

# Multi-year tracking of European sea bass shows large-scale connectivity, summer site fidelity, and repeatability in migration timing

Jena E. Edwards <sup>1,2,\*</sup>, Allert I. Bijleveld <sup>1</sup>, Anthonie D. Buijse<sup>2,3</sup>, Peter Davies <sup>4</sup>, Alice E. Hall <sup>4</sup>, Jeroen Huisman<sup>5</sup>, Inge van der Knaap<sup>5</sup>, Melanie P. Meijer zu Schlochtern<sup>2,6</sup>, Jan Reubens<sup>7</sup>, Emma V. Sheehan <sup>4</sup>, Thomas Stamp <sup>4</sup>, Hendrik V. Winter<sup>2,6</sup>

<sup>1</sup>Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, Landsdiep 4, 1797 SZ, 't Horntje (Texel), the Netherlands

<sup>2</sup>Aquaculture and Fisheries Group, Wageningen University & Research, Droevendaalsesteeg 4, 6708 PB, Wageningen, the Netherlands

<sup>3</sup>Department of Freshwater Ecology and Water Quality, Deltares, Boussinesqweg 1, 2629 HV, Delft, the Netherlands

<sup>4</sup>School of Biological and Marine Sciences, Faculty of Science and Engineering, University of Plymouth, Drake Circus, PL4 8AA, Plymouth, Devon, United Kingdom

<sup>5</sup>Coastal and Marine Systems Group, Van Hall Larenstein University of Applied Sciences, 8901 BV, Leeuwarden, the Netherlands

<sup>6</sup>Wageningen Marine Research, P.O. Box 68, 1970 AB, IJmuiden, the Netherlands

<sup>7</sup>Flanders Marine Institute, Wandelaarkaai 7, 8400, Ostend, Belgium

\*Corresponding author. Jena E. Edwards, Aquaculture and Fisheries Group, Wageningen University & Research, Droevendaalsesteeg 4, 6708 PB, Wageningen, the Netherlands. E-mails: [jena.edwards@nioz.nl](mailto:jena.edwards@nioz.nl); [edwardsj67@gmail.com](mailto:edwardsj67@gmail.com)

## Abstract

Movement data are essential to the effective conservation and management of migratory species. European sea bass, an ecologically and economically important migratory species in the northeast Atlantic, has expanded its range northward in recent decades. However, the dynamics of its large-scale and seasonal movement patterns across much of its range remain poorly understood. Notably, increasing sea bass abundance in the Wadden Sea, amidst widespread population declines across its broader range, highlights the potential significance of seasonal habitats for the species' overall stability. We used acoustic telemetry to explore the importance of northern summer foraging grounds for sea bass, including examination of large-scale migratory connectivity, seasonal residency, and site fidelity. Acoustic detections from 130 adult sea bass ( $L_T = 40\text{--}75$  cm) revealed extensive seasonal migrations spanning 700 km between the Wadden Sea, North Sea, and English Channel. Migration occurred primarily in spring and autumn and highlighted strong regional connectivity between the Wadden Sea and southern North Sea. Larger individuals were associated with shorter migration distances. Within the Wadden Sea, sea bass arrived in spring (median date = May 22) and departed in autumn (median date = Oct 13) and had a median residence period of 136 days. For most fish, the extent of core area use ranged from 0–54 km. Additionally, 79% of returning individuals were detected within 10 km of their activity centres in previous years. Repeatability analyses showed high consistency between years in departure timing, core area extent, and site fidelity, emphasising greater among-individual than within-individual variation. These findings underscore the significance of the Wadden Sea as a summer habitat and shed light on the seasonal and regional behaviours of sea bass across their migration routes. This knowledge is vital for informing management strategies that account for both local and large-scale movements in this highly migratory population.

**Keywords:** movement ecology; acoustic telemetry; migration; residency; repeatability; Wadden Sea; North Sea; English Channel; *Dicentrarchus labrax*

## Introduction

Seasonal migrations allow individuals to optimize trade-offs in growth, survival, and reproduction by tracking favourable conditions across space and time (Olsson et al. 2006, Brönmark et al. 2008, 2014, Jørgensen et al. 2008). For migratory species, the quality of habitats used at either end of the migratory pathway has consequences for individual fitness (Merkle et al. 2022). Understanding migration timing and seasonal habitat use is critical for identifying the ecological factors that shape population abundance and distribution, thereby informing management at both local and regional scales.

The European sea bass (*Dicentrarchus labrax*, hereafter “sea bass”) is a partially migratory species that inhabits coastal waters, estuaries, and brackish lagoons across the northeast Atlantic, including the North, Irish, and Mediter-

anean Seas (ICES 2012, Froese and Pauly 2023). Within the northeast Atlantic, sea bass exhibit high variability in individual migration patterns and site fidelity, resulting in a complex population structure that complicates management (Robinet et al. 2020, Goossens et al. 2024). The International Council for the Exploration of the Sea (ICES) treats sea bass in the northeast Atlantic as four distinct stocks in their management advice and stock assessments (ICES 2012, 2018). However, a lack of genetic differentiation and variability in migration patterns suggest that current stock divisions may not accurately capture the true population structure (Fritsch et al. 2007, Pawson et al. 2007, ICES 2012, Goossens et al. 2024).

Most sea bass research in the northeast Atlantic has examined seasonal migrations between offshore winter spawning sites (e.g. the English Channel, Iroise Sea, and northern

Bay of Biscay), and coastal summer feeding areas, primarily in UK and Irish waters (Kennedy and Fitzmaurice 1972, Holden and Williams 1974, Pawson et al. 1987, Pawson et al. 2007, 2008, Quayle et al. 2009, de Pontual et al. 2019). These studies found small home ranges and strong interannual site fidelity during summer, contributing to an increased susceptibility to local depletion (Pawson et al. 2008, Doyle et al. 2017). Site fidelity to winter spawning sites was also observed in France, along with further evidence of partial migration (de Pontual et al. 2013, 2019, Le Luherne et al. 2022).

While sea bass populations have declined along Europe's Atlantic coasts (ICES 2022), they have expanded their range and increased in abundance in northeastern regions, likely as a result of climate warming. One example of this is the Wadden Sea, in which the species is considered a recent coloniser and supports both commercial and recreational fisheries (Tulp et al. 2008, Cardoso et al. 2015, Tulp et al. 2017: 2). However, little is known about how migratory patterns and movements in such areas are shaped by environmental or anthropogenic factors. Initial tagging results suggest a predominantly westward seasonal migration toward the southern North Sea and English Channel, highlighting the Wadden Sea as a strategic location for studying movement dynamics in seasonally occupied coastal habitats (Goossens et al. 2024).

We used acoustic telemetry to investigate the movement patterns of adult sea bass tagged in the western Dutch Wadden Sea, addressing knowledge gaps on the role of coastal habitats in their annual migrations. By integrating data from local and regional receiver arrays, we examined migration timing and movement within the Wadden Sea and southern North Sea, with additional focus on individual variation and repeatability across multiple years.

## Methods

### Study area

The Wadden Sea is a dynamic coastal system and UNESCO World Heritage Site (Common Wadden Sea Secretariat 2016, UNESCO 2023) shaped by tidal gullies, river outlets, and intertidal mudflats that cover approximately 50% of its surface area (de Jonge et al. 1993). Its diverse habitats include salt marshes along the mainland and Wadden Islands, soft sediments, and patches of hard substrate formed by oyster and mussel reefs (Baptist et al. 2019). The western Dutch Wadden Sea spans roughly  $\sim 1530$  km<sup>2</sup> and encompasses three tidal basins: Marsdiep, Eierlandse Gat, and Vlie (Baptist et al. 2019) (Fig. 1b). With an average depth of 3.5 m, the deepest areas are confined to the gullies and dredged shipping channels (Zimmerman 1976).

In recent decades, warming temperatures and anthropogenic activities such as fishing, dredging, and resource extraction have degraded the Wadden Sea's function as a nursery and feeding ground for North Sea migratory fish populations (Tulp et al. 2008, van Aken 2008, van der Veer et al. 2011, 2015, 2022).

### Fish tagging and ethics statement

Adult sea bass ( $\geq 40$  cm total length) were captured in the western Dutch Wadden Sea (Fig. 1) using the Royal Netherlands Institute for Sea Research (NIOZ) kom-fyke sampling program (van Walraven et al. 2017) and commercial gillnetting (11 cm stretched mesh) (see Supplementary Materials for

details). A total of 208 fish were caught and tagged from early May to early September in 2021 and 2022. Tagging was performed in the manner described by (Edwards et al. 2025), using V13-1x, V13AP-1x, V16-4x acoustic transmitters (Innovasea Systems Inc., Bedford, Canada) and an external T-bar tag anterior to the first dorsal fin. Prior to tagging, fish were sedated in a 0.04% solution of 2-phenoxyethanol in seawater. Acoustic transmitters were surgically implanted into the peritoneal cavity and incisions were closed with 2–4 interrupted sutures. Following surgery, fish were held in recovery tanks with fresh seawater until normal buoyancy, respiration, and swimming behaviour resumed. Tagging was performed in accordance with the Experiments on Animals Act in the Netherlands and approved by the Animal Ethical Commission under permit numbers 2016.D-0041 and 2021.D-0002. See Supplementary Materials for additional details and tag programming.

### Acoustic arrays

This study includes detections recorded by multiple receiver arrays in the Wadden Sea, southern North Sea, and English Channel (Fig. 1), sourced from the European Tracking Network data portal (<https://www.lifewatch.be/etn/>) (see Appendix 1 for array acknowledgements). Data were collected between May 12, 2021, and June 1, 2024.

Range testing was conducted within the Wadden Sea using receivers in the Swimway array (Fig. 1a), indicating midpoint (50%) detection ranges of 149 m for V13 tags and 311 m for V16 tags (or equivalent power output) (Edwards et al. 2024).

### Data analysis

Data filtering and analyses were conducted using R software (R Core Team 2023).

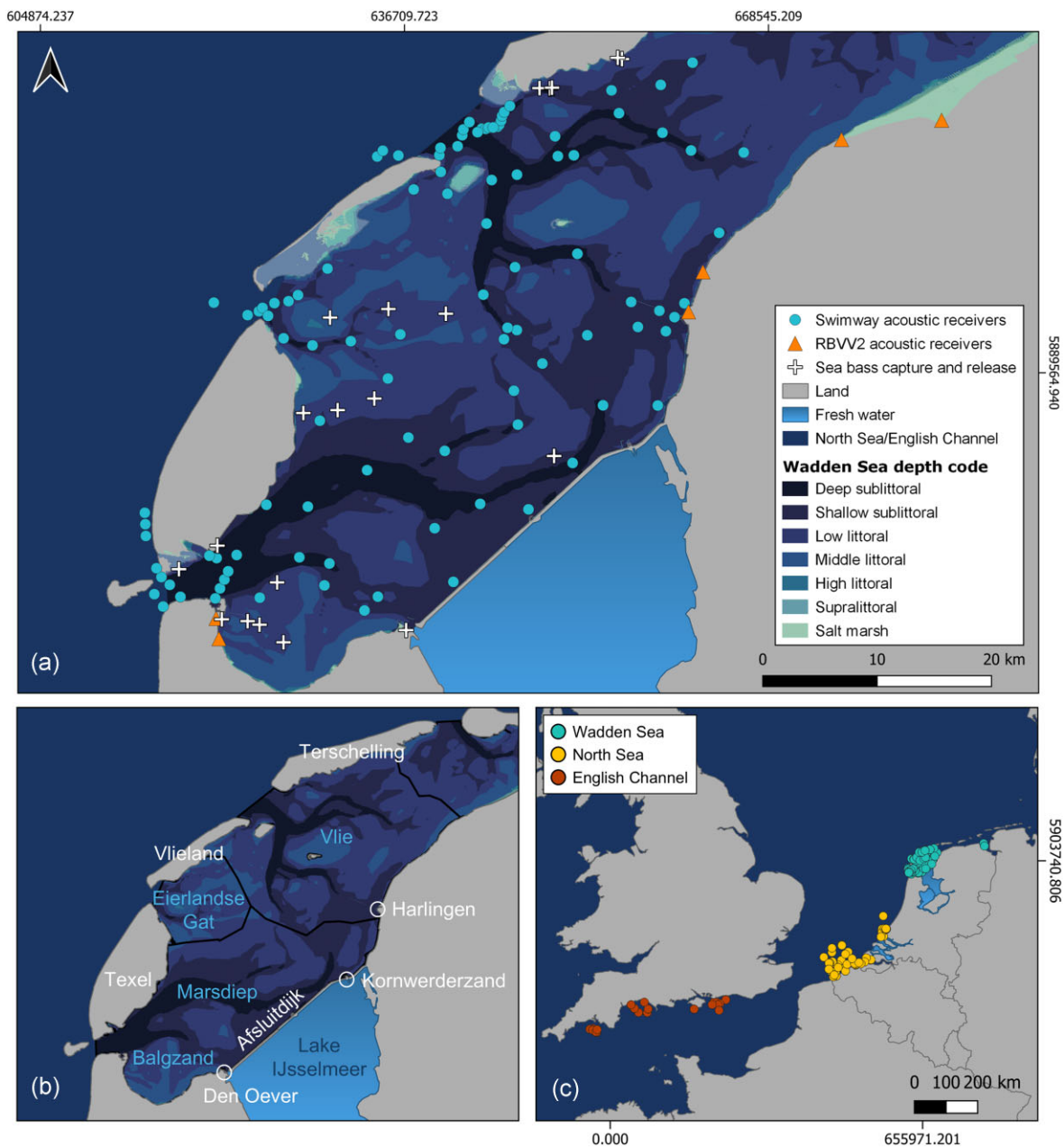
### Data filtering

Detection data were first subjected to a three-step filtering process to remove potential false detections (Brownscombe et al. 2023, Edwards et al. 2025). Detections were removed if they: i) occurred before tag deployment, ii) were part of a pair of detections for the same tag that were simultaneous or occurred within the minimum transmission delay, or iii) were single detections at a station within a 24 h period. In cases of simultaneous detections or those occurring within the minimum transmission delay, only the second detection was removed. Detections were first sorted chronologically, and delays were calculated relative to the previous detection. Detections with delays shorter than the transmission interval – including 0-second delays – were flagged for deletion. For paired simultaneous detections, the first of the pair was compared to the last valid detection and was subsequently retained, while the second detection in the pair was removed.

Suspected mortalities were also assessed via: i) the recapture of internal tags by fishermen or beach combers, or ii) examination of detection profiles (see Supplementary Materials). Individuals identified as likely mortalities were excluded from analyses.

### Sea bass presence and migration across European habitats

The filtered detection dataset was used to compare seasonality and temporal overlap in sea bass presence across the Wadden Sea, southern North Sea, and the English Channel. Temporal



**Figure 1.** Locations of acoustic receiver stations in (A) the western Dutch Wadden Sea and (C) the southern North Sea and English Channel. Locations in panel C include only stations with sea bass (*Dicentrarchus labrax*) detections. Depth contours in the Wadden Sea represent zones described by (Baptist et al. 2019), ranging from areas exposed at low tide (salt marsh to low littoral) to a maximum of ~40 m depth in sublittoral regions. Panel B highlights locations referenced in the text, including the three tidal basins and the Balgzand subregion. Acoustic receiver locations in panels A and C encompass multiple acoustic arrays: (i) Wadden Sea—Swimway and RBV2 arrays, (ii) North Sea—Apelafico, bpns, CODEVCO fish detectors, cpodnetwork, Fish Intel Network, Haringvlietdam, PelFish, and ws1, and (iii) English Channel—Fish Intel Network. Additional detection data were obtained via the database of the European Tracking Network: <https://www.lifewatch.be/etrn/>.

patterns and recurrence rates were examined for individual sea bass in each region.

To assess large-scale connectivity, we calculated the proportion of fish detected in each area to characterise regional detection rates and undetected movements. For receiver stations outside the Wadden Sea, distances from the outermost station in the Swimway array (S 11, Marsdiep Channel) served as a proxy for maximum travel distance. To test whether fish length at capture or season of detection influenced maximum distance travelled, we fitted a Gamma generalised linear mixed model (GLMM) with a log link using the `glmmTMB`

package (Brooks et al. 2017). The model included fish ID as a random intercept to account for repeated seasonal measures, fish length as a continuous fixed effect, and season as a categorical fixed effect, with winter set as the reference level.

#### Patterns of occurrence in the Wadden Sea

Detection data were separated by year and visually examined for spatial patterns in sea bass presence and absence across the western Dutch Wadden Sea. Stations were considered absent of sea bass if they had the potential to detect tagged individ-

uals but recorded no detections. To avoid bias from lost or damaged receivers with reduced detection opportunity, only those that remained functional for at least 90 days in the given year – approximately half of the 6-month deployment period – were included in the analysis. Data from two consecutive deployment periods were then combined to show patterns of detection per year.

To distinguish individual core areas from short-term transient movements, we filtered the detection history of each fish based on detection frequency per receiver station. For each individual, receiver stations were ranked by detection count, and only those contributing to a cumulative sum of 90% of total detections were retained. These high-use stations were interpreted as core areas, under the assumption that higher detection frequencies reflect longer residence times or repeated use. Stations contributing to the remaining 10% of detections were excluded as they likely represent short-term or exploratory visits. The resulting core area dataset was then compared to the full dataset to evaluate the influence of transient movements on overall spatial distribution.

### Timing and duration of Wadden Sea residence

Timing of arrival and departure from the Wadden Sea were evaluated using the dates of first and last detection in each year. As the time of arrival in the tagging year was not known, arrival and departure dates were only examined in subsequent return years. Individual residence duration was defined as the time between first and last detection. To prevent the inclusion of partial residence periods in our analyses, only individuals with residence durations of > 5 d were included (Edwards et al. 2025).

To quantify the spatial extent of detections within the Wadden Sea, we calculated the number of unique receiver stations that detected each individual per year. These counts were summarised to characterise the distribution of detections per individual and across years. Differences in individual station counts across years were assessed using a Kruskal-Wallis rank sum test.

### Detection frequency

To assess individual mobility and space use within the Wadden Sea, we first determined the total number of stations where each fish was detected. We then calculated a Residency Index (RI), adapted here to reflect individual differences in detectability that may be linked to variation in movement and habitat use during Wadden Sea residence. Although this is not the conventional application of RI, this approach has previously been used to compare detectability between grey mullet species in the Wadden Sea (Edwards et al. 2025). RI was calculated as the number of days a fish was detected in the Wadden Sea divided by the residence duration in days (Cochran et al. 2019, Appert et al. 2023, Kraft et al. 2023). Residence duration was defined as the time between an individual's first and last detection and was calculated only for return years in which the timing of arrival could be determined. To minimize the inclusion of partial residence periods – e.g. during which a fish was detected only while entering or leaving the array – only individuals with residence durations > 5 days were included in the analysis (Edwards et al. 2025).

$$RI = \frac{N \text{ detection days}}{\text{Residence duration (days)}}$$

RI values approaching 1 indicate near-continuous detection throughout the seasonal residence period, while lower values suggest infrequent detection, possibly due to movement or residency beyond detection range.

### Space use and site fidelity

Stations included in the 90% core use areas were used to assess variation in space use and site fidelity both within and among individuals. Space use extent was quantified as the maximum pairwise distance between stations within each individual's 90% core area, serving as a coarse proxy to compare the relative scale of space use among individual sea bass.

Site fidelity was assessed based on annual shifts in the centre of activity, calculated as the weighted mean position of receiver stations in the core area with detection frequency used as the weighting factor. This provides a simplified and standardised estimate of central tendency in space use. Pairwise distances between an individual's annual centres of activity were used as a proxy for interannual site fidelity, with smaller distances reflecting greater consistency in space use across years.

### Repeatability analyses

For individuals detected in the Wadden Sea across multiple years, repeatability analyses were conducted using the rptR package (Stoffel et al. 2017) to assess annual repeatability in arrival and departure timing, core area extent, and the distance between activity centres within individuals. This approach applies mixed-effects models with parametric bootstrapping to calculate a repeatability index (R), which quantifies the proportion of total variance attributed to individual differences. R is computed as the among-individual variance divided by the sum of among- and within-individual variances, ranging from 0 to 1, where higher values indicate greater individual consistency over time.

Prior to assessing repeatability, linear mixed-effects models were fitted to each response variable using the *lmer* function in the lme4 package (Bates et al. 2015), with year as a fixed effect and fish ID as a random effect, to assess residual normality. Simulated residuals were generated using the *simulateResiduals* function in the DHARMA package (Hartig 2024). Residuals for distance between activity centres showed right-skew and were normalised using a natural log transformation. However, transformations for departure timing and core area extent failed to normalise the residuals, therefore results should be interpreted with caution.

To evaluate the potential effects of zero inflation, repeatability analyses were conducted using both the full dataset and a filtered subset excluding zeros. As results were highly correlated, final analyses used the full dataset for increased sample size (see Supplementary Materials). Final models were fitted using the rptR package assuming a Gaussian distribution, using the recommended number of 1000 parametric bootstrap iterations and 0 permutations (Stoffel et al. 2017). Fish ID was included as a random effect (also referred to as the grouping factor the rptR syntax), and year was included as a fixed effect for arrival timing, departure timing, and core area extent. As the distance between activity centres, which is a relative measure based on comparisons between two return years, paired years of detection were included as the fixed effect.

## Results

### Tagging summary

A total of 208 adult sea bass were tagged with acoustic transmitters (Fig. 1a), of which 140 individuals were detected (67%). Among these, 10 were identified as confirmed mortalities (via animal or internal tag recovery) or potential mortalities (via prolonged detection at a single station) (see Supplementary Materials). Detection rates were higher for fish captured with fyke nets (94%, 48 fish tagged) than with gillnets (59%, 160 fish tagged). As capture method coincided with factors such as location, timing, and fish size, these differences should be interpreted as associations rather than causal effects.

### Sea bass detections at regional scales

A total of 127 037 filtered detections were recorded by 214 receiver stations in the Dutch Wadden Sea (105 stations, 65% of detections), North Sea (78 stations, 34% of detections), and English Channel (31 stations, 1% of detections) (Table 2, see Supplementary Materials for array summaries). Excluding mortalities, 130 fish were included in the following analyses (40–75 cm total length [TL]; median = 51.1 cm).

Sea bass were detected in each region—Wadden Sea, North Sea, and English Channel—across all seasons (Fig. 1, 2, Table 2). Temporal overlap in fish presence occurred year-round, with fish detected in all regions simultaneously from March–August and from November–December.

Presence in the Wadden Sea spanned from March to December (Table 2). In total, 123 fish were detected in the Wadden Sea, of which 50 (41%) were detected over multiple years (two years:  $N = 24$  [20%], three years:  $N = 25$  [20%], four years:  $N = 1$  [ $<1\%$ ]) (Fig. 2b). Peak detections occurred in May–June and September–October each year, indicating a summer residency period and potential migration through the array en route from and to the North Sea (Fig. 2a).

In the North Sea, fish were detected during all months (Table 2). Peak occurrence aligned closely with trends from the Wadden Sea, with most detections and highest fish counts recorded in spring (April–May) and autumn (October–November) (Fig. 2a). Over 55% of all detected fish were observed in the North Sea ( $N = 72$ ), of which 22 were redetected for two or three years ( $N = 22$ ,  $N = 4$ , respectively) (Fig. 2b).

Lastly, 16 fish were detected in the English Channel, of which 2 were redetected over two years. Detections were recorded throughout most of the year, except September and October, with peak detections recorded in April, May, and December (Table 2, Fig. 2).

### Regional connectivity and seasonal migrations

Sea bass detections outside the Wadden Sea revealed large-scale regional connectivity (Fig. 3). During the study period, 55% of detected fish exhibited westward movements from the Wadden Sea to the southern North Sea (48% detected in both regions; median distance = 200 km, IQR = 186–228), while 12% reached the English Channel—the furthest extent of observed migrations (median distance = 452 km, IQR = 244–600). Thirteen fish were detected in all three regions (Fig. 2), but only one individual was detected east of the

SWIMWAY array area near the Ems-Dollard (Fish ID: SB220) (Fig. 1c, 3).

Westward migrations from the Wadden Sea peaked in autumn (destination North Sea:  $N = 43$  and English Channel:  $N = 10$ ), with fewer movements in spring ( $N = 7$ ,  $N = 2$ ) and summer ( $N = 11$ ,  $N = 1$ ) (Fig. 3). Three individuals were detected in the North Sea before reaching the English Channel. Eastward migrations from the English Channel were less frequent, occurring mostly in spring (North Sea:  $N = 6$ , Wadden Sea:  $N = 2$ ). In contrast, the North Sea showed high bidirectional connectivity with the Wadden Sea, with many fish moving eastward in spring ( $N = 20$ ), followed by autumn ( $N = 11$ ) and summer ( $N = 9$ ) (Fig. 3).

While many large-scale movements were observed, some fish traversed large areas undetected. Six fish were first detected in the North Sea after being tagged in the Wadden Sea, while seven were detected only in the Wadden Sea and English Channel (Fig. 3). Two fish were exclusively detected in the North Sea over 2–3 years (Fish ID: SB26, SB132; Fig. 2b). A further eight fish left and returned to the Wadden Sea over multiple years without detections elsewhere (Fig. 2b).

Maximum distance travelled ranged from 191 to 700 km (median = 244 km) across 74 fish detected outside the Wadden Sea. Fish length had a significant negative effect on maximum distance ( $\beta = -0.029 \pm 0.010$ ,  $P < 0.01$ ), suggesting that larger individuals tended to remain closer to the Wadden Sea. Maximum distance travelled also varied significantly by season, with the shortest distances observed in summer ( $\beta = -1.36 \pm 0.27$ ,  $P < 0.001$ ), followed by autumn ( $\beta = -0.70 \pm 0.26$ ,  $P < 0.001$ ) and spring ( $\beta = -0.58 \pm 0.27$ ,  $P = 0.03$ ), relative to those observed in winter.

### Timing and duration of Wadden Sea residence

Sea bass showed a strong seasonal association with the Wadden Sea with arrival beginning in late March (median date = May 22) (Table 3, Fig. 4a). Departures ranged from early April to late December (median date = Oct 13) (Fig. 3a, Table 3). While in the Wadden Sea, most sea bass were detected by few receiver stations (median = 4, IQR = 3–6) with no significant differences in the median number of stations by which fish were detected across years ( $\chi^2 = 0.96$ ,  $df = 1$ ,  $p$ -value = 0.33) (Fig. 4b). In general, sea bass exhibited low RI values (median = 0.10, IQR = 0.04–0.25), however, strong residency near one or more receiver stations was also observed, reaching a maximum RI of 0.82 (Fig. 4b).

### Patterns of occurrence in the Wadden Sea

Over three years, sea bass detections were broadly distributed throughout the array area, with higher concentrations near the tidal inlets and fewer fish detected in the central Wadden Sea near the inner reaches of the tidal gully systems (Fig. 5a). Relative to the full dataset, 90% core areas included fewer total stations, but showed little difference in overall distribution, indicating that some stations detected only brief forays outside the core use areas (grey dots, Fig. 5b). Receiver stations detected a median 25 fish per year (IQR = 6–156), with most detections recorded in the first tagging year near release locations in the Marsdiep Channel and near Terschelling (Fig. 1b, 5b).

**Table 1.** Overview of sea bass (*Dicentrarchus labrax*) tagged in the Dutch Wadden Sea in summer 2021 and 2022, excluding likely mortalities.

Capture region	Capture method	Tagging months	N tagged	N detected	Median length	Length IQR	V13AP	V13	V16
Texel	Fyke	May-July	48	43	51	46–58	10	31	2
Balgzand	Gillnet	June-July, Sept	94	38	52	49–57	0	28	10
Terschelling	Gillnet	June	32	24	51	49–56	5	18	1
Eierlandse Gat	Gillnet	June-July	24	16	51	48–54	0	12	4
Texel	Gillnet	June	9	9	48	44–50	0	9	0
Kornwerderzand	Gillnet	July	1	1	60		0	0	1

Lengths refer to total length in cm. V13AP, V13, and V16 refer to transmitter models and are listed with numbers deployed.

**Table 2.** Summary of acoustic detections from May 2021 to June 2024 for 130 sea bass (*Dicentrarchus labrax*) tagged in the western Dutch Wadden Sea.

Region	N fish	N stations	N detections	N Years	Months
Wadden Sea	123	105	81 946	4	March-Dec
North Sea	72	78	43 633	4	Jan-Dec
English Channel	16	31	1458	3	Jan-Aug, Nov-Dec

Data sourced from the Swimway array and the European Tracking Network database: <https://www.lifewatch.be/etn/>

### Individual space use and site fidelity in the Wadden Sea

Individual sea bass exhibited diverse movement behaviours characterised by differences in detection frequency, core area extent, and site fidelity. Core area extent and the distance between core area centres were analysed for 34 individuals detected in at least two years, allowing for an assessment of individual repeatability (illustrated for 4 individuals in Fig. 6).

In general, limited space use (small core area extent) was associated with high detection counts and increased site fidelity (short distances between core area centres), whereas larger-scale space use tended to correspond with lower detection counts and reduced site fidelity. Core area extent in a given year ranged from 0 to 54 km (IQR = 0–7.9) with a median of 0 km, indicating limited spatial dispersion during the summer residence period (Fig. 7). For 14 individuals in each year (24 overall), core areas consisted of a single receiver station and were associated with high detection counts (median = 122, IQR = 49–369). In contrast, core areas spanning 2 to 7 stations (median = 2, IQR: 2–3) had lower detection counts (median = 45, IQR: 20–113).

Site fidelity was quantified using pairwise distances between activity centres (the weighted mean coordinates of core area stations) across all detected years. The median distance between activity centres was 3.3 km (IQR = 0–7.5), demonstrating a general pattern of small-scale site fidelity (Fig. 7). Sixteen individuals showed minimal interannual variation, with core area centres separated by <1 km in at least two consecutive years. For four individuals, this pattern persisted across all three years (Fig. 7). Most fish (79%,  $N = 27$ ) had core area shifts of <10 km between years, while only one individual (SB77) exhibited a shift greater than 25 km.

### Repeatability in migration timing and space use

Repeatability analyses were conducted for 42 sea bass that returned to the Wadden Sea over 2–3 consecutive years to assess individual variation in migration timing and space use. Arrival timing showed moderate repeatability, with among-individual variation accounting for 31% of the total variance ( $R = 0.31$ ,  $SE = 0.2$ ,  $P = 0.08$ ) (Fig. 8). Within-individual vari-

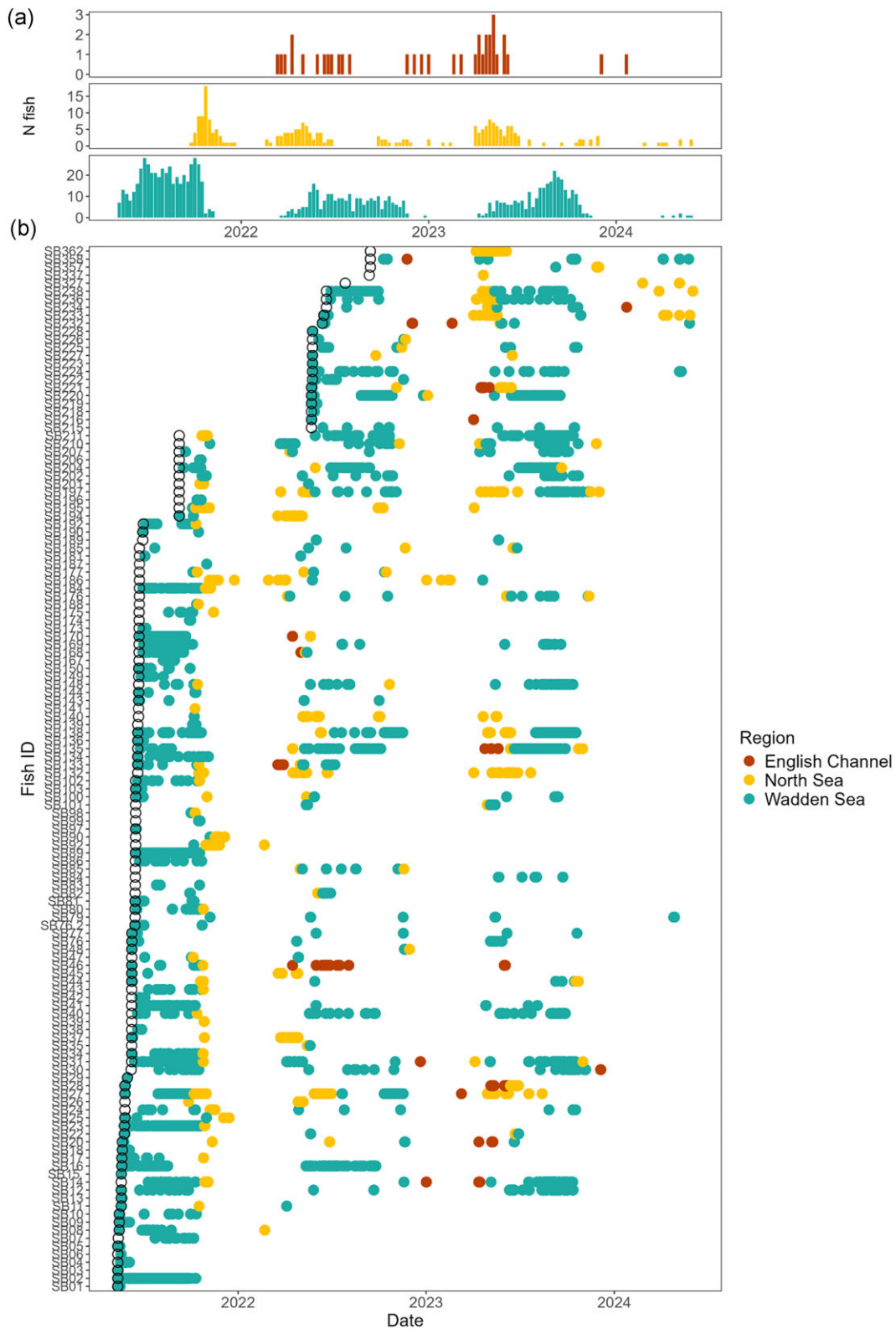
ation accounted for 69% of the total variance, with significant differences across years ( $SE = 7.97$ ,  $t = 2.14$ ,  $P < 0.05$ ).

In contrast, sea bass exhibited high repeatability in departure timing, with among-individual differences explaining 86% of the total variance ( $R = 0.86$ ,  $SE = 0.06$ ,  $P < 0.05$ ) (Fig. 8). Space use (core area extent) was also highly repeatable, indicating consistent individual scales of space use over time ( $R$  (Fig. 8)). Repeatability in the distance between activity centres was very high ( $R = 0.79$ ,  $SE = 0.08$ ,  $P < 0.05$ ), reflecting strong site fidelity across years (Fig. 8).

## Discussion

Sea bass tagged in the Wadden Sea demonstrated large-scale seasonal migrations linking this region to coastal and offshore waters in the Netherlands, Belgium, and the UK. Temporal overlap in sea bass presence was observed across the Wadden Sea, southern North Sea, and English Channel, with most individuals exhibiting summer residency in the Wadden Sea, punctuated by spring and autumn migrations to and from the area and achieving maximum migration distances in winter. Fish length had a negative influence on migration distance, with larger individuals remaining closer to the Wadden Sea. No sea bass were detected in the Wadden Sea during winter, providing no evidence for partial migration in the region. Median arrival and departure dates were in May and October, with a typical summer residence period of ~4.5 months. While migration timing varied among fish, departure dates were highly repeatable. Within the Wadden Sea, individual detection profiles illustrated diverse movement behaviours underlying a broader distribution. Limited space use, characterized by small core areas, was associated with high detection counts and strong site fidelity, while large-scale space use was often associated with lower detection counts and reduced site fidelity.

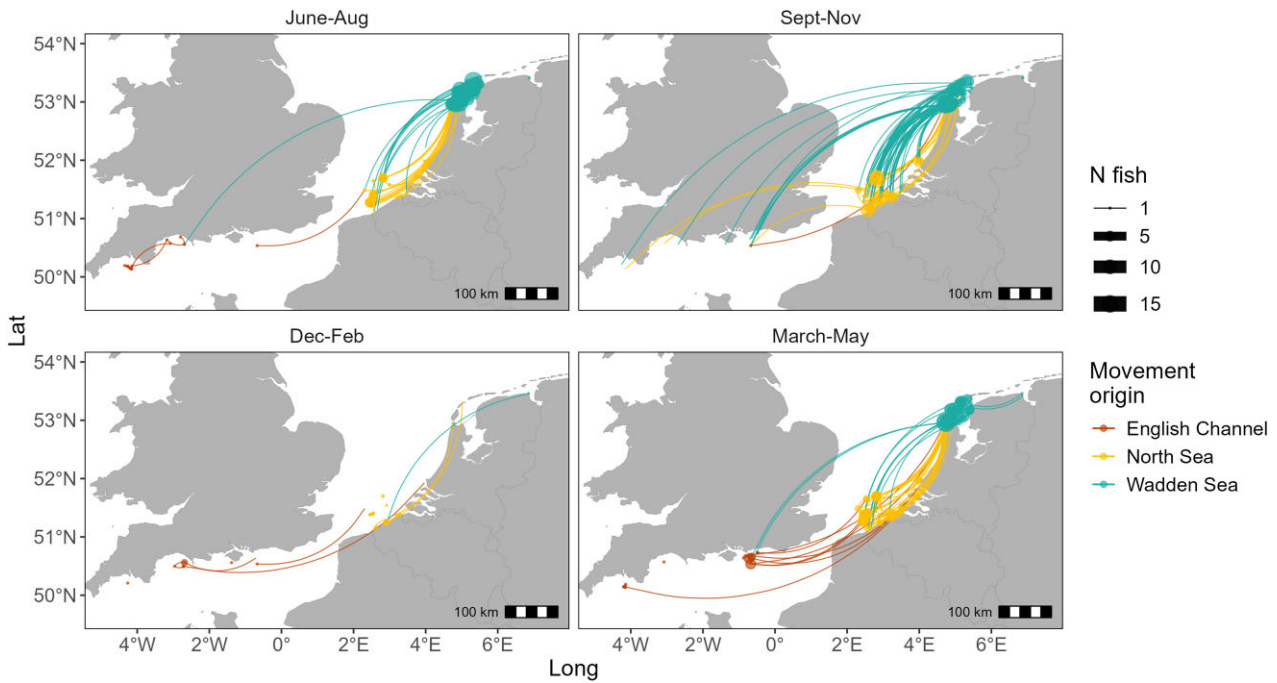
For migratory species, decisions regarding the timing, frequency, and destinations of migration can have profound consequences for both survival and reproductive success (Reséndiz-Infante and Gauthier 2020, Hulthén et al. 2022). Understanding these movements is particularly important for commercially exploited species, where individual migration



**Figure 2.** Detection profiles of sea bass (*Dicentrarchus labrax*) tagged in the Dutch Wadden Sea from May-September 2021 and 2022 and detected from 2021–2024. (A) Number of unique fish detected per week in three regions. (B) Individual detection profiles coloured by region with open circles indicating the date of tagging and release.

patterns also reveal regional connectivity between local populations and stocks, thereby informing fisheries management (Crossin et al. 2017, Özgül et al. 2024). This study used acoustic telemetry to characterise large-scale migrations and local

space use over a vast study area. Many individuals were detected across the Wadden Sea, North Sea, and English Channel, with extensive receiver networks enabling the tracking of full migratory cycles and highlighting strong connectiv-



**Figure 3.** Sea bass (*Dicentrarchus labrax*) movements between the Wadden Sea, North Sea, and English Channel across seasons. Nodes represent individual receiver stations, scaled in size by the number of fish detected. Curved lines represent fish movements between receiver stations and are right-hand curved from origin to destination.

**Table 3.** Arrival and departure dates, residence duration, and Residency Index (RI) for 42 sea bass (*Dicentrarchus labrax*) detected in the Dutch Wadden Sea in subsequent years after tagging ( $N = 59$  observations).

Category	Median	Median date	IQR
Arrival	141	May 22	126–159
Departure	285	Oct 13	263–296
Residence duration	136		98–159
RI	0.10		0.04–0.25

Data include only residence periods  $> 5$  d. Median arrival and departure dates and interquartile ranges (IQR) are shown as day-of-year (DOY).

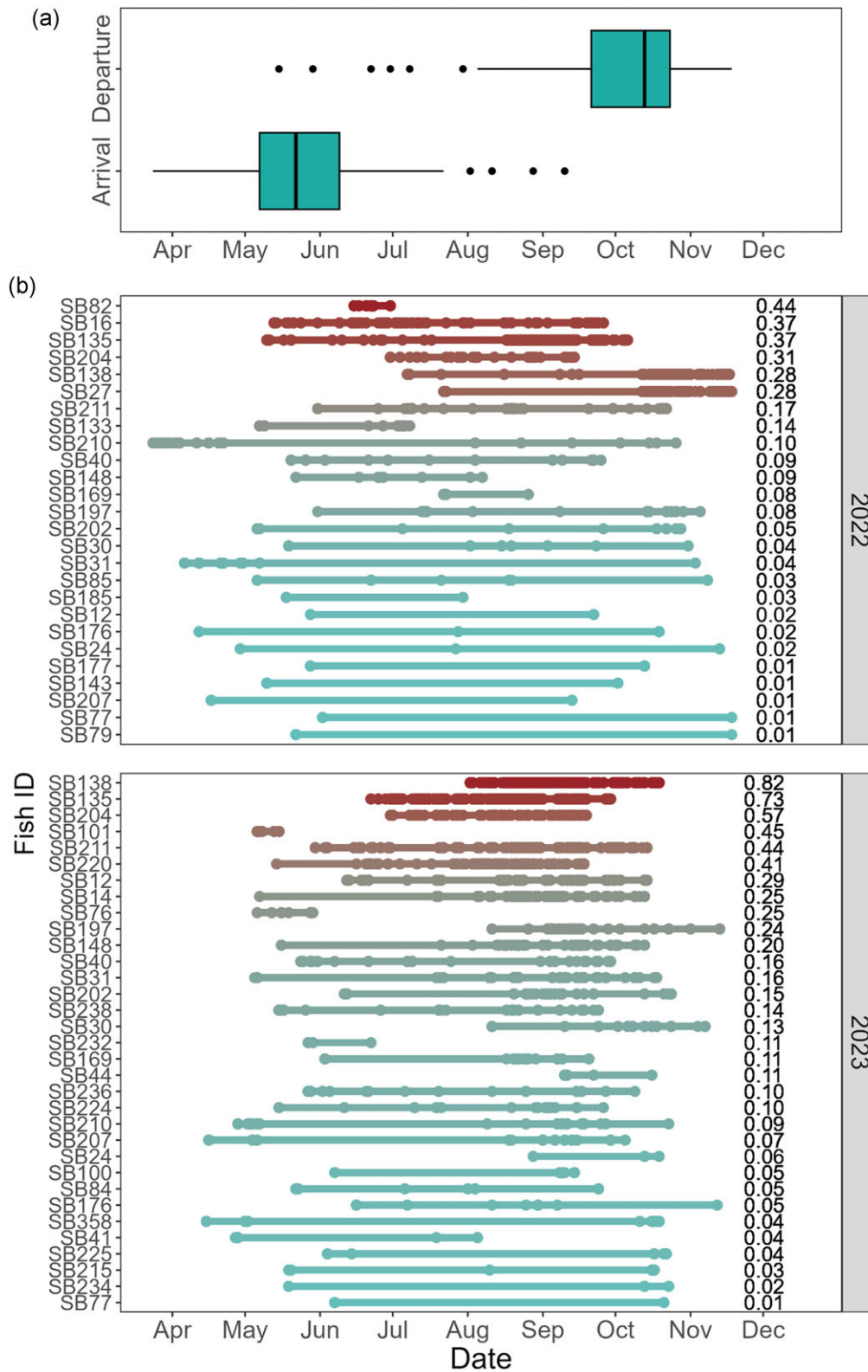
ity between the southern North Sea and Wadden Sea (Fig. 1, 3). However, limited winter detections suggest that potential overwintering and spawning areas used by Wadden Sea migrants are not covered by current receiver networks (Fig. 3). In addition, incompatibility between tags and receivers from different manufacturers continues to limit broad-scale detections, as shown by our inability to track movements into regions covered by alternative systems (e.g. along the northern French coastline), likely preventing the detection of fish migrating to and from the southern English Channel. Greater compatibility across European telemetry networks is needed to enhance data collection and clarify stock mixing (Reubens et al. 2021). Meanwhile, tagging studies from France, Belgium, and the UK have demonstrated the value of data storage tags for identifying important areas beyond current receiver coverage (Quayle et al. 2009, de Pontual et al. 2013, Le Luherne et al. 2022, Goossens et al. 2024). These studies not only improve our understanding of sea bass behaviour, particularly in areas not covered by the current arrays, and but also highlight opportunities to better align receiver networks with fish migrations and spawning habitats.

Constraints on receiver placement in the Wadden Sea resulted in incomplete and unbalanced coverage, posing chal-

lenges for analysing sea bass movements. Low RI values (median = 0.10) suggest that fish spent time outside the array or beyond detection range (Table 3, Fig. 4). Receiver placement was limited to the subtidal gully systems, potentially leading to underestimation of fish presence in intertidal areas. Field observations of large fish crossing submerged mudflats at high tide suggest that use of intertidal areas beyond receiver coverage may have contributed to low RI. Archived depth and temperature data, combined with periods of absence in detections, could provide insights into habitat associations related to tidal height and temperature.

Differences in post-tagging detection probability may reflect both unequal mortality between capture methods and variation in the proximity of release sites to nearby receivers. While physical injuries and longer handling times associated with gillnetting may have increased mortality rates relative to fyke-captured fish, receiver placement may have also contributed to reduced detection rates. Specifically, fyke-captured fish were released near a dense array of receivers in the Marsdiep, a major tidal inlet and migration corridor. In contrast, most gillnet-captured fish were released in the Balgzand, where receiver coverage was sparse due to the extensive intertidal areas.

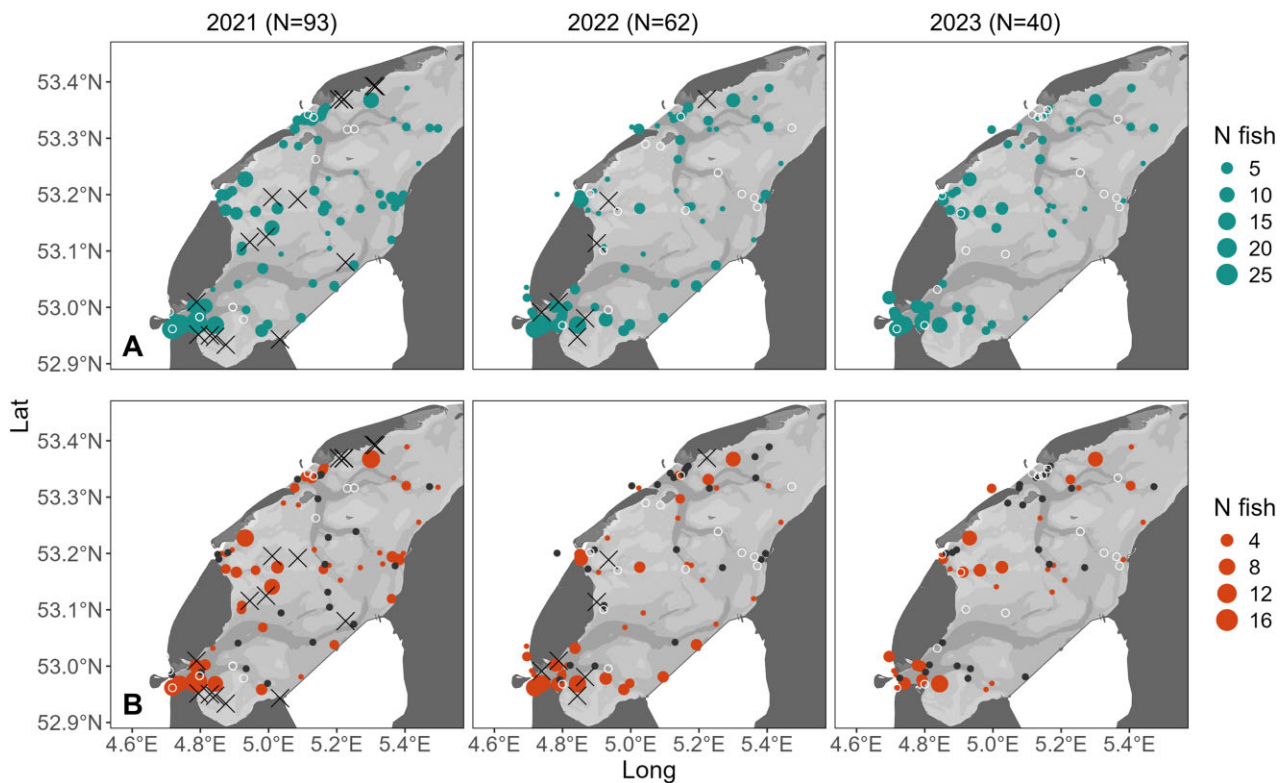
Although our four-year dataset does not allow direct assessment of climate-driven changes, broader evidence indicates that warming can influence migration strategies in partially migratory species (Berthold 2001, Boom 2022). While partial migration occurs elsewhere in the species' range, our data showed no evidence of full-time residency among sea bass tagged in the Wadden Sea, suggesting that strong seasonal cooling may drive sea bass to deeper waters in winter. In Belgium, tagged sea bass overwintered in a marine harbour with a median winter temperature of 6.9°C (Goossens et al. 2023). Anecdotal reports also indicate overwintering near warm-water outflows in Dutch coastal waters (Bierman



**Figure 4.** Timing and duration of seasonal residence for sea bass (*Dicentrarchus labrax*) detected in the Dutch Wadden Sea in subsequent years after tagging. Individuals included had residence durations of > 5 d. (A) Timing of arrival and departure inferred from first and last detections per year. (B) Timing of individual detections (dots) and residence duration (bands). Colour gradient corresponds to the Residency Index (RI) values displayed to the right of each detection profile.

et al. 2010), though these sites were not detected in our array. Given the 1.5°C increase in the Wadden Sea’s temperature over the past 25 years (van Aken 2008), continued warming

may gradually promote year-round residency and partial migration, highlighting the importance of ongoing monitoring at the leading edge of the species’ range.



**Figure 5.** Distribution of sea bass (*Dicentrarchus labrax*) detections in the Wadden Sea. Open circles represent receiver stations without detections. Tagging locations in 2021 and 2022 are denoted by an X. Top panels (A) show 100% of recorded detections while lower panels (B) show receivers included in the 90% core areas of detected individuals (orange) and receivers with detections excluded from the 90% core areas (dark grey).

Consistent individual differences in migratory behaviour and space use have been observed across taxa (Chapman et al. 2011, Ersoy et al. 2024). For sea bass, departure timing, core area size, and distance between activity centres were highly repeatable, indicating individually consistent migratory behaviour and local space use within the Wadden Sea. Comparing the full detection from within the Wadden Sea to the 90% core areas illustrated a broad overall distribution of sea bass with limited individual movements during the summer residence period (Fig. 5). The exclusion of brief forays showed that most fish had core areas covering <10 km, often including only a single receiver station. This, along with high detection rates for short-ranging individuals, indicates fine-scale seasonal residency and strong site fidelity, similar to other summer foraging habitats across Europe (Kennedy and Fitzmaurice 1972, Pawson et al. 1987, Pawson et al. 2007, 2008, Doyle et al. 2017, Stamp et al. 2021, Goossens et al. 2023).

Previous studies have shown that fine-scale residency and high site fidelity increase the vulnerability of sea bass populations to local depletion in coastal foraging areas, potentially affecting mixed populations across their migratory range (Doyle et al. 2017, Goossens et al. 2024). As one of Europe's most valuable fish species, sea bass are targeted in Dutch waters by both recreational and inshore commercial fisheries (vessels <12 m), contributing approximately 3% of total EU landings (EUMOFA 2021). Despite being common across the Wadden Sea (Jager et al. 2009), their low catchability in regional surveys limits our understanding of local population status (Bolle et al. 2009).

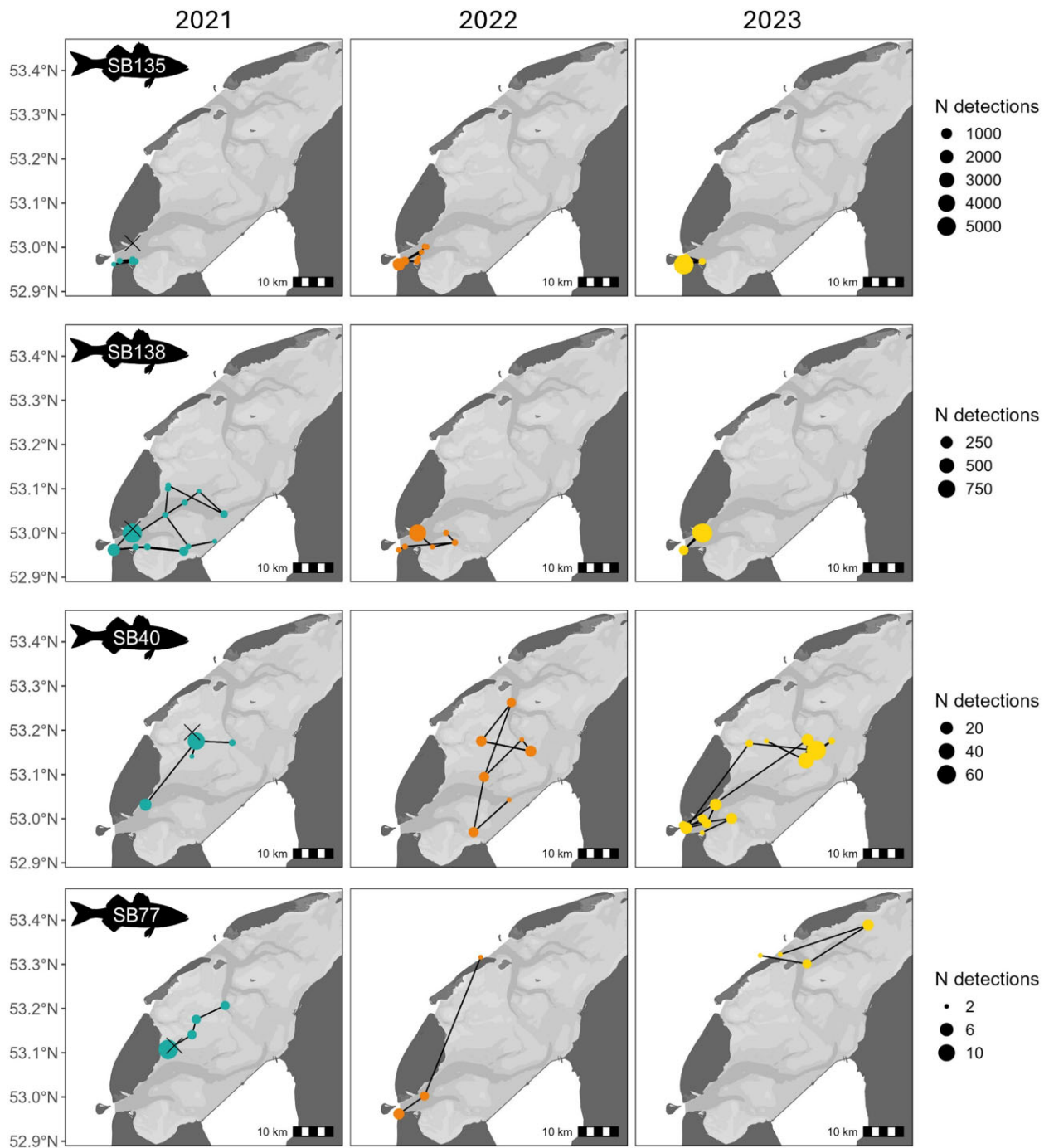
Acoustic telemetry is a powerful tool for assessing behaviours shaping population distribution and abundance.

This study highlights the risk of local depletion in seasonal habitats like the Wadden Sea and emphasises the need for coordinated management across the Wadden Sea, southern North Sea, and English Channel. Further research on fine-scale behaviours in seasonal habitats and the identification of overwintering and spawning habitats in the North Sea and English Channel would be beneficial for effective management.

## Conclusion

In the northeast Atlantic, understanding the large-scale connectivity and seasonal movements of European sea bass is essential for effective fisheries management. Over recent decades, sea bass have expanded their range and increased in abundance in the Wadden Sea, contrasting with declines along the Atlantic coasts and the English Channel. Within the Wadden Sea, sea bass exhibited diverse movement behaviours, including frequent fine-scale residency and localised site fidelity. Our findings also highlight strong regional connectivity between the Wadden Sea, southern North Sea, and English Channel, along with consistent movement patterns within a summer feeding ground.

By linking these movement patterns to stock delineation and potential risks such as localized depletion, this study provides valuable insights for the sustainable management of sea bass populations. Expanding telemetry networks to identify and monitor overwintering and spawning areas will be essential for gaining a more comprehensive understanding of the full migratory cycle.

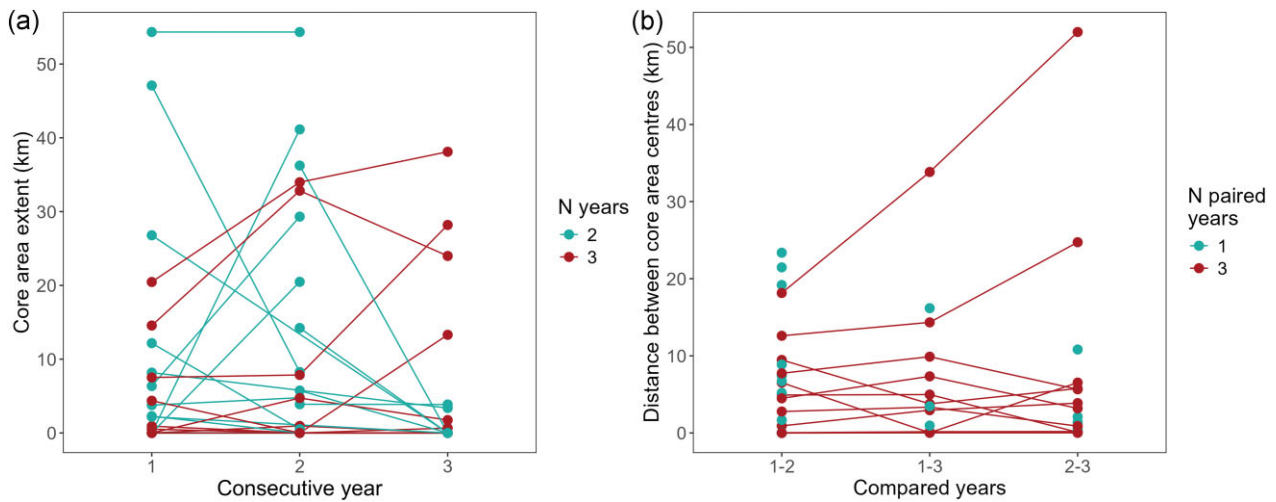


**Figure 6.** Individual multi-year movement patterns for four sea bass (*Dicentrarchus labrax*) detected in the Wadden Sea. X indicates tagging location.

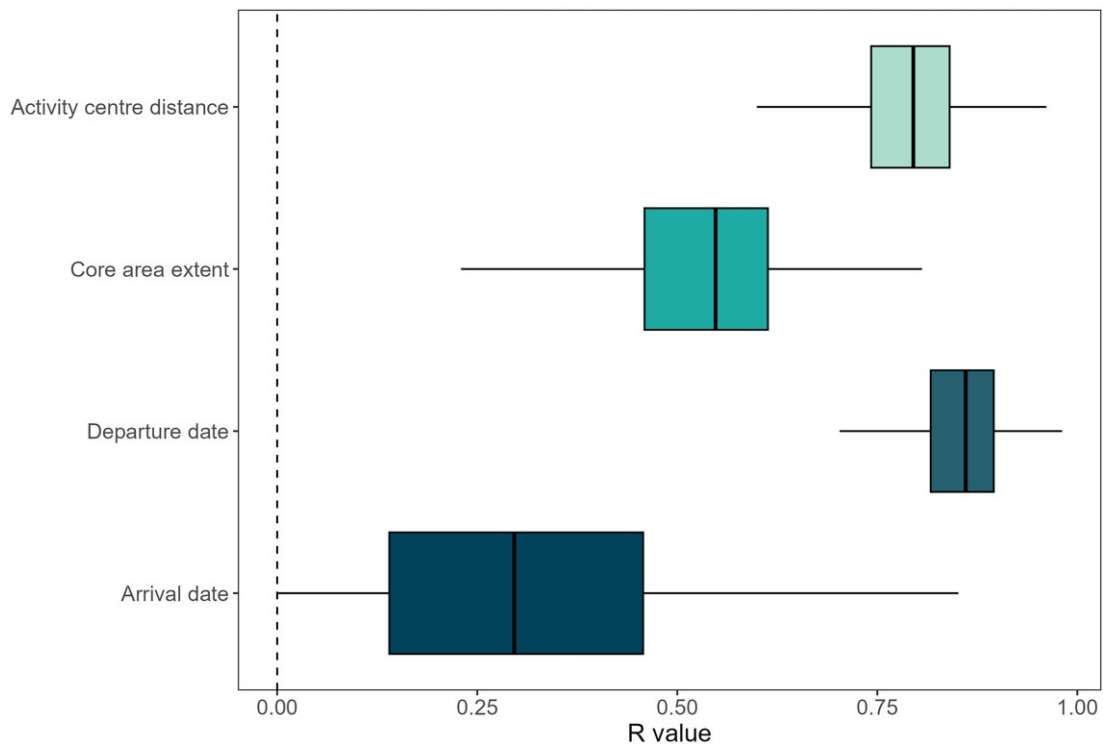
## Acknowledgements

This research made use of data sourced from the European Tracking Network data portal (<https://lifewatch.be/etn/>), developed by the Flanders Marine Institute as part of the Flemish contribution to LifeWatch. Data were derived from several projects, including: Wadden Tools—Swimway Wadden Sea (SWIMWAY) (<https://www.vliz.be/en/imis?module=dataset&dasid=8030>), Van Hall Larenstein: Vissen voor verbinding (RBVV2) (<https://www.vliz.be/en/imis?module=dataset&dasid=7822>), Acoustic Ecology of Pelagic Fish Communities (APELAFICO) (<https://www.vliz.be/en/imis?module=dataset&dasid=7858>), Haringvlietdam—Rhine-Meuse Delta Acous-

tic Network (<https://www.vliz.be/en/imis?module=dataset&dasid=8639>), LifeWatch observatory—Permanent acoustic receiver network in the Western Scheldt; Array 1: Between Breskens & Vlissingen (<https://www.vliz.be/en/imis?module=dataset&dasid=5844>), LifeWatch observatory—Permanent acoustic receiver network in the Belgian Part of the North Sea bpn (<https://www.vliz.be/en/imis?module=dataset&dasid=5843>), CODEVCO (<https://www.lifewatch.be/imis?dasid=8418>), cpodnetwork (<https://www.vliz.be/en/imis?module=dataset&dasid=6550>), Fisheries Innovation for sustainable SHared INTerchannEL resources (FISH INTEL) (<https://www.vliz.be/en/imis?module=dataset&dasid=7881>), and PelFish: Sustain-



**Figure 7.** Repeated measurements of space use for individual sea bass (*Dicentrarchus labrax*) (depicted by each line) during consecutive years of summer residence in the Wadden Sea. (a) Maximum extent between receivers in the 90% core area examined per individual across years. (b) Pairwise distance between core area centres, compared across groups of 2–3 years.



**Figure 8.** Individual repeatability in migration timing (arrival and departure dates) and space use (extent of 90% core areas and distance between activity centres) for sea bass (*Dicentrarchus labrax*) detected over multiple years in the Wadden Sea.

able economic carriers in Flemish coastal fishing communities post-Brexit (<https://www.vliz.be/en/imis?module=dataset&david=8373>).

For help with the SWIMWAY array, we thank Rijkswaterstaat personnel, Arjen Ponger, and crews of the Terschelling and Waddenstroom, as well as Hans Verdaat, Olvin van Keeken, and members of Wageningen Marine Research and NIOZ. Thanks also to Jan Geertsema, Barbera Rodenburg, and their crew, Niels Brevé of Sportvisserij Nederland, and the NIOZ fyke team, including Anieke van Leeuwen, Dennis Mosk, Robert Twijnstra, and Luc de Monte for aid in fishing

activities. Thank you to Gala van der Meer, Samantha Popma, and Sofia Mayorga Paz for assistance in the field, and to the journal editor and anonymous reviewers for their feedback.

### Author contributions

Jena E. Edwards (Conceptualization [equal], Data curation [lead], Formal analysis [lead], Methodology [equal], Visualization [lead], Writing – original draft [lead]), Allert Imre Bijleveld (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Supervision [equal], Writing – re-

view & editing [equal]), Anthonie D. Buijse (Conceptualization [equal], Supervision [equal], Writing – review & editing [equal]), Peter Davies (Data curation [equal], Writing – review & editing [equal]), Alice Elizabeth Hall (Data curation [equal], Writing – review & editing [equal]), Jeroen Huisman (Data curation [equal], Writing – review & editing [equal]), Inge van der Knaap (Data curation [equal], Writing – review & editing [equal]), Melanie P. Meijer zu Schlochtern (Data curation [equal], Writing – review & editing [equal]), Jan Reubens (Data curation [equal], Writing – review & editing [equal]), Emma Victoria Sheehan (Data curation [equal], Writing – review & editing [equal]), thomas stamp (Data curation [equal], Writing – review & editing [equal]), Hendrik V. Winter (Conceptualization [equal], Data curation [equal], Methodology [equal], Supervision [lead], Writing – review & editing [equal]).

## Supplementary data

Supplementary data is available at *ICES Journal of Marine Science* online.

**Conflict of interest:** The Authors declare that there is no conflict of interest.

## Funding

Funding for this study was provided by Waddenfonds, Rijkswaterstaat, the provinces of North Holland, Friesland, and Groningen, and the Dutch Ministry of Agriculture, Nature, and Food Quality as part of the Waddentools Swimway Wadden Sea project. Funding bodies were responsible for facilitation of ship-based fieldwork necessary for our data collection.

## Data availability

The datasets generated by the authors during the current study are archived and published in the NIOZ Digital Archiving System. Additional detection data were sourced from the database of the European Tracking Network data portal: (<http://www.lifewatch.be/etn/>), developed by the Flanders Marine Institute as part of the Flemish contribution to LifeWatch.

## References

- Appert C, Udyawer V, Simpfendorfer CA *et al.* Use, misuse, and ambiguity of indices of residence in acoustic telemetry studies. *Marine Ecology Progress Series* 2023;714:27–44. <https://doi.org/10.3354/meps14300>
- Baptist MJ, van der Wal JT, Folmer EO *et al.* An ecotope map of the trilateral Wadden Sea. *J Sea Res* 2019;152:101761. <https://doi.org/10.1016/j.seares.2019.05.003>
- Bates D, Mächler M, Bolker B *et al.* Fitting linear mixed-effects models using lme4. *J Stat Softw* 2015;67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Berthold P. *Bird Migration: A General Survey*. online edn. Oxford Academic: Oxford University Press, 2001. <https://doi.org/10.1093/oso/9780198507864.001.0001>
- Bierman SM, van Overzee HMJ, Van der Hammen T *et al.* *Kennisdocument Zeebaars*. IJmuiden: IMARES, 2010.
- Bolle LJ, Neudecker T, Vorberg R *et al.* Trends in Wadden Sea Fish Fauna Part I : trilateral Cooperation. 2009
- Boom MP. Rewarding round-trips or tiresome travels?: comparing migratory and non-migratory lifestyles in barnacle geese. 2022
- Brönmark C, Hulthén K, Nilsson PA *et al.* There and back again: migration in freshwater fishes. *Can J Zool* 2014;92:467–79. <https://doi.org/10.1139/cjz-2012-0277>
- Brönmark C, Skov C, Brodersen J *et al.* Seasonal Migration Determined by a Trade-Off between Predator Avoidance and Growth. *PLoS One* 2008;3:e1957. <https://doi.org/10.1371/journal.pone.0001957>
- Brooks ME, Kristensen K, Van Benthem KJ *et al.* glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 2017;9:378. <https://doi.org/10.32614/RJ-2017-066>
- Brownscombe JW, Griffin LP, Morley D *et al.* Spatial-temporal patterns of Permit (*Trachinotus falcatus*) habitat residency in the Florida Keys, USA. *Environ Biol Fishes* 2023;106:419–31. <https://doi.org/10.1007/s10641-022-01332-7>
- Cardoso JFMF, Freitas V, Quilez I *et al.* The European sea bass *Dicentrarchus labrax* in the Dutch Wadden Sea: from visitor to resident species. *Journal of the Marine Biological Association of the United Kingdom* 2015;95:839–50. <https://doi.org/10.1017/S002531541401714>
- Chapman BB, Hulthén K, Blomqvist DR *et al.* To boldly go: individual differences in boldness influence migratory tendency. *Ecol Lett* 2011;14:871–6. <https://doi.org/10.1111/j.1461-0248.2011.01648.x>
- Cochran JEM, Braun CD, Cagua EF *et al.* Multi-method assessment of whale shark (*Rhincodon typus*) residency, distribution, and dispersal behavior at an aggregation site in the Red Sea. *PLoS One* 2019;14:e0222285. <https://doi.org/10.1371/journal.pone.0222285>
- Common Wadden Sea Secretariat. *Report on the State of Conservation of the World Heritage Property “The Wadden Sea (N1314)”*. Wilhelmshaven, Germany, 2016.
- Crossin GT, Heupel MR, Holbrook CM *et al.* Acoustic telemetry and fisheries management. *Ecol Appl* 2017;27:1031–49. <https://doi.org/10.1002/eap.1533>
- de Jonge VN, Essink K, Boddeke R. The Dutch Wadden Sea: a changed ecosystem. *Hydrobiologia* 1993;265:45–71. <https://doi.org/10.1007/BF00007262>
- de Pontual H, Lalire M, Fablet R *et al.* New insights into behavioural ecology of European seabass off the West Coast of France: implications at local and population scales. *ICES J Mar Sci* 2019;76:501–15. <https://doi.org/10.1093/icesjms/fsy086>
- de Pontual H, Ngo T-T, Lalire M *et al.* Understanding the spatial dynamics of European sea bass: new insights on seasonal migration patterns from electronic tagging off the coast of west Brittany. 2013:2008–9.
- Doyle TK, Haberland D, Clohessy J *et al.* Localised residency and inter-annual fidelity to coastal foraging areas may place sea bass at risk to local depletion. *Sci Rep* 2017;7:45841. <https://doi.org/10.1038/srep45841>
- Edwards JE, Buijse AD, Winter HV *et al.* Gone with the wind: environmental variation influences detection efficiency in a coastal acoustic telemetry array. *Animal Biotelemetry* 2024;12:21. <https://doi.org/10.1186/s40317-024-00378-x>
- Edwards JE, Buijse AD, Winter HV *et al.* Seasonal coastal residency and large-scale migration of two grey mullet species in temperate European waters. *Movement Ecology* 2025;13:2. <https://doi.org/10.1186/s40462-024-00528-z>
- Ersoy S, Groothuis TGG, Piersma T *et al.* When slow explorers are fast: personality-related differences in timing of migration in Red Knots (*Calidris canutus*). *Ibis* 2024;166:1146–56. <https://doi.org/10.1111/ibi.13308>
- European Market Observatory for Fisheries and Aquaculture Products (EUMOFA). *Commercial and Recreational Fisheries for Wild Seabass in the Atlantic, Economic and Market Study*. Luxembourg: EUMOFA Publications Office of the European Union, 2021
- Fritsch M, Morizur Y, Lambert E *et al.* Assessment of sea bass (*Dicentrarchus labrax*, L.) stock delimitation in the Bay of Biscay and the English Channel based on mark-recapture and genetic data. *Fish Res* 2007;83:123–32. <https://doi.org/10.1016/j.fishres.2006.09.002>

- Froese R, Pauly D. eds, *FishBase. World Wide Web electronic publication*. 2023. [www.fishbase.org](http://www.fishbase.org)(version 03/2023).
- Goossens J, Villagra D, De Putter G *et al.* Fisheries measures protect European seabass groups with distinct habitat use differently. *ICES J Mar Sci* 2023;80:1899–910. <https://doi.org/10.1093/icesjms/fsad116>
- Goossens J, Woillez M, Wright S *et al.* Elucidating the migrations of European seabass from the southern north sea using mark-recapture data, acoustic telemetry and data storage tags. *Sci Rep* 2024;14:13180. <https://doi.org/10.1038/s41598-024-63347-7>
- Hartig F. DHARMA: residual Diagnostics for Hierarchical (Multi-Level /Mixed). 2024
- Holden MJ, Williams T. the Biology, Movements and Population Dynamics of Bass, *Dicentrarchus Labrax*, in English waters. *Journal of the Marine Biological Association of the United Kingdom* 1974;54:91–107. <https://doi.org/10.1017/S0025315400022098>
- Hulthén K, Chapman BB, Nilsson PA *et al.* Timing and synchrony of migration in a freshwater fish: consequences for survival. *J Anim Ecol* 2022;91:2103–12.
- ICES. *Report of the Inter-Benchmark Protocol on New Species (Turbot and Sea Bass; IBPNew 2012), 1–5 October 2012*. Copenhagen, Denmark: ICES Expert Group reports (until 2018), 2012.
- ICES. *Stock annex: Seabass (Dicentrarchus labrax) in division 4. b–c, 7. a, and 7. d–h (central and southern North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea)*. Denmark: ICES Copenhagen, 2018.
- ICES. *Sea Bass (Dicentrarchus Labrax) in Divisions 4.b–c, 7.a, and 7.d–h (Central and Southern North Sea, Irish Sea, English Channel, Bristol Channel, and Celtic Sea)*. ICES Advice: Recurrent Advice, 2022.
- Jager Z, Bolle LJ, Neudecker T *et al.* Trends in Wadden Sea Fish Fauna, Part I: trilateral Cooperation. 2009
- Jørgensen C, Dunlop ES, Opdal AF *et al.* The Evolution of Spawning Migrations: state Dependence and Fishing-Induced Changes. *Ecology* 2008;89:3436–48. <https://doi.org/10.1890/07-1469.1>
- Kennedy M, Fitzmaurice P. The Biology Of The Bass, *Dicentrarchus Labrax*, In Irish Waters. *Journal of the Marine Biological Association of the United Kingdom* 1972;52:557–97. <https://doi.org/10.1017/S0025315400021597>
- Kraft S, Gandra M, Lennox RJ *et al.* Residency and space use estimation methods based on passive acoustic telemetry data. *Movement Ecology* 2023;11:12. <https://doi.org/10.1186/s40462-022-00364-z>
- Le Luherne E, Daverat F, Woillez M *et al.* Coupling natural and electronic tags to explore spawning site fidelity and natal homing in northeast Atlantic European seabass. *Estuarine Coastal Shelf Sci* 2022;278:108118. <https://doi.org/10.1016/j.ecss.2022.108118>
- Merkle JA, Abrahams B, Armstrong JB *et al.* Site fidelity as a maladaptive behavior in the Anthropocene. *Frontiers in Ecology and the Environment* 2022;20:187–94. <https://doi.org/10.1002/fee.2456>
- Olsson IC, Greenberg LA, Bergman E *et al.* Environmentally induced migration: the importance of food. *Ecol Lett* 2006;9:645–51. <https://doi.org/10.1111/j.1461-0248.2006.00909.x>
- Özgül A, Birnie-Gauvin K, Abecasis D *et al.* Tracking aquatic animals for fisheries management in European waters. *Fisheries Management and Ecology* 2024;31:e12706.
- Pawson MG, Brown M, Leballeur J *et al.* Will philopatry in sea bass, *Dicentrarchus labrax*, facilitate the use of catch-restricted areas for management of recreational fisheries? *Fish Res* 2008;93:240–3. <https://doi.org/10.1016/j.fishres.2008.03.002>
- Pawson MG, Kelley DF, Pickett GD. The distribution and migrations of bass, *Dicentrarchus labrax* L., in waters around England and Wales as shown by tagging. *Journal of the Marine Biological Association of the United Kingdom* 1987;67:183–217. <https://doi.org/10.1017/S0025315400026448>
- Pawson MG, Pickett GD, Leballeur J *et al.* Migrations, fishery interactions, and management units of sea bass (*Dicentrarchus labrax*) in Northwest Europe. *ICES J Mar Sci* 2007;64:332–45. <https://doi.org/10.1093/icesjms/fsl035>
- Quayle VA, Righton D, Hetherington S *et al.* Observations of the Behaviour of European Sea Bass (*Dicentrarchus labrax*) in the North Sea. *Tagging and Tracking of Marine Animals with Electronic Devices*. 2009 103–19.
- R Core Team. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing, 2023.
- Reséndiz-Infante C, Gauthier G. Temporal changes in reproductive success and optimal breeding decisions in a long-distance migratory bird. *Sci Rep* 2020;10:22067. <https://doi.org/10.1038/s41598-020-78565-y>
- Reubens J, Aarestrup K, Meyer C *et al.* Compatibility in acoustic telemetry. *Animal Biotelemetry* 2021;9:33. <https://doi.org/10.1186/s40317-021-00253-z>
- Robinet T, Roussel V, Cheze K *et al.* Spatial gradients of introgressed ancestry reveal cryptic connectivity patterns in a high gene flow marine fish. *Mol Ecol* 2020;29:3857–71. <https://doi.org/10.1111/mec.15611>
- Stamp T, Clarke D, Plenty S *et al.* Identifying juvenile and sub-adult movements to inform recovery strategies for a high value fishery—European bass (*Dicentrarchus labrax*). *ICES J Mar Sci* 2021;78:3121–34. <https://doi.org/10.1093/icesjms/fsab180>
- Stoffel MA, Nakagawa S, Schielzeth H. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. S Goslee (ed.). *Methods Ecol Evol* 2017;8:1639–44. <https://doi.org/10.1111/2041-210X.12797>
- Tulp I, Bolle A, Dänhardt A *et al.* *Fish. Wadden Sea Quality Status Report 2017*. Wilhelmshaven, Germany: Common Wadden Sea Secretariat, 2017
- Tulp I, Bolle LJ, Rijnsdorp AD. Signals from the shallows: in search of common patterns in long-term trends in Dutch estuarine and coastal fish. *J Sea Res* 2008;60:54–73. <https://doi.org/10.1016/j.seares.2008.04.004>
- UNESCO. *Operational Guidelines for the Implementation of the World Heritage Convention*. UNESCO, Paris, 2023
- van Aken HM. Variability of the water temperature in the western Wadden Sea on tidal to centennial time scales. *J Sea Res* 2008;60:227–34. <https://doi.org/10.1016/j.seares.2008.09.001>
- van der Veer HW, Dapper R, Henderson PA *et al.* Changes over 50 years in fish fauna of a temperate coastal sea: degradation of trophic structure and nursery function. *Estuarine Coastal Shelf Sci* 2015;155:156–66. <https://doi.org/10.1016/j.ecss.2014.12.041>
- van der Veer HW, Koot J, Aarts G *et al.* Long-term trends in juvenile flatfish indicate a dramatic reduction in nursery function of the Balgzand intertidal, Dutch Wadden Sea. *Marine Ecology Progress Series* 2011;434:143–54. <https://doi.org/10.3354/meps09209>
- van der Veer HW, Tulp I, Witte JI *et al.* Changes in functioning of the largest coastal North Sea flatfish nursery, the Wadden Sea, over the past half century. *Marine Ecology Progress Series* 2022;693:183–201. <https://doi.org/10.3354/meps14082>
- van Walraven L, Dapper R, Nauw JJ *et al.* Long-term patterns in fish phenology in the western Dutch Wadden Sea in relation to climate change. *J Sea Res* 2017;127:173–81. <https://doi.org/10.1016/j.seares.2017.04.001>
- Zimmerman JTF. Mixing and flushing of tidal embayments in the western Dutch Wadden Sea part I: distribution of salinity and calculation of mixing time scales. *Neth J Sea Res* 1976;10:149–91. [https://doi.org/10.1016/0077-7579\(76\)90013-2](https://doi.org/10.1016/0077-7579(76)90013-2)

Handling editor: Caroline Durif