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European plaice movements show evidence of high residency, site fidelity, and feeding around hard substrates within an offshore wind farm

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Offshore wind farms (OWFs) are expanding rapidly in the North Sea, often creating spatial conflicts with fisheries. Managing such conflicts requires knowledge on the impact of OWFs on the spatial distribution and movement behaviour of fished species. However, such knowledge is still lacking, especially for soft sediment fish such as flatfish, which are vital fisheries resources in the region. Therefore, we used acoustic telemetry to examine the spatial behaviour of European plaice in relation to an OWF and its structures. In a small study area (1.37 km^2), we observed high residency for plaice around the turbines and scour protection layer (SPL), which consists of large rocks around the turbine foundation. The fish primarily resided on sandy sediments near the hard substrates, but showed a diurnal pattern of proximity to the turbine, being closer during the day. Considering their trophic ecology, these findings suggest that plaice moves towards the SPL for feeding opportunities on the hard substrate, potentially leading to increased ecological fish production within OWFs. Although most plaice moved away from the OWF in winter, likely towards spawning grounds, many exhibited high site fidelity returning to the study area after the winter migration. OWFs thus offer protection from fishing mortality as "closed" feeding grounds in spring and summer, but not during winter spawning migrations, which may result in spillover effects. These insights should inform local fisheries management in relation to plaice movement within and around OWFs.

Keywords: acoustic telemetry, artificial reef effect, diurnal patterns, tagging, yaps.

Introduction

Offshore wind power is rapidly expanding in the North Sea region to meet renewable energy targets and to achieve climate neutrality by 2050 in the EU (European Commission, 2019; WindEurope, 2022). A total of 5785 turbines distributed across 122 offshore wind farms (OWFs) already supplied 28.3 GW of power to 12 European countries by the end of 2021 (WindEurope, 2022). Current projections indicate that OWFs will cover ~10% of the total surface area of the North Sea basin by 2040 (EMODnet, 2022). These developments frequently give rise to spatial conflicts with fisheries, since the majority of OWFs prohibit any fishing activities within their boundaries due to safety concerns. As such, fishers have to relocate towards other areas, which might lead to local overfishing (Stelzenmüller *et al.*, 2021).

On the other hand, the development of offshore wind farms (OWFs) introduces hard substrates into predominantly soft-sediment environments, which may influence fished species (Gill *et al.*, 2020). To date, no significant negative effects of OWFs on fish have been identified (Langhamer *et al.*, 2009; Leonhard *et al.*, 2011; Lindeboom *et al.*, 2011; Wilhelmsson and Langhamer, 2014; Stenberg *et al.*, 2015; Wilber *et al.*, 2022). On the contrary, the cessation of fishing activities within OWFs has led to the conclusion that these areas offer refuge to commercially exploited species, comparable to the functioning of marine protected areas (Fenberg *et al.*, 2012; Halouani *et al.*, 2020). Furthermore, the presence of hard substrates, such as turbine foundations and surrounding SPLs, have been found to attract various fish and other motile invertebrates such as crabs and lobsters (Reubens *et al.*, 2011; Wilhelmsson and Langhamer, 2014; Krone *et al.*, 2017). This phenomenon is known as the artificial reef effect and is attributed to increased food and/or shelter opportunities (Degraer *et al.*, 2020). While this effect is evident for species typically associated with hard substrates, its impact on soft-sediment fish species, such as flatfish, is less understood.

Plaice *Pleuronectes platessa* is common in the North Sea and is the most fished flatfish species in terms of volume (Gibson *et al.*, 2015; Polet *et al.*, 2022). They exhibit large-scale migrations from their feeding grounds, where they reside during spring, summer, and early autumn, to various spawning locations during winter (December–March) (Rijnsdorp, 1989; Gibson, 1997). The main spawning areas of plaice are located in deeper waters in the North Sea, English Channel, and Irish Sea (Ellis *et al.*, 2012). A mark–recapture study off the Icelandic coast demonstrated high site-fidelity of plaice towards both feeding and spawning areas, as fish were recaptured only hundreds of metres away from their original release location several years later (Solmundsson *et al.*, 2005). Moreover, catch rates of plaice using bottom trawls are higher during the day,

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particularly in the southern North Sea, which is coupled to their feeding behaviour (Gibson *et al.*, 2015). Plaice primarily depend on visual cues, in addition to chemical signals, to locate their prey within the sediment. Consequently, feeding activities are mainly restricted to daylight hours when they swim short distances in search for food, while maintaining contact with the seabed. As such, they are more vulnerable to be caught by bottom trawling gear during daytime, when they are actively foraging. During nighttime, plaice mobility increases and is reflected in increased swimming activity higher in the water column (Verheijen and De Groot, 1967). Hence, the trawl may pass beneath the fish as they swim higher up in the water column. The daytime feeding pattern is also reflected in their stomach contents, with maximum stomach fullness in the early evening, gradually emptying during night and a recommencing of feeding a few hours before sunrise (De Groot, 1971).

Some studies suggested that flatfish avoid the SPL or remain unaffected by its presence (Krone *et al.*, 2017; van Hal *et al.*, 2017). In contrast, a more recent study indicated a clear attraction effect of plaice *Pleuronectes platessa* towards the SPL in a Belgian wind farm, attributed to the more open organization of the stone blocks and the presence of sandy patches within the SPL (Buyse *et al.*, 2021). Subsequent analysis of the trophic ecology revealed that plaice exhibited distinct dietary patterns on the SPL (both on the short and long term) compared to fish residing on the soft sediment (Buyse *et al.*, 2022, 2023). These observations suggest that certain plaice actively utilize the SPL as a feeding ground, although it remains unclear how much time plaice spends on the SPL, and whether they solely use the SPL for foraging or also as shelter from predators and currents.

To accurately assess the potential effects of OWFs on fished species, it is imperative to understand the small- and large-scale spatial behaviour of the target species in relation to the OWF area. An investigation of fish individual spatial movements around artificial structures within OWFs provides valuable insights into the role these hard structures play for the species (Winter *et al.*, 2010; Reubens *et al.*, 2013; Mitamura *et al.*, 2021). Moreover, the protective capacity of a closed area can change depending on the large-scale movement behaviour of a fished species (Miethe *et al.*, 2010). For example, fish that frequently move in and out of the OWF may derive fewer benefits from its potential protection compared to fish that remain within the OWF boundaries.

Acoustic telemetry is a widely used method to study the spatial movements of fish in the marine environment (Reubens *et al.*, 2013; Keller *et al.*, 2017). It has proven to be instrumental in artificial reef research, coupled to fish residency, site fidelity, and feeding behaviour (Winter *et al.*, 2010; Reubens *et al.*, 2013, 2014; Mitamura *et al.*, 2021). Acoustic telemetry has also been successfully employed to assess the effectiveness of marine protected areas for fish and to explore the potential spillover to adjacent areas (Abecasis *et al.*, 2014; Novak *et al.*, 2020; Villegas-Ríos *et al.*, 2021; Goossens *et al.*, 2023a). In the current study, we used acoustic telemetry to investigate the small and large-scale spatial movements of plaice in relation to an OWF in the Belgian part of the North Sea (BPNS). Specifically, the study aimed (i) to assess plaice residency within the OWF, (ii) to analyse their small-scale movement patterns on and near the SPL, and (iii) to examine their site fidelity to the OWF after their yearly spawning migrations.

Material and methods

Study site

This study was conducted within the Belwind OWF (51° 39′ 36″ N, 2° 48′ 0″ E) in the Belgian part of the North Sea (Figure 1). Belwind is situated on the Bligh Bank, a natural sandbank located 40 km off the Belgian coastline, at depths ranging from 15 to 37 m. The construction of the wind farm commenced in 2009 and involved the installation of 55 turbines (Vestas, 3 MW) on monopile foundations with a diameter of 5 m, spaced at distances of 450–670 m from one another. To prevent erosion of the surrounding sand, an SPL was added around each turbine foundation in a radius of 16.5 m with a total diameter of 38 m, including the turbine. This SPL consists of a filter layer composed of pebbles and an armour layer on top, with a median rock size of 370 mm and a solid rock density of 2.65 tonnes m^{-3} (Coates *et al.*, 2016). In most locations, especially between 5 m from the turbine foundations and the edge of the SPL, there are sandy patches present between the rocks of the armour layer due to sedimentation over the years. Three months before construction started, the entire concession zone, including a 500-m safety perimeter, was closed permanently for all vessel traffic, except for scientific and maintenance activities. In 2016, both areas north and south of Belwind were also closed off to all vessel traffic due to the construction of the neighbouring wind farm.

Receiver arrays

From May 2020 to July 2021, three different arrays of VR2AR receivers (69 kHz, InnovaSea Systems Inc., USA) were deployed during three consecutive periods in the southwestern part of the Belwind OWF (Figure 1). This area exhibits less variation in bathymetry compared to the northern part, thereby enhancing the detectability of the transmitter signals. The deployment and retrieval of all receivers was conducted by the RV Simon Stevin, using tripod moorings that were put on the seabed and subsequently retrieved utilizing an acoustic release system. The mooring setup consisted of a receiver attached to a buoy, which was then connected to both the steel tripod, through an acoustic release system, and a lengthy rope (50 m). For a detailed description of the mooring and retrieval method, see Goossens *et al.* (2020). The spatial design of the three arrays was adapted to the different research questions and objectives.

The first array (May 2020–October 2020) existed of 28 receivers and was specifically designed to assess small-scale movement patterns of plaice around the turbine foundations and on the SPL during the summer–autumn feeding period. To ensure adequate coverage for calculating fish positions based on detections, three turbines were surrounded by six receivers each, positioned ±150 m from the turbine. Additionally, ten receivers were placed on the sand further away in-between the turbines to cover a larger area (total area covered by the receivers = 1.37 km^2), in order to study the residency of plaice to that specific area of the wind farm. During the first month of this setup, a comprehensive study was carried out to assess the detection range, the relationship between the detection probability, and the distance between a transmitter and a receiver, as well as the impact of diverse environmental conditions on the detection probability (Goossens *et al.*, 2022). The model predicted that if plaice was present within the study area, its detection probability over a day was 100% up to a distance of 600 m from a receiver under average noise con-

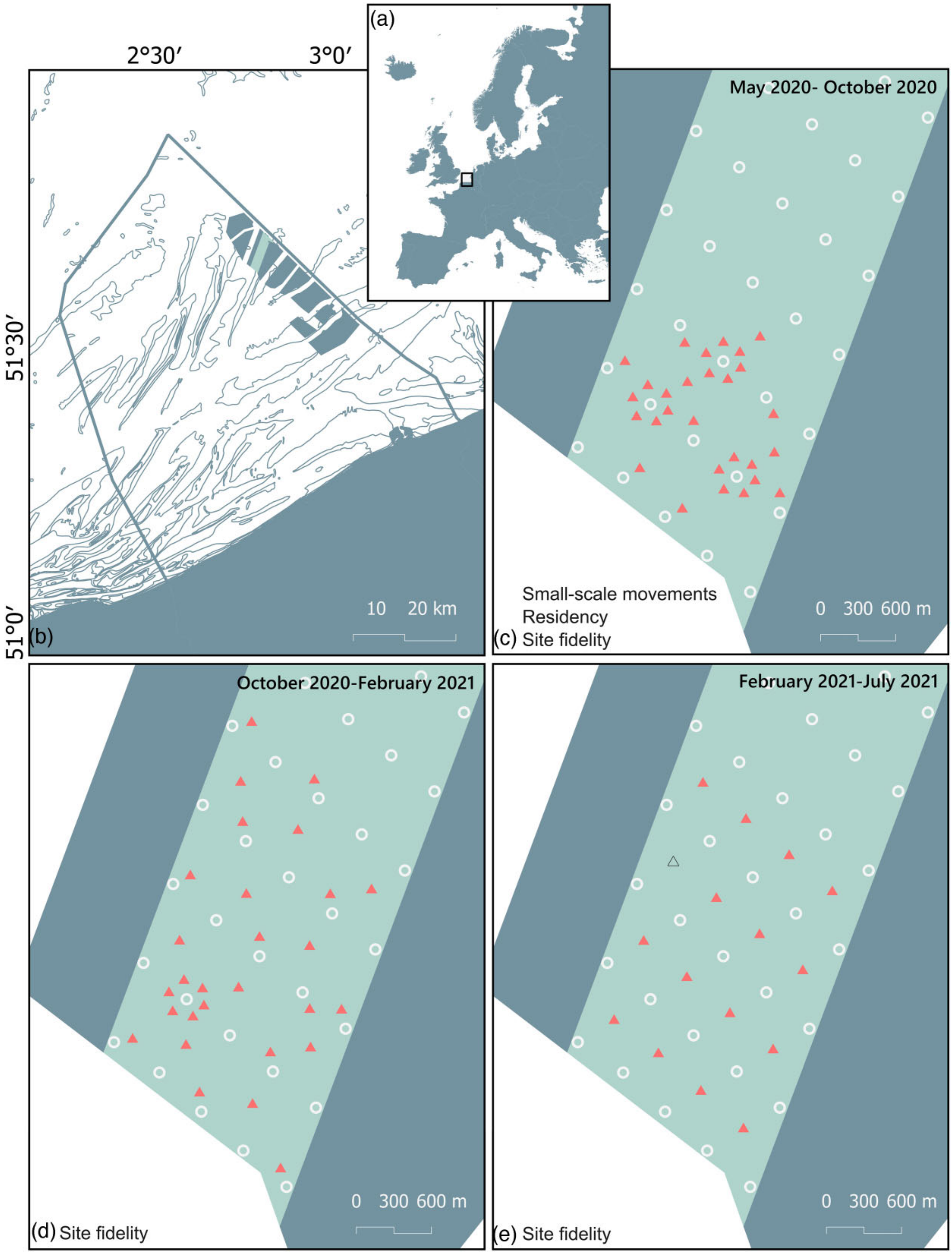

Figure 1. (a–b) Location of the Belgian EEZ (BPNS) and Belwind OWF; (c–e) spatial design of the receiver arrays during the 3 study periods: May 2020–October 2020, October 2020–February 2021, and February 2021–July 2021, respectively. Turbine locations are indicated with white open circles; deployed receivers are indicated as red triangles; and lost receiver indicated as a black open triangle.

ditions. Taking this modelled range into account, it is highly unlikely that plaice, being a slow-moving species, could be present on a certain day within the study area without being detected.

The second array (28 receivers, October 2020–February 2021) was deployed during the spawning period of plaice, primarily to investigate whether fish left the OWF and subsequently returned after spawning. As several tagged fish were still detected around turbine B9 in October 2020, the design with six receivers surrounding it was retained, while the remaining receivers were redeployed either in the middle of four turbines or in close proximity to a turbine to cover an area of ~3.73 km^2. This design facilitated the study of both small-scale movement patterns and the assessment of plaice site fidelity relative to the study area.

The third array (15 receivers, February 2021–July 2021) was also designed to monitor the potential return of individual plaice to the OWF after the spawning period, but less receivers were available and one receiver got lost during this third monitoring period. To enhance the detectability of fish upon their return in a similar area (2.56 km^2) as the second array, the available receivers were evenly distributed throughout the study area.

Tagging procedure

Thelma Biotel MP9 transmitters (69 kHz, 146 dB, 9 × 24.4 mm, 3.6 g in air, 2.1 g in water), emitting an acoustic signal that corresponds to a unique ID, were used to detect the fish in the study area. The transmitters were pre-programmed to emit an acoustic signal at intervals ranging from 70 to 130 s for the initial 200 days after activation. Afterwards, the transmission interval was adjusted to 150–210 s for the subsequent 90 days. For the remaining battery life of the transmitters, the interval was reverted back to 70–130 s. These settings were selected to optimize the battery life of the transmitters (estimated at 522 days) while maintaining the desired data resolution. The 90-day period with the longer transmission interval was timed to coincide with the spawning period of plaice, during which they were expected to have moved out of the study area.

Fish were caught using either (i) hand line fishing conducted from a research vessel or RHIB, or (ii) diving in conjunction with the utilization of a small hand net. Barbed hooks (Gamakatsu, size 1/0) were deliberately avoided to minimize tissue damage to the fish's mouth. Upon capture, the fish were transferred to an aerated water tank until the tagging procedure was conducted. Only fish in good condition and with a minimum size of 29 cm (fish had a total length ranging from 29 to 39.5 cm) were selected for tagging as this resulted in a transmitter-to-fish weight ratio of <1.5%, which is well below the recommended threshold of 2%, and ensures that the potential drag effects from the transmitter are kept to a minimum (Arnold and Holford, 1978; Thorstad *et al.*, 2000; Bégout Anras *et al.*, 2003). The tags were externally attached to the fish, which is a commonly employed tagging method for dorsoventrally compressed species with small peritoneal cavities, and causes less adverse effects in bottom-dwelling flatfish compared to internal tagging (Jepsen *et al.*, 2015; Neves *et al.*, 2018).

The tagging method used in this study is outlined in previous studies, with slight modifications to reduce fish handling time (Bridger and Booth, 2003; Hunter *et al.*, 2003a; Neves *et al.*, 2018). The tagging protocol was approved by the ethical committee of the Flanders Research Institute for Agricultural, Fisheries, and Food (ILVO) (Permit Number: EC 2020/366). The transmitters were initially secured to a stainless steel wire (0.6 mm) using a piece of heat-shrink tubing. The fish were then placed on a foam pad soaked in seawater, with a wet cloth covering the head and gills. The transmitter was attached anterior to the dorsal fin by passing two 19-gauge syringe needles (Terumo Agani) ventrally through the dorsal musculature at a distance equal to the length of the transmitter. Subsequently, both wires on each side of the transmitter were threaded through the needles, which were then removed. On the ventral side, a small rubber piece (25 × 10 × 1 mm) was affixed to the fish's skin to protect it from abrasions. Finally, both wires were secured together using a small metal fishing crimp (brass cylinder, 2 mm × 10 mm). Throughout the procedure, all wounds were disinfected using Betadine, and all equipment was sterilized with 70% ethanol beforehand. The time it took to complete the entire tagging procedure was ~3 min. Afterwards, the fish were transferred into a large, aerated holding tank and, after normal swimming behaviour was observed, the fish were carefully released as close as possible to their original catch location.

Data analysis

Once the data were retrieved from the acoustic receivers, they were scanned for potential spurious detections. A detection was considered spurious when the transmitted ID was only picked up once by a certain receiver on a given day (Meyer *et al.*, 2007; Ramsden *et al.*, 2017). Such detections were checked manually and removed when the signal was picked up by only one receiver within the network.

The site fidelity and long-term presence of plaice in relation to the Belwind OWF was analysed using the presence/absence data per day over all three receiver arrays (May 2020–July 2021). Although ID tags do not facilitate the tracking of fish beyond the confines of the study area (i.e. outside the receiver array), extended absences observed in multiple fish can suggest the occurrence of specific seasonal behaviour (e.g. absences during the spawning period, followed by regular presences after the presumed spawning strongly indicate the migration of fish outside the study area, most probably towards the spawning grounds, and a subsequent return to the studied area for feeding during spring and summer).

Residency of plaice within the study area and small-scale movement patterns around the turbines were studied using the data from the first receiver array period (May 2020–October 2020). Residency was investigated using daily binary presence/absence data of fish that were present during the summer feeding period. The residency index (RI) was calculated for each individual fish as

$$\mathrm{RI} = \text{number of days detected}/\text{days at large},$$

with days at large = last day of detection during first monitoring period—release date of the fish.

Only the data for fish that were at least 20 days at large ($n = 26$) were used to calculate the mean residency index for plaice in the study area.

Small-scale movement patterns were investigated with data from the first receiver array by estimating the positions of those fish that were detected within the study area for at least 20 days ($n = 21$). The day on which a fish was tagged and the following day were removed from the dataset to avoid any effects of the tagging procedure on their behaviour. A fine-scale positioning system was used to estimate the spatial positions of the transmitters using YAPS (Yet Another Positioning Solver), which combines a state-space model applied to the signal time of arrival (TOA) at fixed receiver positions with a random walk movement model (Baktoft *et al.*, 2017, 2019). This method was tested by applying YAPS to data originating from an acoustic transmitter that was towed within a receiver network and compared to a known track (Baktoft *et al*., 2017). This study indicated that 97% of the estimated positions were located within 1 m of the true position, and 87% within 0.5 m. YAPS was chosen over vendor-supplied software, as it was free to use, allowed for complete transparency of the data analysis, and was shown to offer better accuracy and error control than traditional models (Baktoft *et al*., 2017). The VR2AR's built-in transmitters of all the receivers were used as sentinel tags (mean transmission interval of 10 s) for the development of the synchronization model. Synchronization of the array and the validation of the model were applied using the *yaps* package in R (github.com/baktoft/yaps), following the method described in Baktoft *et al.* (2019).

After synchronization, the positions of each fish were individually estimated using the YAPS model. To enhance the effectiveness of the estimation process, each dataset was divided into 4-h bins with a 1-h shift. These overlapping bins were utilized to mitigate any potential edge effects in the modelling. The model was executed five times for each data bin, and only the output from the model with the lowest object score (similar to the Akaike Information Criterion) was retained for subsequent analyses. Furthermore, only detections registered by three or more receivers around the three turbines (each surrounded by six receivers) and located at a maximum distance of 150 m from the turbines (distance at which receivers were placed around the turbines) were retained for further analysis (Espinoza *et al*., 2011). This rigorous filtering was implemented to maximize the reliability of the estimated positions before they were employed in any subsequent analyses.

To study the level of association of plaice with the SPL, the distance of each filtered estimated position to the nearest turbine was calculated. Each position was assigned to one of nine distance intervals from the turbines (0–5, 5–10, 10–15, 15–20, 20–30, 30–40, 40–50, 50–100, and 100–150 m). For each distance interval, the (relative) number of detections was calculated by dividing the number of positions by the surface area of the distance interval. These calculations were performed both for the total number of positions over the three turbines and for each fish separately, to study whether individual preferences existed among fish.

Generalized additive mixed models (GAMMs) were used to investigate the potential relationship between the distance of the fish from the turbines and the explanatory variables that might be associated with behavioural patterns related to feeding or seeking shelter. To examine the influence of light and the potential presence of a diurnal pattern, sunlight time was used to calculate the time elapsed since sunrise (in hours) using the R package *suncalc*. Time relative to sunrise was chosen as an explanatory variable instead of the hour of the day to account for variations in daylight duration between summer and autumn months. Bottom current data were downloaded from a forecast model through the ERDAPP server, from which bottom current speed (m/s) was calculated using the Pythagorean theorem on the eastern and northern vectors (Legrand and Baetens, 2021). This tide-related variable was added to the model to test whether plaice movement was driven by tidal action, which could indicate the use of the SPL for shelter against currents or a more general tidal activity pattern. Fish ID and turbine were included as random variables to incorporate the variance related to individual fish preferences, and differences between turbine environmental conditions and SPL configuration. To fit the model, the data set was split up into a training dataset ($n = 10000$) and a test dataset ($n = 162285$), following a cross-validation approach. Three models were fitted with the *gamm4* R package using the training dataset, with one explanatory variable (either bottom current speed or time relative to sunrise) or two explanatory variables (both variables):

Distance of fish to turbine ~ s (time relative to sunrise, bs = "cs") + s (bottom current speed, bs = "cs"), random = ~ (1| Fish ID) + (1| turbine)
Distance of fish to turbine ~ s (time relative to sunrise, bs = "cs"), random = ~ (1| Fish ID) + (1| turbine)
Distance of fish to turbine ~ s (bottom current speed, bs = "cs"), random = ~ (1| Fish ID) + (1| turbine)

The performance of each model was assessed by calculating the root mean square error (RMSE) between the predicted values from the model and the true values from the test dataset. The model with the simplest structure and the lowest RMSE was chosen as the final model. Subsequently, a visual validation of the model was conducted by examining the residuals. Distance calculations were carried out in QGIS version 3.30.3, while all other calculations and analyses were performed in R version 4.3.0 (R Core Team, 2022).

Results

A total of 31 fish were tagged over the course of the study period, of which 29 during the first study period and 2 during the second study period. From May 2020 to July 2021, the tagged plaice were registered 1724759 times within the Belwind network and only 28 times by other receiver networks. While no spurious detections were identified within the Belwind network, 24 out of the 28 detections on other networks were deemed erroneous and consequently removed.

Residency time

During the first study period (May 2020–October 2020, spanning 150 days), the 29 tagged fish were identified as being present for a duration ranging from 1 to 131 days (Table 1). Many fish remained within the study area for extended uninterrupted periods during the summer and autumn months, with the majority still present at the end of the first study period (Figure 2). Three fish (ID 9257, 9258, and 9262) were only detected for a few days after their release and were not detected thereafter. One fish was captured by a commercial fishing vessel in April 2021, but it was not possible to ascertain its identity or exact capture location.

For the fish that were at least 20 days at large during the first period ($n = 26$), residency values ranged from 0.09 to 1, with an average residency of 0.78 ± 0.23 *SD* (Table 1). Most fish displayed high residency, with 70% of the fish having a residency index of 0.75 or higher.

Small-scale movement patterns around the turbines

A total of 824176 fish positions (21 fish) were estimated within the study area, of which 172285 were withheld for further analyses (Figure 3; see online Supplementary Material for detailed filtering of the detections). The positions had an average standard deviation of 5.1 m for the *x*-coordinate and 4.9 m for the *y*-coordinate. Plaice individuals were observed at a mean distance of 92 ± 48 (*SD*) m from the turbines, with most detections occurring on the sand directly surrounding

Table 1. Summary of the metadata and residency data for the 31 tagged plaice individuals.

Fish ID	Release date	Last detected	Capture method	Capture/Release location	Length (cm)	Total days detected	RI (May–Oct)	Days at large (May–Oct)
T9246	15/05/2020	28/09/2020	Angling	SPL D09	32	131	0.96	137
T9247	15/05/2020	11/11/2020	Angling	SPL C08	29	62	0.82	74
T9248	19/06/2020	19/11/2020	Angling	SPL C08	34	135	0.95	115
T9249	15/09/2020	7/10/2020	Angling	SPL C09	32	15	0.65	23
T9250	17/06/2020	10/07/2021	Diving	SPL C08	32	195	0.98	117
T9251	19/06/2020	14/11/2020	Angling	SPL B09	38.5	149	1.00	115
T9255	14/07/2020	11/07/2021	Angling	SPL C08	34.5	192	0.94	90
T9256	14/07/2020	25/03/2021	Angling	SPL C08	39.5	98	0.97	74
T9257	17/10/2020	18/10/2020	Angling	SPL C08	36	2		
T9258	15/09/2020	19/09/2020	Angling	SPL D09	33	5	1.00	5
T9259	14/08/2020	4/07/2021	Angling	Sand near B09	31	282	1.00	59
T9260	19/06/2020	20/06/2021	Angling	SPL B09	34	250	1.00	115
T9262	17/10/2020	21/10/2020	Angling	SPL C08	31	5		
T9263	17/06/2020	24/03/2021	Angling	SPL D09	34.5	151	0.65	117
T9264	16/06/2020	8/12/2020	Diving	SPL B09	35	92	0.61	117
T9265	17/06/2020	10/11/2020	Angling	SPL D09	34.5	100	1.00	97
T9268	10/09/2020	22/02/2021	Angling	Sand near E08	32.5	2	0.20	5
T9269	15/09/2020	11/07/2021	Angling	SPL D08	39	98	0.78	27
T9272	17/06/2020	23/03/2021	Angling	SPL D09	34.5	244	0.89	116
T9273	17/06/2020	13/12/2020	Angling	SPL D09	35	82	1.00	45
T9274	16/06/2020	20/06/2021	Diving	SPL B09	30	156	0.97	118
T9275	15/09/2020	15/06/2021	Angling	SPL D08	33.5	38	0.12	25
T9276	16/06/2020	4/07/2021	Diving	SPL B09	31.5	40	1.00	1
T9277	17/06/2020	11/07/2021	Angling	SPL D09	37.5	180	0.68	117
T9279	13/08/2020	21/12/2020	Angling	SPL D09	33	67	0.29	55
T9280	10/09/2020	10/07/2021	Angling	SPL C09	31.5	179	0.97	32
T9281	17/06/2020	29/09/2020	Diving	SPL C08	32	103	0.98	105
T9282	19/06/2020	31/10/2020	Angling	SPL B09	32.5	135	1.00	115
T9283	17/06/2020	12/08/2020	Angling	SPL B09	36	5	0.09	57
T9284	14/07/2020	20/06/2021	Angling	SPL C08	35	127	0.77	90
T9285	17/06/2020	06/08/2020	Angling	Sand between row B and C	33	11	0.22	51

The residency index (RI) and the days at large are based on the data of the first receiver array from May to October 2020. No RI was calculated for the two fish tagged in October 2020.

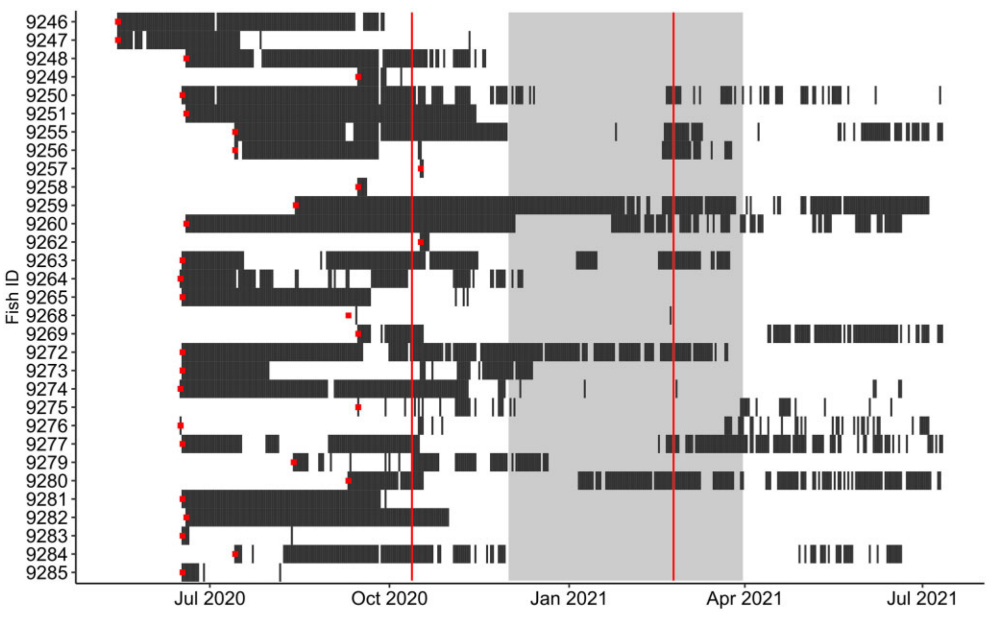

Figure 2. Presence by day of the 31 tagged plaice individuals over all study periods (15/05/2020–11/07/2021) in the Belwind OWF. Red squares indicate the tagging and release dates of the fish. The red vertical lines show the change in receiver array design: study period 1: 15/05/2020–11/10/2020; period 2: 14/10/2020–22/02/2021; and period 3: 25/02/2021–11/07/2021. The grey box represents the yearly spawning period for plaice in the southern North Sea (December–March). A fish was considered to be present in the study area if it was at least detected two times on that particular day.

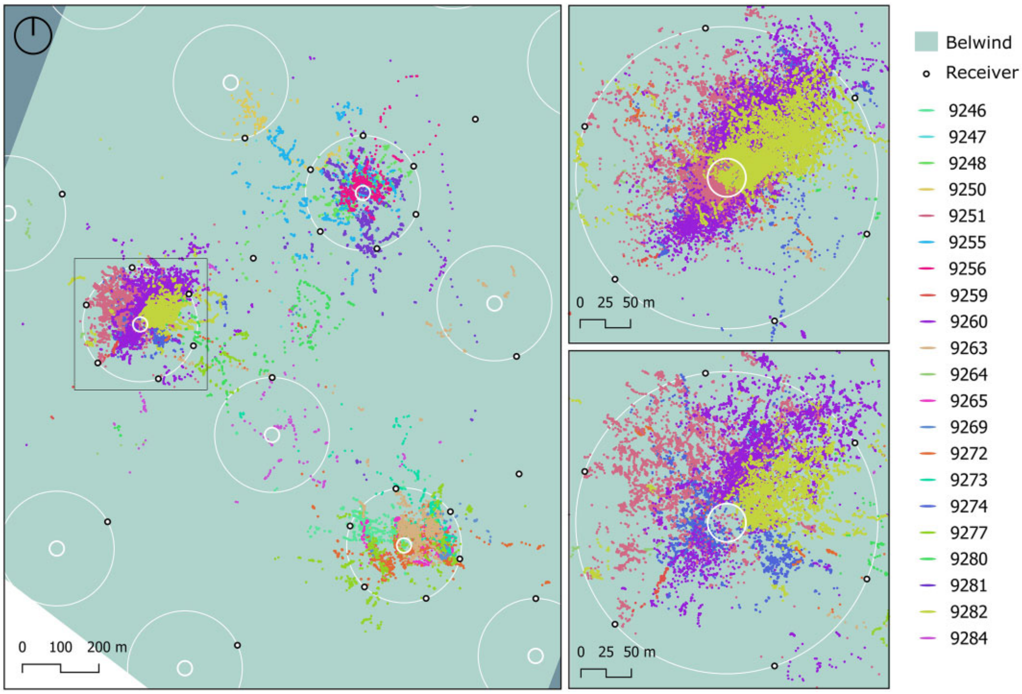

Figure 3. All estimated positions for the 21 fish that were present at least 20 days during the first study period (May 2020–October 2020) and the estimated positions during day- and nighttime around the B9 turbine (see the online Supplementary Material for the day–night comparisons for turbines C8 and D9). The large white circles represent a distance of 150 m around the turbines, while the smaller white circles represent an approximation of the extent of the SPL (16.5 m radius). Each colour represents the position of a different fish. There are fewer detections during nighttime, because night was defined as the period from sunset to sunrise and was considerably shorter than daytime during summer.

the SPL (±25 m from the turbine, SPL extends ~16.5 m from the turbine), and gradually decreasing with a second smaller peak of detections at a distance of 90 m from the turbines (Figure 4).

The distance of plaice from a turbine was best explained by the GAMM with time relative to sunrise as an explanatory variable (see online Supplementary Material for the model output). The model identified a diurnal pattern in the distance of fish to the turbine, with fish being closer during daylight hours compared to nighttime (time relative to sunrise smoother, $F = 1.08$, edf = 8.4, $p < 0.001$). The effective degrees of freedom (edf) reported here is a summary statistic used in generalized additive modelling and reflects the nonlinearity of the relationship (an edf value of 1 indicates a linear relationship; Chiang, 2007; Hunsicker *et al.*, 2016). During the day, the highest density of detections was found on or near the SPL (<15 m from the turbine), while at night, the highest density was found on the surrounding sand (Figures 3–5).

Site fidelity and long-term spatial movements of plaice

Of the 31 fish, 11 were detected after 1 year, and 7 fish were detected within the study area until the final 2 weeks of the study. Significant fewer detections were made in the study area during the winter months (Figure 2). Several fish (9250, 9255, 9256, 9260, 9269, 9275, 9277, 9280, and 9284) were absent for consecutive months, which coincided with the spawning period of plaice (December–March), after which they returned to the study area during spring. One fish (9277) that was tagged on 23/05/20 remained within the wind farm until 16/10/20, with two periods of absence during the first study period. After being completely absent for more than 111 days, fish 9277 was detected twice on 5/02/21 at another receiver station in the western part of the Belgian part of the North Sea (bpns-Westhinder–51° 22′ 52“ N, 2° 27′ 10” E), and 11 days later, it was re-detected at the end of the second study period within the Belwind OWF array and remained present until the end of the third study period (17/07/21).

Discussion

By using acoustic telemetry, we showed that plaice are highly resident to a small area within a Belgian offshore wind farm (OWF) during the summer–autumn feeding period. Plaice remain relatively close to the turbines with most detections occurring on the sand directly surrounding the SPL ±25 m from the turbine foundations. Tagged fish also exhibited clear diurnal spatial movements with fish being detected significantly more during daytime on the SPL compared to the surrounding sand, and were detected significantly more during the night on the surrounding sand compared to within the SPL. Therefore, we hypothesize that plaice undertake feeding excursions towards the SPL during the day, where they find a high prey availability, while they prefer the sand surrounding the SPL for resting and hiding for predators.

During winter, plaice migrate outside the OWF, most likely towards the spawning areas located in deeper waters in the North Sea, Irish Sea, and English Channel (Hunter *et al.*, 2003a; Ellis *et al.*, 2012; Gibson *et al.*, 2015). However, after the spawning season, >30% of all tagged fish were still detected within the study area, indicating that they show a high site fidelity. These results suggest that plaice remain inside OWFs for consecutive years during the feeding season,

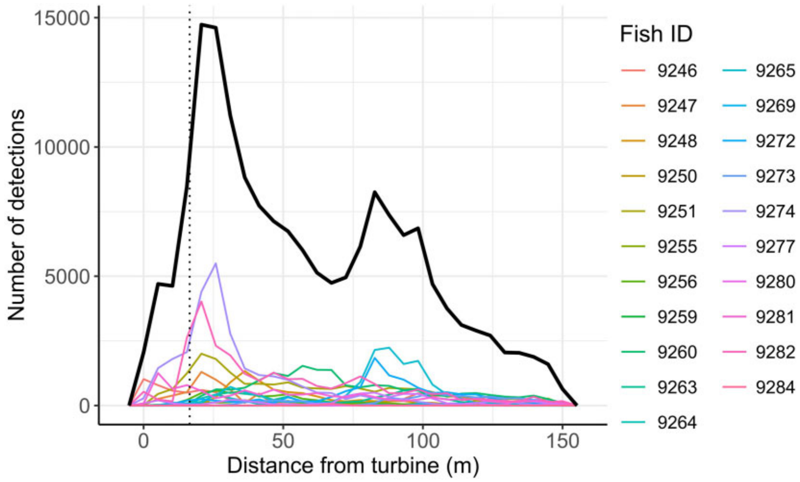

Figure 4. Frequency polygons (middle points of histogram) of the number of detections per fish (coloured lines) and summed detections over the distance from the turbine (black line). The dotted line indicates the distance of the scour protection layer (SPL) by design (16.5 m from the turbine).

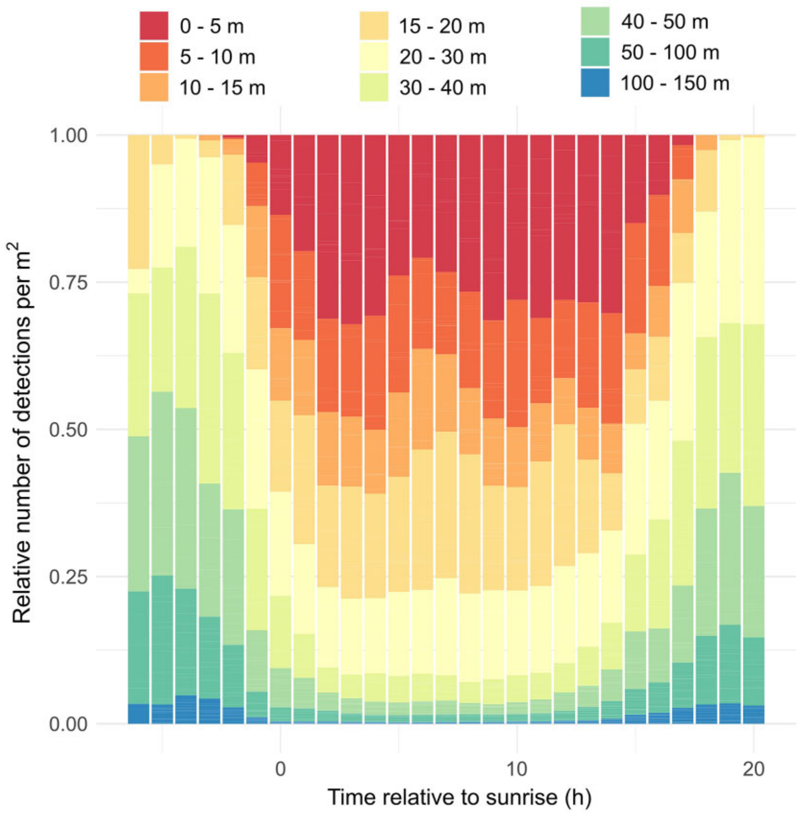

Figure 5. Relative number of fish detections per m^2 for each distance interval over time relative to sunrise around turbines B09, C08, and D09 in the Belwind offshore wind farm (OWF) [end of scour protection layer (SPL) on average 16.5 m from turbines].

where they find food and shelter, and only leave the area for spawning in winter.

Plaice show high residency within OWFs

Plaice showed a high level of residency during summer and early autumn within the studied OWF, even on a relatively small surface area (1.37 km^2). This indicates that, during the feeding season, plaice do not cover extensive distances in search of food, and predominantly remain within the boundaries of the wind farm. Some fish were not detected or absent for days or weeks during the first study period, which most probably means they were still present within the OWF, but could not be detected as they were outside the detection range of the receiver array. Like many other flatfish species, plaice is an opportunistic feeder that relies on the availability of prey in its direct vicinity, which influences its spatial distribution (Gibson, 1997; Shucksmith *et al.*, 2006). A high level of residency within a small area suggests an ample food supply. This is corroborated by a trophic analysis performed within the same OWF, which revealed that plaice had fuller digestive tracts near the turbines compared to fish caught on the surrounding sand in between the turbines (Buyse *et al.*, 2023).

Plaice undertake small-scale feeding excursions to the SPL during day time

The analyses of the small-scale movements of plaice revealed a clear diurnal pattern, with fish being detected closer to the hard substrate during the day than during nighttime. Estimated positions of 21 fish indicated that fish were located on the SPL almost exclusively during daytime, which is reflected in more detections on the SPL (<15 m from the turbine foundations) compared to the surrounding sand (<150 m from the turbines). During the night, the opposite was observed, with more detections on the surrounding sand. Similar movement patterns were found for fish assemblages around an artificial reef in Portugal, with the highest density and species diversity found during the day compared to the night (Santos *et al.*, 2002).

Diurnal patterns in locomotory activity are often correlated to feeding and foraging behaviour in fish, which is also the case for plaice (De Groot, 1971). Plaice mainly forage during daylight hours as it is a visual predator that relies on its sight to detect benthic invertebrates such as polychaetes, bivalves, and echinoderms (Verheijen and De Groot, 1967; Gibson *et al.*, 2015). Trophic and spatial distribution analyses of plaice within the Belwind OWF showed that plaice were not only attracted to the soft sediment patches in between the rocks of the SPL (Buyse *et al.*, 2022), but that the individuals caught close to the turbines also had fuller digestive tracts and a typical hard-substrate diet (Buyse *et al.*, 2023). This difference in diet was observed for a short time span through a stomach content analysis, as well as for a longer time span through a distinctive fatty acid profile. These findings all indicate that plaice actively use the SPL as a feeding ground during the day, related to a high prey availability correlated to the presence of hard substrates in the form of rocks and turbine foundations (Wilhelmsson and Malm, 2008; Degraer *et al.*, 2020; Glarou *et al.*, 2020). It is important to note that plaice might only profit from the SPL if there are sandy patches present in between the rocks where they can rest on (Buyse *et al.*, 2022, 2023). Such patches only develop after some years due to sedimentation processes, and, therefore, the importance of the SPL for plaice and other soft-sediment fish as a feeding habitat might change over time. It is thus important to study temporal patterns, as well as spatial patterns, when monitoring the effects of the SPL on fauna.

Our results showed that the majority of the estimated positions of plaice were located on the soft sediments directly surrounding the SPL, at a mean distance of 92 m with a clear peak at 25 m from the turbines. During diving transects conducted during daylight hours within the same OWF, we recorded higher densities of plaice on the sandy patches in between the rocks of the SPL compared to the adjacent sand (at ~20 m from the turbines) (Buyse *et al.*, 2022). Most probably, some of the fish that undertake feeding excursions to the SPL use these sandy patches for resting in between feeding periods during daytime, while most plaice return to the sandy environment surrounding the hard substrates to bury themselves in the sand as protection against predators. Moreover, plaice tends to swim just above the seabed when foraging during the day, while they show increased swimming activity higher in the water column at night (Verheijen and De Groot, 1967; De Groot, 1971; De Veen, 1978). Such swimming behaviour during the night and increased feeding movements during twilight hours (Gibson, 1973) might also partly explain why more fish were detected outside the SPL during the first study period.

In addition to exhibiting a diurnal movement pattern, individual variations in behaviour among fish are evident. Some fish tend to stay close to the turbine, while others prefer to stay along the edges of the SPL, and some even opt for the adjacent sandy areas. Moreover, while most fish have a preferred turbine, some switch between turbines more frequently (Figure 3). Apart from species-specific behaviours, these individual differences play a crucial role in understanding fish movement and may even be the stronger factor influencing it (Harrison *et al.*, 2019). Since we mainly caught plaice on the SPL, it is important to note that this sample represents fish adapted to this particular environment. Therefore, caution is warranted when generalizing their movement patterns to all plaice within an OWF.

Our results do not support a shelter hypothesis for plaice, as is shown for some other species that use artificial reef structures and SPLs as shelter against predation or currents (Bohnsack, 1989; Langhamer, 2012). On average, the number of detections per hour is twice as high (12.3 ± 8.2) for fish on soft sediments compared to fish present on the SPL (6.2 ± 5.4). However, the transmission of signals from fish present on the SPL might be impeded by the presence of rocks (Payne *et al.*, 2010; Cagua *et al.*, 2013), potentially leading to an underestimation of the number of fish positions on the SPL. Additionally, fish behaviour, such as burial or positioning between the rocks of the SPL, might influence the convergence of the YAPS model and the generation of reliable position estimates. Also, the study by Goossens *et al.* (2022) revealed that ambient noise, primarily originating from tidal currents, may restrict the receivers' ability to detect acoustic signals. However, the consistent diurnal pattern observed in both the total number of detections and the number of reliable position estimates, while such a pattern is absent within the built-in sync tag detections, suggests that the ability of the YAPS model to produce reliable estimates is not dependent on fish behaviour and that the results presented in this study are valid. Moreover, the inclusion of bottom current speed in the GAMM did not enhance the model, indicating that the proximity of fish to the turbines is not influenced by the strength of the tidal currents. It has been shown that plaice can effectively evade strong currents and seek refuge from predators by burying themselves in the sand (Gibson *et al.*, 2015). This further suggests that the rocks of the SPL do not offer significant advantages for shelter use by plaice compared to the surrounding sand.

Plaice shows high-site fidelity towards OWF after spawning

The presence–absence data obtained from the three receiver arrays indicated that 11 out of 31 fish (35%) were detected within the study area 1 year after tagging. Older tagging studies on plaice in the North Sea generally demonstrated strong site fidelity towards spawning and feeding grounds, albeit with limited quantitative information available (De Veen, 1978; Rijnsdorp and Pastoors, 1995; Hunter *et al.*, 2003a). A more recent mark–recapture study conducted on European plaice off the coast of Iceland estimated a 90% fidelity rate to feeding grounds after 1 year, increasing to 100% 2–3 years after tagging (Solmundsson *et al.*, 2005). That study also reported that

38% of males and 50% of females were recaptured within 5 km of their tagging site, with 19% of males and 27% of females being recaptured within 1 km of their tagging site. These results align with our findings, indicating a strong site fidelity to the relative small study area ($\sim$3.7 km^2) within the Belgian OWF.

Moreover, there was a clear link with the spawning period. Nine out of 31 fish (29%) disappeared from the study area for several consecutive months during autumn–winter (which is the main spawning period of plaice) and returned in spring to the study area. Although the use of ID tags does not allow to track fish individuals outside the receiver array and study area, the timing and duration of their absence strongly suggest that they left the study area to spawn. Also, the detection of fish 9277, after an absence of over 4 months, by another receiver in the western part of the BPNS 11 days prior to its return to Belwind, suggests that this individual most probably returned from its spawning area and successfully navigated back to the study area. Some fish (e.g. 9259, 9272, and 9263) remained in the study area during the spawning period. Although we did not collect information on sex or maturity, the maturity ogives, and length–age relationships for plaice in the southern North Sea indicate that 30–80% of the females can still be immature at the age of 4–5 years, which corresponds to fish of 30–35 cm (Rijnsdorp, 1989). As the length of our tagged fish ranged between 29 and 39.5 cm, it is likely that some of these individuals were not yet mature when tagged, and therefore did not leave the OWF area for spawning. Another possibility is that these individuals spawned within the OWF itself, as the northern part of the Belgian part of the North Sea (BPNS) falls within the boundaries of the spawning area of plaice (Hunter *et al.*, 2009).

OWFs protect plaice during the feeding season, but not during spawning migrations

Based on these results, it can be suggested that plaice exhibit high site fidelity towards the feeding grounds within OWFs and that individuals are likely to return to the same OWF after the spawning period. High residency within and high site fidelity towards such a specific area implies that OWFs may serve as refuges for plaice from fishing mortality as no fishing activities are allowed within their borders. This protective capacity would be significantly lower if fish move constantly in and out of the OWF for foraging (Miethe *et al.*, 2010). However, based on our results, it is clear that plaice mainly remain within the OWF during summer and autumn, so OWFs can effectively protect plaice against fishing mortality during the summer feeding season. The results of a study that found increased abundances of plaice within another Belgian wind farm (i.e. C-Power) after its construction supports this hypothesis (Buyse *et al.*, 2022). Combined with the increased food availability on the hard substrates, this may lead to an increase in fish production within OWFs and eventually spillover of adult biomass to surrounding areas. On the other hand, a significant number of individuals leave the OWF area during the spawning season from December to March, which potentially reduces the protection effect offered by the OWF.

Still, for many fished species, including plaice, a fisheries-induced effect has been observed, with a shift towards individuals that reach maturity at a smaller size (Heino *et al.*, 2002; Grift *et al.*, 2003). The installation of marine protected areas (MPAs) may prevent this evolutionary decrease in size at maturity, but only when large adults exhibit low connectivity between the MPA and adjacent fished areas (Miethe *et al.*, 2010). As such, the development of large OWF zones, where fishing activities are prohibited, may act as a buffer to mitigate potential fisheries impacts and to increase local fish production, particularly for relatively sedentary target species like plaice. Nevertheless, more research is needed to investigate whether the positive effects of OWFs on plaice could influence the population on a regional scale or whether they only translate into local effects.

Conclusion and suggestions for further research

This study offers valuable insights into the small-scale spatial movements and long-term presence of plaice in relation to OWFs. The findings clearly demonstrate that OWFs, probably due to the high food availability related to the presence of hard substrates, impact plaice movements. The diurnal movement patterns observed in this study, combined with previous diet analysis results, indicate that plaice actively use the SPL as a feeding hotspot during the day, while they prefer the surrounding sandy areas for resting. The high site fidelity to and residency within a small area demonstrate the potential of OWFs to act as protection areas for plaice against fishing mortality, although mainly during the summer–autumn feeding season. During the spawning season in winter, plaice likely leave the OWF and, as such, likely roam in areas where they can be fished.

This study successfully employed the YAPS model to acquire fish positions from a receiver network using transmitters and receivers from two different manufacturers, namely Thelma Biotel and InnovaSea. Although significant considerations were posed to ensure compatibility between the manufacturers (e.g. utilizing MAP-114 on the acoustic receivers instead of MAP-115 to ensure the detectability of Thelma Biotel transmitters with a R64K protocol), this study demonstrated the feasibility of combining equipment from different vendors. Furthermore, it highlights the applicability of open-source methods, such as YAPS, in obtaining fish positions, thereby enhancing data analysis transparency.

In addition to the utilization of ID-only transmitters, which were suitable for addressing the main research questions, the inclusion of archival tags equipped with pressure (depth) and temperature sensors may offer additional valuable insights to support our findings. Archival tags enable the determination of three-dimensional fish positions, as opposed to the two-dimensional positions obtained from ID-only transmitters, thereby facilitating the integration of depth information to enhance the identification of feeding, resting, or swimming activities (Hunter *et al.*, 2004). Furthermore, as sensor data are continuous logged by archival tags, a geolocation model can estimate fish tracks beyond the receiver array and the OWF, which enables the tracking of plaice from their feeding areas to their spawning grounds and vice versa (Hunter et al., 2003b; Woillez *et al.*, 2016). Since plaice exhibit a distinct movement behaviours during spawning migrations and spawning itself (Hunter *et al.*, 2003a, 2004), depth information may be utilized to determine the timing of spawning behaviour and to explore individual preferences for specific spawning locations (Goossens *et al.*, 2023b).

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Supplementary data

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

Data availability

The acoustic tracking data underlying this article are available at https://doi.org/10.14284/634. All scripts are available on the GitHub repository https://github.com/jolienbuyse/AcousticTelemetryPlaiceOWF/.

Author contributions

JB performed the analyses, drafted the manuscript, and made the visualizations. JR, JG, and JB carried out the field work. JR, JG, KH, ADB, and SD developed the study design. All the authors read and reviewed the drafts of the manuscript and approved the final version.

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Conflict of interest

The authors have no conflicts of interest to declare.

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