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Seasonal migration, site fidelity, and population structure of European seabass (*Dicentrarchus labrax*)

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Large-scale electronic tagging is a very powerful tool to study how fish movements and migrations shape the internal dynamics of populations. This knowledge, crucial for improving fishery management, was still limited for the European seabass, whose stocks in the Northeast Atlantic have declined drastically over the last decade. To better understand the species ecology and the spatio-temporal structure of the population, we tagged seabass in the North Sea, the English Channel, and the Bay of Biscay, from 2014 to 2016. Out of 1220 deployed DSTs, 482 have been recovered by November 2022. Approximately half of them included a period of potential spawning migration. Reconstructed trajectories confirmed seabass to be a partial migratory species, as individuals exhibited either long-distance migrations or residence. Most migrants exhibited fidelity to summer feeding areas and winter spawning areas. Our dataset enriches the knowledge of seabass biological traits (e.g. temperature and depth ranges, vulnerability to predation and fishing). Our results suggest a spatial structure of the Atlantic population that differs from the stock structure currently considered for assessment and management. The consequences should be explored at both the European level and by regional managers involved in conservation outcomes.

Keywords: biologging, depth, *Dicentrarchus labrax*, DST data storage tag, European sea bass, geolocation model, large-scale electronic tagging, movement ecology, spawning site fidelity, stock structure, temperature.

Introduction

As internal dynamics and population structure are shaped by animal movements and migrations (Nathan *et al.*, 2008; Spiegel *et al.*, 2017), the choice of inappropriate spatial and/or temporal scales for monitoring and assessing wild populations can have disastrous effects on their exploitation and conservation (Kerr *et al.*, 2017; Cadrin, 2020). The management units for exploited marine fish—hereafter called stocks, defined as "a marine biological resource that occurs in a given management area", (Anon, 2013)—have not been always spatially delimited on a biological basis. A mismatch between stocks and biological populations—"a group of interbreeding individuals that exist together in time and space" (Hedrick, 2000; in Waples and GaggiottiI, 2006)—can lead to inappropriate management measures. The consequences are detrimental to varying degrees: loss of productivity, loss of biodiversity, and reduced resilience, or, ultimately, the collapse of populations (Kerr *et al.*, 2017; Cadrin, 2020). There have been situations where different populations have failed to be managed as a single stock, for example, the collapse of the walleye pollock fishery in the Aleutian Basin (Bailey, 2011) or the difficulties to rebuild the Atlantic cod fisheries (e.g Hutchinson, 2008; Zemeckis *et al.*, 2014b).

Numerous methods have been developed for delineating populations and exploring their connectivity either at an evolutionary scale—genetics methods—or at a demographical scale—tagging, morphometric/meristic characters, life history

traits such as growth and age at first maturity, chemistry of calcified structures, parasites, etc. (e.g. Cadrin, 2020). Tagging is one of the oldest methods of providing information on fish movement, and Walton reported in "the Compleat Angler", first published in 1653 (in Mc Farlane *et al.*, 1990), its use on Atlantic salmon juveniles, showing natal homing of this species.

The European seabass (*Dicentrarchus labrax*) is one of the most prized species in the Northeast Atlantic. In 2018, commercial landings reached 43.8 M€ in first sale in Europe, while the economic value of recreational fishing was estimated at c.a. 356 M€ (EUMOFA, 2021). The species' distribution ranges from the Scottish and Norwegian coasts in the north and the coasts of Morocco, the Mediterranean Sea, and the Black Sea in the south. Essential habitats vary during the life cycle (Pickett and Pawson, 1994; Lopez *et al.*, 2015). Reproduction generally takes place offshore, although coastal spawning has also been reported. Successful reproduction depends on the advection of eggs and larvae towards estuarine or sheltered coastal areas, which provide favourable habitats to the survival and growth of the juveniles. These nursery areas support the juveniles until they reach maturity at ~35 cm for males and ~42 cm for females (Kennedy and Fitzmaurice, 1972; Pawson and Pickett, 1996). Adults alternate migrations between coastal/inshore feeding areas and offshore spawning grounds.

Classified as coastal and demersal (Froese and Pauly, 2021), seabass was managed locally by national jurisdictions until

the southern Channel/North Sea fisheries showed strong signs of decline in the 2010s. Since 2015, the European Commission has had to take emergency measures for its conservation (e.g. European Commission, 2015). The first international advice regarded NE Atlantic seabass as a single stock (ICES, 2012). Practical considerations then led experts to consider four stocks, two of which are now being assessed by ICES with an analytical assessment (ICES, 2018). The 48th parallel north separates the "northern stock", hereafter designed as NS, comprising the Irish Sea, Celtic Sea, English Channel, and southern North Sea (ICES divisions IVb–c and VIIa, d–h), and the "Bay of Biscay stock", hereafter designed as BOB (ICES divisions VIIIa–b). The two other stocks are in Southern Ireland and Western Scotland (ICES areas VIa, VIIb, and VIIj) and Portugal and Northern Spain (ICES areas VIIIc and IXa). ICES recurrently stresses the need for research on the spatial population structure (ICES, 2021).

Seasonal migrations between inshore feeding areas and offshore spawning areas were shown by conventional tagging (external tags) around British islands (Pawson et al., 1987; Pawson et al., 2007; Pawson et al., 2008). This approach also evidenced fidelity to summer habitats. Fritsch et al. (2007) found low connectivity between the NS and the BOB, but their data showed a very low recapture rate and short time at liberty of recoveries. Electronic tagging (acoustic and archival tags) revealed fine-scale behaviours and confirmed fidelity to summer feeding areas (Quayle et al., 2009; Doyle et al., 2017; de Pontual et al., 2019). Fidelity on spawning grounds in winter was also evidenced as well as the existence of a probable mixing zone of NS/BOB stocks in western Brittany (de Pontual et al., 2019). Seabass is a partially migratory species, with some individuals showing residency in coastal areas (Doyle et al., 2017; O'Neill et al., 2018; de Pontual et al., 2019). Acoustic telemetry recently evidenced residency of juveniles and subadults in inshore habitat (Stamp et al., 2021). Despite these advances, knowledge remains patchy and mainly focused on the NS. The extent to which the identified behaviours and movement patterns are representative for the whole population remains a key question. To address this issue, we carried out a large-scale electronic tagging programme from 2014 to 2016 at 10 sites along the French coast from Dunkirk (southern North Sea) to Capbreton (southern Bay of Biscay). Our objectives were (1) to confirm site fidelity particularly on winter spawning grounds (2) to analyse the connectivity between NS and BOB stocks, and (3) to highlight particular behavioural traits. These objectives required the prior analysis of vertical behaviours (Heerah et al., 2017), with the aim to improve the geolocation model previously developed (Woillez et al., 2016). We then discussed how this new insight on the spatial structure of the Atlantic population challenges the current functioning of its management.

Material and methods

Tagging protocol

Ten tagging surveys were carried out along the French coasts during the summers of 2014, 2015, and 2016 (Table 1 and Figure 1). Tagging followed the protocol developed during a pilot study in the Iroise Sea (de Pontual et al., 2019). The national fishery committee (CNPMEM) charted two to three professional fishing vessels per survey. One or two vessels were in charge of fishing (rods and lines), while another

was used as a support vessel, moored in sheltered waters, where fish were transferred to, tagged, and released on the same day they were caught. Carefully selected fish [>41.5 cm total length (TL), tag to body mass ratio <2%, apparently good condition] were tagged following the protocol of de Pontual et al. (2019). Fish were tattooed by intradermal injection with alcian blue. Ethics rules were strictly observed, and tagging was carried out under a project licence no 01987.02 authorized by the French Ministry of Agriculture and Environment.

The DST type was Cefas G5 long-life 2 Mb, with temperature and pressure sensors and a battery life of 2 years. Tags were calibrated with a pressure range of 0–2000 kPa, allowing a maximum depth record of ~230 m. Pressure and temperature were recorded at 90 s intervals for the first 680 days and at 3 min for the 50 remaining days. Logging regimes were the same for all surveys. In order to increase the recovery rate of DSTs, we used floating tags that could drift ashore in case fish died at sea, regardless of the cause of death.

Experiments were advertised through various media, posters, and mailings to fishers and stakeholders all along the French coasts. Posters in English and Spanish were sent to research institutes in the United Kingdom, Belgium, Netherlands, and Spain to promote the return of tagged fish recaptured abroad. A reward of 100€ was offered for each tagged fish returned to the laboratory (50€ for a DST alone), and a further 1000€ awarded in a prize draw among all participants.

Geolocation model

Trajectories were reconstructed with a geolocation modelling approach (Woillez et al., 2016). The likelihood of daily fish positions was thus estimated with a hidden Markov model (HMM), consisting of a movement model and an observation model (Pedersen et al., 2008; Thygesen et al., 2009). From the daily posterior probability distributions, individual fish tracks were computed as the most probable sequence of positions, i.e. the Viterbi track. Full details on the geolocation approach were outlined in Woillez et al. (2016), but we described the model refinements for the current analysis in the text below.

The observation model linked the time series of measured depth and temperature to the environmental reference fields of temperature at depth and bathymetry. We used the Atlantic-European North West Shelf-Ocean Physics Reanalysis provided by E.U. Copernicus Marine Service Information (CMEMS-NWS Physics) as the temperature reference field. This reanalysis provides ocean temperature at depth produced by a hydrodynamic model at 7 km horizontal resolution. The model assimilates observations (e.g. surface sea temperature from satellite and in situ vertical profiles of temperature) to minimize bias and errors of the temperature at depth fields predicted by the model. For simplicity, we set the standard deviations of temperature at depth to the typical levels of uncertainty for temperatures derived from this hydrodynamic model, i.e. 0.85°C. We used the 2014 30-arcsecond gridded bathymetry data from the General Bathymetric Chart of the Oceans (GEBCO).

The model was adapted to include a behavioural switch. A HMM to identify behavioural states series (Heerah et al., 2017) was applied on the archival depth series to discern low (presence of tidal signals) from high activity states. Following the approach of Pedersen et al. (2008), this daily ac-

Table 1. Synopsis of the tagging surveys.

Survey	Location	#Tagged fish	# Recoveries	Recovery rate (%)	Max. time post tagging (days)[a]
DK (3–13 June 2014)	Dunkirk	150	57	38.0	1474
SQ (17–27 June 2014)	Saint-Quay-Portrieux	152	65	42.8	1437
CB (1–11 September 2014)	Capbreton	123	59	48.0	1237
LT (9–19 September 2014)	La Turballe	143	70	49.0	1533
PB (1–12 June 2015)	Port-en-Bessin	89	39	43.8	1073
AD (9–19 June 2015)	Audierne	179	66	36.9	1230
SM (9–11 September 2015)	Saint-Malo	16	5	31.3	822
IO (7–16 September 2015)	Ile d'Oléron	132	41	31.1	579
SV (21–24 June 2016)	Saint-Vaast-la-Hougue	129	37	28.7	739
NO (31 August–4 September 2016)	Noirmoutier	107	43	40.2	833
Total DSTs		1220	482	39.5	1474

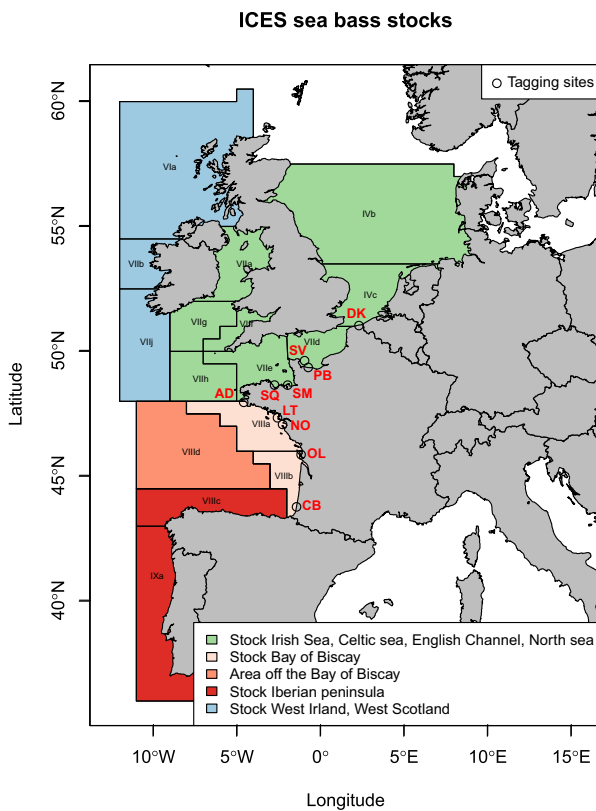[a]For recovered fish only (i.e. excluding DSTs found on the coast).

Figure 1. The ICES seabass stocks and locations of the tagging surveys (DK: Dunkirk; PB: Port-en-Bessin; SV: Saint Vaast-la-hougue; SM: Saint Malo; SQ: Saint Quay-Portrieux; AD: Audierne; LT: La Turballe; NO: Noirmoutier; OL: Ile d'Oléron; and CB: Capbreton). The area off the Bay of Biscay is considered for migration analysis. Figure in colour is available in the online open access version.

tivity state was then incorporated in the movement model and the depth likelihood of the observation model. For the movement model, the parameter of diffusivity (*D*) was estimated in a separate maximum likelihood estimation procedure for the two behavioural states. *D* would be smaller for the low activity state (*D* estimated between bounds of 1 and 6 km²/day) than for high activity (*D* estimated above 6 km²/day). Tide signals were not used to geolocate fish, as it was inefficient for seabass, particularly in BOB, where tide phases and amplitudes are very similar across the whole area.

For the observation model, we implemented a continuous approach for the depth likelihood if the fish showed a high activity level. The depth likelihood computation method assumes that the observed depth at a given position is Gaussian distributed with mean equal to the depth of the bathymetry and variance equal to the estimated bathymetry variance (Pedersen *et al.*, 2008). When a low activity state was detected (with the presence of tidal signals), the depth likelihood resulted in a seabed matching with few meters of uncertainty. The temperature likelihood was estimated for each depth layer of the reference field (0, 3, 10, 15, 20, 30, 50, 75, 100, 125, and 150 m). The depth and temperature likelihood at depth were then multiplied resulting in a single observation likelihood layer per day. When available, the recapture position was used for geolocation if the DST was still actively recording at the time of the recapture.

For the tags showing evidence of a time spent in warm water of power plant plume (expert visual inspection of 5–10°C differences in the temperature time series), an autoregressive model in which the mean of the process switches between two regimes was fit to the temperature time series (Chang-Jin and Nelson, 1999). Thus, a specific observation likelihood model was defined for the days likely spent in the warm plume; with an equal non-null value of data likelihood for grid cells where a nuclear power plant is located and a null value for the rest of the grid cells. Thirteen power plants from France, Belgium, Netherland, and the United Kingdom were considered (Supplementary Table S1).

Individual fish tracks were collated per tagging sites to illustrate post-tagging individual migration histories showing fish location with respect to time and seasons. For every individual, we summarized the estimated fish locations by its daily membership to ICES seabass stocks (as defined in Figure 1). Site fidelity is defined as the fidelity behaviour to a given region. Here, site fidelity or residency to summer feeding grounds was defined as the fish returning or being present in a 50 km radius of its tagging site (as in de Pontual *et al.*, 2019), as seabass are known to return to or stay in very specific locations (Doyle *et al.*, 2017). Site fidelity to spawning grounds was defined as fish returning in the same ICES stock area to reproduce.

Results

Out of the 1220 tags deployed across the 10 sites, 482 (39.5%) tagged fish or tags alone were found by November 2022
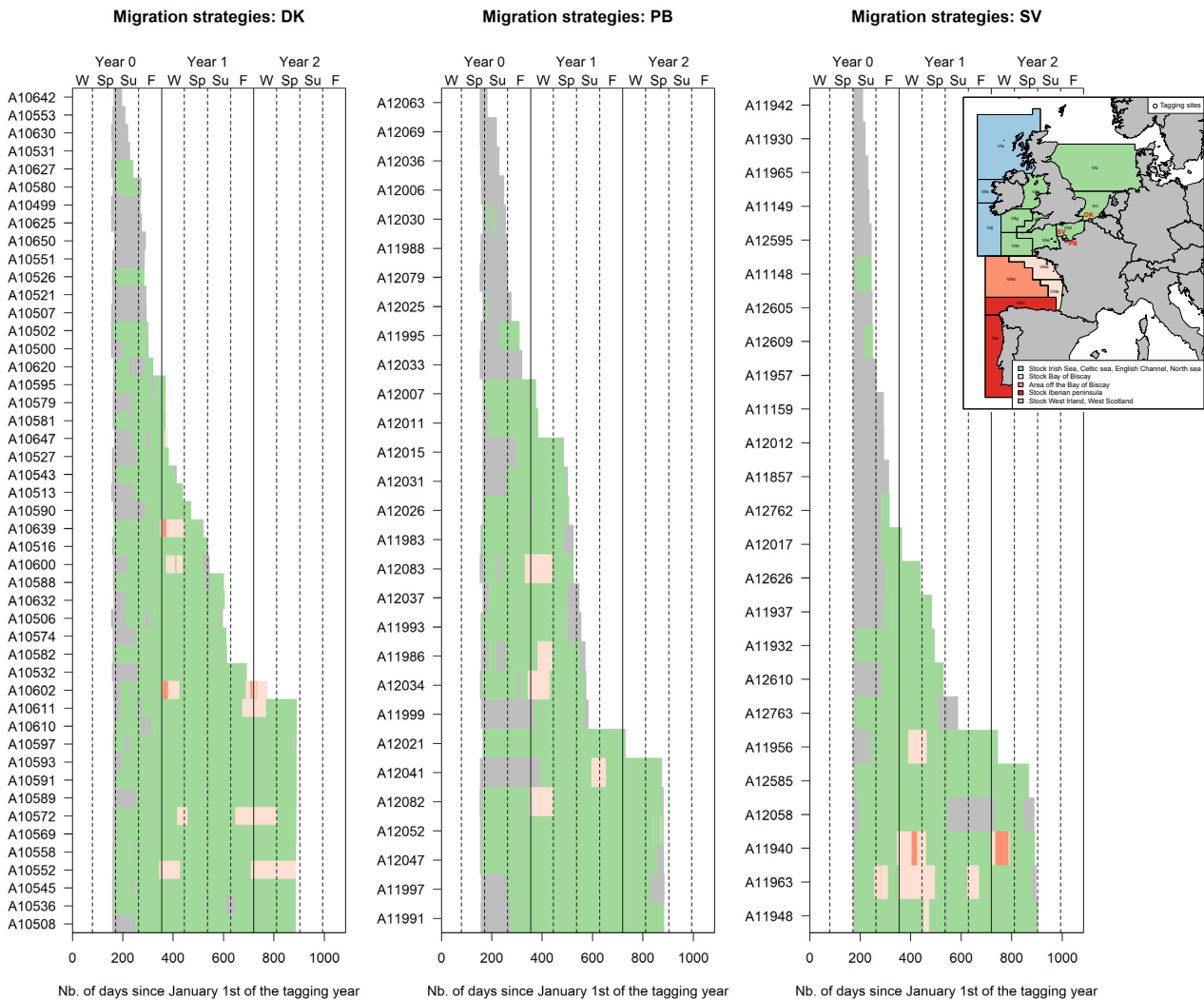
Figure 2. Individual movement histories showing seasonal migrations and occurrences of tagging site fidelity. Results for seabass tagged in the southern North Sea (Dunkirk) and Eastern English Channel (Port-en-Bessin, Saint-Vaast-la-Hougue). The colours indicate fish position according to those of the ICES stocks (shown in the inset plot). The grey colour illustrates the fidelity to the tagging site (fish within 50 km of its tagging site). Time series are temporally aligned among tagging sites using 1 January of the tagging year as a time reference. Vertical dotted lines separate the seasons (W: winter; Sp: spring; Su: summer; F: fall). Solid vertical lines separate the years.

(Table 1). A total of 443 DSTs were physically recovered. Recovery rates varied across sites from 28.7% (Saint-Vaast-la-Hougue) to 49.0% (La Turballe), with the maximum time at liberty ranging from 579 to 1474 days (see Table 1 for all the recovery rates per tagging sites). The tattoo and the tag flotation device proved to be very useful to improve subsequent fish detection or tag recovery. Tags were (1) returned by professional or recreational fishers; (2) discovered at some stage of the commercialization (auction room, fish market, consumer, etc.); or (3) found on the coast after having drifted after the death of the fish (Supplementary Figure S0). Fish were mostly recaptured by net, longline and other lines. Bottom trawlers contributed less (Supplementary Figure S0), whereas the fish returns from other fishing techniques were very few. The contributions of spearfishing and surfcasting were marginal.

For some individuals tagged in Dunkirk ($n = 17$, i.e. 4.7%), sudden rises of $\sim 10^\circ$C above normal temperature at shallow depths were observed all along the year. Those ther-

mal signatures were interpreted as fish incursions into power plant plumes, which positions need to be taken into account in the geolocation model. Supplementary Figure S1 shows depth/temperature series of a fish that stayed in a power plant plume from December to April. Supplementary Figure S2 shows another fish exhibited a quasi-resident behaviour in such water bodies, with a maximum temperature above 32°C.

The experienced thermal minimum was $\sim 6.5^\circ$C (e.g. Supplementary Figure S3). This winter's temperature was more representative of continental or estuarine waters than marine waters. Thermocline position did not limit the amplitude of vertical movements (e.g. Supplementary Figure S4), and temperature gradient that the fish can withstand can be very high (e.g. 10°C in <1 hour for individual #CB_A11107).

Seabass showed some ability to dive deep; some individuals exceeded the maximum depth ($\sim$230 m) defined during the DST calibration (e.g. Supplementary Figure S4).
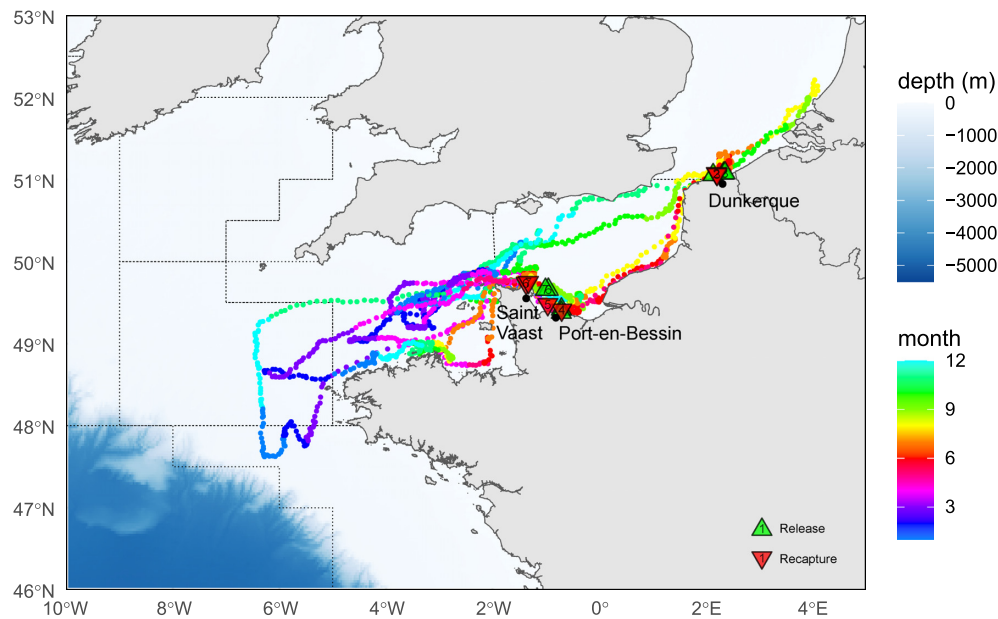
Figure 3. Seven typical reconstructed tracks derived from DST data of seabass tagged in the southern North Sea and in the eastern English Channel (#DK_A10508, #DK_A10506, #DK_A10600, #PB_A11999, #PB_A12015, #SV_A12763, and #SV_A11937), with daily position estimates of the most probable track coloured by calendar month and release and recapture positions represented respectively by green and red triangles. Number inside the triangles corresponds to the rank of the tags ID listed above. Bathymetry data originate from the GEBCO.

DST records provided other environmental signals. For instance, tidal signals could be identified on more or less long time sequences (e.g. Supplementary Figure S5). These were visible on a significant number of tags ($\sim$35%), whether in the Channel or in the Bay of Biscay.

Predation events of seabass by a marine mammals, tuna or lamnid [sharks with varying degrees of thermoregulation capacity (see e.g. Clarke and O'Connor, 2014; Schlaff *et al.*, 2014)] were observed (not counted on the whole dataset). For instance, we found a predation event probably by a lamnid capable of increasing its body temperature by ca. 10°C above that of the surrounding environment (Supplementary Figure S6). Fish #SV_A11857 (Supplementary Figure S7) had been likely eaten by a marine mammal as indicated by a temperature increase to 35°C. Fishing events on seabass by fishers were also observed in the time series (example of a net; Supplementary Figure S8), which were confirmed by their declaration when reporting the recapture information.

Migration strategies

Tagged fish with the longest time at liberty are the most useful to analyse the spatio-temporal structuring of the population in terms of behaviour strategies (residency vs. migration, feeding, and spawning site fidelity at the scale of the stock units). Consequently, trajectories of tagged seabass, whose data were recovered until 31 August 2021, were reconstructed. Most of the time the model runs converged, but some either failed to converge, as diffusion parameters were likely too high, or converged, but they estimated very high values of diffusion parameters, which may be not ecologically relevant ($D > 200$ km^2/day). For those latter tags ($n = 128$, i.e. 32% of the total number of reconstructed tracks), in order to increase the number of reconstructions, the diffusion parameters were fixed to the median values estimated from non-problematic tags of the same tagging site (see supplementary material, Appendix S4, Table S2 for more details). Ultimately, migration strategies were analysed using 364 reconstructions.

Most seabass tagged in Dunkirk (southern North Sea) remained in the NS area except for six fish (#*DK_A10639*, #*DK_A10600*, #*DK_A10602*, #*DK_A10611*, #*DK_A10572*, and #*DK_A10552*), which made incursions in wintertime into the BOB area (Figure 2). However, their trajectories were tangent to the 48th parallel (separating NS and BOB) and did not show any reproductive migration in central BOB (Figure 3). Tagging site fidelity in summer was observed for only three fish tagged in Dunkirk.

The Eastern Channel data (PB and SV) showed the same patterns as in the southern North Sea (Figure 2). Most fish remained in the NS area except nine fish (#PB_A12083, #PB_A11986, etc.), which made incursions, in wintertime (except one in fall), into the BOB area or the area off the BOB. Here again, the trajectories stayed close to the 48°N, and did not go to the central BOB. Feeding site fidelity in summer was observed for ten individuals, which returned to their tagging sites one year after the release date. During wintertime, fish migrate towards west to spawn (Figure 3).

For the western English Channel (fish from Saint-Quay-Portrieux and one fish from Saint-Malo; A12612), a very different pattern is observed (Figure 4). The main migration strategy is towards the south (71%), i.e. mainly the BOB area, and in a lower extent to the area off BOB and the Iberian Peninsula. The occurrences of site fidelity are numerous and concern both feeding site fidelity (in summer; 81% of the DST data that last at least 1 year) and spawning site fidelity (fish migrating to BOB two successive winters; 92% of the DST data that last at least 1.5 years). Two individuals (#SQ_A10788; TL = 67.3 cm, and #SM_A12612; TL = 51.9 cm) remained in the NS (Figure 5), and a third individual showed a mixed tactic (#SQ_A10700; TL = 47 cm) with the first winter in NS
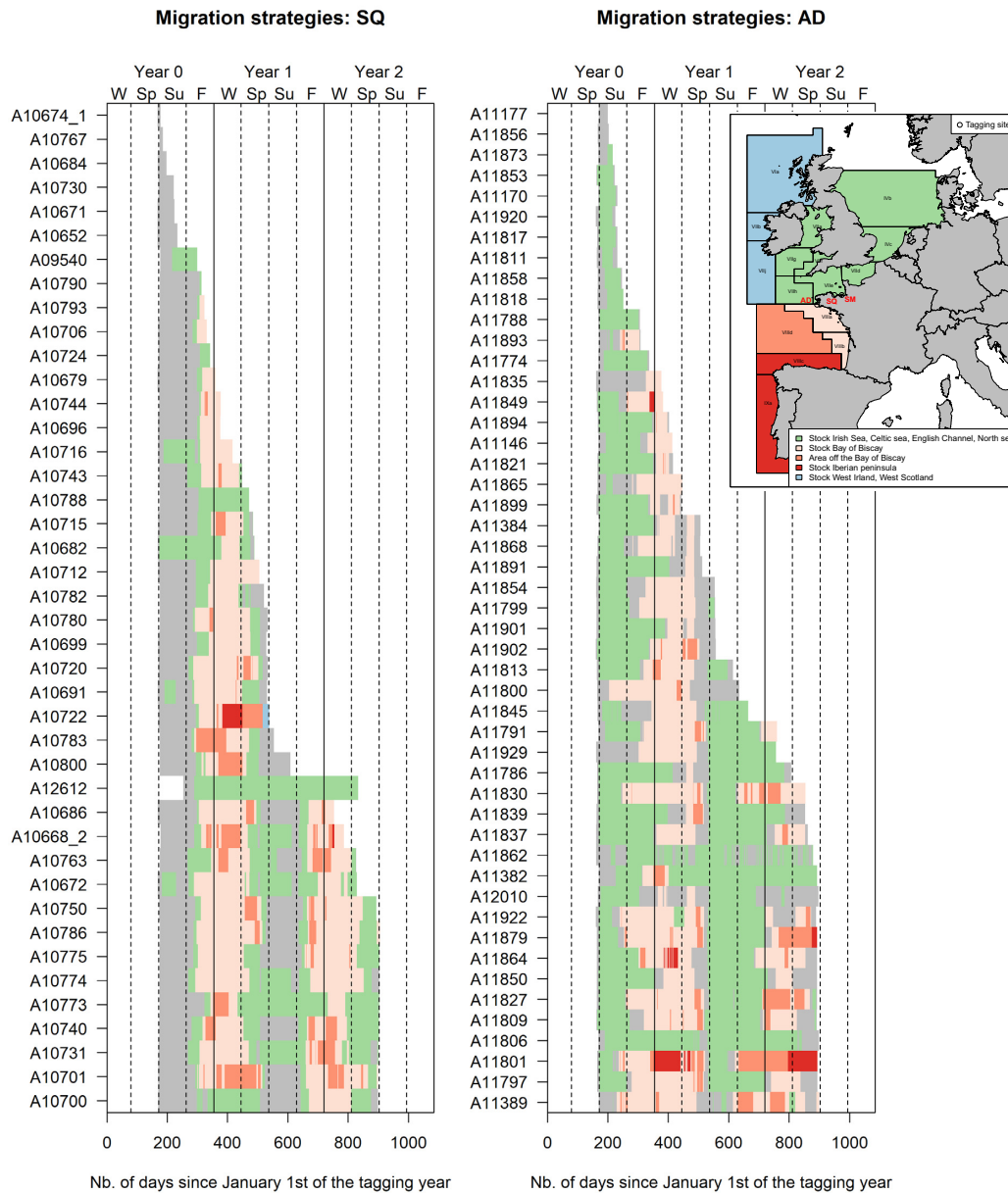
Figure 4. Individual movement histories illustrating seasonal migrations and occurrences of tagging site fidelity. Results for seabass tagged in the western English Channel (Saint-Malo, Saint-Quay-Portrieux, and Audierne). The colours indicate fish position according to those of the ICES stocks (shown in the inset plot). The grey colour illustrates the fidelity to the tagging site (fish within 50 km of its tagging site). Time series are temporally aligned among tagging sites using 1 January of the tagging year as a time reference. Vertical dotted lines separate the seasons (W: winter; Sp: spring; Su: summer; F: fall). Solid vertical lines separate the years.

and the second one in BOB. These results suggested that the Bay of Saint-Brieuc was an area where populations mixed, although most fish bred in BOB (Figures 4 and 5).

The same pattern of migration was observed off the west coasts of Brittany for fish tagged in the Iroise Sea, just north of the 48°N, at the transition between NS and BOB (Figure 4). The main strategy consisted of migrating towards the south, i.e. mainly the BOB area and, to a lesser extent, to the areas off BoB and the Iberian Peninsula (67%). Site fidelity occurrences are numerous both on the summer feeding areas (96% of the DST data that last at least 1 year) and on the winter breeding areas (84% of the DST data that last at least 1.5 years). Note that most fish were migrating when they were tagged, show-

ing proximity to the tagging site when they migrate from the NS to BOB. Five individuals (#AD_A11786, #AD_A11862, #AD_A11382, #AD_A12010, and #AD_A11806) show a different migration strategy: They stay in the NS area or close to the tagging site (Figure 5) or with very short incursions in the BOB area for only one year. The Iroise Sea appears to be an area of mixed populations, with a majority of tagged seabass reproducing in the BOB area (Figure 5).

The further south the European seabass range goes, the more the movement patterns change. Near the Loire River (La Turballe and Noirmoutier; Figures 6 and 7), very few fish migrated to the range of the northern stock (16%). The majority remained in the Bay of Biscay to reproduce (84%), whereas
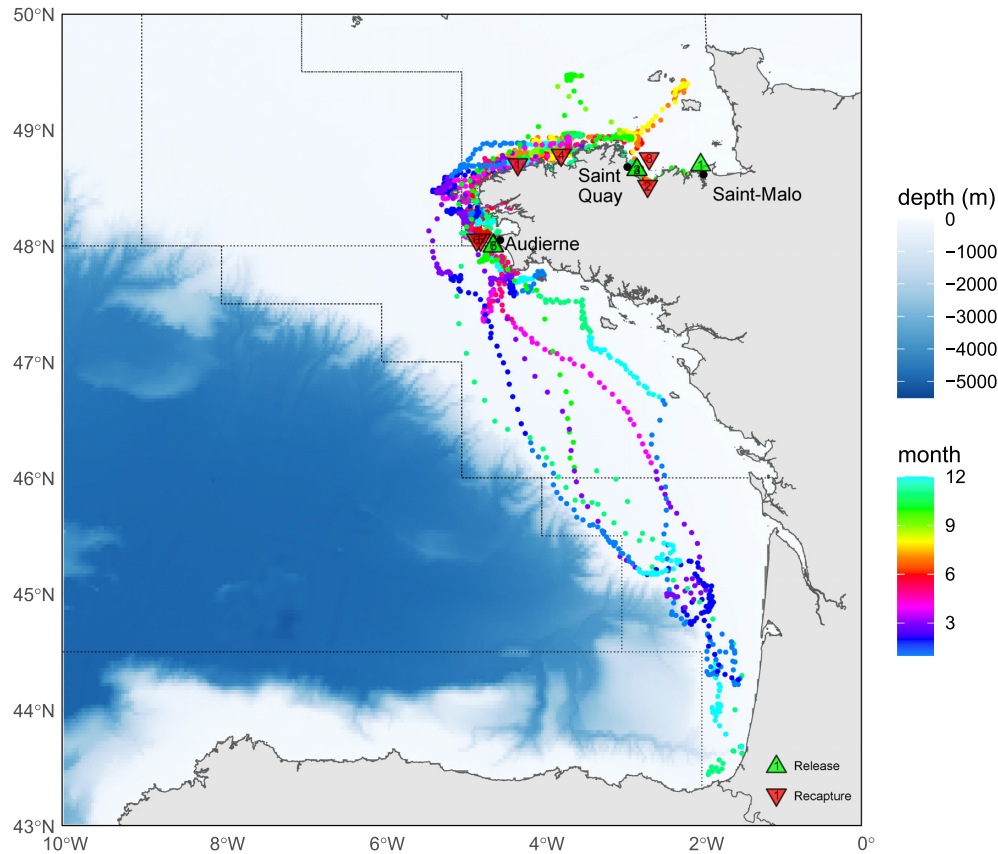
Figure 5. Seven typical reconstructed tracks derived from DST data of seabass tagged in the western English Channel (#SM_A12612, #SQ_A10743, #SQ_A10691, #SQ_A10788, #AD_A11799, #AD_A11806, and #AD_A12010), with daily position estimates of the most probable track coloured by calendar month, and release and recapture positions represented respectively by green and red triangles. Number inside the triangles corresponds to the rank of the tags ID listed above. Bathymetry data originate from the GEBCO.

some migrated to the area off the Bay of Biscay or along the Iberian Peninsula. Many occurrences of site fidelity are observed ($n = 32$).

In île d'Oléron (Figures 6 and 7), the tagged seabass are either resident or they reproduce offshore in the Bay of Biscay. Only 3 out of 36 seabass migrate to the northern area (8%). Fidelity to the summer feeding and winter breeding sites was observed for every tag with enough time at liberty to evaluate respective fidelities.

At Capbreton (Figures 8 and 9), there are many cases of migration towards the open sea of the Bay of Biscay on the one hand and the Iberian Peninsula on the other (2 recaptures in Galicia, 2 in Basque Country, and 29 fish out of 50 having most probably stayed in Iberian waters, i.e. 58%). There would thus be exchanges between the BOB stock and the Iberian stock.

Discussion

Our large-scale electronic tagging programme, conducted at ten sites along the French coast, has provided new evidence of site fidelity behaviour, particularly for reproduction in winter. The connectivity between NS and BOB stocks and the Iroise Sea (western Brittany) could be confirmed as an area of stock mixing, particularly in summer. Some behavioural traits (range of temperatures and dynamics of thermal variations experienced, range of vertical movements and maximum depths achieved, etc.) provided information on the great behavioural

plasticity of the species. The DST data also provided valuable information on predation by top predators (tuna, marine mammals).

DSTs are still being returned to the laboratory, further enriching the unique and valuable dataset from tagging. In particular, the richness of this dataset is due to the geographical extension of the study, covering areas belonging to both NS and BOB stocks as well as a very high recapture rate (39.5%) and long time series covering one or more reproduction seasons. The temporality of the tagging operations needs to be considered as, although they all took place in summer, the windows remained different from one place to another, which could have had some consequences. For example, fish tagged at Audierne in early June (see Figure 4) were typically migrating to the north coasts of Brittany whereas fish tagged a few years earlier, at the same location but in September, remained for a significant time in the area where they were tagged before migrating back to BOB to reproduce (de Pontual et al., 2019). It should be noted that this result could not be related to changes in the geolocation model, which are discussed below. Another example of fish tagged while migrating was in June in Dunkirk, as only three individuals showed site fidelity to this tagging location.

Geolocation models and electronic tracking studies
Geolocation models provide inferences of fish movements from recorded environmental variables such as temperature,
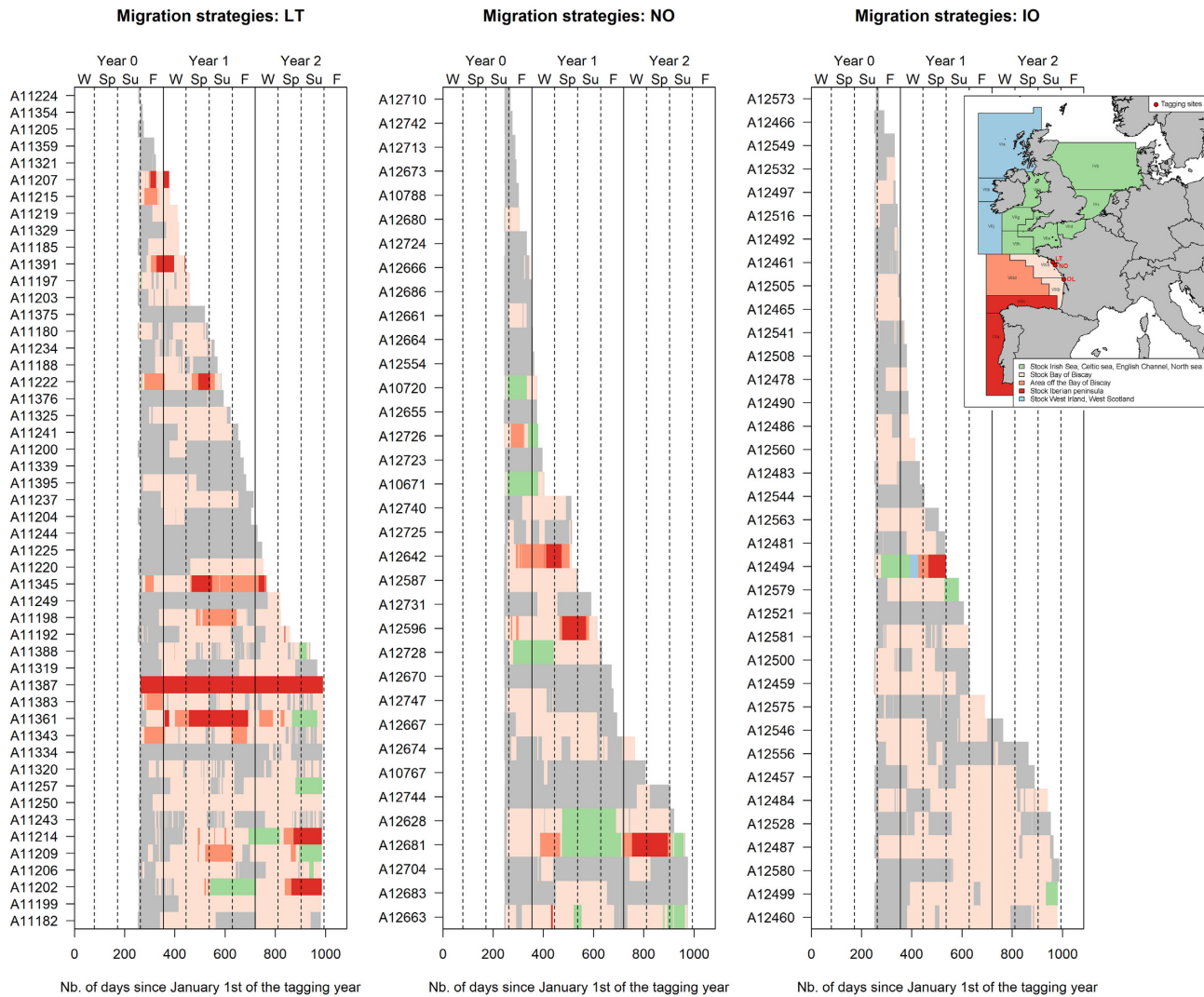
Figure 6. Individual movement histories illustrating seasonal migrations and occurrences of tagging site fidelity. Results for seabass tagged in northern (La Turballe and Noirmoutier) and central Bay of Biscay (Ile d'Oléron). The colours indicate fish position according to those of the ICES stocks (shown in the inset plot). The grey colour illustrates the fidelity to the tagging site. Time series are temporally aligned among tagging sites using 1 January of the tagging year as a time reference. Vertical dotted lines separate the seasons (W: winter; Sp: spring; Su: summer; F: fall). Solid vertical lines separate the years.

depth, light, etc. The model used here has been adapted from Woillez *et al.* (2016) and includes a switching behaviour based on the fish activity level (Heerah *et al.*, 2017). This addition improves the geolocation model greatly. The use of a model with no behavioural change on such a large spatial dataset was not sufficiently specific to model all the spatial diversity of individual behaviours and movements. Behavioural switching was able to partially cope with this. Most of the time, the model runs converged. However, when the model failed to reconstruct some tracks with good confidence (32%), because of convergence issues for D or unrealistically high estimated values of D, using other reconstructions to inform on the value of D was considered as an acceptable solution to increase the sample size of our analysis. The earlier version of this geolocation model has also shown good performances in a validation exercise with simulated tracks and in a sensitivity analysis with or without recapture positions (Woillez *et al.*, 2016). However, the spatial extent of this study has been drastically increased. As stressed by Gatti *et al.* (2021), the model

is likely to be more or less accurate depending on the season, for instance when spatial gradients of environmental variables are low (e.g. temperature in winter, in NS area). Nielsen *et al.* (2019) also stated that model accuracy may decrease and location error may be underestimated, when model assumptions such as data likelihood and grid size are not valid, because the heterogeneity degree of study area was not considered. This is the case of the coastal waters, where strong temperature gradients shaped by fine-scale oceanographic processes occur all year long. Few hydrodynamic model outputs are able to account properly for such highly resolved reference temperature fields. When these model outputs are available, temperature fields extent only over small regions of interest, which is unsuited with the spatial extent of our study, i.e. from the southern Bay of Biscay to the southern North Sea. However, we are confident that the use of a behavioural switching model compensates for the poorly resolved reference field as low activity state (when tide is detected) occurred in the coastal waters, keeping the fish close to the coast, where temperature field
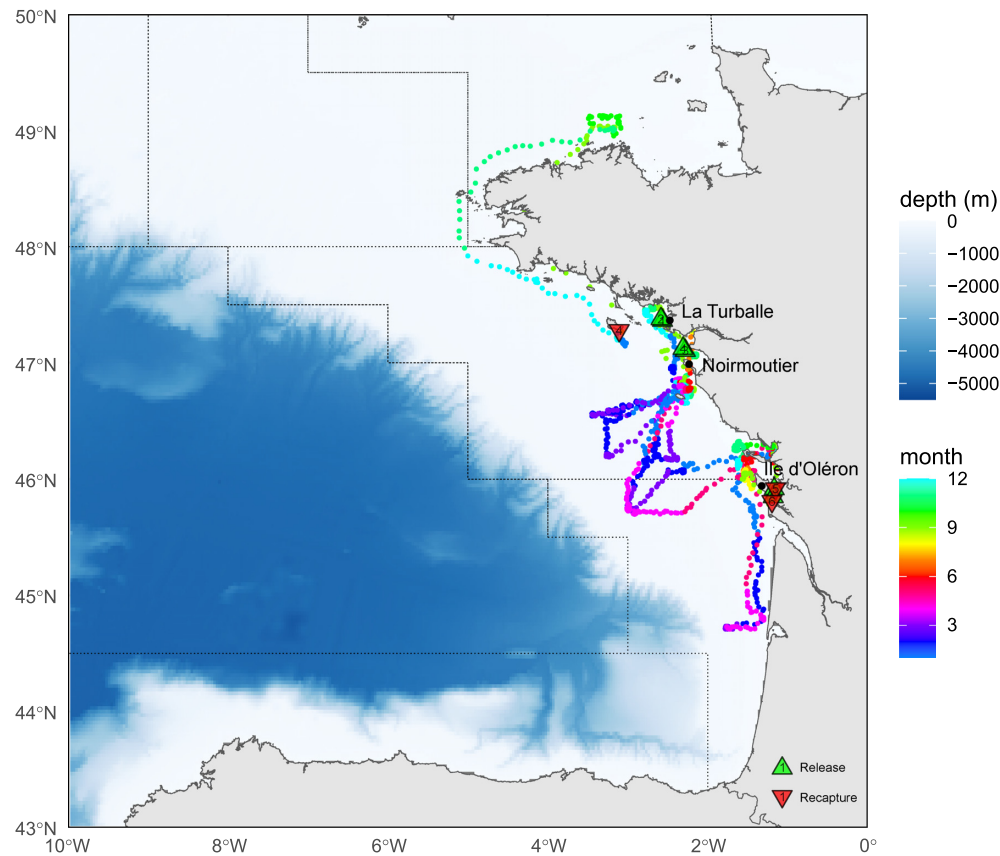
Figure 7. Six typical reconstructed tracks derived from DST data of seabass tagged in the central Bay of Biscay (#LT_A11199, #LT_A11250, #NO_A12704, #NO_A10720, #IO_A12481, and #IO_A12500), with daily position estimates of the most probable track coloured by calendar month, and release and recapture positions represented, respectively, by green and red triangles. Number inside the triangles corresponds to the rank of the tags ID listed above. Bathymetry data originate from the GEBCO.

normally should do the same if correctly resolved. Different validation methods of geolocation have been proposed (Gatti *et al.*, 2021; Haase *et al.*, 2021), but not all seem adapted to large spatial and temporal scales that often characterize investigations on spatio-temporal dynamics of populations. Double tagging—combining DST with other tagging technologies, e.g. acoustic telemetry—is likely promising for improving and validating geolocation models (Goossens *et al.*, 2023).

Site fidelity, partial migration, population structure, and stock mixing

Movements of adult seabass have been long investigated by tagging, demonstrating site fidelity to feeding grounds (Quayle *et al.*, 2009; Doyle *et al.*, 2017; de Pontual *et al.*, 2019) as well as fidelity on spawning areas (de Pontual *et al.*, 2019). DST tagging is the best way to reveal fidelity to offshore (depth > c.a. 100 m) spawning sites except for known recurrent spawning sites where acoustic telemetry could perhaps be deployed and as long as PSAT tags have not been miniaturized. Here we understand "site fidelity" as fidelity to a given region (i.e. NS or BOB) rather than to a specific location, which is a correct scale to study the match/mismatch between biological subpopulations and stocks. Individuals reconstructed tracks confirm the findings of de Pontual *et al.* (2019) at a large scale. Not all bass migrated in winter, which supports the partial migration hypothesis linked to different reproductive strategies, either offshore (migrant contingent) or in coastal

habitats where fish lived all year round (resident contingent). The latter is rarer and observed mainly in the central BOB (LT, NO, and IO) for reasons that are not yet understood. Further investigations are required to state whether the propensity to migrate increases with size and differs between contingents as observed for e.g. striped bass (Secor *et al.*, 2020a; 2020b). Here, most migrants exhibit spawning site fidelity commonly observed in flatfish—e.g. turbot (Florin and Franzen, 2010), plaice (Solmundsson *et al.*, 2005), and halibut (Loher, 2008) but also in roundfish—e.g. cod (Wright *et al.*, 2006; Skjaeraasen *et al.*, 2011; Zemeckis *et al.*, 2014a). The mechanisms underpinning such behaviour in seabass remain largely unknown. They may be genetically driven or induced by a learning mechanism, either asocial—memory of suitable environmental conditions—or social—cultural transmission by older individuals (see e.g. Meager *et al.*, 2018). It can be hypothesized that seabass exhibit regional philopatry *sensu* Chapman *et al.* (2015), i.e. individuals return to the region where they were born but not necessarily to the exact place of their birth. Our data provide an empirical basis for exploring this potential mechanism by coupling reconstructed tracks to genetic markers (Gagnaire *et al.*, in prep) and to otolith chemical signatures (Le Luherne *et al.*, 2022).

This question is all the more important as a recent study described a genetic discontinuity in seabass populations off the Cotentin Peninsula, between the western and eastern Channel (Robinet *et al.*, 2020). Such demographically independent populations would thus have boundaries that do not
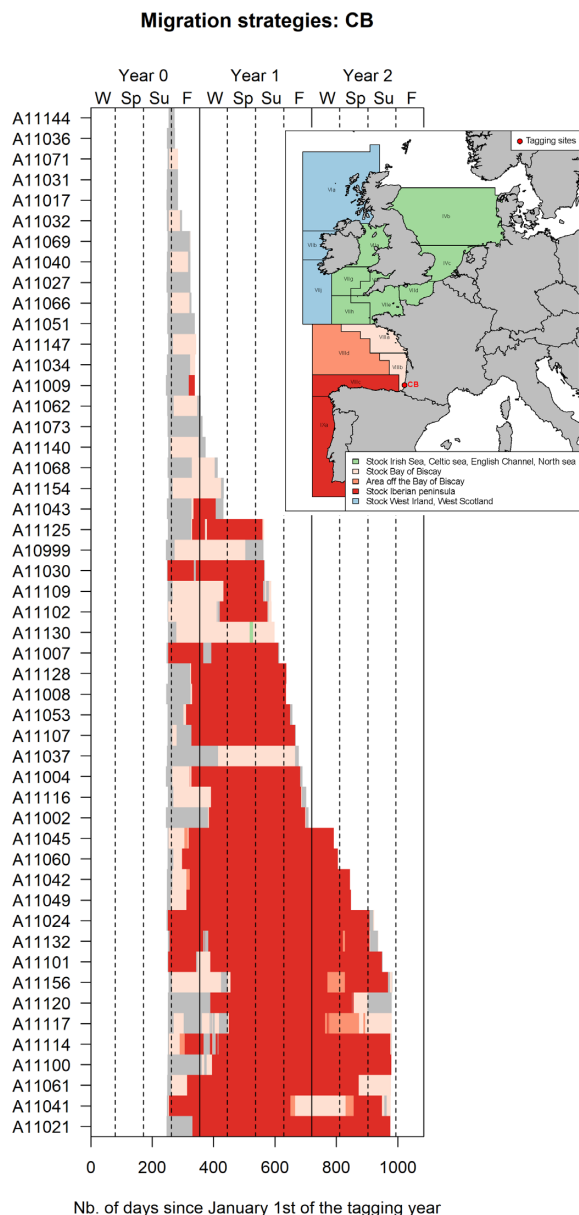
Figure 8. Individual movement histories illustrating seasonal migrations and occurrences of tagging site fidelity. Results for seabass tagged in the southern Bay of Biscay (Capbreton). The colours indicate fish position according to those of the ICES stocks (shown in the inset plot). The grey colour illustrates the fidelity to the tagging site. Time series are temporally aligned among tagging sites using 1 January of the tagging year as a time reference. Vertical dotted lines separate the seasons (W: winter; Sp: spring; Su: summer; F: fall). Solid vertical lines separate years.

correspond to the current definition of NS and BOB stocks. In addition, a significant number of fish tagged in summer in the Western Channel or Iroise Sea (AD and SQ, NS area) breed in the Bay of Biscay (BOB area). This finding indicates that NS and BOB stocks mix in summer. It is also interesting to note that winter spawning migrations are preferentially from NS to BOB ($n = 78$), whereas the reverse is rarely observed ($n = 17$). This finding supports the hypothesis that stock boundaries may not be correctly defined and/or may move seasonally, underlining the importance of refining our current perception of the stock dynamics (delineation and demographic independence). The coupling of individual markers and especially the

joint analysis of genetic structure and reproductive migration patterns should provide answers to these questions.

Management implications

Because they shape the internal dynamics and structure of populations, animal movements are critical information for exploitation and conservation of wild species (Nathan *et al.*, 2008; Spiegel *et al.*, 2017). As seabass is a partial migratory species, local depletion may result from the exploitation of resident contingents. Other seabass life traits such as longevity (>20 years), late maturation (4–6 years), and reproduction in spawning aggregations make this species vulnerable to overexploitation. The latter trait may lead to the "illusion of plenty" (Erisman *et al.*, 2011), especially as there is a lack of fishery-independent data for assessment. This mechanism might well be behind the recent and rapid decline of the NS. Following drastic measures taken by the EU since 2015, this stock is now recovering (ICES, 2021). However, the efforts undertaken are likely to be ineffective if assessment and management do not take into account a correctly defined spatio-temporal structure and dynamics of the population. Our results indicate that a separate and independent assessment of the NS and BOB stocks is inappropriate. The migration patterns observed in our study suggest a metapopulation structure (Cadrin *et al.*, 2019), with subpopulation boundaries probably not at the 48°N, currently separating NS and BOB ICES stocks. Whatever the degree of connectivity of these subpopulations and whatever their geographical boundaries, the two subpopulations probably mix on feeding areas in summer. If there is a consensus about this new paradigm, ICES will need to answer the question of how the current assessment method performs against future alternatives (Cadrin *et al.*, 2019). A step forward would be to extend these results from the individual to population scale by developing a spatially structured population dynamics model of tagged fish to estimate migration rates and mortality (Eveson *et al.*, 2012). Future stock assessment models should determine how including this degree of connectivity affects model estimates and optimal fishing yields.

Conclusions

New knowledge on movements and migrations of the European seabass at the adult stage in the English Channel and Atlantic coasts of France provides a better understanding of the spatio-temporal structure of the population, which is essential to improve diagnostics and advices on its exploitation level. Seabass is a partial migratory species with different contingents (resident vs. migrant) encountered in a same tagging site. Over the whole study area, site fidelity exists on both summer feeding grounds and winter spawning grounds. In some tagging sites of the western coast of France (North and West of Brittany), fidelity was evidenced in addition to different reproductive migratory tactics, illustrating mixing of subpopulations, which translates, in terms of management, into a mixture of stocks. These results challenge the current view of the stock delineation. The data collected constitute a huge dataset providing many information on seabass ecology (thermal preferences, vertical behaviour, vulnerability to predation, etc.). It also opens new avenues on multidisciplinary approaches (genetic analysis of recoveries, otolith and scale microchemistry, tagging on spawning aggregations, and
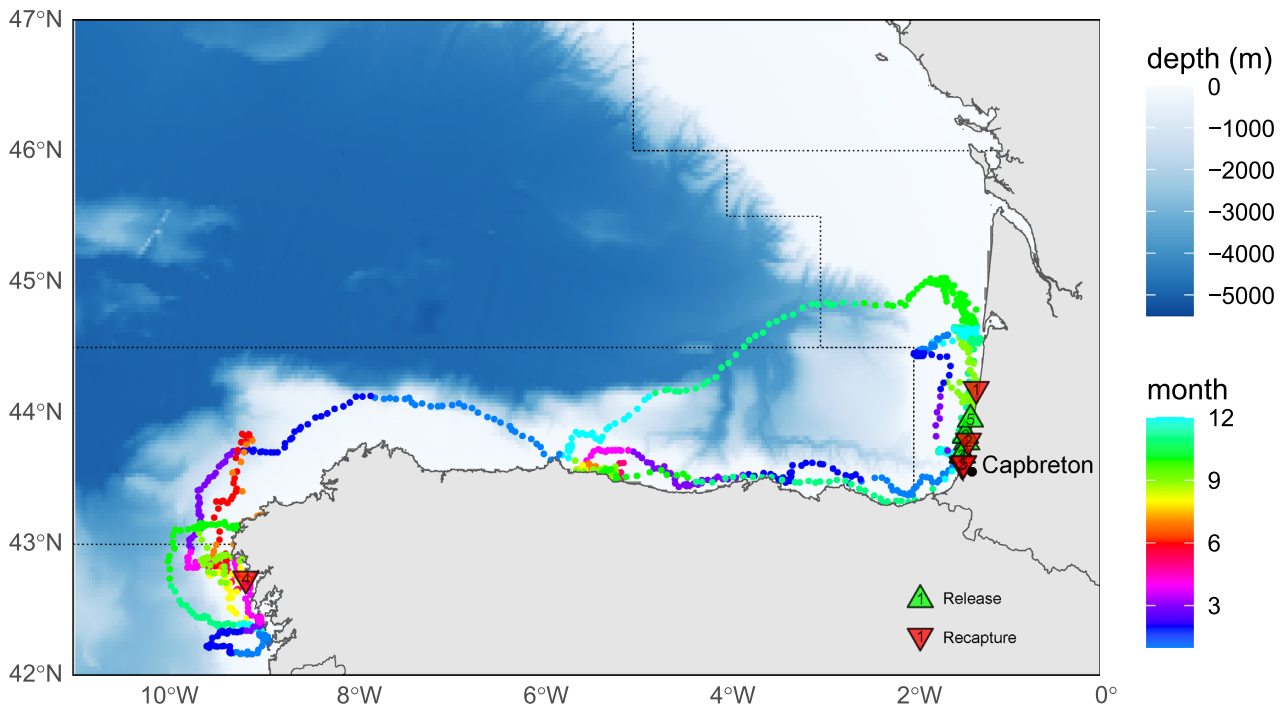
Figure 9. Five typical reconstructed tracks derived from DST data of seabass tagged in the southern Bay of Biscay (#CB_A11002, #CB_A11154, #CB_A11040, #CB_A11042, and #CB_A11073), with daily position estimates of the most probable track coloured by calendar month, and release and recapture positions represented, respectively, by green and red triangles. Number inside the triangles corresponds to the rank of the tags ID listed above. Bathymetry data originate from the GEBCO.

coupling acoustic telemetry to DSTs) that will help the in-depth exploration of mechanisms structuring the seabass population.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

It includes a table on power plant stations considered in the geolocation model, a figure on the typology of recaptures and a series of figures of temperature, depth time series illustrating seabass behavioural ecology and a note detailing how the diffusivity was fixed in certain conditions.

Conflict of interest statement

The authors declare no conflict of interests.

Data availability

Research data are not shared yet. Tagging data will soon be published.

Author contribution

HP designed the research, led the projects and analysed the raw data; FG, LLR, DLR, SM, and HP carried out the fieldwork; MW, KH, and JG developed the geolocation model; MW ran geolocation analyses; HP and MW discussed the results and wrote the manuscript; HP, MW, KH, and JG critically reviewed the manuscript.

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