentially using shallow waters during these seasons, likely driven by the favourable thermal range and the higher prey availability during warmer months (Winkler *et al.*, 2023; Gandra *et al.*, 2024; Garel *et al.*, 2024). Seasonal shift in habitat preferences has also been reported in two closely related species: *Argyrosomus japonicus* in South Australia (Barnes *et al.*, 2019) and *Argyrosomus coronus* off the Angolan coast (Potts *et al.*, 2010, 2018). During the fish migration, the array of APPA was involved as a considerable passage point towards the West Coast, as suggested by his high Betweenness centrality. The narrow continental shelf in this area likely forced meagre to use it as a corridor, and the fact that tuna traps have been deployed in this location supports this phenomenon. In contrast, the very low centrality of Lagos and the low number of detections in that array suggests that individuals did not use this area to reach the West Coast but prefer to move directly from APPA to Sagres, likely aided by warm coastal currents (Garel *et al.*, 2024) and the wider continental shelf outside Lagos compared to where the array of APPA is located. The array of Sagres also represents a transition point between the South and West Coast. The low residency index suggests that individuals do not remain in this area for extended periods. Instead, the high Betweenness centrality values imply that fish were frequently transiting through this region to reach the South-West Coast. Once they arrived in these areas, fish likely remained there for feeding, as suggested by the high residency index of West-Coast North. The high Eigen-centrality showed by Sagres, West-Coast South and West-Coast North, indicates that these arrays were frequently involved in back-and-forth

movement between the Southern and Western Coast of Portugal. In fact, as highlighted by Gandra *et al.*, (2024), some individuals continued their migrations towards the northern region, whereas others returned to the Southern Coast. Our permutation test results also support the hypothesis that meagre did not homogeneously transit along the coast but rather that the high number of movements observed in some locations means they were significantly more involved in the migration. Identifying relevant habitats for marine species has been crucial for the designation and subsequent implementation of MPAs, which enhance the viability and maintain biodiversity of the marine environments (Lea *et al.*, 2016; Perryman *et al.*, 2022; Setyawan *et al.*, 2024). A recent study on reef Manta ray (*Mobula alfredi*) combining acoustic telemetry and spatial network analysis was able to identify critical habitats in the Manta ray migration patterns, calling for the need to include these sites within an MPA network to enhance the conservation of the manta ray population in the Indonesian archipelago (Setyawan *et al.*, 2024).

The current analysis suggests that adult meagre can form large aggregations even in areas far from their spawning grounds and outside the spawning season, as also indicated by Gandra *et al.*, (2024). Many co-occurrences in Sagres, West-Coast South, and West-Coast North were observed from the end of July until the middle of September between 2019 and 2020. Since the spawning season is usually reported to last from March until August (González-Quirós *et al.*, 2011; Winkler *et al.*, 2023), some of the aggregations we observed are outside that range. However, we cannot claim that the observed pattern differed from what would be expected under the null hypothesis of random co-occurrences, as our permutation test was not significant. Nevertheless, when considering the combined results from our social and spatial network analyses (permutation test and residency indexes), we found that certain locations, like West-Coast South, West-Coast North, and Sagres, showed frequent movements of adult meagre and a high number of co-occurrences within the same one-hour interval. Together with other studies (Winkler *et al.*, 2023; Abecasis *et al.*, 2024a, 2024b; Gandra *et al.*, 2024; Garel *et al.*, 2024), this information can be relevant for the species conservation and management planning, as predictable marine aggregations of fish are an easy target for fisheries (Phelan, Gribble and Garrett, 2008). Instances of long and seasonal migrations back and forth from their spawning grounds have been reported among other species of the genus *Argyrosomus*, like the mullet (*Argyrosomus japonicus*) along the South Coast of Australia (Barnes *et al.*, 2019) and in South Africa (Griffiths, 1996) and the West Coast dusky kob (*Argyrosomus coronus*) off the Angolan coast (Potts *et al.*, 2010,

2018). The observed seasonal movement patterns suggest a likely philopatric strategy (Griffiths, 1996; Potts *et al.*, 2010; Barnes *et al.*, 2019), commonly seen in other Sciaenid (Barnes *et al.*, 2019) and also in meagre (Winkler *et al.*, 2023; Abecasis *et al.*, 2024a; Gandra *et al.*, 2024). There are few studies, however, that confirm whether these species form large aggregations at sites different from the spawning grounds. The Blackspotted croaker (*Protonibea diacanthus*), another member of the Sciaenidae family, is reported to form large aggregations off the northern Australian waters. Although evidence on the real drivers of these aggregations is lacking, they may be primarily resource-driven (Phelan, Gribble and Garrett, 2008). Among teleosts, the anadromous Atlantic Sturgeon (*Acypenser oxyrinchus oxyrinchus*) performs extensive marine migrations and can form aggregations between feeding, breeding, and overwintering sites (Lilly *et al.*, 2020), and aggregations at feeding sites are widely reported among elasmobranchs (Schildts *et al.*, 2019; Papastamatiou *et al.*, 2020; Anderson *et al.*, 2021). Aggregating with familiar individuals during feeding events can offer several advantages for elasmobranchs and marine teleosts. Such behaviour may reduce the risk of aggression from conspecifics and facilitate the transfer of knowledge about prey availability and foraging strategies from older to less experienced individuals (Armansin *et al.*, 2016; Meager, Fernö and Skjæraasen, 2018; Schildts *et al.*, 2019; Lilly *et al.*, 2020; Papastamatiou *et al.*, 2020; Anderson *et al.*, 2021). It is worth mentioning that, even if the random test would have yielded a significant p-value, demonstrating that groups of individuals were co-occurring more than expected by chance would not necessarily imply that they were interacting (Wilson, Croft and Krause, 2014). Nevertheless, patterns of co-occurrences higher than random could provide the basis for social interaction (Findlay *et al.*, 2016; Schildts *et al.*, 2019). Yet, to discriminate whether the observed aggregations result from the active choice of the individuals, they should be observed regardless of the presence of environmental drivers (like food resources) (Mourier, Vercelloni and Planes, 2012; Findlay *et al.*, 2016; Lilly *et al.*, 2020). In the current study, we could not properly characterise social interactions among individuals, as acoustic telemetry data could only provide information on whether individuals were present or absent within the range of the receiving station (Lilly *et al.*, 2020). Future studies on meagre and other Sciaenids should include information on localised primary productivity, upwelling, and other environmental variables to be able to assess if the pattern of aggregations observed in the current study could be distinguished from the availability of food resources or other environmental drivers and to evaluate whether social interactions are actually occurring.

Aggregations among individuals of similar size are a common pattern in the marine realms, as they usually provide several benefits due to similar physiological and dietary requirements (Jordan *et al.*, 2010; Mourier, Vercelloni and Planes, 2012; Wilson, Croft and Krause, 2014; Findlay *et al.*, 2016; Ward, Kent and Webster, 2020). In our study, fish of the same size class were not aggregating more with each other than with odd-sized individuals, as suggested by the results of the Mantel test. Notably, 15 out of 19 individuals were assigned to the "medium" size class. For these reasons, the positive correlation might also be an artefact due to the small sample size and limited size range rather than an actual positive correlation driven by the active choice of the individuals. There are different results on the correlations between dyadic relationships and tagging periods across the available literature. In a study on the Yellowfin Tuna (*Thunnus albacares*) social network, the individuals displayed significantly stronger association indices with those they were tagged (Stehfest *et al.*, 2013). Conversely, the tagging period did not correlate with association strength in a social network analysis of Atlantic Sturgeon (*Acipenser oxyrinchus oxyrinchus*) (Lilly *et al.*, 2020). In our study, there was not a significant correlation between the presence of an edge forming a dyad and the period in which the individuals were tagged in none of the five explanatory periods considered (day, month, season, year, and spawning vs. non-spawning period). This result suggests that being tagged within the same period does not significantly influence the likelihood of individuals being detected together at other times during the study period for the social network. Results from the community detection algorithms indicate that we cannot conclusively divide the individuals in the social network into distinct communities based solely on their association strength. The Fast-Greedy algorithm, which yielded the highest modularity score, divided the associating individuals into three communities, although none obtained a significant p-value. While this algorithm is considered well-suited for detecting social network communities (Finn *et al.*, 2014; Pastor-Rollan *et al.*, 2024), the low number of individuals displaying associations (13 out of 19) and the resulting low edge density (18.13%) may reduce the algorithm's efficiency. The Edge-Betweenness algorithm, which is more appropriate for sparse networks (Pastor-Rollan *et al.*, 2024), successfully identified the only possible community based on the measured associations in the social network.

It did not seem that individuals belonging to the same spatial community associated significantly more among them than with individuals assigned to a different community. Despite that, when observing the results from the spatial memberships, we found that some of the highly central fish in the social network (from the Eigen-centrality value) were the ones that

presented a higher residency index on the West Coast and were assigned to community number 2 (IDs 23798, 23804, 23829, 23833, and 23836). In contrast, many of the marginal individuals, with few or no edges with others, usually have no detections at the array along the West Coast and were assigned to community number 1 (IDs 23797, 23802, 23805, 23828, 23830, 23831, 23832). Moreover, we underscore that all individuals belonging to this community had the potential to be detected along the West Coast (i.e., both the tag and the array were available during the social study period), but only a few were detected by those stations, with the majority remaining in the Southern Coast. For instance, IDs 23797, 23802, and 23828 were detected in Sagres for a few days. In contrast, IDs 23805, 23830, 23831, and 23832 were only detected in the Southern region throughout the entire study period and seemed never to have reached Sagres. The results from Gandra *et al.* (2024) partially support these findings. Using models derived from satellite detections Gandra *et al.*, (2024) study showed that individuals 23797 and 23828 clearly passed the West-Coast North array and migrated even northern, arriving in the highly productive region between Ericeira and Peniche, even if no acoustic receiver was able to detect their passage. Furthermore, satellite data suggests that IDs 23800 and 23834 also performed long migrations when they passed the West Coast and arrived at the Northern regions. On the other side, the same models show that even if some individuals arrived in the West Coast region (like 23798, 23829), they did not continue the migration towards the northern region but rather migrated back to the south, and acoustic detections corroborated these observations. This behaviour might be the reason for 23798 and 23829 high Betweenness centrality in the social network. It is, therefore, evident that there was a heterogeneous tendency for movement among the individuals tagged in the study period, with some performing extensive migrations, whereas others remained more resident near the putative spawning estuary and the tagging region. This behaviour has also been observed in the mulloway (*Argyrosomus japonicus*) along the south coast of Australia (Barnes *et al.*, 2019). This species performs horizontal migrations after the spawning season; however, not all the individuals showed the same horizontal distributions, with some being more resident than others (Barnes *et al.*, 2019). Size has been hypothesised as the reason for the observed pattern, despite not being statistically significant (Barnes *et al.*, 2019). A similar pattern has also been hypothesised for one South African population of *A. japonicus*, where differences in the distributions between nuclear and mitochondrial markers might be caused by females being more philopatric than males (Mirimin *et al.*, 2015; Barnes *et al.*, 2019). Nevertheless, the lack of information on the sex of the individuals sampled in the study

prevented the authors from confirming the previous hypothesis (Mirimin *et al.*, 2015).

Long migrations are energetically costly; thus, they take place only when the benefits of the migrations, like the reduced competition between individuals, exploitation of areas with more favourable resources, or escape unfavourable habitat, outweigh the costs of such migration (Bowler and Benton, 2005; Espinoza *et al.*, 2021). However, within the same populations, individuals may exhibit a different tendency to migrate among them, a phenomenon known as "partial migrations" and described in many marine teleosts (Chapman, Hulthén, *et al.*, 2012; Chapman, Skov, *et al.*, 2012; Meager, Fernö and Skjæraasen, 2018; Bryan *et al.*, 2021). Variations in competitive abilities among individuals, along with differences in dietary and physiological requirements, may cause some individuals to migrate towards more favourable grounds while others may choose to remain closer to the spawning ground as it is not advantageous for them to perform long migrations (Chapman *et al.*, 2011; Chapman, Hulthén, *et al.*, 2012; Chapman, Skov, *et al.*, 2012). Nevertheless, the choice to migrate or not is always based on a trade-off between the benefits and the costs that adopting a migratory behaviour could have on the individual's fitness (Childs *et al.*, 2015). A case of partial migrations has been reported within a population of juveniles of *Argyrosomus japonicus* in South Africa (Childs *et al.*, 2015). In this case, the population of juveniles was divided into two "contingents", one inhabiting estuarine water and one more associated with marine waters. Despite that, around one-third of the fish of each contingent frequently made excursions to the other habitat (Childs *et al.*, 2015). Nevertheless, as the estuarine-associated contingents were more vulnerable against possible perturbations, the difference in behaviours between the two subpopulations significantly contributes to maintaining the connectivity among the habitats and, therefore, the whole population's resilience against anthropogenic or environmental stressors (Childs *et al.*, 2015). On a larger geographical scale, individuals with a higher tendency to move may play an essential role in linking distant communities, as was observed in a population of Manta rays in Raja Ampat, West Papua (Perryman *et al.*, 2022).

Highly mobile individuals are fundamental in maintaining the connectivity between distinct subpopulations and, potentially, some level of gene flow (Perryman *et al.*, 2022). As highlighted in a recent study, there is an evident genetic structure between the subpopulation spawning in Tejo and the one spawning in the Guadalquivir (Abecasis *et al.*, 2024a). Larval dispersal has been shown to play little or no role in population connectivity; therefore, the presence of migratory individuals in the Guadalquivir subpopulation is of great

relevance for species conservation (Abecasis *et al.*, 2024a). Adult meagre is suspected to spawn always in the same estuary, a behaviour known as “natal philopatry”, which may further limit the possibility of gene exchange between the two subpopulations (Abecasis *et al.*, 2024a; Gandra *et al.*, 2024). However, a recent study suggests that this phenomenon may be less marked than previously thought, as an individual tagged in the Algarve in 2018 was detected within Tejo during the 2019 spawning season (Abecasis *et al.*, 2024b). Therefore, the long migrations of individuals from the Algarve regions towards the estuary of Tejo possibly support the limited genetic exchange still occurring between these two subpopulations (Abecasis *et al.*, 2024a). Maintenance of gene flow among discrete subpopulations is crucial for conservation purposes (Pavlova *et al.*, 2017). On the one hand, some level of genetic diversity within populations is essential, as it can maintain traits providing advantageous adaptations against environmental changes (Gandra *et al.*, 2021). However, once this phenomenon becomes excessive, it can result in high genetic drift in the population and, ultimately, local extinction (Pavlova *et al.*, 2017). Within the context of marine spatial planning, it has been suggested that “several small” marine reserves, located in the proximity of pivotal spawning grounds, may be the ideal solution for meagre, given this species' low larval dispersal and high genetic fragmentation (Abecasis *et al.*, 2024a). However, with several other studies, we highlight that even migratory individuals can be threatened along their path (e.g., stationary fishing gear) and during their aggregations along the South-West Coast. This information must, therefore, be considered in future conservation projects aimed at protecting this species (Abecasis *et al.*, 2024a; Gandra *et al.*, 2024).

3) RELEVANCE OF NETWORK ANALYSIS FOR MEAGRE CONSERVATION

Individuals' physical and behavioural phenotypes influence their role within a social network and, in turn, the population structure and distribution in space (Childs *et al.*, 2015; Ward, Kent and Webster, 2020; Weiss, Ellis and Croft, 2021; Perryman *et al.*, 2022). Therefore, studying social network systems will be relevant, as it can lead to a better understanding of how external perturbations and disturbances affect the whole population structure (Perryman *et al.*, 2022). As in our study all individuals were approximately the same size and were considered adults (González-Quirós *et al.*, 2011; Morales-Nin *et al.*, 2012); sex could be one variable, other than a possible behavioural phenotype (Perryman *et al.*, 2022), potentially explaining the observed difference in the movement pattern. An individual's sex influences spatial distribution, physiological requirements, and dietary needs (Findlay *et al.*, 2016; Ward, Kent and Webster, 2020; Weiss, Ellis and Croft, 2021; Kraft,

Winkler and Abecasis, 2024). For these reasons, it is essential also to consider this information when managing and conserving marine species, as one sex could be more impacted by fisheries' pressure than the other (Kraft, Winkler and Abecasis, 2024). As far as we know, none of the studies on meagre considered the sex of the individuals in their analysis. Including this information in future studies could be relevant to enhance the conservation and management of this species.

Fish Spawning Aggregations (FSAs) are common across many marine teleost (Claydon, McCormick and Jones, 2012; Meager, Fernö and Skjæraasen, 2018; Lilly *et al.*, 2020; Bryan *et al.*, 2021; Ellis *et al.*, 2023) and Sciaenid species (Phelan, Gribble and Garrett, 2008; Potts *et al.*, 2010; Semmens *et al.*, 2010; Barnes *et al.*, 2019). Unfortunately, little is known about possible aggregations of Sciaenid outside the spawning season and the spawning grounds, with only another paper reporting aggregations of individuals that may not be driven by reproductive purposes (Phelan, Gribble and Garrett, 2008). Life-history traits of many large Sciaenid make them vulnerable to over-exploitation: late attainment of sexual maturity, high longevity, and spawning aggregation that are easy to predict in space and time (Griffiths, 1996; Semmens *et al.*, 2010; Mirimin *et al.*, 2015; Barnes *et al.*, 2019; Winkler *et al.*, 2023). Many studies have already called for a better assessment of their stock and an improvement in their management strategies to avoid population collapse (Phelan, Gribble and Garrett, 2008; Semmens *et al.*, 2010; Mirimin *et al.*, 2015; Potts *et al.*, 2018; Abecasis *et al.*, 2024a; Stratoudakis *et al.*, 2024). Several studies on meagre highlight that the population inhabiting the Portuguese coasts can be divided into two distinct subpopulations: one spawning in the estuary of Tejo and the other in the Guadalquivir estuary (Haffray *et al.*, 2012; Almeida *et al.*, 2022; Abecasis *et al.*, 2024a; Gandra *et al.*, 2024). Based on results obtained by Gandra *et al.*, (2024), which shares some individuals with the present study, we hypothesise that the individuals tagged in the southern Algarve most likely belong to the population spawning in the Guadalquivir. After spawning, adults migrate towards Sagres and reach potential feeding grounds along the Southwestern Portuguese coast, as these areas are known to harbour heterogeneous biodiversity and high primary productivity (Vargas *et al.*, 2003; Gandra *et al.*, 2021; Garel *et al.*, 2024). Combined results from the residency index (high values for West-Coast North array), the movement networks (more than 50% of the overall transitions took place in that region), and the social network (high frequency of co-occurring individuals in that zone) corroborate previous findings, highlighting the importance of that area for meagre migrations and as potential feeding grounds. Migrations between breeding and feeding grounds are a typical

behaviour shared by other teleost fishes and elasmobranchs (Lilly *et al.*, 2020; Espinoza *et al.*, 2021). They could be driven by different factors, like changes in environmental features or density-dependent processes (Bowler and Benton, 2005; Espinoza *et al.*, 2021). The migrations of meagre towards Cape St. Vincent are likely triggered by the warm temperature of the westward water currents during summer, which could favour horizontal movements of adults from their spawning sites towards potential feeding sites along the Vicentine coast (Winkler *et al.*, 2023; Gandra *et al.*, 2024; Garel *et al.*, 2024).

4) CONCLUSION

Our study confirms the relevance of applying Network analysis methodology with acoustic telemetry data to disentangle patterns of space use and social structure among teleost fishes. These results further improve the knowledge of the spatial and behavioural ecology of meagre, a relevant fish for recreational, artisanal, and commercial fishery along the Spanish and Portuguese coast (González-Quirós *et al.*, 2011; Morales-Nin *et al.*, 2012). Future studies should aim to include further information in the available data, like the sex of the individual and the spatial and temporal distributions of resources, to elucidate better patterns of fish associations at the feeding ground, which can significantly contribute to increasing the knowledge about population structure and connectivity along the Iberian Peninsula.

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APPENDIX

Table 4 – Tagging metadata displaying the individual's ID, tagging date, Expected drop date and Length

ID	Tagging date	Expected tag drop date	Length (cm)
23797	2018-09-20	2022-04-04	131
23798	2018-09-20	2022-04-04	128
23799	2019-07-10	2022-12-21	125
23800	2018-09-20	2022-04-04	131
23801	2018-09-20	2022-04-04	127
23802	2018-09-20	2022-04-04	142
23803	2019-07-10	2023-01-22	134
23804	2019-07-10	2023-01-22	134
23805	2019-07-10	2023-01-22	134
23806	2019-07-10	2023-01-22	128
23807	2020-10-15	2024-04-29	132
23808	2020-05-28	2023-12-11	70
23809	2021-07-29	2025-02-10	128
23810	2020-10-15	2024-04-29	120
23811	2020-10-15	2024-04-29	132
23812	2021-07-30	2025-02-11	136
23815	2021-07-30	2025-02-11	130
23816	2021-07-29	2025-02-10	134
23817	2021-07-29	2025-02-10	138
23818	2021-07-29	2025-02-10	131
23819	2021-07-29	2025-02-10	136
23820	2021-07-29	2025-02-10	126
23821	2020-10-15	2024-04-29	128
23822	2020-10-15	2024-04-29	128
23823	2020-10-15	2024-04-29	138
23824	2021-07-30	2025-02-11	138
23825	2020-10-15	2024-04-29	140
23826	2020-10-15	2024-04-29	139
23827	2019-07-22	2023-02-03	100
23828	2019-09-27	2023-04-11	143
23829	2019-09-27	2023-04-11	131
23830	2019-09-27	2023-04-11	130
23831	2019-09-27	2023-04-11	112
23832	2019-09-27	2023-04-11	126
23833	2019-07-09	2023-01-21	124
23834	2019-07-09	2023-01-21	122
23835	2019-07-09	2023-01-21	135
23836	2019-07-09	2023-01-21	126
mean			128.605
Sds			12.639

