Marine Environmental Research 213 (2026) 107727

Contents lists available at ScienceDirect

Marine Environmental Research

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

Effects of electromagnetic fields from an alternating current power cable on the embryogenesis of three benthic associated marine species

Silvia Paoletti [a,*], Robin Brabant [a], Ilona Strammer [a], Peter Sigray [b], Niklas Rolleberg [b], Brian G. Stewart [c], Johan Aerts [d], Steven Degraer [a], Zoë L. Hutchison [e,f,1], Andrew B. Gill [g,1]

[a] Royal Belgian Institute of Natural Sciences (RBINS), Operational Directorate Natural Environment (OD Nature), Aquatic and Terrestrial Ecology (ATECO), Marine Ecology and Management (MARECO), Rue Vautier 29, 1000, Brussels, Belgium
[b] Royal Institute of Technology in Stockholm (KTH), Teknikringen 8, 114 28, Stockholm, Sweden
[c] Strathclyde University, 16 Richmond St, Glasgow, G1 1XQ, United Kingdom
[d] Ghent University, Department of Biology, Stress Physiology Research Group (StressChron), Belgium
[e] Scottish Government, Offshore Wind Directorate, Atlantic Quay, Glasgow, G2 8LU, United Kingdom
[f] University of St Andrews, St Andrew, KY16 9AJ, United Kingdom
[g] Centre for Environment, Fisheries and Aquaculture Science (Cefas), Pakefield Rd, Lowestoft, NR33 0HT, United Kingdom

ARTICLE INFO

Keywords:
EMFs
Subsea power cables
Embryogenesis
Behaviour
Offshore wind farms
Elasmobranch
Cephalopod

ABSTRACT

The global expansion in offshore renewable energy, primarily through offshore wind, is associated with the proliferation of subsea power cables (SPCs) throughout marine and coastal benthic environments. The transmission of electrical power through these SPCs will introduce electromagnetic fields (EMFs) into the seabed and the adjacent water column, which raises questions regarding the potential impact on benthic fauna, particularly during critical developmental early-life stages for which research considering the effects of both the electric and magnetic components of SPC EMFs is lacking. We conducted an experiment on three benthic egg-laying species, – the elasmobranch *Scyliorhinus canicula*, the cephalopod *Loligo vulgaris*, and the cephalopod *Sepia officinalis* – found in areas under consideration for the routing of SPCs. We exposed the embryos to realistic EMF levels (magnetic field 4–6 μT) recreated in the laboratory using an AC power cable set-up that simulated the EMF conditions, and examined the morphological, physiological, and behavioural responses. Our findings indicate subtle responses to EMF exposure in *S. canicula* and *L. vulgaris* with faster growth rates and morphometric differences, but no responses in *S. officinalis*. Our results highlight the value of a multiple end point approach to determine the potential influence of chronic exposure to EMFs on embryogenesis in benthic fauna and provide a baseline for future studies to build upon. Although our study cannot extrapolate the consequences of individual-level effects to population-level impacts, it does underscore the necessity of realistic and longer-term studies to assess the potential consequences of EMFs to marine fauna.

1. Introduction

The electromagnetic fields (EMFs) emitted from subsea power cables (SPCs) are among potential anthropogenic stressors introduced in the marine and coastal environment following the development of offshore renewable energy (ORE, including wind and marine technologies), and power transmission networks (Dannheim et al., 2020), in global efforts to meet net zero and energy security targets. Electricity is transmitted either as alternating current (AC) or direct current (DC) and when the electrical current passes through the cables, magnetic fields are directly propagated into the environment (Albert et al., 2020; Hutchison et al., 2021). In the case of AC cables, electric fields are also induced in the seabed and water, and in each case the EMFs are within the sensitivity range of many species (Gill, 2023). Currently, AC cables are the most numerous connecting multiple energy harnessing devices (*e.g.* wind turbines, wave devices) within the ORE footprint and as export cables to shore (Fjellstedt et al., 2022). Therefore, with the increase in ORE-related SPCs there is an increased likelihood of them being located near ecologically important habitats (*e.g.* natural hard substrates, spawning grounds, marine protected areas). The associated benthic and

* Corresponding author.
E-mail address: silviapaoletti95@gmail.com (S. Paoletti).
[1] Z.L.H and A.B.G contributed equally to this work.

https://doi.org/10.1016/j.marenvres.2025.107727
Received 26 September 2025; Received in revised form 14 November 2025; Accepted 17 November 2025
Available online 17 November 2025
0141-1136/Crown Copyright © 2025 Published by Elsevier Ltd. This is an open access article under the CC BY-NC license (http://creativecommons.org/licenses/by-nc/4.0/).

demersal fauna are therefore expected to be more frequently in closer proximity to SPCs, potentially increasing their encounter rate with EMFs (Hutchison et al., 2020a; Gill, 2023; Hermans et al., 2024), particularly AC EMFs. The life-history traits of a species (*e.g.* mobility and distribution), will determine which life stages of individuals may encounter EMFs and the duration of their potential exposure (Hutchison et al., 2020a; Hermans et al., 2024). Several ecologically important species that can sense EMFs, such as elasmobranchs and cephalopods, lay their eggs on hard substrates, remaining anchored for several weeks to months throughout embryogenesis. Exposure to EMFs during critical early-life stages, may influence growth, development and behaviour (Fey et al., 2019a; Harsanyi et al., 2022), with potential implications for animal fitness and subsequently their populations (Harsanyi et al., 2022; Hutchison et al., 2020a).

Potential effects of both AC and DC EMFs on sensitive marine fauna have been debated, and recent studies have shown variable and sometimes diverging results based on assessments made of exposure to either the electric or magnetic component (for reviews see, Albert et al., 2020; Gill, 2023; Hutchison et al., 2020a). Although studies investigating adult and juvenile responses in elasmobranch and crustacean species have reported signs of behavioural changes associated with exposure to SPC-type EMFs (both magnetic and electric fields on *Raja clavata*, *Scyliorhinus canicula*, *Leucoraja erinacea*, and *Homarus americanus*; Gill et al., 2009; Hutchison et al., 2020b), others have considered magnetic fields alone (on *Cancer pagurus* and *Homarus gammarus*; Scott et al., 2021; Taormina et al., 2020; Albert et al., 2022, on *Necora puber*; Albert et al., 2023, and on *Rhithropanopeus harrisii*; Jakubowska-Lehrmann et al., 2025) and found some or no response. Studies targeting early life stage responses to EMF (*e.g.* (Fey et al., 2019a; Harsanyi et al., 2022), especially of organisms that can sense electric and/or magnetic fields called receptor species (Hermans et al., 2025), are scarcer but needed (Hutchison et al., 2020a).

Research on several teleost fish species exposed to low to medium intensity artificial magnetic fields (15–150 μT) found no response in adults (Chapman et al., 2025) but revealed different behavioural responses at the larval stage: no responses in *Clupea harengus* (Cresci et al., 2020) and *Ammodytes marinus* (Cresci et al., 2022), whereas some responses in *Gadus morhua* and *Melanogrammus aeglefinus* were found (Cresci et al., 2023). Some responses were also recorded during embryogenesis at higher intensities of artificial magnetic fields (1–10 mT) (*Esox lucius*, Fey et al., 2019b; *Coregonus lavaretus* and *C. albula*, Brysiewicz et al., 2017; *Oncorhynchus mykiss*, Stankevičiūtė et al., 2019). In crustaceans (*Homarus gammarus* and *Cancer pagurus*), eggs and larvae morphometric changes were observed by Harsanyi et al. (2022) for 2.8 mT magnetic fields. As shown by Albert et al. (2020) a number of EMF-related studies have targeted invertebrate species (Chapman et al., 2023), however, to our knowledge no study has targeted benthic spawning cephalopods. Furthermore, contrasting results among studies may arise from either technical differences in how the artificial EMFs were generated or due to species-specific and life stage-specific responses (Albert et al., 2020; Hutchison et al., 2020a). In fact, one of the biggest challenges for studying EMF impact on marine fauna remains the production and characterisation of EMFs at intensities representative of SPCs allowing exposure of organisms to realistic scenarios standardised and repeatable way. In controlled laboratory experiments, previous studies have often used set-ups that generate large, unidirectional magnetic field intensities from Helmholtz coil systems (*e.g.*, Harsanyi et al., 2022; Scott et al., 2021; Taormina et al., 2020). However, to be truly representative the desire is to understand animal responses to EMFs observed from SPCs, which requires exposure to magnetic field intensities, which propagate in the same way as SPC EMFs in 3-dimensional space (Gill et al., 2023; Hutchison et al., 2020a, 2021; Albert et al., 2020).

To address the need for studies representative of SPC EMFs, we designed a multiple endpoint study to assess behavioural, developmental and physiological factors, which could lead to the determination of potential impacts of EMFs from AC SPCs on critical early-life stages of benthic associated species. To replicate a realistic SPC exposure scenario, we recreated the EMF environment in a laboratory setting using an AC cable that represented a proxy of an infield cable within an offshore wind farm (OWF). The majority of infield cables used at OWFs are three-core AC power cables (Fjellstedt et al., 2022), which are buried or covered with cable protection therefore the most likely scenario is a physical barrier increasing the distance between the cable surface (EMF source) and the animals. The EMF intensity also decays rapidly with distance, therefore organisms that are on the seabed are plausibly most frequently, likely encounter low to medium-level fields that occur over several metres distance from the cable (Hutchison et al., 2021), rather than the peak fields directly on or above the cable. Furthermore, as wind and electrical load variation occurs with diurnal and seasonal patterns (Kiviluoma et al., 2016), the most representative EMF intensities associated with offshore renewable energy over the several months of species development are at low to medium levels rather than those associated with maximum power loads. This study was, therefore, designed to represent the EMF environment that animals in their early-life stages would most likely encounter if they were located near to an infield cable; such a magnetic field was estimated in the range 0.1–11.9 μT (Hermans et al., 2024; Moray East Offshore Wind Farm Wind Farm Cable Plan, 2019).

We hypothesised that animals exposed to EMFs throughout their embryonic development would manifest measurable responses in growth, development and/or behaviour. To address the hypothesis, we selected three species, the elasmobranch *Scyliorhinus canicula* and the cephalopods *Loligo vulgaris* and *Sepia officinalis* to represent vertebrate and invertebrate animals that have a benthic early-life stages in habitats where cable routing could likely cross (*e.g.* nearshore gravel beds) and are also putatively receptive for (geo)magnetic and bioelectric fields. We exposed the species to the representative magnetic field and examined a selection of morphological, physiological and behavioural variables throughout their embryogenesis and - in cephalopods - at hatching.

2. Methods

2.1. Recreating EMFs in laboratory

The experiments were set up in an isolated laboratory room that was assessed for potential EMF influences. On either side of the room, tables were set out in an L shape, on which multiple individual aquarium tanks were located. One side was exposed to EMFs (Exposed), while the opposite side was not (Control) (Fig. 1a). All equipment and material used in the experiments were also considered with regard to their potential influence on the EMFs in the room. The EMFs which simulated the infield SPC EMFs were created in the exposed area of the laboratory using an AC cable powered through an electrical transformer located outside the room. The cable donated by Elia Transmission Belgium was 24 m in length and had a single copper core of 18 mm in diameter covered by a rubber insulation of 8 mm in thickness. A bespoke electricity transformer generating low voltage (0–10 V), high current (0–1000 A) electricity at 50 Hz was used (Trutech Products, https://www.trutech.co.in/). Settings recreated a constant and continuous EMF emission and exposure scenario. The cable entered the room and passed below the wooden tables through the exposed area (Fig. 1a); the first section of the cable was twisted to minimize EMF emission in unwanted areas, then the cable was fixed to a wooden frame to pass horizontally below the tables at 50 cm from the tabletops, curved back and ran parallel below the other cable section 80 cm from the tabletops. As a result, the exposed animals in tanks above the tabletops were at 50 cm distance from the first cable section. Mild steel sheets (99 % iron, 2 mm thickness) of high permeability to EMFs – and thereby providing some absorption and containment of the EMFs in space – were placed in front of the exposed tables to achieve the same EMF intensities in the tanks and restrict the wider propagation of EMFs ensuring no influence on the

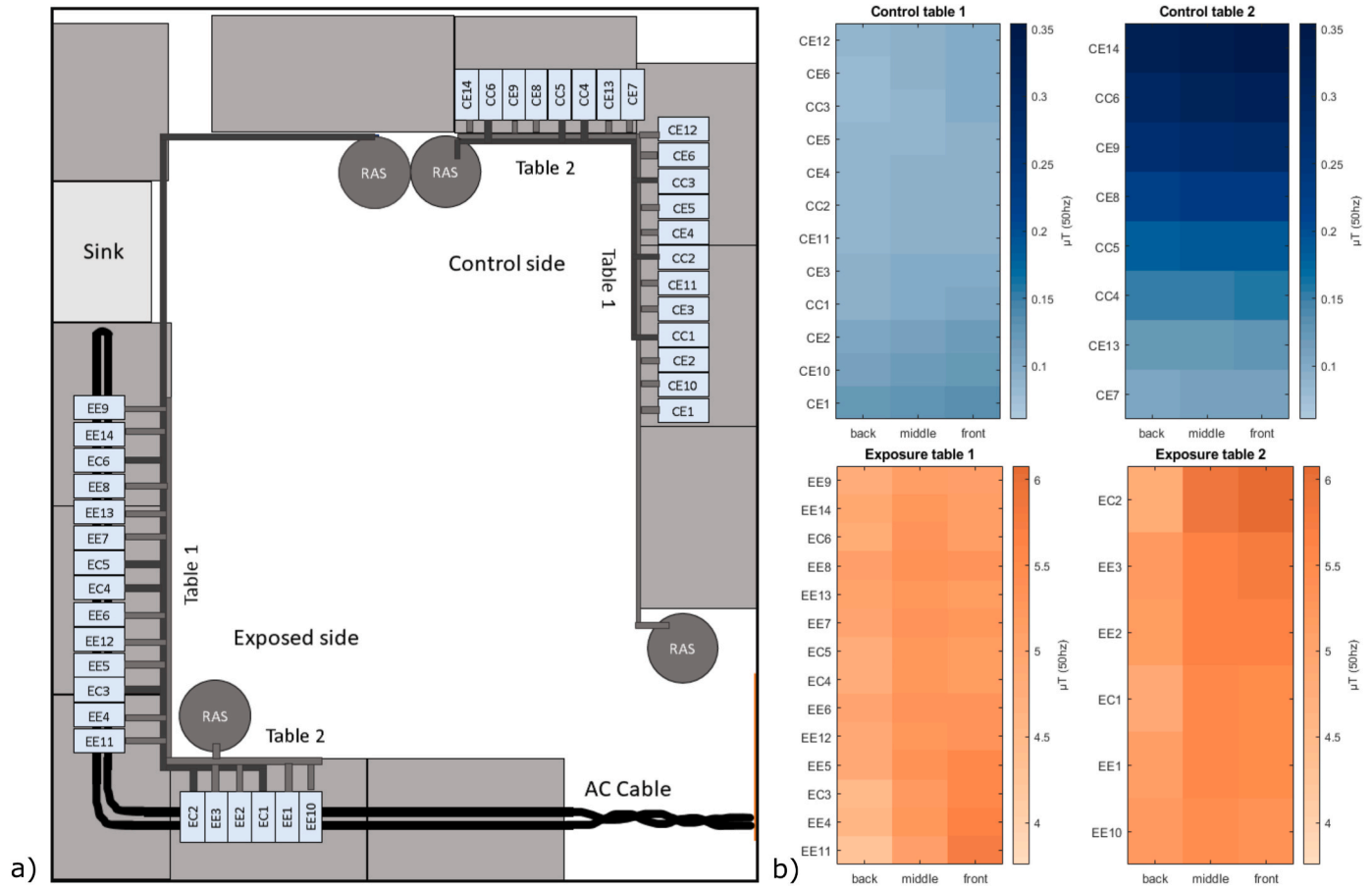

Fig. 1. Reproduction of EMFs in laboratory (4.8 m × 6 m). a) Laboratory room set-up. The power cable entered the room from the door (bottom right) and ran below the tables of the assigned exposed side (drawing simplified to show the dual pathway). On the tables, the randomised sequence of tanks was connected to the respective recirculating aquaculture systems (RAS). Labels EE1-EE14 = exposed elasmobranchs, EC1-EC6 = exposed cephalopod, CE1-CE14 = control elasmobranch and CC1-CC6 = control cephalopods. b) Average magnetic field values measured inside each experimental tank at the back, middle and front. Exposed tanks range from 4 to 6 μT while control tanks range from 0.05 to 0.35 μT, representative of background levels.

control area.

To assist in the experimental design and cable positioning, EMF simulations of the entire room environment with the powered cable were undertaken using COMSOL Multiphysics. This determined approximate cable current settings and geometrical EMF distributions within the environment and the tanks, aiming for EMF intensities and geometries representative of those emitted from an *in-situ* cable at sea within each of the exposed tanks. The targeted level of magnetic fields on the exposure side of the lab was 5–10 μT to reproduce the low to medium EMF levels propagating near infield cables, that spatially represent the most likely scenario for animals located on the seafloor within the zone of emitted EMFs from SPCs. The EMF intensity we used was not only representative, it was also within the range of detection and potential sensitivity of the benthic early-life stage of the receptor species, which can range from small bioelectric fields (μV/cm) to geomagnetic field intensities (25–65 μT). Such low to medium-level EMF exposures were considered biologically meaningful as they are naturally used as cues by receptor species to navigate, orient, prey and migrate and therefore may be expected to elicit behavioural or physiological responses (Hutchison et al., 2020a).

EMF intensities were fully characterised at the start of the experiments at six locations in each tank. The measurements were taken underwater using a magnetic field fluxgate sensor (Bartington model Mag-03MSS1000) and Ag-AgCl electrodes (bespoke electrodes based on disks from In Vivo Metric Systems). Additionally, continuous recordings were obtained from a magnetic field fluxgate sensor in the exposed area to monitor for potential deviations in emitted magnetic field throughout the experimental period. Collectively, these measurements also confirmed that there was no influence of extraneous EMFs from sources external to the laboratory.

2.2. Aquarium set-up

Each elasmobranch system was composed of 14 x 6 L tanks and a total recirculating water body of 120 L, supplied by a water flow of 0.5 L/min. Each cephalopod system was composed of 6 x 11 L tanks and a total recirculating water body of 120 L, with an individual tank water flow of 1 L/min. Average water temperature of 17.5 ± 0.9 °C, relative dissolved oxygen (RDO) of 96.0 ± 0.5 %, pH of 8.2 ± 0.1 and salinity of 35.1 ± 0.7 ppt (mean ± SD) were maintained in all tanks. The light cycle was 12D:12 N with simulated sunrise and sunset. Light intensity was measured over each tank at the beginning and end of the experiment and was on average 53.9 ± 16.1 lux (mean ± SD) for elasmobranch, and 62.6 ± 14.6 lux (mean ± SD) for cephalopods.

Aquarium tanks had separate recirculating water systems (RAS) for elasmobranch and cephalopods per control and exposed systems (Fig. 1a). The same RAS was used for both squid and cuttlefish, but each species was studied over two separate time periods. All components of the RAS were plastic to prevent interference with EMFs. To ensure the independence of the replicate tanks within the RAS, each system had mechanical (activated carbon) and biological filtration (nitrifying bacteria). The recommended time interval for activated carbon renewal is generally 3–4 weeks in aquaria. To ensure maximum metabolite extraction, we renewed activated carbon weekly. Water quality was

monitored three times a week with regular water renewal to maintain minimal ammonium (NH_4^+) and nitrite (NO_2^-) concentrations. The efficiency of the system in ensuring replicate independence was verified by fortnightly sampling of the water outflows of the elasmobranch system (both exposed and control), which was tested for the absence of hormonal markers (see below for details).

2.3. Experimental procedure

2.3.1. Elasmobranchs

Scyliorhinus canicula eggs were supplied weekly in June 2022 from the National Fishery Museum (NAVIGO) in Belgium, where newly deposited eggs were collected, date recorded and monitored until collection. On arrival, all eggs were acclimated over 24 h to the laboratory conditions, labelled and randomly assigned to treatments. Eggs were suspended individually in the water column of each tank in a vertical position. *S. canicula* embryos develop for an average of 20–24 weeks at 17 °C (Musa et al., 2018). We conducted the exposure experiment for 18 weeks, starting from week 0 of development. In total, 28 freshly deposited egg cases were collected and reared in the laboratory, with 14 assigned to control conditions and 14 to exposed conditions, one per tank. Three eggs revealed naturally not viable within the first week and were removed from the experiment, decreasing sample size to 25 (control n = 12, exposed n = 13). The embryonic development of each individual was monitored fortnightly until week 18 by measuring the yolk dimensions and the embryo growth. Eggs were placed next to a ruler in an observational tank in the middle of the room away from the cable EMF and observed against a cold light source while being filmed with a GoPro Hero 8 ("candling" method; Johnson et al., 2016; Musa et al., 2018). The same set-up was used for the entire experiment, ensuring a constant approach (same distance between the tank, camera and light sources; constant water volume). Yolk volume, surface, and embryo total length were calculated from the video frames using Fiji software (Musa et al., 2018). From week 8 onwards, embryos were also filmed to measure their behavioural freeze response (i.e., predatory avoidance behaviour where all movements are interrupted in response to a simulated predatory threat, Ball et al., 2015) and ventilatory frequency (i.e., repeated body movements to oxygenate the egg case, Ripley et al., 2021; Ball et al., 2015). Freeze response was measured in seconds from the end of a predatory threat (in this case handling of the egg case) until the embryo's first movement. Handling followed a consistent approach in scooping the egg from its tank inside a falcon tube and pouring the egg out within the monitoring tank. The time taken for ventilation to restore to normal pre-disturbance levels from the first movement was extracted. After 5 min of being restored, ventilation frequency was measured by counting the tailbeats or mouth pumps per minute (Ripley et al., 2021).

At three time points (T1 = 6 weeks, T2 = 11 weeks, T3 = 16 weeks) three eggs per treatment were removed (total; 9 control, 9 exposed) for stress hormone analysis. Five extra eggs were collected at NAVIGO to provide a hormonal reference at time zero (T0) of no exposure to EMF. Eggs were euthanised by submersion in lethal dosage 0.5 g/L tricaine methanesulfonate (MS-222) buffered with 0.5 g/L sodium bicarbonate (Musa et al., 2018) to be sampled for amniotic fluid, yolk, and embryo (whole body). Concentrations of 1α-hydroxycorticosterone (1α-OHC) were measured in each tissue by ultra-performance liquid chromatography coupled to tandem mass spectrometry (UPLC-MS/MS) (Ruiz-Jarabo et al., 2019). With the progressive removal of embryos for hormone analysis, the total number of filmed embryos decreased from 25 to seven. At week 18, the remaining seven embryos (3 control, 4 exposed) were euthanised, extracted from the egg cases, and filmed for the measurement of additional morphological parameters (Grunow et al., 2022).

2.3.2. Cephalopods

Loligo vulgaris and *Sepia officinalis* egg clusters were collected from passive fishing gear in Belgian coastal waters, during two separate fishing trips in May and June 2022, respectively. Only eggs in the very early stage of embryonic development were taken (squid eggs at stage 1, Feyjoo et al., 2015; cuttlefish eggs below stage 14, Boletzky et al., 2016). After acclimation, squid eggs were separated into individual units (*i.e.* finger-like structures of 50–100 eggs each (Feyjoo et al., 2015)), randomly assigned to treatment and suspended vertically in pairs in each tank. Similarly, cuttlefish egg clusters were separated into individual units and twenty-three random single-egg capsules (Boletzky et al., 2016) were placed in each tank in a suspended net. At 17.5 ± 0.9 °C, the cephalopod embryonic development and exposure lasted 5 weeks in *L. vulgaris* and 8 weeks in *S. officinalis*. Eggs of both species were monitored until hatching. All hatchlings (squid n = 1440, cuttlefish n = 165) were checked for healthiness by assessing buoyancy, reaction to stimulus, prematurity, and presence of malformations. A subsample of hatchlings (squid n = 126, 10 per tank on average; cuttlefish n = 96, 8 per tank) was randomly selected across the hatching period and assessed for healthiness response variables. First, each hatchling was filmed undisturbed with a GoPro Hero 8 (5 min for squid, 2 min for cuttlefish) in an observation tank for categorising species-specific swimming behaviours. Healthy and normally buoyant squid paralarvae are pelagic and rely on jet-and-sink swimming to remain suspended in the water column away from the water surface and the seafloor (Zakroff et al., 2018). Squid hatchlings were then stimulated by being pipetted in a falcon tube to note the presence/absence of a chromatophore reaction (Messenger, 2001). Cuttlefish hatchlings do not have a pelagic phase and, if normally buoyant, immediately seek shelter from currents by anchoring on substrates using an early-stage ventral sucker (O'Brien et al., 2016). Cuttlefish hatchlings were also filmed using a stereomicroscope for ventilatory frequency counting the internal funnel pumps per minute. Both species' hatchlings were then anaesthetized with 2 % ethanol and photographed. All cephalopods were then euthanised within 24 h from hatching using a lethal dose of ethanol that was gradually increased from 0 to 5 % in concentration. The subsample of hatchlings was weighed and dissected for the extraction and photographing of the respective hard structures (*i.e.*, the squid statolith and the cuttlefish cuttlebone). Photographs were analysed in Fiji software for measuring morphological parameters (O'Brien et al., 2016; Boletzky et al., 2016; Villanueva et al., 2007). Unhatched and undeveloped embryos at the end of the hatching period were noted.

2.4. Statistical analysis

An overview scheme of the sample sizes for each statistical analysis is given in the Supplementary materials. All statistical analyses were performed in RStudio (V 4.1.1; RStudio Team, 2020). Continuous data were assessed for normality and homoscedasticity using QQ plots and F-tests. Linear and generalized linear mixed effects models were applied to continuous data (*lme* function, *nlme* package) and proportional data (*glmmPQL* function, *MASS* package) to account for the correlation structures. For the elasmobranch data, models were built to have treatment and time (week) as fixed interacting factors, and egg ID as random factor. Differences in standard deviation between treatments overall and at individual weeks were assessed using *Fisher's F-tests*. *T-tests* were used to compare morphometric and physiological data at individual weeks. For the hormonal analysis no correlation structure was needed, and linear regression models (*lm* function) were used. For the cephalopod data, models were built to have treatment as a fixed factor, and tank ID as a random factor. All models were validated assessing the residuals. For all statistical analyses, an alpha threshold of p = 0.05 was used for statistical significance of the test statistics.

3. Results

3.1. EMFs

With the electricity transformer turned off, background magnetic fields were ubiquitously 0.025 μT and electric fields were 0.0041 mV/m. With the electricity transformer output set on 20 A at 50 Hz, a range of spatially homogeneous magnetic fields of 4–6 μT and induced electric fields of 0.06–0.2 mV/m were obtained in the exposed tanks (values inclusive of background levels) (Fig. 1b). In the control tanks, magnetic fields ranged between 0.05 and 0.3 μT, with the highest values near water pumps on "Table 2" (Fig. 1b). On average, EMFs within the control tanks were over 35 times weaker than exposed tanks and similar to background levels.

3.2. Elasmobranchs

Catshark embryos were visible to the naked eye from week 2 of embryonic development and grew regularly until week 18 (Fig. 2). Growth and yolk consumption curves of control and exposed animals were similar with no statistically significant difference between treatments (control n = 12, exposed n = 13; Fig. 2a and c, Table 1). However, the interaction between time and treatment resulted in statistically significantly different yolk surface curves over time, suggesting a treatment effect on yolk consumption (Fig. 2b). In fact, a clear trend of differentiation was visible from approximately week 10 onwards, where exposed embryos were larger and had smaller yolks at given time points (Fig. 2b and c). At week 18 (control n = 3, exposed n = 4), exposed embryos were on average longer and heavier, had wider heads and smaller remaining yolk mass (Table 1). Moreover, yolk wet weight was statistically significantly lower (*t-test*, t-value = 2.663, p-value = 0.045, df = 5), yolk surface was smaller, yet not significantly (*t-test*, t-value = 2.485, p-value = 0.056), and pectoral fins were statistically significantly longer in exposed embryos (*t-test*, t-value = 2.784, p-value = 0.039).

The behavioural observations of embryos revealed high individual variability in predator avoidance behaviour. The duration of the freeze response, the time to recover ventilatory movements, and, once recovered, the ventilation frequency was not different between treatments but increased over time (Fig. 2d, e and 2f, Table 1). However, at week 10, the variability (expressed as standard deviation) in freeze responses was significantly smaller in exposed individuals (*F-test*, F-value = 8.943, p-value = 0.031). From week 12, the variability (standard deviation) in time taken to recover ventilation was larger in exposed embryos (*F-test*, F-value = 0.034, p-value = 0.018 at week 12; F-value = 0.042, p-value = 0.003 at week 14; F-value = 0.005, p-value = 0.010 at week 16).

No quantifiable traces of the stress hormone 1α-hydroxycorticosterone were observed in the water of the RAS nor in the amniotic fluid of eggs at any time point (below the decision limit (CCα)). Concentrations of the compound were measured in the yolk at each of the time points, and in embryos older than 11 weeks. Concentrations were variable among samples and increased with time, but they were not different between control and exposed animals (Table 1).

3.3. Cephalopods

Both species grew and hatched over the course of five to eight weeks, following a normal distribution with no visible difference between treatments. About 75 % of the squid embryos and 70 % of the cuttlefish embryos on average hatched from their eggs and were observed to be fit, both for EMF exposed and control, while the rest were born either unfit (*i.e.* unable to swim normally), did not develop correctly or did not hatch. All body and hard structure morphometric features were observed to be higher on average in exposed squid hatchlings, despite no - or only marginal - statistical significance (control n = 64, exposed n = 62, Table 2, Fig. 3a). Statoliths in exposed squid hatchlings were statistically significantly longer than in control squids (p-value = 0.030). All squid hatchlings swam normally, except for seven and four hatchlings from the control and exposed treatments, respectively, that were not able to control their buoyancy (Table 2). The time spent jet swimming compared to other swimming categories showed no difference between treatments. Exposed squid hatchlings displayed a chromatophore reaction more often (85 ± 13 % of the times) than controls (67 ±

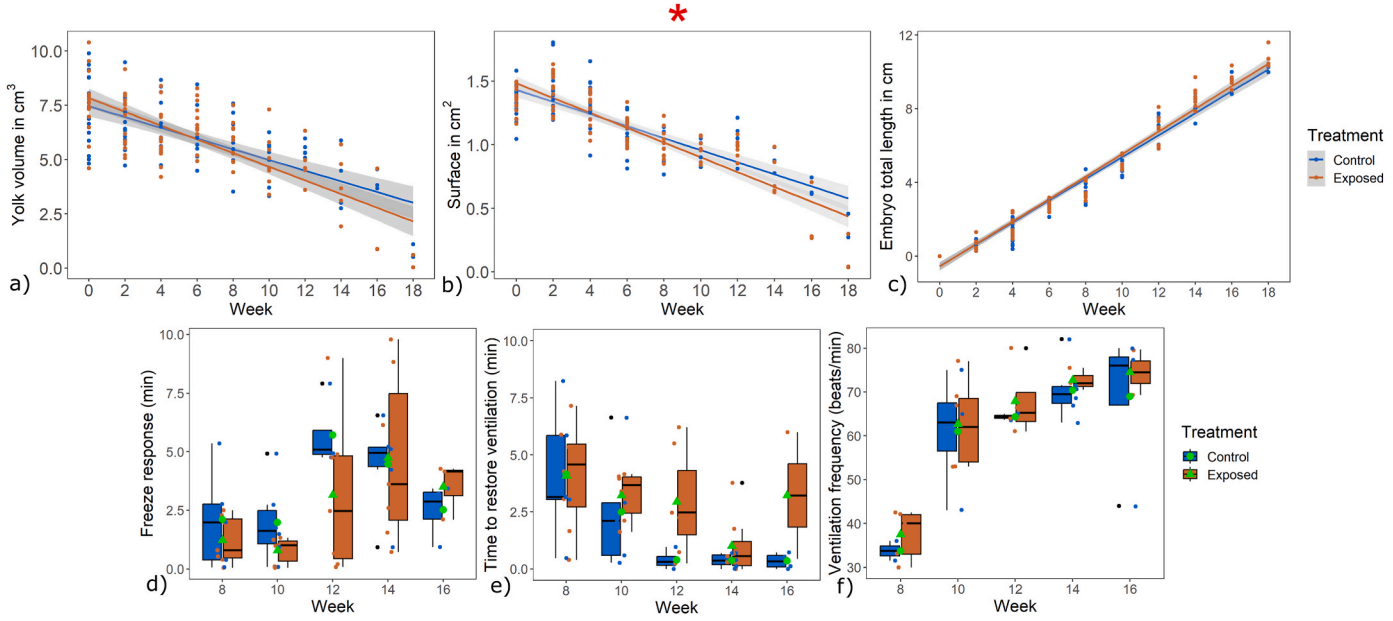

Fig. 2. Elasmobranch *Scyliorhinus canicula* embryonic development and physiological responses from week 1 until week 18. Embryonic development was measured in terms of yolk volume (a), yolk surface area (b), and embryo total length (c) obtained through the method of "candling". Model predictions are shown as trend lines with grey areas representing confidence intervals. Behavioural responses in relation to respiratory activity measured as duration of natural freeze response following handling (d), interval of time from the first movement until ventilation is restored to normal (e), and ventilation frequency (f). Green dots represent means, and the red asterisk indicates a variable with significantly different means between treatments. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Linear mixed effects models used to describe the elasmobranch *Scyliorhinus canicula* embryonic development and physiological responses from week 1 until week 18 (control n = 12, exposed n = 13). Morphological parameters of embryos at week 18 are given as averages with the results of *T-tests* to compare between exposed and control individuals (control n = 3, exposed n = 4). P-values below 0.05 are represented in bold to indicate statistical significance.

Measured morphometric and behavioural variable	Model type	Fixed factor	Coefficient (mean ± SE)	p-value	Summary
Yolk volume (cm^3)	lme	Treatment	0.03 ± 0.26	0.903	No significant differences in the yolk volume change in time between control and exposed individuals.
		Time	1.28 ± 0.03	**<0.0001**	
		Treatment: Time	0.02 ± 0.04	0.504	
Yolk surface (cm^2)	lme	Treatment	0.07 ± 0.05	0.219	Yolk surface significantly changed in time between control and exposed individuals. A trend is visible from week 10.
		Time	−0.10 ± 0.01	**<0.0001**	
		Treatment: Time	−0.02 ± 0.01	**0.040**	
Embryo total length (cm)	lme	Treatment	0.44 ± 0.40	0.284	No significant differences in the embryo total length in time between control and exposed individuals.
		Time	−0.50 ± 0.06	**<0.0001**	
		Treatment: Time	−0.12 ± 0.08	0.127	
Freeze response (min)	lme	Treatment	−4.03 ± 3.36	0.316	No significant differences in freeze response and time to restore ventilation in time between control and exposed individuals. The standard deviation in time to restore ventilation was significantly larger in exposed individuals starting from week 12.
		Time	0.48 ± 0.36	**0.003**	
		Treatment: Time	0.50 ± 0.48	0.306	
Time to restore ventilation (min)	lme	Treatment	−1.65 ± 2.77	0.5613	
		Time	−1.07 ± 0.29	**0.001**	
		Treatment: Time	0.39 ± 0.40	0.335	
Ventilation frequency (beats/min)	lme	Treatment	−2.87 ± 17.19	0.870	No significant differences in the ventilation frequency in time between control and exposed individuals.
		Time	8.60 ± 1.78	**0.0001**	
		Treatment: Time	0.68 ± 2.44	0.783	
Embryo 1α-OHC (μg/kg)	lm	Treatment	0.41 ± 2.21	0.859	No significant differences in the concentration of 1α-hydroxycorticosterone within body and yolk tissue at three time points between control and exposed individuals.
		Time	5.76 ± 2.21	**0.031**	
		Treatment: Time	0.39 ± 3.13	0.905	
Yolk 1α-OHC (μg/kg)	lm	Treatment	0.53 ± 1.04	0.616	
		Time	0.88 ± 0.46	0.070	
		Treatment: Time	−0.18 ± 0.63	0.774	

Morphometric variable measured at 18 weeks	Control (mean ± SD)	Exposed (mean ± SD)	t-value (df = 5)	p-value	Summary
Yolk wet weight (g)	0.82 ± 0.44	0.15 ± 0.23	2.66	**0.045**	Yolk wet weight was significantly lower and yolk surface was marginally significantly lower in exposed individuals.
Yolk surface (cm^2)	0.33 ± 0.11	0.10 ± 0.13	2.49	*0.056*	
Yolk volume (cm^3)	0.72 ± 0.33	0.17 ± 0.28	2.34	0.067	
Total length (cm)	10.19 ± 0.18	10.78 ± 0.57	−1.69	0.152	Pectoral fin length was significantly larger in exposed individuals. The other variables were not significantly different between control and exposed individuals.
Body wet weight (g)	3.38 ± 0.63	3.82 ± 0.48	−1.06	0.338	
Head width (cm)	1.12 ± 0.03	1.23 ± 0.28	−1.77	0.137	
Pectoral fin length (cm)	1.073 ± 0.037	1.220 ± 0.084	−2.784	**0.039**	

13 %) with a near-significant difference (p-value = 0.053) (Fig. 3c). For cuttlefish hatchlings, the average body and hard structure morphometric features were similar between exposed and controls with no visible trend (control n = 49, exposed n = 47; Fig. 3b). Ventilation frequency was comparable between treatments with 69 ± 16 beats per minute overall. All cuttlefish hatchlings swam normally, except for three exposed individuals unable to sink and settle on the substrate. Most hatchlings settled on the tank bottom within 2 min except for nine controls and five exposed individuals. The time spent jet swimming before settling was similar between treatments (Fig. 3d).

4. Discussion

The growth in the number and length of subsea power cables in the marine and coastal environment will increase the exposure of marine fauna to anthropogenic EMFs. To evaluate their impact on receptor species it is crucial to gain knowledge on the types of effects of EMF exposure at relevant life stages and realistic EMF intensities (Gill, 2023; Hutchison et al., 2020a). For these purposes, laboratory studies, complementary to *in-situ* studies, allow controlled studies focused on measurable physiological, developmental and behavioural end points of ecological relevance (Hutchison et al., 2020a). In a literature review on the potential effects of EMFs on benthic elasmobranchs, Hermans et al. (2024) indicated that controlled laboratory experiments would be very suitable to study the almost fully unknown effects on species with embryonic development in egg cases. In this paper, we report the development of a laboratory approach, which examined the responses of three receptor species to chronic exposure to realistic SPCs EMFs throughout their embryonic development. These species have a benthic early-life stage that is associated with natural and artificial habitats crossed or created by cable routing, respectively (Hermans et al., 2024).

Our study provided two key results. First, we developed a method using an AC power cable to generate realistic magnetic and electric field intensities (4–6 μT; 0.06–0.2 mV/m respectively) representative of AC SPCs, demonstrating that cable-based laboratory studies replicating a comparable EMF environment to those measured in the field are possible in controlled conditions. Second, we found that EMFs exposure at 4–6 μT and 0.06–0.2 mV/m did not elicit acute or lethal responses in the growth, development, and early-life stage behaviour of the three species considered, however, two out of three species (*Scyliorhinus canicula* and *Loligo vulgaris*) displayed a range of non-lethal responses. These were at different levels of statistical significance however collectively indicate the effects of SPC EMFs were not null and may be of ecological importance worthy of further investigation.

Specifically, we observed that both exposed elasmobranchs *S. canicula* and cephalopods *L. vulgaris* had an accelerated growth rate

Table 2
Morphological and behavioural parameters of cepalophods hatchlings (*Loligo vulgaris*; control n = 64, exposed n = 62; *Sepia officinalis*; control n = 49, exposed n = 47) with corresponding mixed effects models. P-value below 0.05 is represented in bold to indicate statistical significance.

Species	Measured morphometric variable	Control (mean ± SD)	Exposed (mean ± SD)	Model type	Coefficient (mean ± SE)	p-value	Summary
L. vulgaris	Total length (mm)	4.64 ± 0.26	4.71 ± 0.28	lme	0.11 ± 0.08	0.195	No significant differences in the body features between control and exposed individuals. However, all body features were on average larger in exposed individuals.
L. vulgaris	Wet weight (mg)	3.95 ± 0.54	3.98 ± 0.41	glmmPQL	0.07 ± 0.22	0.750	
L. vulgaris	Mantle length (mm)	2.57 ± 0.25	2.64 ± 0.21	lme	0.11 ± 0.07	0.135	
L. vulgaris	Head width (mm)	1.54 ± 0.09	1.56 ± 0.08	lme	0.02 ± 0.02	0.366	
L. vulgaris	Eye diameter (mm)	0.691 ± 0.047	0.709 ± 0.044	lme	0.020 ± 0.009	0.063	
L. vulgaris	Statolith length (mm)	0.178 ± 0.017	0.193 ± 0.013	lme	0.015 ± 0.005	**0.030**	Statolith length was significantly larger in exposed individuals.
L. vulgaris	Statolith surface (mm^2)	0.011 ± 0.002	0.013 ± 0.003	lme	0.002 ± 0.001	0.104	
S. officinalis	Total length (cm)	1.27 ± 0.15	1.28 ± 0.16	lme	0.004 ± 0.033	0.899	No significant differences in the body features length, width and weight between control and exposed individuals.
S. officinalis	Wet weight (g)	0.165 ± 0.048	0.165 ± 0.054	lme	−0.001 ± 0.011	0.947	
S. officinalis	Mantle length (cm)	0.878 ± 0.100	0.875 ± 0.103	lme	−0.003 ± 0.025	0.902	
S. officinalis	Head width (cm)	0.664 ± 0.065	0.659 ± 0.068	lme	−0.005 ± 0.019	0.779	
S. officinalis	Eye diameter (cm)	0.124 ± 0.019	0.120 ± 0.014	gls	−0.003 ± 0.004	0.330	
S. officinalis	Cuttlebone length (cm)	0.679 ± 0.098	0.680 ± 0.100	lme	0.0007 ± 0.022	0.972	No significant differences in the cuttlebone length and surface between control and exposed individuals.
S. officinalis	Cuttlebone surface (cm^2)	0.438 ± 0.098	0.422 ± 0.104	lme	−0.015 ± 0.024	0.529	

Species	Measured behavioural variable	Control (mean ± SD)	Exposed (mean ± SD)	Model type	Coefficient (mean ± SE)	p-value	Summary
L. vulgaris	Proportion of jet swimming	54.82 ± 32.59	43.59 ± 30.83	glmmPQL	−0.41 ± 0.32	0.226	No significant differences in the natural swimming behaviour between control and exposed individuals.
L. vulgaris	Chromatophore reaction	66.67 ± 12.91	84.72 ± 13.35	glmmPQL	1.02 ± 0.47	*0.053*	Chromatophore reaction was marginally significantly more frequent in exposed individuals.
S. officinalis	Proportion of jet swimming	34.04 ± 32.77	25.25 ± 16.44	glmmPQL	−0.41 ± 0.32	0.226	No significant differences in the natural swimming behaviour between control and exposed individuals.
S. officinalis	Ventilation frequency	69.06 ± 15.64	68.54 ± 17.26	lme	−2.02 ± 3.86	0.612	No significant differences in the ventilation frequency between control and exposed individuals.

and appeared, for some variables measured, more developed than control individuals at the end of the experiments. In the case of *S. canicula*, we detected statistically significantly smaller yolk surfaces from week 10 of embryogenesis in exposed individuals. At the end of the experiment (week 18), they had statistically significantly lighter yolk weight, and a smaller yolk surface, and significantly longer pectoral fins length. As the study did not follow the species development until and beyond hatching, it is not possible to infer the progression and aftermath of such growth divergence. However, changes in yolk consumption rate, as they are linked to changes in metabolic demands, may impact the individual fitness by influencing an effective transition to first feeding and then juvenile survival (Hermans et al., 2025; Fey et al., 2019a, 2019b). A high level of inter-individual variability was observed in hormonal stress levels and early behaviours in *S. canicula* resulting in no clear trend. In a parallel controlled laboratory experiment, Hermans et al. (2025) used our cable EMF set-up to test the potential effects of chronic EMFs exposure at variable intensities (1.8–4.6 μT) on the embryogenesis of the elasmobranch *Raja clavata*. Hermans et al. (2025) observed embryos to be hyperactive and perform more ventilatory movements when exposed to EMF. Such hyperactivity did not translate in visible morphological differences at hatching. However, Hermans et al. (2025) measured only embryo length and weight - parameters for which we also did not observe differences during embryogenesis, however we did observe significant differences for yolk consumption over time and in the fin length at week 18. The differences between our results could derive from habituation of the specimens in our experiment to constant EMF intensities (Hermans et al., 2025). Although potentially stressful leading to morphological and/or metabolic changes in *S. canicula*, they did not elicit a behavioural response.

Similarly, exposed *L. vulgaris* had larger body morphometrics on average and statistically significantly longer statoliths at hatching. However, no difference was detected in hatching and swimming behaviours, with the exception of a higher chromatophore reactivity in exposed *L. vulgaris*. In the fitness trade-offs of a species, the enhancement of a trait usually happens at the expense of another characteristic (Stearns, 1989). In the case of cephalopods with short life cycles, hatching with the right traits and size is even more important as they experience high selective pressure and have limited time for compensating developmental disruptions (Boletzky, 2003). Furthermore, an enhanced chromatophore reactivity in exposed *L. vulgaris* could result in higher vulnerability or lowered fitness due to modifications of the neural pathways and systems controlling the chromatophore contractions (Messenger, 2001).

Through the analysis of multiple variables this study showed that two of three benthic associated species responded to some degree to chronic exposure to EMFs, supporting the hypothesis that exposure during early-life history stages can induce some differences in growth and development, which, if consistent across a proportion of individuals, could lead to responses that have population-level consequences. However, our study could not determine such population impacts because of its small sample sizes and its focus on the early life stages. We used small sample sizes as when working with vertebrates and cephalopods it is recommended they are minimised in accordance with animal ethics and welfare, especially when conducting a pilot study (National Research Council Committee on Recognition and Alleviation of Distress in Laboratory Animals, 2008). Nevertheless, the study provided evidence suggesting there would be a benefit in targeting future research with larger sample sizes. It should also be noted that for the elasmobranch growth repeated measurement experiment, the sample size decreased over time, due to the hormonal assay element of the study. Although this generated a loss of statistical power, data were analysed using mixed-effects models which have been tested to be flexible and

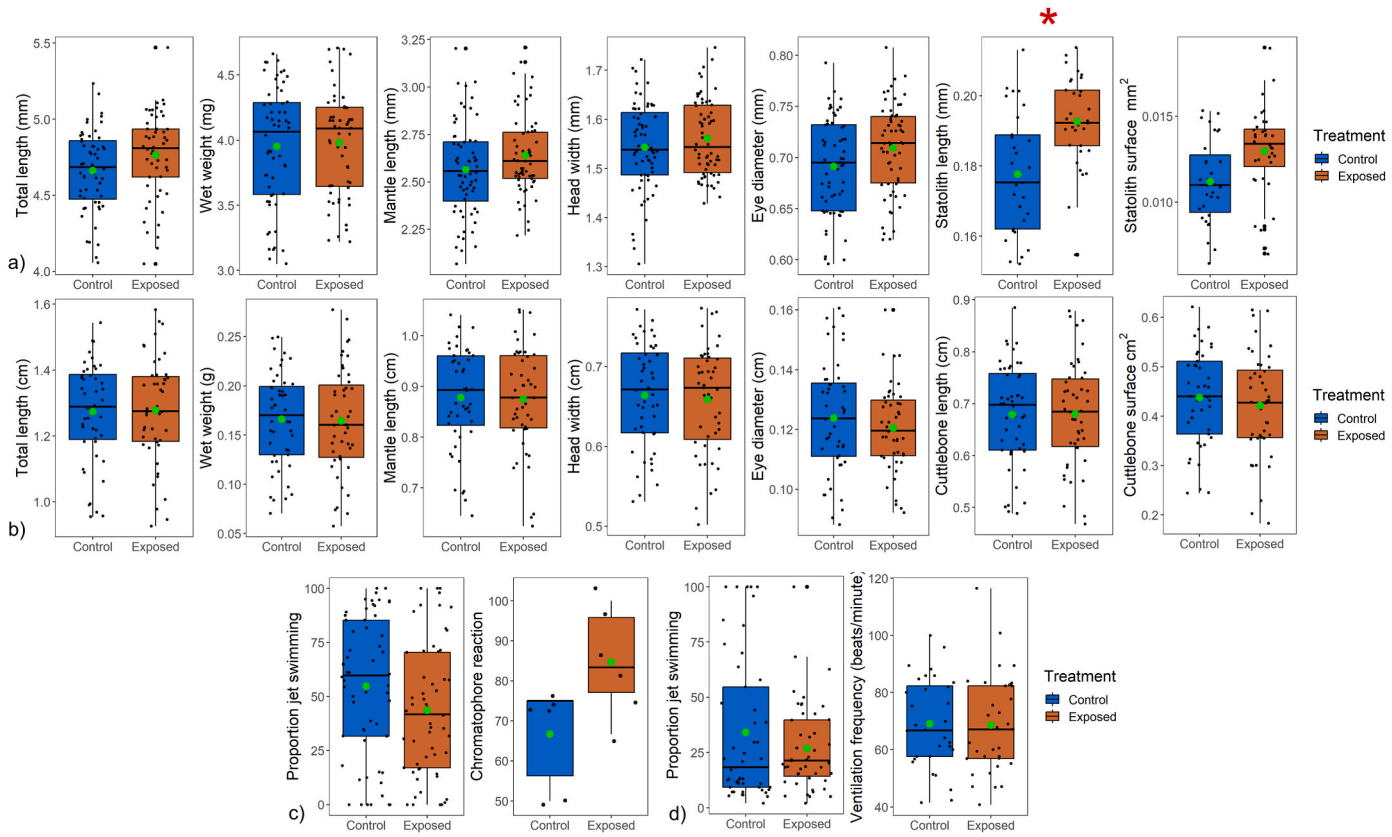

Fig. 3. Boxplots of morphological parameters of a) *Loligo vulgaris* and b) *Sepia officinalis* hatchlings. Boxplots of behavioural parameters of c) squid and d) cuttlefish. Green dots represent means, and the red asterisk indicates a variable with significantly different means between treatments. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

least biased against missing data and imbalances and therefore the analyses are still deemed to be robust (Muhammad, 2023). In the case of growth morphological parameters, the methodology used is expected to detect effect sizes at low power as it measures parameters precisely. The same cannot be said for behavioural parameters in this study.

In general, animals show two distinct strategies to cope with stress: a proactive phenotype trying to control and alter the stress; or a reactive phenotype trying to avoid and withdraw from the stress (Koolhaas et al., 1999). This may be evident in behavioural and/or physiological parameters investigated. The lack of patterns observed in the behavioural parameters in this study could be either the expression of the underlying variability in individuals coping mechanisms between proactive and reactive responses (Skomal and Mandelman, 2012; Creel, 2018; Cresci et al., 2023), or the presence of individual variabilities larger than any effect size.

The study presented here contributes to a call for targeted research on the effects of SPCs EMFs on early-life stage receptor species (Hermans et al., 2024; Hutchison et al., 2020a) and provides a replicable approach for future studies to expand on across EMF intensities and variability. Follow-up studies can build upon the experimental approach presented in this study taking account of recommendations regarding sample sizes to address individual variability. Furthermore, as multiple effects manifested during the embryogenesis could have important consequences for hatchlings, studies should be extended to assess the transition period and specific juvenile life stages as applicable.

The power cable electrical set-up used in this study emitted the same spatio-temporally constant intensities for each of the treatment aquaria, allowing the comparison between individuals exposed to realistic EMFs intensities and individuals under control conditions. The same experimental set up would be suitable for future scenarios of variable EMF intensities through time to better represent the variation in power transmission that occurs as the wind resource varies. Overall, this will contribute to the development of a standardised approach for dose-response research and to deciphering the biological meaningfulness and carry-over effects of the observed responses (Hutchison et al., 2020a; Albert et al., 2020). As noted in other controlled studies (Albert et al., 2020), there is, as yet, no evidence that the EMF effects observed at the individual level will manifest as meaningful impacts on the species population, however, this study does demonstrate that they cannot be excluded without further exploration.

CRediT authorship contribution statement

Silvia Paoletti: Writing – original draft, Investigation, Formal analysis, Conceptualization. **Robin Brabant:** Writing – review & editing, Investigation, Conceptualization. **Ilona Strammer:** Writing – review & editing, Investigation. **Peter Sigray:** Writing – review & editing, Resources, Methodology. **Niklas Rolleberg:** Writing – review & editing, Resources, Methodology. **Brian G. Stewart:** Writing – review & editing, Resources, Methodology. **Johan Aerts:** Writing – review & editing, Resources. **Steven Degraer:** Writing – review & editing, Supervision, Funding acquisition. **Zoë L. Hutchison:** Writing – review & editing, Supervision, Conceptualization. **Andrew B. Gill:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank the staff of the Laboratory of Aquaculture and Artemia Reference Centre (ARC) at Ghent University for hosting the laboratory experiments. We also thank the National Fisheries Museum (NAVIGO) for the supply of elasmobranch eggs, Vincent Vermeylen, Koen Allewerelt and Frank Le Roy for the supply of cephalopods eggs, Yves Laurent at RBINS for his assistance in data collection from video and images, Roger Villanueva and his colleagues at the Institut de Ciencies del Mar in Spain for their advice on cephalopods embryogenesis and husbandry, and Elia Transmission Belgium for the donation of the power cable. This research was conducted in the framework of the EDEN2000 project ('Exploring options for nature-proof development of offshore wind farms inside a Natura 2000 area'), which was commissioned by the Marine Unit of the Belgian Federal Public Service Health, Food Chain Safety and Environment.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107727.

Data availability

The data underlying this article are available in Zenodo at https://doi.org/10.5281/zenodo.17071979.

References

Albert, L., Deschamps, F., Jolivet, A., et al., 2020. A current synthesis on the effects of electric and magnetic fields emitted by submarine power cables on invertebrates. Mar. Environ. Res. 159, 104958.
Albert, L., Olivier, F., Jolivet, A., et al., 2022. Insights into the behavioural responses of juvenile thornback ray *Raja clavata* to alternating and direct current magnetic fields. J. Fish. Biol. 100, 645–659.
Albert, L., Olivier, F., Jolivet, A., et al., 2023. Effects of anthropogenic magnetic fields on the behavior of a major predator of the intertidal and subtidal zones, the velvet crab *Necora puber*. Mar. Environ. Res. 190, 106106.
Ball, R.E., Oliver, M.K., Gill, A.B., 2015. Early life sensory ability-ventilatory responses of thornback ray embryos (*Raja clavata*) to predator-type electric fields. Dev. Neurobiol. 76, 721–729.
Boletzky, S.V., Andouche, A., Bonnaud-Ponticelli, L., 2016. A developmental table of embryogenesis in *Sepia officinalis*. Life Environ. 66, 11–23.
Boletzky, S.V., 2003. Biology of early life stages in cephalopod molluscs. Adv. Mar. Biol. 44, 143–203.
Brysiewicz, A., Formicki, K., Tański, A., et al., 2017. Magnetic field effect on melanophores of the European whitefish *Coregonus lavaretus* (Linnaeus, 1758) and vendace *Coregonus albula* (Linnaeus, 1758) (Salmonidae) during early embryogenesis. Eur. Zool. J. 84, 49–60.
Chapman, E.C.N., Rochas, C.M.V., Piper, A.J.R., et al., 2023. Effect of electromagnetic fields from renewable energy subsea power cables on righting reflex and physiological response of coastal invertebrates. Mar. Pollut. Bull. 193, 115250.
Chapman, E.C.N., Rochas, C.M.V., Burns, Z., et al., 2025. Effects of electromagnetic fields on flatfish activity levels. Mar. Pollut. Bull. 222, 118652.
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, 947–956.
Cresci, A., Allan, B.J.M., Shema, S.D., et al., 2020. Orientation behavior and swimming speed of Atlantic herring larvae (*Clupea harengus*) in situ and in laboratory exposures to rotated artificial magnetic fields. J. Exp. Mar. Bio. Ecol. 526, 151358.
Cresci, A., Perrichon, P., Durif, C.M.F., et al., 2022. Magnetic fields generated by the DC cables of offshore wind farms have no effect on spatial distribution or swimming behavior of lesser sandeel larvae (*Ammodytes marinus*). Mar. Environ. Res. 176, 105609.
Cresci, A., Durif, C.M.F., Larsen, T., et al., 2023. Static magnetic fields reduce swimming activity of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae. ICES J. Mar. Sci. 82, fsad205.
Dannheim, J., Bergström, L., Birchenough, S.N.R., et al., 2020. Benthic effects of offshore renewables: identification of knowledge gaps and urgently needed research. ICES J. Mar. Sci. 77, 1092–1108.
Fey, D.P., Jakubowska, M., Greszkiewicz, M., et al., 2019a. Are magnetic and electromagnetic fields of anthropogenic origin potential threats to early life stages of fish? Aquat. Toxicol. 209, 150–158.
Fey, D.P., Greszkiewicz, M., Otremba, Z., et al., 2019b. 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.
Feyjoo, P., Cabanellas-Reboredo, M., Calvo-Manazza, M., et al., 2015. New insights on the external features of egg capsules and embryo development in the squid *Loligo vulgaris*. J. Nat. Hist. 1–13.
Fjellstedt, C., Ullah, M.I., Forslund, J., Jonasson, E., Temiz, I., Thomas, K., 2022. A review of AC and DC collection grids for offshore renewable energy with a qualitative evaluation for marine energy resources. Energies 15, 5816.
Gill, A.B., Huang, Y., Gloyne-Philips, I., et al., 2009. COWRIE 2.0 Electromagnetic Fields (EMF) Phase 2: Emf-Sensitive Fish Response to EM Emissions from Sub-sea Electricity Cables of the Type Used by the Offshore Renewable Energy Industry. Commissioned by COWRIE Ltd (project reference COWRIE-EMF-1-06).
Gill, A.B., 2023. Effects of subsea cable electromagnetic fields on the non-reproductive behaviour of sensitive receptor species. In: Degraer, S., Brabant, R., Vanaverbeke, J. (Eds.), EDEN 2000 – Exploring Options for a nature-proof Development of Offshore Wind Farms Inside a Natura 2000 Area. Royal Belgian Institute of Natural Sciences, Belgium, p. 359.
Gill, A.B., Hutchison, Z.L., Desender, M., 2023. Electromagnetic Fields (Emfs) from Subsea Power Cables in the Natural Marine Environment. Cefas Project Report for Crown Estate Offshore Wind Evidence and Change Programme, p. 66.
Grunow, B., Reismann, T., Moritz, T., 2022. Pre-hatching ontogenetic changes of morphological characters of small-spotted catshark (*Scyliorhinus canicula*). Fishes 7, 100.
Harsanyi, P., Scott, K., Easton, B.A.A., 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, 564.
Hermans, A., Winter, H.V., Gill, A.B., et al., 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.
Hermans, A., Maas, D.L., de Barros Neta, L.M.V., Spanings, T., Winter, H.V., Murk, A.J., Foekema, E.M., 2025. An egg case study: chronic exposure to AC electromagnetic fields results in hyperactivity in thornback ray (*Raja clavata* L.) embryos. Mar. Environ. Res. 209, 107151.
Hutchison, Z.L., Gill, A.B., Sigray, P., et al., 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.
Hutchison, Z.L., Secor, D.H., Gill, A.B., 2020a. The interaction between resource species and electromagnetic fields associated with electricity production by offshore wind farms. Oceanography 33, 96–107.
Hutchison, Z.L., Gill, A.B., Sigray, P., et al., 2020b. Anthropogenic electromagnetic fields (EMF) influence the behaviour of bottom-dwelling marine species. Sci. Rep. 10, 4219.
Jakubowska-Lehrmann, M., Makaras, T., Normant-Saremba, M., et al., 2025. Exploring the impact of magnetic fields related to submarine power cables on the American mud crab *Rhithropanopeus harrisii*: a behavioural and physiological perspective. Mar. Pollut. Bull. 212, 117492.
Johnson, M.S., Kraver, D.W., Renshaw, G.M.C., et al., 2016. Will ocean acidification affect the early ontogeny of a tropical oviparous elasmobranch (*Hemiscyllium ocellatum*)? Cons. Phys. 4.
Kiviluoma, J., Holttinen, H., Weir, D., Scharff, R., Söder, L., Menemenlis, N., Cutululis, N. A., Danti Lopez, I., Lannoye, E., Estanqueiro, A., Gomez-Lazaro, E., 2016. Variability in large-scale wind power generation. Wind Energy 19 (9), 1649–1665.
Koolhaas, J.M., Korte, S.M., De Boer, S.F., et al., 1999. Coping styles in animals: current status in behavior and stress-physiology. Neurosci. Biobehav. Rev. 23, 925–935.
Messenger, J.B., 2001. Cephalopod chromatophores: neurobiology and natural history. Biol. Rev. Camb. Phil. Soc. 76, 473–528.
Muhammad, L.N., 2023. Guidelines for repeated measures statistical analysis approaches with basic science research considerations. J. Clin. Investig. 133, e171058.
Musa, S.M., Czachur, M.V., Shiels, H.A., 2018. Oviparous elasmobranch development inside the egg case in 7 key stages. PLoS One 13, e0206984.
National Research Council (US) Committee on Recognition and Alleviation of Distress in Laboratory Animals, 2008. Recognition and Alleviation of Distress in Laboratory Animals. National Academies Press (US), Washington (DC). Chapter 4, Avoiding, Minimizing, and Alleviating Distress. Available from: https://www.ncbi.nlm.nih.gov/books/NBK4039/.
O'Brien, C.E., Mezrai, N., Darmaillacq, A.S., et al., 2016. Behavioural development in embryonic and early juvenile cuttlefish (*Sepia officinalis*). Dev. Psychol. 59, 145–160.
Ripley, D.M., De Giorgio, S., Gaffney, K., et al., 2021. Ocean warming impairs the predator avoidance behaviour of elasmobranch embryos. Cons. Phys. 9 coab045.
RStudio Team, 2020. Rstudio: Integrated Development for R. Rstudio. PBC, Boston.
Ruiz-Jarabo, I., Barragán-Méndez, C., Jerez-Cepa, I., et al., 2019. Plasma 1α-Hydroxycorticosterone as biomarker for acute stress in catsharks (*Scyliorhinus canicula*). Front. Physiol. 10, 1217.
Scott, K., Harsanyi, P., Easton, B.A.A., et al., 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, 776.
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. Mol. Integr. Physiol. 162, 146–155.
Stankevičiūtė, M., Jakubowska, M., Pažusienė, J., et al., 2019. Genotoxic and cytotoxic effects of 50 Hz 1 mT electromagnetic field on larval rainbow trout (*Oncorhynchus mykiss*), Baltic clam (*Limecola balthica*) and common ragworm (*Hediste diversicolor*). Aquat. Toxicol. 208, 109–117.
Stearns, S.C., 1989. Trade-offs in life-history evolution. Funct. Ecol. 3, 259–268.

Taormina, B., Di Poi, C., Agnalt, A., et al., 2020. Impact of magnetic fields generated by AC/DC submarine power cables on the behavior of juvenile European lobster (*Homarus gammarus*). Aquat. Toxicol. 220, 105401.
Villanueva, R., Moltschaniwskyj, N.A., Bozzano, A., 2007. Abiotic influences on embryo growth: statoliths as experimental tools in the squid early life history. Rev. Fish Biol. Fish. 17, 101.
Wind Farm Cable Plan, Moray East Offshore Wind Farm, 2019. Moray Offshore Windfarm (East) limited. https://marine.gov.scot/sites/default/files/owf_cable_plan_v2_final_redacted.pdf.
Zakroff, C., Mooney, T.A., Wirth, C., 2018. Ocean acidification responses in paralarval squid swimming behaviour using a novel 3D tracking system. Hydrobiologia 808, 83–106.