Aquatic Conservation: Marine and Freshwater Ecosystems

WILEY

ARTICLE

Floating Offshore Wind Farms Attract Japanese Horse Mackerel

Shimpei Tsuchida[1] | Riko Kato[1] | Shoko Nishitsuji[1] | Sayano Anzai[1] | Siti Syazwani Azmi[1] | Shogo Tanaka[1] | Satoshi Masumi[2] | Jun Uchida[2] | Takashi Aoshima[2] | Katsuya Hirasaka[1] | Shingo Fujimoto[3] | Kenichi Shimizu[1] | Miyuki Hirose[1] | Mitsuharu Yagi[1]

[1]Graduate School of Integrated Science and Technology, Nagasaki University, Nagasaki, Japan | [2]Training Ship Kakuyo-maru, Faculty of Fisheries, Nagasaki University, Nagasaki, Japan | [3]Integrated Technology Center, University of the Ryukyus, Okinawa, Japan

Correspondence: Mitsuharu Yagi (yagi-m@nagasaki-u.ac.jp)

Received: 18 March 2025 | **Revised:** 3 June 2025 | **Accepted:** 7 July 2025

Funding: This work was supported by Nissei Life Foundation 2024-23.

Keywords: East China Sea | ecological risk | environmental DNA | offshore wind farms | *T. japonicus*

ABSTRACT

Floating offshore wind farms (F-OWFs) are becoming key components of renewable energy production, yet their ecological impacts on marine ecosystems remain largely unexplored. Using environmental DNA (eDNA) analysis in the East China Sea, this study investigated the tendency of Japanese horse mackerel (*Trachurus japonicus*) to congregate beneath F-OWFs. Water samples were collected at stations near an F-OWF and control stations farther away at various depths and seasons. A total of 115 samples were analysed, and eDNA of *T. japonicus* was detected in 83% of all samples. eDNA concentrations were significantly higher near an F-OWF (F-OWF stations) than at control stations. The highest recorded eDNA concentration reached 2280 copies/L at an F-OWF station, whereas the maximum concentration at control stations was 783 copies/L. Seasonal variations were also observed, with lower concentrations in summer and higher concentrations from autumn to spring. A generalized linear model (GLM) analysis further revealed that wind turbines had a significant influence on eDNA concentration, whereas other environmental variables, such as water temperature and depth, were not significant. These findings suggest that F-OWFs may function as artificial reefs, providing habitat for *T. japonicus* and influencing fish distributions at both spatial and temporal scales. However, potential conflicts with fisheries due to spatial restrictions, displacement of fishery resources and increased navigation costs necessitate further long-term ecological and socio-economic assessments. Integration of eDNA monitoring with traditional survey methods, such as acoustic surveys and ROV observations, is crucial for coexistence of adaptive offshore wind farm management and sustainable fisheries. Future research should also explore long-term effects of F-OWFs on fish assemblages and biodiversity to support evidence-based decision-making for offshore energy development.

1 | Introduction

Construction of wind power facilities as hubs for clean energy generation has rapidly expanded worldwide. In recent years, many countries have begun exploiting renewable energy sources to reduce greenhouse gas emissions (Graabak and Korpås 2016), and commercial-scale wind power installations have increased significantly globally. According to the Global Wind Energy Council (GWEC), an additional 1021 gigawatts (GW) of wind power capacity were installed in 2023, representing a 13% increase over the previous year (Williams and Zhao 2024). There are two main types of wind power generation: offshore wind farms (OWFs) and land-based wind farms (LWFs). OWFs offer several advantages over LWFs. Specifically, wind speeds are generally higher and more consistent over the ocean compared to onshore locations, leading to greater potential power

generation (Leung and Yang 2012; Msigwa et al. 2022). Large-scale deployment of OWFs contributes to a stable power supply (Kazama 2012). In 2023, OWFs experienced a global capacity increase of 10.9 GW, 24% over the previous year (Williams and Zhao 2024). This trend is expected to accelerate in coming years (Díaz and Guedes Soares 2020). In Japan, deployment of wind power facilities is steadily progressing. In 2024, 170 turbines with a combined capacity of 703.3 MW were installed, representing a 12.8% increase compared to the end of 2023 (JWPA 2024). As for OWFs, the current installed capacity is 253.4 MW (JWPA 2024). However, the Japanese government has set an ambitious target to expand offshore wind capacity to 30–40 GW by 2040 (Government of Japan 2020).

Nonetheless, ecological risks associated with OWFs have not been adequately assessed. It is well known that noise emissions and electromagnetic fields generated during transportation, construction and operation of OWFs can impact marine environments (Kazama 2012). Currently, bottom-fixed offshore wind farms (B-OWFs) are the predominant type, with monopile structures being the most commonly used. This design involves driving a large steel tube (pile) vertically into the seabed, upon which a wind turbine is mounted (Chen and Kim 2022). Due to the piling process, monopile structures have significant environmental and biological impacts. Indeed, construction activities can induce behavioural changes in marine organisms (Thomsen et al. 2006), and extremely high noise emission levels have been reported during installation (Norro et al. 2013). However, some studies suggest that post-construction OWFs may have positive effects on marine life. Offshore structures attract fish, potentially functioning as artificial reefs (Amponsah et al. 2014; Wilson 2007). Additionally, under the United Nations Convention on the Law of the Sea (UNCLOS), except for construction and maintenance purposes, vessels are prohibited from approaching within 500 m of OWFs (Bonsu et al. 2024; United Nations 1982; Reckhaus 2022). As a result, waters adjacent to OWFs effectively function as no-fishing zones, offering protection for marine organisms (Hammar et al. 2016) and potentially benefiting commercial fish species (Bailey et al. 2014). In fact, it has been reported that populations of the harbour porpoise (*Phocoena phocoena*), which declined during OWF construction, recovered to pre-construction levels after completion (Vallejo et al. 2017). Furthermore, post-construction surveys indicate a significant increase in fish abundance (Bergström et al. 2013) Despite these findings, most research to date has focused on B-OWFs, whereas ecological risk assessments of floating offshore wind farms (F-OWFs) remain scarce due to their relatively recent commercial deployment (Farr et al. 2021; Rezaei et al. 2023). Unlike monopile-based designs, F-OWFs employ hybrid spar-type structures, characterized by an elongated cylindrical floating foundation composed of a concrete lower section and a steel upper section, anchored to the seabed using three mooring chains (Sato and Matsunobu 2021). This design allows for deployment in deeper waters, significantly expanding potential installation areas. Given the anticipated large-scale deployment of F-OWFs in offshore regions, understanding their impact on marine ecosystems is an urgent priority.

In this study, using environmental DNA (eDNA) technology, we investigated whether F-OWFs affect the distributions of Japanese horse mackerel (*T. japonicus*). Our study site was located off the coast of the Goto Islands, Nagasaki, Japan, where Japan's only F-OWF is located (Figure 1). Due to consistently strong winds and rough seas in this area, it is challenging to keep a research vessel stationed there for extended periods. Therefore, instead of conventional direct capture or visual surveys, we employed eDNA technology (Jerde et al. 2011), which provides a safer and more efficient method of data collection. Advances in quantification techniques and statistical modelling have enabled eDNA analysis to detect target species and to estimate their relative abundance (Fukaya et al. 2022; Hinz et al. 2022). The probability of species detection and eDNA concentration increase with higher species density (Hering et al. 2018; Yamaguchi et al. 2018). We assumed that if F-OWFs serve as fish aggregation sites, the concentration of *T. japonicus* eDNA should be higher in areas near the F-OWF than in surrounding locations. *T. japonicus* is a commercially valuable species (Igeta et al. 2023). Increasing numbers of F-OWF installations may reduce fishing grounds, potentially causing economic losses to regional fisheries (Methratta et al. 2020). Our findings contribute to understanding the impact of human activities on marine ecosystems and provide critical insights for balancing sustainable energy development with fisheries resource management.

2 | Methods

2.1 | Experimental Design and Water Sampling

To evaluate the aggregation effect of F-OWFs on *T. japonicus* populations, we designed a field survey that incorporated both F-OWF and control sites. F-OWF sites included four stations (E1, E2, E3 and E4) near F-OWFs, approximately 5 km offshore from Fukue Island, Nagasaki, Japan. Control sites included four stations (E5, E6, E7 and E8), 4 nautical miles (7.4 km) south of the F-OWFs

FIGURE 1 | Floating offshore wind power facility (F-OWFs) at the site of this study near the Goto Islands, Kyushu, Japan.

(Figure 2). The F-OWFs in this region consist of one initial turbine, Haenkaze (FH), which was installed in 2015, followed by three additional turbines (F1, F2 and F3) in 2022 (Figure 2). Each turbine has a rotor diameter of 80 m, a total height of 172 m (76 m below the surface and a hub height of 56 m), having a generation capacity of 2100 kW. Latitude, longitude and depth of each station and F-OWFs are provided in Supplementary Table S1.

Water sampling was conducted during a research cruise of the *Kakuyo-maru* (155 tons), the training vessel of the Faculty of Fisheries, Nagasaki University, in April, June, August, October and December 2023. At each station, water was collected from three depths: the surface layer (5 m), the middle layer (50 m) and the bottom layer (80–160 m). Sampling was performed using a CTD profiler (SBE-911 plus, Sea-Bird Electronics, Bellevue, WA, USA) installed on the training vessel, with a Niskin bottle to collect 3 L of sample water (Yamamoto et al. 2016). The Niskin bottle and sampling hose were bleached with a chlorine-based detergent before sampling at each station to prevent contamination. Powder-free nitrile gloves were worn during handling. Using a CTD profiler for sampling significantly reduced the risk of contamination, which is a major challenge in eDNA analysis, while allowing precise water collection at designated depths. Seawater temperature was also measured at each sampling station as an oceanographic parameter. As a field blank, 3 L of artificial seawater (Marine Salt, Kaisuimaren Co. Ltd, Toyama, Japan) was collected using the same method with a Niskin bottle. To inhibit DNA degradation, 3 mL of 10% benzalkonium chloride solution (final concentration: 0.01%) was immediately added to each sample after collection and samples were stored in a cool, dark place (Minamoto et al. 2021). In April 2023, surface water samples at stations E1 and E4 could not be collected due to a malfunction of the CTD observation system. Additionally, in October, surface, middle, and bottom layer samples at station E5 were not obtained due to deteriorating sea conditions. As a result, the total number of samples collected was 115.

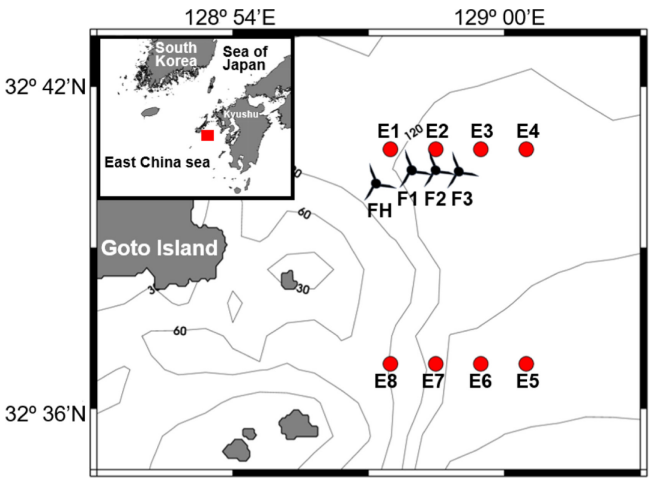

FIGURE 2 | Bathymetric map showing geographic locations of sampling stations (circles: E1 ~ E8) in the East China Sea. E1 ~ E4 is 'F-OWF' and E5 ~ E8 are 'Control' stations. Floating offshore wind power facilities (F-OWFs: FH ~ F3) are also shown. The latitude, longitude, and depth of each station and F-OWFs are provided in Supplementary Table S1.

Within 48 h after collection, water samples were vacuum-filtered using an aspirator (GAS-1N, AS ONE, Osaka, Japan) at the Fish and Ships Lab, Faculty of Fisheries, Nagasaki University. Each 3-L water sample was filtered through a single membrane, with each filtration taking approximately 45 min. To prevent contamination during filtration, the filtration unit was covered with aluminum foil, and each device was decontaminated with 0.1% sodium hypochlorite after processing each sample (Minamoto et al. 2021). Filtration was performed using 47-mm (diameter) glass fiber filters (Whatman GF/F No. 1825-047, retention particle size: 0.07 μm). Filters were wrapped in aluminium foil and stored at −20°C until eDNA extraction.

2.2 | DNA Extraction and qPCR Analysis

eDNA was extracted using a DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) following a modified spin-column method based on the protocols of Ono et al. (2023, 2024) and Yamamoto et al. (2016). Blank samples were processed using the same extraction method. eDNA of *T. japonicus* was quantified using qPCR with the TaqMan probe method. Primers and probes followed Yamamoto et al. (2016) (forward primer: 5′-CAG ATA TCG CAA CCG CCT TT-3′, reverse primer: 5′-CCG ATG TGA AGG TAA ATG CAA A-3′, and probe: 5′-FAM-TAT GCA CGC CAA CGG CGC CT-TAMRA-3′). These primers specifically amplify a 127-bp fragment of the mitochondrial *cytB* gene of *T. japonicus*. The qPCR reaction mixture (total volume: 20 μL) consisted of 900 nM forward and reverse primers, 125 nM TaqMan probe, 2 × Environmental Master Mix (Thermo Fisher Scientific, Waltham, MA, USA), AmpErase Uracil–Glycosylase (Thermo Fisher Scientific, Waltham, MA, USA) and 2 μL of sample DNA. qPCR was performed using a QuantStudio 3 Real-Time PCR System (Thermo Fisher Scientific, Waltham, MA, USA) under the following thermal cycling conditions: 50°C for 120 s, 95°C for 600 s, 55 cycles of 95°C for 15 s and 60°C for 60 s. To ensure quantitative accuracy, a standard curve was generated using a serial dilution of synthetic DNA fragments (1×10^1, 1×10^2, 1×10^3, 1×10^5, 1×10^7 and 1×10^9 copies). The sequence of the synthetic DNA fragment used was: 5′-CCT AGC TAT ACA CTA CAC CTC AGA TAT CGC AAC CGC CTT TAC ATC CGT AGC ACA CAT CTG CCG GGA CGT AAA CTA CGG CTG ACT TAT TCG CAA TAT GCA CGC CAA CGG CGC CTC CTT CTT TTT CAT TTG CAT TTA CCT TCA CAT CGG CCG AGG CCT TTA CTA CGG CT -3′. Each sample was analysed in triplicate during each qPCR run. As a negative control, artificial seawater (2 μL) was analysed via qPCR. Standard curves for all qPCR runs exhibited R^2 values of 0.998–0.999, slopes of −3.67 to −3.56 and intercepts of 40.20–41.42. Based on these standard curves and Ct values of each sample, the mean copy number of the *cytB* gene fragment was calculated from three replicates per sample. The limit of detection (LOD) for quantitative PCR (qPCR) was determined using synthetic DNA. A concentration series (1, 2, 3, 4, 5, 6, 7, 8, 9, 10^1, 10^2, 10^3, 10^5, 10^7 and 10^9 copies/L) was prepared, and each concentration was tested in triplicate. A sample was considered positive if at least one of the three replicates yielded a detectable signal. Based on this criterion, the LOD was determined to be 1 copy/L. Although 2 μL of sample DNA was used for each qPCR reaction, the DNA concentration may vary among samples. To address this, a standard curve was

generated for each run, and target DNA concentrations were calculated based on Ct values using the curve. Therefore, variation in template concentration does not affect the accuracy of quantification. No eDNA was detected in any of the negative controls from either field or laboratory experiments.

2.3 | Data Analysis

Data normality and homogeneity of variance were assessed using the Shapiro–Wilk and Bartlett's tests, respectively. Given that data were not normally distributed, nonparametric tests were applied for statistical analysis. To compare mean eDNA concentrations between F-OWF and control stations, pooled from all sampling periods and layers, the Mann–Whitney U test was employed. Additionally, two-way, nonparametric ANOVA (Scheirer–Ray–Hare test) was conducted to examine effects of station (F-OWF vs. control), water layer (surface, middle and bottom) and their interaction on eDNA concentrations. Furthermore, to analyse differences in monthly mean eDNA concentrations between F-OWF and control stations, a pairwise Wilcoxon rank-sum test with Bonferroni correction was performed following the Scheirer–Ray–Hare test to account for multiple comparisons.

To examine the effects of environmental factors on eDNA concentration, a generalized linear model (GLM) analysis was employed. The response variable was the log-transformed eDNA concentration (log eDNA copies/L) (Sanchez et al. 2022; Maruyama et al. 2018). Explanatory variables included F-OWF presence or absence, water layer (m) and water temperature (°C) as environmental factors. F-OWF was coded as 1 and control as 0. The identity function was used as the link function, and a Gaussian distribution was applied. Variance inflation factor (VIF) values indicated no multicollinearity among explanatory variables, as none exceeded 5 (F-OWF: 1.00, water layer: 1.76, water temperature: 1.75). The significance level was set at 0.05. All statistical analyses were conducted using R version 4.4.2.

3 | Results

T. japonicus eDNA was detected in 95 of 115 samples (83%). At F-OWF stations, 52 of 58 samples (90%) tested positive for eDNA, whereas at control stations, 43 of 57 samples (75%) tested positive (Supplementary Table S2). eDNA concentrations ranged from 8 to 2280 copies/L at F-OWF stations and from 5 to 783 copies/L at control stations. When all monthly and water layer samples were pooled, the mean eDNA concentration was 322.6 copies/L ± 408.0 (standard deviation, S.D.) at F-OWF stations and 157.2 copies/L ± 174.6 (S.D.) at control stations, with a significantly higher concentration at F-OWF stations ($U = 396$, $n = 115$, $p = 0.01$), suggesting a potential attraction of F-OWFs for *T. japonicus* (Figure 3).

Two-way nonparametric ANOVA was conducted to examine the effects of sampling station (F-OWF or control) and water layers (surface, middle, bottom) on eDNA concentration. This analysis revealed that sampling stations had a significant positive effect on eDNA concentration ($p = 0.01$) (Table 1 and Figure 4). In contrast, water layers and their interaction with sampling stations were not significant ($p = 0.38$ and $p = 0.56$, respectively) (Table 1

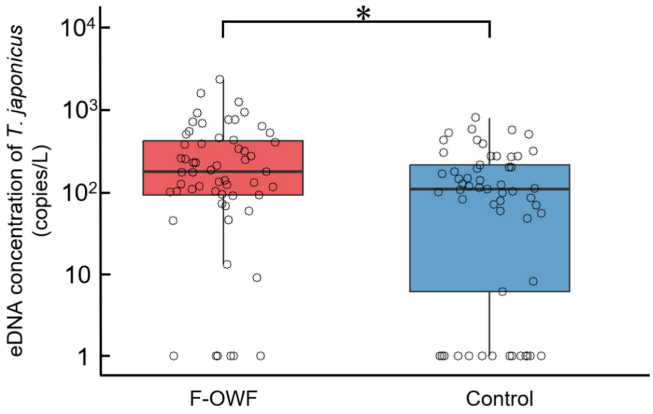

FIGURE 3 | Comparison of *T. japonicus* eDNA concentrations at F-OWF stations and control stations, with data pooled for all sampling periods and water layers. The central line in the whisker plot represents the median, whereas the lower and upper edges of the box indicate the first (25%) and third quartiles (75%), respectively. Whiskers represent minimum and maximum values, and individual data points are displayed as a scatter plot. Statistical significance is indicated as * for $p < 0.05$.

TABLE 1 | Summary of two-way nonparametric ANOVA, assessing effects of sampling station (F-OWF or control) and water layers (surface, middle, bottom) on eDNA concentration. Sampling stations had a significant effect on eDNA concentration. In contrast, water layers (surface, middle, bottom) and their interaction with station location did not significantly affect eDNA concentration. Statistical significance is indicated as "*" for $p < 0.05$.

Factor	d.f	H statistic	*p*
Station (treatment/control)	1	1.96	0.01*
Layer (surface/middle/bottom)	2	6.31	0.38
Interaction (station × layer)	2	1.17	0.56

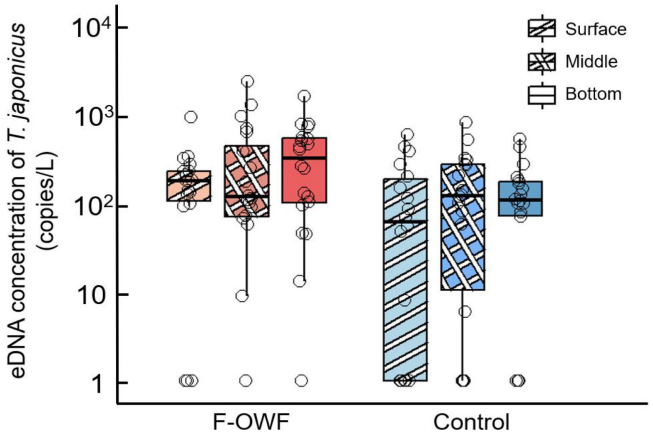

FIGURE 4 | Comparison of eDNA concentrations at F-OWF and control stations across water layers (surface, middle, and bottom). The central line in whisker plots represents the median, whereas the lower and upper edges of the box indicate the first (25%) and third quartiles (75%), respectively. Whiskers represent minimum and maximum values, and individual data points are displayed as a scatter plot.

and Figure 4), indicating that water layers do not influence eDNA concentration, regardless of the sampling station.

Since no significant differences were observed among water layers, Figure 5 presents monthly mean differences in eDNA concentration using pooled data for all water layers. In addition to sampling stations, sampling month also had a significant effect on eDNA concentration ($p = 0.01$, $p = 5.33 \times 10^{-9}$), whereas their interaction was not significant ($p = 0.46$) (Table 2), indicating that the relationship between F-OWF and control stations did not change with the season. The effect of sampling stations on eDNA concentration remained consistently positive throughout the year. Multiple comparisons among groups showed that eDNA concentration at F-OWF stations was highest in October, with significant differences compared to F-OWF and control stations in June and control stations in August (Figure 5). In contrast, eDNA concentration at control stations was lowest in June, with significant differences compared to control stations in April, F-OWF and control stations in October, and F-OWF and control stations in December (Figure 5).

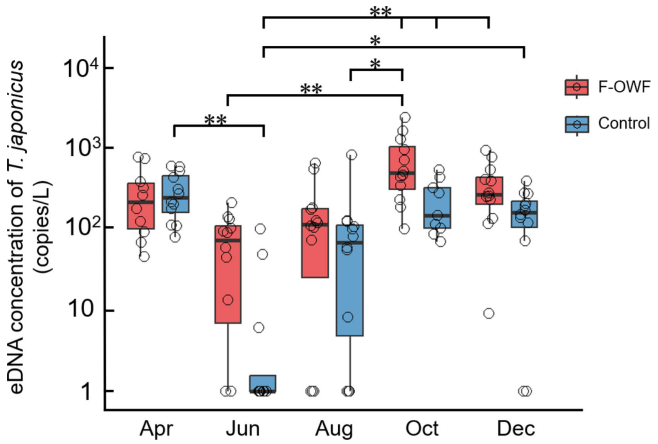

FIGURE 5 | Comparison of eDNA concentrations between F-OWF and control stations and across months (April–December). The central line in whisker plots represents the median, whereas the lower and upper edges of the box indicate the first (25%) and third quartiles (75%), respectively. Whiskers represent minimum and maximum values, and individual data points are displayed as a scatter plot. Statistical significance is indicated as ** for $p < 0.01$ and * for $p < 0.05$.

TABLE 2 | Summary of two-way, nonparametric ANOVA assessing effects of sampling stations (F-OWF and control) and month (Apr ~ Dec) on eDNA concentration. Sampling stations and months have a significant impact on eDNA concentration. In contrast, their interaction did not significantly affect eDNA concentration. Statistical significance is indicated as ** for $p < 0.01$ and * for $p < 0.05$.

Factor	d.f	H statistic	*p*
Station (treatment/control)	1	5.92	0.01*
Month (April/Jun/Aug/Oct/Dec)	4	44.4	5.33×10^{-9}**
Interaction (station × month)	4	3.60	0.46

Results of the GLM analysis showed that among environmental factors (presence of wind turbines, water layer (m) and water temperature [°C]), only wind turbines had a significant effect on eDNA concentration ($p = 6.24 \times 10^{-3}$) (Table 3). This indicates that eDNA concentrations derived from *T. japonicus* are influenced by the presence of wind turbines, regardless of other environmental factors.

4 | Discussion

Using eDNA technology, this study is the first to demonstrate an attraction of OWFs for fish, specifically *T. japonicus*. eDNA analysis is a powerful tool for collecting genetic information from organisms in aquatic or marine habitats, allowing researchers to study species distributions and biodiversity (Thomsen and Willerslev 2015). Additionally, eDNA is released from biological sources such as excretions and tissues, and its concentration correlates with biomass (Doi et al. 2017). This suggests that eDNA concentrations are higher in areas in which the target species is more abundant. However, since this study was conducted in an offshore environment rather than a closed system, careful consideration is required regarding how accurately eDNA reflects the actual biomass at sampling sites. One of the most important factors to consider is the potential persistence of eDNA. Fish-derived eDNA in marine environments decreases by 1.5%–4.6% per hour, meaning that a large proportion of detected eDNA is likely to have been released 1–2 days before sampling (Maruyama et al. 2014). However, an in situ eDNA experiment on *T. japonicus* conducted in Maizuru Bay, Japan, demonstrated that when the current velocity exceeds several tens of L/s, eDNA disperses rapidly, further reducing the presence of older eDNA (Yamamoto et al. 2016). In this study, average current velocities at the sampling sites were 148 mm/s in April, 200 mm/s in June, 181 mm/s in August, 109 mm/s in October and 141 mm/s in December. Therefore, the influence of eDNA persistence on biomass estimation in this study was likely minimal, and detected eDNA concentrations likely reflect the biomass of *T. japonicus* at the time of sampling. Furthermore, it has been suggested that strong currents not only dilute eDNA, but may also physically degrade it (Pastor Rollan et al. 2024). Therefore, the influence of eDNA persistence on biomass estimation in this study was likely minimal, and detected eDNA concentrations likely reflect the biomass of *T. japonicus* at the time of

TABLE 3 | Summary of environmental factors affecting eDNA concentration based on the generalized linear model (GLM). The response variable was the log-transformed eDNA concentration, while explanatory variables included the presence of wind turbines and water layers. Statistical significance is indicated as ** for $p < 0.01$ and * for $p < 0.05$.

Variable	Estimate	SE	*t*-Value	*p*
Intercept	3.24	0.38	8.53	9.3×10^{-14}**
F-OWFs (presence × absence)	1.12	0.40	2.79	0.01*
Depth (m)	0.01	0.04	1.72	0.08

sampling. However, limited knowledge exists regarding the degradation rate of eDNA in marine environments. Future experimental studies are needed to investigate how factors such as water temperature, salinity, ultraviolet radiation, microbial activity and current velocity affect preservation and detectability of eDNA.

In this study, eDNA concentrations of *T. japonicus* at F-OWF sampling stations near F-OWFs were, on average, significantly higher (105.13%) than those at control stations located farther from F-OWFs (Figures 2 and 3). Furthermore, GLM analysis of environmental factors affecting eDNA concentration indicated that the presence of F-OWFs was a significant explanatory variable, showing a positive effect on eDNA concentration (Table 3). Previous studies have reported that floating artificial structures can function as fish aggregation devices (Castro et al. 2002; Inger et al. 2009). For example, Han et al. (2023) demonstrated that floating artificial reefs effectively attract epipelagic fish such as *Nibea albiflora*. Additionally, Okamoto (1992) reported that *T. japonicus* gathers around floating reefs. The results of this study are consistent with these previous findings. Our findings suggest that F-OWFs off the western coast of Kyushu, Japan attract *T. japonicus* and may function as fish aggregation devices.

T. japonicus may utilize F-OWFs throughout its life history. In this study, eDNA concentrations were consistently higher at stations near F-OWFs, regardless of the water layer (Table 1 and Figure 4). F-OWFs in the study area are installed at depths ranging from 100 to 135 m (Table S1) and consist of a floating section (submerged depth: 76 m) and chains extending to the seafloor, forming a vertically structured habitat. This suggests that *T. japonicus* does not aggregate in a specific layer, but rather in all layers around F-OWFs. One possible reason for this pattern is the influence of *T. japonicus*' behavioural ecology at different growth stages. Juvenile *T. japonicus* form schools near the surface and gradually move to deeper waters as they grow (Enomoto et al. 2022; Nakamura and Hamano 2009). In fact, adult fish have been collected using bottom trawl nets at depths of 100–200 m (Takahashi et al. 2012a). The floating structure of F-OWFs may provide shelter that mitigates wave and current impacts, attracting juvenile fish with limited swimming ability. Additionally, these structures may serve as refuges from predators. Indeed, studies have reported that species such as *Caranx crysos* aggregate around floating fish aggregation devices to escape predation (Sinopoli et al. 2015). On the other hand, larger adults, which prefer rocky seabed habitats for shelter (Takahashi et al. 2012b), are likely to aggregate around the chain section of F-OWFs. For fish like *T. japonicus*, which transitions between pelagic and demersal life stages, F-OWFs may provide an attractive habitat for both larval and adult stages. Changes in the underwater environment caused by the installation of F-OWFs are likely to have a positive impact on both marine fish biodiversity and *T. japonicus*, an important biological resource. In particular, F-OWFs may benefit *T. japonicus* by providing shelter and foraging opportunities. In this study, the eDNA concentration of *T. japonicus* was higher in the F-OWF zone; however, it remains unclear whether such a highly mobile species resides continually around wind turbines or merely passes through transiently. To better understand site fidelity and residence time of highly mobile fish species in relation to F-OWFs, future studies should incorporate broader and time-series eDNA sampling that considers distance from F-OWFs and seasonal variation, as well as complementary techniques such as acoustic monitoring.

F-OWFs are likely to attract *T. japonicus* throughout the year. Although seasonal variations in eDNA concentration were observed, the influence of station (F-OWF and control) on eDNA concentration remained consistent throughout the year (Table 2 and Figure 5). In waters off the western coast of Kyushu, Japan, *T. japonicus* reaches its peak abundance during the spawning season in April, after which it is transported to the Sea of Japan by the Tsushima Warm Current over approximately 40 days (Kasai et al. 2008; Sassa et al. 2009). In the southwestern Sea of Japan, juvenile *T. japonicus* abundance peaks along with the seasonal peak in prey availability (Fukataki 1960). In autumn, as water temperatures decline, fish migrate southward, returning to waters off the western coast of Kyushu, Japan. This migration pattern suggests that *T. japonicus* that spawned in western Kyushu move north in the spring, spend the summer in the Sea of Japan and return south in autumn. Results of this study reflect this migratory pattern, as eDNA concentrations of *T. japonicus* decreased in summer and increased from autumn to spring (Figure 5). In the Goto-nada Sea, the study area of this research, previous studies (Takagi 2016) have shown the presence of seasonal residual currents flowing north to northeast, which play an important role in transporting pelagic fish species such as *Engraulis japonicus*. In particular, from winter to spring, a northward flow with daily average speeds of up to 40–56 cm/s has been observed, associated with the northward movement of warm water masses derived from the Kuroshio branch. This northward current likely facilitates the transport of *T. japonicus* and increases the probability of encountering F-OWFs. Furthermore, this area remains under the influence of the Tsushima Warm Current even after summer, and a persistent northward flow has been reported throughout the year (Takagi 2016). The significantly higher eDNA concentrations of *T. japonicus* observed at stations e1–e4 in this study may reflect both the northward migration of pelagic fish and their aggregation around the F-OWFs. In April, the median eDNA concentration was higher at control stations than at F-OWF stations (Figure 5). Japanese horse mackerel (*T. japonicus)* spawn from February to April, and the East China Sea has been identified as a potentially important spawning and nursery ground (Kim et al. 2007). As April corresponds to the peak or immediate post-spawning period, it is likely that widespread eDNA release from adult fish occurred during this time. Furthermore, larvae that had just hatched during this period likely had low swimming ability and were still drifting with ocean currents near the spawning grounds, rather than actively aggregating around structures such as F-OWFs. This may explain why the aggregation effect of the F-OWF was not yet pronounced in April. This finding suggests not only an attraction of F-OWFs for fish but also that the overall eDNA concentration may reflect the abundance of this species in this area. Notably, the effect of station type remained consistent throughout the year, indicating that eDNA concentrations appropriately reflect seasonal fluctuations in actual biomass. However, long-term effects of F-OWFs remain unclear. Long-term monitoring is necessary to evaluate whether F-OWFs

contribute to the establishment of fish schools and local population increases.

eDNA analysis alone cannot determine the size of individual *T. japonicus* congregating around F-OWFs. Although this study focused on a single species, a broader range of species must be examined to fully understand the impact of F-OWFs on fish communities. There are extremely few reports on the impact of F-OWFs on fish communities compared to those of B-OWFs, highlighting the need to investigate a greater taxonomic variety of species. Close to B-OWFs, a shift in the dominant fish species has been observed—from herring (*Clupea harengus*) to sandeel (*Ammodytes* sp.) (Ybema et al. 2009). However, it remains unclear whether this change was directly caused by the wind farm installations or reflects natural fluctuations in the fish community. Other studies have documented significant increases in species such as common sole (*Solea solea*) and Whiting (*Merlangius merlangus*) near B-OWFs (Lindeboom et al. 2011). Furthermore, it has been estimated that fish population densities near wind turbine foundations may be up to 50 times higher than those associated with the surrounding sandy seabed (Vattenfall 2006). B-OWFs also provide refuge for cod (*Gadus morhua*) and pouting (*Trisopterus luscus*), affecting multiple reef-associated and demersal fish species (Stenberg et al. 2015). In addition, transmission cables used to deliver generated electricity emit electromagnetic fields, which may influence movements and navigation of species sensitive to electromagnetic and magnetic fields, particularly elasmobranchs, certain bony fish, decapod crustaceans and sea turtles (Gill 2009; Westerberg and Lagenfelt 2008). These findings indicate that OWFs likely impact a wide range of taxa. Migratory fish, in particular, tend to congregate around floating structures such as artificial reefs (Fréon and Dagorn 2000). Studies have also suggested that combinations of bottom-fixed and floating artificial reefs diversify habitats, attracting a wider variety of fish species (Han et al. 2023; Kellison and Sedberry 1998). The most significant difference between F-OWFs and B-OWFs is their deployment depth. While B-OWFs are restricted to shallower waters, F-OWFs can be installed even in environments exceeding 200 m. If F-OWFs exhibit such reef effects, biomass changes distinct from those observed in B-OWFs may occur. Therefore, to effectively evaluate fish community composition and biomass changes, an integrated biological monitoring approach that combines traditional survey methods with metabarcoding eDNA technology is essential (Hinlo et al. 2017). In this study, water sampling was conducted at multiple spatially independent stations at both F-OWF and control sites. However, a limitation of the study is the insufficient number of replicates at each depth at individual sites. Since only a single sample was collected at each depth per station, statistical comparisons among sites at F-OWF and control areas could not be conducted. In future studies, it will be necessary to increase the number of replicates at each depth in order to enable statistical analyses among stations.

This study demonstrated that F-OWFs influence *T. japonicus* populations both spatially and temporally, but is this necessarily beneficial for fishermen and fish predators? The answer is not simple. Construction of F-OWFs leads to the establishment of no-fishing zones or refugia (Reckhaus 2022). If fish congregate in these restricted areas, fishermen may experience negative impacts on their catches. Additionally, since fishermen must navigate around F-OWFs, they must use extra fuel to avoid them (Nakao 2022). There is also the possibility that fish that would have otherwise entered set nets may instead aggregate around F-OWFs, reducing catch efficiency. However, both fish and fishermen must now coexist with offshore renewable energy generation. Moreover, F-OWFs not only impact fish populations, but also pose potential problems for humans, such as noise pollution, and for birds, in the form of bird strikes (Furness et al. 2013). A large-scale monitoring program should be implemented and integrated with adaptive development of future wind farms. This monitoring should be conducted continuously across all phases—before, during and after construction. Furthermore, it is essential to investigate not only the operational impacts of wind farms, but also the intensity and effects of other human activities in marine environments (Lindeboom et al. 2011).

5 | Conclusion

This study demonstrated that environmental DNA concentrations of *T. japonicus* were significantly higher in areas surrounding F-OWFs than at nearby control areas without such structures. Despite the great swimming ability of *T. japonicus*, our findings suggest that F-OWFs may function as fish aggregating devices by providing feeding opportunities and shelter, leading to the congregation of this ecologically and commercially important species. Seasonal variation in eDNA concentrations, especially anomalously high values at control stations in April, underscores the need to consider reproductive timing and larval dispersal when interpreting species distribution patterns. Although limitations in the number of replicates at each depth remain, our results offer novel insights into the potential ecological role of F-OWFs in supporting marine biodiversity and fisheries resources. Future studies integrating broader spatial–temporal eDNA sampling, acoustic surveys and behavioural tracking will be essential to fully understand the impact of F-OWFs on mobile pelagic fish communities.

Author Contributions

Shimpei Tsuchida: investigation, writing – original draft, visualization. **Riko Kato:** investigation, writing – review and editing. **Shoko Nishitsuji:** investigation, writing – review and editing. **Sayano Anzai:** investigation, writing – review and editing. **Siti Syazwani Azmi:** investigation, writing – review and editing. **Shogo Tanaka:** investigation, writing – review and editing. **Satoshi Masumi:** investigation, writing – review and editing. **Jun Uchida:** investigation, writing – review and editing. **Takashi Aoshima:** investigation, writing – review and editing. **Katsuya Hirasaka:** investigation, writing – review and editing. **Shingo Fujimoto:** investigation, writing – review and editing. **Kenichi Shimizu:** investigation, writing – review and editing. **Miyuki Hirose:** investigation, writing – review and editing. **Mitsuharu Yagi:** conceptualization, methodology, investigation, writing – original draft, supervision, funding acquisition, visualization.

Acknowledgements

We sincerely thank the crew of the training vessel (*T/S*) Kakuyo-Maru for their great support in this research. We also appreciate the staff of the Fish and Ships Laboratory, Faculty of Fisheries, Nagasaki University.

Ethics Statement

The research required no permit approvals.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the supplementary material of this article.

References

Amponsah, N. Y., M. Troldborg, B. Kington, I. Aalders, and R. L. Hough. 2014. "Greenhouse Gas Emissions From Renewable Energy Sources: A Review of Lifecycle Considerations." *Renewable and Sustainable Energy Reviews* 39: 461–475. https://doi.org/10.1016/j.rser.2014.07.087.

Bailey, H., K. L. Brookes, and P. M. Thompson. 2014. "Assessing Environmental Impacts of Offshore Wind Farms: Lessons Learned and Recommendations for the Future." *Aquatic Biosystems* 10: 8. https://doi.org/10.1186/2046-9063-10-8.

Bergström, L., F. Sundqvist, and U. Bergström. 2013. "Effects of an Offshore Wind Farm on Temporal and Spatial Patterns in the Demersal Fish Community." *Marine Ecology Progress Series* 485: 199–210. https://doi.org/10.3354/meps10344.

Bonsu, P. O., J. Letschert, K. L. Yates, et al. 2024. "Co-Location of Fisheries and Offshore Wind Farms: Current Practices and Enabling Conditions in the North Sea." *Marine Policy* 159: 105941. https://doi.org/10.1016/J.MARPOL.2023.105941.

Castro, J. J., J. A. Santiago, and A. T. Santana-Ortega. 2002. "A General Theory on Fish Aggregation to Floating Objects: An Alternative to the Meeting Point Hypothesis." *Aquatic Living Resources* 11: 255–277. https://doi.org/10.1023/A:1020302414472.

Chen, J., and M. H. Kim. 2022. "Review of Recent Offshore Wind Turbine Research and Optimization Methodologies in Their Design." *Journal of Marine Science and Engineering* 10, no. 1: 28. https://doi.org/10.3390/jmse10010028.

Díaz, H., and C. Guedes Soares. 2020. "Review of the Current Status, Technology and Future Trends of Offshore Wind Farms." *Ocean Engineering* 209: 107381. https://doi.org/10.1016/J.OCEANENG.2020.107381.

Doi, H., R. Inui, Y. Akamatsu, et al. 2017. "Environmental DNA Analysis for Estimating the Abundance and Biomass of Stream Fish." *Freshwater Biology* 62, no. 1: 30–39. https://doi.org/10.1111/fwb.12846.

Enomoto, M., S. Ito, M. Takahashi, C. Sassa, T. Higuchi, and K. Shirai. 2022. "Vertical Habitat Shifts of Juvenile Jack Mackerel Estimated Using Otolith Oxygen Stable Isotope." *Progress in Oceanography* 208: 102897. https://doi.org/10.1016/J.POCEAN.2022.102897.

Farr, H., B. Ruttenberg, R. K. Walter, Y. H. Wang, and C. White. 2021. "Potential Environmental Effects of Deepwater Floating Offshore Wind Energy Facilities." *Ocean and Coastal Management* 207: 105611. https://doi.org/10.1016/J.OCECOAMAN.2021.105611.

Fréon, P., and L. Dagorn. 2000. "Review of Fish Associative Behaviour: Toward a Generalisation of the Meeting Point Hypothesis." *Aquatic Living Resources* 10: 183–207. https://doi.org/10.1023/A:1016666108540.

Fukataki, H. 1960. "Consideration of the Recruiting Process of the Jack Mackerel Population in the Tsushima Current Region. I. Consideration From Occurrence and Distribution of Larvae." *Annual Report of the Japan Sea Regional Fisheries Research Laboratory* 6: 69–85 (In Japanese with English abstract).

Fukaya, K., N. I. Kondo, S. Matsuzaki, and T. Kadoya. 2022. "Multispecies Site Occupancy Modelling and Study Design for Spatially Replicated Environmental DNA Metabarcoding." *Methods in Ecology and Evolution* 13, no. 1: 183–193. https://doi.org/10.1111/2041-210X.13732.

Furness, R. W., H. M. Wade, and E. A. Masden. 2013. "Assessing Vulnerability of Marine Bird Populations to Offshore Wind Farms." *Journal of Environmental Management* 119: 56–66. https://doi.org/10.1016/J.JENVMAN.2013.01.025.

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 Report. Accessed May 19, 2025. https://tethys.pnnl.gov/sites/default/files/publications/Sensitive_Fish_Response_to_EM_Emissions_from_Offshore_Renewable.pdf.

Government of Japan. 2020. "Offshore Wind Industry Vision (1st Edition) – Summary." Council for Strengthening the Competitiveness of the Offshore Wind Industry. Accessed 21 May 2025. https://www.meti.go.jp/shingikai/energy_environment/yogyo_furyoku/pdf/001_02_00.pdf.

Graabak, I., and M. Korpås. 2016. "Variability Characteristics of European Wind and Solar Power Resources—A Review." *Energies* 9: 449. https://doi.org/10.3390/en9060449.

Hammar, L., D. Perry, and M. Gullström. 2016. "Offshore Wind Power for Marine Conservation." *Open Journal of Marine Science* 6: 66–78. https://doi.org/10.4236/ojms.2016.61007.

Han, C., K. Liu, T. Kinoshita, et al. 2023. "Assessing the Attractive Effects of Floating Artificial Reefs and Combination Reefs on Six Local Marine Species." *Fishes* 8, no. 5: 248. https://doi.org/10.3390/fishes8050248.

Hering, D., A. Borja, J. I. Jones, et al. 2018. "Implementation Options for DNA-Based Identification Into Ecological Status Assessment Under the European Water Framework Directive." *Water Research* 138: 192–205. https://doi.org/10.1016/j.watres.2018.03.003.

Hinlo, R., E. Furlan, L. Suitor, and D. Gleeson. 2017. "Environmental DNA Monitoring and Management of Invasive Fish: Comparison of eDNA and Fyke Netting." *Management of Biological Invasions* 8, no. 1: 89–100. https://doi.org/10.3391/mbi.2017.8.1.09.

Hinz, S., J. Coston-Guarini, M. Marnane, and J. M. Guarini. 2022. "Evaluating eDNA for Use Within Marine Environmental Impact Assessments." *Journal of Marine Science and Engineering* 10, no. 3: 375. https://doi.org/10.3390/jmse10030375.

Igeta, Y., C. Sassa, M. Takahashi, et al. 2023. "Effect of Interannual Variations of Kuroshio–Tsushima Warm Current System on the Transportation of Juvenile Japanese Jack Mackerel (*Trachurus japonicus*) to the Pacific Coast of Japan." *Fisheries Oceanography* 32, no. 1: 133–146. https://doi.org/10.1111/fog.12622.

Inger, R., M. J. Attrill, S. Bearhop, et al. 2009. "Marine Renewable Energy: Potential Benefits to Biodiversity? An Urgent Call for Research." *Journal of Applied Ecology* 46, no. 6: 1145–1153. https://doi.org/10.1111/j.1365-2664.2009.01697.x.

Japan Wind Power Association (JWPA). 2024. "*Cumulative installed capacity of wind power in Japan: 5,840.4MW (2,720 units).*" Retrieved May 21, 2025. https://jwpa.jp/en/information/11074/.

Jerde, C. L., A. R. Mahon, W. L. Chadderton, and D. M. Lodge. 2011. "'Sight-Unseen' Detection of Rare Aquatic Species Using Environmental DNA." *Conservation Letters* 4, no. 2: 150–157. https://doi.org/10.1111/j.1755-263X.2010.00158.x.

Kasai, A., K. Komatsu, C. Sassa, and Y. Konishi. 2008. "Transport and Survival Processes of Eggs and Larvae of Jack Mackerel *Trachurus japonicus* in the East China Sea." *Fisheries Science* 74, no. 1: 8–18. https://doi.org/10.1111/j.1444-2906.2007.01491.x.

Kazama, K. 2012. "Impacts of Offshore Wind Farms on Marine Ecosystems." *Japanese Journal of Conservation Ecology* 17: 107–122. https://doi.org/10.18960/hozen.17.1_107 (In Japanese with English abstract).

Kellison, G. T., and G. R. Sedberry. 1998. "The Effects of Artificial Reef Vertical Profile and Hole Diameter on Fishes off South Carolina." *Bulletin of Marine Science* 62, no. 3: 763–780.

Kim, H., S. Kimura, and T. Sugimoto. 2007. "Transport of Jack Mackerel (*Trachurus japonicus*) Larvae Inferred From the Numerical Experiment in the East China Sea." *Bulletin of the Japanese Society of Fisheries Oceanography* 71, no. 1: 9–17.

Leung, D. Y. C., and Y. Yang. 2012. "Wind Energy Development and Its Environmental Impact: A Review." *Renewable and Sustainable Energy Reviews* 16, no. 1: 1031–1039. https://doi.org/10.1016/J.RSER.2011.09.024.

Lindeboom, H. J., H. J. Kouwenhoven, M. J. N. Bergman, et al. 2011. "Short-Term Ecological Effects of an Offshore Wind Farm in the Dutch Coastal Zone; A Compilation." *Environmental Research Letters* 6, no. 3: 035101. https://doi.org/10.1088/1748-9326/6/3/035101.

Maruyama, A., K. Nakamura, H. Yamanaka, M. Kondoh, and T. Minamoto. 2014. "The Release Rate of Environmental DNA From Juvenile and Adult Fish." *PLoS ONE* 9, no. 12: e114639. https://doi.org/10.1371/journal.pone.0114639.

Maruyama, A., K. Sugatani, K. Watanabe, H. Yamanaka, and A. Imamura. 2018. "Environmental DNA Analysis as a Non-Invasive Quantitative Tool for Reproductive Migration of a Threatened Endemic Fish in Rivers." *Ecology and Evolution* 8, no. 23: 11964–11974. https://doi.org/10.1002/ece3.4653.

Methratta, E. T., A. Hawkins, B. R. Hooker, A. Lipsky, and J. A. Hare. 2020. "Offshore Wind Development in the Northeast US Shelf Large Marine Ecosystem: Ecological, Human, and Fishery Management Dimensions." *Oceanography* 33, no. 4: 16–27. https://doi.org/10.5670/oceanog.2020.402.

Minamoto, T., M. Miya, T. Sado, et al. 2021. "An Illustrated Manual for Environmental DNA Research: Water Sampling Guidelines and Experimental Protocols." *Environmental DNA* 3, no. 1: 8–13. https://doi.org/10.1002/edn3.121.

Msigwa, G., J. O. Ighalo, and P. S. Yap. 2022. "Considerations on Environmental, Economic, and Energy Impacts of Wind Energy Generation: Projections Towards Sustainability Initiatives." *Science of the Total Environment* 849: 157755. https://doi.org/10.1016/J.SCITOTENV.2022.157755.

Nakamura, T., and A. Hamano. 2009. "Seasonal Differences in the Vertical Distribution Pattern of Japanese Jack Mackerel, *Trachurus japonicus*: Changes According to Age?" *ICES Journal of Marine Science* 66: 1289–1295. https://doi.org/10.1093/icesjms/fsp114.

Nakao, T. 2022. "Approaches to Fisheries Coordination and Coexistence in Offshore Wind Power Projects." *Journal of the Japan Wind Energy Association* 46, no. 2: 331–337. https://doi.org/10.11333/jwea.46.2_331.

Norro, A. M. J., B. Rumes, and S. J. Degraer. 2013. "Differentiating Between Underwater Construction Noise of Monopile and Jacket Foundations for Offshore Windmills: A Case Study From the Belgian Part of the North Sea." *Scientific World Journal* 2013: 897624. https://doi.org/10.1155/2013/897624.

Okamoto, M. 1992. "Studies on the School Behavior of Fish During the Daytime Around the Steel Mid-Layer Floating Reef off Tajima in the Japan Sea." *Nippon Suisan Gakkaishi* 58, no. 7: 1291–1299. https://doi.org/10.2331/suisan.58.1291.

Ono, Y., K. Hirasaka, T. Myosho, S. Fujimoto, and M. Yagi. 2023. "Environmental DNA Concentrations of Japanese Eels in Relation to Habitat Characteristics." *Aquaculture Science* 71, no. 1: 45–48. https://doi.org/10.11233/aquaculturesci.71.45.

Ono, Y., S. Tsuchida, K. Hirasaka, et al. 2024. "Environmental DNA Reveals Geographic Distributions of Two Eel Species, *Anguilla Japonica* and *A. marmorata*, in Western Kyushu, Japan." *Zoological Science* 41, no. 4: 392–399. https://doi.org/10.2108/zs230103.

Pastor Rollan, A., C. D. H. Sherman, M. R. Ellis, et al. 2024. "Current Trends in Biophysical Modeling of eDNA Dynamics for the Detection of Marine Species." *Environmental DNA* 6, no. 5: e70021. https://doi.org/10.1002/edn3.70021.

Reckhaus, N. 2022. "The Ongoing Conflict Between Offshore Wind Farms and the Fishing Industry in the North sea." Master's thesis, University of Groningen. https://tethys.pnnl.gov/sites/default/files/publications/Reckhaus-2022.pdf.

Rezaei, F., P. Contestabile, D. Vicinanza, and A. Azzellino. 2023. "Towards Understanding Environmental and Cumulative Impacts of Floating Wind Farms: Lessons Learned From the Fixed-Bottom Offshore Wind Farms." *Ocean and Coastal Management* 243: 106772. https://doi.org/10.1016/j.ocecoaman.2023.106772.

Sanchez, L., E. Boulanger, V. Arnal, et al. 2022. "Ecological Indicators Based on Quantitative eDNA Metabarcoding: The Case of Marine Reserves." *Ecological Indicators* 140: 108966. https://doi.org/10.1016/j.ecolind.2022.108966.

Sassa, C., K. Yamamoto, Y. Tsukamoto, Y. Konishi, and M. Tokimura. 2009. "Distribution and Migration of Age-0 Jack Mackerel (*Trachurus Japonicus*) in the East China and Yellow Seas, Based on Seasonal Bottom Trawl Surveys." *Fisheries Oceanography* 18, no. 4: 255–267. https://doi.org/10.1111/j.1365-2419.2009.00510.x.

Sato, I., and T. Matsunobu. 2021. "Practical Implementation and Dissemination of a Hybrid Spar-Type Floating Offshore Wind Turbine." *Journal of the Japan Wind Energy Association* 45, no. 4: 610–614. https://doi.org/10.11333/jwea.45.4_610 (In Japanese).

Sinopoli, M., C. Cattano, F. Andaloro, G. Sarà, C. M. Butler, and M. Gristina. 2015. "Influence of Fish Aggregating Devices (FADs) on Anti-Predator Behaviour Within Experimental Mesocosms." *Marine Environmental Research* 112: 152–159. https://doi.org/10.1016/j.marenvres.2015.10.008.

Stenberg, C., J. G. Støttrup, M. Van Deurs, et al. 2015. "Long-Term Effects of an Offshore Wind Farm in the North Sea on Fish Communities." *Marine Ecology Progress Series* 528: 257–265. https://doi.org/10.3354/meps11261.

Takagi, N. 2016. "Structure and Variation of Tidal Residual Currents in the Continental Margin of Amakusa-Nada and Goto-Nada in Relation to Anchovy Catch Fluctuation." *Bulletin of Nagasaki Prefectural Institute of Fisheries* 42: 29–89 (In Japanese).

Takahashi, K., R. Masuda, M. Matsuyama, and Y. Yamashita. 2012b. "Stimulus-Specific Development of Learning Ability During Habitat Shift in Pre to Post-Recruitment Stage Jack Mackerel." *Journal of Ethology* 30, no. 2: 309–316. https://doi.org/10.1007/s10164-012-0328-y.

Takahashi, M., C. Sassa, and Y. Tsukamoto. 2012a. "Growth-Selective Survival of Young Jack Mackerel *Trachurus Japonicus* During Transition from Pelagic to Demersal Habitats in the East China Sea." *Marine Biology* 159, no. 12: 2675–2685. https://doi.org/10.1007/s00227-012-2025-3.

Thomsen, F., K. Lüdemann, R. Kafemann, and W. Piper. 2006. "Effects of Offshore Wind Farm Noise on Marine Mammals and Fish." Biola, Hamburg, Germany, on behalf of COWRIE Ltd.

Thomsen, P. F., and E. Willerslev. 2015. "Environmental DNA—An Emerging Tool in Conservation for Monitoring Past and Present Biodiversity." *Biological Conservation* 183: 4–18. https://doi.org/10.1016/J.BIOCON.2014.11.019.

United Nations. 1982. "United Nations Convention on the Law of the Sea." https://www.un.org/depts/los/convention_agreements/texts/unclos/unclos_e.pdf.

Vallejo, G. C., K. Grellier, E. J. Nelson, et al. 2017. "Responses of Two Marine Top Predators to an Offshore Wind Farm." *Ecology and Evolution* 7, no. 21: 8698–8708. https://doi.org/10.1002/ece3.3389.

Vattenfall. 2006. "Benthic Communities at Horns rev Before, During and After Construction of Horns rev Offshore Wind Farm: Final Report (Report No. 2572–03–005)." BioConsult SH, Report for Vattenfall. https://tethys.pnnl.gov/sites/default/files/publications/Vattenfall_Benthic_Communities_2006.pdf.

Westerberg, H., and I. Lagenfelt. 2008. "Sub-Sea Power Cables and the Migration Behaviour of the European Eel." *Fisheries Management and Ecology* 15, no. 5–6: 369–375. https://doi.org/10.1111/j.1365-2400.2008.00630.x.

Williams, R., and F. Zhao. 2024. "Global Offshore Wind Report 2024." Global Wind Energy Council. https://gwec.net/global-offshore-wind-report-2024/.

Wilson J.C. 2007 "Offshore Wind Farms: Their Impacts, and Potential Habitat Gains as Artificial Reefs, in Particular for Fish." MSc thesis, University of Hull. https://tethys.pnnl.gov/sites/default/files/publications/Their_Impacts_and_Pote.

Yamaguchi, K., Y. Akamatsu, R. Inui, M. Goto, T. Kawano, and K. Kurita. 2018. "Fundamental Study on the Dynamics of Environmental DNA-Containing Substances in Rivers." *Journal of Japan Society of Civil Engineers, Ser. B1 (Hydraulic Engineering)* 74, no. 5: I_409–I_414. https://doi.org/10.2208/jscejhe.74.5_I_409.

Yamamoto, S., K. Minami, K. Fukaya, et al. 2016. "Environmental DNA as a 'Snapshot' of Fish Distribution: A Case Study of Japanese Jack Mackerel in Maizuru Bay, Sea of Japan." *PLoS ONE* 11, no. 3: e0149786. https://doi.org/10.1371/journal.pone.0149786.

Ybema, M. S., D. Gloe, and R. H. L. Lambers. 2009. "OWEZ Pelagic Fish, Progress Report and Progression After T1." (IMARES Report no. C007/09). IMARES Wageningen UR. https://edepot.wur.nl/198566.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.