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Spatial patterns and trends in abundance of larval sandeels in the North Sea: 1950–2005

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Early recruitment indices based on larval fish data from the Continuous Plankton Recorder (CPR) have the potential to inform stock assessments of *Ammodytes marinus* in the North Sea. We evaluate whether the CPR data are reliable for sandeel larvae. Spatially, CPR larval data were comparable with catches by dedicated larval samplers (Gulf and bongo nets) during ICES coordinated surveys in 2004 and 2009. ICES data are also used to explore environmental influences on sandeel distributions. Temporally, CPR data correlate with larval data from plankton surveys off Stonehaven (1999–2005), with sandeel 0-group trawl data at the east Fair Isle ground (since 1984), and with recruitment data (since 1983) for the Dogger Banks stock assessment area. Therefore, CPR data may provide an early recruit index of relative abundance for the Dogger Banks assessment area, where the majority of the commercial catch of *A. marinus* is taken, and the Wee Bankie area that is particularly important for seabird foraging. While warm conditions may stimulate the production of sandeel larvae, their natural mortality is typically greater, in the Dogger Banks and Wadden Sea areas, when the larvae are hatched in warm years and/or with abundant 1-year-old sandeel that are likely to be cannibalistic.

Keywords: environment, keystone, management, modelling, statistical.

Introduction

Sandeels (Ammodytidae) support a large fishery in the North Sea. However, the stock is difficult to assess and manage owing to the short life cycle of sandeels and the reliance of the fishery on new recruits. Sandeels are a key prey species and are consumed by fish (e.g. gadoids; Greenstreet *et al.*, 1998), seabirds (Daunt *et al.*, 2008), and marine mammals (Thompson *et al.*, 2007). Sandeels are also an important commercial species and have been exploited in the North Sea since 1953 by small-meshed industrial fisheries, for oil and meal. Landings of sandeels increased to ~ 600–800 kt year^{-1} during the late 1970s and 1980s before peaking in 1997 at 1150 kt (ICES, 2011). Owing to concern over the potential detrimental effects of the exploitation of sandeel on seabirds and mammals (Daunt *et al.*, 2008), the sandeel fishery was closed off the northeastern UK coast in 2000. A combination of low recruitment since 2002 and restrictions on effort (ICES, 2010a) have reduced subsequent landings for the entire North Sea to between 178 and 356 kt year^{-1}.

ICES ceased to treat lesser sandeels (*Ammodytes marinus*) in the North Sea as a single stock in 2011, following a review of evidence on habitat, larval drift, and regional growth differences that indicated that there were seven subpopulation regions that differed in their vulnerability to exploitation (ICES, 2010a). Although there is some spatial dispersal of larvae between banks up to 300 km apart, most dispersal is <100 km (Proctor *et al.*, 1998; Christensen *et al.*, 2008) and the assessment areas chosen by ICES (2010a) were determined in order to relate local recruitment with spawning-stock biomass (SSB). The scientific and fishery

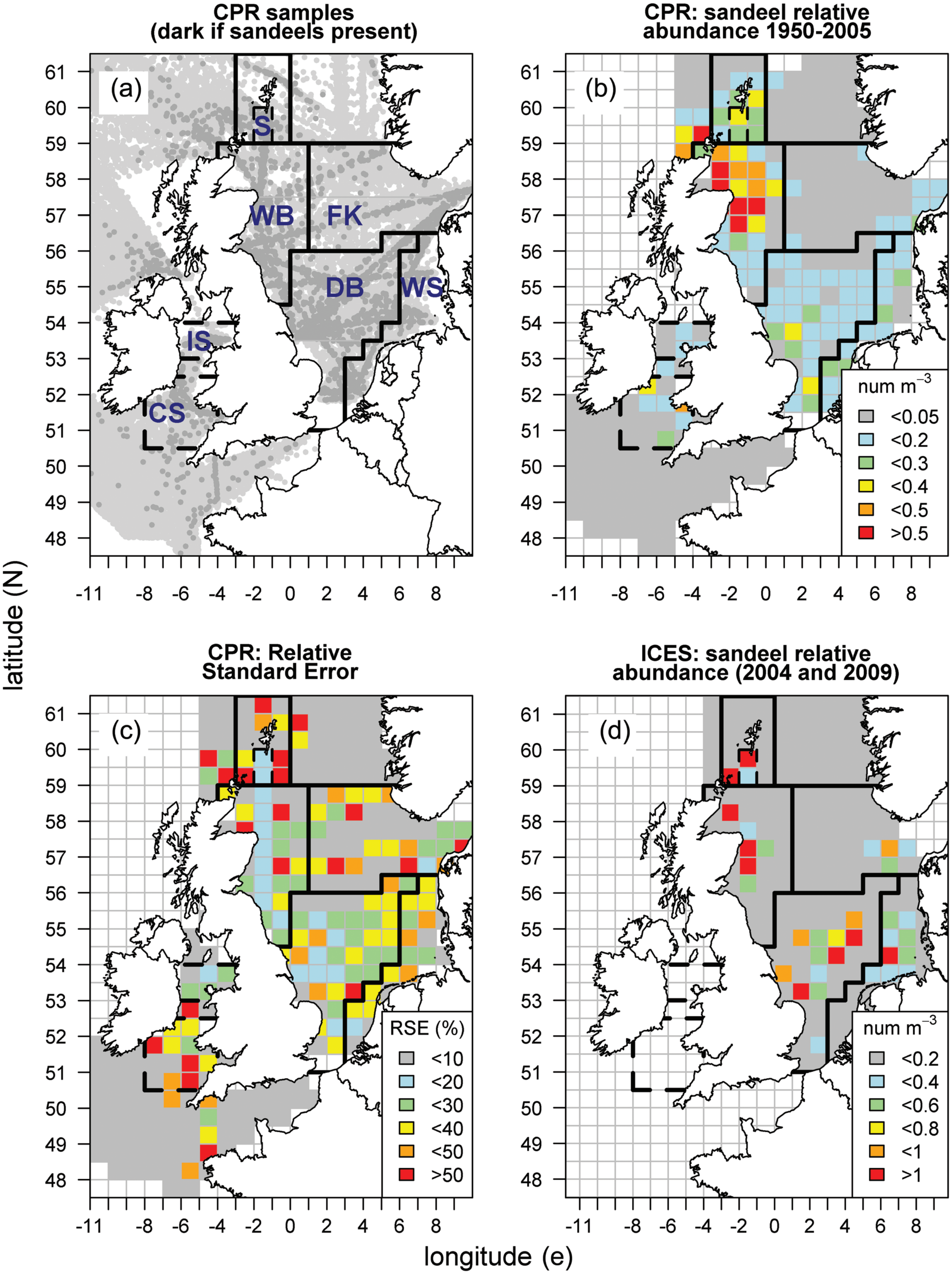

Figure 1. Sampling areas and sandeel abundance. (a) CPR sample locations (light grey points) and presence of Ammodytidae larvae (dark grey circles) from all transects 1950–2005 showing North Sea sandeel assessment regions (solid black lines), the subregion "South of Shetland", and

information available to inform the assessment differs by region, and as a result analytical assessments are only available for the most commercially important of these (ICES, 2010a, 2011). In sandeel assessment areas 1 [Dogger Banks (DB), Figure 1a] and 2 [Wadden Sea (WS)], a dredge survey index from 2004 (collected in area 1 only) is used as a tuning index for an analytical assessment. In sandeel region 3 [Fisher and Klondyke (FK)], the assessment is based on commercial indices only. A dredge survey from 2008 informs the trends-only assessment in area 4 [Wee Bankie (WB)]. No assessment is made in areas 5 (Viking and Bergen Banks, northeastern North Sea) or 6 (Kattegat, Baltic Sea) where the landings are too low or sporadic for an assessment. A recruitment index is available from 1984 to 2007 for area 7 [Shetland (S)], although this region was always treated as a separate stock region and managed under national regulations. No assessments are made in the Irish Sea (ICES division VIIa) or Celtic Sea (ICES divisions VIIfg) because of the lack of large-scale sandeel fisheries there. Given that the sandeel stocks are highly dependent on the incoming year classes (ICES, 2011), short-term forecasts of year-class strength may be improved by early indices of year-class strength.

The Continuous Plankton Recorder (CPR) survey samples throughout the year and the data are considered to be consistent at a monthly resolution. In addition to zooplankton and phytoplankton, fish larvae are retained in the samples. Prior to 1979, identification and enumeration of fish larvae was carried out as part of routine sample analysis. Due to economic restraints and a lack of available expertise, larval fish analysis ceased in 1980. In 2010, retrospective analysis of archived CPR samples for larvae were carried out and the data obtained were combined with the archived pre-1980 data and added to the CPR database. The two most abundant families are the Clupeidae (herring/sprat/pilchard) and Ammodytidae (sandeels; Edwards *et al.*, 2011). A limitation of the current analysis of CPR fish larvae is that the five sandeel species in the North and Irish Seas cannot be distinguished. In the North Sea, the most abundant sandeel species is the commercially important Raitt's or lesser sandeel, *Ammodytes marinus*, which spawns there between December and January (Gauld and Hutcheon, 1990); in the Irish Sea, it spawns between January and March (Nichols *et al.*, 1993). Three additional species of Ammodytidae spawn in the North and Irish Seas: greater sandeel *Hyperoplus lanceolatus* spawns in April and May, smooth sandeel *Gymnammodytes semisquamatus* from April to July, and *Ammodytes tobianus* in autumn (Nichols *et al.*, 1993).

Ammodytes marinus generally prefer habitat with >15% coarse sand and low silt/clay content (Wright *et al.*, 2000; Holland *et al.*, 2005). The demersal eggs typically reside until hatching in the habitat of adult sandeels. In the North Sea, it has been documented that lesser sandeel hatch from February to May and the duration of the larval phase is between 1 and 3 months; larvae are planktonic, until reaching a length of ~25 mm (Nichols *et al.*, 1993; Wright and Bailey, 1996). However, particularly in coastal areas including to the north of the WB, larvae of the less abundant species *H. lanceolatus* increase from April onwards before dominating in July (Heath *et al.*, 2012). In the southern North Sea, larvae of *A. marinus* (<9 mm in length) feed initially on copepod nauplii and to a lesser extent phytoplankton (diatoms and dinoflagellates), turning to an equal mix of copepod nauplii and Appendicularia once the larvae are 9–14 mm long (Ryland, 1964). In the northwestern North Sea, the CPR typically catches *A. marinus* of <15 mm length (range 5–60 mm; Frederiksen *et al.*, 2011). Therefore, predator–prey interactions are considered with the above prey (phytoplankton and zooplankton) species and also the small and abundant cladoceran *Evadne* spp. (Pitois and Fox, 2006).

The primary aim of this study was to evaluate whether the CPR provides a representative index of the spatio-temporal distribution of sandeel larvae. Secondly, the study aimed to assess the potential use of CPR data as a pre-recruit index for regional stock assessments. For sandeels in the North Sea, the overall spatial pattern in CPR data was compared with spatial data collected by dedicated larval fish samplers during ICES coordinated surveys in 2004 and 2009 (ICES, 2007, 2010b). Time-series of larval abundance from the CPR were compared with larval data from a coastal monitoring programme (Heath *et al.*, 2012) and with a range of recruitment indices for stock assessment regions in the North Sea (Wright, 1996; ICES, 2010a, 2011). The final aim of the study was to explore environmental influences on sandeel larvae and their ecological role as predators of plankton. The environment was considered to influence the spatial distribution, and data on physical variables (salinity, temperature, density, and depth) from ICES ichthyoplankton surveys were used to determine the suitable environmental conditions for larvae in the North Sea. Potential relationships between temporal variation in sandeel larval abundance, SSB, prey abundance (see above), and climate [sea surface temperature (SST) and North Atlantic Oscillation (NAO)] was explored to determine the key ecological processes influencing sandeel larvae production and the survival of larvae to the juvenile stage (i.e. recruitment).

Material and methods

CPR sampling methodology

The CPR is a plankton sampling instrument designed to be towed from fast-moving (~15–20 knots) merchant vessels on their normal sailings. Given that the CPR makes use of these "ships of opportunity", the timing of deployments and resulting spatial coverage of the survey are variable. Nevertheless, a network of routes with monthly deployments has been maintained over the history of the survey (Warner and Hays, 1994). The CPR is towed at a depth of ~ 10 m. Water enters through a square aperture, of cross-sectional area 1.61 cm^2, in the nose cone of the CPR (Warner and Hays, 1994). The CPR is designed to filter plankton from the water over long distances (up to 500 nautical miles) on a moving filter band of silk (270 μm mesh size). The filter silk band is wound through the CPR on rollers turned by gears, which are powered by an impeller. The filtering layer is covered by a second band of silk, forming a sandwich with the plankton

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additional areas in the Irish Sea and Celtic Sea (dashed black lines); (b) mean abundance of larvae in CPR samples; (c) relative standard error (%) in the mean in CPR samples by rectangle for all years of data pooled together; (d) ICES coordinated international surveys, where the colours indicate the mean abundance (counts m^{-3}) in February–April of 2004 and 2009. Note: b and c are composite maps with cells in the North Sea and eastern Channel (east of 2°W) based on February–June data only, Celtic Sea (south of 52.5°N) and western Channel (west of 2°W) based on March–July data, and Irish Sea, north of 52.5°N, based on April–August data.

trapped between the two layers of mesh. This silk sandwich is wound onto the storage spool in a tank, which contains a solution of 4% borax-buffered formaldehyde to fix the plankton (Warner and Hays, 1994; Batten *et al*., 2003). On return to the laboratory, the silk sandwich is removed and divided into samples representing 10 nautical miles of towing, and samples are considered to be taken at the mid-point of the corresponding segment of tow track.

Phytoplankton indices (phytoplankton colour index, diatom and dinoflagellate counts) were generated from the CPR database for each sandeel assessment area, and crustacean zooplankton (copepods and cladocerans) and gelatinous zooplankton (Appendicularia, Tunicata) records were selected to explore relationships between larval fish and prey abundance. The CPR is known to underestimate the abundance of zooplankton, particularly small zooplankton, when compared with other datasets (Pitois and Fox, 2006). Therefore, crustacean zooplankton data were corrected for undersampling relative to plankton nets of the standard design (known as "Working Party 2", WP-2; UNESCO, 1968) by using species-specific sampling correction factors (WP-2/CPR ratios) and converted into biomass estimates using species dry weights as described by Pitois and Fox (2006). The abundance of gelatinous Appendicularia was considered separately. Plankton data were limited to the period 1958–2005, because many zooplankton species were not recorded prior to 1958. All zooplankton abundance and biomass values were computed per m^3 of water filtered, assuming a standard volume filtered of 3 m^3 of seawater over 10 nautical miles.

The reliability of a plankton sampler with such a small aperture as the CPR (1.61 cm^2) in studying fish larvae is debatable and is investigated further here. Clearly, fish larvae can grow too large for the CPR to sample, so larval abundances should be interpreted for many species, including sandeels, as early-stage larvae (see Frederiksen *et al*., 2011). To address such concerns, spatial and temporal patterns in the Ammodytidae (sandeel) larval data were verified against other data sources (see below).

Statistical properties of the CPR fish larvae data

The statistical distribution underlying the variability in the larval data was investigated and was well characterized by a negative binomial distribution because of the many zeros in the data with occasional high counts. In order to reduce the proportion of zeros in the dataset, the larval period, i.e. when larvae were present in the surface water, was identified from a visual analysis of abundance by month for each stock unit (Figure 2). Further analyses of the CPR data were restricted to these larval periods.

Spatial variability in the data was explored through maps of overall mean abundance m^{-3} and relative standard error (%) by ICES rectangle. Annual mean abundances with estimates of variability were calculated for each stock assessment region, and annual maps of mean abundance by ICES rectangle were plotted (see Supplementary material, Figure S1). Given the patchiness of larvae in the water column and the short temporal period of availability of larvae to the CPR, sampling events are highly variable. Therefore, a non-parametric bootstrap sensitivity analysis for the computation of mean abundance was conducted (see Supplementary material, Figure S2).

ICES survey sampling methods

The ICES fish egg and larval surveys took place from 15 December 2003 to 13 April 2004 and from 15 December 2008 to 15 March 2009 in the North Sea and eastern English Channel (ICES, 2010b). Comparative analyses were restricted to data from 1 February to 30 April, between 51.5 and 62°N, to be consistent with the CPR data. High-speed samplers (Gulf III and VII, mesh size 270–330 μm and aperture 20–40 cm diameter) and bongo nets (mesh size 330–500 μm, 60 cm opening) were deployed in double oblique hauls for a minimum of 15 min (multiple hauls in shallow water), down to 2 m above the seafloor or a maximum of 100 m (ICES, 2007). Samples were fixed in 96% ethanol or buffered formalin. Larvae were sorted from the preserved samples and identified to the lowest possible taxonomic level according to Munk and Nielsen (2005).

Spatial validation of CPR data with ICES survey data

The spatial structure in the CPR data (mean abundance m^{-3} by ICES rectangle, using February–June data for all available years 1950–2005) was compared with that for February–April from the ICES plankton surveys in 2004 and 2009 (ICES, 2007, 2010b) (Figure 1d). A Mantel correlogram (Borcard *et al*., 2011) was calculated to test the significance of spatial correlation between the two datasets given the spatial structure in the data. For significance testing of Mantel correlograms, the data must meet the condition of second order stationarity, and this was assessed via redundancy analysis (RDA) following Borcard *et al*. (2011).

ICES survey: environmental influences on sandeel larval distribution

Sandeels are known to be limited spatially by the extent of sandy habitat in which they can bury themselves (Wright *et al*., 2000; Holland *et al*., 2005). However, this was not further studied here due to the lack of sediment data of a resolution comparable with the plankton samples. The focus here is on the water column conditions experienced by the larvae. Environmental data (temperature and salinity) were collected by CTD casts at the ICES plankton sampling stations to assist in the classification of suitable environmental conditions. However, when such casts were not completed, supplementary data were extracted from the ICES oceanographic database (http:/ocean.ices.dk). The density was calculated according to UNESCO standards (Millero and Poisson, 1981), and all three hydrographic values were interpolated for depths of 5 m, 20 m, and bottom depth on a regular 0.25 × 0.25 decimal degrees (dec. deg.) grid, by ordinary kriging in Surfer® 8. The horizontal density gradient ($\vec{g}$ in g m^{-3} nautical $mile^{-1}$) was calculated from the interpolated density with the formula (Golden Software, 1999):

$$||\vec{g}|| = \sqrt{\left(\frac{Z_E - Z_W}{2\Delta x}\right)^2 + \left(\frac{Z_N - Z_S}{2\Delta y}\right)^2} \qquad (1)$$

where Z_E and Z_W are adjacent grid points in the East–West direction, Z_N and Z_S are adjacent grid points in the North–South direction, and Δx and Δy are the distances in longitudinal and latitudinal direction, respectively.

The counts of larvae in the ICES surveys were converted to counts m^{-3} and counts m^{-2} of the water column, by dividing the numbers by filtered volume and multiplying by a subsampling raising factor to standardize across gears (counts m^{-3}) and sampled depth (counts m^{-2}). To examine the spatial relationship between sandeel larvae and their environment, the data were split into log-transformed non-zero abundance and binary transformed

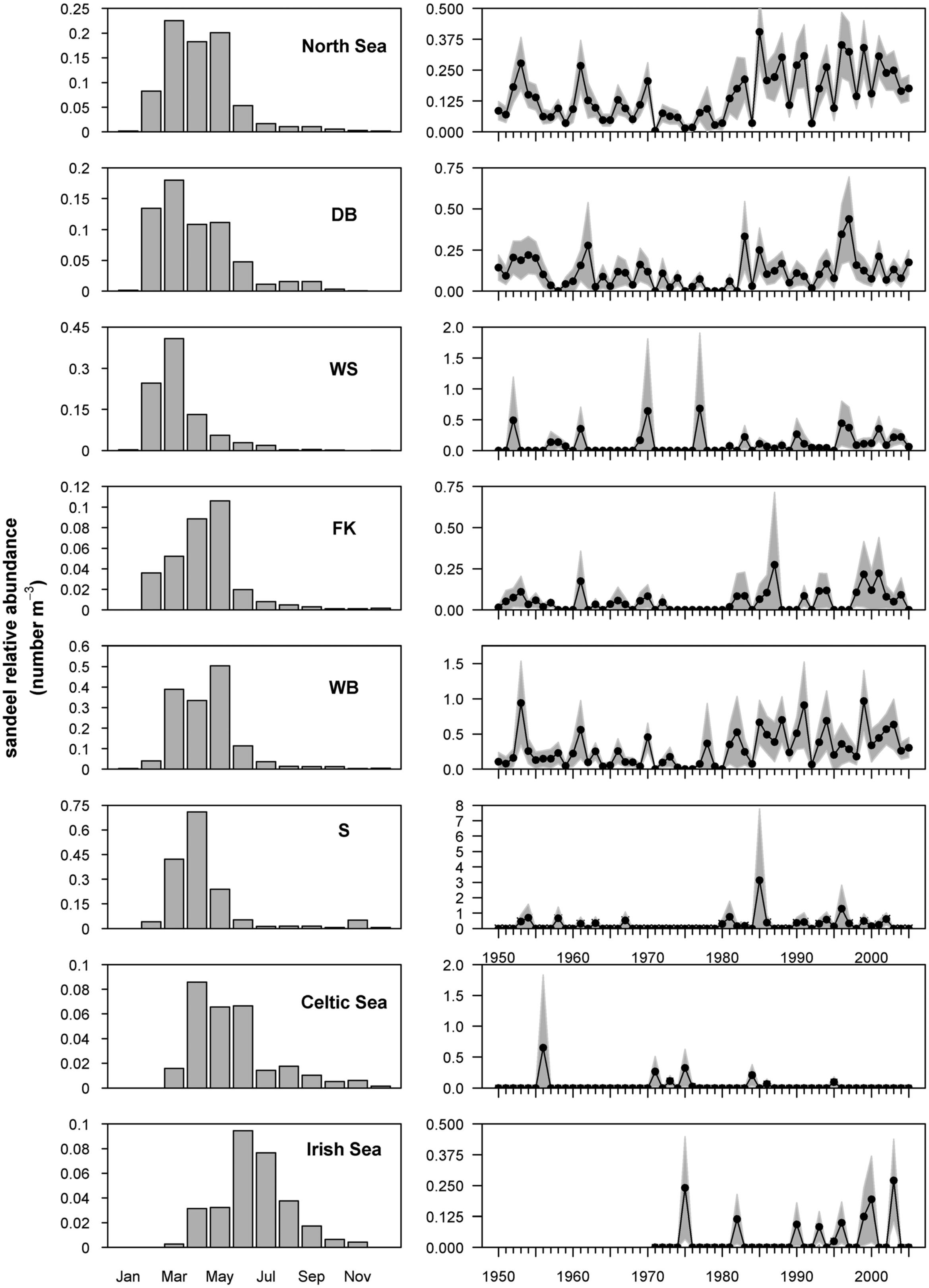

Figure 2. Mean abundance of larvae in CPR samples by region. Left column: average seasonal cycle for all years combined (1950–2005, except the Irish Sea 1971–2005). Right column: annual means of larval abundance in the North Sea and its subareas during February–June, the Celtic Sea during March–July, and the Irish Sea during April–August. Shaded areas indicate the 95% confidence interval based on the standard error of the mean. Subareas (see Figure 1a) from the top row to bottom are: DB, Dogger Banks; WS, Wadden Sea; FK, Fisher and Klondyke; WB, Wee Bankie; S, South of Shetland; CS, Celtic Sea box; IS, Irish Sea box.

presence/absence data. Spatial autocorrelation in the larval data and the average patch size of the larval distribution were modelled with principal coordinates of neighbour matrices (PCNM), following Borcard *et al*. (2011) and Blanchet *et al*. (2008). As in Loots *et al*. (2010), a low *p*-value (0.002) was chosen to avoid inclusion of superfluous submodels.

Generalized additive models (GAMs) were constructed using a Gaussian model for the abundance data and a binomial model for presence/absence, with bottom depth and hydrographic variables as continuous variables and year as a categorical factor. Response variables for larvae were calculated for the ICES survey data only because co-sampled physical and biological data are considered more informative of the local processes influencing the sandeel larvae. Two sets of hydrographic data were constructed to assess whether the surface hydrography affected the larvae directly or whether the bottom hydrography influenced the spawning (parent) population. The "surface" dataset was constituted by the temperature measured at 5 m depth, and salinity and density gradient measured at 20 m: data from 20 m were used because conductivity measurements at this depth were more reliable than at 5 m and the correlation between 5 and 20 m was high ($R^2 > 0.9$). The 'bottom' hydrographic dataset contained temperature, salinity, and density values measured closest to the bottom (within ~2 m). Multicollinearity was investigated through pairwise scatter plots and calculation of the variance inflation factor (VIF). The highest VIF values (6.2 for salinity at 20 m for the surface model and 5.7 for density gradient in the bottom model) were between the critical values (5 and 10) suggested by Zuur *et al*. (2009) and Borcard *et al*. (2011), indicating that the variables required further investigation. However, the smoothing splines in the GAMs did not exhibit any substantial changes, once any one of the hydrographic covariates was removed; therefore, all factors were retained in the initial model. Model reduction was done based on generalized cross-validation (GCV) for Gaussian models or unbiased risk estimator (UBRE) scores for binomial models (Wood, 2006). The choice for the best fitting model between surface and bottom model was based on the Akaike information criterion (AIC). For those variables selected in the final GAMs, variation partitioning (Borcard *et al*., 2011) was conducted to investigate the relative importance of spatial scale and the environmental variables (salinity, temperature, and density) in structuring the distribution of larvae.

Coastal monitoring data and temporal validation of CPR larval fish data

For the Shetland (S) assessment area, an annual sandeel bottom trawl survey using commercial trawls of the 19 Shetland grounds (2–3 samples per ground) was conducted in July/August between 1984 and 2007 (but not 1987 or 1995, as described by Wright, 1996). Both the mean abundance (catch per unit swept area) for all Shetland grounds and that just for the most southerly station the 'east Fair Isle' ground (station 11, ~ 59.5°N, 1.5°W, located in the "South of Shetland" dashed box in Figure 1a) were considered. For the WB area, CPR estimates of larval abundance were compared with February–March larval data from plankton nets tows (100 cm mouth diameter, 350 μm mesh) at a single sampling location off Stonehaven (~ 7°N, 2°W) from 2000 to 2005 (Heath *et al*., 2012), and additionally with 0-group catch rates from a dredge survey in the Firth of Forth during November–December of 1999–2003 (ICES, 2010a).

Each independent time-series was used in correlative analyses with annual relative abundance data from the CPR for the relevant stock unit. Stock units for the North Sea were those adopted by WKSAN (ICES, 2010a). Coverage was poor in the Shetland assessment area and also within the Irish Sea (Figure 1a). Therefore, these regions were represented using regularly sampled subregions: within the Irish Sea, samples were analysed between 53 and 54°N and within the Shetland area between 59 and 60°N and 2 and 1°W (ICES rectangles 47E8 and 48E8, see dashed box S in Figure 1a). Sandeel data were summarized by region on a monthly basis (Figure 2): these data were used to investigate whether or not there was evidence for phenological change in the seasonality of the planktonic larval period thorough simple regression of the mean month of occurrence, m = (month index) × (abundance in month)/(total abundance for year), on year.

Foodweb relationships

Phytoplankton indices and zooplankton prey abundance were related to the abundance of fish larvae through correlative analyses for each stock unit area in the North Sea to explore potential predator–prey linkages. For prey abundances, the seasonal period in which sandeel larvae are expected in the North Sea (February–June) was considered, since this is when phytoplankton, copepod nauplii, and Appendicularia are known to be critical prey items (Ryland, 1964). Hence, copepod species adult abundances were considered proxies for the availability to Ammodytidae of nauplii. The abundant Cladoceran *Evadne* spp. was also considered as a potential prey item. For significance testing of Pearson correlation coefficients throughout the study, the degrees of freedom were corrected for autocorrelation via the modified Chelton method, with the Chatfield estimator, and the number of lags to be considered in computing autocorrelation was taken as one-fifth of the length of the time-series (Pyper and Peterman, 1998); significance values thus corrected for autocorrelation are labelled p_{ACF}.

Climate data and larval production

To measure climatic influences on sandeel larval production and survival, two time-series were considered in order to represent short interannual fluctuations and the slow modes of variability in the climate, namely indices of the NAO and the Atlantic Multidecadal Oscillation (AMO). The NAO data were downloaded from The National Center for Atmospheric Research http://www.cgd.ucar.edu/cas/jhurrell/indices.html. The winter, December–March, index was calculated from the principal component analysis of sea level pressure anomalies over the Atlantic (20–80°N, 90°W–40°E; Hurrell, 1995). When the NAO index is positive, westerly winds are typically strong such that SST warms during April–June in the WB and S areas and to the west of Denmark (Lynam *et al*. 2010). The AMO index of long-term variability in SST of the North Atlantic Ocean ("AMO unsmoothed from the Kaplan SST V2"; Enfield *et al*., 2001) was downloaded from http://www.esrl.noaa.gov/psd/data/timeseries/AMO.

To investigate potential long-term influences on larval production in each stock unit, a correlation matrix was generated for Ammodytidae larval data vs. climate data (long- and short-term variability AMO and NAO, 1950–2005).

Stock assessment data: potential of larval data to inform recruitment levels

Recruitment, landings, and SSB data (1983–2010) for North Sea sandeel stock units were obtained from ICES (2011) along with annual international landings 1952–2010 at the level of the North Sea. For the period 1952–1985, landings data were only available aggregated at the North Sea level. Landings for this historic period were attributed to each stock unit by disaggregating the annual totals by the average proportion of landings in each stock unit annually in the period 1983–2010 (DB, 52%; WS, 10%; FK, 31%; WB, 5%; and S, 1%). Landings were considered to represent the catch of sandeels. Correlative analyses (corrected for autocorrelation as above) were conducted to assess whether the SSB and climate data were indicative of the production of larvae, or whether the larvae, prey, and climate data were indicative of the recruitment level, SSB, and/or eventual catch.

Natural mortality of sandeels

Natural mortality on the larval stage can be measured by the difference in the numbers of larvae successfully hatched (as given by the CPR) and the number of 0-group sandeels that recruit to the adult population (as quantified by the stock assessment). Although there are no absolute data giving the number of successful hatchlings, the CPR dataset provide estimates of the relative abundance of larvae from year to year, which can be used to investigate relative interannual changes in natural mortality of larvae from the age/size at which they are typically sampled. The influence of climate and sandeel-prey on pre-recruit natural mortality was investigated for each stock unit through multiple regression analyses of scaled (minus the mean and divided by the standard deviation) data for log-transformed 0-group recruitment indices regressed against sandeel larval abundances, climate (AMO and winter NAO), and prey (i.e. total crustacean zooplankton biomass, Appendicularia abundance, and phytoplankton indices) during the period February–June. Recruitment with a 1 year lag was also included in the model to account for potential autocorrelation in the data. The regression model assumptions of linearity, homogeneity of variance, normality, and independence of residuals were tested following procedures outlined in Krzanowski (1998).

Results

Statistical properties of the CPR fish larvae data

The relative standard error (RSE, %) in the annual mean abundances indicates that the data are less variable in the North Sea (average annual RSE 24%) than in either the Irish (44%) or Celtic Seas (53%). Within the North Sea, the mean abundance for the DB (35%) and WB (38%) regions are least variable (RSE of each other region >50%). Notably, the spatial map of RSE in Figure 1c suggests that the variability in larval abundance in the Irish Sea is comparable with that at the DB. However, this effect is due to the pooling of data over all available years in the creation of the map; when the RSE calculation is determined on an annual basis and averaged over those years with data, the variability in the Irish Sea data is greater because of the limited sampling levels each year.

The long-term trends in CPR data indicate increases in Ammodytidae larval abundance (counts m^{-3}) in the North Sea and Irish Sea and decreases in the small numbers seen in Celtic Sea (Figure 2). In the North Sea, the long-term trend is dominated by an increase in the WB area since 1978. The second most abundant area for Ammodytidae larvae is the DB area. Other North Sea areas show sporadic high abundances of Ammodytidae larvae without trend. Bootstrapping (Supplementary material, Figure S2) the annual data for the five North Sea regions indicates that the annual means are robust to sampling variability.

Spatial validation of CPR larval fish data

In order to evaluate the spatial patterns, the Ammodytidae data from the CPR were compared visually and statistically with data from ICES larval surveys in the North Sea (Figure 1b and d, Supplementary material, Figure S3). Visual comparison of the maps based on CPR and ICES survey data for 2004, the only year in which both surveys occurred, indicated that they both suggest similar centres of high larval abundance (Supplementary material, Figures S1 and S3). Overall larvae were more abundant in the ICES surveys, peaking at 17.5 m^{-3} in 2004, and were generally abundant along the margins of the North Sea. In both surveys, sandeel larvae were abundant between 56 and 58.5°N off the Scottish east coast, with zero abundance north of 60.5°N. During the ICES surveys, sandeel larvae were only found in water <100 m and typically in temperatures between 4.5 and 7°C (Supplementary material, Figure S4). Abundances of sandeel larvae in 2004 peaked in medium salinities around 34 and in density gradients of 1.5 g m^{-3} nautical $mile^{-1}$ (Supplementary material, Figure S4).

Spatially, the Euclidean distance matrix, created from both CPR and ICES larval abundance data, was considered to meet the condition of second-order stationarity following a redundancy analysis, indicating no true gradient in the spatial pattern ($p = 0.095$). Positive spatial correlation between CPR (1950–2005) and ICES (2004 and 2009) surveys was significant ($p < 0.01$) for distances up to 125 km (i.e. approximately an ICES rectangle; Table 1), albeit with a weak correlation coefficient of ~ 0.1, suggesting that these independent and very different surveys show similar spatial structure in the Ammodytidae larval distribution in the North Sea (Figure 1b and d).

Environmental influences on the spatial distribution of larvae

In the ICES survey data, spatial patterns were determined by PCNMs. Of the 335 PCNMs with positive eigenvalues (labelled V1–V335), five were significant in relation to the distribution of sandeel larvae. These five spatial structures fell into two distinct groups (Supplementary material, Figures S5 and S6): broad-scale

Table 1. Mantel correlogram statistics for spatial comparisons between the CPR data (February–June 1950–2005) and ICES surveys (February–April, 2004 and 2009) for sandeel larval abundance by ICES rectangle.

Distance class (km)	Mantel (Pearson) correlation	Pr(Pearson)	Pr(Holm corrected)
≤75	+0.11	0.001	**0.001**
>75 to ≤125	+0.09	0.001	**0.002**
>125 to ≤175	+0.03	0.042	0.042
>175 to ≤250	0.03	0.095	0.095
>250 to ≤350	−0.02	0.217	0.217
>350 to ≤450	−0.04	0.011	0.043
>450 to ≤600	−0.03	0.049	0.155

Values in bold are significant at $\alpha = 0.01$ after Holm correction for multiple comparison, based on 9999 permutations.

($>$50 nautical miles) and medium-scale ($<$50 nautical miles), and were considered to represent the spawning habitat of the sandeels. Spatial environmental data (surface and bottom temperature, salinity, and depth), and temporal data (year and year day) were incorporated alongside these five spatial structures in statistical analyses by GAMs of larval distribution using the ICES survey data. For both larval presence/absence and non-zero abundance data, the best fitting GAM (explaining 43.0% and 52.9% of the deviance, respectively) was based on the surface, rather than the bottom, hydrography. The final binomial model for the probability of presence P was:

$$\begin{aligned} ln[P/(1-P)] = {} & s(broad\ scale\ V1) + s(broad\ scale\ V4) \\ & + s(medium\ scale\ V7) + s(medium\ scale\ V13) \\ & + s(medium\ scale\ V16) + s(bottom\ depth) \\ & + s(year\ \ day) + s(surface\ temperature) \end{aligned} \tag{2}$$

where smooth terms are indicated by s(variable name) and ‘year day’ refers to the number of days since the beginning of the calendar year (Supplementary material, Figure S7). All five PCNMs were retained as smooth terms, while the categorical factor year, salinity, and density terms were dropped. In contrast, the final Gaussian model for non-zero abundance data (Supplementary material, Figure S8) retained all temporal and environmental (surface temperature, density, and salinity) variables and only a subset of the spatial PCNMs:

$$\begin{aligned} ln(abundance) = {} & factor(year) + medium\ scale\ V7 \\ & + mediumscale\ V16 \quad + s(medium\ scale\ V13) \\ & + s(broad\ scale\ V4) \quad + s(bottom\ depth) \\ & + s(year\ \ day) + s(surface\ temperature) \\ & \quad + s(surface\ salinity) + s(surface\ \alpha_t) \end{aligned} \tag{3}$$

The shape of the bottom depth smooth was similar for both abundance and presence/absence models (Supplementary material, Figures S7 and S8), indicating that sandeels are found in water shallower than 100 m only. In both models, the relationship with temperature peaks between 4 and 6°C. However, this partial relationship differed between models such that the abundance is predicted to increase again above 6°C. Additionally, the abundance model suggested that sandeel abundance is elevated above the mean at salinities $>$34.5, while no effect was found in the presence/absence model. Similarly the abundance of sandeel only was related to the density gradient, with abundance rising steadily between densities of $\sim$0.5 and 1.5 g m^{-3} nautical $mile^{-1}$, but with great uncertainty above this.

For the final set of explanatory variables (selected by the GAM analyses above), variation partitioning revealed differences in the relative importance of the explanatory groups (spatial structures from PCNM vs. environmental and temporal variables) between the models for abundance and presence/absence (Table 2). For the explained variation in abundance, the medium-scale spatial submodels were particularly important (8.6% pure component), whereas the environmental variables and the broad-scale submodels explained much less of the variation. Conversely, the environment contributed most greatly to the probability of occurrence, in terms of both pure and shared components. The contribution of the temporal variables was low in each model and particularly low in the occurrence model. In summary, there is clear spatial structure in the sandeel data at a range of scales, and this is linked in part to the environmental variables considered here (depth and at the surface: temperature, salinity, and density).

Table 2. Variation in the ICES survey data explained by group.

	Abundance model		Occurrence model	
	Shared (%)	**Pure (%)**	**Shared (%)**	**Pure (%)**
Medium-scale	10.8	8.6	13.5	3.5
Broad-scale	5.7	2.7	12.0	9.0
Environment	8.0	2.3	18.7	9.8
Temporal	5.8	3.7	3.8	2.3

“Environment” includes depth and both surface and bottom temperature, salinity, and density gradient. The “Temporal” group contains the year and the year day. “Medium-scale” contains spatial habitat submodels from PCNM with a range of $<$50 NM, and the “Broad-scale” those $>$50 NM. “Pure” is the contribution of each variable group alone and “Shared” is the contribution for each group of variables that interacts with other variable groups.

Temporal validation of CPR larval fish data

The CPR larval data correlate with independent surveys conducted in the Fair Isle channel (south of Shetland, S) and off Stonehaven (north of Wee Bankie, WB). The S time-series is variable, so a rank-based correlation was made between mean abundances from CPR data for the February–June period and the 0-group from the August trawl survey 1984–2005 (not 1987 or 1995): no correlation was evident with the average of all trawl stations (i.e. including the coastal areas not sampled by the CPR), but a significant intermediate correlation was evident for the most offshore ground ‘east Fair Isle’ (Spearman $R = 0.48$, $n = 20$, $p = 0.03$). For the Stonehaven time-series, previous investigations indicated a mix of sandeel species from April on, so the *A. marinus* time-series includes only samples of larvae from February–March of 2000–2005. This short time-series correlated strongly with the CPR larval data for the period February–March (Pearson's $R = 0.91$, $n = 6$, $p = 0.01$), but not the wider February–June period ($p > 0.10$).

Sandeel larval seasonality and phenological change

The period of peak abundance of Ammodytidae in CPR samples in the North Sea is between February and June, whereas in the Celtic Sea and Irish Sea the larval period is later in the year, March–July and April–August, respectively (Figure 2). Sampling in the DB and WB areas indicated sandeel larvae to be common in those areas: data were available throughout the time-series for the entire larval period, and no consistent phenological change (timing in larval emergence) is evident at the monthly scale: no significant linear trend was detected via simple regression in any region ($p > 0.05$) of the mean month of occurrence (see the Material and methods) on year.

Foodweb relationships

Phytoplankton indices (Phytoplankton colour index (PCI), total diatoms, and total dinoflagellates counts) did not significantly correlate with larval Ammodytidae in any region (all $p_{ACF} > 0.10$). For Appendicularia, all correlations with fish larvae abundance were positive, yet only the value for the highly variable FK area was significant ($p_{ACF} < 0.05$). For crustacean zooplankton, intermediate

Table 3. Pearson correlation coefficients between Ammodytidae larval abundance during February – June 1958 – 2005 and the top 12 ranked (1 is greatest biomass) crustacean (copepod and cladoceran) species and also the relative abundance of Appendicularia.

Zooplankton grouping and abundance rank	Copepod assemblage	Peak season	Individual dry weight (mg)	Size rank	Sampling correction factor	Dogger Banks	Wadden Sea	Fisher and Klondyke	Wee Bankie	South of Shetland
Total Crustacean biomass	Not applicable	–	–	–	–	*−0.29*	0.19	0.22	**−0.41**	0.11
1. *Temora longicornis*	Continental shelf	May – Sep	0.0126	6	18.35	−0.18	0.21	0.05	*−0.26*	0.09
2. *Acartia* spp.	Cold – temperate mixed water	May – Sep	0.0082	8	8.71	**−0.34**	0.00	*0.33*	**−0.42***	−0.01
3. *Paracalanus* and *pseudocalanus* spp.	Continental shelf	May – Sep	0.0042	11	13.93	−0.23	0.15	*0.27*	**−0.36**	−0.06
4. *Calanus finmarchicus*	Subarctic	Apr – Jun	0.3192	1	2.45	0.03	0.14	−0.04	0.16	0.11
5. *Oithona* spp.	Not defined	May – Sep	0.0022	12	45.42	−0.23	−0.16	−0.08	**−0.41**	−0.05
6. *Pseudocalanus elongatus* adults	Continental shelf	May – Sep	0.0109	7	11.55	−0.21	0.12	**0.30**	−0.15	−0.03
7. *Calanus* spp. (I – IV)	*Not defined*	Mar – Sep	0.0130	5	2.45	0.08	*0.28*	−0.15	−0.03	0.13
8. *Evadne* spp.	*Not applicable*	May – Sep	0.0055	10	18.16	**−0.33**	−0.07	0.04	**−0.31**	**0.34**
9. *Centropages typicus*	Temperate pseudo-oceanic	Aug – Oct	0.0360	4	1.70	−0.12	-0.07	**0.45***	−0.18	−0.02
10. *Corycaeus* spp.	Not defined	Sep – Nov	0.0062	9	26.80	0.02	0.22	0.22	−0.07	0.07
11. *Metridia lucens*	Cold – temperate mixed water	Sep – Jan	0.0623	3	20.00	0.06	0.03	**0.44***	0.13	−0.02
12. *Calanus helgolandicus*	Temperate pseudo-oceanic	Sep – Oct (Apr – May Dogger Bank)	0.1096	2	2.45	0.13	0.13	**0.49***	0.33	0.13
Appendicularia	*Not applicable*	Apr – Sep	–	–	-	0.10	0.15	**0.45**	0.22	*0.25*

Values in bold with an asterisk indicate $p_{ACF} < 0.01$, bold values without an asterisk $p_{ACF} < 0.05$, and values in italics $p_{ACF} < 0.1$. Individual dry weights (mg) and sampling correction factors (for the CPR relative to WP-2 plankton nets) are those reported by Pitois and Fox (2006) except for dry weight of *Evadne* spp. which was updated using Cladoceran-specific calculations (S. G. Pitois, unpublished). Copepod assemblages are those reported by Beaugrand *et al.* (2009).

negative relationships were found between Ammodytidae larvae in WB and the small but abundant copepods *Acartia* and *Para/Pseudocalanus* spp. and the cladoceran *Evadne* spp. (Table 3). Similarly, *Acartia* and *Evadne* spp. were negatively correlated with Ammodytidae abundance in DB. In contrast, *Evadne* spp. was positively correlated with Ammodytidae abundance in the south of Shetland region. No correlation was found between Ammodytidae larvae and any of the following: *Calanus* stages I–IV, *Calanus finmarchicus*, *Temora longicornis*, or *Corycaeus* spp. Only Ammodytidae abundance in FK was significantly correlated with *Calanus helgolandicus*. Significant positive correlations were also found for Ammodytidae in FK and each of the following: *Pseudocalanus elongatus* adults, *Centropages typicus*, and *Metridia lucens*. No significant correlation ($p_{\mathrm{ACF}} < 0.05$) was found for WS.

Larval production: climate indices

Climate variables [annual AMO, winter (December–March) NAO] alone were considered as indicators of spawning success since no correlation was evident between the larval indices and SSB (1983–2005) with a lag of 0, 1, or 2 years for the three stock assessment areas (DB, WS, and FK, Figure 1a). Following the autocorrelation correction, a single intermediate correlation was significant between the NAO and the abundance of Ammodytidae larvae in the WB area ($R = +\ 0.44$, $n = 56$, $p < 0.001$, d.f.$_{\mathrm{ACF}} = 22.83$, $p_{\mathrm{ACF}} = 0.029$): however, a marginal correlation with the NAO was evident in the FK area ($R = 0.32$, $n = 56$, $p = 0.016$, d.f.$_{\mathrm{ACF}} = 32.91$, $p_{\mathrm{ACF}} = 0.060$) and a marginal correlation with the annual AMO for the DB area ($R = 0.31$, $n = 56$, $p = 0.019$, d.f.$_{\mathrm{ACF}} = 32.14$, $p_{\mathrm{ACF}} = 0.070$).

Relationship of CPR larval data with recruitment data: correlative analyses

The time-series of larval Ammodytidae abundance in the North Sea during the period February–June from the CPR data is significantly correlated with the total recruitment index for the North Sea (recruitment for the three assessment areas where data were available, $R = 0.56$, $n = 23$, $p = 0.005$, d.f.$_{\mathrm{ACF}} = 12.06$, $p_{\mathrm{ACF}} = 0.036$). This correlation is due solely to the DB area where the vast majority of the commercial catch is taken ($R = 0.52$, $n = 23$, $p = 0.010$, d.f.$_{\mathrm{ACF}} = 19.44$, $p_{\mathrm{ACF}} = 0.014$). No separate correlation was found between larval abundance and the separate recruitment indices in WS or FK. A notable difference between the larval data and the recruitment data concerns the high recruitment event in 1996, which the CPR data suggest continued into the subsequent year, in terms of high larval abundance, in both the DB and WS areas. The CPR also picked up high larval abundance in 1996 in the S area, second only to the larval abundance during the earlier good recruitment year, 1985 (Figure 2).

No correlation was evident between the larval indices and either SSB or estimated catch (1955–2005) in DB, WS, or WB areas with and without a 1 year lag to the larval data in each region (Supplementary material, Figure S9), indicating that the larval data can act as indices of incoming recruitment, but not of SSB or catch.

Natural mortality of the larval stage: multiple regression analyses

A high abundance of larval Ammodytidae was a significant ($p < 0.05$) predictor of good recruitment in the DB area only, whereas an abundance of dinoflagellates was indicative of good recruitment in the FK area only (Table 4). In both the DB and WS areas, the previous year's recruitment was significant and negative, indicating a 2 year cycle between high recruitments. SSB was not selected in any area as a predictor of recruitment, whether or not larval abundance or the previous year's recruitment was included in the model. However, in each of the three stock assessment areas, low values of the AMO proved a significant predictor of good recruitments (Table 4).

Table 4. Summary statistics for final linear models of log-transformed recruitment indices of sandeel in three North Sea assessment areas.

	Estimate	s.e.	t	p
Dogger Banks				
Intercept	0.000	0.166	−6E-15	1.000
Lagged recruitment	−0.471	0.180	−2.613	0.0171
Larvae	0.448	0.170	2.637	0.0162
AMO	−0.399	0.180	−2.211	0.0395
$R^2 = 0.46$, $F = 5.3$ on 3 and 19 d.f., $p = 0.008$				
Wadden Sea				
Intercept	0.000	0.152	0.000	1
Lagged recruitment	−0.772	0.199	−3.888	0.0009
AMO	−0.869	0.199	−4.378	0.0003
$R^2 = 0.53$, $F = 10.7$ on 2 and 20 d.f., $p < 0.001$				
Fisher and Klondyke				
Intercept	0.000	0.167	0.000	1
Dinoflagellates	0.383	0.180	2.131	0.0457
AMO	−0.413	0.180	−2.299	0.0324
$R^2 = 0.41$, $F = 7.1$ on 2 and 20 d.f., $p = 0.\ 005$				

Discussion

Utility of the CPR for sandeel larvae: spatial and temporal validation

The comparison of relative abundances m^{-3}, as calculated from CPR (1950–2005) and ICES ichthyoplankton survey data (2004 and 2009), shows that the two main concerns when sampling fish larvae with a CPR, namely the small aperture and the constant and relatively shallow depth of the sampling device, seemingly result in the underestimation of the abundance of larvae in absolute numbers. Yet, because the CPR and ICES surveys show significant spatial correlation in abundance, the CPR is clearly useful in capturing the spatial patterns and relative abundances between areas. The spatial correlation is weak (Table 1); however, this is not unsurprising given the nature of the permutation test, the partial temporal overlap in the datasets, and the great difference in sampling devices. The CPR survey indicates a greater contrast in abundance between WB and DB areas than the ICES survey (Figure 1), which is attributable to the limited number of years in which the ICES survey has been conducted. The annual spatial plots from CPR data indicate that this contrast between WB and DB areas is highly variable and, in the most recent years, decreased from a high contrast in 2002 to a low contrast in 2005 (Supplementary material, Figure S1) similar to that seen in the annual plots from ICES survey data (Supplementary material, Figure S3).

The temporal correlations between the CPR larval abundance data and those from plankton sampling off the eastern Scottish coast (Stonehaven, strong correlation) and from trawl 0-group surveys at the east Fair Isle ground (intermediate correlation) indicate that temporally the sandeel relative abundance data from the CPR are robust. The intermediate correlation with recruitment for the DB area indicates that the larval data are particularly reliable for that area. Additionally, the sandeel biomass modelled by Frederiksen *et al.* (2006) shows a similar trend to the WB larval abundances presented here. The concentrations of sandeel larvae around the Northern Isles and off the eastern UK are also consistent with past plankton surveys (Proctor *et al.*, 1998; Munk *et al.*, 2002).

Several studies (including Pitois and Fox, 2006) have compared the CPR with samplers with larger apertures and similarly found large differences in sampling efficiency. Richardson *et al.* (2004) attributed these large differences to active avoidance and emphasized that this is species specific, which is a problem for describing a plankton community based on CPR, but might be immaterial for a single species. The shallow sampling depth is likely to be problematic when sampling for larvae that exhibit diurnal vertical migrations, leading to increased variability in monthly abundance estimates. For example, sandeel larvae have been found to be most abundant at a depth of 3–11 m during the day and dispersed throughout the water column during the night (Ryland, 1964). Both concerns when sampling with a CPR may be partially alleviated by the much longer deployment time (hours), compared with the 15 min in the plankton surveys, and more frequent deployments with multiple samples per month by both day and night in many areas of the North Sea. As the CPR samples continuously, it can still pick up larvae often enough to give an accurate representation of relative abundance between stock units and between years.

Environmental influences on sandeel larval distribution

Although the spatial pattern in sandeel larvae distribution is consistent between years, the abundance varies, such that ‘year’ is selected by models of abundance but not of occurrence [Equation (3); Supplementary material, Figure S3]. Sandeels hatch between February and May, and the spline (Supplementary material, Figure S7) shows the expected increase in larval occurrence later in that seasonal period. However, this is not mirrored in the abundance, which peaks at the extremes of the sampling period, around day 40 and 80 (Supplementary material, Figure S8). This may indicate two different peaks in hatching, possibly linked to the differences seen between seasonality across assessment regions in CPR data, with earlier hatching in the south and later in the north (Figure 2).

The shape of the spline smooths of abundance (Supplementary material, Figure S8) in relation to the physical variables suggest that sandeel larvae would be most abundant in shallow water, at temperatures >7°C, salinities >34, and density gradients in the high range. The relationship between larval abundance and temperature is interesting (see also Pitois *et al.*, 2012), because the relationship is inverse between larval survival and temperature (Table 4; Arnott and Ruxton, 2002): taken together, these relationships indicate that an optimal temperature range may exist that would balance out the processes leading to production and mortality of larvae. The relationships to salinity and density gradient (Supplementary material, Figures S4 and S8) resemble the findings of Munk *et al.* (2002), who found sandeel larvae related primarily to fronts, where the fresher coastal water interfaces with marine water. As indicated in earlier studies of demersal fish (Loots *et al.*, 2010, 2011; Höffle *et al.*, 2012) and in a general context (Planque *et al.*, 2011), the environmental variables (depth and surface temperature in particular) are more important relatively in structuring the spatial distribution of occurrence of sandeel larvae than of abundance (Table 2). The importance of medium-scale (<50 nautical miles) submodels for abundance indicates a consistent distribution of high and low abundances during the recent ICES surveys.

Foodweb relationships

Since no relationship was found between larval abundance and phytoplankton indices, there is no evidence that high productivity directly implies a high hatching/survival rate of sandeels or that sandeel may consume large amounts of phytoplankton (Table 3). For total crustacean zooplankton biomass, a single negative relationship with larval abundance in WB was significant, suggesting that some top–down control may be exerted by sandeel in this area of peak abundance. If a high abundance of a predator may potentially deplete its prey, the negative relationships between sandeel abundance and the particularly abundant copepod *Acartia* and small cladoceran *Evadne* in both DB and WB could suggest that these species are important prey items, or alternatively proxies for other foodweb processes. Although *Acartia* begin spawning in February (Halsband and Hirche, 2001), both *Acartia* and *Evadne* abundance peaks during summer, and they may be consumed by post-metamorphosis sandeels.

Larval production and pre-recruit natural mortality

A high productivity of plankton may increase sandeel larval survival by providing food for their prey through increased availability of primary production of phytoplankton or secondary production of zooplankton (Eliasen *et al.*, 2011). Frederiksen *et al.* (2006) found that diatom abundance and copepod biomass during the months January–April were significant predictors of sandeel biomass (1973–2002, as modelled from CPR larval abundances from data collected 54 − 59°N and 2°W − 2°E and assumed growth rates).

The finding here, of a positive intermediate correlation between the NAO index and Ammodytidae larval abundance since 1950 in the WB and FK regions, but no link to SSB (since 1983 only), indicates that NAO-related influences may alter the production and/or early mortality of sandeels. Processes related to the NAO have been suggested to alter the inflow of oceanic water and nutrients into the northern North Sea, and alter the abundance of plankton, including *Calanus* species, and of a range of fish and seabird predators (Drinkwater *et al.*, 2003). A positive winter NAO would indicate warm conditions during April–June in the northern North Sea (Lynam *et al.*, 2010) and, in agreement with the GAM models here (i.e. temperature spline in Supplementary material, Figure S8), would suggest a high production of larvae.

The multiple regression (Table 4) characterizing natural mortality of the larval stage in the DB area indicates that recruitment may be enhanced should low AMO (cold) conditions prevail, yet no relationship was found with any plankton index for this area. Similarly, good recruitments are expected in the WS and FK stock units during low AMO regardless of the larval abundance, indicating that natural mortality processes are more important than the production of larvae in determining the recruitment level. The negative parameter estimate for the lagged recruitment term in the DB and WS models, combined with the lack of any relationship to SSB, invokes a number of hypotheses for the poor recruitment of sandeels following a high recruitment year, including: (i) a reduced energy allocation to reproduction by spawning fish in the year subsequent to a large spawning event and thus poor condition of eggs and thus larvae; or (ii) cannibalism of pre-recruits by 1-year-old fish that survived the previous year's spawning. In the DB area, the CPR larval data are indicative of recruitment; if this term fully captures the relative number of pre-recruits, then the lagged recruitment term would relate to the natural mortality experienced and may indicate that cannibalism is a more likely explanation.

While we are currently in a high AMO phase, there is the potential (although uncertain) for a switch to a low phase in the coming decade (Cannaby and Hűsrevoğlu, 2009). However, any increase in the stock should the AMO enter a low phase could potentially be offset by greater cannibalism of larvae by age 1 fish in the southern North Sea (DB and WS) and potentially reduce the suitability of the environmental conditions for larvae at the spawning habitat (see above and Supplementary material, Figure S8). Currently, the stock assessments assume time-invariant natural mortality common to all areas. Yet, the results here (Table 4) indicate that time invariance is not likely given the relationship with the AMO cycle, and the use of a common value is also probably incorrect given the potential area-specific cannibalism found.

Arnott and Ruxton's (2002) analysis of North Sea wide stock assessment data identified climate and environmental effects on sandeel recruitment, and found a significant negative relationship with sea temperature (for the egg and larval period in an area approximating DB and more weakly in an area comparable with FK, in agreement with this study) and a positive relationship with feeding conditions (i.e. *Calanus* stage V and VI abundance). An updated analysis by van Deurs *et al.* (2009) found that sandeel recruitment in the North Sea was positively correlated to the abundance of one copepod species in February: *C. finmarchicus* (stages V and VI). van Deurs *et al.* (2009) also found no relationship between sandeel recruitment and the NAO index. So, while the NAO may be important to larval production in the northern North Sea (WB), the overriding climate influence on survival (particularly in the central and southern North Sea) is through temperature and most probably the effect is felt directly on the metabolism and growth of the larvae. Unfortunately, we cannot say that this temperature effect on survival holds for the WB due to the lack of stock assessment information. Logically, good feeding conditions are a likely factor influencing survival of larvae, but the data do not show this. Either such a signal is obscured by the climate influence or, alternatively, perhaps sandeel larvae very rarely have a short supply of prey.

CPR larval data and its potential to inform stock assessment

Given the spatial and temporal validation of the CPR data by a suite of independent surveys, the relationship between the recruitment data for the DB area and the larval abundances in the area indicate that the data are indicative of recruitments for the well-sampled areas such as the DB and potentially the WB. However, an examination of the performance of such pre-recruit indices within the stock assessment models is required to determine their ultimate value to the assessment. Sandeel stocks in the North Sea are highly dependent on the incoming year classes, which are difficult to forecast. Advice for the commercially important DB area now incorporates data from real-time monitoring of the fishery during April of the year in which the quota is to be set (ICES, 2012). However, ICES (2012) note that the procedure could result in bias as fishing effort is probably concentrated on grounds with the highest CPUE (catch per unit of effort) such that changes in stock abundance may not be as apparent as in fishery-independent survey indices. Therefore, the assessment model and its short-term forecasts of year-class strength should be improved through the inclusion of additional tuning series, such as the early indices of the year-class strength that the CPR can supply.

Unfortunately, the CPR data are not able to provide pre-recruit indices of relative abundance in every stock assessment area in the North Sea. The poor spatial coverage in the S area (CPR sampling limited to the south of Shetland, Figure 1a) coupled with the strong advective processes operating in the region indicate that the CPR data are too limited to provide an early recruitment index for the whole Shetland stock assessment area. Neither of the years with high larval abundance in CPR samples in the south of Shetland area (1996–1997) resulted in high recruitment for the entire Shetland area (ICES, 2010a), potentially indicating the heavy influence of immigration of larvae from the large Orkney ground to the south of Shetland area (Wright, 1996). The lack of correlation between CPR larvae abundance and sandeel recruitment indices for the WS and FK areas indicate that either the CPR data or the indices of recruitment are not robust for these areas or the processes determining larval survival are so great that they obscure any relationship.

Placing sandeel stock assessments in a historical context

The history of deployments in the North Sea by CPR allows assessment data to be set in context: the good recruitments of 1983, 1985, and 1996/1997 in the DB region were probably the greatest events since the high larval abundances recorded in 1962 and the early 1950s. The time-series of larval abundance during the period February–June for the WB area indicates that, other than intermittent peaks in larval abundance (1953, 1961, 1970, and 1978), recruitment was probably low prior to a gradual rise during the 1980s. A similar pattern is shown by the WB larval time-series based on February–March data only (with the exception of low abundances in 1961 and 1970), which is the period in which *A. marinus* dominates the sandeel family in coastal waters (Heath *et al.*, 2012). During the 1990s, the February–March and February–June time-series show some difference. The February–March WB data clearly show the period 1995–2000 to be low in *A. marinus* larval abundance, and a high value in 2001 following the closure of the coastal grounds to the fishery in 2000. In contrast, the February–June WB data display an additional peak in 1999 and average abundance during 2001, with a peak in 2003. Fishery CPUE data show a peak in 2001 and gradually fall thereafter, in agreement with the larval data for February–March (Heath *et al.*, 2012). Research surveys in the WB area during May/June, using hydroacoustic and pelagic trawl surveys, indicate that local recruitment during the period 2000–2009 (no 2004 data) was generally higher each year (with a peak in 2002) than during the lows of 1997–1999 (Heath *et al.*, 2012). Similarly, the CPR February–March data show high larval abundance between 2001 and 2003, with poorer years in 2004 and 2005. The spawning stock continued to decrease throughout the 2000s, indicating elevated mortality of the new recruits (Heath *et al.*, 2012). Given that the CPR also shows increased abundance of larvae since 1995 in April–June relative to February–March, the large landings of sandeels during the open fishery of the 1990s might have reduced the dominance of the *A. marinus* population relative to the later spawning *H. lanceolatus*, a hypothesis worthy of further study.

In conclusion, the CPR data for sandeel larvae provide a spatially and temporally robust signal of relative abundance of pre-recruits and may inform stock assessment, specifically short-term forecasts, for North Sea populations. While global climate change may lead to increased mortality of larvae, this may be offset by an increase in the production of larvae.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of the paper and contains additional information on the computational methods of analysis and nine figures.

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