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Contribution to the Themed Section: '*Decommissioned offshore man-made installations*'

**Original Article**

# Structure in a sea of sand: fish abundance in relation to man-made structures in the North Sea

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Artificial structures in the marine environment may have direct and/or indirect impact on the behaviour and space use of mobile foragers. This study explores whether environmental and physical features in the North Sea—including artificial structures (wrecks, wind turbines, cables, and oil and gas structures) were associated with local abundance of three fish species: cod (*Gadus morhua*), plaice (*Pleuronectes platessa*), and thornback ray (*Raja clavata*). Generalized additive models (GAMs) were used to compare distributions between data collected by fisheries surveys and electronic tags. Distributions of cod, plaice, and ray were correlated with environmental variables including temperature, depth, and substrate, matching findings from previous studies. All species showed seasonal increases in their abundance in areas with high densities of artificial structures, including oil and gas platforms and wrecks. Independent of whether fish purposefully associate with these features or whether structures happen to coincide with locations frequented by these populations, the strong association suggests that greater consideration needs to be given to regulation of habitat alterations, including decommissioning.

**Keywords:** archival tags, artificial structures, fish abundance, oil and gas

## Introduction

The movements and migratory behaviour of fish has been extensively studied using fisheries-dependent (Heesen *et al.*, 2015) and independent techniques (Righton *et al.*, 2010; Reubens *et al.*, 2014; Russell *et al.*, 2014; Hussey *et al.*, 2017). This information has been used to increase understanding of behaviours and spatio-temporal variability in movements, especially for highly migratory fishes such as bluefin tunas (Block *et al.*, 2005) and several species of shark (Campana *et al.*, 2011). Environmental and physical variables can affect the distribution and behaviour of fish. For example, seasonal changes in the behaviour of many elasmobranch species have been linked to temperature and other abiotic factors, such as salinity, oxygen, and photoperiod [see Schlaff *et al.* (2014) for a review].

As well as natural variables influencing movements, the effect of anthropogenic additions, such as artificial structures, is ever more relevant as the installation of infrastructure increases in the marine environment. For example, the demand for energy has increased the number of offshore energy structures. The effect that these structures have on marine communities has been explored in a number of studies (Reubens *et al.*, 2013a; Krone *et al.*, 2017), with both avoidance and attraction to sites depending on several factors, including the structure type, the species, and the location. However, the combined effects of environmental and anthropogenic change on spatio-temporal dynamics is key, if poorly understood, when trying to identify vulnerability to changes in the marine environment (Stelzenmüller *et al.*, 2010) or assess the impact of the addition or removal of artificial structures. For example, many commercially important species, like Atlantic cod, have complex behaviours comprised of daily and seasonal migrations (Righton *et al.*, 2010). The association of these species with artificial structures is difficult to quantify due to the nature of their habitat, even though significant volumes of data on the movement of fish exist (e.g. Block *et al.*, 2005; Pedersen *et al.*, 2008; de Pontual *et al.*, 2013; Woillez *et al.*, 2016). Importantly, a number of factors will affect species vulnerability, with the aggregative behaviour and site fidelity exhibited by a range of fish species making them more vulnerable to anthropogenic impacts (Egil Skjaeraasen *et al.*, 2011). Thus, aggregate extractions and other marine developments will pose a threat if they are located at or near to important spawning areas where fish aggregate (Stelzenmüller *et al.*, 2010). Additionally, the attraction or overlapping space use of fish to artificial structures can have both positive and negative effects. There is the potential for increased foraging opportunity, but structures may aggregate populations which can make them more vulnerable to fishing and predation (Lindberg and Loftin, 1998). The way that fish species interact with highly developed regions provides an indication of potential impacts for future addition and decommissioning of artificial structures.

To quantify the effects of artificial structures on mobile fish populations, previous studies have used both fisheries-dependent (Polovina and Sakai, 1989) and independent surveys (Winter *et al.*, 2010; van Deurs *et al.*, 2012; Reubens *et al.*, 2014). Fisheries-dependent surveys are limited by temporal coverage and gear catchability, though targeted surveys in areas of interest may provide useful insights into biodiversity around sites of interest (Polovina and Sakai, 1989). Fisheries independent surveys, including acoustic telemetry and diving observations, can be used to gain an understanding of site use by individuals at a high spatial and temporal resolution, though these techniques can be affected by the numbers tagged, size of individuals, and the scale of acoustic arrays. In addition to acoustic telemetry, the use of fish tagged with electronic archival tags to gain insights into spatial overlaps in abundance with artificial structures has been little explored but could provide valuable information about species space use.

This study aims to identify whether the space use of three commercially important species (Atlantic cod, *Gadus morhua* L., European plaice, *Pleuronectes platessa* L., and thornback ray, *Raja clavata* L.), may be associated with man-made structures in the North Sea. It uses information from fish, collated from historical datasets which have been gathered over many years from numerous electronic tagging studies. During the period of deployments (1993–2010), there were relatively few windfarms and oil and gas platforms in the areas where the fish were at liberty, so we predict that there will be little overlap or association with these types of structure types, whilst the coverage of cables and wrecks at the time was relatively ubiquitous, so abundance correlations with these sites may be more pronounced.

## Methods

The fish released in the North Sea (between 1993 and 2010) were equipped with electronic archival or data storage tags (DSTs) which record pressure (providing depth) and temperature. To minimize errors when calculating positions, DST time stamps were synchronized at the point of release to an atomic clock standard. Data from tags were used to reconstruct geographic movements that were linked to both physical (depth, substrate, and temperature), structural (man-made structures) and biological (primary production) variables using GAMs. These DST GAMs were then compared with GAMs produced using fisheries survey data on the same species (collected during the International Bottom Trawl Surveys, IBTS). GAMs were compared for consistency and to assess whether fish abundance can be linked to the presence of structures. Some differences between results using these different datasets may be expected as behaviours were explored at different temporal resolutions, with weekly association for DST GAMs and annual association for IBTS GAMs.

### Study area: environmental and physical conditions

To obtain an accurate representation of conditions in the North Sea for the space-use model, a number of physical and biological variables were compiled, including bathymetry, water-column temperature, sediment type, primary production, number of wind turbines, tonnage of wrecks, oil, and gas platforms, and densities of telecommunication cables (Table 1). For further information on the processing of these data layers refer to Posen *et al.* (submitted). All natural substrate information, and structure shape files (telecommunication cables and oil and gas platforms) were scaled to 15 $km^2$ resolution providing the proportion of the cell occupied by these features and sediment types. Numbers of turbines and tonnage of wrecks by grid cell were also derived in addition to mean water-column temperatures and mean bathymetry. These variables were chosen to reflect variables which may affect fish behaviour.

Man-made structures occupy very little space in comparison to the spatial extent of some natural features and to the spatial resolution used in the model. Furthermore, the attributes of most of the datasets of man-made structures did not include their physical dimensions. It was, therefore, necessary to estimate the proportion of grid cell occupied by each type of structure, depending on the characteristics of the latter. Gridded data layers were derived to represent each different structure type as follows:

(1) Point data were output as gridded layers according to the characteristics of individual features (oil and gas platforms; subsurface structures; wind turbines; wrecks).

(2) All point features were overlaid with the different spatial grids and feature count per grid cell was derived.

(3) Buffers were assigned around oil and gas platforms according to their respective tonnage (<10 000 tonnes: 100 m; 10 000–100 000 tonnes: 200 m; >100 000 tonnes: 500 m), overlapping buffer zones were "dissolved" to avoid double counting and the areal values of the resulting buffers were used to derive proportion of grid cell occupied by platforms.

(4) About 50 m buffers were assigned around individual wind turbines (being the KIS-ORCA advisory safety zone for fishing vessels) and these buffers were used to derive proportion of grid cell occupied by turbines.

(5) Subsurface structures (excluding those associated with oil and gas platforms, i.e. not within their assigned buffer zones) were considered to occupy too little space to derive proportion of grid cell occupied, so were produced as count per grid cell only.

(6) Information on wreck abundance was incomplete, so where appropriate, tonnage was calculated depending on wreck type and date sunk using an average tonnage per wreck type. All wreck materials described as wood, plywood, or "wood and plywood" were excluded from analysis and tonnage was weighted depending on the date that the wreck was sunk. In this sense, all the wrecks before 1865 (150 years before

**Table 1.** Data sources used for DST and IBTS models, and manipulations required for model predictions to a 15 km resolution grid.

| | Parameter | Data source | Manipulations | Figure |
|---|---|---|---|---|
| Biological | Abundance | Data storage tags (CTL). | Proportion of time spent by area | 1 |
| | Primary production | GETM-ERSM-BFM hindcast extracts | Mean gross PP by area | |
| Physical | Bathymetry | A merged product of a 6″ digital elevation model (DEM) of the UK continental shelf area (OceanWise, 2011) and the EMODnet-Bathymetry ¼° (equal to 15″) DEM. See Stephens and Diesing (2015) for full methods. | Mean bathymetry by area | S1 |
| | Temperature | Atlantic-European North West Shelf-Ocean physics reanalysis (Wakelin *et al.*, 2015) and the Atlantic-European North West Shelf- Ocean Physics Analysis and Forecast model (McConnell *et al.*, 2017) for dates after 2014. | Mean water-column temperature by area | |
| | Sediment | Merged product derived primarily from the 250 000 resolution Emodnet_seabed_substrate. Areas with "no data" were then supplemented with values from the 1 000 000 resolution Emodnet_seabed_substrate dataset. Remaining "no data" regions were then supplemented with the EUSeaMap_ModelledSeabedHabitats dataset (previous JNCC modelled data). | Proportion of area by type (sand, rock, mixed, coarse, and mud). | S1 |
| Structures | Wind turbines | Point locations of individual wind turbines, substations, and associated meteorological masts in the North Sea from The Kingfisher Information Service—Offshore Renewable and Cable Awareness project (KIS-ORCA)—a joint initiative between Subsea Cables UK and RenewableUK, managed by the Kingfisher Information Service of Seafish (http://www.kis-orca.eu/). | NA | S2 |
| | Wrecks | Point locations with details including wreck type, size, material, depth, and date sunk, purchased from The Wreck Site—wrecksite.eu | Tonnage by area | S2 |
| | Oil and gas platforms | Point locations and details compiled from the Oil & Gas UK (OGUK) Database of North Sea fixed platforms, October 2012—a product of the North Sea Decommissioning Baseline Study joint industry project (oilandgasuk.co.uk/product/north-sea-decommissioning-database; http://www.insitenorthsea.org/about/); and the OSPAR Offshore Installations Inventory, 2015 (odims.ospar.org)). | NA | S2 |
| | Telecomm. cables | Polyline data layer of submarine cables for the North Sea). Source: KIS-ORCA (Offshore Renewable and Cables Awareness) http://www.kis-orca.eu/ subsea cable data, supplemented with additional polyline data from UK Hydographic Office. | NA | S2 |

*Notes:* Figures which appear in the supplementary are denoted with an S.

present, with present being 2015) were eliminated (degraded to the point of removal). Wrecks sunk between 1865 and the present day were assigned a linear weight between 0 and 1 (MacLeod and Harvey, 2015). Once an appropriate tonnage was applied to each wreck, the tonnage was summed by grid cell. Polyline data were output as gridded layers in two formats (pipelines; submarine cables).

(7) Features were overlaid with the different spatial grids and total length of lines per grid cell was derived.

(8) About 25 m buffers were assigned each side of all linear features and the resulting areal values were used to derive proportion of each grid cell occupied by the features. Overlapping buffers were not "dissolved", to account for extra buffer width where neighbouring pipelines or cables cross or coincide.

## Field protocol and DST deployments

Fish were tagged and released between December 1993 and September 2010, with release locations as close to the catch locations as possible. A number of different tag types were used for these deployments including Star Oddi (Marine Device Manufacturing, Iceland) "Milli" and "Centi" tags (cod group 1), LOTEK (Marine Technologies, Canada) 1200 and 1400 tags (cod group 1, plaice groups 2 and 3), Cefas Technology Limited Mk 1 and G5 DSTs (plaice group 2 and 3). For additional information about tag logging regimes and tagging methods refer to manuscripts detailed in Table 2. For analysis purposes, and to reflect that the location and temporal differences in space use may impact association, fish were grouped by species, release location, and by the date of release (Figure 1, Table 2). This resulted in four groups: one cod group based in the western North Sea (referred to as cod group), two plaice groups based in the western North Sea and the central North Sea (referred to as western plaice group and central plaice group), and one thornback ray group from the southern North Sea (referred to as ray group). All releases were from the south west of the North Sea, except for plaice group 3 which were released from the central North Sea (Figure 1). Further information about tagging methods and release characteristics can be

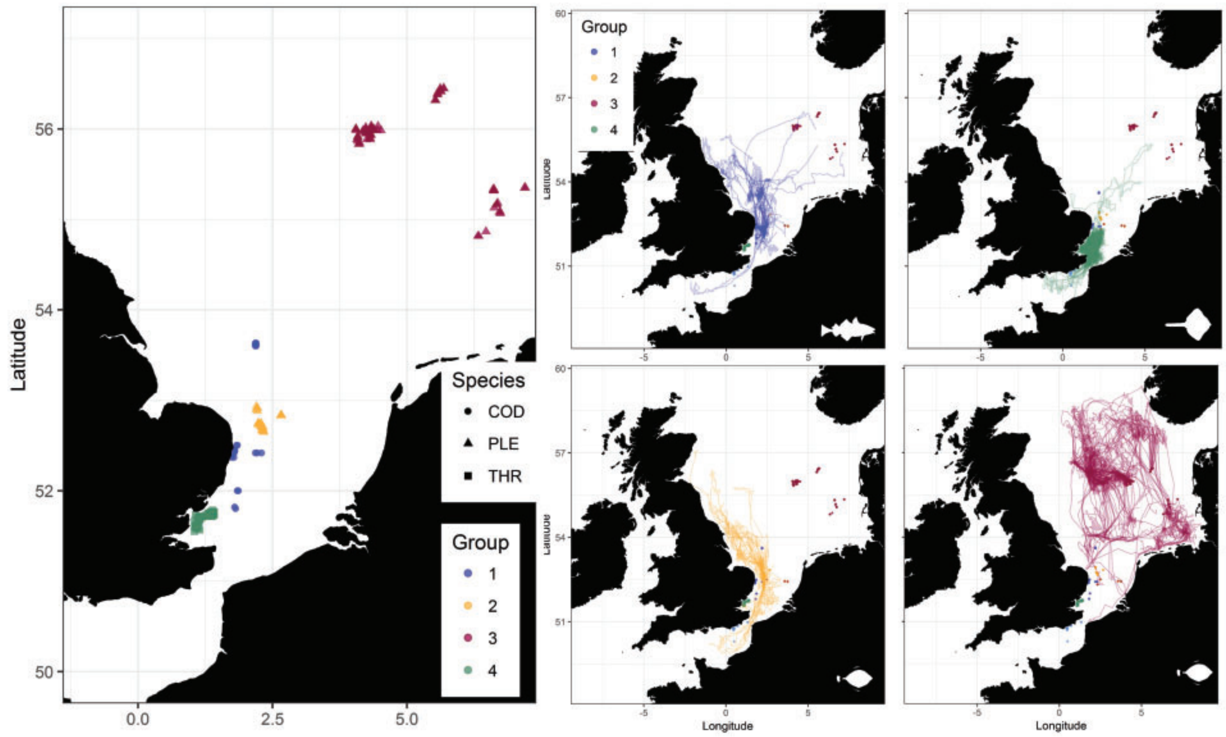


**Figure 1.** Release locations and fish tracks for Atlantic cod (COD), European plaice (PLE), and thornback ray (THR). Daily most probable locations constructed using a HMM for individual fish from groups 1–4.

**Table 2.** Release information for groups 1–4, where *N* reflects the number of individuals used in this analysis, time at liberty is the first and last day at liberty for any fish within the group, and the minimum and maximum latitudes and longitudes.

| Source | Species | Group | Release year | N | Size range (cm) | Type of DST | At liberty First | At liberty Last | Latitude Min | Latitude Max | Longitude Min | Longitude Max | Reference |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DST | Cod | 1 | 1999 | 31 | >45 | (1) Star Oddi | 24/03/1999 | 18/09/2010 | 51.72 | 53.63 | 1.12 | 2.30 | Righton *et al.* (2007, 2010) |
| | | | 2000 | 2 | | ("Milli" and | | | | | | | |
| | | | 2001 | 22 | | "Centi") | | | | | | | |
| | | | 2003 | 2 | | (2) LOTEK 1200 | | | | | | | |
| | | | 2004 | 3 | | and 1400 | | | | | | | |
| | | | 2005 | 2 | | | | | | | | | |
| | | | 2010 | 2 | | | | | | | | | |
| | Plaice | Western (2) | 1993 | 4 | >35 | (1) LOTEK 1200 | 15/12/1993 | 10/08/2006 | 52.65 | 52.93 | 2.20 | 2.67 | Hunter *et al.* (2004a, 2004b) |
| | | | 1998 | 11 | | and 1400 | | | | | | | |
| | | | 2004 | 9 | | (2) CTL Mk 1 | | | | | | | |
| | | | 2005 | 4 | | | | | | | | | |
| | | Central (3) | 1997 | 65 | >35 | (1) LOTEK 1200 | 28/10/1997 | 31/01/2006 | 54.82 | 56.45 | 4.03 | 7.20 | Hunter *et al.* (2003, 2004b) |
| | | | 2004 | 27 | | and 1400 | | | | | | | |
| | | | | | | (2) CTL Mk 1 | | | | | | | |
| | Thornback ray | 4 | 1999 | 48 | 37-60 | LOTEK LTD 1200 | 06/10/1999 | 02/12/2000 | 51.55 | 51.78 | 1.05 | 1.42 | Hunter *et al.* (2005) |
| | | | 2000 | 41 | 36-57 | LOTEK LTD 1200 | 19/10/2000 | 15/03/2002 | 51.55 | 51.78 | 1.05 | 1.42 | |

*Note:* Size range denotes the total length for cod and plaice and disc width for thornback ray.

found for each group in previously published peer-reviewed manuscripts (see Table 2 for references).

## IBTS survey information

IBTS data are collated by ICES and raw data are available from the database of trawl surveys "DATRAS" (http://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx). The data product used here was the quality assured monitoring and assessment data (version 2) set for the "Greater North Sea International Otter Trawl quarter 1 and quarter 3 surveys" (Moriarty *et al.*, 2017). This is a publicly available product, based on data downloaded from DATRAS on 27 August 2015, with supporting technical documentation describing quality assurances and techniques to determine the area swept by each haul (Greenstreet and Moriarty, 2017; Moriarty *et al.*, 2017). The catch data for each haul, for each species was expressed as numbers and biomass and haul data were averaged by species across a 15 $km^2$ resolution grid. Biomass (kg $km^2$) was spatio-temporally matched to locations (matching grid squares) and years when DST tagged cod (>40 cm total length), plaice and thornback ray were at liberty.

## Statistical analysis

### Geolocation

To geolocate fish in this study, the hidden Markov model (HMM) previously described in Pedersen *et al.* (2011) has been adapted. The original HMM uses the maximum depth and tidal signal recorded by the pressure sensors to estimate the daily location of the fish from release to recapture (Pedersen *et al.*, 2008). In addition to bathymetry and tidal amplitude and phase, the revised HMM included sea surface temperature, which aimed to provide additional validation when fish were swimming at or near the surface. Gridded global bathymetry data were obtained from the general bathymetric chart of the oceans (Gebco) (British Oceanographic Data Centre, Liverpool, United Kingdom, 2009). Tidal constituents were obtained from the Oregon State University Tidal Prediction model, as described in Egbert and Erofeeva (2002). Temperature were sourced from the Atlantic-European North West Shelf-Ocean physics reanalysis (Wakelin *et al.*, 2015) and the Atlantic-European North West Shelf- Ocean Physics Analysis and Forecast model (McConnell *et al.*, 2017) for dates after 2014.

Prior to running the model, a number of constraints and input parameters were defined to ensure that the model ran effectively. The recapture information was set as the latitude and longitude where the tag was recovered, and an error was defined based on the level of confidence for each site, i.e. whether the tag was found on a fishing vessel (high confidence: < 5 km error) or on a beach (low confidence: >200 km error). The diffusivity of the model reflects how far the fish could travel each day. Diffusivity was estimated using the method detailed in Pedersen *et al.* (2008). Two values were estimated corresponding to localized (resident) and migratory distances. Smaller values reflect restrictions to movements, with 0 being the same location as the previous day.

The revised HMM was designed to run at 10.8 km resolution providing a result file with a coarse spatial resolution of fish location. The model was then rerun at 1.1 km resolution over the utilized area with a 2 km buffer to obtain a more accurate location estimate of fish position (Figure 1). Daily fish positions were then scaled to a 15 $km^2$ grid matching underlying explanatory variable data layers (Table 1).

### Model description: DST GAM

For each day at liberty, the most probable location (at a 15 $km^2$ resolution) was linked to physical and environmental variables extracted from several sources, as detailed in Table 1. For each group, the first 7 days at liberty were removed from analysis to minimize the effect of release location on the model predictions. For each group (as defined in Table 2), the number of individuals in each gridded area was used to create spatial matrices for each week at liberty. All grid cells used by at least one individual from the group were incorporated in a proportional abundance matrix, providing a weekly abundance layer with zeros where no fish were present.

A generalised additive model (GAM) approach was used to predict abundance of fish in relation to the predictor variables detailed in Table 1. The relationships between the response and predictor variables were assessed using increasingly nonlinear smoothing terms up to a maximum of 4 knots, to minimize the risk of over-fitting. The first model incorporated all explanatory variables, where appropriate (some groups did not spend any time in grids with wind turbines or rock substrate, so these terms were removed for these groups), with subsequent models fitted with insignificant explanatory variables removed, until only significant variables remained:

$$\begin{aligned} FA_p \sim\ & s(\text{week}) + s(\text{depth}) + s(\text{temperature}) \\ & + s(\text{sand substrate}) + s(\text{rock substrate}) \\ & + s(\text{gravel substrate}) + s(\text{mixed substrate}) \\ & + s(\text{oil and gas}) + s(\text{wind turbines}) + s(\text{wrecks}) \\ & + s(\text{telecom. cables}) + s(\text{primary production}) \\ & + \text{offset}(\text{Nind}) \end{aligned} \tag{1}$$

where $FA_p$ represents the expected abundance using a negative binomial distribution with a log link function, including an offset, to allow for variations in the number at liberty by week (offset(Nind)). Thin plate regression splines (s) were applied to each parameter, with cyclic cubic regression splines used for weeks, as the covariate is circular. An extra penalty was applied to each parameter as the smoothing term approached zero allowing the complete removal of terms from the model. All models were fit using the gam function in the mgcv package (Wood 2006), in R (R development core team 2017, version 3.3.2).

### Model description: IBTS GAM

Cod, plaice, and thornback ray catch data from the IBTS surveys were used for comparisons with DST GAM results using the same method as detailed above. For each haul location (at a 15 $km^2$ resolution) by year, biomass (kg/$km^2$) was linked to physical and environmental variables extracted from several sources, as detailed in Table 1 (excluding primary production):

$$\begin{aligned} FA_p \sim\ & s(\text{Year}) + s(\text{depth}) + s(\text{temperature}) + s(\text{sand}) \\ & + s(\text{rock}) + s(\text{gravel}) + s(\text{mixed}) \\ & + s(\text{oil and gas platforms}) + s(\text{wind turbines}) \\ & + s(\text{wrecks}) + s(\text{telecom cables}) \end{aligned} \tag{2}$$

where $FA_p$ represents the biomass (kg/$km^2$) of fish using a negative binomial distribution with a log link function.

### Model evaluation

Model performance was assessed using a number of tools:

(1) Plots of predicted vs. observed abundance were made for each group, with semi-variograms to assess spatial independence of residuals. If a correlation signal was observed in the predicted vs. observed abundance, it was deemed that this criterium was not achieved.

(2) Variance inflation factors to assess multi-collinearity in predictors.

(3) Spearman's rank correlations ($r_s$) to examine the correlation between the DST abundance data and the predictions;

following Lauria *et al.*, (2011) and Sguotti *et al.*, (2016), where, models were accepted when $r_s$ exceeded 0.1 and $p < 0.05$.

(4) Predictive performance was measured through the receiver operating characteristic (ROC) curve and was considered acceptable when the area under the curve (AUC) was greater than 0.5 with $p < 0.05$.

(5) Partial residuals plots for predictors to identify un-explained patterns and the validity of the error structure chosen.

(6) The total deviance explained compared with the deviance explained when each man-made structure variable was individually removed from the GAM.

Models were removed from further analysis if any of the model performance indicators were not achieved.

#### *Assessing the similarity between IBTS and DST abundances*

DST GAMs were compared with GAM results for the same species recorded as part of the IBTS survey at a quarterly time-scale, with quarters 1 and 3 used for comparisons for each group. Quarters 1, 2, 3, and 4 represent dates between January and March, April and June, July and September and October and December, respectively. Significance of explanatory variables were compared between models to assess whether there were any significant differences between models produced using different data sources.

#### *Quantifying effects of man-made structures*

DST-fitted models were used to assess empirically the impact of removing hard structures on the occurrence of species by making predictions across the North Sea grid (all 15 × 15 km cells) with all significant terms in the model and with artificial structures removed. The relative effect of each structure type was standardized given the spatial coverage of each structure type by weighting to the proportion of grid cells in which each structure type was present.

## Results

Between December 1993 and September 2010, a total of 37 191 days of data were recorded for the four fish groups.

### Generalized additive models

The majority of DST and IBTS models exceeded the evaluation criteria (Spearman's $r_s > 0.1$, $p < 0.05$; and AUC $> 0.5$, $p < 0.05$) and had high predictive power (Table 3, Figure 2 for examples), except for the DST-based models for the cod group (full) and the western plaice group (Q1) which had $r_s$ values below 0.1, and for the IBTS-based model for the ray group (Q1), which had positive spatial autocorrelation. These three models were therefore excluded from any further analysis and interpretation. The remaining GAMs described between 12% and 50% of the deviance for DST GAMS and between 8% and 41% of the variation for IBTS GAMs (Table 3).

Six comparisons were made between IBTS and DST GAMs (cod Q1 and Q3, western plaice Q3, central plaice Q1 and Q3 and ray Q3; Table 4). In all instances where there was a significant effect from a predictor in both the IBTS and DST GAMs, the direction was the same for matched quarters (i.e. positive abundance with increasing depth for cod quarter 3 and negative for cod quarter 1). Though, there were many occurrences where significant predictor variables were not found in both IBTS and DST GAMs (i.e. negative effect of depth on abundance for IBTS western plaice Q3 and no effect for the matching DST GAM). The majority of relationships between response and predictors were not inconsistent across month (no opposing negative and positive directions).

### Man-made structure influence

To explore the contributions of artificial structures to GAMs, the proportion of the deviance explained was derived by removing the predictor variable from the full models (Table 5). The influence of windfarms, wrecks, oil and gas platforms, and cables is shown in Figure 3 with weighting for spatial coverage of structures.

#### *Atlantic cod*

For the cod group (group 1), in terms of deviance explained, either depth or temperature were the most important predictor variables for distribution (Table 5), with depth being most important in quarters 1, 2, and 3. Cod preferred shallow in Q1, moderate depths (25-50 m) in Q2 and deep in Q3 (Table 4). In terms of artificial structures, there was a general positive correlation in abundance with cables and negative correlation with wrecks, though an increase in numbers with wrecks occurred in Q2 (Figure 3). In Q3 cod were found in deep areas where primary production was low. Their distribution in Q4 was most explained by temperature (Table 5) with increased abundance in regions with cooler temperatures (< 10°C) and increased abundance with cable coverage and primary production (Table 4).

#### *European plaice*

For western plaice (group 2), artificial structures explained the largest proportion of the variance for all quarters (oil and gas for Q4 and cables for all other quarters and for the combined model, Table 5). For the combined model, and quarters 2 and 4, there was a positive correlation between plaice abundance and depth and density of oil and gas platforms and cables (Table 4, Figure 3). In quarter 2, overall abundance decreased with wrecks and increased with oil and gas platforms and cables (Figure 3).

The distribution of central plaice (group 3) was mostly explained by the depth of the water column. Across all time frames, plaice were in shallow waters and associated with sand or mud-dominated sediments (Table 4). In terms of abundance with structures, plaice had highest densities with oil and gas platforms and lowest with high densities of cables, though the effect was proportionally low compared with other groups (Table 4, Figure 3).

#### *Thornback ray*

GAM results for the thornback ray indicate that ray abundance increased with temperature with a variable relationship with depth depending on the season. The most important predictor variable varied between models (Table 5); with temperature and depth explaining the most variance for quarters 3 and 4, and wrecks explaining the most variance for quarters 1 and 2 (Figure 3). In terms of abundance with structures, all quarters indicated an increase with wrecks (Table 4, Figure 3).

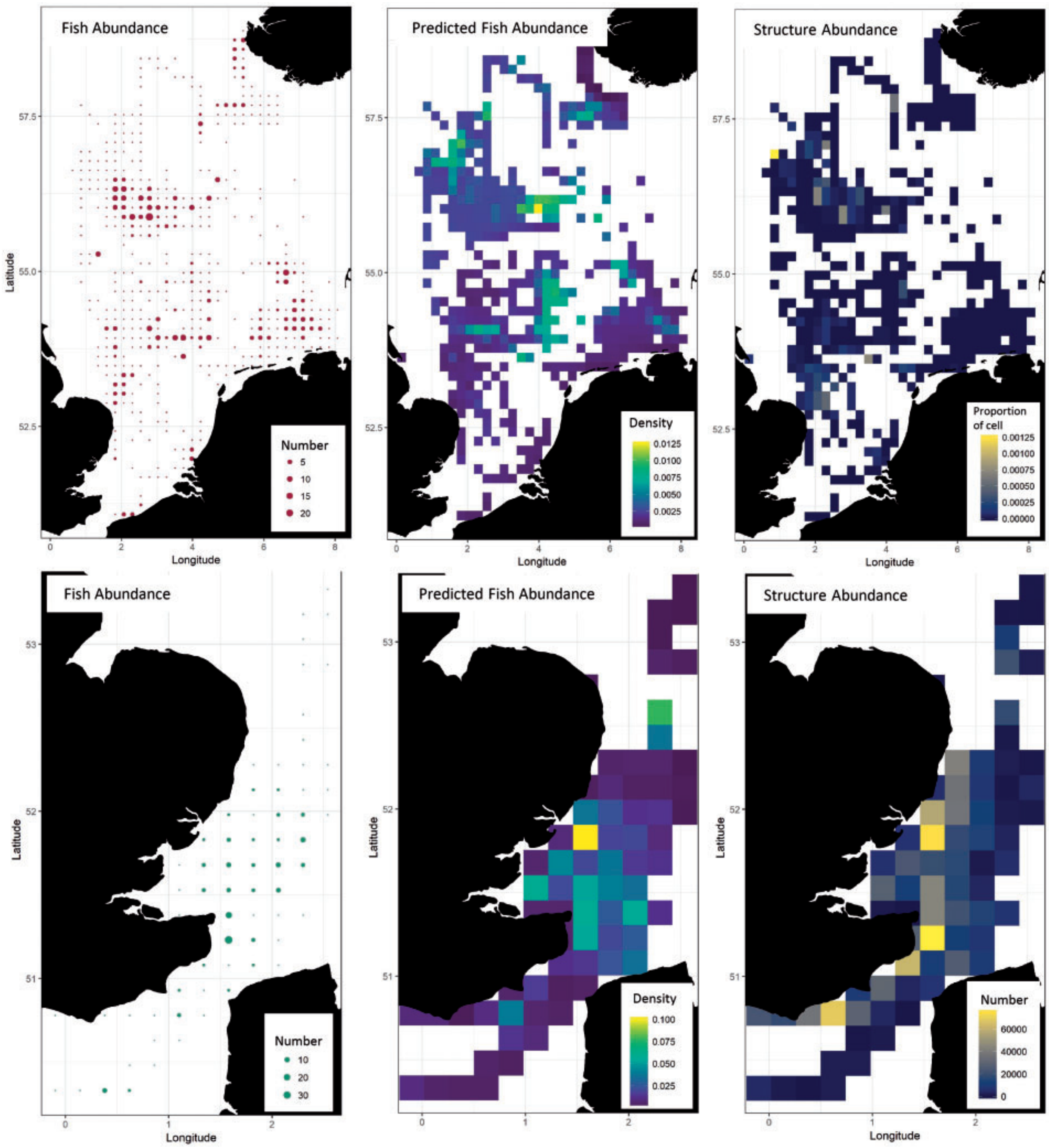


**Figure 2.** Examples of distributions of central European plaice in Q1 (group 3: top figures) and thornback ray in Q2 (group 4: bottom figures). Abundance of fish (left) and predicted abundance by the full GAM model (centre) and corresponding distributions of oil and gas platforms (top right) and wrecks (bottom right) covering the same time period.

## Discussion

This study has shown—based on DST and fisheries survey data—that there are association between cod, plaice, and ray distributions and artificial structures in the North Sea. This was based on consistent patterns in movement that were detected in both fisheries-dependent and independent datasets. The links between artificial structure densities and fish abundance indicate that artificial structures are present in areas where fish spend prolonged periods of time. This study can be considered a baseline, with the potential to explore whether distributions have now changed with the addition of man-made structures in the North Sea. Differences in co-correlation of species with structures highlights the importance of carrying out species-specific studies. Furthermore, implications for major habitat changes, like decommissioning scenarios must also be considered.

## Atlantic cod

### *Natural environment*

Previous studies indicate that North Sea cod spawn between January and April (Brander, 1994; Morgan *et al.*, 2013), with a

**Table 3.** Summary statistics of final GAM models (DST and IBTS) fitted to all explanatory variables via the mgcv package (Wood 2006) in R.

| Data | Species | Gr | GAM type | N | Deviance explained (%) | AUC | $r_s$ | Spatial AC |
|---|---|---|---|---|---|---|---|---|
| DST | Cod | 1 | Full | 64 | 28.24 | 0.64 | **0.09** | F |
| | | | Q1 | 39 | 17.32 | 0.68 | 0.16 | F |
| | | | Q2 | 62 | 32.98 | 0.64 | 0.12 | F |
| | | | Q3 | 25 | 20.31 | 0.65 | 0.14 | F |
| | | | Q4 | 11 | 11.72 | 0.63 | 0.11 | F |
| | Plaice | Western (2) | Full | 24 | 17.38 | 0.69 | 0.12 | F |
| | | | Q1 | 20 | 15.03 | 0.61 | **0.08** | F |
| | | | Q2 | 13 | 17.42 | 0.64 | 0.13 | F |
| | | | Q3 | 22 | 18.46 | 0.68 | 0.18 | F |
| | | | Q4 | 28 | 18.69 | 0.70 | 0.19 | F |
| | | Central (3) | Full | 73 | 36.42 | 0.71 | 0.15 | F |
| | | | Q1 | 64 | 40.53 | 0.66 | 0.14 | F |
| | | | Q2 | 33 | 39.67 | 0.73 | 0.28 | F |
| | | | Q3 | 19 | 44.74 | 0.78 | 0.36 | F |
| | | | Q4 | 73 | 35.27 | 0.71 | 0.18 | F |
| | Thornback ray | 4 | Full | 89 | 47.97 | 0.81 | 0.39 | F |
| | | | Q1 | 75 | 46.91 | 0.81 | 0.50 | F |
| | | | Q2 | 47 | 33.12 | 0.78 | 0.46 | F |
| | | | Q3 | 12 | 12.18 | 0.67 | 0.24 | F |
| | | | Q4 | 89 | 50.42 | 0.76 | 0.36 | F |
| IBTS | Cod | 1 | Q1 | 1281 | 8.35 | – | 0.28 | F |
| | | | Q3 | 213 | 22.26 | – | 0.41 | F |
| | Plaice | Western (2) | Q1 | 1513 | 22.01 | 0.68 | 0.39 | F |
| | | | Q3 | 537 | 21.04 | 0.81 | 0.64 | F |
| | | Central (3) | Q1 | 4852 | 18.95 | 0.83 | 0.56 | F |
| | | | Q3 | 2063 | 19.96 | 0.90 | 0.64 | F |
| | Thornback ray | 4 | Q1 | 1044 | 15.90 | 0.78 | 0.44 | **T** |
| | | | Q3 | 313 | 40.97 | 0.87 | 0.47 | F |

*Notes:* GAM type is defined as full when all data was used for DST deployments, Q1 = January–March, Q2 = April–June, Q3 = July–September, and Q4 = October–December, *N* reflects the number of fish used in DST GAMs and number of unique hauls used in the IBTS GAMs. All *p*-values associated with $r_s$ and AUC were $<$0.001 and whether there was spatial autocorrelation (spatial AC), true or false (T or F). Evaluation criteria which were not met are highlighted in bold.

preference for temperatures between 5°C and 7°C (González-Irusta and Wright, 2016) and a typical thermal range of 1–8°C (Righton *et al.*, 2010). In the present study, cod in Q1 (spawning season) showed a preference for relatively cold waters (compared with available temperatures), with highest abundance in areas with average temperatures <10°C, matching previous results. Seasonal changes in depth reflect increased abundance in relatively shallow waters in Q1 with a movement to progressively deeper waters in Q2 and Q3, as shown in previous studies of cod spatio-temporal distribution in the North Sea (Righton *et al.*, 2007; Neat *et al.*, 2014). Cod in quarter 4 had increased abundance in cooler areas with high primary production, which may link to movement toward feeding grounds in more coastal areas at the end of the year, or simply movement toward inshore spawning grounds in preparation for the spawning season (Righton *et al.*, 2010).

#### *Structures*

In terms of spatial overlap with structures, previous studies have found Atlantic cod associating with oil and gas platforms in the North Sea (Valdemarsen, 1979; Jørgensen *et al.*, 2002; Løkkeborg *et al.*, 2002), and windmill artificial reefs (Reubens *et al.*, 2013a). No association with high densities of oil and gas platforms in the present study, but there was an increase in cod abundance with densities of cables during Q2 and Q4 (and a decrease in Q3) and no correlation during the spawning period (Q1). Increases in abundance with cable densities in quarters 2 and 4 may reflect an increased prey abundance in cells with high proportions of cables, and the association may break down in quarter 1 (spawning season) when prey are presumably less important. An acoustic study (Reubens *et al.*, 2013a) found highest catch-per-unit-effort (and aggregation) of cod around windmill artificial reefs in the southern North Sea during intensive feeding periods (quarters 3 and 4). Cod associated with these windmill artificial reefs ranged from 20 to 62 cm (Reubens *et al.*, 2013b), with increased numbers of small cod observed with these sites throughout the year. There may an ontogenetic difference in the space use of cod in the southern North Sea, with large adults changing behavioural strategy depending on the season, whilst relatively small individuals remain more resident until they reach a critical size.

### European plaice

#### *Natural environment*

There were differences in habitat preference and in significance of predictor variables between plaice inhabiting the western North

**Table 4.** Significant predictor variables for the final DST and IBTS GAM models for the full dataset and for quarters 1 to 4 (where applicable).

| Species | Gr | Variable | Full DST | Q1 DST | Q1 IBTS | Q2 DST | Q3 DST | Q3 IBTS | Q4 DST |
|---|---|---|---|---|---|---|---|---|---|
| Cod | 1 | Deptd | | − | − | ∼ | + | + | |
| | | Temp | | | ∼ | + | | + | − |
| | | Sand | | − | | − | | + | |
| | | Mud | | | − | − | | | |
| | | Coarse | | | | − | − | | + |
| | | Mixed | | | | − | | | |
| | | Cables | | | | + | | − | + |
| | | Wreck | | | | − | | | |
| | | PP | | | | | − | | + |
| PLE | Western (2) | Depth | + | | − | + | | − | + |
| | | Temp | ∼ | | + | | | | |
| | | Sand | + | | + | | | | |
| | | Mud | | | ∼ | | | | |
| | | Coarse | + | | | + | | + | |
| | | Mixed | + | | | | | | |
| | | Rocks | − | | | | | | |
| | | OG | + | | | + | | + | + |
| | | Cables | + | | | + | + | | + |
| | | Wreck | | | ∼ | + | − | − | |
| | | PP | − | | | | − | | − |
| PLE | Central (3) | Depth | − | − | − | − | − | − | ∼ |
| | | Temp | | | − | − | | − | + |
| | | Sand | + | | ∼ | + | | | + |
| | | Mud | + | + | + | + | + | | + |
| | | Coarse | + | | | | | ∼ | |
| | | Mixed | − | | − | | | | |
| | | OG | + | + | | | | | |
| | | Cables | − | − | − | | | − | − |
| | | Wreck | | | | | | | |
| | | PP | | + | | ∼ | | | − |
| THR | 4 | Depth | ∼ | ∼ | | ∼ | | | + |
| | | Temp | + | + | | | + | + | ∼ |
| | | Sand | + | + | | ∼ | | | |
| | | Mud | + | | | − | | | |
| | | Coarse | ∼ | ∼ | | ∼ | − | − | ∼ |
| | | Mixed | ∼ | ∼ | | | | | − |
| | | Rocks | | − | | − | - | | − |
| | | OG | + | + | | − | | | − |
| | | Cables | + | + | | − | | | + |
| | | Wreck | ∼ | + | | + | + | | ∼ |
| | | PP | | | | | | | + |

*Notes:* For clarity, non-significant ($p < 0.05$) predictor variables have been removed. Species are denoted as Atlantic cod (COD), European plaice (PLE), and thornback ray (THR). Variables include depth, temperature (Temp), density of cables, wrecks, oil and gas platforms (OG), primary production (PP), and the proportion of sediments such as sand, mud, coarse, or mixed. Effects show whether there is a positive (+), negative (−), or variable (∼) trend for the predictor variable. When a non-linear trend occurs, the range of values for the highest abundance is denoted. Note, fixed factors (week and year, for DST and IBTS GAMs) are not shown and variables which were not used in the GAMs are denoted in grey.

Sea (group 2) and central North Sea (group 3). Spatially these two groups differ with group 2 limited to the western side of the North Sea and group 3 covering mostly central and eastern areas of the North Sea (Figure 1). Increased abundance in shallow areas for western plaice matched results from the IBTS GAMs and from previous studies on plaice in the English Channel (Hinz *et al.*, 2006), which show that plaice have consistently high abundance in relatively shallow areas, with low salinity, high sand content, and low gravel content (Hinz *et al.*, 2006). In contrast, locations avoided by plaice were characterized by deeper, more saline waters, and sediments with either a high gravel or mud content, matching the shallow, sandy feeding ground reported by (Hunter *et al.*, 2004a).

### *Structures*

Both groups of plaice were found to be more abundant in areas with a high density of oil and gas platforms. Other demersal species have also been shown to have increased abundance in regions with oil and gas structures in the North Sea, including ling (*Molva molva*) and saithe (*Pollachius virens*) (Løkkeborg *et al.*, 2002). The high densities of plaice in regions with high densities of structures does not necessarily reflect that plaice are using these structures directly, but instead, may indicate that these regions with high sand content are optimal for artificial structure placement. Nonetheless, this habitat overlap indicates that alterations to these structures may affect plaice populations close by.

## Thornback ray

### *Natural environment*

There was a seasonal change in the most important predictor variables for thornback ray; these were temperature in quarter 3, and depth in quarter 4 (in line with Sguotti *et al.*, 2016). Abundance in quarter 3 was linked to relatively warm areas, and in quarter 4 with either relatively shallow or deep areas. Previous studies of thornback ray in the Thames estuary indicate that thornbacks move into deeper waters during autumn and shallow waters of the Thames in summer (Hunter *et al.*, 2006). Additionally there was an overall increase in abundance with sandy areas, as found in previous studies of *R. clavata* from the Eastern English Channel (Martin *et al.*, 2005).

### *Structures*

The distribution of thornback rays was generally higher in areas with wrecks, especially in quarters 1 and 2. Thornbacks have their egg laying phase in quarters 1 and 2 (starting in February, peaks in June and ceases in September) (Holden, 1975). A possible association with wrecks may be linked to the fact that these can promote growth of reef organisms; for example, the shipwreck network along the Belgian coast has been shown to enhance biodiversity, and act as stepping stones for hard bottom species (Mallefet *et al.*, 2008). Increases in ray abundance with higher densities of wrecks may also be linked to these areas offering increased refuge and opportunities to feed, as has been found for both benthopelagic and pelagic fish species (Arena, 2011).

## Implications

A number of species in the present study indicate a degree of co-correlation between abundance and man-made structure density. The potential aggregation of species to areas of increased man-made structure presence may increase vulnerability to these fish populations, with the potential for both increased natural predation and anthropogenic population loss through fishing pressure (Lindberg and Loftin, 1998).

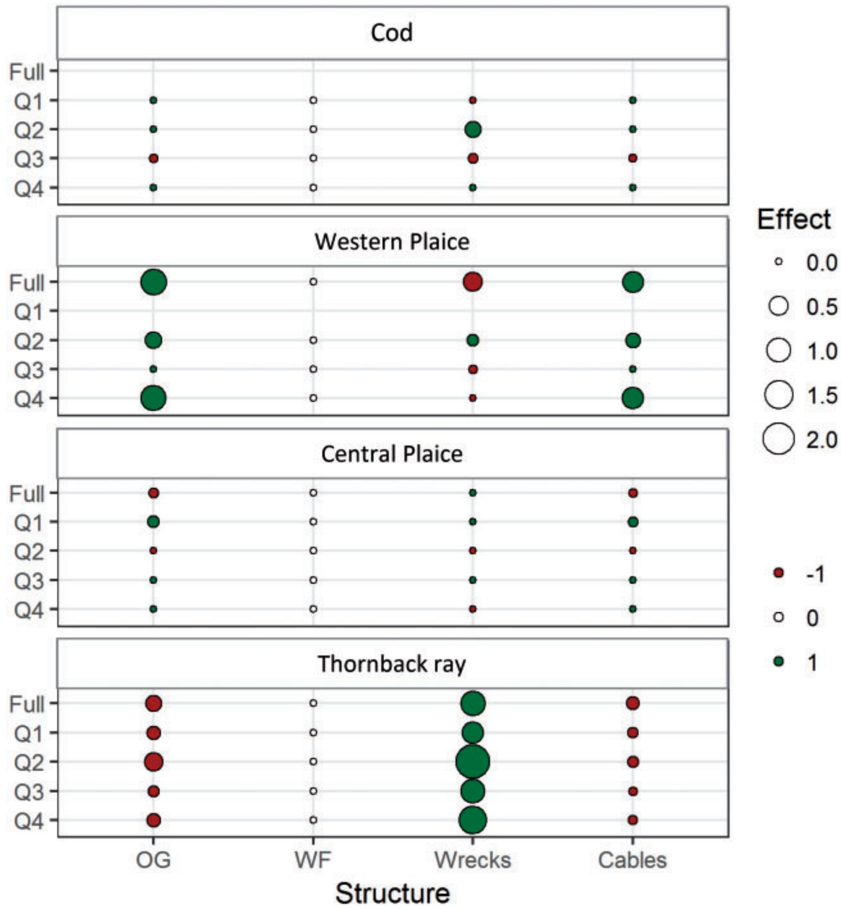


**Figure 3.** Effect of structure types on groups identified through statistical analyses of gridded survey data (significant relationships shown only). A positive effect indicates that the occurrence of the group is increased through the presence of structures, while negative effects indicate the opposite. Bubble size is proportional to the change in probability of occurrence of the group in the region where the relevant structure type is present (so independent of spatial coverage of the structures). Windfarms did not significantly contribute to any of the GAMs, so that their influence is 0 (neither positive or negative).

## Challenges

To a limited extent our results may be compromised, as positional information derived from fish-borne DSTs may be affected by geolocation errors. However, 15 km resolution cells used here to grid abundance have likely limited this effect, and the incorporation of tidal signals and surface temperature have in addition increased the certainty in our geolocation estimates. Moreover, data recorded by the IBTS surveys may not provide full coverage of the North Sea. For example, the IBT surveys are not conducted close to seabed structures to avoid gear damage or loss, so areas dominated by rocky substrate, may not be representatively sampled.

Fish populations explored in this study should be considered as separate subpopulations within the North Sea, and therefore it is not possible to directly extrapolate to the entire North Sea. For example, cod can be considered as several subpopulations within the North Sea (Neat *et al.*, 2014), which results in different environmental conditions, and therefore drivers.

Differences in model predictions likely reflect different temporal coverage for these surveys and limitations of IBTS samples from inshore regions. However, consistencies in the variables explaining abundance between the IBTS and DST models suggests that the analysis technique was effective at highlighting important explanatory variables for the different fish groups, and thus, that the overall patterns of habitat use shown by DSTs are the same as those shown by records logged on the IBTS.

In terms of artificial structure coverage, the spatial extent of some artificial structure features, like cables suggests that further work should identify the condition and whether there is colonization of these structures; for example, whether cables are buried or exposed. Previous studies have already highlighted the importance of cables and pipelines to marine mammals (Russell *et al.*, 2014), but the importance for fish has been little explored. Acoustic tagging studies (e.g. Reubens *et al.*, 2013b) may be an effective tool in identifying whether fish associate with individual structures.

An issue which we were unable to address in this study, is the current state of the structure, i.e. whether the structure is rich in encrusting faunal species or is relatively barren due to wave-action or an exposed position. The state of the structure will affect the suitability of the habitat for mobile species, though this

**Table 5.** Relative importance of variables explaining the variation in fish distribution for groups 1–4.

| Species | Group | GAM type | Predictor variable removed | | | | |
|---|---|---|---|---|---|---|---|
| | | | Wrecks | OG | Cables | Temp | Depth |
| Cod | 1 | Q1 | 0.00 | 0.00 | 0.00 | 5.66 | **7.04** |
| | | Q2 | 1.73 | 0.21 | 5.12* | 1.67 | **9.22** |
| | | Q3 | 0.74 | 0.10 | 0.89* | 0.34 | **1.77** |
| | | Q4 | 0.00 | 0.00 | 8.53* | **12.37** | 1.45 |
| Plaice | Western (2) | Full | 0.00 | 19.64 | **30.24*** | 19.22 | 19.40 |
| | | Q2 | 3.21 | 10.51 | **17.68*** | 0.00 | 2.12 |
| | | Q3 | 2.28 | 0.00 | **41.55*** | −9.70 | 0.00 |
| | | Q4 | −1.77 | **26.06*** | 18.08 | −1.77 | 1.93 |
| | Central (3) | Full | 0.00 | 0.41 | 2.06* | 0.36 | **10.97** |
| | | Q1 | 0.00 | 0.17 | 2.99* | 0.15 | **6.42** |
| | | Q2 | 0.00 | 0.00 | −0.03 | 0.73 | **17.47** |
| | | Q3 | 0.00 | 0.00 | −6.66 | 0.00 | **1.34** |
| | | Q4 | 0.00 | 0.00 | 4.91* | 0.60 | **6.61** |
| THR | 4 | Full | 4.68* | 2.76 | 3.48 | 1.26 | **7.55** |
| | | Q1 | **4.80*** | 2.60 | 2.24 | 2.64 | 4.33 |
| | | Q2 | **22.22*** | 2.90 | 18.84 | 8.00 | 9.90 |
| | | Q3 | 34.65* | 0.90 | 13.96 | **39.49** | 13.96 |
| | | Q4 | 7.79* | 0.77 | 2.62 | 3.95 | **9.16** |

*Notes:* Variables which explained the greatest variation are highlighted in bold, with the structures that contributed the most indicated with an asterisk (*). Note that if all structures were equally important, no structure was highlighted with an asterisk.

was not identified in the current study. Future studies should identify the condition and basic status, to assess whether association can be explained by other environmental or physical variables.

## Conclusions

Data storage tags provide a useful tool in assessing seasonal changes in behaviour with time which can then be linked to structural distributions. Periods where high densities of fish correspond to increased abundance of structures can be used to identify appropriate timings and potential impacts of alterations to anthropogenic structures. Independent of whether fish are purposefully associating with structures or whether structures happen to coincide with locations frequented by fish populations, the link suggests that further considerations are required when deciding on decommissioning scenarios or other structural changes to these sites.

A key issue with this study, is the presence and coverage of large artificial structures. When the data storage tags were deployed (and for the areas used), the number of oil and gas platforms and wind turbines was relatively low. Since this time, the number has increased dramatically (OSPAR, 2010), so this work may be considered a baseline prior to the introduction of many new structures in the North Sea. Future tagging studies with releases from the same sites can be used to see whether there is a change in abundance as the number of structures increase in the region. For example, thornback ray in the Thames estuary may be affected by the increasing number of wind turbines in the region. Additionally, the use of acoustic arrays to monitor particular man-made structures and species of interest may be useful (Reubens *et al.*, 2013a).

## Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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