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Long-term effects of an offshore wind farm in the North Sea on fish communities

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ABSTRACT: Long-term effects of the Horns Rev 1 offshore wind farm (OWF) on fish abundance, diversity and spatial distribution were studied. This OWF is situated on the Horns Reef sand bank in the North Sea. Surveys were conducted in September 2001, before the OWF was established in 2002, and again in September 2009, 7 yr post-establishment. The sampling surveys used a multi-mesh-size gillnet. The 3 most abundant species in the surveys were whiting *Merlangius merlangus,* dab *Limanda limanda* and sandeels *Ammodytidae* spp. Overall fish abundance increased slightly in the area where the OWF was established but declined in the control area 6 km away. None of the key fish species or functional fish groups showed signs of negative long-term effects due to the OWF. Whiting and the fish group associated with rocky habitats showed different distributions relative to the distance to the artificial reef structures introduced by the turbines. Rocky habitat fishes were most abundant close to the turbines while whiting was most abundant away from them. Species diversity was significantly higher close to the turbines. Overall, these results indicate that the artificial reef structures were large enough to attract fish species with a preference for rocky habitats, but not large enough to have adverse negative effects on species inhabiting the original sand bottom between the turbines.

KEY WORDS: Offshore wind farms · Spatial distribution · Fish · Rocky and sandy habitats · BACI design · OWF · Scour protection · Artificial reef

INTRODUCTION

The development of offshore renewable energy is expanding rapidly in Europe as part of the European Union's target to obtain 20% of its energy consumption by this means by 2020. Offshore wind farms (OWFs) are a major component of this strategy. To facilitate the construction of OWFs, and keep establishment and maintenance costs low, most are placed in relatively shallow waters (<20 m depth) and in areas with glacial and marine deposits of sand. Few studies have been published on the impact of these large-scale installations on the marine environment.

Benthic communities (infauna and epifauna) have been studied at several OWFs in Europe: Egmond aan Zee OWF in Holland (Lindeboom et al. 2011); Horns Rev 1 OWF (Leonhard & Pedersen 2006) and Rødsand OWF (Maar et al. 2009) in Denmark; and Thorntonbank OWF in Belgium (Vandendriessche et al. 2014). The general conclusion obtained from these studies was that new communities were established in close proximity to the individual turbine foundation and its scour protection whereas no differences were observed in the sandy areas between turbines.

The long-term impact on local fish abundance of introducing OWFs into sand habitats has so far been investigated only for species of sandeel (van Deurs et al. 2012). However, fish attraction to underwater constructions at OWFs has been reported for different gobiid species (Wilhelmsson et al. 2006, Andersson & Öhman 2010) and for the gadoids, such as cod *Gadus*

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morhua (Winter et al. 2010, Reubens et al. 2013a, 2014) and pouting *Trisopterus luscus* (Reubens et al. 2011, 2013a). The studies by Reubens et al. (2011, 2014) showed that pouting and cod predominantly preyed on amphipods *Jassa hermani* and porcelain crabs *Pisidia longicornis* associated with OWF constructions. From studies of other underwater structures (e.g. wrecks, oil rigs and artificial reefs) it has been documented that fishes are attracted to these areas, where they forage on the associated fauna (Fabi et al. 2006, Page et al. 2007, Leitao et al. 2008, Langhamer & Wilhelmsson 2009).

Here we present the results from a study that combines long-term effects of an OWF on fish abundance and diversity with information on the distribution relative to the turbines. We investigated Horns Rev OWF, deployed in 2002, which was the world's largest OWF at the time.

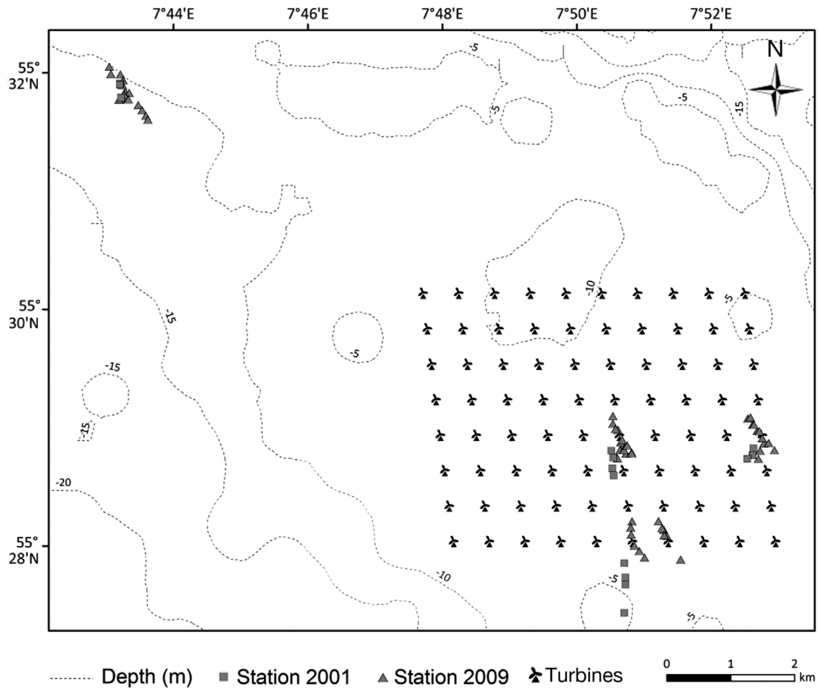

Fig. 1. Sampling locations in the Horns Rev 1 offshore wind farm (OWF) area. Survey years and turbines in the Impact area (built in 2002) are shown by symbols. Stations in the Control area are located northwest of the Impact area. Bathymetry is shown for every 5 m

MATERIALS AND METHODS

Horns Rev 1 OWF is positioned 15 km off western Denmark on the Horns Reef sand bank. The OWF consists of 80 turbines with a total capacity of 160 MW. The turbines are positioned 560 m apart. Each turbine foundation has a diameter of up to 30 m, which includes a scour protection of rocks and boulders. Individual boulders have diameters ranging from 30 to 50 cm and the scour layer is 1 to 1.5 m thick in total. The scour protection constitutes ~0.8% of the total OWF area. The farm covers an area of 27.5 km^2, including a 200 m exclusion zone, and a water depth of 6.5 to 13.5 m.

Field work

Surveys were conducted from 24 September to 7 October 2001 (prior to construction of the OWF, which was initiated in summer 2002), and again 8 yr later, from 11 to 18 September 2009. The pre-impact survey is hereafter referred to as Before and the post-impact survey as After. The surveys covered both the area where the OWF was deployed (Impact) and a reference area (Control), with the same hydrographic and bottom characteristics, 6 km northwest of the OWF (Fig. 1). The area at Horns Reef is characterised by a sandy bottom and salinities between 30 and 32.

Fish were collected with demersal multi-mesh gillnets. Gillnets were deployed at 3 locations (Turbine Nos. 55, 58 and 95) in Impact and 1 location in Control (Table 1). Turbine No. 55 is positioned centrally while Nos. 58 and 95 have peripheral locations in the OWF towards the south and east, respectively (Fig. 1, Table 1). Gillnets were set in the afternoon and re-

Table 1. Gillnet stations in Impact and Control survey areas. Location in the Impact area refers to the turbine reference number in use by the operator Vattenfall Vindkraft A/S

Area	Location	Coordinates		Survey 24 Sep–7 Oct 2001 'Before'	Survey 11–18 Sep 2009 'After'
Impact	55	55° 29.022′ N	7° 50.737′ E	24	24
	58	55° 28.121′ N	7° 50.958′ E	24	23
	95	55° 29.038′ N	7° 52.858′ E	18	24
Control		55° 31.755′ N	7° 43.221′ E	18	25
Sum				84	96

trieved after ~6 h. The nets were set in a north–south direction parallel to the dominant current regime. Start and end positions of each net and the order of mesh size panels were recorded. Each gillnet consisted of 12 panels of different mesh sizes (6.5, 8.5, 11.0, 14.3, 18.6, 24.2, 31.4, 40.9, 53.1, 69.0, 89.8 and 116.7 mm) (for further information on gear specifications see Eigaard et al. 2000). The panels were randomly distributed with a 1 m space between each one to avoid any lead effect (Hamley 1975). The start of the net was set as close to the turbines as weather permitted. Ideally the net covered both the scour protection area and the sandy seafloor.

In order to investigate the effect of inter-turbine distance on species abundance and diversity, gillnets were set at 3 increasing distances from their foundations: near (0 to 100 m), middle (120 to 220 m) and far (230 to 330 m). The near setting was located as close to the turbine as possible. When weather conditions permitted, the gillnets were attached directly to the turbine. For all 3 distances, 2 gillnets were set simultaneously both north and south of the turbine. Gillnets in Control were set at a fixed station (55° 31.755′ N, 7° 43.221′ E) in the same manner as in the Impact area, with 3 settings of increasing distance and 2 settings north/south of the control position. Fishes were identified to the lowest possible taxonomic level, except for sandeels, which were only determined to family level (Ammodytidae). Total length was measured for all fish individuals, and the measurements rounded down to the nearest cm.

Data analysis

Analyses of changes in fish abundance, distribution relative to turbines and fish length followed the Before–After Control–Impact (BACI) design (Smith et al. 1993). The most abundant fish species were analysed at species level while others that occurred only in small quantities were categorised into groups based on their biological characteristics and habitat preferences.

Our primary aim was to analyse interaction effects between area (Control–Impact) and time (Before–After), as these would reveal whether changes that occurred between the Before and After situations could be attributed to the OWF. Catch numbers were assumed to follow a negative binomial distribution (after comparison with a Poisson distribution) and were analysed by a general linear mixed effect model (GLMM) for discrete data using the R software environment (R Core Team 2011) and the AD Model Builder package glmmADMB (Fournier et al. 2012, Skaug et al. 2012). The interaction effects were analysed using the following model:

$$E(\log[C_i]) = \mu + a_1 I_{\text{BA}} + a_2 I_{\text{CI}} + a_3 I_{\text{BA}} I_{\text{CI}} + U_{\text{trip}} \quad (1)$$

where E is the expectation operator, C_i denotes catch (no. ind.) for observation i, I_{BA} and I_{CI} are indicator variables (0 or 1) for the events Before/After and Control/Impact, and U_{trip} is a normally distributed random effect for each survey fishing trip (per day). $U_{\text{trip}} \sim \text{N}(0, \sigma_U)$. The parameters to be estimated were μ, a_1, a_2, a_3 and σ_U.

The spatial distribution expressed as abundance in relation to distance to the nearest turbine in the Impact area in 2009 was analysed in the model:

$$E(\log[C_i]) = \mu + \alpha MeshS_i + \beta Distance_i + U_{\text{trip}} \quad (2)$$

where $\alpha(\ldots_i)$ maps the i'th observation to a categorical effect for each level of the factor. $MeshS_i$ is the mesh size of the i'th gillnet panel and $Distance_i$ is the distance of the mid-point of the i'th gillnet panel to the turbine, C_i and U_{trip} are defined in Eq. (1). The parameters to be estimated were μ, α, β and σ_U.

Changes in fish length distributions were tested using ANOVA. Fish lengths were log transformed prior to tests to ensure homogeneous residuals. Probabilities for pairwise differences in a post hoc test were estimated by the Pdiff function in SAS (SAS 1990–2013).

Species diversity was calculated with the Shannon-Wiener index (H') for each gillnet and analysed using the BACI design. In the After situation, the effect on distance from the 3 investigated turbines in Impact was analysed by a generalized linear model (GLM). The distance to the nearest turbine was calculated using the mid position of each gillnet.

RESULTS

The most abundant species captured in the surveys were the semi-demersal whiting *Merlangius merlangus*, the sand-dwelling dab *Limanda limanda*, and sandeels (Ammodytidae spp.). These species, referred to as key species, constituted 76 to 88% of the catch (Table 2). Key fish species were analysed separately while the remaining fish species were merged into 3 groups: demersal (DEM), pelagic (PEL) and rocky habitat fishes (ROC) (Table 2).

The fish fauna on Horns Reef was dominated by relatively small fishes <30 cm length (Fig. 2a). The whiting, dab and sandeel had modal lengths of 12–14, 20–22 and 12–14 cm, respectively (Fig. 2b).

Table 2. Relative distribution (%) of the observed fish species in the surveys Before and After in Control and Impact areas with total no. ind. per area and survey. The group categories demersal (DEM), pelagic (PEL) and rocky habitat (ROC) are indicated for the less abundant species. CPUE: no. ind. per gillnet setting

Species		Group	Before				After			
			Control		Impact		Control		Impact	
			%	CPUE	%	CPUE	%	CPUE	%	CPUE
American plaice	*Hippoglossoides platessoides*	DEM					0.7	0.037	1.1	0.08
Brill	*Scopthalmus rhombus*	DEM					1.4	0.0741		
Cardine franche	*Lepidorhombus whiffiagonis*	DEM					0.7	0.037		
Cod	*Gadus morhua*	DEM	0.9	0.17	0.8	0.05	2.8	0.1481	5.5	0.42
Dab	*Limanda limanda*		12.1	2.33	12.9	0.77	55.3	2.8889	20.4	1.59
Dover sole	*Solea solea*	DEM	0.9	0.17	5.6	0.33			0.4	0.03
Dragonet	*Callionymus* spp.	DEM	0.3	0.06	1.0	0.06	2.1	0.1111	0.7	0.05
Flounder	*Platichthys flesus*	DEM			0.8	0.05	0.7	0.037	0.4	0.03
Gobies	Gobiidae	DEM					1.4	0.0741		
Goldsinny wrasse	*Ctenolabrus rupestris*	ROC							3.2	0.25
Herring	*Clupea harengus*	PEL					0.7	0.037	3.9	0.30
Hook-nose	*Agonus cataphractus*	DEM	5.8	1.11	5.6	0.33	1.4	0.0741	2.1	0.16
Horse mackerel	*Trachurus trachurus*	PEL			0.5	0.03	1.4	0.0741	0.4	0.03
Lemon sole	*Microstomus kitt*	DEM					0.7	0.037		
Mackerel	*Scomber scombrus*	PEL					5.0	0.2593	1.9	0.15
Plaice	*Pleuronectes platessa*	DEM	4.9	0.94	4.3	0.26	0.7	0.037	0.5	0.04
Pouting	*Trisopterus luscus*	ROC							1.4	0.11
Rock gunnel	*Pholis gunnellus*	ROC	0.3	0.06	0.3	0.02			0.4	0.03
Saithe	*Pollachius virens*	DEM	0.2	0.01						
Sandeel	Ammodytidae		1.4	0.28	7.4	0.44	4.3	0.2222	32.0	2.49
Sculpin	*Myxocephalus* spp.	ROC	0.3	0.06	0.3	0.02			0.5	0.04
Sprat	*Sprattus sprattus*	PEL					1.4	0.0741		0.00
Turbot	*Psetta maxima*	DEM	0.9	0.17	0.5	0.03	0.7	0.037	0.5	0.04
Viviparous eelpout	*Zoarces viviparus*	ROC							0.4	0.03
Whiting	*Merlangius merlangus*		72.3	13.89	60.2	3.59	18.4	0.963	24.1	1.88
Yellow gurnard	*Chelidonichthys lucernus*	DEM							0.2	0.01
Total (no. ind.)			**346**		**394**		**141**		**568**	

Except for DEM, which had a modal length of ~12 cm, the number of fish caught in the functional groups was generally too low to describe the species-specific length distribution (Fig. 2c). There were no statistically significant differences in fish length between the Control and Impact areas and the Before and After periods, for any of the key species and fish groups. The interaction effects on fish length were also insignificant (ANOVA, $p > 0.05$, Table 3).

Abundance

Before establishment of the OWF, the total fish catch in the Control area was approximately 4 times higher than in the area designated for the OWF (Impact area) (Fig. 3a). After establishment of the OWF, fish catch in the 2 areas was similar as a result of a small, but non-significant increase in the Impact area (GLMM, $p > 0.12$) and a large, significant decline in the Control area (GLMM, $p < 0.0001$) (Fig. 3a). This development between areas and peri-

Table 3. Test statistics on fish length (log total length [cm]) for Before (B), After (A), Control (C) and Impact (I) designs. DEM: demersal; PEL: pelagic; ROC: rocky habitat

Species	Source	df	Type III SS	*F*	Pr > *F*
Whiting	CI	1	0.00500704	0.28	0.5975
	BA	1	0.01463392	0.82	0.3679
	BA × CI	1	0.02296263	1.29	0.2603
Dab	CI	1	0.00500704	0.28	0.5975
	BA	1	0.01463392	0.82	0.3679
	BA × CI	1	0.02296263	1.29	0.2603
Sandeel	CI	1	0.00500704	0.28	0.5975
	BA	1	0.01463392	0.82	0.3679
	BA × CI	1	0.02296263	1.29	0.2603
DEM	CI	1	0.00500704	0.28	0.5975
	BA	1	0.01463392	0.82	0.3679
	BA × CI	1	0.02296263	1.29	0.2603
PEL	CI	1	0.06280815	1.26	0.2712
	BA	0	0		
	BA × CI	0	0		
ROC	CI	1	0.0003021	0.06	0.8082
	BA	1	0.00004017	0.01	0.9294
	BA × CI	0	0		

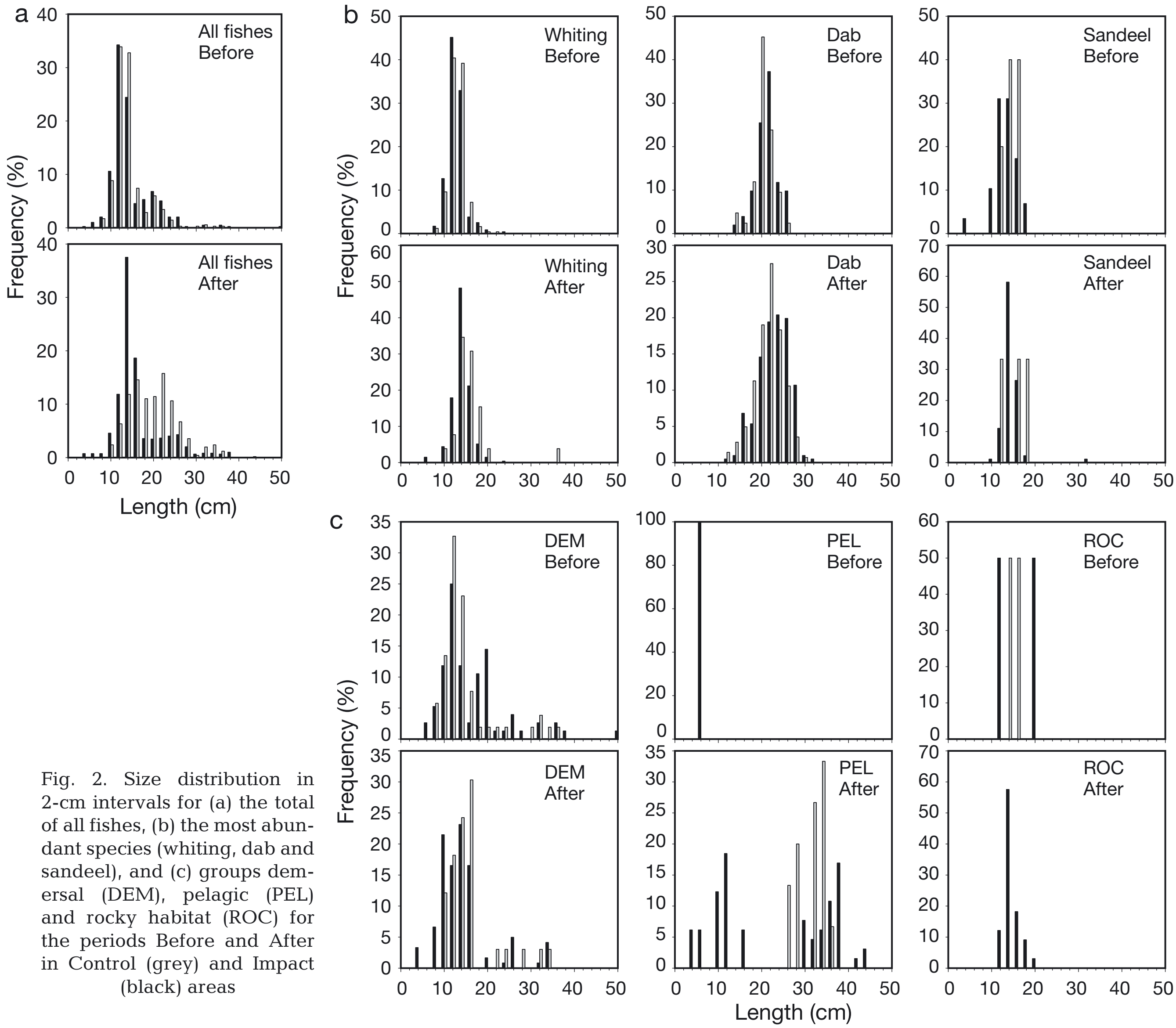

Fig. 2. Size distribution in 2-cm intervals for (a) the total of all fishes, (b) the most abundant species (whiting, dab and sandeel), and (c) groups demersal (DEM), pelagic (PEL) and rocky habitat (ROC) for the periods Before and After in Control (grey) and Impact (black) areas

ods was significantly different (GLMM, interaction effect, $p < 0.0001$). The decline in the Control area was mainly driven by a decrease in whiting but also by a reduction in the DEM group (Fig. 3b,c). This difference in catch rates for whiting and DEM between areas and periods was significant (GLMM, interaction effect, $p < 0.02$). DEM was dominated by Dover sole *Solea solea*, hooknose *Agonus cataphractus* and plaice *Pleuronectes platessa* in the Before period, while cod and hooknose dominated in the After period (Table 2). The catch rate for these dominating DEM species followed the same trend in Impact and Control, except for cod, which increased several fold only in Impact (catch rate increased from 0.05 to 0.4 fish gillnet^{-1}) (Table 2). For dab and sandeels, no significant development was observed between periods and areas (GLMM, interaction effect, sandeel $p > 0.1$; dab $p > 0.6$) (Fig. 3a,b).

Few fish of the PEL and ROC groups were caught in the Before period in either of the areas. The PEL group was dominated by horse mackerel while the ROC group was dominated by a few rock gunnels (*Pholis gunnellus*) and sculpins (*Myxocephalus* spp.). After deployment of the OWF, fish from the PEL group were observed in both areas, whereas those from the ROC group were caught only in the OWF area (Fig. 3c). During this period, mackerel and herring dominated in the PEL group while goldsinny wrasse (*Ctenolabrus rupestris*) and pouting (*Trisopterus luscus*) dominated the ROC group (Table 2). Catch data on PEL and ROC were insufficient for statistical analyses.

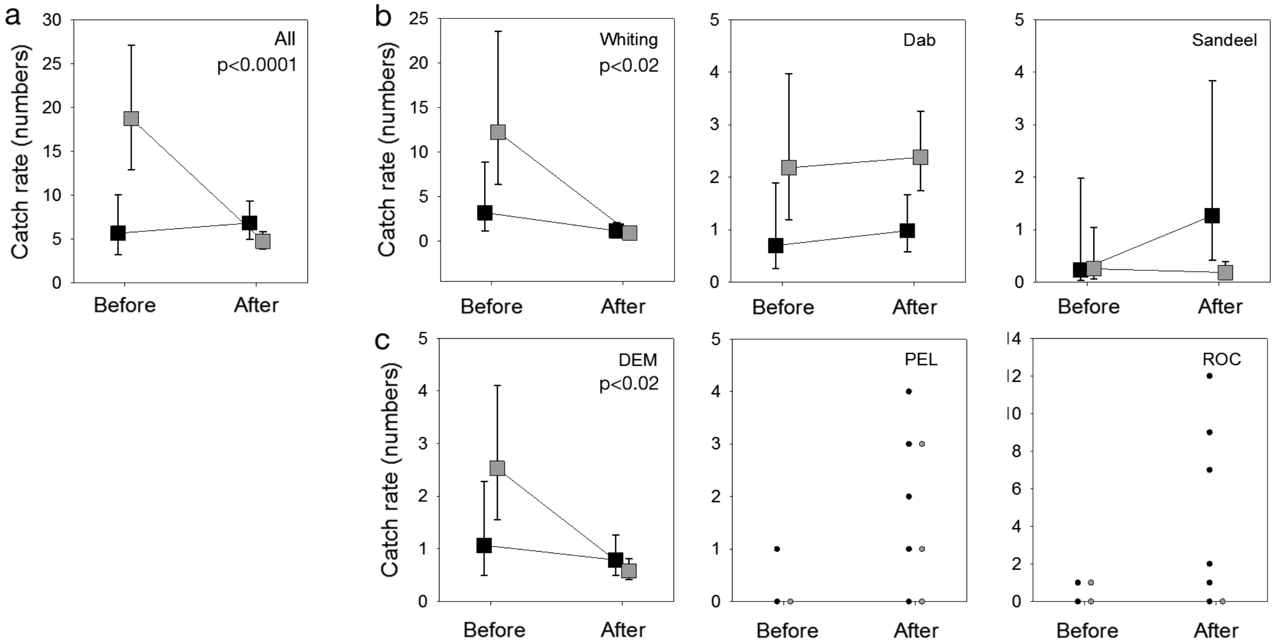

Fig. 3. Mean estimated catch (no. ind.) ± 95% CI (squares) or observed values where the model could not be fitted (circles) for (a) the total of all fishes, (b) the most abundant species (whiting, dab and sandeel), and (c) groups demersal (DEM), pelagic (PEL) and rocky habitat (ROC) for the periods Before and After in Control (grey) and Impact (black) areas. Significant interaction effects of Before–After and Impact–Control are shown where $p < 0.05$. Statistical models do not converge for PEL and ROC

Spatial distribution

The analysis of distribution patterns for the key fish species and fish groups in relation to distance to the specific turbines in the OWF only showed a significant effect for whiting (GLMM, $p < 0.02$) and for fishes belonging to the ROC group (GLMM, $p < 0.04$) (Fig. 4). As expected, the ROC group was most abundant close to the turbines, whereas an opposite trend was observed for whiting.

Species diversity

The BACI analysis of the H' index did not identify any overall significant effect on fish diversity from the deployment of the OWF, nor any significant difference in diversity between Before and After or Control and Impact (Table 4). Yet, inside the Impact area there was a significant effect of distance to the turbines, but not between the 3 investigated turbines nor any cross effects (Table 5). Species diversity was significantly higher close to the turbines and declined with distance (linear regression $r^2 = 0.16$, $p < 0.002$) (Fig. 5). High H' values were, however, observed only for gillnet settings within a distance of 110 m from the turbines. Excluding these settings, we identified no effect of distance to turbine (linear regression $r^2 = 0.008$, $p > 0.55$).

Table 4. Test statistics for a Shannon-Wiener index on effects of period Before (B) and After (A), and Control (C) and Impact (I) areas

Source	df	Type III SS	Mean square	*F*-value	Pr > *F*
CI	1	0.07663850	0.07663850	0.62	0.4313
BA	1	0.01626710	0.01626710	0.13	0.7167
BA × CI	1	0.00116033	0.00116033	0.01	0.9228

DISCUSSION

The significant decrease over time in total fish catch from within the Control area concurrent with the

Table 5. Test statistics for a Shannon-Wiener index on effects of distance to turbine (Dist.), investigated Turbine No. (55, 58 and 95) (TurbNO) and interaction effects (Dist. × TurbNO)

Source	df	Type III SS	Mean square	*F*-value	Pr > *F*
Dist.	1	1.21689354	1.21689354	12.60	0.0008
TurbNO	2	0.05483545	0.02741773	0.28	0.7539
Dist. × TurbNO	2	0.00754802	0.00377401	0.04	0.9617

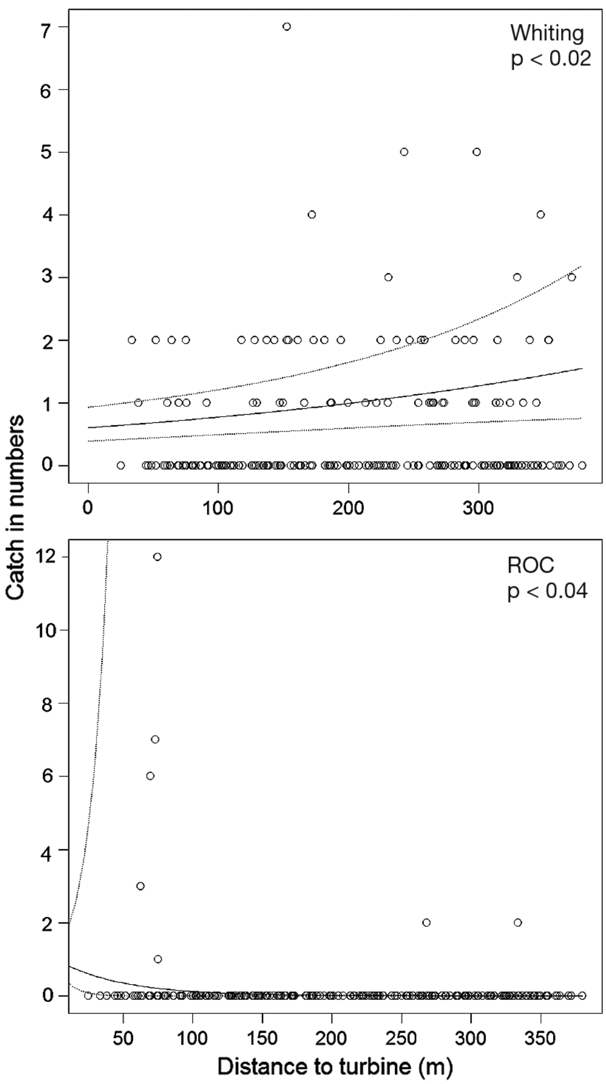

Fig. 4. Estimated catch (no. ind.) of fishes as a function of distance to turbine for the species whiting and the group rocky habitat (ROC). (Solid line) fitted line and (dotted line) 95% CI are shown. Only statistically significant ($p < 0.05$) cases are shown

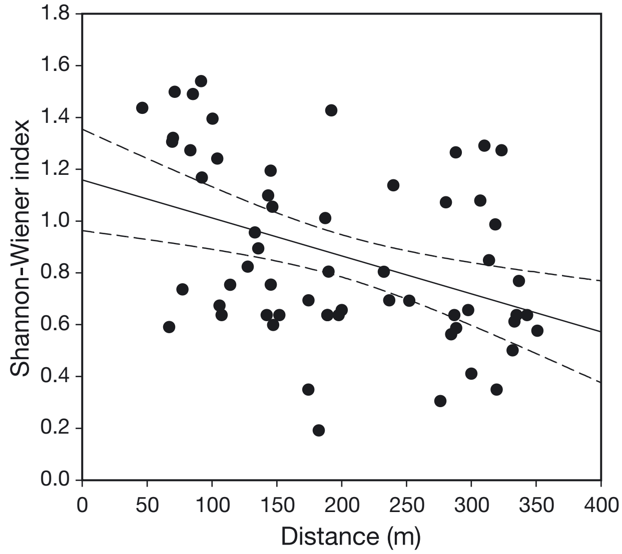

Fig. 5. Shannon-Wiener species diversity index per gillnet setting as a function of distance to turbine. A total of 12 stations were omitted due to no catch or the catch of only a single species. (Solid line) fitted line and (dotted line) 95% CI shown

steady level of fish catch in the Impact area suggested a positive effect of the OWF. This could be due to a refugium effect as fishing is prohibited in the OWF. Refugium effects have been demonstrated for even relatively small areas for the edible crab *Cancer pagurus*, pollock *Pollachius pollachius*, cod *G. morhua* and lobster *Homarus gammarus* (Ashley et al. 2014, Moland et al. 2013). Analysis of VMS (vessel monitoring system) data on the sandeel fishery (van Deurs et al. 2012) and information from local fishermen (J. J. Larsen pers. comm., Danish Fishermen Organisation) indicates, however, that the fishing pressure in both Control and Impact areas at Horns Reef was low.

Species diversity was highest close to the turbines and the lack of a difference in Control and Impact areas prior to the construction of the OWF clearly showed that the introduced hard substratum was utilised by a number of previously scarce or absent fish species. In the studies of Bergstrom et al. (2013), Lindeboom et al. (2011) and Reubens (2013), no significant effects of OWFs on fish diversity were identified. The magnitude of new habitat introduced (<1% of the area in a typical OWF) is probably not large enough to have an overall impact on species diversity in the OWF area. In several other studies, it has been shown that the aggregation of some fish species near OWF turbines is common (Wilhelmsson et al. 2006, Andersson & Öhman 2010, van Hal et al. 2012, Bergstrom et al. 2013, Reubens et al. 2013a), and most likely due to the higher complexity and profile of the introduced habitat relative to the surrounding area creating an 'oasis-like' effect.

The decline in whiting catch levels reflects the general decline of whiting stocks in the North Sea that occurred during this period (ICES 2010). The reason for the less dramatic decline in the OWF area could be greater access to prey. In the North Hoyle OWF (UK), large shoals of juvenile whiting were observed feeding on tube-dwelling amphipods *Jassa falcata* from the underwater structures of the turbine (May 2005). Even though tube-dwelling amphipods *Jassa marmorata* also occur at high densities on Horns Rev OWF (Leonhard & Pedersen 2006), the spatial distribution pattern of the whiting, with a greater abundance away from the turbine foundations, suggests that this species did not utilise this food resource, at least during our study. The equal length distribution, similar catch level in the Impact and Control areas in the After situation, and lack of affiliation to the close proximity of the turbines all point to a limited direct effect of the placement of the turbines on whiting, and thus a low affinity with complex rocky habitats. Whiting is also a dominant species around OWFs off the Dutch coast and here no difference in size or abundance was found between the OWF areas and control sites (van Hal et al. 2012). The reason for this slight discrepancy in our study is not known but stresses the importance of more studies on the effects of OWFs on whiting and fish fauna in general.

OWF development did not appear to affect the sand-dwelling species dab and sandeel, suggesting that that the direct loss of habitat (<1% of the area around the OWF) and indirect effects (e.g. sediment composition) were too low to influence their abundance. Impact assessments on sand-dwelling fish fauna from other OWF studies generally report similar results (Lindeboom et al. 2011, van Deurs et al. 2012, van Hal et al. 2012) with the exception of 2 studies indicating a positive effect on flounder *Platichtys flesus* (Bergstrom et al. 2013), turbot *Psetta maximus* and sole *Solea solea* (Vandendriessche et al. 2014)

The DEM group remained at a low level throughout the study but its large decrease in the Control area resembled that seen for whiting. The shift in the DEM group from flat- to round fishes (such as cod and dragonet) could be interpreted as the introduction of new habitat favoring species capable of benefiting from the new shelter and prey opportunities without having any serious negative effect on the former. Cod are generally caught at higher densities on rough bottoms compared to smooth (Wieland et al. 2009) and it has previously been shown that cod are attracted by shelter and feeding opportunities inside OWFs (Lindeboom et al. 2011, Reubens et al. 2013b).

In conclusion, overall catch rates in the Control relative to the Impact areas indicated a positive effect of the OWF on fish abundance, whereas none of the key fish species or functional fish groups showed any signs of negative effects. The positive effect was mainly evident on a small spatial scale close to the turbines. The placement of the 80 turbines in Horns Rev OWF therefore gave the area a more diverse and complex habitat such that some fish species benefited from it while, concurrently, the impacted size was not large enough to have any adverse effects on sand-dwelling species. Since this study was carried out, another OWF has been established on Horns Reef (Horns Rev 2) and several other OWFs have been planned for adjacent areas. The cumulative effects of additional OWFs in the area are unknown but this study suggests they may increase the recruitment of rocky bottom affiliated fishes.

Horns Rev OWF is, like other current OWFs, situated on soft bottom. One of the major changes to the area after the establishment of the OWF was the introduction of rocky bottom habitat to the otherwise homogeneous sand habitat. The effects on fishes were therefore, not surprisingly, mainly observed in close proximity to these physical changes. The effect on fishes and other fauna in OWFs situated in other, more heterogeneous, environments where rocky habitats are already present may therefore be very different (e.g. Schläppy et al. 2014).

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