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ORIGINAL PAPER

Long-term co-occurrence and gregariousness in the migratory common stingray using network analysis

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Abstract

Aggregations and social interactions play an important role in the movement ecology of many animals, including elasmobranchs. Several of these species have shown the capability of carrying out complex social behaviours, and the importance of sociality in this taxon is being realized. Although it is a growing field of study in the case of these organisms, these processes still need to be better understood, especially to support management and conservation policies. In this study, a long-term acoustic telemetry data set collected on *Dasyatis pastinaca* in a coastal marine protected area was analysed. A co-occurrence network analysis was done to investigate preferential associations among individuals, revealing non-random associations among them. The analysis revealed a few strong and consistent associations that were maintained across inter-migratory periods, as this species performs seasonal migrations to a nearby estuary, suggesting temporal stability of the observed associations. Moreover, individuals had similar average positions and a generally high overlap of space use in both periods, indicating some level of site fidelity to the fully protected area. Groups of up to 64% of tagged individuals were co-detected at a same receiver, particularly in the western side of the array. Despite our limited sample size, likely underestimating associations, these results show that in addition to their large-scale movement pattern, *D. pastinaca* is likely to also present active partner preference and spatial structure at a finer spatial scale. The nature of such results is relevant to support the protection of these species.

Keywords Acoustic telemetry · Aggregation · Association · *Dasyatis pastinaca* · Social network analysis · Sociality

Introduction

Aggregations, or the gathering of individuals in a specific location and time, are an important phenomenon undertaken by many marine animals, from zooplankton and crustaceans to fishes, birds and marine mammals (Genin 2004; Jermacz et al. 2017; Plötz et al. 1991). Aggregations can be passive processes driven by the distribution of suitable habitat or prey, attracting individuals to group in certain areas with no influence of social drivers. For example, animals in the pelagic zone, which is a typically unproductive environment, can be drawn to patches of zooplankton and fish to feed (Genin 2004). Aggregations can also be formed in response to the spatial distribution of shelter and the presence of predators (Jermacz et al. 2017). In some instances, the time and place of these events can also be predictable, such as the seasonal reproductive spawning aggregations of many fishes (Domeier 2012).

Aggregations are also important in that they may represent some of the most simple forms of social behaviour (Deneubourg et al. 2002). Moreover, aggregations are considered a prerequisite for social interactions (Graves and Duvall 1995; Sims et al. 2000) and the development of social groups (Jacoby et al. 2012; Palacios et al. 2023). In this sense, the formation of aggregations may also be socially driven, with or without other environmental influences (Capello et al. 2011; Jermacz et al. 2017). In these

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cases, aggregations are based on active partner choice rather than the result of passive mechanisms.

Non-social aggregations and social interactions, even if different in nature, are also an important part of the movement ecology of species (Spiegel et al. 2017), and understanding their structures and dynamics can be relevant to the development and improvement of conservation efforts (Jacoby et al. 2012; Mourier et al. 2018; Snijders et al. 2017). For example, aggregation areas may increase fishing vulnerability, therefore studying their distribution can lead to the improvement of fishery management strategies (Clark and O'Driscoll 2003). Additionally, the environment can play a role in facilitating social interactions, so understanding where these occur can improve the performance of marine protected areas (Villegas-Ríos et al. 2022).

Animal interactions in the marine environment can be studied using a variety of tools. Under favourable circumstances, data can be collected by direct observation of animal interactions (Mourier et al. 2012; Perryman et al. 2019; Pini-Fitzsimmons et al. 2021). Visual surveys while SCUBA diving, from boats or from the shore, can provide detailed information on the interactions between individuals and on their directionality (Mourier et al. 2012; Pini-Fitzsimmons et al. 2021). However, this can be a demanding task, can be influenced by visual factors (i.e., night-time, high turbidity or currents, structurally-complex environments, study area accessibility), requires the identification of each individual (e.g., photo-ID), and is constrained to factors like fuel availability and diving capacities, making continuous monitoring generally not possible.

On the other hand, automated monitoring systems like passive acoustic telemetry have been used in recent years to study sociality in many aquatic animals (Jacoby et al. 2016). Telemetry data do not have the same resolution and detail on the nature of the interactions as direct observation, although acoustic telemetry data at very fine temporal (seconds) and spatial scales (sub-meter) have been obtained in some cases (e.g., Aspillaga et al. 2021; Baktoft et al. 2017). On the other hand, passive acoustic telemetry systems present advantages like unaffected survey capacities in low visibility conditions, and allow a nearly uninterrupted and long-term monitoring of tagged individuals (Krause et al. 2011).

To analyse acoustic telemetry data, social network analysis is increasingly being applied in studies on elasmobranchs (Mourier et al. 2018). It has proven to be a powerful and adaptable method that can be used to answer a variety of questions about animal social systems (Farine and Whitehead 2015; Krause et al. 2009; Sosa et al. 2021), particularly in species that do not explicitly display social preference or that are hard to study (Snijders et al. 2017). Considering these advantages, marine systems are particularly fitting environments to apply this approach as species in these environments have been historically challenging to study (Hussey et al. 2015).

Compared to taxa like birds and mammals, the study of sociality in fishes is a more recent subject. Most works have been conducted on collective behaviour and structure and the mechanisms driving such individual interactions (Katz et al. 2011). Fishes can present socially intricate interactions, some as complex as cooperative breeding (where breeding animals are assisted by other individuals), increasing the reproductive success of the former (Tanaka et al. 2018). The study of social interactions and aggregations in elasmobranchs is an even newer endeavour (Jacoby et al. 2012). Aggregative behaviour has been reported in a variety of species and across many habitats (McInturf et al. 2023), and a wide array of social behaviours like social grouping, forming and maintaining social structures, dominance hierarchies, leadership, and non-random associations between individuals have also been described (Jacoby et al. 2012, 2016; Mourier et al. 2012; Palacios et al. 2023)., Perhaps the best known example among batoids (superorder Batoidea) are mobulids (Palacios et al. 2023), which are known to display individual preference and associations that last for weeks or months as in dynamic fission–fusion societies (Perryman et al. 2019). Other species in the order Myliobatiformes also show evidence of complex and structured social behaviour, such as *Bathytoshia brevicaudata* (Pini-Fitzsimmons et al. 2021) or *Pateobatis fai* (Furst 2011). However, despite these recent advances, the study of aggregations and associations in elasmobranchs is still in early development and more research is needed (Mourier et al. 2018).

This study focused on *Dasyatis pastinaca*, a medium-sized stingray found in the northeastern Atlantic, from the British Isles to Mauritania, and in the Mediterranean (Last et al. 2016). This is a viviparous stingray of conservation interest, as it is currently catalogued as Vulnerable by the IUCN Red List (IUCN 2020). A long-term acoustic telemetry data set was used to study this species, collected in the Professor Luís Saldanha Marine Park (LSMP), a coastal marine protected area off Portugal, to evaluate if aggregations are formed at specific locations and if so, whether they represent passive gatherings or non-random, socially driven associations. This species is seasonally present in the LSMP, as individuals migrate to the nearby Sado estuary roughly between March and April until October/November (Kraft et al. 2023), which allowed us to compare inter-migratory periods and test the stability of associations and space use over time. Finally, these results were discussed in the context of the conservation of this species in coastal marine protected areas (MPAs) like the LSMP.

Materials and methods

Study area

The LSMP covers 53 km^2 and extends over 38 km of coastline. It is organised into three different protection levels: a total protection area -or marine reserve- of 4.3 km^2, four partial protection areas that cover a total of 21 km^2 and three complementary protection areas or buffer areas of a combined 28 km^2 (Fig. 1). Entrance and any kind of fishing are prohibited in the total protection area. In the partial protection areas, octopus traps and jigs are allowed beyond 200 m from the coastline, while in the buffer areas only local licensed fishing boats under 7 m can operate (Fig. 1).

Terminology

In the context of this study, co-occurrence was defined as "the incidental or deliberate presence of at least-two

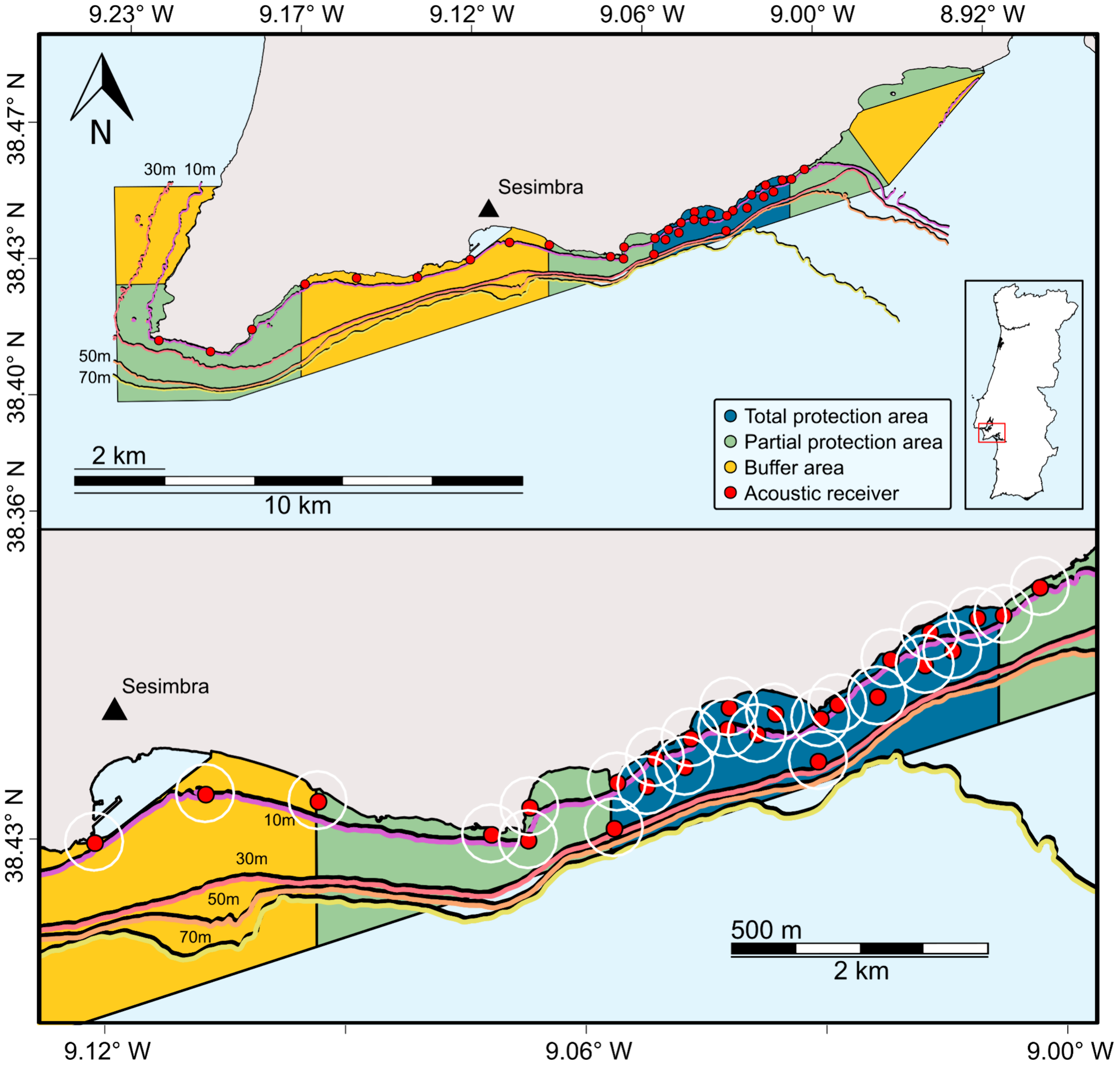

Fig. 1 Top panel: Overview of the Professor Luis Saldanha Marine Park, its three different protection levels, and placement of acoustic receivers (red). Bottom panel: zoom-in to the denser portion of the acoustic array, centred in the total protection area. Detection range of 200 m indicated by white circles; isobaths are colour coded. Map created in R

individuals within the same spatial and temporal boundaries" and aggregations as "the co-occurrence of two or more individuals in space and time due to the deliberate use of a common driver" (McInturf et al. 2023). Following these definitions, their drivers can be social (i.e., interactions with other individuals) or non-social, like as a result of environmental factors such as resources, habitats, and other abiotic conditions (McInturf et al. 2023). To investigate aggregations, the co-detection of two or more individuals at the same receiver during the same time window was used. Social network analysis was interpreted as a co-occurrence network analysis and used a gambit-of-the-group approach, where all individuals in a group were assumed to be associated (Whitehead and Dufault 1999). The term "association" was used to refer to the co-detection of individuals in the context of network analysis, and "dyads" to refer to pairs of individuals.

In this study, the definitions of co-occurrence, aggregation, association, and dyad do not necessarily represent socialization because the resolution and type of data required to confidently assess this was lacking. Although social interactions can drive aggregations, and could still be a possibility in this case, they were interpreted with this caution in mind. Additionally, elasmobranch aggregations are frequently driven by asocial factors like habitat or resource availability, predator avoidance, resting habits, or synchronized patterns of activity (Jacoby et al. 2012; Palacios et al. 2023). Similarly, because of the benthic nature of the study species, establishing a direct equivalency between simultaneous detection and social interaction greatly increases the chances of false positive interactions (Mourier et al 2017).

Tagging and tracking

Individuals were captured in the full and partial protection areas using monofilament trammel nets in 2019 (supplementary material 1). The trammel nets were 500 m in length and 1.6 m in height, with 100 mm inner panels of stretched mesh and outer panels of 600 mm. The fishing gear was deployed at depths between 5 and 40 m, mostly inside the fully protected area and additionally in the partially protected area. Deployments were always in the morning and soaking time was around 24 h. Individuals were brought on board and placed into a container filled with seawater that was changed after every individual. First, a hydrophone was used to detect previously tagged individuals. A measuring tape was used to obtain dorsal total length (TL), dorsal disc width (DW), and clasper length for males. A 2 cm incision was made in the peritoneal cavity using a scalpel to insert the tags and closed the incision using absorbable suture. Three types of Innovasea 69 kHz acoustic tags were used, V9, V13, and V9P with pressure sensor, based on individual size and tag availability. Respective expected battery lifetimes were 651, 1317 and 404 days according to the manufacturer. Additionally, individuals were fitted with a disc tag on the edge of the pectoral fin (www.floytags.com) with a unique ID number and contact information.

The acoustic array was composed of Innovasea VR2W acoustic receivers deployed throughout the LSMP (Fig. 1). Receivers were deployed on a variety of bottom types, which are distributed in patches throughout the area (supplementary material 1). Most receivers were on medium-grained sand (the largest patches), followed by fine-grained sand, coarse-grained sand, and mixed sand that stretched over the outer limit of the array. Other habitats within detection range of the receivers were nearshore reefs, algae on rocks, and muddy sand. Receivers were at depths that ranged between 5 and 17 m (supplementary material 1). Previous studies showed code detection efficiency of 0.54 at 250 m (Abecasis 2013) and no major variation in detection efficiency was found from environmental variables and/or background noises, so it was assumed to be constant across the receiver array (Abecasis et al. 2014). Based on this, a conservative detection range of 200 m was adopted.

Data analysis

For this study, a subset between 23/10/2019 to 04/12/2020 of a larger acoustic telemetry data set on *D. pastinaca* was used to ensure that all individuals had the same probability of being detected throughout the analysed period (full detection plot in supplementary material 2). This avoids biases from individuals entering the studied group later or leaving it for external reasons (e.g., fishing, battery depletion). Before running analyses, the data were filtered and prepared. The first 24 h of detections of each individual were deleted to remove possible anomalies induced by the fishing and tagging processes. To answer our research questions, the data were organized in three sets to study aggregations and perform the co-occurrence network analysis: the first set contained the complete data set with all detections from the LSMP; the second set included the detections obtained in the LSMP during the period before migrating to Sado (LSMP period 1); and the third data set contained the detections obtained in the LSMP during the period after returning from Sado (LSMP period 2). The detections from Sado were not considered because of the sparsity of the array.

Aggregations

The number of individuals co-detected at the same receiver every 15 min was used as a proxy to study aggregations. To assess the spatial distribution of aggregation sizes in the LSMP, the cumulative number of individuals co-detected per interval per receiver were calculated for the study duration and plotted to characterize the distribution of the different aggregation sizes and their frequencies. To investigate the variation of co-detections over time, the daily maximum number of co-occurring individuals at any receiver was obtained. The variation of aggregation size per diel phase was investigated with a Generalized Linear Mixed-Effects Model as implemented in the R package lme4 (Bates et al. 2015). Diel phase (daytime, night, and twilight) was used as fixed effect and receiver as random effect.

Co-occurrence network analysis

Co-occurrence networks were created using the R package asnipe (Farine 2013). Considering the 200 m detection range defined for the VR2W receivers, two or more individuals were determined to be co-occurring if they were detected within this range during the same 15 min window. Although the detection range is too large to confidently determine if two individuals were actually associated, this is offset by the numerous receivers in the array and the long-term nature of the data set, i.e., it should be detected if individuals are actively moving together through the array. The simple ratio index (SRI) was used to weigh network edges. The SRI calculates the probability that individuals A and B are observed together given that at least one of them has been detected (Cairns and Schwager 1987). This index is estimated by dividing the number of times individuals A and B were detected together at the same receiver (x) by the sum of x, plus the times A was detected, and B was not (y_A), plus the times B was detected and A was not (y_B), and when A and B were both detected but not associated, i.e., A and B were at different receivers (y_{A+B}). The formula is: $x/(x+y_A+y_B+y_{A+B})$.

Next, a data stream randomization process was done to test whether the observed network is a result of individuals randomly associating or if it reflects true preferred associations among individuals. For this, the observed association matrix was randomized 10 000 times, and to account for space (i.e., if individuals were randomly occurring at the same sites), randomizations were done among individuals co-detected at the same receiver (therefore, no individuals were randomly shuffled as the structure of the data was conserved). Then, the standard deviation (SD) of each matrix was calculated. SD was used to detect non-random associations because if preferred associations are present, these usually have an association value that is higher than expected for a random association (Farine and Whitehead 2015). Such a network will have a higher SD than a network with only random associations, which would have a low SD. A p value was calculated as the proportion of randomized SDs equal or greater than the observed SD at a significance level of 0.05.

To investigate changes in associations during the day, networks were created for daytime, night, and twilight by separating detections according to diel phase using the R package suncalc (Thieurmel and Elmarhraoui 2019). The time between sunrise and sunset (appearance and disappearance of the sun over the horizon) was considered as “daytime”, morning and evening twilight collectively as “twilight”, and the period between evening twilight and morning twilight as “night”. A Mantel test was performed among networks for each period and diel phase to evaluate if the observed associations are similar among them using the R package vegan (Oksanen et al. 2022).

Reuse of space

To assess if the *D. pastinaca* individuals used the same areas before and after their migration, individual kernel utilization distributions (KUD) were calculated using the R package adehabitatHR (Calenge 2006) with a fixed bandwidth of 200. Because these results will be compared with the associations, the centres of activity (Simpfendorfer et al. 2002) used to estimate KUDs were calculated using the same time window of 15 min. To investigate inter-migratory spatial overlap, separate KUDs were calculated for the *D. pastinaca* that were present before and after their migration. Then an index of reuse was calculated following Morrissey and Gruber (1993), defined as the overlap (intersect) between both areas divided by the cumulative area occupied during both periods.

Results

The study period spanned between 23/10/2019 and 04/12/2020 (409 days) and included 14 individuals (9 males and 5 females, Table 1). Of these individuals, *D. pastinaca* (Dp) 19 (female) was the only one to never be co-detected with other individuals as it was detected only a few times before leaving the study area or dying. The detection plot of the data shows the two periods in the LSMP (Fig. 2).

Aggregations

Because of the low number of individuals that were detected after their migration to Sado (n = 7, 50% of total), aggregations were only assessed for the period before migration. Throughout this period, aggregations of up to 9 individuals were detected at the same receiver. Aggregation sizes of 2–4 were relatively evenly distributed across the array, and more frequently to its western half. As aggregation size increased, their distribution became more skewed towards the west of the array (Fig. 3). A similar pattern was also noted in the number of times each aggregation size was detected, as a same aggregation size tended to be more frequently detected by receivers more to the west side of the fully protected area.

Table 1 Biological data (disc width [DW]) and tracking data (number of days detected [D_d], days between first and last detection [D_i], total monitoring time [D_t], and residency index [IR] as D_d/D_t) of the *Dasyatis pastinaca* individuals used in this study. Tracking data corresponds to the detections from the Luíz Saldanha Marine Park

Dasyatis pastinaca n°	DW (cm)	Sex	First detection	Last detection	D_d	D_i	D_t	I_R
Dp 03	30.8	Female	22-10-2019	10-03-2020	18	141	409	0.04
Dp 05	35.7	Male	02-11-2019	03-12-2020	171	398	409	0.42
Dp 06	35.5	Male	02-11-2019	02-04-2020	153	153	409	0.37
Dp 07	31.1	Male	24-10-2019	04-04-2020	160	164	409	0.39
Dp 08	30.2	Female	24-10-2019	25-02-2020	105	125	409	0.26
Dp 11	36.5	Female	22-10-2019	08-11-2020	110	384	409	0.27
Dp 12	36.0	Male	20-11-2019	22-02-2020	75	95	409	0.18
Dp 13	39.0	Male	13-11-2019	03-12-2020	113	387	409	0.28
Dp 15	39.0	Male	10-11-2019	03-12-2020	134	390	409	0.33
Dp 16	37.5	Male	08-11-2019	03-12-2020	181	392	409	0.44
Dp 17	39.5	Female	23-11-2019	18-11-2020	99	362	409	0.24
Dp 18	41.0	Male	22-10-2019	03-04-2020	135	165	409	0.33
Dp 19	38.5	Female	–	–	–	–	409	–
Dp 20	42.0	Male	08-11-2019	03-12-2020	177	392	409	0.43

Fig. 2 Abacus plot of the *Dasyatis pastinaca* individuals used in the present study, between 23/10/2019 and 04/12/2020. Individuals Dp 03 to Dp 08 were tagged earlier in 2019, and individuals Dp 11 to Dp 20 were tagged at the beginning of the time window used in this study. Detections are colour-coded per receiver location: fully protected area (blue), partially protected area (green), buffer area (yellow), and Sado estuary (red)

Of the 8524 aggregations of 4 or more individuals co-detected at a same receiver every 15 min, in 1113 (13%) the number of males and females was equal, and in 164 (1.9%) the number of females was greater than the number of males. In aggregations of 5 individuals, females and males occurred in same numbers only in 3 instances, while the majority of individuals in all instances of aggregations of 6 individuals and above were males. No statistical analyses of these results were made because of the uneven sex ratio in the sample (9 males and 4 females).

All aggregation size classes were detected in all diel phases (daytime, night, and twilight). The Generalized Linear Mixed-Effects Model found differences in aggregation size among diel phases. Aggregation size was larger during daytime than at night, although by a small difference (diff. 3.2%, $p < 0.001$), but not compared to twilight (diff. 0.9%, $p = 0.19$) (supplementary material 3). The daily maximum number of co-detected individuals varied over time, from 1 to 9 individuals (Fig. 4). Daily maximum aggregation size was equal or larger than 50% of the daily available individuals (number of individuals that were detected at least once on a given day) in 64.5% of days (Fig. 4). Maximum daily aggregation sizes of 0 (no detections) were only obtained after the departure to Sado.

Co-occurrence network analysis

The co-occurrence network of the complete data set was composed of 13 connected individuals, 9 males and 4 females, representing 13 vertices and 75 edges (Fig. 5a). SRI values averaged 0.062 ± 0.082 and ranged from 0.0001 to 0.4035. The significantly higher mean SD ($SD_{obs} = 0.0797$; mean random SD = 0.0794; range 0.0792—0.0797; $p = 0.017$) indicated the presence of preferred associations in the observed network (supplementary material 4). For the networks per diel phase, average SRIs were 0.065 ± 0.085 for daytime, 0.064 ± 0.085 for twilight and 0.060 ± 0.080 for night. Associations were positively correlated among all diel phases (Mantel statistic r: 0.985–0.996, all $p < 0.001$ after 1000 permutations), suggesting that these were consistent across diel phases.

The network for the first period in the LSMP (Fig. 5b) had more nodes than the network of the second period (Fig. 5c) because some individuals progressively stopped being detected over time. Nevertheless, some similarities stand out, like the high association strength of the pair of individuals (dyad) Dp16-Dp20 and their relative isolation from the rest of the individuals in both periods. To compare the networks of each period, the 7 individuals that were

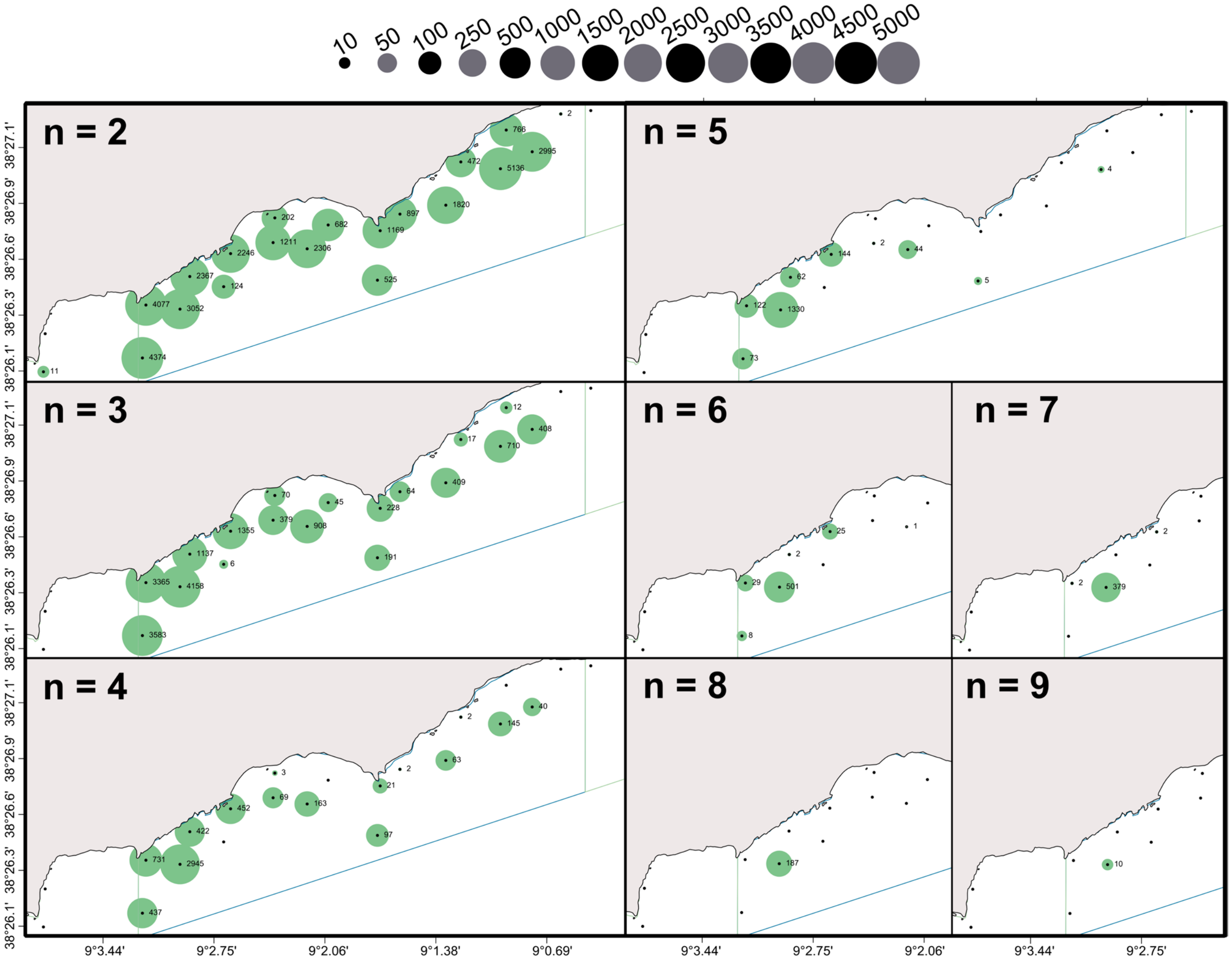

Fig. 3 Cumulative co-detections of *Dasyatis pastinaca* individuals per receiver throughout the first period in the Luiz Saldanha Marine Park. Circle size is proportional to the number of observations and plotted in logarithmic scale for illustration purposes (scale values are not transformed). For aggregation sizes of 6 to 9 individuals only the western side of the fully protected area is shown, where these were detected. Black dots indicate the positions of receivers

detected in both periods were selected to perform a Mantel test. This resulted in a positive correlation among associations (Mantel statistic r: 0.867, p = 0.007). In fact, the spatial distribution also appears to be similar between the two periods, as shown by the respective networks arranged by average position per individual (Fig. 5d, e). In these, the Dp16-Dp20 dyad was spatially segregated from the rest of the network, and the position of all individuals relative to each other was generally similar between both periods. The period in Sado was not included because a smaller acoustic array was used, precluding direct comparisons.

Considering that some dyads maintained a high level of association after migration, the co-detections of Dp13-Dp15 and Dp16-Dp20, two of the dyads with highest association values in both periods, were plotted to describe their area use and to illustrate two contrasting situations (Fig. 6). First, the area use of each dyad was calculated to illustrate the full extent of the space each individual used as the merged 95% KUD of the individuals in each dyad. This resulted in a large area for Dp13-Dp15 that extended throughout most of the array, and a small area for Dp16-Dp20 which was restricted to the east of the array. Regarding the co-detections of the individuals in each dyad, the co-detections of Dp13-Dp15 concentrated on the western end of their combined KUD area, while those of Dp16-Dp20 were noted throughout their combined KUD area. A few co-detections of both dyads were registered in the middle of the array during the first period, but Dp13-Dp15 was scarcely detected here. Similar scenarios were observed during both inter-migratory periods, suggesting consistency in their space use and areas of co-detection. The dyad-level indices of reuse were 55% for Dp13-Dp15 and 72% for Dp16-Dp20. The lower value of the

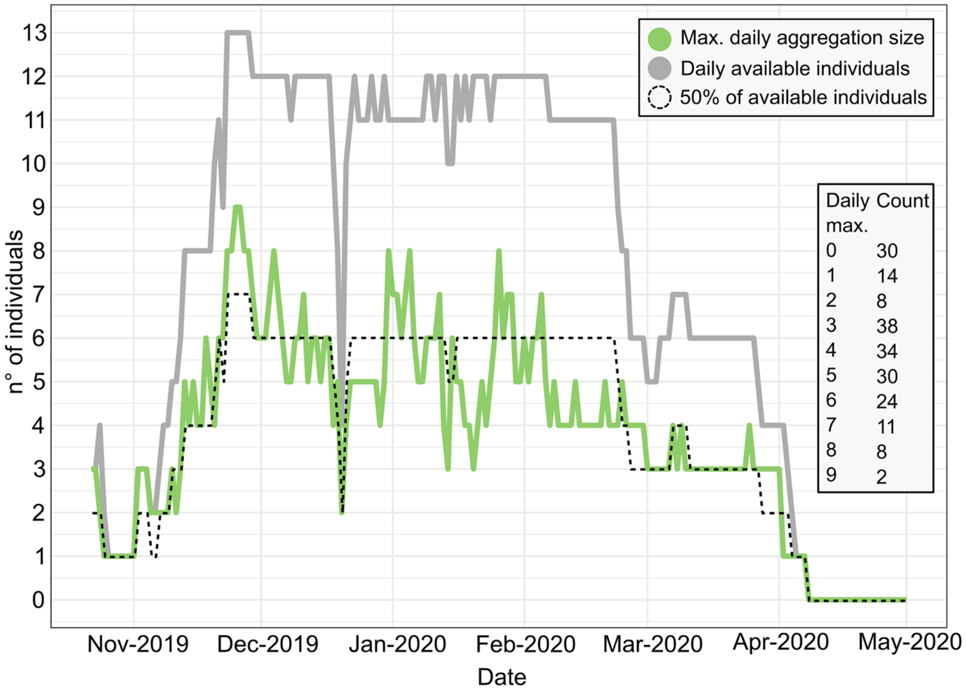

Fig. 4 Daily maximum number of co-detected *Dasyatis pastinaca* individuals in the Luiz Saldanha Marine Park (green line) before the migration to the Sado estuary. The grey line indicates the daily maximum number of available individuals in the marine park (i.e., total number of tags detected in the array each day), and the dashed line indicates 50% of this value (rounded up to only have integers). This did not affect the estimated percentage of daily maximum aggregation size greater than 50% of the available tags

former occurred because of the smaller 95% KUD registered in the second period.

Reuse of space

After their initial period in the LSMP, seven individuals (50%) were detected returning, therefore the IOR between both periods was calculated for these individuals (Table 2). A wide range of values was obtained, the lowest being 18%, but in general the area of reuse was high, averaging an overlap of 54 ± 21% for the 50% KUDs and 64 ± 11% for the 95% KUD.

Discussion

In this study, previous findings that described the seasonal philopatry of *D. pastinaca* to this area (Kraft et al. 2023) were expanded to explore the finer-scale dynamics of aggregations and associations among individuals of this species. Associations were investigated and compared across years, allowing us to examine their long-term stability (i.e., across migrations). Although in this section these results will be interpreted considering the fact that the acoustic telemetry system that was used is not optimal for researching social interactions (Mourier et al. 2017), the longevity of the data set allowed us to obtain interesting insights into the potential social and spatial patterns of *D. pastinaca*.

Aggregations and associations

The first objective of this study focused on identifying and characterizing spatiotemporal patterns of aggregation. Although a low number of tagged individuals was used for this purpose (n = 14), an aggregation site was detected to the west of the array. Here, up to nine *D. pastinaca* were co-detected at the same receiver, representing 64% of tagged individuals or 69% of available individuals on the day of occurrence. Half or more of the daily available individuals were co-detected at least once in 67% of days, indicating that *D. pastinaca* formed larger aggregations with some regularity. An important factor for the interpretation of these results is the presence of untagged *D. pastinaca*, therefore the true aggregation size is unknown and may encompass more individuals. Similarly, the existence of other aggregation sites is also unknown. For this, the fine-scale spatial fidelity of individuals in both inter-migratory periods may provide some clues. For example, considering the presence of unaccounted-for individuals, the spatially isolated Dp16-Dp20 dyad may be part of another spatially separated aggregation.

The second objective of this study was to evaluate whether non-random, potentially social associations are formed between individuals within aggregations, and the co-occurrence network analysis suggested the existence of these. Considering the low number of tagged individuals, it is noteworthy that strong associations were detected among the generally low SRI values. The co-detection of pairs of individuals at receivers throughout the acoustic array also reflects this, which can be interpreted as a

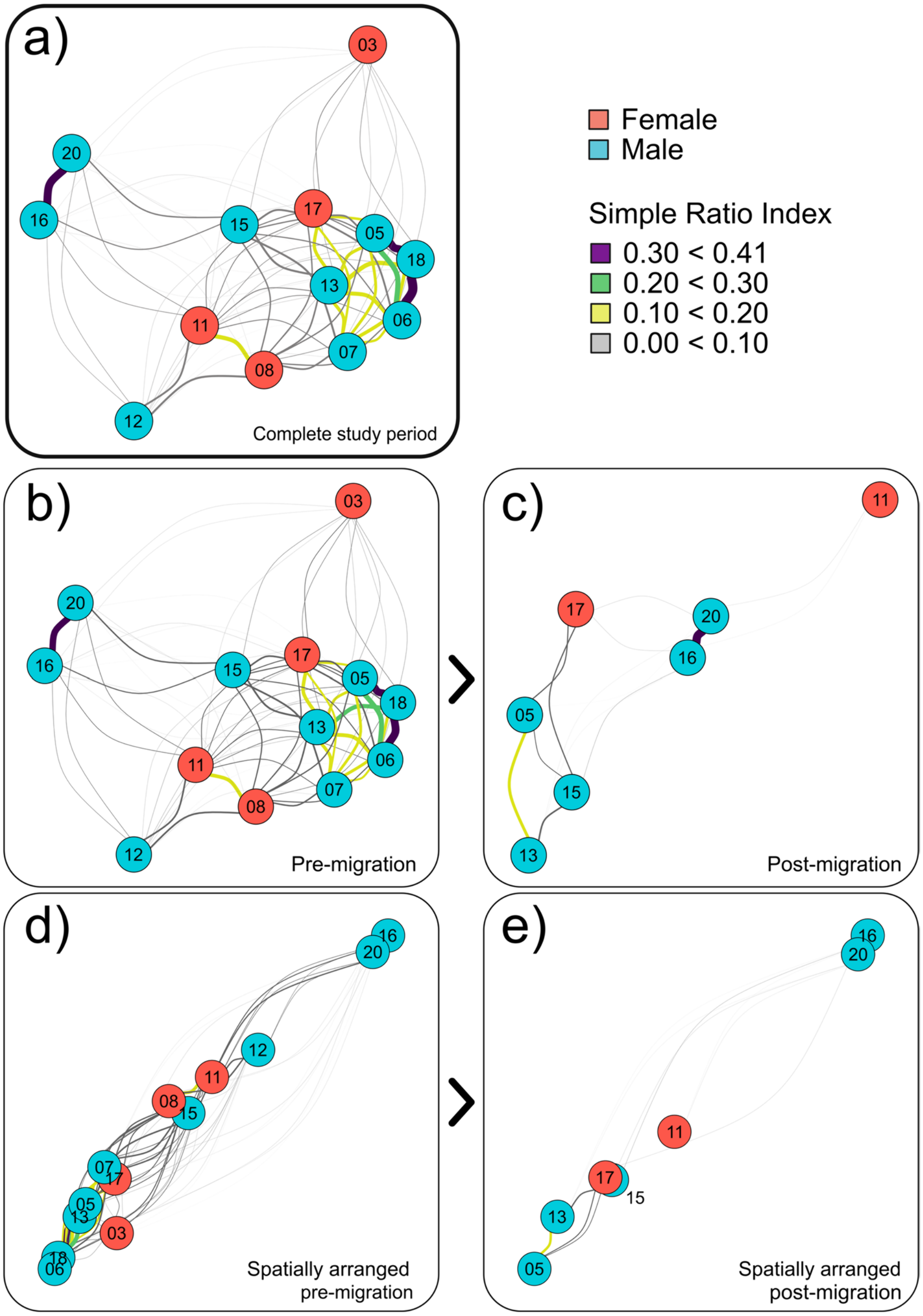

Fig. 5 Co-occurrence networks of *Dasyatis pastinaca* for a) the complete study period, b) Luiz Saldanha Marine Park (LSMP) before the migration to Sado and c) LSMP after the return from Sado; d) and e) show the same networks (b and c, respectively), but spatially organized based on the average position of each individual per period. Dp 19 left quickly after tagging and is not shown

signal of synchronous movement of actively associating individuals. The observed associations were also stable across inter-migratory periods, as shown by the Mantel test. Whether these associations are maintained during their reproductive season or are resumed after returning to the LSMP remains to be evaluated. Regardless of this, these results indicate that the extended seasonal migration this species undergoes (Kraft et al. 2023) did not disrupt the associations detected in the present study.

Other species in the family Dasyatidae have also been observed forming non-random associations, at least under specific conditions such as provisioning sites (Furst 2011; Pini-Fitzsimmons et al. 2021). In these situations, individuals have displayed complex behaviours in the form of different kinds of interactions and social structures akin to despotic societies or size-based social structures (Furst 2011; Pini-Fitzsimmons et al. 2021).

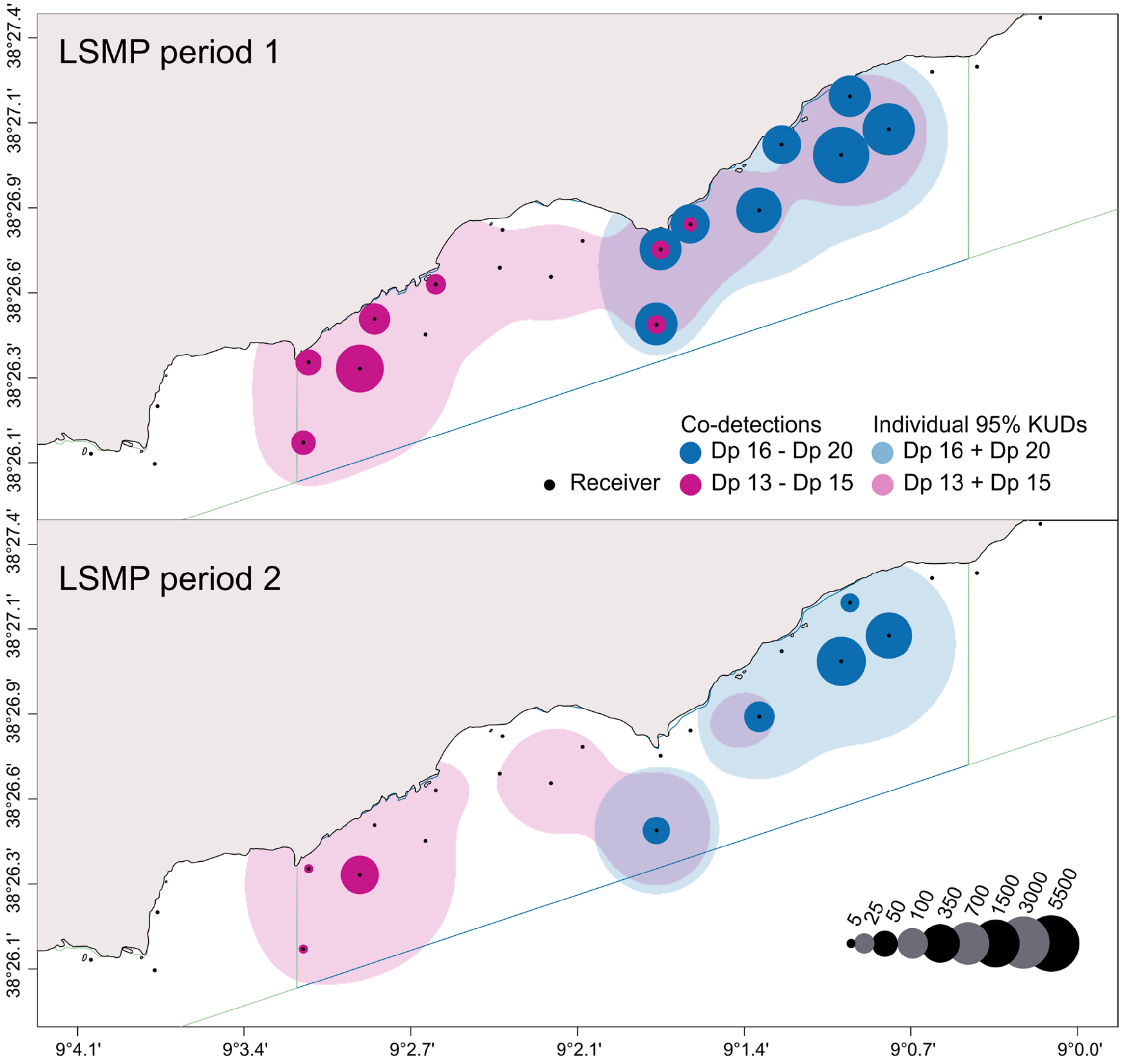

Fig. 6 Receivers at which the *Dasyatis pastinaca* dyads Dp13-Dp15 and Dp16-Dp20 were detected in the Luiz Saldanha Marine Park (LSMP) during the period before migrating to the Sado estuary (LSMP period 1) and after returning (LSMP period 2). The combined 95% Kernel Utilization Distribution areas (KUDs) of the individuals in each dyad are also shown to display the total area covered. Circle size is proportional to the number of observations and plotted in logarithmic scale for illustration purposes (scale values are not transformed)

Table 2 Index of reuse (IOR) for each *Dasyatis pastinaca* that was detected in both periods in the Luiz Saldanha Marine Park, before and after their migration to Sado. Kernel Utilisation Distribution (KUD) at the 50% and 95% levels, their area of overlap, and the area of their combined surfaces are also shown. All units are in km^2 except for the IOR which is in percentage

Dasyatis pastinaca n°	50% KUD (km^2)					95% KUD (km^2)				
	Period 1	Period 2	Total	Overlap	IOR (%)	Period 1	Period 2	Total	Overlap	IOR (%)
Dp 05	0.38	0.27	0.46	0.20	44	1.92	1.30	2.17	1.05	48
Dp 11	0.73	0.93	1.40	0.26	18	3.04	4.99	5.21	2.82	54
Dp 13	0.21	0.21	0.23	0.19	83	1.24	1.18	1.36	1.06	78
Dp 15	0.81	0.35	0.81	0.35	43	3.82	2.69	4.06	2.45	60
Dp 16	0.40	0.29	0.40	0.29	71	1.99	1.72	2.12	1.58	74
Dp 17	0.50	0.37	0.53	0.34	65	2.94	3.27	3.83	2.38	62
Dp 20	0.50	0.32	0.53	0.29	54	1.96	1.84	2.26	1.55	69
Mean	0.51	0.40	0.64	0.27	54	2.41	2.43	3.00	1.84	64
SD	0.21	0.24	0.38	0.06	21	0.88	1.36	1.38	0.71	11

The results presented here complement previous findings on the migratory movement pattern of *D. pastinaca* (Kraft et al. 2023) by using a different approach to characterize their fine-scale movements and the possible social drivers behind them. In combination, these results illustrate the intricacy and stratification of their spatial ecology. Future studies could use a more suitable approach to study the association patterns among individuals in this species, for example proximity loggers or receivers with a shorter detection range (Mourier et al. 2017). Considering that aggregations are a prerequisite for social interactions (Jacoby et al. 2012; Palacios et al. 2023), the site where *D. pastinaca* was observed to aggregate in large numbers could be a candidate to start such a study.

Ecological interpretation of aggregations

Elasmobranchs are known to aggregate across a variety of habitats (McInturf et al. 2023), and several factors can underlie this process. They can passively aggregate as an outcome of habitat or prey distribution, or as the result of synchronized diel or seasonal movements (Jacoby et al. 2012). An example of the latter is the mentioned migration of *D. pastinaca* to the Sado estuary, likely as a response to environmental cues such as temperature (Kraft et al. 2023). Variables like currents, temperature and visibility can play a role in the formation of aggregations, gathering individuals as they seek sites to rest or to accelerate gestation (Jirik and Lowe 2012; Meese and Lowe 2019; Semeniuk and Dill 2005).

Despite the observed difference in *D. pastinaca* agrgegation size per diel phase, the estimated variation (0.9–3.2%) is likely not biologically significant. Although visibility can have an influence in the formation of aggregations, such as through changes in turbidity and environmental light conditions (Semeniuk and Dill 2005), this may not always be enough to increase the aggregation size to large numbers. A study on *Pastinachus ater* showed that this species is more prone to form aggregations in low visibility conditions, but these groups were of around 3 individuals (Semeniuk and Dill 2005). Drawbacks also exist in the formation of large aggregations, like increased conspicuousness and interference among individuals (Semeniuk and Dill 2005), which may explain why large aggregations were rarer. However, this could also be an artifact of the study design. In another example, *Triakis semifasciata* and juvenile *Carcharhinus melanopterus* mostly aggregate during the day, but with the exception of June for the latter, when they aggregate at night as well (Heupel and Simpfendorfer 2005; Nosal et al. 2014).

In the present study, the seafloor where the largest aggregations of *D. pastinaca* were seen was mostly fine, medium, and mixed sand, which are also among the most common bottom types in the LSMP (Henriques et al. 2015) (supplementary material 1). Similarly, most receivers were deployed at depths of around 5–10 m (supplementary material 1), making significant depth-related temperature differences unlikely. This suggests that if the availability of suitable habitat had an effect, it may not be the sole driver of their spatial distribution.

Social factors can also drive group formation in elasmobranchs. Some species engage in active social associations during specific events of their life cycle, like reproduction (Sims et al. 2000). Indeed, *D. pastinaca* has been reported to form breeding aggregations in which behaviours like courtship have been documented (Chaikin et al. 2020; Morey et al. 2006). In the present study area, reproduction likely occurs in the nearby Sado estuary (Kraft et al. 2023), therefore the observed aggregations were likely not for reproductive purposes. Although the observed aggregations were mostly composed of males, these may be an outcome of the unbalanced sex ratio in the studied data subset (9:4), as it did not significantly deviate from an expected 1:1 ratio in the original data set (Kraft et al. 2023). This uneven sex ratio makes it difficult to confidently evaluate whether the observed male-dominated co-occurrences are a natural phenomenon or an artifact of sampling bias. Additionally, discussing the nature of these co-occurrences, whether they are aggregations (non-social) or instances of social grouping, and the advantages for male *D. pastinaca* is limited because of the large uncertainty in the position of the individuals. Male aggregations or social groups in elasmobranchs have been scarcely reported in the literature compared to females (Jacoby et al. 2012).

An important function of aggregations is predator avoidance (e.g., Heupel and Simpfendorfer 2005). This can be particularly important for stingrays when resting, and aggregating allows them to reduce risk by engaging in protective formations, obtain early warning signs and coordinate their escape (Semeniuk and Dill 2005). Although the anti-predator advantages of aggregating greatly rely on the dilution effect of gathering in large numbers, which can occur in non-social situations, in some cases preferential associations can also direct antipredator behaviour. For example, *Pastinachus ater* has been reported to actively choose to rest near individuals of *Himantura australis* because of the latter's faster escape response to predators (Semeniuk and Dill 2006). This indicates an active neighbour selection when deciding on a resting site.

Another important role of social grouping is the transfer of information among group members, an ability that stingrays are likely to possess. Laboratory experiments on *Potamotrygon falkneri* (Potamotrygonidae) have shown this species is capable of social learning and imitation (Thonhauser et al. 2013), which in wild stingrays could mediate the transfer of information in the form of local enhancement (discovery of food patches by observing other group members, Thorpe (1965)). This has also been shown for spatially-organized social communities of *Carcharhinus amblyrhynchos*, in which information is also socially transferred in the form of local enhancement (Papastamatiou et al. 2020).

In conjunction with the previous drivers, social factors can also mediate the spatial distribution of individuals and aggregations. Elasmobranchs are capable of organizing into spatially delimited communities that can arise from non-social factors but also from active partner choice, for example as seen in *Mobula alfredi* (Perryman et al. 2022) and in *C. melanopterus* (Mourier et al. 2012). Other stingrays also display at least some form of spatial memory and can construct spatial maps of their surroundings (Schluessel and Bleckmann 2005), which would enable them to identify spaces and return to known sites after traveling to other areas. This is supported in the present study by the similar average positions and generally high IOR values observed in the two inter-migratory periods, reflecting that some level of fine-scale spatial fidelity that may organize individuals into separate communities was maintained (Chapman et al. 2015).

Conservation and management

Although *D. pastinaca* is not targeted by fisheries in this region, they are nonetheless captured as bycatch in fishing operations targeting other species like flatfishes (Baeta et al. 2010; Batista et al. 2009). In relation to the LSMP, the aggregations formed by *D. pastinaca* were detected by interior receivers in the full protection area, suggesting this aggregation site may be protected from fishing. The neighbouring partial protection areas provide similar protection, as the activities allowed in them do not represent a risk to this species. However, the actual positions of the individuals in these aggregations and their closeness to the marine park's border remains to be better assessed, as the current study design only confirms that they were inside the detection range of a receiver. This is relevant to clarify because the distribution of elasmobranchs can directly influence their susceptibility to fishing (Mucientes et al. 2009; Wearmouth and Sims 2008), which is important information for the management of MPAs.

Susceptibility increases at aggregation sites because the concentration of individuals inside a delimited area facilitates their capture in larger numbers (Palacios et al. 2023), and the closeness of individuals to an MPA's border may exacerbate an individual's (and the aggregation's) exposure to risk (Villegas-Ríos et al. 2021). In turn, this removal of individuals in large numbers can have detrimental effects on the social processes of a population beyond the reduction in numbers. Social learning relies on the structure of social groups, and the disturbance of this structure can reduce the social information available in a population, affecting its adaptability and survival (Wilson and Giske 2023). Excessive harvesting can lead, for example, to the loss of social nodes through which relevant information travels, such as related to feeding or migration routes, and even to the disruption of the general social structure (Villegas-Ríos et al. 2022). Therefore, to avoid irreversible changes in the social processes of populations, and the consequences this can have, understanding the dynamics of aggregations and associations is needed to push for improvements in their management and conservation (Villegas-Ríos et al. 2022).

Conclusion

By building on previous research, this study provided important insights into the aggregation dynamics and potentially social associations of *D. pastinaca* at a site of seasonal philopatry. This study revealed an inter-migration stability in *D. pastinaca*, both in the form of preferred associations that persisted over their seasonal migration and in the form of multi-seasonal area reuse within the MPA as indicated by the acoustic detections at receivers.

Despite the limitations of the acoustic telemetry system that was used and the caution with which these results were interpreted, these findings still offer interesting insights into the potential social behaviour of this species and of elasmobranchs in general, which are still scarcely studied in this aspect.

Finally, monitoring and protecting aggregation sites that were detected or are yet to be found can aid the conservation objectives of the LSMP, and can be expanded to other coastal MPAs. This can help in improving the efforts to reduce the capture of individuals of this species and to protect habitats that are critical to them, ensuring the long-term sustainability of this *D. pastinaca* population.

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Author contributions JM, DA and SK conceptualized and designed the study. SK, ACW and DA captured and tagged the individuals of this study and acquired the data. SK, ACW and DA maintained the receiver network. SK conducted the analyses, prepared the figures for publication, and drafted the article. SK, ACW, DA and JM interpreted the data. SK, ACW, DA and JM revised it critically for important intellectual content. All authors have approved the final article.

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Data availability The data used in this work is deposited in the European Tracking Network data portal (http://www.lifewatch.be/etn/), developed by the Flanders Marine Institute as part of the Flemish contribution to LifeWatch. The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

Declarations

Conflict of interest The authors have no competing interests to declare.

Ethical approval The authors declare no conflicts of interest. Capture, handling, and tagging was done under permits of the Portuguese Institute for Nature Conservation and Forests (permits n°145/2019/CAPT; 13/2020/CAPT; 70/2021/CAPT) and the Veterinary General Directorate (permit n° 2018–08-29 015730). Tagging procedures were also approved by the Animal Welfare Committee of the Centro de Ciências do Mar (CCMAR—ORBEA).

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