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### ► To cite this version:

Hélène de Pontual, Maxime Lalire, Ronan Fablet, Claire Laspougeas, Francois Garren, et al.. New insights into behavioural ecology of European seabass off the West Coast of France: implications at local and population scales. ICES Journal of Marine Science, 2019, 76 (2), pp.501-515. 10.1093/icesjms/fsy086 . hal-02013003

**HAL Id: hal-02013003**

**<https://imt-atlantique.hal.science/hal-02013003>**

Submitted on 9 Feb 2019

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## New insights into behavioural ecology of European seabass off the West Coast of France: implications at local and population scales

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de Pontual, H., Lalire, M., Fablet, R., Laspougeas, C., Garren, F., Martin, S., Drogou, M., and Woillez, M. New insights into behavioural ecology of European seabass off the West Coast of France: implications at local and population scales. – ICES Journal of Marine Science, doi:10.1093/icesjms/fsy086.

Received 31 January 2018; revised 23 April 2018; accepted 19 June 2018.

From 2010 to 2012, 246 data storage tags were deployed on European seabass in the Iroise Natural Marine Park, a marine protected area (MPA) off west Brittany, France. A return rate of 14.6% associated with long time series of data provided new information on fish ecology (e.g. maximum experienced depth greater than 225 m, temperature range 6.80–21.87°C). Depth and temperature series were used to infer individual migration using an innovative hidden Markov model (HMM) especially developed for seabass geolocation. Reconstructed fish tracks revealed that seabass is a partially migratory species, as individuals exhibited either long-distance migrations towards the Bay of Biscay or the Celtic Sea, or residency behaviour in the Iroise Sea. Fidelity to summer feeding areas and to winter spawning areas was demonstrated. These results suggest that the population is spatially structured. The Iroise Sea is likely a mixing zone for different stocks or sub-populations, and may also shelter a resident population. At the population scale, such findings may impact ICES stock assessment and the resulting decisions from EU managers. At the local scale, conservation action could be taken by MPA managers. Besides, this study demonstrates the high potential of archival tags for investigating multi-year behavioural patterns such as site fidelity to offshore spawning areas.

**Keywords:** cod, connectivity, Data Storage Tag (DST), depth, European sea bass, *Dicentrarchus labrax*, geolocation, partial migration, spawning site fidelity, temperature, vertical movement

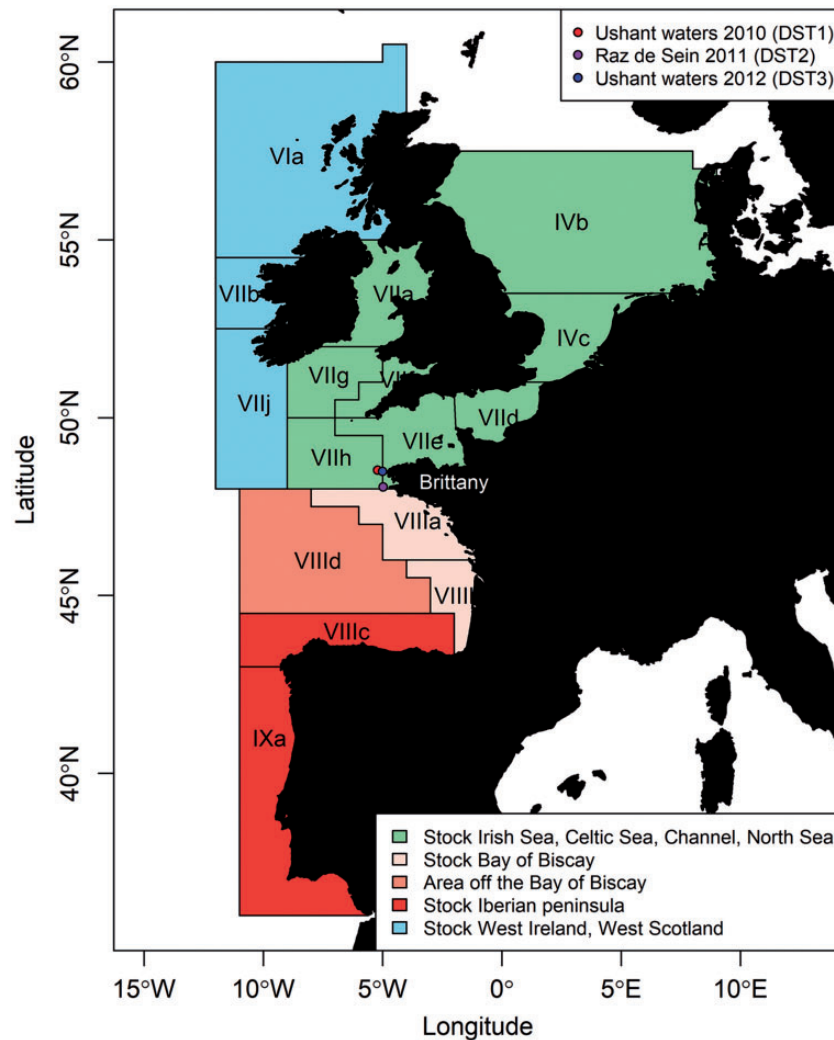
### Introduction

European seabass (*Dicentrarchus labrax*) is found in the north-east Atlantic Ocean from Morocco to Scotland and Norway, in the Black Sea and in the Mediterranean Sea (Pickett and Pawson, 1994). Northward expansion of seabass has been recently reported along the Norwegian coast (Ilestad *et al.*, 2012) and in the Baltic Sea (Bagdonas *et al.*, 2011), probably related to climate change as suggested by these authors. This species has high cultural and economic values and is targeted by both commercial

and recreational fishers. Assessment of the population status for fisheries management currently considers four stocks (Figure 1). The northern seabass stock (also called the Celtic Sea stock) comprises the Irish Sea, Celtic Sea, English Channel, and southern North Sea (ICES divisions IVb–c and VIIa, d–h) while the other three stocks are defined as: (1) west of Scotland and Ireland (ICES divisions VIa and VIIb, j); (2) the Bay of Biscay (ICES divisions VIIIa–b), and (3) coasts around the Iberian peninsula (ICES divisions VIIIc, IXa). Such delineation mainly resulted

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**Figure 1.** Map of the ICES seabass stocks and the location of the tagging surveys. Note that the area off the Bay of Biscay is considered by convenience for the further migration analysis. Figure appears in color on the open access online version.

from practical considerations and allowed the first quantitative assessments of the Celtic Sea stock to be made (ICES, 2012). However, experts have highlighted a lack of biological evidence supporting this delineation and have pointed out the need for further research on population structure. This is important since both increasing fishing pressure and poor recruitment have recently raised concern about stock status (ICES, 2015), leading the European Commission to agree on emergency conservation measures in 2015, 2016, and 2017 (European Commission, 2016) to address a severe decline in the northern seabass stock component.

Genetic data have indicated that the seabass population consists of two lineages, the Atlantic and the Mediterranean, with a contact zone at the Almeria-Oran Front, east of Gibraltar strait (Coscia *et al.*, 2012; Quere *et al.*, 2012; Tine *et al.*, 2014). Whereas the Mediterranean lineage has become differentiated into two groups with the Siculo-Tunisian Strait as a contact zone (Quere *et al.*, 2012), the Atlantic lineage shows weak genetic structure with some evidence of introgression from the Mediterranean (Souche *et al.*, 2015). However, despite this weak genetic

differentiation within the Atlantic lineage, the latter authors favoured the delineation of eight spawning stocks: the five units proposed by Pawson *et al.* (2007), plus three additional ones: the Bay of Biscay, following Quere *et al.* (2010), the coasts off Portugal to Morocco, and the Alboran Sea (their own study, Souche *et al.*, 2015).

Tagging is a useful tool for defining movement and distribution patterns in fish, which can provide information on population structure. Both conventional (e.g. T-bar/dart tagging) and electronic tagging have already challenged traditional views of population structure and stock delineation for various species such as bluefin tuna (e.g. Block *et al.*, 2005), Atlantic cod (e.g. Robichaud and Rose, 2004; Neuenfeldt *et al.*, 2013), and European plaice (e.g. Hunter *et al.*, 2004). Conventional tagging data for seabass in the British Isles (see review by Lopez *et al.*, 2015) showed seasonal migration between inshore summer feeding areas and offshore wintering and spawning areas (Pawson *et al.*, 1987, 2007). Fidelity to summer habitats was demonstrated in these studies (Pawson *et al.*, 1987, 2007, 2008), while fidelity to wintering and spawning areas was not. Also, Pawson *et al.* (2007)

showed that English Channel seabass comprised a mixture of residents and seasonal migrants, however it is unclear if these characteristics are evident at the population scale, particularly for the Bay of Biscay and the Iberian coasts. A unique conventional tagging experiment revealed very low connectivity between the English Channel-Celtic Sea region and the Bay of Biscay (Fritsch *et al.*, 2007). More recently, archival tagging revealed fine-scale behaviour patterns of seabass in relation to migration (Quayle *et al.*, 2009). Acoustic telemetry confirmed fidelity to coastal foraging areas and localised residency (Doyle *et al.* 2017). Considering the large home range of seabass and the diversity of hydroclimatic characteristics of potential habitats, we initiated a tagging programme with Data Storage Tags (DSTs) to investigate movement patterns and population structure, using temperature and depth data to geolocate fish. Our study was conducted in the Iroise Sea, off the west coast of Brittany (Figure 1). This area is at the southern limit of the Celtic Sea stock. It is a transition zone between three ICES-defined ecoregions (Greater North Sea, Celtic Sea, and Bay of Biscay and the Iberian coasts) and includes a marine-protected area (the Iroise Natural Marine Park), a multiple-use MPA that allows for local artisanal use (e.g. fisheries) while preserving natural heritage values. This MPA has been established quite recently and its functional role for species of local importance remains to be established. Our goals were to investigate movements and migrations of adult seabass, both at a large scale to see where fish caught and tagged in the summer went to in the winter, and what stock they belonged to, and at a local scale to identify the functional role of the Iroise Natural Marine Park for this species, which is the most valuable fish species in the area.

## Material and methods

### DST tagging

Three tagging surveys were carried out in the Iroise Sea during summers 2010, 2011, and 2012 (Table 1). Fish were caught by professional rod and line fishers in either Ushant or Raz de Sein waters. In case of over inflation of the swim bladder due to rapid depressurisation, swim bladders were bled to release excess air. Carefully selected fish [ $>45$  cm total length (TL), tag to body mass ratio  $<2\%$ , apparently good condition] were placed in a 600-l tank supplied with flowing seawater until further treatment. The Iroise Sea is a difficult zone to navigate due to very strong currents, which often produce rough sea conditions that prevent immediate tagging on fishing boats. Therefore, two different tagging procedures were tested. The first procedure (survey DST 1) involved a support vessel, moored in sheltered waters, where fish were transferred, tagged, and released on the same day they were caught. The second procedure (surveys DST 2 and DST 3) used shore-based infrastructures where fish were transferred, tagged, and maintained over one night prior to release. The tagging protocol consisted of (1) anaesthesia with IsoEugenol at 80 ppm for 3 min, (2) measurements of TL and weight, (3) positioning on an operating table with water and IsoEugenol at 15 ppm (sedation dose) flowing through the gills, (4) removal of scales and  $\sim 0.5$  cm<sup>2</sup> of caudal fin for age estimation and genetic analyses, (5) external tagging with a T-bar tag (FD-94 Floy Tag<sup>®</sup>) inserted near the first dorsal fin, (6) surgical implantation of a DST in the peritoneal cavity, (7) suture of the wound, and (8) application of Forudine<sup>®</sup>, an antibiotic ointment, on the wound to complete the surgery. Ethics rules were strictly observed and all tagging procedures were carried out under an appropriate

project licence authorized by the French Ministry of Agriculture and Environment.

The DSTs were Cefas G5 long life 2 Mb models, with temperature and pressure sensors and a typical battery life of 2 years. The first two surveys (DST 1 and 2) were conducted with tags calibrated with a pressure range of 0–10 bar, allowing a maximum depth record of  $\sim 110$  m. Seabass being considered as a coastal fish, this value was considered deep enough. As it became obvious that seabass can dive much deeper, the third survey (DST 3) was conducted with tags calibrated with a pressure range of 0–20 bar, allowing a maximum depth record of  $\sim 230$  m, which was also reached by some individuals. At a 12-bit setting, sensor accuracy and resolution were  $\pm 1\%$  of the full scale and better than 0.04% of the full scale, respectively, for depth, and  $\pm 0.1^\circ\text{C}$  and  $0.03125^\circ\text{C}$ , respectively, for temperature. Logging regimes differed between the three surveys although all had a high logging rate during the first year post tagging (pressure and temperature at  $\sim 1$  min intervals). In order to increase the recovery rate of deployed DSTs, we used floating tags that could drift ashore in case fish died at sea, regardless of the cause of death.

The experiments were advertised through various media (newspapers, radio, and TV) and via posters and mailings to fishers and stakeholders. A reward of 100€ was offered for each tagged fish returned to the laboratory (50€ for a DST alone) as well as an additional 1000€ awarded in a prize draw among all participants.

### Geolocation model

Track reconstruction was performed using the geolocation model recently developed by Woillez *et al.* (2016), where seabass positions are estimated based on the high-resolution temperature and depth time series recorded by the DSTs. The model involves two key components (Figure 2). The dynamic model describes the time dynamics of the hidden state (i.e. seabass positions), which are based on a Brownian random walk model with white Gaussian noise as an innovation term. The standard deviation of the latter relates to the Brownian diffusion through a parameter named the diffusion coefficient  $D$ . The coefficient of diffusion characterizes the mean distance covered by the fish daily. The observation model compares whether or not depth and temperature measurements conform to the expected temperature and bathymetry conditions at a given position. For this purpose, satellite-derived sea surface temperature (SST) as well as sea bottom temperature (SBT) and bathymetry issued from the MARS3D hydrodynamic model were used as reference geophysical fields. The bathymetry-driven term of the observation model amounts for a given day to discarded positions for which the depth experienced by the fish is below the depth of the sea bottom. The temperature-driven term evaluates whether or not daily maximum and minimum temperatures experienced by the fish close to the sea surface and below the thermocline conform to the satellite-derived and MARS-derived temperature conditions, respectively. To account for potential inversion of the vertical temperature profiles in winter, when required, daily minimum and maximum temperatures were considered close to the sea surface and below the thermocline, respectively. This makes it possible to maximize the temperature-based geolocation by showing the contrasted water masses explored by the fish. Observation errors for the temperature-driven term follow a zero-mean Gaussian

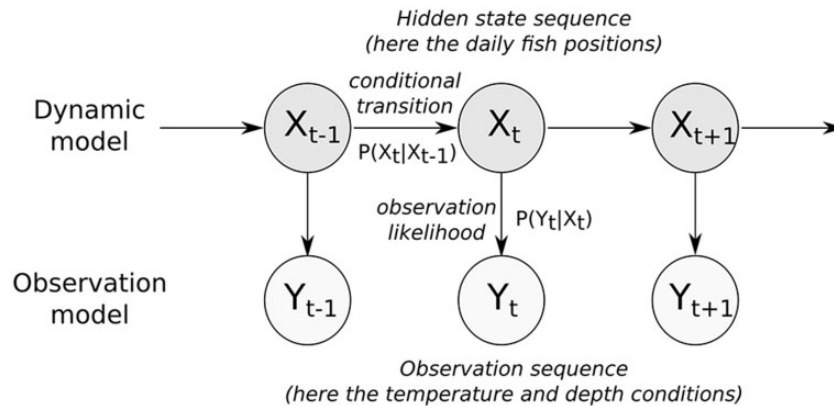
**Table 1.** Synopsis of the tagging surveys in the Iroise Sea.

Survey	Location	# Tagged fish	# Recoveries	Recovery rate (%)	Maximum time post tagging (days)
DST 1—SV (September 2010)	Ushant waters	98	16	16.3	>861 <sup>a</sup>
DST 2—SBI (July 2011)	Raz de Sein	74	8	10.8	1163
DST 3—SBI (September 2012)	Ushant waters	74	12	16.2	1206 <sup>b</sup>
Total DSTs		246	36	14.6	1206

SV, support vessel, SBI, shore-based infrastructures.

<sup>a</sup>Data issued from a beached tag. Data indicated that the fish was not dead when the tag's battery ran out. The actual survival time is thus unknown.

<sup>b</sup>In this case, the fish was recovered, allowing the time at liberty to be calculated.

**Figure 2.** Conceptual diagram of the hidden Markov model for fish geolocation with  $X_t$  being the fish position at time  $t$  (in days), and  $Y_t$  being the temperature and depth conditions experienced by the fish at time  $t$ .

distribution with standard deviations  $\sigma_s$  and  $\sigma_b$  for the sea surface and sea bottom layers, respectively.

Given the proposed model, the geolocation issue resorts to Bayesian inference, which follows the discrete setting proposed by Pedersen *et al.* (2008) and uses a Stochastic iterative Expectation-Maximization procedure (Dempster *et al.*, 1977; Diebolt *et al.*, 1994) to estimate all model parameters jointly (the coefficient of diffusion  $D$ , and the standard deviations  $\sigma_s$  and  $\sigma_b$  of the observation errors for the sea surface and the sea bottom temperature; see Woillez *et al.*, 2016 for more details). Once convergence is reached, the track reconstruction can be illustrated by the most probable track (also called the Viterbi track) or any representative track examples sampled from the posterior likelihood.

The performance of such a geolocation model was evaluated in Woillez *et al.* (2016). Reconstructions from synthetic data showed that this geolocation model performed well, with all parameter estimates within the 95% confidence interval. For real data, the model appeared robust to the absence of recapture position. This is an important result as the number of tags with an unknown position at fish death is quite high in all three tagging surveys (Table 2).

Track reconstructions were performed for every recovered tag from the three tagging surveys carried out in the Iroise Sea. Estimated model parameters, maximum distance from release location, and total distance travelled computed from the most probable track were compiled for every fish in Table 3. The quality of the track reconstruction can be evaluated by looking at the number of days for which a fish was present in the surface observation likelihood layer, in the bottom temperature observation likelihood layer, in no layer, in one layer, or in both layers, the

reconstruction being better resolved when the fish was present more days in the surface temperature layer than in the bottom temperature layer, as the latter layer is a poorly contrasted field. These metrics are also listed in Table 3. Migration strategies were analysed and illustrated with representative tag samples using the most probable track and posterior likelihood summed over time, which provide an explicit representation of uncertainty. Individual post-tagging histories showing fish location with respect to time and seasons were derived using these individual tracks. Every individual was visualized on every given day post tagging and assigned to one of the ICES seabass stocks (as defined in Figure 1) based on fish location, except when this location was within a 100 km radius of the tagging sites. In this case, a grey colour was allocated to these for the subsequent data presentation alongside the colours for the ICES stocks given in Figure 1. The area covered by this exception roughly defines the extent of the Iroise Sea and identifies fish behaviour in the vicinity of the tagging sites as resident or returning migrant. Lastly, 600 representative track examples were sampled to analyse the characteristics of the migration process for a given tag. These tracks were used to analyse the distributions of the total distance travelled over 3 days and the mean compass heading over 3 days, using box plot time series.

## Results

Out of the 246 tagged fish (472–800 mm, total length range at tagging), 36 (14.6%) individuals (fish or tags) were recovered by the end of 2016 (Table 1). Recovery rate ranged from 10.8% to 16.3% depending on the survey. Although most fish were reported by their external T-bar tag numbers, two fish entered



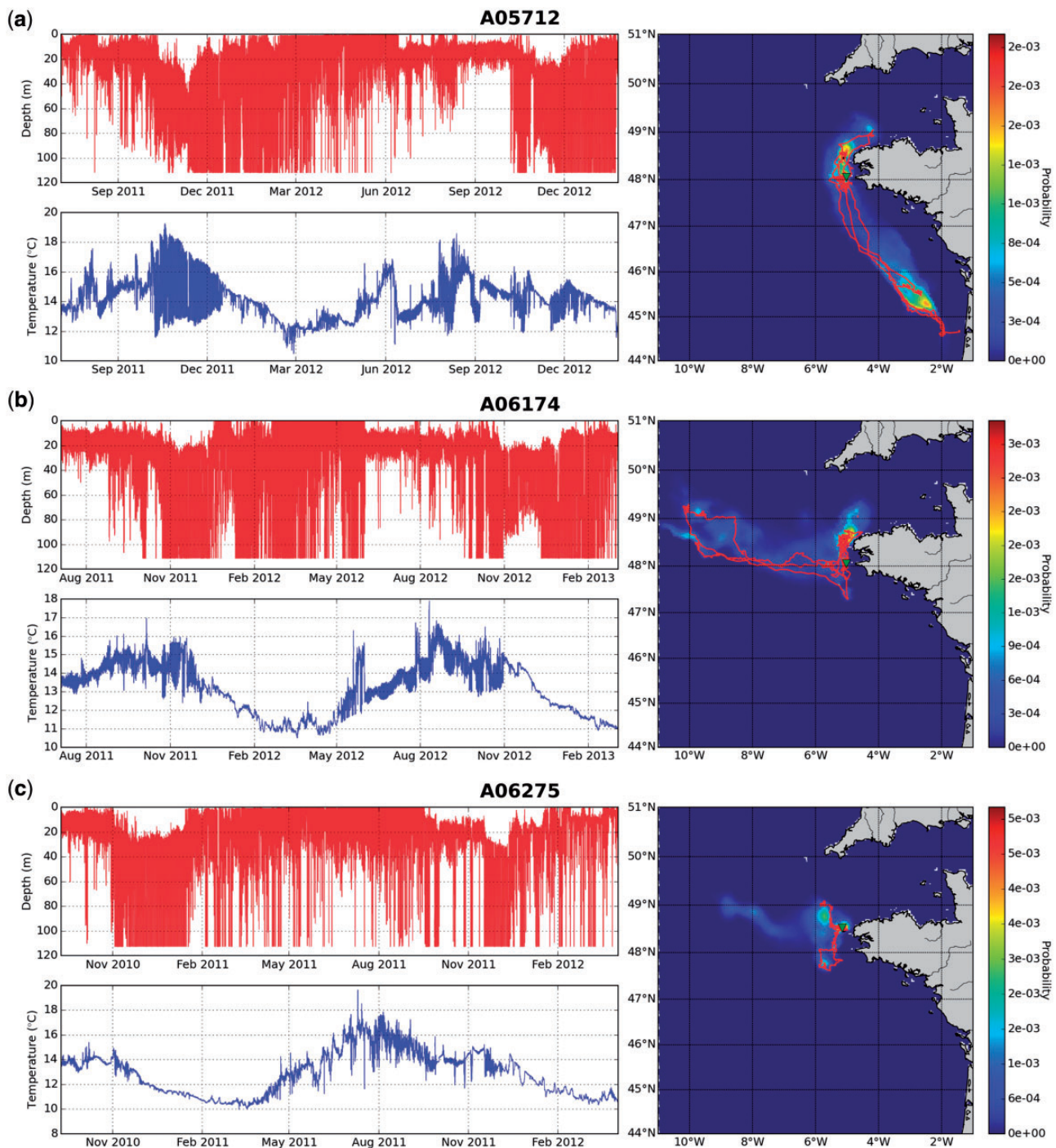
Table 2. Details for individual recoveries.

Tag no.	Survey	Release day	Release position	TL (mm)	Recovery day	Recovery position	Recovery type	Life post tagging (no. of days)	Drift duration (no. of days)	TS end	TS length (no. of days)	Data integrity
A05392	DST 1	9/10/2010	48.521°N, 5.159°W	590	9/27/2011	48.487°N, 5.114°W	PF	382		9/27/2011	383	Full
A05712	DST 2	7/4/2011	48.053°N, 5.019°W	690	1/25/2013		FM	571		1/25/2013	572	Full
A06125	DST 2	7/4/2011	48.053°N, 5.019°W	676	8/16/2011	48.487°N, 5.114°W	PF	43		8/16/2011	44	Full
A06127	DST 2	7/5/2011	48.053°N, 5.019°W	630	9/10/2014		FM	1163		N/A	N/A	None
A06129	DST 2	7/1/2011	48.043°N, 4.751°W	647	8/3/2013	46.2°N, 2.45°W	RF	764		10/14/2012	472	Truncated
A06137	DST 2	7/4/2011	48.053°N, 5.019°W	570	4/1/2014		FM	1002		5/31/2013	698	Truncated
A06174	DST 2	7/4/2011	48.053°N, 5.019°W	590	2/8/2014	45.87°N, 1.26°W	BE	>611	?	3/5/2013	611	Truncated
A06176	DST 1	9/7/2010	48.515°N, 5.14°W	519	5/24/2011	47.083°N, 3.117°W	PF	259		5/24/2011	260	Full
A06177	DST 2	7/4/2011	48.053°N, 5.019°W	674	4/16/2014	50.635°N, 1.576°E	BE	10	1007	7/14/2011	11	Full
A06182	DST 1	9/8/2010	48.521°N, 5.159°W	602	2/16/2011	45.694°N, 2.279°W	FM	161		2/16/2011	162	Full
A06191	DST 1	9/8/2010	48.521°N, 5.159°W	591	2/24/2016	46.692°N, 1.441°W	BE	>580	?	4/3/2012	574	Truncated
A06192	DST 1	9/9/2010	48.521°N, 5.159°W	691	9/1/2011	48.053°N, 5.019°W	FM	357		9/1/2011	358	Full
A06195	DST 1	9/7/2010	48.515°N, 5.14°W	712	12/13/2011	47.281°N, 2.499°W	BE	462	41	11/2/2011	422	Full
A06202	DST 1	9/8/2010	48.521°N, 5.159°W	685	11/20/2010		FM	73		11/20/2010	74	Full
A06205	DST 1	9/8/2010	48.521°N, 5.159°W	680	7/12/2011	48.487°N, 5.114°W	PF	307		7/12/2011	308	Full
A06215	DST 2	7/16/2011	48.053°N, 5.019°W	656	9/28/2011	48.053°N, 5.019°W	PF	84		9/28/2011	85	Full
A06226	DST 1	9/7/2010	48.515°N, 5.14°W	694	6/19/2011	47.469°N, 2.873°W	RF	285		6/19/2011	286	Full
A06271	DST 1	9/10/2010	48.521°N, 5.159°W	725	11/19/2013	48.653°N, 3.947°W	BE	>861	?	4/23/2012	592	Truncated
A06275	DST 1	9/8/2010	48.521°N, 5.159°W	594	9/21/2013	47.539°N, 3.139°W	BE	>838	?	4/2/2012	573	Truncated
A06277	DST 1	9/9/2010	48.521°N, 5.159°W	658	2/10/2011	49.37°N, 0.871°W	BE	15	139	9/24/2010	16	Full
A06280	DST 1	9/8/2010	48.521°N, 5.159°W	549	5/6/2011	47.631°N, 3.398°W	FM	240		N/A	N/A	None
A06294	DST 1	9/8/2010	48.521°N, 5.159°W	596	9/15/2011	48.487°N, 5.114°W	PF	372		9/15/2011	373	Full
A06301	DST 1	9/8/2010	48.521°N, 5.159°W	637	8/29/2011	48.487°N, 5.114°W	PF	355		8/29/2011	356	Full
A06303	DST 1	9/8/2010	48.521°N, 5.159°W	660	12/9/2013		FM	>831		4/3/2012	574	Truncated
A08287	DST 3	9/5/2012	48.487°N, 5.114°W	594	2/2/2013	45.175°N, 1.475°W	PF	150		2/2/2013	151	Full
A08293	DST 3	9/5/2012	48.487°N, 5.114°W	747	12/29/2013	51.679°N, 4.325°W	BE	471	9	12/20/2013	472	Full
A08296	DST 3	9/5/2012	48.487°N, 5.114°W	630	10/26/2014	47.8°N, 4.374°W	BE	>680	?	7/16/2014	680	Truncated
A08302	DST 3	9/8/2012	48.48°N, 4.885°W	584	12/28/2015		FM	1206		7/17/2014	678	Truncated
A09454	DST 3	9/21/2012	48.487°N, 5.114°W	495	10/19/2013	48.658°N, 4.425°W	RF	393		10/19/2013	394	Full
A09455	DST 3	9/19/2012	48.487°N, 5.114°W	691	10/2/2012	48.232°N, 4.439°W	BE	1	12	9/20/2012	2	Full
A09456	DST 3	9/19/2012	48.487°N, 5.114°W	610	11/7/2013	47.149°N, 2.227°W	BE	244	170	5/21/2013	245	Full
A09465	DST 3	9/19/2012	48.487°N, 5.114°W	695	1/31/2013	45.912°N, 1.161°W	PF	134		1/31/2013	135	Full
A09478	DST 3	9/21/2012	48.487°N, 5.114°W	590	11/14/2012	48.712°N, 4.767°W	BE	4	50	9/25/2012	5	Full
A09484	DST 3	9/8/2012	48.48°N, 4.885°W	608	11/6/2014	48.67°N, 4.364°W	BE	>779	?	7/18/2014	679	Truncated
A09486	DST 3	9/19/2012	48.487°N, 5.114°W	560	9/25/2012	48.179°N, 4.298°W	BE	4	2	9/23/2012	5	Full
A09489	DST 3	9/8/2012	48.48°N, 4.885°W	564	11/8/2012	47.535°N, 4.319°W	PF	61		11/8/2012	62	Full

TL, total length at release; PF, professional fisher; RF, recreational fisher; FM, fish market; BE, beached tag; TS, time series. Recovery positions in grey were not used for track reconstruction (beached tags or truncated data due to logging regime/battery life).

**Table 3.** Model parameters, number of days present in an observation likelihood layer, and total distance for individual track reconstructions.

Tag no.	Survey	Diffusion $D$ ( $\text{km}^2.\text{d}^{-1}$ )	Speed from				Total no. of surface (%)	No. of days at bottom (%)	No. of day not in a layer (%)	No. of days in 1 layer (%)	No. of days in 2 layers (%)	Total distance travelled (km)	Average speed ( $\text{km.d}^{-1}$ )	Max. distance from release (km)
			$\sigma_b$ (°C)	$\sigma_s$ (°C)	days	No. of days at surface (%)								
A05392	DST1	74	15	1.80	0.24	383	366 (95.6)	159 (41.5)	3 (0.8)	235 (61.4)	145 (37.9)	2276	5.9	385
A05712	DST2	53	13	0.74	0.36	572	467 (81.6)	432 (75.5)	9 (1.6)	227 (39.7)	336 (58.7)	3305	5.8	460
A06125	DST2	17	7	1.11	0.61	44	25 (56.8)	9 (20.5)	17 (38.6)	20 (45.5)	7 (15.9)	157	3.6	51
A06129	DST2	44	12	0.83	0.21	472	426 (90.3)	333 (70.6)	9 (1.9)	167 (35.4)	296 (62.7)	2918	6.2	497
A06137	DST2	38	11	0.26	0.45	698	509 (72.9)	578 (82.8)	37 (5.3)	235 (33.7)	426 (61)	3732	5.3	315
A06174	DST2	39	11	0.47	0.24	611	443 (72.5)	461 (75.5)	18 (2.9)	282 (46.2)	311 (50.9)	3229	5.3	393
A06176	DST1	23	8	0.83	0.36	260	185 (71.2)	226 (86.9)	0 (0)	109 (41.9)	151 (58.1)	1056	4.1	330
A06177	DST2	7	5	0.10	0.38	11	8 (72.7)	7 (63.6)	2 (18.2)	3 (27.3)	6 (54.5)	41	3.7	11
A06182	DST1	51	13	0.40	0.20	162	147 (90.7)	105 (64.8)	1 (0.6)	70 (43.2)	91 (56.2)	998	6.2	378
A06191	DST1	20	8	0.85	0.39	574	407 (70.9)	422 (73.5)	35 (6.1)	249 (43.4)	290 (50.5)	2189	3.8	240
A06192	DST1	21	8	1.17	0.36	358	298 (83.2)	295 (82.4)	10 (2.8)	103 (28.8)	245 (68.4)	1410	3.9	272
A06195	DST1	42	12	1.62	0.38	422	390 (92.4)	340 (80.6)	8 (1.9)	98 (23.2)	316 (74.9)	2125	5.0	355
A06202	DST1	57	13	0.21	0.08	74	37 (50)	24 (32.4)	21 (28.4)	45 (60.8)	8 (10.8)	404	5.5	117
A06205	DST1	33	10	0.32	0.28	308	244 (79.2)	101 (32.8)	60 (19.5)	151 (49)	97 (31.5)	1302	4.2	216
A06215	DST2	14	7	0.33	0.25	85	48 (56.5)	70 (82.4)	1 (1.2)	50 (58.8)	34 (40)	330	3.9	52
A06226	DST1	114	19	0.73	0.23	286	267 (93.4)	203 (71)	8 (2.8)	86 (30.1)	192 (67.1)	2299	8.0	329
A06271	DST1	68	15	0.23	0.56	592	361 (61)	282 (47.6)	170 (28.7)	201 (34)	221 (37.3)	2999	5.1	390
A06275	DST1	11	6	1.08	0.43	573	427 (74.5)	429 (74.9)	26 (4.5)	238 (41.5)	309 (53.9)	1597	2.8	109
A06277	DST1	68	15	4.19	0.17	16	15 (93.8)	5 (31.2)	1 (6.2)	10 (62.5)	5 (31.2)	92	5.8	66
A06294	DST1	64	14	1.09	0.28	373	317 (85)	247 (66.2)	3 (0.8)	176 (47.2)	194 (52)	2222	6.0	276
A06301	DST1	58	14	1.47	0.32	356	326 (91.6)	253 (71.1)	22 (6.2)	89 (25)	245 (68.8)	2146	6.0	470
A06303	DST1	50	12	0.52	0.44	574	353 (61.5)	366 (63.8)	96 (16.7)	237 (41.3)	241 (42)	2742	4.8	342
A08287	DST3	149	22	0.31	0.36	151	88 (58.3)	121 (80.1)	3 (2)	87 (57.6)	61 (40.4)	1274	8.4	456
A08293	DST3	191	24	1.94	0.17	472	314 (66.5)	222 (47)	95 (20.1)	218 (46.2)	159 (33.7)	3660	7.8	215
A08296	DST3	19	8	1.14	0.58	680	446 (65.6)	533 (78.4)	49 (7.2)	283 (41.6)	348 (51.2)	2320	3.4	250
A08302	DST3	77	16	1.48	0.39	678	597 (88.1)	453 (66.8)	16 (2.4)	274 (40.4)	388 (57.2)	4111	6.1	600
A09454	DST3	128	20	0.45	0.25	394	376 (95.4)	9 (2.3)	18 (4.6)	367 (93.1)	9 (2.3)	2675	6.8	277
A09455	DST3	39	11	0.05	0.11	2	2 (100)	1 (50)	0 (0)	1 (50)	1 (50)	7	3.5	8
A09456	DST3	48	12	0.62	0.07	245	211 (86.1)	167 (68.2)	0 (0)	112 (45.7)	133 (54.3)	1552	6.3	291
A09465	DST3	42	11	0.14	0.45	134	63 (47)	121 (90.3)	3 (2.2)	78 (58.2)	53 (39.6)	835	6.2	347
A09478	DST3	18	8	0.00	0.08	5	5 (100)	0 (0)	0 (0)	5 (100)	0 (0)	12	2.4	10
A09484	DST3	64	14	0.94	0.33	679	473 (69.7)	375 (55.2)	80 (11.8)	350 (51.5)	249 (36.7)	3515	5.2	303
A09486	DST3	263	29	0.92	0.25	5	4 (80)	1 (20)	1 (20)	3 (60)	1 (20)	32	6.4	31
A09489	DST3	54	13	2.16	0.19	62	60 (96.8)	11 (17.7)	0 (0)	53 (85.5)	9 (14.5)	316	5.1	112

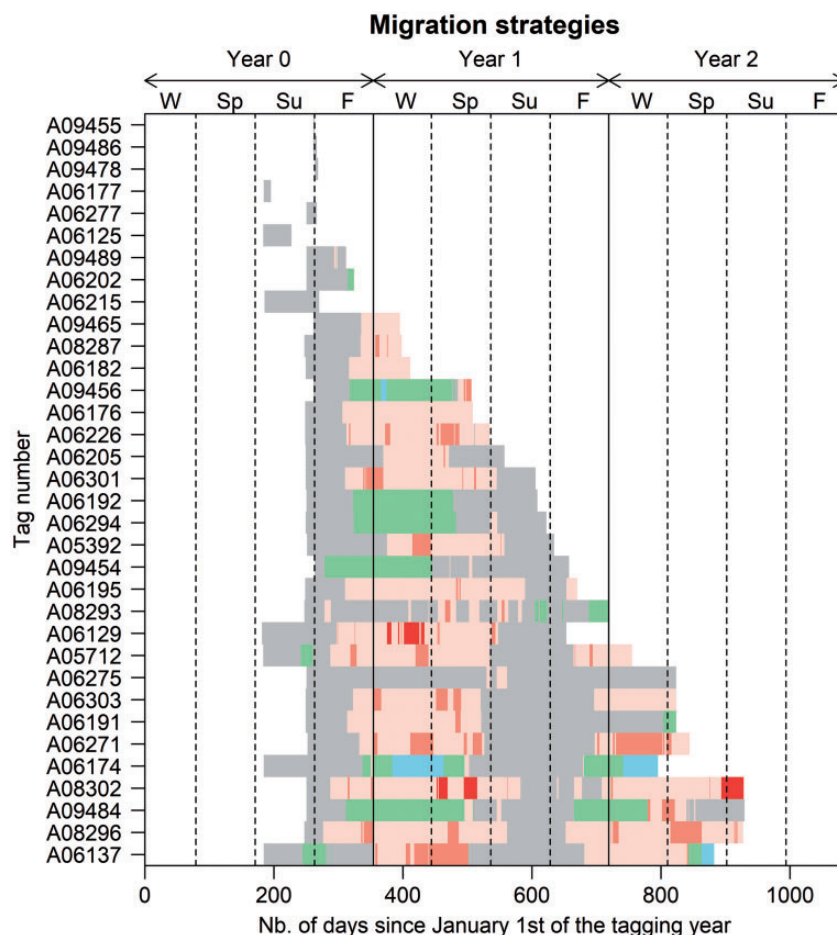


**Figure 3.** Representative samples of three migration strategies: (a) Bay of Biscay migration (tag A05712); (b) Celtic Sea migration (tag A06174); (c) Iroise Sea residency (tag A06275). Reconstructed tracks appear in the right-hand panels (most probable track) with the corresponding depth and temperature profiles in the left-hand panels. The colour gradients indicate the utilization distributions of the tagged seabass (i.e. the probability distributions of the daily positions cumulated over time and normalized by the number of days at liberty). Figure appears in color on the open access online version.

the sale channel where the DSTs were subsequently lost (tags A06127 and A06280, Table 2). Three main types of recoveries occurred: (1) 38.9% of DSTs were sent back by professional or recreational fishermen; (2) 22.2% of DSTs were found at some stage in the sale channel: auction room, fish market, restaurant, or

consumer; and (3) 38.9% of DSTs drifted across the sea after fish death and were washed up on beaches where they were found. In the first case, geographical position at fish death was known and could be used for track reconstruction, except when recapture occurred after the end of recording (e.g. tag A06129, Table 2). For





**Figure 4.** Individual post-tagging histories showing fish habitats with respect to time and seasons. 1st January of the year of tagging is taken as reference for calendar date. Successive seasons are separated by dashed vertical lines. Stock colour code, identical to Figure 1, is as follows: Iroise Sea (grey), Celtic stock (green), Western Ireland stock (blue) Bay of Biscay stock (pink), Western Bay of Biscay (area VIIIId, orange), and Iberian stock (red).

fish that entered the sale channel, recapture positions could be retrieved in only two cases (A06182, A06192, Table 2). Although geographical positions of beached tags were known, these were not used because of uncertainties due to drift. However some of these positions proved to be useful for *a posteriori* corroboration of track reconstruction, particularly when drift duration could be calculated and was sufficiently short (e.g. A06195 and A08293, Table 2). In 20 cases (out of 34), the geolocation model was run without a recapture position (Table 2).

Regarding beached tags, the endpoint analysis suggested two occurrences of predation, probably by a shark (lamnidae) or tuna, based on the temperature and pressure profiles. In three cases (A9486, A9478, and A9455, all deployed in 2012, DST3), endpoints suggested early fish mortality probably due to the tagging procedure (shore-based infrastructures). Tag A08293 had a 9-day “drift time” and was found on Pembrey beach, Wales, UK, a beach used by fishermen to fish with a rod from the beach. This could suggest that the tag was dropped as the fish was gutted, which might also be the case for two other tags. Six beached tags came from fish that had been alive at the end of the recording time (truncated data, Table 2) making the cause of death uncertain.

Time at liberty (Table 2) ranged from 1 to 1206 days (i.e. more than 3 years); however, it did not always match the length of the corresponding time series, as the programmed logging regimes were limited by the 2-year battery life. Nevertheless, most tags (25 out of 34) had time series long enough for analysing spawning migrations, as they included at least one winter.

Daily log data, summed over all tags (corresponding to 12 409 days of data), indicated that the depth range was 0–228.81 m, although the maximum depth that fish experienced was probably higher but could not be recorded because of tag pressure range capacity (see below). Regarding temperature, the observed range was 6.80–21.87°C, but the seabass rarely spent time below 9°C (41 days out of 12409).

### Reconstructed tracks: where do summer-tagged fish go in winter?

Reconstructed tracks show movements and migrations that differ among fish, mainly on a seasonal basis. Some representative tracks are given in Figure 3, together with the corresponding depth and temperature time series. These profiles show behavioural switches in vertical movements on a seasonal scale. All fish moved offshore during winter to depths greater than 110–120 m,

as shown by plateaus in the depth profiles (Figure 3, left panel). Such plateaus were due to the use of 10-bar depth sensors during the first two surveys (2010–2011). It is worth noting that the 20-bar depth sensors subsequently used in the DST 3 survey also failed to record the maximum depth that the seabass experienced. This was revealed by tag A08296, which recorded depth plateaus at 228.81 m. The associated temperature profiles indicated that fish visited areas that differed in thermal regime, temperature range, stratification of the water column, etc., particularly in autumn/winter (Figure 3 left panel). Most of the reconstructed tracks showed long-distance migrations (Table 3). There was a high correlation between the total distance travelled and the total number of days at liberty ( $r=0.92$ ), but not with the diffusion coefficient ( $r=0.12$ ). However, the longer the fish were at liberty, the more variation was seen in the total distances recorded, indicating different individual migration strategies. The maximum distances from the release locations (Table 3), which varied from 8 to 600 km, were more informative than the total distances travelled. The very short distances indicated either early recaptures or residency behaviour (depending on the length of the time series), while the longest distances indicated migration behaviour. Indeed, three different spawning migration strategies occurring during autumn/winter were identified among the fish tagged in summer in the Iroise Sea: (i) migration towards the Bay of Biscay (Figure 3a), (ii) migration toward the Celtic Sea (Figure 3b), or (iii) residency in the Iroise Sea (Figure 3c), as defined above.

Regarding movement characteristics during the entire reconstructed tracks, the averaged horizontal speeds (total distance divided by the number of days in the time series) ranged from 2.4 to 8.4 km.d<sup>-1</sup> (Table 3). These estimates were conservative as they were derived from most probable tracks (Viterbi tracks) known to minimise distances travelled. Speeds, estimated from the equation  $\bar{v} = \sqrt{\pi D}$ , where  $D$  is the diffusion coefficient, see Woillez *et al.* (2016), ranged from 5 to 29 km.d<sup>-1</sup> (Table 3).

### Individual behaviour, habitat maps, and migration features

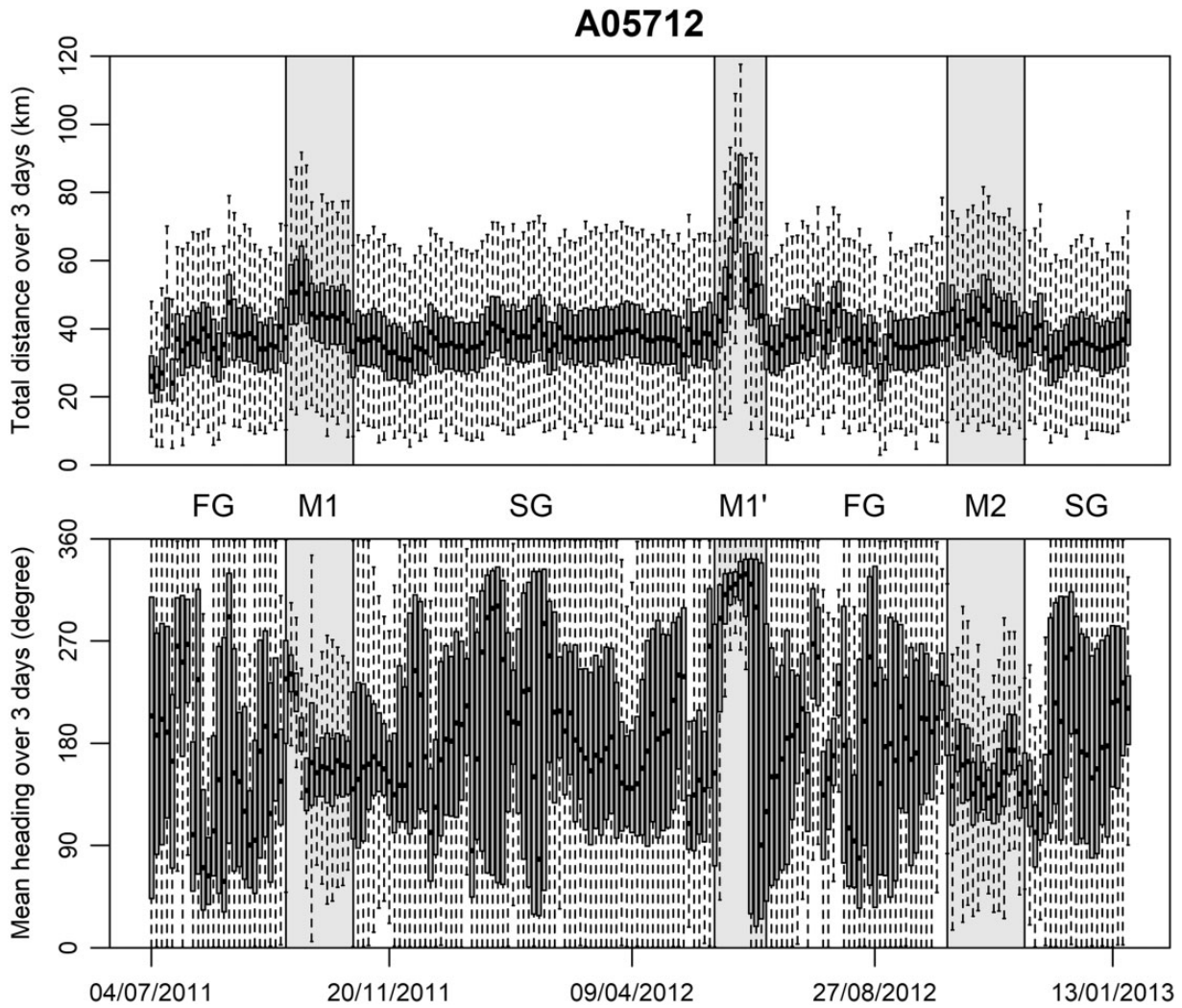
Individual movements and migrations, reconstructed on a daily time-scale, are given in Figure 4. As mentioned above, a colour indicative of an ICES seabass stock was attributed to every individual on every given day post tagging according to fish location, except when this location was within a 100 km radius of the tagging sites. In such cases, a grey colour was used, allowing the characterization of residency or returning migration in the Iroise Sea. 1st January of the tagging year was taken as the reference date in order to compare individual tactics over the post-tagging lifespan. Consequently, the starting points of the individual histories (time series) of fish from different tagging dates do not coincide, particularly between tagging surveys (Table 2). Figure 4 shows that some fish were recovered very shortly after tagging (e.g. A09455, A09486, and A09478), whereas 25 fish (from tags A09465 to A06137) spent at least one winter at sea after release. Out of these 25 fish, 17 (68%) migrated to the Bay of Biscay and adjacent waters, six (24%) moved toward the Celtic Sea and adjacent waters and two (8%) could be considered as resident fish (A08293 and A06275) spending the most time at liberty in the Iroise Sea. However, fish A08293 occasionally made short incursions to both southern and northern adjacent waters, where the tag was eventually found.

The longest time series revealed key behavioural features in terms of spatial dynamics and habitats experienced. First, results highlight site fidelity to summer feeding areas, as all fish that had at least 1 year at liberty (19 fish starting with A06205 on Figure 4) came back to the Iroise Sea during the spring/summer of year 1 post tagging. More importantly, site fidelity to winter spawning areas was also observed for fish that spent two winters at sea after release (9 out of 10 fish starting with A05712 on Figure 4). Except for fish A06191, which had a first spawning migration in the Bay of Biscay (fall/winter, year 0/1) and a second fall/winter spawning season (year 1/2) in the Iroise Sea, spawning site fidelity was observed for all fish, irrespective of migration strategies. More specifically, this was observed for fish utilizing the Bay of Biscay (six fish), the Celtic Sea (two fish), and residents (one fish, namely A06275). On a more general point of view, these results highlight the potential of archival tags to investigate multi-year site fidelity processes on offshore areas.

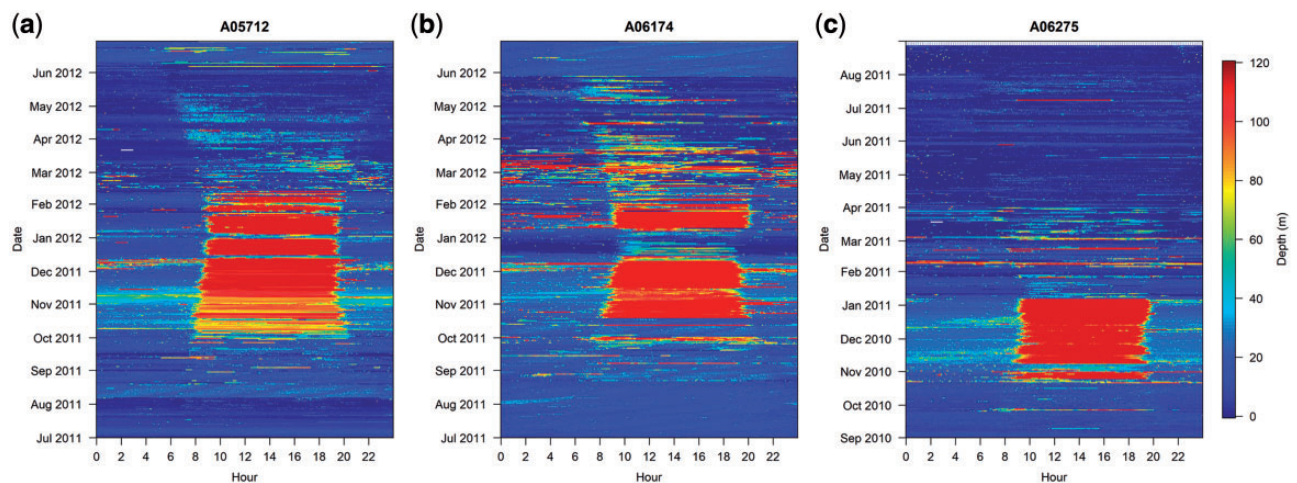
Individual habitat maps can be drawn from daily position probabilities and provide information about habitat range and fine-scale migration dynamics (Figure 3). These maps show that fish spent most of their time either in the summer feeding area (Iroise Sea, in the case of these three fish in the figure) or winter spawning areas (Bay of Biscay or Celtic Sea for migrants or the Iroise Sea for residents). For migrating fish (A05712 and A06174), fidelity to Ushant and Sein waters is strongly marked, whereas the geographical extent of spawning areas appears to be larger, particularly regarding the Celtic Sea pattern (fish A06174). In both cases, maps show low presence probabilities between feeding and spawning areas, which suggests that migrations are rather rapid events. This hypothesis can be verified by estimating the travelling speed (horizontal movements) and direction (fish heading). As an example, such parameters were estimated from 600 tracks sampled from the daily probability maps of fish A05712 (Figure 5). Distribution of speed as a function of time shows periods (identified as M) for which distances travelled were much higher than the median values (Figure 5, top). This is particularly obvious for the migration back to the Iroise Sea (called M1') during which the distance travelled over 3 days exceeded 80 km, around twice the median distance travelled. Moreover long distances were concomitant with oriented headings (Figure 5, bottom), either to the southeast (winter migration to south eastern spawning areas in the Bay of Biscay) or to the northwest (return summer migration to the feeding area in the Iroise Sea).

### Vertical behaviour

Vertical movements not only vary in terms of daily amplitude (Figure 3) but also in terms of daily rhythm (Figure 6). For the representative tag A05712 (Figure 6a), during the first months after release (July–October 2011) there were no apparent trends in diel movement. The four oblique lines that are visible on a 15-day sequence between August and September probably correspond to a tidal inversion-driven behaviour. Clear diel behaviour appears in autumn–winter (October 2011–February 2012) with fish being at greater depths (more than 120 m) during the daytime and ascending to the surface/subsurface at night. However, behaviour changed during short periods (e.g. mid-Dec. to early Jan.), where fish remained in shallower water. Diel behaviour resumed between Feb. and May, though fish actually made several ascents and descents during the day. Finally, such diel behaviour seems to



**Figure 5.** Characteristics of the migration process for the fish tagged A05712: total distance travelled over 3 days (top) and mean compass heading over 3 days (bottom) computed from 600 sampled trajectories. Migrations are indicated by grey boxes. FG, feeding areas; M, migration; SG, spawning areas.



**Figure 6.** Seasonal change in vertical behaviour over the first year of data for seabass corresponding to the three representative samples: tags A05712 (a), A06174 (b), and A06275 (c). Figure appears in color on the open access online version.



be triggered by light intensity changes at dusk and dawn (Figure 6, with Central European Summer Time, i.e. UTC + 2, as the time reference). Such description of vertical behaviour can also be done for other seabass tagged during this study, such as those from the representative tags A06174 and A06275 (Figure 6b and c). The tidal inversion-driven behaviour and the diel behaviour triggered by light intensity changes at dusk and dawn were also observed for these fish, but the timing and duration differed. For instance, the seabass with tag A06275 did not resume diel behaviour in wintertime. Breaks in diel behaviour were longer for the fish with tag A06174 than the one with tag A05712. The fish with tag A06174 also showed several ascents and descents during the day after the winter diel behaviour, but dives were deeper and this behaviour lasted until June.

## Discussion

### Tagging procedure

Following the pioneering DST work on European seabass by Quayle *et al.* (2009), our study provides data from long time series, up to 698 days, that allow new insights into seabass spatial ecology and population structure. By recovering such long time series from sufficient numbers of individuals, we demonstrated the value of DST non-deleterious tagging procedures for seabass, a species often considered to be very sensitive to stress (Samaras *et al.*, 2016). The procedure used during the DST1 survey (a support vessel equipped for “massive tagging” in the best possible conditions) was shown to ensure a high recovery rate, an absence of early post-tagging mortality and a long post-tagging life. Using floating DSTs also significantly increased the recovery rate, accounting for 36% of the total recoveries. The cause of death could not always be determined by endpoint analyses, but predation by lamnid sharks, tunas or billfishes was obvious for two of the tagged seabass. This predation was identified by sudden changes in depth profile and associated temperature rise (from 18°C to 32°C), followed by fluctuating temperatures from 22°C to 32.9°C over more than 4 days (e.g. tag A06195). Such features are characteristic of tunas and sharks (see e.g. Block and Finnerty, 1994; Ciezarek *et al.*, 2016). Predation by marine mammals was not observed in the dataset although such occurrences have been reported in this area by both professional and recreational fishermen.

### Migration patterns, inference on population structure, and management implications

Provided that the geolocation model is reliable (see below), our results yielded important information about migration patterns and behaviour that may have important implications for management, both at the population scale (population spatial structure and stock identification) and at a more local scale (functional role of the Iroise Sea and potential implications for MPA managers).

The observed migratory patterns (migration vs. residency) indicate that seabass display partial migration (see review by Chapman *et al.*, 2012). Among the three types of seasonal partial migration (Shaw and Levin, 2011), the most likely is breeding partial migration where residents and migrants separate to breed. Skipped breeding partial migration is less likely, not only because residency was observed in two successive winters, but also because spawning probably occurs in or near the Iroise Sea (M. Laurans pers. comm.) because young-of-the-year recruitment occurs in this area. Partial migration is unlikely to be related to maturity stage as all fish were

larger than the size at first maturity when they were tagged (42 cm and 36 cm for males and females, respectively) (Kennedy and Fitzmaurice, 1972; Pickett and Pawson, 1994).

At a large scale, our results revealed the long distances travelled by the migrating seabass—about 600 km from their release locations. Long migrations on this scale have already been reported for seabass (Quayle *et al.*, 2009) and might be considered as dispersive mechanisms, although this behavioural trait does not necessarily imply a lack of population structure (e.g. Ruzzante *et al.*, 2006; Pampoulie *et al.*, 2008; Riccioni *et al.*, 2010). The documentation of site fidelity is a significant finding of this study, because of its implications for population structure. Site fidelity to summer feeding areas had already been reported (Pawson *et al.*, 2008; Doyle *et al.*, 2017), but more importantly with regard to population structure, our results show fidelity to winter spawning areas for the first time. Based on these results, it is likely that seabass populations are spatially structured, with subpopulations mixing during part of the annual cycle, as already observed for many species. This raises new questions that might have important management implications. First, the underlying mechanism of fidelity to spawning areas needs to be clarified. We need to discern whether it is associated with genetically driven natal homing (e.g. Bluefin tuna, Thorrold *et al.*, 2001) or whether it results from social learning (e.g. herring, Corten, 2002). Collaborative studies using multiple markers (e.g. next-generation sequencing tools, otolith or scale microchemistry, etc.) could help to unravel this issue (Fromentin *et al.*, 2009). Second, the connectivity rate between subpopulations — or stocks — needs to be assessed. It is worth noting that the most common migration strategy of seabass from the Iroise Sea is towards the Bay of Biscay, thus crossing the 48th parallel, which is considered by ICES to be the frontier between the two stocks. There is therefore a need to examine whether there are significant exchanges between these two stocks that would need to be accounted for in assessment and management. At a still larger scale, we should ask whether biological evidence supports the current stock delineation.

At a local scale, results suggest that the Iroise Sea, is a biogeographic transition zone (Cox *et al.*, 2016) that may play multiple roles for European seabass: (i) a feeding area where different subpopulations mix during spring and summer; (ii) a transit area for fish moving from the Bay of Biscay to the English Channel and vice versa; (iii) and a shelter for a resident seabass population. The latter is supported by the presence of 0-group juveniles in the Iroise Sea in summer months. This new knowledge should be taken into account by the managers of the Iroise Marine Natural Park. They can lead to conservation actions, but this would require the agreement of all the components of the governance structure, which is the specificity of this MPA (Solandt *et al.*, 2014).

On a more general point of view, this study demonstrates the high potential of archival tags for investigating multi-year behavioural patterns such as site fidelity to offshore spawning areas.

Acoustic telemetry, often recommended to obtain data over multiple years, would have likely missed the multi-year offshore spawning contingent because of the lack of prior information on where to put acoustic receivers grid offshore.

### Migration routes (habitat maps, speed, and compass heading)

Habitat maps indicate that the fish spent most of their time either in spring/summer feeding areas or in winter spawning areas. This



may have implications for conservation, as suggested by Pawson *et al.* (2008). Abrupt variations in speed and heading clearly indicate that migrations are rapid events whose triggers need to be investigated. In the North East Atlantic, spawning migration is probably driven by temperature, as growth and ovarian development are reduced in waters  $<9^{\circ}\text{C}$  (Pawson *et al.*, 1987; Pawson and Pickett, 1996; Pawson *et al.*, 2000). Our data corroborate this theoretical threshold, which was reached in only 0.33% of the 12409 days of data summed over 34 fish. The potential difference in proportion between individuals from more eastern/northern areas (e.g. English Channel, southern North Sea) would need to be investigated. However, increasing temperatures in the North Sea may have induced a northward expansion and year-round residence of seabass here and in Norwegian coastal waters (Pawson *et al.*, 2007; Colman *et al.*, 2008). The temperature data will obviously require a more thorough analysis for a better understanding of the migration polymorphism. More specifically, the potential benefit of migrating so far offshore, in water deeper than 200 m, needs to be better understood.

### Vertical behaviour

Seasonal offshore migration patterns were not only inferred from track reconstructions but also formally documented by individual depth profiles, particularly during winter. As mentioned above, maximum experienced depths were below 225 m. To the best of our knowledge, this is the first time that such depths have been reported for seabass and this result challenges the currently held belief that “adults manifest demersal behaviour, inhabit coastal waters down to about 100 m depth but are more common in shallow waters” (Froese and Pauly, 2018).

Biological rhythms of European seabass have been explored in depth using experiments in controlled conditions (see review by Del Pozo *et al.*, 2014). Other than initial observations reported by Quayle *et al.* (2009), information from the field remains scarce. Fish A05712, representative of the Bay of Biscay contingent, showed drastic changes in its vertical activity, with different seasonal, circadian, and ultradian rhythms. In winter, this fish had strong diel vertical movement (DVM) whose proximate trigger was obviously the light intensity changes at dusk and dawn. The advantages of such DVM are probably multifactorial (Mehner, 2012): bioenergetic gain (warmer water at depth in winter in this area), foraging opportunities (following DVM of preys) or predator avoidance. It could be also indicative of spawning behaviour, as suggested for cod (Le Bris *et al.*, 2013). Moreover, the intra-individual plasticity of DVM exhibited by this fish over the different seasons corroborates the hypothesis that seabass would be a dual species (i.e. capable of changing from diurnal to nocturnal activity) as defined by Reeb (2002). Ultradian rhythms were also seen in some periods (between August and September), a rhythm probably driven by the inversion of the tidal current. Given the richness of these data, a thorough analysis of vertical behaviour is needed, which requires dedicated developments such as those proposed by Heerah *et al.* (2017).

### Geolocation model

The geolocation model developed for seabass and pelagic fish showed good performances, as detailed in Woillez *et al.* (2016). Additionally, the numerous track reconstructions undertaken in the present work provide some interesting feedback about the estimated parameters.

In Table 3, the average observation errors are  $0.3^{\circ}\text{C}$  for SST and  $0.9^{\circ}\text{C}$  for SBT. In comparison, the typical levels of uncertainty (in standard deviation units) of the reference geophysical fields are  $0.65^{\circ}\text{C}$  for SST, derived from satellite-based observation (Piolle *et al.*, 2010), and  $1.0^{\circ}\text{C}$  for temperatures, derived from the hydrodynamic model (Lazure *et al.*, 2009). Assuming that the measurement error from tags is very small, as described in technical specifications, observation errors may be underestimated on average, especially for SST. The geolocation model may be seeking to find too close a fit between the solution/track and the observed data values at the surface.

Table 3 also shows observation error outliers. Tags A06202, A09455, A09456, and A09478 show very low observation errors at the surface: below or equal to  $0.11^{\circ}\text{C}$ . For tags with short time series (A09455 and A09478, 5 days at sea or less), this low error level can be explained because tagging was done in summer time, when clouds have a lesser impact on satellite-derived observations. For the remaining tags, A06202 (74 days at sea) and A09456 (245 days at sea), the reconstructions may be questionable. Then, tags A06177, A09455, and A09465 show very low observation errors at the bottom: below or equal to  $0.14^{\circ}\text{C}$ . For tags A06177 and A09455, reconstruction quality was not a concern as these tags could not contribute to seabass migration analysis because of their short time series (11 days at sea or less). Tag A09465 had a long time series (134 days at sea) and more time spent in the bottom layer (90.3%) than in the surface layer (47.0%). Its reconstruction may be uncertain because SBT is a field with little contrast, less useful than SST. Tag A06277 showed a very high value of observation error at the bottom: equal to 4.19. This tag presented a short time series (16 days at sea), with more time spent in the surface layer (93.8%) than in the bottom layer (31.2%). This may indicate that MARS3D had difficulties to properly model the thermal front in the Iroise Sea. None of the other tags with a long time series had doubtful observation error estimates, thus validating our conclusions on seabass migrations.

As previously stated, the speeds derived from the diffusion coefficient ranged from 5 to  $29\text{ km}\cdot\text{d}^{-1}$  (Table 3). Such values are difficult to compare with swimming speeds recorded on juvenile or adult seabass in a controlled environment (reviewed in Lopez *et al.*, 2015). Indeed, swimming performances are usually reported in terms of critical swimming speed (i.e. the speed at which a fish is unable to remove itself from the back grid of a swim chamber). However, acoustic telemetry performed just before the first DST tagging survey in 2010 (de Pontual *et al.* unpublished) showed an average speed of  $60\text{ km}\cdot\text{d}^{-1}$  for one fish tracked over a 24-h period, demonstrating that the estimated values of the diffusion coefficient are all plausible.

The geolocation model could be improved in several ways. First, the observation likelihood layers could include multiple layers of temperature-at-depth information derived from the hydrodynamic model. This would avoid having days without observation likelihood layers when performing the track reconstructions. The bias revealed on the observation error for SST could be compensated by using uncertainty maps derived from the satellite products—here Odyssey North Western Europe, see Piolle *et al.* (2010). They are mainly linked to clouds impacting the derivation of SST from satellite sensors. While the surface error term is currently estimated homogeneously over the entire track, the revised term will vary in time and space over the entire track according to the uncertainty maps. In addition, error from both the environmental field (i.e. bathymetry, sea surface

temperature, and sea bottom temperature) and the tags could be integrated into the geolocation model (Le Bris *et al.*, 2018). Then, unusual thermal signatures, such as those from plumes of nuclear power stations or those of estuaries should also be included as attraction points in the geolocation model. Otherwise, with the geographical extension of the tagging experiments on seabass in the eastern English Channel, tide-driven geolocation, like that developed by Pedersen *et al.* (2008) and extended by Liu *et al.* (2017) on cod, should be included in the model. Indeed, seabass exhibit demersal behaviour when close to the seafloor. The depth observation model could also incorporate a weighting system based on the depth experienced by the fish when tide signals are detected. Seabass movement characteristics are expected to vary depending on the activities of the fish. The geolocation model could be expanded to include some behavioural switches, as in Pedersen *et al.* (2008). Regarding seabass, behavioural switches could be derived from the analysis of vertical data using a segmentation approach, such as the one developed by Heerah *et al.* (2017). The identified behaviours (i.e., various seasonal levels of activity) could be used to adjust the diffusion coefficient of the geolocation model. The joint modelling of vertical and horizontal movements would help interpretation in terms of realized functions, e.g. migration, foraging, or spawning.

## Conclusion

This first DST-tagging experiment off west Brittany revealed that seabass is a partially migratory species, as individuals exhibited either long-distance migrations toward the Bay of Biscay or the Celtic Sea, or a residency behaviour in the Iroise Sea. Migrants had a strong fidelity to the Iroise Sea in summer, probably for foraging. Fidelity to summer feeding areas had been already reported, but fidelity to winter spawning areas was demonstrated here for the first time and in most of the recovered tags with two winters of data. This result suggests that the population is spatially structured, although the underlying mechanisms still need to be understood. The Iroise Sea thus seems to be a mixing zone for different stocks or sub-populations including a resident one. At the population scale, such findings may impact the ICES stock assessment and resulting decisions from EU managers. At the local scale, conservation action could be taken by MPA managers. Ultimately, this work highlights the huge interest of extending such a tagging experiment geographically and making a complementary characterization of tagged fish (genetics, natal origin, etc.). This would provide a better understanding of the spatio-temporal structuring of the seabass population for improved assessment and management at both local and population scales.

## Acknowledgements

This study was funded by Ifremer and the Parc Naturel Marin d'Iroise (PNMI, Agence des Aires Marines Protégées). The authors thank the PNMI staff, fishermen, stakeholders, and everyone who provided assistance with fish tagging and/or recovery. We are grateful to Helen McCombie (BTU-UBO: Translation Bureau of the University of Western Brittany) for editing the manuscript. The authors also thank Dr Arnault Le Bris and two other reviewers for their constructive comments that helped improve the manuscript.

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Handling editor: Jonathan Grabowski