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An egg case study: Chronic exposure to AC electromagnetic fields results in hyperactivity in thornback ray (*Raja clavata* L.) embryos

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ABSTRACT

Subsea power cables, required for offshore generated wind power transport, emit electromagnetic fields (EMFs) into the marine environment. EMFs also occur naturally, resulting from biotic (animals) and abiotic (geomagnetic field) sources. Skate and oviparous shark embryos in the egg can sense EMF from predators and respond by reducing their normal movement ('freezing response') to prevent detection and subsequent predation. When nursery areas overlap with power cables, embryos will be exposed to varying levels of anthropogenic EMFs and effects thereof on embryonic development is currently understudied. Here, we present behavioral responses of thornback ray (*Raja clavata*) embryos to varying field-related EMF levels (1.8–4.6 μT) generated by alternating current throughout embryogenesis (~20 weeks). Chronically exposed individuals were overall more active, including 33 % more tail undulations and 150 % increased body movements, compared to non-exposed individuals. This increased activity suggests that eggs exposed to EMFs generated by subsea power cables might be at risk of increased predation. We found no indications of reduced health or survival after hatching, or changes in development time or biometry. Effects on subsequent life stages cannot be excluded, follow-up studies should observe hatchling development. We did not observe an increase in freezing response resulting from EMF change as described by other researchers who used different types and intensities of EMF cues. We recommend that different species, along with DC exposure, should be studied to gain a more complete insight into the potential effects of EMF exposure during embryogenesis of these EMF-sensitive species.

1. Introduction

The offshore energy transition plays a crucial role in the transition to sustainable energy production (European Court of Auditors). Offshore wind energy generation will be upscaled from 16 GW as of 2024, to 61 GW in 2030, and is projected to be 340 GW by 2050 in European Union waters (European Court of Auditors), (Wind Europe). The wind-generated power is transported to shore with subsea power cables (SPCs) (Taormina et al., 2018), (Boon et al., 2019), of which there are both alternating current (AC) and direct current (DC) power systems deployed at sea. For export cables connecting windfarms <70 km from shore and for infield cables connecting turbines within a windfarm to the offshore high voltage station (OHVS), three phase AC SPCs are most commonly used (Taormina et al., 2018), (Elliott et al., 2016), (Hutchison et al., 2021). The range of perceptible magnetic fields produced depends on cable type and power level transported and could reach up to 120 m around AC cables and up to 240 m around DC cables (Hutchison et al., 2021), (Hermans et al., 2024). The expansion of offshore wind generation and concomitant increase in number, capacity, and length of SPCs will increase anthropogenic EMF exposures that may impact marine life in general and the electro- and magneto-sensitive elasmobranchs (sharks and rays) even more (Hermans et al., 2024).

Elasmobranchs use EMF cues in foraging and activities such as interactions with conspecifics and navigation during migrations (Kalmijn, 1971), (Newton et al., 2019), (Kajiura and Holland, 2002), (Sisneros and Tricas, 2002a). However, it is poorly understood how oviparous elasmobranch embryos might be affected by exposure to EMFs from SPCs (Kempster et al., 2013), (Ball et al., 2016), (Christensen et al., 2023). Over one third of elasmobranch species are oviparous (Musa et al., 2018), (Compagno et al., 2005), (Dulvy and Reynolds, 1997), (Hamlett and Koob, 1999), and the developing embryos can respond to and thus sense EMF cues already from an early developmental stage. Ball et al.

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(2015) showed that Thornback rays (*Raja clavata)* respond to 0.61 mV/cm (RMS) at 1–2 Hz already at one-third of the embryonic development (Ball et al., 2016). It is suggested that this early sensory ability serves to detect potential predators (Christensen et al., 2023), (Paoletti et al., 2023). The freeze response resulting from an external EMF stimuli, reduces emission of EMF from the embryo itself and reduces emission of olfactory cues from the egg which could otherwise be detected by predators (Kempster et al., 2013), (Ball et al., 2016), (Christensen et al., 2023), (Paoletti et al., 2023). A freeze response is characterised by temporarily ceasing pharyngeal respiration while coiling the tail around the body (Kempster et al., 2013), (Sisneros et al., 1998), (Ripley et al., 2021). For example, Brownbanded bamboo shark (*Chiloscyllium punctatum)* embryos show a freeze response when exposed to predator-mimicking electric fields (0.4–2.1 μV/cm at 0–20 Hz) (Kempster et al., 2013). The ability to detect EMFs early in the development of egg cases could disrupt the normal development of elasmobranch embryos when developing within the field of anthropogenic EMFs.

Elasmobranch egg cases are generally deposited close to the seabed in coastal areas (Heessen et al., 2015), (Franco and Thomson, 2016), (Martins et al., 2018). These areas are often also suitable for SPCs, resulting in an overlap of cable routes and nursery areas. IOffshore windfarms have the potential to attract elasmobranchs to deposit their eggs because of newly formed reefs and the absence of bottom trawling (Rodríguez-Cabello et al., 2008), (Coolen et al., 2020), (Degraer et al., 2020). However, chronic EMF exposure due to the SPCs could have adverse effects on embryonic development (Hermans et al., 2024). The sessile egg cases are not likely to move, and when deposited close to an SPC, the EMF exposure encompasses the whole of embryogenesis. The freezing response to avoid being detected by predators is believed to be triggered by the electric component of EMF, induced by the muscle activity of an approaching potential predator. In case of EMFs near SPCs, this refers to the induced electric field, as the direct electric field is shielded within the SPC. Induced electric (iE) fields are considered to be low, in the order of magnitude of 10^{-4} to 10^{-5} V/m (Hutchison et al., 2020a), (European Commission, 2015). However, Small-spotted catshark (*Scyliorhinus canicula)* embryos have demonstrated a response to fields as low as 2.10^{-4} V/m (Paoletti et al., 2023). The electric field levels emitted by SPC overlap with those of predators, which are also in the order of magnitude of 10^{-4} to 10^{-5} V/m, depending on the activity and size of the predator (Bedore and Kajiura, 2013). Therefore, artificial electric fields might be mistaken for predators as research has shown that (at least some) elasmobranchs cannot distinguish between artificial and natural EMFs (Kempster et al., 2013), (Kimber et al., 2011).

Given the inherent variability of SPC EMFs on both short (minutes) and long (hours to months) timescales - driven by the wind forces generating electricity – it's unlikely that habituation to EMF occurs during embryogenesis. (Hermans et al., 2024), (Hutchison et al., 2020b). Christensen et al. (2023) observed habituation by embryos of *Scyliorhinus canicula* when continuously exposed to DC electrical stimuli in a range between 1 μA and 10 mA for 40 min. Most notably, embryos reacted with a freeze response to a change in electrical field, when the field was turned on and again when it was turned off, rather than just the presence of an electric field. Actively responding to these changing EMF levels may increase energy demands that then in turn may affect growth, development (time) and require a higher yolk consumption (Formicki et al., 2019), as has been demonstrated in other marine taxa (Paoletti et al., 2023), (Formicki et al., 2019), (Harsanyi et al., 2022), (Formicki and Winnicki, 1998), (Brysiewicz and Formicki, 2019), (Fey et al., 2019), (Fey et al., 2020). If embryo development is impeded, hatchlings may be smaller in size which has a negative influence on pup survival (Walker et al., 1998), (Matich et al., 2021), (Leonard et al., 1999), (Holmes and McCormick, 2010). Other potential effects include a change in EMF sensitivity after hatching due to epigenetic imprinting as was shown in elasmobranchs for other stressors, such as temperature and trace metals (Ripley et al., 2023), (Paige Beal et al., 2021).

The batoid Thornback ray *Raja clavata* (Linnaeus 1758), a common ray species in the North Sea, was selected as the study species due to its oviparous nature and the potential overlap of its nursery areas with SPCs (Hermans et al., 2024). The development time of *Thornback ray* embryos ranges from 5 to 11 months, depending on temperature (Clark, 1922), (Serra-Pereira et al., 2011). For this species EMF impact studies on juveniles and adults have also been carried out before (Gill, 2009), (Albert et al., 2022), allowing comparative analyses. Finally, its commonly present in public aquaria which demonstrate good husbandry practices and facilatates the sufficient supply of egg cases that are readily available. Tail undulations, body movement and freeze response can be observed within the egg cases. These parameters can be used as a proxy for stress and can therefore serve as an indication of response to EMF (Ball et al., 2016), (Sisneros et al., 1998), (Sisneros and Tricas, 2002b).

Understanding the impact of the increasing EMF exposure by SPCs on embryos of EMF-sensitive elasmobranchs is crucial as the rate that EMF will be exposed to eggs will increase in the areas around SPCs. Chronic embryonic exposure may affect embryonic behaviour, subsequent life stages and ultimately even population success (Ripley et al., 2021), (Di Santo, 2015), (Schröder et al., 2021), (Reynolds et al., 2005), (Pimentel et al., 2014). The present study compares embryonic behavioural responses to EMF stimuli between a treatment group continuously exposed to varying EMF levels and an unexposed control group. In addition, development duration and biometry (weight and length) after hatching are compared.

2. Materials and methods

2.1. Animal collection

Thornback ray (*Raja clavata*) eggs were collected daily over 28 days within 24h after depositing by captive-bred adults from the public aquarium "Dolfinarium" in Harderwijk, Netherlands, during the months of January and February 2023. At the Dolfinarium, each egg was ID-agged with a combination of coloured rubber bands and a zip tie attached to one of the egg horns. In total, 34 egg cases were collected and transferred within 7 days after collection, resulting in 4 batches of egg cases being transported to 'Carus' the animal research facility of Wageningen University & Research, Netherlands, where the experiments were conducted. The eggs were placed in plastic bags filled with ~10L seawater and more than 2/3rd air in styrofoam boxes to maintain temperature. The duration of the transport was ~60 min after which the eggs stayed in the bags for an additional 2h to equalise the temperature in increments of 1,2 °C per 30 min from ~12 °C to ~17 °C.

2.2. Husbandry

Up to the sixth week of development, eggs were kept together in a 90L stock tank until the development of an embryo was visible, distinguishing fertilised and non-fertilised eggs. Egg cases were placed horizontally at the bottom of the tank, mimicking natural conditions. At six weeks after deposition, 18 fertilised eggs were selected and randomly distributed individually in one of the 9 treatments or 9 control aquaria. The aquaria (25L) were filled with artificial seawater (Tropic Marin Zoomix) which was refreshed weekly, 4L 2x per week. Each aerated aquarium (dissolved O_2 concentration 8.2 ± 0.4 mg/L sd) was kept in a temperature-controlled room ± 16 °C with a 12h:12h (light/dark) 2–4 lux photoperiod (Roline RO-1332 lux meter) filtered by a sponge filter (Tetra Brillant Filter). They were placed on a non-ferrous storage rack to prevent interference with the EMF. Daily health checks were performed, consisting of a visual inspection of the yolk and the state and movements of the embryo by shining a torch in the aquaria. Water quality was assessed weekly for pH (8.3 ± 0.1 sd), and daily for temperature (15.8 °C ± 0.3 °C sd), and salinity (34.1 ± 0.7 ppt sd) and adjusted if necessary. In addition, weekly analysis of ammonium (0.07 ± 0.19 sd) and nitrite (0.12 ± 0.13 sd) (Merck MQuant Supelco) were conducted. During the

first 6 developmental weeks in the stock tank, ammonium and nitrite values were sometimes elevated, likely due to the presence of unfertilised eggs undergoing decay. These eggs were removed from the group, and water exchanges (80 % of total volume) were conducted accordingly.

2.3. Experimental set-up

From development week 6 onwards, the treatment aquaria were exposed continuously to an AC magnetic field. The EMF field changed once per 24h, alternating between 1.8 and 4.6 μT, mimicking days with low wind speed and high wind speed, respectively. These data were reported from field measurements 1m from the buried 700 MW 3-phase 50 Hz AC offshore wind export cable from the offshore wind farm Borssele in the Southern North Sea (unpublished data used with permission by T.S.O. TenneT). The corresponding inducted electric field levels were assumed to be 0.06–0.20 mV/m as measured in a comparable set-up by Paoletti et al. (2023). The exposure level was changed every 24h at 10:00 CET, 3 h after the start of the daylight period. The magnetic field was generated by a Trutech Products transformer on loan from Paoletti et al. (2023) (Paoletti et al., 2023) connected to an AC cable (thickness 4 mm, shielding: PVC mantle, length: 30 m, resistance: 0.1 Ω). The cable was positioned underneath the aquaria and fixed in the exact position required to result in the necessary exposure level within the aquaria. Daily magnetic field level measurements were taken with a Narda ELT-400 magnetometer to check the functioning of the transformer, and transformer output was logged throughout the experiment. Mu-metal sheets (2 mm thick, 1 × 1 m) were placed in front of the cable to limit EMF exposure to the Control aquaria placed at >4m. Daily measurements verified that the 9 Control aquaria were only exposed to the background EMF levels of 0.06 μT ± 0.03 sd that resulted from water quality maintenance equipment and the electric infrastructure in the room.

The EMF stimuli trials were carried out between developmental week 17–21 (Fig. 1 middle). The order of the trials was randomised using a randomised complete block design (RCBD). The EMF stimuli experiments consisted of three exposure levels: 0.1, 1.0 or 10 μT ± 0.05 μT sd, conducted with all 18 embryos (Chronically exposed treatment and Control group), resulting in a total of 54 trials (Table S1). The unidirectional exposure level 0.1 μT was distinctly different from the diffuse background level (0.06 μT ± 0.03 sd) in origin, direction and strength. For each individual, the trials were separated by a minimum of 1 day. The trials were conducted between two purpose build Helmholtz coils (coil Ø 83.5 cm, distance between coils: 43 cm), manufactured by WaterProof B.V. The coils were supported by a built in magnetometer, and created a unidirectional field in the centre in which a 1.5 L plastic transparent 'trial-tank' was placed, containing the embryo. The embryo movements were made visible throughout the trial using a candling technique, exposing individuals to ~100 lumen (Roline RO-1332 lux meter). The behaviour of the embryos during each trial was recorded using a camera (Obsbot meet 4k; settings: shutter speed 1/60, ISO 800, contrast 50, quality 1080 P30, video format mkv) mounted above the coil.

Each trial lasted 45 min and was divided into three 15 min intervals:

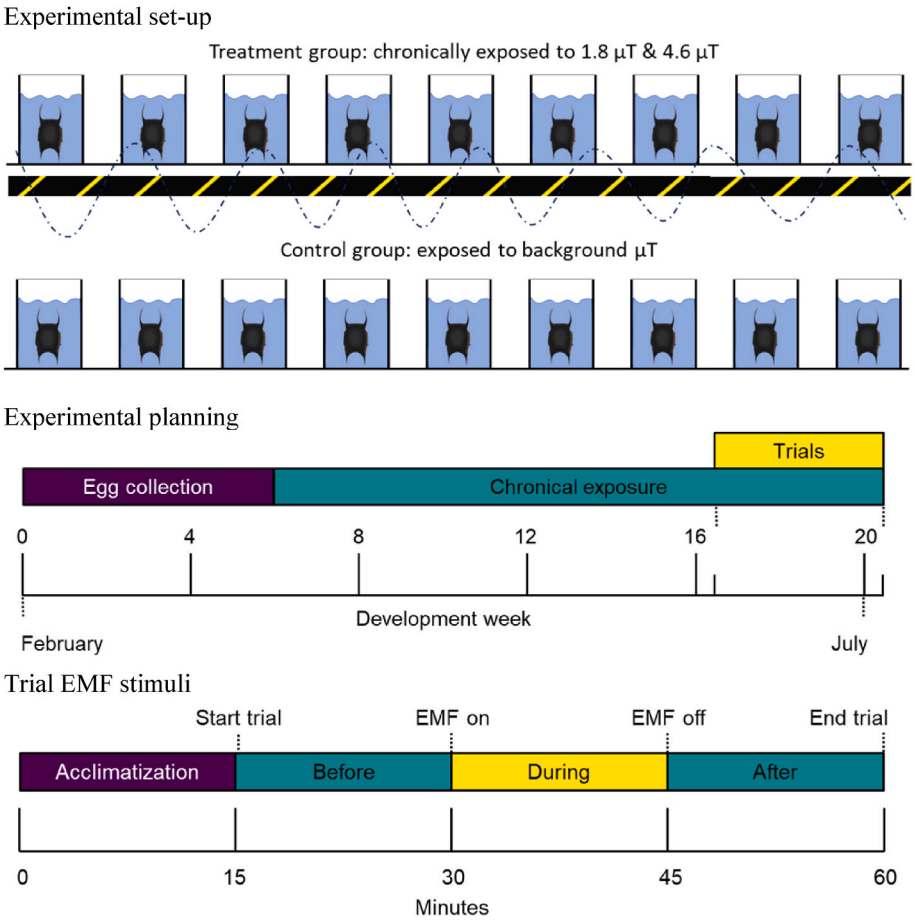


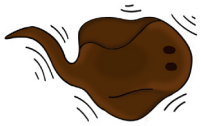
Fig. 1. Schematic overview of (top) experimental set-up, showing 9 egg casesChronically exposed and 9 control egg cases, all individually housed. Experimental planning (middle) with the egg collection period in purple, the exposed period in green and the measurement period superimposed in yellow. Overview of an EMF stimuli trial (bottom), indicating each block of 15 min, including acclimatisation (purple), "Before" exposure (green), "During" the EMF stimuli (yellow) and "After" the EMF stimuli (green). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

"Before" (to observe normal behaviour), "During" (to observe effects of EMF stimuli) and "After" (to observe lasting effects) (Fig. 1 bottom). It took the Helmholtz coil ~5 s to reach the required EMF exposure level. The trials were preceded by 15 min acclimatisation time which was in accordance with other studies (Ball et al., 2016), (Christensen et al., 2023), (Paoletti et al., 2023) and verified by pilot studies where the period of a freeze response due to handling, and the associated recovery to normal behaviour was observed. The behaviours freezing, tail undulating, whole body movement and partial body movement were selected as they could represent a predator avoidance or (stress) response (Kempster et al., 2013), (Christensen et al., 2023), (Paoletti et al., 2023), (Sisneros et al., 1998), (Ripley et al., 2021). The behaviours were scored per occurrence as detailed in the ethogram shown in Table 1. Tail undulation is performed to refresh water in the egg case, creating an influx of oxygenated water and removing metabolic waste products. Before and after the trial, the water quality parameters, temperature, salinity and dissolved O_2 concentration in the trial tank were measured and no deviations from the holding tank levels were recorded. During the trial period, parameters 'age', 'time of day', and 'trial number' were noted to allow for statistical inclusion as covariates to check whether they influenced behavioural responses. After the trials were completed, on the day of hatching, the total development days were calculated, the hatchlings were weighed and photographed to determine the length using ImageJ (v. 1.52).

2.4. Data analysis

The effects of exposure to EMF fields on embryo behaviours (freezing, tail undulation, whole body movement and partial body movement) were statistically analysed in R v. 4.2.2 (R Core Team). An absence of the influence of covariates 'age', 'time of day' and 'trial number' was verified (Table S2). Data were checked for normality and homogeneity of variances through Shapiro-Wilk and Levene's tests, respectively. A Bonferroni correction for multiple testing was applied where appropriate. The difference between Chronically exposed and Control embryo behaviour (occurrence and duration) was tested via a non-parametric general independence test, as the data did not follow assumptions on normality and homogeneity. This permutational test was applied using the *independence_test* function from the *coin* package (Hothorn et al., 2008). Next, during the initiation and termination of the EMF stimuli per trial, the occurrences of freeze response were determined. To see whether differences in behaviour within treatment groups (Control or Chronically exposed individuals) differed between the stage of the trial ("Before", "During" and "After" the EMF stimulus), a Generalised Linear Mixed Model (GLMM) was run using the *glmmTMB* package in R ((Brooks E et al., 2017)). Multiple GLMMs were run with different options as distributions (Poisson or Negative Binomial), and where parameters included were varied: trial order ("Before", "During" and "After"), EMF level (0.1, 1 and 10 μT) and treatment group (Control and Chronically exposed). Trial order, EMF level and treatment group were included as fixed effects and the individual rays were included as random effects. The model with the best fit was selected based on the lowest Akaike Information Criterion (AIC) value, and whether the addition of parameters increased the fit (p-value). Only the results from the model with the best fit were displayed. In order to visualize variation in behaviour between individual embryos, plots were produced of the occurrence of specific behaviours during the "Before" phase of the subsequent trials. For this, the average occurrence of the behaviour of the treatment group (Control or Chronically exposed) as recorded during (randomly assigned)exposure level 1 was used as a starting point. For each embryo the difference (increase or decrease) between the occurrence of the behaviour in the first trial, and in the second and third trial, respectively was calculated and plotted relative to the average occurrence in the first trial. Lastly, on the day of hatching the total development period in days was calculated, the hatchlings were weighed and photographed to determine their length using in ImageJ (v. 1.52).

Table 1
Ethogram of behavioural parameters including freezing, tail undulation, whole body movement and partial body movement in thornback ray embryos.

Behaviour	Definition	Depiction
Freezing	Tail retracts from horn and coils around the body. Embryo ceases all discernible movement for at least 5 s. Behaviour ends when tail undulation or other body movement is performed.	
Tail undulation	Tail undulates in one of the horns. Behaviour starts when tail starts undulating in a horn and ends when the undulation ceases.	
Whole body movement	Movement using the whole body, ranging from small spasms to half turns of body position inside the egg.	
Partial body movement	Body movement using only one body segment (either part of pelvic or pectoral fin).	

3. Results

All 18 embryos, 9 Chronically exposed and 9 Controls, underwent three trials of 45 min to observe differences in behaviour, during development weeks 17–21, totalling 54 trials. All 18 individuals successfully hatched within 21 weeks after egg deposition.

3.1. Effects of chronic EMF exposure

The average developmental time between egg laying and hatching or biometrics upon hatching did not differ significantly between the two treatment groups (Table 2). The number of freezing responses during the EMF stimuli showed no significant change between the Chronically exposed embryos (0.35 ± 0.82 sd occurrences) and the Control group (0.21 ± 0.58 sd occurrences), with a large skew towards zero response in both groups (Table S3). In addition, no freeze responses were observed when EMF levels changed during the initiation (start "During" phase) or termination (start "After" phase) of the stimuli trials, for both the Chronically exposed and the Control animals. Chronically exposed embryos did show increased tail undulation (Independence test: MaxT = −2.92, p-value = 0.015), increased whole body movement (MaxT = −2.70, p-value = 0.035) and more partial body movement (MaxT = −2.78, p-value = 0.005) during the "Before" phase (Fig. 2A, B and C; Table S3). On average, Chronically exposed animals showed 34 % more tail undulation than Control individuals (20.46 ± 5.7 sd versus 15.25 ± 5.7 sd tail undulation occurrences, respectively). Whole body movement was on average 148 % more in the Chronically exposed embryos compared to those in the Control group (4.54 ± 3.8 sd versus 1.82 ± 2.5

Table 2
Table of average time between egg laying and hatching (development time), and biometrics (total length and weight) for the different treatment groups.

Treatment group	development time in days ±sd	Length at hatching in cm ± sd	Weight at hatching in grams ±sd
Chronically exposed	143 ± 6	13.4 ± 0.8	103.6 ± 1.5
Control	145 ± 6	13.6 ± 0.5	104.4 ± 0.9

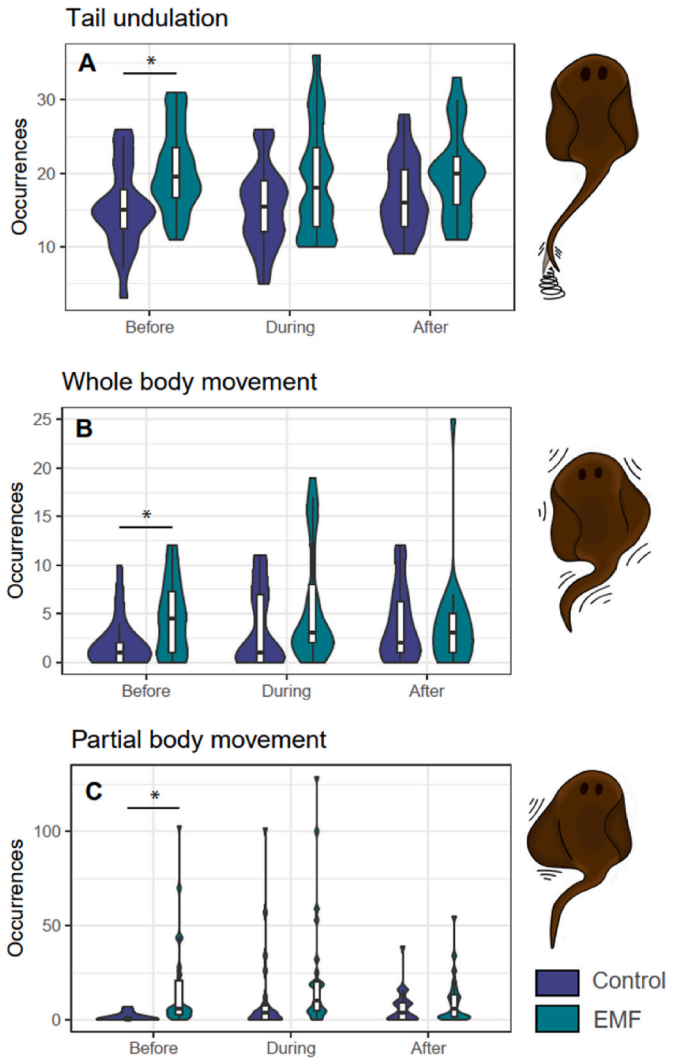


Fig. 2. Violin plots of number of occurrences during three 15-min trial periods ("Before" - background EMF exposure, "During" EMF exposure ranging from background, 1,0 and 10,0 μT and "After" - background EMF exposure) of (A) tail undulation, (B) whole body movement and (C) partial body movement, in thornback ray embryos comparing control with Chronically exposed treatment groups. Blue indicates the control group, and green depicts the Chronically exposed group. EMF levels 0.1, 1 and 10 μT are grouped. During the 'Before' trial period, significantly more occurrences of tail undulation, whole body movement and partial body movement were observed for the Chronically exposed group compared to the control ($p < 0.05$ after Bonferroni correction). The violin plot depicts the data distribution and displays a boxplot in each centre with the median and 25 % intervals. Outliers are depicted as points. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

sd whole body movement occurrences, respectively). Partial body movements occurred approximately 13 times more in the Chronically exposed embryos compared to the Controls (16.79 ± 25.3 sd versus 1.21 ± 2.1 sd, respectively). An absence of an effect of trial order ("Before", "During" and "After") was confirmed for the behaviours tail undulation and whole body movement, as including the fixed effect order did not result in the model with the lowest AIC (Fig. 2, Table S4). Instead, only treatment group (Control and Chronically exposed) and to a lesser extent EMF level and order were kept in the model for tail undulation and whole body movement, but without interactions. For partial body movement, order was kept in the model alongside treatment group, again without interactions. Chronically exposed embryos consistently showed higher occurrence of in tail undulation (GLMM: estimate = 0.22, z = 2.22, p = 0.03), whole body movement (GLMM: estimate = 0.48, z = 2.03, p = 0.04) and partial body movement (GLMM: estimate = 0.86, z = 2.91, p = 0.004) compared to Control embryos.

3.2. Variation in individual response

As indicated above, the occurrences of body movements were higher in the Chronically exposed group compared to the Controls. Although trial number did not prove to be a significant factor in explaining embryonic behaviour, when comparing individual responses an increased variation in individual behaviour can be observed in consecutive trials. During the course of the experiment, illustrated by observations in "Before" Trials 1 to 3, the individuals from the Chronically exposed group showed more changes in the occurrence of movements than the Controls (Fig. 3). This individual variation in change of behaviour is most notable for the partial body movement (Fig. 3 right panel) ranging from 8 to −5 for the Control and 156 to −47 for the Chronically exposed. This variation is also present in whole body movement e.g. ranging from 9 to −1 and 11 to −3 for the Control and Chronically exposed groups, respectively.

4. Discussion

Our results did not show any differences in development duration or hatching biometry between the Chronically exposed Thornback ray (*Raja clavata)* embryos in comparison to the Control group. We observed an increase in overall activity, expressed as more frequent body movements on average and a higher tail undulation activity in the treatment group. No disparity in freezing response between the two treatment groups was found when exposing embryos to changing EMF levels. Below, we elaborate on our findings and provide recommendations for further research.

Despite the observed hyperactive state and changes in tail undulation, neither development time nor biometry were affected. Leonard et al. (1999) determined that active tail beating (categorised as 'tail undulation' in the present study) costs *Raja erinacea* embryos over 53–81 % compared to the standard metabolic rate. Significantly increased tail undulation will therefore seriously increase energy consumption (Leonard et al., 1999) and it would be expected that the increased activity levels would have led to either changes in development time or changed biometry as (partly) shown by Paoletti et al. (2023) (Paoletti et al., 2023). Paoletti et al. (2023) reported increased growth in catshark (*Scyliorhinus canicula)* embryos exposed to EMF from week 10 of development until week 18, accompanied by a corresponding reduction in yolk size and increased length of the embryo (Paoletti et al., 2023). Because the trial was terminated at development week 18, individuals could not be followed to hatching to determine if this trend would lead to earlier hatching. It is worth noting that there are distinct differences in embryology between catsharks and rays, owing to the differences in the evolutionary development of oviparity between these taxa (Dulvy and Reynolds, 1997). Although the heightened metabolic demand did not lead to smaller hatchlings in our study, it may have led to accelerated yolk consumption, reducing the residual yolk supply at hatching and necessitating a quicker transition to successful foraging. However, since we did not measure the residual yolk size after hatching, we cannot determine whether there were differences in residual yolk between the Chronically exposed and Control groups.

Our results show an increased activity level in individuals that were Chronically exposed to variable levels of EMF. The observed hyperactive state might be a stress response to daily changing EMF levels (Ball et al., 2016). We only observed the embryos in the trial set-up, which is different from the housing aquaria in terms of EMF level and lighting levels (2–4 lumen vs. ~100 lumen during candling). Based on our data, we cannot determine if the hyperactive behaviour is a temporarily heightened stress response due to the changed environment during the trials or a persistent state.

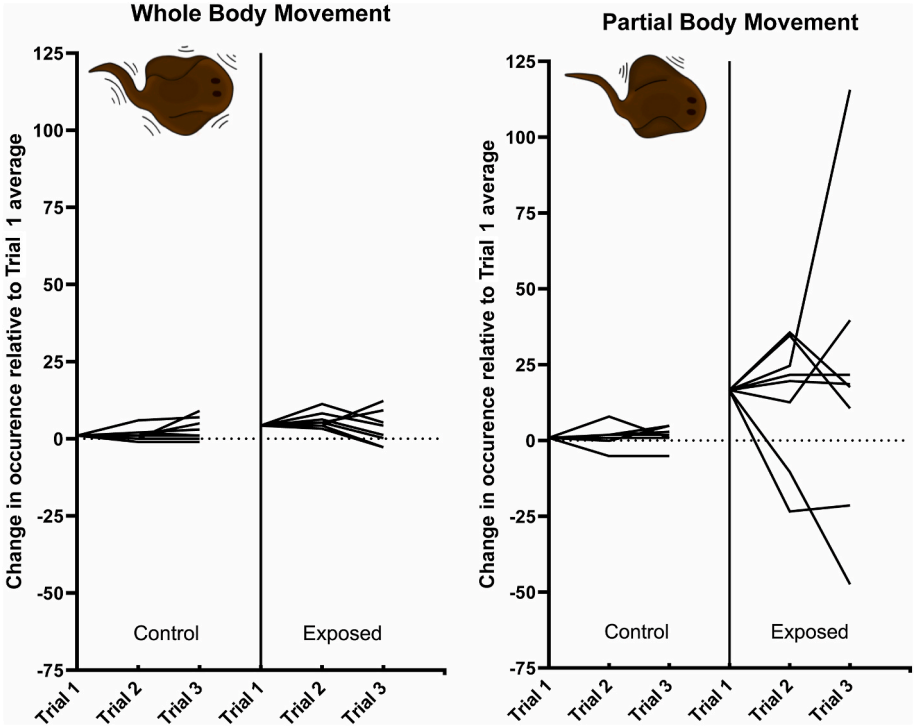


Fig. 3. Plots visualising the deviation in occurrences of (left) whole body movement and (right) partial body movement in thornback ray embryos during the "Before" phase of subsequent trials. Presented are the average occurrences for all embryos in the Control or Chronically exposed groups during Trial 1, and the changes in occurrence for individual embryos between Trial 2 and 3. The figure indicates the direction of the change, i.e. increase or decrease of the occurrence, showing a high individual variability. The averages in Trial 1 of the Chronically exposed group lay higher than in the control group, resulting in a higher starting point.

Before the stimuli trials started, embryos were allowed to acclimatise for 15 min, comparable to durations found in the pilot and other studies (Ball et al., 2016), (Christensen et al., 2023), (Paoletti et al., 2023). Particularly for adjusting to EMF stimuli, this acclimatisation period is considered sufficient due to the necessity for rapid response and recovery from an ecological EMF cue, such as that from an approaching predator. In the "Before" trial phase the embryos are expected to have returned to normal behaviour and recovered from the change in EMF level at the start of the acclimatisation phase (Fig. 1 bottom). During the stimuli trials embryos were exposed to changing EMF levels, but the average activity of the Chronically exposed group and Control group, respectively, did not change significantly (Fig. 2). If the EMF stimuli from the Helmholtz coil would act as a stressor resulting in increased activity, we would expect to see a change in activity in different phases of the trial. Our observations suggest that the EMF levels applied were not experienced by the embryos as (additional) a stressor, if experienced at all. The high light intensity needed for candling could form a stress factor during the trials. To our knowledge, no studies have investigated the effect of candling on elasmobranch embryos. Research applying this technique to zebrafish (Kimber et al., 2014) did not show any effect from increased light intensity. We did not observe specific responses of the embryos. These observations support the hypothesis that Chronically exposed embryos were constantly hyperactive and not only during the trials. If that is the case, the intensity of the hyperactivity was likely insufficient to cause detectable changes in development time or biometry based on our data.

Alternatively, Chronically exposed individuals might respond differently to a stressor (as EMF or intensified light) and may require more than 30 min to recover from a hyperactive state compared to control individuals. This would suggest that the treatment group is only hyperactive during the stimuli trials.

It is possible that the hyperactive state is a result of the fluctuations in chronic EMF exposure levels in our study design. In a study by Paoletti et al. (2023) seven *Scyliorhinus canicula* embryos were exposed to constant AC EMF levels ranging from 4 to 7 μT, comparable to our study, during 18 weeks and showed no changes in tail undulation frequency. The difference in the changes of tail undulation frequency with our study could be due to habituation to invariable exposure levels used by Paoletti et al. (2023). Indeed, several studies also showed habituation to repeated exposure to EMF within a short time-period, independent of exposure level, species and power systems (Ball et al., 2016), (Christensen et al., 2023), (Sisneros et al., 1998), (Kimber et al., 2014). In contrast, intermittent exposure has been shown to lead to a behavioural response in *Thornback ray* (Ball et al., 2016) and it might be especially changes in intensity that causes elevation in behavioural levels. While our study utilised field-relevant EMF levels, the frequency of small-scale variations (minutes/hours) in our simplified experiment set-up is less than with SPC. In our findings, the enhanced activity did not affect development time to hatching or biometry upon hatching. However, if it is the change in EMF level that results in difference in behaviour, a greater number of fluctuations in chronic EMF exposure levels than the current once per 24 h could lead to different effects. Conversely, frequent, predictable changes in EMF exposure might facilitate habituation (Ball et al., 2016), (Christensen et al., 2023), (Sisneros et al., 1998), (Kimber et al., 2014), resulting in less behavioural responses and result in habituation to changing levels. If elevated activity levels persist throughout embryogenesis this may increase te risk of embryos being detected by predators (Ball et al., 2016). This elevated detection risk could result in higher predation rates, ultimately reducing the recruitment of new individuals into the population. However, not much is known about the effects of predation on elasmobranch populations and further study is recommended (Martins et al., 2018), (Schröder et al., 2021), (Cox et al., 1993).

It is possible that EMF exposure during embryogenesis has resulted in effects that do not present themselves at hatching but manifest later in life for example a changed sensitivity to electric or magnetic fields due to

epigenetic selection or behavioural imprinting. Paige Beal et al. (2021) showed epigenetic responses in juvenile *Negaprion brevirostris* from trace metals released during dredging works, and temperature is associated with changes in tissue plasticity in *Scyliorhinus canicula*, as shown by a modelling approach of Ripley et al. (2023). It is possible that a changeable and intense EMF environment present during embryogenesis in combination with the early development of electro-sensitivity (Ball et al., 2016) can lead to a changed sensitivity level or response to EMF cues used in interactions with conspecifics, navigation or foraging later in life. Conversely, if the heightened activity levels found in our trials persist after hatching, this can lead to a higher metabolic demand and reduced individual fitness. Monitoring the further development of hatchlings, preferably in semi-field conditions (mesocosms) to investigate the long-term behavioural implications of altered sensitivity could provide valuable insights into long-term fitness and survival of Chronically exposed individuals.

There was no increase in freezing response during the stimuli trials, either on average through the stimulus exposure period or when the EMF level was altered. Sisneros et al. (1998), Ball et al. (2015) and Kempster et al. (2013) reported freezing by individuals exposed to EMF fields that were 10^2 - 10^3 higher than we used, and with 10 times lower frequencies (e.g., 56 μV/m at 0.5 Hz (Ball et al., 2016), 61 μV/m at 1–2 Hz (Ball et al., 2016) and 40–210 μV/m at 0–20 Hz (Kempster et al., 2013)). Paoletti et al. (2023) is, to our knowledge, the only other study with chronic EMF exposure and with field-relevant exposure levels, during the entire embryogenesis, although without variation in the EMF levels. The authors also reported high variability in freezing response and no difference in freezing between treatment groups (Paoletti et al., 2023). Both Paoletti et al. (2023) and our study used SPC field-relevant EMF levels with the same frequency (50 Hz). The extent to which the EMF source used in our study will mimic a predator needs to be investigated further. For example, the strength of the magnetic field might be comparable, but the frequency of an SPC AC is 25–50 times higher., is to be explored further. Kempster et al. (2013) observed reduced freeze response of *Brownbanded bamboo shark* with increasing frequency from 0 Hz to 20 Hz. It's possible that embryos are more likely to respond with a freezing response to EMF resulting from a biological source (conspecific or predator) with a low frequency than that of a cable with a higher frequency. Exploring the effects of chronic EMF exposure from a DC (0 Hz) cable will show if this different power system has a different impact.

The Chronically exposed group developed much wider variation in partial movement occurrence, ranging from marked decreases to increases in activity during the trials, than the Control group (Fig. 3). These large individual bidirectional changes, e.g. some increase the number of movements and some decrease, reduce the likelihood of demonstrating statistical differences. The significance of this observation lies not in the conventionally tested mean, but in the differences in the number of movements among individuals. It is recommended that further research in this field looks at individual differences in response to EMF and not only the average differences of an experimental group (Finger et al., 2016), (Byrnes and Brown, 2016), (Stuber et al., 2022). The variability in behavioural response within individuals may be attributed to different coping mechanisms in dealing with a stressor (Gallagher et al., 2014), (Creel, 2018), (Skomal and Mandelman, 2012).

Our study sheds light on the potential impact of EMF emitted by SPC on embryos developing in batoid egg cases, typically deposited in shallow coastal ecosystems (Martins et al., 2018), are also areas used for SPC routes (Hermans et al., 2024). While our findings provide valuable insights, it is premature to determine the need for mitigation measures or extrapolate our results to the real-world situation. Further investigation into the locations of egg case nurseries is needed to delineate potential conflict areas. Moreover, it is recommended to study responses to a DC field exposure, which distinctly differs from the AC field employed in our study. DC cables will be used in future planned offshore wind farms with a greater distance to shore (>70 km). For both AC and DC studies, experimental designs including short-term and long-term fluctuations of EMF levels mimicking the field is recommended. It is unknown whether batoid embryos are more sensitive to EMF resulting from DC than AC cable sources.

Given the greater activity during the trial of the Chronically exposed embryos, it is important to further study relative EMF sensing capabilities and behavioural responses upon EMF triggers of juveniles after hatching. Considering interspecies variability in coping with a stressor (Gallagher et al., 2014), (Creel, 2018), (Skomal and Mandelman, 2012), it is recommended to conduct comparative research with different oviparous species with distinctly diverse juvenile behaviour ecology (Hermans et al., 2024). Examples of species groups with different foraging and survival strategies are epibenthic predators as *Scyliorhinidae* or bentho-demersal ambush predators such as batoids (skates and stingrays). It would be appropriate to prioritise populations where the overlap between SPC and egg case nurseries is likely. If more research indicates persistent effects, mitigation measures such as micro cable routing or locally increased burial depth could be explored (Taormina et al., 2018), (Tricas and Gill, 2011). Ultimately, if EMF effects on elasmobranch embryos are minimal, offshore wind farms and cable crossings could serve as de facto protected areas for elasmobranch eggs. The prohibition of bottom trawling within offshore wind farms reduces fishing mortality, allowing adult oviparous elasmobranchs to lay eggs without the risk of bycatch, and ensuring that deposited eggs remain undisturbed by fishing activities (Pardo et al., 2023), (Wright et al., 2020), (Bergström et al., 2014).

5. Conclusions

This study shows that chronic exposure to variable EMF levels from AC cables increased the overall activity of Thornback ray (*Raja clavata)* embryos during trials. This could be attributed to either a heightened stress response or a persistent state of increased activity levels, but did not lead to detectable changes in development time or biometry at hatching. No change in freeze response, a behaviour associated with predator avoidance, was found resulting from EMF exposure. The heightened activity levels observed in Chronically exposed embryos could imply that depositing eggs within SPC-generated EMFs may elevate predation risk. Future research should prioritise effects of long-term DC exposure, observe the behavior of Chronically exposed hatchlings during embryogenesis and include different species, as species-specific responses may differ significantly.

CRediT authorship contribution statement

Annemiek Hermans: Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Diede L. Maas:** Writing – review & editing, Writing – original draft, Visualization, Formal analysis, Data curation. **Lydia M. V. de Barros Neta:** Writing – review & editing, Writing – original draft, Investigation, Data curation. **Tom Spanings:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Hendrik V. Winter:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Albertinka J. Murk:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Edwin M. Foekema:** Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization.

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were carried out in accordance with the project licence and animals were monitored for health issues by a qualified staff member.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107151.

Data availability

Data will be made available on request.

References

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.

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. Dev. Neurobiol. 76 (7), 721–729. https://doi.org/10.1002/dneu.22355.

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.

Bergström, L., et al., 2014. Effects of offshore wind farms on marine wildlife—a generalized impact assessment. Environ. Res. Lett. 9 (3), 034012. https://doi.org/10.1088/1748-9326/9/3/034012.

Boon, A.R., et al., 2019. The Assessment of System Effects of Large-Scale Implementation of Offshore Wind in the Southern North Sea. https://doi.org/10.13140/RG.2.2.23113.60000.

Brooks E, M., et al., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9 (2), 378. https://doi.org/10.32614/RJ-2017-066.

Brysiewicz, A., Formicki, K., 2019. The effect of static magnetic field on melanophores in the sea trout (*Salmo trutta* m. *trutta* Linnaeus, 1758) embryos and larvae. Ital. J. Anim. Sci. 18 (1), 1431–1437. https://doi.org/10.1080/1828051X.2019.1680319.

Byrnes, E.E., Brown, C., 2016. Individual personality differences in P ort J ackson sharks *H eterodontus portusjacksoni*. J. Fish. Biol. 89 (2), 1142–1157. https://doi.org/10.1111/jfb.12993.

Christensen, J., Grønkjær, P., Neuheimer, A.B., Kristiansen, R., 2023. Electroreception by small-spotted catshark (*Scyliorhinus canicula*) embryos in relation to predator detection and avoidance. Mar. Freshw. Behav. Physiol. 1–11. https://doi.org/10.1080/10236244.2023.2221372.

Clark, R.S., 1922. Rays and Skates (Raiae). No. I—Egg Capsules and Young. J Mar Biol Assoc UK.

Compagno, L.J.V., Dando, M., Fowler, S.L., 2005. A field guide to the sharks of the world [Online]. Available: https://api.semanticscholar.org/CorpusID:82517956.

Coolen, J.W.P., et al., 2020. Benthic biodiversity on old platforms, young wind farms, and rocky reefs. ICES J. Mar. Sci. 77 (3), 1250–1265. https://doi.org/10.1093/icesjms/fsy092.

Cox, D.L., Koob, T.J., 1993. 'Predation on elasmobranch eggs', in *The reproduction and development of sharks, skates, rays and ratfishes*. vol. 14. In: Demski, L.S., Wourms, J.P. (Eds.), Developments in Environmental Biology of Fishes, vol. 14. Springer Netherlands, Dordrecht, pp. 117–125. https://doi.org/10.1007/978-94-017-3450-9_10.

Creel, S., 2018. The control of risk hypothesis: reactive vs. proactive antipredator responses and stress-mediated vs. food-mediated costs of response. Ecol. Lett. 21 (7), 947–956. https://doi.org/10.1111/ele.12975.

Degraer, S., et al., 2020. Offshore wind farm artificial reefs affect ecosystem structure and functioning: a synthesis. Oceanography (Wash. D. C.) 33 (4), 48–57. https://doi.org/10.5670/oceanog.2020.405.

Di Santo, V., 2015. Ocean acidification exacerbates the impacts of global warming on embryonic little skate, Leucoraja erinacea (Mitchill). J. Exp. Mar. Biol. Ecol. 463, 72–78. https://doi.org/10.1016/j.jembe.2014.11.006.

Dulvy, N.K., Reynolds, J.D., 1997. Evolutionary transitions among egg–laying, live–bearing and maternal inputs in sharks and rays. Proc. R. Soc. Lond. B Biol. Sci. 264 (1386), 1309–1315. https://doi.org/10.1098/rspb.1997.0181.

Elliott, D., et al., 2016. A comparison of AC and HVDC options for the connection of offshore wind generation in great britain. IEEE Trans. Power Deliv. 31 (2), 798–809. https://doi.org/10.1109/TPWRD.2015.2453233.

European Commission, 2015. Directorate general for research and innovation. *MaRVEN: Environmental Impacts of Noise, Vibrations and Electromagnetic Emissions from Marine Renewable Energy : Final Study Report*. LU. Publications Office [Online]. Available: https://data.europa.eu/doi/10.2777/272281. (Accessed 19 December 2023).

Fey, D.P., Greszkiewicz, M., Otremba, Z., Andrulewicz, E., 2019. Effect of static magnetic field on the hatching success, growth, mortality, and yolk-sac absorption of larval Northern pike Esox lucius. Sci. Total Environ. 647, 1239–1244. https://doi.org/10.1016/j.scitotenv.2018.07.427.

Fey, D.P., et al., 2020. Otolith fluctuating asymmetry in larval trout, Oncorhynchus mykiss Walbaum, as an indication of organism bilateral instability affected by static and alternating magnetic fields. Sci. Total Environ. 707, 135489. https://doi.org/10.1016/j.scitotenv.2019.135489.

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.

Formicki, K., Winnicki, A., 1998. Reactions of fish embryos and larvae to constant magnetic fields. Ital. J. Zool. 65 (Suppl. 1), 479–482. https://doi.org/10.1080/11250009809386870.

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.

Franco, A., Thomson, S., 2016. Follow on to the Development of Spatial Models of Essential Fish Habitat for the South Inshore and Offshore Marine Plan Areas. ' https://doi.org/10.13140/RG.2.2.23092.24969.

Gallagher, A., Serafy, J., Cooke, S., Hammerschlag, N., 2014. Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. Mar. Ecol. Prog. Ser. 496, 207–218. https://doi.org/10.3354/meps10490.

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, Newbury.

Hamlett, W.C., Koob, T.J., 1999. Sharks, Skates, and Rays: the Biology of Elasmobranch Fishes. Johns Hopkins University Press, Baltimore.

Harsanyi, P., et al., 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 (5), 564. https://doi.org/10.3390/jmse10050564.

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.

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.

Holmes, T., McCormick, M., 2010. Size-selectivity of predatory reef fish on juvenile prey. Mar. Ecol. Prog. Ser. 399, 273–283. https://doi.org/10.3354/meps08337.

Hothorn, T., Hornik, K., Wiel, M.A.V.D., Zeileis, A., 2008. Implementing a class of permutation tests: the **coin** package. J. Stat. Softw. 28 (8). https://doi.org/10.18637/jss.v028.i08.

Hutchison, Z.L., Gill, A.B., Sigray, P., He, H., King, J.W., 2020a. 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., Secor, D., Gill, A., 2020b. 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.

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.

Kajiura, S.M., Holland, K.N., 2002. Electroreception in juvenile scalloped hammerhead and sandbar sharks. J. Exp. Biol. 205, 3609–3621.

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., Hart, N.S., Collin, S.P., 2013. 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., 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. Cogn. 17 (1), 55–65. https://doi.org/10.1007/s10071-013-0637-8.

Leonard, J.B.K., Summers, A.P., Koob, T.J., 1999. Metabolic rate of embryonic little skate,Raja erinacea (Chondrichthyes: batoidea): the cost of active pumping. J. Exp. Zool. 283 (1), 13–18. https://doi.org/10.1002/(SICI)1097-010X(19990101)283:1<13::AID-JEZ3>3.0.CO;2-S.

Martins, A., Heupel, M., Chin, A., Simpfendorfer, C., 2018. Batoid nurseries: definition, use and importance. Mar. Ecol. Prog. Ser. 595, 253–267. https://doi.org/10.3354/meps12545.

Matich, P., Plumlee, J.D., Fisher, M., 2021. Grow fast, die young: Does compensatory growth reduce survival of juvenile blacktip sharks (*Carcharhinus limbatus*) in the western Gulf of Mexico? Ecol. Evol. 11 (22), 16280–16295. https://doi.org/10.1002/ece3.8311.

Musa, S.M., Czachur, M.V., Shiels, H.A., 2018. Oviparous elasmobranch development inside the egg case in 7 key stages. PLoS One 13 (11), e0206984. https://doi.org/10.1371/journal.pone.0206984.

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.

Paige Beal, A., Hackerott, S., Franks, B., Gruber, S.H., Feldheim, K., Eirin-Lopez, J.M., 2021. Epigenetic responses in juvenile Lemon sharks (Negaprion brevirostris) during a coastal dredging episode in Bimini, Bahamas. Ecol. Indic. 127, 107793. https://doi.org/10.1016/j.ecolind.2021.107793.

Paoletti, S., et al., 2023. The effect of electromagnetic feilds generated by an alternating current cable on the early-life stages of marine species. EDEN 18, 389–414, 2000.

Pardo, J.C.F., Aune, M., Harman, C., Walday, M., Skjellum, S.F., 2023. A synthesis review of nature positive approaches and coexistence in the offshore wind industry. ICES J. Mar. Sci. https://doi.org/10.1093/icesjms/fsad191.

Pimentel, M.S., et al., 2014. Defective skeletogenesis and oversized otoliths in fish early stages in a changing ocean. J. Exp. Biol. 92635. https://doi.org/10.1242/jeb.092635.

Reynolds, J.D., Dulvy, N.K., Goodwin, N.B., Hutchings, J.A., 2005. Biology of extinction risk in marine fishes. Proc. R. Soc. B Biol. Sci. 272 (1579), 2337–2344. https://doi.org/10.1098/rspb.2005.3281.

Ripley, D.M., De Giorgio, S., Gaffney, K., Thomas, L., Shiels, H.A., 2021. Ocean warming impairs the predator avoidance behaviour of elasmobranch embryos. Conserv. Physiol. 9 (1), coab045. https://doi.org/10.1093/conphys/coab045.

Ripley, D.M., et al., 2023. Warming during embryogenesis induces a lasting transcriptomic signature in fishes. Sci. Total Environ. 902, 165954. https://doi.org/10.1016/j.scitotenv.2023.165954.

Rodríguez-Cabello, C., Sánchez, F., Serrano, A., Olaso, I., 2008. Effects of closed trawl fishery areas on some elasmobranch species in the Cantabrian Sea. J. Mar. Syst. 72 (1–4), 418–428. https://doi.org/10.1016/j.jmarsys.2007.09.010.

Schröder, D., Schröder, G., Wiersma, G., Verhoog, P., Laterveer, M., 2021. Elasmobranch egg case predation in the Dutch North Sea. Proc. Zool. Soc. 74 (2), 211–218. https://doi.org/10.1007/s12595-021-00365-7.

Serra-Pereira, B., et al., 2011. The development of the oviducal gland in the Rajid thornback ray, Raja clavata. Helgol. Mar. Res. 65 (3), 399–411. https://doi.org/10.1007/s10152-010-0232-1.

Sisneros, J.A., Tricas, T.C., 2002a. 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.

Sisneros, J.A., Tricas, T.C., 2002b. 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.

Sisneros, J., Tricas, T., Luer, C., 1998. Response properties and biological function of the skate electrosensory system during ontogeny. J. Comp. Physiol. 183, 97–99. https://doi.org/10.1007/s003590050237.

Skomal, G.B., Mandelman, J.W., 2012. The physiological response to anthropogenic stressors in marine elasmobranch fishes: a review with a focus on the secondary response. Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 162 (2), 146–155. https://doi.org/10.1016/j.cbpa.2011.10.002.

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., et al., 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.

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. BOEMRE, Camarillo, CA, 2011-09.

Walker, T.I., Taylor, B.L., Hudson, R.J., Cottier, J.P., 1998. The phenomenon of apparent change of growth rate in gummy shark (Mustelus antarcticus) harvested off southern Australia. Fish. Res. 39 (2), 139–163.

Wind Europe, 'Wind energy today'. Accessed: December. 30, 2023. [Online]. Available: https://windeurope.org/about-wind/wind-energy-today/.

Wright, S.R., et al., 2020. Structure in a sea of sand: fish abundance in relation to man-made structures in the North Sea. ICES J. Mar. Sci. 77 (3), 1206–1218. https://doi.org/10.1093/icesjms/fsy142.