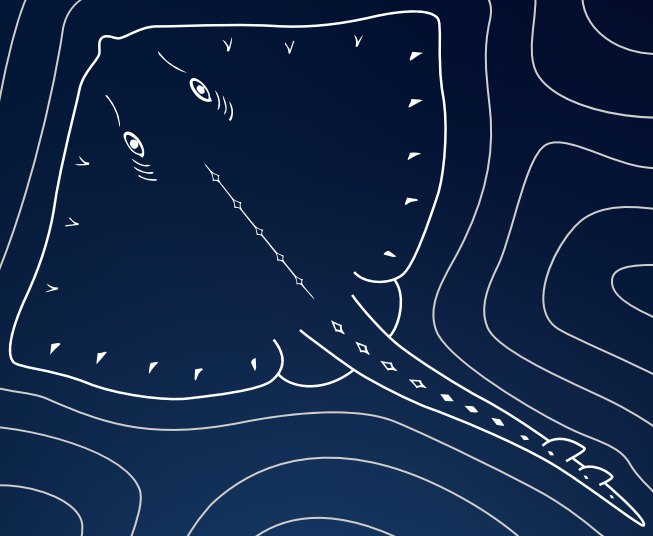
Charged Encounters

Effects of electromagnetic fields on sharks and rays



Annemiek Hermans

Propositions

1. | Offshore electrification restructures the sensory landscapes of elasmobranchs. (this thesis)
2. | Life-history traits predict ecological vulnerability better than taxonomic relatedness. (this thesis)
3. | First authorship is a relic of ego in an age of collaboration.
4. | AI favours scientists with ideas over eloquence in academic research.
5. | Scientific excellence requires a system that fits women, not women fitting the system.
6. | The ecological benefits of offshore wind farms outweigh its environmental costs.
7. | Stopping eating fish will protect ecosystems more than studying subtle impacts.

Propositions belonging tot the thesis, entitled
Charged Encounters
Effects of electromagnetic fields on sharks and rays.

Annemiek Hermans
Wageningen, August 2026

Charged Encounters

Effects of electromagnetic fields on sharks and rays

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This research was conducted under the auspices of the Graduate School Wageningen Institute for Environment and Climate Research (WIMEK)

Charged Encounters

Effects of electromagnetic fields on sharks and rays

Annemiek Hermans

Thesis
submitted in fulfilment of the requirements for the degree of doctor
at Wageningen University
by the authority of the Rector Magnificus,
Prof. Dr C. Kroeze,
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Friday 28 August 2026
at 3.30 p.m. in the Omnia Auditorium.

Annemiek Hermans
Charged Encounters: effects of electromagnetic fields on sharks and rays, 315 pages.

PhD thesis, Wageningen University, Wageningen, the Netherlands (2026)
With references, with summary in English

DOI: 10.18174/681260

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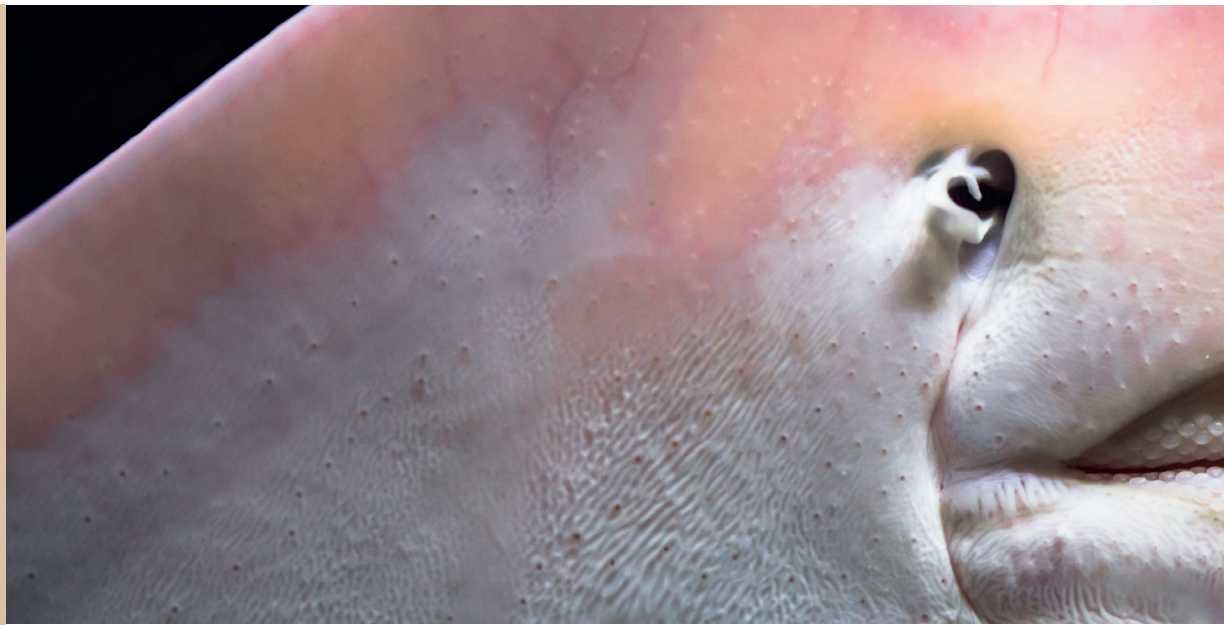
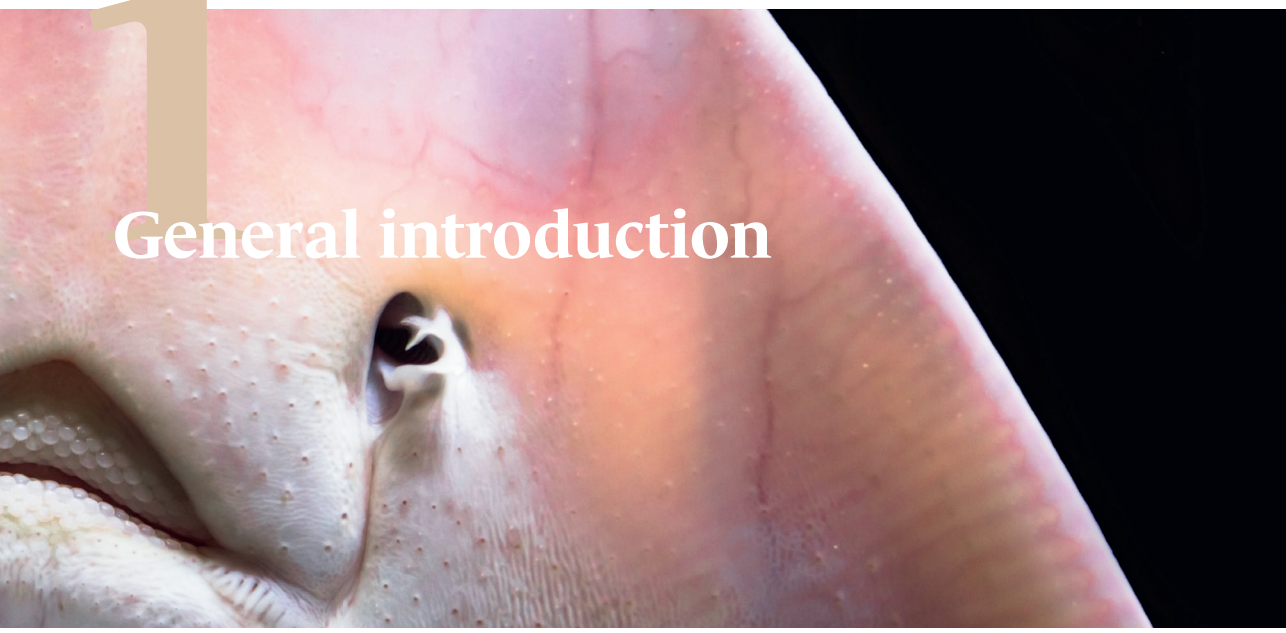


1 General introduction



Earth teems with sights and textures, sounds and vibrations, smells and tastes, electric and magnetic fields. But every animal can only tap into a small fraction of reality's fullness. Each is enclosed within its own unique sensory bubble, perceiving but a tiny sliver of an immense world.

An immense world – Ed Young

1.1 Elasmobranchs have been around for a very long time

Sharks, skates and rays together form the class *Elasmobranchii*, a lineage that has travelled Earth's oceans for over 420 million years (Stein et al. 2018). While their earliest ancestors pre-date the dinosaurs, the species we recognise today began to emerge during the Jurassic period, around 200 million years ago. At present, 1,266 species have been formally described, with discoveries still underway - notably, more than a quarter (>340) of these species have been described since 2001 (IUCN 2024). We are not only learning about new species, but also about the capabilities of this remarkable species group.

Elasmobranchii differ from their bony fish counterparts (*Osteichthyes*) in a number of striking ways. Their skeletons are made of cartilage rather than bone (Moss 1977). Their skin is covered in dermal denticles - tiny tooth-like scales designed to reduce drag - rather than the overlapping scales of bony fishes (Reif 1985). They lack a swim bladder and instead achieve buoyancy through large, oil-rich livers that can comprise up to 25% of body mass in some species (Baldridge 1972). Their gill slits (five to seven pairs) are exposed externally rather than hidden beneath a single protective operculum, and their teeth are not permanently fused to jawbones but are attached to a fibrous band and replaced continuously throughout life (Carrier, Musick, and Heithaus 2010). Their variety in reproductive strategies also set them apart. Males use paired claspers for internal fertilisation, and species exhibit a variety of developmental modes, including viviparity (live birth), ovoviviparity (eggs hatching internally), and oviparity (egg cases), generally producing fewer, but well-developed, young (Carrier et al. 2010).

But perhaps most remarkable of all is their unique sense: the ampullae of Lorenzini, specialised electroreceptors capable of detecting minute electric fields as low as one nanovolt per centimetre of water (Kalmijn 1971). In addition, they can sense magnetic fields which enable them to use the earth's magnetic field for orientation and navigation during migrations. This detection mechanism remains less well understood (Keller et al. 2021; Meyer et al. 2005). These sensory adaptations allow sharks and rays to perceive and navigate their underwater world in ways unlike any other vertebrate group.

1.2 But now their world is changing

Elasmobranchs have survived five mass extinction events, demonstrating their resilience and adaptability. Now, the world of elasmobranchs is rapidly changing in the Anthropocene. From the mid-1900s, populations have been in severe decline by targeted fishing for fins and liver oil, as well as bycatch (Dulvy et al. 2021). Currently, more than one-third of all chondrichthyan species (*Elasmobranchii* plus *Holocephali* or chimaeras), are classified as threatened with extinction under the International Union for Conservation of Nature (IUCN) red list (Dulvy et al. 2021; IUCN 2024). Beyond exploitation pressures, additional stressors such as degradation and loss of critical nursery habitats (Carrier et al. 2010; IUCN 2024) and chemical pollution (Alves et al. 2022; Carrier et al. 2010) pose additional stressors for

these species. Climate change influences species distribution towards higher latitudes and ocean acidification may affect sensory systems and prey availability (Ashur, Johnston, and Dixson 2017; Perry et al. 2005).

On top of all these changes, humans introduced electromagnetic fields (EMFs) generated by subsea power cables (SPC), which could provide a new pressure on this already threatened species class (Taormina et al. 2018). Anthropogenic EMFs may disturb the sensory systems of elasmobranchs (Hutchison, Secor, and Gill 2020). That which gave them a competitive advantage for millions of years, might now potentially place them more at risk from this additional stressor compared to other marine fauna.

1.3 And the North Sea is a prime example

The North Sea is a frontrunner of a rapidly changing habitat for elasmobranchs, having experienced a marked decline in elasmobranch populations over the past 120 years (Sguotti et al. 2016). This heavily utilised marine region concentrates many human activities in a relatively small area, making it a prime example of concentrated anthropogenic impact. Historically, the North Sea has been exploited for transportation, commercial bottom trawling fisheries, sand extraction, and military operations (Ducrotoy, Elliott, and De Jonge 2000; Kenny et al. 2018). More recently, energy production has emerged as a dominant function, initially through oil and gas extraction, and increasingly via intensive offshore wind energy development over the last two decades (Gusatu et al. 2020).

These functions result in spatial competition and conflicting uses, particularly between nature conservation, fisheries, and offshore wind farms (OWFs). OWF development introduces multiple environmental stressors to the marine ecosystem, including underwater noise, increased vessel movements, substrate alteration and EMF in case of SPC use (Bailey, Brookes, and Thompson 2014; Vrooman et al. 2019). Despite these negative impacts, the OWF industry is critically important as a driver of decarbonized, sustainable energy systems. It contributes to energy security and reduces dependence on fossil fuels. The industry is well-suited to shallow, coastal seas with stable wind regimes, such as the North Sea (Bailey et al. 2014; Coelingh, Van Wijk, and Holtslag 1998). Equally, nearshore and deltaic zones as the North Sea represent key habitats for many benthic elasmobranch species (Knip, Heupel, and Simpfendorfer 2010; Leurs 2024; Sguotti et al. 2016), creating spatial overlap with OWF development and EMF. Within OWFs bottom trawling fisheries is not allowed on the Dutch continental shelf, and not common practice in other countries due to the risk of damaging SPC. As bottom trawl fishing is incompatible with a healthy benthic elasmobranch population, OWFs might also provide opportunities for these species. Consequently, the North Sea provides an ideal study area for investigating the potential impacts of EMFs resulting from OWF on elasmobranch ecology, which forms the focus of this thesis (Fig. 1.1).

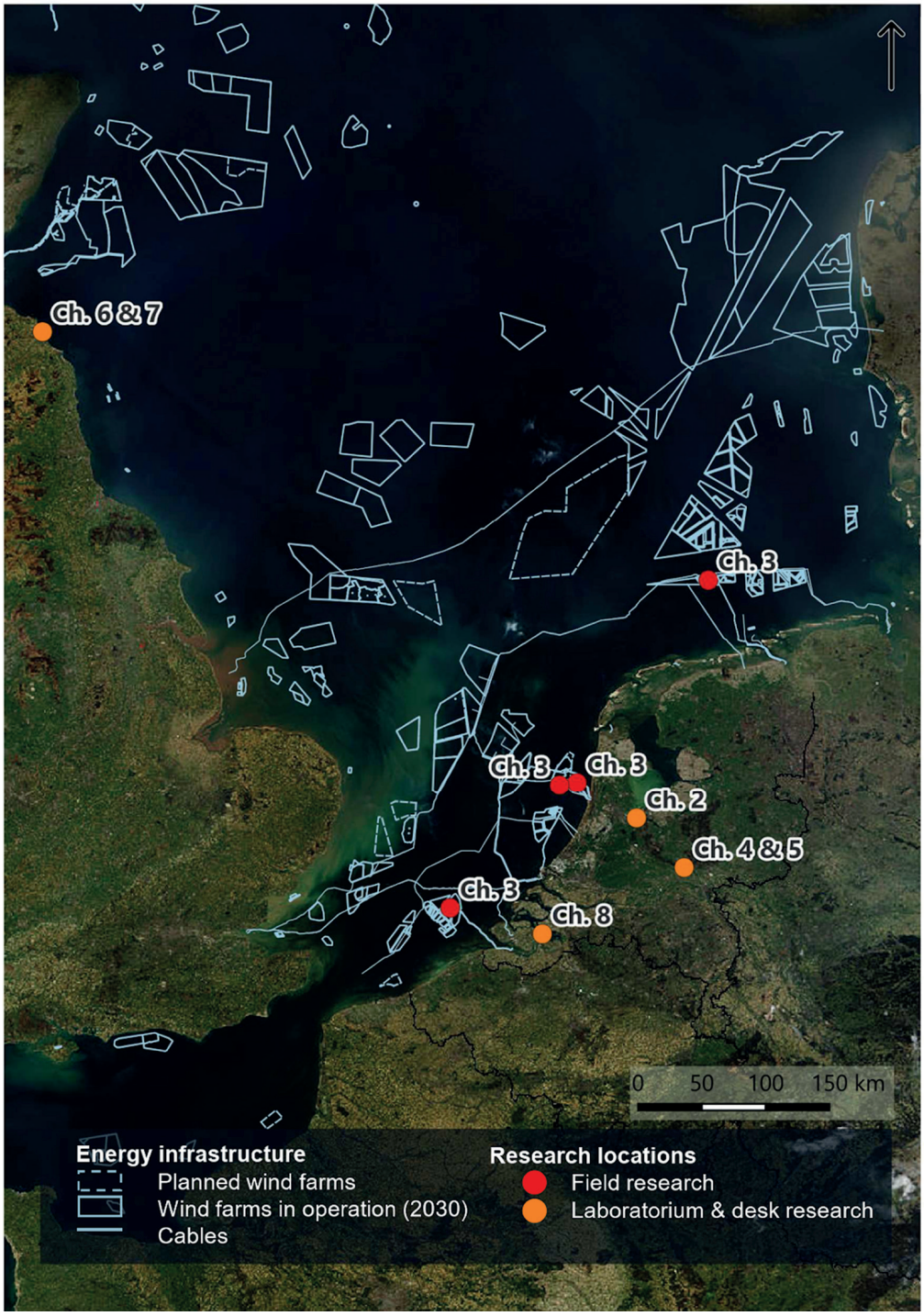


Fig. 1.1 The North Sea ("Spring colour in the North Sea", Image of the Day May 8, 2018, NASA visible earth). Ch. X indicates the location where the research for the thesis chapters is performed.

1.4 Due to the high number of subsea power cables

Subsea cables have been present in the North Sea since the 1870s, following the invention of the Morse code and the subsequent establishment of telecommunication cables connecting countries and continents (Chesnoy and Fouchard 2025). Since then, over 6,000 km of communication cable has been installed in the North Sea (Ministry of Infrastructure and Water Management 2025). However, due to the relatively low electrical currents used in this type of cable, the resulting EMF are considered to be negligible (Carter 2009; Chesnoy and Fouchard 2025; Normandeau, Tricas, and Gill 2011). They have laid the foundation for the introduction of interconnector cables in the 1950s, and four decades later for OWF development. Since then, the number of SPC, including power systems with alternating current (AC) and direct current (DC), and transmission capacities have increased substantially. The need to transport power has resulted in over 1,400 km high voltage SPC in the North Sea (Rijkswaterstaat 2025). This growth, along with more complex installation layouts forming network-like structures within OWFs, has heightened awareness and concern regarding the potential ecological effects of EMF (Hutchison et al. 2020; Taormina et al. 2018).

The fisheries industry has raised concerns about cables routed through important trawling grounds and the physiological impacts of EMF on commercially important species (EMK Foundation 2020; Szostek et al. 2025). Non-governmental organizations (NGOs) have expressed worries about broader ecological consequences, including habitat displacement and ecosystem disruptions through EMF (North Sea Foundation 2022; Vrooman et al. 2019). In response, policy makers are debating the inclusion of EMF impacts under Descriptor 11 (Introduction of Energy) within the Marine Strategy Framework Directive (MSFD) (Hermans and Schilt 2022). The fact that humans lack the modality to sense EMFs makes it difficult to grasp its potential effects, contributing to the uncertainty on how to deal with this subject.

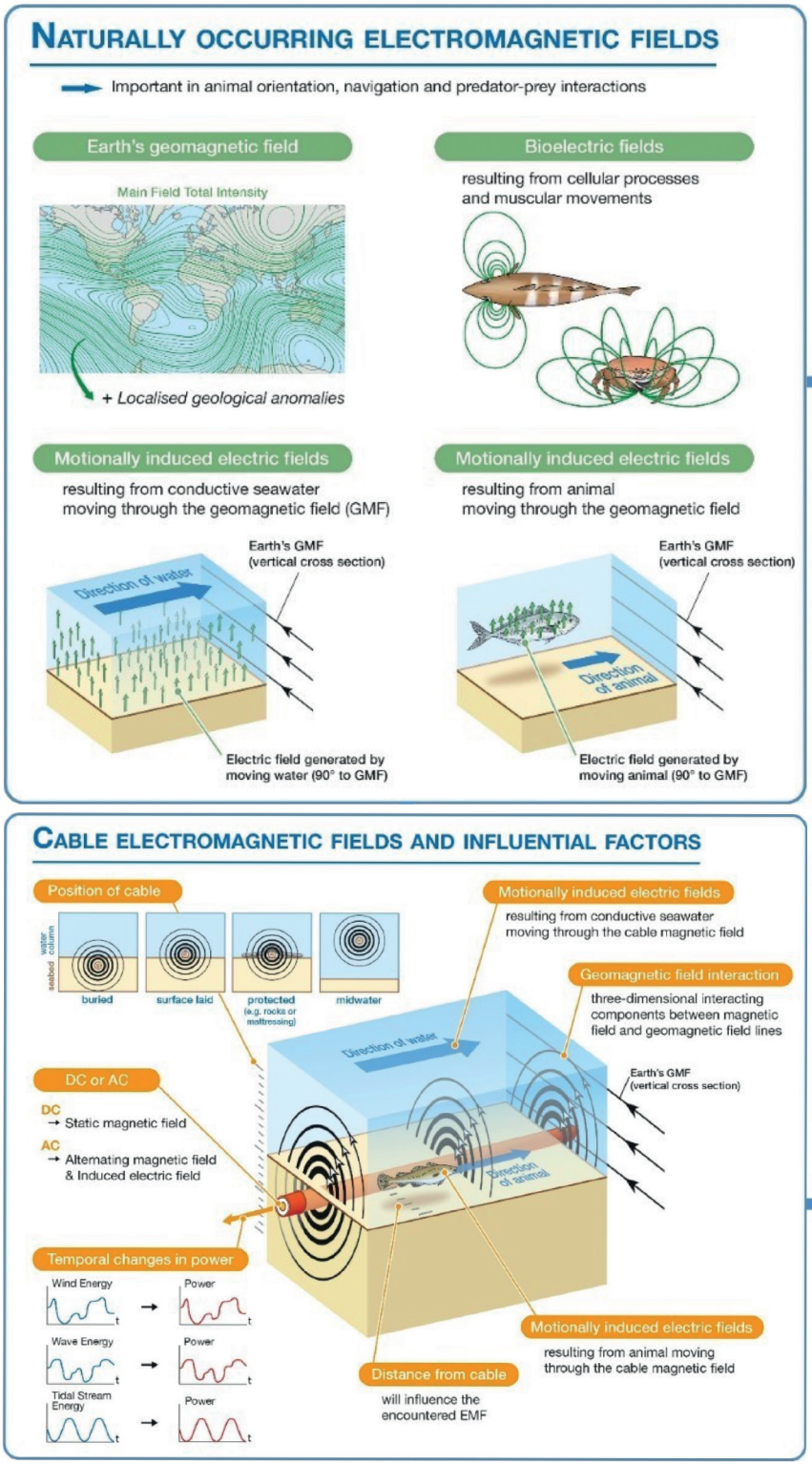
The current lack of robust knowledge regarding potential effects of EMF has led to appeals during the permitting processes in OWF development (Copping 2018). For example, in 2021 the export cable project *Ten Noorden van de Wadden* was cancelled in its existing form following a halted Environmental Impact Assessment (EIA) process, largely due to stakeholder concerns including EMF effects in the Wadden Sea (Kokshoorn 2020). Subsequently the permitting procedure was restarted in the form of the "Programma Aansluiting Wind Op Zee Eemshaven" *PAWOZ-Eemshaven* program in which additional cables routes are under review. In addition, more detailed effect studies were carried out which resulted in a delay of over two years. At the time of writing the route of the cable still has not been decided upon. Providing a better evidence-based insight in exposure-effect levels of EMFs help underpin impact assessments. This can speed up the decision making and permitting processes and allow a well-balanced and urgently needed energy transition to counteract climate change and its severe ecological consequences.

1.5 Which elasmobranchs can sense like no other

In order to determine whether stakeholder concerns are valid, it is important to understand how elasmobranchs use naturally occurring EMFs and how this ability might be affected by anthropogenic EMFs. To sharks and rays, the ocean is structured by electromagnetic cues: the Earth's steady geomagnetic field (~50 μT) for large-scale orientation, and tiny bioelectric fields from prey detectable only within centimetres to <1 m (Newton, Gill, and Kajiura 2019). Strong examples of natural electrosensory use include blue sharks (*Prionace glauca*), which orient to the Earth's magnetic field or to oceanic electric fields, potentially aiding seasonal migration (Carey, Scharold, and Kalmijn 1990); male round stingrays (*Urobatis halleri*), which detect females' electric signals during courtship (Sisneros and Tricas 2002); and the iconic example of small-spotted catsharks (*Scyliorhinus canicula*), which accurately locate buried European plaice (*Pleuronectes platessa*) without the aid of other senses (Kalmijn 1971). Anthropogenic sources now add new signals: AC cables generate magnetic fields and induced electric fields detectable over centimetres to tens of metres, while DC export cables can create magnetic "halos" extending tens to hundreds of metres (Hermans et al. 2024). What sharks perceive is no longer solely a natural EM seascape of the steady geomagnetic field plus ecological cues but a mosaic with added anthropogenic anomalies that must be dealt with during foraging and migration (Fig 1.2).

As offshore wind energy production scales up, more and longer SPC generate stronger and more widespread EMFs, increasing the likelihood that sharks and rays encounter these fields, making it increasingly important to quantify any ecological effects. However, determining whether anthropogenic EMFs have an adverse effect is inherently complex, as exposure and consequences are influenced by multiple interacting factors. These include technical characteristics on the exposure side e.g. different power systems (AC/DC), variability in dependant production and transmission, the relative strength and shape of electric and magnetic components, and the duration of exposure. This complexity makes it difficult to assess effects in the field as well as to replicate EMFs from SPC in a laboratory. Biological variables to consider include life history traits, behaviour, and sensory thresholds, which may differ between species and life stages, and also with size, swimming direction, or the behavioural characteristics of an individual fish. Also, the broader environmental context, including the presence and variability of naturally occurring EMFs, plays a role (Hutchison et al. 2020; Taormina et al. 2018). This complexity is reflected in the variability of results presented in the limited number of currently available studies. They also differ in experimental set-up, often employing non-realistic (high) exposure levels or limited parameterisation (Hermans et al. 2024).

There are other, established and pressing stressors on elasmobranch populations including fisheries (Dulvy et al. 2021) and impulsive underwater sound from pile driving or oil and gas exploration (Hawkins and Popper 2017; Kok et al. 2021). However, these do not negate the need to assess the potential effects of the seemingly less pressing EMF as an anthropogenic stressor adding to these existing pressure factors. The characteristics of EMF


NATURALLY OCCURRING ELECTROMAGNETIC FIELDS
Important in animal orientation, navigation and predator-prey interactions
Earth's geomagnetic field
Main Field Total Intensity
+ Localised geological anomalies
Bioelectric fields
resulting from cellular processes and muscular movements
Motionally induced electric fields
resulting from conductive seawater moving through the geomagnetic field (GMF)
Direction of water
Earth's GMF (vertical cross section)
Electric field generated by moving water (90° to GMF)
Motionally induced electric fields
resulting from animal moving through the geomagnetic field
Direction of animal
Earth's GMF (vertical cross section)
Electric field generated by moving animal (90° to GMF)
CABLE ELECTROMAGNETIC FIELDS AND INFLUENTIAL FACTORS
Position of cable
water column
seabed
buried
surface laid
protected (e.g. rocks or mattressing)
midwater
DC or AC
DC
Static magnetic field
AC
Alternating magnetic field & Induced electric field
Temporal changes in power
Wind Energy
Power
Wave Energy
Power
Tidal Stream Energy
Power
Motionally induced electric fields
resulting from conductive seawater moving through the cable magnetic field
Geomagnetic field interaction
three-dimensional interacting components between magnetic field and geomagnetic field lines
Direction of water
Earth's GMF (vertical cross section)
Direction of animal
Motionally induced electric fields
resulting from animal moving through the cable magnetic field
Distance from cable
will influence the encountered EMF
WHAT THE ANIMAL HAS TO MAKE SENSE OF

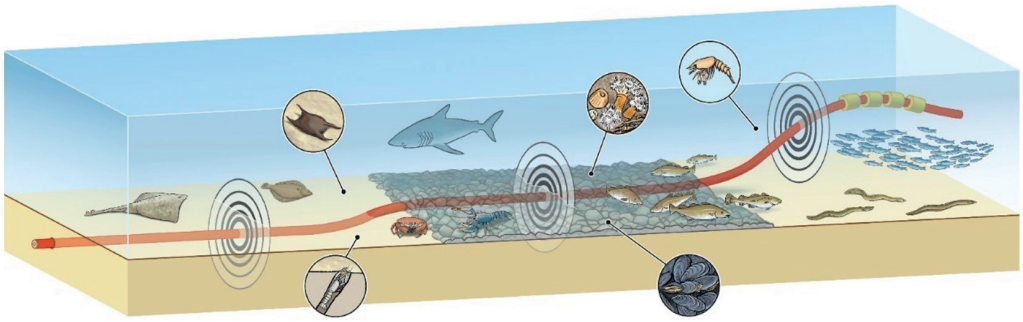


Fig. 1.2 - on the left page and above
Schematic overview of naturally occurring electromagnetic fields and cable magnetic fields and influential factors, printed with permission from Hutchison and Gill (2025), created by Dr. Hendrik Gheerardyn.

as a stressor is very different from more direct population-level effects such as bycatch they are persistent over the entire ~40 year operational lifetime of SPC (Carter 2009), meaning any impacts are long-term. At this time scale, even subtle effects may scale up to population-level consequences through continuous exposure over multiple generations (Soudijn et al. 2020). Similar chronic exposure concerns have been posed for continuous underwater noise from shipping (Frankish et al. 2023; Thomsen et al. 2020), artificial light (Davies et al. 2014; Fobert et al. 2023; Walsh et al. 2024), and persistent contaminants such as low-level discharges of heavy metals, microplastics, or endocrine-disrupting compounds (Andrady 2011; Kersten et al. 1993; Scott and Sloman 2004). In addition, different stressors may interact with each other, and it is important to determine the contribution of EMF to the concert of stressors on elasmobranch populations.

1.6 And which we studied with the help of two species

This thesis focuses on two elasmobranch species: the small-spotted catshark (*Scyliorhinus canicula*) and the thornback skate (*Raja clavata*). They were chosen for their suitability for laboratory research, including well-established husbandry protocols, ease of maintenance, availability of multiple life stages from public aquaria, and their common presence in the North Sea, these species were selected for this research. Both species are among the least threatened in European waters potentially due to their relatively high fecundity compared to other elasmobranchs, with small-spotted catsharks designated as Least Concern and Thornback ray as Near Threatened on the IUCN red list. It is not known whether they are representative models for broader elasmobranch groups, but they share life history traits, and have distinct differences, that may be influenced by EMF exposure. Textbox A presents the key characteristics of these study species.

Textbox A - Study species

Small-spotted catshark, *Scyliorhinus canicula* (Linnaeus, 1758)

The small-spotted catshark is widely distributed throughout the northeast Atlantic Ocean and the Mediterranean Sea, including the North Sea (Compagno, Dando, and Fowler 2005; Heessen, Daan, and Ellis 2015). It is a benthic species commonly found on sandy and muddy substrates and mussel beds from shallow coastal waters to depths of around 800 meters (ĎOnghia et al. 1995; Heessen et al. 2015; Lyle 1983). In the North Sea, small-spotted catsharks are one of the most abundant elasmobranchs, frequently by-caught in commercial fisheries. Adults typically reach lengths of 80 cm, with a maximum size of 100 cm (Heessen et al. 2015; IUCN 2014).

Life history traits of small-spotted catsharks include slow growth and late maturity, with females generally reaching sexual maturity ~9 years of age, at lengths of approximately 53-55 cm (Wearmouth et al. 2013). The species is oviparous, laying paired egg cases throughout much of the year, with peak egg-laying observed from late winter through summer (Ellis and Shackley 1997; Wearmouth et al. 2013). Females produce multiple egg cases per season, with fecundity varying based on environmental conditions and individual size (Sims, Nash, and Morritt 2001; Wearmouth et al. 2013). As an opportunistic predator, small-spotted catsharks primarily feed on small benthic invertebrates such as crustaceans (crabs, shrimp), molluscs, and small fish (Compagno et al. 2005; Heessen et al. 2015; Lyle 1983). Its foraging behaviour is adapted to the demersal environment, relying on electric signals from muscle activity to detect prey in low-light conditions (Fig. 1.3).



Fig. 1.3 Species used in the experimental studies: small-spotted catshark (*Scyliorhinus canicula*) Source: Peter Verhoog.

Thornback skate, *Raja clavata* (Linnaeus, 1758)

The thornback skate is widely distributed across the northeast Atlantic Ocean, from Norway to the Mediterranean Sea, including the North Sea (Dulvy and Reynolds 2002; Heessen et al. 2015). It inhabits continental shelf waters, typically found on sandy, muddy, or gravel substrates at depths ranging from shallow coastal areas down to most commonly 300 meters (IUCN 2014).

In the North Sea, thornback skate is a common benthic elasmobranch species, often caught as bycatch in commercial fisheries. Adults commonly reach lengths of 115 cm, with maximum lengths up to 130 cm (Heessen et al. 2015). It exhibits slow growth and late maturity, with females reaching sexual maturity around 5-8 years of age, at lengths of 60-85 cm (Dulvy and Reynolds 2002; Heessen et al. 2015; Kadri et al. 2014). It is oviparous, laying large, rectangular egg cases throughout much of the year, with peak egg deposition generally occurring in spring and summer (Heessen et al. 2015; Kadri et al. 2014; Schröder et al. 2021). Females produce multiple egg cases per breeding season, with fecundity influenced by size and environmental factors.
The thornback skate is a benthic predator feeding primarily on crustaceans (such as crabs and shrimp), molluscs, and small fish (Heessen et al. 2015).
It uses its flattened body and camouflaging abilities to ambush prey on the seafloor (Fig. 1.4).



Fig. 1.4 Species used in the experimental studies: thornback ray (*Raja clavata*)
Source: Annemiek Hermans

1.7 To answer the following research questions

The rapid expansion of SPC to support OWF is outpacing our willingness to invest in research to enable understanding of the potential impacts of EMF on elasmobranchs. Impact assessments, required for permitting, require information on exposure, species sensitivity, (behavioural) response and ecological relevance; yet robust data on all these aspects are lacking. While this data gap persists, fisheries, NGOs, and policymakers require a fact-based foundation for debate to assess the potential impact of EMF and whether, and how, mitigation is needed. This is made even more pressing as elasmobranchs are a species group already heavily under pressure from other anthropogenic pressures as fishing. As offshore wind development accelerates and EMF becomes a growing concern, the lack of robust data and a clear risk assessment framework may therefore delay permitting processes.

Therefore this thesis aims to provide a better evidence-based insight in exposure-effect levels to help underpin impact assessments of EMFs from SPC on benthic elasmobranchs in the Dutch North Sea.
Following a commonly accepted ecological risk assessment method (Fig. 1.5, (Environmental Protection Agency 1998; Van den Brink 2008)), four research questions were formulated to achieve this aim:

1. | What is known about the nature of EMFs from SPC, and what indications exist for behavioural responses in benthic elasmobranchs from field observations and experimental studies?

2. | What EMFs levels have been reported and are to be expected from SPC?

3. | What are the (lowest) EMFs exposure levels at which behavioural effects of benthic elasmobranchs occur in exposure studies with different life stages?

4. | Which risk level results from the comparison of highest EMF exposure levels and lowest observed effect levels (LOELs) for altered behaviour in benthic elasmobranchs across life stages?

1.8 As described in the following chapters

Chapter 2 establishes the foundation of this thesis through an ecological risk assessment (ERA) applied to EMF from SPC on benthic elasmobranchs in the Dutch North Sea. Combining a literature review with exposure modelling, it allowed to quantify the exposure and hazard, allowing risk characterisation. This analysis identifies key knowledge gaps and pinpoints the behavioural categories or life stages most at risk, guiding the research questions and experimental approaches carried out in the subsequent chapters. A schematic overview of this thesis is provided in Fig 1.6.

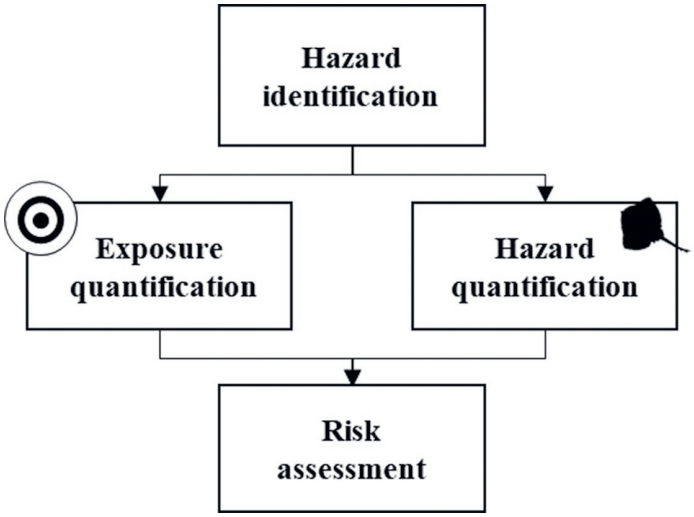


Fig. 1.5 Schematic overview of an ecological risk assessment

Chapter 3 describes the use of eDNA in a field study to address a key knowledge gap e.g. if elasmobranchs return to OWF areas after construction or are deterred by EMF or other stressors, making the habitat unsuitable or disrupting seasonal migration. The thesis then moves to laboratory studies exploring the impacts of EMF exposure at different life stages, where the exposure level and characteristics (e.g., chronic, intermittent, gradient) are tailored to realistic scenarios.

Chapter 4 investigates whether embryos of thornback skate, exposed to alternating artificial AC EMF throughout embryogenesis, show changes in survival, biometry, or behavioural alterations.

Chapter 5 subsequently analyses the effects on EMF sensitivity and activity levels on hatched juveniles of both thornback skate and small-spotted catshark that were exposed during embryogenesis. This chapter also compares species-specific impacts and explores potential differences based on their life history traits.

Chapter 6 determines the behavioural effects on adult small-spotted catshark exposed to a gradient of field relevant EMF, comparable to crossing a SPC. Each animal served as its own control, accounting for intraspecific differences (or characters), and both AC and DC treatments were included.

Chapter 7 then compares the interspecific differences by applying the same experimental set-up as in Chapter 6 to thornback skate. It then evaluates the potential for extrapolating experimental results to other elasmobranch species despite differences in their life history traits.

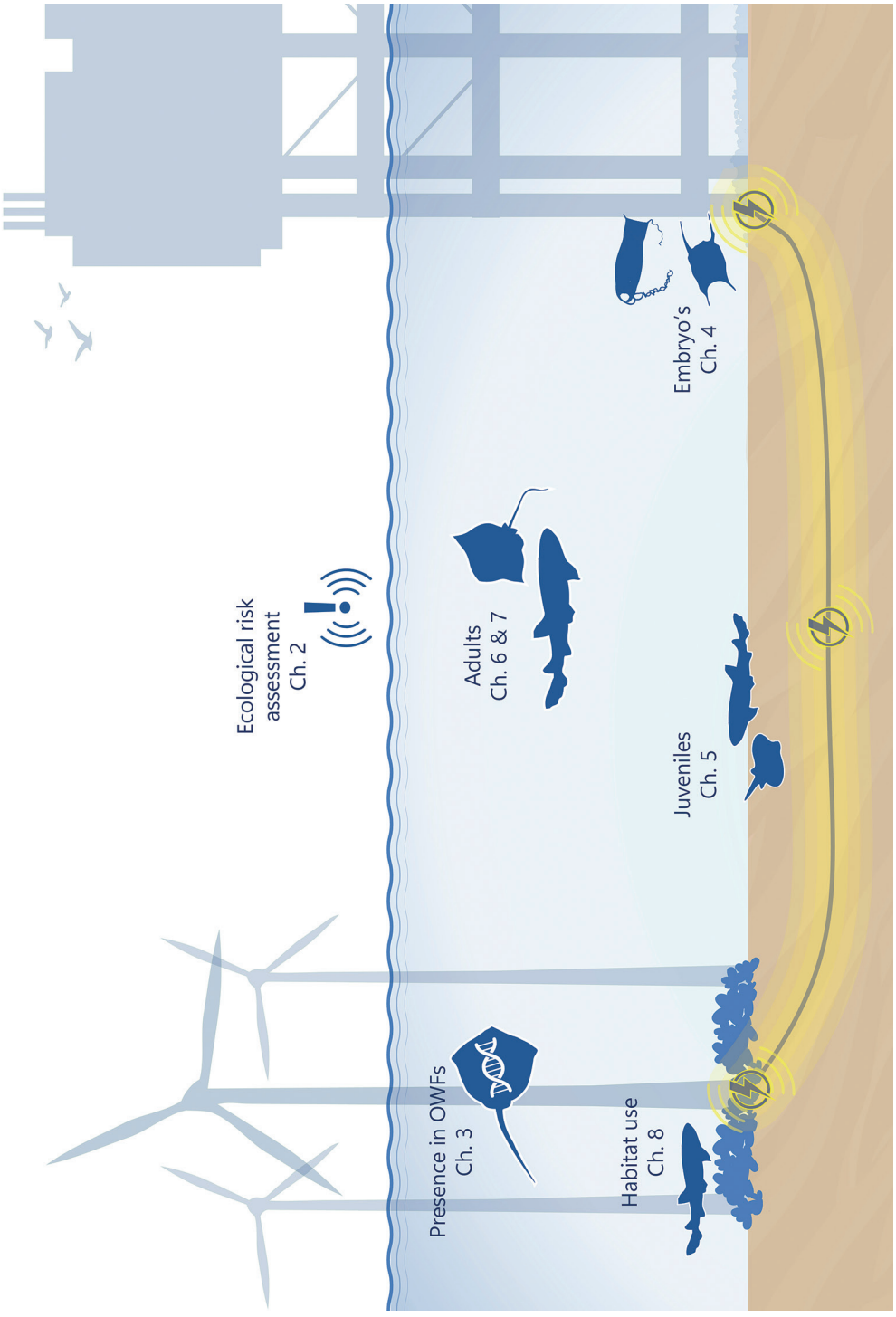
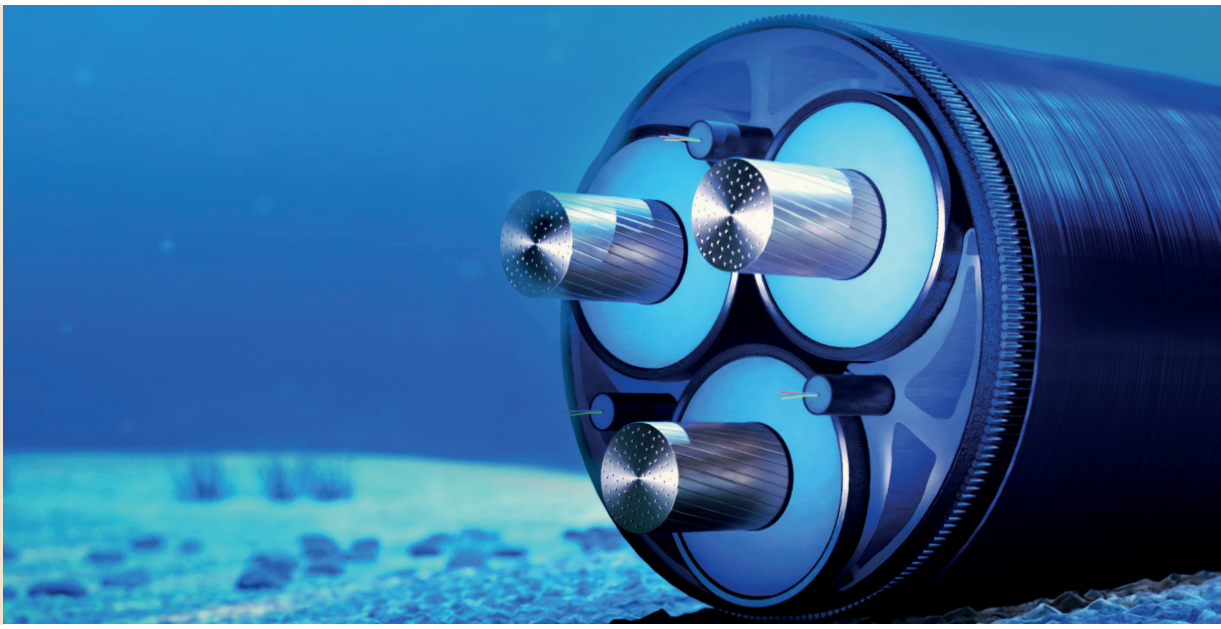


Fig. 1.6 Schematic overview of the Chapters in this thesis.

Chapter 8 presents a first exploration into the impact of EMF on substrate use by juvenile small-spotted catshark, using a preference chamber divided into four quadrants. The individuals were allowed to choose between a substrate with blue mussel (*Mytilus edulis*) and bare substrate, both with and without of EMF exposure.

Finally, **Chapter 9** provides a general discussion that answers the research questions posed in the environmental risk assessment. It highlights the need for a Relative Vulnerability Assessment (RVA), which is subsequently introduced. Based on the outcome of the RVA, field and laboratory research priorities are identified. The chapter further examines the various policy frameworks within which EMF-related information is integrated, followed by an analysis of the precautionary principle's application in this context. It concludes with some overarching considerations.

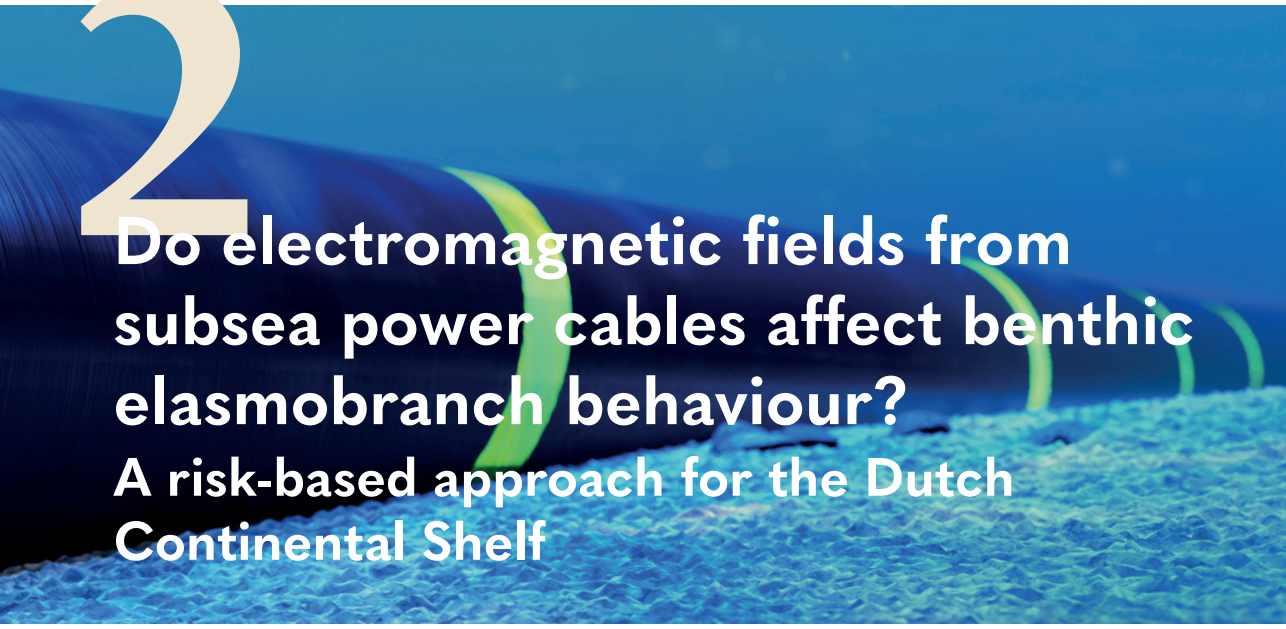


Based on: https://doi.org/10.1016/j.envpol.2024.123570

Abstract

Subsea power cables cause electromagnetic fields (EMFs) into the marine environment. Elasmobranchs (rays, skates and sharks) are particularly sensitive to EMFs as they use electromagnetic-receptive sensory systems for orientation, navigation, and locating conspecifics or buried prey. Cables may intersect with egg laying sites, mating, pupping, and nursery grounds, foraging habitat and migration routes of elasmobranchs and the effects of encountering EMFs on species of elasmobranchs are largely unknown.

Demonstrated behavioural effects include attraction, disturbance and indifference, depending on EMF characteristics, exposed life stage, exposure level and duration. We estimated exposure levels of elasmobranchs to subsea power cable EMFs, based on modelled magnetic fields in the Dutch Continental Shelf and compared these to reported elasmobranch sensory sensitivity ranges and experimental effect levels. We conclude that the risk from subsea power cables has a large uncertainty and varies per life stage and species ecology. Based on estimated no-observed effect levels (from 10^{-3} to 10^{-1} μT) we discuss what will probably be



2 Do electromagnetic fields from subsea power cables affect benthic elasmobranch behaviour?

A risk-based approach for the Dutch Continental Shelf

the most affected species and life stage for six common benthic elasmobranchs in the Southern North Sea. We then identify critical knowledge gaps for reducing the uncertainty in the risk assessments for EMFs effects on benthic elasmobranchs.

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Published in Environmental Pollution | April 2024

2.1 Introduction

The transition from fossil fuel-based energy to renewable energy in the marine environment is considered crucial to meet climate change ambitions and initiatives in many countries (United Nations, 2022). The European Union has set-out targets for an installed capacity of at least 61 GW by 2030 and 340 GW by 2050 (European Court of Auditors, 2023), (WindEurope, 2023). The Southern North sea is well suited for the generation of power from offshore wind because it is shallow (~30m) and average wind speeds are high (>7 m/s) (Government of the Netherlands, 2023; Coelingh et al., 1998). Offshore Wind Farms (OWFs) are planned and realised at an increasing rate, covering ever larger marine areas located increasingly further from shore (WindEurope, 2023; Ministry of economic affairs and climate, 2022; Soares-Ramos et al., 2020).

The North Sea marine environment is already heavily impacted by human activities, and OWFs represents an additional and large-scale activity that will influence marine life (Li et al., 2023). The effects of scour protection functioning as artificial reefs (Lindeboom, 2012; Coolen et al., 2020; Degraer et al., 2020a), exclusion of bottom trawling (Degraer et al., 2020a), collision risks for birds (Fox et al., 2006; Drewitt and Langston, 2006; Furness et al., 2013) and underwater sound risks for marine mammals (Nedwell and Howell, 2004) are relatively well studied. However few studies exist on the effects of sediment resuspension (Boon et al., 2018), destratification (Boon et al., 2018; Cazenave et al., 2016) and marine fauna exposure to EMFs (Martínez et al., 2021). Different types of subsea power cables (SPC) emit EMFs, including infield cables between turbines, export cables that transmit electricity to shore and interconnector cables that enable power exchange between countries (Boon et al., 2018; Anderson et al., 2017; Kalmijn, 1978). Subsea power cables produce a locally changed electric and magnetic environment.

Many marine taxa are regarded as magneto-sensitive, whilst some organisms are electrosensitive and a select group, in particular elasmobranchs, are both (Anderson et al., 2017; Meyer et al., 2005; Keller et al., 2021a). Magneto-sensitivity is mainly assumed to be used for long-distance navigation or orientation (Kalmijn, 1978; Molteno and Kennedy, 2009; Klimley, 1993a; Newton and Kajiura, 2020), which leads to the prediction that the EMFs from SPC export cables that transport electricity to the shore could interfere with migration along the coast. During migration adults will encounter multiple cables of varying EMF strengths which might cause delays as has been shown in migrating eel (Westerberg and Lagerfelt, 2008). In another study salmonids showed a (slight) deviation of course (Wyman et al., 2018). A multitude of species respond to magnetic cues and are sensitive to the direction, magnitude or/and inclination of the Earth's geomagnetic field (Mouritsen, 2018, Wiltschko and Wiltschko, 2005, Nyqvist et al., 2020). The variations in the geomagnetic field are as low as 0.002–0.005 μT/km, and the earth magnetic field ranges between 25 and 70 μT (Nyqvist et al., 2020), therefore the magneto-sensitivity of species using the geomagnetic field is believed to be in the nano tesla range (Anderson et al., 2017; Meyer et al., 2005; Klimley, 1993a; Wiltschko and Wiltschko, 2005; Hodson, 2020).

Electro-sensitivity is used to find prey (Kalmijn, 1971; Kajiura and Holland, 2002; Collin et al., 2015), avoid predation (Sisneros and Tricas, 2002; Kempster et al., 2013a), and find conspecifics/mates (Sisneros and Tricas, 2002; Kempster et al., 2013a; Tricas et al., 1995). Elasmobranchs can detect electric fields as low as 5 (nV/cm) (Kalmijn, 1971).

Benthic elasmobranchs are highly electro- and magneto-sensitive (Hutchison et al., 2020a) and as a taxonomic group they are already greatly impacted by anthropogenic stressors, such as overfishing, bottom trawling rendering them as bycatch and destroying reef structures needed for reproduction (Walker and Heessen, 1996; Batsleer et al., 2020). These fish perform a critical role in the food web linking different trophic levels together and controlling prey populations (Flowers et al., 2021; Carrier et al., 2010). As slow growing, often oviparous species with a late sexual maturity, benthic elasmobranch population success is very vulnerable to bottom trawling fisheries and is therefore expected to benefit from the exclusion of these fishing techniques in OWF (Walker and Heessen, 1996; Rodríguez-Cabello et al., 2008). Conversely, their benthic ecology places them in direct contact with the extensive (and growing) network of subsea cables emitting EMF. Potential effects from EMFs that have been suggested for benthic elasmobranchs, range from 1) disturbance of the reproductive cycle, including embryogenic development or courting behaviour and mating, 2) behavioural changes such as attraction or avoidance

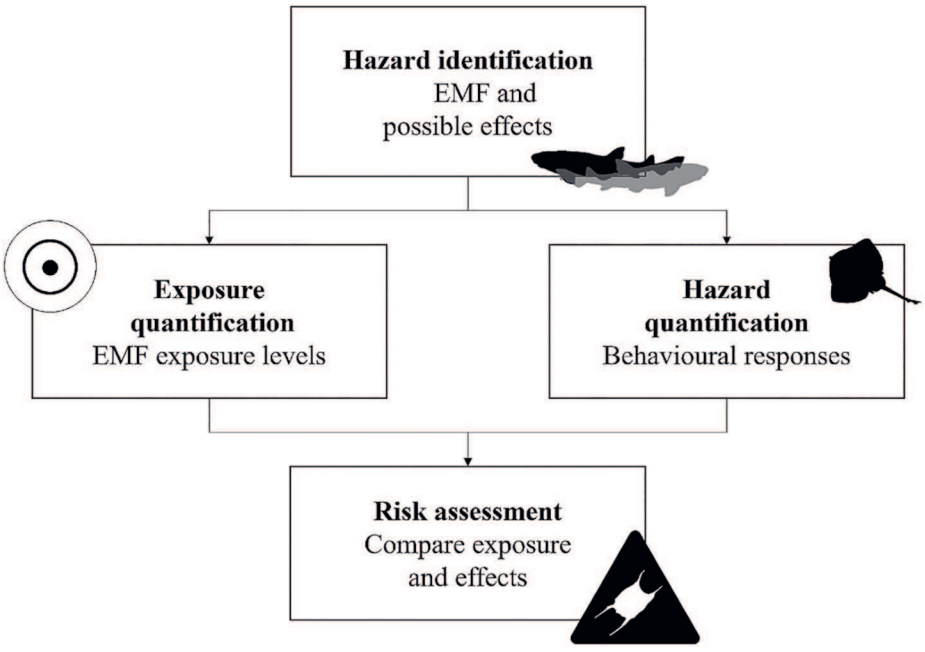

Fig. 2.1 Ecological Risk Assessment approach to determine the risk for behavioural effects of electromagnetic fields (EMFs) resulting from subsea power cables (SPC) on benthic elasmobranchs on the Dutch continental shelf.

(Hutchison et al., 2020a; Gill et al., 2009), which could lead to disrupted predator-prey relations and/or relations between conspecifics or changes in habitat use and 3) impact on migratory behaviour (Ohman et al., 2007). Within category 1), especially, embryos of oviparous species may be continuously exposed to EMF as export cable routes transverse egg laying sites, making egg-cases potentially a particular vulnerable life-stage. This possibility might be exacerbated through the active introduction or recovery of reefs in OWF which could provide additional opportunities for benthic elasmobranchs to lay their eggs within an EMF from a SPC (Rodríguez-Cabello et al., 2008).

Although there is not much known about the effects of EMF on benthic elasmobranchs, their high electro- and magneto-sensitivity and vulnerable life history stages raises concerns, some of which have been expressed by governments (Hermans and Schilt, 2022), NGOs (Hermans and Schilt, 2022) and fisheries organisations (EMK, 2020). These uncertainties might delay the permitting process (Copping, 2018) or lead to a precautionary approach and the requirement for the development and implementation of mitigation measures that are costly and of uncertain added value. A science-based Ecological Risk Assessment (ERA) (Depledge and Fossi, 1994) can support better informed discussions and aid in decision making of whether or where mitigation is needed to reduce potential adverse effects (Hutchison et al., 2020b). An ERA could also serve to indicate which knowledge gaps should be filled with priority to answer remaining critical questions (Normandeau et al., 2011; Gill et al., 2014; Boehlert and Gill, 2011).

This study follows an ERA approach (Fig. 2.1) to assess the risk of EMF emitted by current and planned SPC in the Dutch Continental Shelf in the Southern North Sea for benthic elasmobranchs. The ERA was performed through the following steps:

1. | **Hazard identification:** what is known about the nature of EMFs from SPC, and what indications exist for behavioural responses in benthic elasmobranchs from field observations and experimental studies?

2. | **Exposure quantification:** what EMFs levels have been reported and are to be expected based on modelling from SPC characteristic on the Dutch Continental Shelf?

3. | **Hazard quantification:** what are the (lowest) EMFs exposure levels at which behavioural effects on benthic elasmobranchs occur in exposure studies with different life stages?

4. | **Risk assessment:** comparing highest EMFs exposure levels to lowest effects levels for altered benthic elasmobranch behaviour per life stage in the Dutch North Sea resulting in risk levels.

The ERA is followed by a discussion in which the results from the risk assessment are related to the different specific traits of the benthic elasmobranchs leading to an estimation of the potentially most affected species/life stage, critical knowledge gaps and the need for appropriate mitigation or retirement of the risk for currently deployed SPCs.

2.2 Hazard identification

The hazard identification step evaluated if EMFs may be regarded as having the potential to cause harm to benthic elasmobranchs. Therefore, an overview is provided of the potential risk posed by exposure to EMF and what the characteristics of the EMF should be taken into account. Below an overview is provided of the nature, sources and potential effects reported by EMFs on benthic elasmobranchs.

2.2.1 EMF characteristics

The characteristics of the EMFs depend on whether the cable is transporting Alternating Current (AC) or Direct Current (DC). EMFs consists of an electric (E-field), magnetic (B-field) and induced electric field (iE-field). As an industry standard for both AC and DC cables, the direct E-field is contained by cable armouring in a perfectly grounded cable, but the B-field is emitted into the environment and any water movement generates an induced electric or iE field (Gill et al., 2014). Furthermore, AC cables also create iE fields owing to the asymmetric cycling of the electrical current in the multiple cable cores. The extent of the magnetic field can vary in relative importance of the directional components (x,y,z plane) (Hutchison et al., 2020b). The resultant magnetic component is a sum of these directional components and therefore it has a strength and also a direction (Hutchison et al., 2021). Factors influencing the intensity and direction include amount of power transported, cable design and component geometries, and cable orientation (Gill et al., 2014), (Taormina et al., 2018a). EMFs are linearly related to the amount of power transmitted through the SPC which, in the case of OWFs, depends on the available wind. With AC the frequency depends on the local standard, i.e. 50 Hz in most of Eurasia, Africa and Oceania and 60 Hz in North-America. In addition, the form of the cable component rotations (circle or ellipse shaped) can also vary (Hermans and Schilt, 2022). The vectoral magnetic components interact with other, more variable, natural EMF sources, such as solar radiation (see Nyqvist et al., 2020 for an extensive overview of natural EMF sources). iE fields result from water movement through a magnetic field, for example tidal currents or water displacement by animal movement. The pattern and magnitude of the resulting iE field depends on the direction and flow of seawater (Nyqvist et al., 2020; Kalmijn, 1999) as well as the fish size, shape, orientation, and the speed and direction of its movement (Nyqvist et al., 2020; Haine et al., 2001). The iE fields are expected to be in the range of 10^{-4} to 10^{-5} V/m (Hutchison et al., 2020a; CSA Ocean Sciences Inc, 2019; Thomsen et al., 2016).

2.2.2 Magnetic fields and induced electric fields

The way an organism experiences a specific EMF, and thus the biological relevance, will depend on the species and its life stage (Gill et al., 2012). Both the magnetic field and the iE field can serve as potentially important behavioural cues (Nyqvist et al., 2020; Fisher and

Slater, 2010; Marcotte and Lowe, 2008). When an animal is moving through a magnetic field, it simultaneously experiences the magnetic and the induced electric field (Nyqvist et al., 2020). Due to this biological coupling these fields are difficult to consider separate (Nyqvist et al., 2020; Kalmijn, 1999). However, whilst the iE fields are generated from the magnetic fields, they are difficult to measure and they are heavily dependent on other environmental and biological factors. The exposure quantification applied in this study therefore focused on magnetic fields. As 0.002–0.005 μT/km is the latitudinal geomagnetic field (GMF) change for Dutch waters, 0.005 μT was assumed as the minimum level relevant for benthic elasmobranchs to be able to use the GMF for long-distance navigation (Nyqvist et al., 2020). Following this assumption, in the risk assessment the lower level of the exposure quantification of 0.005 μT was used.

2.2.3 Potential effects of EMF

Previous studies suggest that EMF levels that SPC emit are too low to induce acute health effects, such as permanent (neuro)physiological effects in adult individuals (Nyqvist et al., 2020). The scale of research available on EMF and bentho-pelagic elasmobranchs ranges from empirical evidence of use of the geomagnetic field in e.g. *Sphyrna lewin* (Keller et al., 2021a; Klimley, 1993b) to strong deterrence in *Carcharias taurus* (Polpetta et al., 2021). Although the signature of anthropogenic EMFs from a SPC might be different than natural EMFs, Kimber et al., 2011 have shown that benthic elasmobranchs cannot discriminate between an artificial and natural EMFs. Indeed, a number of experimental studies address how EMFs induce behavioural responses in benthic elasmobranchs and field observations suggest that benthic elasmobranch interact with SPC (Marra, 1989). The suggested behavioural effects can be categorized in three types 1) disturbance during embryogenic development, 2) behavioural changes of local-dwelling animals and 3) interaction with migratory behaviour. Potential effects for these categories of behaviour are indicated below and shown in Fig. 2.2.

1. | Disturbance during embryogenic development Where SPC come to land they often cross estuaries or other coastal areas potentially well suited as benthic elasmobranch egg laying sites or pupping grounds (Leurs et al., 2023; Day et al., 2019). Benthic catsharks, such as Scyliorhinus canicula, are known to deposit eggs in macroalgae in coastal areas and sessile benthic invertebrates (reefs) on offshore grounds (Heessen et al., 2015). Benthic skates, such as Raja clavata, are known to deposit egg cases in sandy shallow waters of the Southern North Sea (MMO, 2016). On the Dutch Continental Shelf SPC routes cross the Oosterschelde inlet. If the sessile egg cases are deposited within the EMFs of a SPC, an embryo will be exposed to the varying EMF levels during embryogenesis. Embryos have been shown respond to electric stimuli after 1/3 of their development phase (Paoletti et al., 2023). Studies have shown a freeze response, (temporarily ceasing respiration) which is suggested to prevent detection by a predator, when exposed to EMF from SPC (Ball et

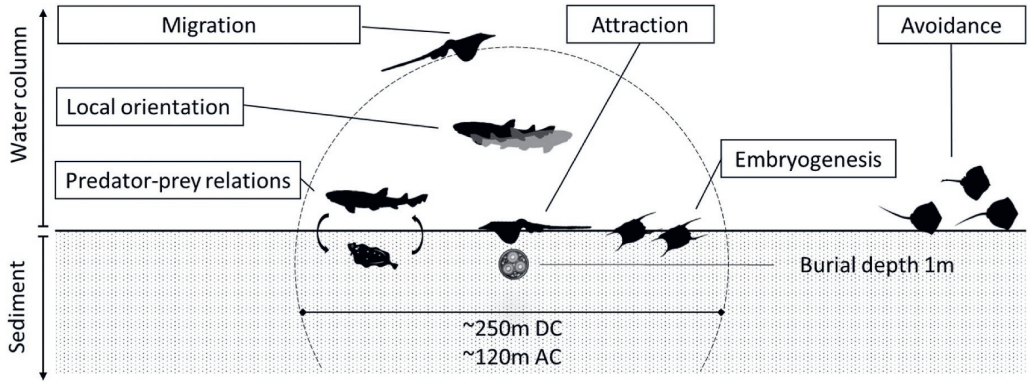

Fig. 2.2 Schematic overview of possible elasmobranch responses exposed to modelled magnetic fields (Figure inspired by Albert et al., 2020). Potential impact range based on a perception level of 0.005 μT, modelled levels for the OWF export cable IJmuiden Ver (2 GW direct current subsea power cable) and Borssele (700 MW alternating current subsea power cable) transporting maximum amount of power is indicated by dotted line. Note: animals are not to scale.

al., 2016; Kempster et al., 2013b; Paoletti et al., 2023; Christensen et al., 2023). Constantly responding to changing EMF levels might cost metabolic energy, resulting in reduced growth and development and lead to higher yolk consumption, which may lead to a longer development time and/or smaller hatchlings, as has been seen in lobster larvae (Harsanyi et al., 2022). Another impact mechanism could be that continuous exposure to EMFs during embryogenesis could exert epigenetic effects, leading to behavioural alterations in adulthood, as shown for other stressors in Negaprion brevirostris and other fish (Paige Beal et al., 2021, Gapp et al., 2014, Cavalieri and Spinelli, 2017) Individuals could become less sensitive to EMFs, or the opposite could be true, where individuals could become hypersensitive. These effects might result in reduced foraging success later in life, increased predation risk because they became less sensitive to EMF signatures of predators or a change in habitat use. Also, magneto sensitive species, such as turtles, but also elasmobranchs are believed to use geomagnetic imprinting to maintain fidelity to reproduction sites (Putman et al., 2013; Lohmann et al., 2008; Feldheim et al., 2014). Continuously altering EMFs from SPC during embryogenesis might disrupt the imprinting process needed to find the way back to reproduction sites.

2. | Behavioural changes during local dwelling The Southern North Sea provides habitat for approximately 18 elasmobranch species of which 12 have a (partly) benthic ecology (Heessen et al., 2015). Species abundance and distributions vary but at least some habitats overlap with areas that are suitable for OWF development. Behavioural changes induced by in-field SPC could include altered natural foraging behaviour and success by i.e. disruption in predator-prey, attraction or avoidance, disruption of conspecifics relationships like courtship or mating and/or changes in habitat use (Normandeau et al., 2011; Taormina et al., 2018b), examples listed in Table 2.2. For example, anecdotal evidence presented by Barry

et al. (2008) showed 126 Raja rhina aggregating around a not powered SPC compared to no individuals during repeated field survey when the SPC was in use. Hutchison et al. reported increased foraging behaviour, such as increased swimming distance and speed, with more sharp turns and changing swimming depth in animals exposed to between 0.3 and 14 μT (Hutchison et al., 2020a).

3. | Interaction with migratory behaviour Benthic elasmobranchs as Raja clavata, Galeorhinus galeus and Mustelus asterias are known to migrate over long distances up to hundreds km per year (Schaber et al., 2022; Hunter et al., 2005; Brevé et al., 2016, Brevé et al., 2020; Keller et al., 2021b; McMillan, 2018). Migrating benthic elasmobranchs have been shown to orient using the inclination, intensity and angle of the magnetic field (Newton and Kajiura, 2020). Therefore, they might respond during migration when crossing a SPC if the characteristics of the local magnetic field are altered by the emitted EMF. This was observed with eels (Westerberg and Lagenfelt, 2008), and with salmonids where individuals were slowed down or showed (slight) deviation of course (Wyman et al., 2018). Complete blockage of migration is not likely given observed migration patterns from tagged benthopelagic elasmobranchs that must have crossed several existing SPCs (Brevé et al., 2016, Brevé et al., 2020). Attraction to the SPC could become point of concern, dependant on the duration of the attraction ranging from short (seconds) as shown by Orr (2016) to longer attraction as shown by Barry et al., (2008). Cumulative minor migration alterations and delays might have energetic consequences resulting (McMillan, 2018) in reduced migration success, missing important ecological timing, reduce overall fitness or increase predation risk when crossing SPC higher in the water column.

2.3 Exposure quantification

2.3.1 Measured magnetic field levels on the Dutch Continental Shelf

In order to assess the risk of any stressor, it is important to quantify the exposure that animals may encounter, estimating frequency of occurrence, variability in EMFs and the range of field strength. To be able to estimate the current and for the nearby future predicted EMF levels as potential exposure of benthic elasmobranchs in the Southern North Sea, a literature review was performed on the measured magnetic field levels over three phase AC and bundled bipolar DC SPC (Table 2.1). The majority of the measurements were performed at the seabed, where the distance to the SPC depends on the burial depth, generally 1.0–2.0 m deep. The reported magnetic field levels above cables transporting AC or DC range from 0.004 μT to 6.540 μT for AC cables and 0.46 μT–20.7 μT for DC cables. The magnetic field levels depend on distances to the SPC, environmental conditions (flow, temperature etc.) and power transported through the SPC at the time of measurement, and could not be measured during high wind conditions for safety reasons. Therefore, the scenario for high intensity EMFs can only be modelled. For assessment of the spatial range

Table 2.1 Magnetic field levels measured above alternating current (AC) 3-phase and bundled bipolar direct current (DC) export and interconnector cables. The values noted in the table are the maximum levels recorded during a measurement. The power transported through the cable at the moment of measurement was not provided in the listed studies.

Alternating Current (AC) Cables - 3-phase

Cable specifications	Maximum levels (μT)	Distance from the cable (m)	Reference
34 kV; 108 MW	0.008 - 0.020	1.5 - 2.0	Snoek et al., 2020
150 kV; 120MW	0.015 - 0.039	1.5 - 2.0	Snoek et al., 2020
150 kV; 129 MW	4	1.5 - 2	Snoek et al., 2020
50 Hz	4	1.0 - 1.5	Thomsen et al., 2015
50 Hz; 70 A	17	15	Thomsen et al., 2015
36 kV; 265 A	600	1.5	Gill et al., 2009
33 kV; 50 A	50	0	CMACS 2003
11 kV; 60 A	56	0	CMACS 2003
150 kV; 120MW; 436 A	6.540	0.5	DNV-GL, 2015 cited in Snoek et al., 2020

Direct Current (DC) Cables - bipolar

Cable specifications	Magnetic field levels (μT)	Maximum levels above GMF (μT)	Distance from the cable (m)	Reference
300kV; 330 MW; 0 A	51.7	0.46	1.3	Hutchison et al., 2020
300kV; 330 MW; 16 A	51.9	0.64	1.3	Hutchison et al., 2020
300kV; 330 MW; 345 A	65.6	14.3	1.3	Hutchison et al., 2020
660 MW; 500 kV; 1320 A	72.0	20.7	1.3	Hutchison et al., 2020
660 MW; 500 kV; 660 A	56.3	4.7	1.3	Hutchison et al., 2020

in exposures benthic elasmobranchs might encounter, the spatial and temporal characteristics of EMF should be taken into consideration and can be approximated with modelling (Hutchison et al., 2020b).

2.3.2 Modelled magnetic field levels for the Dutch Continental Shelf

As a case study, we modelled the local magnetic field levels (in μT) of SPC at the seabed of the Dutch Continental Shelf. The model comprises a 24 year period, from the first cable installation in 2006 up to the planned SPC network to connect the allocated OWF by 2030. Telecommunication cables were not included as their EMF levels are believed to be negligible (<0.005 μT) because of low voltage (10 kV) (Normandeau et al., 2011; Carter et al., 2009; Meiβner et al., 2006). The magnetic fields of 3-phase (commonly used in AC SPC) and bipole (for DC SPC) cables were calculated using the Biot-Savart law (for a detailed description of the calculations refer to the supplementary materials S1). Cable characteristics were obtained from publicly available documentation and/or provided by the cable owners (for details see supplementary materials Table 2.1). The burial depth was assumed to be the legally required minimum of -1m in Dutch waters.

As the capacity of the AC SPC cables has increased in the last decades, the modelled magnetic field increased from a maximum of 1.8 μT in the first Dutch OWF Windpark Egmond aan Zee (OWEZ) which has been operational since 2007 to a maximum of 13.9 μT for the recently build OWF Borssele (Fig. 2.3a). This increase in magnetic field strength also can be observed for DC cables where the capacity and thus output has quadrupled in the same time span from 16.4 μT in NorNed (built in 2008) to 61.3 μT for IJmuiden Ver planned for 2028 (Fig. 2.3b).

As the amount of transported energy and therefore the magnetic field levels above SPC depends on the wind conditions, we modelled seasonal scenarios to provide a realistic exposure range. We assumed the production of an average of 25% of the maximum (designed) power in summer and 80% of the designed power in winter (Fig. 2.3). The percentages used for the scenarios are based on information supplied by the grid operator. For example, a commonly used 700 MW 3-phase AC (Borssele) summer scenario resulted in an average magnetic field of 3.5 μT and the winter scenario 11.1 μT. Without wind, the maintenance power level including the reactive power results was modelled at 0.1 μT and the maximum EMF that the cable can produce is 13.9 μT. The modelled magnetic field levels for planned DC cables are four times higher than for AC cables (Fig. 2.3). Unless OWF generated wind will be converted into e.g. hydrogen at sea, future scenarios (2030–2050) will include more cables with higher capacities transporting electricity over longer distances (Ministry of economic affairs and climate, 2022) which will further increase EMF exposure levels (Hutchison et al., 2020b).

Table 2.2 Overview of reported benthic elasmobranch behavioural responses to anthropogenic magnetic field exposure of alternating (AC) and direct current (DC) power transmission systems or changes in the geomagnetic field (GMF).

Power system (AC/DC)	Type of study	Life stage	Species	Experimental level (μT)
DC	Laboratory	Juvenile	*Carcharhinus plumbeus*	39.4
			Carcharhinus plumbeus	37.3
			Carcharhinus plumbeus	36.03
		Adult	*Raja clavata*	450
			Carcharhinus plumbeus	25
			Urobatis jamaicensis	38
			Urobatis jamaicensis	90
			Cephaloscyllium isabellum	3960
			Leucoraja erinacea	47.8
	Mesocosm		*Leucoraja erinacea*	52.6-65.4
AC	Mesocosm	Adult	*Scyliorhinus canicula*	8
			Raja clavata	8
	Laboratory	Juvenile	*Cephaloscyllium isabellum*	1430
			Raja clavata	450
		Embryo	*Scyliorhinus canicula*	4

2.3.3 5.5% of Dutch Continental Shelf covered with EMF detectable by elasmobranchs by 2030

The magnetic field levels exponentially decrease with distance from the SPC. Based on the lowest perception level of 0.005 μT, the affected area of SPC from export and intercontinental cables considered in this study totals over 550 km2. This is approximately 1.0 % of the Dutch Continental Shelf (~57,800 m2). The potential impact range of 0.005 μT contour differs from roughly 40 metres in diameter for the OWEZ cable to 250 metres for the IJmuiden Ver SPC (supplementary materials Table 2.2). It is important to consider that as the EMFs extend in all directions, and the extent can differ horizontally and verti-

Type of response considered	Reference
behavioural: Strong conditioned reaction swimming towards target increasing tail beat frequency and swim speed towards target	Anderson et al. 2007
behavioural: moderate conditioned reaction, swimming towards target increasing tail beat frequency and swim speed towards target	Anderson et al. 2007
behavioural: weak conditioned reaction, swimming towards target increasing tail beat frequency and swim speed towards target	Anderson et al. 2007
Behavioural: small behavioural change (only in afternoon)	Albert et al 2021
behavioural: conditioned reaction swimming towards target	Meyer et al. 2005
behavioural: choice	Newton and Kajiura 2020a
behavioural: conditioned response	Newton and Kajiura 2020b
Behavioural: small attraction	Orr et al 2016
behavioural: strong attraction, strongly increased distance covered, increased speed of movement, increased number of sharp turns, closer to seabed	Hutchison et al. 2020
behavioural: moderate attraction, foraging and exploratory behaviour, moderately increased distance covered, increased speed of movement, closer to seabed	Hutchison et al. 2020
behavioural: attraction to cable/decreased movement near cable	Gill et al. 2009
behavioural: increased movement in some individuals in EMF	Gill et al. 2009
Behavioural: no response	Orr et al 2016
Behavioural: no significant response	Albert et al 2021
Physiological: changes in growth and development	Paoletti et al 2023

cally. For simplicity in this risk assessment it is assumed that this extension is the same in all directions. This means that not only the seabed but also (most of) the water column is influenced by EMF as the water depth is a maximum 50 meter in the DCS. Besides the export cables, the inter-array cables within the OWF also create an EMF. OWF are planned to occupy 2,600 km2 in 2030 which is circa 4,5% of the Dutch Continental Shelf. Assuming the EMF from the inter array cables covers the entire OWF, 5.5% of the Dutch Continental Shelf will be under the influence of SPC generated EMF detectable by elasmobranchs by 2030. Of course, this exposure will not be limited to the Dutch Continental Shelf as in the surrounding North Sea countries comparable OWF developments are taking place, aiming for a total energy production 61 GW by 2030 in the entire North Sea.

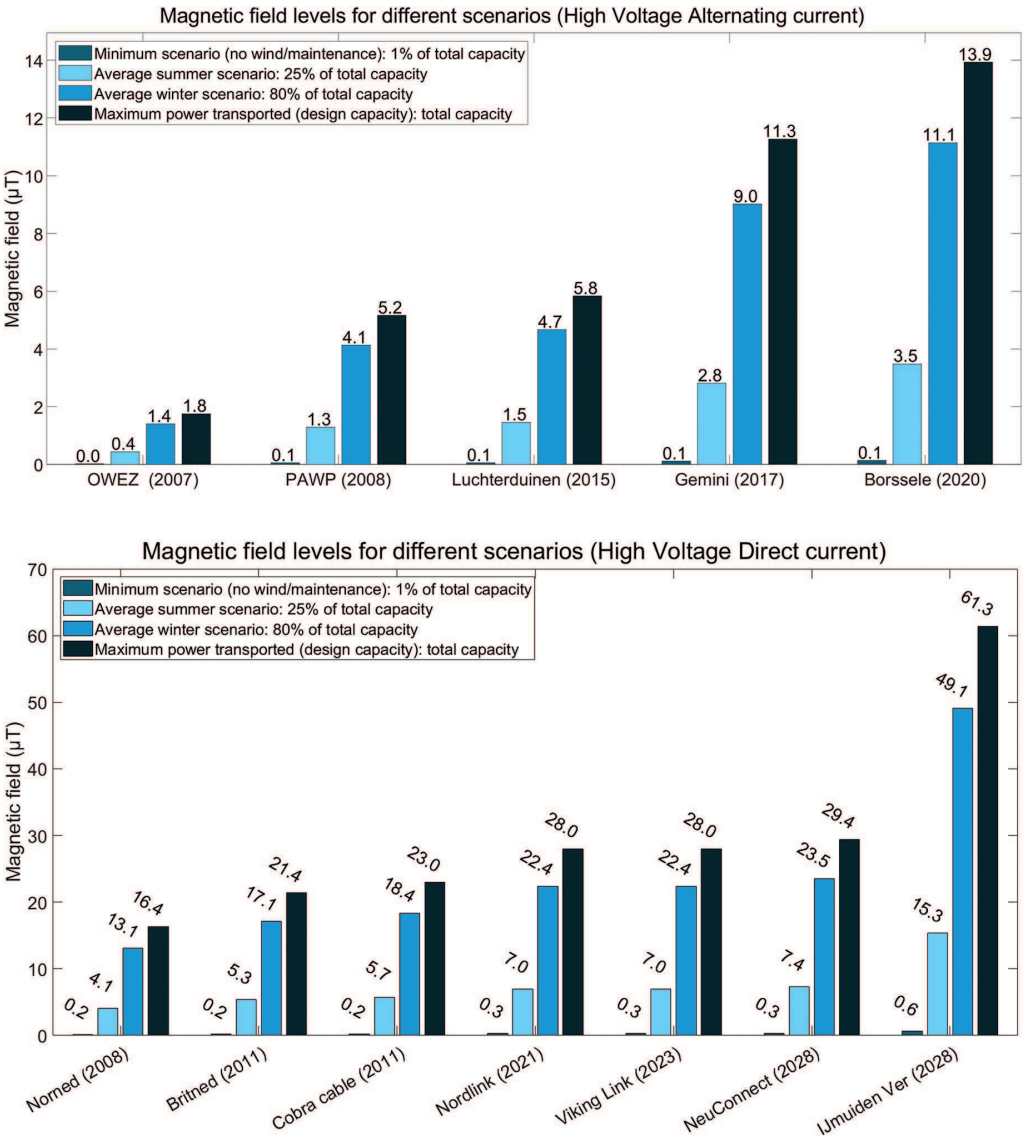

Fig. 2.3 Modelling results of produced magnetic field levels from existing and planned SPCs up to 2030 of (a) from Offshore Wind Farm export and (b) interconnector cables on the Dutch Continental Shelf. Note that the Borssele cable also represents the Hollandse Kust Zuid, Noord and West, and Ten Noorden van de Wadden cables and the IJmuiden Ver cable also represents the Nederwiek cables respectively which are planned but not shown as the cable specification and thus the modelled values are the same. The scenarios are defined as a percentage of the design power (DP) minimum (1% of DP, only maintenance power levels), summer (25% of DP), winter (80% of DP) and maximum (100% of DP).

2.3.4 Rate of encounter

Benthic elasmobranch habitat will not fully overlap, 5.5% of the Dutch Continental Shelf will be under the influence of EMFs by 2030. The species-specific movement ecology and habitat uses will determine encounter rates. For most benthic elasmobranch species these life history characteristics are not yet known. As a first proxy for encounter rate, overlap in spatial occurrence of benthic elasmobranchs and areas under the influence SPC induced EMFs is examined. For this, the number of species caught in the Frisbe and DATRAS fisheries surveys of ICES at a certain location in a period of ~40 years (data collections methods described by Batsleer et al. (2020)) was overlayed by the installed and planned SPC until 2030 (Fig. 2.4). This shows that OWFs overlap habitat of up to four of the studied benthic elasmobranch species. Some export cables (IJmuiden Ver and Borssele) transvers areas are used by up to 5 different species for either migration of local-dwelling.

2.3.5 Comparing measured and modelled EMF levels

It is only possible to validate the modelled magnetic field levels with measured EMF levels if key information that influences field strength is available, such as power transported through the cable at the time of measurement, burial depth and cable characteristics (Hutchison et al., 2021). This is mostly lacking, resulting in apparent discrepancies between measured and modelled magnetic field levels (Thomsen et al., 2016; Degraer et al., 2020b). Hutchison et al. (2020a,b) reported AC levels of >0.005 μT tens to a hundred of metres from the cable recorded at DC cables (Hutchison et al., 2021), which was unexpected. The most likely explanation was interference from the transformation stations. Other measurements report AC magnetic field background values ±0.0325 μT, which were higher than the EMF in references areas without SPC (Snoek et al., 2020). Thomsen et al. (2016) described that magnetic field levels measured at Belgium OWF export cables were higher than calculated (Thomsen et al., 2016). On the other hand, Snoek et al. (2020) measured magnetic field levels up to 0.039 μT at the AC 'PAWP' SPC located in the Dutch North Sea, transporting power generated by wind levels at 3–4 Bft (Snoek et al., 2020). Our modelled levels for those conditions, assuming standard burial depth, were >30 times higher (1.3 μT in the comparable wind scenario, summer scenario, 25% of total capacity) (Table 2.1 and Fig. 2.3). The theoretical transported power does not always reflect the actual transported power and there is an imbalance between the three phases in AC cables that can explain this difference. In addition, the 3-phase cables are helically twisted which reduces the magnetic field level as the fields of the three cores party cancel each other out. This cancellation could not be taken into account in the model, as it would require information on the twist length periodicity (the cores have made a 360° twist around each other), which is currently not provided in cable specifications (del-Pino-L´opez et al., 2022). For bundled DC cables the orientation in which the cables are placed on/in the seabed (vertical, horizonal or diagonal) influences the interaction with the geomagnetic field. The placement orientation is generally not known

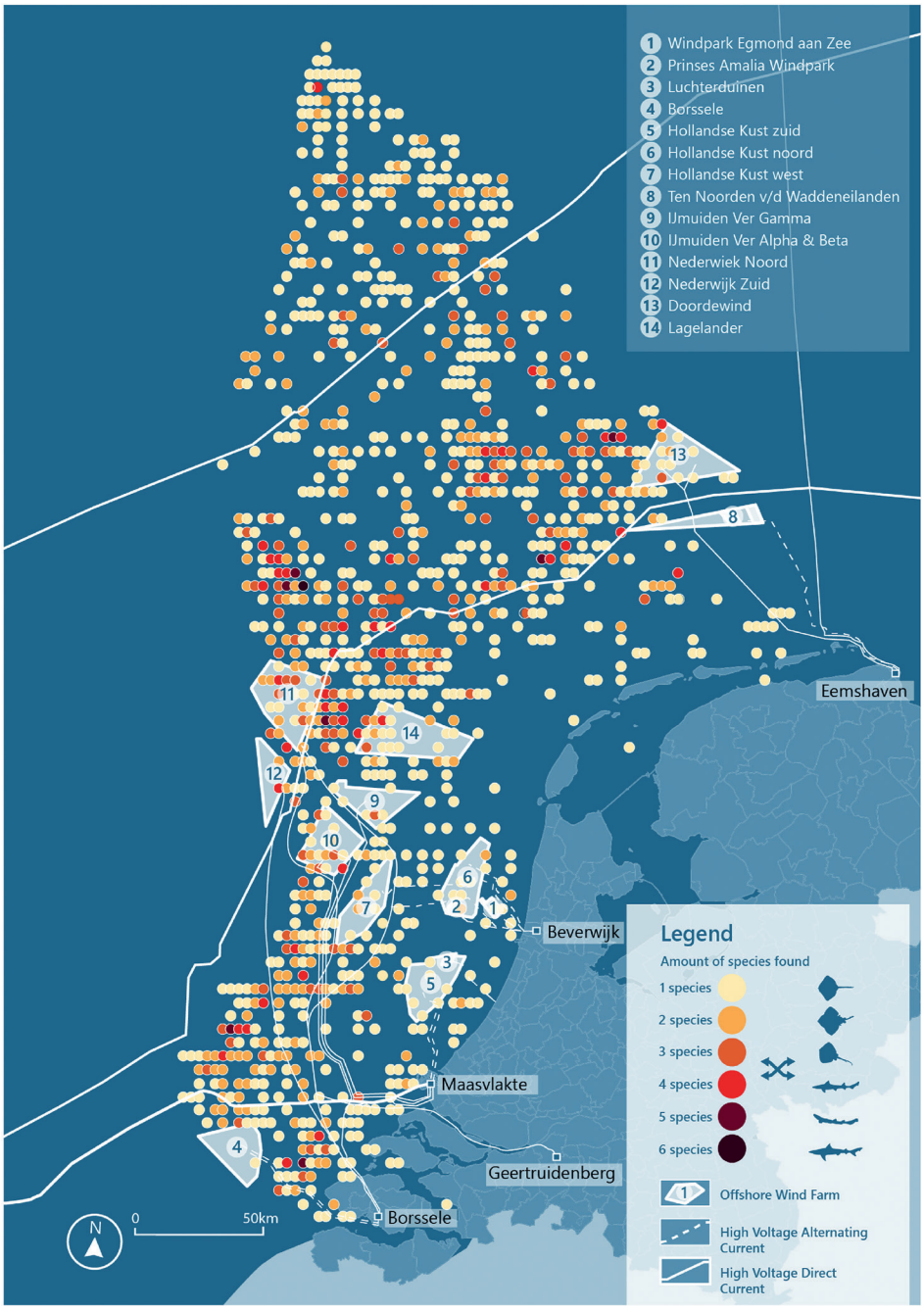

Fig. 2.4 Overview of offshore wind farm export cables and interconnect cables build and planned until 2030 on the Dutch Continental Shelf in relation to the catch data of elasmobranch species. Solid lines indicate direct current cables, dashed lines indicate alternating current cables, data obtained from Informatiehuis Marien Open data viewer. Species richness indicates number of elasmobranch species caught based on Frisbe (1980–2019) and DATRAS (ICES) fisheries database. Figure shows overlap between cable routes and habitat use of Elasmobranchs.

and also not included in the existing models. Therefore, measurements are still needed to account for these uncertainties, and modelled values to be able to include EMFs generated at the highest wind levels. The combination of both methods can provide understanding in the critical knowledge gaps needed to be able to quantify EMF exposure levels for benthic elasmobranchs.

2.4 Hazard quantification

To determine the risk of behavioural effects the No-Observed and/or Lowest Observed Effect Levels (N/LOEL) need to be established to be able to compare these to the exposure levels for the risk assessment. The (No-) effect levels will depend on the species/life stage and exposure type/duration and studied endpoint. In this hazard quantification the N/LOEL was established based on the available literature. EMFs can induce behavioural changes in benthic elasmobranchs and based on a literature review of laboratory and mesocosm studies on behavioural responses to EMF exposure, the No- or Lowest Effect Levels were assessed for DC as well as AC induced EMFs (Table 2.2). In total 9 studies were found, which is very limited for a good hazard quantification. Seven studies were laboratory based and two mesocosm based. When determining the LOEL it is important to consider that dose-response curve is potentially not Sshaped, but maybe show a downward trend or (inverted) U-shape (Thomsen et al., 2016). Lower levels of EMFs might have different effects as they could evoke attraction of a longer duration with less individual variation, which for example may mimic bioelectric fields of prey (Kimber et al., 2011). This might explain why some studies that include high EMF levels (Meyer et al., 2005; Albert et al., 2021) show no effects, whist others with lower levels that are comparable to the levels expected at on the Dutch Continental Shelf, reveal behavioural changes (Hutchison et al., 2020a; Gill et al., 2009).

2.4.1 Reported effects of EMF

The behavioural responses to EMFs exposure that are described in literature are summarised in Table 2.2. The reported effects are clustered for the three behavioural categories distinguished in the hazard quantification: embryonic, local-dwelling and migratory behaviour.

1. | Disturbance during embryogenic development There is only one study that looked into the impact of EMFs during the embryonic phase (Paoletti et al., 2023). Paoletti et al. found no changes in freezing response, nor ventilation frequency, in Scyliorhinus canicula eggs exposed to a constant EMFs levels of 4–7 μT 50 Hz AC during the entire embryogenesis. They also found no changes in stress hormones (1α-hydroxycorticosterone) levels. The authors did find a subtle change in growth rate in the second half of development. The exposed individuals were more advanced in development (smaller yolk sack, larger body size) than the control group at 18 weeks. In the study of Paoletti et al. the embryos were not followed until hatching so an influence on behaviour after hatching was not determined. The

effect on development period, size at hatching and possible developmental alterations could be stronger after longer development. The only available LOEL for AC causing a subtle effect after exposure during 27 weeks is 4 μT. To extrapolate to NOEL, taking into account the relatively short exposure and observation period we apply an extrapolation factor of 10 as is common practice in ecotoxicology, resulting in a NOEL-AC of 0.4 μT. No studies are reported to estimate a N/LOEL for DC exposure. However, it is hypothesized that the effects of DC may be more pronounced compared to 50 Hz AC (AC). This is because DC is considered to be more perceptible and similar to the bioelectric field emitted by a potential predator which causes embryonic stress (Bedore and Kajiura, 2013). We therefore adopt a preliminary NOEL of 0.4 μT for both AC and DC as a rough estimation.

2. | Behavioural changes during local-dwelling In a study by Hutchison et al., (2020a,b) Leucoraja erinacea was exposed in a field-based mesocosm study to a SPC with levels from 0.03 μT DC above the GMF and showed increased swimming distance and speed, more sharp turns and swimming closer to the seabed (Hutchison et al., 2020a). In the same study similar but stronger responses were found at higher levels up to 14 μT DC above GMF. These findings are supported by Anderson et al., (2007) who showed a conditioned response to a magnetic field target at the same minimum value of 0.03 μT DC above GMF in juvenile *Carcharhinus plumbeus*. The response increased with magnetic field strength and stronger responses were noted at 5.3 μT DC above GMF (Anderson et al., 2017). The LOEL was established at 0.03 μT DC.

The LOEL value at which a behavioural response was recorded for AC was 8 μT in another mesocosm experiment with adult *Raja clavata* and *Scyliorhinus canicula* (Gill et al., 2009). Here, for *Raja clavata* some increase in movement was seen and for Scyliorhinus canicula attraction to the SPC combined with decreased movement near the SPC was observed. At higher levels some attraction of *Cephaloscyllium isabellum* to DC was recorded at 3960 μT for DC but not for AC levels at 1430 μT (Orr, 2016). Albert et al., 2021 also worked with high exposure levels (450 μT DC) of juvenile *Raja clavata* and found a small increase in movement , which was dependent on the time of day. The same experiment with AC did not show any changes in behaviour of juvenile *Raja clavata*. None of the reviewed studies found indications for avoidance behaviour. Avoidance is only known for shark deterrent devices in which extremely high magnetic field levels are applied (i.e. 250,000 μT) (O'Connell et al., 2014a; O'Connell et al., 2014b; Smith and O'Connell, 2014). The LOEL for AC is 8 μT. There are indications of a non-S shaped dose-response curve, suggesting lower EMF levels might result in more effect then higher levels as bioelectrical signals of fish (mates, partners and predators) are much lower (Bedore and Kajiura, 2013). Extrapolation from the LOEL to a NOEL for AC is therefore set at an order of magnitude lower, at 0.8 μT AC.

3. | Interaction with migratory behaviour No studies were performed to investigate migratory responses by (benthic) elasmobranchs to EMF from SPC. Based on field observations of delayed migration in eel and salmon (Westerberg and Lagerfelt, 2008; Wyman et al.,

2018) and based on the reasoning that the benthic elasmobranchs can navigate differences in the geomagnetic field as low as 0.002–0.005 μT we assumed that the NOEL for confusion or diversion caused by migrating over SPC are expected to be around 0.005 μT. It is anticipated that disruptive effects may occur when the levels are increased by a factor of 10, placing the LOEL at 0.05 μT. As the geomagnetic field (DC) is used for migration 50 Hz AC levels are not believed to impact migration and therefore no effect, and thus no risk for AC is assumed for this endpoint.

2.5 Risk characterization and assessment

When overlaying the exposure levels presented in literature (Table 2.2) with the modelled EMF levels from the exposure quantification (Fig. 2.3) an overlap of the sensory range of benthic elasmobranchs can be observed (Fig. 2.5). This means there is reason to continue with the ERA where the exposure levels are compared with the NOELs to determine whether the risks occur, to be determined per life stage category. In case there is reason for concern, the spatial encounter risk is determined for the different life stage categories and related to the ecological traits of benthic elasmobranch species.

As the maximum magnetic fields cannot be measured, only modelled exposure levels, we used these as input for the risk assessment: max 61.3 μT DC (projected for IJmuiden Ver, 2028 onwards) and 13.9 μT for AC (current for the OWF Borssele), respectively.

The hazard quantification provided a NOEL of 0.4 μT for embryonic development for both and AC. For behavioural changes during local dwelling, 0.8 μT and 0.003 μT were adopted for AC and DC, respectively. For interaction with migratory behaviour an DC NOEL of 0.005 μT for confusion/diversion and an LOEL of 0.05 μT for disruptive effects was set.

2.5.1 Risks assessed per effect

1. | Disturbance during embryogenic development The maximum EMFs levels elasmobranch embryos are potentially continuously exposed to were 13.9 μT for AC cables and 61.3 μT for DC cables. The exposure levels are highly variable due to the changes in power transported and are likely to vary hourly (small changes) and daily (larger changes). The NOEL for impact on embryonic development is 0.4 μT for both AC and DC. The likelihood of encounter was judged as likely due to the overlap of cable routes and areas that are suitable as egg laying sites which will mean continuous exposure of egg cases when laid within the vicinity of SPCs. The NOEL is two and three orders of magnitude lower than AC and DC exposure levels respectively, which is reason for concern. While experiments are done with constant EMF levels, an extra risk lies in the constant changing EMF level as this may reduce the potential for habituation. As embryos especially react to changing EMF levels, constant adjustment might require extra energy which might disturb growth and development.

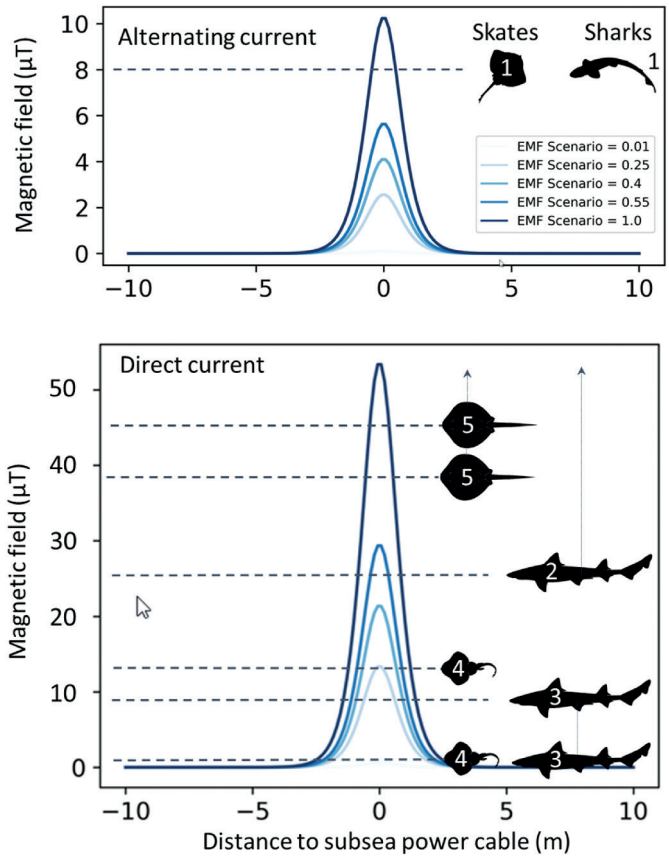

Fig. 2.5 Schematic overview showing overlap of 1) modelled magnetic field levels of alternating current (top) and direct current (bottom) subsea power cables and 2) elasmobranch responses to magnetic stimuli based on mesocosm and laboratory studies (dotted lines). The number in the depicted animals correspond with the studies: 1) Gill et al., 2009: 8 µT 2) Meyer et al., 2005: 25–100 µT 3) Anderson et al., 2007: 0.03–8.00 µT 4) Hutchison et al., 2020a,b: 0.3, 4.0 and 14 µT 5) Newton and Kajiura, 2020 38, 45, 90 µT. Note that lower magnetic field levels (nT) are not visible as the y-axis is not logarithmic, but can extend up to 120 (AC) and 250 (DC) meter from the subsea power cable, depending on cable characteristic and power levels transported.

2. | Behavioural changes during local-dwelling Both infield within the OWF and export cables, transporting the power from the transformation station to shore, can be encountered during local-dwelling by benthic elasmobranchs and might cause behavioural effects. However, the chances of encountering an SPC is largest within OWFs as the cable density is higher. In addition, the infield cables form a network like structure of cable strings connect the turbines to the transformation station. As the EMF levels of infield cables are lower than of export cables this spatial extent will be lower therefore we assumed a lower likelihood of encounter and therefore response. Specifically with the possibly non-S-shaped dose-response relationship, exposure to lower EMF levels might result in more confusion or disturbance then higher levels. Infield cables are not modelled as part of this ERA. However,

the OWEZ cable has comparable characterises to the majority of the infield cables and was used as a proxy for EMF levels. The maximum magnetic field level based on modelling was 1.8 μT. The NOEL for behavioural changes resulting in (different types of) local behaviour changes was set at 0.003 μT and 0.8 μT for DC and AC, respectively. The likelihood of encounter was judged as possible because 5.5% of the Dutch continental shelf is expected to be under influence of EMF in 2030. Most OWF and SPC routes overlap with habitat of up to 6 species of benthic elasmobranchs (Fig. 2.4). The NOEL was an order of magnitude lower than the exposure levels indicating risk of behavioural changes within OWFs. The main risk lies in long term attraction which could result in wasted energy expenditure or possibly changes in foraging and habitat use of 5.5% of the Dutch continental shelf.

3. | Interaction with migratory behaviour The maximum exposure level for migrating individuals was 61.3 μT for DC cables; specifically DC SPC interact with the geomagnetic field. The NOEL for potential confusion to migratory behaviour was set at 0.005 μT, while the possibility of exposure was classified as high as SPC routes are perpendicular to the coast (Fig. 2.4) suggesting multiple encounters when migrating over larger distances. An animal migrating from the North to the South along the Dutch coast might encounter up to 34 cables in 2030 (Table S2.1). When it is traveling longer distances in the Southern North Sea or adjacent seas it might encounter even more cables in Germany, the United Kingdom, Belgium and France. The NOEL for confusion was five orders of magnitude lower, and for disruption it was four times lower than exposure, suggesting a considerable risk and reason for concern for interaction of EMF with migratory behaviour.

2.6 Discussion

In this ERA exposure to EMF from SPC resulted in risks for three different categories of behaviour, 1) disturbance during embryogenesis, 2) behavioural changes during local-dwelling and 3) interaction with migratory behaviour. During embryonic development and migratory behaviour the risks were most pronounced. The number of available studies to base the ERA on is limited, and all those studies were based on a small sample size and/or report large individual variation (Molteno and Kennedy, 2009; Klimley, 1993a; Marcotte and Lowe, 2008; Klimley, 1993b) resulting in a low level of confidence. It is strongly recommended that the N/LOELs reported in this study should be refined. The NOEL for confusion during local dwelling was based on a hypothetically lower sensory range of (benthic) elasmobranchs used for navigation (Nyqvist et al., 2020). This level might be an under estimation of the lower sensory threshold for navigation, which may mean the actual total spatial impact zone is larger.

2.6.1 Species traits dependent risk estimation and priority for further research

In order to provide an impression of the risks from EMF exposure of benthic elasmobranchs with different life cycle traits, to facilitate determining research priorities, a risk matrix

was created to categorise risks ranging from no to high concern. This matrix was based on the probability of the species and life cycle being exposed to EMFs from SPC (y-axis) combined with the severity of the impact (x-axis) (Slabbekoorn et al., 2019; Altenbach, 1995) for the six most common benthic elasmobranchs on the Dutch Continental Shelf. The resulting risk qualification depends on the biology and life histories of different species, e.g. rays, sharks or skates, being resident or migratory, and oviparous or ovoviviparous/viviparous species (Fig. 2.6).

1. | Disturbance during embryogenic development Based on the effects of EMFs on exposed embryos or eggs in other species the severity of impact could range from low (negligible impact), medium (impact on yolk consumption and decreased size) to high (deformities and reduced swimming behaviour). For oviparous species that lay their eggs on sandy substrate such as Raja clavata it is known that nursery areas are located in shallow sheltered areas, which are also often used for the landing of SPCs. Species like Amblyraja radiata are believed to lay eggs throughout the North Sea, including deeper waters (Heessen et al., 2015). This wide distribution of eggs indicates a likelihood of overlap between SPC and egg cases. The probability of encounter can range from low to high depending on the actual overlap of cable routes and egg laying sites. *Scyliorhinus canicula* is an example of an oviparous species that uses reef like structures and benthic invertebrates to attach egg cases (Ellis et al., 2004). SPC on the Dutch Continental shelf are laid in soft sediment areas. Therefore, any exposure might be less likely but the rocks placed on cables crossings, or scour protection of turbines offer potential habitat heterogeneity which might make suitable egg deposition sites. The probability of encounter is therefore judged as low to high. The highest risk can be identified when egg laying sites and SPC routes directly overlap. This would result in continuously exposed egg cases with a potential high severity e.g. physical changes, such as deformities or changed EMF perception. Research should focus on the effects of EMFs during the complete embryogenesis of oviparous elasmobranchs. Of the two power systems used in OWF, DC systems will have a greater spatial extension owing to higher intensities. In addition, DC interacts with the GMF, whereas AC is not expected to and therefore DC research should therefore be prioritized. Conversely, AC could lead to different effects especially in relation to the varying levels (mimicking low wind and high wind days) and potential effects should therefore also be researched. Controlled laboratory experiments would be very suitable to study the effect of EMFs on embryonic development in egg cases. Following a laboratory approach, it is important to choose a model species of which egg cases can be obtained in sufficient numbers, are not classified as endangered and can be reared successfully in captivity as for example *Raja clavata* and *Scyliorhinus canicula*.

2. | Behavioural changes during local-dwelling The local-dwelling phase is not, at present, a priority risk requiring further research. None of the 6 species considered has severity of consequences deemed to be high (Fig. 2.6). Except for *Dasyatis pastinaca* and *Galeorhinus galeus*, however, it cannot be excluded that EMF exposure could be high. The unknowns in species ecology include the spatial extent of foraging behaviours and local

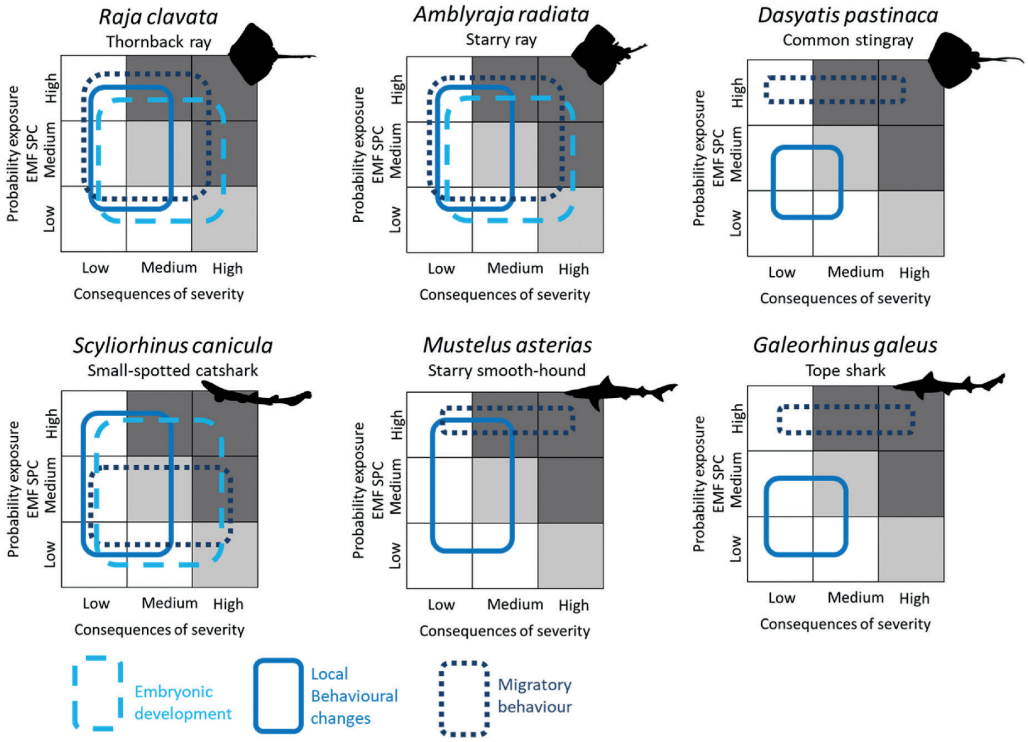

Fig. 2.6 Risk assessment matrices for species with different ecology showing the range of risk for embryonic development, local behavioural changes and migratory behaviour in relation to electromagnetic fields exposure resulting from subsea power cables. The risk is categorized ranging from no to severe concern by assessing individual probability exposure to EMFs from SPC (y-axis) versus the severity of consequence (x-axis) (following Altenback, 1996). The resulting risk range differs depending on the biology and ecology of different species groups, e.g. rays, sharks or skates, resident or migratory, and oviparous or ovoviviparous/viviparous species. The white squares indicate no risk, the lightly shaded squares indicate minor risk and the dark shaded squares indicate high risk.

habitat preference which all affect the probability of encountering SPCs. For species that forage closer to the seabed such as *Mustelus asterias* the chances of disruption in predator-prey relations are more likely than for species that (also) feed pelagically as *Galeorhinus galeus* (Heessen et al., 2015). The impact on foraging might be indirectly increased further for species that feed on prey that may also be influenced by EMF such as crustaceans (Scott et al., 2021) as is the case for *Mustelus asterias* but less so for the piscivore *Galeorhinus galeus*. The location (depth and distance to shore) of the OWF also influences the encounter rate as the habitat suitability will differ between OWFs (Fig. 2.4). For example *Raja clavata* is more frequently caught offshore and *Amblyraja radiata* has a more northly distribution range (Heessen et al., 2015). The effects described in the literature include impact on foraging behaviour and short-term attraction, which are potential reasons for concern but the consequence of severity is considered low to medium. Although there are no studies that suggests avoidance of deployed OWF SPCs, there is only anecdotal

evidence of benthic elasmobranch presence in OWFs and no information to which extent habitats within OWF are used. The main risk lies in OWFs becoming unsuitable habitat for foraging or mating due to the vast network of infield cables. Research could focus on habitat use within OWFs using for example tagging studies or eDNA methods (Brevé et al., 2020; Liu et al., 2022; Hammerschlag et al., 2011; Wearmouth and Sims, 2009; Bird et al., 2020). By establishing behaviourally focused dose-response relationships using varying levels of AC comparable to the EMF levels generated by in-field SPC, valuable insights can be gained regarding the potential disruptions in conspecifics or predator-prey relationships. It is anticipated that these relationships will be most affected, as AC fields are similar to the natural fields produced by fish (Kalmijn, 1971; Bodznick et al., 2003). Research on behavioural changes in OWFs should focus on the species which are expected to have a long(er) resident time within these parks. Studies of this nature can be done in a laboratory setting or in the field with tagging studies or Baited Remote Underwater Video systems (Hammerschlag et al., 2011; Bird et al., 2020; Griffin et al., 2016; Unsworth et al., 2014). In addition, given the potentially longer time spent with the infield cables array, habituation to varying EMF levels is also a highly relevant research route. However, Hutchison et al., 2020a,b hypothesize that elasmobranchs are less prone to habituation to SPC EMFs as these are highly variable in frequency distribution, exposure frequency and duration which makes them less predictable (Hutchison et al., 2020b). Thus, in habituation research this variability should be carefully considered in the research design.

3. | Interaction with migratory behaviour Migratory species as *Mustelus asterias* and *Galeorhinus galeus* with alongshore migration routes during spring and autumn (Heessen et al., 2015; Brevé et al., 2016; Brevé et al., 2020) have a high probability of exposure. Other more resident species, such as *Scyliorhinus canicula*, will have a lower probability of encountering DC SPC alongshore. The biggest risk to date lies in the uncertainty of the severity of impact from SPC on migratory behaviour and can consequently range from low (short duration) to high (strong deviation off course or delays). Long delays and deviation of course could result in failure to meet the migration goal in time or increased changes of predation due to a changed swimming depth. Research efforts could be focussed on reducing the uncertainties in the NOEL for the long-distance migratory species. This can be done for example done through tagging studies with a sensor that combines behavioural parameters (heart stroke volume, temperature, activity, tilt) and environmental parameters (salinity, depth) with a magnetometer. As long-term migration species are believed to use the earth magnetic field (DC), research on migration could be focused on DC cables which interact with the earth magnetic field.

The risks discussed for the different behavioural categories describe single effects. A combination of effects under varying exposure levels, at different life stages and during a range of ecological activities could increase the probability of exposure and therefore the potential severity of the effect. For example, when attraction of females near egg-laying sites is combined with impacts on embryogenesis once eggs are laid then the risks might be classified

as high. The behavioural categories described in this paper were chosen based on existing risks described in literature. Future studies could suggest different types of impact, allowing a more fine-scaled ERA with additional impact categories e.g.: 1) reproductive cycle and output; 2) feeding ecology; 3) movement patterns (resident species vs. migratory species); 4) fine-scale habitat selection (e.g. due to avoidance or deterrence); and 5) physiology to gain a more nuanced understanding of potential impacts.

2.6.2 Validity of EMF exposure modelling approach for other countries

Whilst this study has focussed on the Dutch Continental Shelf as a case study of our approach, it is applicable in all seas with OWF and SPC expansion. In particular for Belgium, United Kingdom, German and Danish North Sea OWFs, as the species distribution range for the species discussed above overlap and migration for some species occur at transboundary scales. Moreover, our approach can also be applied conceptually for species with similar ecological traits. What is important to consider is that SPC will generate different EMFs levels in other countries if regulation results in different specifications, e.g. in cable design, burial depth and frequency on which AC cables operate, all of which will influence the magnetic field. Most notably, on the Dutch Continental Shelf bundled bipolar DC cables are the norm but in many countries the positive and negative cores are laid separately, with up to 250 m distance between them. This will result in elevated magnetic fields of up to 300 μT which is six times the earth magnetic field (~50 μT on the Dutch Continental Shelf) and more than 3 times the maximum levels modelled for the Dutch situation in this study. Different cable specifications resulting in different EMFs could lead to a changed risk profile. Although these regional differences influence the level, characteristics and spatiotemporal fluctuations of EMF exposure, the modelling approach presented here can be applied in other regions as well, provided the different cable specification and regional difference are taken into consideration.

The findings from the research priorities resulting from the ERA should provide valuable insights and support for whether there is a need for the development of any required mitigation strategies or choices with respect to precautionary approaches pending upcoming studies and insights. In the case of observing an effect on embryogenesis, it is likely that rerouting the SPC would be the most suitable mitigation option, considering the localized nature of egg laying sites for benthic elasmobranchs. On the other hand, if the choice for egg-laying sites is related to habitat features associated with SPCs and OWFs this mitigation option should be reconsidered, again showing the need for dedicated research. If evidence for effects on migration is found, investigating SPC corridors (combining multiple cable routes) could be the most appropriate approach to minimize the risk of encounters (Taormina et al., 2018a).

2.6.3 Conclusion

The offshore energy transition is significant and growing across the marine environment. As such it highlights the importance of addressing the risks of EMFs from the huge expansion SPC on benthic elasmobranchs. Filling the knowledge gaps with the highest priority will either retire the risk or support policy decisions to prevent significant ecological impact through mitigation measures. As benthic elasmobranch populations are already under the influence of many anthropogenic stressors (Dulvy et al., 2021), conservation or mitigation actions focussing on reducing impacts from EMFs should be properly considered in relation to other stressors as fishing, shipping and sand mining. The ERA approach set out here is a useful step forward in understanding research priorities for EMF.

Supplementary materials

S1 Description model

The calculations presented here are carried out and visualized using a model developed based on the Biot-Savart law. The Biot-Savart law is expressed as follows:

$$\vec{\mathrm{B}}(\vec{r}) = \frac{\mu_0}{4\pi} \int_C I \frac{d\vec{l} \times \vec{r}}{\vec{r}^3}$$

The magnetic field ($\vec{\mathrm{B}}$) is dependent on the magnetic permeability (μ_0), the amount of current (I) that flows through the cable, the geometry or direction of the cable ($d\vec{l}$) and the distance to the point at which the magnetic field is computed ($d\vec{r}$). When the distance between the cable and the point at which the magnetic field is to be computed is much smaller than the cable length, then the above equation can be simplified to the following:

$$B(r) = \frac{\mu_0 I}{2\pi r}$$

The above equation shows that the magnetic field is directly proportional to current flowing through the cable and inverse proportional to the distance r. The above equation computes the magnetic field for a single cable. In case of DC and AC cables there are multiple cables with different phases that need to be accounted for. Using the method shown by the National Grid of the United Kingdom on the Electric and magnetic fields and health (EMFS) webpage, the total magnetic field at a certain point can be computed as a result of the different phases of the different cables.

Source: How to calculate the magnetic field from a three-phase circuit'. EMFS, maintained by National Grid, https://www.emfs.info/wp-content/uploads/2014/07/Howtocalculatethemagneticfieldfromathree.pdf, accessed on 11-08-2023

OWF cables	Type	Power transmission system	Voltage (kV)	Power (MW)	Number of cables	Core-to-core distance (m)	Modelled magnetic field range (μT)
OWEZ	3-phase	AC	34	108	3	0.060	0.0 - 1.8
PAWP	3-phase	AC	150	120	1	0.078	0.1 - 5.2
Luchterduinen	3-phase	AC	150	129	1	0.082	0.1 - 5.8
Gemini	3-phase	AC	220	600	2	0.100	0.1 - 11.3
Borssele*	3-phase	AC	220	700	4 (12*)	0.106	0.1 - 13.9
IJmuiden Ver**	Bundled	DC	525	2.000	3 (6*)	0.200***	0.6 - 61.3
Interconnector cables							
Norned	Bipolar Bundled (in the Dutch waters)	DC	450	700	1	0.130	0.2 - 16.4
Britned			450	1.000	1	0.119	0.2 - 21.4
CobraCable			320	700	1	0.130	0.2 - 23.0
NeuConnect			500	1.400	1	0.130***	0.3 - 29.4
VikingLink			525	1.400	1	0.130***	0.3 - 28.0

Supplementary Table 2.1
Existing interconnector and Offshore Wind Farm export cables on the Dutch Continental Shelf.
* The design strengths for Borssele are the same for the planned offshore wind parks Hollandse Kust (Zuid, Noord, West) and Ten Noorden van de Wadden and IJmuiden Ver are the same for Nederwiek.
** Cables for IJmuiden Ver are planned to be bundled depending on the technical availably of bundled 2GW cables.
*** Core-to-core distances are assumed when no public information or cable owner information was available.

Supplementary Table 2.2 Impact zone calculated based on the 5 nT zone and the length of the subsea power cable on the Dutch Continental Shelf.

Cable	Length within Dutch Continental Shelf (km)	Amount of cables	5 nT zone (m) from the centre of the cable	Affected area (km2)
Norned	57	1	64	7.3
BRITNED	101	1	73	14.7
Cobra cable	98	1	76	14.9
Neuconnect	349	1	83	57.9
Viking Link	203	1	85	34.5
IJmuiden Ver (alpha)	163	1	124	40.4
IJmuiden Ver (beta)	146	1	124	36.2
IJmuiden Ver (gamma)	152	1	124	37.7
Nederwiek (alpha)	208	1	124	51.6
Nederwiek (beta)	200	1	124	49.6
Nederwiek (gamma)	278	1	124	68.9
OWEZ	15	3	20.7	1.9
PAWP	27	1	71	3.8
Luchterduinen	25	1	74	3.7
Gemini	91	2	52	18.9
Borssele	67	4	57.5	31.1
HK(z)	42	4	57.5	19.5
HK(n)	33	2	57.5	7.7
HK(w)	64	4	57.5	29.7
TNW	82	2	57.5	19.0
Total	**2.401**	**34**	-	**549.1**



Abstract

The development of offshore wind farms (OWFs) in coastal seas presents both risks and opportunities for threatened elasmobranch populations, but their actual influence on elasmobranch presence and habitat use remains unclear. As more OWFs are planned, the lack of available space puts pressure on stakeholders to create multi-use areas as demands from fisheries, conservation and the energy sector become increasingly overlapping. Insight into interactions between these demands is needed to support policymakers in marine spatial planning and management decisions. One of the important questions is to what extent OWFs influence elasmobranch presence and habitat use. Here, we (i) ascertain elasmobranch occurrence in OWFs, (ii) determine whether elasmobranch presence varies between sampling locations, and (iii) investigate the influence of seasonality on elasmobranch presence. We collected 436 seawater samples within four OWFs and the presence of 5 different elasmobranch species (2 sharks, 3 skates) was confirmed. The overall detection probability of elasmobranchs in the four OWFs was 8.5 %. A quarterly sampling campaign over 2 years demonstrated the seasonality of Mustelus asterias

https://doi.org/10.1016/j.ocecoaman.2025.107671

3

Elasmobranchs in offshore wind farms



on the subsea power cables, which corresponded with known migratory movements of this species. Our findings confirm that sharks and skates are present in OWFs. We advise caution when introducing multi-use activities that could counteract the benefits of bottom trawling fisheries exclusion. Investigating how these threatened species use OWFs would aid policymakers in determining the (multi-use) function of OWFs in terms of EU legislative acts including the Habitat Directive, MSFD, Biodiversity Strategy 2030 and the Nature Restoration Law.

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Published in Ocean & Coastal Management | July 2025

3.1 Introduction

The rapid expansion of offshore energy production is considered necessary for advancing the renewable energy transition. In European Union waters, offshore wind capacity is planned to expand from the current ~20 GW–60 GW by 2030, and an anticipated 300 GW by 2050 (EU commission, 2024; European Court of Auditors, 2023; Wind Europe, 2024). This growth necessitates the installation of subsea power cables (SPC) to handle over 15 times the current volume of wind-generated electricity.

Almost 20 species of elasmobranchs inhabit the Greater North Sea (Heessen et al., 2015). Elasmobranchs have historical importance to fisheries and play a key role in marine ecosystems where they regulate prey populations and are prey themselves for larger pelagic and mammalian predators (Heessen et al., 2015; Heithaus et al., 2008). Anthropogenic pressures such as (by-catch in) fisheries and habitat destruction put pressure on elasmobranchs globally, including in the southern North Sea (Bom et al., 2022; Dulvy et al., 2021; Gallagher et al., 2012; Pacoureau et al., 2021; Sguotti et al., 2016). The relatively recent and rapid development of offshore wind farms (OWFs) has raised concerns about the effects of OWFs as expressed by NGO's and fisheries organisations (EMK Foundation, 2020; The North Sea Foundation, 2022), but also within regulatory frameworks aimed at protecting elasmobranchs such as OSPAR and Marine Strategy Framework Directive (MSFD) (Hermans and Schilt, 2022; OSPAR, 2008).

With a design life of over 40 years, it is important to consider the possible effects of OWFs and SPC during the operational phase. Chemical pollution, vessel movements, heat dissipation and electromagnetic fields (EMF) generated during power transport will influence elasmo branch habitat and could influence species distribution or behaviour (Copping et al., 2021; Danovaro et al., 2024; Hasselman et al., 2023; Hendon et al., 2024; Taormina et al., 2018). EMF is considered a particular risk for elasmobranchs as they are highly sensitive to naturally existing electric and magnetic cues. The effects of OWFs and SPC-induced stressors are relatively unknown but are hypothesised to range from attraction to confusion (Gill, 2009; Hermans et al., 2024; Hutchison et al., 2020; Taormina et al., 2018). The exposures occur on a relatively small spatial scale (tens to hundreds of meters). However, the potentially resulting disturbances have a large-scale longitudinal component, as export cables traverse extensive sections of the ocean seabed (hundreds of kilometres) and inter array cables within fixed bottom OWFs form an interconnected network of cables, covering areas of 200–400 km2 (Hermans et al., 2024).

Conversely, the absence of bottom trawl fisheries in OWFs strongly reduces by-catch and relative bottom rest allowing recovery of natural reef formation. These benefits might increase foraging opportunities (Pardo et al., 2023; Wright et al., 2020) and undisturbed embryonic development within sessile egg cases. Additionally, the 'reef effect' from the hard substrate used for scour protection of the turbine foundation may benefit elasmobranchs depending on species-specific habitat and dietary preferences (Degraer et al., 2020; Langhamer, 2012; Pardo et al., 2023; Werner et al., 2024; Zupan et al., 2024). Species such as cod

(Werner et al., 2024) and lobster (Thatcher et al., 2023) have already been shown to benefit from these effects, while this is yet to be demonstrated for elasmobranchs.

The rapid expansion of OWFs has significantly intensified competition for space in the already heavily utilised southern North Sea. Multi-use areas that balance the demands of fisheries, nature conservation, and the energy sector are proposed to overlap these different functions (Li and Jay, 2020; Püts et al., 2023; Stelzenmüller et al., 2022). This results in pressure being placed on the existing ban on bottom trawling in OWFs, such as those present in the Netherlands, which undermines the potential positive effects for sensitive elasmobranch populations. Conversely, it is unclear if there are effects that impact elasmobranchs' ability to utilise these OWF habitats. The lack of comprehensive knowledge regarding the impacts of OWFs on elasmobranch populations complicates policy decisions related to spatial planning and multi-use strategies, including complementary forms of fisheries. Furthermore, EU legislative acts including the Habitat Directive, MSFD, and the Biodiversity Strategy 2030 (part of the European Green Deal), (European Parliament, 1992, 2008, 2020) also face challenges in meeting their objectives due to the limited understanding of OWF impacts on elasmobranchs. In addition, the implementation of habitat restoration measures for sharks and skates is measured by the recently adopted Nature Restoration Law (item 45 Nature Restoration Law, 2024). However, it remains uncertain whether OWFs could serve as suitable habitats for monitoring this species group.

Recent studies have applied Environmental DNA (eDNA) monitoring to study the presence and biodiversity of elasmobranchs, demonstrating greater detection success compared to traditional trawling-based methods from which faster or smaller individuals can escape (Bakker et al., 2017; Cornelis et al., 2024; Dukan et al., 2024; Leurs et al., 2023; Liu et al., 2022). These studies have demonstrated that eDNA may offer a potentially low-cost, non-invasive alternative to traditional survey approaches in temperate waters and can be upscaled for routine monitoring (Miya, 2022).

Despite its potential, eDNA has hardly been used to study elasmobranch populations in fixed-bottom OWFs. Other methods, such as trawling and baited remote underwater video (BRUVs), have reported on the presence of elasmobranchs in fixed-bottom OWFs, including blonde ray *Raja brachyura*, thornback ray, *Raja clavata* and small-spotted catshark, Scyliorhinus canicula in the Arklow sandbank wind farm (Atalah et al., 2013) and Scyliorhinus stellaris in the Walney wind farm (Irish Sea) (Griffin et al., 2016). Labourgade et al. recently showed site fidelity of *S. canicula* at monopiles with scour protection in the OWF Saint Nazaire in France (Labourgade et al., 2024). In the North Sea, elasmobranchs in OWFs have been anecdotally recorded thus far. For example, Wright et al. (2020) used tagging data and GAM modelling to study if artificial structures influence fish abundance, finding that OWFs did not influence *R. clavata* abundance. The few eDNA studies in North Sea OWFs, such as Hestetun et al. (2023) and Doorenspleet et al. (2024), have shown contrasting results in detecting elasmobranchs in OWFs, particularly in *R. clavata*, and have only collected samples in summer.

The limited data on elasmobranchs in OWFs underscores the need for focused research to understand (seasonal) presence and habitat use. This data could subsequently be used to inform policy and management decisions on the role of OWFs for this pressured species group and decide on multiuse developments (Andersson and Öhman, 2010; Bergström et al., 2013; Stenberg et al., 2015; Van Hal et al., 2017; Vandendriessche et al., 2015; Wilhelmsson et al., 2006). To compare elasmobranch biodiversity and seasonality in OWFs in the southern North Sea, 436 eDNA samples were collected from four OWFs and analysed using 12S (MiFish) and COI (*Raja*-specific) metabarcoding. This study aimed to (i) ascertain elasmobranch occurrence in OWFs, (ii) determine whether elasmobranch presence varies between SPCs and other sampling locations, and (iii) investigate the influence of seasonality on elasmobranch presence.

3.2 Materials and methods

3.2.1 Sample area and sampling design

Two types of eDNA sampling campaigns were undertaken: [1] a repeated sampling campaign over two years in OWF "Borssele", and [2] inconsecutive sampling in three additional OWFs - "Gemini (ZeeEnergie)", "Luchterduinen", and "Hollandse Kust Zuid" (HK(z).

The Borssele wind farm is located approximately 25 km from the southwest Dutch coast. Sampling was conducted from the Buoy-Laying Vessel "Rotterdam" or "Terschelling" on eight consecutive occasions at ~ quarterly intervals beginning in March 2022. Nine locations were sampled, three within the OWF, three outside directly above the export cable, and three in a reference location north of the OWF (Fig. 3.1). Each location was sampled in triplicate, yielding 27 1.5 L water samples per sampling campaign and 216 samples in total. A mounted rack holding three 2.5L Niskin bottles (KC Denmark) was suspended 1 m above the seabed to collect seawater. From each Niskin bottle, 1.5 L seawater was decanted into a sterilized 2.5 L brown polypropylene bottle (Table S3.1). The mounted rack, Niskin and brown polypropylene bottles were sterilised using 1:10 dilution of household bleach:-water (<5 % chlorine). During each sampling day, a negative control sample consisting of bottled drinking water was collected. Samples were filtered within 15 min of collection, in parallel through 1.2 μM cellulose nitrate filters (Sartorius) using a vacuum pump (Rocker 400) equipped with a 3 chamber 0.5 L filtration system and stored in 1.5 ml screw cap dorfs containing 400 μL DNA/RNA shield (Zymo). Samples were stored at –20 ◦C until DNA extraction.

The other three OWF were sampled between November 2021 and July 2023 from different vessel types, mainly Crew Transfer Vessels (CTVs). The sampling design for these surveys was not aimed at collecting elasmobranch DNA or potential EMF effects, but the data were deemed suitable for use in this study. In OWF Gemini, eDNA samples within the OWF were taken above a nature enhancement area with outplaced shells and European flat oysters (*Ostrea edulis*). In OWF HK(z), samples were taken from inside monopiles, above

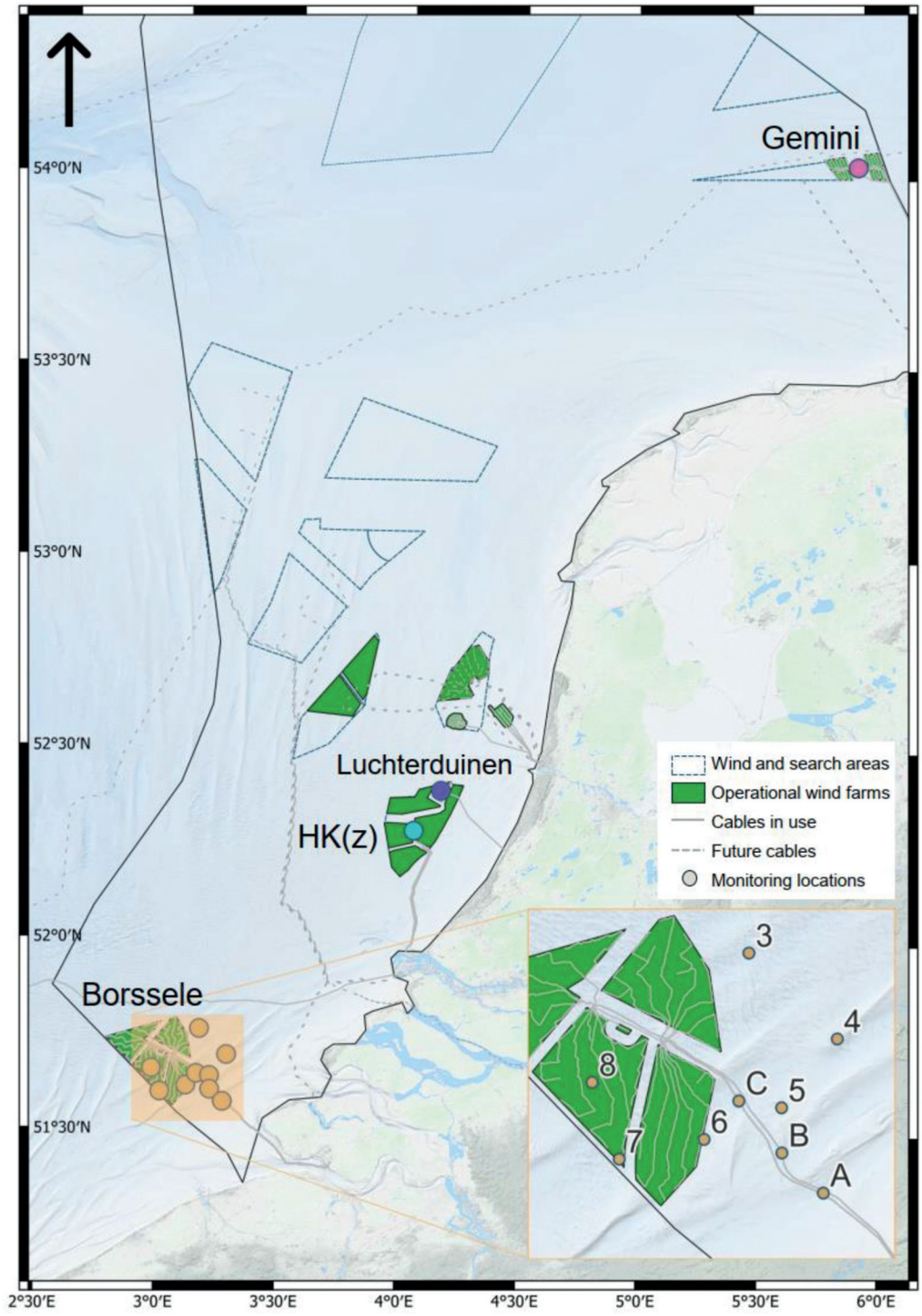

Gemini
Luchterduinen
HK(z)
Borssele
Wind and search areas
Operational wind farms
Cables in use
Future cables
Monitoring locations
54°0′N
53°30′N
53°0′N
52°30′N
52°0′N
51°30′N
2°30′E
3°0′E
3°30′E
4°0′E
4°30′E
5°0′E
5°30′E
6°0′E
3
4
8
C
5
6
B
7
A

Fig. 3.1 - on the left
Overview of the Dutch North Sea where the existing subsea power cables are indicated by the grey lines and future cables are indicated by the dotted lines. The sampling locations in the offshore wind farms (OWF, green areas) are shown with a round dot for Borssele (orange) Hollandse kust Zuid (turquoise), Luch-terduinen (purple) and Gemini (pink). This figure includes an overview of the Borssele OWF indicating the sampling locations within the OWF (6, 7 and 8), on the SPC cable (A, B, C) and outside the OWF in the reference area (3, 4, 5).

the scour protection of monopiles and at locations 50 and 200 m downstream of, or dicular to, the current from the monopiles. The samples from OWF Luchterduinen were also taken above the scour protection and in between turbines above a nature enhancement location with flat oysters. Due to the different sampling designs, the number of replicates varied per campaign (Table S3.1). Other methods were comparable, although samples were taken using single 5L Niskin bottles, so replicates were taken one by one after each other. Filtering took place within 8 h and not in parallel. Overall, 14 campaigns were organised during which a total of 220 samples were taken within the OWFs, but lacking a regular interval.

3.2.2 DNA extraction

DNA extractions were performed using the DNeasy Blood & Tissue kit (Qiagen, Germany), following the manufacturer's tissue sample protocol with some modifications. The modified protocol added 20 µL proteinase K to the Eppendorf tubes containing the eDNA filter and 400 µL DNA/RNA shield. Samples were vortexed and incubated at 56 °C for 1–3 h. Additionally, the volume of AL buffer and >99.8 % ethanol were doubled to 400 µL to maintain equal buffer concentrations. The spin column stage was repeated twice to process the entire volume. Finally, DNA was eluted in 50 µL AE buffer with an incubation time of 5 min. DNA quality and quantity were assessed using a DS-11 spectrophotometer (DeNovix, USA).

3.2.3 Metabarcoding

MiFish U/E primers from Miya et al. (2015), targeting the 12S rRNA gene, were modified to increase the amplification efficiency of the nine most common elasmobranch species in the Dutch North Sea (Table S3.2). This resulted in the adapted forward primer MiFish_U/E_V2_FW (5′ - GTYGGTHAAWCTCGTGCCAGC - 3′) and the adapted reverse primer MiFish_U/E_V2_REV (5′ -ATAGTRGGGTATCTAATCCTAGTTT - 3′).

Specific primers for the *Raja* genus were designed to accurately identify which *Raja* species were detected in the eDNA samples using reference sequences of *Raja* species known to occur in the North Sea (Table S3.2). Specifically, *Raja brachyura*, *Raja clavata* and *Raja montagui* (spotted ray) were used by targeting a ~270 bp fragment of the COI gene, specificity of the primers was tested using non-target elasmobranch species

(Table S3.2). Primers were designed using Geneious Prime (V 11.0.20.1) which resulted in the forward primer Raja_COIF117 (5′ - AGAACTAAGTCAACCCGGGA - 3′) and the reverse primer Raja_COIR304 (5′ - GRACAGGTTGRACAGTCTAC- 3′).

For certain samples (S1), no DNA was amplified using the MiFish primers. However, amplification of longer DNA fragments was achieved using primers targeting the 16S ribosomal gene (~519 bp) (Craeymeersch et al., 2019) or a ~2000 bp fragment spanning the adjacent ribosomal genes 12S and 16S (Doorenspleet et al., 2024). Detailed methodologies for these primers can be found in the respective studies.

Both MiFish primer sets and the *Raja*-genus primers were appended at the 5′ end with an Oxford Nanopore Technologies (ONT) tag so that samples could be multiplexed during ONT sequencing using PCR-based barcoding.

All PCR amplification was performed using 2 ×Phire Tissue Direct PCR Master Mix (ThermoFisher Scientific, USA). The total PCR reaction volume was 10 µL, consisting of 5 µL 2x Phire Tissue Direct PCR Master Mix, 0.1 µL of each primer (10 µM), 3.8 or 4.3 µL nuclease-free water (NFW) and either 1 µL or 0.5 µL undiluted eDNA or 1 µL 10x diluted eDNA template, depending on successful PCR amplification. PCR reactions were run in duplicate. DNA extraction controls and PCR controls were included in each PCR. The 12S rRNA PCR program was as follows: 98 ◦C for 3 min, followed by 35 cycles of 98 ◦C for 10 s, 59 ◦C for 10 s, 72 ◦C for 10 s, and a final extension at 72 ◦C for 3 min. All PCR products were evaluated on a 1.5 % agarose gel via gel electrophoresis before pooling successful replicates.

The PCR amplification for the COI *Raja*-genus specific primer set was performed nearly identical to the MiFish primer set, with duplicate reactions of 0.5 µL undiluted DNA template as input. The COI PCR gram was as follows: 98 ◦C for 3 min, followed by 40 cycles of 98 ◦C for 10 s, 58 ◦C for 10 s, 72 ◦C for 10 s, and a final extension at 72 ◦C for 3 min. Following amplification, PCR products were visualised on a 1 % agarose gel via gel electrophoresis and successful duplicate reactions were pooled and taken forward to library preparation.

3.2.4 Library preparation and ONT sequencing

The 96 PCR barcoding kit (EXP-PBC096) (Oxford Nanopore Technologies, UK) was used to barcode all amplicons. PCR barcoding and library preparation was performed following the same method as described in De Leeuw et al. (2024) for most sequencing runs. The only difference in later sequencing runs performed was that for the last 4 sampling campaigns at Borssele (summer 2023, autumn 2023, winter 2023, spring 2024), the samples were pooled on ice instead of at room temperature due to barcode hopping (mis-assignment of barcodes and samples). Barcode hopping correction was conducted for the earlier samples (all the other OWF samples and the first 4 Borssele samples which had been pooled at room temperature).

3.2.5 Bioinformatics and taxonomic assignment

All fast5 files were basecalled in super accuracy mode to fastq files, using ONT guppy basecalling software version 6.5.7 and config file: dna_r10.4.1_e8.2_400bps_5khz_sup.cfg. Processing, filtering and analysis of the basecalled reads was performed using the Decona pipeline as described in Doorenspleet et al. (2024). To run Decona for the MiFish 12S rRNA amplicon the following command was used: decona -T 28 -f -q 10 -l 150 -m 240 -g "GTYGGTHAAWCTCGTGCCAGC; max_error_rate =0.1; min_overlap =17 ... CAAACTAGGATTAGATACCCYACTAT; max_error_rate =0.1; min_overlap =21" -c 0.96 -n 10 -r -o 1 -R 500 -k 6 -M -b/path/nt_euk.

The.pod5 files generated for the *Raja* spp. primer set were basecalled using dorado version 7.4.13 to super accuracy mode using the config file dna_r10.4.1_e8.2_400bps_sup@v4.3.0.cfg. Then, the resulting reads were processed by Decona (v1.5) using the following command: decona -T 28 -f -l 200 -m 240 -g "AGAACTAAGTCAACCCGGGA; max_error_rate =0.1; min_overlap =15 ... GTAGACTGTYCAACCTGTYC; max_error_rate =0.1; min_overlap =15" -c 0.99 -n 100 -o 1 -r -k 6 -M -b/path/ nt_euk. The reference database used for classification through BLAST (integrated in the Decona pipeline) consisted of the complete eukaryotic nucleotide database downloaded from NCBI (downloaded 11-04-2024). Decona's output was further analysed using R (v4.3.0) in R studio (v2022.02.3), making use of the tidyr (v1.3.0) and dplyr (v1.1.2) packages. Percentage identity for species identification was set to>99 % in order to be taken for final data analysis. Tag leakage was observed in some sequencing runs, therefore a 0.6 % tag leakage read correction was performed as described in De Leeuw et al. (2024).

The methods outlined were specifically applied to OWF Borssele. For the other OWFs, slight variations in methodology occurred due to earlier data collection. Most notably, the PCR reactions for the Borssele samples were performed in triplicate biological replicates, and duplicate technical replicates, whereas triplicate PCR replicates and one to nine

logical replicates were used for the other OWFs. Samples from HK(z), Luchterduinen, and Gemini were processed using the original MiFish U/ E primers from Miya et al. (2015). Earlier versions of Decona and the nucleotide database targeting elasmobranch species were used for these samples. These methodological differences are not expected to influence the overall results of the analysis.

The MiFish U/E primers could not differentiate sufficiently between *Raja* spp. therefore, *Raja*-specific COI primers were used on these eDNA samples. Amplification success was limited, with eight of the eighteen eDNA samples showing a positive target amplification using gel electrophoresis. All eight samples were sequenced, but after the matics pipeline only four resulted in the detection of one or more *Raja* spp. In two instances, the initial detection of R. clavata (MiFish) and R. miraletus (18S) was reduced to just *R. clavata*. The other two instances confirmed the initially detected species of *R. clavata*, as *R. montagui* and *R. brachyura*, respectively.

Descriptive statistics such as the number of detections, mean ± standard deviation and percentages were used to determine the detection rate and the seasonality of *Mustelus asterias*. Months were described as seasons based on the meteorological seasons for the northern sphere, where March, April and May are considered spring, June, July and August are summer, September, October, November are autumn and December, January and February are winter.

3.3 Results

Using the adapted MiFish U/E primers (Miya et al., 2015) the detection rate of elasmobranch species across all samples was 8.5 % of the total 436 samples. *M. asterias* was the only elasmobranch detected in 12 out of 216 samples at the OWF Borssele, predominantly in autumn and spring (Fig. 3.2). At OWF Gemini, samples in which *R. clavata* was detected were collected predominantly in the autumn (Fig. 3.2). At OWF Hk(z) *Cetorhinus maximus* (basking shark) eDNA was abundantly detected but only seen in winter 2021. At OWF Luchterduinen, only spring (May) was sampled, and *R. clavata* and *R. montagui* were detected. The most common elasmobranch species across the four OWFs was *R. clavata*,

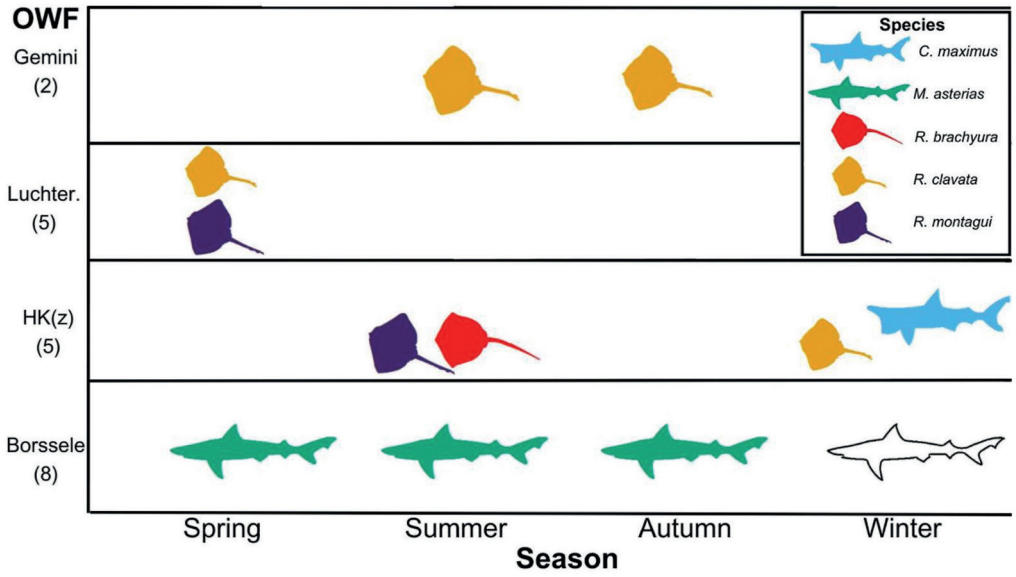


Fig. 3.2 Presence of elasmobranch species for each offshore wind farm (OWF) (from north to south) across the four seasons. The coloured icons represent species: *Cetorhinus maximus* (light blue), *Mustelus asterias* (green), *Raja brachyura* (red), *Raja montagui* (dark blue), and *Raja clavata* (orange). The sampling effort (# of campaigns indicated in brackets) differed for each OWF. The outline of *M. asterias* indicates that OWF Borssele was sampled in the winter season, but no elasmo-branch DNA was found.

detected in 3 of the 4 OWFs, recorded in 57.1 % of the samples in OWF Gemini, 2.1 % of the samples in OWF HK(z) and 1.6 % in OWF Luchterduinen, showing a high variability in detection rate across the OWFs. The rarest elasmobranch was *R. montagui*, detected only once (1.6 %) in OWF Luchterduinen. In OWF Gemini, only *R. clavata* was found (Table 3.1), but the sampling effort was low (n = 14) compared to the other OWFs. All three skates were detected in OWF Hk(z) samples (Table 3.1), with *C. maximus* being the only shark species, but also the most detected species (6.9 %). It's important to note that sampling frequency varied across the different OWFs (Table S3.1), potentially skewing the data as the rate of encountering an elasmobranch differs from a well-balanced sampling design. In addition, only sampling campaigns of OWFs with at least one detection were included in the dataset.
OWF Borssele was sampled every season in 2022 and 2023; therefore, the seasonality of *M. asterias* could be determined. Using adapted MiFish U/E primers, *M. asterias* was most often found above the SPC, detected in four of the eight seasons sampled (Fig. 3.3). By comparison, *M. asterias* was only found in summer within the OWF and at the reference site. The seasonality observed in the SPC samples is confirmed in Brevé et al. (2016) as a known migration route of *M. asterias*.

3.4 Discussion

Five different species of elasmobranchs were found in the four operational OWFs in the Dutch North Sea in different seasons using eDNA. The most frequently detected species was *Mustelus asterias* across the four OWFs while the rarest species was *Raja montagui*. The overall detection rate of elasmobranchs in OWFs was 8.5%, although this is biased as only OWF data with at least one detection were included in the dataset (with exception to OWF Borssele). The two-year quarterly sampling campaign in OWF Borssele demonstrated the seasonality of *M. asterias*, which was more frequently detected above an SPC rather than in the OWF. However, the overall detection rate of *M. asterias* was still less than 10% in the SPC samples.

3.4.1 Elasmobranch presence and habitat use

Our data reveals the presence of at least five different elasmobranch species within OWFs across various seasons in the southern North Sea. These findings suggest that any potential stressors associated with OWFs are either not acting directly enough or are not strong enough to cause large-scale deterrence for these species. These findings are corroborated by research in the Irish Sea and the French Atlantic coast, where similar elasmobranch species e.g. *Raja brachyura*, *Raja clavata*, *Scyliorhinus canicula* and *Scyliorhinus stellaris* were found within OWFs in summer using different techniques e.g. trawling fisheries, tagging and stereo BRUVs (Atalah et al., 2013; Griffin et al., 2016; Labourgade et al., 2024). Conversely, a GAM modelling study based on tagging data showed that *R. clavata* were absent

from OWFs, favouring shipwrecks (Wright et al., 2020). The difference with our findings may be due to the relatively few, small and young OWFs at the time of the data collection by Wright et al. (1999–2002) described in Wright et al. (2020), when reef habitats in OWFs were developing or construction was still ongoing, causing disturbances. Our results confirm the presence of elasmobranch in OWFs. The next step is to study how elasmobranchs use OWF habitats and whether the EMF around SPC will induce subtle or long-term effects.

The presence of *M. asterias* DNA in spring to autumn in both OWF and SPC Borssele (Fig. 3.3) coincides with the seasonal migration of this species (Brevé et al., 2016, 2020). These data suggest that OWFs do not hamper migration for this species. In December, *C. maximus* DNA was found at several sampling locations in OWF Hk(z). Being an opportunistic filter-feeding elasmobranch, it is expected to be in the southern North Sea in the summer months for feeding (Austin et al., 2019; Cotton et al., 2005; Skomal et al., 2004; Witt et al., 2012). Tagging data shows *C. maximus* has an optimal temperature preference of 13 °C–20 °C (Skomal et al., 2004) and spends most of the winter months in warmer waters (Braun et al., 2018). However, studies show large individual differences in winter migration patterns (Braun et al., 2018) and *C. maximus* are regionally endothermic, producing and retaining heat in only specific parts of their bodies, which may enable them to exploit zooplankton in colder conditions (Dolton et al., 2023). In addition, citizen science has confirmed infrequent but yearly observations in winter in the last decade, indicating a consistent presence (Observation.org, 2024). Although, based on literature, it is reasonably possible that an individual was present in the OWF, it could be that the

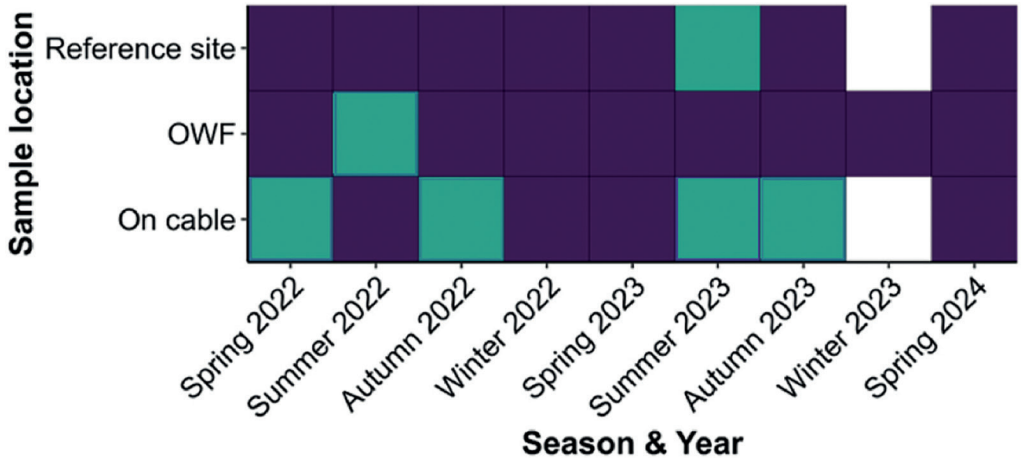


Fig. 3.3 Seasonal and spatial variation in eDNA detections of M. asterias shown as presence (green), absence (purple) or no data (white) at the Borssele offshore wind farm. Note that there were eight sampling campaigns, but due to weather constraints, the winter 2023 campaign stretched into the spring 2024 season.

DNA found originated from a dead individual transported by currents, or was carried along following a ship collision, from more southern regions. The most common skate species found was *R. clavata*, which coincides with the recent reports of a recovering population (Sguotti et al., 2016; Staeudle et al., 2024). We can only speculate on what the habitat is used for as the species reproduces all year (Saglam and Ak, 2012) and has shown partial migration movements (Hunter et al., 2005; Kraft et al., 2024; Sguotti et al., 2016). Possible behaviour of *R. clavata* in OWFs could include foraging and reproduction or other life history traits, as suggested by a tagging study for another elasmobranch species, *Scyliorhinus canicula* (Labourgade et al., 2024). *R. brachyura* and *R. montagui* were also observed in our study, but less frequently and only in summer and autumn. Tagging individuals with acoustic transmitters in combination with a receiver array would provide more information about the habitat use of elasmobranchs in OWFs (Kraft et al., 2024; Labourgade et al., 2024, 2024, 2024; Papadopoulo et al., 2023). Using BRUVs, unbaited camera systems, or high resolution acoustic cameras could provide additional information, depending on the experimental set-up, to explore small-scale behaviour of elasmobranchs as interaction with prey and conspecifics or residence time (Griffin et al., 2016; Unsworth et al., 2014).

Over the two years of sample collection in and around the Borssele OWF, we observed a higher *M. asterias* presence on the export SPC (eight detections) as opposed to inside the OWF (one detection) and the reference sites (three detections) (Fig. 3.3). This could be attributed to the SPC acting as an attractant, similar to the aggregation behaviour of the skate *Raja rhina* as shown in anecdotal evidence Barry et al. (2008)or exploratory/foraging behaviour as shown in *Leucoraja erinacea* (Hutchison et al., 2020). Alternatively, (activities or infield cables in) the OWF may have acted as a deterrent during migrations from the north toward the delta area, or maybe it was just the preferred route. Using archival tags with a magnetometer and overlapping the data with SPC locations could help further the understanding of migratory behaviour in relation to SPC.

3.4.2 Suitability of eDNA as a monitoring tool in OWFs

Overall, relatively few elasmobranch species [5] were detected in all four OWFs with a relatively low read count (Table S3.1). Of the four shark (*M. asterias, Squalus acanthias, Galeorhinus galeus, S. canicula*), two skates (*R. clavata, Raja montaqui*) and one ray (*Dasyatis pastinaca*) species regularly observed in the North Sea (Heessen et al., 2015), two shark and both skate species were observed in the present dataset but in low numbers. The low detection rate can be explained by the generally low abundance and biomass of elasmobranchs in the North Sea (Heessen et al., 2015; Sguotti et al., 2016). Detection rates varied significantly across OWFs and specific sampling campaigns, ranging from 0.6 % to 78.6 %, indicating a degree of randomness. The lower sampling rates of *R. brachyura* (0.6 %) and *R. montagui* (1.6–1.8 %) are in accordance with the low read count of elasmobranch DNA observed in the Belgian North Sea (0.5 %), in comparable conditions. The low elasmobranch diversity is especially pronounced in the OWF Borssele, where only *M. asterias* was found, despite

OWF	# Sampling campaigns	Total # samples	Species					Total elasmobranch samples
			C. maximus	*M. asterias*	*R. brachyura*	*R. clavata*	*R. montagui*	
Gemini	2	14	–	–	–	8 (57.1 %)	–	8
Luchter.	5	62	–	–	–	1 (1.6 %)	1 (1.6 %)	2
HK(z)	5	144	10 (6.9 %)	–	1 (0.7 %)	3 (2.1 %)	1 (0.7 %)	15
Borssele	8	216	–	12 (5.6 %)	–	–	–	12
Total	20	436	10	12	1	12	2	**37 (8.5 %)**

Table 3.1 Detection rates, calculated as % from the overall sampling effort of elasmobranch species for each offshore wind farm (OWF).

the two-year monitoring effort. This corresponds with the single species count observed with bottom trawl surveys on the OWF site prior to commissioning (Hermans et al., 2024). These findings suggest that the habitat of the OWF Borssele may be less suitable for elasmobranchs. While other elasmobranch species were observed in the OWFs HK(z), Luchterduinen, and Gemini, sampling was performed on an opportunistic and intermittent basis, so the detection rate cannot be put in a temporal perspective and may have underestimated the species diversity. For example, *Scyliorhinus canicula* was not detected in any sample, despite using genus-specific primers. However, it is frequently reported in the Dutch North Sea (Heessen et al., 2015; Kingma and Walker, 2021) and we would have expected a detection in our samples. The species has been confirmed in OWFs, showing site fidelity to monopiles on sandy substrates with scour protection (Labourgade et al., 2024) and was reported in five out of seven monitoring stations in the Wadden Sea (Tulp et al., 2022). Studies on the presence of *S. canicula* in the southern North Sea are limited, how-ever, the species was omitted from the North Sea endangered species list due to its frequency in occurrence (Bos et al., 2020). This is further congruent with the Dutch elasmobranch association report which lists *S. canicula* as "least concern" (Kingma and Walker, 2021). It is possible that their patchy distribution, together with the limited sampling efforts, has resulted in the species eluding detection in our samples.

Frequent and long-term sampling Before-After-Control-Impact (BACI) studies of OWF sites (Methratta, 2021; Stenberg et al., 2015), would greatly improve insights into spatial and temporal movements of elasmobranchs. In future research, eDNA may be used to estimate the abundance of species, or environmental RNA (eRNA) could be used for routine monitoring and may be able to provide a more accurate representation of recent biodiversity in OWFs because eRNA degrades faster compared to eDNA (Giroux et al., 2022; Marshall et al., 2021; Yates et al., 2021). In addition, using complementary techniques, such as BRUVs, or data storage tags, could improve the detection rate of target species and further our understanding of elasmobranch behaviour in OWFs.

While eDNA has proven itself a valid biodiversity monitoring technique for elasmobranchs (Bakker et al., 2017; Cornelis et al., 2024; Dukan et al., 2024; Leurs et al., 2023; Liu et al., 2022), eDNA can be transported by currents and influenced by environmental factors (Blackman et al., 2024). In the present study, elasmobranchs were frequently detected in only one biological replicate out of two or three (Table S3.1), emphasising the importance of collecting sample replicates to increase the likelihood of target detection in dynamic environments such as the North Sea (Klymus et al., 2020). The accuracy of target detection depends on, but is not limited to, the gene region of interest, environmental factors (e.g. water currents), the source of eDNA (e.g. faeces, skin, mucus etc), the time taken between sample collection and the accuracy of the water sampling from the location of interest (Barnes et al., 2014; Collins et al., 2018; Holman et al., 2022; Rodriguez-Ezpeleta et al., 2021). For example, at the SPC locations, the area of interest is relatively narrow (<200m), due to the limited spatial effects of the cable (Hermans et al., 2024). The accuracy of water collection using a Niskin is also limited, as the exact depth and

location of the bottle cannot be verified underwater, especially when sampling during high currents (>1 m/s), which are often present in the Borssele offshore area. Depending on the local environmental conditions, the optimal water collection approach should be optimised and validated in future research as the behaviour and decay of eDNA in the North Sea is currently unknown. Remotely Operated Vehicles (ROVs) equipped with eDNA collection equipment and equipment to localise the SPC under water could visually verify the eDNA sampling location underwater, and mesocosm studies could be designed to understand eDNA behaviour in turbid marine environments.

3.4.3 Future of elasmobranchs in OWFs

The seasonality of *M. asterias* in OWF Borssele presented in this study reflects known migratory periods (Brevé et al., 2016, 2020). This suggests that *M. asterias* is, at minimum, using the habitat in OWFs as a migration corridor. However, it is unclear at this stage whether the "reef effect" is occurring and if elasmobranchs are using the OWF habitats for other functions such as mating, nurseries or foraging. Importantly, our data suggest that the detected elasmobranch species were not strongly deterred by the OWF cables or other possible stressors associated with OWFs, such as vessel traffic. The longer-term broad-scale effects of OWFs, such as attraction and disorientation by EMF or the impacts of chemical pollution, cannot be assessed by the current dataset. Therefore, continued research is essential to determine whether OWFs provide additional habitat opportunities such as foraging, egg-laying and development or nursery areas.

Insight into elasmobranch habitat use in OWFs is essential to understanding how these habitats could complement conservation efforts. Multi-use areas could provide an answer to spatial planning challenges, but care should be taken when allowing bottom trawling in OWFs, as the benefits of by-catch reduction and seafloor integrity will be lost. Our findings could be used to inform several legislative tools in the marine domain. Firstly, environmental impact assessments (EIAs) on the effects of OWFs on elasmobranchs can be supported, which are required for permits for offshore developments under European Union Directive (European Union, 2014). Secondly, our findings play a small role in exploring potential effects of EMF that can put pressure on the marine environment, as is described in the MSFD, descriptor 11 'Energy' (Annex I, European Parliament, 2008). Marine Spatial Planning could benefit from understanding the role OWFs play as a possible refuge for threatened elasmobranch species. For example, the possibility to apply habitat restoration measures for sharks and rays, as described in the Nature Restoration Act, in OWFs. Lastly, our findings befit the understanding needed for the OSPAR framework, which aims to keep the seas biologically diverse, and identify and mitigate the impacts of human activities and protect the marine environment in Europe.

3.5 Conclusion

This study confirms that elasmobranch use OWFs as a habitat, and further research is essential to investigate the behaviour and the purpose of habitat use by elasmobranchs in and around OWFs and SPCs. To support this vulnerable species group, caution is needed when introducing multi-use activities that could counteract the benefits of reduced bycatch, bottom rest, or the reef effect. Future studies should integrate ROV eDNA collection, BRUV, or data storage tagging to enhance detection and gain deeper insights into elasmobranch behaviour in OWFs.

Supplementary materials

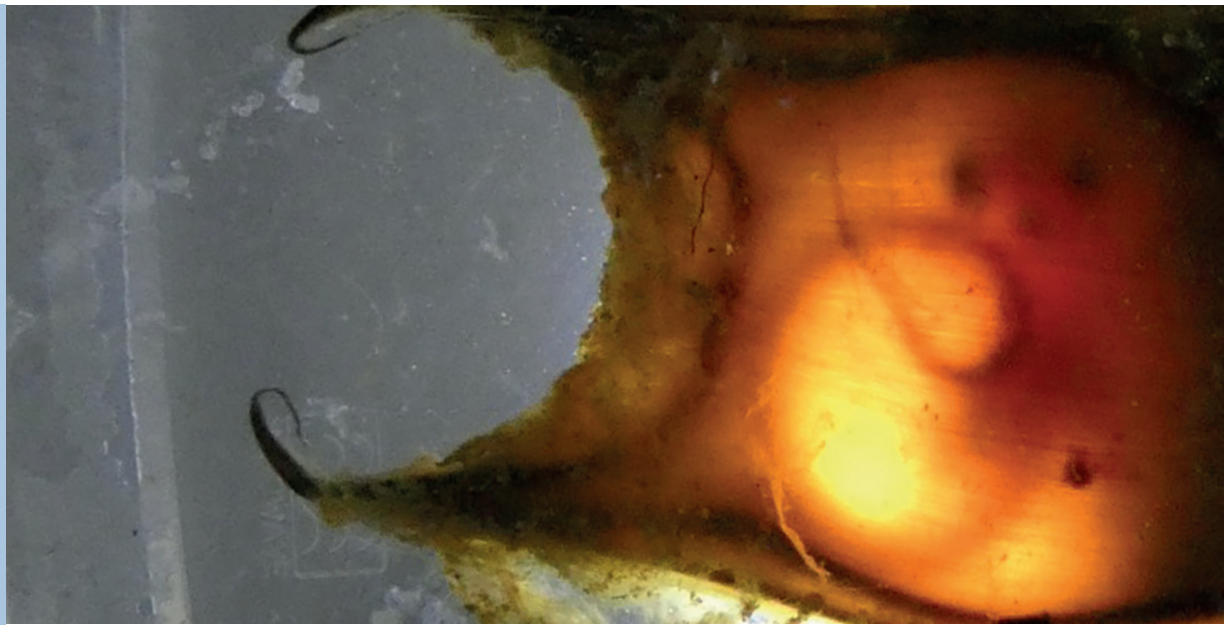
Table S3.1 - on page 72-73
Overview of all eDNA sampling data containing elasmobranch DNA collected in four Offshore Wind Farms during 2021-2023. The total read count given shows the read number after all Decona filtering and removal of microbial DNA, effectively only showing vertebrate reads. The majority of the samples were amplified using an adapted version of the Mifish primers (Miya et al., 2015) (no symbol), two samples with ~2000 bp fragment spanning the adjacent ribosomal genes 12S and 16S (Doorenspleet et al., 2024) (indicated by *) and three targeting the 16S mitochondrial region (Craeymeersch et al., 2019) (indicated by **).

OWF	Location	Sample ID	Species	Sample Date	Biological replicates	Sp. Read Count	Total Read Count
Gemini	OWF	GEM_1	*R. clavata*	16-11-2021	Single	668	16.316
Gemini	OWF	GEM_2	*R. clavata*	16-11-2021	Duplicate	1078	25.839
Gemini	OWF	GEM_3	*R. clavata*	16-11-2021	Duplicate	544	37.770
Gemini	OWF	GEM_4	*R. clavata*	16-11-2021	Single	448	17.098
Gemini	OWF	GEM_6	*R. clavata*	16-11-2021	Duplicate	297	28683*
Gemini	OWF	GEM_7	*R. clavata*	16-11-2021	Duplicate	659	32.678
Gemini	OWF	G1_GEM_rif_1	*R. clavata*	28-07-2023	Triplicate	45	7.027
Gemini	OWF	R3_GEM_ref_3	*R. clavata*	28-07-2023	Triplicate	48	2.972
Luchterduinen	OWF	LUD_10A	*R. clavata*	08-05-2023	Duplicate	52	2.033
Luchterduinen	OWF	LUD_11A	*R. montagui*	08-05-2023	Duplicate	13	6.683
HK(z)	OWF	VFM3A_8	*R. clavata*	13-12-2021	Sextuple	66	5146*
HK(z)	OWF	VFM3B_1	*C. maximus*	17-12-2021	Duplicate	6196	49.166**
HK(z)	OWF	VFM3B_11	*C. maximus*	17-12-2021	Nonuple	1899	15.028**
HK(z)	OWF	VFM3B_12	*C. maximus*	17-12-2021	Nonuple	164	38.873
HK(z)	OWF	VFM3B_14	*C. maximus*	17-12-2021	Nonuple	504	62.400
HK(z)	OWF	VFM3B_15	*C. maximus*	17-12-2021	Nonuple	63	4.124
HK(z)	OWF	VFM3B_15	*R. clavata*	17-12-2021	Nonuple	88	27.192
HK(z)	OWF	VFM3B_17	*R. clavata*	17-12-2021	Nonuple	850	44.001
HK(z)	OWF	VFM3B_3	*C. maximus*	17-12-2021	Sextuple	710	10.215**
HK(z)	OWF	VFM3B_5	*C. maximus*	17-12-2021	Sextuple	509	84.171

OWF	Location	Sample ID	Species	Sample Date	Biological replicates	Sp. Read Count	Total Read Count
HK(z)	OWF	VFM3B_7	*C. maximus*	17-12-2021	Sextuple	41	33.416
HK(z)	OWF	VFM3B_8	*C. maximus*	17-12-2021	Sextuple	877	51.611
HK(z)	OWF	VFM3B_9	*C. maximus*	17-12-2021	Nonuple	581	44.675
HK(z)	OWF	B1B	*R. montagui*	04-06-2022	Triplicate	249	63.340
HK(z)	OWF	B1B	*R. brachyura*	04-06-2022	Triplicate	113	63.340
Borssele	OWF	8A	*M. asterias*	24-08-2022	Triplicate	229	7.924
Borssele	SPC	K1A	*M. asterias*	23-08-2022	Triplicate	275	12.803
Borssele	SPC	K1A	*M. asterias*	31-05-2022	Triplicate	102	18.233
Borssele	SPC	K1B	*M. asterias*	31-05-2022	Triplicate	698	29.362
Borssele	SPC	K2C	*M. asterias*	15-11-2022	Triplicate	565	26.290
Borssele	SPC	K3C	*M. asterias*	24-08-2022	Triplicate	66	21.052
Borssele	Reference	5C	*M. asterias*	16-08-2023	Triplicate	363	9.459
Borssele	SPC	K1C	*M. asterias*	14-08-2023	Triplicate	122	9.949
Borssele	Reference	5C	*M. asterias*	16-08-2023	Triplicate	363	9.459
Borssele	SPC	K1B	*M. asterias*	16-10-2023	Triplicate	20	2.232
Borssele	SPC	K1C	*M. asterias*	16-10-2023	Triplicate	146	5.584
Borssele	Reference	3A	*M. asterias*	15-08-2024	Triplicate	814	11.781

Table S3.2 Overview of elasmobranch species that can be potentially amplified and have a 100% match with the used MiFish_U/E_V2 primer adapted from Miya et al., (2015), targeting the 12S rRNA gene (elasmobranchs with a known presence in the North Sea are listed). Species used to design and test the specificity of the *Raja*-genus primers, targeting ~270bp of the COI gene are indicated in bold. The sharks were used as a control to ensure no sharks were amplified.

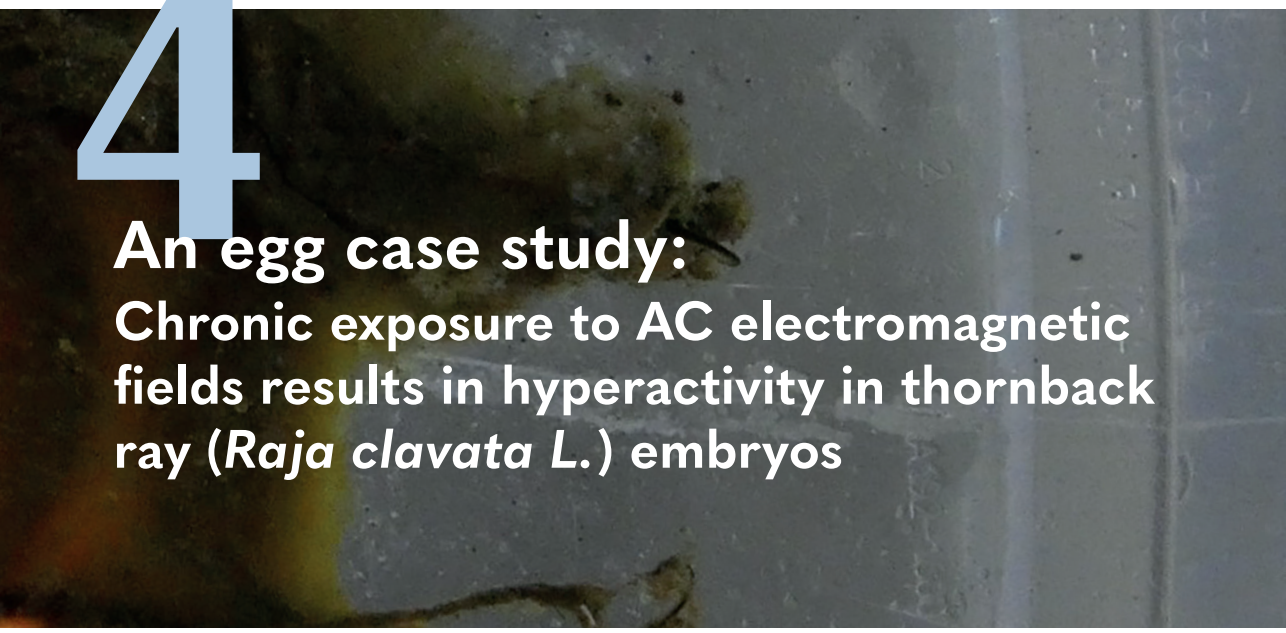
Sharks		**Rays**	
Scientific name	**English name**	**Scientific name**	**English name**
Alopias vulpinus	Common thresher	Amblyraja radiata	Starry ray
Cetorhinus maximus	Basking shark	Dasyatis pastinaca	Common stingray
Lamna nasus	Porbeagle	**Dipturus batis**	**Common/ blue skate**
Mustelus asterias	**Starry smooth hound**	Leucoraja naevus	Cuckoo ray
Mustelus mustelus	Smooth hound	**Raja brachyura**	**Blonde ray**
Scyliorhinus canicula	**Lesser spotted dogfish**	**Raja clavata**	**Thornback ray**
Scyliorhinus stellaris	Nursehound	**Raja montagui**	**Spotted ray**
Somniosus microcephalus	Greenland shark	Raja undulata	Undulate ray
Squalus acanthias	Picked dogfish	Torpedo marmorata	Marbled electric ray
Squatina squatina	**Angelshark**		
Galeorhinus galeus*	**Tope shark**		



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 behavioural 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.

https://doi.org/10.1016/j.marenvres.2025.107151



4

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

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.

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Published in Marine Environmental Research | August 2025

4.1 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. (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 branch 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 *Scylio rhinus 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.

4.2 Materials and methods

4.2.1 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-tagged 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.

4.2.2 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 O2 concentration 8.2 ±0.4 mg/L sd) was kept in a tempera-

ture-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.

4.2.3 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) 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. 4.1 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 S4.1). 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,

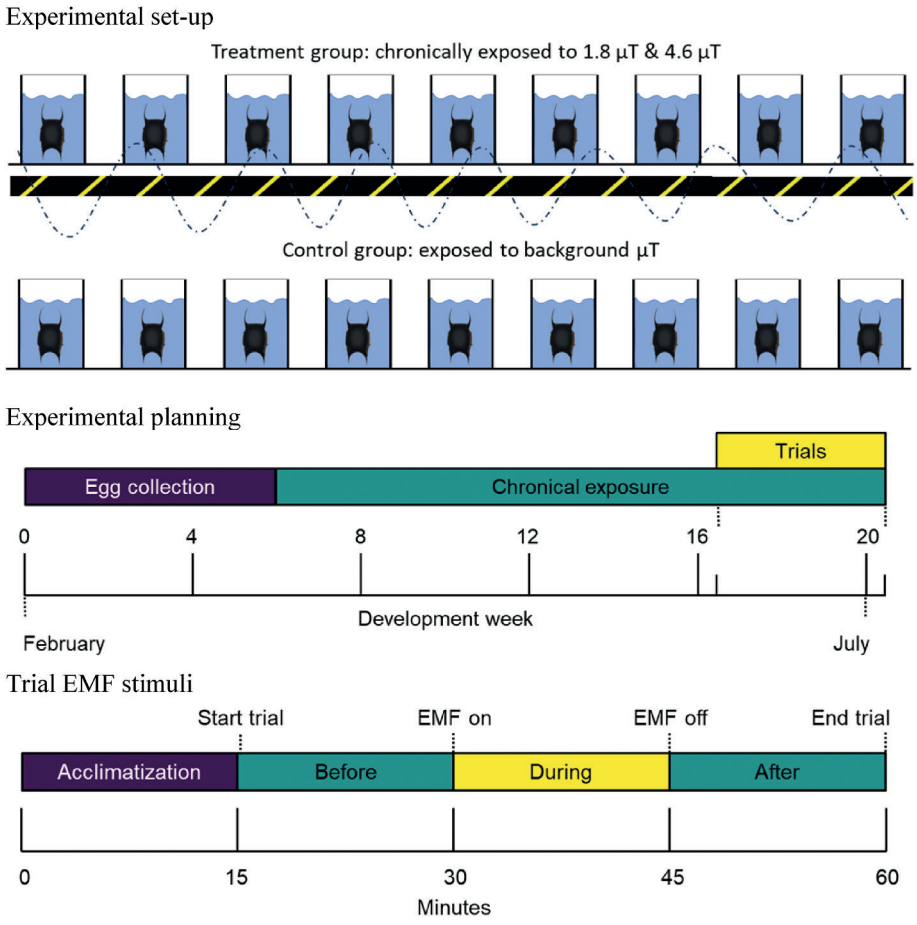


Fig. 4.1 Schematic overview of (top) experimental set-up, showing 9 egg cases Chronically exposed and 9 control egg cases, all individually housed. Experimental planning (middle) with the egg collection period in purple, the exposed period in green and the measurement period superimposed in yellow. Overview 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).

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: "Before" (to observe normal behaviour), "During" (to observe effects of EMF stimuli) and "After" (to observe lasting effects) (Fig. 4.1 bottom). It took the Helmholtz coil ~5 s to reach the requi-

red 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 4.1. 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 O2 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).

Table 4.1 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 seconds. 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).	

4.2.4 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 S4.2). 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).

4.3 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.

4.3.1 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 4.2). 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 S4.3). 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. 4.2A, B and C; Table S4.3). 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 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. 4.2, Table S4.4). 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.

Table 4.2 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

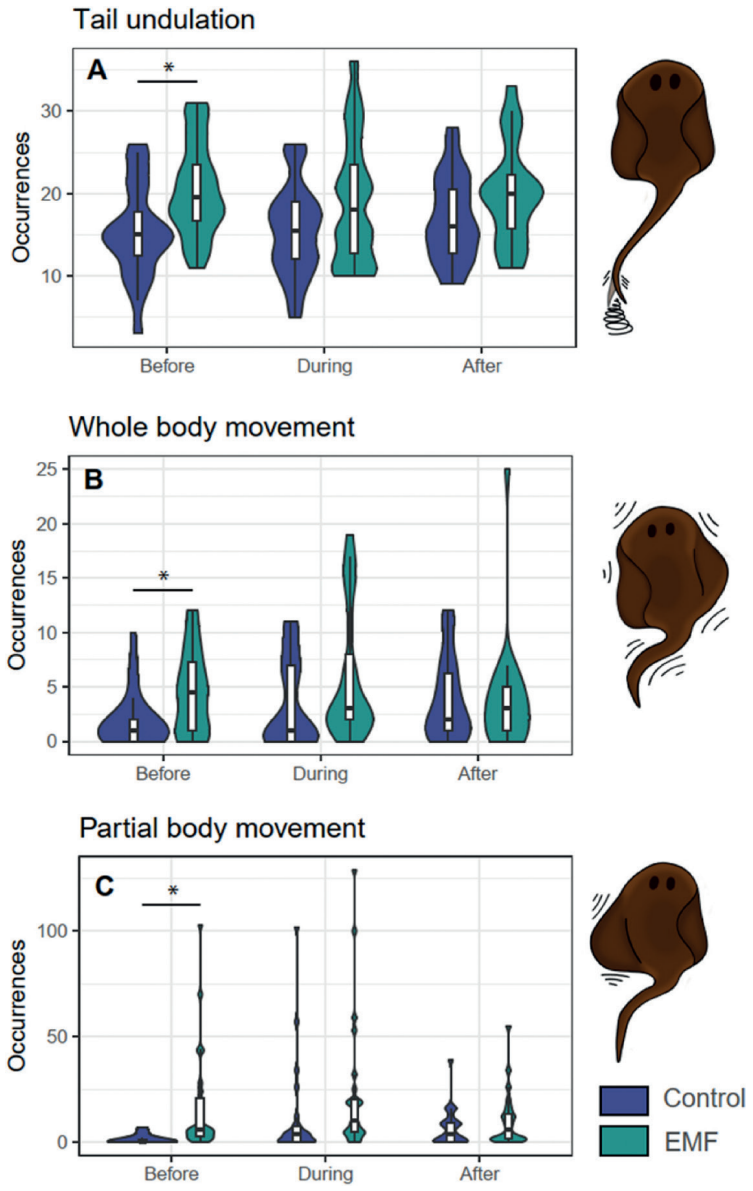


Fig. 4.2 Violin plots of number of occurrences during three 15-min trial periods ("Before" - background EMF exposure, "During" EMF exposure ranging from background, 1,0 and 10,0 µT and "After" - background EMF exposure) of (A) tail undulation, (B) whole body movement and (C) partial body movement, in 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.

4.3.2 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. 4.3). This individual variation in change of behaviour is most notable for the partial body movement (Fig. 4.3 right panel) ranging from 8 to −5 for the Control and 156 to −47 for the Chronically exposed. This variation is also present

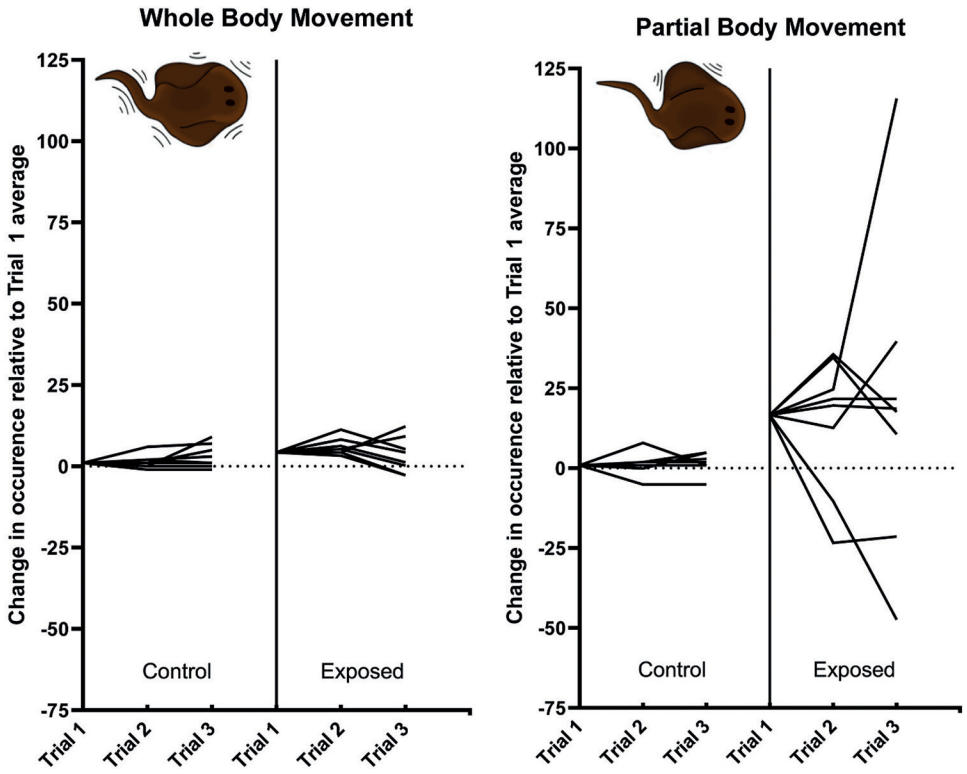


Fig. 4.3 Plots visualising the deviation in occurrences of (left) whole body movement and (right) partial body movement in thornback ray embryos during the "Before" phase of subsequent trials. Presented are the average occurrences for all embryos in the Control or Chronically exposed groups during Trial 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.

in whole body movement e.g. ranging from 9 to −1 and 11 to −3 for the Control and Chronically exposed groups, respectively.

4.4 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. 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.

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 acclimatisa-

tion 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. 4.1 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. 4.2). 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 embryogen esis 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 tivity 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 102 - 103 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. 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. 4.3). 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).

4.5 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.

Supplementary materials

Tabel S4.1 Overview of trials carried out in developmental weeks

Embryo ID	Treatment group (exposed/control)	Trial order (age embryo in weeks)		
		1	**2**	**3**
RC14	Control	20,3	20,6	20,7
RC22	Control	18,7	19	19,1
RC23	EMF	18,6	18,9	19
RC25	EMF	18,1	18,4	18,6
RC27	EMF	17,9	18,1	18,3
RC28	Control	18,6	18,7	18,9
RC29	EMF	18,6	18,7	18,9
RC30	Control	18,6	18,7	18,9
RC31	EMF	18,3	18,4	18,6
RC32	Control	18,1	18,3	18,4
RC34	EMF	18,3	18,9	19
RC37	Control	18,1	18,7	18,9
RC38	Control	18,1	18,6	18,9
RC39	Control	18,1	18,6	18,9
RC40	EMF	18,1	18,6	18,9
RC44	EMF	17,6	18	18,3

Table S4.2 Verification of the absence of significant influences of covariates 'age', 'time of day' and 'trial number' on Thornback ray embryo behaviour. The statistical test, test statistic, p-value and adjusted p-values are reported.

Age			
Parameter (Independence test)	**Test statistic (rho)**	**p-value**	**Adjusted p-value**
Freezing occurrences	0.07	0.41	1
Freezing duration	0.08	0.34	1
Tail undulation occurrence	0.05	0.53	1
Tail undulation duration	0.17	0.04	0.37
Whole body movement occurrence	-0.14	0.10	0.86
Whole body movement duration	-0.11	0.19	1
Partial body movement occurrence	-0.09	0.29	1
Time of day			
Parameter (Spearman correlation)	**Test statistic (rho)**	**p-value**	**Adjusted p-value**
Freezing occurrences	0.13	0.12	1
Freezing duration	0.13	0.13	1
Tail undulation occurrence	0.03	0.70	1
Tail undulation duration	-0.12	0.15	1
Whole body movement occurrence	0.05	0.54	1
Whole body movement duration	0.03	0.76	1
Partial body movement occurrence	0.15	0.07	0.67
Trial number			
Parameter (Spearman correlation)	**Test statistic (maxT)**	**p-value**	**Adjusted p-value**
Freezing occurrences	1.40	0.34	1
Freezing duration	1.74	0.19	1
Tail undulation occurrence	1.28	0.41	1
Tail undulation duration	2.33	0.05	0.47
Whole body movement occurrence	1.96	0.12	1
Whole body movement duration	1.16	0.47	1
Partial body movement occurrence	1.97	0.12	1

Table S4.3 General independence tests for behavioural differences between chronically exposed and control thornback ray embryos. Behavioural parameters, test statistics MaxT, p-values and adjusted p-values are displayed. WBM = whole body movement, PBM = partial body movement.

Occurrence			
Parameter	**Test statistic (maxT)**	**p-value**	**Adjusted p-value**
Freezing	-1.32	0.19	0.95
Tail undulation	-2.91	0.003	0.015
WBM	-2.7	0.007	0.035
PBM	-2.78	0.005	0.025
Duration			
Parameter	**Test statistic (maxT)**	**p-value**	**Adjusted p-value**
Freezing	-0.82	0.41	1
Tail undulation	0.16	0.88	1

Table S4.4 Generalized Linear Mixed Models (GLMM) for negative binomial distributions for behavioural differences between chronically exposed and control thornback ray embryos. Exposure (Control and Chronically Exposed), EMF level (0, 1 and 10μT), and trial order ("Before", "During" and "After") were included as fixed effects, and individual rays as random effects. Only models with lowest AIC are displayed in the table. Fixed effects estimates, standard errors, z-values, and p-values are displayed.

Tail undulation				
	Estimate	**SE**	**Z-value**	**p-value**
Intercept	2.70090	0.07810	34.58	<2e-16
ExposureEMF	0.21825	0.09851	2.22	0.0267
EMF_level1	0.12713	0.05572	2.28	0.0225
EMF_level10	0.02636	0.05714	0.46	0.6446
Whole Body Movement				
	Estimate	**SE**	**Z-value**	**p-value**
Intercept	1.0732	0.2081	5.156	2.52e-07
ExposureEMF	0.4782	0.2356	2.030	0.0423
EMF_level1	-0.3428	0.2030	-1.689	0.0913
EMF_level10	0.1500	0.1831	0.819	0.4127
Partial Body Movement				
	Estimate	**SE**	**Z-value**	**p-value**
Intercept	1.5196	0.2833	5.365	8.11e-08
ExposureEMF	0.8626	0.2965	2.909	0.00362
OrderDuring	0.5870	0.2173	2.701	0.00691
OrderAfter	0.2911	0.2223	1.309	0.19047

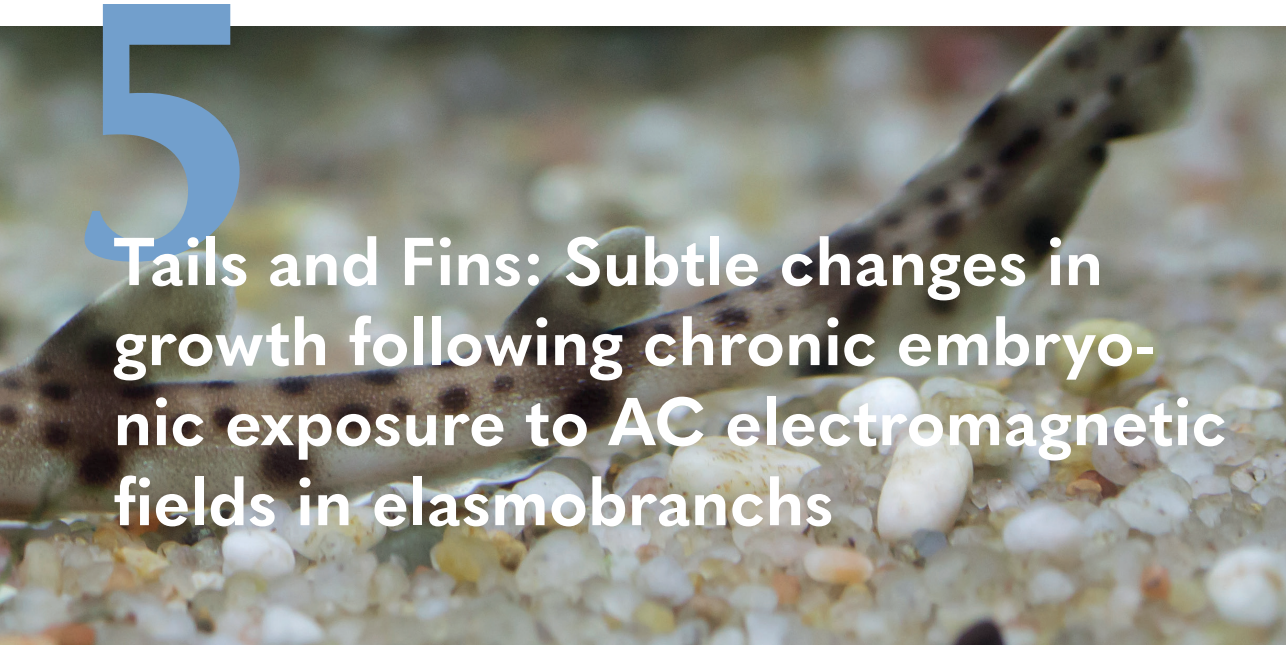


Abstract

Subsea power cables used to transport offshore wind-generated energy emit electromagnetic fields (EMFs) into the marine environment. These anthropogenic fields overlap with naturally occurring biotic and abiotic EMFs that elasmobranchs can detect and use for navigation, prey detection and predator avoidance. When egg-laying sites overlap with subsea cables, embryos may be chronically exposed to EMFs throughout development, yet the effects remain largely unknown.

We compared the morphology and behaviour of thornback skate (Raja clavata) and small-spotted catshark (Scyliorhinus canicula) juveniles exposed to alternating current EMFs (1.8 and 4.6 μT) throughout embryogenesis, with an unexposed control group. In skates, tail length was significantly shorter (5.3%) in exposed individuals at both one and three months post-hatching, while in exposed sharks, the pectoral fins were 11.2% larger at birth, a transient effect that disappeared after one month. These results may indicate subtle changes in growth of EMF exposure. As tail/fin-to-body ratios were unchanged, the extremities could be proxy for overall differences in length, possibly obscured by postural variation.

https://doi.org/10.1016/j.marpolbul.2026.119937



5 Tails and Fins: Subtle changes in growth following chronic embryonic exposure to AC electromagnetic fields in elasmobranchs

Activity levels and ventilation rates did not differ between treatments, nor were startle or avoidance responses observed following acute EMF exposure. However, sharks showed a significant difference in ventilation rate between 0.1 µT (background) and 10 µT, indicating EMF detection. We conclude that chronic exposure during embryogenesis causes subtle, species-specific growth effects without behavioural impairment. Although ecological relevance of these findings is unclear, it highlights the need for caution when extrapolating EMF sensitivity across elasmobranch species.

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Published in Marine Pollution Bulletin | October 2026

5.1 Introduction

5.1.1 Electromagnetic fields from offshore generated energy transport

To fulfil the growing demand for green energy, marine renewable energy developments are expanding, resulting in energy transport through subsea power cables over large distances (Sutton, Lewin and Swingler, 2017; Taormina et al., 2018). Both alternating (AC) and direct current (DC) cables used for this purpose generate an electromagnetic field (EMF) (Worzyk, 2009). Where the electric field is shielded within the cable, the magnetic field typically radiate 10's m (AC) to 100's m (DC) into the marine environment (Henkel, Suryan and Lagerquist, 2014; Copping and Hemery, 2020). The intensity and inclination of the magnetic fields are dependent on the power level, orientation and cable design, ranging up to 500 μT DC and 50 μT root mean square (RMS) AC for the most commonly used systems (Albert et al., 2020; Copping and Hemery, 2020; Hermans et al., 2024). Movement through the magnetic field by animals or water currents results in induced electric fields which are generally small (10−4 to 10−5 V/m) but detectable by electrosensitive species. Anthropogenic EMFs have been shown to influence the natural EMFs and the magneto- or electrosensitive marine life within (Albert et al., 2020; Hermans et al., 2024). Understanding the extent of the impact on sensitive species is not well known but growing in recent years (Albert et al., 2020; Copping and Hemery, 2020; Klimley et al., 2021; Scott et al., 2021; Hermans et al., 2024; Verhelst et al., 2025).

5.1.2 Elasmobranch and EMFs

Sharks and skates play important roles in many ecosystems, fulfilling the roles of predator, competitor, facilitator, nutrient transporter, and prey This species group is heavily under threat with more than 1/3rd of the species nearing extinction (Dulvy et al., 2021). Sharks and skates belong to the elasmobranchii which is one of the few taxonomic groups that can detect both magnetic and electric fields Using their electrosensitive ampullae of Lorenzini, they can detect bioelectric fields which are used throughout different life stages:, foraging and magnetic field is believed to be used in navigation, shown in laboratory studies and through field observations. The growing evidence base also highlights interspecies differences in EMF usage and sensitivity, depending on life history and morphology (Kempster, McCarthy and Collin, 2012; Bedore and Kajiura, 2013; Newton, Gill and Kajiura, 2019). EMF from subsea power cables could disrupt these natural behaviours, and the degree of impact may vary among species depending on the reliance on EMF.

5.1.3 Impact of EMFs on developing embryos

Early life stages of elasmobranchs are particularly vulnerable to pressures as they have a higher predation pressure then adult, and potential EMF effects might influence subse-

quent life stages, with potential consequences for population development (Reynolds et al., 2005; Di Santo, 2015; Ripley et al., 2021; Schröder et al., 2021). There is a risk of EMF exposure on elasmobranchs during embryogenesis as well as juveniles as spawning and egg-laying sites overlap with cables routes (Hermans et al., 2024). Embryos developing in sessile egg cases are at risk of prolonged EMF exposure when eggs are laid directly within an anthropogenic EMF. Exposure during critical stages of skeletal and tissue development may alter body morphology or sensitivity to EMF (Taormina et al., 2018; Paoletti et al., 2023; Hermans et al., 2025) and/or interfere with the imprinting of background electromagnetic fields as is shown in turtle hatchlings (Lohmann, Putman and Lohmann, 2008). Several studies have shown responses of electric stimuli by embryos of oviparous shark and skate, ranging from freezing response (temporarily ceasing respiration) during acute exposure (Kempster, Hart and Collin, 2013; Ball, Oliver and Gill, 2016) to short term tolerance buildup in
S. canicula during repeat exposure of several electrical stimuli over a 40-min period, indicating that habituation may occur (Christensen et al., 2023). In earlier work with we showed that chronically exposed (1.8-4.6 μT AC) individuals of skate (*Raja clavata*) embryo's were overall more active during exposure, including 33% more tail undulations and 150% increased body movements, compared to non-exposed individuals (Hermans et al., 2025). The increased activity might result in an increased risk of being detected by predators. No indications of reduced health or survival after hatching were found, or changes in development time or biometry, but the skates were not followed after hatching. Paoletti et al. studied 14 small-spotted catsharks (*Scyliorhinus canicula*) exposed to 4-7 μT AC, and 14 control animals, throughout embryogenesis and found indications of enlarged pectoral fins, but aborted the study at 18 weeks, not following the embryos to hatching (Paoletti et al., 2023). Alberts et al. observed juvenile skates (*R. clavata*) exposed to 1-h of 450 μT AC (50 Hz) and DC fields and found no significant behavioural effects in the morning, but small increased activity under DC fields in the afternoon (Albert et al., 2022). To date, no studies have investigated the morphological or behavioural changes in juveniles that were exposed to EMF during embryonic development, despite this being a likely scenario in the field.

5.1.4 Differences in elasmobranchs

Sharks and skates exhibit variation in the morphology and use of their electro- and magnetosensory systems, shaped by differences in foraging, mating, and navigation strategies (Sisneros and Tricas, 2002; Egeberg et al., 2014; Newton, Gill and Kajiura, 2019). It is possible that these interspecies differences also results in a different response to EMF from subsea power cables. However, differences in experimental designs across the limited number of EMF studies make cross-species comparisons challenging (Hutchison et al., 2020; Newton and Kajiura, 2020; Albert et al., 2022; Paoletti et al., 2023). Marcotte and Lowe (2008) directly compared the responses of scalloped hammerheads (*Sphyrna*

lewini) and leopard sharks (*Triakis semifasciata*) to strong electric fields (mean intensities of 18.50 ± 13.27 V/m and 9.64 ± 10.28 V/m), finding comparable behaviours such as increased head twitching and retreating, but with hammerheads retreating at higher levels indicating species-specific behavioural thresholds. Importantly, these deterrent-level field strengths are at least 4 orders of magnitude higher than the electric fields typically emitted by subsea power cables measured directly at the cable. Port Jackson sharks (*Heterodontus portusjacksoni*) and western shovelnose skates (*Aptychotrema vincentiana*), share a similar habitat and feed on similarly sized prey items but differ significantly in their electrosensory system morphology. When compared, they showed a similar sensitivity to electric-field gradients (<1 nV cm−1) but the authors outlined species-specific differences in spatial resolution and directionality of electroreception e.g. ability to pinpoint the exact location of a prey (Kempster et al., 2016). In this study, we compare the responses of two benthic elasmobranch species: the skate *Raja clavata* and the shark *Scyliorhinus canicula*, to EMF from subsea power cables. These species share key ecological traits, including overlapping diets (crustaceans and small fish), similar benthic habitats in the North Sea, limited migratory behaviour, and high site fidelity (Sims, Nash and Morritt, 2001; Rodríguez-Cabello et al., 2004; Heessen, Daan and Ellis, 2015; Bird et al., 2020; Papadopoulo et al., 2023; Labourgade et al., 2024). However, they differ in hunting strategy, with *S. canicula* acting as an locomotive opportunistic scavenger and *R. clavata* as an stationarity ambush predator (Šantić, Rađa and Pallaoro, 2012). They also exhibit distinct electro sensory morphology: sharks possess ampullae of Lorenzini concentrated around the snout, whereas in skates these are primarily located on the ventral surface of the disc (Newton, Gill and Kajiura, 2019). For both species egg laying sites are likely to overlap with subsea power cables routes. In addition, they are both common, non-threatened, easy to maintain in captivity, and have readily available egg cases from public aquaria, making them suitable model species for EMF impact studies.

5.1.5 Aim and approach

This study aims to assess the effects of field-relevant EMF exposure during embryogenesis on post-hatching body morphology and behaviour of a benthic skate and shark species in a controlled laboratory experiment. Observed interspecies differences and similarities in response to EMF will be used to explore the potential for extrapolating laboratory findings on one species to others by determining what these species have in common and differ in response.

5.2 Materials and Methods

5.2.1 Animal collection and husbandry

The experiments with thornback skate (*Raja clavata*) were conducted in 2023, and with small-spotted catshark (*Scyliorhinus canicula*) in 2024. In 2023, eighteen *R. clavata* eggs were sourced in from the public aquarium "Dolfinarium" in Harderwijk, the Netherlands, and transported within one week from deposition to a climate controlled room of the animal research facility of Wageningen University & Research, the Netherlands. The skate eggs hatched from August to September 2023. The next year, nineteen *S. canicula* were obtained from the Zeeaquarium in Bergen aan Zee, Netherlands and hatched from August to November 2024. They were collected in two batches due to the low fertility rate of the first batch. The eggs were split in two groups, an treatment group chronically exposed to EMF and a control group.

Individuals of both species, ten treatment and nine control *S. canicula* and eight treatment and nine control *R. clavata*. One control skate died due to reasons unrelated to the experiment and was subsequently excluded from the analyses. All individuals were kept under identical conditions in 25 L aquaria with artificial seawater (Tropic Marin Zoomix) for the duration of the experiment. All aquariums were part of a recirculating aquaculture system (RAS), in which water circulated continuously through all tanks and was filtered between cycles. Water flow rates were maintained between 110 and 140 L h^{-1}. Each tank was lined with a layer of sand to mimic the natural habitat and provide enrichment (Cau et al., 2017, Greenway et al 2017). The photoperiod was set to a 12 h light:12 h dark cycle (lights on at 07:00 h, off at 19:00 h), with an intensity of 2–4 lux measured in the tank using a Roline RO-1332 lux meter.

Environmental parameters, including temperature, dissolved oxygen, salinity, and pH, were monitored daily using a WTW Multi 3630 IDS meter with appropriate probes (FDO 925 for oxygen, TetraCon 925 for salinity, and SenTix 940 for pH). For *Raja clavata*, mean water temperature across all tanks was 15.64 ± 0.39 °C, oxygen concentration was 8.13 ± 0.10 mg L^{-1}, salinity was 33.47 ± 0.71 PSU, and pH was 8.214 ± 0.036. For *Scyliorhinus canicula*, mean water temperature across all tanks was 16.32 ± 0.03 °C, oxygen concentration was 8.68 ± 0.04 mg L^{-1}, salinity was 33.19 ± 0.04 PSU, and pH was 8.179 ± 0.043. RAS performance was checked weekly for ammonium (Merck Aquamerck Colorimetric Ammonium test) and nitrite (Merck Aquamerck Colorimetric Nitrite test) and did not exceed <0.1 mg L-1 and <0.1 mg L-1 respectively.

5.2.2 Experimental set-up

During embryogenesis, the treatment group was exposed to dynamic 50 Hz AC magnetic field levels alternating between 1.8 and 4.6 μT, changing every 24 hours to simulate conditions associated with low and high wind speeds ~1 m from the cable (minimum burial

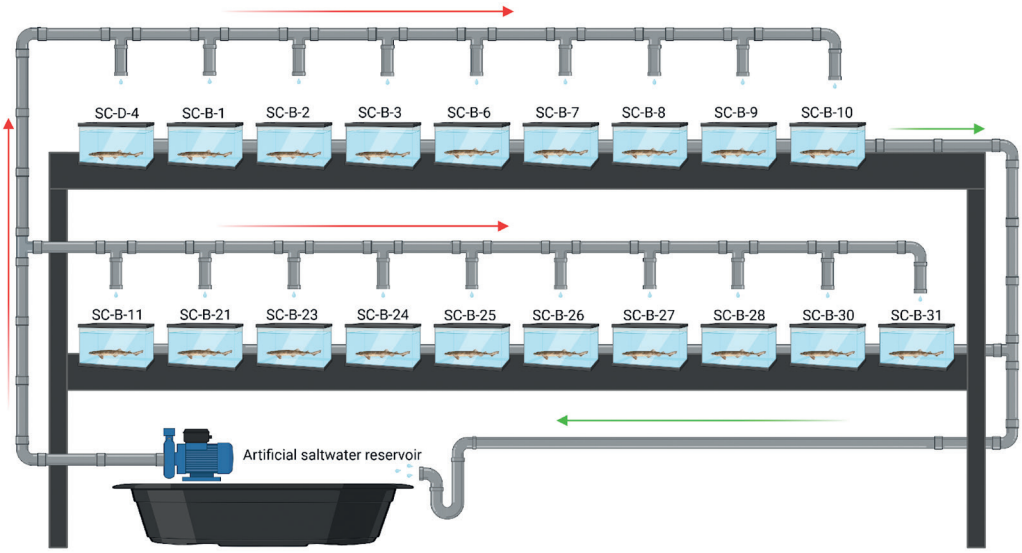


Fig. 5.1 Schematic overview of Recirculating Aquaculture System (RAS) set-up for *Scyliorhinus canicula* juveniles (after hatching), the set-up was comparable for *Raja clavata*. The juveniles' code number is indicated above each tank.

depth), respectively (Hermans et al., 2025). These magnetic field levels corresponded to estimated electric fields of 0.06–0.20 mV/m. To prevent interference, treatment and control groups were housed at opposite ends of a climate-controlled room, separated by more than 4 meters and shielded by Mu-metal plates to contain the magnetic field around the cable. The EMF values were measured bi-weekly using a magnetometer (Narda ELT-400, frequency range: 1 Hz – 400 kHz). Embryos on the control side of the room were exposed only to background magnetic fields, measured at 0.05 μT ± 0.073 for *R. clavata* and 0.07 ± 0.043 μT for *S. canicula*, with minor variation explained by their proximity to electrical equipment in the room. After hatching, all individuals were relocated to the control side of the room and all fish were randomly allocated to an aquarium. The juvenile fish were no longer exposed to EMFs beyond background levels, except during the acute exposure trials (Fig. 5.1). *S. canicula* were hand-fed herring (*Clupea harengus*) every other day. *R. clavata* were started on artemia and as they grew on a mixed diet of North Sea whitefish of predominantly *C. harengus*.

To test the response to EMF stimuli, acute EMF exposure trials were conducted when the animals reached 11 weeks post hatching (Fig. 5.2). For *S. canicula*, additional trials were performed at 5 weeks, and for *R. clavata*, at both 5 and 8 weeks; however, these earlier trials were not included in further analysis. Against the background level of 0.07-0.08 μT, the acute EMF stimuli experiments included two field strengths 1, and 10 μT (± 0.05 μT SD), and were conducted on individuals from both the control and treatment groups, yielding a total of 111 trials for both species combined (Table S5.1). Trial order was randomized using

a randomized complete block design. Each acute exposure trial was performed in a Helmholtz coil setup, comprising two coils with a diameter of 83.5 cm and a separation of 43 cm, generating a unidirectional magnetic field. It took the Helmholtz coil ~5 s to reach the required EMF exposure level. Trials commenced within a maximum of 6 days after individuals reached 11 weeks. All 3 trials were completed within 7 days, separated by a minimum interval of 48 hours. Fish behaviour was recorded using an overhead camera (Obsbot Meet 4K) with the following settings: shutter speed 1/60, ISO 800, contrast 50, resolution 1080P at 30 fps, and video format MKV, and logged by OBS studio (29.1.3, 2023).

Each trial started after the animals were allowed to acclimatise for 20 min (*S. canicula*) and 10 min (*R. clavata*), respectively. The difference in acclimatisation time between the two species was based on pilot tests, observing the duration after which animals returned to

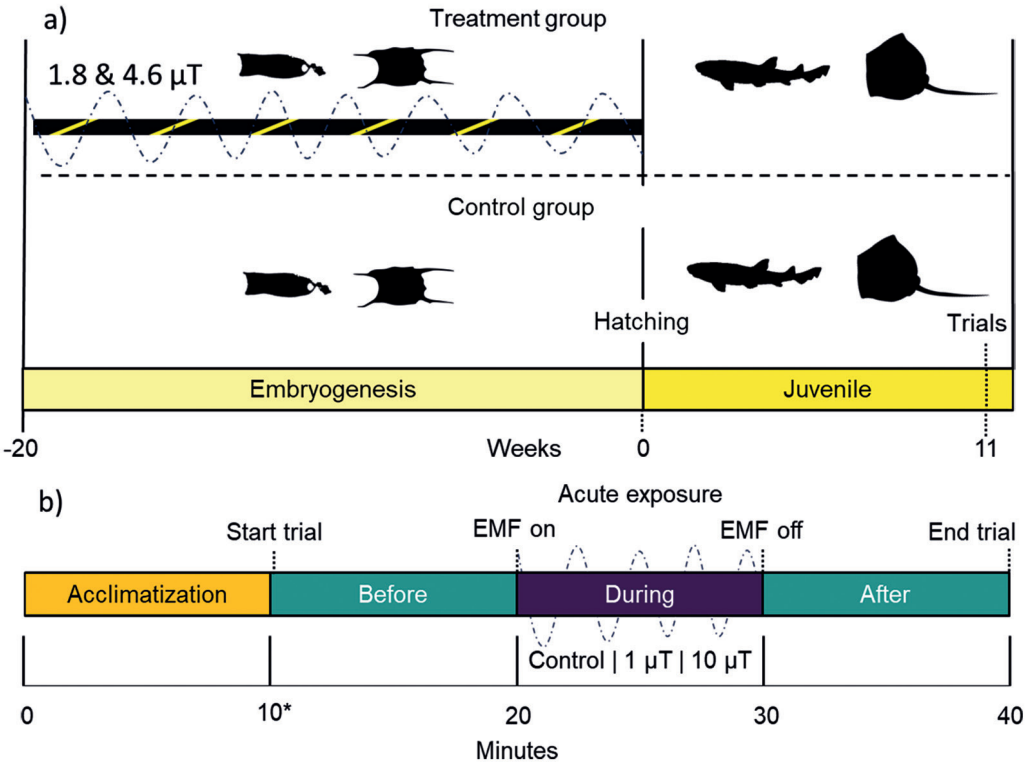


Fig. 5.2 (a) schematic overview of experimental set-up, showing exposure of the embryos in the treatment group to AC induced electromagnetic fields and a control group for both *Scyliorhinus canicula* (sharks), and *Raja clavata* (rays). After hatching individuals were only exposed to a set of acute stimuli trials at ~11 weeks.
(b) schematic overview of the acute trial protocol, indicating each block of 10 min, including acclimatisation (orange), "Before" exposure (green), "During" the acute EMF exposure (purple) (control, 1 µT or 10 µT) and "After" the EMF stimuli (green). *Note that for the sharks the acclimatization phase was extended to 20 min.

inactive behaviour and in accordance to previous studies (Ball, Oliver and Gill, 2016; Christensen et al., 2023; Paoletti et al., 2023; Hermans et al., 2025). Each trial, after acclimatisation, lasted 30 min and was divided into three 10 min phases: "Before" (to observe normal behaviour without EMF stimuli), "During" (to observe effects of the acute EMF stimuli) and "After" (to observe the behaviour after the EMF stimuli had ended) (Fig. 5.2 bottom). The behaviours in terms of time activity, ventilation rate (count/minute), and the occurrence and duration of surface breaking and horizontal breaching in sharks and burying movements, occurrence and duration of horizontal resting, stepping and surface breaking in skates, were scored using open-access program BORIS (V. 9.1.1) (Friard and Gamba, 2016). Ventilation rate was determined by counting the number of gill movements (*S. canicula*) or spherical movements (*R. clavata*) during the first and last minute of each phase (six times for each trial). Lastly, after each acute exposure trial a photo was taken of the individual with a ruler inside the container, to determine total length, pectoral fin length and width in sharks, and disk width and tail length in skates (Serra-Pereira et al., 2011) using ImageJ (v. 1.52). The juveniles sharks were weighed after the third trial and the skates before the first trial.

5.2.3 Data Analysis

The effects of EMF treatment on behaviour and biometrics were statistically analysed in R v. 4.2.2 (R Core Team). Multiple Generalised Linear Mixed Model (GLMM) were run using the *glmmTMB* package in R (Brooks et al., 2017), with different error distributions (Gaussian, Poisson or Negative Binomial). We determined the influence of treatment during embryogenesis on the morphological measures over time and baseline behaviour levels ('before' acute exposures) of activity and ventilation rate, and we included time of day, trial number, and – for skates – sex as additional explanatory variables. It was not (yet) possible to determine the sex of the sharks. For determining the response to acute exposures we included the exposure level (0.1 (background levels), 1, or 10 μT) and its interaction with treatment in the full model. In all models the individual was included as a random effect. The model with the best fit was selected based on the lowest Akaike Information Criterion (AICc) value. When the covariate 'treatment' was not part of the best model, but required to answer the research question, we added it to the final model anyway. We ran the final models and reported the summary statistics and p-values. Model outputs were checked for normality and homogeneity of variances based on visual inspection of the residual plots. When pairwise comparisons were needed to compare responses to different acute exposure levels, we used a post hoc Tukey test from the emmeans package (Lenth, 2025). Result plots were made using ggplot2 in R (Wickham, 2016).

5.3 Results

All 18 skates and 19 sharks, from both the treatment and control group successfully hatched, with no statistical differences in embryogenesis duration (*S. canicula*: control = 158.00 days, exposed = -1.33, p = 0.348; *R. clavata*: control = 144.43 days, exposed = 2.07, p = 0.372) between the treatment groups.

5.3.1 Morphological differences

There was no difference in body length at birth between treatment groups of neither species (*S. canicula* intercept = 11.92, treatment = 0.47, p = 0.150, *R. clavata*: intercept = 13.42, treatment = -0.33, p = 0.221) or weight (*S. canicula*: intercept = 4.84, treatment = 0.14, p = 0.532, *R. clavata*: intercept = 12.37, treatment = -0.51, p = 0.153). For skates, a non-significant trend suggested that males were smaller at hatching (Intercept = 13.42, males = -0.51, p = 0.061).

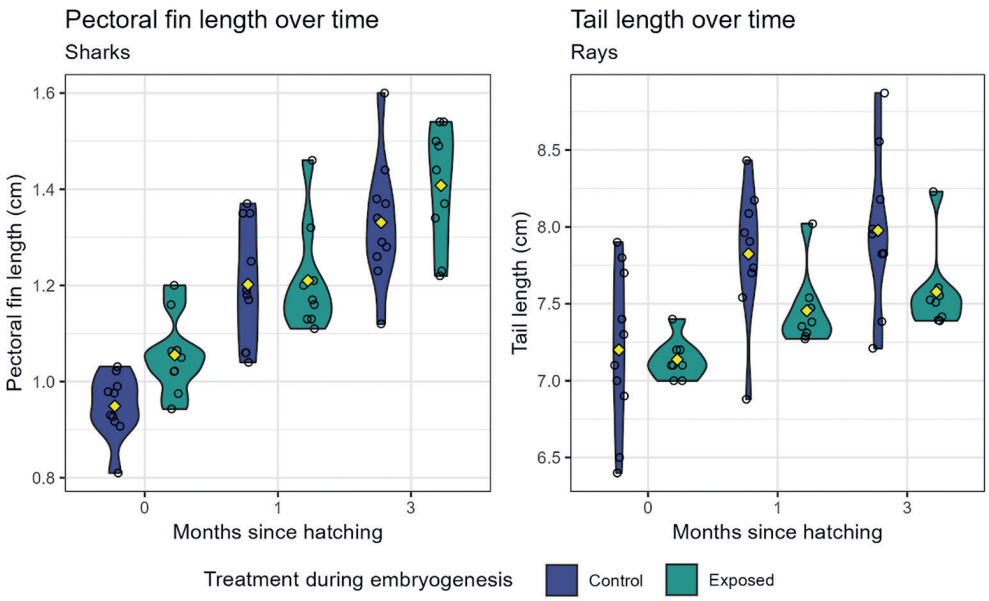


Fig. 5.3 Violin plots of biometric development of pectoral fin length in cm of *Scyliorhinus canicula* (sharks) left, and tail length of *Raja clavata* (rays) right, comparing control (blue) with treatment groups chronically exposed to AC induced electromagnetic fields throughout embryogenesis (green) over time. For the sharks the pectoral fin length different significantly at hatching but this corrected in the first month. The tail length of the rays was normal after hatching but differences became evident after one month.

However, sharks that were exposed to EMF during embryogenesis had a non-significant trend larger pectoral fin length (intercept = 1.01, exposed = 0.06, p = 0.075; Fig. 5.3), this was irrespective of time as the interaction between month and treatment was not part of the final model. We run additional t-tests to assess the difference between treatments for each timestamp in development, and found that pectoral fin length was significantly larger in EMF treated sharks at hatching (t = -3.12, p = 0.007), but not at 1 (t = -0.15, p = 0.886) or 3 (t = -1.31, p = 0.207) months. In skates, EMF exposure during embryogenesis led to significantly smaller tails (intercept = 7.9, p = 0.006; Fig. 5.3), irrespective of time. T-tests revealed no differences at hatching (t = 0.94, p = 0.370) and non-significant trends for smaller tails in exposed skates at 1 (t = 2.15, p = 0.052) and 3 (t = 2.01, p = 0.067) months. Additionally, visual observation of the plot suggests that the treatment group exhibited a narrower distribution in tail length compared to the controls (Fig. 5.3). We ran similar model selections for body total length (both species) and disc length (skates), but treatment during embryogenesis was not part of the final models here, indicating the lack of influence of treatment in contrast to pectoral fin length and tail length.

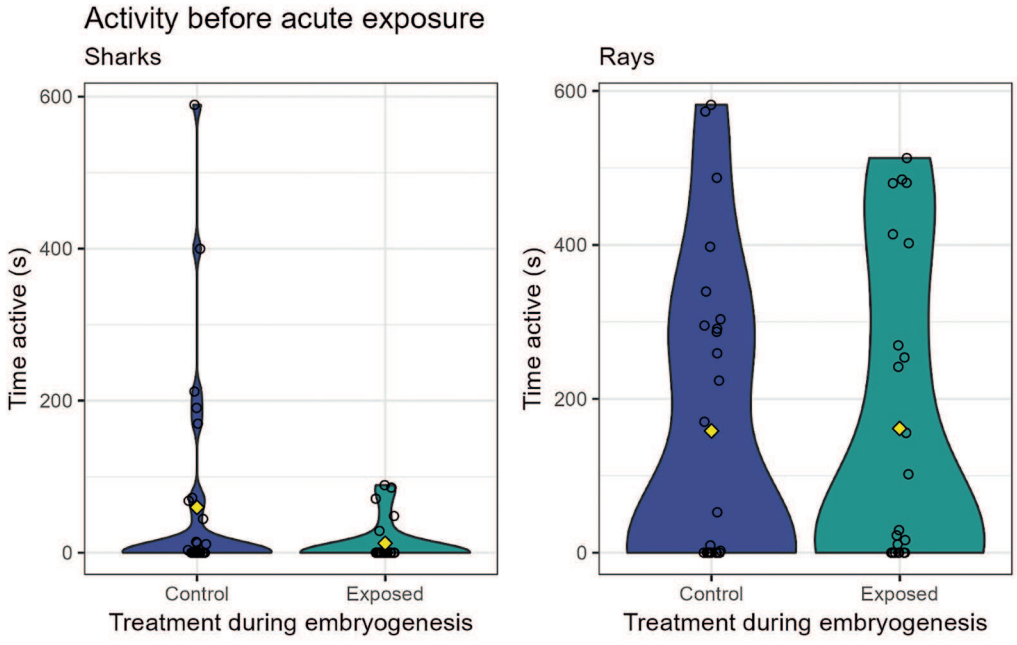


Fig. 5.4 Violin plots of activity before acute exposure of *Scyliorhinus canicula* (sharks) left, and *Raja clavata* (rays) right, comparing control (blue) with treatment groups chronically exposed to AC induced electromagnetic fields throughout embryogenesis (green). No significant differences in the activity level of both species was observed.

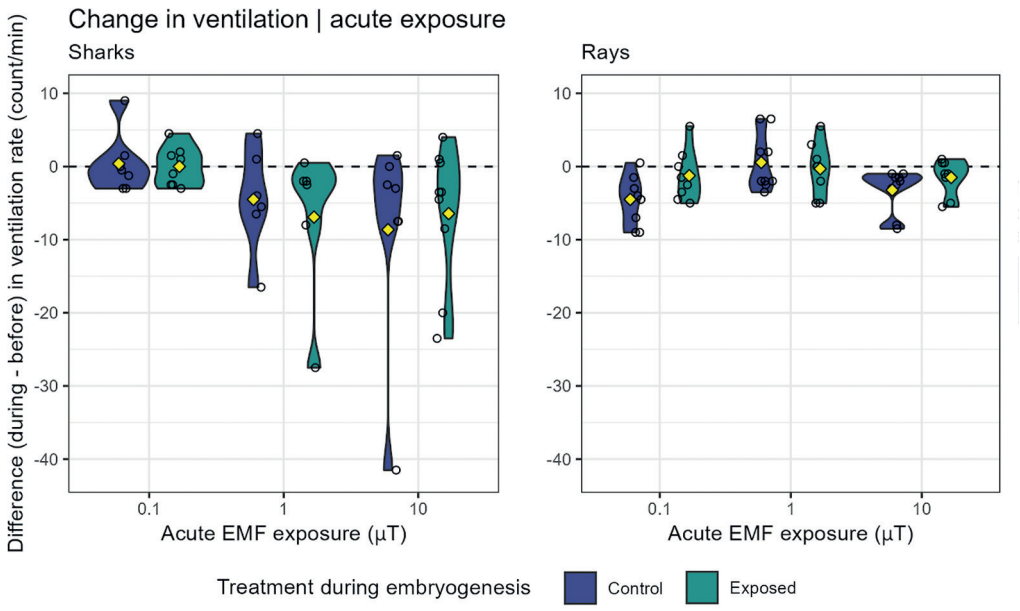


Fig. 5.5 Violin plots of change in ventilation during acute exposure of *Scyliorhinus canicula* (sharks) left, and *Raja clavata* (rays) right, comparing control (blue) with treatment groups chronically exposed to AC induced electromagnetic fields throughout embryogenesis (green), shown for 0.1 µT (control conditions), 1 µT and 10 µT. No significant differences in the change of ventilation of both species was observed between the exposed and control group.

5.3.2 Behaviour

No differences were found in the baseline (before acute stimulus) activity levels between treatment and control groups for neither species. In both species, many individuals did not move at all during the Before phase, this was not different between treatments (zero-inflated model *S. canicula*: intercept = 0.32, treatment = 1.23, p = 0.169, *R. clavata*: intercept = -0.98, treatment = -0.56, p = 0.512; Fig. 5.4). The activity level (duration) of individuals that did move was also not different (*S. canicula*: intercept = 5.78, treatment = -1.18, p = 0.217, *R. clavata*: intercept = -3.42, treatment = -0.16, p = 0.929; Fig. 5.4). During the acute EMF exposures, there were no clear changes in activity level relative to the Before phase for neither species. This confirmed by the absence of statistical differences between the acute exposures, including the control, in the change in activity level in neither species (0.1, 1, and 10 µT, in sharks all pairwise comparisons p > 0.862, and in skates all comparisons p > 0.606; Fig. S4.1). Additionally their treatment during embryogenesis was not part of the final model, indicating this did not affect their response (or lack thereof) to the acute exposure.

For the ventilation rate before the acute EMF exposure, no significant difference was found for skates, comparing treatment and control. For sharks there was a non-significant trend of a higher ventilation rate in exposed individuals (*S. canicula*: intercept = 69.49, treatment = 6.61, p = 0.078, *R. clavata*: intercept = 44.72, treatment = -2.24, p = 0.400). For their response in ventilation rate to the acute EMF exposure, treatment during development was not part of the best models indicating the treatment during embryogenesis did not affect responses. Irrespective of treatment, sharks reduced their ventilation rate significantly during the acute EMF exposure to 10 μT compared to 0.1 μT (background levels) (Tukey post hoc test: estimate = -7.59, p = 0.042; Fig. 5.5). Exposure to 1 μT did not result in a significant change in ventilation rate compared to the 0.1 μT control (-5.89, p = 0.180; Fig. 5.5). In skates, the absolute changes in ventilation rate upon acute EMF exposures were smaller than in sharks. During the control exposure (0.1 μT), ventilation rate still went down (i.e. was different from zero: intercept = -2.97, p < 0.001), indicating that not all animals had reached stable baseline levels of ventilation rate. This decrease was similar during the 10 μT exposure (pairwise comparison with 0.1 μT: estimate = 0.56, p = 0.875; Fig. 5.5). The decrease in ventilation rate was significantly less strong during the 1 μT exposure (pairwise comparison with 0.1 μT: estimate = -3.12, p = 0.023; Fig. 5.5).

No significant differences were found in any of the other behavioural parameters assessed. These included the occurrence and duration of surface-breaking and horizontal breaching in *S. canicula*, as well as burying behaviour, and the occurrence and duration of horizontal resting, stepping, and surface-breaking in *R. clavata* (Table S5.2).

5.4 Discussion

This study examined effects on the morphology and behaviour of the juvenile sharks and skates until 3 months after hatching, after being exposed to EMFs during embryogenesis. In sharks, the pectoral fin length was significantly larger at hatching in the treatment group, although this difference was no longer evident after one month. In skates, tail length was significantly shorter in the treatment group until the end of the experiment, but this was only evident after one month post-hatching. No significant differences in baseline activity or ventilation rate were observed between treatment groups, for neither species, nor following acute exposure to an EMF stimulus, except for the difference between 0.1 μT (background) with 10 μT exposure in shark, indicative of EMF detection.

5.4.1 Differences in morphology

All fish appeared in good condition during the final sampling, three months after hatching, with no significant differences in weight or overall body length between treatment and control groups. Nevertheless, subtle differences in the length of extremities were detected. In skates, tail length was significantly shorter (5.3%) in exposed individuals at both one and

three months, while in sharks, pectoral fin length was larger (11.2%) in exposed individuals at birth. In combination with the fact that no statistically significant changes in overall body size were found, these findings may suggest that chronic EMF exposure influences specific aspects of biometry by allometric growth. Another explanation could be that tail and fin length represents the most reliable proxy for total length, as postural variation e.g. sharks lifting on pectoral fins or skates arching their disc or not laying completely still, can introduce measurement error and obscure proportional changes. While accuracy could be improved by measuring animals outside of the water, this would also increase handling stress.

Analysis of individual growth rates (Fig. S5.2) did not provide further insights. A non-significant trend was observed which showed EMF exposure lead towards smaller male skates at hatching, but further analysis showed no clear differences between the treatments (Fig. S5.3). Although the observed differences may become more evident with larger sample sizes or improved measurement techniques, they remain relatively minor. In natural field conditions, such subtle effects would likely have limited ecological significance, unless they are a symptom or result of other processes.

Embryogenic *R. clavata* exposed to the same EMF levels as used in this study, showed hyper active behaviour e.g. 150% increased body movements and 33% more tail undulations (Hermans et al., 2025). It was assumed the increased body movements resulted in additional metabolic waste, which required additional water exchange in the egg accomplished by increased tail beating. Since during embryo development the nutrient availability (via the yolk) is fixed from the start, it is likely that embryo's that spend more energy on movement will be smaller at hatching then those that were more 'relaxed' in the egg. If we accept that tail-length is the best proxy for total body length this argumentation could explain our findings, that EMF exposure of embryo's results in smaller skates at hatching.

The results of the altered growth of the shark fin in this study support the trend observed by Paoletti et al. (2023), who also reported enlarged pectoral fins of *S. canicula* under similar levels of chronic EMF exposure during embryogenesis, up to 18 weeks in development, after which the study was terminated (Paoletti et al., 2023). Interestingly, Paoletti et al. also did not find significant differences in overall body length or in the fin-length body-length ratio. Similarly, our data provide no solid evidence for altered morphology in EMF-exposed sharks, although a potential effect cannot be fully excluded. It is possible that, as posed by Paoletti et al, altered energy allocation during late embryogenesis may have led to the larger pectoral fins, leading to localized overdevelopment of certain structures like fins and implying an energetic inefficiency or loss (Huveneers et al., 2011; Paoletti et al., 2023). The outcomes of our study addressed several other questions raised by Paoletti et al., specifically finding no evidence of earlier hatching or significantly increased body size in sharks following EMF exposure.

It is not uncommon for exposure to a stressor during early developmental stages to cause abnormalities in fin or tail growth, as shown in intensive rearing conditions in aquaculture, development during increased temperature, acidification, vibrations and sound exposure (Koumoundouros et al., 1997; Pimentel et al., 2014; Nedelec et al., 2015; Jeradi

and Franz-Odendaal, 2022). The shape of the pectoral fin is important in shark swimming performance (Fish and Shannahan, 2000; Hoffmann, Buser and Porter, 2020), and environmental stressors have been linked to deformations in for example sharpnose shark (*Rhizoprionodon porosus*) (Lopes et al., 2020). Studies on other fish species e.g. Gilthead Seabream (*Sparus aurata*) and Zebra seabream (*Diplodus cervinus*), indicate that comparable changes in growth as found in our study can influence individual fitness through e.g. reduced swimming performance or impairing predator avoidance (Corriere et al., 2020; Mhalhel et al., 2023).

Both species show changes in growth, but the expression differs. This may relate to differences in body shape, the positioning in the egg, or of the ampullae of Lorenzini, or species-specific use of EMF, such as differing hunting strategies (e.g., ambush predator vs. opportunistic feeder). Additionally, skates may employ different compensatory mechanisms than sharks, as their tails serve different functional roles.

5.4.2 No differences in behavioural parameters

The EMF exposure levels used in this study (1.8 - 4.6 μT) were more within the range of realistic field-relevant values reported for subsea power cables (Hermans et al., 2025) when compared to some other studies (Scott et al., 2021; Albert et al., 2022; James, Ghodsi and Ford, 2025). No significant changes in activity, either in frequency or duration, were observed during the baseline period of acute exposure trials for either species, indicating limited short-term effects on behavior (Fig. 5.4). Furthermore, no species-specific differences were detected. These findings are consistent with Alberts et al. (2022), who reported minimal behavioural responses in juvenile *R. clavata* exposed to 450 μT DC fields (not exposed during embryogenesis), although they noted a diel pattern in responsiveness which was not assessed in the present study (Albert et al., 2022). In line with previous research (Byrnes and Brown, 2016; Finger et al., 2016; Dhellemmes et al., 2021), substantial inter-individual variability was observed (Fig. 5.4, 5.5, S5.1), suggesting intrinsic differences in behavioural coping styles or differences in genetics or physiological state. No significant differences were detected between treatment groups in the expression of stress-related behaviors such as surface breaking or ventral swimming (Table S5.2).

When exposing both treatments groups to an acute EMF stimulus, again no significant differences in the change in activity levels of either species were observed. This suggests that chronic EMF exposure during embryogenesis does not change the short-term behavioural or stress response of an acute (10 minute) EMF stimulus (Fig. S5.1).

Visually there seems to be a trent of decreased ventilation rate for *S. canicula* when exposed to an EMF stimuli (Fig. 5.5). Although not significant, save the difference between 0.1 μT (background) with 10 μT exposure, this is indicative of detection of the experimental EMF. However, no difference in ventilation rate were observed between treatment groups, suggesting that chronic EMF exposure during embryogenesis does not significantly influence sensitivity of antropogenic EMFs ≤10 μT resulting from AC cables. Overall, a

greater reduction in ventilation rate was observed in sharks compared to skates. However, this difference may partly reflect methodological limitations, as ventilation rate is sometimes underestimated in *S. canicula* using visual observations; branchial movements are occasionally subtle, or disrupted by a freezing response, and become increasingly obscured during swimming. While ventilation rate is a commonly used external proxy for physiological response to stimuli (Kramer, 1987), these measurements should be interpreted with caution. Accuracy could be improved through the use of implantable data loggers that allow continuous, internal monitoring (Whitney et al., 2018). Another explanation is that species-specific behavioural responses occur, as demonstrated by Gill et al. (2009). In their mesocosm study with the same species examined here, skates increased their swimming speed when the cable was energized, whereas sharks altered its spatial distribution, spending more time in the zone of EMF emission.

5.4.3 Recommendations

The outcomes of this study reaffirm that caution is warranted when extrapolating the effects of EMF exposure from one elasmobranch species to another, particularly between species with distinct body morphologies (e.g. fusiform sharks and dorsoventrally flattened skates) as shown in adults (Marcotte and Lowe, 2008; Kempster et al., 2016). Our findings suggest that while some effects, such as allometric growth, may occur across species and appear to be of a similar order of magnitude, the specific nature of these changes likely varies. In contrast, the lack of significant impact on behaviour appears to be more consistent, at least for the two species examined here.

There are uses of electro- or magnetic senses in elasmobranchs that might be impacted, that were not part of the study design as changes in navigation, foraging success and/or conspecific interaction. To determine EMF exposure during embryogenesis on these vital functions, it is recommended to follow animals longer term in a more natural setting like a mesocosm to see how the differences in growth alter over time and if this interferes with longer-term survival and fitness. A carefully compiled study design, that could include tagging, would even allow explorations of impacts from cumulative exposure and generational effects. For example, some species show site fidelity as Flapper skate (*Dipturus intermedius*) and Port Jackson shark (*Heterodontus portusjacksoni*) (Powter and Gladstone, 2008; Martins et al., 2018; Bass et al., 2021; Dodd et al., 2022), a mechanism that might be aided by geoimprinting, as seen with turtles (Lohmann, Putman and Lohmann, 2008; Brothers and Lohmann, 2015). This maybe affected by EMF DC exposure during embryogenesis, underscoring the importance of further research focused specifically on DC fields.

5.5 Conclusions

Chronic exposure to low-level, AC-induced EMF during embryogenesis resulted in no significant differences in weight between treatment and control groups. A subtle reduction in growth was found in rays, whereas sharks showed indications of a transient increase in size; both effects are likely to be obscured by natural variation in the field. No significant behavioural differences were detected under baseline conditions or during acute EMF exposure between EMF and control individuals, suggesting limited direct effects on behavior or stress. To better understand potential impacts on fitness, foraging success, and social behavior, we recommend long-term mesocosm studies. As our research shows interspecies differences, we recommend caution when extrapolating effects of EMF research to other elasmobranch species.

Supplementary materials

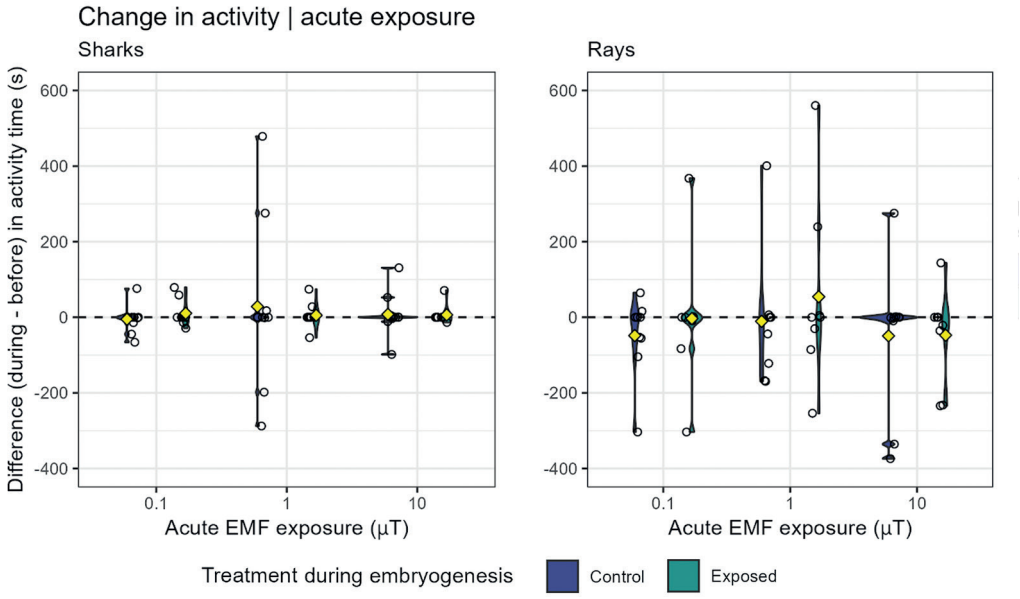


Fig. S5.1 Violin plots of the change in activity during acute exposure of *Scyliorhinus canicula* (sharks) left, and *Raja clavata* (rays) right, comparing control (blue) with treatment groups chronically exposed to AC induced electromagnetic fields throughout embryogenesis (green). No significant differences in the change in activity level during acute exposure of both species was observed.

Tabel S5.1 Overview of trials carried out showing trial date of fish in weeks, were SC stands for *Scyliorhinus canicula* and RC for *Raja clavata*, symbols indicating the exposure level of the trial: 0.1 µT ♣, 1.0 µT ♥, 10.0 µT ♦.

Fish ID	Treatment group	Trial dates		
SC-D-4	control	21/10/2024 ♥	23/10/2024 ♦	25/10/2024 ♥
SC-B-1	exposed	21/10/2024 ♥	23/10/2024 ♦	25/10/2024 ♣
SC-B-2	exposed	21/10/2024 ♦	23/10/2024 ♥	25/10/2024 ♣
SC-B-7	exposed	29/10/2024 ♥	31/10/2024 ♣	04/11/2024 ♦
SC-B-6	control	31/10/2024 ♦	04/11/2024 ♥	06/11/2024 ♣
SC-B-3	control	01/11/2024 ♥	04/11/2024 ♦	06/11/2024 ♣
SC-B-8	control	05/11/2024 ♦	07/11/2024 ♣	11/11/2024 ♥
SC-B-11	exposed	05/11/2024 ♥	07/11/2024 ♦	11/11/2024 ♣
SC-B-10	control	06/11/2024 ♣	08/11/2024 ♦	11/11/2024 ♥
SC-B-9	control	12/11/2024 ♥	15/11/2024 ♦	18/11/2024 ♣
SC-B-21	control	08/01/2025 ♥	10/01/2025 ♣	13/01/2025 ♦
SC-B-23	control	16/01/2025 ♦	20/01/2025 ♣	22/01/2025 ♥
SC-B-24	exposed	16/01/2025 ♣	20/01/2025 ♥	22/01/2025 ♦
SC-B-25	exposed	20/01/2025 ♦	22/01/2025 ♥	24/01/2025 ♣
SC-B-26	control	20/01/2025 ♣	22/01/2025 ♥	24/01/2025 ♦
SC-B-28	control	05/02/2025 ♣	07/02/2025 ♥	10/02/2025 ♦
SC-B-30	exposed	06/02/2025 ♦	10/02/2025 ♥	12/02/2025 ♣
SC-B-27	exposed	10/02/2025 ♣	12/02/2025 ♦	14/02/2025 ♥
SC-B-31	exposed	10/02/2025 ♥	12/02/2025 ♣	14/02/2025 ♦
RC52	exposed	14/12/2023 ♣	18/12/2023 ♦	20/12/2023 ♥
RC53	control	11/12/2023 ♦	13/12/2023 ♣	15/12/2023 ♥
RC57	control	11/12/2023 ♥	13/12/2023 ♣	15/12/2023 ♦
RC59	control	27/11/2023 ♣	29/11/2023 ♥	01/12/2023 ♦
RC64	exposed	11/12/2023 ♦	13/12/2023 ♣	18/12/2023 ♥
RC66	exposed	15/12/2023 ♣	19/12/2023 ♦	21/12/2023 ♥
RC67	control	11/12/2023 ♥	13/12/2023 ♣	15/12/2023 ♦
RC68	exposed	18/12/2023 ♥	20/12/2023 ♦	22/12/2023 ♣
RC69	control	13/12/2023 ♣	15/12/2023 ♦	18/12/2023 ♥

Fish ID	Treatment group	Trial dates		
RC70	exposed	18/12/2023 ♦	20/12/2023 ♣	22/12/2023 ♥
RC73	control	18/12/2023 ♥	20/12/2023 ♦	22/12/2023 ♣
RC74	exposed	12/12/2023 ♦	14/12/2023 ♥	19/12/2023 ♣
RC75	exposed	08/12/2023 ♦	11/12/2023 ♣	13/12/2023 ♥
RC76	control	04/12/2023 ♥	06/12/2023 ♦	08/12/2023 ♣
RC79	exposed	14/12/2023 ♣	18/12/2023 ♦	20/12/2023 ♥
RC82	control	14/12/2023 ♦	19/12/2023 ♣	21/12/2023 ♥
RC92	control	14/12/2023 ♣	19/12/2023 ♥	21/12/2023 ♦

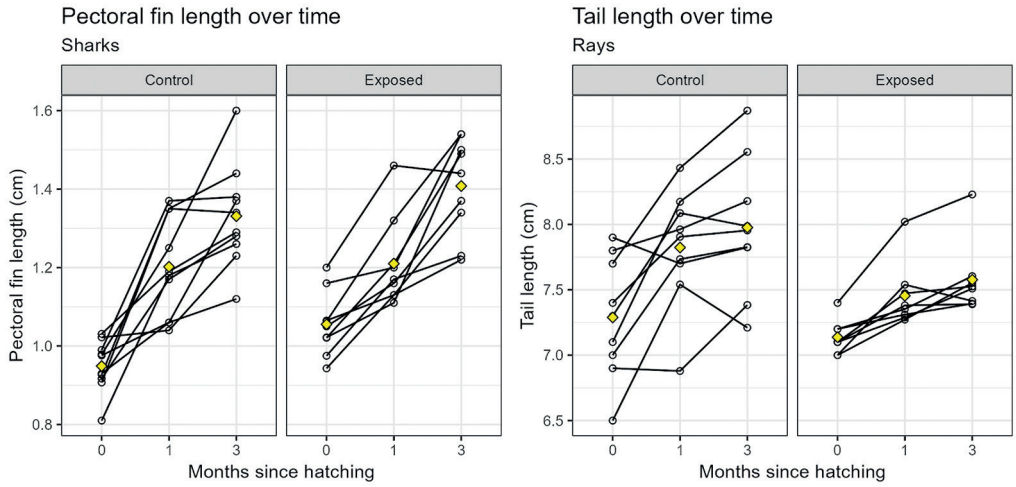


Fig. S5.2 Line plot showing the individual growth rate of the pectoral fin length of the shark *Scyliorhinus canicula* (left) and the tail length of the skate *Raja clavata* (right), of individuals chronically exposed to electromagnetic fields during embryogenesis (Exposed) and the control groups. Some lines show a downward movement of <1 mm between the 1st and 3rd month indicating some uncertainty in the measurement technique.

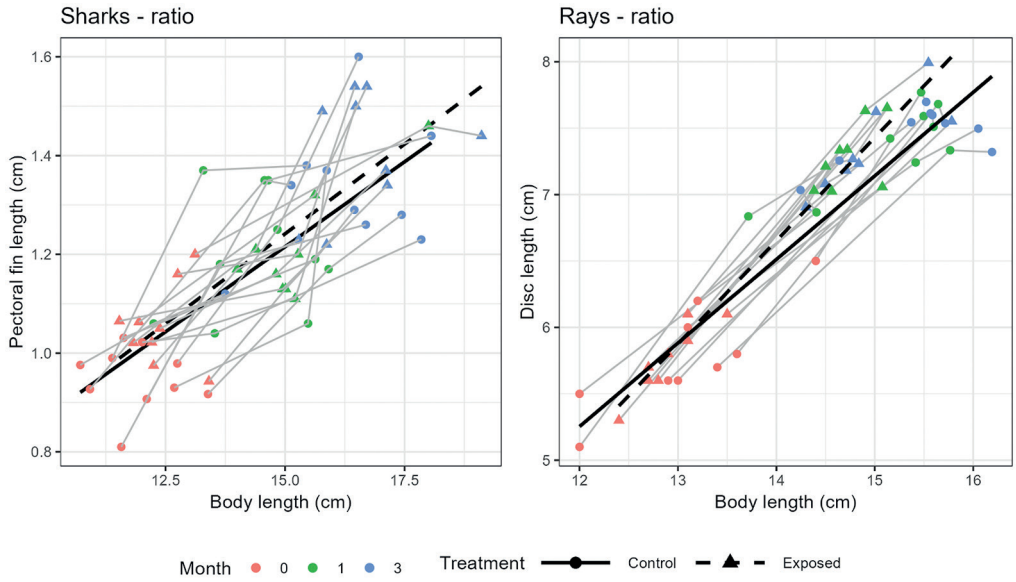


Fig. S5.3 Scatterplot showing the ratio of total body length (cm) versus pectoral fin length in the shark *Scyliorhinus canicula* (left) and the skate *Raja clavata* (right) exposed to electromagnetic fields throughout embryogenesis.

Table S5.2 Overview of the statistical test of all parameters, showing baseline behavioural parameters (also part of exposure phases), biometrics over time and acute exposure for the shark *Scyliorhinus canicula*, followed by the same values for the skate *Raja clavata*. Blank cells indicate data that was not collected.

Sharks - baseline

Behavioural parameters	Treatment	Mean	SD	Median	Q25	Q75	Min	Max
Horizontal Breaching occurrence	Control	2,3	7,0	0,0	0,0	0,0	0,0	35,0
Horizontal Breaching occurrence	Exposed	0,4	1,0	0,0	0,0	0,0	0,0	4,0
Inactivity occurrence	Control	2,3	2,1	1,0	1,0	3,0	1,0	9,0
Inactivity occurrence	Exposed	1,6	1,4	1,0	1,0	1,0	1,0	7,0
Inactivity time in seconds	Control	528,6	159,1	600,0	563,1	600,0	10,8	600,0
Inactivity time in seconds	Exposed	587,5	27,3	600,0	599,5	600,0	511,1	600,0
Locomotion occurrence	Control	1,6	2,5	0,0	0,0	3,0	0,0	10,0
Locomotion occurrence	Exposed	0,6	1,4	0,0	0,0	0,0	0,0	6,0
Locomotion time in seconds	Control	59,7	134,3	0,0	0,0	36,9	0,0	589,2
Locomotion time in seconds	Exposed	12,5	27,4	0,0	0,0	0,0	0,0	88,9
Surface breaking occurrence	Control	7,3	18,7	0,0	0,0	1,0	0,0	68,0
Surface breaking occurrence	Exposed	1,1	2,4	0,0	0,0	0,0	0,0	9,0
Surface breaking time seconds	Control	33,9	64,0	0,0	0,0	28,0	0,0	202,2
Surface breaking time seconds	Exposed	9,9	22,4	0,0	0,0	0,0	0,0	81,4
Ventilation occurrence	Control	123,4	43,7	137,5	108,8	151,0	0,0	191,0
Ventilation occurrence	Exposed	152,9	15,0	154,0	140,0	161,5	126,0	187,0
Ventilation_per_min	Control	70,2	13,0	72,8	63,3	76,4	37,3	95,5
Ventilation_per_min	Exposed	76,1	6,8	77,0	71,0	80,5	63,0	89,5

Sharks - Biometrics over time *SE = standard error*

Biometric parameters	Treatment	Mean	SD	Median	Q25	Q75	Min	Max
Weight_at_birth	Control	4,8	0,6	4,8	4,4	5,4	3,8	5,6
Weight_at_birth	Exposed	5,0	0,3	5,1	4,7	5,2	4,3	5,4
Weight_11_weeks	Control	11,1	1,8	11,5	9,7	12,2	8,2	14,1
Weight_11_weeks	Exposed	11,1	2,0	10,5	9,6	12,2	8,6	15,2
Width_at_birth	Control	1,4	0,1	1,4	1,3	1,5	1,3	1,5
Width_at_birth	Exposed	1,4	0,1	1,4	1,4	1,4	1,2	1,5
Width_5_weeks	Control	1,6	0,1	1,7	1,5	1,7	1,4	1,9
Width_5_weeks	Exposed	1,7	0,1	1,7	1,6	1,7	1,5	1,9
Width_11_weeks	Control	1,8	0,1	1,8	1,8	1,9	1,7	2,0
Width_11_weeks	Exposed	1,8	0,1	1,8	1,8	1,9	1,7	2,0
pectoral_fin_length_at_birth	Control	0,9	0,1	1,0	0,9	1,0	0,8	1,0
pectoral_fin_length_at_birth	Exposed	1,1	0,1	1,1	1,0	1,1	0,9	1,2
pectoral_fin_lenght_5	Control	1,2	0,1	1,2	1,1	1,4	1,0	1,4
pectoral_fin_lenght_5	Exposed	1,2	0,1	1,2	1,1	1,2	1,1	1,5
pectoral_fin_lenght_11	Control	1,3	0,1	1,3	1,3	1,4	1,1	1,6
pectoral_fin_lenght_11	Exposed	1,4	0,1	1,4	1,3	1,5	1,2	1,5
Size_pectoral_fin_at_birth	Control	0,8	0,1	0,8	0,7	0,8	0,7	0,9
Size_pectoral_fin_at_birth	Exposed	0,9	0,1	0,8	0,8	0,9	0,7	1,0

Size_pectoral_fin_5	Control	1,2	0,2	1,2	1,1	1,4	0,9	1,4
Size_pectoral_fin_5	Exposed	1,3	0,2	1,2	1,2	1,2	1,1	1,7
Size_pectoral_fin_11	Control	1,5	0,2	1,5	1,4	1,6	1,1	2,0
Size_pectoral_fin_11	Exposed	1,6	0,2	1,6	1,6	1,6	1,3	1,9
Length_at_birth	Control	11,9	0,8	11,8	11,4	12,7	10,7	13,4
Length_at_birth	Exposed	12,4	0,6	12,3	11,9	12,8	11,5	13,4
Length_5_weeks	Control	14,4	1,1	14,6	13,5	15,5	12,3	15,9
Length_5_weeks	Exposed	15,3	1,1	15,0	14,8	15,3	14,0	18,0
Length_11_weeks	Control	16,3	1,3	16,5	15,5	17,4	13,8	18,1
Length_11_weeks	Exposed	16,7	1,1	16,5	15,9	17,1	15,3	19,1
SE_A_Fin_11_weeks	Control	0,1	0,1	0,1	0,1	0,1	0,0	0,2
SE_A_Fin_11_weeks	Exposed	0,1	0,1	0,1	0,1	0,1	0,1	0,2
SE_A_Fin_5_weeks	Control	0,1	0,1	0,1	0,1	0,2	0,0	0,3
SE_A_Fin_5_weeks	Exposed	0,1	0,0	0,1	0,1	0,1	0,1	0,2
SE_Lenght_11_weeks	Control	0,4	0,2	0,3	0,2	0,5	0,0	0,9
SE_Length_11_weeks	Exposed	0,3	0,2	0,4	0,2	0,4	0,0	0,7
SE_Length_5_weeks	Control	0,3	0,2	0,3	0,1	0,5	0,1	0,8
SE_Length_5_weeks	Exposed	0,4	0,2	0,4	0,3	0,5	0,1	0,8
SE_Length_Fin_11_weeks	Control	0,1	0,0	0,1	0,1	0,1	0,0	0,2
SE_Length_Fin_11_weeks	Exposed	0,1	0,0	0,1	0,1	0,1	0,0	0,1

SE_Length_Fin_5_weeks	Control	0,1	0,0	0,1	0,1	0,1	0,0	0,1
SE_Length_Fin_5_weeks	Exposed	0,1	0,0	0,1	0,0	0,1	0,0	0,1
SE_Width_11_weeks	Control	0,0	0,0	0,0	0,0	0,1	0,0	0,2
SE_ Width_11_weeks	Exposed	0,0	0,0	0,0	0,0	0,1	0,0	0,1
SE_Width_5_weeks	Control	0,1	0,0	0,1	0,0	0,1	0,0	0,1
SE_Width_5_weeks	Exposed	0,0	0,0	0,0	0,0	0,1	0,0	0,1

Sharks - Acute exposure

Behavioural parameters	**Treatment**	**Phase**	**Mean**	**SD**	**Median**	**Q25**	**Q75**	**Min**	**Max**
Horizontal Breaching occurrence	Control	baseline	2,3	7,0	0,0	0,0	0,0	0,0	35,0
Horizontal Breaching occurrence	Control	EMF	3,1	9,1	0,0	0,0	0,0	0,0	43,0
Horizontal Breaching occurrence	Control	recovery	2,4	5,1	0,0	0,0	0,0	0,0	19,0
Horizontal Breaching occurrence	Exposed	baseline	0,4	1,0	0,0	0,0	0,0	0,0	4,0
Horizontal Breaching occurrence	Exposed	EMF	1,1	3,0	0,0	0,0	0,0	0,0	12,0
Horizontal Breaching occurrence	Exposed	recovery	0,1	0,4	0,0	0,0	0,0	0,0	2,0
Inactivity occurrence	Control	baseline	2,3	2,1	1,0	1,0	3,0	1,0	9,0
Inactivity occurrence	Control	EMF	3,0	3,3	1,0	1,0	4,0	1,0	16,0
Inactivity occurrence	Control	recovery	2,2	1,9	1,0	1,0	2,0	1,0	8,0
Inactivity occurrence	Exposed	baseline	1,6	1,4	1,0	1,0	1,0	1,0	7,0
Inactivity occurrence	Exposed	EMF	1,7	1,3	1,0	1,0	2,0	1,0	5,0
Inactivity occurrence	Exposed	recovery	1,3	1,0	1,0	1,0	1,0	1,0	6,0

Inactivity time in seconds	Control	baseline	528,6	159,1	600,0	563,1	600,0	10,8	600,0
Inactivity time in seconds	Control	EMF	517,4	163,7	600,0	541,8	600,0	69,2	600,0
Inactivity time in seconds	Control	recovery	531,4	132,2	600,0	515,8	600,0	39,5	600,0
Inactivity time in seconds	Exposed	baseline	587,5	27,3	600,0	599,5	600,0	511,1	600,0
Inactivity time in seconds	Exposed	EMF	580,1	36,7	600,0	582,5	600,0	486,3	600,0
Inactivity time in seconds	Exposed	recovery	594,1	21,8	600,0	600,0	600,0	500,1	600,0
Locomotion occurrence	Control	baseline	1,6	2,5	0,0	0,0	3,0	0,0	10,0
Locomotion occurrence	Control	EMF	2,3	3,8	0,0	0,0	3,8	0,0	17,0
Locomotion occurrence	Control	recovery	1,4	2,2	0,0	0,0	1,8	0,0	8,0
Locomotion occurrence	Exposed	baseline	0,6	1,4	0,0	0,0	0,0	0,0	6,0
Locomotion occurrence	Exposed	EMF	0,7	1,3	0,0	0,0	1,0	0,0	4,0
Locomotion occurrence	Exposed	recovery	0,3	1,0	0,0	0,0	0,0	0,0	5,0
Locomotion time in seconds	Control	baseline	59,7	134,3	0,0	0,0	36,9	0,0	589,2
Locomotion time in seconds	Control	EMF	70,1	143,9	0,0	0,0	58,0	0,0	530,8
Locomotion time in seconds	Control	recovery	68,6	132,2	0,0	0,0	84,2	0,0	560,5
Locomotion time in seconds	Exposed	baseline	12,5	27,4	0,0	0,0	0,0	0,0	88,9
Locomotion time in seconds	Exposed	EMF	19,9	36,7	0,0	0,0	17,5	0,0	113,7
Locomotion time in seconds	Exposed	recovery	5,8	21,9	0,0	0,0	0,0	0,0	99,9
Surface breaking occurrence	Control	baseline	7,3	18,7	0,0	0,0	1,0	0,0	68,0
Surface breaking occurrence	Control	EMF	7,3	17,1	0,0	0,0	5,0	0,0	67,0
Surface breaking occurrence	Control	recovery	6,6	15,0	0,0	0,0	5,3	0,0	68,0

Surface breaking occurrence	Exposed	baseline	1,1	2,4	0,0	0,0	0,0	0,0	9,0
Surface breaking occurrence	Exposed	EMF	1,2	2,9	0,0	0,0	1,0	0,0	14,0
Surface breaking occurrence	Exposed	recovery	0,4	1,4	0,0	0,0	0,0	0,0	6,0
Surface breaking time seconds	Control	baseline	33,9	64,0	0,0	0,0	28,0	0,0	202,2
Surface breaking time seconds	Control	EMF	46,1	98,9	0,0	0,0	55,2	0,0	476,6
Surface breaking time seconds	Control	recovery	34,0	57,5	0,0	0,0	60,0	0,0	224,6
Surface breaking time seconds	Exposed	baseline	9,9	22,4	0,0	0,0	0,0	0,0	81,4
Surface breaking time seconds	Exposed	EMF	14,7	29,0	0,0	0,0	11,6	0,0	107,6
Surface breaking time seconds	Exposed	recovery	4,2	18,3	0,0	0,0	0,0	0,0	94,1
Ventilation occurrence	Control	baseline	123,4	43,7	137,5	108,8	151,0	0,0	191,0
Ventilation occurrence	Control	EMF	116,7	46,4	125,0	99,0	144,8	0,0	193,0
Ventilation occurrence	Control	recovery	122,6	37,7	128,5	108,3	143,0	0,0	179,0
Ventilation occurrence	Exposed	baseline	152,9	15,0	154,0	140,0	161,5	126,0	187,0
Ventilation occurrence	Exposed	EMF	140,7	30,3	143,0	133,5	159,5	76,0	194,0
Ventilation occurrence	Exposed	recovery	144,4	20,6	146,0	133,5	159,0	101,0	186,0
Ventilation_per_min	Control	baseline	70,2	13,0	72,8	63,3	76,4	37,3	95,5
Ventilation_per_min	Control	EMF	66,6	15,3	70,3	57,8	74,9	34,0	96,5
Ventilation_per_min	Control	recovery	68,4	12,1	69,3	62,5	75,9	39,3	89,5
Ventilation_per_min	Exposed	baseline	76,1	6,8	77,0	71,0	80,5	63,0	89,5
Ventilation_per_min	Exposed	EMF	72,6	13,3	71,5	69,5	81,0	40,0	97,0
Ventilation_per_min	Exposed	recovery	72,4	9,6	73,0	67,5	78,5	50,5	93,0

Rays - baseline

Behavioural parameters	Treatment	Mean	SD	Median	Q25	Q75	Min	Max
Activity_time	Control	158,3	195,8	9,5	0,0	293,1	0,0	582,1
Activity_time	Exposed	161,5	197,7	26,0	0,0	302,7	0,0	512,9
burying_movement_occurance	Control	1,4	1,8	1,0	0,0	2,5	0,0	7,0
burying_movement_occurance	Exposed	2,5	3,5	1,0	0,0	3,3	0,0	10,0
horizontal_resting_occurance	Control	11,6	14,8	3,0	1,0	18,0	1,0	48,0
horizontal_resting_occurance	Exposed	8,8	11,9	3,0	1,0	11,8	1,0	50,0
horizontal_resting_time_s	Control	441,7	195,8	590,5	306,9	600,0	17,9	600,0
horizontal_resting_time_s	Exposed	438,5	197,7	574,0	297,3	600,0	87,1	600,0
stepping_occurance	Control	13,8	17,2	2,0	0,0	27,5	0,0	49,0
stepping_occurance	Exposed	10,6	14,9	2,0	0,0	19,3	0,0	56,0
stepping_time_s	Control	104,6	126,6	7,8	0,0	207,3	0,0	385,6
stepping_time_s	Exposed	122,6	157,6	24,7	0,0	224,4	0,0	472,8
surface_breaking_occurance	Control	3,5	8,4	0,0	0,0	0,5	0,0	33,0
surface_breaking_occurance	Exposed	3,5	6,9	0,0	0,0	4,0	0,0	26,0
surface_breaking_time_s	Control	47,0	120,7	0,0	0,0	1,8	0,0	450,4
surface_breaking_time_s	Exposed	32,8	81,9	0,0	0,0	18,5	0,0	334,6
ventilation_per_minute	Control	44,7	7,5	43,5	40,3	46,3	32,5	69,0
ventilation_per_minute	Exposed	42,5	4,6	43,5	39,8	46,1	33,5	51,0

Rays - Biometrics over time

Biometric parameters	Treatment	Age	Mean	SD	Median	Q25	Q75	Min	Max
Disk_length_at_birth	Control	0	5,8	0,4	5,8	5,6	6,1	5,1	6,5
Disk_length_at_birth	Exposed	0	5,8	0,3	5,8	5,6	6,0	5,3	6,1
Disk_width_at_birth	Control	0	8,1	0,5	8,2	8,1	8,3	7,0	8,8
Disk_width_at_birth	Exposed	0	8,2	0,4	8,2	8,0	8,4	7,7	8,8
Ratio_DW_DL	Control	0	1,4	0,0	1,4	1,4	1,4	1,3	1,4
Ratio_DW_DL	Exposed	0	1,4	0,1	1,4	1,4	1,4	1,3	1,5
Ratio_TL_DL	Control	0	2,2	0,1	2,3	2,2	2,3	2,0	2,4
Ratio_TL_DL	Exposed	0	2,2	0,1	2,2	2,2	2,3	2,1	2,3
Weight_at_birth	Control	0	12,4	1,0	12,3	11,8	13,1	10,6	13,6
Weight_at_birth	Exposed	0	11,9	0,5	11,8	11,7	11,8	11,3	13,1
Disk_length_age	Control	5	7,4	0,3	7,4	7,2	7,6	6,8	7,8
Disk_length_age	Control	14	7,5	0,2	7,5	7,3	7,6	7,0	7,7
Disk_length_age	Exposed	5	7,3	0,3	7,3	7,1	7,4	7,0	7,7
Disk_length_age	Exposed	14	7,4	0,3	7,3	7,2	7,6	6,9	8,0
Disk_width_age	Control	5	9,6	0,4	9,7	9,4	9,8	8,8	10,2
Disk_width_age	Control	14	9,7	0,3	9,8	9,6	9,9	9,2	10,2
Disk_width_age	Exposed	5	9,5	0,2	9,5	9,4	9,7	9,2	9,7
Disk_width_age	Exposed	14	9,6	0,3	9,5	9,4	9,8	9,1	10,0

Ratio_DW_DL_age	Control	5							
Ratio_DW_DL_age	Control	14	1,3	0,0	1,3	1,3	1,3	1,3	1,3
Ratio_DW_DL_age	Exposed	5							
Ratio_DW_DL_age	Exposed	14	1,3	0,0	1,3	1,3	1,3	1,2	1,3
Ratio_TL_DL_age	Control	5							
Ratio_TL_DL_age	Control	14	2,1	0,1	2,0	2,0	2,1	2,0	2,2
Ratio_TL_DL_age	Exposed	5							
Ratio_TL_DL_age	Exposed	14	2,0	0,1	2,1	2,0	2,1	2,0	2,1
Total_length_age	Control	5	15,2	0,7	15,5	15,2	15,6	13,7	15,8
Total_length_age	Control	14	15,4	0,6	15,6	15,4	15,7	14,2	16,2
Total_length_age	Exposed	5	14,7	0,3	14,7	14,5	14,9	14,4	15,1
Total_length_age	Exposed	14	14,9	0,5	14,8	14,7	15,1	14,3	15,8
Weight_age	Control	5							
Weight_age	Control	14	14,1	1,1	14,1	13,6	15,0	11,9	15,4
Weight_age	Exposed	5							
Weight_age	Exposed	14	14,0	1,2	14,2	13,4	14,6	11,7	15,5
Tail_lenght_5_weeks	Control	5	7,8						
Tail_lenght_5_weeks	Exposed	5	7,5						
Tail_lenght_14_weeks	Control	14	8,0	0,4					
Tail_lenght_14_weeks	Exposed	14	7,6	0,2					

Rays - Acute exposure

Behavioural parameters	Treatment	Phase	Mean	SD	Median	Q25	Q75	Min	Max
Activity_time	Control	baseline	158,3	195,8	9,5	0,0	293,1	0,0	582,1
Activity_time	Control	EMF	122,2	176,1	4,0	0,0	165,0	0,0	589,4
Activity_time	Control	recovery	121,5	195,9	0,0	0,0	159,3	0,0	581,9
Activity_time	Exposed	baseline	155,2	196,1	22,5	0,0	269,5	0,0	512,9
Activity_time	Exposed	EMF	162,8	198,7	72,4	0,0	278,8	0,0	576,9
Activity_time	Exposed	recovery	123,2	199,6	0,0	0,0	250,7	0,0	525,7
burying_movement_occurance	Control	baseline	1,4	1,8	1,0	0,0	2,5	0,0	7,0
burying_movement_occurance	Control	EMF	1,7	2,2	1,0	0,0	3,0	0,0	9,0
burying_movement_occurance	Control	recovery	1,1	1,8	0,0	0,0	1,0	0,0	6,0
burying_movement_occurance	Exposed	baseline	2,4	3,4	1,0	0,0	3,0	0,0	10,0
burying_movement_occurance	Exposed	EMF	2,2	2,5	1,5	0,0	3,0	0,0	8,0
burying_movement_occurance	Exposed	recovery	1,3	2,4	0,0	0,0	1,3	0,0	7,0
horizontal_resting_occurance	Control	baseline	11,6	14,8	3,0	1,0	18,0	1,0	48,0
horizontal_resting_occurance	Control	EMF	9,5	12,4	2,0	1,0	13,5	1,0	50,0
horizontal_resting_occurance	Control	recovery	7,6	9,7	1,0	1,0	13,5	1,0	32,0
horizontal_resting_occurance	Exposed	baseline	8,5	11,7	3,0	1,0	11,0	1,0	50,0
horizontal_resting_occurance	Exposed	EMF	6,6	7,9	4,0	1,0	7,5	1,0	30,0
horizontal_resting_occurance	Exposed	recovery	5,4	8,0	1,0	1,0	7,5	1,0	30,0

horizontal_resting_time_s	Control	baseline	441,7	195,8	590,5	306,9	600,0	17,9	600,0
horizontal_resting_time_s	Control	EMF	477,8	176,1	596,0	435,0	600,0	10,6	600,0
horizontal_resting_time_s	Control	recovery	478,5	195,9	600,0	440,7	600,0	18,1	600,0
horizontal_resting_time_s	Exposed	baseline	444,8	196,1	577,5	330,5	600,0	87,1	600,0
horizontal_resting_time_s	Exposed	EMF	437,2	198,7	527,6	321,2	600,0	23,1	600,0
horizontal_resting_time_s	Exposed	recovery	476,8	199,6	600,0	349,3	600,0	74,3	600,0
stepping_occurance	Control	baseline	13,8	17,2	2,0	0,0	27,5	0,0	49,0
stepping_occurance	Control	EMF	12,4	16,4	1,0	0,0	16,5	0,0	49,0
stepping_occurance	Control	recovery	10,8	16,1	0,0	0,0	19,0	0,0	46,0
stepping_occurance	Exposed	baseline	10,2	14,7	2,0	0,0	19,0	0,0	56,0
stepping_occurance	Exposed	EMF	9,4	11,7	4,5	0,0	18,0	0,0	34,0
stepping_occurance	Exposed	recovery	6,0	10,9	0,0	0,0	7,8	0,0	37,0
stepping_time_s	Control	baseline	104,6	126,6	7,8	0,0	207,3	0,0	385,6
stepping_time_s	Control	EMF	82,3	105,5	3,3	0,0	130,5	0,0	359,0
stepping_time_s	Control	recovery	77,2	109,8	0,0	0,0	143,1	0,0	360,5
stepping_time_s	Exposed	baseline	117,8	156,2	21,2	0,0	223,7	0,0	472,8
stepping_time_s	Exposed	EMF	125,5	155,6	66,8	0,0	195,7	0,0	460,2
stepping_time_s	Exposed	recovery	91,3	159,9	0,0	0,0	128,8	0,0	437,2
surface_breaking_occurance	Control	baseline	3,5	8,4	0,0	0,0	0,5	0,0	33,0
surface_breaking_occurance	Control	EMF	4,1	9,8	0,0	0,0	1,0	0,0	40,0

surface_breaking_occurance	Control	recovery	4,8	10,7	0,0	0,0	0,0	0,0	38,0
surface_breaking_occurance	Exposed	baseline	3,4	6,8	0,0	0,0	4,0	0,0	26,0
surface_breaking_occurance	Exposed	EMF	3,6	6,9	0,0	0,0	3,5	0,0	26,0
surface_breaking_occurance	Exposed	recovery	2,0	4,8	0,0	0,0	0,0	0,0	15,0
surface_breaking_time_s	Control	baseline	47,0	120,7	0,0	0,0	1,8	0,0	450,4
surface_breaking_time_s	Control	EMF	33,8	90,4	0,0	0,0	1,2	0,0	369,6
surface_breaking_time_s	Control	recovery	38,7	96,0	0,0	0,0	0,0	0,0	339,3
surface_breaking_time_s	Exposed	baseline	31,5	80,4	0,0	0,0	15,8	0,0	334,6
surface_breaking_time_s	Exposed	EMF	31,4	71,8	0,0	0,0	10,3	0,0	308,8
surface_breaking_time_s	Exposed	recovery	27,8	83,1	0,0	0,0	0,0	0,0	341,6
ventilation_per_minute	Control	baseline	44,7	7,5	43,5	40,3	46,3	32,5	69,0
ventilation_per_minute	Control	EMF	42,3	8,4	40,0	37,3	46,5	30,5	68,0
ventilation_per_minute	Control	recovery	41,5	7,8	40,5	38,0	43,0	30,0	68,0
ventilation_per_minute	Exposed	baseline	42,3	4,6	43,0	39,0	46,0	33,5	51,0
ventilation_per_minute	Exposed	EMF	41,5	5,7	41,0	38,9	44,9	28,0	51,5
ventilation_per_minute	Exposed	recovery	40,3	6,1	40,0	36,9	45,6	28,5	51,5

Sharks - baseline

Behavioural parameters	Treatment	Mean	SD	Median	Q25	Q75	Min	Max
Horizontal Breaching occurrence	Control	2,3	7,0	0,0	0,0	0,0	0,0	35,0
Horizontal Breaching occurrence	Exposed	0,4	1,0	0,0	0,0	0,0	0,0	4,0
Inactivity occurrence	Control	2,3	2,1	1,0	1,0	3,0	1,0	9,0
Inactivity occurrence	Exposed	1,6	1,4	1,0	1,0	1,0	1,0	7,0
Inactivity time in seconds	Control	528,6	159,1	600,0	563,1	600,0	10,8	600,0
Inactivity time in seconds	Exposed	587,5	27,3	600,0	599,5	600,0	511,1	600,0
Locomotion occurrence	Control	1,6	2,5	0,0	0,0	3,0	0,0	10,0
Locomotion occurrence	Exposed	0,6	1,4	0,0	0,0	0,0	0,0	6,0
Locomotion time in seconds	Control	59,7	134,3	0,0	0,0	36,9	0,0	589,2
Locomotion time in seconds	Exposed	12,5	27,4	0,0	0,0	0,0	0,0	88,9
Surface breaking occurrence	Control	7,3	18,7	0,0	0,0	1,0	0,0	68,0
Surface breaking occurrence	Exposed	1,1	2,4	0,0	0,0	0,0	0,0	9,0
Surface breaking time seconds	Control	33,9	64,0	0,0	0,0	28,0	0,0	202,2
Surface breaking time seconds	Exposed	9,9	22,4	0,0	0,0	0,0	0,0	81,4
Ventilation occurrence	Control	123,4	43,7	137,5	108,8	151,0	0,0	191,0
Ventilation occurrence	Exposed	152,9	15,0	154,0	140,0	161,5	126,0	187,0
Ventilation_per_min	Control	70,2	13,0	72,8	63,3	76,4	37,3	95,5
Ventilation_per_min	Exposed	76,1	6,8	77,0	71,0	80,5	63,0	89,5

Sharks - Biometrics over time	SE = standard error							
Biometric parameters	**Treatment**	**Mean**	**SD**	**Median**	**Q25**	**Q75**	**Min**	**Max**
Weight_at_birth	Control	4,8	0,6	4,8	4,4	5,4	3,8	5,6
Weight_at_birth	Exposed	5,0	0,3	5,1	4,7	5,2	4,3	5,4
Weight_11_weeks	Control	11,1	1,8	11,5	9,7	12,2	8,2	14,1
Weight_11_weeks	Exposed	11,1	2,0	10,5	9,6	12,2	8,6	15,2
Width_at_birth	Control	1,4	0,1	1,4	1,3	1,5	1,3	1,5
Width_at_birth	Exposed	1,4	0,1	1,4	1,4	1,4	1,2	1,5
Width_5_weeks	Control	1,6	0,1	1,7	1,5	1,7	1,4	1,9
Width_5_weeks	Exposed	1,7	0,1	1,7	1,6	1,7	1,5	1,9
Width_11_weeks	Control	1,8	0,1	1,8	1,8	1,9	1,7	2,0
Width_11_weeks	Exposed	1,8	0,1	1,8	1,8	1,9	1,7	2,0
pectoral_fin_length_at_birth	Control	0,9	0,1	1,0	0,9	1,0	0,8	1,0
pectoral_fin_length_at_birth	Exposed	1,1	0,1	1,1	1,0	1,1	0,9	1,2
pectoral_fin_lenght_5	Control	1,2	0,1	1,2	1,1	1,4	1,0	1,4
pectoral_fin_lenght_5	Exposed	1,2	0,1	1,2	1,1	1,2	1,1	1,5
pectoral_fin_lenght_11	Control	1,3	0,1	1,3	1,3	1,4	1,1	1,6
pectoral_fin_lenght_11	Exposed	1,4	0,1	1,4	1,3	1,5	1,2	1,5
Size_pectoral_fin_at_birth	Control	0,8	0,1	0,8	0,7	0,8	0,7	0,9
Size_pectoral_fin_at_birth	Exposed	0,9	0,1	0,8	0,8	0,9	0,7	1,0

Size_pectoral_fin_5	Control	1,2	0,2	1,2	1,1	1,4	0,9	1,4
Size_pectoral_fin_5	Exposed	1,3	0,2	1,2	1,2	1,2	1,1	1,7
Size_pectoral_fin_11	Control	1,5	0,2	1,5	1,4	1,6	1,1	2,0
Size_pectoral_fin_11	Exposed	1,6	0,2	1,6	1,6	1,6	1,3	1,9
Length_at_birth	Control	11,9	0,8	11,8	11,4	12,7	10,7	13,4
Length_at_birth	Exposed	12,4	0,6	12,3	11,9	12,8	11,5	13,4
Length_5_weeks	Control	14,4	1,1	14,6	13,5	15,5	12,3	15,9
Length_5_weeks	Exposed	15,3	1,1	15,0	14,8	15,3	14,0	18,0
Length_11_weeks	Control	16,3	1,3	16,5	15,5	17,4	13,8	18,1
Length_11_weeks	Exposed	16,7	1,1	16,5	15,9	17,1	15,3	19,1
SE_A_Fin_11_weeks	Control	0,1	0,1	0,1	0,1	0,1	0,0	0,2
SE_A_Fin_11_weeks	Exposed	0,1	0,1	0,1	0,1	0,1	0,1	0,2
SE_A_Fin_5_weeks	Control	0,1	0,1	0,1	0,1	0,2	0,0	0,3
SE_A_Fin_5_weeks	Exposed	0,1	0,0	0,1	0,1	0,1	0,1	0,2
SE_Lenght_11_weeks	Control	0,4	0,2	0,3	0,2	0,5	0,0	0,9
SE_Length_11_weeks	Exposed	0,3	0,2	0,4	0,2	0,4	0,0	0,7
SE_Length_5_weeks	Control	0,3	0,2	0,3	0,1	0,5	0,1	0,8
SE_Length_5_weeks	Exposed	0,4	0,2	0,4	0,3	0,5	0,1	0,8
SE_Length_Fin_11_weeks	Control	0,1	0,0	0,1	0,1	0,1	0,0	0,2
SE_Length_Fin_11_weeks	Exposed	0,1	0,0	0,1	0,1	0,1	0,0	0,1

SE_Length_Fin_5_weeks	Control	0,1	0,0	0,1	0,1	0,1	0,0	0,1
SE_Length_Fin_5_weeks	Exposed	0,1	0,0	0,1	0,0	0,1	0,0	0,1
SE_Width_11_weeks	Control	0,0	0,0	0,0	0,0	0,1	0,0	0,2
SE_ Width_11_weeks	Exposed	0,0	0,0	0,0	0,0	0,1	0,0	0,1
SE_Width_5_weeks	Control	0,1	0,0	0,1	0,0	0,1	0,0	0,1
SE_Width_5_weeks	Exposed	0,0	0,0	0,0	0,0	0,1	0,0	0,1

Sharks - Acute exposure

Behavioural parameters	**Treatment**	**Phase**	**Mean**	**SD**	**Median**	**Q25**	**Q75**	**Min**	**Max**
Horizontal Breaching occurrence	Control	baseline	2,3	7,0	0,0	0,0	0,0	0,0	35,0
Horizontal Breaching occurrence	Control	EMF	3,1	9,1	0,0	0,0	0,0	0,0	43,0
Horizontal Breaching occurrence	Control	recovery	2,4	5,1	0,0	0,0	0,0	0,0	19,0
Horizontal Breaching occurrence	Exposed	baseline	0,4	1,0	0,0	0,0	0,0	0,0	4,0
Horizontal Breaching occurrence	Exposed	EMF	1,1	3,0	0,0	0,0	0,0	0,0	12,0
Horizontal Breaching occurrence	Exposed	recovery	0,1	0,4	0,0	0,0	0,0	0,0	2,0
Inactivity occurrence	Control	baseline	2,3	2,1	1,0	1,0	3,0	1,0	9,0
Inactivity occurrence	Control	EMF	3,0	3,3	1,0	1,0	4,0	1,0	16,0
Inactivity occurrence	Control	recovery	2,2	1,9	1,0	1,0	2,0	1,0	8,0
Inactivity occurrence	Exposed	baseline	1,6	1,4	1,0	1,0	1,0	1,0	7,0
Inactivity occurrence	Exposed	EMF	1,7	1,3	1,0	1,0	2,0	1,0	5,0
Inactivity occurrence	Exposed	recovery	1,3	1,0	1,0	1,0	1,0	1,0	6,0

Inactivity time in seconds	Control	baseline	528,6	159,1	600,0	563,1	600,0	10,8	600,0
Inactivity time in seconds	Control	EMF	517,4	163,7	600,0	541,8	600,0	69,2	600,0
Inactivity time in seconds	Control	recovery	531,4	132,2	600,0	515,8	600,0	39,5	600,0
Inactivity time in seconds	Exposed	baseline	587,5	27,3	600,0	599,5	600,0	511,1	600,0
Inactivity time in seconds	Exposed	EMF	580,1	36,7	600,0	582,5	600,0	486,3	600,0
Inactivity time in seconds	Exposed	recovery	594,1	21,8	600,0	600,0	600,0	500,1	600,0
Locomotion occurrence	Control	baseline	1,6	2,5	0,0	0,0	3,0	0,0	10,0
Locomotion occurrence	Control	EMF	2,3	3,8	0,0	0,0	3,8	0,0	17,0
Locomotion occurrence	Control	recovery	1,4	2,2	0,0	0,0	1,8	0,0	8,0
Locomotion occurrence	Exposed	baseline	0,6	1,4	0,0	0,0	0,0	0,0	6,0
Locomotion occurrence	Exposed	EMF	0,7	1,3	0,0	0,0	1,0	0,0	4,0
Locomotion occurrence	Exposed	recovery	0,3	1,0	0,0	0,0	0,0	0,0	5,0
Locomotion time in seconds	Control	baseline	59,7	134,3	0,0	0,0	36,9	0,0	589,2
Locomotion time in seconds	Control	EMF	70,1	143,9	0,0	0,0	58,0	0,0	530,8
Locomotion time in seconds	Control	recovery	68,6	132,2	0,0	0,0	84,2	0,0	560,5
Locomotion time in seconds	Exposed	baseline	12,5	27,4	0,0	0,0	0,0	0,0	88,9
Locomotion time in seconds	Exposed	EMF	19,9	36,7	0,0	0,0	17,5	0,0	113,7
Locomotion time in seconds	Exposed	recovery	5,8	21,9	0,0	0,0	0,0	0,0	99,9
Surface breaking occurrence	Control	baseline	7,3	18,7	0,0	0,0	1,0	0,0	68,0
Surface breaking occurrence	Control	EMF	7,3	17,1	0,0	0,0	5,0	0,0	67,0
Surface breaking occurrence	Control	recovery	6,6	15,0	0,0	0,0	5,3	0,0	68,0

Surface breaking occurrence	Exposed	baseline	1,1	2,4	0,0	0,0	0,0	0,0	9,0
Surface breaking occurrence	Exposed	EMF	1,2	2,9	0,0	0,0	1,0	0,0	14,0
Surface breaking occurrence	Exposed	recovery	0,4	1,4	0,0	0,0	0,0	0,0	6,0
Surface breaking time seconds	Control	baseline	33,9	64,0	0,0	0,0	28,0	0,0	202,2
Surface breaking time seconds	Control	EMF	46,1	98,9	0,0	0,0	55,2	0,0	476,6
Surface breaking time seconds	Control	recovery	34,0	57,5	0,0	0,0	60,0	0,0	224,6
Surface breaking time seconds	Exposed	baseline	9,9	22,4	0,0	0,0	0,0	0,0	81,4
Surface breaking time seconds	Exposed	EMF	14,7	29,0	0,0	0,0	11,6	0,0	107,6
Surface breaking time seconds	Exposed	recovery	4,2	18,3	0,0	0,0	0,0	0,0	94,1
Ventilation occurrence	Control	baseline	123,4	43,7	137,5	108,8	151,0	0,0	191,0
Ventilation occurrence	Control	EMF	116,7	46,4	125,0	99,0	144,8	0,0	193,0
Ventilation occurrence	Control	recovery	122,6	37,7	128,5	108,3	143,0	0,0	179,0
Ventilation occurrence	Exposed	baseline	152,9	15,0	154,0	140,0	161,5	126,0	187,0
Ventilation occurrence	Exposed	EMF	140,7	30,3	143,0	133,5	159,5	76,0	194,0
Ventilation occurrence	Exposed	recovery	144,4	20,6	146,0	133,5	159,0	101,0	186,0
Ventilation_per_min	Control	baseline	70,2	13,0	72,8	63,3	76,4	37,3	95,5
Ventilation_per_min	Control	EMF	66,6	15,3	70,3	57,8	74,9	34,0	96,5
Ventilation_per_min	Control	recovery	68,4	12,1	69,3	62,5	75,9	39,3	89,5
Ventilation_per_min	Exposed	baseline	76,1	6,8	77,0	71,0	80,5	63,0	89,5
Ventilation_per_min	Exposed	EMF	72,6	13,3	71,5	69,5	81,0	40,0	97,0
Ventilation_per_min	Exposed	recovery	72,4	9,6	73,0	67,5	78,5	50,5	93,0

Rays - baseline

Behavioural parameters	Treatment	Mean	SD	Median	Q25	Q75	Min	Max
Activity_time	Control	158,3	195,8	9,5	0,0	293,1	0,0	582,1
Activity_time	Exposed	161,5	197,7	26,0	0,0	302,7	0,0	512,9
burying_movement_occurance	Control	1,4	1,8	1,0	0,0	2,5	0,0	7,0
burying_movement_occurance	Exposed	2,5	3,5	1,0	0,0	3,3	0,0	10,0
horizontal_resting_occurance	Control	11,6	14,8	3,0	1,0	18,0	1,0	48,0
horizontal_resting_occurance	Exposed	8,8	11,9	3,0	1,0	11,8	1,0	50,0
horizontal_resting_time_s	Control	441,7	195,8	590,5	306,9	600,0	17,9	600,0
horizontal_resting_time_s	Exposed	438,5	197,7	574,0	297,3	600,0	87,1	600,0
stepping_occurance	Control	13,8	17,2	2,0	0,0	27,5	0,0	49,0
stepping_occurance	Exposed	10,6	14,9	2,0	0,0	19,3	0,0	56,0
stepping_time_s	Control	104,6	126,6	7,8	0,0	207,3	0,0	385,6
stepping_time_s	Exposed	122,6	157,6	24,7	0,0	224,4	0,0	472,8
surface_breaking_occurance	Control	3,5	8,4	0,0	0,0	0,5	0,0	33,0
surface_breaking_occurance	Exposed	3,5	6,9	0,0	0,0	4,0	0,0	26,0
surface_breaking_time_s	Control	47,0	120,7	0,0	0,0	1,8	0,0	450,4
surface_breaking_time_s	Exposed	32,8	81,9	0,0	0,0	18,5	0,0	334,6
ventilation_per_minute	Control	44,7	7,5	43,5	40,3	46,3	32,5	69,0
ventilation_per_minute	Exposed	42,5	4,6	43,5	39,8	46,1	33,5	51,0

Rays - Biometrics over time

Biometric parameters	Treatment	Age	Mean	SD	Median	Q25	Q75	Min	Max
Disk_length_at_birth	Control	0	5,8	0,4	5,8	5,6	6,1	5,1	6,5
Disk_length_at_birth	Exposed	0	5,8	0,3	5,8	5,6	6,0	5,3	6,1
Disk_width_at_birth	Control	0	8,1	0,5	8,2	8,1	8,3	7,0	8,8
Disk_width_at_birth	Exposed	0	8,2	0,4	8,2	8,0	8,4	7,7	8,8
Ratio_DW_DL	Control	0	1,4	0,0	1,4	1,4	1,4	1,3	1,4
Ratio_DW_DL	Exposed	0	1,4	0,1	1,4	1,4	1,4	1,3	1,5
Ratio_TL_DL	Control	0	2,2	0,1	2,3	2,2	2,3	2,0	2,4
Ratio_TL_DL	Exposed	0	2,2	0,1	2,2	2,2	2,3	2,1	2,3
Weight_at_birth	Control	0	12,4	1,0	12,3	11,8	13,1	10,6	13,6
Weight_at_birth	Exposed	0	11,9	0,5	11,8	11,7	11,8	11,3	13,1
Disk_length_age	Control	5	7,4	0,3	7,4	7,2	7,6	6,8	7,8
Disk_length_age	Control	14	7,5	0,2	7,5	7,3	7,6	7,0	7,7
Disk_length_age	Exposed	5	7,3	0,3	7,3	7,1	7,4	7,0	7,7
Disk_length_age	Exposed	14	7,4	0,3	7,3	7,2	7,6	6,9	8,0
Disk_width_age	Control	5	9,6	0,4	9,7	9,4	9,8	8,8	10,2
Disk_width_age	Control	14	9,7	0,3	9,8	9,6	9,9	9,2	10,2
Disk_width_age	Exposed	5	9,5	0,2	9,5	9,4	9,7	9,2	9,7
Disk_width_age	Exposed	14	9,6	0,3	9,5	9,4	9,8	9,1	10,0

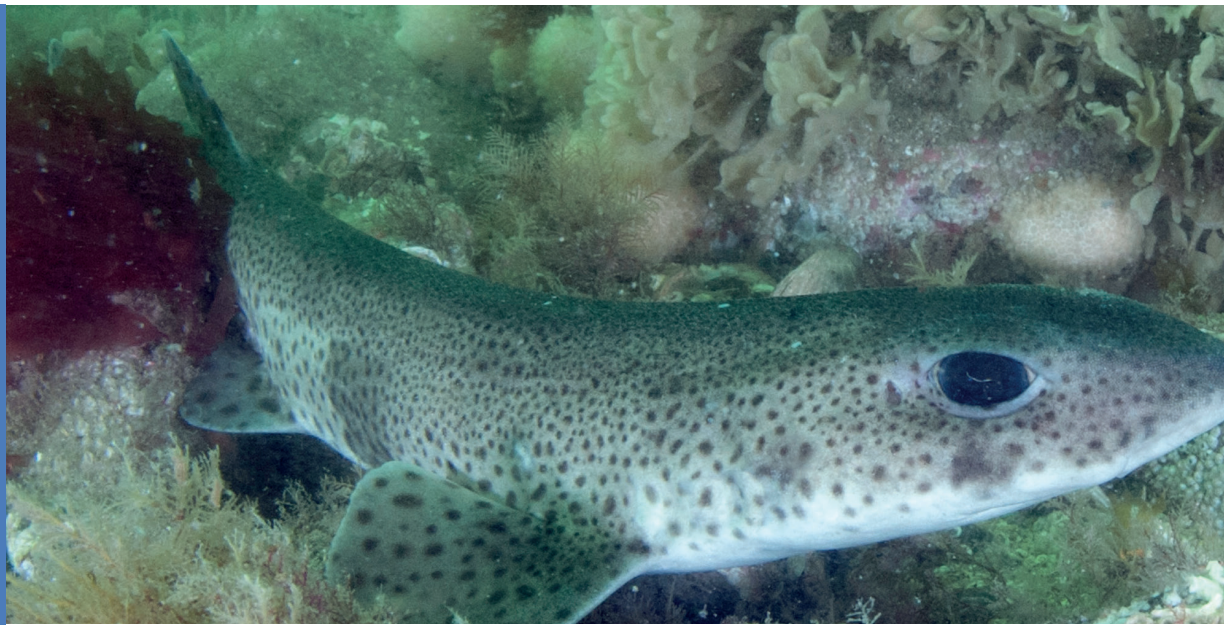
Ratio_DW_DL_age	Control	5							
Ratio_DW_DL_age	Control	14	1,3	0,0	1,3	1,3	1,3	1,3	1,3
Ratio_DW_DL_age	Exposed	5							
Ratio_DW_DL_age	Exposed	14	1,3	0,0	1,3	1,3	1,3	1,2	1,3
Ratio_TL_DL_age	Control	5							
Ratio_TL_DL_age	Control	14	2,1	0,1	2,0	2,0	2,1	2,0	2,2
Ratio_TL_DL_age	Exposed	5							
Ratio_TL_DL_age	Exposed	14	2,0	0,1	2,1	2,0	2,1	2,0	2,1
Total_length_age	Control	5	15,2	0,7	15,5	15,2	15,6	13,7	15,8
Total_length_age	Control	14	15,4	0,6	15,6	15,4	15,7	14,2	16,2
Total_length_age	Exposed	5	14,7	0,3	14,7	14,5	14,9	14,4	15,1
Total_length_age	Exposed	14	14,9	0,5	14,8	14,7	15,1	14,3	15,8
Weight_age	Control	5							
Weight_age	Control	14	14,1	1,1	14,1	13,6	15,0	11,9	15,4
Weight_age	Exposed	5							
Weight_age	Exposed	14	14,0	1,2	14,2	13,4	14,6	11,7	15,5
Tail_lenght_5_weeks	Control	5	7,8						
Tail_lenght_5_weeks	Exposed	5	7,5						
Tail_lenght_14_weeks	Control	14	8,0	0,4					
Tail_lenght_14_weeks	Exposed	14	7,6	0,2					

Rays - Acute exposure

Behavioural parameters	Treatment	Phase	Mean	SD	Median	Q25	Q75	Min	Max
Activity_time	Control	baseline	158,3	195,8	9,5	0,0	293,1	0,0	582,1
Activity_time	Control	EMF	122,2	176,1	4,0	0,0	165,0	0,0	589,4
Activity_time	Control	recovery	121,5	195,9	0,0	0,0	159,3	0,0	581,9
Activity_time	Exposed	baseline	155,2	196,1	22,5	0,0	269,5	0,0	512,9
Activity_time	Exposed	EMF	162,8	198,7	72,4	0,0	278,8	0,0	576,9
Activity_time	Exposed	recovery	123,2	199,6	0,0	0,0	250,7	0,0	525,7
burying_movement_occurance	Control	baseline	1,4	1,8	1,0	0,0	2,5	0,0	7,0
burying_movement_occurance	Control	EMF	1,7	2,2	1,0	0,0	3,0	0,0	9,0
burying_movement_occurance	Control	recovery	1,1	1,8	0,0	0,0	1,0	0,0	6,0
burying_movement_occurance	Exposed	baseline	2,4	3,4	1,0	0,0	3,0	0,0	10,0
burying_movement_occurance	Exposed	EMF	2,2	2,5	1,5	0,0	3,0	0,0	8,0
burying_movement_occurance	Exposed	recovery	1,3	2,4	0,0	0,0	1,3	0,0	7,0
horizontal_resting_occurance	Control	baseline	11,6	14,8	3,0	1,0	18,0	1,0	48,0
horizontal_resting_occurance	Control	EMF	9,5	12,4	2,0	1,0	13,5	1,0	50,0
horizontal_resting_occurance	Control	recovery	7,6	9,7	1,0	1,0	13,5	1,0	32,0
horizontal_resting_occurance	Exposed	baseline	8,5	11,7	3,0	1,0	11,0	1,0	50,0
horizontal_resting_occurance	Exposed	EMF	6,6	7,9	4,0	1,0	7,5	1,0	30,0
horizontal_resting_occurance	Exposed	recovery	5,4	8,0	1,0	1,0	7,5	1,0	30,0

horizontal_resting_time_s	Control	baseline	441,7	195,8	590,5	306,9	600,0	17,9	600,0
horizontal_resting_time_s	Control	EMF	477,8	176,1	596,0	435,0	600,0	10,6	600,0
horizontal_resting_time_s	Control	recovery	478,5	195,9	600,0	440,7	600,0	18,1	600,0
horizontal_resting_time_s	Exposed	baseline	444,8	196,1	577,5	330,5	600,0	87,1	600,0
horizontal_resting_time_s	Exposed	EMF	437,2	198,7	527,6	321,2	600,0	23,1	600,0
horizontal_resting_time_s	Exposed	recovery	476,8	199,6	600,0	349,3	600,0	74,3	600,0
stepping_occurance	Control	baseline	13,8	17,2	2,0	0,0	27,5	0,0	49,0
stepping_occurance	Control	EMF	12,4	16,4	1,0	0,0	16,5	0,0	49,0
stepping_occurance	Control	recovery	10,8	16,1	0,0	0,0	19,0	0,0	46,0
stepping_occurance	Exposed	baseline	10,2	14,7	2,0	0,0	19,0	0,0	56,0
stepping_occurance	Exposed	EMF	9,4	11,7	4,5	0,0	18,0	0,0	34,0
stepping_occurance	Exposed	recovery	6,0	10,9	0,0	0,0	7,8	0,0	37,0
stepping_time_s	Control	baseline	104,6	126,6	7,8	0,0	207,3	0,0	385,6
stepping_time_s	Control	EMF	82,3	105,5	3,3	0,0	130,5	0,0	359,0
stepping_time_s	Control	recovery	77,2	109,8	0,0	0,0	143,1	0,0	360,5
stepping_time_s	Exposed	baseline	117,8	156,2	21,2	0,0	223,7	0,0	472,8
stepping_time_s	Exposed	EMF	125,5	155,6	66,8	0,0	195,7	0,0	460,2
stepping_time_s	Exposed	recovery	91,3	159,9	0,0	0,0	128,8	0,0	437,2
surface_breaking_occurance	Control	baseline	3,5	8,4	0,0	0,0	0,5	0,0	33,0
surface_breaking_occurance	Control	EMF	4,1	9,8	0,0	0,0	1,0	0,0	40,0

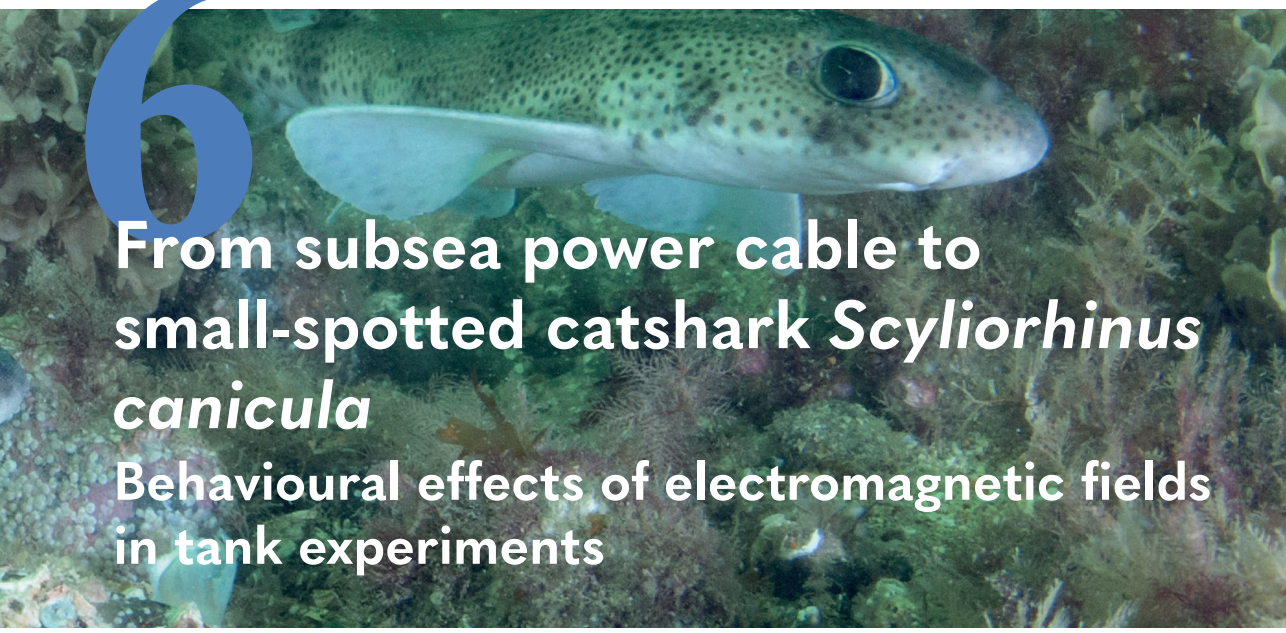
surface_breaking_occurance	Control	recovery	4,8	10,7	0,0	0,0	0,0	0,0	38,0
surface_breaking_occurance	Exposed	baseline	3,4	6,8	0,0	0,0	4,0	0,0	26,0
surface_breaking_occurance	Exposed	EMF	3,6	6,9	0,0	0,0	3,5	0,0	26,0
surface_breaking_occurance	Exposed	recovery	2,0	4,8	0,0	0,0	0,0	0,0	15,0
surface_breaking_time_s	Control	baseline	47,0	120,7	0,0	0,0	1,8	0,0	450,4
surface_breaking_time_s	Control	EMF	33,8	90,4	0,0	0,0	1,2	0,0	369,6
surface_breaking_time_s	Control	recovery	38,7	96,0	0,0	0,0	0,0	0,0	339,3
surface_breaking_time_s	Exposed	baseline	31,5	80,4	0,0	0,0	15,8	0,0	334,6
surface_breaking_time_s	Exposed	EMF	31,4	71,8	0,0	0,0	10,3	0,0	308,8
surface_breaking_time_s	Exposed	recovery	27,8	83,1	0,0	0,0	0,0	0,0	341,6
ventilation_per_minute	Control	baseline	44,7	7,5	43,5	40,3	46,3	32,5	69,0
ventilation_per_minute	Control	EMF	42,3	8,4	40,0	37,3	46,5	30,5	68,0
ventilation_per_minute	Control	recovery	41,5	7,8	40,5	38,0	43,0	30,0	68,0
ventilation_per_minute	Exposed	baseline	42,3	4,6	43,0	39,0	46,0	33,5	51,0
ventilation_per_minute	Exposed	EMF	41,5	5,7	41,0	38,9	44,9	28,0	51,5
ventilation_per_minute	Exposed	recovery	40,3	6,1	40,0	36,9	45,6	28,5	51,5



Abstract

Subsea power cables are expanding in number and capacity due to increasing demand to transport offshore generated energy. Energy transported through a cable creates an electromagnetic field (EMF). Elasmobranchs are dependent on their perception of the earth's magnetic field and biologically induced electric fields, for orientation, navigation, locating conspecifics and detecting prey. EMF levels from subsea power cables will add to natural signals potentially disrupting elasmobranch perception, but the effects are not fully understood. Reported behavioural responses include attraction, disturbance, and indifference, varying with exposure type, level and experimental set-up. In this study, the effects of EMF on swimming behaviour of 14 individual small-spotted catshark *Scyliorhinus canicula* were studied. All sharks were exposed to field-relevant EMF gradients cables in three trials: 15.0 μT AC, 19.6 μT DC, and a control treatment. Sharks showed no startle response to EMF onset, did not alter movement towards or away from the cable, and crossed it as frequently as in control trials. Hidden Markov Models showed that behavioural states were best explained by EMF treatment, trial order

https://doi.org/10.1016/j.marenvres.2025.107127



6 From subsea power cable to small-spotted catshark *Scyliorhinus canicula*

Behavioural effects of electromagnetic fields in tank experiments

and sex. Sharks showed 25 % less time transiting during DC trials when compared to AC and control trials. These findings indicate reason for further refined studies to better determine behavioural effects from direct current subsea power cables with *S. canicula*, for example using tagging studies. In addition, exploring effects on other species will help obtain a broader understanding of the potential impacts of EMF on benthic elasmobranchs.

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Published in Marine Environmental Research | June 2025

6.1 Introduction

Offshore energy production plays a crucial role in the transition to renewable energy and is expanding rapidly. To scale up from 16 GW offshore wind energy today, to 61 GW in 2030 and the projected 340 GW by 2050 in European Union waters, subsea power cables (SPC) must transport over 20 times more wind generated power (European Court of Auditors, 2023; Wind Europe, 2023). SPC generate electromagnetic fields (EMF) which consist of an electric field (between two charged particles) and a magnetic field (between to magnetic poles). The direct electric field is confined inside the cable due to shielding. The magnetic field protrudes into the environment and generates an induced electric field in flowing water, which is most notable for alternating current (AC) and negligible for direct current (DC) cables. AC cables carry current that periodically reverses direction (50 Hz in Europe), generating a time-varying magnetic field, while DC cables carry constant current, producing a steady magnetic field that can interact with the Earth's magnetic field. As an EMF is a magnetic field generated around moving charged particles, the electric and magnetic field components are closely related. Naturally, magnetic fields are omnipresent, such as the Earth's magnetic field (25–65 μT), and create induced electric fields in the marine environment (Gill et al., 2014; Hayakawa et al., 2004). In 2030, an estimated 5.5 % of the Dutch continental shelf will be influenced by SPC-generated EMF (Hermans et al., 2024). The range and intensity of EMF depend on cable characteristics, amount of power transported, and the power type e.g. AC or DC (Hutchison et al., 2021; Normandeau et al., 2011; Taormina et al., 2018). Modelling indicates that EMF from export SPC can be detectable above background levels, up to 60 m from high voltage 220 kV AC (export) cables and up to 125 m for bundled (phase conductors joint together) high voltage 525 kV DC cables, decreasing approximately as an inverse square of the distance to the cable. The potential exposure of marine organisms to EMF depends on the burial depth and the cable configuration. Cables that are buried deeper result in lower EMF levels on the seabed and in the water column. Cables within an offshore windfarm, or infield cables, are AC and have a network-like structure. Conversely, export cables cross long sections perpendicular to the coast and can be both AC (closer to shore) or DC (further from shore). EMF from SPC might affect the way electro- or magneto sensitive organisms perceive the environmental or biological cues and it is therefore possible that this influences their behaviour.

Various marine taxa can detect electrical or magnetic fields, including crustaceans, sea turtles, birds, mammals and fish, e.g. eel, salmon and sturgeon (Albert et al., 2020; Nyqvist et al., 2020; Wiltschko and Wiltschko, 2005). The only taxonomic group that is known to detect both electrical and magnetic fields are elasmobranchs; i.e. sharks, rays and skates (Anderson et al., 2017; Collin et al., 2015; Crooks, 2019; Meyer et al., 2005). Elasmobranchs use bioelectric fields for detection of predators, conspecifics and prey, and the geomagnetic field for navigation (local and long-distance migrations) (Ball et al., 2016; Kalmijn, 1971; Kempster et al., 2013; Klimley, 1993; Klimley et al., 2005; Newton and Kajiura, 2017, 2020; Sisneros and Tricas, 2002). All species of this subclass have highly sensitive ampullae

of Lorenzini which are used for electroception (Newton et al., 2019). It is not yet understood how magnetic field reception works, but three empirical drivers are hypothesised: (1) induction-based electroreception (2) magnetite-based magnetoreception and (3) radical pair mechanism (Albert et al., 2022; Anderson et al., 2017; Nyqvist et al., 2020). SPC routes intersect with elasmobranchs' habitat. This is especially relevant for bottom-dwelling (benthic) elasmobranchs, as their close proximity to cables in the seabed increases the rate of encountering elevated EMF (Hermans et al., 2024; Hutchison et al., 2020; Orr, 2016).

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

Elasmobranchs are highly electrosensitive and are reportedly able to detect down to a threshold limit of 5 nV/cm (Kalmijn, 1971). The magneto sensitivity is hypothesised to be at least 5 nT to perceive changes in the earth magnetic field needed for local and large-scale orientation (Hermans et al., 2024; Nyqvist et al., 2020). Behavioural responses to EMF depends on species, intensity, cable characteristics and frequency distribution of the signal (Bedore and Kajiura, 2013). A first exploration indicates that elasmobranchs may be unable to discriminate between artificial (dipole electrode) and natural (live crabs) EMF (Kimber et al., 2011). A variety of behavioural changes could be elicited from SPC-induced EMF during key activities such as foraging, mating, and/or migration (Hermans et al., 2024; Hutchison et al., 2020; Taormina et al., 2018). Mesocosm experiments indicated changes in foraging, or exploratory behaviour and shifts in habitat use in small-spotted catshark (*Scyliorhinus canicula*), thornback ray (*Raja clavata*) and little skate (*Leucoraja erinacea*) (Gill, 2009; Hutchison et al., 2020). Alterations in migratory patterns, such as course deviations and delays have been observed in magnetically sensitive species such as Chinook salmon (*Oncorhynchus tshawytscha*) and European eel (*Anguilla anguilla*) (Öhman et al., 2007; Westerberg and Lagenfelt, 2008; Wyman et al., 2018) and may also occur in elasmobranchs. Changes in activity levels induced by anthropogenic EMF stimuli could lead to less time foraging, reduced overall fitness, or an increased risk of predation due to reduced mobility, as suggested from experiments with crabs (Scott et al., 2021). Repeated behavioural changes (e.g. delays in migration, reduced swimming depth) when crossing export SPC might increase predation risk and hinder migration, potentially delaying encounters with important ecological cues like feeding or mating opportunities.

To study the potential effects of EMF on sharks, *S. canicula* (Linnaeus, 1758) was chosen as the test species due to its small size, hardiness and high abundance. *S. canicula* is a demersal shark and is very common in the north-east Atlantic (Compagno et al., 2005). It can be obtained relatively easily as it is commonly caught as bycatch of commercial fishing

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

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

6.2 Method & materials

6.2.1 Animals and holding conditions

In April 2023, 15 *S. canicula* were line-caught by anglers off the coast of Port Logan (Dumfries and Galloway, Scotland, UK). Animals were kept in fishing ponds prior to being transported to St Abbs Marine Station. All animals underwent a visual health check upon arrival (parasite presence, abrasions or lesions, and overall fitness) to ensure animal condition and assess whether the animals were at the desired level of fitness for participation in the experiments. Individuals were subsequently sexed (17M:14F), weighed, measured (total length), photographed and tagged using T-bar anchor tags (Hallprint fish tags) to allow for individual identification. All animals were held together in a 13 000 L tank measuring 7.5x1.7 ×1.0 m (LxWxH), provided with a constant flow of ambient temperature seawater, pumped from the North Sea in the Berwickshire Marine Reserve. Several recirculation filtration systems (Tropical Marine Centre) were used, providing UV, mechanical and biological filtration to the tank. Additional Fluval FX6 filters and air stones were added to maintain good water quality and oxygen levels, respectively. pH, ammonia, nitrite and nitrate were assessed weekly. The holding facility had a transparent roof, allowing the animals to be exposed to a natural photoperiod. Over the period of the experiment, there were an average of 17.33

±0.25 (sd) hours of daylight. Environmental enrichment, in the form of PVC shelter tubes (Ø 15 and 25 cm), rocks and fronds of seaweed were provided. Animals were fed 3 % of their bodyweight per week, late in the afternoon every other day, with a diet of Californian squid (*Loligo opalescens*), king prawn (*Penaeus vannamei*) and sand eel (*Amnodytes marinus*). Any food left uneaten was removed after 24 h and prior to the next batch of feeding. Supplements, including vitamins and iodine were added to the feeding regimen. Visual welfare checks were conducted on each individual daily.

6.2.2 Technical set-up

The experimental tank was custom-built 15.0x1.65 × 1.60 m (LxWxH), filled to a water level of 0.90 m and made of non-ferrous materials (fibreglass and wood), with opaque sides to prevent any visual disturbances from outside (Fig. 6.1). All possible sources for electromagnetic interference were shielded with radio-frequency identification (RFID) EMF shielding fabric (Lexiangnong, 20 % Nylon copper, 80 % polyester mesh and Lvfeier, 100 % Nylon). Two PVC pipes (1m Ø0.15 m) were placed at the 5 and 10 m mark to provide shelter opportunities during the trials. To monitor behaviour during the trials, 16 remote controlled infra-red cameras (Reolink RLC-810A) were suspended above the tank and recorded behaviour throughout the trials. The cameras did not interfere with the geomagnetic or solenoid generated EMF. The water was controlled in a closed recirculation system during the trials. Between trials, 50 %–100 % of the tank volume was replenished with seawater, depending on the tide, with full exchanges only possible at high tides. Inflowing seawater was filtered using filter socks to prevent sediment build-up.

The electromagnetic field was generated by two solenoids fixed to an aluminium frame connected to a Keysight N6715C DC Power Analyser with two 20 W Source/Measure units. Both solenoids were 1.9 × 2.9 m (WxH) and contained 32 turns of 1.25 mm2 copper wire. The solenoid system was placed at the 5-m mark of the 15-m experimental tank, to create an EMF gradient in the tank (Fig. 6.1). In the DC configuration, only the lower solenoid was in use and the maximum field generated was 19.6 μT. The magnetic field levels were measured at 135 points in the tank, before any experimentation began, with a Twinleaf VMR sensor and SYNC4 data acquisition system (Fig. S6.1c). In AC configuration, one solenoid was located on the horizontal frame and the other on the vertical frame. By controlling the two solenoids, coupled with the same frequency of 50 Hz, but with a phase difference of 90°, a rotating field was generated in the water volume around the frame, similar to a 3-phase AC transport cable. By setting the amplitude of the current in the horizontal solenoid twice as strong as the amplitude of the vertical solenoid, a circular rotating field was created in the centre of the vertical solenoid. The maximum AC magnetic field generated was 15.0 μT Root Mean Square (RMS) (Fig. 6.1b and S6.1b in more detail). The difference in AC and DC level can be explained by the physical changes in the coil positioning. The magnetic field generator was designed and fabricated by the Netherlands Organisation for Applied Scientific Research (TNO).

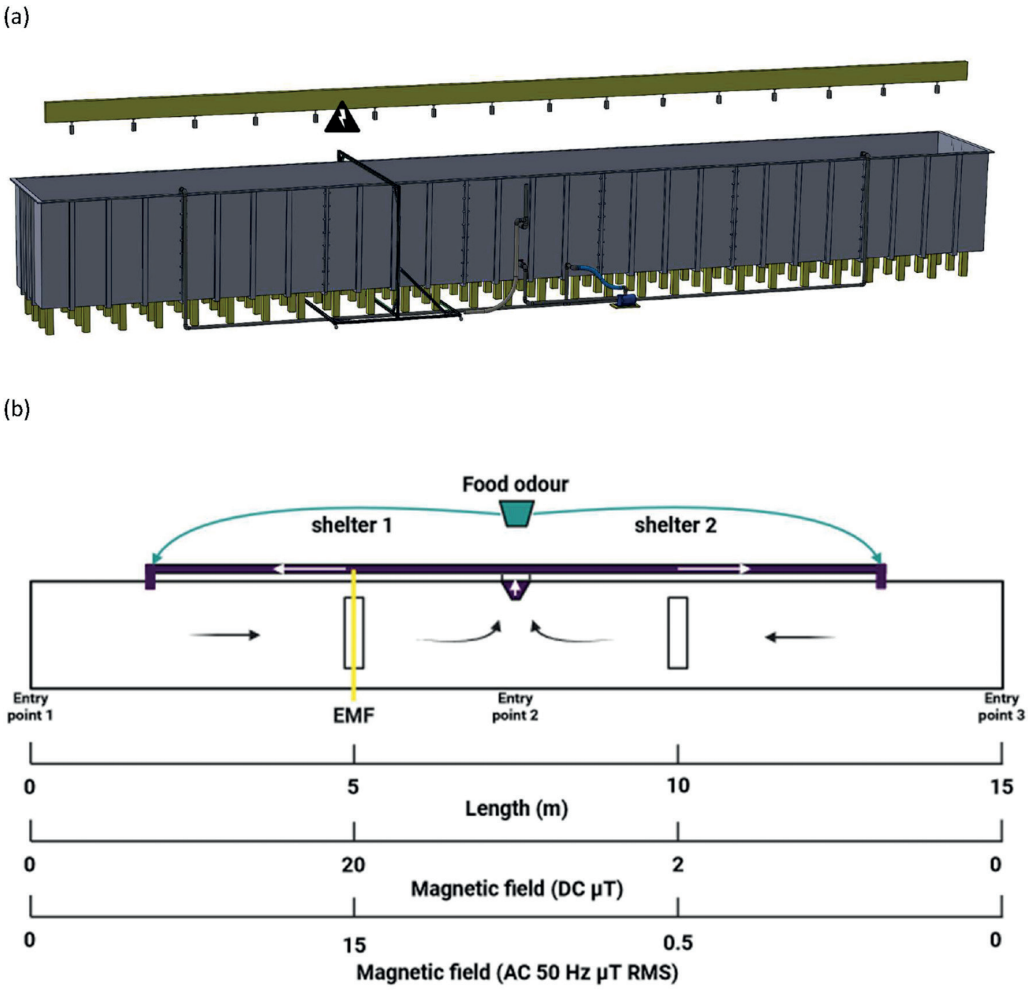


Fig. 6.1 (a) Schematic overview of the experimental tank indicting the proportions, the location of the coil and the cameras above the tank. The solenoids (enclosed in the black frame) are indicated by the power symbol in the black triangle and located at the 5m mark **(b)** Top view schematic overview of the experimental tank (15m × 1.65m x 1.6m; L x W x H). Sharks were entered at one of three randomized entry points. Two PVC pipe shelters (1m, 25 øcm) were located in the tank at 5 and 10m and the solenoid system (yellow line), to induce the EMF, was situated at the 5m shelter. Food odour was added at the start of treatment time (Fig. 6.2b) to promote foraging behaviour, which was dispersed to the far ends of tank using a water pump. Black and white arrows indicate the water flow through the tank during experiments. Green arrows indicate the entry points of food odour. An indication of the total magnetic field intensity for both DC, after subtraction of the geomagnetic field (solid line) and 50 Hz AC trials (broken line) at the mid-width and bottom of the tank. Image created with https://BioRender.com.

The magnetic field intensities were modelled to field measurements of the high voltage 220 kV 50 Hz AC Borssele offshore wind export cable (NL) and the high voltage 525 kV bundled DC Norned interconnector cable, measured at 1m from the cable (minimum required burial depth), data used with permission from T.S.O. TenneT. The average static ambient field (geomagnetic field) in the experimental facility was 50.7 μT (Fig. S6.1a).

6.2.3 Experimental procedure

The number of sharks (15) was selected to ensure the experiment could be conducted within a three-month period, minimizing potential seasonal effects while maintaining sufficient explanatory power. One individual died due to reasons unrelated to the experiment and was subsequently excluded from the analyses. Each of the resulting 14 sharks (weight: 587.7 ± 83.2g, length: 55.3 ± 6.1 cm), were used for three trials in the experimental tank supplied with ambient seawater (13.2 ± 1.2 °C, 33.9 ± 0.2 salinity ppt, 109.4 ± 8.7 % dissolved oxygen): receiving three treatments (one per trial) in a randomized order 1) EMF resulting from AC, 2) EMF resulting from DC, and 3) EMF not powered (Control). The experimental tank was thoroughly cleaned by siphoning the waste out once halfway through the trials to remove sediment and improve visibility. Pilot trials were carried out to determine the most appropriate acclimatisation period, aimed at returning to 'normal' behaviour. The acclimatisation time was set accordingly for 1h:30m to 1h:45m (depending on the speed at which the animal was caught). Considering the twilight and nocturnal activity pattern of *S. canicula* (Papadopoulo et al., 2023), trials were conducted at dusk, starting 2h:45m before sunset (Fig. 6.2). This schedule was selected, as opposed to nighttime trials, as preliminary trial runs indicated that the animal tracking software was unable to identify the shark less than 45 min before sunset due to a shortage of natural light and ineffectiveness of infrared. In treatment trials, EMF (either AC or DC) was remotely

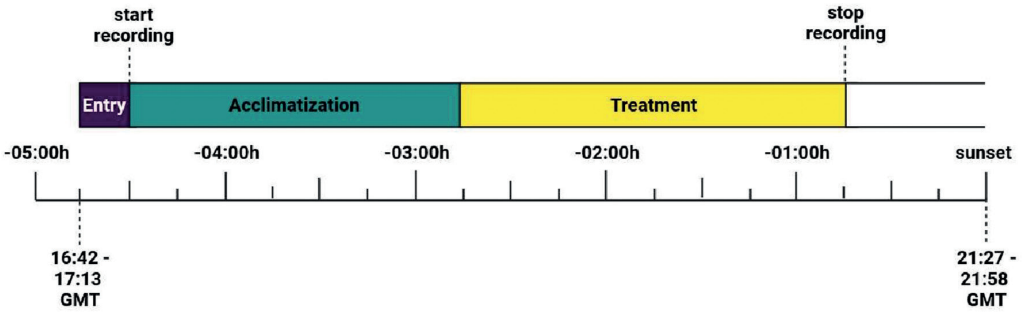


Fig. 6.2 Overview of the time schedule used during the trials. Time of entry was between 4h45m and 4h30m before sunset, after which sharks were given 1h45m to acclimatize to the new environment. The treatment lasted 2h and finished 45m before sunset to ensure proper light conditions for cameras. Food odour was added at the start of experimental treatment to promote foraging behaviour. Trials ran from May 22nd until July 14th, 2023.

activated for 2:00 h after acclimatisation, ending 45 min before sunset to ensure proper animal tracking. On the day of the trial, the individual was not fed, to ensure that it would respond to the olfactory incentive during the trial. 500 mL of food odour was added to the experimental tank at the start of the treatment period using a DD H2Ocean P1 dosage pump to promote movement and foraging behaviour during the trials. The olfactory stimulus was prepared by defrosting five frozen king prawns (Pennaeus vannamei) in 500 mL seawater. This was added at the inflow of the circulation pump allowing the odour to enter the experimental tank through the outflow at both ends of the tank (Fig. 6.1 bottom). A shark was released in the experimental tank at a randomly selected position, either in the middle or one of the far ends, to mitigate entry-side bias. A minimum interval of three weeks between trials was selected for each individual to ensure sufficient time for the sharks to regain naivety, and avoid habituation, based on Kimber et al. (2014). The order of trials was randomized, as an animal being introduced to a novel arena may not behave in the same way than when introduced to the same arena again (Dhellemmes et al., 2021; Finger et al., 2016). The animal remained in the experimental tank until the next morning when it was returned to the holding tank.

6.2.4 Data processing and analysis

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

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

Discrete-time hidden Markov models (HMMs) were used to examine if the EMF treatment affected the time spent in various behavioural states by the sharks. The HMMs were applied in R using the package 'momentuHMM' (version 1.5.5; McClintock & Michelot, 2018). Initially, the sharks' horizontal step length (speed) (Fig. 6.3a) and turning angle (Fig. 6.3b) were used to fit the HMMs, but because the swimming behaviour and derived behavioural states were strongly influenced by the corners of the experimental tank,

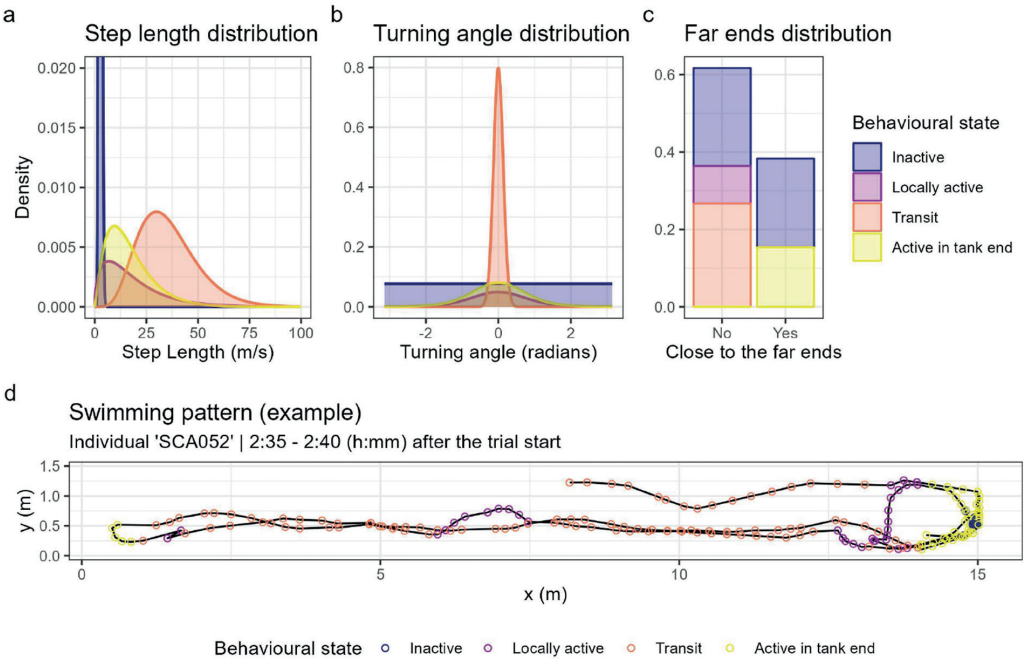


Fig. 6.3 Distribution of step length (a), turning angle (b), and being in the tank end (c) of the four behavioural states (colours) a classified by the hidden Markov model (HMM). We used the behavioural state 'Active in tank end' (yellow) to compensate for the 'tank effect': forced turning behaviour at the ends of the tank. (d) An overview of a 5-min swimming track, with the classified behavioural states.

a variable stating whether the shark was within 1 m from one of the far ends of the experimental tank was added (Fig. 6.3c). HMM null models were fitted with 1 up to 4 states and the AIC scores were compared to determine the number of behavioural states that were best supported by the models. The model with 4 states had the best fit (Table S6.1) and the behavioural states were labelled as follows: (1) Inactive; low step length and a flat distribution of turning angles, (2) Locally active; moderate step length and a low degree of directionality, (3) Transiting; large step lengths and highly directional swimming, (4) active swimming at the ends of the experimental tank, moderate step length and a low degree of directionality, confined within 1 m of the experimental tank ends (Fig. 6.3). Combinations of the covariates EMF treatment (AC, DC, Control), order, weight, sex, and length were added as state transition probability covariates to select the best fitting model. Comparison of AIC scores indicated that the inclusion of Treatment, Order, and Sex resulted in the best fitting model (Table S6.2). For this model, stationary state probabilities with 95 % confidence intervals were determined. When intervals of two levels of a covariate did not overlap, these levels were considered significantly different.

6.3 Results

6.3.1 No evident attraction or avoidance

Overall, considerable inter- and intraindividual variation in sharks behaviour during EMF exposure was observed (Figures S6.2, S6.3 and S6.7). The mean distance from the EMF highpoint (mean ± standard deviation) was measured at 594 ± 182 cm for AC, 514 ± 171 cm for DC, and 586 ± 199 cm for the control group. These differences were not significant (all pairwise comparison p-values ≥0.34, Fig. 6.4 top panel, distance to EMF), suggesting no attraction or avoidance behaviour. The weight of the shark was part of the best model and had a non-significant negative correlation with the distance from the EMF (intercept: 6.46, slope = $-1.35*10^{-4}$, p-value: 0.65). The number of EMF highpoint crossings per km was 44.6 ± 21.3 for AC, 41.4 ± 26.2 for DC, and 43.2 ± 21.8 for control treatments, with no significant difference (all pairwise comparison p-values ≥0.99, Fig. 6.4 middle panel, number of times EMF highpoint crossed). The weight of the shark was part of the best model and had a non-significant positive correlation with the number of crossings (intercept: 2.98, slope: 1.39*10-3, p-value: 0.45). The distance travelled per hour was 622 ± 344 m for AC, 590 ± 553 m for DC, and 569 ± 435 m for control treatments. These differences were not significant (all pairwise comparison p-values ≥0.99, Fig. 6.4 lower panel, Distance travelled) The weight was again part of the best model with a nonsignificant positive correlation with the distance travelled (intercept: 5.81, slope: $1.07*10^{-3}$, p-value: 0.73). Furthermore, there were no startle responses (indicated by a sudden change in behaviour) observed when the EMF was turned on after the acclimatisation period. During the trials, only two sharks made use of the shelters for 59 min (SCA069, trial 29, Control) and 8 min (SCA069, trial 43, DC) respectively, both during the acclimatisation period, indicating that EMF did

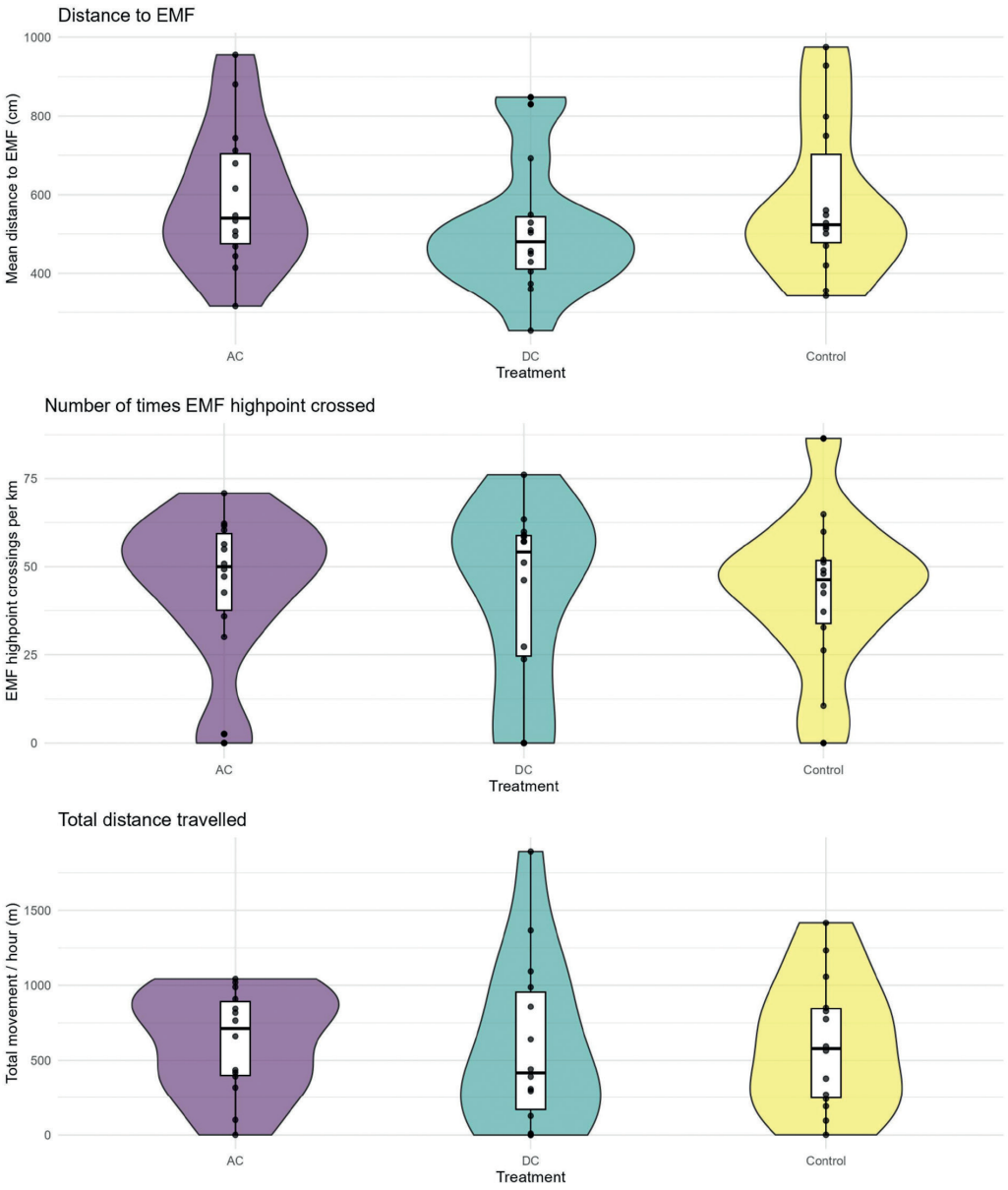


Fig. 6.4 Violin plots showing the mean distance to the centre of the electromagnetic field (EMF) (top), the number of times the centre of the (EMF) was crossed per km travelled (middle), and total distance travelled in meters per hour (bottom) for alternating current (AC), direct current (DC) and control treatments. Top and bottom figures are corrected for total treatment time as some trials were cut short due to a lack of visibility. No statistical significance was found between the treatments in all three parameters. The control trials are close to a random distribution as the experimental tank housed an a-symmetric setup which resulted in relatively more data closer to coil (0–5 m) than far from the coil (10–15 m).

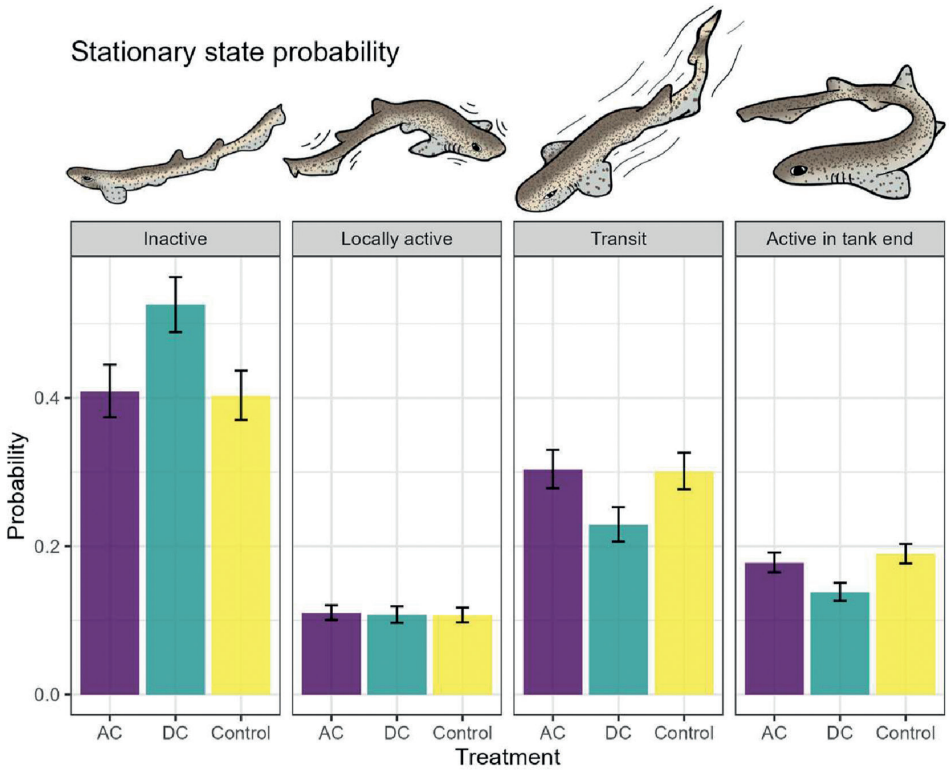


Fig. 6.5 The stationary state probability of the behavioural states of the 14 sharks during the experimental treatments. This is the Hidden Markov Model (HMM) output for the best model fit which included the parameters treatment, sex and trial order. The error-bars represent the 95 % confidence interval, when the error-bars of different treatment do not overlap, there is a significant treatment effect. The sharks were significantly more inactive, transited less, and spend less time active in the tank ends during the DC treatment.

not increase sheltering behaviour. Because of the lack and scarcity of startle responses and hiding behaviour respectively, no inferential statistics were performed here.

6.3.2 Changes in behavioural states

Overall, on average, sharks spent almost half of the trial time being inactive, a quarter of the time transiting, and the remainder of the time was spent active in the tank ends or locally active. During the DC treatment, sharks were spend significantly more time being inactive, and spend significantly less time transiting and moving at the experimental tank ends, compared to both AC and control conditions (Fig. 6.5). The total distance covered during the trials did not differ significantly (Fig. 6.4 lower panel), indicating a higher swimming speed for sharks under DC conditions when active. This is also evident from the step length distribution during the locally active and transit states, with longer step lengths during DC trials (Fig. 6.6 for all states). Sharks were mostly inactive during the first trial, which significantly changed as the number of trials progressed, regardless of the treatment order which

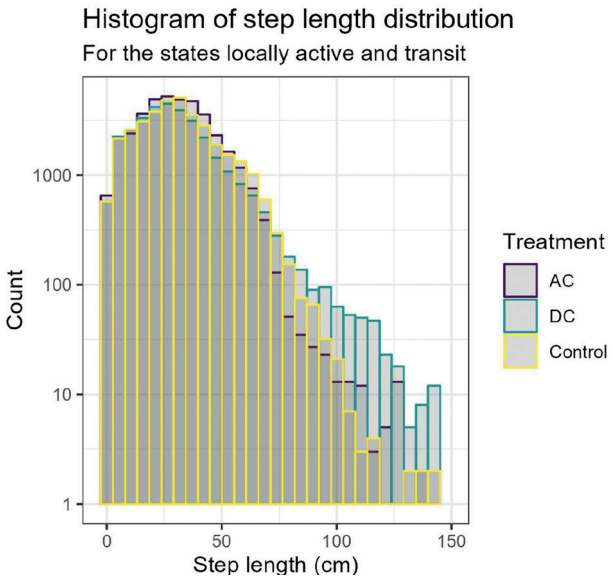


Fig. 6.6 The step length distribution, as histogram, during the experimental treatment, for the locally active and transit behavioural state only. For the DC trials a higher amount of larger step lengths can be seen, indicating a higher swimming speed when they are active.

was randomized (Fig. S6.4). No significant effects of sex on the time spent in the different behavioural states was found (Fig. S6.5).

6.4 Discussion

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

6.4.1 Movement behaviour

There were no signs of attraction or avoidance to EMF, contrary to suggestions by other studies with comparable field intensities. Barry et al. (2008) showed anecdotal evidence attraction of 126 longnose skates (*Raja rhina*) around an unused power and data cable (MARS, no cable specifications provided), but no such aggregation was shown when the cable was in use suggesting there no longer was an attraction to the SPC. Gill et al. (2009)showed attraction to a 50 Hz offshore wind AC cable with exposures up to 8 μT and decreased movement near the cable in S. canicula. In accordance with our findings,

Hutchison et al. (2020)demonstrated no clear attraction or avoidance in *Leucoraja erinacea* in a mesocosm experiment above a live DC cable (14 μT), but did see increased exploring/foraging behaviour based on spatial distribution, total distance travelled, speed of movement and proportions of large turns. In our study, if there was attraction to AC or DC, we would have expected to see a shorter mean distance to cable, or more crossings of the solenoid midline, which were not significant. Individuals crossed the cable as frequently in all treatments, so the EMF levels associated with SPC did not serve as a barrier. EMF-deterrence devices can serve as barrier, but this was shown at ~250 000 μT, which is 105 higher than the EMF intensities used in this study design (Doherty et al., 2022; O'Connell et al., 2014a; 2014b; Smith & O'Connell, 2014).

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

The observed differences between results obtained from this study and others may be caused by differences in study design, species-specific responses or exposure levels. For instance, the EMF levels employed by Albert et al. (2022) were >20 times higher (450 μT) as may be seen in unbundled DC cables. The magnitude difference in exposure could have led to a different response, depending on the unknown EMF dose-response curve. Additionally, Albert et al. (2022) studied juvenile *Raja clavata*, while we examined adult *S. canicula*; sensory abilities vary with age and species due to life history traits like mating and foraging. Almost all studies reported high inter-individual variability and a small sample size, which

likely also contributed to the observed differences. Although the individual differences make it more difficult to determine a population mean, they might be indications of behavioural phenotypes in response to EMF. Stuber et al. (2022) described that those differences in movement, habitat use, and home range behaviour make up spatial personalities; behaviours that might be influenced by EMF. Consistent intraindividual differences, or personalities (Roche et al., 2016), might help species to adapt to increasing anthropogenic stressors by rapid behavioural adaptation due to differences in stress response (Smith and Blumstein, 2013; Stuber et al., 2022). For example, shy and bold behavioural phenotypes may respond differently to an SPC EMF. If one of these trait-related responses results in reduced fitness of one trait, this could lead to impact at population level.

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

6.4.2 No startle response or shelter use

No direct effect of the EMF onset was observed in the trials. Sharks that where lying in the vicinity of the EMF at the time of it being turned on did not change their behaviour instantly. This suggests that the EMF levels used where not sufficient to elicit an immediate behavioural response in contrast to the responses to 105 times higher exposure levels used from pulse fisheries or shark deterrence devices (Boute, 2022; De Haan et al., 2009; O'Connell et al., 2014a,2014b; Smith and O'Connell, 2014). However, it cannot be excluded that an unobserved stress or freeze response occurred. Combining biologging tags to monitor physiological stress indicators, such as respiratory rate, heart rate, and stroke volume, with video analysis can enhance our understanding of stress responses that do not manifest as overt movements (Barkley et al., 2020; Laurioux et al., 2024; Meira et al., 2024).

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

6.4.3 Influence of trial order, sex and body length

In the observed trials, treatment, order, and sex emerged as primary predictors of shark behavioural states, with body length also presented as a potentially contributing factor. The order of trials significantly influences behaviour, as sharks showing more exploratory behaviour in subsequent trials, even though trials were spaced by >3 weeks. Evidence suggests that elasmobranchs can retain knowledge of a novel area for extended periods, e.g. showing the retention of visual cues for >50 days(Brown and Schluessel, 2023; Fuss and Schluessel, 2015). While the first experience in the experimental tank might have been highly novel, familiarity with the tank or procedure likely increased during subsequent trials, shown by more locally active and transit and less inactive behaviour (Fig. S6.4). This is in line with observations in lemon sharks (*Negaprion brevirostris*) displaying increasing rate of movement and exploratory behaviour over repeated introductions in the novel arena (Dhellemmes et al., 2021; Finger et al., 2016). Three weeks might still have been sufficient for re-naivety to EMF cues, as wild sharks frequently encounter varying EMFs from shifting prey and conspecifics conditions, while habitat appearance remains more stable. Conversely, evidence suggests yellow stingray (*Urobatis jamaicensis*) can retain EMF memory for 180 days when conditioned to associate a magnetic field with a food reward, highlighting the need for more understanding on how EMF us used by different species of elasmobranchs (Newton and Kajiura, 2017). Even though no direct significant effect of sex and EMF treatment was found, including sex gave a higher explanatory power in the selection of the model. This indicates that sex might play a role in explaining variation in behaviour, either by differences in behaviour between sexes in general, or by sex-specific responses to EMF-fields (Table S6.2). To disentangle this further, a follow-up study with larger sample size per sex would be needed. Especially, as research shows sexual dimorphism in the ampullae of Lorenzini (Kempster et al., 2013), and male *S. canicula* are reported to have longer ampullae and alveoli, higher number of alveolar bulbs, larger sensory epithelial surface areas and a greater number of sensory receptor cells in the ampullae than females (Crooks and Waring, 2013) which is believed to increase the capability of males to detect females. In addition, sexual behavioural dimorphism in relation to electric stimuli has been shown and is linked to differing reproductive strategies and resultant sexual conflict (Kimber et al., 2009; Rodríguez-Cabello et al., 2007; Sims et al., 2001). The interaction between sex and EMF-response may be an interesting focus for future studies.

Shark body length shows a relation with treatment response (Table S6.2). Older, and thus larger, sharks have a lower electroreceptive resolution, as the pores grow further away from the ampullae, and will gain in receptor sensitivity and a larger sensory field that samples a greater area (Newton et al., 2019). As the older/larger sharks have a changed sensitively to EMF, they could respond differently to the EMF resulting from SPCs. Alternatively, larger individuals may have higher cruising speeds, potentially resulting in the same distance travelled when related to as body lengths per second. In the wild, larger sharks were found to exhibit reduced activity space, indicating that as length increased, their

range of movement decreased (Papadopoulo et al., 2023). This could imply that the relation between body size and treatment response is not EMF related, contrary to what our data suggest.

6.4.4 Implications for future studies

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

The absence of data on habituation of EMF from SPC in adult individuals, both in this study and others, precludes an assessment of cumulative EMF impacts. For example, if a shark reduces its movement by a third every time it comes across a cable during migration, the accumulated time lost might have a larger negative effect on the migration goal than when it habituates and does not slow down. In addition, it is not known if the reduction measured in the lab will also occur in the field, and what the duration of the reduction will be. To the contrary, if the shark does habituate to SPC EMF cues, this might impair the sensitively to natural EMF cues and result in reduced foraging success or disturbed conspecific interaction. It is likely that sharks can habituate to stimuli, as habituation is one of the most primitive learning mechanisms (Heinrich et al., 2022). However, habituation does not necessarily exclude the masking of relevant (EMF) cues.

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

above mentioned different potential effects is relevant for environmental risk assessments and should address EMF effects on different life stages, especially embryogenesis and migration (Hermans et al., 2024).

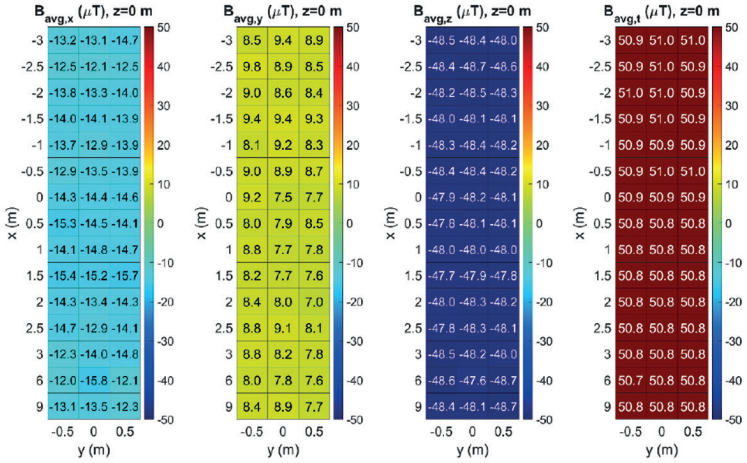
6.5 Conclusion

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

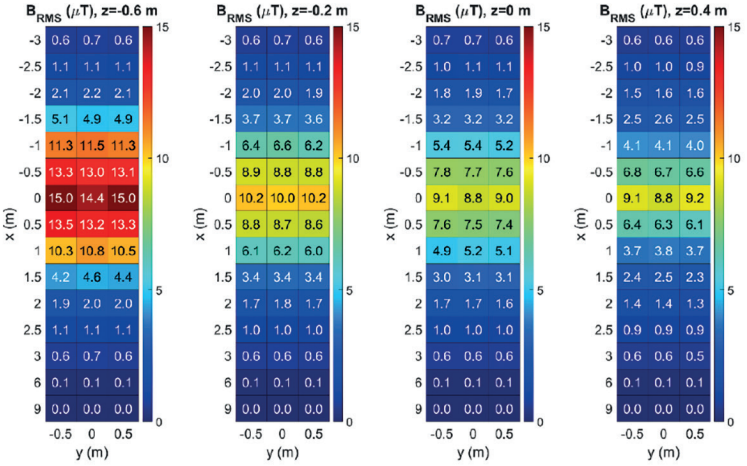
Supplementary materials

Fig. S6.1 - On the right page
(a) Average values (static background field) in all measuring points at height (z) 0 m (= middle of the coil), decomposed into components in x, y and z direction. The fourth column shows the total static field.
(b) Total B-fields (xyz) RMS values of the 50 Hz AC field generated in μT at different levels in the tank, where z = -0.6 m the bottom of the tank, z = -0.2 m 40 cm above the bottom, z = 0 m in the middle of the coil and z = 0.4 m at the water surface.
(c) Static field measured at the configuration "DC 1.25 A" after subtraction of the geomagnetic field (-14.4, 8.9, -47.8 μT) at the bottom of the tank. Note: Values need to be halved as only one solenoid was in use during the DC trials, effectively halving the generated magnetic field level.

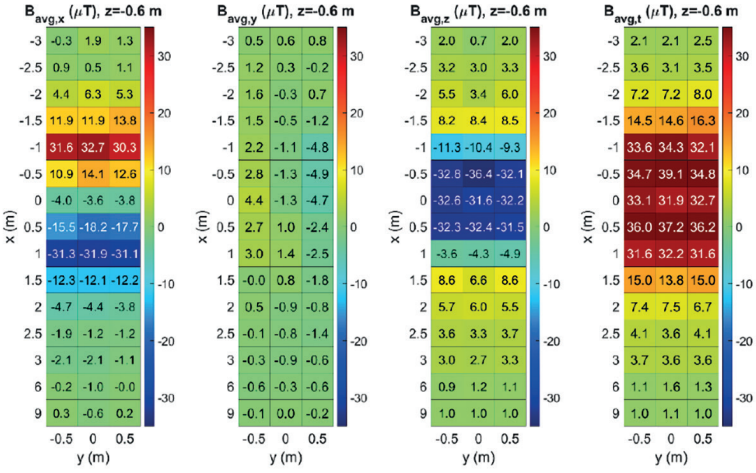
(a)


$B_{avg,x}$ (μT), z=0 m
$B_{avg,y}$ (μT), z=0 m
$B_{avg,z}$ (μT), z=0 m
$B_{avg,t}$ (μT), z=0 m
x (m)
y (m)

(b)


B_{RMS} (μT), z=-0.6 m
B_{RMS} (μT), z=-0.2 m
B_{RMS} (μT), z=0 m
B_{RMS} (μT), z=0.4 m
x (m)
y (m)

(c)


$B_{avg,x}$ (μT), z=-0.6 m
$B_{avg,y}$ (μT), z=-0.6 m
$B_{avg,z}$ (μT), z=-0.6 m
$B_{avg,t}$ (μT), z=-0.6 m
x (m)
y (m)

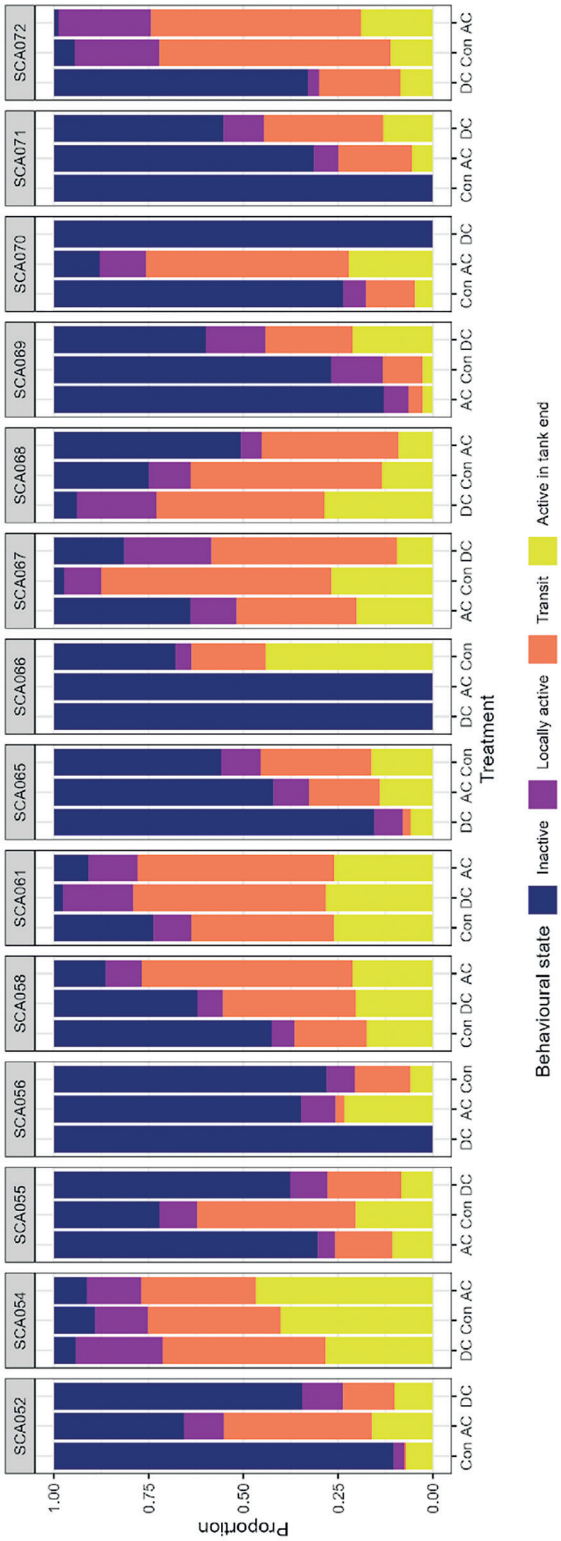


Fig. S6.2 State distribution for each of the 14 individual sharks in the order of treatments (first treatment displayed first), depicting a high within and between individual behavioural variability. Control on the x-axis is abbreviated as 'Con'.



Fig. S6.3 Depicting the mean distance to the EMF highpoint (top), number of times the EMF highpoint of the electromagnetic field (EMF) was crossed per km travelled (middle) and total distance travelled in meters per hour (bottom) for all 14 shark trials for the treatments alternating current (AC) (purple), direct current (DC) (green) and control (yellow). The order of the bars corresponds to the order of the treatments for each shark. Top and bottom figures are corrected for total treatment time as some trials were cut short due to a lack of visibility.

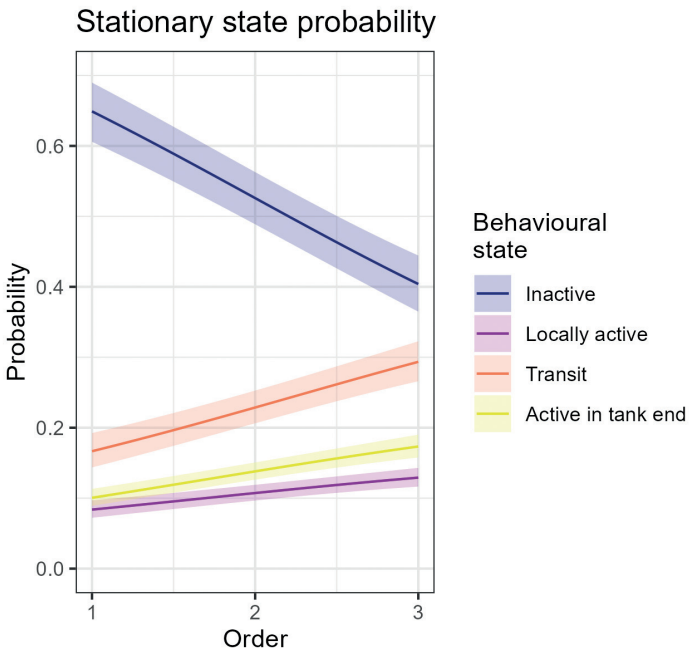


Fig. S6.4 Stationarity state probability over trial order. All states changed significantly over consecutive trials and indicate that sharks became more active over consequtive trials.

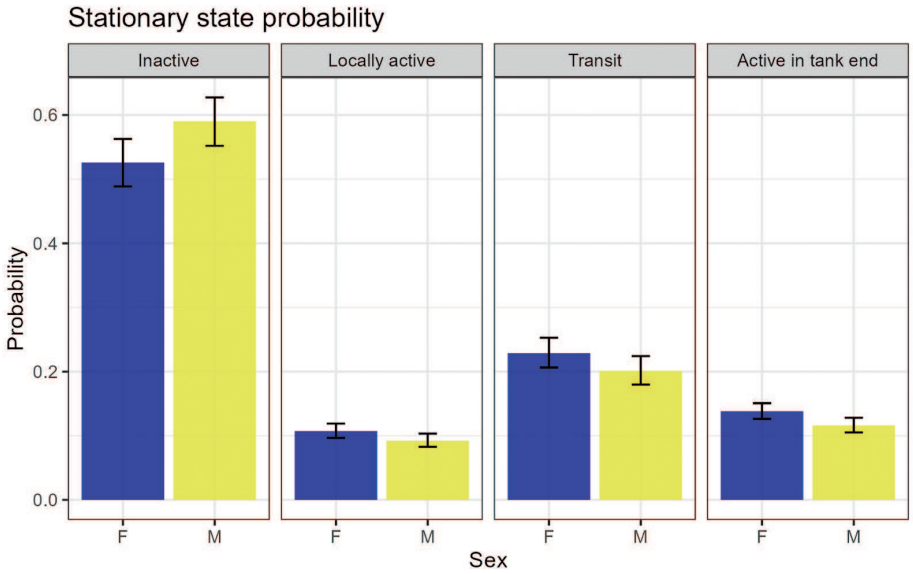


Fig. S6.5 Stationary state probability of both sexes, indicating female (blue) and male (yellow), for all four behavioural states (the panels). The results reveal no significant sex differences.

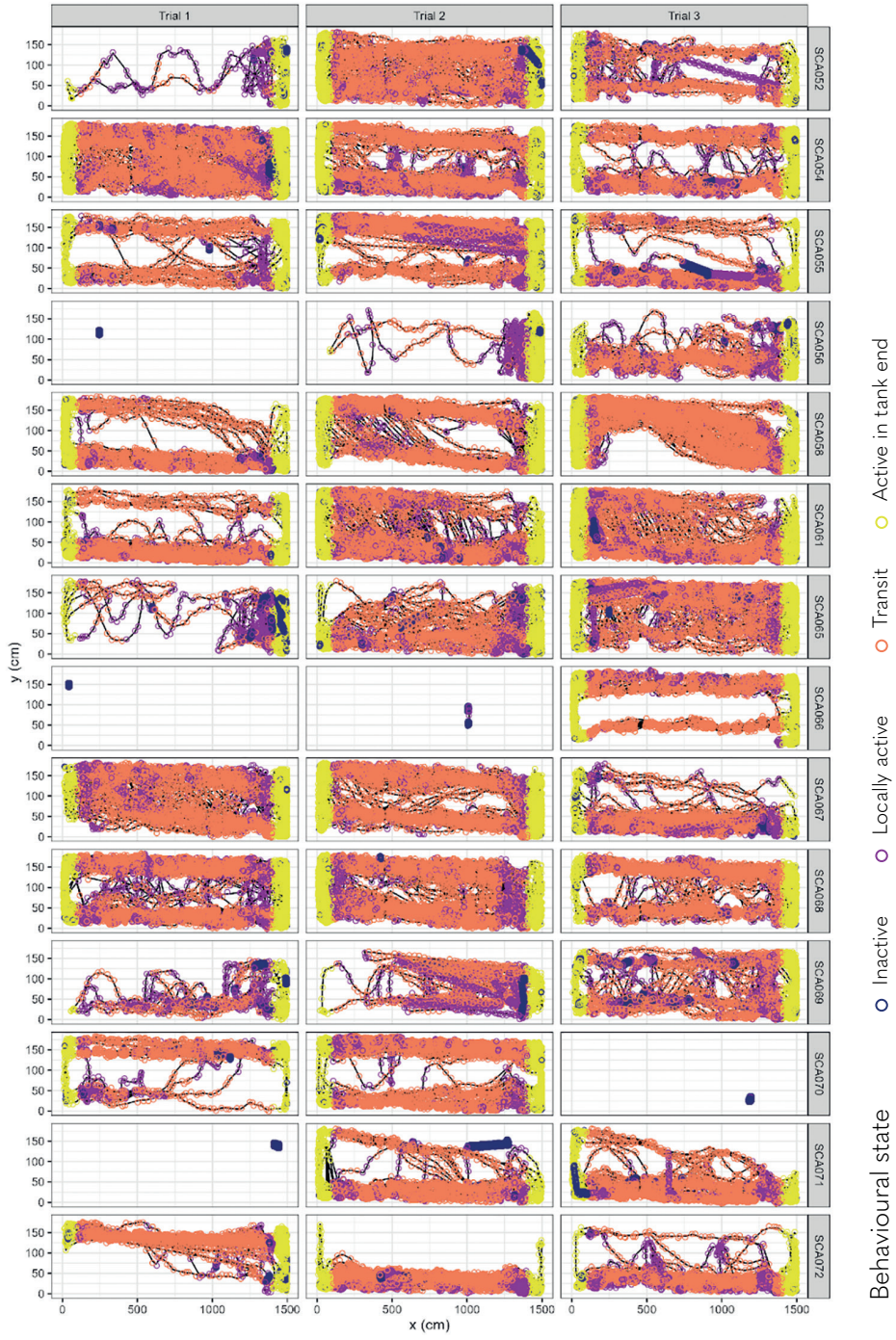


Fig. S6.6 Individual tracks of all 14 sharks in order of trials, with the behavioural states indicated by the colour: inactive (blue), locally active (pink), transit (orange) and active in tank end (yellow). The tracks show high individual variability. The labels on the right, starting with 'SCA0', refer to the individuals. Note that the x- and y-axes are not proportional.



Abstract

The rapid expansion of offshore wind energy has increased the number and capacity of subsea power cables, introducing anthropogenic electromagnetic fields (EMFs) in marine environments. Elasmobranchs use electro- and magnetoreception for prey detection, navigation, and other vital functions, yet the behavioural consequences of cable-related EMFs remain poorly studied. This study experimentally tested the responses of thornback skates (*Raja clavata*) to field-relevant alternating current (AC) and direct current (DC) EMFs under controlled laboratory conditions. Eighteen individuals (8 males, 10 females) were exposed to three treatments (control, AC, DC) in a 15m long experimental tank. Swimming behaviour and space use were quantified using automated tracking. Results showed no attraction to or avoidance of EMFs, and spatial use did not differ between treatments. However, subtle (15%pt.) but significant sex-specific changes in behaviour were observed. Hidden Markov model results indicated that females showed reduced inactivity and increased transiting under AC exposure, whereas males exhibited increased inactivity and reduced movement under both AC and DC exposure. Results indicate that cable-related



7 Torn in their side? Subtle sex-dependent behavioural responses of a batoid to AC and DC electromagnetic fields

EMFs do not act as barriers for *R. clavata* but can induce small, sex-dependent shifts in activity patterns. Although modest, the consequences of such changes could compound with repeated exposure. Given the anticipated growth in offshore power transmission, particularly via DC systems, field-based studies are needed to assess whether these responses persist under natural conditions and at ecologically relevant scales.

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Submitted to Environmental Science and Technology

7.1 Introduction

Since the installation of the first subsea power cables in the early 1800s, the number, size, and transmission capacity of these cables has increased rapidly. This has been further accelerated to meet the growing demand for transporting offshore wind energy to shore (Díaz & Guedes Soares, 2020; Taormina et al., 2018). The transmission of energy, i.e. electricity, through cables generates electromagnetic fields (EMFs). While the electric field is typically contained within the cable, the magnetic field extends into the surrounding marine environment and induces secondary electric fields when seawater or organisms move through it (Gill et al., 2014). These anthropogenic EMFs interact with natural sources of electromagnetic variation, including the geomagnetic field, solar activity, animal movement, and geological anomalies (Newton et al., 2019; Nyqvist et al., 2020). These natural electric and magnetic cues are used by a multitude of marine species across their life history. Among these species are the elasmobranchs (sharks, skates, and rays), which use electro- and magnetoreception for prey detection (Bedore & Kajiura, 2013; Kajiura & Holland, 2002), navigation (Anderson et al., 2017a; Kalmijn, 1978; Keller et al., 2021; Klimley et al., 2021; Naisbett-Jones & Lohmann, 2022; Newton & Kajiura, 2020b, 2020b, 2020b), predator avoidance (Ball et al., 2016; Christensen et al., 2023; Hermans, Maas, et al., 2025; Ryan M. Kempster et al., 2013; Paoletti et al., 2023), and communication (Kempster et al., 2013; Sisneros & Tricas, 2000; Tricas et al., 1995). Elasmobranchs play a key role in maintaining balanced coastal ecosystems (Dedman et al., 2024) but are severely under pressure, with one third of species threatened with extinction (Dulvy et al., 2021; Ferretti et al., 2010). Despite overlapping habitat with subsea cable routing and sensory capabilities comparable to the cable EMF strengths (Hermans et al., 2024), the ecological consequences of cable EMFs for elasmobranchs remain poorly understood (Garavelli et al., 2024).

Elasmobranchs detect electric fields through the ampullae of Lorenzini, i.e. specialized sensory organs that measure potential differences between the body core and the skin. Differences in stimulation across these organs enable precise detection of electrical cues from prey, mates, or other targets (Adair et al., 1998; Collin et al., 2015). Their magnetic sense is less understood and may involve electric induction via electroreception, although alternative mechanisms have also been proposed (Collin et al., 2015; Nyqvist et al., 2020). From the few behavioural studies available, it is evident that the effects are subtle and that controlled laboratory and mesocosm studies can help understand the responses. Hutchison et al. (2020) exposed little skates (*Leucoraja erinacea*) to a direct current (DC) subsea cable in a field-based mesocosm (Hutchison et al., 2020a). Skates increased swimming distances and speeds, made more frequent sharp turns, and swam closer to the seabed at intensities as low as 0.3 μT above the geomagnetic field (GMF). Stronger responses were observed at higher levels, up to 14 μT above GMF (Hutchison et al., 2020a). Anderson et al. demonstrated a conditioned food-induced target search response of juvenile sandbar sharks (*Carcharhinus plumbeus*) to magnetic fields, with behavioural changes apparent at 1.2-1.4 μT and increasing in strength up to 5.3-8.0 μT above GMF (Anderson et al., 2017b).

Our previous work showed that small-spotted catsharks (*Scyliorhinus canicula*) reduced swimming activity when exposed to field-relevant DC EMF (19.0 μT), but exhibited no changes in behaviour under alternating current (AC) exposure when compared to controls (Hermans et al., 2025). Albert et al. reported small, time-of-day–dependent increases in activity in juvenile *R. clavata* at high DC intensities (450.0 μT), while no behavioural effects were observed under AC conditions (Albert et al., 2021). Although strong deterrence has been hypothesised, largely based on the use of magnetic shark repellents (i.e.~250 000 μT) (Marcotte & Lowe, 2008; O'Connell, Andreotti, et al., 2014; O'Connell et al., 2014; Smith & O'Connell, 2014), there is little evidence that deterrence occurs at EMF strengths typical of offshore wind farms. Additionally, an increasing body of evidence indicates the presence of elasmobranchs within offshore wind farms, including eDNA surveys, acoustic telemetry, and telemetry tagging studies (Couturier et al., 2025; Labourgade et al., 2024). And some studies suggesting that attraction, under certain circumstances, may be more likely than avoidance (Gill et al., 2009; Hutchison et al., 2020a).

Elasmobranch species vary in structure and function of their electro- and magneto-sensory systems, reflecting adaptations to distinct foraging, mating, and navigational strategies (Egeberg et al., 2014; Newton et al., 2019; Sisneros & Tricas, 2002). Such interspecific differences could also lead to variation in responses to EMFs from subsea power cables. However, as experimental designs differ widely across the relatively small number of studies conducted so far, making robust cross-species comparisons remains difficult (Albert et al., 2022; Hutchison et al., 2020b; Newton & Kajiura, 2020a; Paoletti et al., 2023). As an example, Marcotte and Lowe compared scalloped hammerheads (*Sphyrna lewini*) and leopard sharks (*Triakis semifasciata*) under high-intensity electric fields (mean 18.50 ± 13.27 V/m and 9.64 ± 10.28 V/m, respectively) aimed at exploring shark deterrent devices. Both species exhibited similar behaviours such as increased head twitching and retreating, though hammerheads only withdrew at higher intensities, suggesting species-specific behavioural thresholds (Marcotte & Lowe, 2008). Notably, the deterrent-level fields used in Marcotte & Lowe (2008) are at least four orders of magnitude stronger than those typically measured at subsea power cables (Hermans et al., 2024). Other work has examined more subtle differences: Port Jackson sharks (*Heterodontus portusjacksoni*) and western shovelnose skates (*Aptychotrema vincentiana*) occupy similar habitats and exploit prey of comparable size but differ markedly in electro-sensory system morphology. While both species responded to very low electric-field gradients (<1 nV cm−1), they showed contrasting spatial resolution and directional accuracy in detecting prey items (Kempster et al., 2016). In mesocosm experiments with adult *R. clavata* and *S. canicula*, exposed to AC EMFs of 8.0 μT, species-specific differences were evident: *R. clavata* showed a slight increase in movement, whereas *S. canicula* displayed attraction to the cable coupled with decreased movement in close proximity (Gill et al., 2009).

As research on the effects of EMFs is still emerging and there is a large diversity in elasmobranch species it is important to know if and under which conditions findings can be extrapolated. Against this background, the present study presents the behavioural responses

to field-relevant (i.e. around subsea power cables) AC and DC EMF exposure of a common benthic elasmobranch, *R. clavata*. Their abundance, non-threatened status, availability of egg cases from public aquaria, and suitability for captive maintenance make them adequate models for EMF impact research. No avoidance is expected, but attraction might be evident as this was seen in mesocosm studies (Gill et al., 2009; Hutchison et al., 2020b). The swimming patterns might also be influenced as previous work in the same experimental set-up with *S. canicula* showed a 25%pt. reduction in transiting but increased swimming speed during DC trials (Hermans et al., 2025b).

7.2 Materials and Methods

7.2.1 Animal collection and holding conditions

A first group of animals (n = 14) was collected by angling in Loch Linnhe (LL) (Fort William, Scotland, UK) on 13th September 2024 and subsequently transported to St Abbs Marine Station the same day. In order to increase the replicate number, for more robust analyses, a second group of animals (n = 4) was collected from the Solway Firth (SF) on 30th April 2025, using similar methods. All individuals underwent a health check, were photographed upon arrival and underwent an acclimation period of at least two weeks in the facility. Overall condition, lesions presence and parasite presence were assessed. Additionally, all individuals were checked by veterinary surgeons and deemed fit for the experiment. Individuals were sexed (8M:10F), weighed (mean = 1261 g ± 582) and their disc width measured (mean = 40.5 cm ± 4.4) one week after their arrival to establish baseline measurements. Sizes and weights for both groups were comparable. For details of each individual, see supplementary materials (Table S7.1). Skates were subsequently weighed immediately after each of their trials to allow continued health monitoring. Individual skin patterns were used as means of identification.

The two groups were held in separate tanks, and both were supplied with natural seawater from the North Sea. Both tanks were on a flow-through system, with additional filtration units (Tropical Marine Centre and Fluval FX6), providing mechanical, biological and Ultra-Violet (UV) filtration. Water temperature (10.4 °C ± 3.2), salinity (33.94 ppt ± 0.5), and dissolved oxygen (99.2% ± 6.4) were assessed daily, and pH (7.9 ± 0.09), ammonia (0.07 ppm ± 0.12), nitrite (1.49 ppm ± 3.10) and nitrate (1.41 ppm ± 2.38) were assessed weekly. The aquarium facility had a translucent roof, which provided the animals with natural photoperiods. The experimental trials took place between 15th May 2025 and 18th July 2025, with an average of 17.22 (± 0.35) hours of daylight per day.

Animals were fed every day, in the late afternoon, with the equivalent of 2% bodyweight (BW) per day, with a regimen of king prawn (*Pennaeus vannamei*), mackerel (*Scomber scombrus*), sand eel (*Ammodytes marinus*) and Californian squid (*Loligo opalescens*). Any uneaten food was removed from the holding tanks the following morning. Nutritional supplements (International Zoo Veterinary Group elasmobranch tablets) including iodine

and various vitamins were added to the diet (crushed and mixed with the food). Daily individual welfare checks were conducted including observations of their external aspect (clinical signs), general behaviour (stress behaviour) and feeding behaviour.

7.2.2 Experimental set-up

The experimental arena consisted of a custom-built tank (Fig. 7.1) of 15.00 x 1.65 x 1.60 m (LxWxH). The tank was built using opaque non-ferrous materials (fiberglass and wooden frame) to avoid magnetic interference. Animal behaviour was recorded using an array of 16 Close Circuit TeleVision (CCTV) cameras (Reolink RLC-810A), which were affixed above the tank, evenly spaced along the tank-length. The water level was set at 0.90 m (total volume = 22 275 L) and circulated throughout the tank during the trials by an external pump. In between trials, each day, a partial water change (50-100%) was done with raw seawater (filtered through 400 μm mesh), and the bottom of the tank was cleaned of any accumulated sediment.

The artificial EMFs were generated by two solenoids attached to an aluminium frame and powered by a Keysight N6715C DC Power Analyser, both at a frequency of 50 Hz, as described in (Hermans et al., 2025). Each solenoid was composed of 32 turns of 1.25 mm2 copper wire and placed in an inverted T position, one below (horizontally) and one around (vertically) the tank. In DC configuration, only the horizontal solenoid was powered (1.25 A), and the maximum field strength was 19.6 μT above the average geomagnetic field (GMF), which was 50.7 μT. In AC configuration, both solenoids were powered, out-of-phase, in order to simulate a 3-phase AC cable. The current amplitude in the horizontal solenoid was twice the one of the vertical solenoid, therefore creating a circular rotating field in the centre of the vertical solenoid. The maximum EMF strength in the AC configuration was 15.0 μT RMS above GMF. The EMF generating device was designed, built and commissioned by the Netherlands Organisation for Applied Scientific Research (TNO). EMF values were modelled based on field measurements taken where the burial depth of the cable exceeded 1m (the minimally required burial depth) of the Borssele offshore windfarm (AC) export cable and the NorNed (DC) interconnector cable. Values in the tank were modelled, then measured and verified by TNO, using a Twinleaf VMR sensor and SYNC4 data acquisition system.

7.2.3 Experimental procedure

Each individual skate underwent three trials (one for each treatment: control, AC, DC) (Table S7.2). The order of treatments was randomised for each animal with an elapsed period of at least 3 weeks in between each trial. Water parameters (temperature, salinity, dissolved oxygen) were measured in the holding tank and the experimental tank prior to every trial, to ensure conditions were similar. The skate was transferred to the experimental arena prior to feeding that day. The entry point was also randomised for each trial.

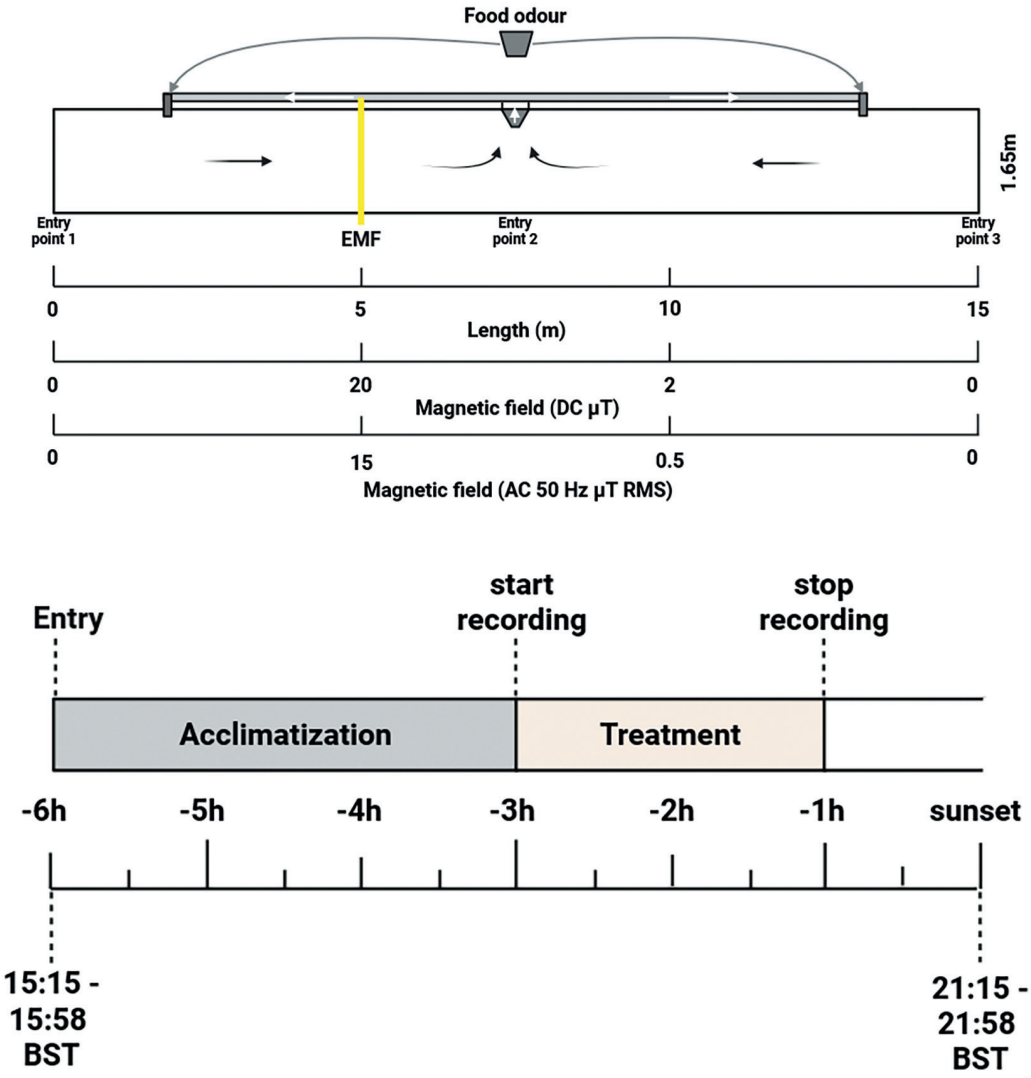


Fig. 7.1 (a) Top view schematic of the experimental tank (15.0m × 1.7m x 1.6m; L x W x H). Skates entered at one of three randomised entry points. The solenoid system is indicated by the yellow line at 5m. Food odour was added at the start of treatment time to promote foraging behaviour, which was dispersed to the far ends of tank using a recirculation system (trapeze). Black and white arrows indicate the water flow through the tank during experiments. An indication of the total magnetic field intensity for both DC, after subtraction of the geomagnetic field (solid line) and 50 Hz AC trials (broken line) at the mid-width and bottom of the tank.
(b) Overview of the time schedule used during the trials. Time of entry was 6 hours before sunset, after which skates were given 3 hours to acclimate to the new environment. The treatment lasted 2h and finished 1 hour before sunset to ensure proper light conditions for cameras. Trials ran from 15th May 2025 until 18th July 2025.
Created in BioRender.

The skate was then allowed to acclimate for three hours. The exposure started three hours before sunset and ended one hour before sunset, resulting in a 2-hour experimental time window (Fig. 7.1). When the exposure started, an olfactory food cue (prawn concentrate) was added to both ends of the tank through the recirculation system, to encourage movement. The animal was retrieved the following morning, weighed, and returned to its holding tank. One mortality (unrelated to the nature of the experiment) occurred over the experimental period (Skate ID 208). This individual, having completed two of its three trials (a control and a DC), died one month after its last trial. It was not deemed an outlier, since its weight and behaviour (Fig. S7.1 and S7.2) closely matched those of the other animals; accordingly, it was retained in the analyses.

7.2.4 Data processing and analysis

Video recordings of all 16 cameras were edited using Adobe Premiere Pro (version 25.3.0) into one 2h video file, displaying a full overview of the experimental arena. Individual skates were tracked using EthovisionXT (Noldus, version 16.0), with a sampling rate of 5 points per second. The automatically generated track (x and y coordinates) was manually verified and edited where required.

Statistical analyses were conducted in R (version 4.5.0). From the swimming tracks, the following parameters were calculated for each trial: [1] mean distance to the EMF highpoint, [2] number of EMF highpoint crossings per kilometre, and [3] total distance travelled per hour. These response variables were analysed in generalised linear mixed models with Gaussian error distribution and identity-link function for the mean distance from the EMF highpoint, and zero-inflated negative binomial error distributions with log-link function for the number of crossings and total distance swam. The models were implemented using the R-packages lme4 and glmmTMB (Bates et al., 2015; Brooks et al., 2017). Skate ID was included as random effect to account for repeated measures of individuals. Weight, sex, EMF treatment (AC, DC, control), order of the treatment, and origin (LL, SF) were included as covariates in the full model. Model selection was based on the lowest Akaike Information Criterion (AIC) score among all possible covariate combinations using the R-package MuMIn (Bartoń, 2025). When EMF treatment was not retained in the best-supported model, it was included in the final model since assessing EMF effects was a primary objective of the study. The final models were then fitted and all covariate effects were reported. For the EMF treatment, Tukey post hoc tests were used to perform pairwise comparisons using the R-package emmeans (Lenth, 2025). Water temperature was strongly correlated with treatment order and was therefore not included as separate covariate in the models.

Discrete-time hidden Markov models (HMMs) were used to examine whether EMF treatment affected the time rays spent in various behavioural states. The HMMs were implemented in R using the package 'momentuHMM' (version 1.5.6; (McClintock & Michelot, n.d.)). The skates' horizontal step length (horizontal speed; Fig. 7.2a) and turning angle (Fig. 7.2b) were used as observation variables in the HMMs. Null HMMs with one to three

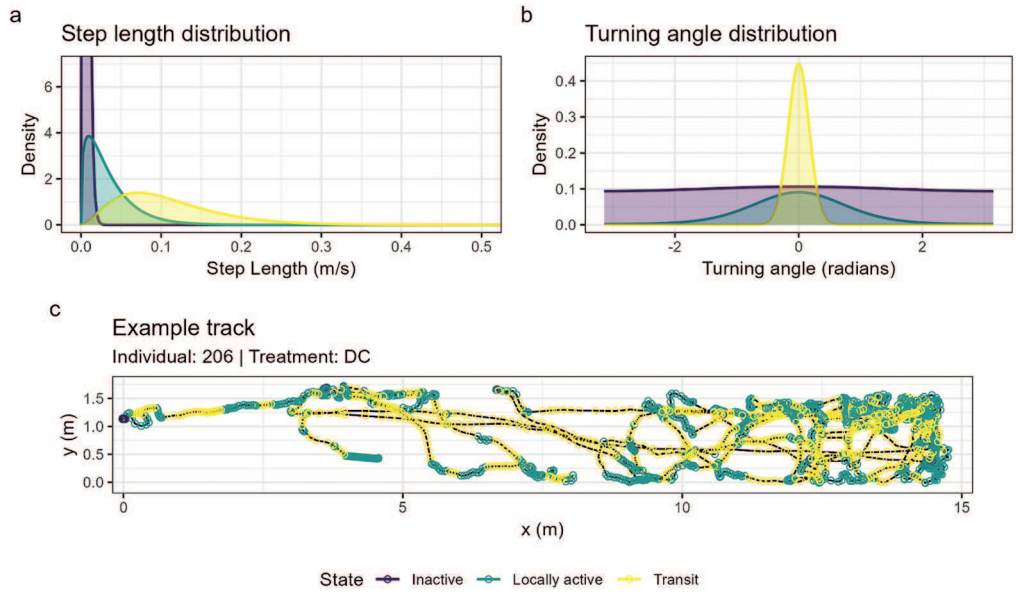


Fig. 7.2 Distribution of step length (a) and turning angle (b) of the three behavioural states (colours), as classified by the hidden Markov model (HMM). (c) An example swimming track of a 2-h trial of one of the rays, with the inferred behavioural states (colours).

behavioural states were fitted, and AIC was used to determine the number of states best supported by the data. A maximum of three states was tested since model selection criteria applied to HMMs often favour models with more states than biologically interpretable (Pohle et al., 2017). The three-state model provided the best fit (Table S7.3). The behavioural states were labelled as: (1) Inactive; characterised by low step lengths and an approximately uniform distribution of turning angles, (2) Locally active; characterized by moderate step lengths and intermediate directionality, (3) Transiting; characterised by large step lengths and highly directional movement (Fig. 7.2). Combinations of the covariates EMF treatment (AC, DC, control), treatment order, weight, origin (LL, SF), sex, and interaction between sex and treatment were tested as state transition probability covariates. Forward model selection based on AIC comparison was used to identify the most parsimonious model, which included origin, sex, order, treatment, and the interaction between treatment and sex (Table S7.4). The significance of the covariates on state transition probabilities was assessed using likelihood ratio tests (LRTs) comparing the best model to reduced models in which the focal covariate, and any associated interaction terms, were removed. Stationary state probabilities (i.e. the modelled proportion of time an individual would spend in each state under constant covariate conditions) of the best-fitting model were calculated with 95% confidence intervals and plotted to visualize the size and direction of covariate effects (Fig. S7.3, S7.4 and S7.5).

Individuals from LL and SF were analysed in a single model because both groups were balanced with respect to sex (LL: 6M:8F; SF: 2M:2F), had overlapping weights (means LL:

1785 g ± 786; SF: 1396.5 g ± 267) and disc widths (means LL: 40.7 cm ± 4.8; SF 39.9 cm ± 2.4), and all but one individual (from LL) underwent all treatments, and for both groups in a balanced order (Table S7.1). Variation attributable to individuals' origin (as well as and sex and weight; the latter was removed during model selection) was accounted for in the models, as explained above. In addition, it was verified whether significance of covariates, based on LRTs, was retained when analyses were restricted to individuals from LL only.

7.3 Results

All individuals maintained or gained weight over their time in captivity and overall stayed in good condition. A total of 53 trials were conducted. No signs of stress behaviour were noted after completion of any of the trials. For the mean distance from the EMF highpoint, a linear mixed-effects model (LMM, Gaussian family) indicated that the null model was best-supported based on AIC. The EMF treatment was added to the final model to test significance anyway, and Tukey post hoc comparisons revealed no significant differences between treatments (all pairwise $p \geq 0.33$; Fig. 7.3a). For the number of crossings, zero-inflated negative binomial (ZINB) models were used. Again, the null model was best-supported, and adding EMF treatment revealed no significant differences between treatments (all $p \geq 0.23$, Fig. 7.3b). For the total distance swam, the best-supported ZINB model included both treatment and origin. Nevertheless, pairwise comparisons showed no differences between treatments (all $p \geq 0.53$, Fig. 7.3c). Skates from the SF, collected in April 2025, travelled significantly shorter distances than those from LL, collected in September 2024 (estimated difference on the log scale = −1.56 ± 0.45 SE, $z = -3.44$, $p < 0.001$).

On average, skates were inactive approximately 63% of the time, and locally active and transiting for both halves of the remainder period. However, substantial variation was observed among individuals and trials (Fig. S7.1 & S7.2). The best-fitting hidden Markov model revealed a significant main effect of treatment (LRT: $\chi^2 12 = 208.3$, $p < 0.001$), and a significant interaction between sex and EMF treatment (LRT: $\chi^2 12 = 112.9$, $p < 0.001$). During AC trials, females spent approximately 15%pt. less time inactive and ~12.5%pt. more time transiting compared with DC and control trials. In contrast, males were ~14%pt. more inactive during both AC and DC trials, were 4%pt. less locally active during AC trials when compared to control trials and spent 9%pt. less time transiting during AC and DC trials (Fig. 7.4). Sex also had a significant effect on behavioural state transition probabilities (LRT: $\chi^2 6 = 279.7$, $p < 0.001$), however differences in stationary state probabilities between sexes were small, with substantial overlap of 95% confidence intervals, indicating limited differences in long-term behavioural state occupancy (Fig. S7.3). The origin of the skates also influenced the state transition probabilities (LRT: $\chi^2 6 = 364.6$, $p < 0.001$), with skates from SF being more inactive (~30%pt.) and less locally active (~14%pt.) and transiting (~18%pt) than skates from LL (Fig. S7.4). Significance of all covariates was retained when analyses were restricted to individuals from LL only (all still $p < 0.001$, Table S7.5). Lastly, a significant treatment order effect (LRT: $\chi^2 6 = 253.4$, $p < 0.001$) was observed, with

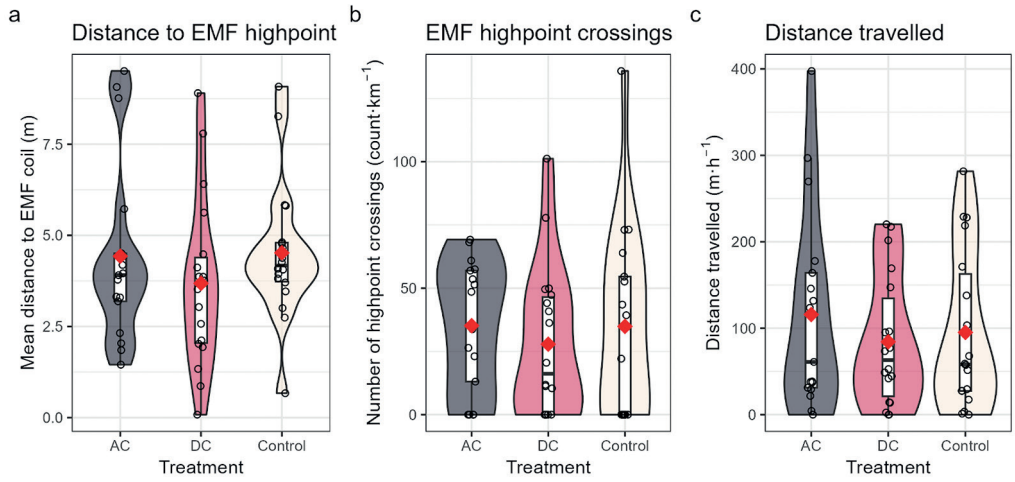


Fig. 7.3 Violin plots with boxplots showing the **(a)** mean distances to the centre of the electromagnetic field (EMF) of each trial, **(b)** the number of times the centre of the EMF was crossed per km travelled, and **(c)** total distance travelled in meters per hour (right) for alternating current (AC) in grey, direct current (DC) in pink and control treatments in white. The red dot indicates the average for all trials. No statistical significances were found between the treatments in all three behavioural parameters.

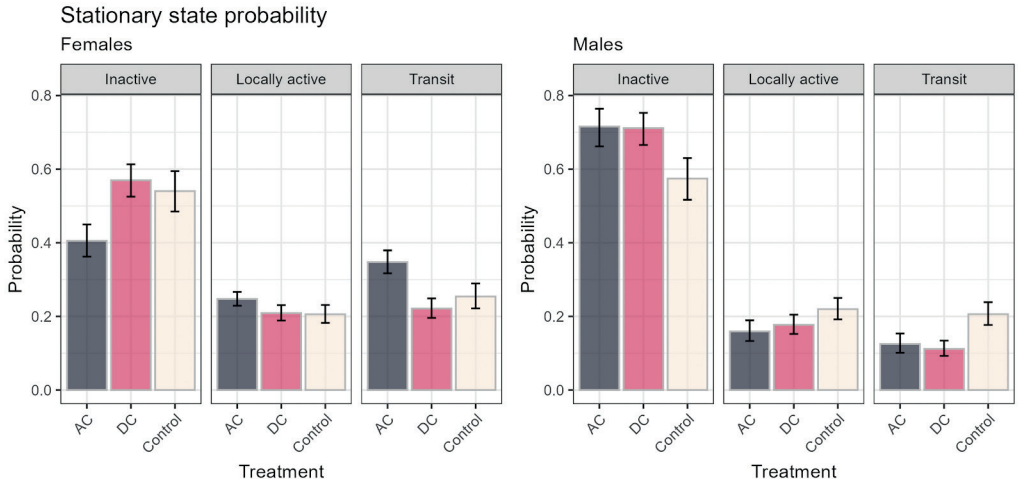


Fig. 7.4 The stationary state probability with 95% confidence intervals of the behavioural states of the skates during the experimental treatments, with females (left, n = 10) and males (right, n = 8) separated. This is the Hidden Markov Model (HMM) output for the best model fit which included the covariates treatment, sex, the interaction between them, trial order, and origin (e.g. location of capture). Likelihood ratio tests indicate a significant treatment effect and interaction with sex. Female rays were less inactive and transiting more during AC treatments, and males were more inactive during both AC and DC treatment when compared to the control, less locally active during AC trials when compared to controls, and transiting less during AC and DC trials. For the stationary state probabilities shown, covariates not depicted in the figure were set to the following reference values: Origin = Loch Linnhe, Order = 1.

increased transiting behaviour only in the third trial compared to the second (Fig. S7.5). The treatment order was colinear with temperature, which increased over the course of the experiment, suggesting that part of the observed order effect may be attributable to temperature rather than the order alone.

7.4 Discussion

The swimming behaviour of *R. clavata* was examined under exposure to AC and DC EMFs comparable to those generated by subsea power cables. No evidence of attraction to, or avoidance of, the EMFs was observed, and spatial use within the experimental tank did not differ between EMF and control trials. Hidden Markov model analyses revealed sex-specific behavioural responses: females exhibited reduced inactivity (15%pt.) and increased transiting behaviour (12.5%pt.) during AC exposure, compared to control conditions. Males showed increased inactivity (14%pt.) under both AC and DC conditions, reduced local activity (4%pt.) during AC exposure, and decreased transiting (9%pt.) during both AC and DC treatments compared to control. These results indicate subtle, sex-dependent changes of activity patterns in response to EMF exposure.

Across all trials, no evidence was found for avoidance of EMF exposure, indicating that the fields did not function as a (behavioural) deterrent. The absence of avoidance is consistent with previous experimental and field observations, where similar responses were reported (Gill et al., 2009; Hermans, Maris, et al., 2025; Hermans, Sumner-Hempel, et al., 2025; Hutchison et al., 2020b; Orr, 2016). Conversely, earlier studies with similar field relevant exposure levels, i.e. around subsea power cables, have reported that AC EMFs may elicit attraction (Gill et al., 2009; Hutchison et al., 2020b), a pattern not observed in this study. One explanation may lie in differences in experimental context: prior work was largely conducted in mesocosm or field-based tagging studies, where electroreception operates in context with chemical, hydrodynamic, and visual cues that were absent under laboratory conditions. It is possible that fish in a structurally enriched environment are more prone to engage in prey-searching behaviour than those in a bare tank. Other laboratory AC EMF exposure studies also give no indication of attraction for *S. canicula* (Hermans et al., 2025), Bouwman and Hermans et al., under review). Behavioural responses to anthropogenic EMFs may only show-up when embedded within ecologically realistic sensory and foraging contexts as present in the field.

The results reveal sex-specific differences in behaviour during EMF exposure. Females exhibited reduced inactivity and increased transiting behaviour, but only under AC exposure, whereas males showed the opposite pattern, with increased inactivity and reduced transiting under both AC and DC conditions. Sex-specific responses to anthropogenic EMF were found in other species as well: a behavioural study on *S. canicula* showed differences in foraging activity between females and males, and between single-sex groups and mixed-sex groups, under exposure to artificial prey-type electric fields (Kimber et al., 2009). The authors discussed that the sexes' physical sensory capabilities were likely not different, sugge-

sting that the response to EMF was behavioural. Sexual dimorphism of the electro-sensory system has been shown in blue-spotted fantail stingray (*Taeniura lymma*) (Kempster et al., 2013), which does suggest perceptual differences in this species. In the European green crab (*Carcinus maenas*), females showed strong attraction to EMF while males showed no preference (James et al., 2025), supporting broader evidence of sex-dependent EMF sensitivity. Although differences in perception cannot be ruled out in the present study species, there are sex-related differences in behaviour that might explain the difference in EMF-related responses. Tagging studies show temporal variation in *R. clavata* habitat use (Papadopoulo et al., 2023; Simpson et al., 2021), where females show a higher presence in nearshore waters, and overall presence peaking in summer. These sex-specific differences likely reflect shifts in foraging, mating, and/or migratory behaviour, all potentially associated with EMF use. As the current experiment was conducted in summer, males and females may have been in different behavioural modes, as mating season lasts from February to September, peaking in June (Holden, 1975). It is recommended that sex is considered in future study design and subsequently added as a covariate in behavioural analyses, particularly for responses involving social interactions and seasonal movements.

The origin of the skates showed significant influence on the behavioural states. Animals came from two different locations, a semi-enclosed sea loch (LL) and an open estuary (SF). The two habitats differ significantly in depth (LL: >30m; SF: <5m), visibility (LL: >5m; SF: <1m), turbidity, general habitat and substrate (LL: rocky and sandy with algal growth; SF: barren sand). These different conditions may reflect inherent differences in baseline activity levels between populations. Additionally, the two groups were captured at different times of year (LL: September; SF: April), potentially corresponding to different reproductive or physiological states, such as pre- versus post-spawning condition, which could influence activity patterns. The duration of captivity prior to experimentation also differed substantially between groups (LL: 8M; SF: 1M). The LL group may have become habitually familiar to the confines of a tank and regular feeding. In contrast, the SF animals may have experienced residual capture/handing stress which may have contributed to their reduced swimming activity. The body condition if the animals, calculated as weight: length ratio, was comparable for both groups. Overall, the two groups had an heterogenous background, but as they were well balanced in relation to other covariates, they were not expected to bias the results from the study. This was confirmed by testing the significance of all covariates, which was retained when the analysis was restricted to the LL group alone. The significance of the observed behavioural responses, despite the heterogeneous experimental population, increases confidence in the robustness of the observed behavioural patterns.

The order of trials influenced the animals' behaviour, with skates displaying less inactivity and more transiting behaviour during the third trial. A possible explanation for this pattern is habituation, i.e. individuals progressively recognising and becoming familiar with the experimental arena, leading to a difference in baseline behaviour over consecutive trials. Acclimatization to experimental conditions has been demonstrated in elasmobranchs

(Finger et al., 2016; Kimber et al., 2014), and a very similar effect was observed in catsharks in the previous study (Hermans et al., 2025). Additionally, other cognitive studies have demonstrated the ability of other elasmobranch species to retain certain information over longer periods of time (Brown & Schluessel, 2023; Newton & Kajiura, 2017). Although these findings strongly suggest that reduced novelty over successive trials may underlie the observed behavioural changes, the order of the trials was also strongly correlated with water temperature. As the experiments took place over two months, under natural seawater conditions, the temperature increased slightly for each subsequent trial, from 12.1 °C the first week to 15.9 °C the last week (7-day average). Seasonal shifts in temperature are known to be a major driver of movement behaviour in ectothermic animals as elasmobranchs, with higher activity levels recorded with higher temperatures and represent therefore another possible contributing factor in this study (Hunter et al., 2005; Papadopoulo et al., 2023; Papadopoulo, Villegas-Ríos, et al., 2023; Schlaff et al., 2014).

Given the documented interspecific variability in EMF-exposure responses (Egeberg et al., 2014; Gill et al., 2009; Kempster et al., 2016; Marcotte & Lowe, 2008) and the impossibility of testing all species, it is important to determine under which conditions and for which trait-grouped species responses to experimental EMF can be extrapolated to other elasmobranchs. Consistent with the findings on skate response presented here, a former experiment on *S. canicula* with the same experimental set-up, no attraction to or avoidance of EMF exposure and no changes in spatial use were observed (Hermans, Maris, et al., 2025). However, *S. canicula* exhibited a reduction of ~25%pt. in transiting behaviour during DC exposure, a pattern comparable to that observed in male skates, although notably in skates this response occurred under both AC and DC exposure. As sex-treatment interactions were not examined in the shark study, it remains unclear whether similar sex-specific differences were present. A mesocosm study also compared the responses of these two species, where *R. clavata* showed a slight increase in movement and *S. canicula* exhibited attraction to the cable with reduced movement in close proximity under max. 8.0 μT AC (Gill et al., 2009). Although the reported behavioural changes were different, they align with the subtlety and observed species-specific differences observed here, particularly in female skates. The majority of the responses, or the lack thereof, of the sharks and skates to the EMF exposure are similar. This could be explained as *S. canicula* and *R. clavata* share several ecological features for which they may use EMF: a predominantly benthic lifestyle in overlapping benthic habitats in the North Sea, and broadly similar diets consisting of crustaceans and small fishes (Bird et al., 2020; Heessen et al., 2015; Labourgade et al., 2024; Papadopoulo et al., 2023; Rodríguez-Cabello et al., 2004; Sims et al., 2001). The subtly distinct responses to EMF exposure may be explained by several life history traits for which electro and/or magnetosensitivity is used. There are basic differences in sensory sensitivity as the ampullae of Lorenzini are clustered around the snout in sharks but distributed across the ventral disc in skates as shown in other elasmobranch species (Collin et al., 2015; Egeberg et al., 2014; Sisneros & Tricas, 2002). The movement patterns of the two species differ, where *R. clavata* are believed to have

longer regional migrations [48], [49], [50] compared to *S. canicula* which remains more local (Labourgade et al., 2024; Papadopoulo et al., 2023; Rodríguez-Cabello et al., 2007). Although both nocturnal, *S. canicula* acts as a more mobile opportunistic scavenger and *R. clavata* predominantly feeds on benthic species (crustations, bivalves, polychaetes) but is also known to feed pelagically (Demirhan et al., 2005; Mate Šantić et al., 2012; M. Šantić et al., 2012). These mechanisms likely interact, and further research is required to disentangle the combined roles of sensory physiology, ecology, behavioural context and sex in relation to response to anthropogenic EMFs. Overall, despite ecological differences between the species, behavioural responses were activity-based and of a similar order of magnitude. Moreover, the absence of strong effects (attraction, avoidance, or altered spatial distribution) was consistent for both species, aiding in assessing potential impacts of subsea power cables on benthic elasmobranchs. Note that greater divergence might be expected in species with more contrasting traits, such as resident versus migratory lifestyles or differing foraging strategies and caution is advised extrapolating EMF effects across elasmobranch species.

The absence of avoidance of EMF in this study supports the hypothesis that habitat within OWFs remains available to elasmobranchs, consistent with observations in other studies (Couturier et al., 2025; Hermans, Sumner-Hempel, et al., 2025; Maire et al., 2025). No influence on EMF crossing was observed, suggesting that export cables do not form a hard barrier. The lack of avoidance behaviour towards EMFs implies that these fields will not deter use as spawning habitat, potentially resulting in greater exposure of embryonic and larval stages and subsequent ecological impacts (Hermans et al., 2025). However, the subtle changes in swimming behaviour detected here, and in other studies (Hermans, Maas, et al., 2025; Hermans et al., 2025), may affect time available for foraging, conspecific interaction and/or long range movements at repeated exposure, e.g. every time a cable is encountered. As these aspects may ultimately impact fitness, growth and reproduction, migration, foraging success, and mating, they warrant targeted investigation (Hermans et al., 2024; Hutchison & Gill, 2025). It remains critical to determine whether habituation occurs and whether these responses persist under natural field conditions, aspects which both should be taken into account in Environmental Impact Assessments (EIAs).

Offshore power transmission is rapidly increasing, particularly through DC cables as energy is transported over longer distances (Zhichu et al., 2024), making the present DC-related findings especially relevant. Field research on effects of DC cables remains limited (Garavelli et al., 2024; Hutchison et al., 2021), and the extent to which increased inactivity or altered movement translates to natural settings is still unknown. It is therefore recommended to conduct fine-mesh in-situ acoustic telemetry studies to validate these laboratory results within a more complex sensory environment.

7.5 Conclusions

Subsea cable-related EMFs, both AC and DC, did not elicit attraction, avoidance, or changes in spatial distribution in *R. clavata*. However, small but statistically significant (15%pt.), sex-specific shifts in activity patterns were detected under both AC and DC exposure, which might carry further importance when considering reproductive behaviours. These findings suggest that EMFs from offshore power cables are unlikely to function as behavioural barriers for this species at field-relevant intensities, but might reduce time available for ecologically vital behaviours. While these effects were subtle, their ecological relevance under repeated exposure remains uncertain and warrants validation through further laboratory as well as field studies.

Supplementary materials

Table S7.1 Overview of biometric data, capture location and date and trial order of individual skates that participated in the trials.

Animal ID	Sex	Disc width (cm)	Weight before trials (g)	Capture location	Date in facility	Trial order
202	F	45.8	1316	Loch Linnhe	13/09/2025	DC-AC-CT
203	M	31.9	912	Loch Linnhe	13/09/2025	CT-AC-DC
204	F	44.1	2460	Loch Linnhe	13/09/2025	AC-CT-DC
205	M	36.5	1308	Loch Linnhe	13/09/2025	CT-AC-DC
206	F	40.6	1640	Loch Linnhe	13/09/2025	CT-AC-DC
208	M	37.1	1226	Loch Linnhe	13/09/2025	CT-DC-AC
209	M	34.3	1002	Loch Linnhe	13/09/2025	DC-CT-AC
210	F	45.5	3032	Loch Linnhe	13/09/2025	AC-DC-CT
211	M	38.3	1040	Loch Linnhe	13/09/2025	AC-DC-CT
215	F	40.8	1616	Loch Linnhe	13/09/2025	AC-CT-DC
216	M	36.3	1000	Loch Linnhe	13/09/2025	DC-CT-AC
217	F	46.1	2614	Loch Linnhe	13/09/2025	DC-AC-CT
218	F	45.1	2738	Loch Linnhe	13/09/2025	CT-DC-AC
219	F	47.3	3086	Loch Linnhe	13/09/2025	DC-CT-AC
301	F	36.9	1272	Solway Firth	01/05/2025	DC-AC-CT
304	F	40.9	1808	Solway Firth	01/05/2025	CT-DC-AC
305	M	43.3	1426	Solway Firth	01/05/2025	AC-CT-DC
306	M	38.7	1080	Solway Firth	01/05/2025	AC-DC-CT

Table S7.2 Overview of trials showing fish ID, the trial, date when it was carried out and the number of the trial for that individual. Skate IDs in bold indicate animals from the second group (Solway Firth).

Skate ID	Trial	Date	#
203	Control	15-05-2025	1
211	AC	16-05-2025	1
204	AC	17-05-2025	1
219	DC	18-05-2025	1
205	Control	19-05-2025	1
301	DC	20-05-2025	1
215	AC	21-05-2025	1
202	DC	22-05-2025	1
218	Control	23-05-2025	1
209	DC	26-05-2025	1
206	Control	27-05-2025	1
217	DC	28-05-2025	1
306	AC	30-05-2025	1
305	AC	31-05-2025	1
304	Control	01-06-2025	1
208	Control	02-06-2025	1
210	AC	03-06-2025	1
216	DC	04-06-2025	1
203	AC	05-06-2025	2
204	Control	07-06-2025	2
219	Control	08-06-2025	2
205	AC	09-06-2025	2
301	AC	10-06-2025	2
215	Control	11-06-2025	2
202	AC	12-06-2025	2
218	DC	13-06-2025	2
209	Control	14-06-2025	2
206	AC	15-06-2025	2
217	AC	16-06-2025	2
306	DC	17-06-2025	2
305	Control	18-06-2025	2
304	DC	19-06-2025	2
208	DC	20-06-2025	2
210	DC	21-06-2025	2
216	Control	25-06-2025	2
203	DC	26-06-2025	3
211	DC	27-06-2025	2
204	DC	28-06-2025	3
219	AC	29-06-2025	3
205	DC	30-06-2025	3
301	Control	01-07-2025	3
215	DC	02-07-2025	3
202	Control	03-07-2025	3
218	AC	04-07-2025	3
209	AC	05-07-2025	3
206	DC	06-07-2025	3
217	Control	08-07-2025	3
306	Control	09-07-2025	3
305	DC	10-07-2025	3
304	AC	11-07-2025	3
210	Control	14-07-2025	3
216	AC	16-07-2025	3
211	Control	18-07-2025	3

Table S7.3 Model selection results to determine optimal number of behavioural states using Hidden Markov Models to explain ray behaviour during the experimental treatment. The AIC is the Akaike Information Criterion, and the lowest AIC refers to the best model [*]. In the case, a three-state model was best-supported.

Number of states	AIC
3*	-169555.8
2	-31348.16
1	494849.5

Table S7.4 Model selection results to determine the covariates for the best fit to explain skate behaviour during the experimental treatment. Covariates used: origin, sex, order of trials, treatment, weight of skate, and the interaction between sex and treatment. The null model, without covariates is indicated by 'NULL'. The AIC is the Akaike Information Criterion, and the lowest AIC indicates the best model [*].

#	Covariates	AIC
1*	Origin + Sex + Order + Treatment + Treatment:Sex	-170712.2
2	Origin + Sex + Order + Treatment	-170623.3
3	Origin + Sex + Order	-170439.0
4	Origin + Sex + Treatment	-170401.9
5	Origin + Sex	-170216.8
6	Origin + Order	-170163.8
7	Origin + Weight	-170137.9
8	Origin + Treatment	-170128.9
9	Origin + Sex + Order + Treatment + Treatment:Sex + Weight	-169923.3
10	Origin	-169921.8
11	Sex	-169850.3
12	Order	-169817.8
13	Origin + Sex + Order + Weight	-169762.4
14	NULL	-169555.8
15	Weight	-168538.2

Table S7.5 Covariate significance of Hidden Markov model for the total group (all) and without the four individuals from Solway Firth (LL). Covariate significance was assessed using likelihood ratio tests (LRTs), comparing models with and without the focal covariate while keeping all other components identical. The table provides the differences in degrees of freedom (Δdf), the likelihood ratio (LR) test statistic, and the associated p-value based on a χ^2 distribution.

Covariate	**Δdf**		**LR statistic**		**p-value**	
	All	**LL**	**All**	**LL**	**All**	**LL**
Sex:Treatment	12	12	112.896	63.997	< 0.001	< 0.001
Treatment	12	12	208.321	218.699	< 0.001	< 0.001
Sex	6	6	279.679	218.845	< 0.001	< 0.001
Order	12	12	253.426	269.050	< 0.001	< 0.001
Origin	6	NA	364.563	NA	< 0.001	NA

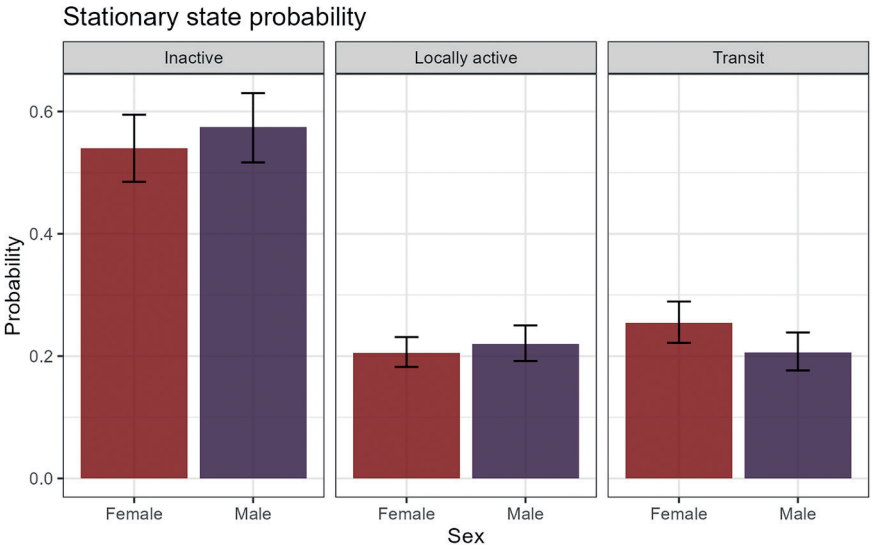


Fig. S7.1 Stationary state probability of both sexes, indicating female (red) and male (purple), for all three behavioural states. Stationary state probabilities showed only minor differences between sexes, despite a significant effect of sex on state transition probabilities. For the stationary state probabilities shown, covariates not depicted in the figure were set to the following reference values: Origin = Loch Linnhe, Order = 1, Treatment = Control.

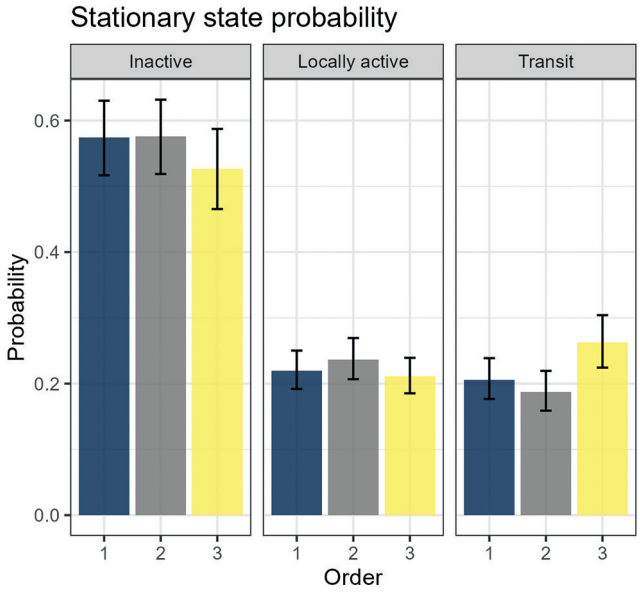


Fig. S7.2 Stationarity state probability over trial order. There was a significant effect of trial order, with more transiting behaviour in the third trial when compared to the second one. For the stationary state probabilities shown, covariates not depicted in the figure were set to the following reference values: Origin = Loch Linnhe, Sex = Male, Treatment = Control.

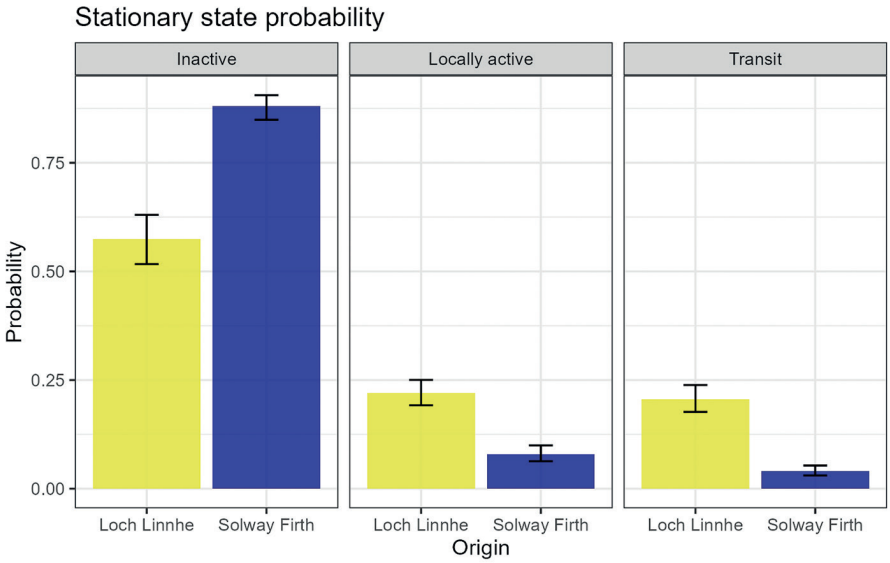


Fig. S7.3 Stationary state probability of origin (e.g. location of capture), indicating Loch Linnhe (n = 14) (yellow) and Solway (n=4) (blue), for all three behavioural states (the panels). The results reveal significant differences between origins, with rays from Solway being more inactive and less locally active and transiting. For the stationary state probabilities shown, covariates not depicted in the figure were set to the following reference values: Order = 1, Sex = Male, Treatment = Control.

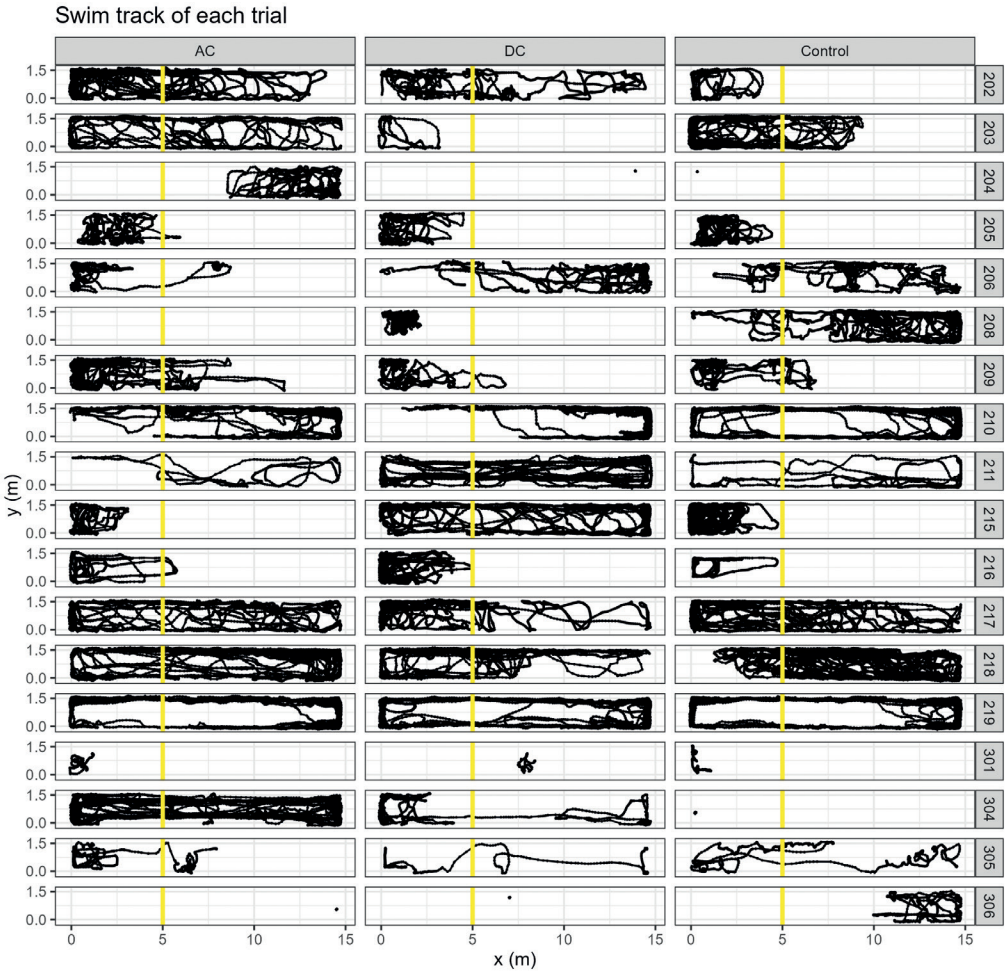


Fig. S7.4 Individual tracks of all 18 skates (rows), for all their trials (columns). The tracks show high individual variability. The yellow line indicates the location of the solenoid system, which was physically present but switched off in the control condition. Note that the x- and y-axes are not proportional.

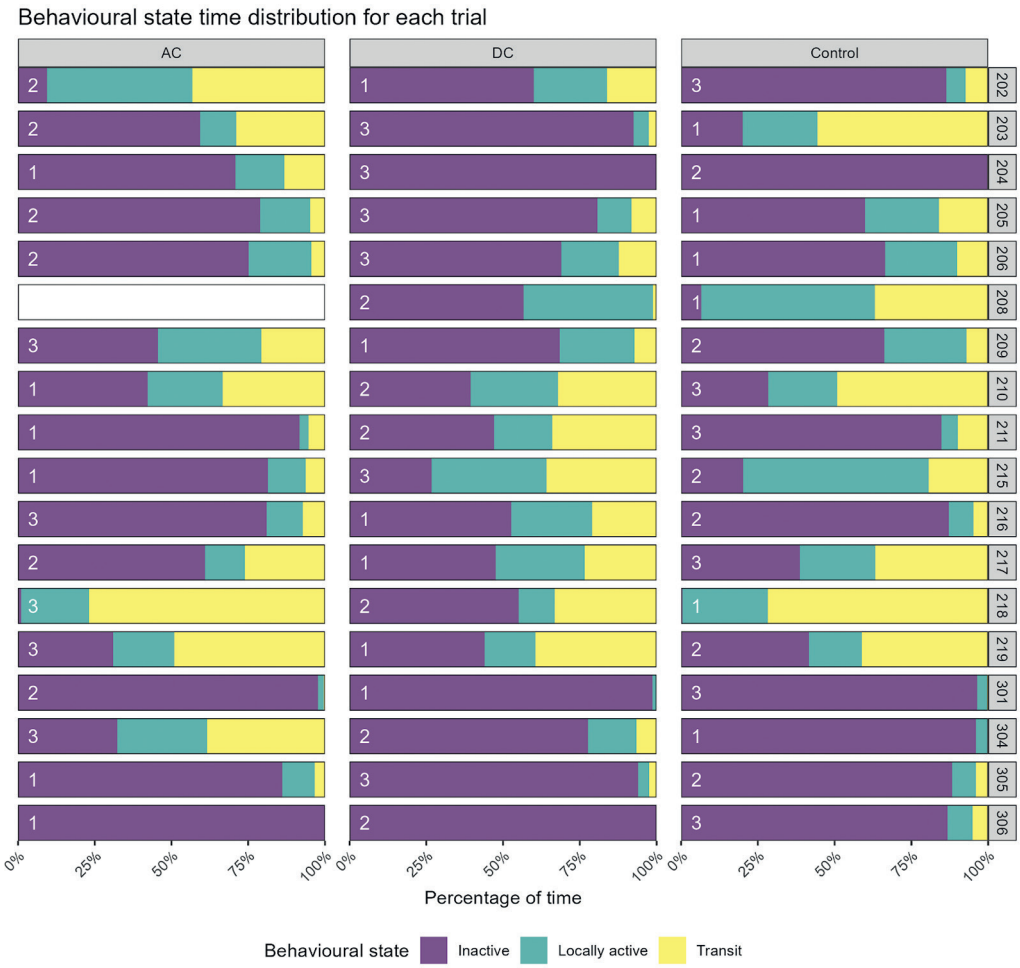
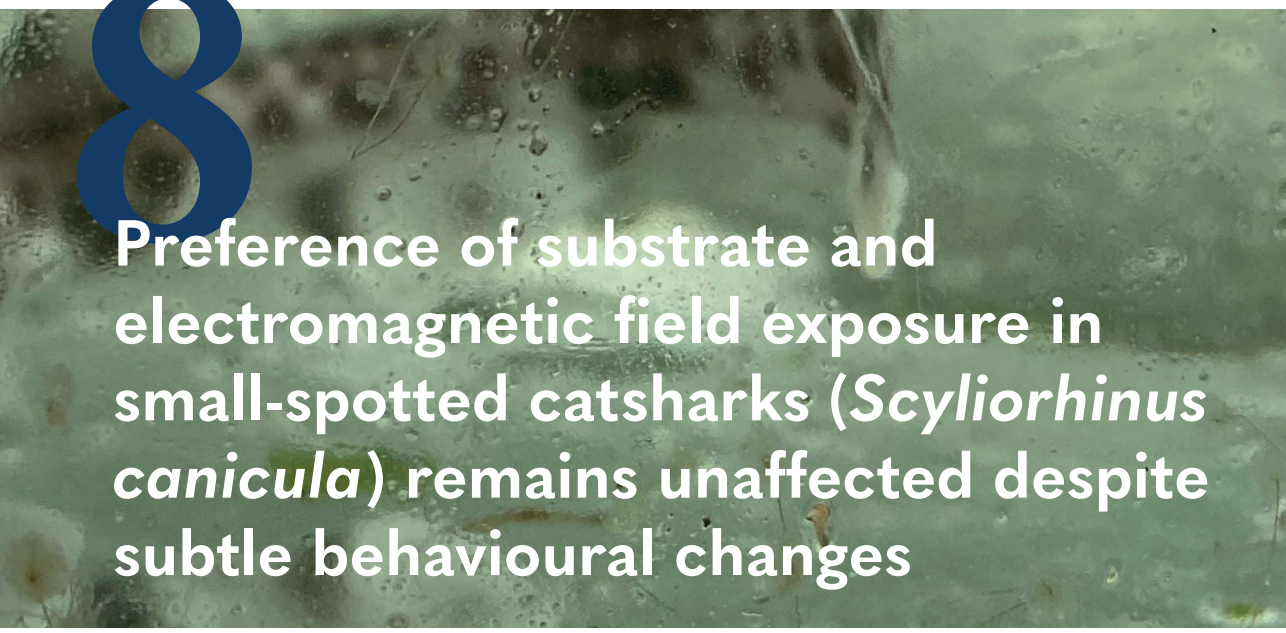


Fig. S7.5 State distribution for each of the 18 individual skates (rows) for each of their trials (columns), the white number indicated the trial order. The overview depicts a high intra- and interindividual behavioural variability.



Abstract

Offshore wind energy plays a crucial role in the transition to low-carbon power generation. The expansion of offshore wind farms (OWFs) introduces anthropogenic electromagnetic fields (EMFs) from subsea power cables. Elasmobranchs, including sharks and rays, are sensitive to natural electric and magnetic fields used for navigation and prey detection, making them potentially vulnerable to anthropogenic EMFs as it may alter orientation, foraging, or habitat use. Coastal shelf seas, where most OWFs are constructed, often overlap with essential elasmobranch habitats, including complex biogenic structures such as mussel beds that provide foraging- and refuge opportunities. We aimed to determine whether exposure to an AC-EMF representative of subsea power cables, and/or complex mussel substrate over non-complex substrate influences behaviour, or modifies substrate preferences in juvenile small-spotted catsharks (*Scyliorhinus canicula*). This study investigated the behavioural responses of 14 juvenile *S. canicula* exposed to a gradient of Alternating Current (AC) EMF (max. RMS 2 μT) and complex biogenic mussel substrate in a 22 factorial design in a circular preference chamber. Across 28 trials, time spent and dis-



8

Preference of substrate and electromagnetic field exposure in small-spotted catsharks (*Scyliorhinus canicula*) remains unaffected despite subtle behavioural changes

tance travelled in each quadrant did not differ with EMF exposure and/or the presence of complex biogenic substrate. Hidden Markov Models revealed subtle but significant changes in behavioural states (inactive, local activity, transit), where sharks become more inactive (+6%pt.) and less locally active (-5%pt.) in the EMF + mussel quadrant compared to the bare and EMF-only quadrants, and increased transiting behaviour (+6%pt.) in the mussel-only quadrant relative to the EMF + mussel quadrant. These findings show that, *S. canicula* juveniles show no preference in substrate nor alternating-current EMF exposure, but did subtly change their behaviour. Future work should examine direct-current systems and field-based tracking and assess the extent to which these observations generalize to field settings and other elasmobranchs.

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Accepted by Journal of Fish Biology | Juli 2026

8.1 Introduction

8.1.1 Electromagnetic fields from offshore generated energy transport

Offshore wind farms represent a sustainable and expanding source of energy for countries bordering the sea (Díaz and Guedes Soares 2020; Isaksson et al. 2025). As part of offshore infrastructure, subsea power cables are required to transport electricity from turbines to high-voltage offshore substations and subsequently to shore via export cables (Henkel, Suryan, and Lagerquist 2014; Taormina et al. 2018; Worzyk 2009). These cables generate electromagnetic fields (EMFs), introducing anthropogenic EMFs into the marine environment (Garavelli et al. 2024; Henkel, Suryan, and Lagerquist 2014; Taormina et al. 2018). Naturally occurring EMFs in the ocean arise from the earth's geomagnetic field, ocean currents, and geomorphological features, and the bioelectric fields produced by marine organisms (CSA Ocean Sciences Inc. and Exponent 2019; Gill et al. 2014; Hutchison et al. 2020). Natural EMFs are used by different marine taxa for ecological purposes including navigation, foraging, and interaction with conspecifics (Albert et al. 2020; Hermans et al. 2024; Verhelst et al. 2025). Despite increasing awareness, the effects of anthropogenic EMFs on marine species remain poorly understood (Garavelli et al. 2024; Hermans et al. 2024; Hutchison and Gill 2025; Verhelst et al. 2025). With the predicted expansion of offshore wind farms, creating a reticulated EMF network across benthic habitats (Hermans et al. 2024). However, knowledge gaps remain regarding the behavioural consequences for elasmobranch populations of such exposure, particularly in relation to benthic habitats common in offshore wind farms.

8.1.2 Elasmobranch and EMFs

Elasmobranchs, including sharks, are capable of detecting natural electric and magnetic fields, making them potentially susceptible to changes in EMFs (Kalmijn 1971; Kalmijn 1982; Meyer, Holland, and Papastamatiou 2005). As ecologically important predators, increasingly threatened by human activities, understanding factors that may affect their behaviour and habitat use is essential to understand the potential impact on these species (Dedman et al. 2024; Dulvy et al. 2021; Flowers, Heithaus, and Papastamatiou 2021). Elasmobranchs detect electric fields primarily through specialized sensory organs known as the Ampullae of Lorenzini, which are distributed over the head and pectoral region (Newton, Gill, and Kajiura 2019; Sisneros and Tricas 2000). There is less consensus on how magnetic fields are sensed, but this is hypothesised to occur either indirectly through the same organs that detect electric fields or via magnetite-based receptors, enabling navigation over large distances (Crampton 2019; Nyqvist et al. 2020). Electro- and magneto-sensitivity play critical roles in foraging (Bedore and Kajiura 2013; Kajiura and Holland 2002), mating interactions (Kempster et al. 2013; Sisneros and Tricas 2000; Tricas, Michael, and Sisneros 1995) and navigation (Anderson et al. 2017; Kalmijn 1978; Keller et al. 2021; Naisbett-Jo-

nes and Lohmann 2022). These senses also aid in predator avoidance during embryogenesis, as the embryo senses a predator and response by ceasing all movement reducing the chance of detection (Ball, Oliver, and Gill 2016; Christensen et al. 2023; Hermans, Maas, et al. 2025; Kempster, Hart, and Collin 2013; Paoletti et al. 2023), underscoring their importance for survival. Anthropogenic EMFs generated by subsea power cables may interfere with these natural cues, potentially altering habitat selection or foraging efficiency (Hermans et al. 2024; Hutchison, Secor, and Gill 2020). To investigate these potential effects, we focus on the small-spotted catshark (*Scyliorhinus canicula*) (Linnaeus, 1758), a species well-suited for controlled experiments due to its small size, tolerance of captivity, relatively high abundance and ex-situ availability (Compagno, Dando, and Fowler 2005; Heessen, Daan, and Ellis 2015; IUCN 2008). Juveniles were selected as relevant study subjects, as early developmental stages are often more sensitive to environmental perturbations (Ball, Oliver, and Gill 2016; Hermans et al. 2024; Hermans et al. 2025; Wheeler 2023), and impacts during this period may carry over to later life stages.

8.1.3 Potential impact of EMFs on habitat preference

Benthic sharks such as *S. canicula* commonly inhabit shallow coastal environments including sandy areas, rocky substrates, and biogenic reefs formed by Sabellaria worms, mussels or other shellfish, which provide both shelter and foraging opportunities (Heessen, Daan, and Ellis 2015; Martin et al. 2012; Papadopoulo et al. 2023; Pizzolla 2008). Mussels are ecosystem engineers that represent a structurally complex substrate that supports diverse benthic prey communities and prevails in deltaic regions (Buschbaum et al. 2009), where subsea cable routes are frequent. Mussel also colonise artificial structures, including platforms and potentially scour protection around offshore wind farms (Degraer et al. 2020; Maar et al. 2009; Ter Hofstede et al. 2022). Moreover, mussels aquaculture is globally widespread in soft-sediment coastal systems (Ysebaert, Hart, and Herman 2009).

The diet of *S. canicula* includes a wide variety of benthic organisms, including species associated with mussel presence, but commonly not mussels directly (Kousteni, Karachle, and Megalofonou 2017; Pizzolla 2008). If anthropogenic EMFs alter habitat preferences, this could render large areas less suitable for sensitive species through deterrence, or conversely attract individuals potentially reducing energy expenditure efficiency (Hutchison, Secor, and Gill 2020; Labourgade et al. 2024; Taormina et al. 2018). There are studies that indicate such attraction (Gill 2009; Hutchison et al. 2020; Labourgade et al. 2024). Most critically, EMFs may interfere with prey detection, for example by masking bioelectric cues, thereby disrupting foraging patterns and effectively reducing suitable habitat for species already under ecological pressure (Hermans et al. 2024; Hutchison, Secor, and Gill 2020; Newton, Gill, and Kajiura 2019; Taormina et al. 2018). Over 5.5% of the Dutch continental shelf, an important habitat for this species, is projected to be exposed by anthropogenic EMF by 2030 in a high wind scenario. Understanding these dynamics is essential to assess offshore wind impacts, optimize cable routing, and identify potential mitigation needs.

8.1.4 Aim and approach

We aimed to determine whether juvenile *S. canicula* prefer complex substrate over bare substrate, and whether exposure to an AC-EMF representative of exposure at 1m (minimum burial depth) of a 700 MW subsea power cable, modifies their substrate choice and behaviour under controlled laboratory conditions. To address this objective, we employed a circular preference chamber divided into four quadrants representing EMF- and complex substrate presence/absence in a 22 factorial design. As a proxy for ecologically relevant and complex substrate, the chamber bottom was covered with live blue mussels (*Mytilus edulis*) for two quadrants as against two quadrants with bare bottom. A local electromagnetic field, with EMF values comparable to those on a seafloor generated by subsea power cables, was generated using a solenoid. This design allowed us to disentangle the effects of EMF exposure and presence of substrate structure on substrate preference and shark behaviour. The documented attraction to anthropogenic EMF (Gill 2009; Hutchison et al. 2020; Labourgade et al. 2024) and the perceived preference to biogenic reefs (Heessen, Daan, and Ellis 2015; Martin et al. 2012; Papadopoulo et al. 2023; Pizzolla 2008) leads to the hypothesis that EMF and substrate complexity influence behaviour and spatial distribution of juvenile *S. canicula*.

8.2 Materials and Methods

8.2.1 Test animals

Fourteen juvenile *S. canicula* of 6-9 months old were obtained from Wageningen University and transported to the WUR Yerseke facility. During transport, sharks were placed in plastic bags containing ~10L seawater and filled with 2/3rd 100% oxygen and transported in Styrofoam boxes to maintain temperature. The transport duration was approximately 120 min. At the start of the experiment in May 2025, the juveniles were photographed for individual ID and weighted, and assessed to be in good health (e.g. no ectoparasite presence, abrasions or lesions, good overall condition). Half of the individuals used in this experiment were not naïve to anthropogenic AC EMF, as they were chronically exposed to low level AC EMF (1.8-4.6 μT) during embryogenesis. All individuals were exposed 2 times to a brief 10 min EMF stimulus (1 μT and 10 μT) at 5 and 11 weeks respectively. Their behaviour and biometric parameters were assessed following the earlier exposure, and no significant changes in behaviour or body condition were found (Hermans et al. 2025). To ensure conscious and responsible use of experimental animals, sharks were considered naïve again after a period of three months without further exposure.

8.2.2 Husbandry

Sharks were housed in a sound- and temperature-isolated climate room (Wageningen Marine Research, Yerseke, Zeeland, The Netherlands) was temperature-controlled at ± 16 °C, corresponding to the outside temperature at the time of the experiment. A 12:12h light:dark photoperiod was automatically maintained, with dim light (5 lx; Lutron LX-107, sensitivity = ± 0.05%) from 7 am to 7 pm for simulation of underwater light conditions. To familiarise the sharks and mimic a more varied environment, ~20% of the tank bottom was covered with live mussels. Sharks were group-housed in a 470 L light-grey-coloured propylene housing tank measuring 119 x 79 x 75 cm (LxWxH) subdivided into two sections using a propylene grid, with individuals moved to the other section after completing their initial trial. During the day, a constant inflow (3 L per minute) of ambient temperature seawater was pumped from the Eastern Scheldt, passed through a coarse sand filter, into the housing tank and aerated with air stones to maintain stable oxygen levels. Water quality was assessed daily at noon (portable multiparameter, HANNA HI98194) for temperature (17.21 °C ± 1.11 sd), pH (7.98 ± 0.14 sd), dissolved oxygen (74.69% ± 12.58 sd) and salinity (27.46 ppm ± 0.71 sd). Sharks were fed ad libitum, with a minimum of 3-4 cubes (~0.5 cm3 each) of fresh whiting (Merlangius merlangus) and pouting (Trisopterus luscus) daily (visually checked), equalling ~2.5% of wet body mass. Additional feed was placed on the tank floor, ensuring that feed remained available for consumption at a later stage. Leftover food was removed the next day, prior to feeding. During feeding, visual welfare checks confirmed active swimming and feeding behaviour of each individual. Maximum background EMF levels in the housing tank were 0.13 μT ± 0.06 sd (Narda ELT-400 magnetometer).

8.2.3 Experimental set-up

A sand-coloured polypropylene circular preference chamber with a 190 cm diameter (Dye et al. 2024a; Post et al. 2017; Schram et al. 2013) was used to assess the potential influence of electromagnetic fields (EMF) and habitat preference of juvenile sharks. The chamber design was adapted from Myrick et al. (2004) and has been used in previous behavioural studies with different fish species (Dye et al. 2024b; Post et al. 2017; Schram et al. 2013). The chamber was comprised of a central compartment and three rings: a mixing channel; a swimming channel; and an effluent channel. Sharks were placed in the swimming channel with a width of 19 cm, in which the sharks could move freely. Water entered the mixing channel at eight evenly spaced inlets, passing evenly through circular apertures into the swimming channel and then the effluent ring, draining via the central section to five 60-L storage tanks beneath. More detailed descriptions can be found in Dye et al. (2024) and Schram et al. (2013).

The circular chamber was placed in the same climate room as the housing tank, under the same light- and temperature conditions. In the chamber, the swimming channel was equally divided into four quadrants of a 90 degrees angle. Each of the four quadrants contained a different experimental condition: (1) bare substrate without EMF exposure,

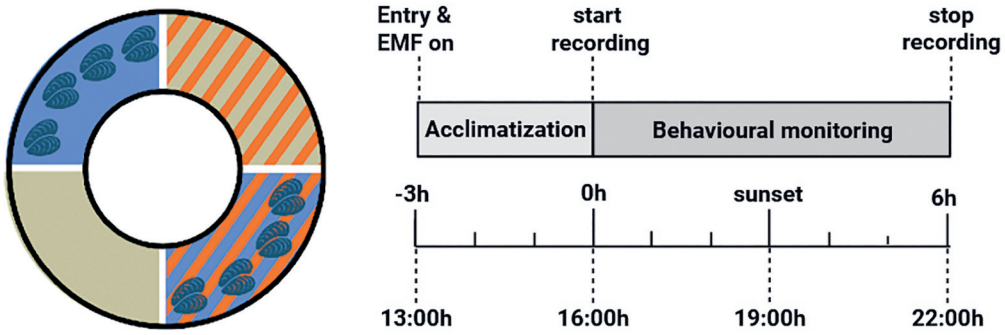


Fig. 8.1 (a) Schematic overview of the habitat preference chamber indicating the different conditions per quadrant, where blue indicates mussels and orange stripes indicate exposure of electromagnetic fields.
(b) Overview of the time schedule used during the trials. Time of entry was at 13h00m, 3 hours before sunset, after which sharks were given 3h to acclimatize to the new environment. The trial lasted 6h and finished 3h after sunset to capture behavioural changes in both light and dark conditions. *Image created with https://BioRender.com*

(2) bare substrate with EMF exposure, (3) mussel substrate with EMF exposure, and (4) mussel substrate without EMF exposure. This design enabled direct comparison of habitat use between complex (mussel) and non-complex (bare) substrates under both EMF and non-EMF conditions (Fig. 8.1). As a proxy for complex biogenic substrate, live mussels forming a 3D structure on the bottom of the swimming channel were used. For each trial, 1 to 1.2 kilograms of live blue mussels (Mytulis edulis) originating from the Eastern Scheldt were used, forming a bed of mussels in the complex substrate condition quadrants. Before use, epifauna was removed and they were rewatered for at least 12h to filter out sand to eliminate any confounding factors. Four overhead cameras (Basler 1300-60gm; monochrome; 1.3 Mp; 60 fps) paired with four infrared led-lights (Raytec VAR2-i2-1; IR 850 nm), were positioned above the chamber to record shark swimming patterns during light and dark conditions.

During the experiments, seawater from five 60-L storage tanks underneath the chamber was circulated continuously through the chamber via eight inlet points. A constant inflow of 3 L of ambient temperature seawater per minute was maintained for the chamber, administered in the storage tanks. Directly before and after each trial, water quality was recorded for every quartile of the circular chamber, resulting in averaged water temperature (17.6 °C ± 1.2 sd), pH (8.0 ± 0.1 sd), dissolved oxygen (5.55 mg/l ± 0.97 sd) and salinity (34.1 ppt ± 0.7 sd) values across all trials (portable multiparameter, HANNA HI98194). At the end of each trial, after water quality measurements, all water in the preference chamber was refreshed to remove any chemical cues from the previous individual.

The EMF was generated by a solenoid fixed to a High-Density Polyethylene (HDPE) frame connected to an Accel Instruments TS250 Waveform Amplifier, set to Hi-Z and 20 dB gain (hereafter referred to as the EMF coil). The solenoid, with a diameter of 800 mm

and 155 turns of 1.5 mm^2 copper wire, was paired with a fixed oneaxis fluxgate magnetometer positioned 30 cm behind it. All components were customdesigned and integrated by Waterproof Marine Consultancy & Services BV. Background AC EMF levels were elevated relative to natural conditions originating from the interfering structural elements of experimental room which could not be removed (0.32 ± 0.15), yet remained stable at over six times lower than the exposure condition. Directly before and after each trial, the highest observed EMF values were recorded at four equally spaced positions per quadrant, to determine if the exposure values were as planned (Narda ELT-400 magnetometer). For trials 1 to 4, the EMF level of only one position per quadrant was measured, and therefore linearly interpolated for positions in between. From trial 5 onwards, four EMF values for every quadrant were recorded (16 positions in total), increasing the resolution of the EMF gradient across the chamber. Measured just before and after all 28 trials, the average recorded EMF values in the swimming channel were: 2.04 μT ± 0.5 sd in front of the EMF coil; 0.49 μT ± 0.43 sd in the edge zones of the EMF field; and 0.32 μT ± 0.15 sd in the position opposite the EMF coil (bare/ bare + mussel condition).

8.2.4 Experimental protocol

The EMF coil and substrate were positioned and the field was activated before the sharks entered the preference chamber, to prevent any novelty effects (onset response) associated with EMF exposure or mussels. Sharks were tested individually to eliminate behavioural influences from conspecifics. For each trial, an individual was randomly selected from the housing tank and placed into one of the eight zones (at random) of the circular chamber between 12:00 and 13:00. Data collection started only after three hours to minimise behavioural effects associated with environmental acclimation and recovery from handling. Handling behaviours were observed as moments of surface bobbing and elevated swimming speed, for which the duration varied between individuals from at least five minutes to up to two hours after entering the preference chamber. Hence, between two to three hours, no novelty- nor handling effects were observed anymore and sharks resumed usual behaviour. Swimming behaviour was recorded for six hours – from 3 hours before to 3 hours after artificial sunset at 19:00 (i.e.16:00-22:00) – to capture light-dark changes in activity. Each individual completed two trials, separated by at least three days to reduce effects of habituation and carry-over effects, resulting in a total of 28 trials.

The EMF coil location was randomly assigned to one of five possible positions, locations adjacent to the housing tank were excluded to avoid exposing stock fish to EMF (Fig. 8.5). The location of the mussel condition was also randomly assigned, with the second mussel condition quadrant placed opposite the first to ensure clear choice opportunities.

EthovisionXT v.17.5 (Noldus et al., 2001) was used to record swimming patterns, yielding an XY position every 0.2 s for subsequent analyses. Movements of less than 0.5 cm were ignored to prevent detection interference by mussels (Ethovision setting: track smoothing). Tracking was conducted independently per camera, producing four XY

coordinate streams that were subsequently merged for each trial. Positional data were then corrected to match arena dimensions and the randomised experimental conditions per quadrant for each trial. This process produced a continuous XY position dataset for each shark, annotated with the corresponding experimental condition at each time step. For both trials 5 and 16, the last hour of XY datapoints were excluded due to a recording problem in EthovisionXT. To account for this reduced recording time, behavioural metrics were scaled to a standardised 6-hour duration prior to analysis.

8.2.5 Statistical analyses

To check whether a sharks' release location e.g. condition upon entering the preference chamber influenced the number of minutes spent per condition, a Kruskal-Wallis rank sum test was performed. Quadrant use was determined by comparing the time spent and the distance travelled between quadrants, both for all trials (n = 28), and averaged/summed per individual (n = 14). When comparing quadrants across trials, the trials were considered repeated measures by individual shark, whereas data was considered independent when comparing across individuals. Prior to performing statistical comparisons, data were inspected for normality and homogeneity of variances using standard diagnostic tests (Shapiro and Levene's test). Because assumptions for parametric testing were not met, all subsequent analyses were performed using the non-parametric Friedman rank sum test (comparing across trials) and Kruskal-Wallis rank sum tests (comparing across sharks). Analyses were performed using R Statistical Software (v4.4.1; R Core Team 2024).

Next, we analysed behavioural dynamics using discrete-time hidden Markov models (HMMs), which infer behavioural states from observed time series data. The HMMs were run in R using the package 'momentuHMM' (version 1.5.6; (McClintock and Michelot n.d.)). The sharks' horizontal step length (speed) (Fig. 8.2a) and turning angle (Fig. 8.2b) were used as input data for model fitting. To identify the number of behavioural states best supported by the input data, null models with one up to three states were compared using AIC scores. We used three states a maximum because model selection criteria applied to HMMs often favour models with more states than biologically interpretable (cf Pohle et al. 2017). The three-state model had the best fit (Table S8.1) and we labelled the states as (1) Inactive – low step length and an uniform distribution of turning angles, (2) Locally active – moderate step length and a low directionality, (3) Transiting – large step lengths and highly directional movement (Fig. 8.2). Combinations of the covariates: quartile (Bare, EMF, EMF + Mussels, Mussels), order, body length, and light condition (Light, Dark) were included as predictors of state transition probabilities. Forward model selection based on AIC comparison indicated that the model including all covariates provided with the best fit (Table S8.2). The significance of covariate effects on state transition probabilities was assessed using likelihood ratio tests (LRTs) comparing models with and without the focal covariate. For the best-fitting model, stationary state probabilities (i.e. the modelled proportion of time an individual would spend in each state under constant covariate conditions) were calculated with

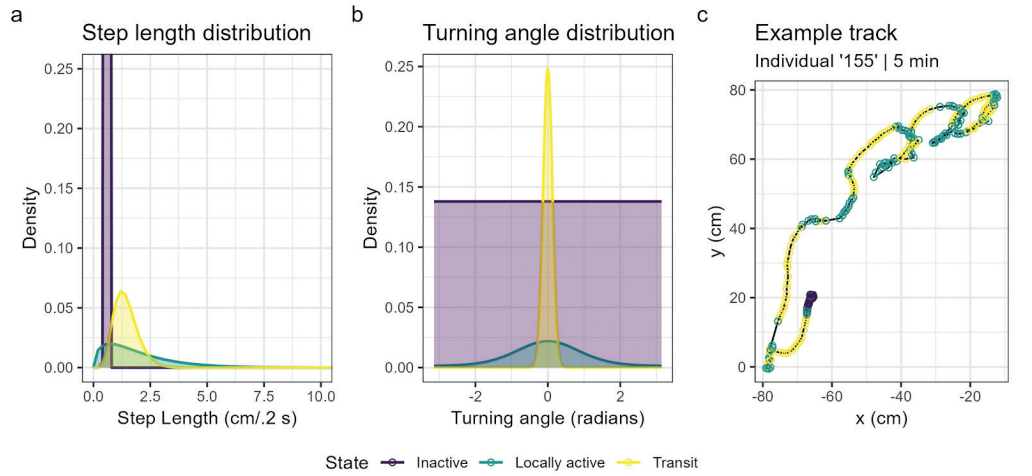


Fig. 8.2 Distribution of step length (a), and turning angle (b) of the three behavioural states (colours) as classified by the hidden Markov model (HMM). (c) Top view of a 5 minute swimming track, with the classified behavioural states.

95% confidence intervals and plotted to visualize the size and direction of covariate effects.

8.3 Results

A total of 26 six-hour trials and two five-hour trials were conducted using 14 juvenile *S. canicula* to assess differences in preference and behaviour between four quartiles with(out) EMF exposure, and with(out) complex biogenic substrate. All 14 individuals appeared healthy from the beginning to the end of the study.

8.3.1 Habitat preferences

All individuals actively moved around in the circular preference chamber during at least one of their two trials (Fig. 8.5). When checking the swimming tracks, release location did not affect where sharks spent the greatest proportion of time based on visual evaluation (Fig. 8.5). Correspondingly, no association between release location and time spent per condition was observed (Kruskal-Wallis rank sum, $p = 0.5102$, $\chi^2_3 = 2.3123$). No abnormal or stress-related behaviours such as belly swimming or surface bobbing were observed during the trials. No statistically significant differences were found between the number of minutes spent across the four quadrants with different experimental conditions (1) bare substrate without EMF exposure, (2) bare substrate with EMF exposure, (3) mussel substrate with EMF exposure, and (4) mussel substrate without EMF exposure across trials (Friedman rank sum test, $p = 0.8839$, $\chi^2_3 = 0.65414$) nor distance travelled between condition across trials (Friedman rank sum test, $p = 0.4057$, $\chi^2_3 = 2.9098$). Similarly, no significant difference

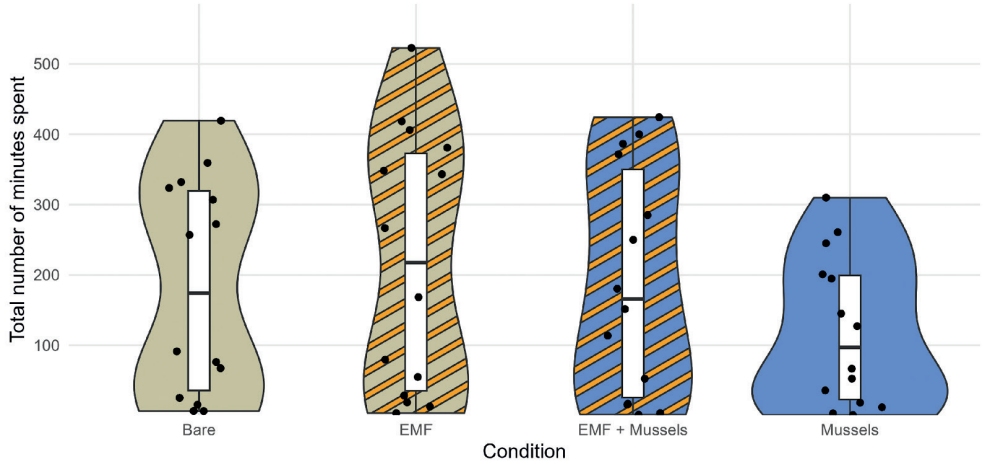


Fig. 8.3 Time spent per individual shark (minutes; n = 14) at four quadrants, each representing a distinct experimental condition (1) bare substrate without EMF exposure, (2) bare substrate with EMF exposure, (3) mussel substrate with EMF exposure, and (4) mussel substrate without EMF exposure. For each shark, data were summed across two 6-hour trials, with trials 5 and 16 corrected for their 5-hour recording only. Violin plots depict the distribution across individuals; inset boxplots show the median and interquartile range. The number of minutes spent did not differ significantly among conditions (Kruskal-Wallis rank sum, $p = 0.4129$, $\chi^2_3 = 2.8652$).

was observed in number of minutes spent between conditions across sharks (Kruskal-Wallis rank sum, $p = 0.4129$, $\chi^2_3 = 2.8652$, Fig. 8.3), nor in total distance travelled between conditions across sharks (Kruskal-Wallis rank sum, $p = 0.713$, $\chi^2_3 = 1.367347$). Overall, these results indicate that neither EMF exposure nor presence of mussels influenced the quadrant selection of juvenile sharks in this experiment.

8.3.2 Behavioural changes

On average, sharks were inactive for approximately 85% of the trial, with the remaining time roughly evenly divided between transiting and locally active (Fig. 8.5). Individual variation was high in both overall activity and quadrant use (Fig. 8.5; Fig. S8.1), and several individuals showed different behaviour between trials (e.g., individuals 186, and 25).

The quartile (bare, EMF, EMF + Mussels, Mussels) had a significant effect on behavioural state transition probabilities (LRT: $\chi^2_{18} = 1381.3$, $p < 0.001$). Differences in stationary state probabilities among quartiles are generally small, with sharks being more inactive (up to 6%pt.) and less locally active (up to 5%pt.) in the EMF + Mussels quartile when compared to the bare and EMF quartiles, and transiting more (6%pt.) in the Mussels quartile than in the EMF + Mussels quartile, as indicated by non-overlapping 95% confidence intervals. State transitions were significantly influenced by diel light conditions (LRT: $\chi^2_6 = 849.3$, $p < 0.001$), with both locally active and transiting increasing during dark

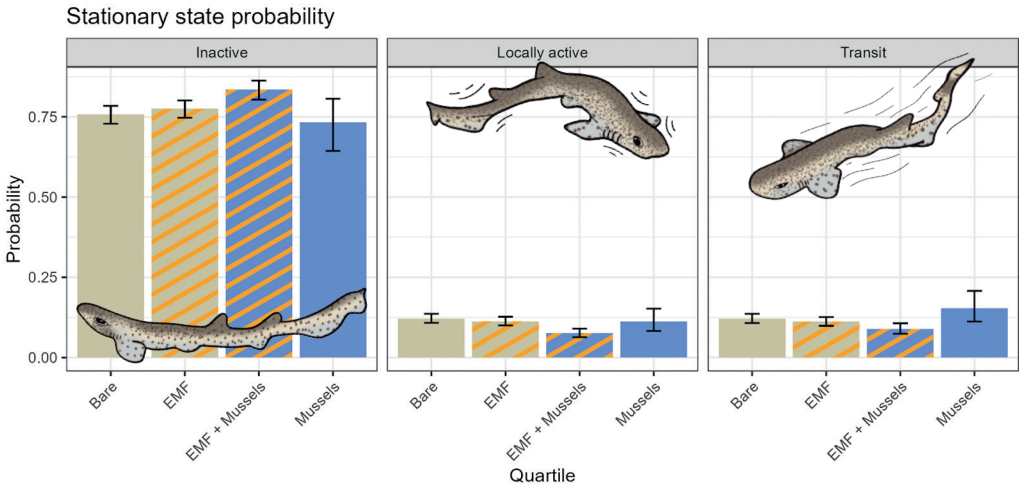


Fig. 8.4 The stationary state probability of the three behavioural states of the 14 sharks, for each condition (1) bare substrate without EMF exposure, (2) EMF exposure with bare substrate, (3) EMF exposure with mussel substrate, and (4) mussel substrate without EMF exposure. The error bars represent the 95 % confidence interval. In the EMF exposure with mussel substrate condition, the sharks spent more time being inactive than at EMF exposure with bare substrate.

hours, reducing inactivity with ~20%pt. (Fig. S8.2). Trial order also had a significant effect (LRT: $\chi^2_6 = 7750.2$, $p < 0.001$), with sharks being slightly less likely to move (~3%pt.) in the second trial (Fig. S8.3). Additionally, body length had a significant effect on state transition probabilities (LRT: $\chi^2_6 = 593.1$, $p < 0.001$) with larger individuals being more inactive than smaller sharks (Fig. S8.4).

8.4 Discussion

Substrate preference and swimming behaviour of juvenile *S. canicula* exposed to SPC-related EMFs and two substrate types were assessed using a controlled preference experiment. No differences in overall space use were detected among quadrants representing the different experimental conditions. However, sharks exhibited subtle but significant shifts in behavioural state transition probabilities, with increased inactivity (+6%pt.) and reduced local activity (-5%pt.) in the EMF + mussel quadrant compared to the Bare and EMF-only quadrants, and increased transiting behaviour (+6%pt.) in the mussel-only quadrant relative to the EMF + mussel quadrant.

Neither time spent per quadrant nor total distance travelled differed significantly between the elevated EMF and the background EMF quadrants, nor in the mussel or bare quadrants. Based on previous studies (Gill 2009; Hutchison et al. 2020; Labourgade et al. 2024), an attraction to AC EMF exposure might have been expected. A possible explanation for the lack of behavioural change is that previous studies were conducted in mesocosm-

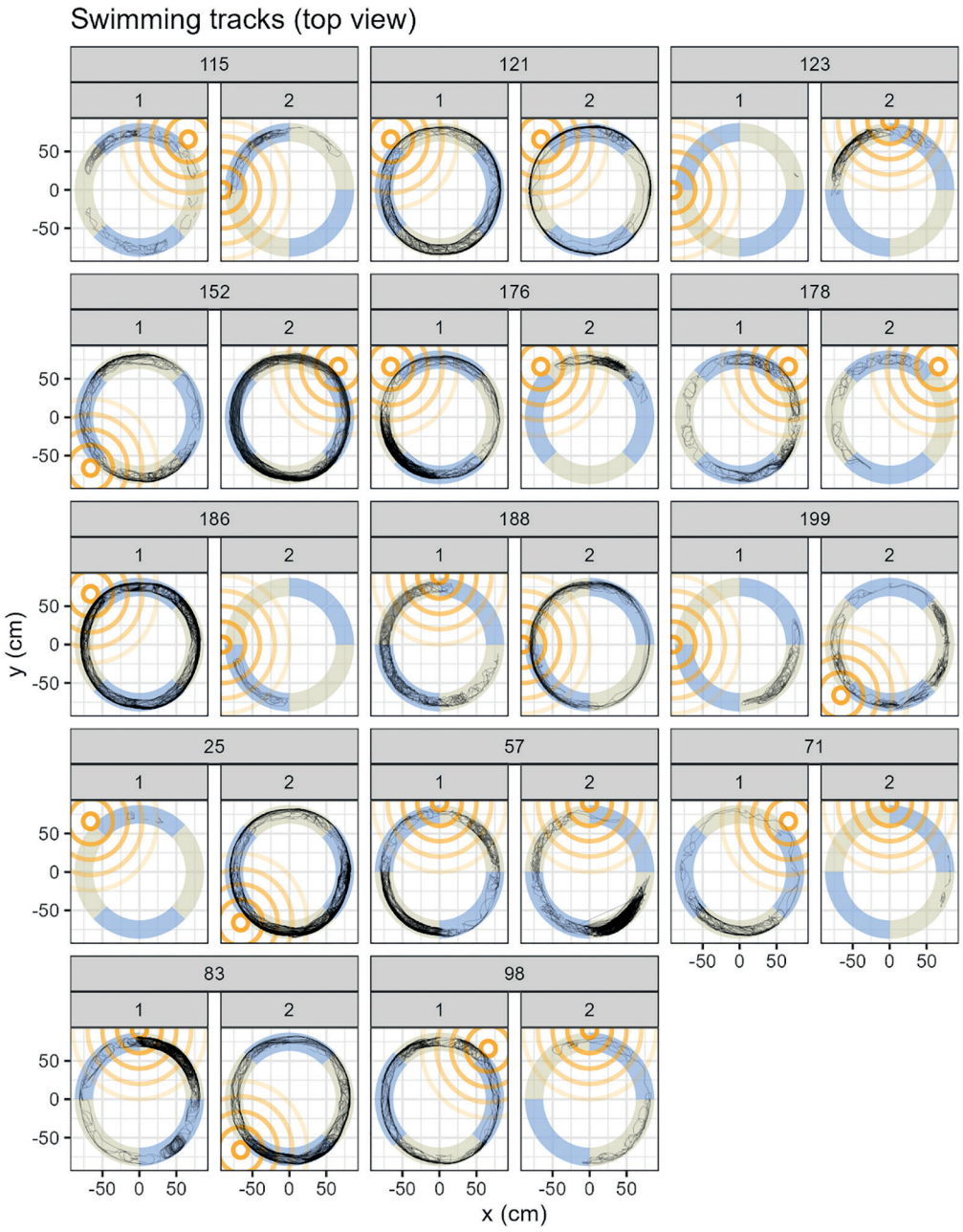


Fig. 8.5 Top view of the swim tracks of all individuals in both their trials. The bar above two tracks indicates the individual, and the bar below indicates whether this was the first or second trial. The shaded background of the tracks indicates the substrate (blue = mussels, beige = bare). The centres of orange circles indicate the position of the EMF coil, note that EMF spreads elliptical rather than circular in reality. In a few trials, the shark did not move much, hence the swimming track is very small.

or field-based tagging contexts, where electroreception is used in concert with chemical, mechanical, and visual signals, which are lacking in a laboratory setting. Altered behavioural responses to anthropogenic EMF may only emerge in more natural conditions were animals are required to continuously integrate multiple sensory cues, potentially interfering with foraging behaviour or predator-prey interaction. Feeding motivation was likely low in the present study, as sharks were fed ad libitum and no food or odour cues were provided to trigger active prey-search behaviour.

The proportions of inactive and transiting behaviour differed significantly between treatments, although the magnitude of these changes was small (5-6%pt.). Although this behavioural effect was observed, considerable interindividual variation was evident in the data, consistent with previous findings for elasmobranchs (Dhellemmes et al. 2021; Finger et al. 2016; Hermans et al. 2025). Individual sharks also did not consistently select the same quadrants across repeated trials (Fig. 8.5 and Fig. S8.1), indicating that quadrant selection was not driven by individual preferences. Whether these subtle behavioural shifts would be amplified under natural conditions with more complex sensory cues, or attenuated against environmental background variability, remains unclear. Overall, while a behavioural effect was detected, its ecological relevance and applicability to field settings cannot yet be resolved.

No significant differences were found in time spend across the four quadrants or behaviour based on the different substrate types provided. Live mussel substrates have been shown to influence fish behaviour, such as providing shelter for European eel (Schwartzbach et al. 2020). Mussel farmers in the Eastern Scheldt report elasmobranch species, including *Dasyatis pastinaca*, *Mustelus asterias* and *Raja clavata*, during the management of shellfish plots (personal observation). A preference for complex biogenic substrate over non-complex substrate, would seem more in line with natural behaviour as it more closely resembles their natural habitat (Heessen, Daan, and Ellis 2015; Martin et al. 2012; Papadopoulo et al. 2023; Pizzolla 2008). The absence of a substrate effect in the present experiment may reflect the opportunistic nature of *S. canicula*, as it is known to inhabit a wide range of substrates (IUCN 2008), possibly favouring one substrate over another based on incentives such as foraging or mating cues. Sharks did not display mussel-specific selection, suggesting possible ecological implications that merit further investigation, especially in the light of (shellfish) aquaculture practices.

Even though mussels were included in the housing tank to familiarise the sharks, the absence of preferences for conditions may relate to the use of lab-reared individuals that lack prior experience with complex natural environments and foraging contexts. Sharks displayed diel activity patterns aligned with light conditions (Fig. S8.2), suggesting that at least part of their behavioural repertoire appears comparable to that of wild individuals, and supporting the relevance of their responses to potential field conditions. The covariates that best explained shark behavioural states resulting from the HMM, e.g. trial order, light condition and body length (Table S8.2), can be explained by literature. The observed order effect (Fig. S8.3) is also seen in other studies and may reflect a reduction in novelty or exploratory motivation in individuals over consecutive trials (Dhellemmes et al. 2021; Finger

et al. 2016). The observed change in activity levels between day and night (Fig. S8.2), being higher at night which is in line with normal behaviour in the wild, and was already discussed above (Papadopoulo et al. 2023). And consistent with previous tagging studies on *S. canicula* (Papadopoulo et al. 2023), larger individuals exhibited reduced swimming activity (Fig. S8.4).

Results from this controlled experiment indicate that AC-generated EMFs influence behaviour, albeit subtly but not substrate preference in *S. canicula*. The data does suggest no barrier resulting from AC EMFs associated with both export cables (running perpendicular to the coastline and transporting electricity from offshore wind farms to shore), and infield cable networks (connecting turbines to the offshore high-voltage station). However, the outcome warrants further research as it suggests that AC fields may influence swimming behaviour in this (juvenile) benthic shark.

It is important to recognise that laboratory experiments, while controlled, represent a simplification of the natural environment, where substrate preference and behaviour are influenced by multiple interacting sensory cues (Winkler and Murphy 1973), including chemical, hydrodynamic, and social information. Furthermore, the experimental design did not include all behavioural end points that may be influenced by EMF, including complex predator-prey interaction, migration and interaction with conspecifics. To capture these dynamics, fine-meshed field-based telemetry studies above subsea power cables are needed to investigate habitat use and behavioural responses in ecologically realistic contexts including both natural prey availability and conspecific interactions (Papadopoulo et al. 2023; Reubens et al. 2019). In addition, previous studies demonstrate interspecific differences in elasmobranch responses to EMF, highlighting the importance of testing whether the present results generalise to other elasmobranch species.

A number of studies have found comparable subtle or context-dependent effects of EMF (Gill 2009; Hermans et al. 2025; Hermans et al. 2025; Hutchison, Secor, and Gill 2020; Orr 2016). However, these minor negative impacts must be weighed against potential positive effects, e.g. a refuge benefit that offshore wind farms may provide due to the lack of bottom trawling fisheries. Large areas within OWFs are closed to fishing, the primary source of mortality for elasmobranchs populations, which could result in a net positive conservation outcome even if small behavioural effects occur. Additional data are required to evaluate this balance. Our findings contribute to this perspective by suggesting that EMF itself may result in subtle behavioural changes, but not a barrier for *S. canicula*. Nonetheless, other anthropogenic pressures (e.g., noise, construction disturbance, habitat alteration) are associated with OWFs and warrant parallel investigation.

Looking ahead, offshore power transmission is expected to rely increasingly on direct current (DC) systems, as wind farms are built further offshore and DC transmission minimizes energy loss over long distances (Ryndzionek and Sienkiewicz 2020). Consequently, in the future, the rate of exposure to DC fields will be higher for elasmobranchs and other species (Hermans et al. 2024). The biological relevance of this change is notable, as DC and low-frequency AC (<20 Hz) fields, comparable to conspecifics and prey, are more readily

detected by elasmobranchs than the 50 Hz AC currently used in most grids (Bedore and Kajiura 2013). Moreover, DC systems, though nominally constant, can generate transient low-frequency AC fluctuations due to variable power loads, producing a more complex electromagnetic environment. Lastly, the geomagnetic field is a DC field, and sharks are believed to use this for navigation, underscoring the importance of further understanding and studying behavioural responses to DC EMFs.

8.5 Conclusions

In this controlled laboratory experiment, juvenile *S. canicula* showed no change in time spent nor distance travelled depending on AC-EMF exposure or the presence of mussels as proxy for complex biogenic substrate. Subtle but significant changes (5-6%pt.) were found in behavioural states. These findings indicate that AC subsea cable fields, at intensities comparable to those found around offshore wind infrastructure, are unlikely to form a hard barrier. Additionally, juvenile sharks did not display mussel-specific selection, indicating a null preference that may carry ecological relevance for aquaculture managers. While only one minor significant behavioural effect was detected, its ecological relevance and applicability to field settings cannot yet be resolved for juveniles of this benthic shark species. Future research should validate these responses in-situ to determine whether the largely absent behavioural effects hold under natural environmental conditions and for different elasmobranch species. In addition, the influence of antropogenic DC fields on habitat selection and swimming behaviour should be further explored.

Supplementary materials

Table S8.1 Model selection to determine optimal number of behavioural states using Hidden Markov Models to explain shark behaviour during the experiment. The AIC is the Akaike Information Criterion, and the lowest AIC refers to the best model [*]. In the case, a 3-state model was supported best.

Number of states	AIC
3*	1196546
2	1732541
1	3527098

Table S8.2 Model selection to determine the covariates for the best fit to explain shark behaviour during the experiment. The null-model, without covariates is indicated by [~1]. The AIC is the Akaike Information Criterion, and the lowest AIC indicates the best model [*].

#	Covariates	AIC
*1	Light condition + Quadrant + Order + Body length	1992768
2	Light condition + Quadrant + Order	1193349
3	Light condition + Quadrant	1194237
4	Light condition + Order	1194479
5	Light condition	1195355
6	Order	1195474
7	Quadrant	1195493
8	~1	1196546
9	Light condition + Quadrant + Body length	1200506
10	Light condition + Body length	1566701
11	Body length	1567758

Table S8.3 Overview dates of all trials dates and entry and EMF coil positions.

Shark	Trial 1			Trial 2		
ID	Date	Position Entry	Position coil	Date	Position Entry	Position coil
199	20-5-2025	3	2	12-6-2025	2	2
25	21-5-2025	6	3	27-5-2025	4	3
121	23-5-2025	6	3	23-6-2025	2	3
176	24-5-2025	1	3	26-6-2025	7	3
115	26-5-2025	2	5	17-6-2025	4	5
178	02-6-2025	1	5	10-6-2025	7	5
83	28-5-2025	2	4	09-6-2025	3	4
188	29-5-2025	6	4	20-6-2025	3	4
98	03-6-2025	1	5	11-6-2025	3	5
186	04-6-2025	8	3	16-6-2025	4	3
57	05-6-2025	5	4	13-6-2025	8	4
123	08-6-2025	8	2	19-6-2025	2	2
152	22-5-2025	5	1	25-6-2025	7	1
71	24-6-2025	2	5	27-6-2025	4	5



Fig. S8.1 State distribution for each of the 14 sharks in each quadrant. The numbers on the right indicate the individual shark ID, overarching trial 1 and 2 representing the two trials of each shark. The numbers in the bar represent the amount of time spent in that quadrant (XY positions recorded). The asterisks indicates the release position of the shark at the start of the acclimation (3 hours prior to the behavioural monitoring).

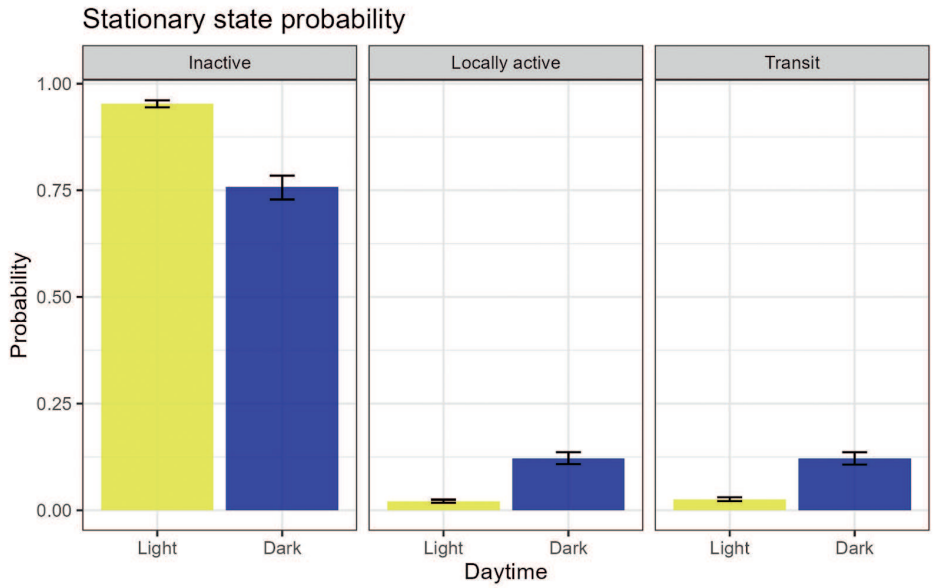


Fig. S8.2 Stationary state probability of the behavioural states during light-time and dark-time. Sharks were significantly more active during dark-time, both locally active and transiting.

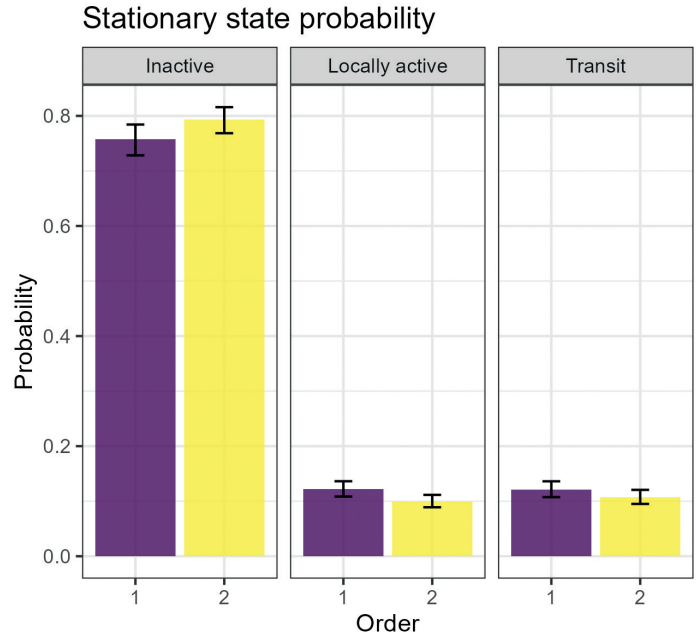


Fig. S8.3 Stationary state probability during the first and second trial of each individual. No significant effect of order was found.

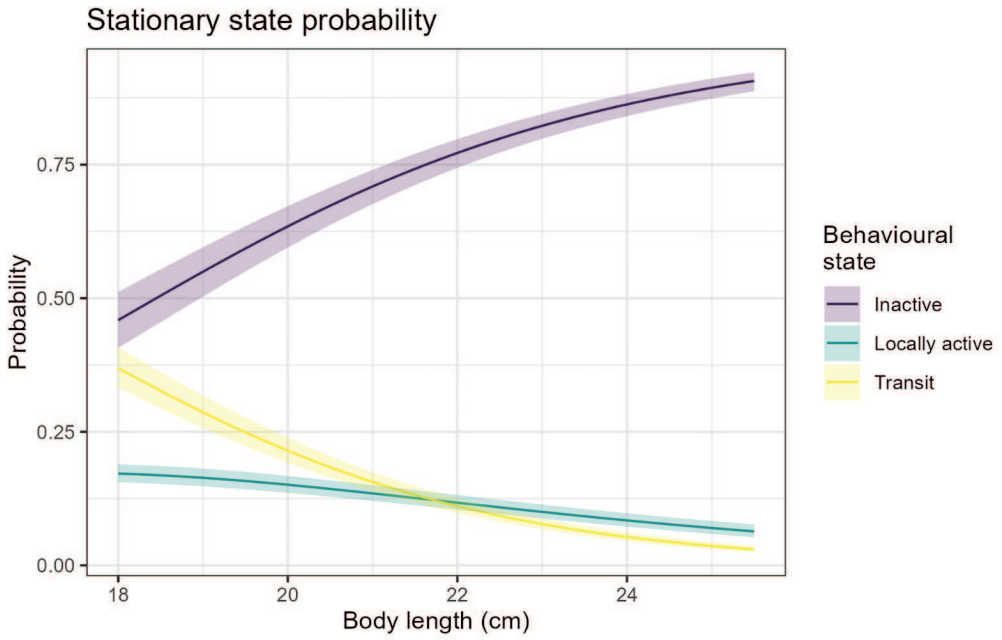
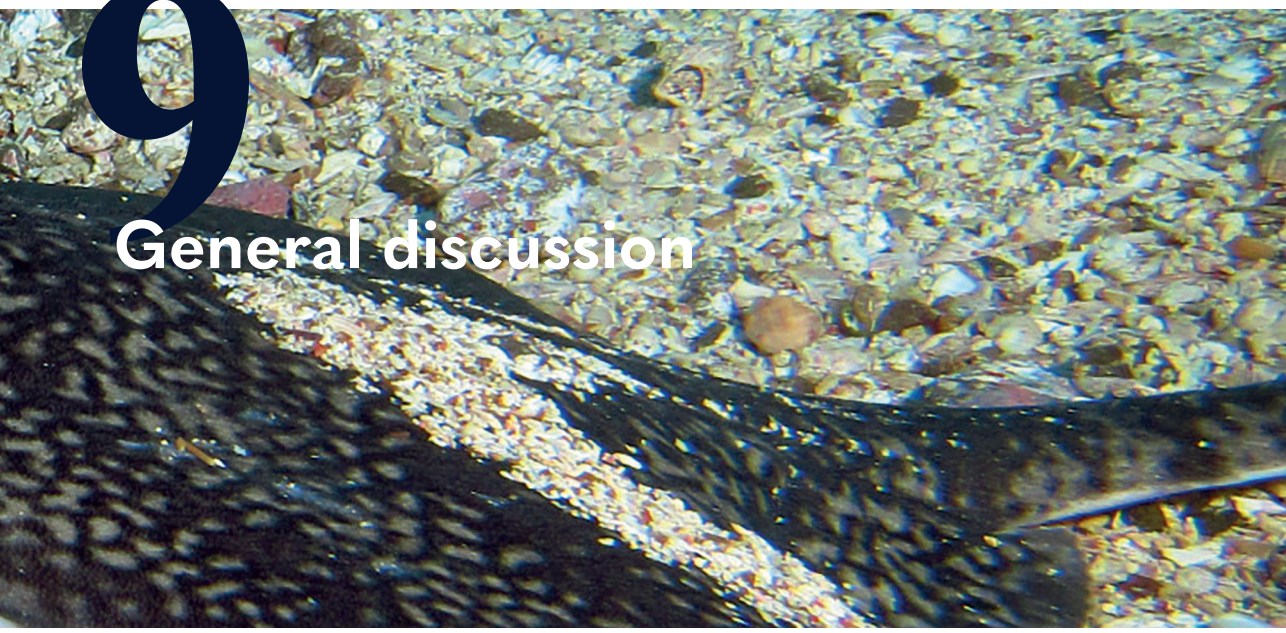


Fig. S8.4 Stationarity state probability over trial body length of the sharks, shaded area indicates the 95% confidence interval. Larger individuals spent more time being inactive.



9 General discussion



> *It speaks to the awesome nature of magnetoception.*
>
> An immense world – Ed Young

9.1 Now it is time to wrap it up

This thesis aimed to provide evidence-based insight in exposure-effect levels to support impact assessments of electromagnetic fields (EMFs) from subsea power cables (SPC) on benthic elasmobranchs in the Dutch North Sea. This can facilitate decision making and permitting processes and allow more appropriate balance of considerations of environmental impact resulting from the transition to the non-fossil fuel based offshore wind industry. The research started with an environmental risk assessment (ERA), combining a literature study, EMF measurements and modelling, to assess the risk of EMFs from SPC to elasmobranchs in the Dutch North Sea (Chapter 2). In-situ EMF measurements revealed that exposure levels are considerably lower than those used in most experimental studies found in literature, but also are highly variable in time (wind-dependant) and space. Modelling results indicated that by 2030, approximately 5.5% of the Dutch Continental Shelf will be influenced by anthropogenic EMFs, intersecting elasmobranch egg-laying sites, foraging habitats, and migration routes. DC fields are potentially detectable up to 250 m from cables (with the specs used in this research) and potential effects on elasmobranchs include attraction of adults, disruption of embryonic development within spawning habitats, interaction with prey and conspecifics and migration. The risk level strongly depends on life stage and species ecology, represented by three key life stage categories: embryonic development-specifically in the egg, local dwelling and migratory behaviour.

The ERA was followed by a field study where eDNA analyses confirmed the presence of multiple elasmobranch species within Dutch offshore wind farms (Chapter 3). In laboratory experiments the effects of EMF on shark and skate embryogenesis were studied under controlled conditions. Exposure to variable AC EMFs did not affect development time, hatching success or body condition, but induced hyperactivity of embryos inside their egg cases which could increase their risk of being detected by predators. Significant differences in body growth were observed in the shark and skate hatchlings but these had a small effect size and are believed to fall within natural variability (Chapter 4). After hatching, no differences in stress response to EMF exposure or swimming behaviour were found between animals that had developed in EMFs compared to the control animals, and all skate juveniles appeared healthy (Chapter 5). Large tank experiments with adult sharks and skates showed no evidence of avoidance, nor attraction or stress-related behaviour under either a gradient of AC or DC exposure. Swimming behaviour, however, was altered in small-spotted catshark, with a ~25%pt. decrease in total swimming time and an increase in swimming speed during DC trials, where no effect was observed under AC exposure or control conditions (Chapter 6). Male skates showed a similar pattern, but less pronounced (~14%pt.), and also in AC EMFs. Conversely, female skates showed an opposite trend, with no significant difference between DC and control, but ~15%pt. increased activity in AC (Chapter 7). Presence of AC EMF did not influence the preference of juvenile small-spotted catsharks for mussel-covered versus bare substrates in the tank, suggesting no EMF-associated effect on substrate choice (Chapter 8). There were, however, behavioural changes

in which sharks showed more inactivity (~5-6%pt.) in the experimental quadrant with both mussels and EMF exposure, compared to control. Notably, sharks and skates exhibited species-specific responses to EMF exposure. In sharks, embryonic exposure was associated with increased growth, and behavioural changes were evident for adults only under DC conditions. In contrast, skates showed reduced growth following embryonic exposure and pronounced sex-dependent differences in swimming behaviour under AC exposure (and under both AC and DC in males). In addition, substantial individual variability in behaviour was observed, with significant differences in responses to EMF. An overview of the findings resulting from this thesis is summarised in Table 9.1.

Reading guide General Discussion

This General Discussion first revisits the research questions that guided this PhD project in 9.2, following the ERA framework which was introduced in Chapter 2. These questions

Tabel 9.1 Providing an overview of the main findings from the Chapters presented in this thesis. eDNA denotes environmental DNA, AC alternating current, DC direct current, EMF electromagnetic fields and OWF Offshore Wind Farm.

Chapter	Study type	Method	Exposure	Life stage
2	Desk study	ERA & EMF exposure modelling	AC & DC, various scenarios	NA
3	Field study	eDNA in OWF field study	3-core 33 & 66 kV AC	NA
4	Controlled laboratory experiment	Embryonic exposure	AC 1.4 & 4.6 μT	Embryo
5		Juvenile stimuli response	AC 1 & 10 μT	Juvenile
6		Gradient exposure trials sharks	AC 15.0 μT & DC 19.6 μT	Adult
7		Gradient exposure trials skates	AC 15.0 μT & DC 19.6 μT	Adult
8		Habitat preference in circular preference chamber	AC <2.2 μT	Juvenile

are addressed again, interpreted through the lens of the results obtained over the course of this thesis, with special focus on the three life-stage-specific categories: embryonic development, local dwelling and migration. Subsequently, this information is used in 9.3 to identify species that are expected to be most vulnerable within each life stage category based on their species-specific traits. From this analysis, key knowledge gaps are identified and specific research priorities recommended in 9.4. The policy implications of the findings from this PhD work are discussed in 9.5, addressing how these insights can support evidence-based management of offshore wind development at different decision-making levels. This General Discussion concludes in 9.6 with a reflection on the balance between positive and negative effects of offshore wind energy on elasmobranch populations in the North Sea and opportunities provided by offshore wind development for the recovery and protection of elasmobranch populations. An overview of this approach is presented in Fig. 9.1. Note that while EMFs occur naturally, hereafter "EMF" refers specifically to anthropogenic fields associated with subsea power cables, unless otherwise stated.

Results

- Cables intersect with egg-laying sites, foraging habitats, and migration routes.
- 5.5% of Dutch Continental Shelf with EMF from subsea cables by 2030.
- EMF detectable by benthic elasmobranchs can reach 250 m for direct current cables.

- Five elasmobranch species were detected in OWFs across different seasons using eDNA.
- Elasmobranchs use OWFs as a habitat, understanding habitat use needs further study.

- Chronically Exposed embryos show hyperactivity including 33% more tail undulations and 150% increased body movements, compared to non-exposed, individuals but unchanged development.
- Increased predation risk could result from enhanced embryonic activity near cable routes.

- Skates showed 5.3% shorter tails; sharks had larger pectoral fins (11.2%) but no impact on juveniles weight, body-to-fin/tail ratios or behaviour.
- Sharks detected EMF differences between 0.1 μT and 10 μT exposures.

- Small-spotted catsharks showed no attraction or avoidance to EMF.
- No startle responses were observed after EMF onset.
- 25%pt. decrease in transiting but with increased swimming speed during DC trials

- AC and DC EMFs did not cause attraction or avoidance in thornback skates
- Subtle (15%pt.), sex-dependent changes of activity patterns in response to EMF
- EMF-induced changes in male skates matched the magnitude seen in a benthic shark

- No change in habitat or substrate preference in juvenile catsharks
- Only the condition 'EMF + mussels' resulted in increased inactivity of 5-6%pt.

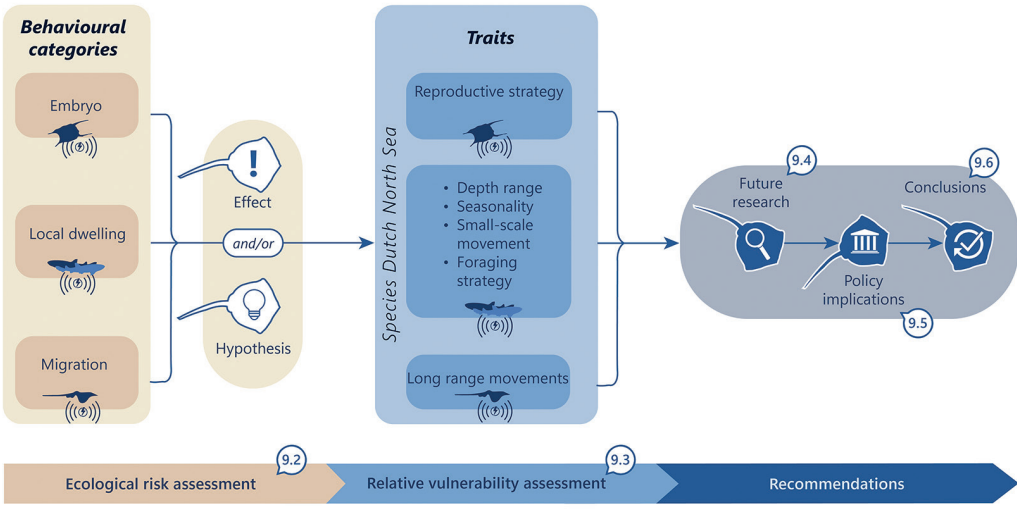


Fig. 9.1 Schematic overview of the topics covered in the General Discussion, showing how the environmental risk assessment (paragraph 9.2), translates into a species specific relative vulnerability assessment (paragraph 9.3), followed by recommendations for future research (paragraph 9.4) and implications for policy (paragraph 9.5). After drawing conclusion from the ecological risk assessment and relative vulnerability assessment, the policy implications are discussed, future perspectives and advice for further research.

9.2 Returning to the questions that guided this thesis

Hazard identification

RQ 1 | What is known about the nature of EMFs from SPCs, and what evidence exists for behavioural responses in benthic elasmobranchs from field and experimental studies?

The EMF characteristics are rooted in physics and explained in section 9.1 and 9.2 of the ERA paper (Chapter 2). The findings confirm our assumed lowest measurable level of exposure i.e. 0.005 μT. It has become increasingly clear by our work and that of others that the way an organism senses a specific EMF depends on its life stage and duration of exposure (Hutchison & Gill, 2025). For example, embryos developing while chronically exposed to variable AC react with increased movement when challenged with exposure to EMF (Chapter 4), whilst exposed juveniles presented with a similar stimulus do not show change in activity (Chapter 5). Adult sharks and male skates show a similar reduction of movement to DC exposure but male skates also respond to AC EMF. The responses seem sex-dependant, with the opposite reaction for female skates. Contrary to our ERA in 2024, these findings suggest that skates and rays do show minor physical effects after chronic AC exposure during embryogenesis (Chapter 4), indicating that physical effects resulting from

chronic exposure should be considered in an ERA. Note that although EMFs comprise both electric and magnetic components, this analysis is based on the magnetic field (μT), which governs the induced electric fields experienced by elasmobranchs near subsea power cables.

1. | Embryogenic development SPC often cross coastal habitats that serve as egg-laying or pupping grounds for benthic elasmobranchs, meaning embryos can be chronically exposed to EMFs during development (Hermans et al., 2024; Hutchison et al., 2020; Paoletti et al., 2026). As hypothesised (Ball et al., 2016; Hutchison et al., 2020; Taormina et al., 2018) it was found that EMF exposure leads to changes in movement, increasing metabolic costs and alter growth (Chapter 4 and 5). Notable, freezing is often mentioned as an EMF response, but we found hyperactivity instead with variable field strengths. Based on the documented detection of EMF ((Ball et al., 2016; Christensen et al., 2023; Kempster et al., 2013), Chapter 4) it is possible that there are EMF-induced imprinting-processes, which could be explained by epigenetic mechanisms, and might lead to behavioural changes later in life (Cavalieri & Spinelli, 2017; Gapp et al., 2014; Paige Beal et al., 2021).

2. | Local dwelling There is growing evidence that attraction to SPC, possibly leading to time lost searching for prey or mates, is of greater concern than avoidance of locations were prey could be found. Acoustic telemetry research showed attraction of small-spotted catshark to SPC and associated EMFs (Labourgade et al., in prep), consistent with earlier laboratory, mesocosm, and field studies (Barry et al., 2008; Gill, 2009; Hutchison et al., 2020; Orr, 2016). As we recorded five species of elasmobranchs within OWFs using eDNA (Chapter 3), avoidance by SPC appears unlikely. Also thresher shark (*Alopias vulpinus*) and small-spotted catshark have been found in eDNA surveys in the OWF Hollandse Kust Zuid (NL) by the Rich North Sea programme (unpublished data). Acoustic telemetry also revealed the presence of undulate ray (*Raja undulata*) around the St-Brieuc export cables, including individuals crossing the cable, while porbeagle (*Lamna nasus*) were detected within St-Brieuc OWF and subsequently migrated to the Isle of Wight (UK). Furthermore, starry smooth-hound (*M. asterias*) were recorded in both the St-Nazaire and YEU-Noirmoutier OWFs (Couturier et al., 2025). Complementary eDNA surveys along 5 km transects at St-Nazaire OWF detected undulate ray, marbled electric ray (*Torpedo marmorata*), and thresher shark (Maire et al., 2025). Together, these findings suggest that in-field and export cables are unlikely to act as EMF barriers to elasmobranch local dwelling. This is supported by evidence presented in Chapter 8, which, despite small behavioural changes, gives no indication for substrate preference under influence of EMF by juvenile small-spotted catshark. The possible effects of EMF on local dwelling remain to include altered natural foraging behaviour or reduced foraging success by e.g. disruption in predator-prey or conspecifics relationships which could result in reduced food uptake or reduced reproductive output (Hutchison et al., 2020; Normandeau et al., 2011; Taormina et al., 2018). Despite improved understanding, current evidence is insufficient to confirm or refute these hypotheses, it cannot yet be determined whether EMF is a hazard for successful local dwelling behaviour.

3. | Migratory behaviour The evidence base for elasmobranchs crossing SPC during migration is growing, as probable for starry smooth-hound with eDNA (Chapter 5) and with acoustic telemetry demonstrating movements from the St-Nazaire OWF (France) to the YEU–Noirmoutier OWF, 23 km away (Couturier et al., 2025). In addition, mark–recapture and tracking studies of starry smooth-hound (Brevé et al., 2016, 2020) and tope sharks (Schaber et al., 2022) demonstrate that individuals routinely cross multiple subsea power cables during migration, indicating that the key question is not whether SPCs are crossed, but whether crossings result in delays or impediments for some individuals. In our experimental setup, swimming activity was reduced in response to DC generated EMF for sharks and male skates (Chapter 6 & 7). It cannot be excluded that (repeated) alterations or delays in migration result in energetic costs, disrupt ecological timing, reduce fitness by increasing energy expenditure or increase predation risk, particularly if SPC are crossed higher in the water column to avoid too high EMF levels. These aspects require validation in the field, were environmental complexity and natural behaviour are fully expressed, and are challenging to study in a controlled experimental set-up for animals in migration mode.

Exposure quantification

RQ 2 | What EMF levels have been reported and are expected from SPC?

To assess risk from SPCs, it is essential to quantify exposure by estimating (i) the temporal and spatial variability of EMF and (ii) the frequency of encounter; both can be addressed with field measurements or exposure modelling, or a combination. This outcome strongly depends on individual behaviour and population-level spatial distribution, which should be taken into account when determining encounter rates. Recent in-situ measurements commissioned by transmission system operator (T.S.O.) TenneT and conducted by Waterproof B.V. provide a more robust exposure characterization then available during the ERA in Chapter 2 as they extended monitoring to 13 months. This longer time series captures longer-term seasonal variability (see Textbox B), resulting in a better understanding of the exposure profile. Overall, these measurements largely correspond with the measured values reported in literature which resulted in the exposure range used for the ERA in Chapter 2, Table 2.1, thereby validating the earlier exposure quantification.

In addition to addressing research question 2, this section reflects on how the exposure levels measured by TenneT relate to the experimental conditions described in Chapters 3-8. The chronic exposure protocols incorporated temporal variability of field strengths to mirror the frequent changes in EMF that developing embryos experience in situ (Chapters 4 and 5). This dynamic exposure is the central hypothesis of the embryogenic studies - that temporal variability, rather than a constant field, governs biological responses under field-like conditions. The gradient-based research set-up designed to mimic spatial heterogeneity and creating a situation comparable to approaching a cable in the field, representing a level of realism not commonly used in comparable studies was used in Chapters 6 and 7.

Textbox B - Magnetic field measurements

- Borssele 220 kV 700 MW export AC cables measured 13 months from July 2021 to August 2022 with a land based stationary monitoring 1m from the cable, 0.5 μT tot 5 μT, peaking at 6.0 μT (Snoek et al., 2022)
- Borssele 220 kV 700 MW export AC cables transect measurements at sea in September 2021, towing a sensor over the buried cable, measuring 0.25 - 0.75 μT at 3 bft, measurable at maximum 35m from cable, where the land station measured 2 μT at the time of measurement (Snoek et al., 2022)
- HK(z) 220 kV 700 MW AC export cable measured 3 months from April to June 2024 with a minimum of 2.2 μT and peaking at 6.5 μT with wind speeds 6-7 Bft (Neut & Brinkkemper, 2025)
- Norned 450 kV 700 MW interconnector DC cable max. 290 μT separated (unbundled) at the landstation and between 1-2 μT transect measurements (bundled) at sea, all measured 1m from the cable (Snoek et al., 2021)
- Southern Iberian Peninsula 400 kV 1400 MW export AC cables measured max. 43 μT i.e. 0.01 μT - 0.03 μT above the background geomagnetic field, measurable at maximum 250m from cable, burial depth not specified (Donázar-Aramendía et al., 2025)

Notably, the exposure coil used in those experiments was designed to reproduce not only the measured field strengths but also the circular geometry of the EMF resulting from a SPC. This contributes to creating a more realistic three-dimensional exposure environment, as opposed to a more traditional unidirectional Helmholtz-coil, enhancing the ecological relevance and translational value of the results.

The data from the measurement campaigns can be used to validate modelling as shown in Chapter 2. It is evident that the measured long-term magnetic-field intensities were consistently lower than the values predicted by the modelling in Chapter 2. Several factors may account for this discrepancy. First, finite lay-length and the three-core geometry of AC cables induce mutual shielding and field cancellation along the conductor, attenuating near-field strengths fivefold comparing ∞ 5 m (Schilt et al., 2025). Many models assume infinite lay-length, effectively producing worst-case (highest) field estimates; incorporating finite lay-length would likely reduce predicted exposures (Buenau et al., 2022; Hutchison et al., 2021). Inquiries with cable owners indicate that precise lay-length and conductor arrangement data are not readily available, introducing structural uncertainty into input parameters. In addition, there are other cable characterises that govern modelling results, and discussion with the cable manufactures is essential to obtain the required input. Secondly, when SPC transect longer spans, a nonzero current baseline (the so-called blind or baseline current) must be maintained to ensure power delivery, which sustains a continuous

magnetic field even when mechanical power input from the wind turbines is low. For the HK(z) cables, this minimum field is about 3.7 μT (unpublished data TenneT). Together, these factors can explain why measurements and modelled values are not always aligned and underscore the need to incorporate realistic lay-length distributions and baseline-current estimates in exposure modelling to improve accuracy.

Exposure of benthic elasmobranchs depends on encounter rates with SPC, which are determined by both the development of the spatial expansion of offshore wind infrastructure and the movement and distribution patterns of the animals. The aim of the Dutch government is to have a production capacity of 70 GW offshore wind energy by 2050 (Structuurvisie Windenergie op Zee; Brief regering; Windenergie op zee 2030-2050, 2022). Until 2040 the ambition is bracketed between 30 to 40 GW which results in two scenarios, dependent on politic drivers (Het Windenergie Infrastructuurplan Noordzee, 2025; Structuurvisie Windenergie op Zee; Brief regering; Het Windenergie Infrastructuurplan Noordzee, 2025). In both scenarios, it is assumed that the four smaller parks built before 2018 are decommissioned or repowered, and that existing and currently planned wind parks contribute approximately 6 GW of capacity. Hydrogen production is not included in these scenarios because this development is currently halted; consequently, all energy is assumed to be transported via SPCs.

- Minimal scenario 2040: Up to 30 GW total offshore wind capacity (12×2 GW new parks = 24 GW, plus ~6 GW existing/planned). Resulting in 12 additional DC export cables.

- Maximum scenario 2040: Up to 40 GW total offshore wind capacity (17×2 GW new parks = 34 GW + ~6 GW existing/planned). Resulting in 17 additional DC export cables.

The additional cables implied by the minimal and maximum Offshore Wind scenarios add to the Dutch Continental Shelf cable inventory described in Chapter 2 and are essential input for estimating encounter rates. Routing decisions of these new cables must be integrated into spatial planning processes to determine feasible, low-exposure wiring layouts while maintaining grid optimisation. Section 9.5 (Policy Implications) provides recommendations to translate these results into actionable routing guidance for regulators and developers.

Hazard quantification

RQ 3 | What are the lowest EMF exposure levels at which behavioural effects occur in benthic elasmobranchs across different life stages?

This thesis presents five experimental studies (Chapters 4-8) that provide additional evidence to strengthen the hazard quantification developed in the ERA (Chapter 2). To date, no additional laboratory or mesocosm studies on elasmobranch responses to EMFs

have been published, other than those presented in this thesis. However, relevant research is ongoing, including the Tintreach project (Tracking INTeractions between Renewable Energy and ElasmobranCHs) at Queen's University Belfast, which focuses on biotelemetry and movement, the EMFish project from the Flanders Marine Institute and a PhD project at the University of Southampton investigating the impacts of acoustics and EMFs on marine fishes with laboratory-based experiments.

The Lowest Observed Exposure Level (LOEL) resulting from this thesis are organized again in the three life stage categories distinguished in the hazard quantification: embryonic development, local-dwelling and migratory behaviour. In Chapter 2, the LOEL was used to derive a No Observed Effect Level (NOEL); however, in this discussion, a Predicted No Effect Level (PNEL) is applied instead, as no empirical evidence supports a NOEL for any life stage.

1. | Embryogenic development In the embryogenesis experiment with thornback skate (Chapter 3), embryos were chronically exposed to two alternating levels of AC EMF (1.8 and 4.6 μT, alternating every 24 h). In addition, they received short-term EMF stimuli (10 min) of 1 and 10 μT. No freeze responses, or other signs of detection, were observed at the onset or termination of the stimuli. However, chronically exposed animals showed a significant increase in activity (tail undulation, whole-body, and partial-body movements), indicating that the chronic exposure levels were perceived by the embryos. Embryos may have responded only at the highest exposure level (4.6 μT). Chapter 5 presents a study on juvenile small spotted-catshark and thornback skate following there behaviour after hatching to determine any carry-over effects from chronic embryonic exposure. Individuals were subjected to short-term EMF stimuli (10 min) of 1 and 10 μT. A significant increase in ventilation rate was observed in the control group when exposed to the 10 μT stimulus in sharks, but swimming or stress-related behaviour remained unchanged. Based on these findings, the AC LOEL remains at 4.0 μT, and the PNEL remains determined a factor 10 lower i.e. 0.4 μT (Chapter 2). For DC exposure, no new evidence is available; however, the assumed NOEL of 0.4 μT is retracted because it was based on the premise that AC and DC elicit similar responses. The demonstrated differences between AC and DC in adults (Chapters 6 and 7), and fact that the static or moving field may be perceived quite differently as AC and DC have quite distinct differences, make that this assumption is unlikely to hold for embryos. Consequently, a DC PNEL is currently not defined due to the lack of embryonic data.

2. | Local-dwelling When exposed to gradients of up to 15.0 μT AC and 19.6 μT DC, adult sharks and male skates were more inactive in DC (~25%pt. and ~14%pt. respectively), and the male skates showed a similar behaviour in AC. The female skates showed the opposite behaviour, with increased activity in AC (~15%pt.), all compared to control trials. No evidence of attraction, avoidance, or startle responses to EMF onset was observed under either AC or DC exposure for any of the animals (Chapter 6 & 7). Juvenile small spotted-ca-

tshark show statistically significant but subtle (~5-6%pt.) reduction in swimming activity in a quadrant with mussel substrate and EMF exposure of 2.0 μT AC (Chapter 8). This behavioural response warrants revising the AC LOEL from 8 μT to 2 μT, which put the PNEL at 0.2 μT based on the assumed ten-fold factor. For DC, no new data are available and the LOEL remains 0.03 μT. Although a DC NOEL was not defined in Chapter 2, the PNEL is set at 0.003 μT (ten-fold below the LOEL), consistent with the PNEL applied for migratory behaviour (see below). Similar life-stage-specific sensitivity may plausibly apply to both local dwelling and migration.

3. | Migratory behaviour Although more studies on elasmobranch migration have been published, no new evidence on EMF effects has emerged since Chapter 2 to refine LOEL or PNEL values for migratory responses. The previously assumed LOEL of 0.05 μT and PNEL of 0.005 μT for DC exposure are therefore maintained. As no migratory hazard has been identified for AC exposure, no LOEL or NOEL is defined for AC.
An overview of the LOEL and PNEL are presented in Table 9.2.

Risk assessment

RQ 4 | Which risk level results from the comparison of the highest EMF exposure levels and the lowest observed effect levels (LOELs) for altered behaviour in benthic elasmobranchs across life stages?

In the ERA described in Chapter 2, it was established that the sensory range and habitat use of benthic elasmobranchs overlap with the zones influenced by EMF from SPC, indicating a risk for effects. The actualised hazard quantification in this General Discussion has led to changes in the LOEL/PNEL namely for local dwelling (Table 9.2). Both newly acquired

Table 9.2 Lowest observed effect levels (LOELs) and Predicted No Effect Levels (PNELs) for the three life stages derived from the ecological risk assessment, compared with measured electromagnetic field levels from high-voltage alternating current (HVAC) and direct current (HVDC) cables to assess the Risk Coefficient (RC) range (depicted in dark blue). Italic grey values indicate those reported in Chapter 2 which have been updated according to the findings in this thesis. The RC is determined by Exposure/PNEL. ND denotes no data and NA not applicable.

	Embryonic (μT)		**Local-dwelling (μT)**		**Migration (μT)**	
	AC	**DC**	**AC**	**DC**	**AC**	**DC**
LOEL	4	ND	2 *8*	0.03	NA	0.05
PNEL	0.4	ND *0.4*	0.2 *0.8*	0.003 *ND*	NA	0.005
Exposure	1.8-6.5	NA	1.8-6.5	1-2	NA	1-2
RC	4.5-11.5	NA	9-32.5	330-660	NA	200-400

and previously available measurements show exposure levels that exceed the LOEL/PNEL for all life stages (Textbox B), consisted with the findings in Chapter 2. In addition, rate of exposure is expected to increase in the future under the maximum offshore wind farm development scenario in the Dutch North Sea for 2040 with an expansion with approximately 17 additional OWFs and their associated SPC infrastructure. As the exposure increases, so does the risk. Below the risk is characterised and assessed for this maximum scenario, performed per life stage (Table 9.2). In addition, key knowledge gaps are listed in Table 9.3.

1. | Embryogenic development The current PNEL for AC EMF remains at 0.4 μT. Long-term measurements at HVAC cables provide values of 1.8-4.6 μT at Borssele and 2.2-6.5 μT at HKz. These exposure levels exceed the PNEL, indicating a risk coefficient (Exposure/PNEL) of 4.5-11.5, indicating risk for impact on embryonic development associated with AC exposure. The hazard of embryonic exposure to DC fields remains a knowledge gap.

Elasmobranchs are most sensitive to DC and low Hz AC fields (Bedore & Kajiura, 2013). DC SPC fields will interact with the geomagnetic field, changing local DC signals. Temporary events such as rapid energisation or de-energisation can create short low Hz AC. The combination of DC and low frequency AC exposure may have more pronounced impact on embryonic activity than 50 Hz AC. It is possible chronic embryonic exposure to EMF results in epigenetic effects changing EMF sensitivity. This could result in impact on conspecific interaction, foraging success and consequently fitness in later life, but remains a knowledge gap.

2. | Local-dwelling The current PNEL for AC EMF is adjusted to 0.2 μT, and is weighted against the same measurements as above (1.8-4.6 μT at Borssele and 2.2-6.5 μT at HKz), resulting in a risk coefficient of 9-32.5, indicating risk for impact on local dwelling associated with AC exposure. The DC PNEL was newly determined at 0.003 μT. Measurements at Norned HVDC cables reported exposure levels of 1-2 μT, exceeding the PNEL. This results in a relatively high risk coefficient of 333.3-666.7 for impact on local-dwelling resulting from DC cables, denoting a larger knowledge gap for DC as opposed to AC.

Attraction to cables near EMF sources has been suggested as a plausible response in several field/mesocosm studies (Gill, 2009; Hutchison et al., 2020; Labourgade et al., 2024). Although it does not becomes evident from the laboratory data presented in this thesis, attraction remains a prominent risk when it results in a negative effect on fitness, reproduction or survival. However, it is still unknown whether such responses persist over time or diminishes through habituation, representing a key knowledge gap. There is currently no evidence that SPC EMF causes avoidance. Possible indirect effects such as altered foraging efficiency or changes in conspecific interactions, also present a knowledge gap, particularly if combined with attraction or prolonged residency near cables. Another option is the reduced ability

to detect electric signals of prey due to masking of these signals by an overruling artificial EMF around cables. These behavioural mechanisms have not been sufficiently investigated, and no new research has resolved these uncertainties.

3. | Migratory behaviour Disturbance of migration routes or long-range movement behaviour remains a risk, as DC EMF levels along cable routes (measured at 1-2 μT) exceed the PNEL of 0.005 μT, resulting in a relatively high-risk coefficient (>100) of 200-400, indicating a clear knowledge gap. As AC is not expected to influence this life stage as migration movements are believed to be based on the DC geomagnetic field, no NOEL/PNEL has been determined.

The chance of exposure is expected to increase with the expansion from 12-17 cables by 2040. This is particularly relevant for species undertaking long-distance migrations. Given findings that European eel (Anguilla anguilla) are delayed in their migration (Westerberg & Lagenfelt, 2008) there is reason for concern, resulting in a need for addressing this knowledge gap. The reduced movement of sharks exposed to DC EMF observed in Chapter 6, supports further study of this concern under field conditions, particularly for species in a migratory mode. Exposure during migration could encompass both deviation in course as well as hesitation to pass the SPC, or even attraction as shown in (Hutchison et al., 2020), all potentially resulting in delays which may cause individuals to miss critical environmental conditions, including periods of optimal foraging and reproduction. In contrast to the effects during local dwelling, habituation is not expected to readily occur due to the strong spatial and temporal variability in EMF intensity, emphasising the knowledge gap.

Concluding the Ecological Risk Assessment

In summary, EMF-related risks to benthic elasmobranchs were identified for embryonic development and local dwelling under AC exposure, and for local dwelling and migration under DC exposure (Table 9.2), as indicated by the risk coefficient. The risk coefficient is evaluated against the PNEL; but even at the LOEL, exposure levels exceed the thresholds, underscoring the risk. The relatively high-risk coefficient (>100) for DC exposure, emphasises the knowledge gap for local dwelling and migration. Across all behavioural categories, the risk is not associated with pronounced acute responses, but with subtle behavioural modifications. During embryonic development, behaviour is altered in ways that may increase vulnerability; however, the ecological significance of these effects (e.g. leading to increased predation, altered EMF sensitivity influencing conspecific interactions, less foraging success) remains a key knowledge gap. For local-dwelling behaviour, risk arises from changes in swimming activity under both AC and DC exposure. For migratory behaviour, a potential risk is delays associated with (temporary) route diversions or hesitation behaviour when crossing DC cables.

Although these effects appear to be modest, they remain important as these artificial EMFs are chronic stressors operating over long temporal scales (cable lifetimes of ~40 years) and large spatial scales (>5% of the Dutch continental shelf). Therefore, an accumulation of in itself small individual-level effects may still add up to population-level consequences (Soudijn et al., 2020). It is not known what this chronic exposure actually will result in, but the endpoints presented in this thesis suggests that they will be negative. This is particularly relevant in natural systems where multiple mechanisms may interact; for example, EMF attraction combined with increased egg deposition on cable crossings or scour protection, or reduced foraging efficiency due to less efficient prey detection.

This thesis applied the ERA framework to EMF for the first time (Gallagher et al., 2012). The approach proved suitable for evaluating a chronic stressor with a multitude of behavioural endpoints, providing a structure to link mechanistic effects to risk levels. It can be considered an appropriate tool for data-limited stressors with U-shaped or non-linear response (Calabrese & Baldwin, 2001; Davis & Svendsgaard, 1990). These elements allow for extending it to other poorly understood anthropogenic pressures resulting from offshore wind such as operational vibration or low-frequency continuous sound, or to other species groups potentially affected by EMF like migratory teleosts or sea turtles (Lohmann et al., 2022).

Despite its suitability the ERA approach has challenges and limitations, specifically in taking variation in temporal exposure regimes into account. In addition, it is difficult to account for the complex nature of the EMF signature that animals can perceive e.g. the (interaction of) electric and magnetic signals, instead of exposure to a single component. As exposure to EMF depends on the species traits and species specific differences in effects are found (Chapters 5 and 7, (Gill, 2009; Hutchison et al., 2020)), the next section dives deeper into the relative vulnerability of these risks per species (Hobday et al., 2011; Werry & Meager, 2025; Williams et al., 2011) which allows EMF risks to be assessed in relation to species specific life-history traits. This approach identifies the species and life stages most at risk without the need to test every species individually, which would be unethical and impractical.

9.3 Exploring relative vulnerability

In the ERA the risks were determined per life stage category (Fig. 9.1; Table 9.3, columns 1-3). These effects may influence individuals through several impact pathways, including increased energetic expenditure, reduced food intake, less reproductive output, or elevated mortality (Table 9.3, column 4). Identifying the most vulnerable species is essential for prioritising research and conservation. To this end, a Relative Vulnerability Assessment (RVA) is conducted below, adapted from (Hobday et al., 2011; Werry & Meager, 2025; Williams et al., 2011). The EVA extends the risk assessment by systematically distinguishing species most susceptible to EMF based on life history traits.

The presented RVA focusses on elasmobranch species recorded in the Dutch North Sea, as listed in the Shark Action Plan (Ministry of Agriculture, Fisheries, Food Security

Table 9.3 Overview of risks per life stage, the available evidence to support the impact, or when this was missing hypotheses, and how these link to the impact pathways and corresponding criteria for a species-level risk assessment, which knowledge gaps exist and which future research will provide additional insight. Sources see end of Chapter 9.

Behavioural category	Observed Effect	Hypothesis or potential consequence	Impact pathways
Embryogenic development	• AC: Direct increased embryonic movement [1] • AC: Change in growth [1], [2] • AC: Changes in yolk sack consumption [2]	• AC: Indirect effect upon hatching on conspecific interaction (mating), foraging success and consequently fitness [2], [3] • DC: Abnormal growth or increased energy expenditure during embryogenesis.	Direct increased energy expenditure Indirect reduced reproductive output
Local dwelling	• DC: attraction and increased speed of movement, increased distance covered [5] • AC/DC: decreased/ movement [6] [7]	AC/DC: • Attraction, and subsequent energy loss due to fruitless foraging or lost energy/ time [3], [5] • Disruption or changed sensitivity in sensing prey, masking, resulting in reduced foraging success [3], [4] • Disruption mating interaction, reduced mating success	Direct increased energy expenditure Indirect reduced food uptake or reduced reproductive output
Migration	No data available	Reduced migration success due to delay [3], [4]	Direct increased energy expenditure Indirect reduced food uptake or reduced reproductive output

and Nature, 2023). To apply the RVA towards EMF impacts, species-specific life history traits were translated to exposure scores (on a scale from 1 (less vulnerable) to 3 (highly vulnerable)) (Galic et al., 2024) across the three life stage categories (Table 9.4). Criteria selection followed an ecologically grounded rationale based on observed response patterns in this thesis and published literature (Textbox C), building upon the species based conceptual framework introduced in Chapter 2 (Figure 2.6). Assessing the trait- based vulnerability to SPC generated EMF for the 16 elasmobranch species described for the Dutch North Sea results in a relative scoring, presented in Table 9.5 and Fig. 9.2. In addition to relative vulnerability, Table 9.5 and Fig. 9.2 also include the IUCN conservation status, which is based on five quantitative criteria; population reduction, geographic range, population size and decline, very small population thresholds, and extinction risk modelling (IUCN

Trait based vulnerability criteria	Knowledge gaps	Research suggestion
Reproductive strategy	• DC: abnormal growth or increased energy expenditure • AC: Probability and extent effects conspecific interaction, foraging success [4]	• DC: Lab experiments with chronic DC exposure during embryogenesis • AC/DC: Mesocosm experiment tracking exposed individuals, measuring foraging success and interaction with conspecifics
• Depth range • Residency • Foraging strategy	AC/DC: • Habituation • Extent attraction and subsequent energy loss [8], [9] • Probability and extent disruption foraging success [4] • Probability and extent disruption mating interaction	AC/DC: • Lab/ mesocosm: cumulative exposure effect study determining habituation, • Field: acoustic telemetry combined with fine mesh receiver network surrounding cable [8], using HHM to determine (un)successful foraging • Lab/ mesocosm: foraging/mating success with adult individuals
Long range movements	DC: Probability and extent of delay [4]	DC: Field: Acoustic telemetry with large scale combined with fine mesh network, ideally in Before After Control Impact (BACI) design

Standards and Petitions Committee, 2024) and thus reflect a species' overall vulnerability to anthropogenic pressures. Species with poorer conservation status are expected to have reduced capacity to compensate for further stress, making any additional impact proportionally more severe.

For embryonic development, oviparous skates represent the most vulnerable group (score 3) as eggs are deposited on the seabed and remain immobile during development potentially within an EMF, unlike ovoviviparous species. Eight species are therefore particularly vulnerable, with the common skate complex (consisting of flapper skate and blue skate, *Dipturus batis-intermedius* complex, referred here as *Dipturus spp*.) standing out due to its Critically Endangered (CR) status. During local-dwelling, species with a predominantly benthic lifestyle and high residency are assessed to be most vulnerable, as most skate/ray

Textbox C - Definition of trait-based vulnerability criteria

Exposure score - Life-history traits were used as proxies for species vulnerability, capturing spatial and temporal exposure and behavioural susceptibility to EMF.

Embryonic development	**Reproductive strategy (spatial overlap)** was based on the likelihood that embryogenesis overlaps with EMF sources. Oviparous species were assigned higher scores because eggs are deposited onto the seabed, close to the seabed, where the spatial extent of EMF is greatest, resulting in prolonged, immobile exposure when deposited in direct vicinity of cables. Species that utilise defined nursery areas received additional weighting, as spatial clustering of egg deposition may lead to exposure of a large proportion of a cohort.
Local dwelling	**Depth range (spatial overlap)** Depth range was included as an indicator of proximity to EMF sources, as field strength is highest near the seabed and attenuates with distance. Benthic species were therefore assigned the highest scores due to their relatively higher use of near-cable environments, resulting in longer and higher exposure. This assessment does not account for floating offshore wind systems, where cables may be suspended in the water column, nor for EMFs generated by turbines themselves, (potentially affecting pelagic species), both forming limitations of this RVA. **Residency (temporal overlap)** Residency was used to quantify presence and the likelihood of repeated exposure. Species demonstrating prolonged occupancy in the Dutch North Sea were assigned higher scores, as this increases cumulative EMF exposure through repeated encounters. Ranging from high site fidelity (e.g. Small-spotted catshark) (Papadopoulo et al., 2023) to seasonal/incidentally observed species (e.g. Basking shark) (Austin et al., 2019; Berrow & Heardman, 1994; Finucci et al., 2021). Note that this approach does not account for potential exposure to EMF in other locations, where cable density (exposure) may also be high. This assessment is based on current species distributions, which are reduced compared to their historical, unfished ranges and abundances.

	Foraging strategy Foraging strategy was included as a proxy for mechanistic exposure risk. Benthic feeders were assigned higher scores to reflect their increased time spent close to the seabed where the spatial extent of EMF largest. Additionally, emerging evidence indicates that benthic prey such as crustaceans may themselves be affected by EMF exposure, potentially leading to indirect effects on elasmobranch as reduced foraging efficiency through disruption of predator–prey interactions (Albert et al., 2020; Chapman et al., 2026; James et al., 2025; Scott et al., 2021). This dual pathway, direct exposure and indirect trophic effects, justifies higher exposure weighting for benthic feeders as opposed to planktonic/filter feeders as basking shark, or the intermediately scored pelagic feeders as thresher shark
Migration	**'Long range movements'** was used as a proxy for encounter rate with offshore export cables during migration. Species undertaking long-distance migrations are expected to intersect a greater number of cable routes along their migration routes, increasing the frequency of EMF exposure and the potential for cumulative effects, such as repeated delays due to reduced swimming or attraction, resulting in a higher score. In contrast, species with limited movement or high site fidelity are likely to encounter fewer cables and therefore experience lower cumulative exposure.

Table 9.4 Overview of species-specific vulnerability scoring across traits categorised in three vulnerability levels, detailing the literature sources used to determine each score.

Exposure score	1	2	3
Reproductive strategy	viviparity/ovoviviparity	oviparity - scattered	oviparity - nursery area/ unknown
Depth range	pelagic species	benthopelagic	benthic species
Residency	incidental	seasonal	resident
Foraging strategy	planktonic/filter feeding	pelagic feeding	benthic feeding
Long range movements	high-site fidelity	regional	migration/unknown

Table 9.5 Estimated species-specific vulnerability of all elasmobranchs on the Dutch continental shelf [10] based on the trait-related expected exposure per behavioural category. When insufficient data was unavailable to assess the trait, the highest category was assumed (values indicated in *italic*). Conservation status information was sourced from the IUCN Red List species assessments, specifically the "Habitat and Ecology" sections [11], where LC denotes Least Concern, NT Near-Threatened, VU Vulnerable, EN Endangered and CR Critically Endangered. The study species used in this thesis are indicated in bold. The respective reproductive strategies, depth range and foraging strategies are based on [11], [12], [13], the sources for residency and long range movement are indicated in the last row.

Traits	Tope shark (Galeorhinus galeus)	Spurdog (Squalus acanthias)	Angelshark (Squatina squatina)	Basking shark (Cetorhinus maximus)	Thresher (Alopias vulpinus)	Porbeagle (Lamna nasus)
Embryonic development						
Reproductive strategy	1	1	1	1	1	1
Local dwelling						
Depth range	2	2	3	1	1	1
Residency	1	1	1	1	*1*	1
Foraging strategy	3	3	3	1	2	2
Average score	**2.0**	**2.0**	**2.0**	**1.0**	**1.3**	**1.3**
Migration						
Long range movements	3	3	*2*	3	*3*	3
	IUCN Conservation status					
	CR	VU	CR	EN	VU	VU
Sources *See end of Chapter 9*	[14], [15], [16];	[17], [18];	[19], [20];	[21], [22], [23];	[24], [25], [26];	[27], [28], [29];

Starry smooth-hound (Mustelus asterias)	**Small-spotted catshark (Scyliorhinus canicula)**	Flapper skate (Dipturus spp)	Undulate skate (Raja undulata)	Blonde skate (Raja brachyura)	**Thornback skate (Raja clavata)**	Spotted ray (Raja montagui)	Cuckoo skate (Leucoraja naevus)	Thorny skate (Amblyraja radiata)	Common stingray (Dasyatis pastinaca)
1	3	3	3	3	3	3	3	3	1
2	3	3	3	3	3	3	3	3	3
2	3	3	*3*	3	3	3	*1*	3	2
3	3	3	3	3	3	3	3	3	3
2.3	**3.0**	**3.0**	**3.0**	**3.0**	**3.0**	**3.0**	**2.3**	**3.0**	**2.7**
3	1	*2*	*2*	*2*	*2*	*2*	*2*	*2*	*3*
IUCN Conservation status									
NT	LC	CR	NT	NT	NT	LC	NT	VU	VU
[14], [30], [31];	[8], [32], [33];	[34], [35];	[36], [37], [38];	[39], [40];	[40], [41], [42], [43], [44];	[41], [45];	[46], [47];	[26], [48];	[14], [49].

Tope shark
Galeorhinus galeus
Spurdog
Squalus acanthias
Angelshark
Squatina squatina
Basking shark
Cetorhinus maximus
Thresher
Alopias vulpinus
Porbeagle
Lamna nasus
Starry smooth-hound
Mustelus asterias
Small-spotted catshark
Scyliorhinus canicula
Flapper/Blue skate
Dipturus spp
Undulate skate
Raja undulata
Blonde skate
Raja brachyura
Thornback skate
Raja clavata
Spotted skate
Raja montagui
Cuckoo skate
Leucoraja naevus
Thorny skate
Amblyraja radiata
Common stingray
Dasyatis pastinaca
3
2,5
2
1,5
1
0,5
0
Embryogenesis
Local dwelling
Migration
Extinct in wild
Extinct
Threatened
Critically endangered
Endangered
Vulnerable
Near threatened
Least Concern
EW
EX
CR
EN
VU
NT
LC

Fig. 9.2 - On the left page
Radial plot showing the relative vulnerability levels to the effects of electromagnetic fields per species, at a scale from 1 (relatively invulnerable) to 3 (relatively vulnerable), where the different lines depict the different life stages e.g. embryogenic development (beige), local dwelling (light blue) and migratory behaviour (dark blue line). The IUCN conservation status is indicated in the circles.

species and small-spotted catshark (Table 9.5). Next to the CR *Dipturus spp*., the common stingray and thorny skate are of particular interest given their vulnerability index of 3.0 and 2.7, respectively, as well as the two CR shark species, tope and angel shark, that score 2.0. Migration is particularly relevant for most sharks due to their high mobility, placing six shark and one ray species in the high-vulnerability class; when combined with conservation status, the tope shark and angel shark (both CR) emerge as species of particular interest, whereas the highly resident small-spotted catshark is least at risk with respect to migration.

The two species chosen for our experimental studies in this thesis (thornback skate and small-spotted catshark) were selected based on practical considerations: multiple life stages were available from public aquaria; have been used in laboratory research before and both species are known to be relatively stress-resilient during capture and handling (Enever et al., 2009; Ruiz-García et al., 2025; Schram et al., 2024; Skomal & Mandelman, 2012). The thornback skate and small-spotted catshark both show the highest-vulnerability score in the embryogenic development and local dwelling categories as a consequence of their oviparous benthic lifestyle. They have limited vulnerability during migration as especially small-spotted catshark makes limited long-range movements. This makes both species suitable species to continue research, particularly for studies on embryonic and local-dwelling effects.

RVA scores are often assumption-based due to limited life-history data, introducing uncertainty (Galic et al., 2024). Movement is particularly uncertain: many skates are considered seasonally resident with regional migrations (IUCN Species Survival Commission Shark Specialist Group et al., 2024), but residency is better documented though local mark-recapture and acoustic telemetry studies, than long-range movements (satellite tagging). For example, common blue skate (Dipturus batis) shows high site fidelity, but knowledge on movement patterns are incomplete as males have been suggested to migrate offshore seasonally (Wearmouth & Sims, 2009), resulting in a migratory score of 2. Estimated RVA scores are shown in italics in Table 9.5. Moreover, large individual variation in movement patterns can be observed within many elasmobranch species (Lubitz et al., 2022).

It should be noted that the RVA identifies potential EMF sensitivity only; low scores do not imply low conservation risk, and high severity reflects population vulnerability rather than direct EMF causality. For threatened species, even minor, but especially chronic effects may have serious consequences when existing anthropogenic pressures have already caused a population to be endangered. The RVA framework and the ERA introduced here

for elasmobranchs are readily transferable to other electro- or magneto-sensitive taxa, including diadromous species such as eels (*Anguillidae*), salmonids (*Salmonidae*) or sturgeons (*Accipenseridae*) that undertake long-distance migrations (Chapman et al., 2026; Hermans et al., 2025; Verhelst et al., 2025).

9.4 Formulating recommendations to improve our understanding

The ecological risk assessment (Section 9.2) identifies key knowledge gaps and associated research priorities (Table 9.3). The species-specific relative EMF vulnerability assessment (Section 9.3) then allows translation of these priorities to the species that are already under severe anthropogenic pressure, as shown by their poor conservation status. The RVA also highlights which factors drive vulnerability but remain uncertain (italicised scores). Where such parameters are estimated, they define critical knowledge gaps and guide the prioritisation of future research to improve vulnerability estimates, as is discussed below, and inform mitigation decisions (Section 9.5).

Laboratory and mesocosm studies

For **embryonic development**, chronic DC exposure experiments should best be conducted in a laboratory to determine effects on behaviour and body condition. This is then ideally followed by mesocosm trials with juveniles to assess changes in foraging and behavioural states under (semi-)natural conditions, under AC and DC exposure. For adults, mesocosm studies seem suitable to examine habituation and cumulative exposure in relation to foraging efficiency and reproductive success, which are key components of the **local dwelling** life stage category. From the species identified as vulnerable (Table 9.5) flapper skate (CR) and thorny skate (IUCN status Vulnerable (VU)) are of particular concern due to their unfavourable conservation status; however, their rarity limits feasibility for experimental research. Thornback skate represents a feasible alternative for the near threatened species, due to the availability of ex-situ egg cases and existing foundational work, including studies presented in this thesis (Chapter 4, 5, 7).

Field-based behavioural studies

To assess behavioural changes during **local dwelling**, acoustic telemetry with fine-scale receiver arrays seems the best option to test for changes in local movement patterns, attraction, and reduced foraging efficiency in the field (Labourgade et al., 2024; Reubens et al., 2019). Given that dense receiver arrays can only cover relatively small areas compared with the open sea, this method is most suitable for species resident in small home ranges. If spatial use is unknown, it is recommended conduct a pilot study to determine the target species' scale of movement before deploying a denser network. Of the species with high vulnerability scores, blue skate (CR), thorny ray (VU), and common stingray (VU),

only the latter occurs seasonally in sufficient numbers to make tagging studies feasible. In addition, thornback skate (NT, 3.0) is a strong candidate to study mechanisms that might possibly also be applicable to other species with similar traits due to its availability and suitability for laboratory and mesocosm experiments on embryogenesis. This combination will allow integration of multiple life stages within a single species and thereby improving inference across the full exposure pathway. Lastly, basking sharks, thresher sharks and cuckoo skates could be prioritised for studies in regions where they are more abundant, as substantial uncertainty remains regarding their residency behaviour.

To evaluate risks during **migration**, field research should best target DC export cables, ideally applying a BAG (Before, After, Gradient) experimental design where possible (Methratta, 2020). A BAG is well suited as it allows for the propagation of EMF in the environment as the animals cross a SPC. Tagging studies, particularly archival pop-up satellite tags with a depth and magnetometer, i.e. a sensor that measures magnetic induction (magnetic field intensity), can quantify the field exposure to determine effects on migration and substantially reduce uncertainty in migratory patterns for approximately two-thirds of the species assessed in the RVA (Goossens et al., 2023). Substantial new data are expected to elucidate migratory behaviour, as tagging studies are currently underway for starry smoothhound, small-spotted catshark, tope shark, common stingray, spotted skate, blonde skate, and thornback skate (Poos et al., 2023; Winter & Batsleer, 2023). Collaboration with the Dutch Rijkswaterstaat MONS ("Monitoring en Onderzoek Natuurversterking en Soortenbescherming") programme and ongoing studies in surrounding North Sea countries (DTO-Track, DTO-Straits), such as Belgium (Reubens et al., 2019) is strongly recommended, as its expanding of the Dutch North Sea tracking infrastructure will support multiyear deployment and data integration across species (MONS, 2025). This increasing international body of movement data, organised within the European Tracking Network platform and central database (Özgül et al., 2024) enables to further assess long range movements. The tope shark and porbeagle are of particular interest, combining a poor conservation status (CR) with high vulnerability (3.0). The basking shark (EN, 3.0), angel shark (CR, 2.0), and flapper/blue skate (CR, 2.0) are also of concern but are (presently) less accessible for tagging in Dutch waters. To explore interspecies variability the shark M. asterias represents a strong candidates due to high catchability, seasonal presence and an existing evidence base (Brevé et al., 2016, 2020). For the batoids, thornback skate (NT, 2.0) and common stingray (VU, 3.0), supported by their relative abundance and seasonal presence in the Eastern Scheldt, are suitable candidates for tagging and monitoring.

Future analyses are recommended to include behavioural phenotype as an explanatory variable to account for intraspecies differences in EMF responsiveness. Unpublished findings from this thesis showed personality traits could partly explain individual variation in responses. Indeed, recent work on gadoid larvae shows EMF effects differ by personality type, particularly under DC exposure (22-156 μT) (Cresci et al., 2022). This is important as there is intraspecific behavioural variation in responses to EMF exposure. Such behavioural phenotypes, shaped by genetic diversity and/or experience, might influence responses.

Furthermore, they may even be subject to selection under chronic exposure, providing a potential mechanism for adaptation to this emerging stressor.

Insights gained from these research efforts will allow refinement of EMF exposure thresholds. And potentially more crucially, gain an improved understanding the nature, signature and variability of cues linked to EMF exposure, as these will determine biological responses and impacts. The gathered data can improve encounter rate estimates, and by iteratively updating the ERA and RVA frameworks an increasingly accurate risk assessment can be obtained. Leading to either risk retirement or informing mitigation and improve support for policy decisions.

9.5 Considering implications on policy

As the North Sea is an increasingly busy place, EMF is only one of multiple stressors to take into consideration when assessing ecological impact. An operational offshore wind farm results in changes to the marine environment e.g. continuous noise, currents, light, vessel traffic, vibration and substrate. In addition, within the North Sea elasmobranchs already encounter human pressures such as fisheries, sand extraction, military activity and climate change. Policy makers are required to evaluate the risk and effect-size of EMF alongside these factors, within multiple legislative frameworks. And not only governments, but with the introduction of the Corporate Sustainability Reporting Directive (CSR-D) (Directive (EU) 2022/2464 of the European Parliament and of the Council of 14 December 2022 Amending Regulation (EU) No 537/2014, Directive 2004/109/EC, Directive 2006/43/EC and Directive 2013/34/EU, as Regards Corporate Sustainability Reporting, 2022), companies must report ecological risks resulting from their operations and provide data-based information to guide resource allocation. The work presented in this thesis provides data and knowledge that supports decision-making across three policy levels, e.g. individual/population impact, cumulative impact of multiple stressors acting simultaneously and multi criteria decision assessments stressors (Fig. 9.3). Given the uncertainties identified in the ERA and RVA, application of the precautionary principle could be considered, with corresponding implications for mitigation measures, all discussed below.

Individual level impact assessments evaluate the impact of a single stressor of a single species on habitat use and/or dispersal of the species under consideration. These can form the basis for more complex evaluations such as **population-level impact** assessments based on extrapolating impact on increased energetic expenditure, reduced food intake or reproductive output and elevated mortality (Soudijn et al., 2020). In addition to the research described in section 9.4, progress in providing the knowledge base for these assessments is being made through the Dutch Sharks and Ray Action Plan (HARON) 2022–2027 (Dutch Elasmobranch Association, 2023). The Ministry of Agriculture, Fisheries, Food Security and Nature (LVVN) developed the HARON to contribute to the sustainable management of Dutch elasmobranch. The action plan considers activities that may affect the survival of

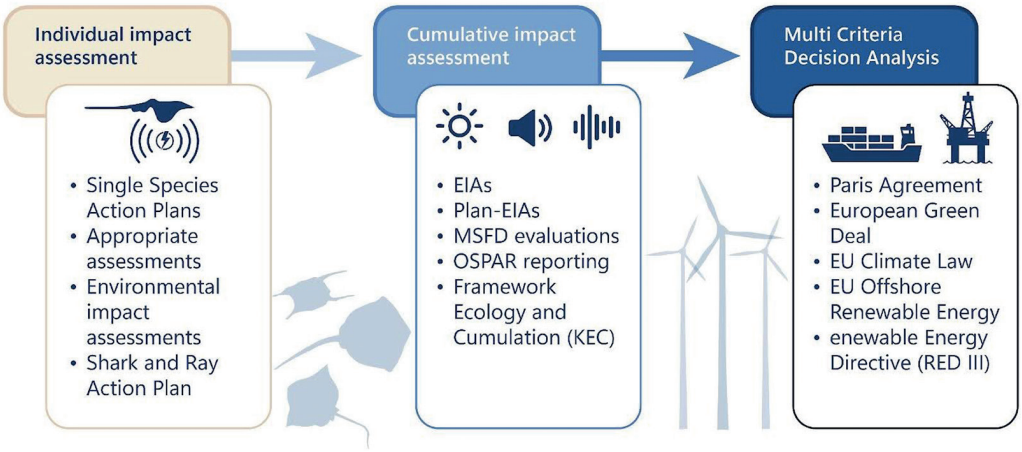


Fig. 9.3 Schematic overview of different decision-making levels on which risk categorisation and knowledge on impact of electromagnetic field have an influence. EIA denotes Environmental Impact Assessment, MSFD Marine Strategy Framework Directive and EU European Union.

these species, such as sustainable energy production at sea resulting in EMF, specifically for the Dutch waters. Conversely, the Single Species Action Plan (SSAP), required under the Convention of Migratory Species (CMS) is a conservation tool which coordinates initiatives in all countries of the species distribution. A SSAP is currently being formulated for tope shark in the Northeast Atlantic and Mediterranean. This plan includes an overview of the threats for the populations of the species, which includes EMFs.

Other policy frameworks are designed to consider the effects of stressors when an initiative is developed in the North Sea. For example, the Environmental and Planning Act, requires an Appropriate Assessment when installing a new export or interconnector cable (Environmental and Planning Act, 2025). This assessment includes a detailed ecological evaluation carried out for plans or projects near Nature conversation sites (e.g. the European Natura 2000 sites) to determine potential negative impacts, including those resulting from EMFs. Its purpose is to provide more confident risk assessments that the site's natural features will not be harmed; if this cannot be assured, alternatives or mitigation measures (as presented in this thesis) must be considered before a permit can be granted. In addition, an Environmental Impact Assessment (EIA) is a broader study that describes the expected environmental effects of a plan or project, including alternatives, to minimise harm to the environment. For example, when evaluating EMF-related risks, shorter cable routes (resulting in less exposure) or areas that do not include Important Shark and Ray Areas (ISRAs) could be assigned a more favourable score. Lastly, in the Common Fisheries Policy of the EU the potential of EMF influencing the long term distribution of (prey)species is included in the population developments assessment.

The results presented in this thesis provide several key inputs for these policy frameworks: realistic exposure levels and thresholds (Chapter 2) and risks retiring including

avoidance, EMF induced stress behaviours and large influence of EMF on substrate preference (Chapters 3, 5, 6, 7). However, enhanced embryo movement and changed swimming activity under EMF exposure highlight the need for continued consideration. The RVA provides life-stage-specific EMF vulnerability profiles that can be directly integrated into future assessments based on the presence of a species in a project area. In addition, the interpretation of the precautionary principle regarding EMF effects, together with the suggested mitigation measures (see below), can inform policy development. It is important to recognize that future cables are expected to have substantially higher capacity, resulting in a wider area of influence, and it remains necessary to verify whether these findings remain valid under such conditions.

Cumulative impact assessments such as EIAs, Plan-EIAs, Marine Strategy Framework Directive (MSFD) evaluations (descriptor 11), OSPAR reporting, and the Dutch "Kader Ecologie en Cumulatie" (KEC) require understanding how EMFs interacts with other pressures. This thesis provides realistic, technically and ecology founded boundary conditions that help define the scale of possible EMF impacts and enable comparison with other stressors. By situating EMF within the broader North Sea system and adjacent seas, including ISRAs, fishing pressure and the potential refuge effects of OWFs, this work facilitates evaluating EMF not in isolation but as part of a multi-stressor environment. For example, the scale of effects observed in this thesis underscores that stressors causing direct mortality, such as fisheries, and those leading to habitat degradation/loss remain dominant pressures. However, the behavioural changes presented here, such as embryonic hyperactivity or changed swimming behaviour, may accumulate over decades of exposure and are particularly relevant for large-scale long-term planning tools. These might include Plan-EIAs and Marine Spatial Planning, noting that these tools are not always adapted to deal with chronic stressors.

Multi-criteria decision analysis (MCDA) frameworks weigh environmental stressors against societal benefits of offshore wind, which are anchored in climate commitments under the Paris Agreement (2015), the European Green Deal (2020), the EU Climate Law (2021), and the EU Offshore Renewable Energy Strategy (RED III). By clarifying the risks, this thesis reduces uncertainty and supports a more fact-based societal dialogue among transmission system operators, OWF developers, policy makers, fishery organisations and NGOs. Overall, the findings presented in this work do not suggest that the effects of EMF directly impact elasmobranch populations through mortality. There are however potential effects of other impact pathways identified e.g. reduced reproductive output, reduced food uptake or increase energy expenditure. Following the research suggestions and targeted mitigation resulting from this thesis should aid in decision making towards a well-balanced and urgently needed energy transition, which requires a more holistic approach or view.

Textbox D Precautionary principle

The precautionary principle originates from international environmental law and reflects the recognition, since the 1990s, that human activities can cause serious and irreversible environmental damage, often under conditions of scientific uncertainty. The principle holds that a lack of full scientific certainty about actual or potential impacts should not prevent states from taking appropriate measures when such impacts may be severe or irreversible. In European law it is considered part of customary law (Atapattu, 2002) and is therefore legally binding, including for the Netherlands. It is also embedded in regulations such as Article 6(3) of the Habitat Directive and implemented through instruments like Environmental Impact Assessments. Moreover, it is referenced in international agreements relevant to electromagnetic fields, including the OSPAR Convention and the Marine Strategy Framework Directive.

The 'precautionary principle'

In environmental policy a concept exists to guide policy makers in situations where there is concern and uncertainty about the impact of a stressor: the precautionary principle (see Textbox D). According to Customary International Law (CIW) (Atapattu, 2002), the precautionary principle applies when two conditions are met: A. when scientific knowledge is lacking on the impact of a stressor, and B., there are concerns about serious or irreversible harm. The ERA and RVA provide evidence that substantiate such concerns, as they identify the potential impact and knowledge gaps on the impact of EMF (Table 9.3, 9.5).
When the conditions of the precautionary principle are assessed for EMFs it becomes evident that:

A | there is insufficient scientific certainty to fully assess the risk e.g. the likelihood or severity regarding the damage, providing reason for concern (Copping & Hemery, 2020; Hutchison et al., 2020; Klimley et al., 2021);

B | due to the relatively long temporal scale (cable lifetime >40 years) and large spatial scale (>5% of the Dutch continental shelf is under the influence of EMF (Hermans et al., 2024)), there is the potential that chronic or cumulative effects might cause serious or irreversible harm to elasmobranch populations, which may result in irreparable or long-lasting impact.

Together, these conditions create an obligation to take preventive measures to avoid or mitigate potential damage (Koeman et al., 2010; Smits, 2023). Actions under the precautionary principle should be proportionate to the level of risk. This does not imply that all cable

installation must be halted. While no strict guidelines exist on what constitutes proportionality, the principle dictates that the greater the risk, the stronger the required response. When determining whether measures are necessary, both the potential consequences of inaction and the associated uncertainties must be considered. In this context, and given the risk identified in the ERA, it follows that proportionate action could include (continued) investment in research, mandatory data sharing on cable characteristics by cable owners and accessibility to cables, and feasible, cost-effective mitigation measures. Applying the precautionary principle can help policy makers justify and allocate funding for the research agenda outlined in Section 9.4.

It is important to note that while some suggest that EMF risks may be retired, although this statement is based on the current scale of marine renewable energy (Garavelli et al., 2024), application of the precautionary principle indicates that this conclusion is premature. Instead, the emphasis should be on asking the right questions and conducting appropriate research by addressing the most urgent knowledge gaps that follow from the ERA and RVA presented here, before risks are dismissed.

Mitigation Measures

Ideally, key knowledge gaps would be resolved before formulating mitigation measures, but the pace of offshore wind development is currently outstripping the willingness to invest in research to generate the necessary ecological evidence. Following the precautionary principle there are several readily actionable measures available, that make sense based on the evidence presented in this thesis. Firstly, recruitment is one of the most sensitive stages in elasmobranch population dynamics due to low fecundity and late maturity. Because early-life survival heavily influences population health, uncertainties around EMF effects during embryogenesis warrant a precautionary approach. Targeted mitigation, such as micro-routing of cables to avoid ISRAs, especially nursery grounds of egg laying species, offers a feasible and justifiable mitigation strategy. In addition, locally increasing burial depth could be assessed, avoiding seabed disturbance through techniques as horizontal drilling - noting that this, in many cases, does not prevent EMF exposure but reduces the EMF exposure area. The theory of a U-shaped dose-response curve suggests high EMF intensities can deter animals which results in an acute response, but thereby reduce the likelihood of chronic exposures during sensitive stages (e.g. embryogenesis or migration), which might otherwise result in ecologically consequential losses of time or fitness. However, as no avoidance of EMF was demonstrated in the present experiments, at the levels expected from SPC, minimising the spatial extent of EMF is preferable. This can be achieved (in part) by deeper burial which is however heavily dependent on local technical feasibility, influenced by e.g. substrate type, water depth and distance to shore. In terms of local movement and migration, increasing burial depth is unlikely to be cost-effective given the broadscale nature these behaviours, but cable straights or bundling can reduce EMF intensity which then reduces the extent of the EMF zone and potentially encounter rates by sharks, skates and rays.

9.6 Leaving you with these final thoughts

This thesis has advanced our understanding of how EMFs from SPC may influence elasmobranchs in the Dutch North Sea across different life stages. The Ecological Risk Assessment identified risks of behavioural changes for embryonic development and local dwelling under AC exposure, and a high risk for local dwelling and migration under DC exposure. No data were previously available to assess the effect of EMF on embryogenesis, denoting a clear knowledge gap. The experiments carried out in this thesis revealed that, while avoidance can be readily ruled out, species- and life stage-specific effects can be expected in the field. The species-specific differences have prompted a species-specific Relative Vulnerability Assessment which has helped prioritise future research and translate findings into evidence-based policy advice.

We have moved beyond the question of whether EMFs pose a risk: they do, but the extent of the risk is complex, requiring consideration of long-term impacts. Their ecological significance lies in the scale of exposure, both spatially (>5% of the Dutch Continental Shelf) and temporally (>40 years), making EMF a chronic stressor. The key question now is if/how the effects found in this thesis cumulate over prolonged and/or repeated exposure, and whether elasmobranchs can adapt through habituation or learning. Does the absence of acute avoidance behaviour lead to prolonged exposure ultimately resulting in long-term harm? And how does this work in concert with other stressors? In what way to the observed intraspecific differences, showing the individual character of sharks, rays and skates, play a role in determining the effect of EMF? This variation may buffer populations against OWF-driven change by diversifying responses, but understanding this adaptive capacity requires sustained time, resources, resulting from policy commitment.

Progress in understanding EMF-related risks follows the path of other stressors that introduce energy and additional complex cues in the marine environment, such as underwater sound. Especially continuous noise forms a chronic complex stressor that also deals with many behavioural endpoints including masking, confusion, chronic stress and behavioural disturbances (Slabbekoorn et al., 2010). Knowledge development in relation to underwater sound shows us that with international collaboration, effect-understanding can expand rapidly. The ability to expand the knowledge base when appropriate resources are applied, does not only translate to effect-understanding of anthropogenic EMF, but also on elasmobranch ecology itself. Both aspects are needed to better understand risks and mitigation measures as offshore wind development accelerates.

Ultimately, when considering EMFs alongside demonstrably severe pressures such as fisheries, even small additional negative effects matter for populations which are heavily under threat as is the case for many elasmobranch species. Understanding whether offshore wind farms act as yet another stressor, or work constructively as a potential refuge from fishing, will be key to striking a responsible balance between renewable energy growth and the conservation of these remarkable species.

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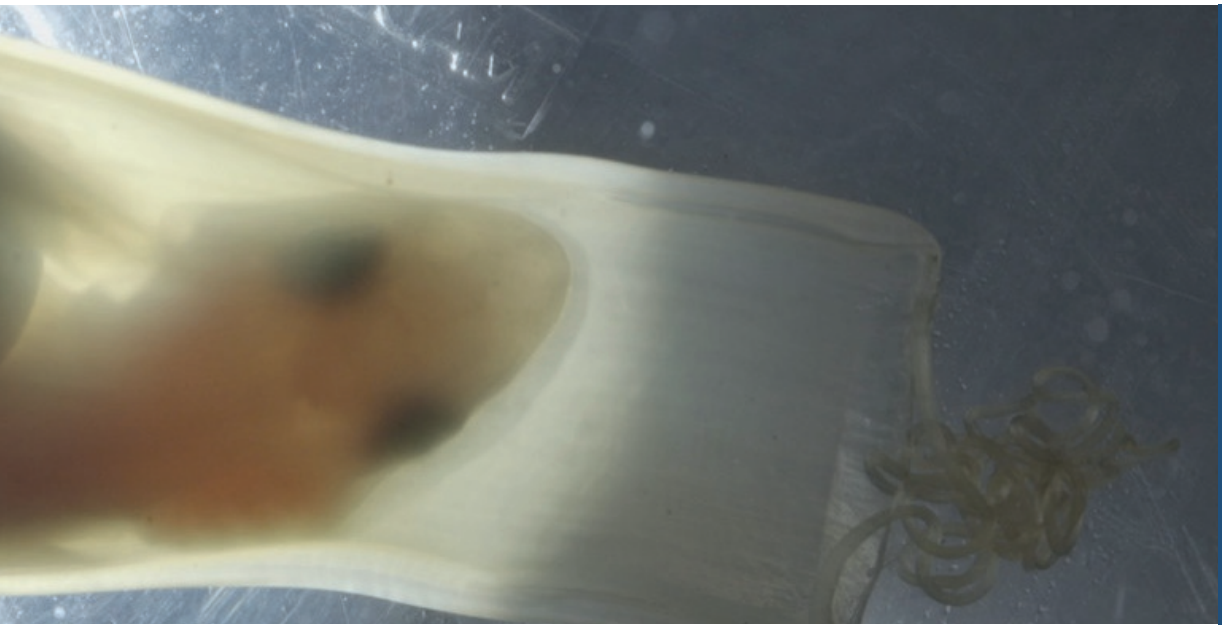

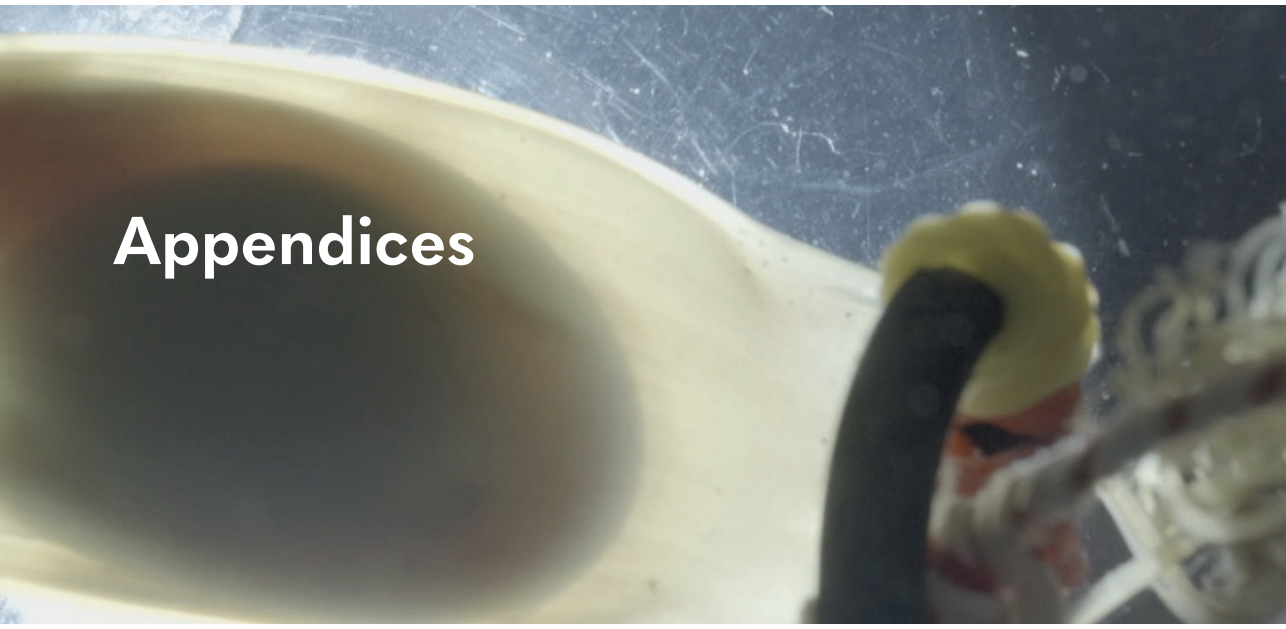

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English Summary

Offshore wind energy is expanding rapidly in the North Sea, bringing with it an extensive and growing network of subsea power cables (SPCs). These cables generate electromagnetic fields (EMFs) that extend into the marine environment. While EMFs are invisible to humans, they fall within the sensory domain of elasmobranchs (sharks, skates and rays), which rely on electro- and magnetoreception for foraging, orientation, and social interactions. At the same time, elasmobranch populations are among the most threatened marine vertebrates globally, already under pressure from fisheries, habitat degradation, and climate change. Against this backdrop, this thesis asks whether anthropogenic EMFs from SPCs constitute an additional ecological stressor for benthic elasmobranchs in the Dutch North Sea, and how such effects should be interpreted within ecological risk assessment and marine policy.

Overall aim and research questions

The overall aim of this thesis, presented in **Chapter 1**, is to assess the ecological risk of electromagnetic fields generated by subsea power cables for benthic elasmobranchs in the Dutch North Sea. Using an ecological risk assessment (ERA) framework, four research questions guide the work:

1. | What is known about the nature of EMFs from SPCs, and what evidence exists for behavioural responses in benthic elasmobranchs from field and experimental studies?

2. | What EMF levels have been reported and are expected from SPC?

3. | What are the lowest EMF exposure levels at which behavioural effects occur in benthic elasmobranchs across different life stages?

4. | Which risk level results from the comparison of the highest EMF exposure levels and the lowest observed effect levels (LOELs) for altered behaviour in benthic elasmobranchs across life stages?

Scientifically, the thesis aims to move beyond isolated experimental outcomes towards a structured, risk-based evaluation of a subtle and chronic stressor. Societally, it seeks to provide an evidence base for environmental impact assessments (EIAs), spatial planning, and application of the precautionary principle in offshore wind development, enabling the balancing of renewable energy and marine conservation priorities.

Chapter 2 establishes the conceptual and analytical foundation of the thesis by applying an ecological risk assessment to EMFs from SPCs for benthic elasmobranchs on the Dutch Continental Shelf. Combining a systematic literature review with exposure modelling, this chapter quantifies both hazard (potential biological effects) and exposure (spatial

extent and intensity of EMFs), allowing risk assessment. The analysis demonstrates that EMF footprints overlap with key elasmobranch habitats, including egg-laying grounds and migration routes, and identifies three behavioural categories likely to be affected: embryonic development, local dwelling, and migration. Importantly, the ERA reveals substantial knowledge gaps, particularly regarding effects at realistic exposure levels and species-specific sensitivity, thereby guiding the design of subsequent field and laboratory studies that are presented in the next chapters of this thesis.

Chapter 3 addresses a central uncertainty highlighted in the ERA: whether elasmobranchs continue to use offshore wind farm (OWF) habitats after construction or are deterred by EMF or other OWF associated stressors. Using environmental DNA (eDNA) surveys within four operational OWFs over two years, the study detects five elasmobranch species inside wind farm areas. These findings provide the first field-based evidence within this thesis that OWFs and associated cables do not constitute large-scale barriers to elasmobranch presence or movement. The results thus "retire" the hypothesis of broad habitat exclusion, while leaving open the possibility of more subtle behavioural effects due to the resulting exposure.

The thesis then moves to controlled laboratory experiments that examine life-stage-specific responses under realistic exposure scenarios. **Chapter 4** investigates embryonic development of thornback skate (*Raja clavata*) chronically exposed to varying AC EMF throughout embryogenesis. No effects were found on hatching success, development time, or hatching weight. However, embryos exhibited hyperactive movement (150%) under exposure, suggesting elevated energetic costs and potentially elevating predation risk. Significant but minor biometric differences (5-11 %) in hatchlings were observed.

Chapter 5 follows these individuals into the juvenile stage and extends the comparison to small-spotted catshark (*Scyliorhinus canicula*). Juveniles that had been exposed during embryogenesis showed no differences in stress or swimming behaviour relative to controls, and all individuals appeared healthy. These results indicate that early exposure did not translate into overt impairments at the juvenile stage for either species. A knowledge gap remains in effects on foraging, navigation and conspecific interaction, while highlighting that subtle behavioural changes may not persist uniformly across life stages.

Chapter 6 examines behavioural responses of adult small-spotted catshark exposed to spatial gradients of field-relevant EMFs, simulating the experience of crossing a subsea cable. Each individual served as its own control, and both AC and DC treatments were included. No evidence of stress behavioural, attraction, avoidance, or altered space use was detected. However, under DC exposure sharks reduced activity by ~25%pt., indicating a subtle but statistically significant change in activity patterns. These results suggest that while SPCs do not act as behavioural barriers, DC fields in particular may influence movement dynamics.

Chapter 7 applies the same experimental framework used in Chapter 6 to thornback skate, enabling a direct interspecific comparison. As with sharks, skates showed no

attraction or avoidance, overt signs of stress, and no changes in spatial use. Hidden Markov modelling (HMM) revealed small but statistically significant sex-specific responses: females were less (~15%pt.) inactive and more transitory under AC exposure, whereas males were more (~14%pt.)inactive under both AC and DC conditions, all compared to control trials. These findings demonstrate that even when overall responses are subtle, behavioural effects may differ between species and sexes, underscoring the limitations of extrapolating results from a single model species.

Chapter 8 explores whether EMF influences habitat use by juvenile small-spotted catshark in a circular preference chamber offering quadrants with a combination of mussel-covered versus bare substrate, with and without EMF exposure. No differences in substrate choice or space use were detected, but a significant but subtle increase in inactivity (5-6%pt.) was revealed by HMM analysis in the quadrant with mussels and EMF exposure. This experiment provides further evidence that EMF likely does not lead to habitat avoidance at small spatial scales, even when biologically meaningful habitat features are available. This underscores the importance of investigating more subtle behavioural responses under field conditions.

Chapter 9 integrates these empirical findings within the ERA framework and answers the original research questions. First, it confirms that EMF exposure levels in the field are generally lower than those used in many experimental studies, but exhibit high temporal variability. It emphasises that spatial extent and encounter rates are likely to increase with future offshore wind development. Second, it shows that behavioural effects, where present, are subtle, life-stage-dependent, and species- and sex specific, with no evidence for strong deterrence or barrier effects. Third, it demonstrates that risk persists primarily because EMF is a chronic, long-term stressor acting over decades and across large spatial scales, and knowledge on habituation is absent. The ERA results in risk coefficients, used to indicate relative risk levels (exposure levels/Precited No Effect Levels), of 4.5-11.5 for embryogenesis and 9-32.5 for local dwelling both for AC and 333-667 for local dwelling for DC and migration 200-400 for DC.

Recognising the heterogeneity of responses among species, Chapter 9 introduces a Relative Vulnerability Assessment (RVA) that builds on life-history traits (e.g., reproductive strategy, depth range, residency, foraging strategy, long range movements) to identify which elasmobranch species are most vulnerable to EMF exposure. This framework highlights oviparous, benthic, resident species, such as large skates, as higher-risk groups for the life stages embryonic development and local dwelling. Conversely, as most shark species are more migratory, they are most at risk during migration. The RVA highlights interspecific differences, identifies key life-history knowledge gaps and provides a transparent tool for prioritising future research and informing conservation management.

From a policy perspective, EMF is situated within existing regulatory frameworks, including EIAs, the Marine Strategy Framework Directive, and the application of the

precautionary principle originating from Customary International Law. The results suggest that EMF effects are unlikely to justify delaying offshore wind development but advocates for continued monitoring, targeted research on high-risk species and life stages, and pragmatic mitigation measures such as micro-routing to avoid critical habitats.

Overall conclusions and implications

Collectively, this thesis demonstrates that EMFs from subsea power cables do not block migration routes, do not cause strong acute stress responses nor cause large-scale habitat loss for benthic elasmobranchs in the North Sea. Nonetheless, subtle, context-dependent behavioural effects occur, varying by life stage, species, and sex. Because EMF is a persistent stressor operating over long temporal and spatial scales, even small individual-level changes may accumulate and interact with other anthropogenic pressures. Scientifically, the work advances EMF research from isolated experiments to a structured, risk-based framework that integrates exposure, effects, and species ecology. Societally, it provides regulators, developers, and stakeholders with an evidence-based foundation for assessing EMF alongside other stressors, supporting responsible offshore wind expansion while minimising additional pressure on already vulnerable elasmobranch populations.

Dutch Summary

Offshore windenergie breidt zich snel uit in de Noordzee en gaat gepaard met een steeds omvangrijker netwerk van onderzeese stroomkabels (subsea power cables; SPC's). Deze kabels genereren elektromagnetische velden (EMV's) die zich uitstrekken in het mariene milieu. Hoewel EMV's voor mensen onzichtbaar zijn, vallen zij binnen het zintuiglijke bereik van elasmobranchen (haaien en roggen), welke elektro- en magnetoreceptie gebruiken voor onder meer foerageren, oriëntatie en sociale interacties. Tegelijkertijd behoren elasmobranch populaties wereldwijd tot de meest bedreigde mariene vissoorten, en staan zij onder druk door visserij, habitatdegradatie en klimaatverandering. Tegen deze achtergrond onderzoekt dit proefschrift of antropogene EMV's afkomstig van SPC's een aanvullende ecologische stressfactor vormen voor benthische elasmobranchen in de Nederlandse Noordzee, en hoe dergelijke effecten geïnterpreteerd dienen te worden binnen milieu effect rapportages en marien beleid.

Algemene doelstelling en onderzoeksvragen

De overkoepelende doelstelling van dit proefschrift, zoals gepresenteerd in **Hoofdstuk 1**, is het beoordelen van het ecologisch risico van elektromagnetische velden afkomstig van onderzeese stroomkabels voor benthische elasmobranchen in de Nederlandse Noordzee. Aan de hand van een ecologische risicoanalyse (Ecological Risk Assessment; ERA) worden vier onderzoeksvragen behandeld:

1. | Wat is bekend over de aard van EMV's afkomstig van SPC's, en welk bewijs bestaat er voor gedragsreacties van benthische elasmobranchen op basis van veld- en experimentele studies?

2. | Welke EMV-niveaus zijn gerapporteerd en worden verwacht rondom SPC's?

3. | Wat zijn de laagste blootstellingsniveaus waarbij gedragsveranderingen optreden bij benthische elasmobranchen in verschillende levensstadia?

4. | Welk risiconiveau volgt uit de vergelijking tussen de hoogste EMV-blootstellingen en de laagste waargenomen effectniveaus (LOEL's) voor gedragsveranderingen over levensstadia heen?

Wetenschappelijk beoogt dit proefschrift verder te gaan dan geïsoleerde experimentele uitkomsten, en bij te dragen aan een gestructureerde, risico-gebaseerde evaluatie van een subtiele en chronische stressor. Maatschappelijk beoogt het een onderbouwde basis te bieden voor milieueffectrapportages, ruimtelijke planning en de toepassing van het voorzorgsbeginsel binnen de ontwikkeling van offshore windenergie, zodat er een nieuwe balans gevonden kan worden tussen hernieuwbare energieproductie en mariene natuurwaarden.

Hoofdstuk 2 legt het conceptuele en analytische fundament van het proefschrift door een ecologische risicoanalyse toe te passen op EMV's van SPC's voor benthische elasmobranchen in de Nederlandse Noordzee. Door een systematische literatuurstudie te combineren met blootstellingsmodellering worden zowel de potentiële effecten (hazard) als de ruimtelijke omvang en intensiteit van blootstelling gekwantificeerd. De analyse laat zien dat EMV-velden overlappen met belangrijke habitats, waaronder paaigebieden en migratieroutes, en identificeert drie gedragsdomeinen die waarschijnlijk beïnvloed worden: embryonale ontwikkeling, lokaal verblijf en migratie. Tegelijkertijd worden substantiële kennislacunes zichtbaar, met name rond realistische blootstellingsniveaus en soortspecifieke gevoeligheid, die richting geven aan de opzet van de daaropvolgende veld en laboratorium studies.

Hoofdstuk 3 adresseert een kernonzekerheid uit de ERA: blijven elasmobranchen gebruikmaken van habitats binnen offshore windparken (OWF's) na aanleg, of worden zij ontmoedigd door EMV's of andere OWF-gerelateerde stressoren? Met behulp van eDNA-metingen binnen vier operationele windparken over twee jaar werden vijf haaien en roggensoorten gedetecteerd. Deze resultaten leveren het eerste bewijs binnen dit proefschrift dat OWF's en bijbehorende kabels geen harde barrières vormen voor aanwezigheid of verplaatsing. De hypothese van brede habitatvermijding kan daarmee worden verworpen, terwijl ruimte blijft voor subtielere gedragsveranderingen.

Het proefschrift richt zich vervolgens op gecontroleerde laboratoriumexperimenten die levensfase specifieke gedragsveranderingen onderzoeken bij realistische blootstellingsscenario's. **Hoofdstuk 4** onderzoekt de embryonale ontwikkeling van de stekelrog (*Raja clavata*) onder chronische blootstelling aan AC-EMV. Er werden geen effecten gevonden op uitkomstsucces, uitkomstgewicht of ontwikkelingsduur, maar wel een sterke toename in embryoactiviteit (150%), wat kan wijzen op verhoogde energiekosten en predatierisico. Bij de uitgekomen dieren werden significante maar beperkte biometrische verschillen (5–11%) vastgesteld.

Hoofdstuk 5 volgt deze individuen in het juveniele stadium en vergelijkt hen met de hondshaai (*Scyliorhinus canicula*). Juveniele die tijdens de embryonale ontwikkeling waren blootgesteld, vertoonden geen verschillen in stress of zwemgedrag ten opzichte van de controlegroep, en alle individuen leken in goede gezondheid. Deze resultaten geven aan dat vroege blootstelling niet heeft geleid tot duidelijke beperkingen in het juveniele stadium voor beide soorten. Er blijft echter een kennislacune bestaan met betrekking tot effecten op foerageren, navigatie en interacties met soortgenoten, en benadrukt dat subtiele gedragsveranderingen mogelijk niet voortduren in volgende levensstadia.

Hoofdstuk 6 onderzoekt de gedragsresponsen van volwassen hondshaaien die werden blootgesteld aan ruimtelijke gradiënten van veld-relevante EMV's, waarmee de ervaring van het kruisen van een SPC werd gesimuleerd. Elk individu fungeerde als zijn eigen controle, en zowel AC- als DC-blootstellingen waren onderdeel van de proef. Er werd geen bewijs

gevonden voor stressgedrag, aantrekking, vermijding of veranderingen in ruimtegebruik. Echter, onder DC-blootstelling verminderden de haaien hun activiteit met ~ 25%pt., wat wijst op een subtiele maar statistisch significante verandering in activiteitspatronen. Deze resultaten suggereren dat SPC's geen gedragsmatige barrières vormen, maar dat met name DC-velden de bewegingsdynamiek kunnen beïnvloeden.

In **Hoofdstuk 7** is hetzelfde experimentele als in Hoofdstuk 6 uitgevoerd met de stekelrog (*Raja clavata*), waardoor een directe interspecifieke vergelijking mogelijk wordt. Net als bij de haaien vertoonden de roggen geen aantrekking of vermijding, geen duidelijke tekenen van stress en geen veranderingen in ruimtegebruik. Hidden Markov-modellering (HMM) toonde echter kleine maar statistisch significante geslacht specifieke reacties: vrouwtjes waren minder (~15%pt.) inactief en vertoonden meer transitiegedrag onder AC-blootstelling, terwijl mannetjes meer inactief waren (~14%pt.) onder zowel AC- als DC-condities, telkens vergeleken met de controleproeven. Deze bevindingen laten zien dat zelfs wanneer reacties subtiel zijn, gedragsmatige effecten kunnen verschillen tussen soorten en tussen de seksen, wat de beperkingen onderstreept van het extrapoleren van onderzoeksresultaten op basis van één modelsoort.

Hoofdstuk 8 onderzoekt of EMV het habitatgebruik beïnvloedt van juveniele hondshaaien in een ronde voorkeursopstelling met kwadranten die een combinatie boden van met mosselen bedekt versus kaal substraat en met en zonder EMV-blootstelling. Er werden geen verschillen in substraatkeuze of ruimtegebruik gevonden, maar HMM-analyse toonde een significante maar subtiele toename in inactiviteit (5-6%pt.) in het kwadrant met zowel mosselen als EMV-blootstelling. Dit experiment levert aanvullend bewijs dat EMF waarschijnlijk niet leidt tot habitatvermijding op kleine ruimtelijke schaal, zelfs wanneer biologisch relevante habitatkenmerken aanwezig zijn. Dit onderstreept het belang van het onderzoeken van meer subtiele gedragsveranderingen in een natuurlijke setting.

Hoofdstuk 9 integreert deze empirische bevindingen binnen het ERA-raamwerk en beantwoordt de oorspronkelijke onderzoeksvragen. Ten eerste bevestigt het dat EMV-blootstellingsniveaus in zee over het algemeen lager zijn dan die in veel experimentele studies worden gebruikt, maar dat zij een hoge temporele variabiliteit tonen. Daarnaast wordt benadrukt dat zowel de ruimtelijke omvang als de kans op blootstelling naar verwachting zullen toenemen met de verdere ontwikkeling van offshore windenergie. Ten tweede laat het zien dat gedragseffecten, waar aanwezig, subtiel zijn, levensfase-afhankelijk en soort- en geslachtsspecifiek, zonder aanwijzingen voor sterke afschrikking- of barrière effecten. Ten derde toont het aan dat het risico met name zit in het feit dat EMV een chronische, langdurige stressor is die over decennia en op grote ruimtelijke schaal aanwezig is, terwijl kennis over mogelijke habituatie ontbreekt. De ERA resulteert in risico coëfficiënten, gebruikt om relatieve risiconiveaus aan te geven (blootstellingsniveaus/Predicted No Effect Levels), van 4,5-11,5 voor embryonale ontwikkeling en 9-32,5 voor lokaal verblijf bij AC, en 333-667 voor lokaal verblijf en 200-400 voor migratie bij DC.

Gezien de heterogeniteit in reacties tussen soorten introduceert Hoofdstuk 9 een Relative Vulnerability Assessment (RVA), gebaseerd op levensgeschiedeniskenmerken (zoals voortplantingsstrategie, diepte, mate van residentie, foerageerstrategie en lange-afstandsbewegingen), om te identificeren welke rog en haai soorten het meest kwetsbaar zijn voor EMV-blootstelling. Dit raamwerk toont dat ovipare, benthische en residente soorten, zoals grote roggen, een hogere risicogroep vormen voor de levensfasen embryonale ontwikkeling en lokaal verblijf. Daarentegen lopen de meeste haaiensoorten, die meer migrerend zijn, vooral risico tijdens migratie. De RVA maakt interspecifieke verschillen inzichtelijk, identificeert belangrijke kennislacunes in levensgeschiedenisgegevens en biedt een transparant instrument voor het prioriteren van toekomstig onderzoek en het informeren van natuurbeheer.

Vanuit beleidsmatig perspectief wordt EMV geplaatst binnen bestaande regelgevende kaders, waaronder milieueffectrapportages (mer), de Kaderrichtlijn Mariene Strategie en de toepassing van het voorzorgsbeginsel. De resultaten suggereren dat de effecten van EMV geen aanleiding vormt om de ontwikkeling van offshore windenergie te vertragen. Er wordt gepleit voor voortgezette monitoring, gericht onderzoek naar hoog-risicosoorten en -levensfasen, en pragmatische mitigerende maatregelen, zoals microroutering om kritieke habitats te vermijden.

Algemene conclusies en implicaties

Gezamenlijk laat dit proefschrift zien dat EMV van SPC migratieroutes niet blokkeren, geen sterke acute stressreacties veroorzaken en niet leiden tot grootschalig habitatverlies voor benthische elasmobranchen in de Noordzee. Desondanks treden er subtiele, contextafhankelijke gedragsmatige effecten op, die variëren per levensfase, soort en geslacht. Omdat EMV een chronische stressor is die over lange temporele en ruimtelijke schalen werkzaam is, kunnen zelfs kleine veranderingen op individueel niveau zich in de tijd opstapelen en interageren met andere antropogene drukfactoren. Wetenschappelijk draagt dit werk bij aan de ontwikkeling van EMV-onderzoek door te verschuiven van geïsoleerde experimenten naar een gestructureerd, risicogebaseerd raamwerk waarin blootstelling, effecten en soort-
eigen ecologie geïntegreerd worden. Maatschappelijk biedt het beleidsmakers, ontwikkelaars en andere belanghebbenden een empirisch onderbouwde basis om EMV te beoordelen in samenhang met andere stressoren, en ondersteunt het een verantwoorde uitbreiding van offshore windenergie waarbij wordt gestreefd naar het minimaliseren van aanvullende druk op reeds kwetsbare roggen en haaien populaties.





Curriculum Vitae

Annemiek Hermans was born on September 11, 1985, in Amsterdam, The Netherlands. At the age of four, she took an art class at the aquarium of the Artis Zoo, where her love for the ocean was sparked. At 15, during her secondary vocational education at Groenhorst College, she completed internships rescuing seal pups at the Seal Rehabilitation Center Pieterburen, followed by an internship at the shark and ray pool at Dolfinarium Harderwijk. She then attended Van Hall Larenstein University of Applied Sciences from 2005-2010, where she earned double Bachelor's degrees in Integrated Coastal Zone Management and Environmental Sciences. Annemiek subsequently moved to the United Kingdom to obtain her MSc in Oceanography from the University of Southampton.

Upon graduating with distinction in 2011, she secured her first job at dredging company Boskalis. For six years, she travelled to most continents as an environmental engineer, conducting water quality monitoring, observing marine mammals, making underwater sound recordings of humpback whales, counting sea turtle nests, and learning about people and the world in general.

When starting a family, she decided to find a position closer to home and began working as a marine ecologist at engineering firm Witteveen+Bos early 2018. She still works there, advising government, NGOs, and industry on developments in the North Sea, focusing on both the positive and negative effects of offshore wind development. In this role, she has been working with transmission system operator TenneT since 2018, advising on the effects of electromagnetic fields from the export cables and the nature-inclusive design of the offshore grid.






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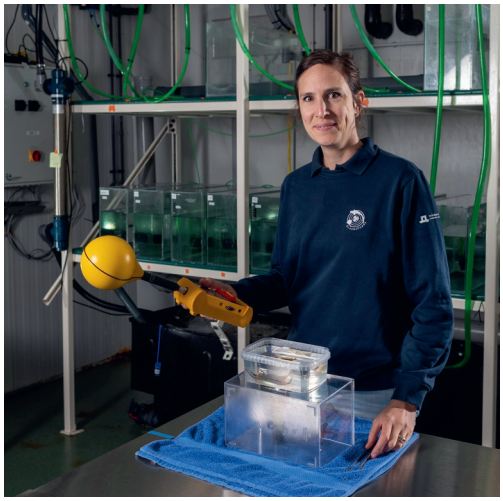





During a meeting with Tinka Murk, not long after Annemiek started at Witteveen+ Bos, Annemiek asked Tinka why Wageningen University was not researching the understudied effects of electromagnetic fields. Tinka replied, "Why aren't you?" Together, they wrote a research proposal that was granted in 2019, and Annemiek started her PhD in September 2020.

Throughout her professional career, Annemiek has contributed to several research projects, in addition to ElasmoPower, focusing on the effects of offshore wind development and particularly electromagnetic fields. She aims to continue this role in a position as a part-time researcher at the Marine Animal Ecology chair group.



Authorship statement

PhD candidate's name:	Annemiek Hermans
First promotor:	Professor A. J. Murk
Title of PhD thesis:	Charged encounters
Date of public defence:	August 2026

Chapter 1 General Introduction. The research questions were formulated jointly with my promotor. I developed an outline for the general introduction which was reviewed once by my supervisory team. Based on the agreed structure, I then wrote the full chapter and subsequently revised the text following one round of feedback from my promotor and co-promotors.

Chapter 2 Do electromagnetic fields from subsea power cables effect elasmobranch behaviour? A risk-based approach for the Dutch Continental Shelf. I conceptualised the study, and the methodology was developed jointly with my promotor. Based on the agreed structure, I then conducted the literature review and data analysis, except the EMF-modelling of the magnetic field values. Subsequently, I then wrote the final version after several revisions with comments of my promotor and co-promotors.

Chapter 3 Elasmobranchs in Offshore Wind Farms. I conceptualised the study. The methodology was developed jointly with one of my co-promotors. The data collection was carried out by several co-authors, including myself. I then wrote the initial outline of the manuscript. After one revision round incorporating comments from all co-authors and feedback from the last author, the co-first author and I prepared the full manuscript, which was reviewed once by the co-authors and then finalised jointly.

Chapter 4 An egg case study: chronic exposure to AC electromagnetic fields results in hyperactivity in thornback ray *Raja clavata* embryos. I conceptualised the study, and the methodology was developed jointly with one of my co-promotors. The data collection was carried out by MSc students that I supervised. I wrote the initial outline of the manuscript. After one revision round incorporating comments from all co-authors and feedback from the last author, I prepared the full manuscript, which was reviewed once by the co-authors, after which I wrote the final version.

Chapter 5 Tails and Fins: Subtle changes in growth following chronic embryonic exposure to AC electromagnetic fields in elasmobranchs I conceptualised the study, and the methodology was developed jointly with one of my co-promotors. The data collection was carried out jointly with MSc students that I supervised. I wrote the initial outline of the manuscript. After one revision round incorporating comments from all co-authors and

feedback from the last author, I prepared the full manuscript, which was reviewed once by the co-authors, after which I wrote the final version.

Chapter 6 From Subsea Power Cable to Small-spotted Catshark *Scyliorhinus canicula*: behavioural effects of electromagnetic fields in tank experiments. I conceptualised the overarching research goals, and developed the methodology jointly with the co-first author. The data collection was carried out by co-authors and MSc students that I supervised. I carried out the initial drafting of the manuscript together with co-authors. After one round of revisions with comments from all co-authors, and with several discussions with the last author, I then wrote the final version of the manuscript.

Chapter 7 Torn in their side? Subtle sex-dependant behavioural responses of a batoid to AC and DC electromagnetic fields. The research questions and methodology were developed jointly with the co-first author. I then wrote the initial outline of the manuscript. After one revision round incorporating comments from all co-authors and feedback from the last author, the co-first author and I prepared the full manuscript, which was reviewed once by the co-authors and then finalised jointly.

Chapter 8 Preference of substrate and electromagnetic field exposure in small-spotted catsharks (*Scyliorhinus canicula*) remains unaffected despite subtle behavioural changes. The research questions and methodology were developed jointly with the co-first author, as was the initial drafting of the manuscript. After one revision round incorporating comments from all co-authors, and feedback of the last author, the co-first author and myself then wrote the full version of the manuscript, which was reviewed once by the co-authors and finalised jointly with the co-first author and myself.

Chapter 9 General discussion. I wrote the first draft of the text after just one discussion with my co-promotor on the subjects and arguments to be included. I revised the text once, after comments of my promotor and co-promotors.

In all chapters, with the exception of 2, 4 and 6, I have used ChatGPT to provide language support, and to enhance the clarity of the text. I am fully responsible for the final content and interpretation of the research. I have used OpenAI. (2025). ChatGPT (GPT-5.2) [Large language model]. https://chat.openai.com

Date: 13th February 2026

Signature PhD candidate



Signature promotor for agreement



Scientific publications

In this thesis

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. Environmental Pollution, 346, 123570. https://doi.org/10.1016/j.envpol.2024.123570

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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. Marine Environmental Research, 209, 107151. https://doi.org/10.1016/j.marenvres.2025.107151

Hermans, A., Hubert, J., Chiovaro, A. P., Witsen, E., Spanings, T., Winter, H. V., & Foekema, E. (2025). Tails and Fins: Subtle changes in growth following chronic embryonic exposure to AC electromagnetic fields in elasmobranchs. SSRN. https://doi.org/10.2139/ssrn.5900598

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Bouwman, L. and **Hermans, A.**, Hubert, J., Nijland, R., Jansen, H., Schotanus. J. & Winter, H. V. (under review). Preference of substrate and electromagnetic field exposure in small-spotted catsharks (Scyliorhinus canicula) remains unaffected despite subtle behavioural changes. Submitted to Journal of Fish Biology.

Hermans, A. and Rochas, C., Hubert, J., Chapman, E., Burns, Z., Foekema, E. M., Harsányi, P., Scott, K., & Winter, H. V. (under review). Thorn in their side? Subtle sex-dependant behavioural responses of a batoid to AC and DC electromagnetic fields. Submitted to Environmental Science & Technology Letters.

Other

Chapman, E. C. N., Rochas, C. M. V., Burns, Z., Harsányi, P., **Hermans, A.**, & Scott, K. (2026). Effects of electromagnetic fields on flatfish activity levels. Marine Pollution Bulletin, 222, 118652. https://doi.org/10.1016/j.marpolbul.2025.118652

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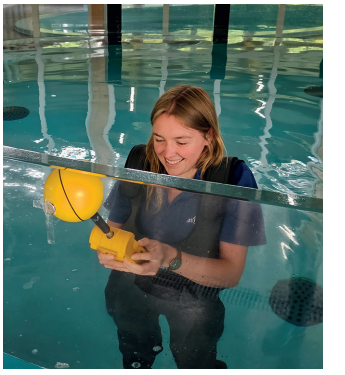
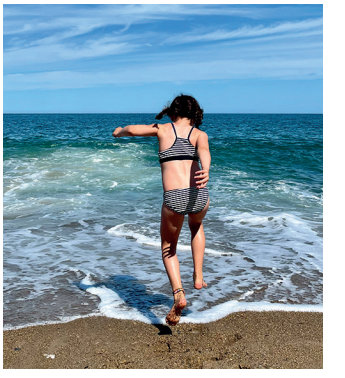
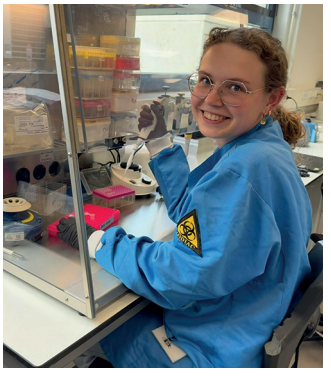




Acknowledgements

To those who helped me navigate the currents

Some PhDs stories are of ups and downs, of mountains climbed, hardship and perseverance and sometimes stress. Mine is really quite different. I loved every minute of my 6 years and now, as the cherry on top, I would like to thank the people who shared the joy with me.

First of all, I thank the fish, as I think for them it was not always a joyride - at least now you are all free.

Tinka, my promotor, you were and are the source of my inspiration. Even after the umpteenth revision of that first manuscript - you never gave up and made me trust in my own researcher capabilities, thank you. But moreover, you have my gratitude for starting a chair group, in an academic world made by and for men, underfunded, and outnumbered, labeled as an 'experiment'. Thank you for making it a safe space for women and men, where I did not have to fight as you had to. I hope that if my daughters choose to make the same journey, they will do so in a world where being a mother and doing a PhD is seen as a sign of strength, supported and celebrated as an example of strong positive parenting, leading by example.

Erwin, I have not yet met anyone who is your equal in kindness, or in your ability to explain complex shark ecology so simply that I never felt lost. Thank you for sharing your profound quest for shark knowledge with me.

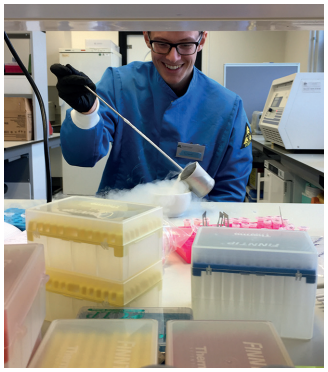
Reindert, thank you for treating all my plans as if they were magnificent and doable, and for supporting countless side quests with equal enthusiasm. I am happy that our adventures continue.

Edwin, how lucky we were to find each other and become such an excellent student–co-promotor team. Thank you for helping me untangle data with too many parameters, and for teaching me how to read the story the data are telling.

Steering group members, headed by Dr. Andrew Gill, your advice and continued link industry, our unique collaboration, it was refreshing! A special thanks to Saskia Jaarsma of TenneT and Martine Graafland of WOZEP for seeing the need for this work and backing it up with data and resources, getting the ball rolling.

Witteveen+Bos colleagues, firstly and most importantly, Just and Britte - thank you for your brains, and allowing me to spar with them. It satisfies me greatly to work with people of your caliber. Maartje Smit thank you for discussions on that strange and often misunderstood fickle beast - the precautionary principle. Rijn van Kampen, thanks for rescuing me from an ugly fate and making sure my final figures were up to scratch. A special heartfelt thanks to Marcel Klinge who, more then anyone, gave me the opportunity to combine the academic and consultancy world and helped shape my carrier.

Samantha, Hilmar, Niels, Robbert, Max, Maxime, Stella, Ditte, Ties, Lydia, Sophie, Eva, Stan, Sytse and Antonio, my dear students. How the world has changed from when I was a student. I have tried to be the best supervisor I could be for you. And in turn you were excellent students, motivated, hard working with a continued sharp eye for the welfare of the












animals. I also worried about you, as at times you were anxious, feeling the pressure and setting the bar so high. I hope you will grow up to be strong, independent and carefree(er) people. You collected so much (and mostly ;) high quality data, and made this work possible - thank you.

All at MAE, or the marine animal ecology chair group, you made my Friday's on campus a true escape from corporate world. If the WUR was my Hogwarts, then you were my Gryffindors: all brave, courageous and full of determination to make the world a bit better. And where I felt like Harry Potter, in my story Diede and Jeroen are most definitely my Ron and Hermione - Thank you.

I quickly figured out that science is best done, when done together. Research takes a long time, something about it not being the destination but the journey. Well, now that I have arrived at my destination, I can say that the journey was much more enjoyable with my co-authors - and most especially with my co-first-authors, Auriel Sumner-Hempel, Corentine Rochas and Lotte Bouwman. Special thanks to Daniël van Berkel, Xantia van den Brink, Valentin Bordoux and Anouk Langerak for co-piloting the side quests with me.

Marlies Bult, you raised the bar for thesis graphic design. I am quite certain that no thesis has ever looked this good - and received the level of love and attention to lay-out detail as this one, thank you.

Paranymphs, Harm and Jacob, thanks for taking me to the Lampas Symposium, I felt infinitely more prepared for my defense, having been able to practice the art of proper scientific debate.

Mom, my foundation. You gave me those most essential of building blocks for PhD success, perseverance and the ability to structure. Our carriers are more alike than you might think - both discovering a world that had yet to be discovered. Thank you for all those Tuesdays taking care of my kids when I was off doing science. Dad, ♥ you engrained me with a sense of adventure, more times than I can count I have seen us doing fieldwork onboard the Zeewoelf, eating frozen pizzas and watching VHS videos, or fixing the bow thruster. I am sure you did not miss one step of my adventure, thank you for sailing with me. You both shaped me into a person that could not only do a PhD, but enjoying it tremendously - Thank you.

And then, Casper Edze and the Girls - Anne-Noor, my baby, the start of my PhD was also when you started your life. As I begun, I imagined who you would be at 5 years old. And now I know, and you are bigger, better and more full of life then I could have ever imagined. Thank you for reminding me how fast life is going and the joy of laughing unreservedly. Emma, thank you for loving the ocean with me and showing me how my mind works. You are so much like me, don't ever let anyone give you the feeling your brain is anything less then absolutely magnificent. And thank you both for never growing tired of guessing my favorite animal is a ray.

Edze, when all is said and done, you were there at the start of this PhD, you are here during the celebrations at the end, and you will be there for the next chapter in our lives, unconditionally and real and above all full of love - our love truly is one of epic proportions. Thank you.

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The research described in this thesis was financially supported by the Dutch Research Counsil NWO PPS grant ENW PPS-fonds 2019 (*grant number ENPPS.TA.019.005*). As part of the PPS grant, the project received *in-cash* and *in-kind* funding from T.S.O. TenneT, Wind at sea Ecological Program of *Rijkswaterstaat*, Witteveen+Bos and The North Sea foundation.

DOI: 10.18174/681260

Cover design by Marlies Bult
Printed by ProefschiftMaken on recycled paper

This thesis should be cited as:
Hermans, A. (2026) Charged Encounters: effects of electromagnetic fields on sharks and rays. PhD thesis. Wageningen University & Research, Wageningen, the Netherlands. https://doi.org/10.18174/681260

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