ELSEVIER

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev



From subsea power cable to small-spotted catshark *Scyliorhinus canicula*: Behavioural effects of electromagnetic fields in tank experiments

Annemiek Hermans ^{a,*}, Ties Maris ^a, Jeroen Hubert ^{a,c}, Corentine Rochas ^d, Kevin Scott ^d, Albertinka J. Murk ^a, Hendrik V. Winter ^b

- ^a Marine Animal Ecology Group, Wageningen University, P.O. Box 338, 6700 AH, Wageningen, the Netherlands
- ^b Wageningen Marine Research, Wageningen University and Research, P.O. 68, 1970 AB, IJmuiden, the Netherlands
- ^c Institute of Biology Leiden, Leiden University, Sylviusweg 72, 2333 BE, Leiden, the Netherlands
- ^d St Abbs Marine Station, The Harbour, St Abbs TD14 5PW, UK

ARTICLE INFO

Keywords: Elasmobranchs Behavioral response Benthic species environmental impact Offshore wind marine renewable energy development

ABSTRACT

Subsea power cables are expanding in number and capacity due to increasing demand to transport offshore generated energy. Energy transported through a cable creates an electromagnetic field (EMF). Elasmobranchs are dependent on their perception of the earth's magnetic field and biologically induced electric fields, for orientation, navigation, locating conspecifics and detecting prey. EMF levels from subsea power cables will add to natural signals potentially disrupting elasmobranch perception, but the effects are not fully understood. Reported behavioural responses include attraction, disturbance, and indifference, varying with exposure type, level and experimental set-up. In this study, the effects of EMF on swimming behaviour of 14 individual small-spotted catshark *Scyliorhinus canicula* were studied. All sharks were exposed to field-relevant EMF gradients cables in three trials: $15.0~\mu$ T AC, $19.6~\mu$ T DC, and a control treatment. Sharks showed no startle response to EMF onset, did not alter movement towards or away from the cable, and crossed it as frequently as in control trials. Hidden Markov Models showed that behavioural states were best explained by EMF treatment, trial order and sex. Sharks showed 25 % less time transiting during DC trials when compared to AC and control trials. These findings indicate reason for further refined studies to better determine behavioural effects from direct current subsea power cables with *S. canicula*, for example using tagging studies. In addition, exploring effects on other species will help obtain a broader understanding of the potential impacts of EMF on benthic elasmobranchs.

1. Introduction

Offshore energy production plays a crucial role in the transition to renewable energy and is expanding rapidly. To scale up from 16 GW offshore wind energy today, to 61 GW in 2030 and the projected 340 GW by 2050 in European Union waters, subsea power cables (SPC) must transport over 20 times more wind generated power (European Court of Auditors, 2023; Wind Europe, 2023). SPC generate electromagnetic fields (EMF) which consist of an electric field (between two charged particles) and a magnetic field (between to magnetic poles). The direct electric field is confined inside the cable due to shielding. The magnetic field protrudes into the environment and generates an induced electric field in flowing water, which is most notable for alternating current (AC) and negligible for direct current (DC) cables. AC cables carry current that periodically reverses direction (50 Hz in Europe), generating a

time-varying magnetic field, while DC cables carry constant current, producing a steady magnetic field that can interact with the Earth's magnetic field. As an EMF is a magnetic field generated around moving charged particles, the electric and magnetic field components are closely related. Naturally, magnetic fields are omnipresent, such as the Earth's magnetic field (25–65 μ T), and create induced electric fields in the marine environment (Gill et al., 2014; Hayakawa et al., 2004). In 2030, an estimated 5.5 % of the Dutch continental shelf will be influenced by SPC-generated EMF (Hermans et al., 2024). The range and intensity of EMF depend on cable characteristics, amount of power transported, and the power type e.g. AC or DC (Hutchison et al., 2021; Normandeau et al., 2011; Taormina et al., 2018). Modelling indicates that EMF from export SPC can be detectable above background levels, up to 60 m from high voltage 220 kV AC (export) cables and up to 125 m for bundled (phase conductors joint together) high voltage 525 kV DC cables, decreasing

E-mail address: Annemiek.hermans@wur.nl (A. Hermans).

^{*} Corresponding author.

approximately as an inverse square of the distance to the cable. The potential exposure of marine organisms to EMF depends on the burial depth and the cable configuration. Cables that are buried deeper result in lower EMF levels on the seabed and in the water column. Cables within an offshore windfarm, or infield cables, are AC and have a network-like structure. Conversely, export cables cross long sections perpendicular to the coast and can be both AC (closer to shore) or DC (further from shore). EMF from SPC might affect the way electro- or magneto sensitive organisms perceive the environmental or biological cues and it is therefore possible that this influences their behaviour.

Various marine taxa can detect electrical or magnetic fields, including crustaceans, sea turtles, birds, mammals and fish, e.g. eel, salmon and sturgeon (Albert et al., 2020; Nyqvist et al., 2020; Wiltschko and Wiltschko, 2005). The only taxonomic group that is known to detect both electrical and magnetic fields are elasmobranchs; i.e. sharks, rays and skates (Anderson et al., 2017; Collin et al., 2015; Crooks, 2019; Meyer et al., 2005). Elasmobranchs use bioelectric fields for detection of predators, conspecifics and prey, and the geomagnetic field for navigation (local and long-distance migrations) (Ball et al., 2016; Kalmijn, 1971; Kempster et al., 2013; Klimley, 1993; Klimley et al., 2005; Newton and Kajiura, 2017, 2020; Sisneros and Tricas, 2002). All species of this subclass have highly sensitive ampullae of Lorenzini which are used for electroception (Newton et al., 2019). It is not yet understood how magnetic field reception works, but three empirical drivers are hypothesised: (1) induction-based electroreception (2) magnetite-based magnetoreception and (3) radical pair mechanism (Albert et al., 2022; Anderson et al., 2017; Nyqvist et al., 2020). SPC routes intersect with elasmobranchs' habitat. This is especially relevant for bottom-dwelling (benthic) elasmobranchs, as their close proximity to cables in the seabed increases the rate of encountering elevated EMF (Hermans et al., 2024; Hutchison et al., 2020; Orr, 2016).

Elasmobranchs play a vital role in many ecosystems, acting as a link between various trophic levels and regulating prey populations (Heithaus et al., 2008). Many elasmobranchs are threatened by anthropogenic pressures such as bycatch in fisheries or habitat destruction (Dulvy et al., 2021; Gallagher et al., 2012; Pacoureau et al., 2021; Stevens, 2000). This makes elasmobranchs a priority taxon under several regulatory frameworks including the Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR), the Common fisheries policy of the European Union, the Convention on Migratory Species (CMS) and the Convention in Trade of Endangered Species (CITES).

Elasmobranchs are highly electrosensitive and are reportedly able to detect down to a threshold limit of 5 nV/cm (Kalmijn, 1971). The magneto sensitivity is hypothesised to be at least 5 nT to perceive changes in the earth magnetic field needed for local and large-scale orientation (Hermans et al., 2024; Nyqvist et al., 2020). Behavioural responses to EMF depends on species, intensity, cable characteristics and frequency distribution of the signal (Bedore and Kajiura, 2013). A first exploration indicates that elasmobranchs may be unable to discriminate between artificial (dipole electrode) and natural (live crabs) EMF (Kimber et al., 2011). A variety of behavioural changes could be elicited from SPC-induced EMF during key activities such as foraging, mating, and/or migration (Hermans et al., 2024; Hutchison et al., 2020; Taormina et al., 2018). Mesocosm experiments indicated changes in foraging, or exploratory behaviour and shifts in habitat use in small-spotted catshark (Scyliorhinus canicula), thornback ray (Raja clavata) and little skate (Leucoraja erinacea) (Gill, 2009; Hutchison et al., 2020). Alterations in migratory patterns, such as course deviations and delays have been observed in magnetically sensitive species such as Chinook salmon (Oncorhynchus tshawytscha) and European eel (Anguilla anguilla) (Öhman et al., 2007; Westerberg and Lagenfelt, 2008; Wyman et al., 2018) and may also occur in elasmobranchs. Changes in activity levels induced by anthropogenic EMF stimuli could lead to less time foraging, reduced overall fitness, or an increased risk of predation due to reduced mobility, as suggested from experiments with crabs (Scott et al.,

2021). Repeated behavioural changes (e.g. delays in migration, reduced swimming depth) when crossing export SPC might increase predation risk and hinder migration, potentially delaying encounters with important ecological cues like feeding or mating opportunities.

To study the potential effects of EMF on sharks, S. canicula (Linnaeus, 1758) was chosen as the test species due to its small size, hardiness and high abundance. S. canicula is a demersal shark and is very common in the north-east Atlantic (Compagno et al., 2005). It can be obtained relatively easily as it is commonly caught as bycatch of commercial fishing along European coasts (Revill et al., 2005) and is suited to be held in captivity. It exhibits opportunistic scavenging feeding behaviour as well as engages as an active predator, interacting with the substratum to consume a diverse array of benthic species (Heessen et al., 2015; Martinho et al., 2012; Šantić et al., 2012). It frequents sand, gravel, or mud substrates, mostly from coastal areas down to depths of 400m (Finucci et al., 2020), from the west coast of Norway down to the Senegalese coast (Compagno et al., 2005). This shark is known to be electrosensitive as shown by Kalmijn (1972, 1971) and Peters and Evers (1985). While the magnetosensitivity of most shark species, including S. canicula, has not been shown, its ability to detect electric fields suggests that it might also be sensitive to magnetic fields, as these are closely related senses in elasmobranchs (Nyqvist et al., 2020). The wide habitat range and relatively small home range of S. canicula makes it probable that SPC are encountered frequently, e.g. resulting in a high rate of encounter (North Sea Energy, 2023; Ocean Biodiversity Information System (OBIS), 2023; Papadopoulo et al., 2023; Rodriguez-Cabello et al., 2004).

The objective of this study was to determine the behavioural responses of *S. canicula* to AC and DC generated EMF at levels comparable to realistic in situ conditions around SPC. Sharks were exposed during three trials, each separated by three weeks, to either an AC or DC treatment, or a control. Spatial utilization disparities (attraction or avoidance to EMF), frequency of EMF crossings, variance in distance travelled, startle response, shelter use, and alterations in behavioural states were quantified and compared to the control scenario.

2. Method & materials

2.1. Animals and holding conditions

In April 2023, 15 S. canicula were line-caught by anglers off the coast of Port Logan (Dumfries and Galloway, Scotland, UK). Animals were kept in fishing ponds prior to being transported to St Abbs Marine Station. All animals underwent a visual health check upon arrival (ectoparasite presence, abrasions or lesions, and overall fitness) to ensure animal condition and assess whether the animals were at the desired level of fitness for participation in the experiments. Individuals were subsequently sexed (17M:14F), weighed, measured (total length), photographed and tagged using T-bar anchor tags (Hallprint fish tags) to allow for individual identification. All animals were held together in a 13 000 L tank measuring $7.5x1.7 \times 1.0$ m (LxWxH), provided with a constant flow of ambient temperature seawater, pumped from the North Sea in the Berwickshire Marine Reserve. Several recirculation filtration systems (Tropical Marine Centre) were used, providing UV, mechanical and biological filtration to the tank. Additional Fluval FX6 filters and air stones were added to maintain good water quality and oxygen levels, respectively. pH, ammonia, nitrite and nitrate were assessed weekly. The holding facility had a transparent roof, allowing the animals to be exposed to a natural photoperiod. Over the period of the experiment, there were an average of 17.33 \pm 0.25 (sd) hours of daylight. Environmental enrichment, in the form of PVC shelter tubes (Ø 15 and 25 cm), rocks and fronds of seaweed were provided. Animals were fed 3 % of their bodyweight per week, late in the afternoon every other day, with a diet of Californian squid (Loligo opalescens), king prawn (Pennaeus vannamei) and sand eel (Amnodytes marinus). Any food left uneaten was removed after 24 h and prior to the next batch of feeding. Supplements,

including vitamins and iodine were added to the feeding regimen. Visual welfare checks were conducted on each individual daily.

2.2. Technical set-up

(a)

The experimental tank was custom-built $15.0x1.65 \times 1.60$ m (LxWxH), filled to a water level of 0.90 m and made of non-ferrous materials (fibreglass and wood), with opaque sides to prevent any visual disturbances from outside (Fig. 1). All possible sources for electromagnetic interference were shielded with radio-frequency identification (RFID) EMF shielding fabric (Lexiangnong, 20 % Nylon copper, 80 % polyester mesh and Lvfeier, 100 % Nylon). Two PVC pipes (1m \emptyset 0.15 m) were placed at the 5 and 10 m mark to provide shelter opportunities during the trials. To monitor behaviour during the trials, 16 remote controlled infra-red cameras (Reolink RLC-810A) were suspended above the tank and recorded behaviour throughout the trials. The cameras did not interfere with the geomagnetic or solenoid

generated EMF. The water was controlled in a closed recirculation system during the trials. Between trials, 50 %–100 % of the tank volume was replenished with seawater, depending on the tide, with full exchanges only possible at high tides. Inflowing seawater was filtered using filter socks to prevent sediment build-up.

The electromagnetic field was generated by two solenoids fixed to an aluminium frame connected to a Keysight N6715C DC Power Analyser with two 20 W Source/Measure units. Both solenoids were $1.9\times2.9~m$ (WxH) and contained 32 turns of $1.25~mm^2$ copper wire. The solenoid system was placed at the 5-m mark of the 15-m experimental tank, to create an EMF gradient in the tank (Fig. 1). In the DC configuration, only the lower solenoid was in use and the maximum field generated was $19.6~\mu T$. The magnetic field levels were measured at 135~points in the tank, before any experimentation began, with a Twinleaf VMR sensor and SYNC4 data acquisition system (Fig. S1c). In AC configuration, one solenoid was located on the horizontal frame and the other on the vertical frame. By controlling the two solenoids, coupled with the same

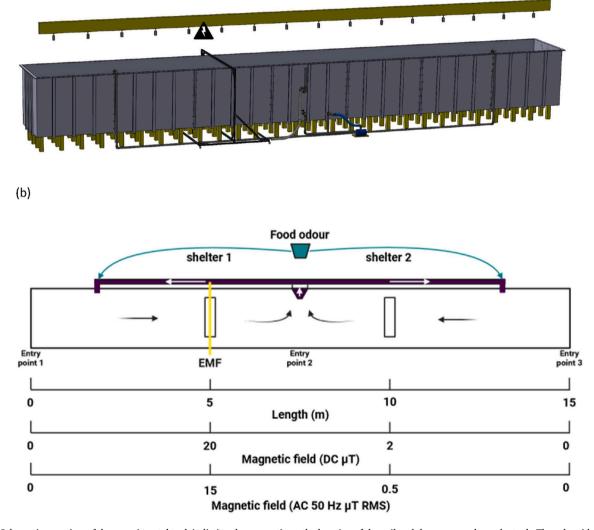


Fig. 1. (a) Schematic overview of the experimental tank indicting the proportions, the location of the coil and the cameras above the tank. The solenoids (enclosed in the black frame) are indicated by the power symbol in the black triangle and located at the 5m mark (b) Top view schematic overview of the experimental tank (15m \times 1.65m x 1.6m; L x W x H). Sharks were entered at one of three randomized entry points. Two PVC pipe shelters (1m, 25 \varnothing cm) were located in the tank at 5 and 10m and the solenoid system (yellow line), to induce the EMF, was situated at the 5m shelter. Food odour was added at the start of treatment time (Fig. 2b) to promote foraging behaviour, which was dispersed to the far ends of tank using a water pump. Black and white arrows indicate the water flow through the tank during experiments. Green arrows indicate the entry points of food odour. An indication of the total magnetic field intensity for both DC, after subtraction of the geomagnetic field (solid line) and 50 Hz AC trials (broken line) at the mid-width and bottom of the tank. Image created with https://BioRender.com. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

frequency of 50 Hz, but with a phase difference of 90°, a rotating field was generated in the water volume around the frame, similar to a 3phase AC transport cable. By setting the amplitude of the current in the horizontal solenoid twice as strong as the amplitude of the vertical solenoid, a circular rotating field was created in the centre of the vertical solenoid. The maximum AC magnetic field generated was 15.0 μT Root Mean Square (RMS) (Fig. 1b and S1b in more detail). The difference in AC and DC level can be explained by the physical changes in the coil positioning. The magnetic field generator was designed and fabricated by the Netherlands Organisation for Applied Scientific Research (TNO). The magnetic field intensities were modelled to field measurements of the high voltage 220 kV 50 Hz AC Borssele offshore wind export cable (NL) and the high voltage 525 kV bundled DC Norned interconnector cable, measured at 1m from the cable (minimum required burial depth), data used with permission from T.S.O. TenneT. The average static ambient field (geomagnetic field) in the experimental facility was 50.7 μT (Fig. S1a).

2.3. Experimental procedure

The number of sharks (15) was selected to ensure the experiment could be conducted within a three-month period, minimizing potential seasonal effects while maintaining sufficient explanatory power. One individual died due to reasons unrelated to the experiment and was subsequently excluded from the analyses. Each of the resulting 14 sharks (weight: 587.7 \pm 83.2g, length: 55.3 \pm 6.1 cm), were used for three trials in the experimental tank supplied with ambient seawater (13.2 \pm 1.2 °C, 33.9 \pm 0.2 salinity ppt, 109.4 \pm 8.7 % dissolved oxygen): receiving three treatments (one per trial) in a randomized order 1) EMF resulting from AC, 2) EMF resulting from DC, and 3) EMF not powered (Control). The experimental tank was thoroughly cleaned by siphoning the waste out once halfway through the trials to remove sediment and improve visibility. Pilot trials were carried out to determine the most appropriate acclimatisation period, aimed at returning to 'normal' behaviour. The acclimatisation time was set accordingly for 1h:30m to 1h:45m (depending on the speed at which the animal was caught). Considering the twilight and nocturnal activity pattern of S. canicula (Papadopoulo et al., 2023), trials were conducted at dusk, starting 2h:45m before sunset (Fig. 2). This schedule was selected, as opposed to nighttime trials, as preliminary trial runs indicated that the animal tracking software was unable to identify the shark less than 45 min before sunset due to a shortage of natural light and ineffectiveness of infra-red. In treatment trials, EMF (either AC or DC) was remotely activated for 2:00 h after acclimatisation, ending 45 min before sunset to ensure proper animal tracking. On the day of the trial, the individual was not fed, to ensure that it would respond to the olfactory incentive during the trial. 500 mL of food odour was added to the experimental tank at the start of the treatment period using a DD H2Ocean P1 dosage pump to

promote movement and foraging behaviour during the trials. The olfactory stimulus was prepared by defrosting five frozen king prawns (*Pennaeus vannamei*) in 500 mL seawater. This was added at the inflow of the circulation pump allowing the odour to enter the experimental tank through the outflow at both ends of the tank (Fig. 1 bottom). A shark was released in the experimental tank at a randomly selected position, either in the middle or one of the far ends, to mitigate entry-side bias. A minimum interval of three weeks between trials was selected for each individual to ensure sufficient time for the sharks to regain naivety, and avoid habituation, based on Kimber et al. (2014). The order of trials was randomized, as an animal being introduced to a novel arena may not behave in the same way than when introduced to the same arena again (Dhellemmes et al., 2021; Finger et al., 2016). The animal remained in the experimental tank until the next morning when it was returned to the holding tank.

2.4. Data processing and analysis

The footage recorded from each camera was stitched together using Adobe Premiere Pro (version 22.2.0) to one 3h45m file (acclimatisation and treatment) with a full overview of the entire experimental tank. Sharks in each trial were tracked 25 times per second using Ethovision XT Pro software by Noldus, resulting in a single file with x and y coordinates over time for each trial. The tracking was conducted automatically with the software and manually adjusted when the software failed to identify the shark due to decreased light availability, splashing of the water surface or proximity of the animal to the experimental tank's edge. Further analyses were carried out using R (4.2.1). Initial exploration of the data was done using heatmaps and showing the trajectory of the shark in each trial. The behavioural parameters explored were: [1] distance to the highest EMF level in the gradient in cm (hereafter: EMF highpoint) [2] times crossing the EMF highpoint per km travelled [3] total distance travelled per hour [4] startle response (immediately visible response) when EMF was turned on after acclimatisation period (yes/no) and [5] shelter use in minutes. The acclimatisation period was not included in the data analysis as shark behaviour was expected to be influenced by handling. The unit crossings per km was selected (parameter 2) as sharks exhibiting higher swimming activity would inherently encounter the EMF more frequently and thus the number of crossings was normalized by dividing it by the total distance covered. We analysed these response variables in generalized linear mixed models with a Gamma error distribution and log-link function. Sharks' ID were included as random effect, and their body length (cm), weight (gram), sex, EMF treatment (AC, DC, Control), order of the treatments, and interaction between weight and EMF treatment as covariates in the full model. The best model was selected based on the lowest AICc score of all possible covariate combinations. When EMF treatment was not part of the best model, it was added to the final model

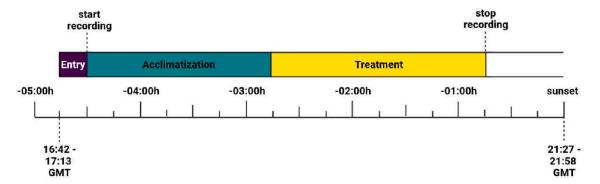


Fig. 2. Overview of the time schedule used during the trials. Time of entry was between 4h45m and 4h30m before sunset, after which sharks were given 1h45m to acclimatize to the new environment. The treatment lasted 2h and finished 45m before sunset to ensure proper light conditions for cameras. Food odour was added at the start of experimental treatment to promote foraging behaviour. Trials ran from May 22nd until July 14th 2023.

anyway because the study was designed to get insight into EMF effects. The final models were ran and all covariate effects reported. For the EMF treatment effects, a Tukey post hoc test was conducted for pairwise comparisons. Environmental factors could have influenced activity levels (Hyatt et al., 2018; Papadopoulo et al., 2023; Schlaff et al., 2014) but these factors showed limited variation over the experimental period, and were therefore not included in subsequent analysis. Individual factors such as sex, body length, and weight, which may have impacted overall behaviour and specifically foraging behaviour (e.g. researching different food types and sizes) were used in analyses (Papadopoulo et al., 2023; Rodriguez-Cabello et al., 2004; Šantić et al., 2012; Sims et al., 2006).

Discrete-time hidden Markov models (HMMs) were used to examine if the EMF treatment affected the time spent in various behavioural states by the sharks. The HMMs were applied in R using the package 'momentuHMM' (version 1.5.5; McClintock & Michelot, 2018). Initially, the sharks' horizontal step length (speed) (Fig. 3a) and turning angle (Fig. 3b) were used to fit the HMMs, but because the swimming behaviour and derived behavioural states were strongly influenced by the corners of the experimental tank, a variable stating whether the shark was within 1 m from one of the far ends of the experimental tank was added (Fig. 3c). HMM null models were fitted with 1 up to 4 states and the AIC scores were compared to determine the number of behavioural states that were best supported by the models. The model with 4 states had the best fit (Table S1) and the behavioural states were labelled as follows: (1) Inactive; low step length and a flat distribution of turning angles, (2) Locally active; moderate step length and a low degree of directionality, (3) Transiting; large step lengths and highly directional swimming, (4) active swimming at the ends of the experimental tank, moderate step length and a low degree of directionality, confined within 1 m of the experimental tank ends (Fig. 3). Combinations of the covariates EMF treatment (AC, DC, Control), order, weight, sex, and length

were added as state transition probability covariates to select the best fitting model. Comparison of AIC scores indicated that the inclusion of Treatment, Order, and Sex resulted in the best fitting model (Table S2). For this model, stationary state probabilities with 95 % confidence intervals were determined. When intervals of two levels of a covariate did not overlap, these levels were considered significantly different.

3. Results

3.1. No evident attraction or avoidance

Overall, considerable inter- and intraindividual variation in sharks behaviour during EMF exposure was observed (Figures S2, S3 and S7). The mean distance from the EMF highpoint (mean \pm standard deviation) was measured at 594 \pm 182 cm for AC, 514 \pm 171 cm for DC, and $586\pm199~\text{cm}$ for the control group. These differences were not significant (all pairwise comparison p-values ≥0.34, Fig. 4 top panel, distance to EMF), suggesting no attraction or avoidance behaviour. The weight of the shark was part of the best model and had a non-significant negative correlation with the distance from the EMF (intercept: 6.46, slope = $-1.35*10^{-4}$, p-value: 0.65). The number of EMF highpoint crossings per km was 44.6 \pm 21.3 for AC, 41.4 \pm 26.2 for DC, and 43.2 \pm 21.8 for control treatments, with no significant difference (all pairwise comparison p-values >0.99, Fig. 4 middle panel, number of times EMF highpoint crossed). The weight of the shark was part of the best model and had a non-significant positive correlation with the number of crossings (intercept: 2.98, slope: 1.39*10-3, p-value: 0.45). The distance travelled per hour was 622 \pm 344 m for AC, 590 \pm 553 m for DC, and 569 ± 435 m for control treatments. These differences were not significant (all pairwise comparison p-values >0.99, Fig. 4 lower panel, Distance travelled) The weight was again part of the best model with a nonsignificant positive correlation with the distance travelled (intercept:

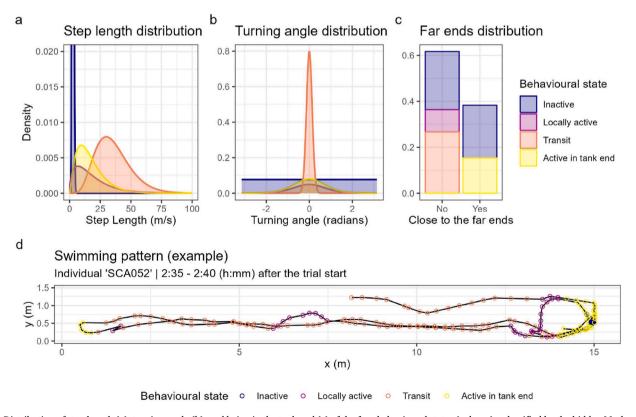


Fig. 3. Distribution of step length (a), turning angle (b), and being in the tank end (c) of the four behavioural states (colours) a classified by the hidden Markov model (HMM). We used the behavioural state 'Active in tank end' (yellow) to compensate for the 'tank effect': forced turning behaviour at the ends of the tank. (d) An overview of a 5-min swimming track, with the classified behavioural states. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

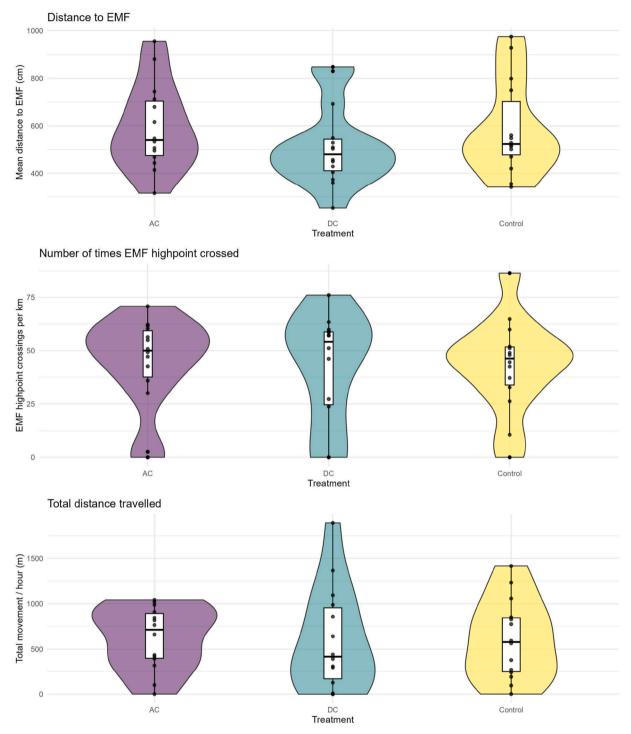


Fig. 4. Violin plots showing the mean distance to the centre of the electromagnetic field (EMF) (top), the number of times the centre of the (EMF) was crossed per km travelled (middle), and total distance travelled in meters per hour (bottom) for alternating current (AC), direct current (DC) and control treatments. Top and bottom figures are corrected for total treatment time as some trials were cut short due to a lack of visibility. No statistical significance was found between the treatments in all three parameters. The control trials are close to a random distribution as the experimental tank housed an a-symmetric setup which resulted in relatively more data closer to coil (0–5 m) than far from the coil (10–15 m).

5.81, slope: $1.07*10^{-3}$, p-value: 0.73). Furthermore, there were no startle responses (indicated by a sudden change in behaviour) observed when the EMF was turned on after the acclimatisation period. During the trials, only two sharks made use of the shelters for 59 min (SCA069, trial 29, Control) and 8 min (SCA069, trial 43, DC) respectively, both during the acclimatisation period, indicating that EMF did not increase sheltering behaviour. Because of the lack and scarcity of startle responses and hiding behaviour respectively, no inferential statistics were

performed here.

3.2. Changes in behavioural states

Overall, on average, sharks spent almost half of the trial time being inactive, a quarter of the time transiting, and the remainder of the time was spent active in the tank ends or locally active. During the DC treatment, sharks were spend significantly more time being inactive, and

spend significantly less time transiting and moving at the experimental tank ends, compared to both AC and control conditions (Fig. 5). The total distance covered during the trials did not differ significantly (Fig. 4 lower panel), indicating a higher swimming speed for sharks under DC conditions when active. This is also evident from the step length distribution during the locally active and transit states, with longer step lengths during DC trials (Fig. 6 for all states). Sharks were mostly inactive during the first trial, which significantly changed as the number of trials progressed, regardless of the treatment order which was randomized (Fig. S4). No significant effects of sex on the time spent in the different behavioural states was found (Fig. S5).

4. Discussion

Behavioural responses of *S. canicula* to SPC-related EMF stimuli were studied in a controlled experiment. No attraction or avoidance behaviour was observed in response to EMF exposure, nor were any differences detected in spatial utilization. No shark showed a startle response when turning on the EMF and there was no reluctance to cross the EMF or alterations in shelter use. Based on HHM analysis, sharks subjected to the DC EMF showed a 25 % reduction in transiting time coupled with an 30 % increase in inactivity and on average higher swimming speeds.

4.1. Movement behaviour

There were no signs of attraction or avoidance to EMF, contrary to suggestions by other studies with comparable field intensities. Barry et al. (2008) showed anecdotal evidence attraction of 126 longnose skates (*Raja rhina*) around an unused power and data cable (MARS, no

Histogram of step length distribution For the states locally active and transit

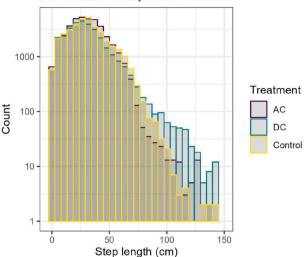


Fig. 6. The step length distribution, as histogram, during the experimental treatment, for the locally active and transit behavioural state only. For the DC trials a higher amount of larger step lengths can be seen, indicating a higher swimming speed when they are active.

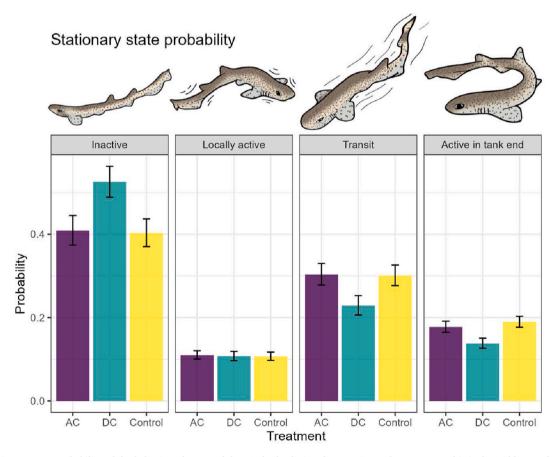


Fig. 5. The stationary state probability of the behavioural states of the 14 sharks during the experimental treatments. This is the Hidden Markov Model (HMM) output for the best model fit which included the parameters treatment, sex and trial order. The error-bars represent the 95 % confidence interval, when the error-bars of different treatment do not overlap, there is a significant treatment effect. The sharks were significantly more inactive, transited less, and spend less time active in the tank ends during the DC treatment.

cable specifications provided), but no such aggregation was shown when the cable was in use suggesting there no longer was an attraction to the SPC. Gill et al. (2009) showed attraction to a 50 Hz offshore wind AC cable with exposures up to 8 μT and decreased movement near the cable in S. canicula. In accordance with our findings, Hutchison et al. (2020) demonstrated no clear attraction or avoidance in Leucoraja erinacea in a mesocosm experiment above a live DC cable (14 µT), but did see increased exploring/foraging behaviour based on spatial distribution, total distance travelled, speed of movement and proportions of large turns. In our study, if there was attraction to AC or DC, we would have expected to see a shorter mean distance to cable, or more crossings of the solenoid midline, which were not significant. Individuals crossed the cable as frequently in all treatments, so the EMF levels associated with SPC did not serve as a barrier. EMF-deterrence devices can serve as barrier, but this was shown at \sim 250 000 μ T, which is 10⁵ higher than the EMF intensities used in this study design (Doherty et al., 2022; O'Connell et al., 2014a; 2014b; Smith & O'Connell, 2014).

Conversely, there was a change in time spent in the behavioural states in the DC trials, where individuals on average spend 30 % more time inactive and 25 % less time transiting. This observed decrease in activity for DC exposure contrasts findings of other studies, involving different species or power systems. For instance, in a mesocosm experiment, little skates (Leucoraja erinacea) exposed to a comparable EMF level (14 µT DC) showed altered swimming time, with effects varying by exposure sequence (3 % increase or 29 % decrease) (Hutchison et al., 2020). Juvenile thornback rays (Raja clavata) exposed to a >20 times higher DC stimulus (450 µT), in a study by Albert et al. (2022), demonstrated a time-dependent 20 % increase in activity, showing only a response in the afternoon and not in the morning, differing from this study's results. In a choice experiment, Kimber et al. (2011) found a significant preference of S. canicula for stronger DC fields (90 µA, resulting in a higher magnetic field level), as opposed to lower DC fields (9 μA , resulting in a lower magnetic field level). In this case, μT cannot directly be calculated from μA as the coil turns, distance, and medium properties are not known. The experiment of Kimber et al. could indicate that stronger DC fields resulting from e.g. unbundled SPC might result in different effects than observed in our study. Gill et al. (2009) observed decreased movement in a mesocosm experiment with S. canicula, which seems comparable to findings in this study. However, the SPC in the study of Gill et al. was an AC cable, and although of comparable EMF intensities (maximum of 8 μ T), the data from our study did not show behavioural differences during AC exposure. Atlantic lumpfish (Cyclopterus lumpus) show a comparable decrease of swimming velocity by 16 % when exposed to a 230 μT DC EMF. Comparable to our study, swimming activity and distance travelled were not affected in the lumpfish (Durif et al., 2023).

The observed differences between results obtained from this study and others may be caused by differences in study design, species-specific responses or exposure levels. For instance, the EMF levels employed by Albert et al. (2022) were >20 times higher (450 μ T) as may be seen in unbundled DC cables. The magnitude difference in exposure could have led to a different response, depending on the unknown EMF dose-response curve. Additionally, Albert et al. (2022) studied juvenile Raja clavata, while we examined adult S. canicula; sensory abilities vary with age and species due to life history traits like mating and foraging. Almost all studies reported high inter-individual variability and a small sample size, which likely also contributed to the observed differences. Although the individual differences make it more difficult to determine a population mean, they might be indications of behavioural phenotypes in response to EMF. Stuber et al. (2022) described that those differences in movement, habitat use, and home range behaviour make up spatial personalities; behaviours that might be influenced by EMF. Consistent intraindividual differences, or personalities (Roche et al., 2016), might help species to adapt to increasing anthropogenic stressors by rapid behavioural adaptation due to differences in stress response (Smith and Blumstein, 2013; Stuber et al., 2022). For example, shy and bold

behavioural phenotypes may respond differently to an SPC EMF. If one of these trait-related responses results in reduced fitness of one trait, this could lead to impact at population level.

Another explanation for the different findings between studies is that the dose-response curve of elasmobranch responses to EMF may not follow a traditional S-shaped pattern. Instead, it might exhibit an inverse-parabolic U-shaped curve where very low stimuli mimicking natural EMF signals and very high stimuli overloading the system may induce behavioural changes, but medium levels may not elicit a significant behavioural response. The limited availability of studies, differences in study design, combined with a potential non-chromatic doseresponse curve, necessitates caution in interpreting the study results, rendering them preliminary in nature.

4.2. No startle response or shelter use

No direct effect of the EMF onset was observed in the trials. Sharks that were lying in the vicinity of the EMF at the time of it being turned on did not change their behaviour instantly. This suggests that the EMF levels used where not sufficient to elicit an immediate behavioural response in contrast to the responses to 10^5 times higher exposure levels used from pulse fisheries or shark deterrence devices (Boute, 2022; De Haan et al., 2009; O'Connell et al., 2014a,2014b; Smith and O'Connell, 2014). However, it cannot be excluded that an unobserved stress or freeze response occurred. Combining biologging tags to monitor physiological stress indicators—such as respiratory rate, heart rate, and stroke volume—with video analysis can enhance our understanding of stress responses that do not manifest as overt movements (Barkley et al., 2020; Laurioux et al., 2024; Meira et al., 2024).

Additionally, the animals did not make more use of the shelter in any of the treatments. Increase in sheltering versus roaming behaviour under the influence of EMF has been observed in edible crabs (Cancer pagurus), at EMF field intensities that were an order of magnitude higher than those used in this study (>500 μT) (Scott et al., 2021). Our experiment was conducted during the twilight period, chosen for heightened shark activity (Papadopoulo et al., 2023). Sheltering behaviour was not expected during the trials, as it was only observed during the daytime in the holding tank, consistent with natural behaviour. Any alterations in daytime sheltering behaviour during the trial may therefore have been an indication of stress of discomfort.

4.3. Influence of trial order, sex and body length

In the observed trials, treatment, order, and sex emerged as primary predictors of shark behavioural states, with body length also presented as a potentially contributing factor. The order of trials significantly influences behaviour, as sharks showing more exploratory behaviour in subsequent trials, even though trials were spaced by > 3 weeks. Evidence suggests that elasmobranchs can retain knowledge of a novel area for extended periods, e.g. showing the retention of visual cues for >50 days(Brown and Schluessel, 2023; Fuss and Schluessel, 2015). While the first experience in the experimental tank might have been highly novel, familiarity with the tank or procedure likely increased during subsequent trials, shown by more locally active and transit and less inactive behaviour (Fig. S4). This is in line with observations in lemon sharks (Negaprion brevirostris) displaying increasing rate of movement and exploratory behaviour over repeated introductions in the novel arena (Dhellemmes et al., 2021; Finger et al., 2016). Three weeks might still have been sufficient for re-naivety to EMF cues, as wild sharks frequently encounter varying EMFs from shifting prey and conspecifics conditions, while habitat appearance remains more stable. Conversely, evidence suggests yellow stingray (Urobatis jamaicensis) can retain EMF memory for 180 days when conditioned to associate a magnetic field with a food reward, highlighting the need for more understanding on how EMF us used by different species of elasmobranchs (Newton and Kajiura, 2017).

Even though no direct significant effect of sex and EMF treatment was found, including sex gave a higher explanatory power in the selection of the model. This indicates that sex might play a role in explaining variation in behaviour, either by differences in behaviour between sexes in general, or by sex-specific responses to EMF-fields (Table S2). To disentangle this further, a follow-up study with larger sample size per sex would be needed. Especially, as research shows sexual dimorphism in the ampullae of Lorenzini (Kempster et al., 2013), and male S. canicula are reported to have longer ampullae and alveoli, higher number of alveolar bulbs, larger sensory epithelial surface areas and a greater number of sensory receptor cells in the ampullae than females (Crooks and Waring, 2013) which is believed to increase the capability of males to detect females. In addition, sexual behavioural dimorphism in relation to electric stimuli has been shown and is linked to differing reproductive strategies and resultant sexual conflict (Kimber et al., 2009; Rodríguez-Cabello et al., 2007; Sims et al., 2001). The interaction between sex and EMF-response may be an interesting focus for future studies.

Shark body length shows a relation with treatment response (Table S2). Older, and thus larger, sharks have a lower electroreceptive resolution, as the pores grow further away from the ampullae, and will gain in receptor sensitivity and a larger sensory field that samples a greater area (Newton et al., 2019). As the older/larger sharks have a changed sensitively to EMF, they could respond differently to the EMF resulting from SPCs. Alternatively, larger individuals may have higher cruising speeds, potentially resulting in the same distance travelled when related to as body lengths per second. In the wild, larger sharks were found to exhibit reduced activity space, indicating that as length increased, their range of movement decreased (Papadopoulo et al., 2023). This could imply that the relation between body size and treatment response is not EMF related, contrary to what our data suggest.

4.4. Implications for future studies

The results of this study indicate that DC induced EMF reduces shark activity with 25 %. It is important to acknowledge that the study design does not fully addresses the potential impact on foraging, including factors such as prey masking and fruitless foraging in EMF due to false suggestions of prey presence. For example, a different experimental setup, with live prey or a choice-experiment could provide more information on the effects of EMF in relation to foraging (Hubert et al., 2021; Kimber et al., 2011; Williams et al., 2023). Our experimental set-up did not allow for the measuring of changes in swimming depth as reported in a mesocosm study by Hutchison et al. (2020). The parameter depth could be recorded by including side-angle cameras or tagging individuals with a depth sensor (Ellis et al., 2019; Sims et al., 2006) and would increase the understanding of potential EMF effects. Lastly, further research is recommended to explore how behavioural responses vary among species and life stages with differing traits, such as habitat use or food choice. Behavioural responses to electromagnetic fields may vary between species, especially those with different migratory patterns. Species that undertake long-distance migrations, unlike the more localized movements of our study species, could perceive and react differently to changes in their magneto sensitive environment. Studies using tags with a magnetometer and depth sensor could provide further insight in the effect of EMF on migration.

The absence of data on habituation of EMF from SPC in adult individuals, both in this study and others, precludes an assessment of cumulative EMF impacts. For example, if a shark reduces its movement by a third every time it comes across a cable during migration, the accumulated time lost might have a larger negative effect on the migration goal than when it habituates and does not slow down. In addition, it is not known if the reduction measured in the lab will also occur in the field, and what the duration of the reduction will be. To the contrary, if the shark does habituate to SPC EMF cues, this might impair the sensitively to natural EMF cues and result in reduced foraging

success or disturbed conspecific interaction. It is likely that sharks can habituate to stimuli, as habituation is one of the most primitive learning mechanisms (Heinrich et al., 2022). However, habituation does not necessarily exclude the masking of relevant (EMF) cues.

It is believed that sharks can learn and ignore electric stimuli repeatedly not resulting in prey capture as shown in a laboratory study by Kimber et al. (2014). In their natural habitats, there is also evidence of learning to ignore non-profitable stimuli, as for example low yielding foraging patches or hard-to-catch prey (Heinrich et al., 2022). However, habituation might be less likely as there is a large temporal and spatial variability in EMF from SPC and habituation most often occurs if the repeat exposure has comparable stimuli (Hutchison et al., 2021). An experimental design focussed on possible habituation for the above mentioned different potential effects is relevant for environmental risk assessments and should address EMF effects on different life stages, especially embryogenesis and migration (Hermans et al., 2024).

5. Conclusion

This study showed no attraction or avoidance behaviour by adult *S. canicula* to field-relevant exposure levels of EMF. No change in shelter use, startle response or number of cable crossings was observed. We observed 25 % less swimming activity, and correspondingly more inactivity in sharks exposed to a DC field. As the animals covered the same distance, this indicates an increased swimming speed when active. It is advised to study whether this behavioural change is a stress response and whether habituation would occur after longer or repeated exposure to variable field intensities. Additionally, insights should be gained in differences in effects of EMF exposure to species with other ecological traits. Ideally, the behaviour of sharks around DC cables would be studied in the field using pop-up or archival tags for movement and EMF intensities.

CRediT authorship contribution statement

Annemiek Hermans: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. Ties Maris: Writing – original draft, Visualization, Methodology, Data curation, Conceptualization. Jeroen Hubert: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis. Corentine Rochas: Writing – review & editing, Supervision, Methodology, Data curation. Kevin Scott: Writing – review & editing, Methodology, Albertinka J. Murk: Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. Hendrik V. Winter: Writing – review & editing, Validation, Supervision, Methodology, Investigation, Formal analysis, Conceptualization.

Funding and ethics

Funding for this project was granted by the NWO PPS grand ENW PPS-fonds 2019 (*grand number ENPPS.TATA.019.005*). St. Abbs Marine Station was accredited for the use of animals for scientific purposes, the project was licenced under the ANIMALS (SCIENTIFIC PROCEDURES) ACT 1986 (UK) (*PPL number: PP4707747*, Granted: 11 Oct 22). All procedures were carried out in accordance with the project licence and animals were monitored for health issues by qualified staff members.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Annemiek Hermans (Corresponding author) is employed part-time by engineering firm Witteveen + Bos and in that role is seconded to T.S.O.

TenneT. All authors declare that they have no known competing financial interests or personal relationships that would influence the work reported in this paper.

Acknowledgements

Students from Wageningen University are thanked for conducting pilot studies, data collection and exploratory analysis: Samantha Popma, Hilmar Derksen, Niels van Houten, Stella de Zeeuw and Max Goessens; The staff at St Abbs Marine Station is thanked for animal welfare and husbandry; the ElasmoPower steering group for guidance, Eugene Lepelaars and Max Geljon from TNO designing and building the coil; Peet Hovenkamp for visualisation of the experiment tank; Jochem Boersma from engineering firm Witteveen+Bos for support in scripting the exposure levels and Max Willems for the visualisation of the small-spotted catsharks in Fig. 5. We would like to thank the reviewers for their time and critical thinking resulting in a stronger manuscript, and the editor for considering our work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107127.

Data availability

Data will be made available on request.

References

- Albert, L., Deschamps, F., Jolivet, A., Olivier, F., Chauvaud, L., Chauvaud, S., 2020.
 A current synthesis on the effects of electric and magnetic fields emitted by submarine power cables on invertebrates. Mar. Environ. Res. 159, 104958. https://doi.org/10.1016/j.marenvres.2020.104958.
- Albert, L., Olivier, F., Jolivet, A., Chauvaud, L., Chauvaud, S., 2022. Insights into the behavioural responses of juvenile thornback ray *Raja clavata* to alternating and direct current magnetic fields. J. Fish. Biol. 100 (3), 645–659. https://doi.org/ 10.1111/jfb.14978
- Anderson, J.M., Clegg, T.M., Véras, L.V.M.V.Q., Holland, K.N., 2017. Insight into shark magnetic field perception from empirical observations. Sci. Rep. 7 (1), 11042. https://doi.org/10.1038/s41598-017-11459-8.
- Ball, R.E., Oliver, M.K., Gill, A.B., 2016. Early life sensory ability—ventilatory responses of thornback ray embryos *Raja clavata* to predator-type electric fields. Develop. Neurobiol. 76 (7), 721–729. https://doi.org/10.1002/dneu.22355.
- Barkley, A.N., Broell, F., Pettitt-Wade, H., Watanabe, Y.Y., Marcoux, M., Hussey, N.E., 2020. A framework to estimate the likelihood of species interactions and behavioural responses using animal-borne acoustic telemetry transceivers and accelerometers. J. Anim. Ecol. 89 (1), 146–160. https://doi.org/10.1111/1365-2656.13156.
- Barry, J.P., Kuhnz, L., Buck, K., Lovera, C., Whaling, P.J., 2008. Potential Impacts of the MARS Cable on the Seabed and Benthic Faunal Assemblages. Monterey Bay Aquarium Research Institute.
- Bedore, C.N., Kajiura, S.M., 2013. Bioelectric fields of marine organisms: voltage and frequency contributions to detectability by electroreceptive predators Physiol. Biochem. Zool 86 (3), 298–311. https://doi.org/10.1086/669973.
- Boute, P.G., 2022. Effects of Electrical Stimulation on Marine Organisms. Wageningen University. https://doi.org/10.18174/566867.
- Brown, C., Schluessel, V., 2023. Smart sharks: a review of chondrichthyan cognition. Anim. Cognit. 26 (1), 175–188. https://doi.org/10.1007/s10071-022-01708-3.
- Collin, S.P., Kempster, R.M., Yopak, K.E., 2015. How elasmobranchs sense their environment. In: Fish Physiology, vol. 34. Elsevier, pp. 19–99. https://doi.org/ 10.1016/B978-0-12-801289-5.00002-X.
- Compagno, L.J.V., Dando, M., Fowler, S.L., 2005. A field guide to the sharks of the world. https://api.semanticscholar.org/CorpusID:82517956.
- Crooks, N., 2019. Chondrichthyes navigation. In: Vonk, J., Shackelford, T. (Eds.), Encyclopedia of Animal Cognition and Behavior. Springer International Publishing, pp. 1–8. https://doi.org/10.1007/978-3-319-47829-6_1030-1.
- Crooks, N., Waring, C.P., 2013. A study into the sexual dimorphisms of the Ampullae of Lorenzini in the lesser-spotted catshark, Scyliorhinus canicula (Linnaeus, 1758). Environ. Biol. Fish. 96 (5), 585–590. https://doi.org/10.1007/s10641-012-0048-8.
- De Haan, D., Van Marlen, B., Velzeboer, I., Van der Heul, J., Van de vis, J., 2009. The effects of pulse stimulation on biota-Research in relation to ICES advice-Effects on dogfish. Imares. https://edepot.wur.nl/133168.
- Dhellemmes, F., Finger, J., Smukall, M.J., Gruber, S.H., Guttridge, T.L., Laskowski, K.L., Krause, J., 2021. Personality-driven life history trade-offs differ in two subpopulations of free-ranging predators. J. Anim. Ecol. 90 (1), 260–272. https:// doi.org/10.1111/1365-2656.13283.

- Doherty, P.D., Enever, R., Omeyer, L.C.M., Tivenan, L., Course, G., Pasco, G., Thomas, D., Sullivan, B., Kibel, B., Kibel, P., Godley, B.J., 2022. Efficacy of a novel shark bycatch mitigation device in a tuna longline fishery. Curr. Biol. 32 (22), R1260–R1261. https://doi.org/10.1016/j.cub.2022.09.003.
- Dulvy, N.K., Pacoureau, N., Rigby, C.L., Pollom, R.A., Jabado, R.W., Ebert, D.A., Finucci, B., Pollock, C.M., Cheok, J., Derrick, D.H., Herman, K.B., Sherman, C.S., VanderWright, W.J., Lawson, J.M., Walls, R.H.L., Carlson, J.K., Charvet, P., Bineesh, K.K., Fernando, D., et al., 2021. Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. Curr. Biol. 31 (21), 4773–4787.e8. https://doi.org/10.1016/j.cub.2021.08.062.
- Durif, C.M.F., Nyqvist, D., Taormina, B., Shema, S.D., Skiftesvik, A.B., Freytet, F., Browman, H.I., 2023. Magnetic fields generated by submarine power cables have a negligible effect on the swimming behavior of Atlantic lumpfish (*Cyclopterus lumpus*) juveniles. PeerJ 11, e14745. https://doi.org/10.7717/peerj.14745.
- Ellis, T., Rimmer, G., Parker, S.-J., Joiner, C., Sebire, M., Verner-Jeffreys, D., Lines, J., 2019. In-tank underwater cameras can refine monitoring of laboratory fish. Anim. Welf. 28 (2), 191–203. https://doi.org/10.7120/09627286.28.2.191.
- European Court of Auditors, 2023. Offshore renewable energy: EU auditors highlight green dilemma. Curia Rationum. https://www.eca.europa.eu/en/news/news-sr-2023-22
- Finger, J.S., Dhellemmes, F., Guttridge, T.L., Kurvers, R.H.J.M., Gruber, S.H., Krause, J., 2016. Rate of movement of juvenile lemon sharks in a novel open field, are we measuring activity or reaction to novelty? Anim. Behav. 116, 75–82. https://doi. org/10.1016/j.anbehav.2016.03.032.
- Finucci, B., Derrick, D., Neat, F.C., Pacoureau, N., Serena, F., VanderWright, W.J., 2020. Scyliorhinus canicula: The IUCN Red List of Threatened Species 2021: e. T161307554A124478351. https://doi.org/10.2305/IUCN.UK.2021-2.RLTS.T16130 7554A124478351.en.
- Fuss, T., Schluessel, V., 2015. Something worth remembering: visual discrimination in sharks. Anim. Cognit. 18 (2), 463–471. https://doi.org/10.1007/s10071-014-0815-3.
- Gallagher, A.J., Kyne, P.M., Hammerschlag, N., 2012. Ecological risk assessment and its application to elasmobranch conservation and management. J. Fish. Biol. 80 (5), 1727–1748. https://doi.org/10.1111/j.1095-8649.2012.03235.x.
- Gill, A.B., 2009. 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., Gloyne-Philips, I., Kimber, J., Sigray, P., 2014. Marine renewable energy, electromagnetic (EM) fields and EM-sensitive animals. In: Shields, M.A., Payne, A.I. L. (Eds.), Marine Renewable Energy Technology and Environmental Interactions. Springer, Netherlands, pp. 61–79. https://doi.org/10.1007/978-94-017-8002-5 6.
- Hayakawa, M., Hattori, K., Ando, Y., 2004. Natural electromagnetic phenomena and electromagnetic theory: a review. IEEJ Trans. Fundament. Mater. 124 (1), 72–79. https://doi.org/10.1541/jeejfms.124.72.
- Heessen, H.J.L., Daan, N., Ellis, J.R., 2015. Fish Atlas of the Celtic Sea, North Sea and Baltic Sea: Based on International Research-Vessel Surveys. Wageningen Academic Publishers.
- Heinrich, D.D.U., Huveneers, C., Houslay, T.M., Dhellemmes, F., Brown, C., 2022. Shark habituation to a food-related olfactory cue. Anim. Behav. 187, 147–165. https://doi. org/10.1016/j.anbehav.2022.03.003.
- Heithaus, M.R., Frid, A., Wirsing, A.J., Worm, B., 2008. Predicting ecological consequences of marine top predator declines. Trends Ecol. Evol. 23 (4), 202–210. https://doi.org/10.1016/j.tree.2008.01.003.
- Hermans, A., Winter, H.V., Gill, A.B., Murk, A.J., 2024. Do electromagnetic fields from subsea power cables effect 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.
- Hubert, J., Van Bemmelen, J.J., Slabbekoorn, H., 2021. No negative effects of boat sound playbacks on olfactory-mediated food finding behaviour of shore crabs in a T-maze. Environ. Pollut. 270, 116184. https://doi.org/10.1016/j.envpol.2020.116184.
- Hutchison, Z.L., Gill, A.B., Sigray, P., He, H., King, J.W., 2020. Anthropogenic electromagnetic fields (EMF) influence the behaviour of bottom-dwelling marine species. Sci. Rep. 10 (1), 4219. https://doi.org/10.1038/s41598-020-60793-x.
- Hutchison, Z.L., Gill, A.B., Sigray, P., He, H., King, J.W., 2021. A modelling evaluation of electromagnetic fields emitted by buried subsea power cables and encountered by marine animals: considerations for marine renewable energy development. Renew. Energy 177, 72–81. https://doi.org/10.1016/j.renene.2021.05.041.
- Hutchison, Z., Secor, D., Gill, A., 2020. The interaction between resource species and electromagnetic fields associated with electricity production by offshore wind farms. Oceanography (Wash., D.C.) 33 (4), 96–107. https://doi.org/10.5670/ oceanog.2020.409.
- Hyatt, M.W., Anderson, P.A., O'Donnell, P.M., 2018. Influence of temperature, salinity, and dissolved oxygen on the stress response of bull *Carcharhinus leucas* and bonnethead *Sphyrna tiburo* sharks after capture and handling. J. Coast Res. 344, 818–827. https://doi.org/10.2112/JCOASTRES-D-17-00118.1.
- Kalmijn, 1972. Bioelectric fields in sea water and the function of the ampullae of Lorenzini in elasmobranch fishes. Scripps Inst. Ocranogr., Ref. Ser. (72–83), 1–21.
- Kalmijn, A.J., 1971. The electric sense of sharks and rays. J. Exp. Biol. 55 (2), 371–383. https://doi.org/10.1242/jeb.55.2.371.
- Kempster, R.M., Garza-Gisholt, E., Egeberg, C.A., Hart, N.S., O'Shea, O.R., Collin, S.P., 2013a. Sexual dimorphism of the electrosensory system: a quantitative analysis of nerve axons in the dorsal anterior lateral line nerve of the blue-spotted fantail stingray *Taeniura lymma*. Brain Behav. Evol. 81 (4), 226–235. https://doi.org/ 10.1159/000351700.
- Kempster, R.M., Hart, N.S., Collin, S.P., 2013b. Survival of the stillest: predator avoidance in shark embryos. PLoS One 8 (1), e52551. https://doi.org/10.1371/ journal.pone.0052551.

- Kimber, J.A., Sims, D.W., Bellamy, P.H., Gill, A.B., 2009. Male–female interactions affect foraging behaviour within groups of small-spotted catshark, Scyliorhinus canicula. Anim. Behav. 77 (6), 1435–1440. https://doi.org/10.1016/j.anbehav.2009.02.014.
- 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), 1–8. https://doi.org/10.1007/s00227-010-1537-y.
- Kimber, J.A., Sims, D.W., Bellamy, P.H., Gill, A.B., 2014. Elasmobranch cognitive ability: using electroreceptive foraging behaviour to demonstrate learning, habituation and memory in a benthic shark. Anim. Cognit. 17 (1), 55–65. https://doi.org/10.1007/ s10071-013-0637-8.
- Klimley, A.P., 1993. Highly directional swimming by scalloped hammerhead sharks, Sphyrna lewini, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. Mar. Biol. 117 (1), 1–22. https://doi.org/10.1007/BF00346421.
- Klimley, A.P., Kihslinger, R.L., Kelly, J.T., 2005. Directional and non-directional movements of bat rays, *Myliobatis californica*, in tomales bay, California. Environ. Biol. Fish. 74 (1), 79–88. https://doi.org/10.1007/s10641-005-3997-3.
- Laurioux, A., Huveneers, C., Papastamatiou, Y., Planes, S., Ballesta, L., Mourier, J., 2024. Abiotic drivers of the space use and activity of gray reef sharks *Carcharhinus amblyrhynchos* in a dynamic tidal environment. J. Fish. Biol. 15825. https://doi.org/10.1111/jfb.15825.
- Martinho, F., Sá, C., Falcão, J., Cabral, H.N., Pardal, M.A., 2012. Comparative feeding ecology of two elasmobranch species, *Squalus blainville* and *Scyliorhinus canicula*, off the coast of Portugal. Fish. Bull. 110 (1), 71–84. Fishery Bulletin, 110(1), 71–84.
- McClintock, B. T., & Michelot, T. (2018). momentuHMM: R Package for Analysis of Telemetry Data Using Generalized Multivariate Hidden Markov Models of Animal Movement.
- Meira, A., Carvalho, F., Castro, P., Sousa, R., 2024. Applications of biosensors in nonnative freshwater species: a systematic review. NeoBiota 96, 211–236. https://doi. org/10.3897/neobiota.96.128038.
- Meyer, C.G., Holland, K.N., Papastamatiou, Y.P., 2005. Sharks can detect changes in the geomagnetic field. J. R. Soc. Interface 2 (2), 129–130. https://doi.org/10.1098/ psif 2004.0021
- Newton, K.C., Gill, A.B., Kajiura, S.M., 2019. Electroreception in marine fishes: chondrichthyans. J. Fish. Biol. 95 (1), 135–154. https://doi.org/10.1111/jfb.14068.
- Newton, K.C., Kajiura, S.M., 2017. Magnetic field discrimination, learning, and memory in the yellow stingray (*Urobatis jamaicensis*). Anim. Cognit. 20 (4), 603–614. https://doi.org/10.1007/s10071-017-1084-8.
- Newton, K.C., Kajiura, S.M., 2020. The yellow stingray (*Urobatis jamaicensis*) can use magnetic field polarity to orient in space and solve a maze. Mar. Biol. 167 (3), 36. https://doi.org/10.1007/s00227-019-3643-9.
- Normandeau, E., Tricas, T., Gill, A.B., 2011. Effects of EMFs from undersea power cables on elasmobranchs and other marine species. U.S. Dept. Of the Interior, Bureau of Ocean Energy Management, Regulation, and Enforcement, Pacific OCS Region. OCS Study BOEMRE 2011-09, Camarillo, CA.
- North Sea Energy, 2023. Interactive map of subsea power cables. Energy Atlas. https://north-sea-energy.eu/en/energy-atlas/.
- Nyqvist, D., Durif, C., Johnsen, M.G., De Jong, K., Forland, T.N., Sivle, L.D., 2020. Electric and magnetic senses in marine animals, and potential behavioral effects of electromagnetic surveys. Mar. Environ. Res. 155, 104888. https://doi.org/10.1016/ j.marenvres.2020.104888.
- Ocean Biodiversity Information System (OBIS), 2023. Scyliorhinus canicula (linnaeus, 1758). https://obis.org/taxon/105814.
- O'Connell, C.P., Andreotti, S., Rutzen, M., Meÿer, M., He, P., 2014a. The use of permanent magnets to reduce elasmobranch encounter with a simulated beach net. 2. The great white shark (Carcharodon carcharias). Ocean Coast Manag. 97, 20–28. https://doi.org/10.1016/j.ocecoaman.2012.11.006.
- O'Connell, C.P., He, P., Joyce, J., Stroud, E.M., Rice, P.H., 2014b. Effects of the SMARTTM (Selective Magnetic and Repellent-Treated) hook on spiny dogfish catch in a longline experiment in the Gulf of Maine. Ocean Coast Manag. 97, 38–43. https://doi.org/10.1016/j.ocecoaman.2012.08.002.
- Öhman, M.C., Sigray, P., Westerberg, H., 2007. Offshore windmills and the effects of electromagnetic fields on fish. AMBIO A J. Hum. Environ. 36 (8), 630–633. https:// doi.org/10.1579/0044-7447(2007)36[630:OWATEO]2.0.CO;2.
- Orr, M.A., 2016. The Potential Impacts of Submarine Power Cables on Benthic Elasmobranchs [Doctoral Thesis]. The University of Auckland, 2016.
- Pacoureau, N., Rigby, C.L., Kyne, P.M., Sherley, R.B., Winker, H., Carlson, J.K., Fordham, S.V., Barreto, R., Fernando, D., Francis, M.P., Jabado, R.W., Herman, K.B., Liu, K.-M., Marshall, A.D., Pollom, R.A., Romanov, E.V., Simpfendorfer, C.A., Yin, J. S., Kindsvater, H.K., Dulvy, N.K., 2021. Half a century of global decline in oceanic sharks and rays. Nature 589 (7843), 567–571. https://doi.org/10.1038/s41586-020-03173-9.
- Papadopoulo, K., Villegas-Ríos, D., Mucientes, G., Hillinger, A., Alonso-Fernández, A., 2023. Drivers of behaviour and spatial ecology of the small spotted catshark

- (Scyliorhinus canicula). Aquat. Conserv. Mar. Freshw. Ecosyst. 33 (5), 443–457. https://doi.org/10.1002/aqc.3943.
- Peters, R.C., Evers, H.P., 1985. Frequency selectivity in the ampullary system of an elasmobranch fish (*Scyliorhinus canicula*). J. Exp. Biol. 118 (1), 99–109. https://doi. org/10.1242/jeb.118.1.99.
- Revill, A.S., Dulvy, N.K., Holst, R., 2005. The survival of discarded lesser-spotted dogfish (Scyliorhinus canicula) in the Western English Channel beam trawl fishery. Fish. Res. 71 (1), 121–124. https://doi.org/10.1016/J.FISHRES.2004.07.006.
- Roche, D.G., Careau, V., Binning, S.A., 2016. Demystifying animal 'personality' (or not): why individual variation matters to experimental biologists. J. Exp. Biol., 146712 https://doi.org/10.1242/jeb.146712.
- Rodríguez-Cabello, C., Sánchez, F., Olaso, I., 2007. Distribution patterns and sexual segregations of *Scyliorhinus canicula* (L.) in the Cantabrian Sea. J. Fish. Biol. 70 (5), 1568–1586. https://doi.org/10.1111/j.1095-8649.2007.01444.x.
- Rodriguez-Cabello, C., Sánchez, F., Fernández, A., Olaso, I., 2004. Is the lesser spotted dogfish (Scyliorhinus canicula) population from the Cantabrian Sea a unique stock? Fish. Res. 69 (1), 57–71. https://doi.org/10.1016/j.fishres.2004.04.002.
- Šantić, M., Rađa, B., Pallaoro, A., 2012. Feeding habits of small-spotted catshark (*Scyliorhinus canicula* Linnaeus, 1758) from the eastern central Adriatic Sea. Mar. Biol. Res. 8 (10), 1003–1011. https://doi.org/10.1080/17451000.2012.702912.
- Schlaff, A.M., Heupel, M.R., Simpfendorfer, C.A., 2014. Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev. Fish Biol. Fish. 24 (4), 1089–1103. https://doi.org/10.1007/s11160-014-9364-8.
- Scott, K., Harsanyi, P., Easton, B.A.A., Piper, A.J.R., Rochas, C.M.V., Lyndon, A.R., 2021. Exposure to electromagnetic fields (EMF) from submarine power cables can trigger strength-dependent behavioural and physiological responses in edible crab, *Cancer pagurus* (L.). J. Mar. Sci. Eng. 9 (7), 776. https://doi.org/10.3390/jmse9070776.
- Sims, D., Nash, J., Morritt, D., 2001. Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. Mar. Biol. 139 (6), 1165–1175. https://doi.org/10.1007/ s002270100666
- Sims, D.W., Wearmouth, V.J., Southall, E.J., Hill, J.M., Moore, P., Rawlinson, K., Hutchinson, N., Budd, G.C., Righton, D., Metcalfe, J.D., Nash, J.P., Morritt, D., 2006. Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. J. Anim. Ecol. 75 (1), 176–190. https://doi.org/10.1111/j.1365-2656.2005.01033.x.
- Sisneros, J.A., Tricas, T.C., 2002. Neuroethology and life history adaptations of the elasmobranch electric sense. J. Physiol. Paris 96 (5–6), 379–389. https://doi.org/10.1016/S0928-4257(03)00016-0.
- Smith, B.R., Blumstein, D.T., 2013. Animal personalities and conservation biology. In: Carere, C., Maestripieri, D. (Eds.), Animal Personalities: Behavior, Physiology, and Evolution. The University of Chicago Press. https://discover.libraryhub.jisc.ac.uk/se arch?ti=Animal%20personalities%3A%20behavior%2C%20physiology%2C%20and %20evolution.
- Smith, L.E., O'Connell, C.P., 2014. The effects of neodymium-iron-boron permanent magnets on the behaviour of the small spotted catshark (Scyliorhinus canicula) and the thornback skate (Raja clavata). Ocean Coast Manag. 97, 44–49. https://doi.org/ 10.1016/j.orgcoamar.2013.05.010
- Stevens, J., 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 57 (3), 476–494. https://doi.org/10.1006/jmsc.2000.0724.
- Stuber, E.F., Carlson, B.S., Jesmer, B.R., 2022. Spatial personalities: a meta-analysis of consistent individual differences in spatial behavior. Behav. Ecol. 33 (3), 477–486. https://doi.org/10.1093/beheco/arab147.
- 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. Sustain. Energy Rev. 96, 380–391. https://doi.org/10.1016/j.rser.2018.07.026.
- Westerberg, H., Lagenfelt, I., 2008. Sub-sea power cables and the migration behaviour of the European eel. Fish. Manag. Ecol. 15 (5–6), 369–375. https://doi.org/10.1111/i.1365-2400.2008.00630.x.
- Williams, J.P., Jaco, E.M., Scholz, Z., Williams, C.M., Pondella, D.J., Rasser, M.K., Schroeder, D.M., 2023. Red rock crab (Cancer productus) movement is not influenced by electromagnetic fields produced by a submarine power transmission cable. Cont. Shelf Res. 269, 105145. https://doi.org/10.1016/j.csr.2023.105145.
- Wiltschko, W., Wiltschko, R., 2005. Magnetic orientation and magnetoreception in birds and other animals. J. Comp. Physiol. 191 (8), 675–693. https://doi.org/10.1007/ s00359-005-0627-7.
- Wind Europe, 2023. Wind energy today. https://windeurope.org/about-wind/wind-energy-today/.
- 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 (8), 134. https://doi.org/10.1007/s00227-018-3385-0.