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Running title: Fish egg distribution in the North Sea

Linking spawning ground extent to environmental factors - patterns and dispersal during the egg phase of four North Sea fishes.

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Abstract

Previous studies have shown that four commercially important demersal species, namely cod (Gadus morhua), haddock (Melanogrammus aeglefinus), whiting (Merlangius merlangus) and plaice (Pleuronectes platessa) spawn in distinct areas across the North Sea. Based on two comprehensive ichthyoplankton surveys in 2004 and 2009, the present study uses Generalized Additive Mixed Models (GAMMs) to delimit these spawning grounds using the distribution of recently spawned eggs, investigates their relationship to specific environmental conditions and examines egg dispersal during their development. Results indicate that presence/absence of early stage eggs is more related to temporal and topographic variables, while egg densities are closely linked with hydrography. Egg distribution patterns were relatively consistent during development and only changed near hatching. Compared to historic observations, the location of the spawning grounds appeared stable on the broad scale but centres of egg abundance varied between the surveyed years. Potential effects of long-term climate change and anthropogenic short-term disturbances, such as seismic surveys, on fish reproduction are discussed, pointing out the demand for multi-species studies on these issues.

Keywords: Spawning distribution, dispersal, seismic surveys, climate change, demersal fish
Introduction

Annually visited spawning grounds are a common feature in the life cycle of many fish populations (Daan et al. 1981; Heath et al. 1994), and have been demonstrated for a number of commercially important fish species in the North Sea (e.g. Brander 1994; González-Errusta and Wright 2016a; 2016b). Such stability in reproductive strategy is thought to have evolved to ensure that, during the average lifetime enough offspring are placed into suitable environments to ensure the population’s survival. Suitable conditions for survival may be found in the vicinity of the spawning ground or in nurseries with good connectivity to the spawning grounds. Bakun (1996) coined the term ‘ocean triads’ for areas where zooplankton is plentiful due to enrichment from nutrients, and where fish offspring are retained in a given water mass. In the North Sea, such conditions could be found at tidal and salinity fronts (Simpson et al. 1993). For fish spawning in late winter and spring salinity fronts may be more important (Munk et al. 2002; Munk et al. 2009) as increased freshwater runoff during fall and winter widens the region of freshwater influence (ROFI), particularly in the southern North Sea (Simpson et al. 1991). Previous studies have suggested that the four commercially important species cod (Gadus morhua), haddock (Melanogrammus aeglefinus), whiting (Merlangius merlangus) and plaice (Pleuronectes platessa) all make use of recurrent spawning grounds in the North Sea which may be linked to such hydrographic features.

In the southern North Sea cod spawns in relatively cool water (5-7°C) beyond the 32 isohaline (Aurich 1941). North Sea cod appears to have four distinct spawning grounds, the Southern and German Bights, the southern and eastern flanks of Dogger Bank and off Flamborough (Aurich 1941; Lelièvre et al. 2010; Daan 1978). The recurrent use of the latter area could, however, not be confirmed from findings of a more recent survey in 2004 (Fox et al. 2008). Further north, ripe and running cod have been observed on the Great Fisher and Ling Banks as well as in the coastal areas (<100 m depth) of Scotland (Graham 1934;
González-Irusta and Wright 2016a). In the 2000s the main cod spawning grounds in the northern North Sea were found off the north and east Scottish coasts and east of Shetland towards Viking Bank (González-Irusta and Wright 2016a). Cod in the North Sea do not appear to be a single stock as recent genetic evidence indicates that fish in the deeper northern waters east of Shetland are genetically distinct from other North Sea populations (Heath et al. 2014). In the northernmost North Sea, haddock spawning predominates in the Atlantic influenced water of the deeper outer shelf, (González-Irusta and Wright 2016b; Heath et al. 1994). Haddock rarely spawns in the southern North Sea, spawning has only been extending as far south as the German Exclusive Economic Zone (EEZ) during a pulsed recruitment (Aurich 1941). In the North Sea, haddock egg production appears highest outside the Moray Firth and east of Orkney, though the eggs and larvae spawned to the west of Scotland are advected into the North Sea (Heath and Gallego 1998) and the two regions are treated as one stock for management purposes (ICES 2015).

North Sea whiting is divided into two genetically distinct northern and southern spawning populations (Charrier et al. 2007). This species is among the most prolific spawners in the North Sea, and it has both individually and collectively, an extended spawning period (Aurich 1941). Compared to cod it appears to spawn in warmer water, having an optimum of 5–8°C, and eggs can be found in the southeastern inshore areas (Lelièvre et al. 2010). The main centres for egg production of the southern population are on the western side, off Flamborough, south of the Dogger Bank and in the Southern Bight, while the northern population has its centre south of Shetland (Loots et al. 2011b).

North Sea plaice spawns in a large area of the southeastern North Sea, from the Southern Bight northwards through the German Bight and along the coast of Jutland (Taylor et al. 2007). On the western side of the North Sea, plaice eggs have been found from Flamborough up to the Moray Firth and further northeast off Shetland. The southwestern populations of
plaice appear to spawn mainly in the Southern Bight and partially in the eastern English
Channel (Houghton and Harding 1976; Hunter et al. 2004). Generally plaice spawns further
offshore than most other flatfish species, with the main egg production observed 50-200 km
offshore, in salinities >32 (Rijnsdorp 1989). Freshwater from the river plumes apparently has
a strong effect on spawning outside the core areas (Lelièvre et al. 2014). The location of the
spawning areas is thought to offer good connectivity to inshore, spatially limited, soft
sediment nursery grounds (Hufnagl et al. 2013).

Life-cycle closure requires a succession of suitable habitats and appropriate mechanisms for
transiting between them (Petitgas et al. 2013). There are concerns that predicted climate
change may not only affect reproduction directly but also affect early life stage habitats and
the connectivity between them (Collins et al. 2013). The changes would have a series of
direct and indirect effects, taking place on scales ranging from individuals to populations. It
has already been seen that North Sea fish distributions have responded to rising sea
temperatures (Perry et al. 2005) whilst changes in wind patterns and restricted transport of
Calanus finmarchicus into the North Sea have been implicated in cod recruitment (Rindorf
and Lewy 2006; Fromentin and Planque 1996). Under climate change the location of salinity
fronts, which may direct spawning, could also change (Collins et al. 2013; Perry et al. 2005).
Such changes may be especially detrimental for fish species on the southern edge of their
range, while other species may be able to extend into the North Sea (Dulvy et al. 2008;
Planque and Frédou 1999). Many North Sea stocks have also suffered decades of overfishing,
leading to low spawning stock biomasses (SSBs) and truncated age structures. Such stocks
may have reduced resilience against changes in the abiotic environment (Ottersen et al.
2006). Other human activities may put additional stress on spawners and their offspring,
particularly in a heavily industrialized area like the North Sea, containing nearly a thousand
active above- and sub-surface structures (De Groot 1996; OSPAR Commission 2014). Except
for specific accidents these structures, may, however, only be local disturbances and may
even serve as habitat (Løkkeborg et al. 2002; Fujii 2015). Other disturbances might come
from seismic exploration which nowadays uses airguns that cause direct physical damage in a
much narrower zone than the explosives used in the past (5 m, McCauley et al. 2000). Effects
on adults may rather be indirect, causing avoidance of approaching survey vessels. Since
seismic surveys are not supposed to be undertaken during periods of fish spawning, or are
supposed to use mitigation measures such as soft-starts (Smithies 2014), knowledge of the
extent and timing of spawning is essential for proper Environmental Impact Assessment
(EIA). Therefore, evaluating the overlap between intense seismic operations and spawning
grounds is a normal requirement for EIAs undertaken before seismic operations commence.
In 2004 and 2009, dedicated surveys and additional sampling during routine surveys were
coordinated by ICES, affording the possibility to examine fish spawning using egg
distribution data separated by 5 years.
Here we use the egg distribution of the four most abundant species, cod, haddock, whiting
and plaice in order to (i) construct statistical models, relating the spawning habitat inferred
from stage I eggs, up to the onset of gastrulation, to the abiotic environment; (ii) examine
how distribution patterns changed over time by constructing interpolated distribution maps
and by statistically comparing the distribution of the successive egg development stages; (iii)
evaluate to which extent spawning distribution overlaps with industrial activities and how
these, in concert with climate change, may affect future spawning distribution and success.
Materials and methods

Survey design and field sampling

Sampling was carried out across the North Sea (Fig. 1a) by five participating countries, either during the annual International Bottom Trawl Survey for the first quarter (IBTS 1Q) or in dedicated surveys between the 16\textsuperscript{th} February and 23\textsuperscript{rd} of March 2004 and between 17\textsuperscript{th} of January and 6\textsuperscript{th} of March 2009 (Table 1).

The samples were taken with Gulf III/Nackthai (Gehringer 1962; Nellen and Hempel 1969), Gulf VII (Nash et al. 1998), BONGO (Posgay and Marak 1980) and WP2 (Fraser 1968; Tranter 1968) nets, covering the entire North Sea from 51.5\textdegree N to 62\textdegree N. The Gulf and BONGO nets were deployed in double oblique hauls, while the WP2 was deployed in vertical hauls, in both cases down to five metres above sea bottom or a maximum of 100 m depth.

Double oblique hauls lasted at least 10 minutes with multiple hauls ensuring the minimum deployment time in shallow water (ICES 2008). To determine cod-like eggs to species level, single eggs without oil globules and diameters of 1.1–1.75 mm (Fox et al. 2008) or 0.97–1.89 mm (Lelièvre et al. 2010) were fixed for later genetic analysis, either in 96\% ethanol (Fox et al. 2008) or in a pigment preserving Battaglia-solution containing buffered 0.864\% formalin, BHA (butylated hydroxyanisole), EDTA (ethylenediaminetetraacetic acid) and monopropylene glycol and ascorbic acid (Mastail and Battaglia 1978; Bigot 1979).

The locations of installations for oil extraction, seismic survey areas and the outlines of exclusive economic zones were extracted from public online databases (Fig. 1b, OSPAR Commission 2014; Ministerie van Economische Zaken 2015; Oljedirektoratet 2015). Depth and shoreline data were downloaded from NOAA databases (NOAA (NGDC) 2016a; NOAA (NGDC) 2016b).
Egg and larvae identification

Subsamples of at least 100 eggs in the desired size range (>1.16 mm, Russell 1976) were staged (Ryland et al. 1975; Geffen and Nash 2012) and visually identified to the lowest possible taxonomic level (Munk and Nielsen 2005; Russell 1976). Preserved cod-like eggs were identified either with TaqMan probes (Fox et al. 2008) or cytochrome $b$ PCR–RFLP (Lelièvre et al. 2010). Accuracy of TaqMan probes is >98% for cod, haddock and whiting (Taylor et al. 2002) while cytochrome $b$ PCR-RFLP confirmed 98% of visual identifications for late-stage cod eggs and 71% for late-stage whiting eggs (Lelièvre et al. 2010). The identified gadoid eggs were assigned to each species according to the proportion obtained from genetic analyses. For stations where this was not possible, the proportion in 2004 was derived from a multinomial Generalized Additive Model (GAM) over the whole survey area (Fox et al. 2008) and in 2009 from the average proportion for the other stations in the same ICES square. Counts of fish eggs were raised by the fraction of the whole sample examined and then converted to density (eggs m$^{-2}$), by dividing by the sampled volume and multiplying by the sampled depth.

Geostatistics

Hydrographic data were obtained from CTD hauls during the survey and augmented with data from the ICES oceanographic database (ICES 2009). After pre-screening for erroneous measurements, density anomalies $\sigma_i$ (kg m$^{-3}$-1000) were calculated from temperature and salinity according to UNESCO standards (Millero and Poisson 1981) using the R package cce (Kelley 2013). To calculate the density gradient, an experimental variogram for $\sigma_i$ was calculated in Surfer 10 (Golden Software 2011) and a linear theoretical variogram model fitted to the experimental variogram, using least square regression. Using ordinary kriging, the density anomaly was then interpolated onto a regular grid of $0.25^\circ \times 0.25^\circ$ and
subsequently smoothed to half that grid resolution. From the interpolated horizontal density anomaly the density gradient in g m\(^{-3}\) n.mi.\(^{-1}\) was calculated using the formula (Golden Software 1999):

\[
\|\mathbf{g}\| = \sqrt{\left(\frac{Z_E - Z_W}{2\Delta x}\right)^2 + \left(\frac{Z_N - Z_S}{2\Delta y}\right)^2}
\]

Where \(\mathbf{g}\) is the density gradient, \(Z_E\) and \(Z_W\) are adjacent grid points in East-West direction; \(Z_N\) and \(Z_S\) are adjacent grid points in North-South direction, \(\Delta x\) and \(\Delta y\) the distances in either direction, respectively.

For visual representation, temperature and salinity were interpolated on a 1 n.mi. \(\times\) 1 n.mi. grid using the R package gstat (Pebesma 2004). Analogous to the procedure for \(\sigma_t\), an experimental variogram was calculated and a Gaussian, exponential or spherical theoretical variogram was fitted to the experimental variogram using least-square regression and eye-fit. The chosen model was then used for the interpolation. Average temperature and salinity data for the 2000s was also interpolated following the same procedure. However, the value plotted here was the variation, to visually compare the distribution of stage I fish eggs with the variation of hydrography.

Similarly, data for each egg development stage were split into presence/absence and log-transformed non-zero abundance and then interpolated using an ordinary kriging procedure on the default grid in gstat (Pebesma 2004). The values for abundance were then weighted with the probability of occurrence on a cell-by-cell basis and the final maps created by kriging onto the same 1 n.mi. \(\times\) 1 n.mi. grid that was used for hydrography.
Statistical comparisons of egg density distributions between stage I and the later stages were performed using the Syrjala test in the R package ecespa (de la Cruz 2008). The Syrjala test computes a modified two-sample Cramér–von Mises test for a difference between the cumulative distribution functions of two populations (Syrjala 1996). As the test is sensitive to where the coordinate system has its origin, it is performed once for each of the four corners of the hypothetical rectangle encompassing all sampling sites and then averaged. Although the test is insensitive to sample size, each sample was transformed to $\%$ of the sum of the respective stage before conducting the test.

Modelling spatial autocorrelation

Spatial autocorrelation and average patch size were modelled with Moran’s eigenvector maps (MEMs) using the R package pcnm (Legendre et al. 2013). A truncated distance matrix was computed by converting all distances farther than the longest distance between immediate neighbours to four times that value (Borcard and Legendre 2002). Since there are no interactions in the population of fish eggs, only the MEMs with positive eigenvalues were retained. Before running a global test on all MEMs with positive eigenvalues the hellinger-transformed abundances were detrended to remove any spatial trend. Individual Moran’s Eigenvectors (MEVs) were selected by regression-based forward selection with the R package packfor (Blanchet et al. 2008; Dray et al. 2013) using p-value and adjusted $r^2$ as stopping criteria. Similar to Loots et al (2010a) the threshold p-value was set to a low 0.002, to avoid building too complex spatial models. The spatial scale was then determined by first computing a Gaussian variogram for each MEM (Bellier et al. 2007). Then the selected MEMs’ eigenvalues were plotted against these ranges and subdivided into sub-models for a fine, medium, medium-broad and broad scale.
Explanatory models

To examine the relationships between the distributions of stage I eggs and the abiotic environment, data from both years were used to construct a generalized additive mixed model (GAMM) with the R package gamm4 (Wood and Scheipl 2014; Wood 2006). As for the kriged distribution maps, separate models were constructed for presence/absence and non-zero abundance, resulting in a hurdle-model. Potential independent variables were temporal (year, day of the year), bathygraphic (bottom depth), hydrographic (temperature, salinity, and $\sigma_t$-gradient; from the surface and bottom) and the selected MEVs. These variables were examined for collinearity with pair plots and variance inflation factors (AED, Zuur 2010), entailing the exclusion of the year. Hydrographic values were taken from the CTD casts taken at the locations of the individual samples or, if not available or erroneous, were extracted from the interpolated surfaces. The measurements from 5 m depth and the bottom were strongly correlated. Instead of excluding one or the other, separate models using either surface or bottom measurements were constructed and compared. MEVs were treated as random effects, while the day of the year (=year day), bottom depth and the hydrographic covariates were the fixed-effects. Using either presence/absence in a binomial model with a logit-link or log-transformed non-zero egg densities in a Gaussian model with identity-link as response, the general form of the GAMM was (Wood 2006; Höffe et al. 2014):

\[
y_i = \beta + f_1(x_{1i}) + f_2(x_{2i}) + \cdots + f_n(x_{ni}) + Z_i b + \epsilon_i
\]

$y_i$ being the response, $\beta$ the intercept, $f_i$ the smooth functions for the fixed effects $x_k$, $b$ a random effects coefficient vector from the matrix $Z_i$ and the residual error vector $\epsilon_i$. 

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The risk of over-fitting the individual models was reduced by restricting the degrees of freedom to four and by using the Bayesian Information Criterion (BIC, Schwarz 1978) as an indicator of improvement during the backward selection of the optimal models. Initial models contained hydrographic measurements from either the surface (5 m) or the bottom depth. Following the optimization of these models the decisions between either surface or bottom models were based on BIC, Akaike’s Information Criterion (AIC, Akaike 1974) and in case of disagreement between the two on the predictive power of the models. Formal assessment of the goodness of fit, since not possible from the GAMM itself (Wood 2006; Zuur et al. 2009), was done by estimating the deviance explained from a generalized additive model (GAM) using the same fixed-effects covariates (Gilman et al. 2012). Post-hoc testing included an evaluation of the random effects’ contribution, using the residuals from the GAM as response (Wood 2006). Hereby, linear fixed-effects and mixed models are compared, by using a constant parameter and in the mixed model the random effects. The two models are then compared by AIC, BIC and the log-likelihood ratio test.

The effect of the random covariates on the spatial autocorrelation was evaluated by Moran’s I correlograms on the models’ residuals, setting a separation distance of 0.7° for non-zero egg densities of cod and plaice, 2.1° for all other models, corresponding to the maximum distance between nearest neighbours (Diniz-Filho et al. 2003; Borcard et al. 2011). The number of lags to cover the entire study area was then 15 and 5, respectively. P-values were adjusted using Holm’s correction (Borcard et al. 2011).

The performance of individual fixed covariates was evaluated using three different indicators. Firstly, by dropping each covariate individually and then calculating the log-likelihood ratio between the reduced model and the model selected in the fitting process. Secondly, by computing the ROC AUC (Receiver Operating Characteristic Area Under the Curve) for binomial and the $r^2$ between response values predicted from individual covariates and the
observations for Gaussian models using the R package MuMIn (Barton 2013). Lastly, partial
linear regression and adjusted $r^2$ were used to partition the explained variation explained by
the individual covariates using the R package vegan (Oksanen et al. 2013; Peres-Neto et al.
2006).

Results

Hydrography

In both years hydrography was characterized by a pool of relatively warm (>7°C) and saline
(>34.5) water in the northern and central North Sea and cooler, fresher water along the
margins, which was more pronounced in the East (Fig. 2). Salinity (Figs 2b, d) as well as
density gradients (max. 4.3 g m$^{-3}$ n.mi.$^{-1}$ off Norway) were steeper on the eastern side of the
North Sea. Surface hydrography was more structured than at the bottom. The main difference
between 2004 (Fig. S1) and 2009 (Fig. S2) was that in the southern North Sea water ≤6°C
extended further westwards in 2009. The water in the German Bight was more than 1°C
colder than in 2004 and salinity gradients from coastal to offshore waters were shallower,
particularly north of the Frisian Islands where a prominent plume of relatively fresh (≤34.25)
water extended far offshore. North of 57°N the situation was the opposite with the salinity
gradient steeper in 2009 (Fig. S2) than 2004 (Fig. S1).

Spatial structuring

The threshold for truncating the distance matrix was 2°. Of the MEMs, 355 were found to
have positive eigenvalues. Two of these were significant for cod, four each for haddock and
plaice and one for whiting. When plotting eigenvalues against the variogram range, there
were four distinct groups (Fig. 3), on ranges of 0-40 n.mi. (fine), 40-75 n.mi. (medium), 75-
100 n.mi. (medium-broad) and above 100 n.mi. (broad).
Egg distribution

Stage I egg densities on the scale of the entire North Sea were in both years in the same general areas (Fig. 4). High egg densities of cod (Fig. 4a) and plaice (Fig. 4p) were found in the Southeast, along the continental coast, extending as far north as Viking Bank. Whiting and haddock were more common in the western part. The centre of egg densities for haddock was limited to the Northwest (Fig. 4f), two patches on either side of the Fladen Ground and a third, smaller, patch outside the Firth of Forth. Peak densities of whiting eggs also occurred in three locations but they were farther apart. One centre of abundance was east of the Shetland Isles (Fig. 4k) around the Forties, the second, larger, area was between Flamborough and the Dogger Bank and a third area was in the Southern Bight.

The overall pattern in the development over time was one of decline and dispersal. For cod and whiting (Figs 4a-e, 4k-o) this process appeared to be quicker compared with haddock and plaice with a sharp drop in egg densities between stages I and II and a lower rate of decline thereafter. For haddock and plaice the peak densities did not decline as quickly (Figs 4f-j, 4p-t), densities of the same magnitude as in stage I were still observed in stages IV and V (Figs 4i, 4t). However, the area covered by high densities shrank and in the case of haddock divided into several smaller well-separated patches.

The main differences between the years (Figs S3, S4) were that the centres of abundance for cod and plaice were further north and offshore in 2004 than in 2009 and that the rate of dispersal differed between the years for each individual species. In 2004 high cod and plaice densities covered a larger area (Figs S3a-e, S3p-t), from the transition area between the Bights up to the southern edge of the Norwegian trench. For cod in 2009 this area was smaller, more inshore, off the Frisian Islands, while egg densities were higher in the northern patch around Viking Bank (Fig. S4a-e). For plaice the overall location was similarly changed,
extending along an east-west axis rather than a north-south axis, but the extent of the area was similar to 2004. Peak densities of cod eggs and the area covered with such densities, quickly declined in 2009, while in 2004 high densities were still found in stage III (Fig. S3c). There was no such difference for plaice, although in later stages (Figs S3s and S3t) the location of peak densities was similar to 2009. High egg densities of haddock covered much larger areas in 2004 (Figs S3f-j) than in 2009 (Figs S4f-j) and the distribution pattern did not disperse as quickly and completely. Whiting egg densities were generally lower in 2009 than in 2004 (Fig. S4k-o) but there was little difference in how quickly the eggs dispersed.

However, the overall pattern was different (Fig. S3k-o) with high densities in the Southern Bight in 2009 while in the earlier year the centres of abundance were off Flamborough and east of Shetland.

The Syrjala-test did not fully confirm the patterns suggested by the interpolated maps (Table 2). The distribution patterns of stage IV and V were more often dissimilar from stage I than those of earlier stages, but that pattern was not consistent across species or years. Although stage IV was significantly dissimilar for all species when comparing mean distributions, it never was for whiting in any of the single years. Similarly, the distribution of stage V was significantly different for all species in 2004, but not in 2009 or for mean distributions. Stage III never exhibited significant dissimilarity to stage I, although there were three cases of significantly different distributions between stages I and II.

## Explanatory models

The overall trends in the explanatory models were twofold. Firstly, the best fitting models for non-zero egg density tended to be more complex than those for the probability of occurrence (Table 3, Figs 5, 6). Secondly, although the difference was marginal, three out of four models exhibited a better fit when using hydrographic measurements at the bottom for the probability
of occurrence, while for egg densities it was the opposite. Deviations explained by the corresponding GAMs ranged between 15% for the density of stage I cod eggs and 57% for the presence/absence of haddock eggs. The models for these two species also consistently retained the least fixed-effects covariates (3) for both cod models and the most (5) for both haddock models (Table 3).

Bottom depth and year day were the only fixed-effects covariates retained in every model. They also exhibited similarly shaped relationships for three of the four species (Figs 5a, b).

Cod, Haddock and Whiting exhibited an increasing trend towards the end of the period. Plaice differed from the other species, exhibiting a dome shaped relationship between days 30 and 70. The relationships of cod and plaice egg densities with the year day were of similar shape and peaked earlier than their probabilities of occurrence (days 45 and 35; Fig. 6a).

Whiting egg densities exhibited an early and a late peak around days 20 and 80, respectively. Haddock egg densities were linearly and positively related to the year day.

Probabilities of occurrence for cod and plaice exhibited overall decreasing trends of similar shape with peak probabilities at ca. 50 m (Fig. 5b). Haddock exhibited a similar pattern, but shifted towards greater depths, with a peak at around 100 m and an increasing trend towards the end of the observed depth range. The probability of finding stage I eggs of whiting declined with increasing depth, becoming zero at ≥150 m (Fig. 5b). Relationships between egg densities and bottom depth were of similar shape for cod, whiting and plaice, with peaks at shallower depth than peak probabilities of occurrence (Fig. 6b). Haddock egg densities exhibited a Gaussian distribution around 100 m.

Other than for time and depth, the relationships between the probability of presence and the hydrographic covariates were more species specific with no consistent patterns between any two species. Temperature did not contribute to the model for the occurrence of cod eggs and exhibited negative and positive trends for plaice and whiting, respectively (Fig. 5c). For
haddock the probability of finding eggs was high across the temperature range, except for a local decline around 6°C. Unlike for probability of occurrence, the smooth terms for egg densities related to hydrographic measurements exhibited similarities between two or more species. Haddock consistently differed from the other species, exhibiting linear or near-linear increases in egg densities in relation to year day, salinity and density gradient. Temperature contributed to all models for egg density with the peak occurring as low as ca. 5°C for plaice and as high as 9°C for whiting. The smooth terms for cod and plaice were similar in shape and both egg densities peaked at nearly the same temperatures. Observations at either end of the observed temperature range were few and therefore have wide confidence intervals.

Salinity contributed to the model for the probability of occurrence of cod eggs (Fig. 5d) but did not contribute to the model for egg densities (Fig. 6d). Cod probability of occurrence exhibited a weakly declining trend towards higher surface salinities, while haddock was strongly positive related to bottom salinity. Salinity was only retained in the models for egg densities of whiting and plaice, exhibiting similar shapes of the smooth terms, with peaks at the lower end of the range and at salinities of 34. Haddock eggs were only observed in a narrow salinity range and the trends of probability of occurrence as well as egg densities were strongly positive. The density gradient was retained in the presence/absence models for haddock and whiting (Fig. 5e) and the egg density models for these two species as well as for plaice (Fig. 6e). Egg densities of all three species were linearly related to density gradients.

Across all species the relationships to the MEVs describing spatial autocorrelation were linear or dome shaped (Figs S5 – S8). Spatial autocorrelation in the residuals was by a factor of 1.5 to 7.5 lower than in the data used for fitting. However, on the first lag it remained significant (Table 3).

Predictive power of the selected models was highest for the presence/absence of haddock, the egg density model of whiting and lowest for both models for cod (Table 4). Individual
covariates with high predictive power strongly affected the log-likelihood ratios as well

(Table 5). Concerning explained variation this consistency in performance of individual
covariates was limited to cod (Table 6). The variation explained by the fixed-effects
covariates was lowest for cod and highest for haddock. The highest percentage of explained
variation in presence/absence was related to bottom depth for plaice and year day for all other
species. For the egg densities the highest percentage of explained variation was related to
temperature for cod, salinity for haddock, and density gradient for whiting and plaice,
respectively. This increased importance of hydrographic variables in the egg density models
was not reflected in the predictive power or the log-likelihood ratios where these covariates
were usually weaker than either year day or bottom depth.

The comparison between the GAMMs and their corresponding GAMs using only the fixed-
effects covariates revealed that the MEVs only contributed significantly to the models for
whiting (Table 7). However, even for whiting the GAM was more parsimonious, as the AIC
and BIC was for all GAMs lower.

Comparison with decadal hydrography and oil installations

Averaged over the 2000s the variation in bottom temperature exhibited a range of interannual
variability between <1°C and >1.6°C (Fig. 7a). The lower part of this range was found in
large areas of the central and southern North Sea, while the rest of the North Sea proper
exhibited intermediate variation. High variability was primarily indicated on the northern
margins of the North Sea and between the Shetland and Orkney Isles as far south as the
Moray Firth. High egg densities across all four species were primarily found at the
boundaries between the areas of low, intermediate and high variability. The mean density of
stage I eggs across all species, compared to the distribution of oil extraction and seismic
survey areas in the eastern North Sea showed that at this time of the year areas of high egg
densities primarily overlapped with the oil industry in the southeastern North Sea in the
Dutch and German EEZs (Fig. 7b).

Discussion

The results of the present study indicate that presence/absence and non-zero abundance of
cod, haddock, whiting and plaice eggs are primarily governed by different environmental
variables. Presence/absence was mainly linked with the day of the year as well as bottom
depth whilst non-zero abundance was linked to one or more of the hydrographic covariates.
Overall, the spawning of cod and plaice appears more common in the southeastern North Sea,
while spawning of haddock and whiting were concentrated in the western areas, and in the
case of haddock further limited to the northern North Sea. The overall spawning areas seem
to have remained stable, compared to historical observations. However, the, smaller, actual
spawning grounds used within those areas varied between the two years surveyed depending
on prevailing conditions.

Egg distribution

Where spawning locations persist over many years their use must allow sufficient offspring
to survive to sustain the population size (see Hufnagl et al. 2013). Our observations of
geographically relatively stable spawning areas contrast findings for other species such as,
e.g. mackerel (*Scomber scombrus*, Beare and Reid 2002). However, even for mackerel the
spawning occurs mainly along the shelf-break and this location may be linked to patterns in
secondary production driven by internal waves (Sharples et al. 2009). Areas of the North Sea
where high abundances of cod, haddock, whiting and plaice eggs were found are consistent
with earlier studies (Coull et al. 1998; Heath et al. 1994). However, their extent at higher
population levels might be greater and at the present time the maximal extent of the spawning
areas may be better indicated by egg occurrence (Brander 1994). The overall better fit for the
presence/absence models when including hydrographic measurements from the bottom rather
than from the surface may be due to the generally demersal behaviour of the adult fish. On
the other hand the better fits for egg densities using surface hydrography may be based in the
distribution of pelagic eggs in the upper part of the water column (Coombs et al. 1990;
Fritsch 2005). After rising to the surface layer, eggs will be advected from the spawning site.
However, in the observed temperature range the eggs develop to the end of stage I within a
few days (Thompson and Riley 1981; Geffen and Nash 2012). At common winter current
velocities (Sündermann and Pohlmann 2011), dispersal during that time should have been on
about the same scale as the survey. This is supported by recent studies on the distribution of
mature adults which largely corroborate the finding from the egg surveys (González-Irusta
and Wright 2016a; González-Irusta and Wright 2016b; Loots et al. 2011b) The only major
difference was that the northern core spawning grounds of whiting extended further south
than was observed in the egg surveys (Loots et al. 2011b). Therefore, the distribution of stage
I eggs observed in 2004 and 2009 may be considered a reliable source of information on
spawning distribution.

**Relationship with the abiotic environment**

Compared to Otto and Zimmermann (1990) and the studies underlying that review (Goedcke
et al. 1967; Tomczak and Goedcke 1962), the overall pattern of hydrography in the North
Sea in 2004 and 2009 was not much changed since the 1960s. Patterns were also similar
between the sampled years with the main differences in temperature and salinity occurring
south of 57°N. A major difference between the two survey years were the higher egg
densities of whiting in the Southern Bight in 2009. The difference in egg densities in the
Southern Bight correlates with the hydrographic differences, as whiting may have spawned
across the boundary between the cool, low salinity coastal water and the warmer water from the South, corresponding to the species preferences (Aurich 1941). In the southern North Sea a comparable data set is available from a series of surveys using the Continuous Underway Fish Egg Sampler (CUFES, Lelièvre 2010). In this study high egg densities of all species were found in the Southern Bight in 2006 and 2008, but to a lesser extent in 2007 (Lelièvre et al. 2012). In 2006 low salinity was not restricted to the German Bight and the interface between fresh and saline water was further offshore, resembling the situation in 2009. From the comparison of the years we deduce that a more seaward position of the boundary between freshwater influenced areas and marine water may attract more spawning fish to the area. The present observations on cod egg distribution are consistent with Aurich (1941) and Brander (1994). The latter author identified the western-central North Sea (2°W-2°E and 52.3-56°N) as a minor contributor to the spawning of cod, and the German and Southern Bights as major contributors in alternating periods, 1948-1956 and 1958-1972, respectively. In 2004 and 2009, the distribution of cod eggs in the Southern Bight was limited to a few patches, while in the German Bight cod eggs were widespread, similar to the pattern described by Brander (1994).

Densities of cod eggs peaked in areas shallower than 100 m, corresponding to results of previous ichthyoplankton studies (Munk et al. 2002) and in line with González-Irusta and Wright (2016a) who reported that the abundance of cod in spawning condition declined at more than125 m water depth (González-Irusta and Wright 2016a). The temperature (ca. 4°C) at these locations corresponded to the distribution of spawners which declined when temperatures increased to above 5°C (González-Irusta and Wright 2016a). Cod larvae tend to aggregate at or slightly inshore of a frontal system (Munk et al. 1999) but for the presence/absence and abundance of cod eggs the gradient in water density did not appear to be an important covariate in our analyses. Hence, the aggregation around fronts may only
become established by selective processes or behaviours taking place in the larval stage.

Patterns of egg production were not entirely consistent with predictions based on the catches of mature female cod in research surveys (Fox et al., 2008). This was particularly the case in the northern North Sea where the bulk of the cod stock is presently located and where high egg production would be expected. Cod in the northern population centred around Viking Bank spawn several weeks later than those in the southern North Sea (González-Irusta and Wright 2016a), which may call for changes in the timing of future ichthyoplankton surveys.

The greatest spawning concentrations of haddock have historically been reported from the plateau between the Orkney-Shetland Isles and Norway in water deeper than 100 m (Thompson 1928). A statistical model developed for spawning haddock west of Scotland also indicated a decline at greater depths, which corroborates the egg-based model in the present study (González-Irusta and Wright 2016b). Spawning aggregations have also been reported east of the Moray Firth, at the Buchan and Farne deeps, the Gut and the Fisher Banks. Saville (1959) found haddock eggs to be widely distributed across the northern North Sea from the Scottish coast to the Norwegian deeps except for the Moray Firth and an area around the Fladen Ground. The low egg densities around the Fladen Ground appear a consistent feature, as they were also noted by Damas (1909), González-Irusta and Wright (2016b) and in the present study. The extent of haddock eggs found by Heath et al. (1994) in 1992 was comparable with that of Saville’s study, although eggs were concentrated further north and west. Heath and Gallego’s (1998) study estimated high egg production from mature fish for the Moray Firth, the Scottish east coast and Shetland Isles, which is reflected in the results of the two surveys. However, their model did not predict high abundances to the immediate east of the Shetland Isles, which were present in 2004, 2009 and earlier egg surveys. High abundances of haddock eggs south of the Moray Firth were only found in 2004. In earlier plankton surveys Heath et al. (1994) found a spatial segregation of late stage cod and
haddock eggs, in colder North Sea water and on the warmer outer shelf, respectively. These findings support the suggested preferences for different zones of a frontal system between these gadoids (Munk et al. 1999). More common occurrence and higher abundance of haddock eggs on the offshore side of a frontal system, was also seen in the relationships to the environmental covariates. Observations of haddock eggs were limited to a narrow part of the species’ salinity range (30-36, Laurence and Rogers 1976). Within the observed range, the probability of occurrence as well as egg densities increased. Likewise the warmer offshore water, where a local peak was found at 7°C in the present study, falls within the species’ temperature range (4-10°C, Laurence and Rogers 1976). Similarly, spawning haddock reached peak probability of presence and abundance at 7°C and exhibited peaks at salinities >34 and >35, respectively (González-Irusta and Wright 2016b). Density gradients in the northern North Sea were lower than in the South. Nevertheless, they positively affected the abundance and to a lesser extent the occurrence of haddock eggs. This may be related to the observed high numbers of eggs on the oceanic side of the front between the Atlantic and the North Sea water in the northwestern North Sea (Heath et al. 1994).

It has been suggested that the whiting population consist of two stocks in the North Sea, one east of England and one east of the Shetland Isles (Charrier et al. 2007). Such separation is consistent with our findings. The preferred habitat of adult whiting can be characterized by shallow depths and relatively high winter temperatures of 6-9°C (Damas 1909). This preference was apparently reflected in the higher probability to find whiting eggs as well as higher egg densities in the upper temperature range. Egg abundance peaked not only at temperatures >7°C but also at sub-optimal temperatures of 4°C, but still within the thermal range for egg survival (Povoa et al. 2011). Probability of occurrence and abundance peaked in the 20-40 m range identified as preferred depth range for spawning by Aurich (1941). The likelihood to find whiting eggs increased at high density gradients, while the egg densities
declined, partially corroborating the findings of Munk et al (1999), who found that whiting eggs were uncommon at central parts of fronts. Whiting has a long spawning period, from February to June with increasingly later spawning at higher latitudes (Hislop 1984). Hence, the earlier sampling period in 2009 may partially explain the difference to 2004, particularly in the northern spawning grounds east off Shetland. In 2009 spawning east of Shetland may not have begun at the time of the survey. However, in 2004 stage IV and V eggs were abundant in the North, while early stages occurred more in the southern North Sea, contrary to the observations by Hislop (1984) and Aurich (1941). As individual whiting spawn many batches over a period between 1.5 and 2 months into late spring (Hislop 1984), the 2004 survey may have sampled the early stages of a later spawning batch in the South, while in the North the previous batch was sampled in the later stages.

The relatively homogenous distribution of plaice eggs in the German Bight and along the Danish coast, particularly in 2004, is a good representation of this species’ large spawning area in the southern North Sea and English Channel (Aurich 1941; Metcalfe 2006). Moray Firth, Firth of Forth and the area off Flamborough Head are further suitable for plaice spawning (Loots et al. 2010b) and some eggs were found there, in earlier surveys (Aurich 1941) and in the present study. To develop successfully, plaice eggs need a temperature range of 2-8°C (Wegner et al. 2003), which was reflected in the above average abundance of eggs at 4-6°C. The probability of finding plaice eggs was similarly highest at the lowest observed temperatures and declined linearly over the observed range, indicating that within the species’ thermal range the lower part is preferred (Wegner et al. 2003). The high densities of plaice eggs at salinities ≥34 corroborated earlier studies indicating high salinities as optimal for plaice eggs (Aurich 1941; Cushing 1990). The linear relationship between egg densities and density gradient was negative and had a similar slope to that for whiting. This result
supports earlier studies indicating more offshore spawning grounds than other flatfish (Lelièvre et al. 2014).

Overall, egg densities declined quickly between stages I and II and at a lesser rate towards later development stages. However, distribution patterns remained largely the same up to stage IV. Therefore, one can assume that the decline was primarily driven by the high mortality of fish eggs (Bunn et al. 2000), and that mortality rates were similar across the North Sea. Contrary, dispersal may be rather slow. In the southern North Sea, eggs are adected at about 5 km d\(^{-1}\) (Brander 1994), resulting in a transport of around a 100 km from spawning to hatching, based on temperature dependent egg development (Thompson and Riley 1981; Geffen et al. 2006). This slow dispersal may explain why distribution patterns remained similar until the later stages. As indicated by \(p\)-values in the Syrjala-test, distribution patterns of stages I and III were often more similar than those of stage I and II. This may be due to the difference in duration of development stages. It is less likely to find stage II eggs during a survey, as it is comparatively short (Fox et al. 2003; Geffen et al. 2006).

Areas with high densities of haddock eggs, similar to densities in stage I, were maintained longer than for cod and whiting. Partially this might be due to a larger contiguous area with high densities to start with. Another factor may be that the distribution of adult haddock in the first quarter changes little (Hedger et al. 2004), suggesting that predators were satiated by a continuous supply of freshly spawned eggs rather than feeding on the less numerous later stages. A similar mechanism may be at work in case of plaice, which also started out with a large area of high densities that shrank but did not disappear over time.
**Individual covariates**

The greater importance of the hydrographic variables concerning explained variation, and to a lesser extent predictive power and the log-likelihood ratios, in the egg density models contrasts with the findings of earlier studies. In the present study the year day was the most influential covariate in determining presence/absence. However, earlier studies indicated that environmental covariates are more important for defining the boundaries of a population’s habitat, rather than the distribution within (Loots et al. 2011a; Loots et al. 2010a). However, it is not without precedent. Although they used a different measure, Gonzáles-Irusta and Wright (2016a) came to a similar result for the abundance of North Sea cod in spawning condition. In their study, temporal covariates were likewise the most important ones, followed by salinity as the most important hydrographic covariate. Still, the importance of the year day must be interpreted with care, due to the time series being short and the survey periods differing by about three weeks. Longer time series with several samples on the same year day may reduce its influence (e.g. Höffle et al. 2014; Lelièvre et al. 2014). The distribution of populations on the edge of their environmental range may experience a stronger influence of the environment, which may apply to cod and haddock. Haddock is environmentally restricted to the northern North Sea and while distributed across the North Sea, cod still experiences a strong influence of temperature, because the North Sea stock is one of the most southernmost ones (Hedger et al. 2004; Drinkwater 2005).

MEMs are a powerful tool to deal with spatial autocorrelation. However, the additional covariates may be penalized in model selection (Loots et al. 2011a). This may be one reason why only the models for whiting exhibited a significant difference in the log-likelihood ratio test, as they only contained a single MEV on the broad scale. Broad scale structures were also those with the most discernible patterns when plotting observations against predictions,
indicating that these structures were likely more important for characterising the spatial
distribution of spawning than those on smaller scales.

Long-term change and short-term disturbances

The four species in the present study may be affected in different ways by long-term changes
in environmental conditions of the North Sea, potentially compounded by short-term
disturbances (Collins et al. 2013; Petitgas et al. 2013). The debate whether recent changes in
the distribution of some North Sea species are related to climate change or to changes in local
populations is still ongoing (Neat and Righton 2007; Holmes et al. 2014). The present study
indicates that effects would be species specific, with cod and haddock experiencing stronger
direct effects of rising temperatures (Hedger et al. 2004; Drinkwater 2005). However,
Petitgas et al. (2013) highlighted the potential impact of indirect effects on species with
specific habitat requirements for spawning grounds or nurseries as well as on the connectivity
between these areas. Plaice appears to be particularly vulnerable as spawning grounds are
offshore and the, narrowly defined, nursery areas inshore (Hufnagl et al. 2013). North Sea
plaice is one of the more southern populations and suitable spawning grounds and nurseries
may decrease in size (Petitgas et al. 2013). Connectivity may be affected by accelerated
development and changing current patterns through changes in wind and runoff patterns. For
the period 1975 to 2006 Hufnagl et al. (2013) observed a decrease in connectivity related to
an increase in temperature, for the spawning grounds in the German Bight and in the English
Channel, while connectivity for other areas increased. For cod, connectivity may be affected
in the opposite way, as climate change may entail more natal retention (Heath et al. 2008).
However, other studies suggested a displacement to the North (Rindorf and Lewy 2006).
Whiting may also be affected by changes in salinity and subsequently stronger density
gradients in its, previously more homogenous, spawning areas (Loots et al. 2011a).
While the effects of changes in climate are long-term, short-term disturbances may interact with them. Noise producing activities, such as seismic surveys as well as construction work and the ensuing avoidance reactions, may lead to delays in spawning or avoidance of optimal spawning grounds and therefore interfere with successful connectivity between spawning and nursery areas. Together with minor injuries and their effects on long-term survival such indirect effects of noise pollution are understudied and call for further research (Wahlberg and Westerberg 2005; Payne 2004). Such impacts are considered in the EIA that must be undertaken before seismic surveys are conducted. Where potential impacts are judged serious then mitigation measures must be taken. Mitigation can include restricting the timing of work so it is outside of the spawning season or other measures such as soft-starts for pile-driving and air gun surveys. It is therefore important that up-to-date information is available regarding spawning locations and timing so that offshore exploration and construction activities can be properly controlled. Of the four species in the present study, cod and plaice overlap with areas for seismic surveys, whether for oil exploration or construction work, in the southeastern North Sea (Ministerie van Economische Zaken 2015). Cod may be vulnerable due to its SSB being below $B_{\text{trigger}}$, the biomass triggering management actions, while plaice is vulnerable due to its dependence on successful connectivity between early life stages.

**Conclusion**

Spawning areas appear to be defined by few, time-invariant variables, while centres of abundance within these areas are influenced by the interannual variability of the hydrographic conditions. Explanatory power of the statistical models varied between 15% explained deviation for cod egg density and 57% for haddock egg presence/absence. Models for cod spawning distribution, whether they use eggs or ripe and running adults as response, appear
to be difficult to define as even a far larger number of covariates barely yielded double the 
explained deviation (González-Irusta and Wright 2016a). Considering that the cod stock is 
currently the most vulnerable one in the North Sea, the investigation of further drivers 
governing the spawning distribution should concentrate on this species. Performance of 
individual covariates indicates that the occurrence of spawning in a given location of the 
North Sea is more dependent on covariates that do not vary over time, as the most important 
covariates for these models were year day and bottom depth. Contrary, egg densities were to 
a greater extent governed by covariates that change over time. This suggests that changes in 
the ocean climate, not exceeding the fishes’ physiological limits, may cause centres of 
abundance to shift within spawning areas that remain the same. Such centres of abundance 
should be avoided by potentially damaging activities, and aggregate maps of spawning 
habitats and egg distributions, such as in the present study and Lelièvre et al. (2014), would 
be valuable tools in the management of marine areas, protecting the successful reproduction 
of fishes.

Supplements

Surface and bottom hydrography as well as the distribution of development stages for 
individual years are available as online supplements (Figs S1-S4). Supplementary figures 
presenting predicted versus observed values illustrate the information on predictive power of 
individual covariates given in Table 4 (Figs S5-S8).

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Table 1: Survey cruises in this study. For the BONGO nets only the mesh size for the samples used in the analysis is given.

<table>
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<th>Year</th>
<th>Country</th>
<th>Survey</th>
<th>Ship</th>
<th>Start Date</th>
<th>End Date</th>
<th>Gear</th>
<th>Mesh size (µm)</th>
<th>Nos. Hauls</th>
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<td>137</td>
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<td>BONGO</td>
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<td>Scotia</td>
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<td>6.3.09</td>
<td>BONGO</td>
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*) Abbreviations: add. IBTS = Additional IBTS-Sampling, IHLS = International Herring Larvae Surveys, PLACES = Plaice and Cod Egg Surveys, PCEGGS = Planning Group on North Sea Cod and Plaice Egg Surveys
Table 2: Syrjala-test between Stage I and subsequent development stages, for each year and both years combined. P <0.5 indicates that the distribution patterns are significantly dissimilar.

<table>
<thead>
<tr>
<th></th>
<th>Stage II</th>
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<th>Stage III</th>
<th></th>
<th>Stage IV</th>
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<th>Stage V</th>
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<td></td>
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<td>0.072</td>
<td>0.18</td>
<td>0.067</td>
<td>0.70</td>
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<td>0.532</td>
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<td><strong>0.018</strong></td>
<td>1.36</td>
<td>0.061</td>
<td>0.16</td>
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<td><strong>0.014</strong></td>
<td>0.22</td>
<td><strong>0.038</strong></td>
<td>2.21</td>
<td>0.221</td>
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<td>1.01</td>
<td>0.061</td>
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<td>------</td>
<td>------</td>
</tr>
<tr>
<td>Plaice</td>
<td>4.65</td>
<td>0.058</td>
<td>0.36</td>
<td>0.061</td>
<td>1.49</td>
<td>0.144</td>
<td>0.22</td>
</tr>
<tr>
<td><strong>Mean</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cod</td>
<td>3.33</td>
<td>0.089</td>
<td>0.16</td>
<td>0.159</td>
<td>2.06</td>
<td>0.219</td>
<td>0.17</td>
</tr>
<tr>
<td>Haddock</td>
<td>3.10</td>
<td><strong>0.01</strong></td>
<td>0.17</td>
<td><strong>0.042</strong></td>
<td>1.56</td>
<td>0.116</td>
<td>0.14</td>
</tr>
<tr>
<td>Whiting</td>
<td>2.43</td>
<td>0.066</td>
<td>0.20</td>
<td>0.070</td>
<td>3.40</td>
<td>0.104</td>
<td>0.24</td>
</tr>
<tr>
<td>Plaice</td>
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<td>0.144</td>
<td>0.15</td>
<td>0.138</td>
<td>0.44</td>
<td>0.521</td>
<td>0.08</td>
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</tbody>
</table>

997
Table 3: Model formulae, explained deviation, AIC, BIC and Moran’s I in the residuals for the best fitting GAMMs fit to presence/absence and density of fish eggs. Of the Moran’s I only the values for the first lag are presented.

<table>
<thead>
<tr>
<th>Species</th>
<th>Type</th>
<th>N</th>
<th>Model Formula</th>
<th>GAM - Dev. Expl. (%)</th>
<th>AIC</th>
<th>BIC</th>
<th>Moran’s I</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cod</td>
<td>Presence/absence</td>
<td>696</td>
<td>( YD + s(b\text{ depth, } 4) + s5, (1</td>
<td>MEV2) + (1</td>
<td>MEV5) )</td>
<td>18.5</td>
<td>688.1</td>
</tr>
<tr>
<td></td>
<td>Egg density</td>
<td>510</td>
<td>( s(YD, 4) + s(b\text{ depth, } 4) + s(t5, 4), (1</td>
<td>MEV2) + (1</td>
<td>MEV5) )</td>
<td>14.6</td>
<td>1131.2</td>
</tr>
<tr>
<td>Haddock</td>
<td>Presence/absence</td>
<td>696</td>
<td>( s(YD, 4) + s(b\text{ depth, } 4) + s(tb, 4) + cs(sb) + \sigma_{gb}, (1</td>
<td>MEV3) + (1</td>
<td>MEV10) + (1</td>
<td>MEV28) + (1</td>
<td>MEV83) )</td>
</tr>
<tr>
<td></td>
<td>Egg density</td>
<td>336</td>
<td>( YD + s(b\text{ depth, } 3) + s(tb, 3) + s(sb, 3) + \sigma_{gb}, (1</td>
<td>MEV3) + (1</td>
<td>MEV10) + (1</td>
<td>MEV28) + (1</td>
<td>MEV83) )</td>
</tr>
<tr>
<td>Whiting</td>
<td>Presence/absence</td>
<td>696</td>
<td>( s(YD, 4) + b\text{ depth} + tb + s(\sigma_{gb}, 4), (1</td>
<td>MEV2) )</td>
<td>29.8</td>
<td>672.8</td>
<td>709.2</td>
</tr>
<tr>
<td></td>
<td>Egg density</td>
<td>448</td>
<td>( s(YD, 4) + s(b\text{ depth, } 4) + s(t5, 4) + s(s5, 4) + \sigma_{g5}, (1</td>
<td>MEV2) )</td>
<td>34.8</td>
<td>1081.8</td>
<td>1131.0</td>
</tr>
<tr>
<td>Plaice</td>
<td>Presence/absence</td>
<td>696</td>
<td>( s(YD, 4) + s(b\text{ depth, } 4) + tb, (1</td>
<td>MEV2) + (1</td>
<td>MEV8) + (1</td>
<td>MEV12) + (1</td>
<td>MEV15) )</td>
</tr>
<tr>
<td></td>
<td>Egg density</td>
<td>363</td>
<td>( s(YD, 4) + s(b\text{ depth, } 4) + s(t5, 4) + s(s5, 4) + \sigma_{g5}, (1</td>
<td>MEV2) + (1</td>
<td>MEV8) + (1</td>
<td>MEV12) + (1</td>
<td>MEV15) )</td>
</tr>
</tbody>
</table>
Model formulae show the fixed-effects covariates, either as linear or smooth (s()) terms with degrees of freedom. The prefix cs. indicates a scaling function applied to a linear term. Explained deviation was calculated with a GAM using the same fixed effects. MEVs were included as random covariates, e.g. (1|MEV1). YD, day of the year; b_depth, bottom depth; t5, temperature at 5 m depth; s5, salinity at 5 m depth; σt5, gradient of σt at 5 depth; tb, bottom temperature; sb, bottom salinity; σgb, gradient of σb at the bottom. MEVs

Significance levels: **: ≤0.001, *: >0.001
Table 4: Predictive performance of the selected models and single covariates. The performance for presence/absence models is given as Receiver Operating Characteristic Area Under the Curve (ROC AUC) while for the egg densities it is the $r^2$ between predictions and observations. N is 636 for presence/absence of all species, for the non-zero abundance it is: $N_{\text{Cod}}=510$, $N_{\text{Haddock}}=336$, $N_{\text{Whiting}}=448$, $N_{\text{Plaice}}=363$.

<table>
<thead>
<tr>
<th>Response</th>
<th>Covariates\textsuperscript{a}</th>
<th>Cod</th>
<th>Haddock</th>
<th>Whiting</th>
<th>Plaice</th>
</tr>
</thead>
<tbody>
<tr>
<td>Presence/Absence (ROC AUC)</td>
<td>Selected Model</td>
<td>0.71</td>
<td>0.85</td>
<td>0.79</td>
<td>0.74</td>
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<tr>
<td></td>
<td>Year Day</td>
<td>0.64</td>
<td>0.78</td>
<td>0.72</td>
<td>0.63</td>
</tr>
<tr>
<td></td>
<td>Bottom Depth</td>
<td>0.54</td>
<td>0.77</td>
<td>0.50</td>
<td>0.71</td>
</tr>
<tr>
<td></td>
<td>Temperature\textsuperscript{5}</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Salinity\textsuperscript{5}</td>
<td>0.50</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>$\sigma_t$-Gradient\textsuperscript{5}</td>
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<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Temperature\textsuperscript{b}</td>
<td>-</td>
<td>0.77</td>
<td>0.60</td>
<td>0.63</td>
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<td>Salinity\textsuperscript{b}</td>
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<td>0.81</td>
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<tr>
<td></td>
<td>$\sigma_t$-Gradient\textsuperscript{b}</td>
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<td>0.63</td>
<td>0.62</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Random</td>
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<td>0.50</td>
<td>0.50</td>
<td>0.50</td>
</tr>
<tr>
<td>Egg Density ($r^2$)</td>
<td>Selected Model</td>
<td>0.45</td>
<td>0.62</td>
<td>0.72</td>
<td>0.51</td>
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<tr>
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<td>0.38</td>
<td>0.59</td>
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<tr>
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<td>0.56</td>
<td>0.61</td>
<td>0.39</td>
</tr>
<tr>
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<td>Temperature\textsuperscript{5}</td>
<td>0.42</td>
<td>-</td>
<td>0.57</td>
<td>0.43</td>
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<td>Salinity\textsuperscript{5}</td>
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<td>-</td>
<td>0.58</td>
<td>0.38</td>
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<td>0.59</td>
<td>0.31</td>
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<td>$\sigma_t$-Gradient\textsuperscript{5}</td>
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<td>0.50</td>
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<tr>
<td>Temperature\textsuperscript{b}</td>
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<tr>
<td>Salinity\textsuperscript{b}</td>
<td></td>
<td></td>
<td>0.35</td>
<td>-</td>
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<tr>
<td>$\sigma_t$-Gradient\textsuperscript{b}</td>
<td></td>
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<td>0.36</td>
<td>0.34</td>
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<tr>
<td>Random</td>
<td>0.56</td>
<td>0.30</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\textsuperscript{a) Suffixes 5 and b indicate whether a value was measured at the surface (5 m) or at the bottom.}
Table 5: Log-likelihood ratio test between the selected models and models with each of the covariates removed in turn. Bold font indicates significant p-values.

<table>
<thead>
<tr>
<th>Species</th>
<th>Dropped Covariate&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Presence/Absence</th>
<th>Egg density</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>( \chi^2_{0.05} )</td>
<td>df</td>
</tr>
<tr>
<td>Cod</td>
<td>Year Day</td>
<td>124.0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Bottom Depth</td>
<td>37.1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Temperature&lt;sup&gt;5&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Salinity&lt;sup&gt;5&lt;/sup&gt;</td>
<td>5.0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>( \sigma_t )-Gradient&lt;sup&gt;5&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Haddock</td>
<td>Year Day</td>
<td>181.0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Bottom Depth</td>
<td>12.0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Temperature&lt;sup&gt;b&lt;/sup&gt;</td>
<td>35.3</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Salinity&lt;sup&gt;b&lt;/sup&gt;</td>
<td>40.4</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>( \sigma_t )-Gradient&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6.7</td>
<td>1</td>
</tr>
<tr>
<td>Whiting</td>
<td>Year Day</td>
<td>134.9</td>
<td>2</td>
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<tr>
<td></td>
<td>Bottom Depth</td>
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<td>1</td>
</tr>
<tr>
<td></td>
<td>Temperature&lt;sup&gt;5&lt;/sup&gt;</td>
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<td>-</td>
</tr>
<tr>
<td></td>
<td>Salinity&lt;sup&gt;5&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>( \sigma_t )-Gradient&lt;sup&gt;5&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Temperature&lt;sup&gt;b&lt;/sup&gt;</td>
<td>34.1</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Salinity&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>( \sigma_t )-Gradient&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.0</td>
<td>2</td>
</tr>
<tr>
<td>Plaice</td>
<td>Year Day</td>
<td>35.5</td>
<td>2</td>
</tr>
<tr>
<td>--------</td>
<td>----------</td>
<td>------</td>
<td>---</td>
</tr>
<tr>
<td>Bottom Depth</td>
<td>78.2</td>
<td>2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Temperature&lt;sup&gt;5&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Salinity&lt;sup&gt;5&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>σ&lt;sub&gt;θ&lt;/sub&gt;-Gradient&lt;sup&gt;5&lt;/sup&gt;</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Temperature&lt;sup&gt;b&lt;/sup&gt;</td>
<td>9.5</td>
<td>1</td>
<td>0.002</td>
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<tr>
<td>Salinity&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>-</td>
<td>-</td>
</tr>
<tr>
<td>σ&lt;sub&gt;θ&lt;/sub&gt;-Gradient&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-</td>
<td>1</td>
<td>-</td>
</tr>
</tbody>
</table>

<sup>o</sup> Suffixes 5 and b indicate whether a value was measured at the surface (5 m) or at the bottom.
Table 6: Variation explained by the fixed effects.

<table>
<thead>
<tr>
<th>Covariates</th>
<th>Cod (%)</th>
<th>Haddock (%)</th>
<th>Whiting (%)</th>
<th>Plaice (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Presence/Absence</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year Day</td>
<td>16.1</td>
<td>33.2</td>
<td>25.7</td>
<td>1.3</td>
</tr>
<tr>
<td>Bottom Depth</td>
<td>3.1</td>
<td>27.2</td>
<td>10.8</td>
<td>8.6</td>
</tr>
<tr>
<td>Temperature</td>
<td>-</td>
<td>33.0</td>
<td>15.3</td>
<td>8.3</td>
</tr>
<tr>
<td>Salinity and $\sigma_g$</td>
<td>0.9</td>
<td>22.0</td>
<td>5.1</td>
<td>-</td>
</tr>
<tr>
<td>Total</td>
<td>15.9</td>
<td>47.1</td>
<td>29.1</td>
<td>9.6</td>
</tr>
<tr>
<td>Egg density</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year Day</td>
<td>1.7</td>
<td>7.0</td>
<td>1.7</td>
<td>4.4</td>
</tr>
<tr>
<td>Bottom Depth</td>
<td>2.1</td>
<td>17.4</td>
<td>4.5</td>
<td>2.9</td>
</tr>
<tr>
<td>Temperature</td>
<td>5.0</td>
<td>21.4</td>
<td>6.8</td>
<td>1.1</td>
</tr>
<tr>
<td>Salinity and $\sigma_g$</td>
<td>-</td>
<td>28.9</td>
<td>9.2</td>
<td>7.9</td>
</tr>
<tr>
<td>Total</td>
<td>5.0</td>
<td>30.5</td>
<td>9.9</td>
<td>13.2</td>
</tr>
</tbody>
</table>

$^a$) Variation partitioning only allows for four components. Therefore salinity and density gradient were, if necessary, grouped. Values for single covariates contain a pure component and a component shared with other covariates. Hence, the terms sum up higher than the total variation explained. $\sigma_g = $ density gradient.
Table 7: Log-likelihood ratio test between GAMM and corresponding GAM models for presence/absence as well as density of eggs for the four species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Type</th>
<th>AIC</th>
<th>GAM</th>
<th>AIC</th>
<th>GAM</th>
<th>Log-likelihood ratio test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>GAMM</td>
<td>GAM</td>
<td>GAMM</td>
<td>GAM</td>
<td>χ^2 0.05</td>
</tr>
<tr>
<td>Cod</td>
<td>Presence/Absence</td>
<td>1938.8</td>
<td>1930.0</td>
<td>1957.0</td>
<td>1939.1</td>
<td>4.8</td>
</tr>
<tr>
<td></td>
<td>Egg density</td>
<td>1079.6</td>
<td>1076.2</td>
<td>1096.6</td>
<td>1084.7</td>
<td>0.6</td>
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<td>Haddock</td>
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<td>1653.9</td>
<td>1622.5</td>
<td>5.2</td>
</tr>
<tr>
<td></td>
<td>Egg density</td>
<td>672.5</td>
<td>659.7</td>
<td>695.4</td>
<td>667.3</td>
<td>4.8</td>
</tr>
<tr>
<td>Whiting</td>
<td>Presence/Absence</td>
<td>1921.2</td>
<td>1914.4</td>
<td>1934.8</td>
<td>1923.5</td>
<td>4.7</td>
</tr>
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<td></td>
<td>Egg density</td>
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<td>998.7</td>
<td>1017.9</td>
<td>1006.9</td>
<td>4.9</td>
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<tr>
<td>Plaice</td>
<td>Presence/Absence</td>
<td>2046.1</td>
<td>2037.9</td>
<td>2073.3</td>
<td>2046.9</td>
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<td>Egg density</td>
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<td>574.2</td>
<td>608.1</td>
<td>582.0</td>
<td>2.6</td>
</tr>
</tbody>
</table>
Figure 1: Panel (a) shows the ichthyoplankton stations for 2004 and 2009 over a bathymetric map of the North Sea. Panel (b) exhibits the operational installations related to oil extraction; color-coded depending on the operating country on the same bathymetric map. Red lines depict Exclusive Economic Zones (EEZs). Areas shaded pink; show the areas with planned or ongoing seismic surveys in the Norwegian and Dutch sectors. Germany is not conducting seismic surveys and for the UK and Denmark no information is publicly available.

Figure 2: Mean Temperature and Salinity at the surface (5 m; panels (a, b) and at bottom depth (c, d), based on data from the first quarter of 2004 and 2009. Black dots indicate individual CTD hauls.

Figure 3: Range of structures of spatial autocorrelation (a) for the individual species. Broken lines indicate where the structures were grouped into the scales depicted, in the order fine to broad, on the maps on panels (b) to (e). The plotted structures are those for haddock, except on medium-broad scale (d) where there was only a single structure, for cod.

Figure 4: Mean interpolated surfaces for the distribution of eggs in each stage, drawing from both surveys. Interpolated areas beyond 200 m bottom depth are blanked out. Black dots on panel (a) indicate the sampling stations for both years.
Figure 5: Predicted probability of occurrence for stage I eggs of all four species, on
the range of the covariates in the best fitting models. Broken lines indicate models
using hydrographic values measured at the surface. Hatches at the bottom of each
panel indicate the values observed at samples. As cod was related to surface salinity,
while haddock was related to bottom salinity on a narrower range, the
corresponding observations are depicted in colours corresponding to the smooth
terms. Shaded areas indicate the 95% confidence interval.

Figure 6: Predicted log-transformed stage I egg density for stage I eggs of all four
species, related to the covariates in the best fitting models. Broken lines indicate
models using hydrographic values measured at the surface. Observations with non-zero egg densities for the individual species are indicated by hatches, in the same
colour as the smooth term, at the bottom of each panel. Shaded areas indicate the
95% confidence interval.

Figure 7: Panel (a) shows the average stage I egg density for each ICES rectangle on
the interpolated surface of bottom temperature variability, based on CTD data for
the 1st quarter of the entire 2000s. Panel (b) depicts installations of the oil industry,
categorized as above-surface (red dots) or subsurface structures (white squares)
the position of oil industry installation and the seismic survey areas for Norway and
the Netherlands, shaded blue, on top of the average distribution of stage I eggs for
all four species combined.