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Citation

Knaap, I. E. J. van der, Slabbekoorn, H. W., Moens, T., Eynde, D. van den, & Reubens, J. (2022). Effects of pile driving sound on local movement of free-ranging Atlantic cod in the Belgian North Sea. *Environmental Pollution*, 300. doi:10.1016/j.envpol.2022.118913

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Note: To cite this publication please use the final published version (if applicable).



Effects of pile driving sound on local movement of free-ranging Atlantic cod in the Belgian North Sea[☆]

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ARTICLE INFO

Keywords:

Pile driving
Atlantic cod
Acoustic telemetry
Wind farm
Movement behaviour

ABSTRACT

Offshore energy acquisition through the construction of wind farms is rapidly becoming one of the major sources of green energy all over the world. The construction of offshore wind farms contributes to the ocean soundscape as steel monopile foundations are commonly hammered into the seabed to anchor wind turbines. This pile driving activity causes repeated, impulsive, low-frequency sounds, reaching far into the environment, which may have an impact on the surrounding marine life. In this study, we investigated the effect of the construction of 50 wind turbine foundations, over a time span of four months, on the presence and movement behaviour of free-swimming, individually tagged Atlantic cod. The turbine foundations were constructed at a distance ranging between 2.3 and 7.1 km from the cod, which resided in a nearby, existing wind farm in the southern North Sea. Our results indicated that local fish remained in the exposed area during and in-between pile-driving activities, but showed some modest changes in movement patterns. The tagged cod did not increase their net movement activity, but moved closer to the scour-bed (i.e. hard substrate), surrounding their nearest turbine, during and after each piling event. Additionally, fish moved further away from the sound source, which was mainly due to the fact that they were positioned closer to a piling event before its start. We found no effect of the time since the last piling event. Long-term changes in movement behaviour can result in energy budget changes, and thereby in individual growth and maturation, eventually determining growth rate of populations. Consequently, although behavioural changes to pile driving in the current study seem modest, we believe that the potential for cumulative effects, and species-specific variation in impact, warrant more tagging studies in the future, with an emphasis on quantification of energy budgets.

1. Introduction

The number and size of offshore wind farms is growing worldwide with potentially diverse consequences for aquatic wildlife during the construction and operational phases (Gill, 2005; Gill et al., 2020; Lindeboom et al., 2011; Nabe-Nielsen et al., 2018). Predictions are that around 70 GW of Europe's energy will come from offshore wind turbines by 2030 (Nghiem and Pineda, 2017). By 2050, this could expand to 450 GW, 380 GW of which is to be produced in the North Sea (Freeman et al., 2019). Wind turbine foundations are anchored to the seabed, typically surrounded by a scour-protection layer of rocks or other hard substrate,

which creates artificial reef structures (Ashley et al., 2014; Petersen and Malm, 2006; Reubens et al., 2013a). Especially invertebrate animal communities benefit from these new artificial reef habitats. These communities include bivalves, anemones and crustaceans (Mavraki et al., 2020), which in turn attract a variety of fish species (De Mesel et al., 2015; Paxton et al., 2020; Reubens et al., 2014). However, construction and operation of wind farms also bring changes to the acoustic environment, the impact of which on marine wildlife is as yet insufficiently understood and may not always be beneficial (Gill et al., 2020).

Once the wind farm is operational, turbine vibrations, altered flow conditions around turbines, and wind park maintenance vessels all

[☆] This paper has been recommended for acceptance by Prof. Pavlos Kassomenos.

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<https://doi.org/10.1016/j.envpol.2022.118913>

Received 25 October 2021; Received in revised form 8 January 2022; Accepted 25 January 2022

Available online 31 January 2022

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contribute to a growing ambient sound level (Madsen et al., 2006; Popper and Hawkins, 2019a; Sertlek et al., 2019; Slabbekoorn et al., 2010; Tougaard et al., 2009; Tougaard et al., 2020; Wahlberg and Westerberg, 2005; Duarte et al., 2021). However, the most dramatic acoustic events are associated with the park's construction phase (Dahl et al., 2015; Lippert et al., 2018). Elevated sound levels usually start long before actual construction, as a seismic survey and multi-beam sonar is often required for seabed mapping. When the seabed at an offshore location is considered suitable, the preparation phase is initiated with seabed preparations (i.e. deposition of hard substrate to reduce sediment erosion and flattening of the seabed), followed by pile driving. After foundations have been anchored, the turbines and blades are attached, which is then followed by the operational phase.

Especially the sound event train with long periods of loud series of impulsive sounds associated with pile driving for turbine foundation placements have a high potential to negatively affect marine wildlife (Duarte et al., 2021; Popper and Hastings, 2009; Popper and Hawkins, 2019; Slabbekoorn, 2019; Slabbekoorn et al., 2010). The most common type of offshore turbine foundation is a steel monopile, that ranges in diameter from 4 to 8 m and is piled into the sediment from a rigid platform using a hydraulic hammer. Piling one monopile 30 m into the seabed typically takes over 3500 strikes, lasting around 1.5–4.5 h, depending on the density of the sediment. Hammer strikes are associated with low-frequency (100–1000 Hz) sound, reaching levels above 200 dB re 1 μ Pa close to the source, including sharp pulse rise times and inter-pulse intervals of 2–4 s (Ainslie et al., 2020; Hildebrand, 2009). Strikes create downward sound waves that spread cylindrically from the pile wall into the water column and seafloor (Dahl et al., 2015; Martin and Barclay, 2019; Zampolli et al., 2013). The total duration of the construction phase depends on the size of the wind farm but usually takes between 2 and 6 months.

Fish can be directly affected by pile driving through immediate physical and behavioural effects, or indirectly through the effect of piling on their predators (Thompson et al., 2020) and prey (Roberts et al., 2016). Exposure effects from multiple impulsive pile strikes at close range have been investigated in captivity and include damage to internal organs, including the inner ear, swim bladder, liver, kidney, and gonads (Casper et al., 2017, 2013; Halvorsen et al., 2012a,b), which may eventually result in fish death (Slabbekoorn et al., 2010; Popper and Hawkins, 2019). Acoustic modelling has recently demonstrated that lethal and sub-lethal injury could occur at distances as far as 1.8 and 3.1 km from the pile driving location, respectively (Ainslie et al., 2020). In addition, indoor studies with exposure to moderate levels of impulsive sound have found increased gill ventilation rates, indicative of a stress response, in several but not all fish species (Bruintjes et al., 2016; Spiga et al., 2017).

Similar to stress responses, behavioural effects of impulsive sounds may occur at a large spatial scale (Duarte et al., 2021; Popper and Hawkins, 2019; Slabbekoorn et al., 2010). Groups of captive seabass (*Dicentrarchus labrax*) in a small indoor basin increased their swimming depth and group cohesion, and swam faster, in response to both continuous and impulsive sounds, but during the latter, they took twice as long to return to their baseline levels (Neo et al., 2015, 2014). Impulsive sound exposure in a larger outdoor pen, in shallow harbour conditions, revealed stronger effects from exposure at night compared to daytime conditions, and showed a potential for habituation to repeated exposure, at least for seabass (Hubert et al., 2020b; Neo et al., 2018, 2016). Pile-driving playback on schooling behaviour of juvenile seabass, again in lab conditions, demonstrated that groups became less cohesive, less directionally ordered, and individuals became less correlated in speed and directional changes (Herbert-Read et al., 2017). Captive exposure and response patterns may not accurately reflect free-ranging conditions qualitatively nor quantitatively, but observations and analyses in captivity may provide important complementary insights to studies in the wild (Hubert et al., 2020b).

Examining the behaviour of tagged individuals during pile driving at

sea is more challenging than observing fish in captivity, but such *in situ* studies provide better insight into potential consequences of noisy events in nature. Iafrate et al. (2016) reported that individual sheepshead (*Archosargus probatocephalus*) were little affected by 35 days of pile driving at a busy wharf in Florida, but four grey snappers (*Lutjanus griseus*), with high prior site fidelity, had relatively low day-time residency during piling, and two left the area within the first three days of the noisy activities. In a recent study, we showed that impulsive sounds from another loud anthropogenic source (an experimental seismic survey) resulted in delayed deterrence from a wind farm area, interrupted diurnal activity cycles, and likely reduced foraging activity in free-ranging Atlantic cod (*Gadus morhua*) (van der Knaap et al., 2021a). However, we are unaware of any published data on effects of pile driving on tagged individuals for this species.

During summer, Atlantic cod stay several months around the hard-bottom structures of wind turbine foundations in the southern part of the North Sea (Reubens et al., 2013a, 2013c; Winter et al., 2010). They use these structures to forage and seek shelter (Reubens et al., 2013b; van der Knaap et al., 2021a; Winter et al., 2010). Atlantic cod also play an important role in the local food web (Reubens et al., 2014), are commercially and culturally important for fisheries (Hutchings, 2004; Rose, 2004), and have shown dramatic population declines, related to overfishing and climate change (Engelhard et al., 2014; Pitcher et al., 2009; Worm et al., 2006). Consequently, Atlantic cod at wind farms are a feasible and important model species for sound impact studies (van der Knaap et al., 2021a, 2021b). Moreover, a captive study (Thomsen et al., 2010) as well as a theoretical evaluation (Hammar et al., 2014) both reported that impulsive sounds from pile driving could be a potential risk to cod.

In this study, we examined the presence and movement of free-swimming Atlantic cod at an existing offshore wind farm (OWF) in the Belgian North Sea, in response to nearby pile driving in 2016. Within a period of four months, 50 monopiles were hammered into the seabed for a new wind farm, adjacent to an existing wind farm. This provided a unique opportunity to monitor cod presence and movement *in situ* during offshore piling operations. We used acoustic telemetry to monitor individual presence and movement in the area to answer the following questions: 1) Do cod move out of the study area in response to pile driving? And 2) Does piling affect the general spatial behaviour of cod, their distance to the nearest turbine (indication for the distance to the scour bed), and their distance to the pile-driving location, taking into account the time interval between consecutive piling events?

2. Methods

2.1. Study site

Fifty steel monopile wind turbine foundations were hammered into the seabed using pile driving between May 16 and September 22, 2016 (Table S1) for the construction of the wind farm 'Nobelwind' at the North-Eastern edge of the Belgian Part of the North Sea. The farm was built around the existing wind farm 'Belwind' (completed in 2013) situated on the Blich Bank, about 50 km from the coastal harbour of Zeebrugge (Fig. 1A). The water depth at the study site varied between 15 and 37 m, including tidal fluctuations. Main currents in the wind farm run from northeast to southwest (Brabant et al., 2013). Steel monopiles were piled into the seabed using a hydraulic piling hammer (IHC Hydrohammer B.V.) from a rigid platform. Each pile strike creates downward energy, forcing the pile into the seabed. As a by-product this creates a low-frequency, high-intensity acoustic energy wave that radiates into the air, water and seabed (Lippert et al., 2018).

Sound pressure was recorded using a hydrophone (Brüel & Kjaer hydrophones type 8104) suspended at 10 m depth from a drifting Zodiac workboat. Ambient sound levels were recorded at three locations without construction activities (on July 12 and 13, 2016 see Degraer et al., 2017), and sound recordings during construction were made at

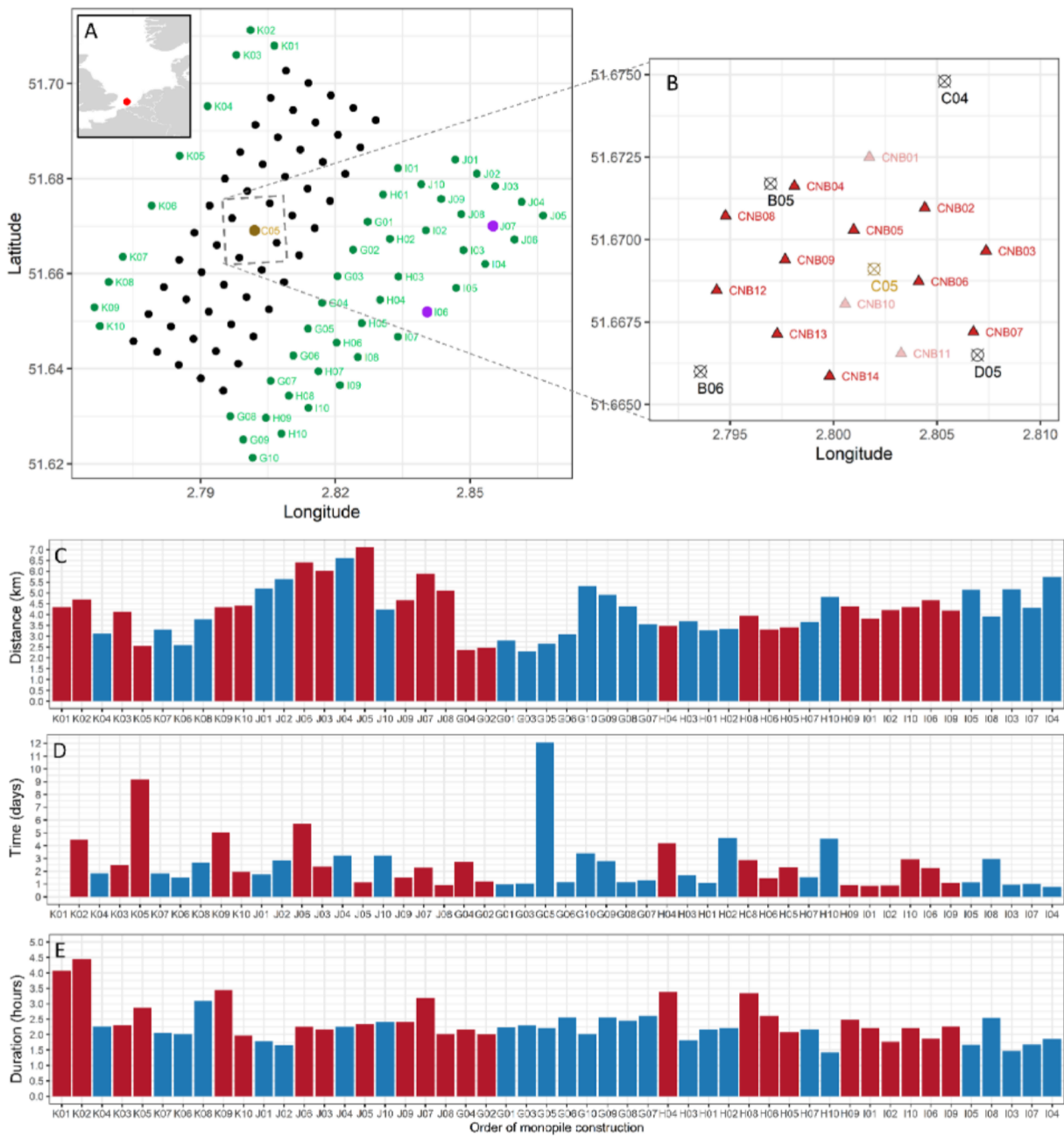


Fig. 1. Overview of location and study setup. A) Location of Belwind (black dots) and Nobelwind (green dots) wind turbines in the Belgian part of the North Sea (red dot in overview map). The turbine C05 (golden dot) in Belwind is the centre of our fish tagging site. Purple dots in Nobelwind indicate locations of sound measurements during construction. B) Receiver setup around Belwind turbine C05. 14 acoustic receivers (red triangles) were deployed on April 4, 2016 around turbine C05 (orange dot). During the deployment period, 3 receivers were lost (shaded red triangles). C), D) and E) order in which the Nobelwind turbines were constructed and the distance of the piling event (C), time since last event (D), and the duration of an event (E). The red bars indicate the piling events that were included in the movement analysis. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

400 m and 1700 m from monopile I06 (lat. 51.65195, long. 2.84043, September 13, 2016 Fig. 1) and at 500 m from monopile J07 (lat. 51.67005, long. 2.85506, July 12, 2016 Fig. 1). Ambient sound pressure levels (SPL) varied between 114 dB and 138 dB (re1 μPa) on average. During piling operations, the zero-to-peak SPL reached 199, 196 and 188 dB at 400, 500 m and 1700 m distance from the sound source, respectively. Single strike sound exposure levels (SELs) were on average 176, 175, and 168 dB (re1 $\mu\text{Pa}^2 \cdot \text{s}$), respectively (adopted from Degraer et al., 2017).

2.2. Experimental setup

In 2016, 14 acoustic receivers (12 VR2AR and 2 VR2Tx, Innovasea) with an internal sync-tag were deployed around the Belwind turbine C05 to form a network of receivers that allowed to locate the positions of the tagged fish (Fig. 1B) (Smith, 2013). The deployment period ran from April 4 to October 25. Nine receivers were operational during the whole period of deployment and provided continuous presence and movement data for the tagged cod after retrieval. Three receivers (CNB01, CNB10, CNB11) were lost and no data was retrieved, while two receivers (CNB07 and CNB14) stopped recording before the end of the study (18 September and 8 August, respectively) (Fig. 1B). Overall, 64.9% of

synctag transmissions were logged on 3 or more receivers.

Fifteen Atlantic cod, with a total length range of 40–49.5 cm (Table S2), were internally tagged with V13P tags (Innovaseas) on April 4, as per Reubens et al. (2013c; c. f. van der Knaap et al., 2021a, 2021b). They were caught using hook and line, all close to the wind turbine C05 (Fig. 1A). Soon after tagging, fish were released again at the catch site. Acoustic tags had a pressure sensor and transmitted a coded signal with information on tag ID. The tags measured pressure at a random delay between 140 and 220 s. Catching and tagging of free-ranging animals was performed after ethical approval (certificate number LA1400452) and in line with official guidelines for animal welfare in Belgium.

2.3. Data analysis

After recovery of the receivers, corrections for internal clock drift of the receivers during the deployment period were done by applying a linear time correction over the entire sampling period (VUE, Innovasea). Of the 15 tagged cod, one was not detected after release and therefore excluded from further analysis (Table S2). Additionally, we excluded the first 24 h of data from the first day after the animals were tagged, as it is expected that cod take a variable amount of time to resume their natural behaviour, but typically within this time period (Hubert et al., 2020a). We furthermore scanned the data for any stationary tags which could indicate fish that died or lost their tag during the study. No such stationary tags were found.

2.4. Presence/absence

We determined half hour presence/absence over the entire study period for the 14 cod (Fig. 3A, tag ID's numbers ranged from 8 to 22). Fish were considered present if they were detected at least once within a half hour bin. We applied a discrete-time hidden Markov model (HMM) to analyse the effect of piling on the presence/absence of the fish. HMMs intrinsically deal with temporal autocorrelation and are able to predict the probability at which animals are in a certain mutually exclusive behavioural state, based on telemetric detection data (Langrock et al., 2012; McClintock and Michelot, 2020; Hubert et al., 2020a). Half hourly observations of presence/absence (Bernoulli distribution) per individual (14 fish in total) were fitted to the states 'Onsite' or 'Offsite'.

We tested whether cod had spent more time in the Offsite state, during piling; soon after each piling event (50 in total); or soon after the first or last piling event in particular, as a previous study on the impact of impulsive sound on cod indicated a delayed leaving effect (van der Knaap et al., 2021a). We therefore included a piling decay variable, which was 1 during piling, after which it exponentially decayed to 0 over a 24-h period. This piling decay variable tested whether the chance that cod would depart was highest during piling and exponentially became smaller afterwards. We then also included a piling order variable with four levels: no-piling, first piling event (K01), all middle piling events, and last piling event (I04). We checked for collinearity between these two variables (piling-decay and -order) by excluding them one-by-one from the HMM and looking at the model results. If the model results did not change, we assumed that collinearity was not an issue for the significance of our model. If they did change, one of the covariates causing the collinearity was left out.

Other covariates considered in the departure probability analyses were: day of the year (as $\cos(2\pi t/365 \text{ d})$ and $\sin(2\pi t/365 \text{ d})$), current speed (ms^{-1}), tidal elevation (m), sun angle (degrees, relative to the hours in a day), and fish length (cm). Current speed and tidal elevation were estimated based on a hydrodynamic model (COHERENS, operated by RBINS Belgium). Model selection was done based on AIC comparison using model dredging ('MuMin' version 1.43, Table S3). The best model (lowest AIC, Table S3) was: presence/absence ~ decay after each piling event + piling order + fish length + day of the year + current speed. HMMs were applied in R (version 4.0.4) using the 'momentuHMM' package (version 1.5.1).

2.5. Movement behaviour

The individual detections were converted into 2-dimensional positions (latitude, longitude) through time difference of arrival (TDOA) triangulation (Voegeli et al., 2001) (Innovasea). A position could only be determined when the tag signal was detected by at least three receiver stations (van der Knaap et al., 2021b). The associated horizontal positioning error (HPE, a unit-less error metric Innovasea) was then used to filter out the top 2% most erroneous positions (Smith, 2013). This excluded one fish whose positions were at the edge of, or outside our detection area and therefore had a high HPE. Furthermore, we removed fish 11 which had only very few positions. To understand how a piling event affected cod movement, we defined three fish movement metrics (Table 1), i.e. step length (distance moved) (Fig. 2A), distance to the scour bed (Fig. 2A) and relative distance to the piling event (Fig. 2B).

We investigated the effect of a piling event on these three movement metrics by filtering the dataset to include positions before, during, and after each piling event. The duration of each sound exposure varied per piling event and we set the before and after period to match each exposure period, which led to equal periods for comparison per event (Fig. 1E). Piling operations took place during day and night and it took an average of 3353 blows to fully anchor a turbine foundation ca 30 m into the seabed, which lasted between 1.65 and 4.45 h (Fig. 1E). We only included piling events and fish if we had data for all three periods (before, during, and after). This resulted in 24 piling events with sufficient data, including 11 fish with data for 1–18 piling events per individual. We then analysed the effect of piling on cod movement, averaging the movement metrics over half hour time bins, taking the following parameters into account: piling period (before, during, and after), distance of the piling event (km between piling location and turbine C05, range 2.3–7.1 km (Fig. 1C)), and time since last piling event (hours since end of last event, range 0–220 h (Fig. 1E)). Other variables included: current speed (ms^{-1}), tidal elevation (m), sun angle (degrees), and we added fish length (cm) to the movement models to account for variation attributable to the individual.

We then used linear and generalised mixed models (LMM and GLMM) to model the effect of piling on cod movement behaviour. Fish ID (fish ID) and piling location (piling ID) were set as the random variables in all movement models. We checked for temporal autocorrelation and when found, included a correlation for a continuous time covariate (autoregressive process (AR (1))). Model selection from the full model (Table S4) was done based on AIC comparison using model dredging ('MuMin' version 1.43, Table S4). We used the R package 'lme4' (version 1.1) for both LMMs and GLMMs. Cod half-hour step length was log-transformed (\log_{10}) to obtain a normally distributed dataset. The best model (lowest AIC, Table S4) for cod step length was an LMM and included: $\log(\text{step length}) \sim \text{sun angle} + \text{tidal elevation} + \text{current speed} + (1|\text{piling ID}) + (1|\text{fish ID})$. For the distance to the scour-bed protection layer, the best model was an LMM including: $\text{distance scour-bed} \sim \text{period} + \text{distance to piling event} + \text{sun angle} + \text{tidal elevation} + \text{current speed} + \text{period} * \text{distance to piling event} + (1|\text{piling ID}) + (1|\text{fish ID})$. The top model for cod relative distance to the piling location was a GLMM (distribution gamma, link = log) including: $\text{relative distance piling} \sim \text{period} + \text{distance to piling event} + \text{hours since last event} + \text{tidal elevation} + \text{current speed} + \text{period} * \text{distance to piling location} +$

Table 1
Cod movement metrics.

Movement metric	Calculated as
Step length (m)	Linear distance between consecutive average half hour fish positions (Fig. 2A)
Distance to turbine scour-bed (m)	Distance of each fish position to the centre of the scour-bed of the closest turbine (Fig. 2A)
Relative distance to piling event (m)	Relative distance of each fish position to the piling event corrected for the distance of the event to the C05 turbine (i.e. centre turbine of the study site, Fig. 2B)

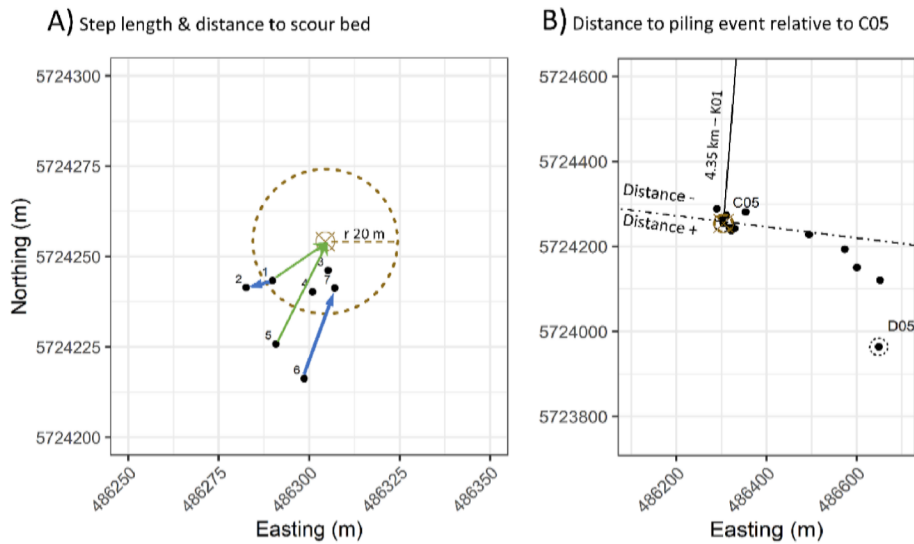


Fig. 2. An example of how cod movement metrics are assessed. Black dots in both panels represent fictitious cod positions. A) Black dots indicate seven fictitious half-hour consecutive positions around Belwind turbine C05. The crossed circle at the centre is the turbine C05 and the dashed line is the edge of the scour-bed protection layer at 20 m from the turbine. The calculation of step length between consecutive positions and cod distance to the centre of the scour bed (i.e. position of the closest turbine) are indicated by blue and green arrows, respectively (both in meters). B) Distance of a cod position to the pile driving location, before, during and after each event, was calculated for all cod positions relative to the distance between the piling events and the centre of C05. Black dots represent fictitious fish positions and the dashed-dotted line served as a reference line to determine whether the relative distance changes of the fish to the piling event were positive (moved further from the piling event) or negative (moved closer to the piling event). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

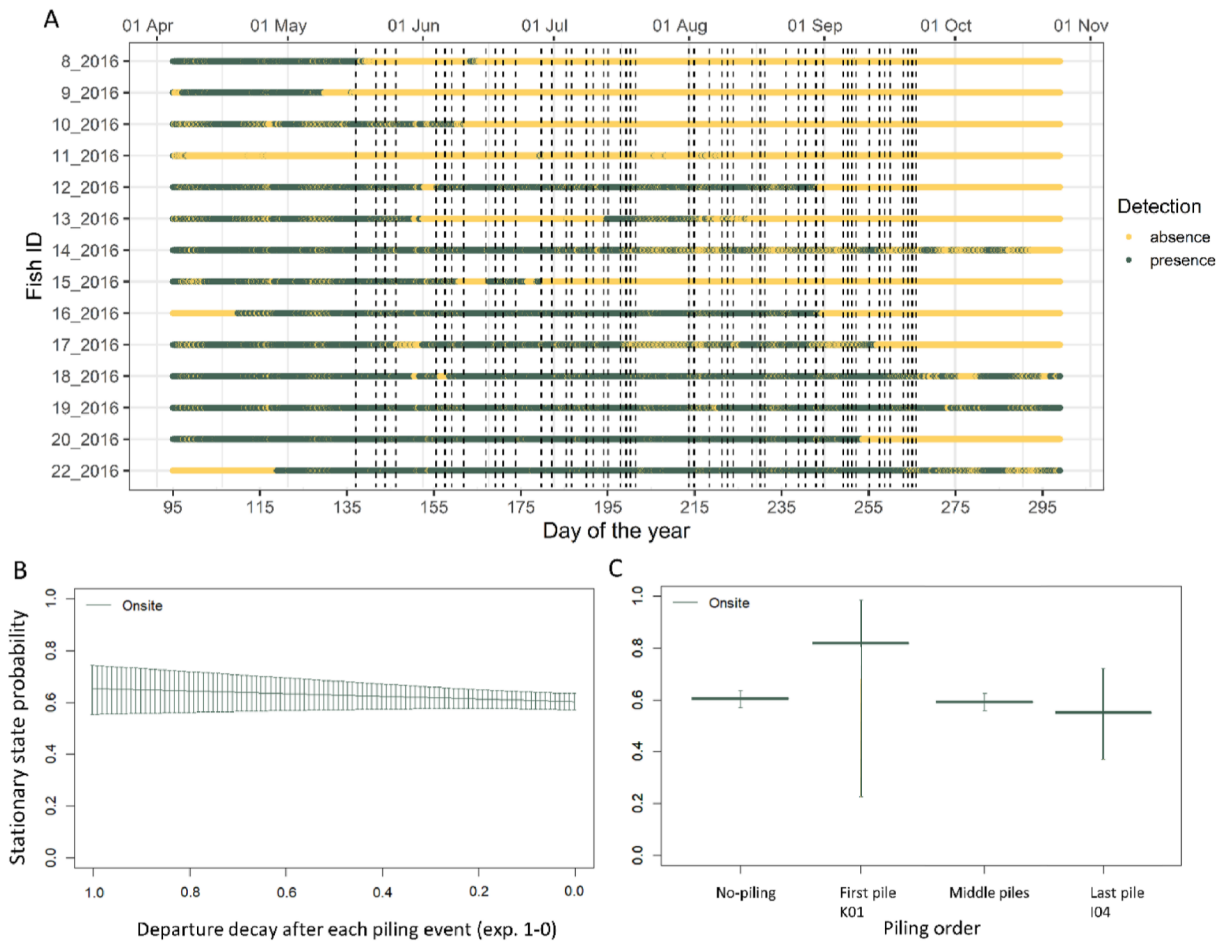


Fig. 3. A) Half hour presence/absence of individual cod (fish ID on the y axis) over the entire study period (5 April – October 30, 2016). The dotted vertical lines represent the 50 piling events during which monopile foundations were piled into the seabed for the construction of the Nobelwind wind farm. Hidden Markov model (HMM) predicted stationary state probabilities of cod in the Onsite behavioural state including the 95% confidence intervals (CI). B) Effect of pile driving on Onsite probability, including a 24 h exponential decay after the end of each piling period (value of 1 during piling followed by an exponential decay to 0 (representing 24 h later) after each individual piling period ended). C) Effect of piling order on Onsite probability, including a level for the first, last and middle piling events and for all non-piling moments.

tidal elevation*current speed + (1|piling ID) + (1|fish ID).

3. Results

3.1. Presence/absence

Cod presence within reach of our receiver network fluctuated over the study period (Fig. 3A). However, we found no significant effect of pile driving on the probability that cod moved out of the study area, with or without the 24 h decay period after each piling event (which means that the probability that cod spent less time in the Onsite state did not change significantly over the exponential decay 1–0, Fig. 3B). In addition, we also did not find any significant differences in time spent in the Onsite state (the 95% confidence intervals (CI) overlapped between the four levels of the piling order variable), from before to after the first or last piling event in comparison to events in the middle or moments when there was no piling activity (Fig. 3C). Day of the year strongly affected the departure from the area, as over time more cod are expected to leave (Reubens et al., 2013c) and spend less time in the Onsite state (Fig. S1). After the first week of August, day 220, 50% of the tagged fish had left the area (Fig. 3A).

3.2. Movement behaviour

Our data revealed unprecedented detail in individual tracks of free-ranging fish during piling events. The individual tracks and positions of the tagged cod around turbine C05 revealed highly variable movement patterns per individual (Fig. 4). For example, fish with the tag ID numbers 12, 16 and 20, when present during these four piling events, were always very close to the turbine before, during, and after piling. Fish 18 and 19, when present, tended to move around at some distance from the turbine before piling in three of the events, but always moved closer to the turbine during and especially after piling, typically also moving away from the direction of the sound source. Fish 14 was close to the turbine in two of the examples before the piling started, and moved closer to and further from the turbine when the sound source was nearby (Fig. 4A) and when it was further away, respectively (Fig. 4B). Fish 15 was also close before the piling started in the same two examples, but moved away when the piling source was nearby (Fig. 4A) and stayed close to the turbine during and after the piling at a more distant location (Fig. 4B).

In the best model for step length period, distance and time between piling events were not included and we were therefore unable to further investigate any significant effects of these factors. We did plot the step length against piling period, distance, and time for visual comparison and saw that step length was fairly similar among periods (Fig. 5A). Environmental variables that influenced the step length significantly were: sun angle ($p < 0.0001$, estimate: -0.005), step lengths were largest during night time; current speed ($p < 0.0001$, estimate: -0.82), step lengths increased with increasing current speed; and tide ($p < 0.03$, estimate: 0.722), step lengths were largest during absolute low tide.

We also found significant variation in cod distance to the scour-bed among the piling periods (Fig. 5B). Cod significantly reduced their distance (m) to the closest scour-bed from before to during ($p < 0.03$), and from during to after ($p < 0.002$) the piling, and were thus moving closer towards the turbine (Fig. 5B left panel). In addition, this effect showed an interaction with the distance to the piling location ($p < 0.001$, Fig. 5B middle panel), with a relatively stronger effect at large distances ($\sim 4\text{--}7$ km) before pile driving and a relatively weaker effect at large distances after pile driving. Other variables included in the model that had a significant effect were: sun angle ($p < 0.0001$, estimate: -0.006), during day time fish were closer to the scour-bed; tide ($p < 0.0001$, estimate: -0.162), distance fluctuated with tidal changes; and current speed ($p < 0.0001$, estimate: 1.286), when current speeds increased, so did fish distance to the scour-bed.

Piling also had a significant effect on the relative distance of cod to

the piling location; cod were positioned closer to a piling location before piling started than during ($p < 0.0001$) or after ($p < 0.0001$) piling (Fig. 5C). The trend of cod moving away from the piling location was strongest at large absolute distances of the pile driving (Fig. 5C middle panel). At these piling events, fish were positioned closer to the pile driving location before the pile driving started (relative distance was less than 0) and the effect of movement away from the piling sources was strongest for these animals, resulting in a significant interaction with piling period (Fig. 5C middle panel). There was no effect of the time since the previous piling event on cod relative distance alone. There was, however, a significant interaction between the change in relative distance to the piling location and the length of the preceding interval between consecutive piling events, with cod positioning themselves closer to the piling location in the hours before the event started after a longer interval (Fig. 5C). Other variables influencing relative distance were: tide ($p < 0.0001$, estimate: 11.504), during absolute low tide fish were further from the turbine C05 than during high tide; and current speed ($p < 0.0001$, estimate: -34.581), during low current speeds the fish were closer to the turbine C05.

4. Discussion

Our results indicate that: 1) pile driving at distances between 2.3 and 7.1 km did not cause cod to leave the detection area during exposure, but that 2) there were several more subtle effects of piling on cod spatial behaviour. Over the six-and-a-half-month study period, cod left the detection area over time, however, this was statistically unrelated to the piling activity. Cod moved closer to the local turbine scour-bed during and after each piling event compared to the periods before pile-driving. Cods' relative distances to the pile driving location were correlated with the absolute distance to the location of the event: when piling took place at larger distances, the fish were positioned relatively closer to the sound source before the piling started and moved to an area further away from the source during and after piling. Time since last piling event in itself had no effect on cod movement, but a significant interaction indicated that with longer time intervals cod were positioned relatively closer to the sound source before piling started, which caused the effect of moving away during and after piling at large absolute distances to be stronger.

4.1. Disturbance-related departure decisions

We found no indication that cod left the area sooner than expected when exposed to pile driving sounds. Iafate et al. (2016) found that tagged grey snappers (*Lutjanus griseus*) were more likely to leave an area when they were exposed to piling sounds. However, that effect was species-specific, as the same researchers found no effect of piling on the residency of sheepshead (*Archosargus probatocephalus*) (Iafate et al., 2016). They argued that this difference in response could be caused by a general species-specific difference in site fidelity. From previous work on the residency of cod at offshore wind farms, we know that during summer months, cod often stay close to one turbine base for several months, only making occasional excursions to other turbines (Reubens et al., 2013c). This site fidelity of cod during the summer could explain why we did not find a change in presence. In line with the data on sheepshead (Iafate et al., 2016), species with long residence periods may thus be less easily deterred by loud sounds. Our model did show that over time, cod moved out of the detection area. We expected to find this pattern as cod could move to another turbine outside of our detection range during the summer (Winter et al., 2010) and in addition, at the end of the summer, many move away from the offshore areas towards coastal areas (Reubens et al., 2013c).

The behavioural results of the current study differ from those observed during an earlier study on the effects of seismic survey sounds on Atlantic cod within the same wind farm (van der Knaap et al., 2021a). In that study, cod left the area shortly after the experimental exposure had ended (van der Knaap et al., 2021a). This difference may relate to

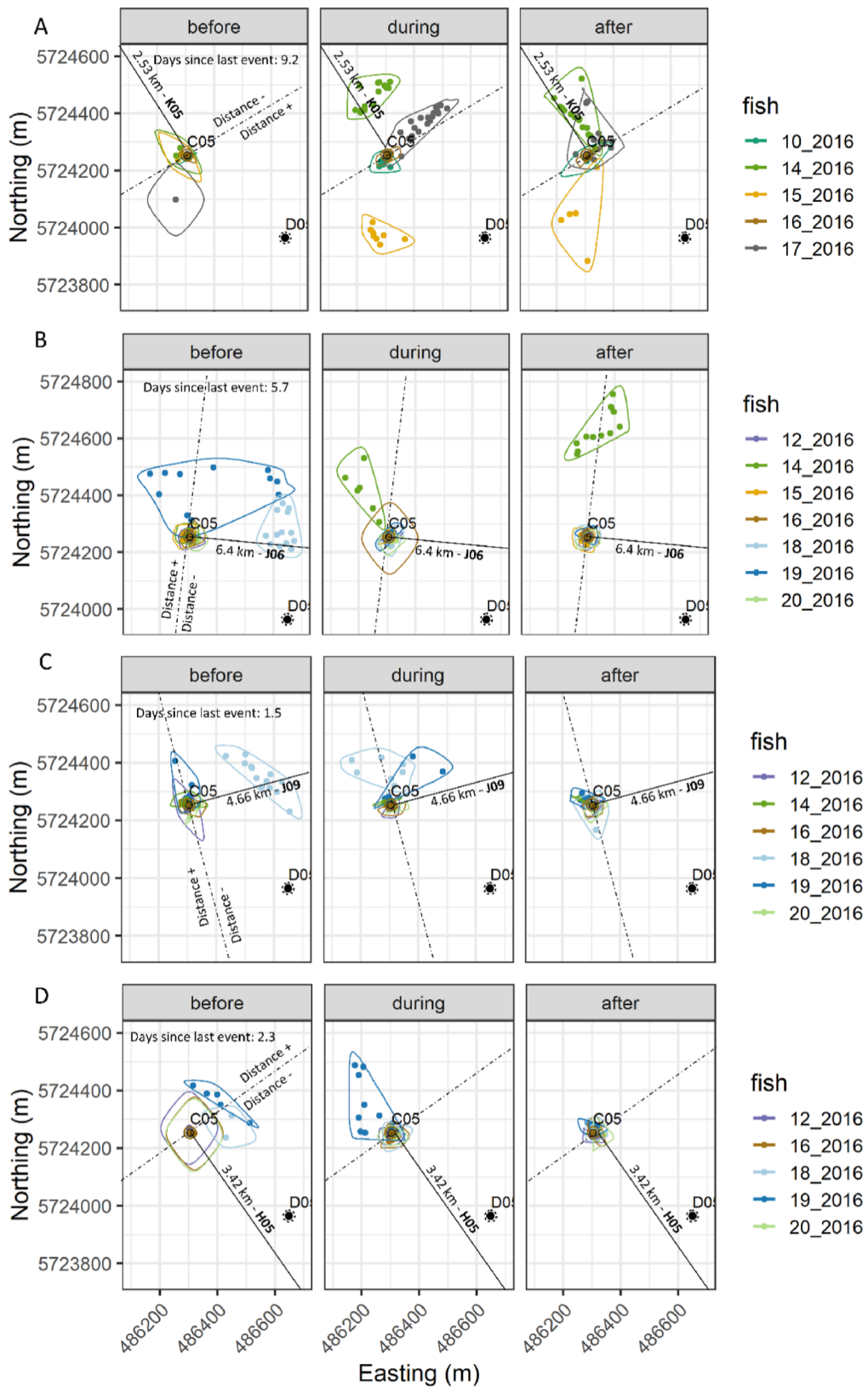


Fig. 4. Examples of cod positions before, during and after four piling events in chronological order of construction, for wind turbines A) K05, B) J06, C) J09, and D) H05. The distance in kilometres and time since the previous piling event in days, are indicated in the panels. Individual fish are colour-coded and the turbines are at the junction of the direction line towards the piling event and the distance reference line (dashed-dotted lines). The contour around each individual fish illustrates the distribution of positions and does not represent an area use quantification. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

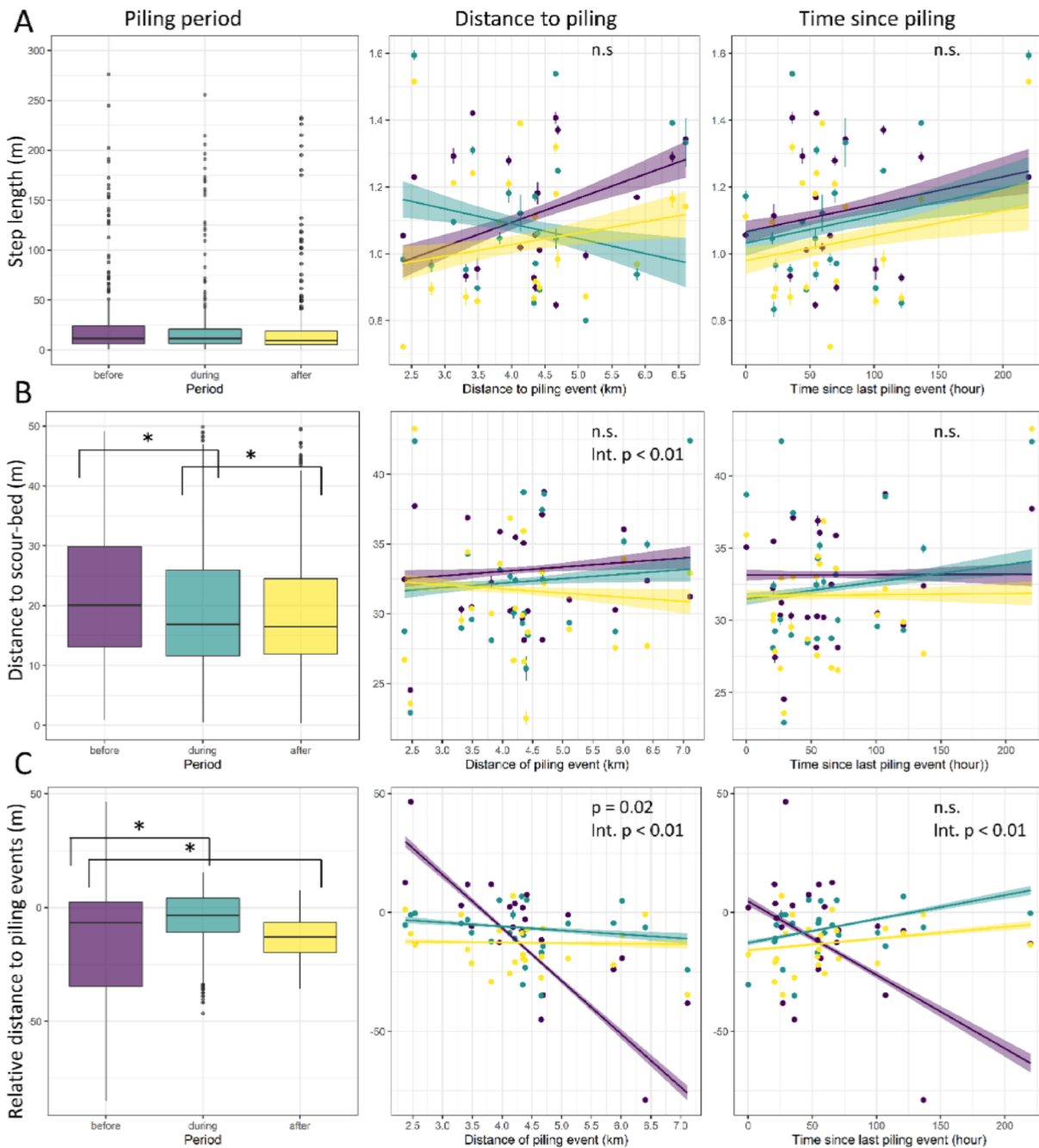


Fig. 5. From left to right the effect of: piling period, distance to the piling event and time since last event, on A) cod step length (m) (not included in the best model and therefore no measurable effect), B) cod distance to scour-bed (m) and C) cod relative distance to the piling event (m). For piling period the significant differences are indicated with an asterisk (*, indicating a $p < 0.05$). For the two interactions with period (of distance of piling event and time since last event), the significance of the overall trend is indicated (n.s. = not significant) as well as that of the interaction (Int.).

the different nature of sound exposure, as pile driving and seismic surveys differ from each other in a number of ways. Sound exposure periods of a single piling event are relatively short: ca 1.5–4.5 h, in comparison to a full seismic survey: continuously over four days in (van der Knaap et al., 2021a), but often weeks to months for actual surveys (Day et al., 2017; Slabbekoorn et al., 2019). The pulse rate intervals also differ, with 2–4 s for pile driving and 8–15 s for seismic surveys. In addition, pile driving occurs at a fixed location, with subsequent pile driving events making discrete steps in space, while a seismic survey typically moves back and forth across an area for longer periods of gradual changes in space. We obviously need more data on more seismic survey and pile driving events to gain general understanding about which parameters

are critical for fish departure tendencies. We also need data on more species at the time, as species may interact and vary in their residence tendency, and on the energetic trade-offs associated with abandoning local resources (Iafate et al., 2016; Kok et al., 2021; Soudijn et al., 2020; van der Knaap et al., 2021a).

4.2. Scour-bed related positioning

We found that cod moved closer to the scour-bed during and after the piling periods, from an average distance of 20 m before to 16 m during and after. Around the turbine base, a scour-bed rocky protection layer ($r = 20$ m) is deposited, which provides fish with food and hiding places

(Reubens et al., 2013a). In our study area in the Belgian part of the North Sea, cod have a diurnal activity cycle (Reubens et al., 2013c; van der Knaap et al., 2021a) and are most active during twilight periods when they move around searching for food (Reubens et al., 2013b). This diurnal activity pattern is probably caused by a trade-off between light-dependent foraging success (Reubens et al., 2013b) and predation pressure (Scheidat et al., 2011; Todd et al., 2009). In the current study, piling events occurred both during day and night and we found a general effect of time of day (i.e. sun angle), in which cod were positioned on top and closer to, the centre of the scour bed during the day and moved towards the edges during night time, which could reflect a diurnal cycle in food searching behaviour.

The effect size of the response is only a few meters but could be related to some sort of general anxiety response. A typical response of fish to impulsive sounds is moving down the water column and forming tighter aggregations (e.g. Hawkins et al., 2014; Neo et al., 2018). Our tags included a pressure sensor, but with insufficient resolution (± 0.5 m at 30 m depth (Innovasea)) for the small range in depth variation. Cod in the southern North Sea live in relatively shallow water and are closely associated with the seabed (Reubens et al., 2013c), which makes vertical avoidance by downward movement an unlikely response for this species here and any changes in depth inherently small. Additionally, the area around the turbines' scour-beds is sandy bottom that does not provide many hiding places. Cod movement towards the scour-bed during and after piling could therefore be indicative of cod seeking shelter closer to the turbine base and in-between the rocks.

This result of moving towards the scour-bed again differs from the findings in van der Knaap et al. (2021a), where cod moved away from the scour-bed during and after a four-day impulsive seismic survey (van der Knaap et al., 2021a). Those earlier results were in line with the observed gradual departure of cod from the detection area after the sound exposure period in that study. In the present study, however, cod did not leave the area. The benefits of staying in a noisy area may outweigh those of moving to a more silent one. Schools of herring that were exposed to seismic sounds did not cease their feeding activity (Pena et al., 2013). Pena et al. (2013) explained their finding by a strong motivation of the school to feed, a lack of suddenness of the exposure and an increased level of tolerance to the type of sound. Atlantic cod around offshore wind turbines are highly motivated to stay for food during summer, but apparently either the disturbance was different for the experimental seismic survey (van der Knaap et al., 2021a) and the pile driving (current study), or the consequences of leaving differed among the years of study, leading to the differences in their spatial behaviour relative to the scour bed.

4.3. Horizontal displacements relative to the sound source

Another interesting finding of the current study is that cod were positioned closer to the location of the sound source before piling started irrespective of the direction of the piling activity to the location of the fish. This was particularly so when the source was further from the fish and when the time since the last event was longer. This could be an indication that sounds from preparatory activities before the onset of piling may already be somehow deterrent when nearby, but that the very same sounds, when from larger distances and fainter, could be attractive and elicit phonotaxis. Indeed, certain sounds or sound levels can attract fish (Gordon et al., 2019; Neo et al., 2016). Radford et al. (2011) demonstrated how juvenile reef fish find their way back to their reef using environmental sound cues. In addition, man-made sounds can also attract fish as Chapman et al. (1974) observed how different fish species were attracted to the low-frequency sounds of scuba diving equipment.

Most studies investigating the movement of fish in response to impulsive sounds are done in captivity, which hampers a proper assessment of horizontal displacement (Davidsen et al., 2019; Neo et al., 2016). Potential horizontal displacements have been observed for

free-swimming pelagic fish species in response to seismic sound (Engås and Løkkeborg, 1996; Løkkeborg et al., 2012). In the current study, we were unable to observe directional swimming behaviour but did find that fish were positioned closer to the piling location before piling started, in particular when piling preparations were happening at larger absolute distances. The type and level of sounds produced by these activities (vessel manoeuvring, on-board handling of heavy materials) could potentially have attracted the fish into the direction of the piling location before the actual start of pile driving. The displacements are only several meters, but since the area use of the cod is restricted to the scour-bed surrounding the turbine base ($r = 20$ m), they indicate that the cod stay above the scour-bed during and after the piling exposure more than before.

We also observed distinct individual positioning and movement patterns of cod around the turbine. Individual personalities have been identified for Atlantic cod and have been linked to different response styles to environmental changes (Villegas-Ríos et al., 2017, 2018), which might also apply to the responsiveness to anthropogenic sounds. Individual body condition may also affect response patterns, as Harding et al. (2020) showed that damselfish (*Chromis viridis*) with a poorer body condition startled later at shorter distances due to a predator threat during boat noise exposure, than did fish with a good body condition. We did not investigate the effect of individual differences further in our data set, but inter-individual variation could be an important factor in understanding animal responses to sound and has also been recognised as an important factor in translating behavioural effects to population dynamics in fish (Bolnick and Ballare, 2020).

4.4. Potential effects of habituation

Cod were exposed to a total of 50 piling events spread over four months. Although the interval between consecutive piling events varied from 1 to 12 days, we found no effect of time since last piling event on cod step length or their distance to the scour-bed. We only found an interaction between piling period and time since last piling event for relative distance to the piling site. The repetitive nature of the sound exposure may also have contributed to the lack of impact on departure, as over accumulating exposure time, fish may become more tolerant to the sound levels. Nedelec et al. (2016) demonstrated that juvenile reef fish (*Dascyllus trimaculatus*) exposed to boat noise reduced their hiding behaviour as well as their respiration rates (indicator for stress) after two weeks of exposure. Repeated exposure to impulsive sound has also been shown to reduce the disturbance response in seabass (*Dicentrarchus labrax*) over time (Radford et al., 2016).

Each piling event, in the current study, was precluded by a period of increased human activity at the piling site which might have served as some sort of ramp-up scenario, i.e. slowly increasing sound levels, providing animals with a warning signal, before sound exposure levels rise to the high levels of pile driving. We found that cod did not leave during or after the piling events, which might also be due to these slowly increasing sound levels, which may have accommodated habituation to the repeated occurrence of piling. However, we still know very little about the effect of fluctuating sound levels (Neo et al., 2014), and a net-pen study demonstrated little or no effect of a ramp-up exposure scenario on responsiveness in seabass (Neo et al., 2016).

5. Conclusions

The current study revealed that exposure to pile driving sounds at relatively close range of a few kilometres did not cause free-ranging cod to leave an area. We were able to show, however, several more subtle response patterns in their movement behaviour: they moved a couple of meters closer towards the scour-bed of the nearest turbine and also moved away from the sound source location. Spatial positioning before pile driving started suggested phonotactic approach behaviour in response to preparatory sounds at relatively large distances. Such

changes in behaviour seem modest but can lead to changes in energy expenditure, which could potentially accumulate to population-level consequences (Soudijn et al., 2020). Offshore energy acquisition through the construction of wind farms is part of the EU's plans to move towards becoming climate-neutral by 2050 (European Commission, 2018), which will result in more piling in the North Sea in the coming years. Further studies are therefore needed to understand whether subtle behavioural changes like the ones we observed also occur with alternative construction strategies such as vibropiling, or while taking mitigation measures into account, such as bubble screens or acoustic deterrent devices. We also need to know whether the behavioural changes have any consequences for individuals or populations, whether there are any cumulative effects of co-occurrence of multiple stressors, and whether our findings can be extrapolated to other species. We therefore believe that raised awareness and more studies into anthropogenic under-water noise are warranted. More insight may allow us to detect and prevent unwanted detrimental effects of green alternatives to fossil energy resources on conservation of marine fish species like cod as well as their coastal habitat.

Author statement

Inge van der Knaap: Methodology, Formal analysis, Visualization, Writing – original draft. **Hans Slabbekoorn:** Funding acquisition, Writing – review & editing, Supervision. **Tom Moens:** Resources, Funding acquisition, Writing – review & editing, Supervision. **Dries Van den Eynde:** Software, Writing – review & editing. **Jan Reubens:** Conceptualization, Methodology, Investigation, Writing – review & editing

Declaration of competing interest

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

Acknowledgements

P. Verhelst assisted with the set-up of the receivers, data collection, and fish capture. We thank L. Thomas for help and advice regarding the data analysis and C. ten Cate for feedback on the manuscript. Parkwind is acknowledged for their kind cooperation and for allowing access to the offshore wind farm Belwind. This work was supported by the E&P Sound and Marine Life Joint Industry Programme (JIP) as part of the 'PCAD4Cod' project. Infrastructure for fieldwork (RV Simon Stevin, RHIB Zeekat and receiver deployment) were provided by Flanders Marine Institute and funded by the Research Foundation - Flanders (FWO) as part of the Belgian contribution to LifeWatch. This work is supported by COST Action CA18102. We thank the reviewers for their constructive feedback.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.envpol.2022.118913>.

References

- Ainslie, M.A., Halvorsen, M.B., Müller, R.A.J., Lippert, T., 2020. Application of damped cylindrical spreading to assess range to injury threshold for fishes from impact pile driving. *J. Acoust. Soc. Am.* 148, 108–121. <https://doi.org/10.1121/10.0001443>.
- Ashley, M.C., Mangi, S.C., Rodwell, L.D., 2014. The potential of offshore windfarms to act as marine protected areas - a systematic review of current evidence. *Mar. Pol.* 45, 301–309. <https://doi.org/10.1016/j.marpol.2013.09.002>.
- Bolnick, D.I., Ballare, K.M., 2020. Resource diversity promotes among-individual diet variation, but not genomic diversity, in lake stickleback. *In: J. Ecol. Lett.*, pp. 495–505

- Brabant, R., Degraer, S., Rumes, B., 2013. Monitoring offshore wind farms in the Belgian part of the North Sea: setting the scene, pp. 1–5.
- Bruintjes, R., Simpson, S.D., Harding, H., Bunce, T., Benson, T., Rossington, K., Jones, D., 2016 July. The impact of experimental impact pile driving on oxygen uptake in black seabream and plaice. *In: Proceedings of Meetings on Acoustics 4ENAL*, p. 010042. Vol. 27, No. 1, Acoustical Society of America.
- Casper, B.M., Halvorsen, M.B., Carlson, T.J., Popper, A.N., 2017. Onset of barotrauma injuries related to number of pile driving strike exposures in hybrid striped bass. *J. Acoust. Soc. Am.* 141, 4380–4387. <https://doi.org/10.1121/1.4984976>.
- Casper, B.M., Smith, M.E., Halvorsen, M.B., Sun, H., Carlson, T.J., Popper, A.N., 2013. Effects of exposure to pile driving sounds on fish inner ear tissues. *Comp. Biochem. Physiol. Mol. Integr. Physiol.* 166, 352–360. <https://doi.org/10.1016/j.cbpa.2013.07.008>.
- Chapman, C.J., Johnstone, A.D.F., Dunn, J.R., Creasey, D.J., 1974. Reactions of fish to sound generated by divers' open-circuit underwater breathing apparatus. *Mar. Biol.* 27, 357–366. <https://doi.org/10.1007/BF00394372>.
- Dahl, P.H., de Jong, C., Popper, A.N., 2015. The underwater sound field from impact pile driving and its potential effects on marine life. *Acoust. Today* 11, 18–25.
- Davidson, J.G., Dong, H., Linné, M., Andersson, M.H., Piper, A., Prystay, T.S., Hvam, E. B., Thorstad, E.B., Whoriskey, F., Cooke, S.J., Sjørusen, A.D., Rønning, L., Netland, T. C., Hawkins, A.D., 2019. Effects of sound exposure from a seismic airgun on heart rate, acceleration and depth use in free-swimming Atlantic cod and saithe. *Conserv. Physiol.* 7, 1–19. <https://doi.org/10.1093/conphys/coz020>.
- Day, R.D., McCauley, R.D., Fitzgibbon, Q.P., Hartmann, K., Semmens, J.M., 2017. Exposure to seismic air gun signals causes physiological harm and alters behavior in the scallop *Pecten fumatus*. *Proc. Natl. Acad. Sci. U.S.A.* 114, E8537–E8546. <https://doi.org/10.1073/pnas.1700564114>.
- De Mesel, I., Kerckhof, F., Norro, A., Rumes, B., Degraer, S., 2015. Succession and seasonal dynamics of the epifauna community on offshore wind farm foundations and their role as stepping stones for non-indigenous species. *Hydrobiologia* 756, 37–50. <https://doi.org/10.1007/s10750-014-2157-1>.
- Degraer, S., Brabant, R., Rumes, B., Vigin, L., 2017. Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea: A Continued Move towards Integration and Quantification. Royal Belgian Institute of Natural Sciences, OD Natural Environment, Marine Ecology and Management Section, Brussels.
- Duarte, C.M., Chapuis, L., Collin, S.P., Costa, D.P., Devassy, R.P., Eguiluz, V.M., Erbe, C., Gordon, T.A.C., Halpern, B.S., Harding, H.R., Havlik, M.N., Meekan, M., Merchant, N.D., Miksis-Olds, J.L., Parsons, M., Predragovic, M., Radford, A.N., Radford, C.A., Simpson, S.D., Slabbekoorn, H., Staerman, E., Van Opzeeland, I.C., Winderen, J., Zhang, X., Juanes, F., 2021. The soundscape of the Anthropocene ocean. *Science* 371, 1–10. <https://doi.org/10.1126/science.aba4658>.
- Engås, A., Løkkeborg, S., 1996. Effects of seismic shooting on local abundance and catch rates of cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). *Can. J. Fish. Aquat. Sci.* 53, 2238–2249.
- Engelhard, G.H., Righton, D.A., Pinnegar, J.K., 2014. Climate change and fishing: a century of shifting distribution in North Sea cod. *Global Change Biol.* 20, 2473–2483. <https://doi.org/10.1111/gcb.12513>.
- European Commission, 2018. A Clean Planet for All. A European Long-Term Strategic Vision for a Prosperous, Modern, Competitive and Climate Neutral Economy. Com, p. 773.
- Freeman, K., Frost, C., Hundley, G., Roberts, A., Valpy, B., Holtinen, H., Ramírez, L., Pineda, I., 2019. Our Energy, Our Future: How Offshore Wind Will Help Europe Go Carbon-Neutral. Wind Europe.
- Gill, A.B., 2005. Offshore renewable energy: ecological implications of generating electricity in the coastal zone. *J. Appl. Ecol.* 42, 605–615. <https://doi.org/10.1111/j.1365-2664.2005.01060.x>.
- Gill, A.B., Degraer, S., Lipsky, A., Mavraki, N., Methratta, E., Brabant, R., 2020. Setting the context for offshore wind development effects on fish and fisheries. *Oceanography* 33, 118–127. <https://doi.org/10.5670/oceanog.2020.411>.
- Gordon, T.A.C., Radford, A.N., Davidson, I.K., Barnes, K., McCloskey, K., Nedelec, S.L., Meekan, M.G., McCormick, M.I., Simpson, S.D., 2019. Acoustic enrichment can enhance fish community development on degraded coral reef habitat. *Nat. Commun.* 10, 1–7. <https://doi.org/10.1038/s41467-019-13186-2>.
- Halvorsen, M.B., Casper, B.M., Matthews, F., Carlson, T.J., Popper, A.N., 2012a. Effects of exposure to pile-driving sounds on the lake sturgeon, Nile tilapia and hogchoker. *Proc. R. Soc. B Biol. Sci.* 279, 4705–4714. <https://doi.org/10.1098/rspb.2012.1544>.
- Halvorsen, Michele B., Casper, B.M., Woodley, C.M., Carlson, T.J., Popper, A.N., 2012b. Threshold for onset of injury in chinook salmon from exposure to impulsive pile driving sounds. *PLoS One* 7, 2–12. <https://doi.org/10.1371/journal.pone.0038968>.
- Hammar, L., Wikström, A., Molander, S., 2014. Assessing ecological risks of offshore wind power on Kattegat cod. *Renew. Energy* 66, 414–424. <https://doi.org/10.1016/j.renene.2013.12.024>.
- Harding, H.R., Gordon, T.A.C., Wong, K., McCormick, M.I., Simpson, S.D., Radford, A.N., 2020. Condition-dependent responses of fish to motorboats. *Biol. Lett.* 16 <https://doi.org/10.1098/rsbl.2020.0401>, 20200401.
- Hawkins, A.D., Roberts, L., Cheesman, S., 2014. Responses of free-living coastal pelagic fish to impulsive sounds. *J. Acoust. Soc. Am.* 135, 3101–3116. <https://doi.org/10.1121/1.4870697>.
- Herbert-Read, J.E., Kremer, L., Bruintjes, R., Radford, A.N., Ioannou, C.C., 2017. Anthropogenic noise pollution from pile-driving disrupts the structure and dynamics of fish shoals. *Proc. R. Soc. B Biol. Sci.* 284, 20171627. <https://doi.org/10.1098/rspb.2017.1627>.
- Hildebrand, J.A., 2009. Anthropogenic and natural sources of ambient noise in the ocean. *Mar. Ecol. Prog. Ser.* 395, 5–20. <https://doi.org/10.3354/meps08353>.

- Hubert, J., Campbell, J.A., Slabbekoorn, H., 2020a. Effects of seismic airgun playbacks on swimming patterns and behavioural states of Atlantic cod in a net pen. *Mar. Pollut. Bull.* 160, 111680. <https://doi.org/10.1016/j.marpolbul.2020.111680>.
- Hubert, J., Neo, Y.Y., Winter, H.V., Slabbekoorn, H., 2020b. The role of ambient sound levels, signal-to-noise ratio, and stimulus pulse rate on behavioural disturbance of seabass in a net pen. *Behav. Process.* 170, 103992. <https://doi.org/10.1016/j.beproc.2019.103992>.
- Hutchings, J.A., 2004. The cod that got away. *Nature* 428, 899–900. <https://doi.org/10.1038/428899a>.
- Iafate, J.D., Watwood, S.L., Reyier, E.A., Scheidt, D.M., Dossot, G.A., Crocker, S.E., 2016. Effects of pile driving on the residency and movement of tagged reef fish. *PLoS One* 11, 1–17. <https://doi.org/10.1371/journal.pone.0163638>.
- Kok, A.C.M., van Hulten, D., Timmerman, K.H., Lankhorst, J., Visser, F., Slabbekoorn, H., 2021. Interacting effects of short-term and long-term noise exposure on antipredator behaviour in sand gobies. *Anim. Behav.* 172, 93–102. <https://doi.org/10.1016/j.anbehav.2020.12.001>.
- Langrock, R., King, R., Matthiopoulos, J., Thomas, L., Fortin, D., Morales, J.M., 2012. Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. *Ecology* 93, 1–22. <https://doi.org/10.1890/11.2241.1>.
- Lindeboom, H.J., Kouwenhoven, H.J., Bergman, M.J.N., Bouma, S., Brasseur, S., Daan, R., Fijn, R.C., De Haan, D., Dirksen, S., Van Hal, R., Hille Ris Lambers, R., Ter Hofstede, R., Krijgsveld, K.L., Leopold, M., Scheidat, M., 2011. Short-term ecological effects of an offshore wind farm in the Dutch coastal zone; a compilation. *Environ. Res. Lett.* 6, 1–13. <https://doi.org/10.1088/1748-9326/6/3/035101>.
- Lippert, T., Ainslie, M.A., von Estorff, O., 2018. Pile driving acoustics made simple: damped cylindrical spreading model. *J. Acoust. Soc. Am.* 143, 310–317. <https://doi.org/10.1121/1.5011158>.
- Løkkeborg, S., Ona, E., Vold, A., Salthaug, A., 2012. Sounds from seismic air guns : gear- and species- specific effects on catch rates and fish distribution. *Can. J. Fish. Aquat. Sci.* 69, 1278–1291. <https://doi.org/10.1139/F2012-059>.
- Madsen, P.T., Wahlberg, M., Tougaard, J., Lucke, K., Tyack, P., 2006. Wind turbine underwater noise and marine mammals: implications of current knowledge and data needs. *Mar. Ecol. Prog. Ser.* 309, 279–295. <https://doi.org/10.3354/meps309279>.
- Martin, S.B., Barclay, D.R., 2019. Determining the dependence of marine pile driving sound levels on strike energy, pile penetration, and propagation effects using a linear mixed model based on damped cylindrical spreading. *J. Acoust. Soc. Am.* 146, 109–121. <https://doi.org/10.1121/1.5114797>.
- Mavraki, N., De Mesel, I., Degraer, S., Moens, T., Vanaverbeke, J., 2020. Resource niches of co-occurring invertebrate species at an offshore wind turbine indicate a substantial degree of trophic plasticity. *Front. Mar. Sci.* 7, 1–17. <https://doi.org/10.3389/fmars.2020.00379>.
- McClintock, A.B., Michelot, T., 2020. momentHMM: R package for analysis of telemetry data using generalized multivariate hidden Markov models of animal movement. <https://doi.org/10.1111/2041-210X.12995>.
- Nabe-Nielsen, J., van Beest, F.M., Grimm, V., Sibly, R.M., Teilmann, J., Thompson, P.M., 2018. Predicting the impacts of anthropogenic disturbances on marine populations. *Conserv. Lett.* 11, 1–8. <https://doi.org/10.1111/conl.12563>.
- Nedelec, S.L., Mills, S.C., Lecchini, D., Nedelec, B., Simpson, S.D., Radford, A.N., 2016. Repeated exposure to noise increases tolerance in a coral reef fish. *Environ. Pollut.* 216, 428–436. <https://doi.org/10.1016/j.envpol.2016.05.058>.
- Neo, Y.Y., Hubert, J., Bolle, L., Winter, H.V., Ten Cate, C., Slabbekoorn, H., 2016. Sound exposure changes European seabass behaviour in a large outdoor floating pen: effects of temporal structure and a ramp-up procedure. *Environ. Pollut.* 214, 26–34. <https://doi.org/10.1016/j.envpol.2016.03.075>.
- Neo, Y.Y., Hubert, J., Bolle, L.J., Winter, H.V., Slabbekoorn, H., 2018. European seabass respond more strongly to noise exposure at night and habituate over repeated trials of sound exposure. *Environ. Pollut.* 239, 367–374. <https://doi.org/10.1016/j.envpol.2018.04.018>.
- Neo, Y.Y., Seitz, J., Kastelein, R.A., Winter, H.V., ten Cate, C., Slabbekoorn, H., 2014. Temporal structure of sound affects behavioural recovery from noise impact in European seabass. *Biol. Conserv.* 178, 65–73. <https://doi.org/10.1016/j.biocon.2014.07.012>.
- Neo, Y.Y., Ufkes, E., Kastelein, R.A., Winter, H.V., ten Cate, C., Slabbekoorn, H., 2015. Impulsive sounds change European seabass swimming patterns: influence of pulse repetition interval. *Mar. Pollut. Bull.* 97, 111–117. <https://doi.org/10.1016/j.marpolbul.2015.06.027>.
- Nghiem, A., Pineda, I., 2017. *Wind Energy in Europe: Scenarios for 2030*. Wind Europe.
- Paxton, A.B., Shertzer, K.W., Bachele, N.M., Kellison, G.T., Riley, K.L., Taylor, J.C., 2020. Meta-analysis reveals artificial reefs can be effective tools for fish community enhancement but are not one-size-fits-all. *Front. Mar. Sci.* 7, 282. <https://doi.org/10.3389/fmars.2020.00282>.
- Pena, H., Handegard, N.O., Ona, E., 2013. Feeding herring schools do not react to seismic air gun surveys. *ICES J. Mar. Sci.* 70, 1174–1180.
- Petersen, J.K., Malin, T., 2006. Offshore windmill farms: threats to or possibilities for the marine environment. *AMBIO A J. Hum. Environ.* 35, 75–80. [https://doi.org/10.1579/0044-7447\(2006\)35\[75:owfto\]2.0.co;2](https://doi.org/10.1579/0044-7447(2006)35[75:owfto]2.0.co;2).
- Pitcher, T., Kalikoski, D., Pramod, G., Short, K., 2009. Not honouring the code. *Nature* 457, 658–659. <https://doi.org/10.1038/457658a>.
- Popper, A.N., Hastings, M.C., 2009. The effects of anthropogenic sources of sound on fishes. *J. Fish. Biol.* 75, 455–489. <https://doi.org/10.1111/j.1095-8649.2009.02319.x>.
- Popper, A.N., Hawkins, A.D., 2019. An overview of fish bioacoustics and the impacts of anthropogenic sounds on fishes. *J. Fish. Biol.* 94, 692–713. <https://doi.org/10.1111/jfb.13948>.
- Radford, A.N., Lèbre, L., Lecaillon, G., Nedelec, S.L., Simpson, S.D., 2016. Repeated exposure reduces the response to impulsive noise in European seabass. *Global Change Biol.* 22, 3349–3360. <https://doi.org/10.1111/gcb.13352>.
- Radford, C.A., Stanley, J.A., Simpson, S.D., Jeffs, A.G., 2011. Juvenile coral reef fish use sound to locate habitats. *Coral Reefs* 30, 295–305. <https://doi.org/10.1007/s00338-010-0710-6>.
- Reubens, J., Braeckman, U., Vanaverbeke, J., Van Colen, C., Degraer, S., Vincx, M., 2013a. Aggregation at windmill artificial reefs: CPUE of Atlantic cod (*Gadus morhua*) and pouting (*Trisopterus luscus*) at different habitats in the Belgian part of the North Sea. *Fish. Res.* 139, 28–34. <https://doi.org/10.1016/j.fishres.2012.10.011>.
- Reubens, J., De Rijcke, M., Degraer, S., Vincx, M., 2013b. Diel variation in feeding and movement patterns of juvenile Atlantic cod at offshore wind farms. *J. Sea Res.* 85, 214–221. <https://doi.org/10.1016/j.seares.2013.05.005>.
- Reubens, J., Pasotti, F., Degraer, S., Vincx, M., 2013c. Residency, site fidelity and habitat use of Atlantic cod (*Gadus morhua*) at an offshore wind farm using acoustic telemetry. *Mar. Environ. Res.* 90, 128–135. <https://doi.org/10.1016/j.marenvres.2013.07.001>.
- Reubens, J.T., Degraer, S., Vincx, M., 2014. The ecology of benthopelagic fishes at offshore wind farms: a synthesis of 4 years of research. *Hydrobiologia* 727, 121–136. <https://doi.org/10.1007/s10750-013-1793-1>.
- Roberts, L., Harding, H.R., Voellmy, I., Bruintjes, R., Simpson, S.D., Radford, A.N., Breithaupt, T., Elliott, M., 2016. Exposure of benthic invertebrates to sediment vibration: from laboratory experiments to outdoor simulated pile-driving. *Proc. Meet. Acoust.* 27, 010029. <https://doi.org/10.1121/2.0000324>.
- Rose, G.A., 2004. Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years. *Can. J. Fish. Aquat. Sci.* 61, 1553–1557. <https://doi.org/10.1139/f04-173>.
- Scheidat, M., Tougaard, J., Brasseur, S., Carstensen, J., Van Polanen Petel, T., Teilmann, J., Reijnders, P., 2011. Harbour porpoises (*Phocoena phocoena*) and wind farms: a case study in the Dutch North Sea. *Environ. Res. Lett.* 6, 025102. <https://doi.org/10.1088/1748-9326/6/2/025102>.
- Sertlek, H.Ö., Slabbekoorn, H., ten Cate, C., Ainslie, M.A., 2019. Source specific sound mapping: spatial, temporal and spectral distribution of sound in the Dutch North Sea. *Environ. Pollut.* 247, 1143–1157. <https://doi.org/10.1016/j.envpol.2019.01.119>.
- Slabbekoorn, H., 2019. Noise pollution. *Curr. Biol.* 29, R942–R995. <https://doi.org/10.1016/j.cub.2019.06.066>.
- Slabbekoorn, H., Bouton, N., Opzeeland, I., Van, Coers, A., ten Cate, C., Popper, A.N., 2010. A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends Ecol. Evol.* 25, 419–427. <https://doi.org/10.1016/j.tree.2010.04.005>.
- Slabbekoorn, H., Dalen, J., Haan, D., Winter, H.V., Radford, C., Ainslie, M.A., Heaney, K. D., Kooten, T., Thomas, L., Harwood, J., 2019. Population-level consequences of seismic surveys on fishes: an interdisciplinary challenge. *Fish Fish.* 20, 653–685. <https://doi.org/10.1111/faf.12367>.
- Smith, F., 2013. Understanding HPE in the VEMCO Positioning System (VPS). Innovasea <https://doi.org/10.1016/j.vemco.2013.05.007>.
- Soudijn, F.H., Kooten, T., Van, Slabbekoorn, H., Roos, A.M. De, 2020. Population-level effects of acoustic disturbance in Atlantic cod: a size-structured analysis based on energy budgets. *Proc. R. Soc. B* 287, 20200490.
- Spiga, I., Aldred, N., Caldwell, G.S., 2017. Anthropogenic noise compromises the anti-predator behaviour of the European seabass, *Dicentrarchus labrax* (L.). *Mar. Pollut. Bull.* 122, 297–305. <https://doi.org/10.1016/j.marpolbul.2017.06.067>.
- Thompson, P.M., Graham, I.M., Cheney, B., Barton, T.R., Farcas, A., Merchant, N.D., 2020. Balancing risks of injury and disturbance to marine mammals when pile driving at offshore windfarms. *Ecol. Solut. Evid.* 1, 1–12. <https://doi.org/10.1002/2688-8319.12034>.
- Thomsen, F., Mueller-Blenkle, C., Gill, A., Metcalfe, J., McGregor, P.K., Bendall, V., Andersson, M.H., Sigra, P., Wood, D., 2010. Effects of pile driving on the behavior of cod and sole. In: Popper, A.N., Hawkins, A.D. (Eds.), *The Effects of Noise on Aquatic Life*. Springer New York, New York, NY, pp. 387–388.
- Todd, V.L.G., Pearse, W.D., Tregenza, N.C., Lepper, P.A., Todd, I.B., 2009. Diel echolocation activity of harbour porpoises (*Phocoena phocoena*) around North Sea offshore gas installations. *ICES J. Mar. Sci.* 66, 734–745. <https://doi.org/10.1093/icesjms/fsp035>.
- Tougaard, J., Henriksen, O.D., Miller, L.A., 2009. Underwater noise from three types of offshore wind turbines: estimation of impact zones for harbor porpoises and harbor seals. *J. Acoust. Soc. Am.* 125, 3766–3773. <https://doi.org/10.1121/1.3117444>.
- Tougaard, J., Hermanssen, L., Madsen, P.T., 2020. How loud is the underwater noise from operating offshore wind turbines? *J. Acoust. Soc. Am.* 148, 2885–2893. <https://doi.org/10.1121/10.0002453>.
- van der Knaap, I., Reubens, J., Thomas, L., Ainslie, M.A., Winter, H.V., Hubert, J., Martin, B., Slabbekoorn, H., 2021a. Effects of a seismic survey on movement of free-ranging Atlantic cod. *Curr. Biol.* 1–8. <https://doi.org/10.1016/j.cub.2021.01.050>.
- van der Knaap, I., Slabbekoorn, H., Winter, H.V., Moens, T., Reubens, J., 2021b. Evaluating receiver contributions to Acoustic Positional Telemetry: a case study on Atlantic cod around wind turbines in the North Sea. *Anim. Biotelemetry* 9, 1–12. <https://doi.org/10.1186/s40317-021-00238-y>.
- Villegas-Ríos, D., Freitas, C., Moland, E., Olsen, E.M., 2018. Personalities influence spatial responses to environmental fluctuations in wild fish. *J. Anim. Ecol.* 87, 1309–1319. <https://doi.org/10.1111/1365-2656.12872>.
- Villegas-Ríos, D., Réale, D., Freitas, C., Moland, E., Olsen, E.M., 2017. Individual level consistency and correlations of fish spatial behaviour assessed from aquatic animal telemetry. *Anim. Behav.* 124, 83–94. <https://doi.org/10.1016/j.anbehav.2016.12.002>.

- Voegeli, F.A., Smale, M.J., Webber, D.M., Andrade, Y., O'Dor, R.K., 2001. Ultrasonic telemetry, tracking and automated monitoring technology for sharks. *Environ. Biol. Fish.* 60, 267–281. <https://doi.org/10.1023/A:1007682304720>.
- Wahlberg, M., Westerberg, H., 2005. Hearing in fish and their reactions to sounds from offshore wind farms. *Mar. Ecol. Prog. Ser.* 288, 295–309. <https://doi.org/10.3354/meps288295>.
- Winter, H., Aarts, G., van Keeken, O., 2010. Residence Time and Behaviour of Sole and Cod in the Offshore Wind Farm Egmond Aan Zee (OWEZ). IMARES - Institute for Marine Resources & Ecosystem Studies.
- Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Sala, E., 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314, 787–791. <https://doi.org/10.1126/science.1137946>.
- Zampolli, M., Nijhof, M.J.J., de Jong, C.A.F., Ainslie, M.A., Jansen, E.H.W., Quesson, B. A.J., 2013. Validation of finite element computations for the quantitative prediction of underwater noise from impact pile driving. *J. Acoust. Soc. Am.* 133, 72–81. <https://doi.org/10.1121/1.4768886>.