



Effects of electromagnetic fields on flatfish activity levels

Erica C.N. Chapman^{a,*}, Corentine M.V. Rochas^a, Zoe Burns^a, Petra Harsányi^a,
Annemiek Hermans^b, Kevin Scott^a

^a St Abbs Marine Station, The Harbour, St Abbs TD14 5PW, United Kingdom

^b Wageningen University, Droevendaalsesteeg 4, 6708 PB Wageningen, the Netherlands

ARTICLE INFO

Dataset link: [Effects of electromagnetic fields on flatfish activity levels \(Original data\)](#)

Keywords:

Circadian rhythm
Electromagnetic fields
European flounder
Platichthys flesus
European plaice *Pleuronectes platessa*
Subsea power cables

ABSTRACT

The offshore renewable energy industry is expanding rapidly due to decarbonisation commitments and need for energy security. This will change the marine environment in ways that are not fully understood, including more subsea power cables in the sea. Movement of electricity through these cables generates an electromagnetic field (EMF), which might affect marine species. To aid in ensuring the industry expands sustainably, this study aims to improve our understanding of how flatfish might be affected by EMFs. Behaviour of 61 European flounder (*Platichthys flesus*) was recorded in a large tank, with one section exposed to EMF. Two types of common EMFs were generated at realistic levels (alternating current [AC] maximum ca. 15 μ T RMS and direct current [DC] maximum ca. 19.6 μ T). A small pilot study was also conducted using 15 European plaice (*Pleuronectes platessa*). Results from blind video analysis showed no evidence of attraction, avoidance, or differences in behaviours inside vs outside the EMF. In control trials, flounder were more active during the day compared to the hour before sunset until the end of the trial. Continuous exposure to EMF removed this rhythm, with flounder exposed to EMF staying active throughout the trial period. At sunset, EMF-exposed fish were at least twice as likely to be transiting compared to control. Further research is needed to determine what the underlying cause(s) might be, and whether these results happen through a full 24-hour cycle, are comparable to the wild, or lead to long term impacts.

1. Introduction

With global commitments to net-zero emissions and requirements for energy security becoming increasingly critical, the renewable energy sector is expanding rapidly. Unfortunately, the full effects of offshore marine renewable energy devices (MREDs) on the marine environment are not entirely understood (Dannheim et al., 2019; Normandeau Associates Inc. et al., 2011). Better insight into their environmental impacts will allow for appropriate planning and mitigation to ensure the sector progresses sustainably. One significant knowledge gap is the effects of electromagnetic fields (EMFs) on marine species. Anthropogenic EMFs are generated from offshore MRED subsea power cables, which are used for a variety of purposes (e.g. inter-array cables, cables to power storage banks, and export cables from deployment sites to shore) (Taormina et al., 2018). The electrical current may be alternating current (AC) or direct current (DC) and the EMFs consist of both electric (E-

field) and magnetic fields (B-field). The insulation system of subsea power cables is designed to constrain the generated electrical field within the cable, but this is not practically possible for magnetic fields. Even though E-fields can be shielded, movement through or by the magnetic field can create an induced electric field (iE-field) (De Luca, 2009; Rzepoluch et al., 2025). It is, therefore, the magnetic B-field, and in certain instances, an iE-field, that animals may be exposed to in the marine environment.

Electric and magnetic fields are also generated naturally, for example, from the Earth's magnetic field (usually 30–70 μ T) and bioelectric signals from animals. Various species, across a range of taxa, use these signals for migration or locating food, predators, or conspecifics (e.g. Gill et al., 2009; Normandeau Associates Inc. et al., 2011). Anthropogenic EMFs have the potential to interact with these natural sources, which may or may not impact marine life (e.g. Chapman et al., 2023; Cresci et al., 2023; Gill et al., 2009; Kimber et al., 2011;

* Corresponding author.

E-mail addresses: erica.chapman@marinestation.co.uk, ericachapam@posteo.uk (E.C.N. Chapman), corentine.rochas@marinestation.co.uk (C.M.V. Rochas), zoe.burns@marinestation.co.uk (Z. Burns), petra.harsanyi@marinestation.co.uk (P. Harsányi), annemiek.hermans@wur.nl (A. Hermans), kevin.scott@marinestation.co.uk (K. Scott).

<https://doi.org/10.1016/j.marpolbul.2025.118652>

Received 20 June 2025; Received in revised form 27 August 2025; Accepted 28 August 2025

Available online 5 September 2025

0025-326X/© 2025 The Author(s). Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Normandeau Associates Inc. et al., 2011). Exposure to magnetic fields may also penetrate living tissues and could trigger physiological or developmental changes (Ghodbane et al., 2013; Harsanyi et al., 2022; Kulkarni and Gandhare, 2014; Tang et al., 2015; Tilden et al., 2003). Due to the complex nature of EMF emissions, the uncertainty of how some animals detect and use magnetic and electric fields, and the range of mixed results that currently exist, there is a lot of doubt on how anthropogenic EMFs may impact marine life, both at the species and wider trophic levels.

One species group of particular concern is flatfish. Many flatfish species are commercially and ecologically important (DEFRA, 2024; Gibson et al., 2014; Lee et al., 2010). Flatfish have been observed in the vicinity of various offshore windfarms (e.g. Stenberg et al., 2015; ter Hofstede et al., 2022; Vandendriessche et al., 2015; Winter et al., 2010), and due to their demersal and broad geographical distribution, are likely to interact with offshore MREDs during different life history stages (Barbut et al., 2020). In general terms, modelling and abundance studies have shown positive (Bicknell et al., 2025; Buyse et al., 2023a; Raoux et al., 2017; Vandendriessche et al., 2015), or no (Bicknell et al., 2025; Stenberg et al., 2015; Winter et al., 2010) effects of offshore windfarms on flatfish. However, the large-scale biological significance of these effects is unknown (Gill et al., 2024). There is also a lack of evidence with regards to how flatfish might respond specifically to anthropogenic EMFs generated from subsea power cables. It has been suggested that European plaice (*Pleuronectes platessa*) may use an external directional cue for orientation, but it is not known if this is the electrical field generated by the flow of sea water through the geomagnetic field, the Earth's magnetic field itself, or another source (Metcalf et al., 1993). Whilst not studied on both feeding and spawning grounds, European plaice have shown a normal movement pattern of feeding around wind turbines, leaving at the expected time of spawning, then returning successfully to the feeding ground (Buyse et al., 2023b). This may be less likely for species where there is evidence of a magnetic compass or map sense, such as Gulf flounder (*Paralichthys albigutta*) (Naisbett-Jones et al., 2022). European flounders (*Platichthys flesus*) were shown not to cross over a 132 kV 50 Hz AC cable buried at 1 m depth during periods of high electrical production, but did cross over during low production (Hvidt et al., 2006). However, due to the position of the nets used in the study, it is difficult to attribute the differences to the cable itself. A pilot study conducted over subsea power cables noted that flatfish were very active, but no further details were given, and no quantitative analysis could be conducted (Snoek et al., 2020). In a study using a relatively high-strength magnetic field, the survival of young flounder was not affected when exposed to a static 3.7 milli-Tesla (mT) DC magnetic field for four weeks (Bochert and Zettler, 2004). Anthropogenic EMF studies on other fish species have had mixed results on animal behaviour and physiology (Cada et al., 2012; Cresci et al., 2022; Formicki et al., 2004; Gill et al., 2012; Kilfoyle et al., 2018; Loghmannia et al., 2015; Ohman et al., 2007; Sedigh et al., 2019; Taormina et al., 2018; Woodruff et al., 2012; Wyman et al., 2018).

Given the current knowledge gaps associated with the potential impacts of EMF emissions from subsea power cables, in addition to a lack of understanding of how marine groups such as flatfish detect EMF, the primary objective of this study is to gain insight into the potential effects of real-world EMF intensities from AC and DC power systems on flatfish behaviour. Specifically, the study seeks to determine whether flatfish exhibit any observable behavioural changes, including signs of attraction or avoidance, erratic behaviour, or shift in general activity levels, when exposed to AC or DC induced EMF. The main study focuses on European flounder, and a small pilot study on European plaice is also included.

2. Methods

2.1. Animal acquisition and welfare

All procedures and animal welfare were carried out in accordance with the Animals (Scientific Procedures) Act 1986 from the UK Home Office (PPL number PP4103519, granted 27 March 2024), by trained personnel and under the direction of named animal care and welfare officers and veterinary surgeons.

Animals were wild-caught along the southeast (SE) coast of Scotland, UK (Fig. 1). Plaice were caught as by-catch from local prawn trawlers. Flounder were caught by line fishing from five different locations along the SE coast of Scotland. Animals were then transported to St Abbs Marine Station where they were kept in tanks with local raw sea water conditions that were similar to where they were caught.

Fifteen plaice were caught between 14 February and 20 August 2024 (weight 176–364 g with a mean 244.37 ± 62.70 g, length ca. 26.25–40.5 cm with a mean 30.87 ± 3.41 cm). Sixty-one flounder were caught between 17 September and 10 November 2024 (weight 76–956 g, mean 326.31 ± 174.36 g, length 20.5–42.0 cm, mean 29.67 ± 5.10 cm).

Wild-caught animals are expected to have some level of unknown parasite burden or possible medical condition. Any visible parasites (e.g. sea lice) were removed either manually or by using a freshwater bath. Any fish with a high burden were not kept. Once onsite, fish also underwent a quarantine and acclimation period of at least one week. During this time and prior to experimentation, fish were examined by trained personnel to assess their health and condition (e.g. wounds, infection, body condition, behaviour). Animals that did not meet appropriate health and condition requirements were not used (i.e. no large wounds or severely thin fish).

Fish were fed one of cockle, mackerel, mussel, or squid daily. A minimum of 1 % of their total body weight was given daily, as per standard operating procedure approved with veterinarians. Any uneaten food was removed the following day prior to the next feeding. Plaice were target fed to guarantee food was being consumed. Flounder did not target feed, therefore, body weights were taken to ensure individual fish were maintaining or gaining weight.

2.2. Experimental set-up

Experimental trials were conducted from May to September 2024 (plaice) and September to December 2024 (flounder) at St Abbs Marine Station, a facility purpose-built for EMF research, located on the SE coast of Scotland, near where animals were caught (Fig. 1). The facility has a low magnetic footprint and natural conditions, including raw seawater pumped directly from the sea and natural photoperiod from a translucent roof. Environmental parameters (light levels [lux], water temperature [°C], salinity [ppt], and dissolved oxygen [%]) were monitored throughout, showing 48.49 ± 32.22 lx, 12.84 ± 2.14 °C, 34.17 ± 0.43 ppt salinity, and 105.12 ± 8.07 % DO for plaice trials and 9.92 ± 6.52 lx, 9.04 ± 1.87 °C, 34.52 ± 0.25 ppt salinity, and 103.77 ± 2.62 % DO for flounder trials.

A combination of two coils, each made up of 32 turns of 1.25 mm² copper wire, were powered by a Keysight N6705C DC Power Analyzer with two 20 W source/measure units to generate AC (maximum ca. 15 μ T RMS) or DC (maximum ca. 19.6 μ T) EMFs. The magnetic field generator was designed, fabricated, and commissioned by the Netherlands Organisation for Applied Scientific Research (TNO). EMF strengths used in this study were based on modelled values from field measurements of the NorNed and Borssele cables in the Netherlands (Hermans et al., 2024). In-situ EMF levels in the tank were measured with a Twinleaf VMR sensor and SYNC4 data acquisition system to verify emission levels. The average static ambient geomagnetic field inside the experimental tank, when the coils were turned off, was 50.7 μ T. Further details on the static geomagnetic field throughout the experimental tank

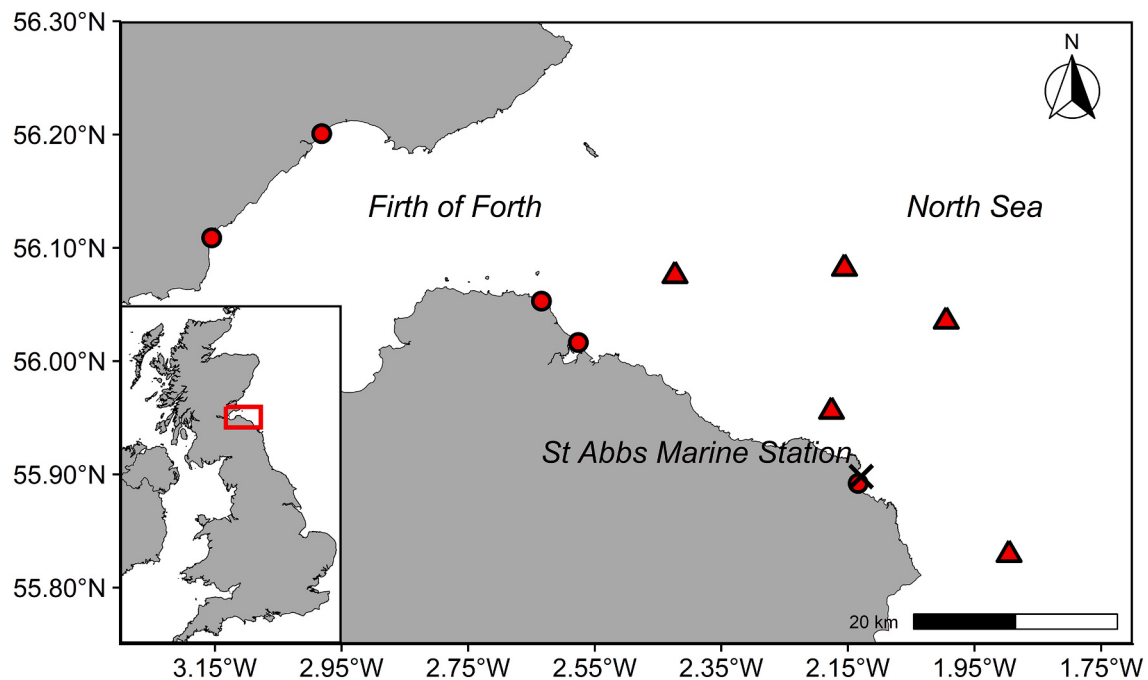


Fig. 1. Map showing locations where flatfish were caught along the southeast coast of Scotland, UK. European plaice (*Pleuronectes platessa*) were caught as by-catch from prawn trawlers with approximate catch locations represented by triangles (Δ). European flounder (*Platichthys flesus*) were caught by shore-based sea anglers, with catch locations represented by circles (o). The location of the research aquarium, St Abbs Marine Station, is indicated by an 'x'.

are provided in the Supplementary materials.

In the DC configuration, only the horizontal solenoid under the bottom of the tank was powered (1.25 A) (Fig. 2). In the AC configuration, the solenoids were placed in an inverted T configuration (horizontal and vertical) (Fig. 2) and were powered out of phase, simulating a 3-phase AC transport cable. The amplitude of the current in the horizontal solenoid (1.25 A) was twice as strong as the amplitude of the vertical solenoid (0.625 A), creating a circular rotating field in the centre of the vertical solenoid, mimicking the circular field emitted by live AC subsea power cables. Both solenoids had a frequency of 50 Hz. Details of the xyz components of the emitted B-fields are found in the Supplementary materials.

The experimental tank was approximately $15 \times 2 \times 1.5$ m, with a floor area of 15.2×1.6 m. The main EMF exposure area was equivalent to a 2×2 m area at the bottom of the tank and was positioned off centre (Figs. 2 & 3). Due to how EMFs are emitted and dissipate, very low levels of EMF (ca. three times less than the highest) were detected outside of this main EMF area (Fig. 3).

Raw local seawater filtered through a filter sock was used to fill the tank to a water depth of 0.3 m.

The tank size and EMF position allowed animals to be exposed to an EMF gradient from two sides of the EMF source, whilst also leaving parts of the tank unexposed to EMF (Fig. 3). This gave a relatively realistic

environment that can be more easily related to the animals' natural behaviour surrounding subsea power cables.

To limit magnetic interference with the EMF exposure area, the experimental tank was built using non-ferrous materials, principally fiberglass and wood. Electronics and ferrous materials were removed from around the exposure area. The tank had high sides to visually block the surrounding environment, thus reducing external stimuli. During trials, access to the experimental tank area was also restricted to prevent acoustic disturbance.

A camera system, consisting of 16 infra-red cameras (Reolink, RLC-810A), was set-up above the experimental tank (Fig. 2) and connected to a network video recorder (Reolink NVR 16 channel recorder) with a monitor. Cameras were positioned a minimum of 2 m away from the base of the tank to avoid any EMF interference. Cameras were spaced to create an overlapping field of view, creating a full overview of the experimental tank.

2.3. Experimental procedure

Environmental conditions were measured prior to animal transfer to ensure conditions between holding tanks and the experimental tank were similar. A single fish was randomly placed into the experimental tank at one of three entry points (far left, middle, far right)

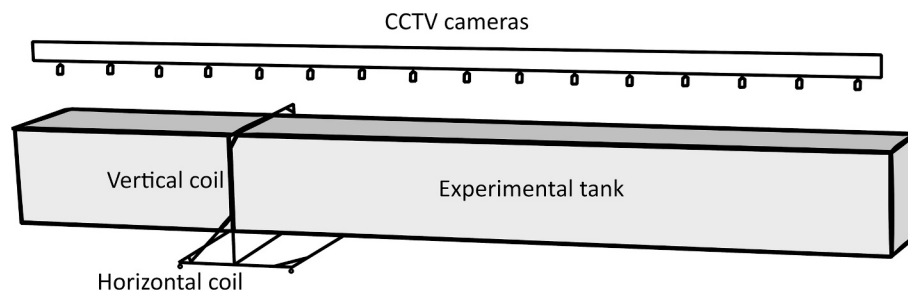


Fig. 2. The experimental tank (internal measures: $15.20 \times 1.64 \times 1.6$ m) with 16 closed-circuit television (CCTV) cameras placed above and coils that generate the artificial electromagnetic fields (EMFs).

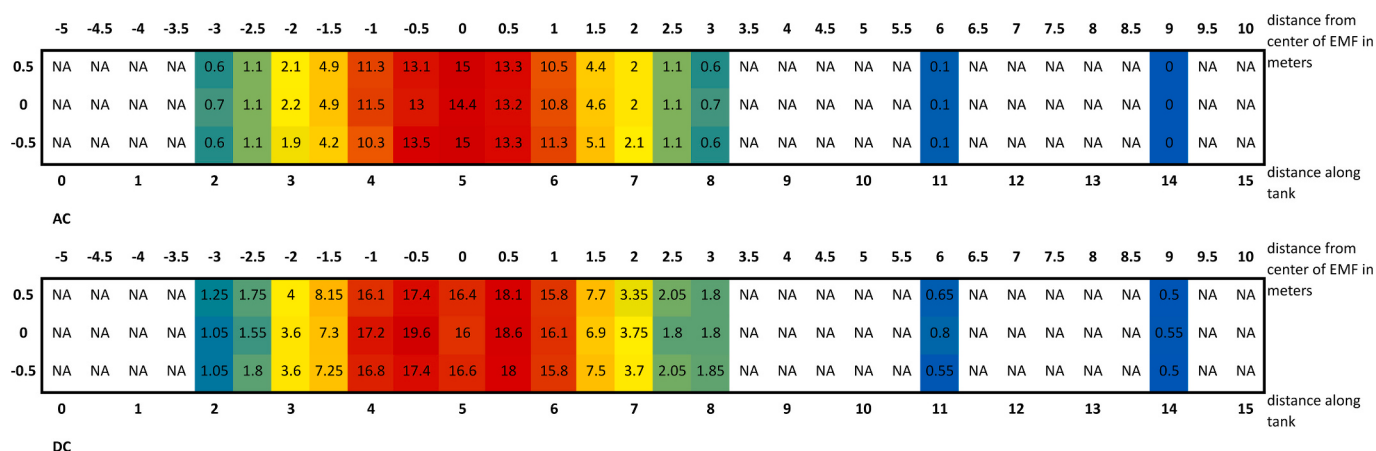


Fig. 3. Electromagnetic field (EMF) values measured throughout the bottom of a 15 m tank. Top: Alternating current (AC) with 1.25 A through horizontal solenoid and 0.625 A through vertical, both 50 Hz frequency. Bottom: Direct current (DC) with constant 1.25 A current through bottom solenoid.

approximately one hour prior to the start of the trial for an acclimation period. Time of entry, sunset, and trial start were noted. To cover day and night periods, each trial began approximately four hours before sunset and ended two hours after sunset, equating to a total trial length of six hours. During the acclimation and experimental period, the infrared CCTV camera system recorded the full length of the experimental tank.

After each trial, water parameters were recorded, and fish were weighed and their length measured. After a minimum one-week observation period, fish were released back into the sea.

Between each trial, any settled sediment was removed from the bottom of the tank, seawater was exchanged, and air-stones were used to aerate the water.

A pilot study of fifteen plaice was carried out (5 of each AC, DC, and control treatments) in two groups, in spring (4–17 May 2024, 5 individuals who had been tagged in the posterior dorsal muscle with Hallprint t-bar anchor tags for identification) and summer (23 July–1 September 2024, 10 individuals).

A total of 61 flounder trials were completed 23 September–26 December 2024 (20 AC, 21 DC and 20 control).

2.4. Video analysis

For each trial, video files from the CCTV footage were combined into one six-hour file using Adobe Premiere Pro (v.25.1.0), allowing for a full overview of the experimental tank. The stitched video was then analysed through Behavioral Observation Research Interactive Software (BORIS, v8.27.7 2024/08/23, <https://www.boris.unibo.it>) (Friard and Gamba, 2016), a free open-source event logging software, and Noldus Ethovision XT (v.16.0), a commercial video tracking software. Video analysis was conducted blind, with treatment of the trial unknown to the analyst.

In BORIS the behaviour (stationary, moving, or changing direction) and location (left of EMF, in EMF, right of EMF, or in the corners) of the fish throughout each trial were logged (start and stop time). Durations of behaviours were then calculated. Behaviours in and around the EMF were also logged separately as a tally (cross through EMF, enter EMF and exit through the same side, turn just before EMF).

In Ethovision, fish location coordinates, and therefore fish tracks, were generated (Fig. 5 in Supplementary materials). Due to the limitations of the software in the context of this study (i.e. large tank, small animal, suboptimal lighting conditions), which led to position errors and missing values, a large amount of manual editing was required. Therefore, only a one-hour subset, starting at sunset, of each six-hour trial was used for this stage of the analysis.

2.5. Data handling and analysis

R studio (version 1.5.57) and R (version 4.4.1) were used for data exploration and all analysis (R Core Team, 2024). The presence of outliers, zero inflation, collinearity, relationships, and independence between variables was assessed with boxplots, Cleveland dotplots, frequency plots, pairplots, Pearson/Spearman correlation coefficients, multi-panel scatter plots, and conditional boxplots (Zuur et al., 2010).

Plaice data were summarised but not statistically analysed beyond an analysis of variance (ANOVA), due to the smaller sample size.

The number of times a fish entered the EMF area, classified as approximately one meter on either side of the centre of the EMF high-point, was tallied. To account for the fact that more active fish will be more likely to enter the EMF area, EMF occurrences were also normalised by dividing the number of EMF occurrences by the time the fish spent moving. This was then reported as a number of EMF occurrences per hour of locomotion time.

BORIS data were analysed from each trial as a whole, irrespective of relation to EMF (i.e. combining behaviours inside and outside the EMF), to represent changes in behaviour when an EMF source was in the vicinity. This included movement and the proportional amount of time spent changing direction. As the corners of the tank physically forced fish to change direction or stop, time spent in the corners was removed from the analysis. The proportional amount of time spent changing direction was therefore calculated as the total amount of time spent changing direction not in corners divided by the total trial time spent anywhere in the tank except the corners.

Time spent moving was also broken down and analysed per hour to investigate any diurnal patterns.

Within each trial, behaviours were also compared inside versus outside the EMF area. This analysis included time spent moving and time spent changing direction. Data were adjusted to account for the difference in behaviour found in corners and ends of the tank, compared to elsewhere. Due to the nature of the enclosed tank, fish often swam along the perimeter of the tank. Fish naturally spent more time in either end of the tank due to there being more wall space to travel along. These sections of the tank were therefore given proportionally more weight based on the length of wall space. Corner behaviours were also removed from these analyses. Trials where fish did not experience both the EMF area and outside the EMF area were excluded from inside vs outside proportional comparisons.

Different generalised linear models (GLMs) and generalised mixed models (GLMMs) were used to investigate the significance of explanatory variables (e.g. treatment, fish length, and tank temperature) on each response variable. Details are provided in the methods section of the Supplementary materials. Where no significance results were found

from the GLMs or GLMMs, Kruskal-Wallis rank sum tests were carried out with the built-in function from base R, to compare the medians of the three treatments.

The one-hour subset of Ethovision data was analysed using discrete-time Hidden Markov Models (HMMs) with momentuHMM (v.1.5.5; McClintock and Michelot, 2018), as done by Hermans et al. (2025), to determine whether EMF exposure affected the behavioural states of flatfish. Ethovision data were diluted from every 0.2 s to a position every two seconds for computational reasons. Step length, turning angle, and whether the animal was within 1 m of either end of the tank, were used as parameters to distinguish between behavioural states. All step lengths less than 2 cm were set to zero. Null HMMs were fitted with one to four behavioural states. Akaike information criteria (AIC) were used for model selection on the most suitable number of behavioural states. Combinations of variables were then added as state transition probability covariates. These variables included treatment, fish length, water temperature, dissolved oxygen, whether or not the fish was in the EMF zone, how long the fish spent in the EMF, and distance to the EMF highpoint. AIC were used for model selection, and stationary state probabilities with 95 % confidence intervals from the best model were plotted.

3. Results

A total of 76 six-hour flatfish trials were conducted with separate individuals (15 plaice and 61 flounder). Fish rarely showed an avoidance type behaviour (i.e. turning immediately outside the EMF area) (26 individuals, 56 total observations with mean one per fish and range 0–8), therefore, this was not analysed statistically.

There were few observations (86 total observations with mean one per fish and range 0–12) of fish entering the EMF area from one side and exiting on the same side, therefore, these numbers were added to the number of times a fish swam through the EMF. The variable of occurrences in the EMF was used for analysis.

3.1. Plaice pilot study

All plaice entered the EMF area of the experimental tank. Any fish that turned immediately outside the EMF area (1–8 occurrences from 9 different fish), also entered the EMF area multiple times (75–282 individual occurrences). There was no significant difference in the number of times plaice entered the EMF across the three treatments (ANOVA, $F(2,12) = 3.453$, $p = 0.0654$) (Fig. 4). The power of this test was low (10 %) and the effect size medium/moderate (Cohen rules from 0.246 omega squared). A summary of results for all variables is provided in Table 1.

3.2. Flounder

Pearsons/Spearman correlation coefficients and variance inflation factors (VIFs) showed collinearity in explanatory variables. Trial date, sunset time, and water temperature were correlated (date vs sunset time: $r_s(59) = -0.94$, $p < 0.001$, date vs temperature: $r_s(59) = -0.94$, $p < 0.001$), with date and sunset showing the highest VIFs (date 17.89 and sunset 11.41). Therefore, only temperature was used for the analysis. Fish weight and length were also correlated ($r_s(59) = 0.98$, $p < 0.001$), therefore, only fish length was used in the analysis, as it is a more consistent measurement.

Overall, adding water temperature or fish length did not alter the significance of the treatments on flounder behaviour. See results section in the Supplementary materials for details on model findings.

During one DC trial, four video cameras did not record. These were not the cameras over the EMF area, therefore, this trial was used for occurrences within the EMF area but not for behaviours elsewhere in the tank or inside vs outside the EMF. To account for the limitations of this trial, an additional DC trial was run.

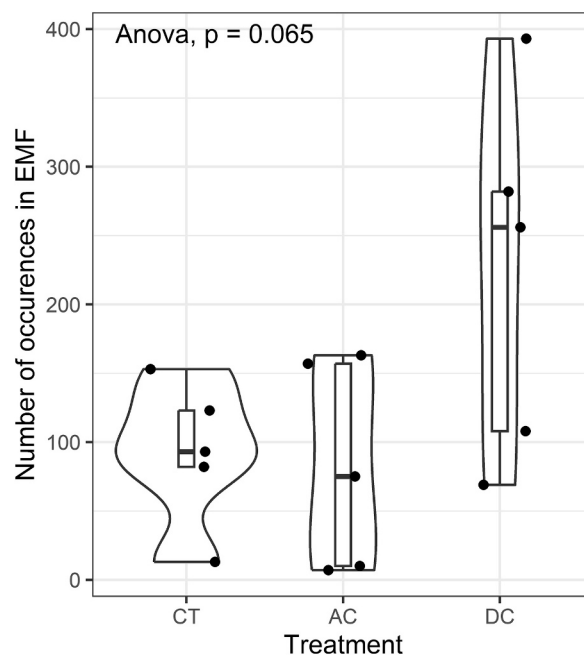


Fig. 4. Number of occurrences each European plaice (*Pleuronectes platessa*) entered the electromagnetic field (EMF) area within the 15 m experimental tank over the six-hour trial period for each treatment (CT = control, AC = alternating current, DC = direct current).

Table 1

Pilot study summary of behavioural results for European plaice (*Pleuronectes platessa*) exposed to electromagnetic fields. Reported as mean and standard error (SE), then minimum and maximum.

Parameter	Control	Alternating current (AC)	Direct current (DC)
Occurrences in EMF	92.8 (52.5) 13–153	82.4 (75.9) 7–163	221.6 (132.7) 69–393
Occurrences in EMF by hour of moving	40.7 (5.3) 33.0–47.5	34.8 (18.8) 18.0–55.7	56.4 (10.7) 41.5–70.3
Time in EMF (min)	31.3 (13.4) 11.4–44.1	25.3 (14.9) 3.7–37.8	48.8 (52.0) 10.3–138.1
Proportion of time changing direction (min) not including corners	0.02 (0.02) 0.003–0.06	0.03 (0.03) 0.01–0.08	0.03 (0.01) 0.02–0.05
Moving time (min)	134.4 (68.4) 20.0–193.1	113.4 (78.1) 22.8–175.4	241.0 (137.8) 66.5–370.0

3.2.1. Avoidance or attraction

No clear avoidance or attraction was seen to the EMF. Changing direction within a close proximity of the EMF before entering the main EMF area was seen 1–4 times across 17 different flounder (7 CT, 7 AC, 3 DC) for a total of 29 times. In most cases, the fish crossed through the EMF area multiple times before displaying this behaviour.

Of the 61 flounder used, there was a wide range in the number of times a fish entered the EMF area. Eleven fish did not enter the EMF area (3 CT, 2 AC, 6 DC), and a further 14 flounder entered fewer than 10 times (5 CT, 5 AC, 4 DC). Eleven fish (3 CT, 4 AC, 4 DC), however, entered the EMF area more than 100 times. Two fish, whilst only entered once, spent the entire trial in the EMF area (1 AC, 1 DC).

There was no significant difference in the number of times fish entered the EMF across the three treatments, either as a whole (Kruskal-Wallis, $\chi^2(2, N = 61) = 0.98498$, $p = 0.6111$) or adjusted for activity level of individual fish (Kruskal-Wallis, $\chi^2(2, N = 56) = 3.3472$, $p = 0.1876$).

3.2.2. Movement

When comparing the proportion of time spent changing direction throughout each trial, three trials were omitted. The one with the missing footage (DC), and two where the fish stayed in one corner for the full trial (one AC and one DC), as corner behaviours were removed due to the tank effect. There was no significant difference in the proportion of time fish spent changing direction across the three treatments (Kruskal-Wallis, $\chi^2(2, N = 58) = 0.29065$, $p = 0.8647$).

There were 12 fish that did not spend time both inside and outside the EMF and were therefore not used for the analysis of proportional time or behaviours inside vs outside the EMF area. This brought the sample size to 49 flounder (17 CT, 18 AC, 14 DC). There was no significant difference in the proportion of time fish spent changing direction (Kruskal-Wallis, $\chi^2(2, N = 49) = 1.6689$, $p = 0.4341$) or moving (Kruskal-Wallis, $\chi^2(2, N = 49) = 0.16702$, $p = 0.9199$) in the EMF area across the three treatments.

3.2.3. Hourly activity levels

A significant difference in time spent moving across the different hours was seen in control trials (Kruskal-Wallis, $\chi^2(5, N = 120) = 28.688$, $p = 2.67\text{e-}05$), but not EMF trials (AC: $\chi^2(5, N = 120) = 8.0725$, $p = 0.1523$, DC: $\chi^2(5, N = 120) = 9.3565$, $p = 0.09566$) (Fig. 5). In the control trials, significantly more time was spent moving in the first two hours (both daytime) compared to the last three hours (one hour before sunset until end of trial/two hours after sunset) (Wilcoxon rank sum exact test, $p = 0.00075\text{--}0.05$), except between hour two and five (Wilcoxon rank sum exact test, $p = 0.06527$).

3.2.4. Hidden Markov model

Using the position data from the hour at sunset, the best null HMM classified four behavioural states based on step length, turning angle, and whether the fish was in the ends of the tank (Fig. 6 Supplementary materials). These could be labelled as inactive in and not in the ends of the tank (large number of 0 cm step lengths and a nonspecific turning angle distribution), active in the end of the tank (smaller step lengths and wider distribution of turning angles), and transiting (larger step length and narrow turning angle distribution, i.e. travelling in a straight line). A visualisation of combined swim tracks is provided in the Supplementary materials (Fig. 7 Supplementary materials).

When testing various combinations of variables as state transition

probability covariates, the best model included treatment and an interaction with the fish being in the EMF area or not (AIC 234252.1, other models ranged from 234,280.1–352,496.9).

Within this hour after sunset analysed by the HMM, AC (25 %) and DC (20 %) trial fish were more likely to be transiting than control (10 %) fish when looking at behavioural states anywhere in the tank (Fig. 6). AC trials had the largest steps, then DC, then control (Fig. 7). Step size was significantly different across treatments (Kruskal-Wallis, $\chi^2(2, N = 21,538) = 1026.5$, $p = <2.2\text{e-}16$), with all post-hoc pairwise comparisons also significant (Wilcoxon rank sum test with continuity correction $p = <2.2\text{e-}16$).

4. Discussion

European flounder did not exhibit any obvious avoidance or attraction to anthropogenic AC (maximum ca. 15 μT RMS) or DC (maximum ca. 19.6 μT) EMFs in the laboratory. Using changing direction as an indicator, exposure to EMFs did not appear to cause flounder to behave erratically. They also did not move more or less within the EMF compared to outside the EMF. The circadian cycle, observed as hourly activity levels, differed between treatments, with time spent moving varying per hour in control trials but not EMF trials. Control trials showed a reduction in activity from sunset until the end of the trial, two hours later. Looking specifically at the hour starting at sunset, EMF trials showed elevated movement, with EMF trials being more likely to be transiting (CT 10 %, AC 25 %, DC 20 %) and swimming faster.

European plaice did not exhibit any obvious behavioural changes, although more data is required to complete meaningful analysis. Whilst the European plaice pilot study appeared to show that plaice were potentially more active in DC trials, it did not show any significant difference in EMF occurrences. The power of this test, however, was very low and will not be discussed in detail. It does highlight the need for more research on plaice, not only to gain appropriate statistical power, but if a significance is found in overall activity levels in DC trials, this would potentially show a difference in how closely related species are affected by EMFs.

4.1. Circadian rhythms

AC and DC EMFs altered the circadian rhythm of flounder in this

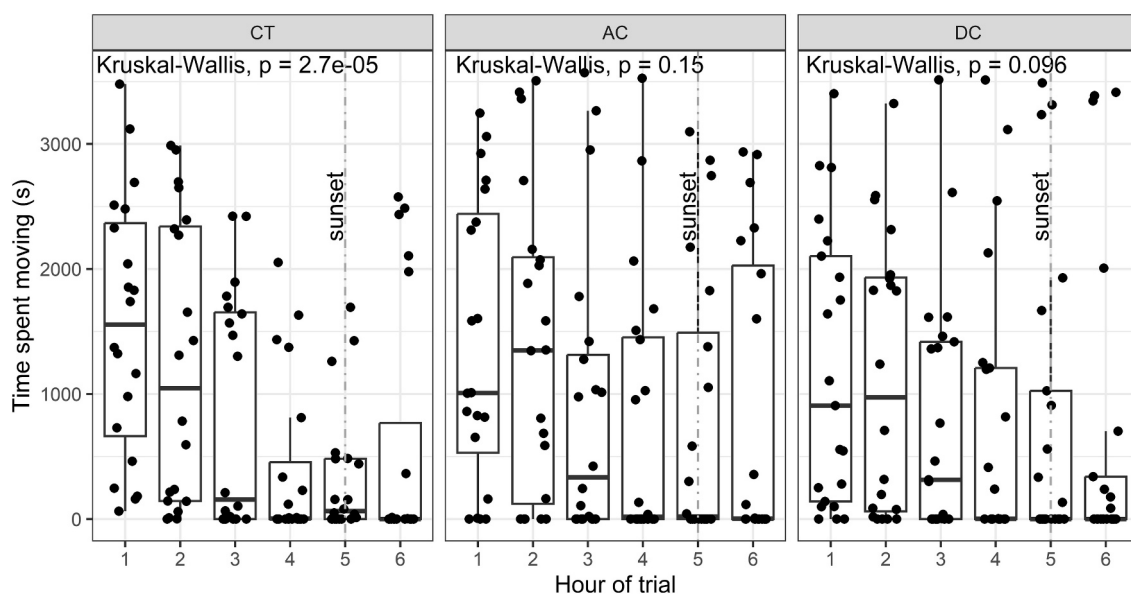


Fig. 5. Time European flounder (*Platichthys flesus*) spent moving during each hour for the three different treatments (CT = control, AC = alternating current, DC = direct current). The first 2 h of the control trials are all significantly different from the last 3 h, except hours 2 and 5. Sunset occurred at the beginning of hour five, as indicated by the labelled dashed line.

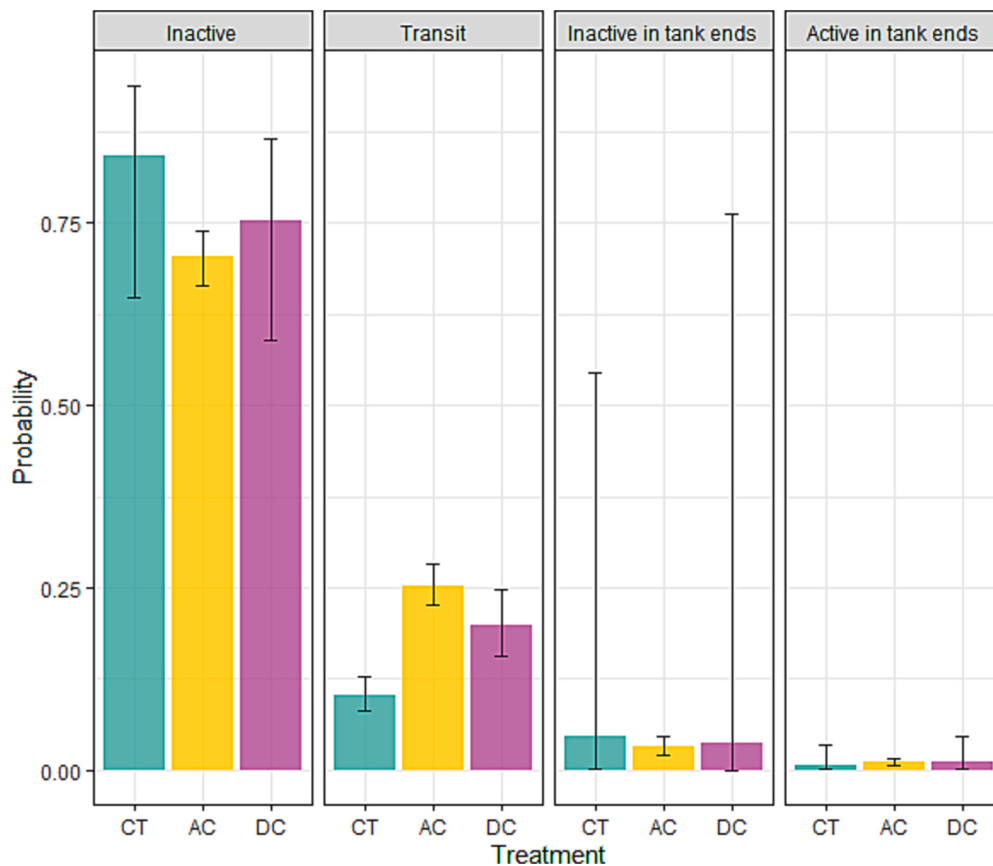


Fig. 6. Stationary state probabilities for each treatment (CT = control, AC = alternating current, DC = direct current), as calculated by a hidden Markov model. Error-bars represent 95 % confidence intervals.

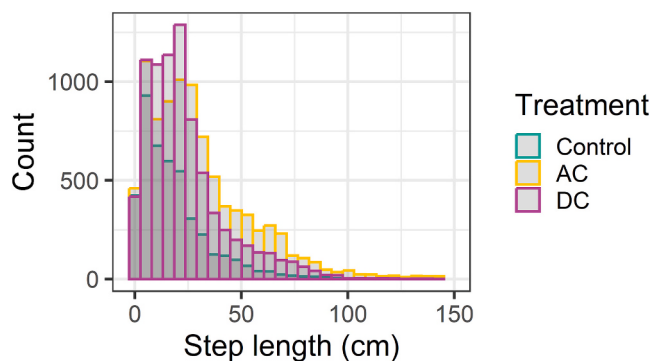


Fig. 7. Histogram of step length for transit and active in tank ends states (i.e. moving states calculated by a hidden Markov model) for each treatment as a whole. CT = control, AC = alternating current, DC = direct current.

study. Whilst it cannot be said if the same would be seen in the field, the rhythm observed in unexposed fish during this study is in line with other laboratory studies (De Groot, 1971; Verheijen and De Groot, 1967).

Generally, flounder have been shown to feed and have more bottom activity during the day and be more mobile throughout the water column at night (Macdonald and Waiwood, 1987; Verheijen and De Groot, 1967). Insufficient information exists on activity levels and circadian rhythms of flatfish around windfarms. European plaice have shown a diurnal pattern of being close to turbines during the day to feed, then being further away from turbines at night (Buyse et al., 2023b). Although that study showed diurnal differences in spatial movement, resting and swimming behaviour near and away from turbines, or EMF zones, were not assessed. As part of the Dutch government's offshore

wind ecological programme (WOZEP), a pilot study using an EMF-sled, equipped with three go-pro cameras, over a 150 kV AC export cable from a 120 MW windfarm noted that European flounder were very active (Snoek et al., 2020). No further details are given, and no quantitative analysis could be conducted. It was also not possible to match-up the recorded flounder sightings with EMF exposure levels. Although authors note they were likely below 0.034 μT , as this study could only be conducted in relatively low wind conditions, therefore, only low EMF levels were monitored.

Both AC and DC EMFs have been shown to change activity levels or alter circadian rhythms in other marine species. Exposure to 50 Hz AC 1000 μT EMF for eight days caused an increase in burrowing activity of a ragworm (*Hediste diversicolor*), with no avoidance or attraction shown (Jakubowska et al., 2019). Altered behaviour of prey species due to EMF exposure could indirectly affect flatfish feeding behaviour and should be investigated in future EMF studies. A laboratory study on Atlantic salmon (*Salmo salar*) and American eels (*Anguilla rostrata*) saw no difference between the level or rhythmicity of locomotor activity from weak, extremely low frequency electric fields (60 or 75 Hz electric fields of 0.07 V/m or 0.7 V/m) or a 50 μT magnetic field (Richardson et al., 1976). Whereas the swimming activity of haddock larvae (*Melanogrammus aeglefinus*) was reduced during 50 to 150 μT DC EMF exposure (Cresci et al., 2022). Using the same EMF emissions as this study, lesser spotted catsharks (*Scyliorhinus canicula*) exposed to a DC EMF were less likely to be transiting compared to AC or control trials (Hermans et al., 2025). These two studies had shorter exposure periods (10 min and 2 h), therefore no information on possible circadian rhythm changes is available. Other studies showed that in addition to changes in magnetic field intensity, altered geomagnetic field direction can also modify fish behaviour. When the horizontal component of the geomagnetic field was artificially altered in laboratory conditions, directional preferences

of zebrafish (*Danio rerio*) changed, and locomotor activity significantly increased (Osipova et al., 2016). Other stressors, such as dichlorodiphenyltrichloroethane (DDT), have also shown increased activity levels in flounder, in this case, likely due to effects on the nervous system (Bengtsson and Larsson, 1981).

In the field, movement patterns and activity levels of flatfish tend to correlate with environmental factors, such as water temperature, light, current velocity, tidal state, pressure, and turbulence (Gibson, 1997, 1973; Gibson et al., 2015). Internal mechanisms, such as endogenous rhythmicity and physiological state, are also important (Gibson, 1997). It is likely that a combination of environmental and/or internal factors work together, and the intricacies of what factor(s) influence flatfish behaviour will vary depending on location and/or life stage (Burrows et al., 1994; Gibson, 1997). Responses to any stressor are not only life stage dependent but also differ based on the time of day when the stress occurs. Nocturnal species show stronger responses if stress occurs during the day, while diurnal fish react strongly at night (López-Olmeda et al., 2013; Sánchez-Vázquez et al., 2019). As most environmental factors are constant or vary by the same degree within a laboratory setting, or were shown not to be significant during modelling, it is most likely internal mechanisms that have caused the divergence of activity levels in EMF trials during this study.

Whilst various mechanisms for specific and nonspecific magnetoreceptions have been considered in previous research and reviews, the study of nonspecific reactions in particular, has no one leading theory (example reviews: Binhi and Prato, 2017; Formicki et al., 2019). Generally, studies on nonspecific magnetoreception are unique and often have poor reproducibility, as results often vary across species and even individuals, and may depend on local conditions (Binhi and Prato, 2017). This discussion will therefore focus on general connections between EMFs and alterations to circadian rhythms specifically. With further study it may be that other pathways exist and the mechanisms within these pathways are determined.

One molecule linked to circadian rhythms that may be disturbed during EMF exposure is melatonin, either directly or indirectly. The circadian rhythms of haemolymph L -lactate and α -glucose, for example, in edible crabs (*Cancer pagurus*) were disrupted by a 2800 μ T EMF in the laboratory (Scott et al., 2018). Shifts in these hormones can be caused by alterations in melatonin levels, which has been shown to be affected by EMF exposure in fish (Lerchl et al., 1998). Lerchl et al. (1998) speculated that their 40 μ T 110 mA pulsing DC EMF exposure may have caused an increased flow of calcium, which led to the increase of melatonin production in brook trout (*Salvelinus fontinalis*). Conversely, melatonin production has been repressed by EMF exposure in mammals (Stevens and Davis, 1996). Lerchl et al. (1998) also speculate that indirect effects from electric fields on the sensory system may have led to the shifts in pineal melatonin due to a secondary stress response. European flounder have a circadian fluctuation in plasma melatonin, with higher levels at night compared to day (Kulczykowska et al., 2001). Where and how EMFs might alter this pattern, if at all, is unknown.

Melatonin does not only play a role in circadian rhythms of fish but may also be an important component in fish reproduction, stress response, and endocrine-immune system interactions (Esteban et al., 2013; López-Olmeda et al., 2013; Zhao et al., 2022). Melatonin changes in fish can be very sensitive to environmental stressors, as daily rhythms exist along the hypothalamic-pituitary-interrenal (HPI) axis, which controls their stress response (Sánchez-Vázquez et al., 2019). For example, in rainbow trout (*Oncorhynchus mykiss*), salinity changes increased melatonin at night (López-Patiño et al., 2011), and chasing and high stocking densities reduced melatonin during the day and at night (López-Patiño et al., 2014). If melatonin alterations are involved in the behavioural changes seen in this study, then wider impacts may be possible, as melatonin is involved in other processes within the body. For example, a fish's ability to integrate rhythmic environmental information (López-Patiño et al., 2014), cope with osmotic challenges (López-Patiño et al., 2011), fight disease (Esteban et al., 2013), camouflage

(Feng et al., 2023), and/or reproduce effectively (Hong et al., 2021; Kim et al., 2013).

Further physiological studies are needed to establish whether exposure to EMFs alters the circadian pattern of melatonin levels and internal physiological processes it regulates in flounder, or if another component of the complex circadian system is involved. Whilst melatonin is the principal circadian hormone, the fish circadian system also involves melatonin-producing organs (e.g. pineal gland and retina), circadian clock genes, and circadian oscillators (i.e. oscillating cells and structures) (Zhdanova and Reeb, 2005). Specifically, it has been suggested that European flounder have circadian oscillators within the pineal organ (Kulczykowska et al., 2001). Additionally, molecular clock genes are expressed in various tissues in Senegalese sole (*Solea senegalensis*) (Martín-Robles et al., 2012) and turbot (*Scophthalmus maximus*) (Ceinos et al., 2019). A 100 μ T 50 Hz EMF has been shown to alter the expression of various clock genes in human dermal fibroblasts (Manzella et al., 2015), whereas a 580 μ T 50 Hz EMF did not affect the expression of two clock genes in mice (Lundberg et al., 2019).

5. Conclusion

Flounder did not show any indication of avoidance, attraction, or erratic behaviours indicating a stress response to EMF, as shown from blind video analysis. Exposure to AC and DC induced EMF altered the activity level circadian rhythm of flounder in an aquarium around sunset. Additional studies are needed to establish whether the trend observed in this study extends to the full 24-hour cycle and whether the change is caused by disruptions in the circadian system (e.g. melatonin hormone) and/or a physiological stress response. Further research is also required to determine if this increased activity and potential loss or alteration of a circadian rhythm is seen in the field, and whether other factors (e.g. EMF effects on prey) or multi-stressors (e.g. vibrations and/or altered hydrodynamics) will also have an influence.

CRedit authorship contribution statement

Erica C.N. Chapman: Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Corentine M.V. Rochas:** Writing – review & editing, Validation, Resources, Methodology, Investigation. **Zoe Burns:** Writing – review & editing, Resources, Investigation. **Petra Harsányi:** Writing – review & editing, Validation, Supervision, Resources, Methodology. **Annemiek Hermans:** Writing – review & editing, Validation, Supervision, Methodology. **Kevin Scott:** Writing – review & editing, Validation, Supervision, Methodology.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Erica Chapman reports financial support was provided by Renewable Grid Initiative. Annemiek Hermans reports a relationship with Witteveen Bos that includes: employment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

A huge thank you to all the staff and volunteers at the St Abbs Marine Station for all your hard work during this project. Thank you to the crews of fishing vessels *Endeavour* and *Arcturus* for collecting the plaice. Thank you to all the anglers who gave advice and assisted us in catching flounder, especially the anglers of the Bass Rock shore angling league and competitors of the Iain Reid Memorial match. Thank you to Jeroen

Hubert for his hidden Markov model code. Many thanks to Ana Miljanović Rusan and Evripidis Karatsivos for your valuable feedback and suggestions. Thank you to the reviewers for your time and constructive comments to improve our manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2025.118652>.

Data availability

Data is available on Mendeley Data doi: 10.17632/dh3nzps8z8.1
Effects of electromagnetic fields on flatfish activity levels (Original data) (Mendeley Data)

References

- Barbier, L., Vastenhou, B., Vigin, L., Degraer, S., Volckaert, F.A.M., Lacroix, G., 2020. The proportion of flatfish recruitment in the North Sea potentially affected by offshore windfarms. *ICES J. Mar. Sci.* 77, 1227–1237. <https://doi.org/10.1093/icesjms/fsz050>.
- Bengtsson, B.-E., Larsson, Å., 1981. Hyperactivity and changed diurnal activity in flounders, *Platichthys flesus*, exposed to DDT. *Mar. Pollut. Bull.* 12, 101–102. [https://doi.org/10.1016/0025-326X\(81\)90201-0](https://doi.org/10.1016/0025-326X(81)90201-0).
- Bicknell, A.W.J., Gierhart, S., Witt, M.J., 2025. Site and species dependent effects of offshore wind farms on fish populations. *Mar. Environ. Res.* 205, 106977. <https://doi.org/10.1016/j.marenvres.2025.106977>.
- Binh, V.N., Prato, F.S., 2017. Biological effects of the hypomagnetic field: an analytical review of experiments and theories. *PLoS One* 12, e0179340. <https://doi.org/10.1371/journal.pone.0179340>.
- Bochert, R., Zettler, M.L., 2004. Long-term exposure of several marine benthic animals to static magnetic fields. *Bioelectromagnetics* 25, 498–502. <https://doi.org/10.1002/bem.20019>.
- Burrows, M.T., Gibson, R.N., Robb, L., Comely, C.A., 1994. Temporal patterns of movement in juvenile flatfishes and their predators: underwater television observations. *J. Exp. Mar. Biol. Ecol.* 177, 251–268. [https://doi.org/10.1016/0022-0981\(94\)90240-2](https://doi.org/10.1016/0022-0981(94)90240-2).
- Buyse, J., Hostens, K., Degraer, S., De Troch, M., Wittoeck, J., De Backer, A., 2023a. Increased food availability at offshore wind farms affects trophic ecology of plaice *Pleuronectes platessa*. *Sci. Total Environ.* 862, 160730. <https://doi.org/10.1016/j.scitotenv.2022.160730>.
- Buyse, J., Reubens, J., Host Ens, K., Ev En Degr Aer, S., Goossens, J., De Backer, A., 2023b. European plaice movements show evidence of high residency, site fidelity, and feeding around hard substrates within an offshore wind farm. *ICES J. Mar. Sci.*, fsad179 <https://doi.org/10.1093/ICESJMS/FSAD179> (1–13).
- Cada, G.F., Bevelhimer, M.S., Fortner, A.M., Riemer, K.P., Schweizer, P.E., 2012. Laboratory Studies of the Effects of Static and Variable Magnetic Fields on Freshwater Fish. <https://doi.org/10.2172/1038484> (USA).
- Ceinos, R.M., Chivite, M., López-Patiño, M.A., Naderi, F., Soengas, J.L., Foulkes, N.S., Míguez, J.M., 2019. Differential circadian and light-driven rhythmicity of clock gene expression and behaviour in the turbot, *Scophthalmus maximus*. *PLoS One* 14, e0219153. <https://doi.org/10.1371/journal.pone.0219153>.
- Chapman, E.C., Rochas, C.M., Piper, A.J., Vad, J., Kazanidis, G., 2023. Effect of electromagnetic fields from renewable energy subsea power cables on righting reflex and physiological response of coastal invertebrates. *Mar. Pollut. Bull.* 193, 115250. <https://doi.org/10.1016/j.marpolbul.2023.115250>.
- Cresci, A., Durif, C.M.F., Larsen, T., Bjelland, R., Skiftesvik, A.B., Browman, H.I., Nelson, K.E., 2022. Magnetic fields produced by subsea high-voltage direct current cables reduce swimming activity of haddock larvae *Melanogrammus aeglefinus*. *PNAS Nexus* 1, pgac175. <https://doi.org/10.1093/pnasnexus/pgac175>.
- Cresci, A., Durif, C.M.F., Larsen, T., Bjelland, R., Skiftesvik, A.B., Browman, H.I., 2023. Static magnetic fields reduce swimming activity of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae. *ICES J. Mar. Sci.* 0, 1–8. <https://doi.org/10.1093/icesjms/fsad205>.
- Dannheim, J., Bergström, L., Birchenough, S.N.R., Brzana, R., Boon, A.R., Coolen, J.W.P., Dauvin, J.-C., De Mesel, I., Derweduwen, J., Gill, A.B., Hutchison, Z.L., Jackson, A.C., Janas, U., Martin, G., Raoux, A., Reubens, J., Rostin, L., Vanaverbeke, J., Wilding, T.A., Wilhelmsson, D., Degraer, S., 2019. Benthic effects of offshore renewables: identification of knowledge gaps and urgently needed research. *ICES J. Mar. Sci.* 1–17. <https://doi.org/10.1093/icesjms/fsz018>.
- De Groot, S.J., 1971. On the interrelationship between morphology of the alimentary tract, food and feeding behaviour in flatfishes (Pisces: Pleuronectoformes). *Neth. J. Sea Res.* 5, 121–196. [https://doi.org/10.1016/0077-7579\(71\)90008-1](https://doi.org/10.1016/0077-7579(71)90008-1).
- De Luca, R., 2009. Lorentz force on sodium and chlorine ions in a salt water solution flow under a transverse magnetic field. *Eur. J. Phys.* 30, 459–466. <https://doi.org/10.1088/0143-0807/30/3/004>.
- DEFRA, 2024. Fisheries Management Plan for North Sea and Eastern Channel Mixed Flatfish. Policy Paper.
- Esteban, M.Á., Cuesta, A., Chaves-Pozo, E., Meseguer, J., 2013. Influence of melatonin on the immune system of fish: a review. *Int. J. Mol. Sci.* 14, 7979–7999. <https://doi.org/10.3390/ijms14047979>.
- Feng, J., Yang, J., Jiang, Z., Zhou, N., Liu, X., Zhang, G., Yan, X., Wang, J., Xu, X., Guo, S., Wang, T., 2023. Melatonin modulates the hypothalamic-pituitary neuroendocrine axis to regulate physiological color change in teleost fish. *Int. J. Biol. Sci.* 19, 2914–2933. <https://doi.org/10.7150/ijbs.81055>.
- Formicki, K., Sadowski, M., Tanski, A., Korzelecka-Orkisz, A., Winnicki, A., 2004. Behaviour of trout (*Salmo trutta* L.) larvae and fry in a constant magnetic field. *J. Appl. Ichthyol.* 20, 290–294. <https://doi.org/10.1111/j.1439-0426.2004.00556.x>.
- Formicki, K., Korzelecka-Orkisz, A., Tański, A., 2019. Magnetoreception in fish. *J. Fish Biol.* 95 (1), 73–91. <https://doi.org/10.1111/jfb.13998>.
- Frard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods Ecol. Evol.* 7, 1325–1330. <https://doi.org/10.1111/2041-210X.12584>.
- Ghodbane, S., Lahbib, A., Sakly, M., Abdelmelek, H., 2013. Bioeffects of static magnetic fields: oxidative stress, genotoxic effects, and cancer studies. *Biomed. Res. Int.* 2013. <https://doi.org/10.1155/2013/602987>.
- Gibson, R.N., 1973. Tidal and circadian activity rhythms in juvenile plaice, *Pleuronectes platessa*. *Mar. Biol.* 22, 379–386. <https://doi.org/10.1007/BF00391398>.
- Gibson, R.N., 1997. Behaviour and the distribution of flatfishes. *J. Sea Res.* 37, 241–256. [https://doi.org/10.1016/S1385-1101\(97\)00019-1](https://doi.org/10.1016/S1385-1101(97)00019-1).
- Gibson, R.N., Nash, R.D.M., Geffen, A.J., van der Veer, H.W., 2014. Flatfishes: Biology and Exploitation. Wiley. <https://doi.org/10.1002/9781118501153>.
- Gibson, R.N., Stoner, A.W., Ryer, C.H., 2015. The behaviour of flatfishes. In: Flatfishes: Biology and Exploitation: Second Edition. Wiley Blackwell, pp. 314–345. <https://doi.org/10.1002/9781118501153.ch12>.
- Gill, A.B., Huang, Y., Gloyne-Phillips, I., Metcalfe, J., Quayle, V., Spencer, J., Wearmouth, V., 2009. COWRIE 2.0 Electromagnetic Fields (EMF) Phase 2: EMF-Sensitive Fish Response to EM Emissions From Sub-sea Electricity Cables of the Type Used by the Offshore Renewable Energy Industry. COWRIE.
- Gill, A.B., Bartlett, M., Thomsen, F., 2012. Potential interactions between diadromous fishes of U.K. conservation importance and the electromagnetic fields and subsea noise from marine renewable energy developments. *J. Fish Biol.* 81, 664–695. <https://doi.org/10.1111/j.1095-8649.2012.03374.x>.
- Gill, A.B., Bremner, J., Vanstaen, K., Blake, S., Mynott, F., Lincoln, S., 2024. Limited evidence base for determining impacts (or not) of offshore wind energy developments on commercial fisheries species. *Fish Fish.* 26, 155–170. <https://doi.org/10.1111/faf.12871>.
- Harsanyi, P., Scott, K., Easton, B.A.A., de la Cruz Ortiz, G., Chapman, E.C.N., Piper, A.J. R., Rochas, C.M.V., Lyndon, A.R., 2022. The effects of anthropogenic Electromagnetic Fields (EMF) on the early development of two commercially important crustaceans, European lobster, *Homarus gammarus* (L.) and Edible crab, *Cancer pagurus* (L.). *J. Mar. Sci. Eng.* 10, 564. <https://doi.org/10.3390/jmse10050564>.
- Hermans, A., Winter, H.V., Gill, A.B., Murk, A.J., 2024. Do electromagnetic fields from subsea power cables affect benthic elasmobranch behaviour? A risk-based approach for the Dutch Continental Shelf. *Environ. Pollut.* 346, 123570. <https://doi.org/10.1016/j.envpol.2024.123570>.
- Hermans, A., Maris, T., Hubert, J., Rochas, C., Scott, K., Murk, A.J., Winter, H.V., 2025. From subsea power cable to small-spotted catshark *Scyliorhinus canicula*: behavioural effects of electromagnetic fields in tank experiments. *Mar. Environ. Res.* 107127. <https://doi.org/10.1016/j.marenvres.2025.107127>.
- Hong, B.S., Lee, H. Bin, Park, J.Y., Yoon, J.H., Lee, I.Y., Lim, H.K., 2021. Effects of photoperiod, water temperature, and exogenous hormones on spawning and plasma gonadal steroid in starry flounder, *Platichthys stellatus*. *Isr. J. Aquacult. Bamidgheh* 73. <https://doi.org/10.46989/001C.28425>.
- Hvidt, C.B., Klausrup, M., Leonhard, S., Pedersen, J., 2006. Fish Along the Cable Trace Nysted Offshore Wind Farm Final Report 2004.
- Jakubowska, M., Urban-Malinga, B., Otremba, Z., Andruliewicz, E., 2019. Effect of low frequency electromagnetic field on the behavior and bioenergetics of the polychaete *Hediste diversicolor*. *Mar. Environ. Res.* 150, 104766. <https://doi.org/10.1016/j.marenvres.2019.104766>.
- Kilfoyle, A.K., Jermain, R.F., Dhanak, M.R., Huston, J.P., Spieler, R.E., 2018. Effects of EMF emissions from undersea electric cables on coral reef fish. *Bioelectromagnetics* 39, 35–52. <https://doi.org/10.1002/bem.22092>.
- Kim, B.-H., Lee, C.-H., Hur, S.-W., Hur, S.-P., Kim, D.-H., Suh, H.-L., Kim, S.-Y., Lee, Y.-D., 2013. Long photoperiod affects gonadal development in olive flounder *Paralichthys olivaceus*. *Dev. Reprod.* 17, 241–246. <https://doi.org/10.12717/dr.2013.17.3.241>.
- Kimber, J.A., Sims, D.W., Bellamy, P.H., Gill, A.B., 2011. The ability of a benthic elasmobranch to discriminate between biological and artificial electric fields. *Mar. Biol.* 158, 1–8. <https://doi.org/10.1007/s00227-010-1537-y>.
- Kulczykowska, E., Warne, J.M., Balment, R.J., 2001. Day-night variations in plasma melatonin and arginine vasotocin concentrations in chronically cannulated flounder (*Platichthys flesus*). *Comp. Biochem. Physiol. Part A* 130, 827–834. [https://doi.org/10.1016/S1095-6433\(01\)00444-5](https://doi.org/10.1016/S1095-6433(01)00444-5).
- Kulkarni, G., Gandhare, W., 2014. Effect of extremely low frequency electromagnetic fields on brain activity. *Int. J. Med. Sci. Public Health* 3 (1). <https://doi.org/10.5455/ijmsph.2014.080520141>.
- Lee, S. Il, Aydin, K.Y., Spencer, P.D., Wilderbuier, T.K., Zhang, C.I., 2010. The role of flatfishes in the organization and structure of the eastern Bering Sea ecosystem. *Fish. Sci.* 76, 411–434. <https://doi.org/10.1007/s12562-009-0201-2>.
- Lerchl, A., Zachmann, A., Ali, M.A., Reiter, R.J., 1998. The effects of pulsing magnetic fields on pineal melatonin synthesis in a teleost fish (brook trout, *Salvelinus fontinalis*). *Neurosci. Lett.* 256, 171–173. [https://doi.org/10.1016/S0304-3940\(98\)00778-2](https://doi.org/10.1016/S0304-3940(98)00778-2).

- Loghmannia, J., Heidari, B., Rozati, S.A., Kazemi, S., 2015. The physiological responses of the Caspian kutum (*Rutilus frisii kutum*) fry to the static magnetic fields with different intensities during acute and subacute exposures. *Ecotoxicol. Environ. Saf.* 111, 215–219. <https://doi.org/10.1016/j.ecoenv.2014.10.020>.
- López-Olmeda, J.F., Blanco-Vives, B., Pujante, I.M., Wunderink, Y.S., Mancera, J.M., Sánchez-Vázquez, F.J., 2013. Daily rhythms in the hypothalamus-pituitary-interrenal axis and acute stress responses in a teleost flatfish, *Solea senegalensis*. *Chronobiol. Int.* 30, 530–539. <https://doi.org/10.3109/07420528.2012.754448>.
- López-Patiño, M.A., Rodríguez-Illamola, A., Gestó, M., Soengas, J.L., Míguez, J.M., 2011. Changes in plasma melatonin levels and pineal organ melatonin synthesis following acclimation of rainbow trout (*Oncorhynchus mykiss*) to different water salinities. *J. Exp. Biol.* 214, 928–936. <https://doi.org/10.1242/jeb.051516>.
- López-Patiño, M.A., Gestó, M., Conde-Sieira, M., Soengas, J.L., Míguez, J.M., 2014. Stress inhibition of melatonin synthesis in the pineal organ of rainbow trout (*Oncorhynchus mykiss*) is mediated by cortisol. *J. Exp. Biol.* 217, 1407–1416. <https://doi.org/10.1242/jeb.087916>.
- Lundberg, L., Sienkiewicz, Z., Anthony, D.C., Broom, K.A., 2019. Effects of 50 Hz magnetic fields on circadian rhythm control in mice. *Bioelectromagnetics* 40, 250–259. <https://doi.org/10.1002/bem.22188>.
- Macdonald, J.S., Waiwood, K.G., 1987. Feeding chronology and daily ration calculations for winter flounder (*Pseudopleuronectes americanus*), American plaice (*Hippoglossoides platessoides*), and ocean pout (*Macrozoarces americanus*) in Passamaquoddy Bay, New Brunswick. *Can. J. Zool.* 65, 499–503. <https://doi.org/10.1139/Z87-078>.
- Manzella, N., Bracci, M., Ciarapica, V., Staffolani, S., Strafella, E., Rapisarda, V., Valentino, M., Amati, M., Copertaro, A., Santarelli, L., 2015. Circadian gene expression and extremely low-frequency magnetic fields: an in vitro study. *Bioelectromagnetics* 36, 294–301. <https://doi.org/10.1002/bem.21915>.
- Martín-Robles, A.J., Whitmore, D., Sánchez-Vázquez, F.J., Pendón, C., Muñoz-Cueto, J. A., 2012. Cloning, tissue expression pattern and daily rhythms of *Period1*, *Period2*, and *Clock* transcripts in the flatfish Senegalese sole, *Solea senegalensis*. *J. Comp. Physiol. B.* 182, 673–685. <https://doi.org/10.1007/s00360-012-0653-z>.
- McClintock, B.T., Michelot, T., 2018. momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods Ecol. Evol.* 9, 1518–1530. <https://doi.org/10.1111/2041-210X.12995>.
- Metcalfe, J.D., Holford, B.H., Arnold, G.P., 1993. Orientation of plaice (*Pleuronectes platessa*) in the open sea: evidence for the use of external directional clues. *Mar. Biol.* 117, 559–566. <https://doi.org/10.1007/BF00349766>.
- Naisbett-Jones, C., Lohmann, L., Lohmann, C.M.F., Bruno, J.F., Sockman, K.W., Fodrie, J. F., Kenneth, J., 2022. Magnetic Navigation, Magnetoreception, and Migration in Fishes. University of North Carolina.
- Normandeau Associates Inc, Exponent Inc, Tricas, T., Gill, A., 2011. Effects of EMFs From Undersea Power Cables on Elasmobranchs and Other Marine Species.
- Ohman, M.C., Sigra, P., Westerberg, H., 2007. Offshore windmills and the effects of electromagnetic fields on fish. *Ambio* 36, 630–633. [https://doi.org/10.1579/0044-7447\(2007\)36](https://doi.org/10.1579/0044-7447(2007)36).
- Osipova, E.A., Pavlova, V.V., Nepomnyashchikh, V.A., Krylov, V.V., 2016. Influence of magnetic field on zebrafish activity and orientation in a plus maze. *Behav. Process.* 122, 80–86. <https://doi.org/10.1016/j.beproc.2015.11.009>.
- R Core Team, 2024. R: A Language and Environment for Statistical Computing.
- Raoux, A., Tecchio, S., Pezy, J.-P., Lassalle, G., Degraer, S., Wilhelmsson, D., Cachera, M., Ernande, B., Le Guen, C., Haraldsson, M., Ben, 2017. Benthic and fish aggregation inside an offshore wind farm: which effects on the trophic web functioning? *Ecol. Indic.* 72. <https://doi.org/10.1016/j.ecolind.2016.07.037>.
- Richardson, N.E., McCleave, J.D., Albert, E.H., 1976. Effect of extremely low frequency electric and magnetic fields on locomotor activity rhythms of Atlantic salmon (*Salmo salar*) and American eels (*Anguilla rostrata*). *Environ. Pollut.* 10, 65–76. [https://doi.org/10.1016/0013-9327\(76\)90096-3](https://doi.org/10.1016/0013-9327(76)90096-3).
- Rzempoluch, J., Goddard, K., Chaudhary, S., Callender, G., Olsen, R.G., Dix, J., Lewin, P., Renew, D., 2025. Electric fields induced by water movement in proximity to HVDC submarine cables. *IEEE J. Ocean. Eng.* <https://doi.org/10.1109/JOE.2025.3556152>.
- Sánchez-Vázquez, F.J., López-Olmeda, J.F., Vera, L.M., Mígaud, H., López-Patiño, M.A., Míguez, J.M., 2019. Environmental cycles, melatonin, and circadian control of stress response in fish. *Front. Endocrinol. (Lausanne)* 10. <https://doi.org/10.3389/fendo.2019.00279>.
- Scott, K., Harsanyi, P., Lyndon, A.R., 2018. Understanding the effects of electromagnetic field emissions from Marine Renewable Energy Devices (MREDS) on the commercially important edible crab, *Cancer pagurus* (L.). *Mar. Pollut. Bull.* 131, 580–588. <https://doi.org/10.1016/j.marpolbul.2018.04.062>.
- Sedigh, E., Heidari, B., Roozati, A., Valipour, A., 2019. The effect of different intensities of static magnetic field on stress and selected reproductive indices of the zebrafish (*Danio rerio*) during acute and subacute exposure. *Bull. Environ. Contam. Toxicol.* 102, 204–209. <https://doi.org/10.1007/s00128-018-02538-1>.
- Snoek, R., Böhm, C., Dideren, K., Lengkeek, W., Driessen, F., Maathuis, M., 2020. Potential Effects of Electromagnetic Fields in the Dutch North Sea. Phase 2 - Pilot Field Study.
- Stenberg, C., Støttrup, J.G., Van Deurs, M., Berg, C.W., Dinesen, G.E., Mosegaard, H., Grome, T.M., Leonhard, S.B., 2015. Long-term effects of an offshore wind farm in the North Sea on fish communities. *Mar. Ecol. Prog. Ser.* 528, 257–265. <https://doi.org/10.3354/meps11261>.
- Stevens, R.G., Davis, S., 1996. The melatonin hypothesis: electric power and breast cancer. *Environ. Health Perspect.* 104 (Suppl. 1), 135–140. <https://doi.org/10.1289/ehp.96104s1135>.
- Tang, J., Zhao, W., Chi, J., Liu, G., Yu, X., Bian, L., 2015. Effects of magnetic treatment on growth and immune and digestive enzyme activity in the juvenile sea cucumber *apostichopus japonicus* (Selenka). *Aquaculture* 435, 437–441. <https://doi.org/10.1016/j.aquaculture.2014.10.022>.
- Taormina, B., Bald, J., Want, A., Thouzeau, G., Lejart, M., Desroy, N., Carlier, A., 2018. A review of potential impacts of submarine power cables on the marine environment: knowledge gaps, recommendations and future directions. *Renew. Sust. Energ. Rev.* 96, 380–391. <https://doi.org/10.1016/j.rser.2018.07.026>.
- ter Hofstede, R., Driessen, F.M.F., Elzinga, P.J., Van Koningsveld, M., Schutter, M., 2022. Offshore wind farms contribute to epibenthic biodiversity in the North Sea. *J. Sea Res.* 185, 102229. <https://doi.org/10.1016/j.seares.2022.102229>.
- Tilden, A.R., Brauch, R., Ball, R., Janze, A.M., Ghaffari, A.H., Sweeney, C.T., Yurek, J.C., Cooper, R.L., 2003. Modulatory effects of melatonin on behavior, hemolymph metabolites, and neurotransmitter release in crayfish. *Brain Res.* 992, 252–262. <https://doi.org/10.1016/j.brainres.2003.08.053>.
- Vandendriessche, S., Derweduwen, J., Hostens, K., 2015. Equivocal effects of offshore wind farms in Belgium on soft substrate epibenthos and fish assemblages. *Hydrobiologia* 756, 19–35. <https://doi.org/10.1007/s10750-014-1997-z>.
- Verheijen, F.J., De Groot, S.J., 1967. Diurnal activity pattern of plaice and flounder (*Pleuronectidae*) in aquaria. *Neth. J. Sea Res.* 3, 383–390. [https://doi.org/10.1016/0077-7579\(67\)90011-7](https://doi.org/10.1016/0077-7579(67)90011-7).
- Winter, H.V., Aarts, G., van Keeken, O.A., 2010. Residence Time and Behaviour of Sole and Cod in the Offshore Wind farm Egmond aan Zee (OWEZ). Netherlands.
- Woodruff, D.L., Schultz, I.R., Marshall, K.E., Ward, J.A., Cullinan, V.I., 2012. Effects of Electromagnetic Fields on Fish and Invertebrates. Task 2.1.3: Effects of Aquatic Organisms. Fiscal Year 2011 Progress Report. Environmental Effects of Marine Hydrokinetic Energy, Environmental Effects of Marine and Hydrokinetic Energy. Richland, Washington, USA.
- Wyman, M.T., Peter Klimley, A., Battleson, R.D., Agosta, T.V., Chapman, E.D., Haverkamp, P.J., Pagel, M.D., Kavet, R., 2018. Behavioral responses by migrating juvenile salmonids to a subsea high-voltage DC power cable. *Mar. Biol.* 165. <https://doi.org/10.1007/s00227-018-3385-0>.
- Zhao, C., Xu, S., Liu, Y., Feng, C., Xiao, Y., Wang, Y., Liu, Q., Li, J., 2022. Changes of melatonin and its receptors in synchronizing turbot (*Scophthalmus maximus*) seasonal reproduction and maturation rhythm. *Acta Oceanol. Sin.* 41, 84–98. <https://doi.org/10.1007/s13131-021-1923-y>.
- Zhdanova, I.V., Reeb, S.G., 2005. Circadian rhythms in fish. In: Sloman, K.A., Wilson, R. W., Balshine, S. (Eds.), *Fish Physiology*. Elsevier, pp. 197–238. [https://doi.org/10.1016/S1546-5098\(05\)24006-2](https://doi.org/10.1016/S1546-5098(05)24006-2).
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.