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Residency, home range and inter-annual fidelity of three coastal fish species in a Mediterranean coastal lagoon

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Abstract :

In the Gulf of Lion (NW Mediterranean), fish species such as gilthead sea bream Sparus aurata, European seabass Dicentrarchus labrax, and salema Sarpa salpa show seasonal occupation of coastal lagoons, presumably as feeding grounds during their adult life stage. The role of the lagoons in these species' life cycles remains unknown, particularly with respect to their residency, space-use, and inter-annual fidelity. Using acoustic telemetry, the movements of 72 seabream, 58 seabass, and 81 salema were monitored over four years within Prévost Lagoon (Hérault Department, Occitania Region), to characterise (1) the main seasonal patterns of space use inside the lagoon and (2) their annual migrations between the lagoon and the sea. Overall, all three species were highly resident in the lagoon during the spring/summer foraging season; seabass was the only species that also displayed high residency to the lagoon throughout the winter breeding season. The three species showed differences in their space use, although they all mainly inhabited the deep lagoon centre and adjacent shellfish farms, with very small individual home ranges (mean ± SD, 0.12 ± 0.06 km2 over all species). All species showed some inter-annual fidelity to the lagoon (>43% at minimum for seabream) although these fidelity rates were probably underestimated due to fishing mortality, which is probably high during the winter breeding season. Overall, this study reveals that coastal lagoons are key foraging habitats for these species in the Gulf of Lion. The high residency and inter-annual fidelity suggest that any increase of anthropogenic pressure within the lagoon could negatively impact these fish populations. Therefore, protection of such productive habitats could be beneficial for long-term management of emblematic coastal species and the fisheries that they support.

Keywords : Multi-species, Acoustic telemetry, Space utilization, Migration, Foraging, Reproduction

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List of symbols and abbreviations:

-RI: Residency index
-EFS: Expected Foraging Season
-EBS: Expected Breeding Season
-KUD: Kernel Utilization Distribution

Introduction

Preserving marine biodiversity requires a thorough understanding of patterns of spatial and temporal variability of marine biota (Ward et al., 1999). For animals, understanding their movements is crucial in spatially structured populations (Morales et al., 2010) and for species that display large scale migrations (Putman, 2018). Fish movements are mainly shaped by their reproductive strategy or breeding behaviour (Sheaves et al., 1999; Bolden, 2000), food availability (Phiri & Shirakihara, 1999), predator and prey interactions (Gilliam & Fraser, 2001; Herbert-Read et al., 2015), and environmental parameters (Lucas & Batley, 1996; Garrett & Bennett, 1995). In an era of global erosion of marine biodiversity (Halpern et al., 2008), understanding movements is a fundamental element of conservation and resource management (Nathan et al., 2008, Collenge et al., 2010).

Acoustic telemetry uses transmitters attached to or implanted within an animal that emit coded ultrasonic signals that travel through water and can be logged by receivers (Heupel & Webber, 2012; Whoriskey & Hindell, 2016). With a suitable receiver network, this approach can provide fine-scale spatial information for coastal species (Heupel et al., 2006; Hussey et al., 2015). Acoustic telemetry has been particularly valuable for tracking movements of marine fishes at a fine scale in relatively enclosed inshore habitats, such as coastal lagoons (e.g. Abecasis & Erzini, 2008; Abecasis et al., 2009; Reyier et al., 2011; Wada et al., 2017; Noda et al., 2021).

Coastal lagoons are transitional ecosystems, between land and open sea, that provide many valuable ecosystem services (Erzini et al., 2022). In particular, they are important nurseries (Erzini et al., 2022) and seasonal feeding grounds for numerous species of marine fish. As nurseries, lagoons can provide good environmental conditions for growth and survival of post-larvae at settlement and for the ensuing juveniles (Beck et al., 2001; Gillanders et al., 2003; Vasconcelos et al., 2008; Tournois et al., 2017). The use of lagoons as seasonal feeding grounds by older life stages allows fishes to constitute reserves for overwintering and reproduction (Clark, 1998; Costa et al., 2002).

Of the 97 main species captured by the French coastal fishery in the Gulf of Lion (3 379 t in 2018; Weiss et al., 2019), three species comprised 24 % (814 t), namely gilthead seabream (*Sparus aurata*), seabass (*Dicentrarchus labrax*), and salema (*Salpa salpa*). These species provide almost 32 % of the fishery’s income (15 M€ in 2018, Weiss et al., 2019). They all occur in lagoons, although limited data is available on historical and current fishing pressure in the lagoons (Cataudella et al., 2015). There are currently no regional stock assessment or management measures for these species, mainly because of the lack of consistent long-term fisheries data (Mehanna, 2007; 2010; Fateh, 2018).

The Gulf of Lion is a large and highly productive continental shelf (14000 km²), characterized by an extensive complex of lagoons formed about 5600 years ago (Sabatier et al., 2010) that stretch more than 300 km along the French Mediterranean coast (Cataudella et al., 2015). The lagoons of the Gulf of Lion appear to play a key role as foraging grounds in the life cycle of seabass, gilthead seabream, and salema during their juvenile and adult stages (Elliott & Dewailly, 1995; Franco et al., 2006; Abecasis et al., 2012). A proportion of local adult populations migrates into the coastal lagoons at the onset of spring, to feed, grow, and establish reserves, then migrates back out in late autumn to reproduce at sea in winter (Lo Bianco, 1909; Barnabé, 1973; Lasserre, 1976, Anato & Ktari, 1983; Antolic et al., 1994; Tancioni et al., 2003; Mercier et al., 2012). Although the migratory cycle of seabream has been studied (Mercier et al., 2012), very little is known about seabass and salema (Abecasis et al., 2012, Lopez et al., 2015). Furthermore, the significance of lagoon habitats as foraging habitats for adult fishes during the life cycle of the three species remains poorly understood. Notably, little information is available about many key issues such as whether individuals are transient or resident at specific sites for extended periods; the scale of local movements; the level of intra- and inter-annual site fidelity, and whether migration events are driven by intrinsic or extrinsic factors. Patterns of habitat use can be remarkably complex, for example many fish species perform stochastic movements (apparently random out and back movements) between seasonal feeding grounds and the open sea, including *S. aurata* between coastal lagoons and the sea (Katselis et al., 2007; Nathan et al., 2008; Hansson & Akesson, 2014).

Multi-species tracking of fishes is challenging (Nash et al., 2013; Henninger et al., 2020), yet of particular relevance to identify hotspots for conservation because if an area is occupied intensively by several species with widely different life histories, it is likely to be of major ecological significance (Raymond et al., 2015; Lea et al., 2016). Gilthead seabream, seabass and salema have very different ecologies, life history traits, and levels of vulnerability to fishing pressure (Kara & Quignard, 2018a, Kara & Quignard, 2018b). Investigating space utilization and site fidelity of these species in a common lagoon foraging ground will provide decision makers with an improved understanding of the importance of these ecosystems for these species (Pendoley et al., 2014; Osgood & Baum, 2015; Mouillot et al., 2016).

We used acoustic telemetry to track the seasonal movements of 211 individuals from the three species, inside and outside of a lagoon in the Gulf of Lion over 4 years. The aim of the study was to investigate residency and space use in the lagoon at different spatio-temporal scales, and inter-annual fidelity to the lagoon after spawning seaward migrations.

2. Materials and methods

2.1. Study site

Prévost Lagoon (43° 31’ 13.70’’ N, 3° 54’ 33.31’’ E, Mediterranean Sea, Gulf of Lion, France) stretches out in a south west-north east direction near the town of Palavas-les-Flots (Figure 1). It is 3.3 km long and 0.8 km wide, with an average depth of 0.8 m (maximum 2 m) and is directly connected to the sea by the 30 m wide Prévost Inlet. It also has three connections to adjacent lagoons (Arnel, Pierre Blanche, and Mejean) forming a large lagoon complex. It has a wide (15 m) connection with the Rhône to Sète Canal in the middle north of the lagoon; a 12 m wide channel traversing Palavas-les-Flots in the south-west and a 1 m wide pipeline connection to the Pierre Blanche Lagoon. The Rhône to Sète Canal is connected to the Lez River, which feeds into the sea at Palavas-les-Flots as well as into the other lagoons surrounding Prévost. (Figure 1). Other indirect connections to the sea include the Rhône to Sète Canal that connects the ports of Frontignan, Palavas-les-Flots and Carnon. Bivalve farms (mussels and oysters) are located in the deeper part (2 m) of the lagoon near the inlet.

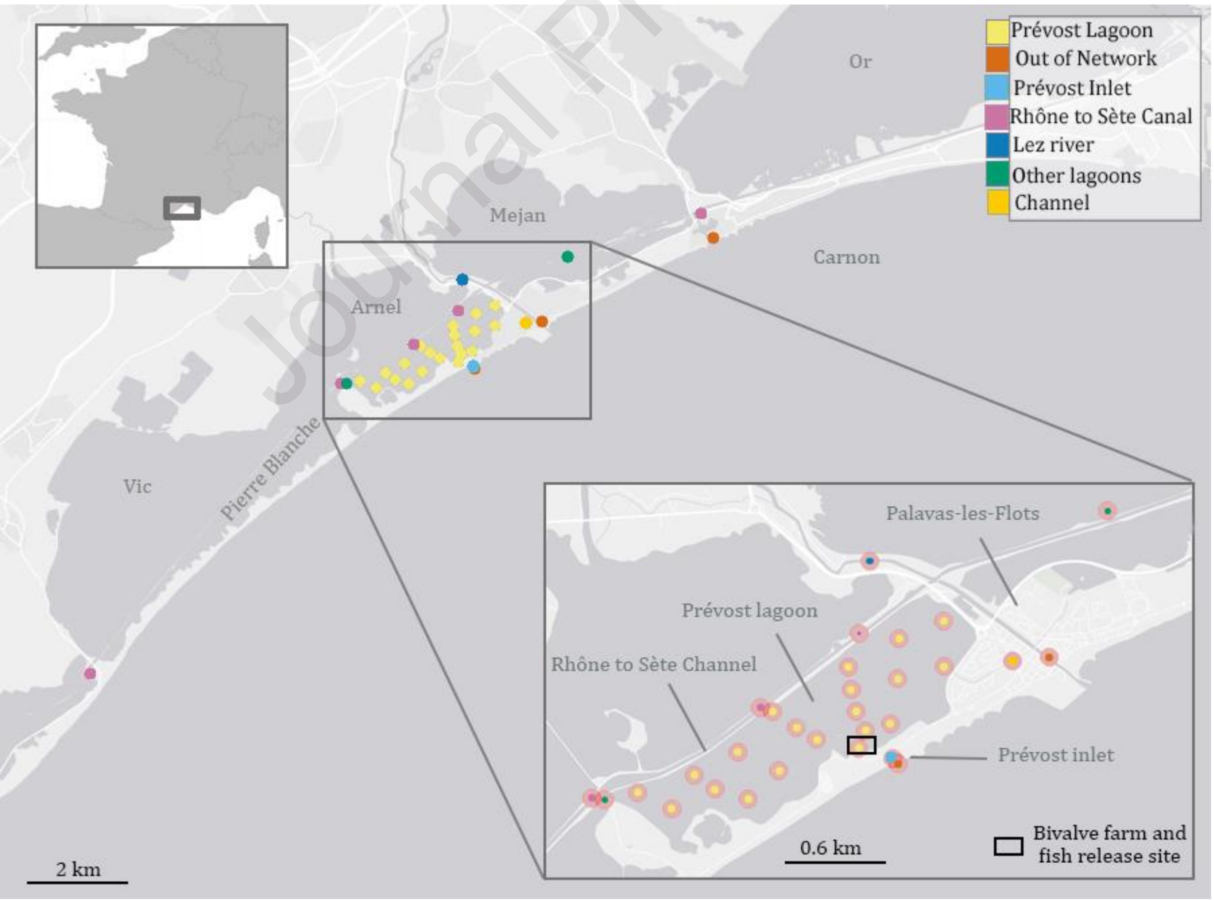

Figure 1. Location of receivers inside the lagoon complex. Pink circles around receivers locations illustrate their detection range (119 m according to range tests). COLORS SHOULD BE USED

2.2. Experimental design

A fixed array of 33 acoustic receivers (VR2W, Innovasea, Bedford, Canada) was deployed to monitor fish spatial and temporal movement patterns (Figure 1). The array was designed to investigate: (1) movements inside the lagoon using 20 receivers and (2) movements out of the main receiver network, using three receivers in Prévost, Palavas-les-Flots and Carnon inlets to detect the movements of fish between the lagoon receiver network and the sea; (3) all connections with adjacent lagoons and connecting channels with nine receivers located in the Rhône to Sète Canal, the Lez River, and all connections with adjacent lagoons and ports. To investigate movement patterns within the network, the overall study area was divided into 7 zones: Prévost Lagoon itself, Prévost Inlet, Lez River, Rhône to Sète Canal, Other lagoons, Channel, or Out of network (Figure 1). The "Out of network" zone refers to when fish exited the receiver network through inlets connecting the network to the sea, the Rhône to Sète Canal, or Other lagoons.

In the lagoons, receivers were weighted and affixed to wooden stakes driven into the bottom with receivers pointing upwards. In the canals and ports, receivers were affixed to existing structures with ropes and cable ties. The monitoring period extended from 01/05/2017 to 01/06/2021.

Range tests performed in March 2017, prior to the study, showed a 50 % detection probability at 119 m in the lagoon (See Richard et al., 2020 for details). The detection range was variable, as expected in shallow coastal habitats (Payne et al., 2010, Weinz et al., 2021).

2.3. Fish sampling

Fish were captured between 2017 and 2020 from May to October (see Figure 2 and Table S.1 for details). A total of 81 gilthead seabream (mean ± SD, 272 ± 64 mm total length – TL), 59 seabass (383 ± 95 mm TL) and 86 salema (279 ± 35 mm TL) were sampled in Prévost Lagoon. Most fishes (n = 187) were captured using traditional net fish traps ('Capechades'), as described in Bach et al. (1992). Others were captured using rigid baited fish traps (60 × 40 × 40 cm) in the shallower parts of the lagoon (n = 21) and rod and line (n = 65). Most captures occurred in the centre of the lagoon (Figure 1).

It is well known that size, maturity and sex all influence space use in marine fishes, and so these variables are usually worthy of investigation when studying spatial behaviour and migrations (Mittelbach, 1981; Minns, 1995; Shapiro, 1986; Schlosser, 1987; Miranda et al., 2008; Jonsson & Gravem, 1985). None of these species are sexually dimorphic, *S. aurata* and *S. salpa* are protandrous hermaphrodites whose sex and associated maturity are usually determined by size but are highly variable in both species, according to individuals and areas (Lasserre, 1976; Chaoui, 2006; Buslé-Sicard & Fourcault, 1997; Criscoli et al., 2006). Nevertheless, all tagged seabream and salema were expected to be mature (size at maturity: 183 mm TL for seabream; Fateh et al., 2018 and 200 mm TL for salema; Pallaoro et al., 2008) For seabass, size at maturity depends on sex (Barnabé, 1976) and sex of individuals could not be assigned. We, therefore, could not investigate the effect of sex or maturity on the behavioural patterns of the three species. Finally, since the standard deviation of sampled size for the three species was low (Figure S.1), we did not investigate the effect of size on the spatial behaviour of tagged individuals.

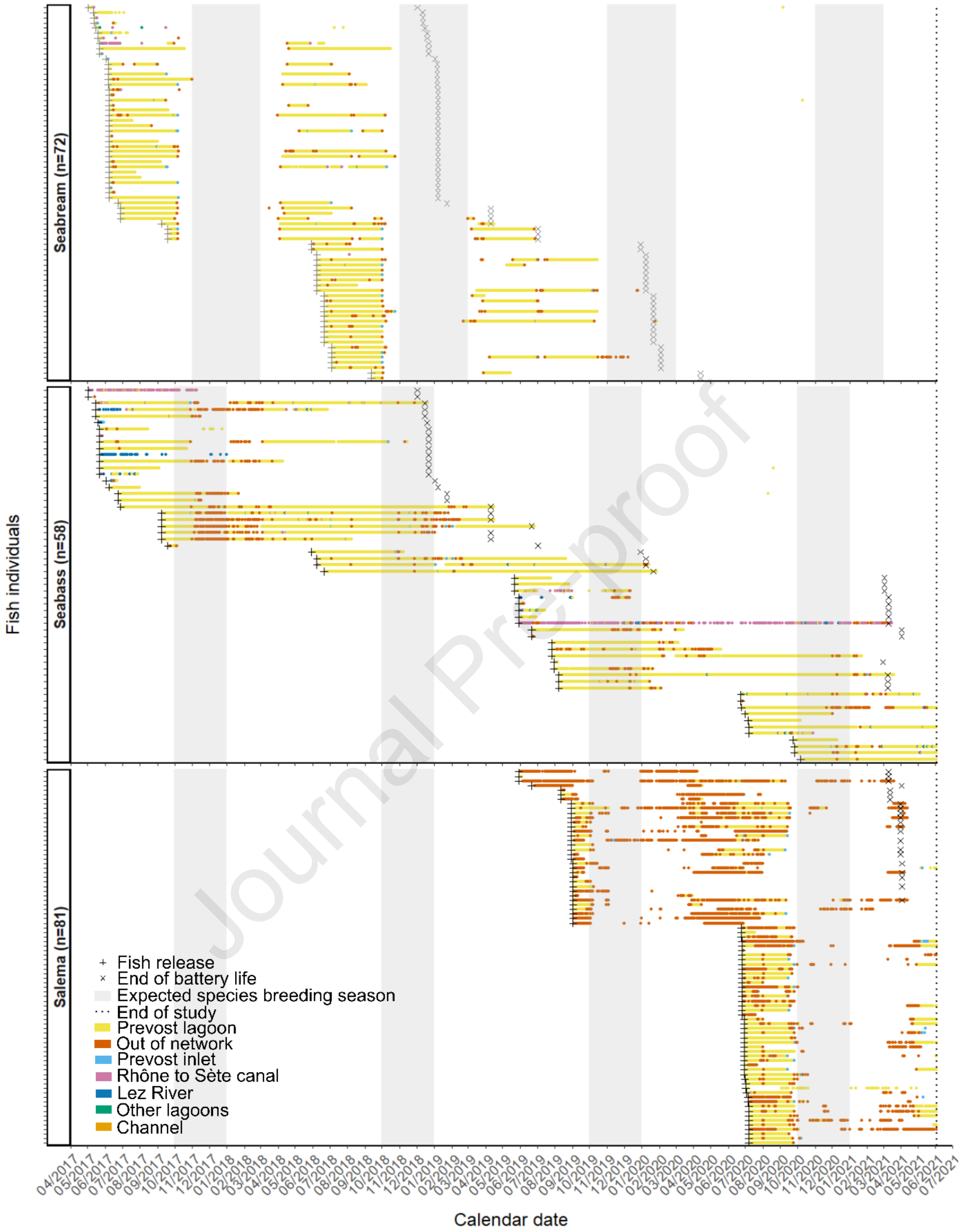

Figure 2. Chronogram of the movements of fish in the receiver network*. Each line corresponds to a fish ID. Each dot corresponds to a detection and the colour to the zone where it was detected as defined in the legend and Figure 1. Grey bars represent the Expected Breeding Season of each species and white bars represent their Expected Foraging Season.* ***COLORS SHOULD BE USED***

2.4. Tagging

After capture, fish were immediately sedated in a 50 L tank containing a 0.025 g.L^{-1} benzocaïne (Benzocaine ethyl 4-Aminobenzoate, VWR, www.vwr.com) solution in aerated seawater, then anesthetized in a 0.1 g.L^{-1} benzocaïne solution. Once anesthetized, total length and weight were measured and individuals were placed ventral side up in a padded V-shaped tagging cradle. A 10 mm incision was made by scalpel in the ventral midline, between the pelvic fins and the anus. A coded acoustic transmitter (Innovasea V9-1X, delay 130 - 230 s; Innovasea V9-2X, delay 60 - 120 s; Innovasea V13-1X, delay 80 - 160 s) was inserted into the peritoneal cavity and the incision closed with absorbable monofilament sutures (Monosyn, glyconate monofilament absorbable, needle DS24, thickness 2/0, Braun, www.bbraun.fr). Additionally, each fish was tagged externally with a plastic dart tag (Hallprint Pty.Ltd) with a reward advertised in case of recapture. Three blue dots (SIGMA, Alcian blue 8GX) were tattooed on the pectoral girdle of tagged individuals as a second external marking method. Fish recovered in a circular 50 L tank of aerated seawater until equilibrium and normal swimming was regained (typically 3 - 5 min). All fish were released back into the lagoons near the mussel farms (Figure 1).

2.5. Data analysis

2.5.1. Data filtering

False detections were filtered by removing all non-deployed tag IDs. Tag emissions detected by two or more receivers in the denser parts of the array were filtered out; detections of the same tag emission on multiple receivers were removed if the timestamp between the detections was below the minimum emission delay of the tag. To avoid potential effect of tagging on fish behaviour, we removed the first 48 h of detections following release. Finally, using individual reconstructed tracks (Campbell et al., 2012) which show movements between receivers, we classified the fate of individuals for which signals were suddenly lost as “caught” and the others as “alive”.

2.5.2. Monthly breakdown of the dataset

To investigate the seasonality of movement patterns amongst species, all analyses were performed on a monthly basis. All metrics were first averaged monthly per year and study year was then tested in the models as a response factor but its effect was negligible. Therefore all metrics were then averaged monthly across all years. The first tagging month for each fish extends from the tagging day to the last day of the month. Similarly, when a fish left the receiver network (or was captured), the last month of that year extends until the last detection in the network.

The Expected Breeding Season (EBS) for each species inside the Mediterranean Sea was estimated from the literature and considered in the analysis. The EBS was estimated to extend from November to February for seabream (Audouin, 1962; Lasserre, 1976; Mercier et al., 2012), from December to March for seabass (Barnabé, 1973; Morretti, 1999; Bakhoum et al., 2015) and from October to December for salema (Anato et al., 1983; Criscoli et al., 2006). Although all three species probably also feed during their EBS, we denoted the months when species are not expected to breed as their “Expected Foraging Season” (EFS).

2.5.3. Residency in the receiver network

Residency indices (RI; March et al., 2010; Villegas-Ríos et al., 2013, Appert at al., 2023, Kraft et al., 2023) were calculated monthly for each individual as the total time (hours) spent in each of the 7 study zones divided by the duration of a given month (hours). We considered that an individual was present in a zone as long as it was not detected elsewhere. The time spent in a specific zone by a fish was calculated as the time difference in hours between its first and last detection in the zone and these durations were summed by zones to calculate the total time spent in each zone per month. Residency indices inside Prévost Lagoon were also calculated monthly for each individual as the number of days detected inside the lagoon divided by the total duration of the considered month in days for each species to determine if each species was detected inside the lagoon daily (March et al., 2010). RI inside Prévost Lagoon and in other zones were calculated for each fish and compared across all combinations of species and months. RI data distribution was verified to be quasibinomial using the *descdist* function (fitdistrplus package, Muller & Dutang, 2015). A linear generalized model was then applied on all individuals’ RI, with species, months and season (EFS or EBS) as factors (*glm* function, R Core Team 2022). Tukey post-hoc tests were used to identify significant differences (*emmeans* function, emmeans package (Lenth 2021)). Homoscedasticity and independence of the residuals were verified visually.

2.5.4. Home ranges

2.5.4.1 Home range calculations

Individual core home ranges (derived from 50 % Kernel Utilization Distribution - KUD) were estimated for each species, season, month and photoperiod phase (day or night) in Prévost Lagoon using kernel utilization distributions (Worton, 1989). Only detections inside the lagoon were used for calculations, in order to compare home ranges of the three species. Home range estimations were calculated in a grid with a 50 × 50 m resolution, using the adehabitat package in R (Calenge, 2006). Kernel bandwidth was set at 119 m, which corresponded to the 50 % probability of detection range in Prévost Lagoon (Richard et al., 2020) (see March et al., 2010). Day and night periods were determined using the *sunriset* function from maptools package (Bivand & Lewin-Koh, 2021).

Overall core home ranges and extended home ranges (derived from 95 % KUD) were calculated seasonally for all individuals of a given species, to assess global space utilization inside the lagoon.

2.5.4.2 Home range sizes

Home range sizes were likewise estimated using the *kernel area* function from the adehabitat package (Calenge, 2006). Home range size were verified to be gamma distrusted using the *descdist* function (fitdistrplus package, Muller & Dutang, 2015), and a mixed generalized model thus applied on all individual home range sizes, for the factors species, month, photoperiod (day or night) and season. Tukey post-hoc tests were used to identify where significant differences lay. Homoscedasticity and independence of the residuals were verified visually.

2.5.4.3 Home range overlaps

To estimate changes in individual home ranges over diel period, overlap derived from 50 % KUD between day and night was calculated using the *kerneloverlaphr* (Calenge, 2006) function. To standardize overlap calculations to yield only positive values, the overlap area was calculated as the proportion of the smallest home range area covered by the largest of the two. Overlap data distributions were quasibinomial and thus a mixed generalized model was applied on all individuals' overlaps for the factors species and months.

Likewise, overlaps derived from 50% KUD across pairs of consecutive months were calculated for each individual using the *kerneloverlaphr* (Calenge, 2006) function. Overlap data distributions were quasibinomial and thus a mixed generalized model was then applied on all individuals' overlaps for the factors species, seasons, and consecutive pairs of months. In all cases, Tukey post-hoc tests were used to identify significant differences; homoscedasticity and independence of the residuals were verified visually.

2.5.5. Inter-annual site fidelity

As all three species breed at sea, we determined mean breeding migration dates when fish left the lagoon at the beginning of their respective EBS, and then levels of inter-annual site fidelity when fish were detected inside the lagoon again at the next EFS. We considered their mean breeding migration date as the mean of last individual detection dates within the receiver network (Figure 1) of their tagging year since all seabream left the lagoon for an extended period of time before their EBS (Figure 2). The migrating pattern for seabass and salema was less clear, as both species moved in and out of the lagoon before and during their EBS (Figure 2). Therefore, we considered an individual's breeding migration date to be the date of their first migration out of the receiver network starting from the month before the beginning of the species' EBS (October for seabass, Rafail, 1971; Barnabé, 1973; Bouain, 1977; Kara, 1997 and September for salema, Criscoli et al., 2006; Anato et al., 1983).

In addition to expected movements associated with breeding behaviour, fish also performed more unpredictable movements in and out of the lagoon which we have defined as ‘stochastic’. These stochastic movements were quantified as the number of detections at the receiver located in Prévost Inlet (Figure 1), regardless of the directionality of the movement. The number of detections was calculated monthly and normalized by the number of fish detected each month. The time difference between these movements and sunrise and sunset was also quantified using the function *difftime* (R Core Team, 2022).

All fish were tagged during an EFS, so we quantified and categorised their inter-annual fidelity to Prévost Lagoon into four categories: a) fish that were not detected inside the lagoon during the subsequent EBS or the following EFS; b) fish that were detected inside the lagoon during the subsequent EBS but not during the following EFS; c) fish that were not detected inside the lagoon during the subsequent EBS but were detected again in the following EFS, and d) fish that were detected inside the lagoon during their EBS and during the following EFS. Site fidelity for each species was calculated as the proportion of fish in each group among the total number of tagged fish during their first EFS, minus individuals caught during the first EFS. Capture rates were calculated as the number of individuals estimated to be “caught” by fishermen throughout the study, divided by the total number of tagged fish, before removing the individuals that remained less than two days inside the lagoon following release.

To calculate inter-annual site fidelity for each individual at their home range scale, overlaps derived from 50 % KUD between either their first EFS, EBS and next EFS were calculated using the *kerneloverlaphr* (Calenge, 2006) function. To standardize overlap calculations to yield only positive values, the overlap area was calculated as the proportion of the smallest home range area recovered by the largest of the two distributions. As the overlaps data distribution was quasibinomial, a mixed generalized model was thus applied on all individuals’ overlaps for the factors species and months. Tukey post-hoc tests were used to identify where significant differences lay. Homoscedasticity and independence of the residuals were verified visually.

3. Results

The tracking period extended from the May 4 2017 to June 1 2021. The total dataset, after the cleaning and filtering process, comprised 6,155,058 detections. Monitoring data are summarized in Table S1 and a chronogram illustrates movements between the different zones of the lagoon for all individuals (Figure 2).

As 15 fish (9 seabream, 1 seabass and 5 salema) left the receiver network within 48h post-release, the final dataset comprised data from 72 seabream, 58 seabass, and 81 salema. Several seabream undertook isolated movements into the lagoon that did not reflect the overall seasonal movements of the species. In November 2019, a seabream undertook a few very short (< 1 hour) excursions into Palavas-les-Flots Inlet from the sea. In December 2019, a different seabream was detected inside the lagoon for less than 48 h. Another individual undertook short excursions into the lagoon over less than 48 h in January 2020. Finally, two seabream entered the lagoon in late February 2019, whilst undertaking movements between the lagoon and the sea (Figure 2). These isolated phenomena were not included in the following analysis of seabream movements.

3.1. Seasonal residency within the lagoon receiver network

The RI values in the various zones are given in Figure S.2. All three species remained mostly in Prévost Lagoon (RI: 71 ± 37 % across all species) or were “out of network” (18 ± 31 % across all species) significantly more than all other zones over all months (Prévost Inlet, Lez River, Rhône to Sète Canal, other lagoons and channels; 4 ± 16 %), except in March when seabream used Prévost Inlet (32 ± 39 %) as much as Prévost Lagoon (32 ± 32 %) and “out of network” (36 ± 38 %). Since all fish were either inside the lagoon or at sea outside of the network, only the Prévost Lagoon residency index was considered to characterize fish residency (Figure 3).

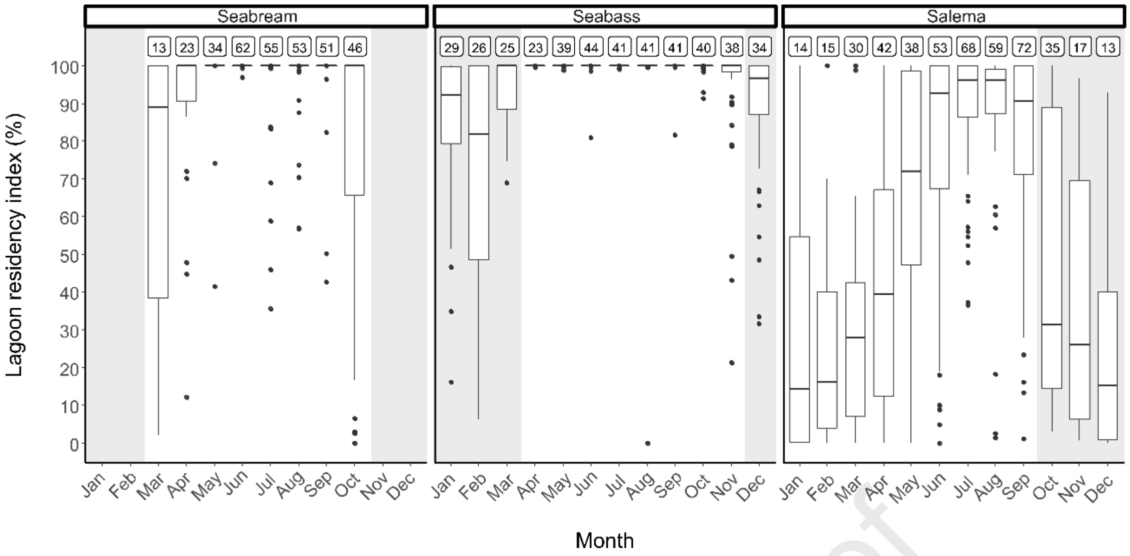

Figure 3. Monthly residency indices of each species inside Prévost Lagoon. *The boxplots represent the median, hinges and whiskers of RI values calculated for each fish, for a given month and dots represent outliers. Gray areas represent the EBS for each species and the white area the EFS. The number of fish for a given combination of species and months is indicated in the white boxes at the top of each subplot.*

All three species spent significantly more time inside the lagoon during their EFS (94 ± 19 % for seabream, 99 ± 8 % for seabass and 69 ± 35 % for salema) than during their EBS (88 ± 22 % for seabass and 41 ± 37 % for salema). More precisely, salema spent significantly more time in the lagoon from May to September (82 ± 26 %) than other months (37 ± 33 %). It is also worth noting that salema undertook significantly more excursions out to sea than other species in any month (Figure S.3) and that most of these movements occurred two hours before sunrise (Figure S.4) or two hours after sunset (Figure S.5). Despite undertaking many stochastic movements in and out of the lagoon during their EFS (Figure S.3), salema were actually detected inside the lagoon almost every day at the height of their EFS, from June to August (Figure S.6, 91 ± 22 %).

Seabass was significantly more resident than the other two species during both EFS and EBS while salema was the least resident of all species during both seasons.

3.2. Diel home ranges size and overlap

Day and night home ranges sizes are presented in Figure 4. Home range size did not vary between day and night for any combination of species and months except for salema from April to September, when home ranges at night (0.09 ± 0.04 km^2) were significantly lower than home ranges during the day (0.14 ± 0.07 km^2). The 24 h mean individual core home ranges were significantly larger in May and June (0.14 ± 0.08 km^2) than other months (0.11 ± 0.04 km^2) for seabream and from October to December (0.15 ± 0.06 km^2) than other months (0.13 ± 0.05 km^2) for seabass. Home range size did not vary between months for salema night home ranges, however, day home ranges were significantly larger in May, July and August (0.15 ± 0.07 km^2) than in other months (0.12 ± 0.06 km^2). Seabass have the largest 24h home range during both their EFS (0.14 ± 0.06 km^2) and EBS (0.15 ± 0.07 km^2) compared to the other species (EFS: 0.12 ± 0.06 km^2 for seabream and 0.11 ± 0.06 km^2 for salema; EBS: 0.11 ± 0.04 km^2 for seabream and 0.1 ± 0.04 km^2 for salema) although salema and seabass had the largest day home range during the EFS (0.13 ± 0.06 km^2 for seabass and 0.14 ± 0.07 km^2 for salema) compared to seabream (0.12 ± 0.06 km^2). The 24h mean individual core home range size was 0.13 ± 0.07 km^2 for gilthead seabream, 0.13 ± 0.05 km^2 for seabass, and 0.14 ± 0.08 km^2 for salema. Considering that Prévost Lagoon has a surface area of 2.5 km², the area used by individuals daily was small.

There was a very high overlap of home ranges for each fish between day and night (Figure S.7, 80 ± 27 % across all months and species). Globally, overlaps did not differ month-to-month for any species, although salema displayed a significantly lower overlap between day and night home ranges (73 ± 33 %) than did the other species (84 ± 25 % for seabream and 85 ± 21 % for seabass) during their EFS. Salema was the only species to differ in their home ranges between day and night.

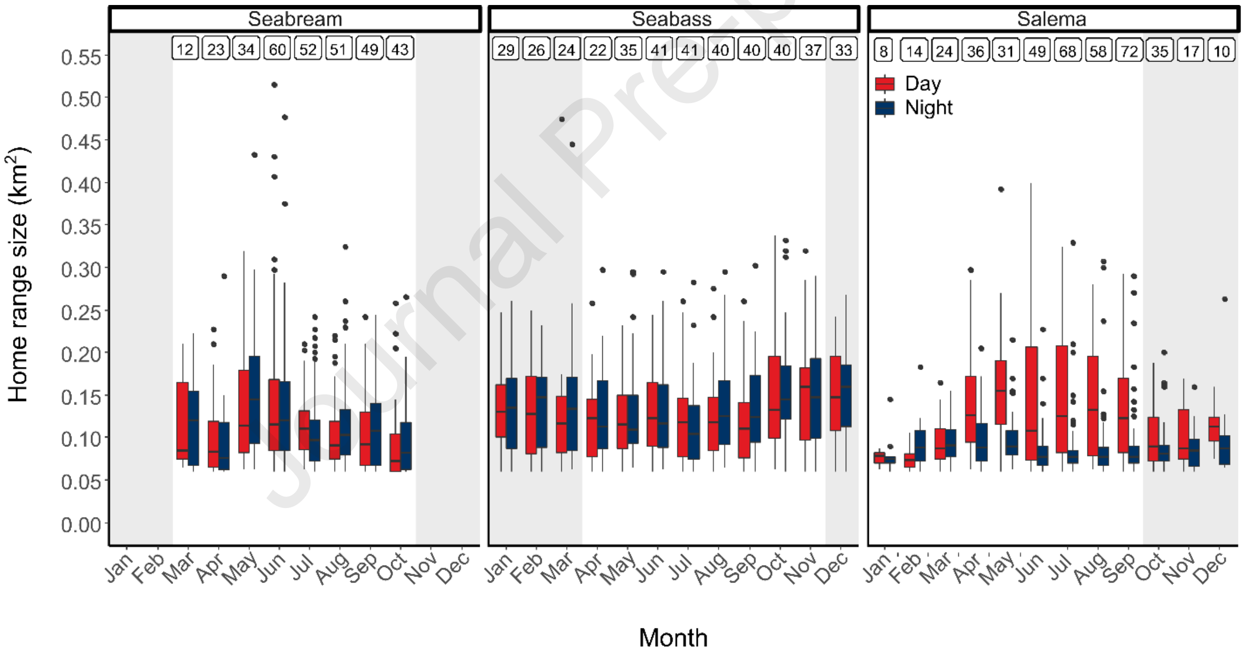

Figure 4. Diel home ranges size derived from 50% presence probability for all three species per months. *Each panel displays the median, hinges, whiskers and outliers of all individual home ranges size values between day and night for each species per month. The number of fish for a given combination of species and month is indicated in the white boxes at the top of each subplot.* ***COLORS SHOULD BE USED***

3.3. Inter-annual lagoon fidelity

3.3.1. Site fidelity and capture success

All species undertook group migrations seaward at the beginning of their EBS and then displayed a degree of inter-annual fidelity to the lagoon (Table 1, Figure 2). Seabream outward migrations were synchronized before their EBS (October 6 ± 6 days) and 43 % of individuals returned the following EFS (March 31 ± 13 days). Seabass left the lagoon in a less synchronized manner, around November 1 ± 15 days, and 50 % actually remained in the lagoon all year long, demonstrating long-term fidelity to the lagoon. However, 30 % of seabass never returned after leaving the lagoon before their first EBS and 20 % did not return after leaving during their second EBS. Salema migrated around the same time as seabream, around September 24 ± 12 days, and 73 % displayed inter-annual fidelity to the lagoon. Among these latter, 60 % remained in the lagoon during their EBS and throughout next EFS, while 13 % left before their EBS and came back for their next EFS. Estimated captures rates for each species are displayed in Table 1.

Table 1. Percentages of inter-seasonal fidelity to the lagoon for each species between their EBS and New EFS (NFS). Columns in bold font indicate the inter-annual fidelity percentages to Prévost Lagoon.

	Are no longer detected during their EBS and are not detected during their NFS	Are still detected during their EBS and are not detected during their NFS	**Are no longer detected during their EBS and are detected during their NFS**	**Are still detected during their EBS and are detected during their NFS**	Capture rate
Seabream (n = 61)	57 %	0 %	**43 %**	**0 %**	17 %
Seabass (n = 46)	30 %	20 %	**0 %**	**50 %**	31 %
Salema (n = 80)	10 %	17 %	**13 %**	**60 %**	7 %

3.3.2. Seasonal home range overlaps

Overlaps of individual home ranges between the first EFS, EBS, and subsequent EFS are shown in Figure 5. The overlap was high (81 ± 24 % for all season combinations and species) with no significant differences among species or across seasons. That is, from one season to the next, individuals in all species used the same area in the lagoon.

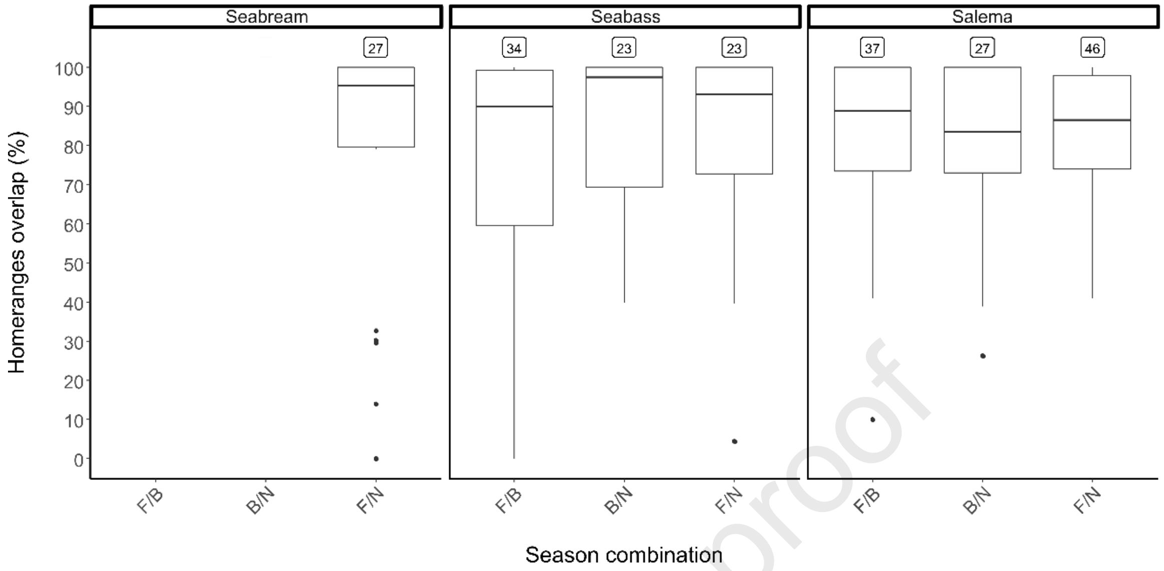

Figure 5. Overlap between home ranges between pairs of either EFS (F), EBS (B) and Next EFS (N) for seabream, seabass and salema. *Panels show median, hinges, whiskers and outliers of all individual overlap values between both seasons indicated in the left sidebars. The number of fish for a given combination of species and season is indicated in the white boxes at the top of each subplot.*

3.4. Seasonal home ranges

Home range overlaps between consecutive months were overall very high for all species (Figure S.8, 84 ± 23 %). There was no significant difference across all month combinations and species, except for the overlap between April and May for salema (69 ± 32 %) that was significantly smaller than other monthly combinations (84 ± 19 %), probably because its home range in May is the largest observed over all months (Figure 4). Therefore, home ranges were considered to be stationary over time and overall home ranges for all three species could be calculated seasonally. Home range sizes are displayed in Table S.2. Species home ranges within Prévost Lagoon are shown in Figure 6. The three species all mainly used the area close to the inlet and rarely explored the East and West, except for seabream who displayed the most extensive use of the lagoon (Table S.2). Seabass tended to venture further north of the lagoon towards the connection with the Rhône to Sète Canal and therefore their home range was at the centre of the lagoon, stretching towards the opening to the Rhône to Sète Canal. They also displayed the largest core home range of the three species (Table S.2). On the other hand, salema home ranges were the smallest (Table S.2) and were centred around the mussel farms. During their EBS, home ranges of seabass and salema were more centred around the mussel farms close to the connection with the sea and were smaller than during the EFS (Table S.2).

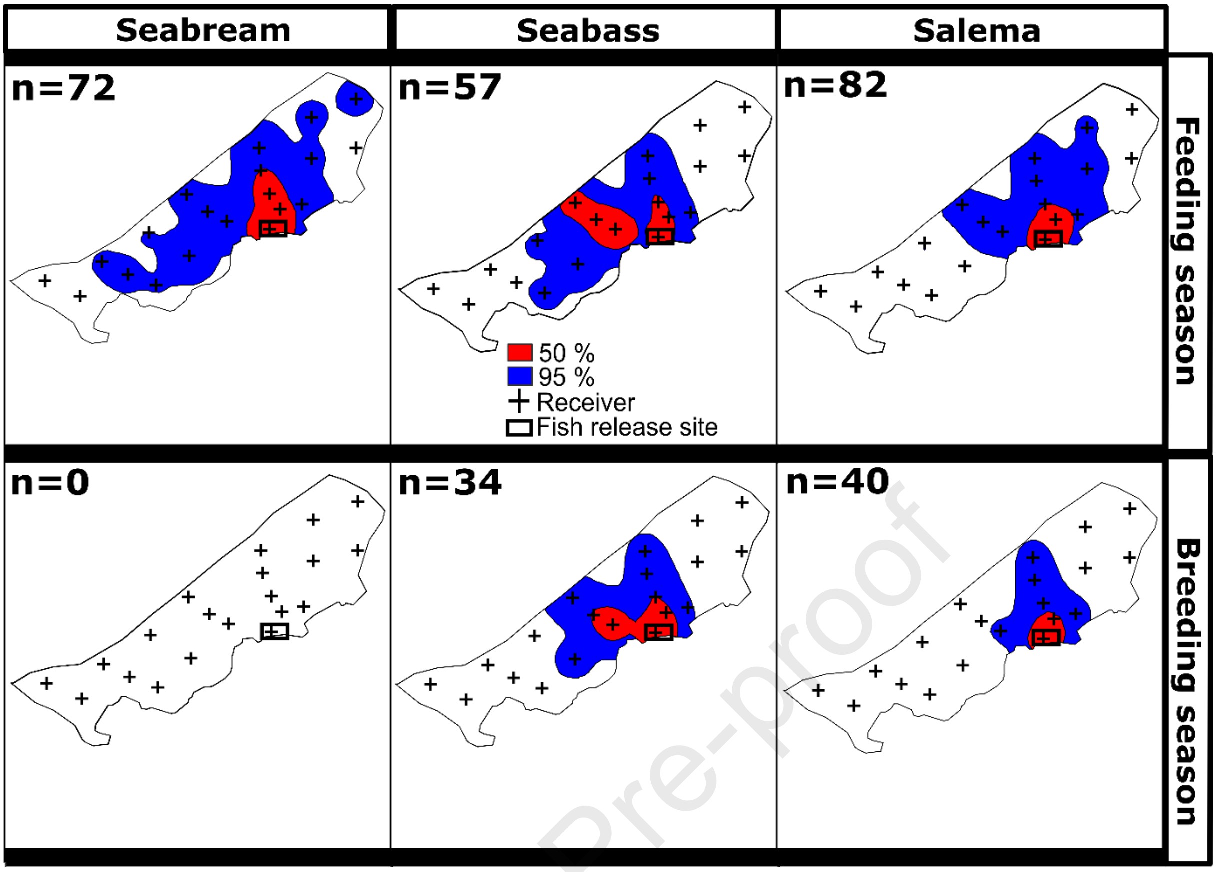

Figure 6. Home ranges of the three species calculated as kernel distributions during their respective EFS and EBS. COLORS SHOULD BE USED

4. Discussion

4.1. Residency and space utilization within Prévost Lagoon during the foraging season

Given that lagoons are particularly productive areas along the coastline, it is not surprising that marine fishes often use them as feeding grounds (Milardi et al., 2019)**.** Prévost Lagoon is small (2.5 km²) and situated in the middle of a vast lagoon network in which all three species occur (Franco et al., 2008). The results from this study suggest that none of the species use Prévost Lagoon as a mere transition zone because the vast majority of individuals remained as residents inside the lagoon (Figure 3). Seabass can tolerate freshwater (Chervinsky, 1974) and was the only species to venture into the Lez River (Figure S.2, Vázquez & Muñoz-Cueto, 2014).

However, the three species showed divergent use of Prévost Lagoon. Seabass displayed the highest residency in the lagoon during both (EBS and EFS) seasons (> 90 % of fidelity) but with a lot of excursions at sea during EBS. Seabream also displayed high fidelity to the lagoon during their EFS (> 90 % of residency) but also undertook short stochastic excursions to sea during EFS. A high residency in seasonal foraging grounds has been reported for *D. labrax* in an estuary in southern Ireland (Doyle et al., 2017), for *S. aurata* in Ria Formosa coastal lagoon (Abecasis & Erzini, 2008) and also for other sparid species in transitional habitats (Abecasis et al., 2009). However, with the exception of Doyle et al. (2017), other studies investigating site fidelity were largely based on short-term tracking and relatively low sample sizes. Our large plurinannual dataset confirms that coastal lagoons play a critical role as foraging grounds during the life cycle of seabass and seabream (Able et al., 2014). Salema, although quite resident inside the lagoon during their EFS, spent a significant proportion of their time (> 30 % of residency out of the network over both seasons) at sea. This higher residency at sea relative to other species is linked with daily excursions in the lagoon, mainly at dusk and dawn (Figures S.3, S.4 and S.5). Increased activity at sunrise and sunset is well known for fishes (Helfman, 1986) and was reported by Jadot et al. (2006) and Baeyaert et al. (2018) for *S. salpa*. Thus, even though this could have led to increased stochastic movements beyond the receiver network, they were still detected inside the lagoon most days. Thus, all three fish species displayed high residency in the lagoon, but in different ways. Both seabream and seabass were characterized as having much higher residency during EFS than during EBS, supporting the hypothesis that their predicted EFS corresponds to their actual EFS. Many fish species use lagoons in their life cycle as feeding ground but very few breed inside them, possibly because of the unpredictability and variability of environmental conditions inside the lagoons (Yafiez-Arancibia et al., 1994). Other acoustic telemetry studies have revealed high residency in coastal lagoons by other species. For example, juvenile and sub-adult *Diplodus sargus* and *Diplodus vulgaris* in the Ria Formosa in Portugal (Abecasis et al., 2009), adult red drum, *Sciaenops ocellatus* in shallow Florida lagoons (Reyier et al., 2011), adult striped bass *Morone saxatilis* in a southern New Jersey estuary (Ng et al., 2007), and several fish species in salt marshes in England (Green et al., 2012) and South Carolina, United States (Potthoff et al., 2003). These studies also highlight the importance of coastal lagoons and estuaries as feeding grounds for many fish species.

The high fidelity to Prévost Lagoon extended further than to just the lagoon in general. All three species were particularly faithful to certain zones of the lagoon (Figures 4, 5 and 6). This small-scale fidelity is even more apparent when evaluating home range sizes, with core home ranges representing 5 % of the total surface of Prévost Lagoon for seabream and seabass and 7.2 % for salema (Figure 4). The fact that individuals were all released at the same place adjacent to the mussel farm could be interpreted as a limitation of the study as this may affect the location of their home range and residency times. Likewise, the majority of fish were captured close to the center of the lagoon, owing to the location of the capechades, which may partly explain why the home ranges of the three species were determined to be centered on this area of the lagoon, which could be interpreted as a bias. However, all three species are known to have homing abilities (Abecasis & Erzini, 2008; Pawson et al., 2008, Jadot et al., 2006). Given that most individuals were captured in the center of the lagoon and that their core home ranges were also determined to be located in the same area demonstrates that they were able to return to their home range even when released away from it, further showing a very high degree of home range fidelity. Day and night home ranges had similar sizes and overlapped to a great degree (> 80 %, Figure S.7), suggesting that seabream and seabass did not display diel patterns in space utilization. This behaviour is consistent with other studies that observed diel activity patterns in these species (Bégout & Lagardère, 1995; Bégout Anras et al., 1998 Abecasis & Erzini, 2008). In contrast, salema displayed smaller home ranges at night than during the day (Figure 4) and lower day/night home ranges overlaps than other species (Figure S.7), suggesting that salema are more active during the day and likely rest at night, as reported by Jadot et al. (2006) and Baeyaert et al. (2018). It is also possible that this lower overlap between day and night is caused by a higher rate of movement between the lagoon and sea at dawn and dusk (Figures S.4 and S.5), shifting their night time home range towards the inlet.

Little is known about the size of foraging areas used by coastal fish or how much time they spend at particular foraging locations (Mather et al., 2009; Doyle et al., 2017). Although small home ranges for salema and seabream in coastal lagoons is in agreement with two previous studies (Abecasis & Erzini, 2008; 2012), home ranges of seabass in coastal lagoons have not been evaluated. In estuaries, the species seems to be restricted to small areas of less than about 3 linear km (Pita & Freire, 2011; Doyle et al., 2017). Fish home range size and fidelity to foraging grounds is often associated with territorial behaviour (Armstrong, 1947; Low, 1971) or food availability (Hansen & Closs, 2005). Gilthead seabream are very territorial (Folkedal et al., 2018) and have been observed to display social hierarchy in tanks (Papadakis et al., 2016) for access to food (Karplus et al., 2000) or space (O'Connor, Metcalfe & Taylor, 2000). This territoriality has also been observed in the wild in other Sparidae (*Pagrus major* and *Evynnis japonica,* Kudoh et al., 2004). This may explain such strong fine scale site fidelity. Both seabass and salema displayed homing ability in previous studies (Pawson et al., 2008, Jadot et al., 2006) which serves a similar purpose to "territoriality" (Green, 1971; Crossman, 1977). Thus, territoriality could explain the small home ranges of the three fish species. However, territory size is predicted to be smaller at high population densities and with increasing food availability (Cowlishaw, 2014). Differences in space utilization inside the lagoon by the three species are more likely to be attributed to their different trophic ecologies, as foraging is a primary determinant of fish movement (Phiri & Shirakihara, 1999). Fish define their home range where the food is neither limiting nor widely used by other species (Barnes, 1989). Given that *S. salpa* is the only algae-grazing fish in the lagoon (Houziaux et al., 1993), competition for resources is limited. By contrast, seabream and seabass are carnivores and may compete for the same prey (Barnabé, 1976; Andrade et al., 1996; Pita et al., 2002; Vázquez & Muñoz-Cueto, 2014). This could explain why, overall, salema had larger individual home ranges than did seabream and seabass.

4.2. Breeding migration and overwintering

Seabream are known to perform ontogenic migrations (Lasserre, 1976; Mercier et al., 2012; Tournois et al., 2017) between their foraging sites in coastal lagoons (Arias, 1976; Suau & Lopez, 1976; Arias, 1980; Pita et al., 2002; Chaoui et al., 2006) and spawning sites at sea (Audouin, 1962; Mercier et al., 2012). They spawn in winter from November to February with a peak in January-February (Audouin, 1962), as do Mediterranean seabass populations, which migrate to sea to spawn from December to March with a peak in January (Rafail, 1971; Barnabé, 1973; Bouain, 1977; Kara, 1997). Little is known about salema migratory patterns, which spawn at sea with two distinct spawning periods along the Italian coast: one in spring, from March to May, and the other in autumn, from the end of September to November (Criscoli et al., 2006) but only once in the Gulf of Tunis from October to December (Anato et al., 1983). We found that all three species showed strong but different patterns of spawning migration. The fact that seabream left the lagoon in a synchronized manner at the end of their EFS is a typical feature of spawning migrations. Finely tuned associations between migrating organisms and their migration triggers ensures that migratory movements are initiated when environmental conditions are optimal for reproduction and offspring survival (Crossin, 2009). Such a synchronized departure is most probably triggered by environmental factors, such as temperature (Lehodey et al., 2006) or photoperiod (Lennox et al., 2016) in order to avoid unfavourable conditions and arrive at destination at an appropriate time (Crossin, 2009). Water temperature in Prévost Lagoon may be low in winter (9.5 ± 2 °C from December 2017 to March 2018, Richard et al., 2020) and gilthead seabream is sensitive to low temperature (Ibarz et al., 2003, Critical Minimum Temperature = 9.3 ± 0.5 °C in juveniles acclimated to 25 °C, Kir, 2020). Seabream probably stayed at sea until March to avoid these cold temperatures, and then came back when the temperature increased at the onset of their EFS.

It was interesting that seabass migration was less synchronised than gilthead seabream, since migration of the species from a coastal lagoon has not been evaluated previously. Doyle et al. (2017) found that most tagged seabass left their feeding ground in estuaries within 6 weeks, between October and November. It seems therefore that these migrations were most probably for spawning. What triggers these departures for migration is unknown, but temperature may again be a key factor (Barnabé, 1976). Breeding sites for seabass in the Gulf of Lion are poorly documented. Several spawning sites are known to exist all along the coast of the Gulf of Lion with some possibly being not far from their feeding grounds (Dufour et al., 2009), a proximity that may explain the highest density of stochastic movements in and out of Prévost Lagoon in November and December (Figures 2 and S.3). Seabass are quite resilient to cold temperatures, which may explain why 59 % overwintered inside the lagoon (Dendrinos & Thorpe, 1985; Venturini et al., 1992; Dülger et al., 2012) although they stop feeding at 7 °C (Kara & Quignard, 2018a).

The fact that salema departed around the same date as seabream, albeit in a less synchronized manner, indicates that the same environmental cues could trigger departures from the lagoon. Salema spawning sites in the Gulf of Lion are unknown but other studies indicate that their spawning season likely starts in October (Anato et al., 1983, Criscoli et al., 2006), so we can assume that these migrations are linked to spawning. In addition, residency inside the lagoon and number of individuals in the lagoon was low from October to March, increasing again in April (Figure 3). It is unlikely that their EBS lasted 6 months. Little is known about salema's tolerance to cold water, although Van der Walt (2019) estimated that their critical minimum temperature was on average 7.1 °C. Therefore, cold conditions may prevent salema from being resident in the lagoon before March. Nevertheless, a few individuals were able to spend several days inside the lagoon during their EBS.

4.3. Inter-annual fidelity to Prévost Lagoon

We found strong site fidelity to Prévost Lagoon both seasonally and between years; such fidelity has been observed in both seabream and seabass, which return inter-annually from offshore to coastal feeding grounds (Andouin 1962; Pawson et al. 2007; Doyle et al. 2017). In seabass, return rates were 55 % by mark-recapture (Pawson et al. 2007) and 93 % by acoustic telemetry (Doyle et al., 2017). Inter-annual feeding site fidelity to a lagoon has not previously been recorded for *S. salpa*. Overall inter-annual site fidelity to the lagoon confirms the significance of the ecosystem in the life cycle of all three species and may be related to the presence of seasonally predictable and energetically valuable resources (Driggers et al., 2014). Such inter-annual site fidelity has been recorded for other fishes, including adult striped bass *Morone saxatilis* in a Southern New Jersey, USA, estuary (Ng et al., 2007), mummichogs (*Fundulus heteroclitus*) in an Atlantic Canadian estuary (Skinner et al., 2005), bonnethead sharks *Sphyrna tiburo* to specific estuaries in South Carolina, USA (Driggers et al., 2014) and red drum *Sciaenops ocellatus* to natal estuarine nursery grounds (Burnsed et al., 2020), again highlighting the importance of coastal lagoons and estuaries in the life cycle of many fish species.

It is worth noting that observed inter-annual site fidelity rates were probably underestimated. Seabream and seabass are targeted by the Mediterranean French artisanal fishery (respectively 960 t and 250 t in 2018, Weiss et al., 2019), although landings of salema are somewhat lower (100 t, Weiss et al., 2019). Given that we estimated that between 7 % and 31 % of the individuals of each species were fished inside the lagoon during the study period and that fishing pressure at sea during the spawning season may be higher (Sadovy de Mitcheson et al., 2013), we believe that individuals that departed from the lagoon also faced considerable fishing pressure at sea (e.g. Erisman et al., 2011). Our fidelity estimates should therefore be considered as lower bound estimates. Interestingly, the least targeted species, salema, is the one that showed the greatest inter-annual fidelity (73 %).

The species were not only faithful to Prévost Lagoon through different seasons but also displayed fine-scale site fidelity within the lagoon. Overlaps amongst home ranges for the three species over seasons were very high (> 80 %, Figure 5), showing that individuals tended to frequent the same specific area they used the previous year. This inter-annual site fidelity behaviour has been recorded before for *D. labrax*. Pawson et al. (2007) and Doyle et al. (2017) showed that most seabass returning to their feeding ground did so to very localised coastal foraging areas. However, the present study represents the first time that such fine scale inter-annual site fidelity has been recorded for both gilthead seabream and salema. It has also been reported for marine reptiles (Siegwalt et al., 2020), birds (Baylis et al., 2015) and other fishes (Martins et al., 2017), most probably because of familiarity with the area, territoriality and foraging efficiency, all of which benefit reproductive success (López-Sepulcre & Kokko, 2005; Martins et al., 2017).

6. Acknowledgements

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7. Supplementary materials

7.1. Tables

Fish ID	Release date (dd/mm/YYYY)	Fishing technique	Species	Fate	Total length (mm)	Weight (g)	Tag format	Battery life (day)	Number of detections	Number of receivers	Number of days detected	Total period of detection (day)
1	02/05/2017	Capechade	Seabass	Alive	375	489	V9-1x	579	27	8	2	2
2	02/05/2017	Capechade	Seabass	Caught	331	391	V9-1x	579	4742	17	128	188
3	02/05/2017	Capechade	Seabream	Alive	242	182	V9-1x	579	2063	12	10	10
7	11/05/2017	Capechade	Seabream	Caught	249	229	V9-1x	579	548	16	26	52
9	12/05/2017	Capechade	Seabream	Alive	256	194	V9-1x	579	1704	20	10	36
11	12/05/2017	Capechade	Seabream	Alive	264	259	V9-1x	579	594	17	3	3
14	15/05/2017	Capechade	Seabream	Alive	264	240	V9-1x	579	545	10	12	433
15	15/05/2017	Capechade	Seabass	Alive	291	252	V9-1x	579	28957	19	179	181
16	15/05/2017	Capechade	Seabass	Alive	301	268	V9-1x	579	39738	29	306	405
17	15/05/2017	Capechade	Seabass	Alive	285	238	V9-1x	579	110904	23	514	582
26	19/05/2017	Fish trap	Seabream	Alive	203	117	V9-1x	579	924	15	10	138
28	19/05/2017	Fish trap	Seabream	Caught	267	259	V9-1x	579	976	8	33	49
30	19/05/2017	Fish trap	Seabass	Alive	254	154	V9-1x	579	1096	12	9	9
33	22/05/2017	Capechade	Seabass	Alive	355	445	V9-1x	579	1874	14	40	65
34	22/05/2017	Capechade	Seabass	Alive	430	854	V9-1x	579	9359	18	105	105
35	22/05/2017	Capechade	Seabream	Alive	204	108	V9-1x	579	393	10	3	3
36	22/05/2017	Capechade	Seabream	Alive	309	378	V9-1x	579	53797	20	328	509
38	22/05/2017	Capechade	Seabream	Alive	248	200	V9-1x	579	7265	25	100	393
39	22/05/2017	Capechade	Seabass	Caught	306	282	V9-1x	579	34564	23	281	319
40	22/05/2017	Capechade	Seabass	Alive	231	126	V9-1x	579	525	1	50	221
42	22/05/2017	Capechade	Seabass	Caught	298	278	V9-1x	579	20319	18	153	153
43	22/05/2017	Capechade	Seabass	Alive	290	240	V9-1x	579	21482	23	397	538
44	22/05/2017	Capechade	Seabass	Alive	296	261	V9-1x	579	64	10	3	3
45	22/05/2017	Capechade	Seabass	Alive	245	157	V9-1x	579	4610	16	88	212
51	02/06/2017	Fish trap	Seabream	Alive	203	118	V9-1x	579	294	6	2	2
52	02/06/2017	Fish trap	Seabass	Caught	425	700	V9-1x	579	595	14	11	11
56	06/06/2017	Capechade	Seabream	Alive	204	117	V9-1x	579	43880	17	263	452
57	06/06/2017	Fish trap	Seabream	Alive	207	120	V9-1x	579	27412	22	146	146
60	06/06/2017	Fish trap	Seabream	Alive	246	213	V9-1x	579	27995	16	221	422
61	06/06/2017	Capechade	Seabream	Caught	203	111	V9-1x	579	298	6	3	3
62	06/06/2017	Capechade	Seabream	Alive	394	847	V9-1x	579	17213	18	143	391
64	07/06/2017	Capechade	Seabream	Alive	277	278	V9-1x	579	16347	15	122	122
65	07/06/2017	Capechade	Seabream	Alive	241	171	V9-1x	579	1168	12	8	8

66	07/06/2017	Capechade	Seabream	Alive	224	153	V9-1x	579	419	12	3	3
68	07/06/2017	Capechade	Seabream	Alive	206	113	V9-1x	579	7904	23	120	120
71	07/06/2017	Capechade	Seabream	Caught	256	219	V9-1x	579	2993	10	54	54
72	07/06/2017	Capechade	Seabream	Caught	202	102	V9-1x	579	8534	19	45	45
73	07/06/2017	Capechade	Seabream	Alive	204	112	V9-1x	579	21101	27	257	486
75	07/06/2017	Capechade	Seabream	Caught	240	179	V9-1x	579	12866	21	90	90
76	07/06/2017	Capechade	Seabream	Alive	277	259	V9-1x	579	13763	23	292	501
77	07/06/2017	Capechade	Seabream	Alive	250	203	V9-1x	579	42707	21	294	485
78	07/06/2017	Capechade	Seabass	Alive	306	277	V9-1x	579	6216	15	53	53
79	07/06/2017	Capechade	Seabream	Alive	242	190	V9-1x	579	18414	17	120	120
80	07/06/2017	Capechade	Seabream	Alive	251	217	V9-1x	579	5821	19	84	84
82	07/06/2017	Capechade	Seabream	Alive	200	100	V9-1x	579	523	10	4	4
83	07/06/2017	Capechade	Seabream	Alive	281	422	V9-1x	579	16185	19	250	479
85	07/06/2017	Capechade	Seabream	Alive	230	162	V9-1x	579	2228	11	70	72
87	07/06/2017	Capechade	Seabream	Alive	244	214	V9-1x	579	37957	19	310	484
88	07/06/2017	Capechade	Seabream	Caught	260	228	V9-1x	579	8883	16	103	103
89	07/06/2017	Capechade	Seabream	Alive	247	202	V9-1x	579	4309	16	40	348
90	07/06/2017	Capechade	Seabream	Alive	208	118	V9-1x	579	10852	21	100	100
91	07/06/2017	Capechade	Seabream	Alive	240	194	V9-1x	579	575	17	6	6
92	07/06/2017	Capechade	Seabream	Alive	210	113	V9-1x	579	3708	19	21	121
97	23/06/2017	Rod	Seabass	Alive	284	234	V9-1x	579	13519	12	145	145
99	23/06/2017	Rod	Seabass	Alive	371	546	V9-1x	579	14653	17	206	209
100	23/06/2017	Rod	Seabream	Alive	424	1132	V9-1x	579	6591	12	195	373
101	28/06/2017	Rod	Seabream	Alive	499	1729	V9-1x	579	18166	15	173	619
102	28/06/2017	Rod	Seabream	Caught	446	1283	V9-1x	579	56477	16	182	369
103	28/06/2017	Rod	Seabass	Alive	449	1040	V9-1x	579	206258	17	640	654
104	28/06/2017	Fish trap	Seabream	Alive	262	263	V9-1x	579	64489	18	224	404
106	08/09/2017	Rod	Seabream	Alive	312	440	V9-1x	579	9691	18	230	582
107	19/09/2017	Rod	Seabass	Alive	346	425	V9-1x	579	8796	13	14	14
108	08/09/2017	Rod	Seabass	Alive	298	257	V9-1x	579	42883	22	325	333
109	19/09/2017	Rod	Seabream	Alive	306	461	V9-1x	579	89156	25	289	644
110	08/09/2017	Rod	Seabass	Alive	304	263	V9-1x	579	29057	22	436	478
111	19/09/2017	Rod	Seabream	Alive	305	420	V9-1x	579	6545	5	16	16
112	08/09/2017	Rod	Seabass	Alive	332	334	V9-1x	579	88529	26	615	654
113	19/09/2017	Rod	Seabream	Alive	327	486	V9-1x	579	59202	17	309	642
114	08/09/2017	Rod	Seabass	Alive	287	333	V9-1x	579	43039	27	545	582
115	30/05/2018	Rod	Seabream	Alive	345	588	V9-1x	579	29986	14	123	123
116	08/09/2017	Rod	Seabass	Alive	388	491	V9-1x	579	39461	27	486	503
117	30/05/2018	Rod	Seabream	Alive	255	278	V9-1x	579	12141	15	66	66
119	30/05/2018	Capechade	Seabass	Caught	377	549	V9-1x	579	5497	18	152	159

120	08/06/2018	Rod	Seabream	Caught	300	371	V9-1x	579	65149	19	322	563
122	08/06/2018	Rod	Seabream	Caught	271	311	V9-1x	579	12175	14	69	69
123	08/06/2018	Rod	Seabream	Alive	270	252	V9-1x	579	23624	16	109	113
125	08/06/2018	Rod	Seabream	Alive	347	617	V9-1x	579	20029	13	114	114
126	08/06/2018	Rod	Seabream	Alive	420	1015	V9-1x	579	10250	14	114	114
127	08/06/2018	Rod	Seabream	Alive	434	1198	V9-1x	579	22304	23	146	363
128	08/06/2018	Rod	Seabream	Alive	203	111	V9-1x	579	58821	21	254	491
129	08/06/2018	Rod	Seabream	Alive	265	246	V9-1x	579	2	1	1	1
130	08/06/2018	Rod	Seabass	Alive	499	1238	V9-1x	579	40362	25	560	582
131	08/06/2018	Rod	Seabass	Alive	435	892	V9-1x	579	87592	21	422	437
134	21/06/2018	Rod	Seabream	Alive	282	327	V9-1x	579	12894	13	101	101
136	21/06/2018	Rod	Seabream	Alive	306	379	V9-1x	579	24233	14	99	99
137	21/06/2018	Rod	Seabream	Alive	289	352	V9-1x	579	19703	13	101	101
140	21/06/2018	Rod	Seabream	Alive	223	158	V9-1x	579	14163	14	101	101
141	21/06/2018	Rod	Seabream	Alive	287	345	V9-1x	579	87876	26	341	582
142	21/06/2018	Rod	Seabream	Alive	232	158	V9-1x	579	15798	14	100	104
143	21/06/2018	Rod	Seabream	Alive	243	187	V9-1x	579	72327	18	320	478
144	21/06/2018	Rod	Seabream	Alive	230	156	V9-1x	579	18765	14	100	100
145	21/06/2018	Rod	Seabream	Alive	224	132	V9-1x	579	22692	23	199	374
146	21/06/2018	Rod	Seabream	Alive	315	615	V9-1x	579	28481	15	123	279
147	21/06/2018	Rod	Seabass	Alive	434	869	V9-1x	579	118834	25	581	582
149	04/07/2018	Rod	Seabream	Alive	338	545	V9-1x	579	16299	14	89	89
150	04/07/2018	Rod	Seabream	Alive	295	353	V9-1x	579	17373	14	88	88
151	04/07/2018	Rod	Seabream	Alive	275	319	V9-1x	579	57880	21	280	519
152	04/07/2018	Rod	Seabream	Alive	218	154	V9-1x	579	15181	15	89	91
153	04/07/2018	Rod	Seabream	Alive	215	145	V9-1x	579	15688	15	87	93
154	12/09/2018	Rod	Seabream	Alive	335	562	V9-1x	579	3386	11	18	18
155	12/09/2018	Rod	Seabream	Alive	324	496	V9-1x	579	12949	20	67	241
160	22/05/2019	Rod	Seabass	Alive	388	533	V9-2x	803	31716	24	102	202
161	22/05/2019	Rod	Seabass	Caught	379	500	V9-2x	803	40181	22	95	95
162	22/05/2019	Rod	Seabass	Caught	420	700	V9-2x	803	28973	17	63	63
165	29/05/2019	Capechade	Seabass	Alive	445	917	V9-2x	803	28277	27	354	653
166	29/05/2019	Capechade	Seabass	Caught	415	771	V9-2x	803	12531	15	30	30
167	29/05/2019	Capechade	Seabass	Caught	372	507	V9-2x	803	15088	22	40	44
168	29/05/2019	Capechade	Seabass	Alive	303	266	V9-2x	803	2809	16	8	8
170	29/05/2019	Capechade	Seabass	Alive	299	236	V9-2x	803	11205	25	39	193
176	29/05/2019	Capechade	Salema	Alive	259	207	V9-2x	803	126742	17	393	654
177	29/05/2019	Capechade	Salema	Caught	300	400	V9-2x	803	2018	13	5	5
178	29/05/2019	Capechade	Salema	Alive	310	385	V9-2x	803	47339	18	173	313
210	21/06/2019	Capechade	Seabass	Alive	331	367	V9-2x	803	523	12	2	2

211	21/06/2019	Capechade	Seabass	Caught	373	485	V9-2x	803	95601	21	240	265
215	21/06/2019	Capechade	Salema	Caught	294	331	V9-2x	803	31024	16	93	295
275	26/07/2019	Rod	Seabass	Caught	418	590	V9-2x	803	109931	23	521	544
276	26/07/2019	Rod	Seabass	Caught	378	580	V9-2x	803	137971	25	295	296
277	26/07/2019	Rod	Seabass	Caught	380	550	V9-2x	803	76505	22	213	221
291	30/07/2019	Capechade	Seabass	Alive	334	400	V9-2x	803	20712	24	166	171
292	30/07/2019	Capechade	Seabass	Caught	445	870	V9-1x	579	497	10	6	6
297	08/08/2019	Rod	Seabass	Alive	402	640	V9-1x	579	34286	20	175	178
298	08/08/2019	Rod	Seabass	Alive	372	490	V9-1x	579	36201	25	159	159
299	08/08/2019	Rod	Seabass	Alive	360	440	V9-1x	579	111822	24	582	587
301	12/08/2019	Capechade	Salema	Caught	305	435	V9-1x	579	13758	16	54	246
303	12/08/2019	Capechade	Salema	Alive	310	442	V9-1x	579	29660	19	138	349
304	12/08/2019	Capechade	Salema	Alive	315	444	V9-1x	579	544	11	4	4
345	02/09/2019	Capechade	Salema	Alive	280	360	V9-2x	803	23140	18	103	297
346	02/09/2019	Capechade	Salema	Alive	304	350	V9-2x	803	34678	20	163	327
347	02/09/2019	Capechade	Salema	Alive	310	460	V9-2x	803	37075	19	202	373
348	02/09/2019	Capechade	Salema	Alive	307	520	V9-2x	803	29916	19	132	525
349	02/09/2019	Capechade	Salema	Alive	305	370	V9-2x	803	16011	13	61	224
350	02/09/2019	Capechade	Salema	Alive	292	450	V9-1x	579	48987	16	263	587
351	02/09/2019	Capechade	Salema	Caught	315	510	V9-2x	803	6452	15	30	208
353	02/09/2019	Capechade	Salema	Alive	275	370	V9-2x	803	13281	17	51	136
355	02/09/2019	Capechade	Salema	Alive	310	550	V9-2x	803	6931	11	30	30
356	02/09/2019	Capechade	Salema	Alive	285	410	V9-1x	579	1515	3	6	6
357	02/09/2019	Capechade	Salema	Alive	284	450	V9-1x	579	28715	20	168	581
358	02/09/2019	Capechade	Salema	Alive	315	500	V9-2x	803	17493	17	92	636
360	02/09/2019	Capechade	Salema	Alive	285	320	V9-1x	579	17756	18	73	331
362	30/08/2019	Capechade	Salema	Alive	280	410	V9-2x	803	4166	9	18	18
363	30/08/2019	Capechade	Salema	Alive	285	400	V9-1x	579	20952	18	107	343
364	30/08/2019	Capechade	Salema	Alive	283	400	V9-1x	579	36660	15	135	372
365	30/08/2019	Capechade	Salema	Alive	322	490	V9-2x	803	7128	15	34	34
366	30/08/2019	Capechade	Salema	Alive	320	570	V9-1x	579	40910	19	217	323
367	30/08/2019	Capechade	Salema	Alive	275	320	V9-2x	803	21320	19	125	376
368	30/08/2019	Capechade	Salema	Alive	290	420	V9-1x	579	24754	18	136	374
369	30/08/2019	Capechade	Salema	Alive	300	380	V9-1x	579	47266	20	228	580
370	30/08/2019	Capechade	Salema	Alive	288	360	V9-1x	579	6880	16	31	224
371	30/08/2019	Capechade	Salema	Alive	290	440	V9-1x	579	46689	19	258	587
372	30/08/2019	Capechade	Salema	Alive	275	350	V9-1x	579	35721	19	198	581
373	30/08/2019	Capechade	Salema	Alive	285	370	V9-1x	579	81681	17	366	586
374	30/08/2019	Capechade	Salema	Alive	286	370	V9-1x	579	39688	19	207	582
499	24/06/2020	Capechade	Seabass	Alive	380	526	V9-2x	803	107232	24	301	340

501	24/06/2020	Capechade	Salema	Alive	320	487	V9-1x	579	13224	16	88	88
502	24/06/2020	Capechade	Salema	Caught	293	336	V9-2x	803	5274	11	23	23
503	24/06/2020	Capechade	Salema	Alive	267	258	V9-2x	803	14287	16	92	92
514	23/06/2020	Capechade	Seabass	Alive	450	802	V13-1x	1349	586	4	2	2
515	23/06/2020	Capechade	Seabass	Alive	480	1090	V13-1x	1349	119506	26	295	313
516	25/06/2020	Capechade	Salema	Alive	314	432	V9-2x	803	2258	10	22	22
517	25/06/2020	Capechade	Salema	Alive	310	394	V9-2x	803	12775	15	82	82
518	25/06/2020	Capechade	Salema	Alive	320	412	V9-2x	803	19597	16	130	334
519	25/06/2020	Capechade	Salema	Alive	290	364	V9-2x	803	13064	13	91	91
520	25/06/2020	Capechade	Salema	Alive	300	355	V9-2x	803	12635	14	81	81
521	25/06/2020	Capechade	Salema	Alive	275	303	V9-2x	803	6015	14	42	90
522	25/06/2020	Capechade	Salema	Alive	270	274	V9-2x	803	18322	13	93	96
523	25/06/2020	Capechade	Salema	Alive	275	263	V9-2x	803	5104	7	36	36
524	25/06/2020	Capechade	Salema	Alive	295	344	V9-2x	803	11209	17	79	79
525	25/06/2020	Capechade	Salema	Alive	337	520	V9-1x	579	11937	16	87	87
526	25/06/2020	Capechade	Salema	Alive	345	541	V9-2x	803	11289	16	87	87
527	25/06/2020	Capechade	Salema	Alive	283	317	V9-2x	803	20652	18	133	339
529	25/06/2020	Capechade	Salema	Alive	297	318	V9-2x	803	12092	10	86	290
530	25/06/2020	Capechade	Salema	Alive	315	474	V9-2x	803	14255	12	91	332
531	25/06/2020	Capechade	Salema	Alive	270	279	V9-2x	803	187	5	2	2
532	25/06/2020	Capechade	Salema	Alive	260	240	V9-1x	579	31050	15	165	334
533	25/06/2020	Capechade	Salema	Alive	270	275	V9-2x	803	18547	14	127	331
545	29/06/2020	Capechade	Salema	Alive	237	175	V9-1x	579	12324	18	102	110
546	29/06/2020	Capechade	Salema	Alive	315	452	V9-2x	803	22900	18	109	335
547	29/06/2020	Capechade	Salema	Alive	260	241	V9-2x	803	3665	9	21	21
548	29/06/2020	Capechade	Salema	Alive	230	164	V9-1x	579	12195	13	88	88
549	29/06/2020	Capechade	Salema	Alive	230	197	V9-2x	803	9501	17	81	305
550	29/06/2020	Capechade	Salema	Alive	275	294	V9-2x	803	16050	14	91	102
551	29/06/2020	Capechade	Salema	Alive	298	406	V9-2x	803	15296	14	75	306
552	29/06/2020	Capechade	Salema	Alive	210	140	V9-2x	803	43215	15	146	330
553	29/06/2020	Capechade	Salema	Alive	209	134	V9-2x	803	27073	15	88	88
554	29/06/2020	Capechade	Salema	Alive	210	124	V9-2x	803	31819	16	111	315
555	29/06/2020	Capechade	Salema	Alive	209	130	V9-2x	803	29854	13	90	317
556	29/06/2020	Capechade	Salema	Alive	210	127	V9-2x	803	39634	21	137	335
557	29/06/2020	Capechade	Salema	Alive	210	134	V9-2x	803	19747	15	77	335
558	30/06/2020	Capechade	Seabass	Alive	685	3235	V13-1x	1349	52956	23	153	153
559	30/06/2020	Capechade	Salema	Alive	264	244	V9-2x	803	19371	16	89	92
561	02/07/2020	Capechade	Salema	Alive	187	97	V9-2x	803	114	2	17	84
563	02/07/2020	Capechade	Salema	Alive	288	367	V9-2x	803	20214	12	84	84
565	03/07/2020	Capechade	Salema	Alive	285	327	V9-2x	803	16664	18	97	277

567	06/07/2020	Capechade	Salema	Alive	256	223	V9-2x	803	23497	16	94	283
568	06/07/2020	Capechade	Salema	Alive	297	385	V9-2x	803	16301	15	74	296
569	06/07/2020	Capechade	Seabass	Caught	343	410	V9-2x	803	34578	16	91	91
571	07/07/2020	Capechade	Salema	Alive	300	380	V9-2x	803	15561	16	78	78
572	07/07/2020	Capechade	Salema	Alive	275	288	V9-2x	803	18480	19	79	90
573	07/07/2020	Capechade	Salema	Alive	277	300	V9-2x	803	12437	16	70	70
574	07/07/2020	Capechade	Seabass	Caught	430	739	V13-1x	1349	32036	24	111	112
575	07/07/2020	Capechade	Salema	Alive	247	212	V9-2x	803	27861	19	151	297
576	07/07/2020	Capechade	Salema	Alive	270	254	V9-2x	803	16809	15	84	327
577	07/07/2020	Capechade	Seabass	Alive	472	1232	V13-1x	1349	104806	21	322	327
578	07/07/2020	Capechade	Salema	Alive	275	265	V9-2x	803	38503	16	152	268
579	07/07/2020	Capechade	Salema	Alive	214	131	V9-2x	803	45944	20	119	327
580	07/07/2020	Capechade	Salema	Alive	210	127	V9-2x	803	38263	20	148	327
581	07/07/2020	Capechade	Salema	Alive	210	136	V9-2x	803	22828	14	124	322
628	23/09/2020	Capechade	Seabass	Caught	735	3775	V13-1x	1349	22374	16	76	76
629	25/09/2020	Capechade	Seabass	Alive	490	1059	V13-1x	1349	89309	23	243	247
630	25/09/2020	Capechade	Seabass	Alive	440	795	V13-1x	1349	87398	20	233	247
631	06/10/2020	Net	Seabass	Alive	535	1638	V13-1x	1349	68194	20	236	236

Table S.1. Monitoring data for each individual of each species. *The number of days detected corresponds to the number of days a fish was detected at least once by one of the receivers. The number of receivers corresponds to the number of receivers which detected a fish at least once. The total period of detection corresponds to the number days between a fish's first and last detection.*

Percentage level for KUD derived home range estimation	**Species**		
50%	Seabream	Seabass	Salema
EFS	0.22	0.28	0.15
EBS	0.24	0.21	0.01
95%	Seabream	Seabass	Salema
EFS	1.73	1.35	1.23
EBS	0.81	1.07	0.63

Table S.2. 50% and 95% KUD derived home ranges sizes for all species and seasons. *Values are in km*^{2}.

7.2. Figures

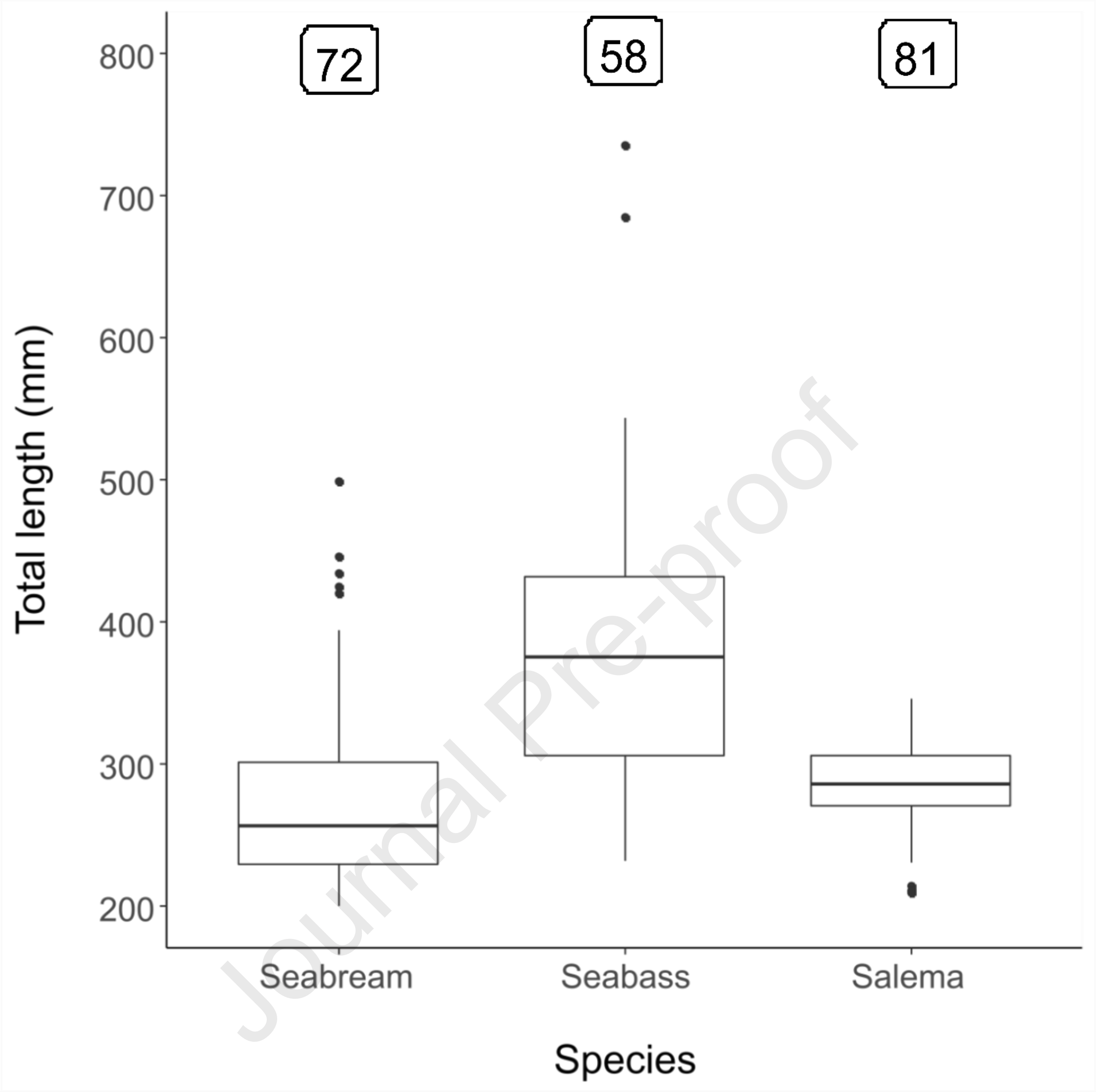

Figure S.1. Mean total lengths of tagged individuals. *Boxplots displays the median, hinges, whiskers and outliers of all individuals total length values between species. The number of fish for a given species is indicated in the white boxes at the top of each boxplot.*

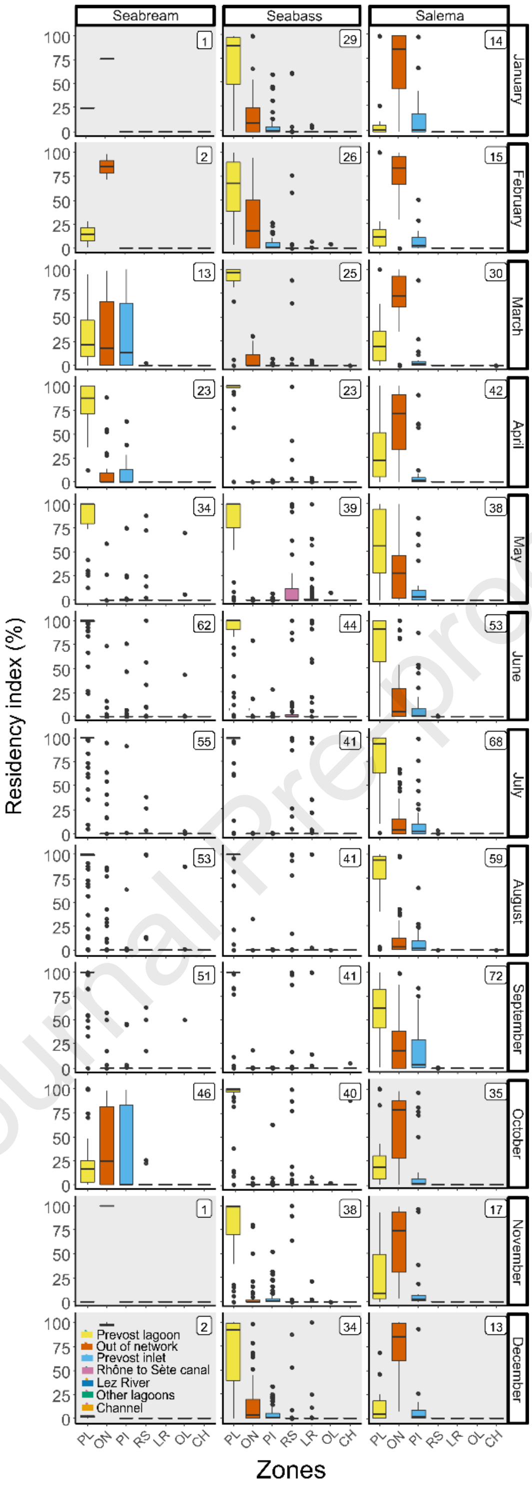

Figure S.2. Monthly residency indices for each species as a function of the zones defined in Figure 1. *The boxplots represent the median, hinges and whiskers of RI values calculated for each fish, for a given species, zone (PL: "Prévost Lagoon", ON: "Out of network", PI: "Prévost Inlet", RS: "Rhône to Sète Canal", LR: "Lez River", OL: "Other lagoons", CH: "Channel",) and month and dots represent the outliers. The number of fish for a given combination of species and seasons is indicated in the white boxes at the top of each subplot. The gray area represents the EBS for each species versus the white area which represents the EFS.* ***COLORS SHOULD BE USED***

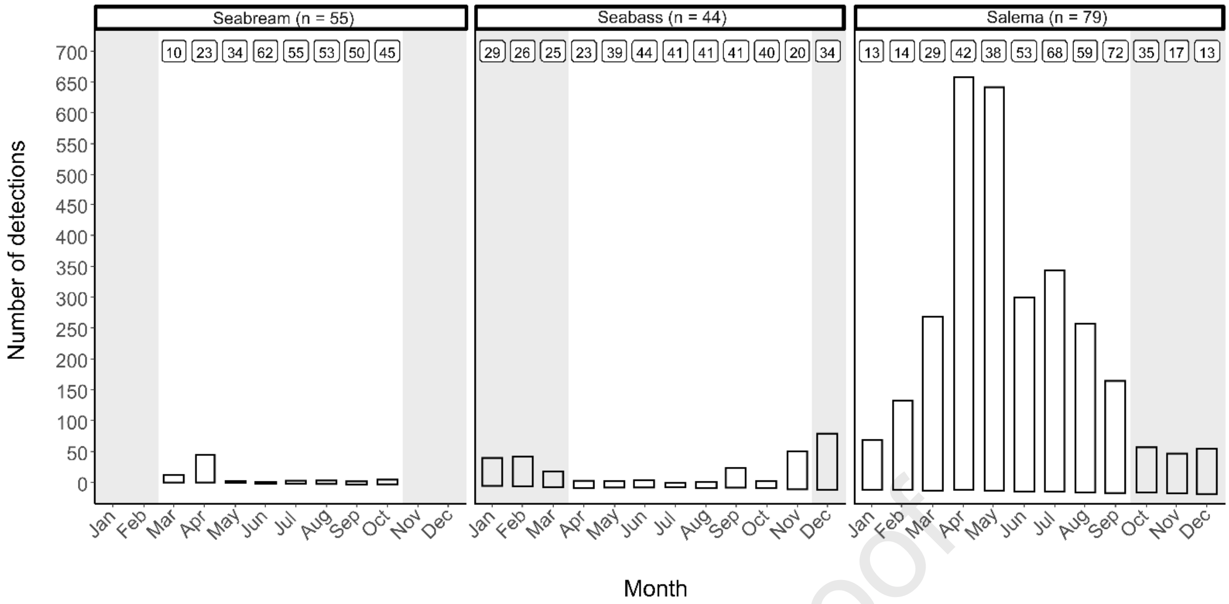

Figure S.3*. Monthly number of detections by the "Out of network" receivers for each species normalized by the number of individuals,** *indicated in the white boxes at the top of each bar. The grey area represents the EBS for each species versus the white area which represents the EFS.* ***COLORS SHOULD BE USED

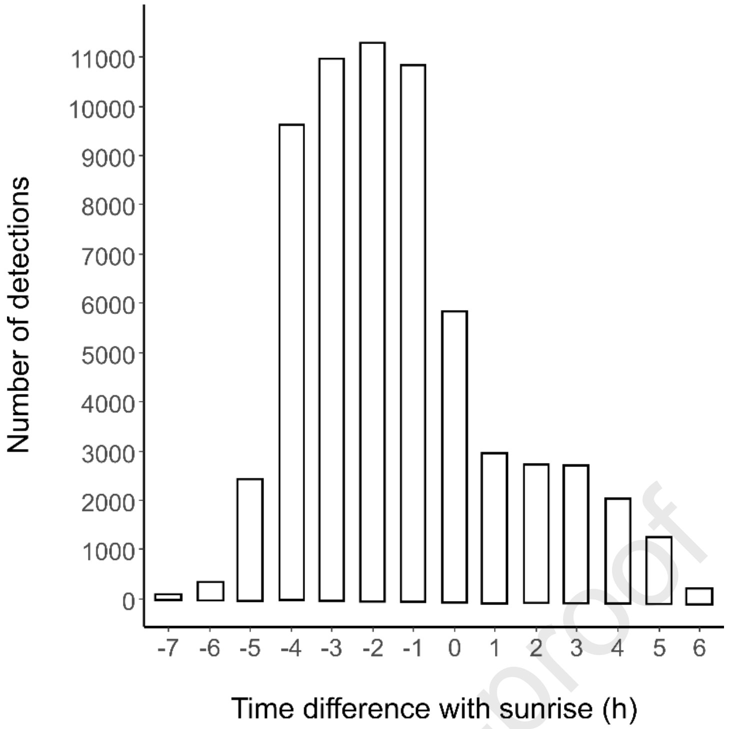

Figure S.4. Number of detections by the "Out of network" receivers of tagged salemas as a function of the time difference between detection and sunrise times.

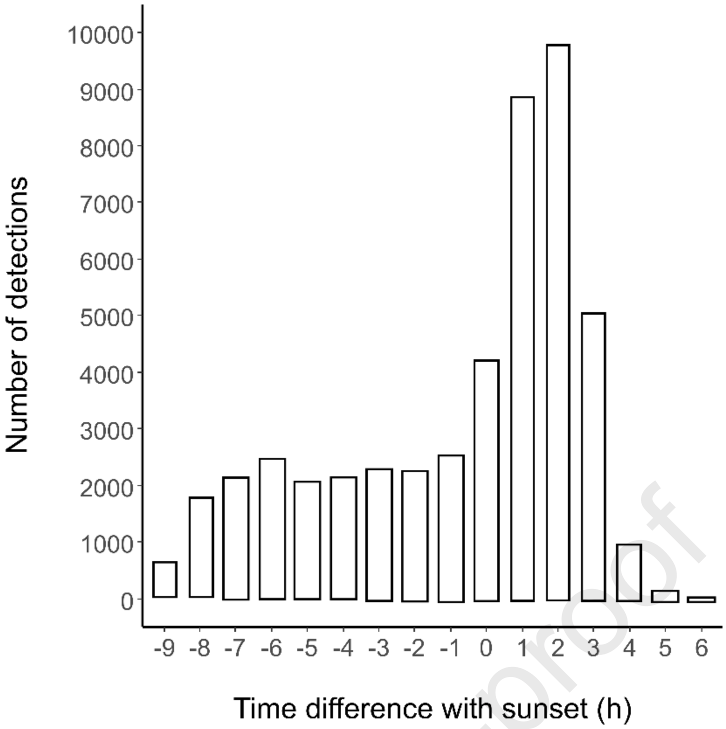

Figure S.5. Number of detections by the "Out of network" receivers of tagged salema as a function of the time difference between detection and sunset times.

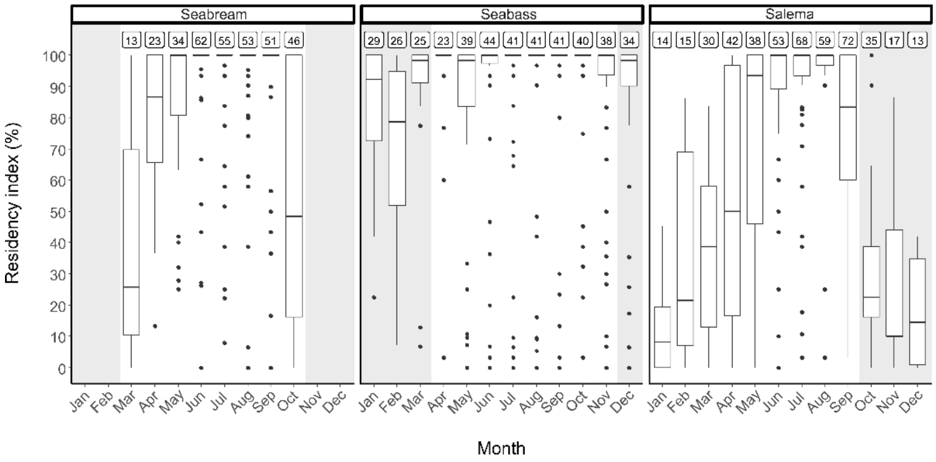

Figure S.6. Monthly residency indices of each species inside Prévost Lagoon in terms of number of days detected. *The boxplots represent the median, hinges and whiskers of RI values calculated for each fish, for a given species and month and dots represent the outliers. The grey area represents the EBS for each species versus the white area which represents the EFS. The number of fish for a given combination of species and month is indicated in the white boxes at the top of each subplot.*

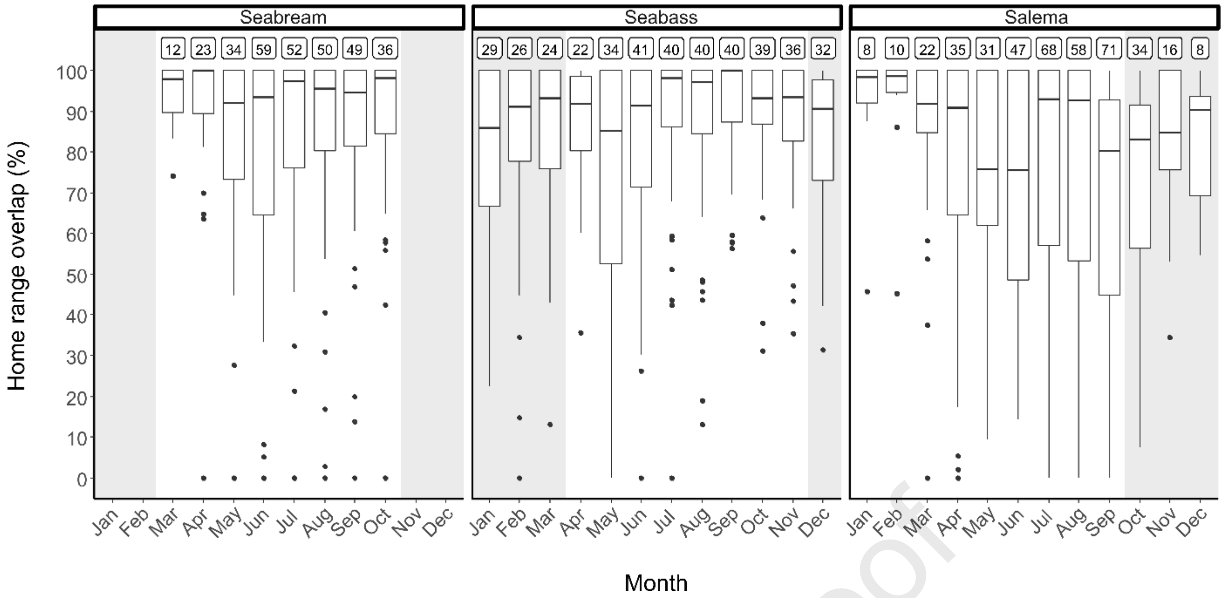

Figure S.7. Overlap between home range areas for home ranges derived from 50% between day and night for all three species and months. *Each panel displays the median, hinges, whiskers and outliers of all individual overlap values for a given month and species. The grey area represents the EBS for each species versus the white area which represents the EFS. The number of fish for a given combination of species and month is indicated in the white boxes at the top of each subplot.*

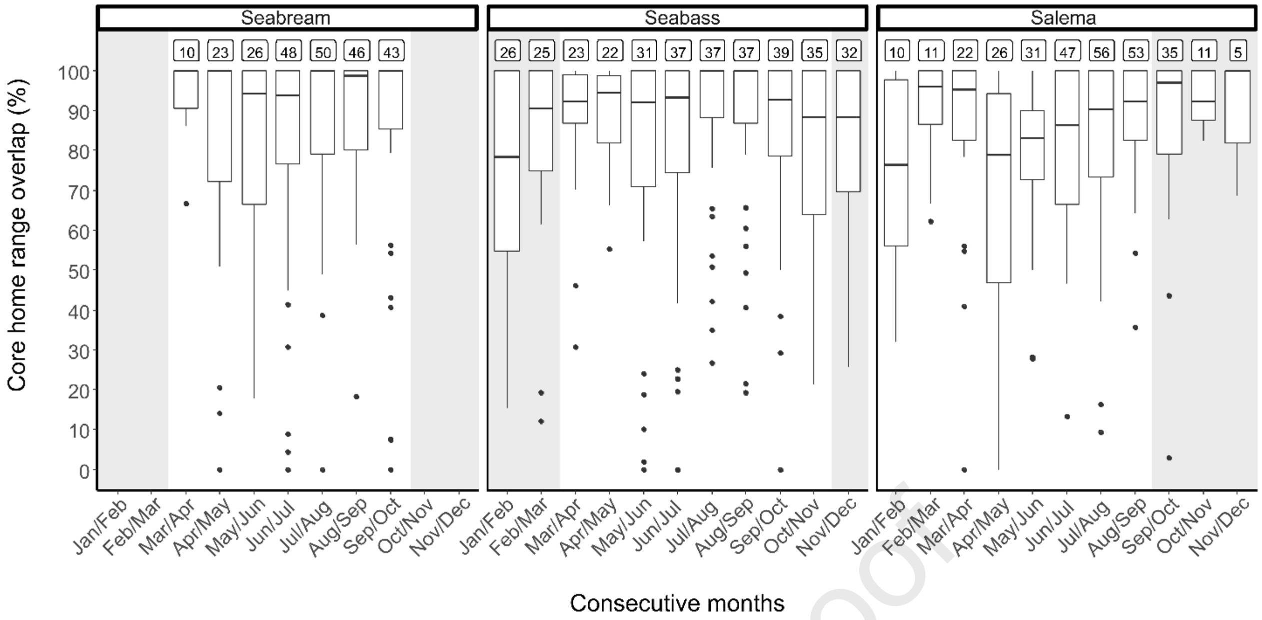

Figure S.8. Overlap between consecutive months home ranges. *Each panel displays the median, hinges, whiskers and outliers of all individual overlap values. The grey area represents the EBS for each species versus the white area which represents the EFS. The number of fish for a given combination of months is indicated in the white boxes at the top of each subplot.*

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Highlights

- All three species are highly resident inside the lagoon during their foraging season

- All three species show contrasted space use with very small individual home ranges

- All three species show some inter-annual fidelity to the lagoon

- Multi-species tracking shows the importance of a lagoon as a key foraging site

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: