CHAPTER 3

EFFECTS OF OFFSHORE WIND FARMS ON THE ECOLOGY OF FLATFISH: A CASE STUDY ON PLAICE *PLEURONECTES PLATESSA*

BUYSE Jolien*, DE BACKER Annelies & HOSTENS Kris

Flanders Research Institute for Agriculture, Fisheries and Food (ILVO), Jacobsenstraat 1, 8400 Oostende, Belgium.

* Corresponding author: Jolien.Buyse@ilvo.vlaanderen.be

Abstract

The ecological effects of offshore wind farms (OWFs) on adult plaice were investigated in terms of their spatial distribution, diet, and movements. Spatial distribution was studied on the turbine and wind farm scale using a combination of visual diving transects and beam trawl samples. A trophic analysis study combined gut content analysis with a biomarker approach (fatty acid analysis) to obtain diet information on both short and longer time scales. Condition was studied by calculating several morphometric (i.e., Fulton's K index) and organosomatic condition indices (fullness-, gonadosomatic-, hepatosomatic- and digestive-somatic index) while the movements of plaice were investigated trough an acoustic telemetry study. Results show that plaice is affected by the presence of OWFs, with the artificial hard substrate within the OWFs providing an important habitat for individual plaice by increasing prey availability through the artificial reef effect. Furthermore, our findings suggest that OWFs may act as a refuge for plaice, potentially mitigating direct fishing mortality. We did not find any evidence that the increased prey availability leads to a better condition of plaice, but our sample size might have been too small to detect differences in condition. Results from this study suggest that existing OWFs likely enhance ecological production for plaice. It remains to be investigated whether this translates to spillover effects into adjacent areas where fishing is permitted and how such effects could influence fisheries given the anticipated large-scale expansion of offshore renewable energy.

1. Introduction

The installation of hard substrates in soft sediment environments, which is associated with the development of offshore wind farms (OWFs), can cause changes that may affect local fauna (Inger *et al.* 2009; Langhamer & Wilhelmsson 2009; Lindeboom *et al.* 2011; Raoux *et al.* 2017). In addition, the energy emissions from turbines and cables (such as noise, electromagnetic fields, and light) can impact the behavior of present fauna and potentially reduce their fitness if the effect is significant (Bailey *et al.* 2014; Hutchison *et al.* 2020). However, many fish species and other megafauna are drawn to the scour protection layer (SPL) and turbine foundations in OWFs through the artificial reef effect (Langhamer & Wilhelmsson 2009; Andersson & Öhman 2010; Krone *et al.* 2017; Degraer *et al.* 2020).

The epifauna growing on the hard substrate increases food availability for higher trophic levels, and the rocks and foundations provide a complex habitat that serves as shelter for different organisms. The attraction of certain fish species, such as cod *Gadus morhua*, to artificial structures such as oil and gas platforms, shipwrecks, and OWFs, has been well documented (Reubens *et al.* 2011; Bergström *et al.* 2013; Krone *et al.* 2017; Wright *et al.* 2020). However, the effects of turbine foundations and scour protection on typical soft-sediment fish species (e.g., flatfish) are not yet well understood.

Two distinct hypotheses have been proposed to explain the increased fish abundance around artificial reefs. According to the attraction hypothesis, fish are either attracted to or redistributed around the structures (Bohnsack & Sutherland 1985; Lindberg 1997; Wilson *et al.* 2010; Bergström *et al.* 2013). In contrast, the production hypothesis proposes that the presence of artificial structures increases the carrying capacity of the area, leading to a greater abundance and biomass of fish (i.e., ecological production) within its boundaries. However, few studies have been able to provide evidence of fish production within OWFs (Wilhelmsson *et al.* 2006; Reubens *et al.* 2014; Mavraki *et al.* 2021). The attraction and production hypothesis are not mutually exclusive and are considered to be two extremes on a continuous scale (Osenberg *et al.* 2002). The potential effects of hard substrates within OWFs as artificial reefs likely vary depending on the species and life stage in relation to the SPL material, rock density and surface area, as well as the water depth, location and foundation type (Brickhill *et al.* 2005; Glarou *et al.* 2020).

Additionally, OWFs may also fulfill a similar role as marine protected areas (MPAs) for certain (target) species, as these concession areas are often closed to any commercial fishing activities and can as such be considered as no-take zones (Steins *et al.* 2021). No-take zones can protect fish species, especially those that are targeted by fisheries, and enhance fish biomass, which might even lead to a spillover in nearby fishing areas (Langhamer 2012; Florin *et al.* 2013). Such spillover effects, resulting from the combined artificial reef and refuge effects, have been predicted through modelling approaches (Raoux *et al.* 2017; Halouani *et al.* 2020), but in-situ studies were not able to confirm this yet.

This chapter summarizes the findings of different papers (Buyse *et al.* 2021, 2023; Buyse 2023) that were consolidated within the framework of a PhD study on the effects of OWFs on the ecology of the plaice *Pleuronectes platessa*, a commercial flatfish species, with the following research questions:

- What are the effects of OWFs on the spatial distribution of plaice at the turbine and wind farm scale?
- Which small- and large-scale movements does plaice perform in relation to OWFs?
- What are the effects of OWFs on the diet and condition of plaice?
- Does plaice production occur in OWFs?

Integrating knowledge on the effects of an OWF on plaice' spatial and temporal distribution, diet and condition and spatial (small scale) movements enables us to discuss whether ecological production is occurring within OWFs, which would indirectly imply that OWFs have a protection potential for this species. Fish production is considered likely if we can demonstrate attraction towards and a high association to the hard substrates with a diet consisting mainly of colonizing prey species, a higher food availability (gut fullness), a high residency and increased fish abundances, condition and size within the wind farm area.

2. Material and methods

2.1. Spatial distribution

The spatial distribution of plaice was examined at two different scales, namely the turbine and wind farm scale, in the

C-Power and Belwind offshore wind farms (OWFs) to determine if an attraction effect towards the wind farm and hard structures could be detected (Fig. 1). At the wind farm scale, we utilized beam trawl samples in a Before-After/Control-Impact (BACI) design (Vandendriessche *et al.* 2015; De Backer *et al.* 2022). The samples were collected during the annual autumn monitoring campaigns as part of the WinMon.BE program (period 2004–2019 for C-Power and 2008–2019 for Belwind). The potential attraction of plaice at the turbine scale was investigated through visual diving transects over the scour protection layer (SPL) and the immediate surrounding sand around turbines selected at

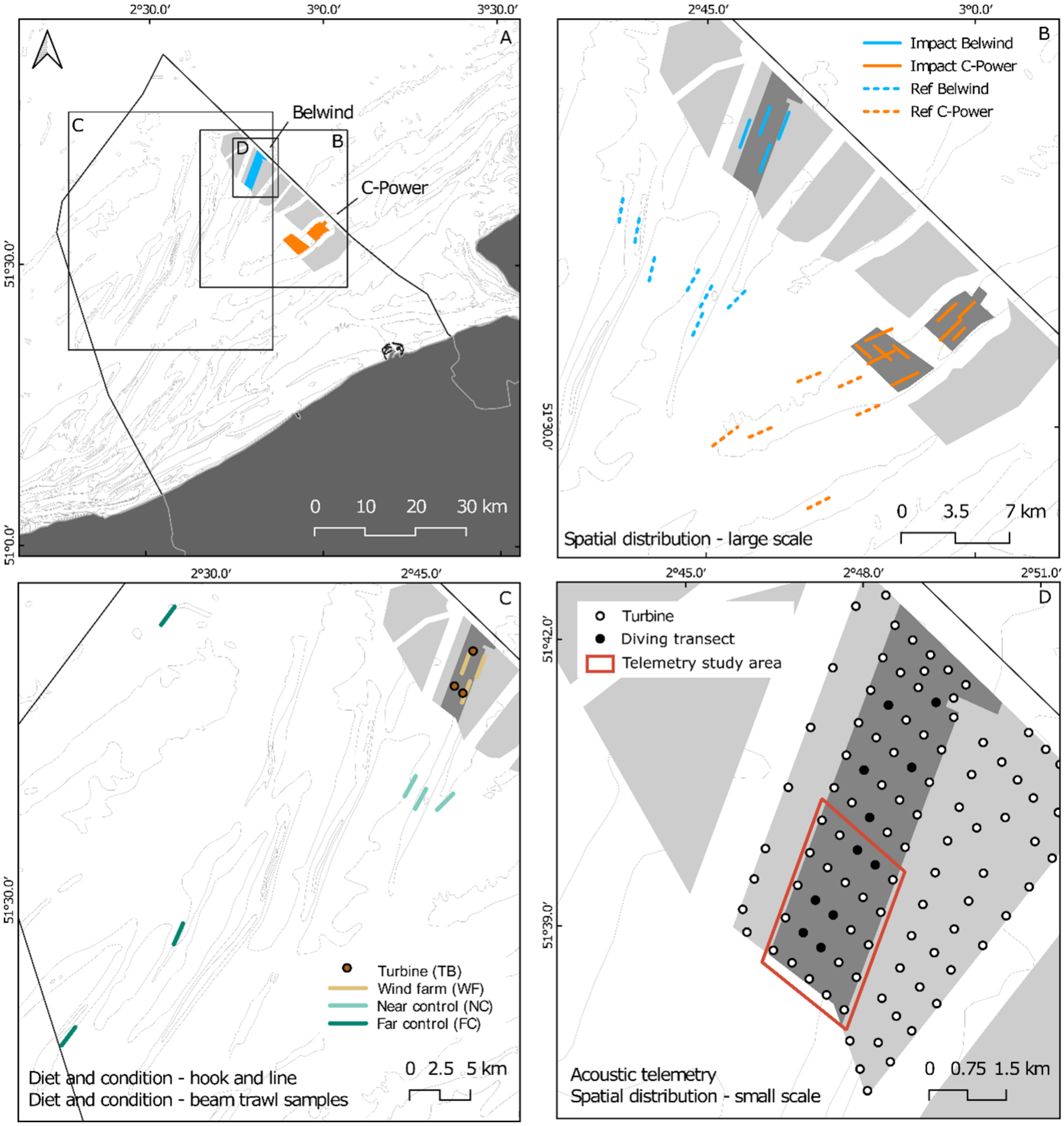

Figure 1. Map showing (**A**) the location of Belwind and C-Power within the Belgian EEZ, (**B**) the locations of the beam trawl samples (Before/After-Control/Impact design) used to study the large scale spatial distribution of plaice, (**C**) the beam trawl and hook-and-line sampling locations for the diet and condition study and (**D**) the turbines where diving transects were carried out for the small-scale spatial distribution study and the area within Belwind where the acoustic telemetry study took place.

random in the Belwind wind farm. For a more detailed explanation of the sampling design and methods, the reader is referred to Buyse *et al.* (2022).

2.2. Diet and condition

The effects of OWFs on the diet and condition of plaice were investigated in four different groups: the turbine group (TB), comprising fish caught by hook-and-line on the SPL of three randomly chosen turbines in Belwind; and the wind farm group (WF), the near control group (NC) and the far control group (FC), comprising fish caught by an 8 m-beam trawl (20 mm mesh size) in between the turbines of Belwind (± 250 m from the turbines), close to the wind farm area, and further away from the wind farm area respectively. A total of 72 fish (18 fish per sample group, six replicates per turbine or haul) were randomly selected and their gut, ovaries or testes, liver, and otoliths were stored for further analyses. The lengths of the fish ranged from 17.5 to 36.5 cm ($\bar{x} = 25.8 \pm 4.3$ SD). Additionally, muscle tissue samples were taken from each fish, and their length and weight before and after evisceration were determined.

The diet composition was studied on a short temporal scale (< 10 h) using gut content analysis, while fatty acid and stable isotope analyses of the muscle samples provided insight into the diet on a longer time scale. A relative abundance method was used to determine the contribution of each prey item to the diet (Amundsen & Sánchez-Hernández 2019), whereby the volume of each prey item for both stomach and gut was visually estimated and expressed as a percentage of a total of 100%. Relative abundances from the stomach and gut were summed to provide a more comprehensive picture of the diet. The stomach fullness index was calculated for each fish based on the weights of the prey relative to the weight of the fish (Mahesh *et al.* 2018). Different morphometric indices (Fulton and Fulton with eviscerated weight) and condition indices (gonadosomatic, digestive-somatic, and hepatosomatic index) were calculated to investigate whether a difference in diet also led to differences in condition or fecundity. Linear mixed models were used, including haul or turbine as random factors. The sampling design, methods, and analyses are thoroughly described in Buyse *et al.* (2023).

2.3. Residency, site fidelity and small-scale movements

In order to examine the presence and spatial movements of plaice within and in relation to OWFs, 31 fish were tagged with acoustic transmitters and subsequently released within a network of acoustic receivers. This study was conducted between May 2020 and August 2021, in the southern region of the Belwind OWF (approx. 3.5–5.5 km^2). Over the course of the study, three different receiver designs were utilized during three consecutive time periods (period 1: 15/05/2020–11/10/2020; period 2: 14/10/2020–22/02/2021; period 3: 25/02/2021–11/07/2021). During the initial period, to obtain a high resolution 2D-positioning, six receivers were arranged in a circular formation around three turbines (B9, C8 and D9), each situated at a distance of 150 meters from the turbines. For the remaining two periods, the receivers were repositioned to cover the largest possible area (approx. 5.5 km^2) whilst still maintaining overlapping detection ranges. The acoustic transmitters emit unique signals at random intervals, which are detected by receivers when the fish swim in their close proximity. Using this presence data, a residency index was computed for the May–October feeding period, reflecting the degree of association between the fish and the OWF area. Triangulation (utilizing the yaps package, available on http://github.com/baktoft/yaps) was employed to estimate the 2D positions of fish that remained in the study area for at least 20 days during the first study period. This facilitated the examination of small-scale movement patterns of plaice in relation to the hard substrates (Baktoft *et al.* 2017, 2019). The estimated positions were utilised to compute the distance between each calculated position and the nearest turbine.

To gain a better understanding of the spatial distribution of fish in the vicinity of the turbines (< 150 m), the number of detections with available positions was calculated per square metre for several distance intervals (0–20 m per 5 m, 20–50 m per 10 m, and 50–150 m per 50 m). In order to investigate the existence of a diurnal pattern in the distance between fish and the hard substrate, information on sunlight times was used to generate a categorical variable *light* consisting of four different levels: dawn, day, dusk, and night. Nautical dusk and dawn times (when the sun is 12° below the horizon) were used to differentiate between dusk/dawn and night, while sunrise and sunset times were used to distinguish between dusk/dawn and day. A linear mixed model (LMM) with a Gaussian distribution was employed to fit the distance of the fish to the nearest turbine as a response variable. The model included light as a fixed effect and fish ID as a random variable to account for the variance between the different fish. The final model that was fitted was: Distance to the turbine ~ *light* + (1 | fish ID).

For a comprehensive overview of the acoustic network, tagging methodology, and data analysis techniques, the reader is referred to Buyse (2023).

3. Results

3.1. Spatial distribution

Over 190 beam trawl samples, 5186 plaice individuals were caught ($\bar{x}=0.18 \pm 0.16$ ind. 100 m^{-2}) across a trawled area of 3.37 km^2 within the Belwind and C-Power offshore wind farms (OWFs). The BACI analysis conducted at the wind farm level yielded contrasting results (Fig. 2). A clear wind farm effect was observed for C-Power

Figure 2. A. Plaice abundance in beam trawl samples (approx. 200 m from the turbines) for C-Power and Belwind OWFs in reference and impact areas (period 2004–2019 and 2008–2019, respectively). The vertical dark grey line indicates the before and after construction period as considered in this study, which also coincides with the moment that fisheries activities were suspended for the second and third phase of C-Power and Belwind (the area around the 6 GBFs in C-Power (first construction phase) was closed in 2008). LOESS-smoothers with a span of 0.7 were fitted to the data to facilitate interpretation. Orange and blue bands indicate the standard error 95% confidence intervals for the impact and reference areas, respectively. **B**. Plaice abundances along the visual diving transects with estimated marginal means for the final GLMM showing the number of plaice per 100 m^2 for both habitat types (SPL = scour protection layer).

($p=0.0008, Z=-3.35$), which resulted in plaice abundances almost 4.5 times higher within the impacted OWF area after construction (0.27±0.09 ind. 100 m^{-2}, $CI_{0.95}[0.13–0.53]$) compared to before construction (0.06±0.02 ind. 100 m^{-2}, $CI_{0.95}[0.03–0.12]$). No significant difference in plaice abundance before and after construction was found for reference samples ($p=0.13$, $Z=-1.53$). Additionally, a significant difference in plaice abundances between reference and impact samples after construction was observed ($p=0.03$, $Z=2.22$), while this was not the case in samples taken before construction ($p=0.05$, $Z=-1.93$). On the other hand, no wind farm effects were observed for Belwind ($p=0.25$, $Z=1.16$).

During the 21 visual diving transects, a total of 31 plaice individuals were observed. Among these, 23 were found on the SPL habitat (total searched area=1028 m^2), while only eight were found on the open sand surrounding the SPL (total searched area=1436 m^2). As a result, the abundance of plaice was four times higher on the sandy patches between the rocks of the SPL (2.08±0.55 ind. 100 m^{-2}, $CI_{0.95}[1.24–3.49]$) compared to the surrounding sand (0.53±0.20 ind. 100 m^{-2}, $CI_{0.95}[0.25–1.11]$). It was observed that fish were not uniformly distributed on the SPL habitat, and were mainly found where the rock density was relatively low, as opposed to locations where rocks were closely stacked on top of each other.

3.2. Diet and condition

The lengths of the 72 plaice individuals differed significantly among the sample groups, except between the two control groups. The largest fish were found in the TB and WF groups (median length TB: 30.2 cm, WF: 26.2 cm, NC: 23 cm, FC: 23 cm; $F_{3,68}=21.8$, $p<0.001$). The sex ratio also varied across the different groups, with a strong dominance of females in the TB (0.88) and WF group (0.83), while sexes for the control groups were more evenly distributed (NC: 0.67, FC: 0.5). However, the age of the fish did not differ among the sample groups ($\bar{x}=3.42\pm1.77$ SD; $F_{3,68}=0.62$, $p=0.60$).

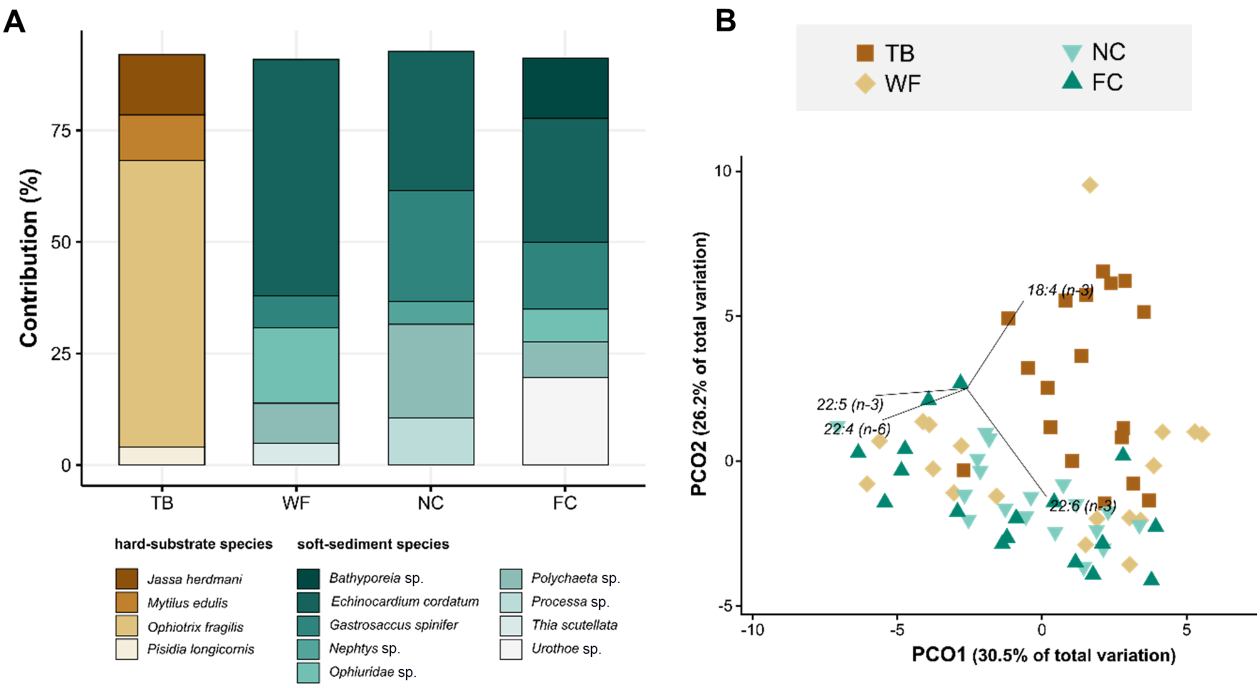

Figure 3. A. Principal coordinates analysis (PCO) results of combined stomach and intestine content using relative abundances of prey items per sample group. The overlay vector shows prey species with a multiple correlation > 0.4. **B**. Contribution of the most abundant prey species (cut-off level 90%) in stomachs and intestines per sample group according to a SIMPER analysis.

The gut content analysis revealed that plaice caught on the SPL had a distinctive diet consisting of typical hard substrate prey species such as *Mytilus edulis*, *Ophiothrix fragilis*, *Jassa herdmani*, and *Pisidia longicornis* ($p_{Permanova}$, pseudo-$F_{3,67}=3.15$, $p=0.005$) (Fig. 3). In contrast, the diet of fish caught on the sand in between the turbines (WF) and outside the Belwind OWF (NC and FC) consisted of prey usually found in soft sediments such as *Echinocardium cordatum* and *Gastrosaccus spinifer*. The fatty acid analysis showed differences in FA profiles between fish caught right next to the turbines (TB) and in between the turbines (WF) versus the control areas (NC and FC).

The fullness index and the Fulton's K index based on the total weight of fish were highest for the turbine group (TB) and decreased as the distance from the hard substrate increased (Fig. 4). However, significant differences were not found between the impact and control groups, likely due to high variability in the data. Additionally, no wind farm effect was observed for the gonadosomatic and hepatosomatic indices, but the digestive-somatic index was significantly higher for fish in the turbine group when compared to the two control groups.

3.3. Residency, site fidelity and small-scale movements

Out of the 31 fish that were tagged, many were found in the Belwind OWF for extended uninterrupted periods after being released during the summer of 2020, and most of them were still present at the beginning of autumn (Fig. 5). Three fish (ID 9257, 9258 and 9262) were only detected for a few days after their release. Eleven individuals (35%) were (re) detected after one year in spring 2021, and seven fish (20%) were detected in the wind farm until the last two weeks of the study. Fewer detections were registered in the study area during the winter months. Several fish (ID 9250, 9255, 9256, 9260, 9269, 9275, 9277, 9280 and 9284) were absent for a long consecutive period, which coincided with the spawning period of plaice (December–March), after which they returned to the study area during the spring of the following year. The residency for fish that were present in the OWF for at least 20 days during the first period (May–October 2020, n=24) ranged from 0.09–1, with an average residency of 0.78±0.29. Overall, 70% of the fish had a residency index of at least 0.75.

The 21 fish individuals that were present within the study area for at least 20 days during the first monitoring period, were observed at a mean distance of 92±48 m from the turbines with most detections occurring on the sand directly surrounding the SPL (±25 m from the turbine) with a second peak of detections around±90 m from the turbines (Figs 5–6). The fish positions showed a diurnal pattern in distance from the turbine ($\chi^2=6251.6$, $p<0.001$). Fish were located closer to the hard substrate during the day (84.6 m, $CI_{0.95}$[64.6–105]) and at dawn (80.6 m, $CI_{0.95}$[60.6–101]), compared to dusk (109.8 m, $CI_{0.95}$[89.7–130]) and at night (101.0 m, $CI_{0.95}$[80.9–121]). Most of the detections per m^2 were located on the SPL during daytime, while at night (21:00–01:00 UTC), almost no fish were located close the turbines (0–10 m) (Fig. 6).

4. Discussion

To summarise, the results from the different studies indicate that adult plaice are affected in terms of their spatial distribution, diet and movements by the presence of offshore wind farms (OWFs). The artificial hard substrate structures within the OWFs appear to be an important habitat for individual plaice, providing increased prey availability through the artificial reef effect. Moreover, our findings suggest that OWFs may act as a refuge for plaice, as indicated by the skewed sex ratio and larger fish size, potentially mitigating direct fishing mortality. These collective results suggest that OWFs may enhance ecological production for plaice, but it remains to be investigated whether this translates to spillover effects into adjacent areas where fishing is permitted and if such effects could benefit fisheries.

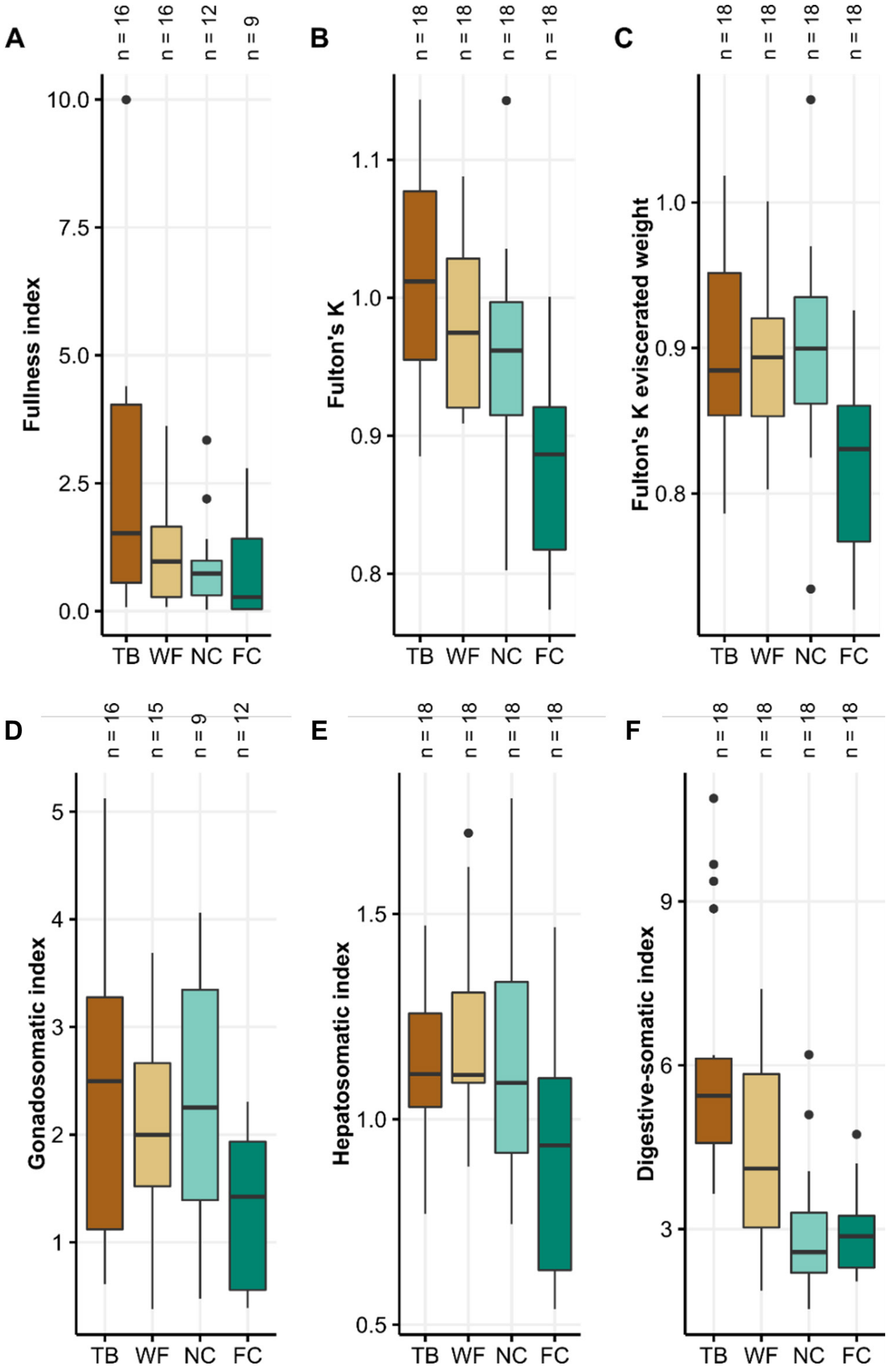

Figure 4. Boxplots of (**A**) fullness index of non-empty stomachs (n = 53), (**B**) Fulton's K condition index calculated with fish total weight, (**C**) Fulton's K condition index calculated with fish eviscerated weight, (**D**) gonadosomatic (GSI), (**E**) hepatosomatic (HSI) and (**F**) digestive-somatic (DSI) index for each sample group with n representing the number of samples used to calculate the index. For the calculation of the GSI, only females were used.

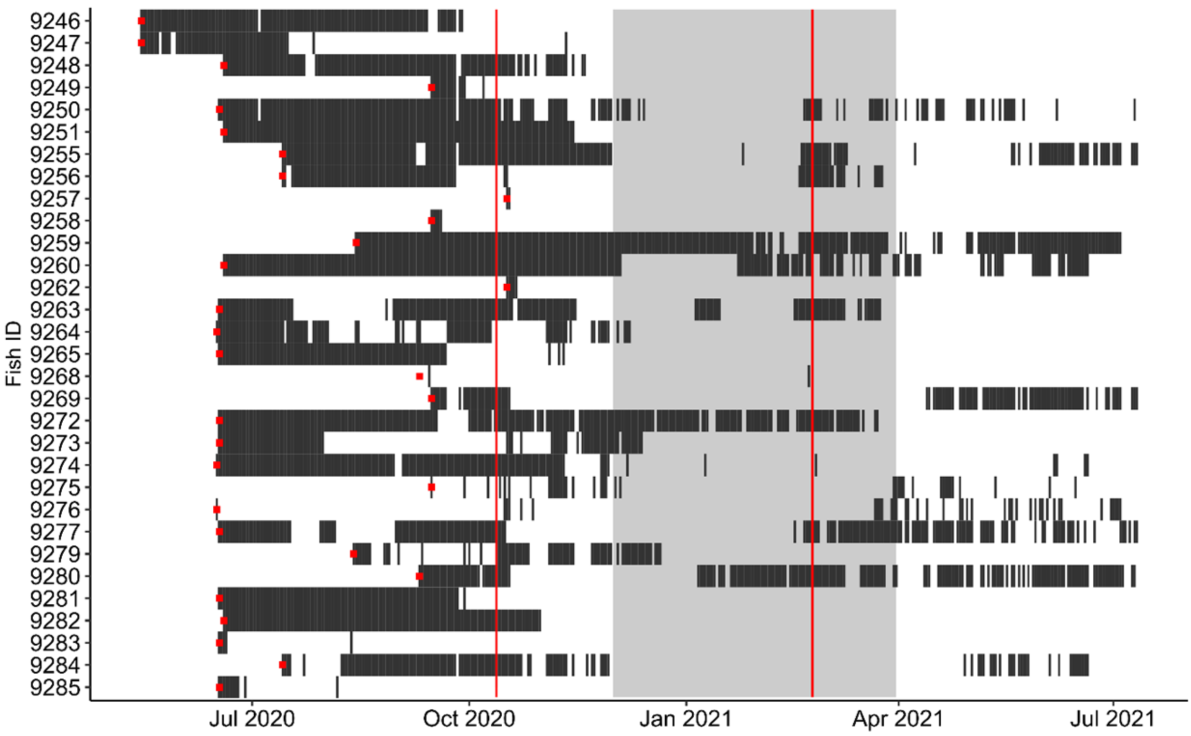

Figure 5. Daily presence of the 31 tagged plaice over the study period (15/05/2020–11/07/2021) in Belwind OWF. Red squares indicate the tagging and release date of the fish, while the red vertical lines show the change in receiver array design., The grey box represents the yearly spawning period for plaice in the southern North Sea (December–March with a peak in January). A fish was considered to be present in the study area if it was detected at least two times on that particular day.

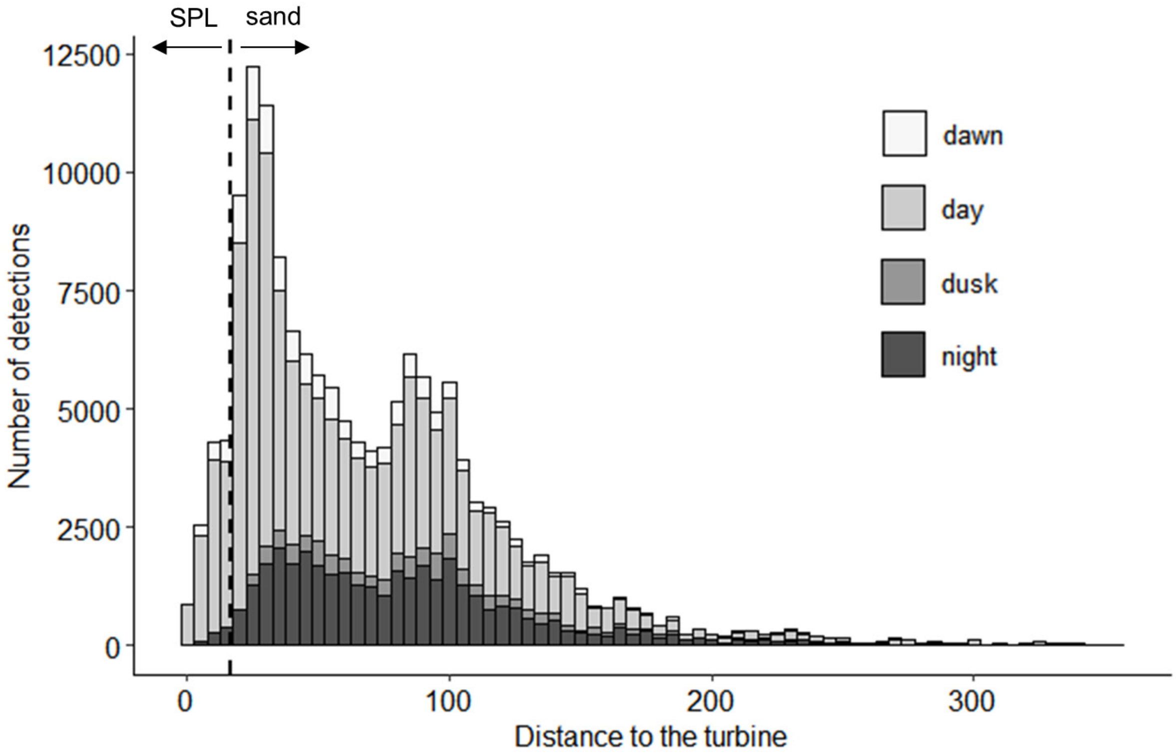

Figure 6. Number of detections over the distance to the nearest turbine for the 21 fish for which positions were estimated. The dashed vertical line indicates the average width (16.5 m from the turbine) of the scour protection layer (SPL) based on the design plans.

Our visual census revealed that plaice is attracted to the habitat formed by the scour protection around turbine foundations. Moreover, the trophic analysis indicated that fish in the vicinity of the turbine (TB) had fuller digestive tracts (higher digestive-somatic index) and consumed primarily hard substrate prey, whereas plaice farther from the turbine consumed mainly soft-sediment prey. This difference was not only observed in

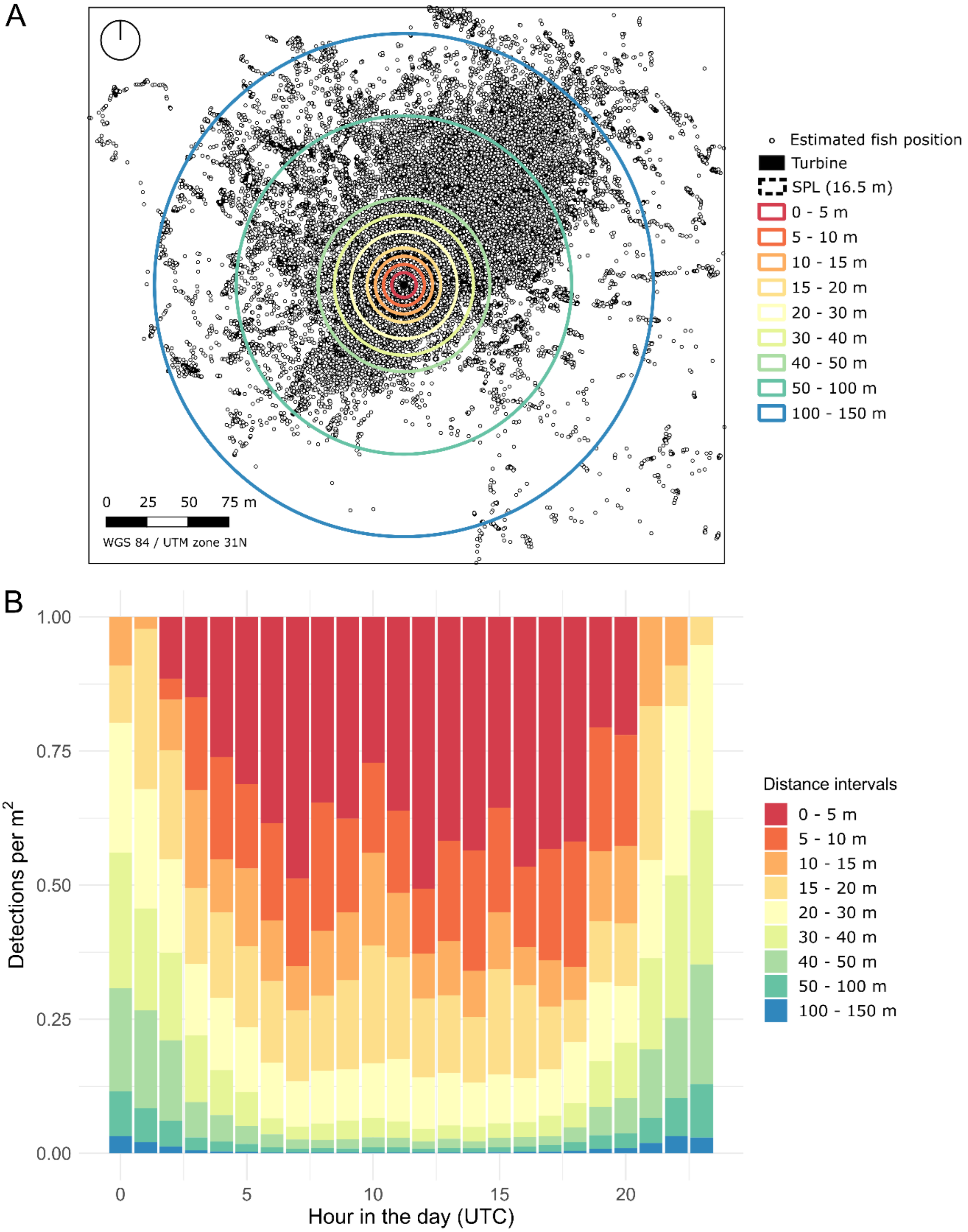

Figure 7. A. Estimated fish positions around turbine B9 in the Belwind OWF from June till October 2020. **B**. Relative number of fish detections per m^2 per hour around turbines B09, C08 and D09 for each distance interval (between 0 and 150 m).

short-term diet analyses but also in assimilated fatty acids, indicating a longer-term diet shift. This suggests that the attraction observed is likely due to the increase in prey availability on and near the hard substrates, known as the artificial reef effect (Bohnsack & Sutherland 1985; Petersen & Malm 2006). While shelter may be another reason for attraction, our tagging study indicated that most detections were located just outside the SPL, making this explanation unlikely for plaice. The tagging study results further support the hypothesis that the observed attraction is linked to feeding behaviour, as a diurnal pattern was found in the distance of the fish to the turbine, with fish being closer to it during the day and at dawn than during night hours and at dusk. During daylight hours, the highest density of detections was even found in the immediate vicinity of the turbine (< 15 m). As plaice is a daytime feeder that relies on its sight to locate and identify prey (Gibson *et al.* 2015), these findings suggest that they undertake ‘feeding excursions’ towards the SPL and return to the soft sediment to rest. By doing so, they can benefit from the increased prey availability near the hard substrates while still being able to bury themselves into the sand directly surrounding the SPL.

In contrast to our findings, several studies conducted in other offshore wind farms did not report any attraction towards the hard substrates (Krone *et al*. 2017; van Hal *et al.* 2017). During the diving transects, plaice were only seen resting on the sandy patches between the rocks of the SPL, not on top of the rocks. Hence, we speculate that plaice can benefit from the increased prey availability offered by the hard substrates, but only if soft sandy sediment is present in the immediate vicinity. Consequently, we can propose some suggestions for modifying the SPL to improve its ecological role for plaice and flatfish species in general. Since the existence of soft sediment is likely a crucial factor for their attraction, adapting the rock density of the SPL to allow for sand patches between the hard substrate will considerably increase prey accessibility for plaice and potentially other soft sediment fish species.

In addition to an artificial reef effect, our findings suggest that OWFs can also have a refuge effect on plaice. As commercial fishing activities within OWFs are often prohibited, they can be considered as no-take zones, similar to marine protected areas (MPAs) (Ashley *et al.* 2014). Previous studies have reported an increase in fish size, abundance, and total biomass within MPAs compared to adjacent fished areas (Di Franco *et al.* 2009; Florin *et al.* 2013; Guidetti *et al.* 2014; Félix-Hackradt *et al.* 2018). Our study revealed that there is a higher number of plaice present within the C-Power wind farm in between the turbines and that fish within the Belwind wind farm are larger, which indicates the existence of a refuge effect. Additionally, our findings show a higher female-to-male ratio within samples taken in Belwind. Plaice is a sexual dimorphic species, with females growing faster and for a longer time than males. In undisturbed populations, this results in a dominance of male individuals among smaller individuals and a dominance of females among larger individuals, with an even sex ratio for the total population. A higher catchability of larger (and thus more likely female) individuals in fished areas can lead to a decrease in fish size and a higher proportion of males (van Walraven *et al.* 2010; Florin *et al.* 2013). The increased female-to-male ratio of plaice found within Belwind might therefore be a consequence of the cessation of fishing activities. Although the sample size used in the trophic analysis study was sufficient to test differences among groups in diet composition and fatty acid profiles, it was likely too low to study differences in life-history traits and demographic variables (e.g., size, age, sex ratio) due to the inherent large variation within such data. A follow-up study that specifically aims at investigating the existence of refuge effects using larger sample sizes is needed to confirm the findings presented here. In general, monitoring programmes should not only focus on fish abundances alone, as research within MPAs has shown that effects on fish size and age (and thus biomass) are often easier to detect than changes in abundances (Florin *et al.* 2013).

The observed attraction effect is evident, but does it also result in ecological production? There are various proposed mechanisms through which the introduction of artificial hard substrates into soft sediment environments can lead to production (Wilson *et al.* 2001; Mavraki *et al.* 2021). These mechanisms include increasing food availability or feeding efficiency, providing shelter from predation, offering recruitment habitat for settling individuals, and freeing space in the natural habitat for other fish by attracting fish to the artificial reefs (Randall 1963; Stone *et al.* 1979; Bohnsack 1989). We have demonstrated that plaice feeds on the prey typically found on the hard substrates in OWFs, which could result in ecological production for this species. Moreover, prey on rocks or turbine foundations might be more easily accessible to plaice compared to prey buried in the sand, potentially increasing their feeding efficiency. Although we did not observe a higher number of plaice between the turbines in the Belwind wind farm compared to outside, there could still be a higher fish abundance when the entire wind farm area is considered. The tagging study suggests that these fish may be located in the sandy environment closer to the hard substrate. Therefore, the total fish biomass within the OWF area could be higher, without being detected by beam trawling at a distance of approximately 250 m from the turbines. In C-Power, where scour protection is absent around most of the turbines, the aggregation effect near the turbines is likely smaller, and thus, the attraction effect is more visible in the beam trawl samples with higher plaice abundance between the turbines compared to reference areas. These results underscore the importance of considering different spatial scales, e.g., turbine and wind farm, when investigating spatial distribution patterns in OWFs, as they can influence each other. Additionally, they indicate that it is crucial to account for environmental and physical conditions, foundation type, and surrounding fishing pressure when studying OWF effects on fish.

Whether a closed area (i.e., excluding fisheries) can efficiently enhance the biomass of a certain fish species depends largely on its mobility (Shipp 2003). A species that constantly moves in and out of the protected area will profit less from a spatial closure than a relatively stationary species (Miethe *et al.* 2010). The tagging study indicated that plaice has a high residency within the OWF area with most individuals showing a preference for a single turbine during the feeding period. However, plaice also undertakes large-scale spawning migrations during winter, which makes them vulnerable to fishing mortality on the spawning areas and during the migration events itself (Gibson *et al.* 2015). Therefore, any protection effect offered by the OWF areas might equally be nullified at a later stage.

Research has shown that successfully managed MPAs can support (small-scale) fisheries through a reduction of the fishing mortality on commercial species and enhancing their production through an increase in food availability (Friedlander *et al.* 2007; Florin *et al.* 2013; Guidetti *et al.* 2014). In such a case, the combined effect of offering refuge and enhancing production leads to a spillover of adults or juveniles into adjacent fishable areas, thereby increasing fish biomass (Davies *et al.* 2021). It has been estimated that spillover can increase catches outside an OWF with 7% (Halouani *et al.* 2020). However, empirical evidence showing the existence of spillover from OWFs is still lacking. Although BACI designs are effective in identifying impacts, a gradient design that involves taking control samples along a distance gradient from the impacted area may be more suitable for detecting spillover effects (Methratta 2020; De Backer *et al.* 2022). This is because one would expect a gradient in effect size with distance from the OWF.

This study addressed some important knowledge gaps on the ecological effects of OWFs on adult plaice at the scale of individuals and single wind farms and we could demonstrate that ecological production at the adult level on wind farm scale is very likely (Fig. 8). It is clear that individual adult fish profit from the increased prey availability around the hard substrates in an OWF. However, this might not cause any changes on the fish population level, even though the effect size on the individual level is high. For management purposes, it is crucial to further upscale the observed effects to the population level (May *et al.* 2019). To understand how OWFs can impact fish populations, it is crucial to obtain knowledge on how the underlying processes, such as recruitment, growth and mortality, might be affected by the cumulative presence of OWFs (Gill *et al.* 2020). For example, changes in recruitment due to OWFs (e.g., eggs do not reach nursery areas due to increased turbulence) might have more important consequences for the population than changes that mainly affect adults (e.g., food availability on offshore feeding grounds). Therefore, it is important to include different life stages when studying OWF effects on a certain species and to determine which changes in certain processes result in the largest impact at the population level (Gill *et al.* 2020).

5. Conclusions

In this study, we analysed the spatial distribution, trophic ecology and small-scale movements in time and space of the commercial flatfish species plaice *Pleuronectes platessa* at the individual adult level. We conclude that OWFs likely enhance ecological fish production through the existence of an artificial reef effect in combination with a refuge effect. Our findings suggest that plaice is attracted towards the scour protection due to the increased hard substrate prey availability, and that they perform ‘feeding excursions’ from the surrounding sand towards the SPL during daylight hours. Although our results indicate that OWFs likely increase plaice

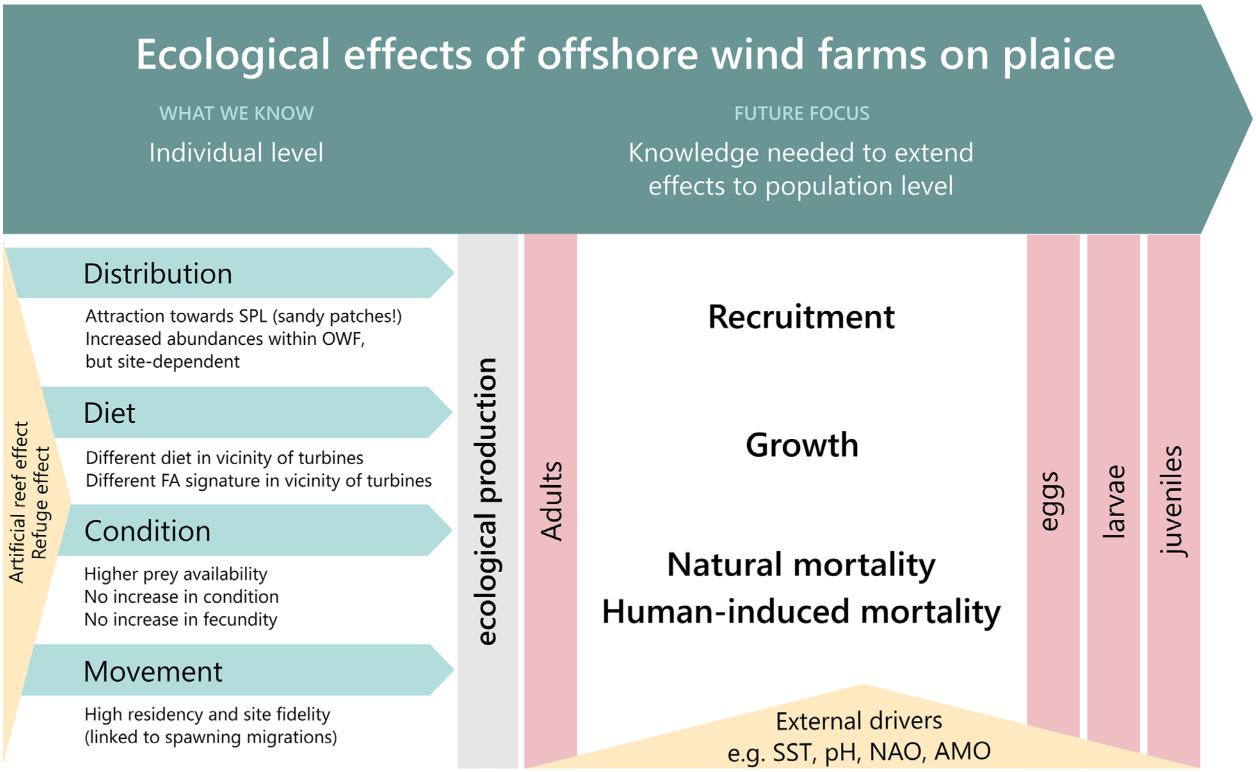

Figure 8. Schematic overview of the most important findings within this PhD study (Buyse 2023) at individual level, and the knowledge gaps for upscaling the observed effects towards the population level.

biomass, it remains unclear whether this could lead to spillover into adjacent areas. Follow-up research should focus on investigating refuge and spillover effects in-situ, and aim at upscaling the effects of OWFs by studying which population-driving processes are most impacted by the large-scale expansion of offshore wind energy developments.

Acknowledgements

The authors would like to express their sincere gratitude to the VLIZ scientific diving team and the RBINS scientific diving team for their commitment during the fieldwork. We also thank VLIZ for providing ship time and infrastructure, and the crews of RV *Simon Stevin* and RV *Belgica* for their excellent assistance during the fieldwork. Our sincere thanks also go to Parkwind NV and C-Power for their cooperation. We acknowledge our ILVO colleagues for their support during the study and Daan Wintein for sharing his knowledge concerning hook-and-line fishing. Finally, we thank the Belgian Science Policy (Belspo and RBINS-OD Nature) for providing shiptime for this research project.

References

Amundsen, P.A. & Sánchez-Hernández, J. 2019. Feeding studies take guts – critical review and recommendations of methods for stomach contents analysis in fish. *Journal of Fish Biology* 95: 1364–1373. https://doi.org/10.1111/jfb.14151

Andersson, M.H. & Öhman, M.C. 2010. Fish and sessile assemblages associated with wind-turbine constructions in the Baltic Sea. *Marine and Freshwater Research* 61: 642–650. https://doi.org/10.1071/MF09117

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. *Marine Policy* 45: 301–309. https://doi.org/10.1016/j.marpol.2013.09.002

Bailey, H., Brookes, K.L. & Thompson, P.M. 2014, September 14. Assessing environmental impacts of offshore wind farms: Lessons learned and recommendations for the future. *Aquatic Biosystems* 10: e8. https://doi.org/10.1186/2046-9063-10-8

Baktoft, H., Gjelland, K.Ø., Økland, F. & Thygesen, U.H. 2017. Positioning of aquatic animals based on time-of-arrival and random walk models using YAPS (Yet Another Positioning Solver). *Scientific Reports* 7: e14294. https://doi.org/10.1038/s41598-017-14278-z

Baktoft, H., Gjelland, K., Økland, F., Rehage, J., Rodemann, J., Corujo, R.S., Viadero, N. & Thygesen, U. 2019. Opening the black box of high resolution fish tracking using yaps. bioRxiv. https://doi.org/10.1101/2019.12.16.877688

Bergström, L., Sundqvist, F. & Bergström, U. 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

Bohnsack, J.A. 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? *Bulletin of Marine Science* 44 (2): 631–645.

Bohnsack, J.A. & Sutherland, D.L. 1985. Artificial reef research: a review with recommendations for future priorities. *Bulletin of Marine Science* 37: 11–39.

Brickhill, M.J., Lee, S.Y. & Connolly, R.M. 2005. Fishes associated with artificial reefs: attributing changes to attraction or production using novel approaches. *Journal of Fish Biology* 67: 53–71. https://doi.org/10.1111/j.0022-1112.2005.00915.x

Buyse, J. 2023. *Ecological Impacts of Offshore Wind Farms on Flatfish with Emphasis on Plaice Pleuronectes platessa, a Species of Commercial Interest in the Southern North Sea*. PhD thesis, Ghent University. 255 pp.

Buyse, J., De Backer, A. & Hostens, K. 2021. Small-scale distribution patterns of flatfish on artificial hard substrates in a Belgian offshore wind farm. *In*: Degraer, S., Brabant, R., Rumes, B. & Vigin, L. (eds) *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea. Attraction, Avoidance and Habitat Use at Various Spatial Scales*: 69–76.

Buyse, J., Hostens, K., Degraer, S. & De Backer, A. 2022. Offshore wind farms affect the spatial distribution pattern of plaice *Pleuronectes platessa* at both the turbine and wind farm scale. *ICES Journal of Marine Science* 79 (6): 1777–1786. https://doi.org/10.1093/icesjms/fsac107

Buyse, J., Hostens, K., Degraer, S., De Troch, M., Wittoeck, J. & De Backer, A. 2023. Increased food availability at offshore wind farms affects trophic ecology of plaice *Pleuronectes platessa*. *Science of the Total Environment* 862: 160730. https://doi.org/10.1016/j.scitotenv.2022.160730

Davies, B.F.R., Holmes, L., Rees, A., Attrill, M.J., Cartwright, A.Y. & Sheehan, E.V. 2021. Ecosystem approach to fisheries management works — how switching from mobile to static fishing gear improves populations of fished and non-fished species inside a marine-protected area. *Journal of Applied Ecology* 58 (11): 2463–2478. https://doi.org/10.1111/1365-2664.13986

De Backer, A., Van Hoey, G., Wittoeck, J. & Hostens, K. 2022. Describing the epibenthos and demersal fish communities in the Belgian part of the North Sea in view of future OWF monitoring. *In*: Degraer, S., Brabant, R., Rumes, B. & Vigin, L. (eds) *Environmental Impacts of Offshore Wind Farms in the Belgian Part of the North Sea. Memoirs on the Marine Environment*: 19–36.

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

Di Franco, A., Bussotti, S., Navone, A., Panzalis, P. & Guidetti, P. 2009. Evaluating effects of total and partial restrictions to fishing on Mediterranean rocky-reef fish assemblages. *Marine Ecology Progress Series* 387: 275–285. https://doi.org/10.3354/meps08051

Félix-Hackradt, F.C., Hackradt, C.W., Treviño-Otón, J., Pérez-Ruzafa, Á. & García-Charton, J.A. 2018. Effect of marine protected areas on distinct fish life-history stages. *Marine Environmental Research* 140: 200–209. https://doi.org/10.1016/j.marenvres.2018.06.012

Florin, A.-B., Bergström, U., Ustups, D., Lundström, K., Lundström, L. & Jonsson, P.R. 2013. Effects of a large northern European no-take zone on flatfish populations. *Journal of Fish Biology* 83: 939–962. https://doi.org/10.1111/jfb.12097

Friedlander, A.M., Brown, E.K. & Monaco, M.E. 2007. Coupling ecology and GIS to evaluate efficacy of marine protected areas in Hawaii. *Ecological Applications* 17: 715–730.

Gibson, R.N., Nash, R., Geffen, A. & Van der Veer, H. 2015. *Flatfishes: Biology and Exploitation*. Wiley Blackwell, Oxford. 542 pp.

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

Glarou, M., Zrust, M. & Svendsen, J.C. 2020. Using artificial-reef knowledge to enhance the ecological function of offshore wind turbine foundations: Implications for fish abundance and diversity. *Journal of Marine Science and Engineering* 8 (5): e332. https://doi.org/10.3390/jmse8050332

Guidetti, P., Baiata, P., Ballesteros, E., Di Franco, A., Hereu, B., Macpherson, E., Micheli, F., Pais, A., Panzalis, P., Rosenberg, A.A., Zabala, M. & Sala, E. 2014. Large-scale assessment of mediterranean marine protected areas effects on fish assemblages. *PLoS ONE* 9: e91841. https://doi.org/10.1371/journal.pone.0091841

Halouani, G., Villanueva, C.M., Raoux, A., Dauvin, J.C., Ben Rais Lasram, F., Foucher, E., Le Loc'h, F., Safi, G., Araignous, E., Robin, J.P. & Niquil, N. 2020. A spatial food web model to investigate potential spillover effects of a fishery closure in an offshore wind farm. *Journal of Marine Systems* 212: e103434. https://doi.org/10.1016/j.jmarsys.2020.103434

Hutchison, Z.L., Secor, D.H. & Gill, A.B. 2020. The interaction between resource species and electromagnetic fields associated with electricity production by offshore wind farms. *Oceanography* 33: 96–107. https://doi.org/10.5670/oceanog.2020.409

Inger, R., Attrill, M.J., Bearhop, S., Broderick, A.C., James Grecian, W., Hodgson, D.J., Mills, C., Sheehan, E., Votier, S.C., Witt, M.J. & Godley, B.J. 2009. Marine renewable energy: potential benefits to biodiversity? An urgent call for research. *Journal of Applied Ecology* 46: 1145–1153. https://doi.org/10.1111/j.1365-2664.2009.01697.x

Krone, R., Dederer, G., Kanstinger, P., Krämer, P., Schneider, C. & Schmalenbach, I. 2017. Mobile demersal megafauna at common offshore wind turbine foundations in the German Bight (North Sea) two years after deployment – increased production rate of *Cancer pagurus*. *Marine Environmental Research* 123: 53–61. https://doi.org/10.1016/j.marenvres.2016.11.011

Langhamer, O. 2012. Artificial reef effect in relation to offshore renewable energy conversion: State of the art. *The Scientific World Journal* 2012: e386713. https://doi.org/10.1100/2012/386713

Langhamer, O. & Wilhelmsson, D. 2009. Colonisation of fish and crabs of wave energy foundations and the effects of manufactured holes - A field experiment. *Marine Environmental Research* 68: 151–157. https://doi.org/10.1016/j.marenvres.2009.06.003

Lindberg, W.J. 1997. Can science resolve the attraction-production issue? *Fisheries* 22: 10–13.

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. *Environmental Research Letters* 6: e035101. https://doi.org/10.1088/1748-9326/6/3/035101

Mahesh, V., Ambarish, P.G. & Rekha, J.N. 2018. Stomach content analysis techniques in fishes. *In*: *ICAR Sponsored Winter School on Recent Advances in Fishery Biology techniques for Biodiversity Evaluation and Conservation, 1–21 December 2018, Kochi*: 104–115.

Mavraki, N., Degraer, S. & Vanaverbeke, J. 2021. Offshore wind farms and the attraction – production hypothesis: insights from a combination of stomach content and stable isotope analyses. *Hydrobiologia* 848: 1639–1657. https://doi.org/10.1007/s10750-021-04553-6

May, R., Masden, E.A., Bennet, F. & Perron, M. 2019. Considerations for upscaling individual effects of wind energy development towards population-level impacts on wildlife. *Journal of Environmental Management* 230: 84–93. https://doi.org/10.1016/j.jenvman.2018.09.062

Methratta, E.T. 2020. Monitoring fisheries resources at offshore wind farms: BACI vs. BAG designs. *ICES Journal of Marine Science* 77: 890–900. https://doi.org/10.1093/icesjms/fsaa026

Miethe, T., Dytham, C., Dieckmann, U. & Pitchford, J.W. 2010. Marine reserves and the evolutionary effects of fishing on size at maturation. *ICES Journal of Marine Science* 67 (3): 412–425. https://doi.org/10.1093/icesjms/fsp248

Osenberg, C.W., Mary, C.M.S., Wilson, J.A. & Lindberg, W.J. 2002. A quantitative framework to evaluate the attraction – production controversy. *ICES Journal of Marine Science* 59: S214–S221. https://doi.org/10.1006/jmsc.2002.1222

Petersen, J.K. & Malm, T. 2006. Offshore windmill farms: Threats to or possibilities for the marine environment. *Ambio* 35 (2): 75–80.

Randall, J.E. 1963. An analysis of the fish populations of artificial and natural reefs in the Virgin Islands. *Caribbean Journal of Sciences* 3: 31–47.

Raoux, A., Tecchio, S., Pezy, J.P., Lassalle, G., Degraer, S., Wilhelmsson, D., Cachera, M., Ernande, B., Le Guen, C., Haraldsson, M., Grangeré, K., Le Loc'h, F., Dauvin, J.C. & Niquil, N. 2017. Benthic and fish aggregation inside an offshore wind farm: Which effects on the trophic web functioning? *Ecological Indicators* 72: 33–46. https://doi.org/10.1016/j.ecolind.2016.07.037

Reubens, J., Degraer, S. & Vincx, M. 2011. Aggregation and feeding behaviour of pouting (*Trisopterus luscus*) at wind turbines in the Belgian part of the North Sea. *Fisheries Research* 108: 223–227. https://doi.org/10.1016/j.fishres.2010.11.025

Reubens, J., De Rijcke, M., Degraer, S. & Vincx, M. 2014. Diel variation in feeding and movement patterns of juvenile Atlantic cod at offshore wind farms. *Journal of Sea Research* 85: 214–221. https://doi.org/10.1016/j.seares.2013.05.005

Shipp, R.L. 2003. A Perspective on Marine Reserves as a Management Tool. *Fisheries* 28: 10–21. https://doi.org/10.1577/1548-8446(2003)28[10:APOMRA]2.0.CO;2

Steins, N.A., Veraart, J.A., Klostermann, J.E.M. & Poelman, M. 2021. Combining offshore wind farms, nature conservation and seafood: Lessons from a Dutch community of practice. *Marine Policy* 126: 104371. https://doi.org/10.1016/j.marpol.2020.104371

Stone, R.B., Pratt, H.L., Parker, R.O. & Davis, G.E. 1979. A comparison of fish populations on an artificial and natural reef in the Florida Keys. *Marine Fisheries Review* 41: 1–11.

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

van Walraven, L., Mollet, F.M., van Damme, C.J.G. & Rijnsdorp, A.D. 2010. Fisheries-induced evolution in growth, maturation and reproductive investment of the sexually dimorphic North Sea plaice (*Pleuronectes platessa* L.). *Journal of Sea Research* 64: 85–93. https://doi.org/10.1016/j.seares.2009.07.003

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

Wilhelmsson, D., Malm, T. & Öhman, M.C. 2006. The influence of offshore windpower on demersal fish. *ICES Journal of Marine Science* 63 (5): 775–784. https://doi.org/10.1016/j.icesjms.2006.02.001

Wilson, J., Osenberg, C.W., Mary, C.M.S., Watson, C.A. & Lindberg, W.J. 2001. Artificial reefs, the attraction-production issue, and density dependence in marine ornamental fishes. *Aquarium Sciences and Conservation* 3: 95–105. https://doi.org/10.1023/A:1011343312031

Wilson, J.C., Elliott, M., Cutts, N.D., Mander, L., Mendão, V., Perez-Dominguez, R. & Phelps, A. 2010. Coastal and offshore wind energy generation: Is it environmentally benign? *Energies* 3: 1383–1422. https://doi.org/10.3390/en3071383

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