Ocean and Coastal Management 266 (2025) 107671

Contents lists available at ScienceDirect

Ocean and Coastal Management

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

Elasmobranchs in offshore wind farms

Annemiek Hermans[a,*], Auriel Sumner-Hempel[a], Xantia van den Brink[a], Daniël van Berkel[a], Renate A. Olie[b], Hendrik V. Winter[c], Albertinka Murk[a], Reindert Nijland[a]

[a] Marine Animal Ecology Group, Wageningen University, P.O. Box 338, 6700 AH, Wageningen, the Netherlands
[b] The North Sea Foundation, Arthur van Schendelstraat 600, 3511 MJ, Utrecht, the Netherlands
[c] Wageningen Marine Research, Wageningen University and Research, P.O. 68, 1970 AB, IJmuiden, the Netherlands

ARTICLE INFO

Keywords:
Habitat use
eDNA
Electromagnetic fields
Subsea power cables
Sharks
Rays

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* 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.

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

---

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

https://doi.org/10.1016/j.ocecoaman.2025.107671
Received 15 December 2024; Received in revised form 10 March 2025; Accepted 2 April 2025

fields (EMF) generated during power transport will influence elasmobranch 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 km^2 (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. Multiuse 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.

2. Materials and methods

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. 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 S1). 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 Eppendorfs 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 the scour protection of monopiles and at locations 50 and 200 m downstream of, or perpendicular 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 S1). Other methods were comparable, although

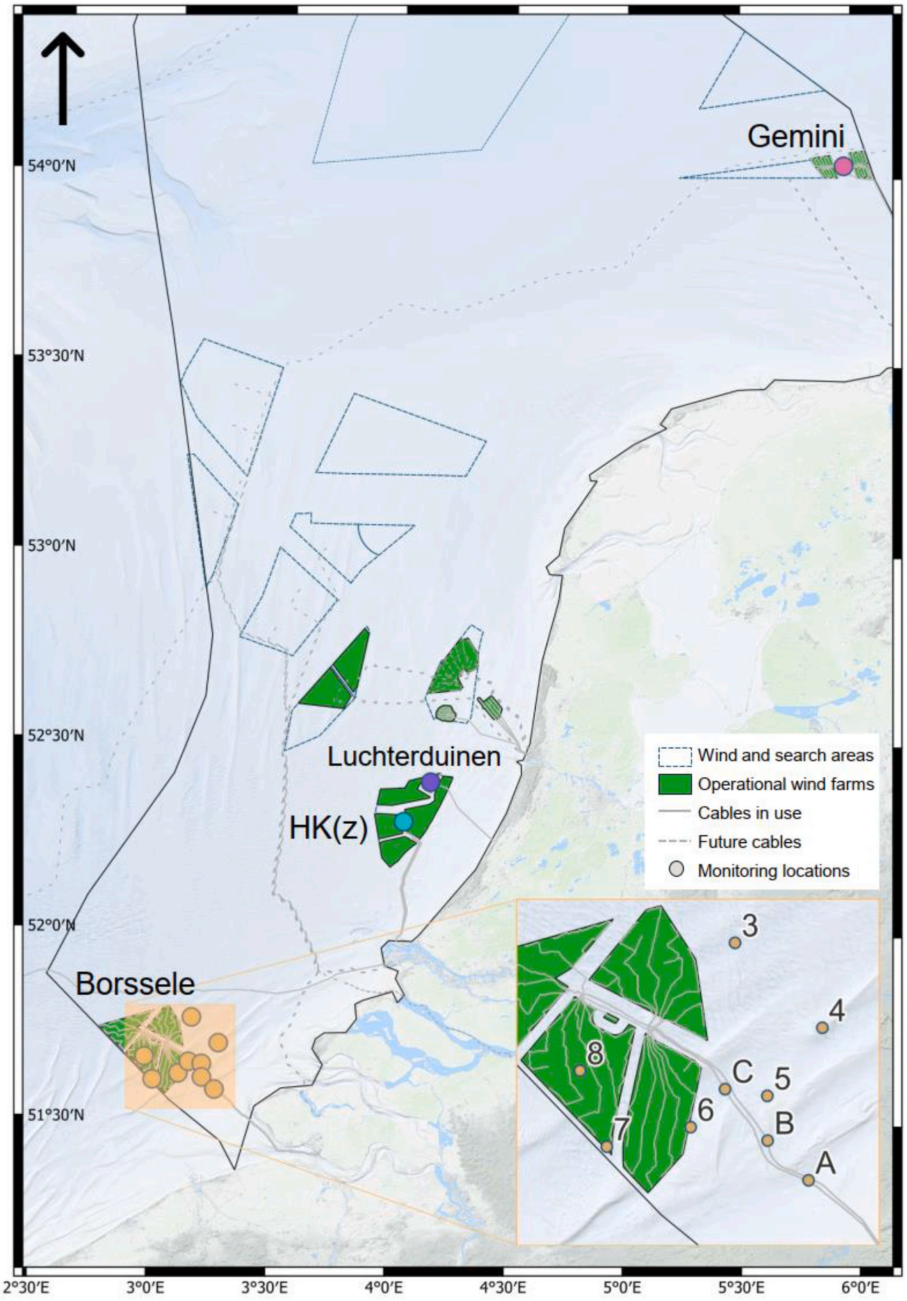

Fig. 1. Overview of the Dutch North Sea where the existing subsea power cables are indicated by the grey lines and future cables are indicated by the dotted lines. The sampling locations in the offshore wind farms (OWF, green areas) are shown with a round dot for Borssele (orange) Hollandse kust Zuid (turquoise), Luchterduinen (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). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

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 where a total of 220 samples were taken within the OWFs, but lacking a regular interval.

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).

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 S2).

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 S2). 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 S2). 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 program 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.

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).

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 biological 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 bioinformatics 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 hemisphere, 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. 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. 2). At OWF Gemini, samples where *R. clavata* was detected were collected predominantly in the autumn (Fig. 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*, 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

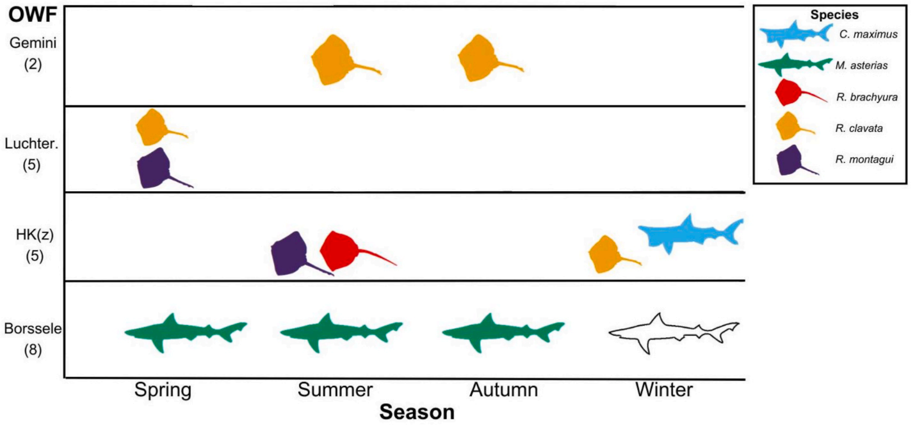

Fig. 2. Presence of elasmobranch species for each offshore wind farm (OWF) (from north to south) across the four seasons. The coloured icons represent species: *Cetorhinus maximus* (light blue), *Mustelus asterias* (green), *Raja brachyura* (red), *Raja montagui* (dark blue*)*, and *Raja clavata* (orange). 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 elasmobranch DNA was found. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

(1.6 %) in OWF Luchterduinen. In OWF Gemini, only *R. clavata* was found (Table 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 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 S1), 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). 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*.

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.

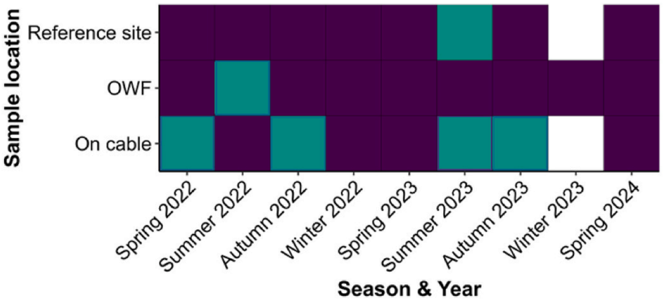

Fig. 3. Seasonal and spatial variation in eDNA detections of *M. asterias* shown as presence (green), absence (purple) or no data (white) at the Borssele offshore wind farm. Note that there were eight sampling campaigns, but due to weather constraints, the winter 2023 campaign stretched into the spring 2024 season. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

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,

Table 1
Detection rates, calculated as % from the overall sampling effort of elasmobranch species for each offshore wind farm (OWF).

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 %)**

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) 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 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). 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.

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 S1). 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 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, however, 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 S1), 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 underwater could visually verify the eDNA sampling location underwater, and mesocosm studies could be designed to understand eDNA behaviour in turbid marine environments.

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.

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.

CRediT authorship contribution statement

Annemiek Hermans: Writing – review & editing, Writing – original draft, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Auriel Sumner-Hempel:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis. **Xantia van den Brink:** Writing – review & editing, Writing – original draft, Methodology, Data curation. **Daniël van Berkel:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Data curation. **Renate A. Olie:** Writing – review & editing, Resources, Methodology, Data curation. **Hendrik V. Winter:** Writing – review & editing, Supervision, Conceptualization. **Albertinka Murk:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Reindert Nijland:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Formal analysis, Conceptualization.

Funding

Funding for this project was provided by the NWO PPS grant ENW PPS-fonds 2019 (*grant number ENPPS.TA.019.005*) named ElasmoPower. The Rich North Sea programme was funded by a Dream Fund of the Dutch National Postcode Lottery, granted in 2019.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Annemiek Hermans (Corresponding author) is employed part-time by engineering firm Witteveen + Bos and in that role is seconded to T.S.O. TenneT. All authors declare that they have no known competing financial interests or personal relationships that would influence the work reported in this paper.

Acknowledgements

We would like to express our gratitude to the Dutch Ministry of Infrastructure and Water Management, specifically the WOZEP (Wind at sea ecological program) and the crew of the *Rijksrederij* for providing vessel time, and the Borssele offshore wind farm. Special thanks are extended to Hans Verdaat, Daan Nieuwendijk, Jack O'Callahan and Britte Schilt for their careful efforts in data collection. We are most obliged to The Rich North Sea programme for the use of the eDNA data that were gathered with the support of Gemini, Eneco and Vattenfall in each of their wind farms. Additionally, we are grateful to the members of the steering group ElasmoPower for their guidance and support throughout this study.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2025.107671.

Data availability

Data will be made available on request.

References

Andersson, M.H., Öhman, M.C., 2010. Fish and sessile assemblages associated with wind-turbine constructions in the Baltic Sea. Mar. Freshw. Res. 61 (6), 642. https://doi.org/10.1071/MF09117.

Atalah, J., Fitch, J., Coughlan, J., Chopelet, J., Coscia, I., Farrell, E., 2013. Diversity of demersal and megafaunal assemblages inhabiting sandbanks of the Irish Sea. Mar. Biodivers. 43 (2), 121–132. https://doi.org/10.1007/s12526-012-0139-y.

Austin, R.A., Hawkes, L.A., Doherty, P.D., Henderson, S.M., Inger, R., Johnson, L., Pikesley, S.K., Solandt, J.-L., Speedie, C., Witt, M.J., 2019. Predicting habitat suitability for basking sharks (Cetorhinus maximus) in UK waters using ensemble ecological niche modelling. J. Sea Res. 153, 101767. https://doi.org/10.1016/j.seares.2019.101767.

Bakker, J., Wangensteen, O.S., Chapman, D.D., Boussarie, G., Buddo, D., Guttridge, T.L., Hertler, H., Mouillot, D., Vigliola, L., Mariani, S., 2017. Environmental DNA reveals tropical shark diversity in contrasting levels of anthropogenic impact. Sci. Rep. 7 (1), 16886. https://doi.org/10.1038/s41598-017-17150-2.

Barnes, M.A., Turner, C.R., Jerde, C.L., Renshaw, M.A., Chadderton, W.L., Lodge, D.M., 2014. Environmental conditions influence eDNA persistence in aquatic systems.

Environmental Science & Technology 48 (3), 1819–1827. https://doi.org/10.1021/es404734p.

Barry, J.P., Kuhnz, L., Buck, K., Lovera, C., Whaling, P.J., 2008. Potential Impacts of the MARS Cable on the Seabed and Benthic Faunal Assemblages. Monterey Bay Aquarium Research Institute.

Bergström, L., Sundqvist, F., Bergström, U., 2013. Effects of an offshore wind farm on temporal and spatial patterns in the demersal fish community. Mar. Ecol. Prog. Ser. 485, 199–210. https://doi.org/10.3354/meps10344.

Blackman, R., Couton, M., Keck, F., Kirschner, D., Carraro, L., Cereghetti, E., Perrelet, K., Bossart, R., Brantschen, J., Zhang, Y., Altermatt, F., 2024. Environmental DNA: the next chapter. Mol. Ecol. 33 (11), e17355. https://doi.org/10.1111/mec.17355.

Bom, R.A., Brader, A., Batsleer, J., Poos, J.-J., Van Der Veer, H.W., Van Leeuwen, A., 2022. A long-term view on recent changes in abundance of common skate complex in the North Sea. Marine Biology 169 (11). https://doi.org/10.1007/s00227-022-04132-w.

Braun, C.D., Skomal, G.B., Thorrold, S.R., 2018. Integrating archival tag data and a high-resolution oceanographic model to estimate basking shark (Cetorhinus maximus) movements in the western atlantic. Front. Mar. Sci. 5, 25. https://doi.org/10.3389/fmars.2018.00025.

Brevé, N.W.P., Winter, H.V., Van Overzee, H.M.J., Farrell, E.D., Walker, P.A., 2016. Seasonal migration of the starry smooth-hound shark *Mustelus asterias* as revealed from tag-recapture data of an angler-led tagging programme. J. Fish. Biol. 89 (2), 1158–1177. https://doi.org/10.1111/jfb.12994.

Brevé, N.W.P., Winter, H.V., Wijmans, P.A.D.M., Greenway, E.S.I., Nagelkerke, L.A.J., 2020. Sex differentiation in seasonal distribution of the starry smooth-hound *Mustelus asterias*. J. Fish. Biol. 97 (6), 1870–1875. https://doi.org/10.1111/jfb.14548.

Collins, R.A., Wangensteen, O.S., O'Gorman, E.J., Mariani, S., Sims, D.W., Genner, M.J., 2018. Persistence of environmental DNA in marine systems. Commun. Biol. 1 (1), 1–11. https://doi.org/10.1038/s42003-018-0192-6.

Copping, A.E., Hemery, L.G., Viehman, H., Seitz, A.C., Staines, G.J., Hasselman, D.J., 2021. Are fish in danger? A review of environmental effects of marine renewable energy on fishes. Biol. Conserv. 262, 109297. https://doi.org/10.1016/j.biocon.2021.109297.

Cornelis, I., De Backer, A., Maes, S., Vanhollebeke, J., Brys, R., Ruttink, T., Hostens, K., Derycke, S., 2024. Environmental DNA for monitoring the impact of offshore wind farms on fish and invertebrate community structures. Environmental DNA 6 (4), e575. https://doi.org/10.1002/edn3.575.

Cotton, P.A., Sims, D.W., Fanshawe, S., Chadwick, M., 2005. The effects of climate variability on zooplankton and basking shark (*Cetorhinus maximus*) relative abundance off southwest Britain. Fish. Oceanogr. 14 (2), 151–155. https://doi.org/10.1111/j.1365-2419.2005.00331.x.

Craeymeersch, J.A., Faasse, M.A., Gheerardyn, H., Troost, K., Nijland, R., Engelberts, A., Perdon, K.J., Van Den Ende, D., Van Zwol, J., 2019. First records of the dwarf surf clam Mulinia lateralis (Say, 1822) in Europe. Marine Biodiversity Records 12 (1), 5. https://doi.org/10.1186/s41200-019-0164-7.

Danovaro, R., Bianchelli, S., Brambilla, P., Brussa, G., Corinaldesi, C., Del Borghi, A., Dell'Anno, A., Fraschetti, S., Greco, S., Grosso, M., Nepote, E., Rigamonti, L., Boero, F., 2024. Making eco-sustainable floating offshore wind farms: siting, mitigations, and compensations. Renew. Sustain. Energy Rev. 197, 114386. https://doi.org/10.1016/j.rser.2024.114386.

De Leeuw, J.J., Van Den Brink, X., Gabrielsen, G.W., Nijland, R., 2024. DNA metabarcoding reveals high diversity of fish and macrofaunal species in diets of little auks and other Arctic seabird species in Svalbard. Polar Biol. 47 (10), 1013–1023. https://doi.org/10.1007/s00300-024-03276-3.

Degraer, S., Carey, D., Coolen, J., Hutchison, Z., Kerckhof, F., Rumes, B., Vanaverbeke, J., 2020. Offshore wind farm artificial reefs affect ecosystem structure and functioning: a synthesis. Oceanography (Wash. D. C.) 33 (4), 48–57. https://doi.org/10.5670/oceanog.2020.405.

Directorate-General for Energy, EU commission, 2024. Offshore Renewable Energy. European Commission. https://energy.ec.europa.eu/topics/renewable-energy/offshore-renewable-energy_en.

Dolton, H., Jackson, A., Deaville, R., Hall, J., Hall, G., McManus, G., Perkins, M., Rolfe, R., Snelling, E., Houghton, J., Sims, D., Payne, N., 2023. Regionally endothermic traits in planktivorous basking sharks Cetorhinus maximus. Endanger. Species Res. 51, 227–232. https://doi.org/10.3354/esr01257.

Doorenspleet, K., Jansen, L., Oosterbroek, S., Kamermans, P., Bos, O., Wurz, E., Murk, A., Nijland, R., 2024. The long and the short of it: Nanopore based eDNA metabarcoding of marine vertebrates works; sensitivity and specificity depend on amplicon lengths. https://doi.org/10.1101/2021.11.26.470087.

Dukan, N., Cornelis, I., Maes, S., Hostens, K., De Backer, A., Derycke, S., 2024. Vertical and horizontal environmental DNA (eDNA) patterns of fish in a shallow and well-mixed North Sea area. Sci. Rep. 14 (1), 16748. https://doi.org/10.1038/s41598-024-66912-2.

Dulvy, N.K., Pacoureau, N., Rigby, C.L., Pollom, R.A., Jabado, R.W., Ebert, D.A., Finucci, B., Pollock, C.M., Cheok, J., Derrick, D.H., Herman, K.B., Sherman, C.S., VanderWright, W.J., Lawson, J.M., Walls, R.H.L., Carlson, J.K., Charvet, P., Bineesh, K.K., Fernando, D., Simpfendorfer, C.A., 2021. Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. Curr. Biol. 31 (21), 4773–4787. https://doi.org/10.1016/j.cub.2021.08.062 e8.

EMK Foundation, 2020. Major concerns offshore renewable energy. https://visserij.nl/wp-content/uploads/2020/10/Fisheries-protest-letter.pdf.

European Court of Auditors, 2023. Offshore renewable energy: EU auditors highlight green dilemma. Curia Rationum. https://www.eca.europa.eu/en/news/news-sr-2023-22.

European Parliament, 1992. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. https://eur-lex.europa.eu/eli/dir/1992/43/oj.

European Parliament, 2008. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive). https://eur-lex.europa.eu/eli/dir/2008/56/oj.

European Parliament, 2020. COM/2020/380 Communication from the Commission to the European Parliament, the Council, the European Economic and Social Committee and the Committee of the Regions EU; Biodiversity Strategy for 2030 Bringing nature back into our lives. https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=celex:52020DC0380.

Gallagher, A.J., Kyne, P.M., Hammerschlag, N., 2012. Ecological risk assessment and its application to elasmobranch conservation and management. J. Fish. Biol. 80 (5), 1727–1748. https://doi.org/10.1111/j.1095-8649.2012.03235.x.

Gill, A.B., 2009. EMF-Sensitive Fish Response to EM Emissions from Sub-sea, Electricity Cables of the Type Used by the Offshore Renewable Energy Industry. COWRIE.

Giroux, M.S., Reichman, J.R., Langknecht, T., Burgess, R.M., Ho, K.T., 2022. Environmental RNA as a tool for marine community biodiversity assessments. Sci. Rep. 12 (1), 17782. https://doi.org/10.1038/s41598-022-22198-w.

Griffin, R.A., Robinson, G.J., West, A., Gloyne-Phillips, I.T., Unsworth, R.K.F., 2016. Assessing fish and motile fauna around offshore windfarms using stereo baited video. PLoS One 11 (3), e0149701. https://doi.org/10.1371/journal.pone.0149701.

Hasselman, D.J., Hemery, L.G., Copping, A.E., Fulton, E.A., Fox, J., Gill, A.B., Polagye, B., 2023. 'Scaling up' our understanding of environmental effects of marine renewable energy development from single devices to large-scale commercial arrays. Sci. Total Environ. 904, 166801. https://doi.org/10.1016/j.scitotenv.2023.166801.

Heessen, H.J.L., Daan, N., Ellis, J.R., 2015. Fish Atlas of the Celtic Sea, North Sea and Baltic Sea: Based on International Research-Vessel Surveys. Wageningen Academic Publishers.

Heithaus, M.R., Frid, A., Wirsing, A.J., Worm, B., 2008. Predicting ecological consequences of marine top predator declines. Trends Ecol. Evol. 23 (4), 202–210. https://doi.org/10.1016/j.tree.2008.01.003.

Hendon, R., Serafy, J., Walter, J., Lipsky, A., Curtis, T., Di Natale, A., Rouyer Tristan Hanke, A., Alvarez-Berastegui, D., Orbesen, E., Lauretta, M., Stelzenmüller, V., 2024. Offshore wind energy development and highly migratory species: ecological, fishery and management implications. ICCAT Recueil de Documents Scientifiques/Collective Volume of Scientific Paper. 81 (4), 1–21.

Hermans, A., Schilt, B., 2022. Current State of Knowledge Electromagnetic Fields Electromagnetic Fields and the Marine Strategy Framework Directive Descriptor 11—Energy. Witteveen+Bos, p. 53, 129373/22-013.411.

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.

Hestetun, J.T., Ray, J.L., Murvoll, K.M., Kjølhamar, A., Dahlgren, T.G., 2023. Environmental DNA reveals spatial patterns of fish and plankton diversity at a floating offshore wind farm. Environmental DNA 5 (6), 1289–1306. https://doi.org/10.1002/edn3.450.

Holman, L.E., Chng, Y., Rius, M., 2022. How does eDNA decay affect metabarcoding experiments? Environmental DNA 4 (1), 108–116. https://doi.org/10.1002/edn3.201.

Hunter, E., Buckley, A.A., Stewart, C., Metcalfe, J.D., 2005. Migratory behaviour of the thornback ray, *raja clavata* , in the southern north sea. J. Mar. Biol. Assoc. U. K. 85 (5), 1095–1105. https://doi.org/10.1017/S0025315405012142.

Hutchison, Z.L., Gill, A.B., Sigray, P., He, H., King, J.W., 2020. Anthropogenic electromagnetic fields (EMF) influence the behaviour of bottom-dwelling marine species. Sci. Rep. 10 (1), 4219. https://doi.org/10.1038/s41598-020-60793-x.

Klymus, K.E., Merkes, C.M., Allison, M.J., Goldberg, C.S., Helbing, C.C., Hunter, M.E., Jackson, C.A., Lance, R.F., Mangan, A.M., Monroe, E.M., Piaggio, A.J., Stokdyk, J.P., Wilson, C.C., Richter, C.A., 2020. Reporting the limits of detection and quantification for environmental DNA assays. Environmental DNA 2 (3), 271–282. https://doi.org/10.1002/edn3.29.

Kraft, S., Winkler, A.C., Abecasis, D., 2024. Seasonal movement dynamics of the commercially important thornback ray (Raja clavata) in a coastal marine protected area. Ocean Coast Manag. 254, 107210. https://doi.org/10.1016/j.ocecoaman.2024.107210.

Labourgade, P., Couturier, L.I.E., Bourjea, J., Woillez, M., Feunteun, E., Reubens, J.T., Trancart, T., 2024. Acoustic telemetry suggests the lesser spotted dogfish Scyliorhinus canicula stays and uses habitats within a French offshore wind farm. Mar. Environ. Res. 202, 106802. https://doi.org/10.1016/j.marenvres.2024.106802.

Langhamer, O., 2012. Artificial reef effect in relation to offshore renewable energy conversion: state of the art. Sci. World J. 1–8. https://doi.org/10.1100/2012/386713, 2012.

Leurs, G., Verkuil, Y.I., Hijner, N., Saalmann, F., Dos Santos, L., Regalla, A., Ledo Pontes, S., Yang, L., Naylor, G.J.P., Olff, H., Govers, L.L., 2023. Addressing data-deficiency of threatened sharks and rays in a highly dynamic coastal ecosystem using environmental DNA. Ecol. Indic. 154, 110795. https://doi.org/10.1016/j.ecolind.2023.110795.

Li, S., Jay, S., 2020. Transboundary marine spatial planning across Europe: trends and priorities in nearly two decades of project work. Mar. Pol. 118, 104012. https://doi.org/10.1016/j.marpol.2020.104012.

Liu, Z., Collins, R.A., Baillie, C., Rainbird, S., Brittain, R., Griffiths, A.M., Sims, D.W., Mariani, S., Genner, M.J., 2022. Environmental DNA captures elasmobranch diversity in a temperate marine ecosystem. Environmental DNA 4 (5), 1024–1038. https://doi.org/10.1002/edn3.294.

Marshall, N.T., Vanderploeg, H.A., Chaganti, S.R., 2021. Environmental (e)RNA advances the reliability of eDNA by predicting its age. Sci. Rep. 11 (1), 2769. https://doi.org/10.1038/s41598-021-82205-4.

Methratta, E.T., 2021. Distance-based sampling methods for assessing the ecological effects of offshore wind farms: synthesis and application to fisheries resource studies. Front. Mar. Sci. 8, 674594. https://doi.org/10.3389/fmars.2021.674594.

Miya, M., 2022. Environmental dna metabarcoding: a novel method for biodiversity monitoring of marine fish communities. Ann. Rev. Mar. Sci 14 (1), 161–185. https://doi.org/10.1146/annurev-marine-041421-082251.

Miya, M., Sato, Y., Fukunaga, T., Sado, T., Poulsen, J.Y., Sato, K., Minamoto, T., Yamamoto, S., Yamanaka, H., Araki, H., Kondoh, M., Iwasaki, W., 2015. MiFish, a set of universal PCR primers for metabarcoding environmental DNA from fishes: detection of more than 230 subtropical marine species. R. Soc. Open Sci. 2 (7), 150088. https://doi.org/10.1098/rsos.150088.

Nature Restoration Law, 2024. COM(2022)0304 – C9-0208/2022 – 2022/0195(COD). https://www.europarl.europa.eu/doceo/document/TA-9-2024-0089_EN.html#title1.

Observation.org, 2024. Stichting observation international and local partners. https://observation.org/.

OSPAR, 2008. *Background Document on potential problems associated with power cables other than those for oil and gas activities* (370/2008). https://www.ospar.org/documents?v=7128.

Pacoureau, N., Rigby, C.L., Kyne, P.M., Sherley, R.B., Winker, H., Carlson, J.K., Fordham, S.V., Barreto, R., Fernando, D., Francis, M.P., Jabado, R.W., Herman, K.B., Liu, K.-M., Marshall, A.D., Pollom, R.A., Romanov, E.V., Simpfendorfer, C.A., Yin, J. S., Kindsvater, H.K., Dulvy, N.K., 2021. Half a century of global decline in oceanic sharks and rays. Nature 589 (7843), 567–571. https://doi.org/10.1038/s41586-020-03173-9.

Papadopoulo, K., Villegas-Ríos, D., Mucientes, G., Hillinger, A., Alonso-Fernández, A., 2023. Drivers of behaviour and spatial ecology of the small spotted catshark. Aquat. Conserv. Mar. Freshw. Ecosyst. 33 (5), 443–457. https://doi.org/10.1002/aqc.3943.

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

Püts, M., Kempf, A., Möllmann, C., Taylor, M., 2023. Trade-offs between fisheries, offshore wind farms and marine protected areas in the southern North Sea – winners, losers and effective spatial management. Mar. Pol. 152, 105574. https://doi.org/10.1016/j.marpol.2023.105574.

Rodriguez-Ezpeleta, N., Morissette, O., Bean, C.W., Manu, S., Banerjee, P., Lacoursière-Roussel, A., Beng, K.C., Alter, S.E., Roger, F., Holman, L.E., Stewart, K.A., Monaghan, M.T., Mauvisseau, Q., Mirimin, L., Wangensteen, O.S., Antognazza, C.M., Helyar, S.J., de Boer, H., Monchamp, M.-E., et al., 2021. Trade-offs between reducing complex terminology and producing accurate interpretations from environmental DNA: comment on “Environmental DNA: what’s behind the term?”. In: Pawlowski, et al. (Eds.), Molecular Ecology, vol. 30, pp. 4601–4605. https://doi.org/10.1111/mec.15942, 19.

Saglam, H., Ak, O., 2012. Reproductive biology of Raja clavata (elasmobranchii: rajidae) from southern black sea coast around Turkey. Helgol. Mar. Res. 66 (2), 117–126. https://doi.org/10.1007/s10152-011-0252-5.

Sguotti, C., Lynam, C.P., García-Carreras, B., Ellis, J.R., Engelhard, G.H., 2016. Distribution of skates and sharks in the North Sea: 112 years of change. Glob. Change Biol. 22 (8), 2729–2743. https://doi.org/10.1111/gcb.13316.

Skomal, G.B., Wood, G., Caloyianis, N., 2004. Archival tagging of a basking shark, *Cetorhinus maximus* , in the western North Atlantic. J. Mar. Biol. Assoc. U. K. 84 (4), 795–799. https://doi.org/10.1017/S0025315404009968h.

Staeudle, T.M., Parmentier, B., Poos, J.J., 2024. Accounting for spatio-temporal distribution changes in size-structured abundance estimates for a data-limited stock of *Raja clavata*. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. https://doi.org/10.1093/icesjms/fsae106 fsae106.

Stelzenmüller, V., Letschert, J., Gimpel, A., Kraan, C., Probst, W.N., Degraer, S., Döring, R., 2022. From plate to plug: the impact of offshore renewables on European fisheries and the role of marine spatial planning. Renew. Sustain. Energy Rev. 158, 112108. https://doi.org/10.1016/j.rser.2022.112108.

Stenberg, C., Støttrup, J., Van Deurs, M., Berg, C., Dinesen, G., Mosegaard, H., Grome, T., Leonhard, S., 2015. Long-term effects of an offshore wind farm in the North Sea on fish communities. Mar. Ecol. Prog. Ser. 528, 257–265. https://doi.org/10.3354/meps11261.

Taormina, B., Bald, J., Want, A., Thouzeau, G., Lejart, M., Desroy, N., Carlier, A., 2018. A review of potential impacts of submarine power cables on the marine environment: knowledge gaps, recommendations and future directions. Renew. Sustain. Energy Rev. 96, 380–391. https://doi.org/10.1016/j.rser.2018.07.026.

Thatcher, H., Stamp, T., Wilcockson, D., Moore, P.J., 2023. Residency and habitat use of European lobster (*Homarus gammarus*) within an offshore wind farm. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 80 (5), 1410–1421. https://doi.org/10.1093/icesjms/fsad067.

The North Sea Foundation, 2022. The Potential Ecological Effects of Electromagnetic Fields Posed by Offshore Wind Farms, p. 9. https://s3-eu-west-1.amazonaws.com/noordzee/app/uploads/2022/02/16230457/Electromagnetic-fields-DEF.pdf.

Unsworth, R.K.F., Peters, J.R., McCloskey, R.M., Hinder, S.L., 2014. Optimising stereo baited underwater video for sampling fish and invertebrates in temperate coastal habitats. Estuar. Coast Shelf Sci. 150, 281–287. https://doi.org/10.1016/j.ecss.2014.03.020.

Van Hal, R., Griffioen, A.B., Van Keeken, O.A., 2017. Changes in fish communities on a small spatial scale, an effect of increased habitat complexity by an offshore wind farm. Mar. Environ. Res. 126, 26–36. https://doi.org/10.1016/j.marenvres.2017.01.009.

Vandendriessche, S., Derweduwen, J., Hostens, K., 2015. Equivocal effects of offshore wind farms in Belgium on soft substrate epibenthos and fish assemblages. Hydrobiologia 756 (1), 19–35. https://doi.org/10.1007/s10750-014-1997-z.

Werner, K.M., Haslob, H., Reichel, A.F., Gimpel, A., Stelzenmüller, V., 2024. Offshore wind farm foundations as artificial reefs: the devil is in the detail. Fish. Res. 272, 106937. https://doi.org/10.1016/j.fishres.2024.106937.

Wilhelmsson, D., Malm, T., Öhman, M.C., 2006. The influence of offshore windpower on demersal fish. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 63 (5), 775–784. https://doi.org/10.1016/j.icesjms.2006.02.001.

Wind Europe, 2024. Wind energy in Europe. In: 2023 Statistics and the Outlook for 2024-2030 (P. 56). https://windeurope.org/intelligence-platform/product/wind-energy-in-europe-2023-statistics-and-the-outlook-for-2024-2030/.

Witt, M., Hardy, T., Johnson, L., McClellan, C., Pikesley, S., Ranger, S., Richardson, P., Solandt, J., Speedie, C., Williams, R., Godley, B., 2012. Basking sharks in the northeast Atlantic: spatio-temporal trends from sightings in UK waters. Mar. Ecol. Prog. Ser. 459, 121–134. https://doi.org/10.3354/meps09737.

Wright, S.R., Lynam, C.P., Righton, D.A., Metcalfe, J., Hunter, E., Riley, A., Garcia, L., Posen, P., Hyder, K., 2020. Structure in a sea of sand: fish abundance in relation to man-made structures in the North Sea. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 77 (3), 1206–1218. https://doi.org/10.1093/icesjms/fsy142.

Yates, M.C., Derry, A.M., Cristescu, M.E., 2021. Environmental RNA: a revolution in ecological resolution? Trends Ecol. Evol. 36 (7), 601–609. https://doi.org/10.1016/j.tree.2021.03.001.

Zupan, M., Coolen, J., Mavraki, N., Degraer, S., Moens, T., Kerckhof, F., Lopez Lopez, L., Vanaverbeke, J., 2024. Life on every stone: characterizing benthic communities from scour protection layers of offshore wind farms in the southern North Sea. J. Sea Res. 201, 102522. https://doi.org/10.1016/j.seares.2024.102522.

European Union, 2014. Directive 2014/52/EU of the European Parliament and of the Council of 16 April 2014 amending Directive 2011/92/EU on the assessment of the effects of certain public and private projects on the environment. https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=celex%3A32014L0052.