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Original Article

Integrating the scale of population processes into fisheries management, as illustrated in the sandeel, *Ammodytes marinus*

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Aggregations of site-attached populations can show marked differences in density due to variation in local productivity and mortality processes. Matching management actions to the scale of biological processes is therefore important for sustainable fisheries management. This study examined the adequacy and appropriate scale of a spatially explicit management regime for sandeel, *Ammodytes marinus*, in the North Sea. Information from biophysical model simulations of larval transport and otolith chemistry was used to estimate the scale of mixing among aggregations. Together, these approaches indicated that there was negligible exchange of pre-settled sandeel among aggregations >200 km apart. Additionally, a re-analysis of tag-recapture experiments and distribution data indicated that the dispersive range decreased further after settlement. Significant differences in length at maturity and year-class strength not only reflect the limited mixing across the North Sea, but also point to regional differences in productivity and thereby vulnerability to fishing pressure. We conclude that the current management regime comprised of multiple assessment areas enable these differences to be considered in advice on annual fishing quotas.

Keywords: *Ammodytes*, biophysical model, maturity, otolith chemistry, population structure, tagging.

Introduction

While fish stock units are often based on a compromise between biological structure, data availability, and management requirements, they are usually assumed to reflect a discrete group of fish in a particular geographical area, which shows little mixing with adjacent groups, and that have the same vital rates (Gulland, 1983; Stephenson, 2002). However, several studies have demonstrated a mismatch between the scale of populations and fishery management units (Stephenson, 2002; Reiss *et al.*, 2009; Barth *et al.*, 2017). Management that ignores population structure may lead to overfishing of less productive populations and under-fishing of more productive populations within a managed unit (Jardim *et al.*, 2018) and ultimately the progressive erosion of local spawning groups (Smedbol and Stephenson, 2001). However, redrawing management boundaries to align with population units requires a detailed understanding of mixing scale and life-history variation (Cadrin *et al.*, 2014; Kerr *et al.*, 2017).

The challenges posed when attempting to include population structure in management advice are clearly illustrated by historical changes in the management of sandeels (primarily *Ammodytes marinus*) in the North Sea. Sandeels not only support a large industrial fishery but are also an important prey to fish, seabirds, and marine mammals (Daan *et al.*, 1990; Furness, 2008; Engelhard *et al.*, 2014). Before 1995, the North Sea was divided into two large stocks (northern and southern) and two smaller stocks (Shetland and the Skagerrak–Kattegat area). These stock divisions were based on differences in growth rate reported by an ICES working group on Norway pout (*Trisopterus esmarkii*) and sandeels (Anon., 1977). However, subsequent analyses of the spatial and temporal variability in growth rate and uncertainty about the scale of movements led ICES to amalgamate the northern and southern assessment areas into a single North Sea stock (ICES, 1995a). Further concern about management scale arose following an expansion of the fishery off the north east UK coast in the 1990s, as this was associated with a decline in breeding success of sandeel-reliant seabirds at adjacent colonies (Rindorf *et al.*, 2000; Daunt *et al.*, 2008). A precautionary fishing closure was established in 2000, within a region of importance to nesting seabirds that appeared to reflect a reproductively isolated aggregation of sandeels (Proctor *et al.*, 1998; Wright *et al.*, 1998). This evidence of limited scale of mixing across the North Sea, together with a large retrospective bias in assessments following a historic low in the recruitment in 2002, led ICES to once again review stock structure in 2010 (ICES, 2010). Seven new stocks were proposed, with boundaries based on <5% average annual exchange of larvae as predicted from a biophysical model (Christensen *et al.*, 2008a, b). The move to seven stocks was intended to account for regional differences in productivity and catch rates, and to avoid local depletion (ICES, 2010). When ICES repeated the exercise in 2016, differences in management among the stock areas outlined in 2010 had led to large spatial differences in fishing pressure, as well as biological and commercial data collection. This led ICES to further change some stock definitions and, currently, analytical assessments are provided for the four main fished stocks (SA1r, 2r, 3r, 4; Figure 1).

In this study, we examined how ontogenetic dispersal shapes population structure of North Sea sandeel and investigated whether the current management areas encompass the main dispersal barriers and differences in productivity. Following the synthesis of stock identification methods proposed by Cadrin *et al.* (2014), this study integrated information on mixing scale and movements of *A. marinus*. Demographic and maturity data were then used to consider the spatial variation in life history traits. Model simulations were used to estimate the time to recover after depletion for different population areas. Results were compared with the stock structure used in management since 2016, where multiple assessment areas are intended to account for differences in productivity and population dynamics.

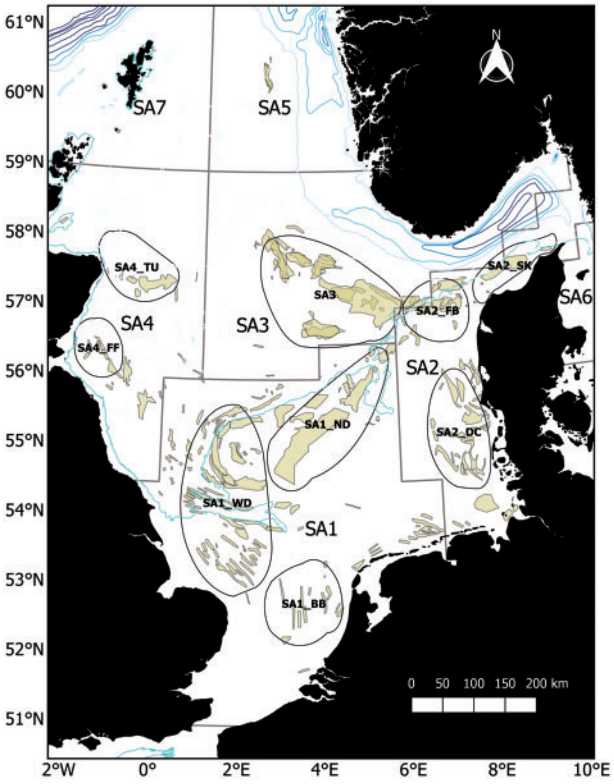

Figure 1. Chart showing sample areas for maturity at length analysis and the fishing grounds they cover within the four assessment areas. Labels refer to stock area and banks: TU—Turbot; FF—Firth of Forth; BB—Browns; WD—West Dogger; ND—North Dogger; DC—Danish coast; FB—Fisher.

Material and methods

Larval transport modelling

Transport indices were computed using the individual-based modelling framework IBMlib (Christensen *et al.*, 2018). Biological dynamics of sandeel larvae were modelled according to Christensen *et al.* (2008a), using March 20 as larval hatch day, settlement length at 40 mm and growth as described by model 3 in Table 2. To assess inter-annual variability in transport, indices were computed for years 2004–2013 and averaged over this period. The hydrographic dataset applied for simulating larval drift 2004–2013 was the Baltic-North Sea ocean-ice model HBM (HIROMB-BOOS Model) in the operational setup of the Danish Meteorological Institute. The HBM setup for the present hydrographic dataset has a horizontal grid spacing of six nautical miles (nm) in the North Sea and Baltic Sea, and 1 nm in the inner Danish waters. The model has up to 50 vertical levels in the North Sea and Baltic Sea, and 52 vertical levels in the inner Danish waters with a top layer thickness of 2 m. The HBM setup performance has been validated on several occasions, e.g. She *et al.* (2007). Sandeel fishing grounds (Jensen *et al.*, 2011) were used to represent spawn locations. To have a simple representation of transport indices, sandeel fishing grounds were projected onto a 10 × 10 km grid cell (corresponding to the resolution of the hydrodynamic model), and transport indices were computed as the probability of successful transport from one cell to another by releasing larvae in each cell at hatch time, following all larvae by drift simulation, and recording where they ended at settlement time, as outlined in Christensen *et al.* (2008a, b). Since 596 grid cells are occupied by sandeel grounds, the transport indices constitute a 596 × 596 matrix, giving the probability of transport between all 355 216 (directional) pairs of 10 km grid cells.

Verification of larval origins

As there is significant regional variation in otolith edge chemistry, representing the juvenile chemical signature, across the North Sea, the magnitude of differences in otolith elemental composition accreted during the early larval phase (near core chemistry) was examined in relation to predicted distance between juvenile origins (Wright *et al.*, 2018). The IBMlib framework (Christensen *et al.*, 2018), with the same biological and physical setup as described above, was used to hind cast the origins of 0-group juvenile sandeel sampled in 2011, whose otolith elemental composition was known based on laser ablation inductively coupled mass spectrometry (Wright *et al.*, 2018). Ground specific estimates of average hatch date (calendar day 63–83), and settlement date, based on daily increment counts (Wright, 1993), were used as input for the hind cast model. It was assumed that age 0 sandeel overwintered in their settlement area, and so the period between hatch date and settlement could be used to infer the onset and duration (54–76 days) of the larval phase. For each ground, 1000 realizations of the model were summarized into a geographic mean and range of potential origins. Advection length scale L and diffusion length scale K was calculated using a Gaussian advection–diffusion kernel.

Spatial similarity in otolith elemental signatures from seven grounds in the Wright *et al.* (2018) study were used to first test the inferred relationship between chemistry and distribution, by comparing Random Forest classification errors in assignment to a ground, based on near edge chemistry, with distance among grounds. A dissimilarity matrix of juvenile chemical signature was calculated as the average misclassification between pairs of sites obtained from Random Forest classification of near edge signatures. Then, the correlation between this matrix and a matrix of geographic distances between sampling sites was estimated using a Mantel test. The dissimilarity in the chemical signature of the near core region of the otolith, was obtained from the unsupervised Random Forest approach as described in Wright *et al.* (2018). In this approach, the frequency at which two individuals end up in the same terminal node of the classification trees reflects the dissimilarity between them (close to 0 for individuals frequently classified together, or close to one for individuals almost never ending in the same terminal node). In a similar way, correlation between the dissimilarity matrix of larval chemical signatures and a matrix of distances between geographic mean larval origins was estimated using a Mantel test.

As the distance between hatching and eventual settlement may be related to the water mass that the fish inhabits, the average difference in the otolith elemental ratios from larval to settlement was compared for two of the important discriminatory elements that are expected to reflect water chemistry (Thomas *et al.*, 2017): manganese (Mn) and rubidium (Rb). The average difference in elemental ratios (delta-Mn and delta-Rb) was compared with the average displacement distance from the IBMlib model using linear regression for the seven grounds.

Post-settled distribution and movements

The distribution of fished grounds from Jensen *et al.* (2011) was used as a proxy of settled *A. marinus* distribution. The catch per hour of age 0 in relation to distance from the fishing grounds was examined using data from the ICES International 0-group Gadoid Survey (I0GS) for the North Sea between 54 and 58°N. This survey caught sandeel >30 mm total length (TL) in the water column using a pelagic trawl (PT154) with a 15 mm cod end deployed in a stepped tow, and was conducted in June–July. Similarly, counts and catch per hour of *A. marinus* were available from the four quarterly North Sea International Bottom Trawl Surveys (NS-IBTS) conducted between 1991 and 1997. Data were downloaded from DATRAS database (DAtabase of TRAwl Surveys; www.ices.dk). While the trawl used in the bottom trawl survey (Grande Ouverture Verticale trawl with a 20 mm cod end liner) has too coarse a mesh to provide reliable quantitative estimates of abundance, sandeels are frequently caught by this gear. Distances between hauls and fished grounds were calculated in QGIS using the DDJOIN plugin. The numbers of age 0 and 1+ were identified from all survey hauls based on length modal analysis with age 1+ typically being > 100 mm TL. Differences in cumulative catch rate between age 0 and older sandeels in quarter 2 and among 1+ in the four seasons relative to distance to ground were compared using a Kolmogorov–Smirnov test.

The scale of post-settled sandeel movement was considered from the results of two large-scale tag-recapture experiments undertaken in 1958, 1959, 1963, and 1968 in the southern and central North Sea (Bertelsen and Popp Madsen, 1958; K. Popp Madsen, unpublished data) and in 1980–1985 around the Shetland Isles (Kunzlik *et al.*, 1986; Gauld, 1990). In both sets of experiments, sandeels were captured by bottom trawling, tagged internally by the insertion of a non-corrosive steel tag into the abdominal cavity and released either close to the recapture site or transplanted at distances of up to 10.3 km or 128 km away from known fished grounds, in the North Sea and Shetland experiments, respectively. All but one of the transplanted sites occurred close to sandy areas and/or other known aggregations identified from the NS-IBTS analysis. The tag size was reduced over time, being 20 × 4.5 × 1 mm in 1958 (Bertelsen and Popp Madsen, 1958), 15 × 3 × 0.5 mm in later North Sea tags releases and 7 × 4 × 0.4 mm and 0.5 × 3 × 0.7 mm in Shetland releases (Gauld, 1990). Recent evidence based on larger pit tags suggests that these tags should not have adversely affected swimming ability (Jørgensen *et al.*, 2017). Because of the limitations of body cavity and short life span, tagging was limited to length a range of 91-179 mm (1+ age group). Releases involved groups of 50–1000 sandeels per ground, with tags coded by ground of release and year. Tags were recovered at fish reduction plants, which incorporated magnets in the processing line. Proportion recovery efficiencies (E) were 0.77–0.90 and 0.88 at the Esbjerg and Shetland plants, respectively, based on known quantities of dead sandeels containing tags being introduced into the storage hoppers. These estimates of recovery efficiency were used to raise actual recaptures to predicted recapture rate.

An estimate of return rate ($R_{i,\,j}$) was calculated for fish tagged in year i and recaptured in year j using a modification of the site fidelity relationship of Zemeckis *et al.* (2014) to account for the annual mortality of later recaptures, as:

$$R_{i,j} = \frac{returned.nb_{i,j}}{released.nb_i \times (1 - M - F - T) - \sum_i^{j-1} returned.nb}$$

where the number of fish tagged in year i and returned in year j is:

$$returned.nb_{i,j} = recaptured_{i,j} \times \frac{1}{E}$$

With $recaptured.nb_{i,j}$ the number of tags recovered in year j.

Annual natural mortality, M, was set at 0.63 based on an average for age 2 (ICES, 2017) and fishing mortality, F, was set at 0.4, consistent with estimates for Shetland in the early 1980s. Tagging-induced mortality, T, was set as 0.02, based on tank experiments (Kunzlik *et al.*, 1986). The term $\sum returned.nb$ is used to account for fish recaptured in the years between tagging (year i) and recapture (year j) and is equal to 0 if fish are recaptured on the year of tagging (year i). R was then compared with distance to nearest fishing ground from release point to estimate the minimum distance travelled. Location information on fished grounds came directly from the experiments or from Jensen *et al.* (2011). A binomial generalized additive model with a logit link was used to model the relationship between proportion R and distance weighted by the number of tags released. The two experiments were treated as a factor and the number of knots in the smooth of distance constrained to 3 to avoid overfitting.

Regional variation in demography and stock trends

Spatial variation in sandeel maturity at length was examined from samples collected over a range of banks in the winter during research dredge surveys in 2017 (Figure 1). Sub-samples of catches were measured for TL (cm) and age estimated following the protocol of ICES (1995b). Proportion mature was estimated using a logistic regression model (McCullagh and Nelder, 1983), which included length as a continuous variable and region as a categorical variable. Variable age was removed from the model due to complete separation precluding a maximum likelihood estimate for the regression parameters associated with this variable. Minimum adequate models were derived by stepwise deletion of all non-significant terms and an additional measure of model fit, based on a pseudo-coefficient of determination (Swartzman *et al.*, 1995). Post-hoc *z*-tests with corrections for multiple pairwise comparisons were used to estimate the significance of pairwise differences in maturity at length among regions.

Regional variation in age 1 abundance

Commercial landings and effort data by ICES rectangle were used to examine coherence in recruitment in relation to distance. Mantel tests were used to estimate the correlation between the matrix of pairwise correlation-based distances in catch per unit effort (CPUE) in numbers of age 1 fish per day of fishing of a 200 GRT vessel (ICES, 2017) (where pairwise distance between two ICES rectangles = 1 – |correlation in CPUE age 1|) and pair-wise geographic distances between the centre of ICES rectangles with at least 5 years of data. Clustering was then undertaken on correlation-based distances between ICES rectangles using partitioning around medoid (PAM) and hierarchical clustering with different agglomeration methods (Ward's minimum variance method, single, complete or average linkage, and the centroid method). Clustering was done with the base and cluster 2.0.7-1 packages in R. The number of clusters was set at 4 to correspond with the current number of sandeel assessment areas.

Simulations of recovery time after local depletion

The time to recovery after local depletion events was simulated for three locations (SA1r: Dogger; SA2r: Horns Reef and Fisher Bank) using the spatially explicit sandeel population model of Christensen *et al.* (2008b). In the model, fish larvae were produced by a spawning stock biomass distributed homogenously within sandeel fishing grounds (see Figure 1). The larvae drift trajectories followed oceanographic transport via a coupling to the larvae transport model described in a previous section and in Christensen *et al.* (2008a, b). Settlement occurred at a predefined threshold size with growth rates modelled as a function of temperature. The oceanographic regime in a given simulation year was randomly selected among an assembly of oceanographic regimes in the period from 2004 to 2013. After settlement fish were either sedentary or moved around randomly within habitat patches at rates of 30 km per year (see Jensen *et al.*, 2011). In each simulation, the local sandeel biomass was removed ("fished down to zero") at time 0 within circles of diameter 50, 150, or 300 km, and repopulation was tracked in the model for a period of 11 years.

Results

Pre-settled dispersal

Figure 2 shows a scatterplot of transport probability between sandeel grounds, aggregated into 10 km grid cell vs. the distance. The hydrodynamic transport probability is not a clear function of distance, but has a significant spatial variability, so that larvae originating from different banks have a significantly different dispersal pattern. The average drift distance was 67 km. The maximum distance between North Sea fishing grounds was 700 km. A quantile averaging of data, with bins of 10 km, shows that on average transport becomes negligible for distances beyond ~200 km. Fitting the spherical average of the Gaussian advection–diffusion kernel to the quantile regression in Figure 2 (for details, see Supplement 1) confirms that the peak (most likely) transport distance is $K \sim 75$ km but L is difficult to resolve statistically, when $L < K$. Supplement 1 shows a nonparametric bivariate kernel density estimate of the scatter data in Figure 2; the distribution has a clear pivot point around 50 km beyond which the spatial variation causes the distribution to flatten. Since transport events at distances > 200 km are very rare, the distribution consequently condenses for small values of transport probability.

When the origins of 0-groups sampled in 2011 for microchemistry analyses were hind casted using the same transport model as above, there was substantial overlap in the distribution of predicted origin for some sample locations within assessment areas, but little to no overlap among assessment areas (Figure 3). Distance between pairs of sampling sites was significantly positively related to the pairwise Random Forest discriminant scores of edge chemistry, especially >300 km (Figure 4a; Mantel $r = 0.71$; $p = 0.001$) showing overlap in the signature of spatially close sampling sites. Average dissimilarity in natal elemental signatures significantly increased with geographic distance between the geographic mean larval origin of the 8 grounds, especially > 300 km (Figure 4b; Mantel $r = 0.62$; $p = 0.01$). Delta Mn was negatively related to the estimated displacement distance ($R^2 = 0.77$, $F_{1,\ 6} = 20.62$, $p = 0.004$, Figure 5), whereas a similar

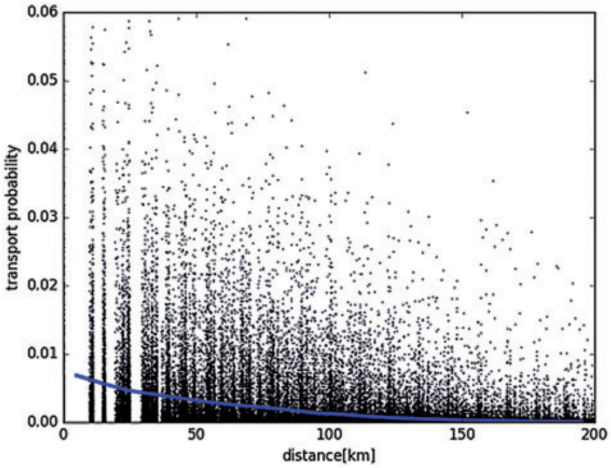

Figure 2. Relation between the probability of larval transport and distance for *A. marinus*. Each point represents a pair of grounds with a known distance sorted in 10 km bins. The blue line is the quantile regression of data, aggregated in 10 km bins. Note that the pixellation for small distances is due to aggregation of sandeel grounds into 10 km grid cells.

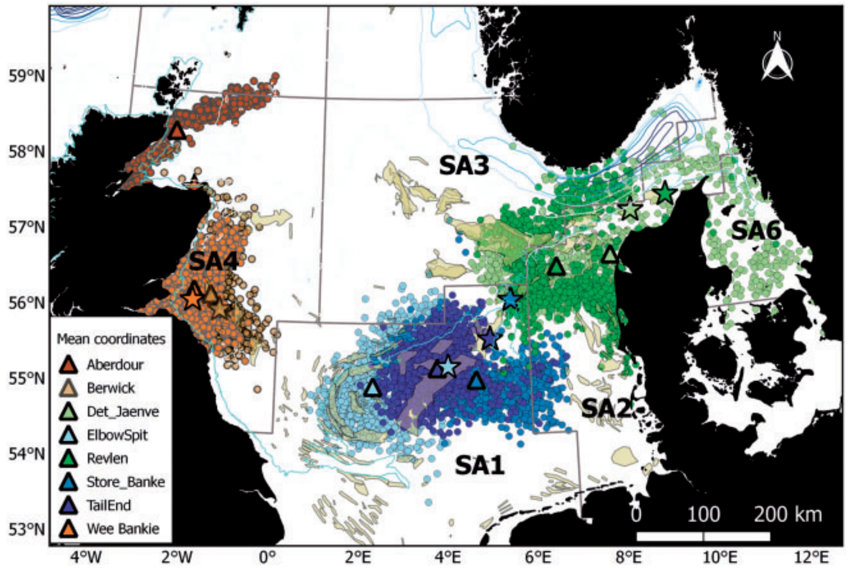

Figure 3. Chart showing distributions of possible larval origins (dots) based on model hind casts of otoliths collected in 2011. Stars indicate capture location and triangles indicate geographic means for each cluster of hind casts. Fishing grounds are also shown.

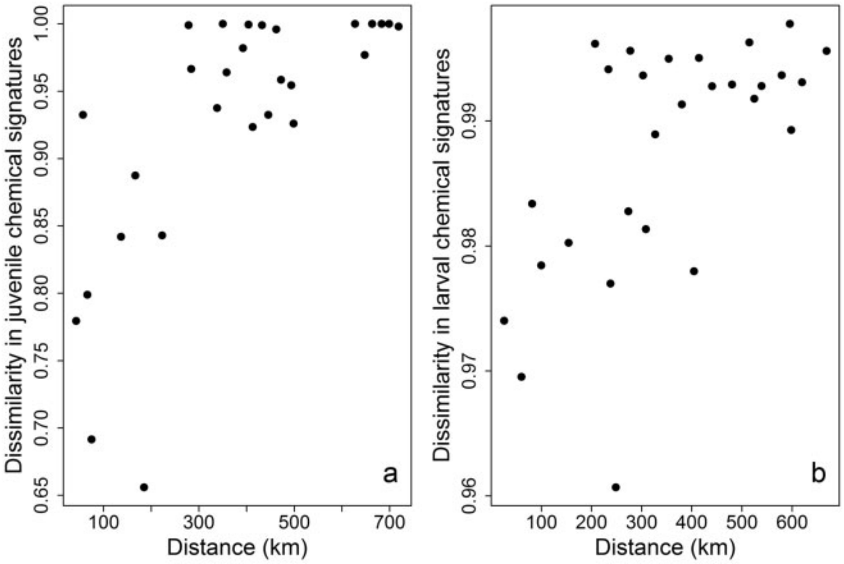

Figure 4. (a) Relationship between the dissimilarity in juvenile chemical signature (otolith edge) and distance between pairs of sampling sites. (b) Relationship between the dissimilarity in larval chemical signature (otolith core) and distance between pairs of larval origin sites.

relationship for delta Rb was nearly significant ($R^2 = 0.49$, $F_{1,6} = 5.88$, $p = 0.051$).

Distribution of 0-group and 1+ in relation to fished grounds

The proportion cumulative catch of 0-group caught in June/July from the I0GS and 1+ sandeels caught each quarter in the NS-IBTS by distance to fished grounds is given in Figure 6. The age 0 caught in June/July were more widely dispersed with only 38% caught < 10 km of grounds. In contrast, 85–100% of sandeels in the bottom trawl surveys were caught <10 km of grounds. The cumulative proportion caught differed with season, with significantly higher numbers in quarter 4 compared with quarters 2 and 3 (KS test; $p = 0.02$) but not compared with quarter 1 ($p = 0.19$).

Post-settled movement

The negative relationship between proportion of fish recaptured and release distance from grounds is similar between the two studied regions (Figure 7) though the significant difference in intercept means that the two sources were not strictly comparable. Corrected proportion returning (R) from releases on grounds ranged from 0.14 to 0.64. However, corrected proportion recaptures R were 0.05 and 0.18 at 10 km for the North Sea and Shetland, respectively. This declined to 0.03 at 30 km for

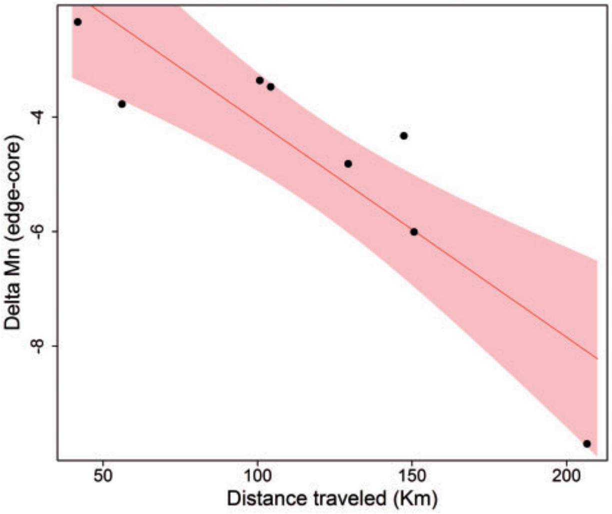

Figure 5. Relationship between delta Mn (change in Mn between core and edge) and average displacement distance as estimated by the particle tracking model.

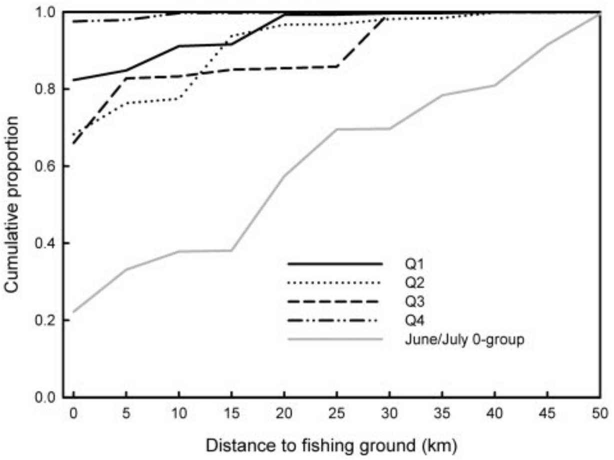

Figure 6. Proportion cumulative catch of 0-group caught in June/July from International 0-group gadoid surveys and 1+ sandeels caught each quarter in NS-IBTS in relation to distance from fishing grounds.

Shetland. There was a single high outlier due to a release 30 km east of the Shetland mainland. Although the time to recapture of transplanted releases tended to increase with displacement distance with an average of 38% recaptures of transplanted sandeels in the first year of the North Sea experiments while Shetland recaptures only began the year after release recaptures continued for 3 years in both regions and from releases on grounds.

Maturity at length

Maturity ogives fitted by logistic regression indicated significant effects of length ($\chi^2(1) = 5609.4$, $p < 0.0001$), sample area ($\chi^2(8) = 182.6$, $p < 0.0001$) and their interaction ($\chi^2(8) = 15.5$, $p < 0.049$) with a pseudo-coefficient of determination r^2 of 0.7. Figure 8 shows the variation in proportion mature at length among sample areas. Post-hoc tests of pairwise differences in maturity at length indicated three significantly different groups with fish from the Browns Bank in SA1 maturing at the shortest lengths and the converse for Fisher Bank (SA2), SA3 and the Firth of Forth (SA4). Sandeels from around the Dogger Bank across to the Danish coast had a similar length at maturity.

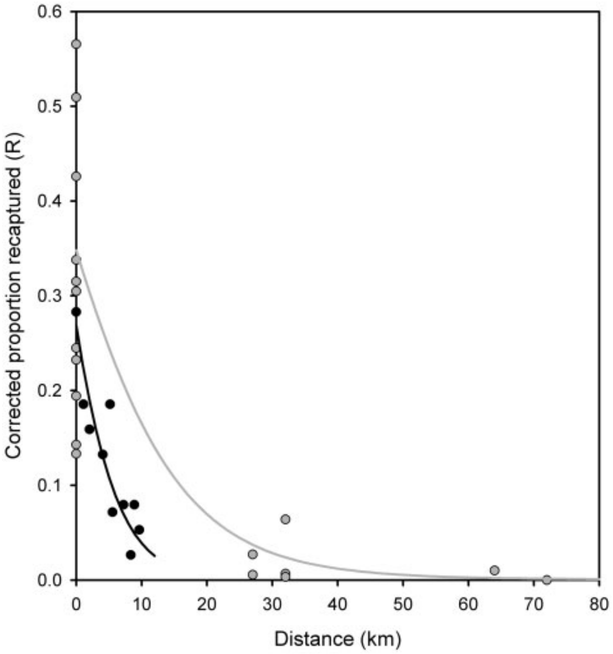

Figure 7. Relationship between the corrected proportion of fish recaptured (R) and release distance from grounds. Data and smoothed fits for the North Sea (black dots and lines) and Shetland (grey dots and lines) are shown.

Regional variation in age 1 abundance

Correlation in age 1 abundance (CPUE) among ICES rectangles was positively related to the logarithm of distance (Mantel statistic: $r = 0.47$; $p < 0.001$), although the variance increased in rectangles that were 90–150 km apart (Figure 9). Clustering always distinguished the rectangles within SA4 from all other rectangles. Also, some rectangles of Dogger (within SA1) were distinguished from rectangles further east, whereas, no clear geographical pattern emerged among the rectangles in the eastern part of the North Sea (Supplement 2).

Localized recovery simulations

On the basis of the simulations, recovery from a depletion ranged from 1 to 3 years at a scale of 50 km with the fastest recovery predicted for Fisher Bank, where larval dispersal range tends to be high (Figure 10). Recovery time increased with size of the depleted areas, in particular for Dogger Bank.

Discussion

Effect of ontogenetic dispersal on population structure

Oceanographic processes appeared to be the primary influence on the scale of inter-mixing of sandeel. The larval transport model predictions suggested that larval mixing among grounds < 67 km apart was common, whereas the probability of mixing was very low among grounds > 200 km apart. This confirms results from simpler larval transport models (Christensen

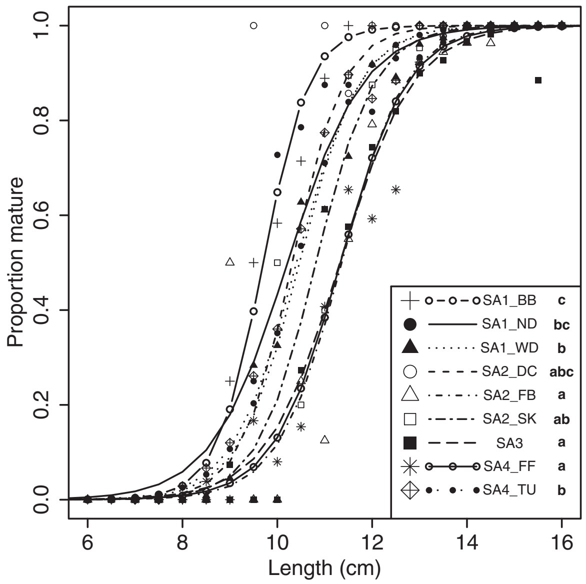

Figure 8. Proportion of mature fish at length. Data points and the fit of a logistic regression including length and region as independent variables are provided. Region indicated by a distinct letter (a, b, or c) are significantly different based on post-hoc *z*-test with corrections for multiple pairwise comparisons.

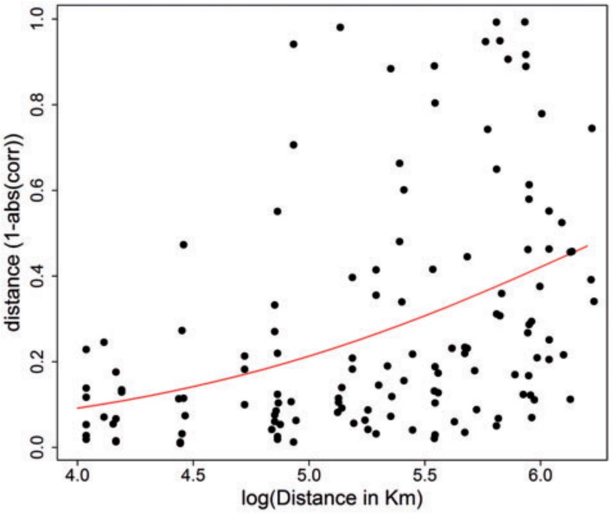

Figure 9. Relationship between pairwise correlation-based distances in age 1 CPUE and pairwise geographic distances between ICES rectangles (log transformed). The regression line of a logit GLM indicating a significant effect of geographic distance ($\chi^2(1) = 41.3$, $p < 0.001$) is only presented for illustrative purposes.

et al., 2008a, b; Proctor *et al.*, 1998). Predictions (model hind casts) of hatch origin for the 2011 samples appeared to explain the spatial variation in natal otolith chemistry, as differences in natal chemistry between sampling sites were positively related to distance between sampling sites. Furthermore, distance between predicted hatch origin and settlement location explained the difference between natal and edge chemical composition. Hence, the larval model and otolith chemistry variation suggested a similar scale of segregation of pre-settled stages across the North Sea, driven mainly by currents.

The larval transport model often predicted advection away from the sandeel banks (Proctor *et al.*, 1998), which may explain why many age 0 sandeel occurred far from grounds in the June-July pelagic trawl surveys. This is in line with previous otolith microstructural analysis, which indicated that some cohorts of juveniles did not reach the Shetland sandeel grounds until late July (Wright, 1996). Active horizontal migration towards suitable habitat has been proposed as an explanation for the frequently observed sudden disappearance of larvae and juvenile sandeels from the water column and the observed restriction in the spatial distribution of larger larvae during the time of settlement (Macer, 1965; Blackburn and Anderson, 1997). A lack of quantitative information on the pre-settlement behaviour meant that the biophysical model could not account for a phase of active movement. However, we can infer that the extent of active movement does not lead to significantly greater exchange among grounds than that predicted from the biophysical model, as any subsequent mixing of juveniles would lead to a greater homogeneity in the near core otolith chemistry than found here. Accurate large scale natal homing is not likely to have occurred, since this would have reduced the differences in Mn signals between the core of the otoliths and the edge and created a mismatch between model hind casts and microchemistry.

The proximity to known fishing grounds explained where most sandeel were caught in survey bottom trawls during quarters 1 and 4, when *A. marinus* are predicted to spend most of their time buried in sand (van Deurs *et al.*, 2010). As knowledge of sandeel habitat is inferred from known fishing grounds, this indicates that there are no major unknown sandeel aggregations. The higher proportion of catches in quarters 2 and 3 surveys away from these grounds may reflect a higher degree of active movements but the proportion declined markedly beyond around 10 km. In contrast to species that home, such as cod, *Gadus morhua*, where the proportion returning can range from 0.39 to 0.95 (Zemeckis *et al.*, 2014), proportion recapture declined to 0.03 beyond 30 km from grounds. Hence, although Gauld (1990) emphasized the ability of post-settled *A. marinus* to move, as 4 out of 996 individuals released 64 km from fished grounds were recaptured, the synthesis of tag-recapture experiments suggests movement is generally limited to a few km from grounds. Moreover, whereas sandeels released on the same ground were mostly recaptured in the following weeks, recaptures from transplant experiments involving over 27 km displacement occurred 1–3 years after release (see also Kunzlik *et al.*, 1986; Gauld, 1990). While it was not possible to correct for effort or spatial variation in mortality, all experiments were undertaken during months and years when the fishery was active. The probability that a fish will return to fished grounds depends on their ability to home, swimming performance and mortality. The low number of transplanted returns indicated a lack of homing behaviour or increased natural mortality during homing. The tag-recapture evidence for a limited scale of movement is consistent with observations made using acoustics, where the daily movement of *A. marinus* seemed constrained to within a few km from their burying habitat (van der Kooij *et al.*, 2008). Further, schools of *A. tobianus* made daily return migrations of around 1 km between shallow and deeper waters (Kühlmann and Karst, 2010) and age 0 *A. hexapterus* occupied the same habitat patch for up to 8 weeks (Haynes and Robinson, 2011). So, while further work is needed to understand the fine scale movements of settled *A. marinus* among neighbouring habitat patches, all present evidences

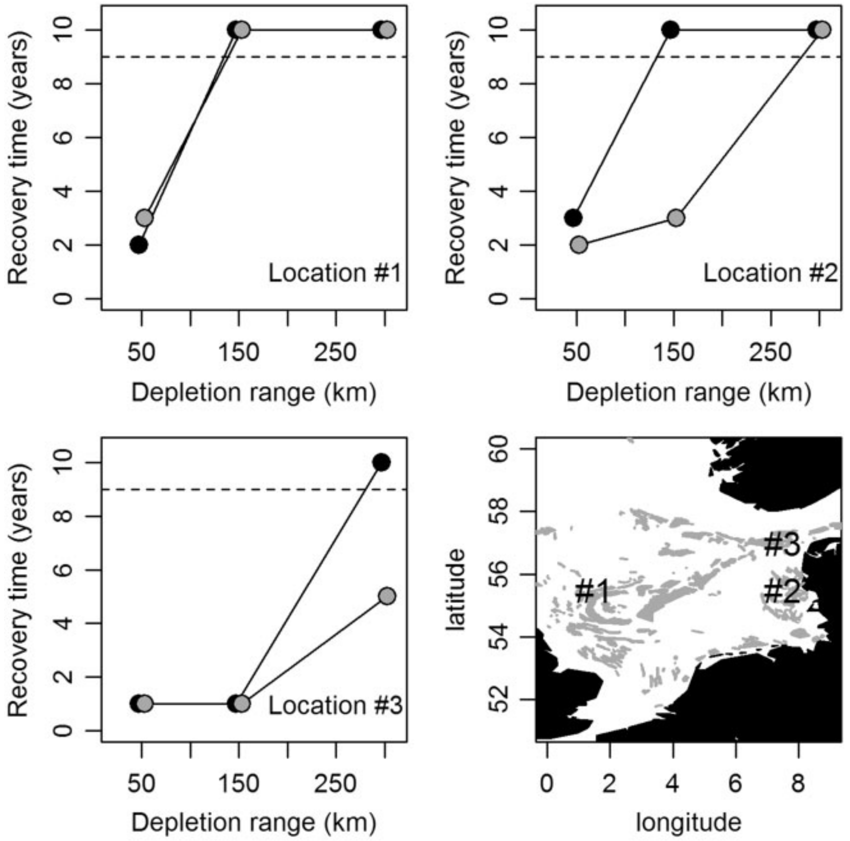

Figure 10. Simulated local recovery time at three locations in the North Sea. The simulations explored local depletion scenarios at three different geographical scales (*Y*-axis) represented by spherical completely depleted (population density of zero) areas of diameter 50, 150, and 250 km, respectively. Simulations were carried out both with (grey) and without (black) the assumption of post-settled random movement within habitat patches. Recovery time was defined as the number of years it took for the population to reach 50% of the population density at time 0. The dashed horizontal line indicates that 10 on the *Y*-axis represent recovery times of at least 10 years.

suggest that active mixing between banks separated by >30 km is unlikely. Even within continuous stretches of suitable habitat, the scale of adult mixing appears to be confined to c. 30 km, as suggested by variation in length compositions (Jensen *et al.*, 2011).

Spatial variation in vital rates

As seen in an earlier study of four sandeel aggregations across the North Sea in 1999 and 2004 (Boulcott *et al.*, 2006), *A. marinus* from Fisher Bank matured at a larger length than those inhabiting Dogger Bank grounds in our study. Bergstad *et al.* (2001) reported a similar length at maturity for *A. marinus* from banks adjacent to Fisher bank. However, in contrast to Boulcott *et al.* (2006), length at maturity for the Firth of Forth banks was not significantly different from that of Fisher Bank in 2017, although in all years of study, only a relatively small proportion of the Firth of Forth sandeels matured at age 1. Length at age has been found to be lowest in the Firth of Forth Banks and increases from west to east across the North Sea (Rindorf *et al.*, 2016). As a consequence of their low growth and late maturity, together with a lower fecundity at length than other regions (Boulcott and Wright, 2011), the Firth of Forth aggregation is likely to have a lower reproductive potential than the remaining North Sea stocks.

The rapid decrease in spatial correlation in year-class strength with distance within the North Sea contrasts with the high correlation in year-class strength found among many adjacent stocks in the North Atlantic (Myers *et al.*, 1997) and species within the North Sea (Pécuchet *et al.*, 2015). This variation may reflect regional differences in the timing and extent of copepod biomass production (Fransz *et al.*, 1991), which appears to be an important driver of year-class strength (Wright and Bailey, 1996; Régnier *et al.*, 2017). Spatial variation in year-class strength is liable to perpetuate further differences because of a positive effect of spawning stock biomass and a negative interaction between age-classes (van Deurs *et al.*, 2009), possibly due to cannibalism (Eigaard *et al.*, 2014).

The simulations of recovery after local depletion in an area of 50 km in diameter, suggested that re-colonization from adjacent grounds should lead to recovery within 1–3 years depending on the hydrographic isolation of the depleted area. This would suggest that recovery after this scale of depletion may be rapid, and have little impact relative to stock areas as these are generally substantially larger. However, landings data indicate that some grounds have failed to recover for >8 years (Johannessen and Johnsen, 2015), which may have been because a very large area had been depleted, as is consistent with the present model predictions, showing recovery times of >9 years when areas much >50 km are depleted. However, delayed recovery can also be caused by environmental changes leading to recruitment failure in the depleted area and adjacent areas (Clausen *et al.*, 2018).

Re-colonization may also be affected by behaviour as settling age 0 tend to favour some grounds over others (Wright, 1996).

Comparison of population and stock structure used in management

Whereas the basis for the SA4 stock boundary is strongly supported by data, the biologically "ideal" set of boundaries separating SA1, SA2, and SA3 are less definite, and the decision on these boundaries may rest on the relative priority given to variation in productivity, life history traits, and larval transport. SA4 contains the least productive aggregations of sandeel, which are largely disconnected from the remainder of the North Sea, both in terms of physical barriers to mixing (i.e. geographical isolation), population dynamics and larval dispersal. Indeed, early evidence on the isolation of SA4 aggregations was important in the designation of the north east UK closed area (Wright *et al.*, 1998). However, defining the "best" set of permanent stock boundaries for the rest of the North Sea is more challenging because of the lack of biophysical barriers to population mixing, which may create a situation where sandeel aggregations near a boundary between two assessment areas have a stronger connection to those in the neighbouring area, rather than concentrations at the opposite end of the area that they are assigned to.

Securing prey for sandeel reliant predators may require additional measures of protection. For example, the north east UK closed area in SA4, encompassing the foraging range of breeding seabirds (Wakefield *et al.*, 2017), was designed to avoid local depletion on time scales that may not be critical to sustain the sandeel stock in the larger SA4 area, but could have a major impact on predator populations (Wright *et al.*, 1998; Daunt *et al.*, 2008). However, further studies are warranted to investigate the biological effect of implementing closed areas (Christensen *et al.* 2008b). In this respect, an evaluation of the Norwegian rotational closed area management system (Johannessen and Johnsen, 2015) could provide much needed direct evidence as to the effect of such spatial measures on reducing local depletion.

In summary, there is substantial evidence for limited mixing upholding a complex of spatially segregated sandeel population components in the North Sea, displaying different dynamics and levels of productivity. The temporal scale over which these persist is unresolved, but if oceanographic segregation of pre-settled life-stages is the most important mechanism, then a stepping stone type of exchange (Kimura and Weiss, 1964) over many generations could potentially support North Sea scale population mixing and re-colonizations on an ecologically rather than evolutionary time-scale, which is consistent with the lack of genetic differentiation found to date (Naevdal and Thorkildsen, 2002). This implies that peripheral up-current population components are relatively more vulnerable to over-exploitation than central and down-current components. While highly segregated populations, as that in SA4, are likely to be well managed by the current separate stock assessments and catch predictions, the ideal management system for stocks with a more gradual change from one set of stock characteristics to another requires further investigation.

The present study illustrates the range of evidence needed to fulfil the requirements of a stock identity review, such as those undertaken by ICES benchmarks. The work presented answers many of the questions from stakeholders and assessment scientists about the scale of population processes and rationale for the new boundaries for management units. As such, this study provides a guide for future stock identity studies, especially where genetic evidence of population structuring is not available. Redrawing management boundaries can have a profound effect on the perception of stock dynamics and measures needed to conserve stocks. While new biological findings are leading to further revisions of the input data for stock assessments, it is clear that sustainable levels of fishing mortality differ considerably among the new sandeel stocks (Christensen *et al.*, 2013; ICES, 2017), so highlighting the importance of incorporating population structure into fisheries management advice.

Supplementary data

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

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