

Influence of larval transport and temperature on recruitment dynamics of North Sea cod (*Gadus morhua*) across spatial scales of observation

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Abstract

The survival of fish eggs and larvae, and therefore recruitment success, can be critically affected by transport in ocean currents. Combining a model of early-life stage dispersal with statistical stock–recruitment models, we investigated the role of larval transport for recruitment variability across spatial scales for the population complex of North Sea cod (*Gadus morhua*). By using a coupled physical–biological model, we estimated the egg and larval transport over a 44-year period. The oceanographic component of the model, capable of capturing the interannual variability of temperature and ocean current patterns, was coupled to the biological component, an individual-based model (IBM) that simulated the cod eggs and larvae development and mortality. This study proposes a novel method to account for larval transport and success in stock–recruitment models: weighting the spawning stock biomass by retention rate and, in the case of multiple populations, their connectivity. Our method provides an estimate of the stock biomass contributing to recruitment and the effect of larval transport on recruitment variability. Our results indicate an effect, albeit small, in some populations at the local level. Including transport anomaly as an environmental covariate in traditional stock–recruitment models in turn captures recruitment variability at larger scales. Our study aims to quantify the role of larval transport for recruitment across spatial scales, and disentangle the roles of temperature and larval transport on effective connectivity between populations, thus informing about the potential impacts of climate change on the cod population structure in the North Sea.

KEYWORDS

Atlantic cod, biophysical model, larval transport, North Sea, populations, stock–recruitment, temperature

Romagnoni and Kvile contributed equally to the article.

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1 | INTRODUCTION

Recruitment of fish stocks depends largely on survival during the first year and in particular during the pelagic early-life stages (ELS) in broadcast spawning teleost fish (Houde, 2008; Leggett & Deblois, 1994). A number of factors affect the ELS survival, including temperature, food availability and predation (Folkvord, 2005; Peck & Hufnagl, 2012). In addition to these factors, the interannual variability in recruitment can be influenced by advective transport of eggs and larvae from spawning to nursery areas (Bailey, 1981; Henriksen et al., 2018). Recent physical–biological modelling studies have related larval transport and success to recruitment using various approaches (Peck & Hufnagl, 2012), including comparisons between modelled larval survival and observed recruitment (Daewel, Schrum, & Gupta, 2015) and between modelled and observed juvenile distributions (Huyer, Hinrichsen, Hussy, & Eero, 2016). One alternative approach to assess the effect of larval transport on recruitment is the application of stock–recruitment models. Historically, parametric stock–recruitment models have been used to link variation in stock size with recruitment success. While the predictive capability of these models remains limited (Subbey, Devine, Schaarschmidt, & Nash, 2014), inclusion of environmental variables such as temperature (Akimova, Núñez-Riboni, Kempf, & Taylor, 2016; Planque, Fox, Saunders, & Rockett, 2003), the North Atlantic Oscillation index (NAO) (Brander & Mohn, 2004), surface wind speed (Hare, Brooks, Palmer, & Churchill, 2015), zooplankton prey availability (Olsen et al., 2011) and interactions between these factors (Duplisea & Robert, 2008; Olsen et al., 2011) can help to identify key biological mechanisms driving the interannual variability in stock–recruitment. We hypothesise that accounting for transport variability in stock–recruitment models can help to explain parts of the observed recruitment variability. In fact, it has been suggested that ELS transport could be one of the drivers behind the unclear relationship between spawning stock size and recruitment (Huyer et al., 2016). While some studies have included proxies of larval transport in stock–recruitment relationships (Baumann et al., 2006; Zimmermann, Claireaux, & Enberg, 2019), few have included direct estimates of larval transport (but see Hidalgo et al., 2019).

Moreover, transport can influence connectivity among populations (e.g. through interannual variability in oceanographic current patterns, Huwer et al., 2016; Kvile, Romagnoni, Dagestad, Langangen, & Kristiansen, 2018) and recruitment dynamics across large geographic scales (Cadrin, Goethel, Morse, Fay, & Kerr, 2019; Henriksen et al., 2018; Hinrichsen, Von Dewitz, & Dierking, 2018) and thereby population management (Fogarty & Botsford, 2007; Hidalgo et al., 2019; Ramesh, Rising, & Oremus, 2019). Critically, the spatial scale of observation can affect the stock–recruitment relationship, providing contrasting results across scales (Chang, Chen, Halteman, & Wilson, 2016). The importance of environmental drivers for recruitment can also differ across subunits within a stock (Brosset et al., 2018). We therefore expect the importance of larval transport variability for recruitment to differ across spatial scales (i.e. basin vs. sub-basin) and between individual populations. In this study, we explore alternative approaches to explicitly include larval transport

in stock–recruitment functions, and quantitatively assess the effect of transport on recruitment across spatial scales. We use annual estimates of larval retention and population connectivity, obtained through a coupled physical–biological model of larval drift, focusing on North Sea cod (*Gadus morhua*) as a case study.

We initially include retention anomaly as an environmental covariate in traditional parametric stock–recruitment model formulations and compare its effect to alternative covariates, namely sea surface temperature (SST) and the North Atlantic Oscillation index (NAO). In addition, we propose a novel approach for inclusion of the effect of larval transport in stock–recruitment models by weighting spawning stock biomass (SSB) according to yearly retention and advection rates, providing a measure of “effective biomass.” Two alternative approaches are proposed to account for effective biomass: including only retention in the spawning area of origin (retention-only SSB, *rSSB*), and including retention and inflow of larvae from other areas (net drift SSB, *ndSSB*), effectively accounting for connectivity. Additionally, we quantify temporal patterns in population connectivity and their relationship with SST and NAO.

2 | MATERIALS AND METHODS

2.1 | Ocean circulation in the North Sea

Ocean circulation in the semi-enclosed North Sea basin is influenced by topography and inflow of North Atlantic water, separating the basin into a shallow southern and a deeper northern area. The northern area is influenced by inflow of saline Atlantic water flowing along the western slope of the Norwegian Trench. This current transports the planktonic copepod, *Calanus finmarchicus*, an important food source for larval cod (Nicolas, Rochette, Llope, & Licandro, 2014) and other species, into the region. The current flows along the Norwegian Trench and into Skagerrak, where it enters the “Skagerrak loop.” It follows a counterclockwise trajectory along the Skagerrak coast, and after mixing with the less saline Norwegian coastal current, flows north-westward along the eastern slope of the Norwegian Trench and into the Norwegian Sea (Huserbråten, Moland, & Albretsen, 2018). The southern North Sea is dominated by continental freshwater run-off and tidal patterns, which in combination with wind and wave turbulence and shallow topography result in permanent mixing. The intermediate saline current from the English Channel and the coastal, low saline Jutland Current flow along the continental coast and into the Skagerrak, entering the “Skagerrak loop” (Sundby, Kristiansen, Nash, & Johannessen, 2017).

2.2 | Cod populations in the North Sea

Although managed as one stock (ICES, 2018c), North Sea cod comprises a number of spatially segregated units, with limited overlap and varying degree of connectivity (Heath et al., 2014; Neat et al., 2014). The main units are the Viking and the South populations. The latter is

often separated into a South proper (centred around the Dogger Bank) and a Northwest unit; these two subpopulations are genetically homogeneous but show contrasting demographic trends and limited adult connectivity, so their relationship is as yet unclear (Neat et al., 2014). In this study, we considered alternative scenarios with three populations (Viking, South and Northwest), two populations (Viking and South including Northwest) and a single population (aggregating Viking, South and Northwest), the latter roughly corresponding to the current management unit. The populations' spatial extent (Figure 1) was based on ICES (2015). We calculated larval connectivity between the populations and assessed drift into the Skagerrak (which is excluded from our populations) and the Norwegian Sea, Scottish sea and English Channel (hereafter called "outside"; Figure 1). Particles leaving the study area (i.e. entering the "outside" area) were considered lost.

2.3 | Early-Life Stage (ELS) dispersal model

To quantify larval retention and connectivity between populations, we used a coupled physical-biological model

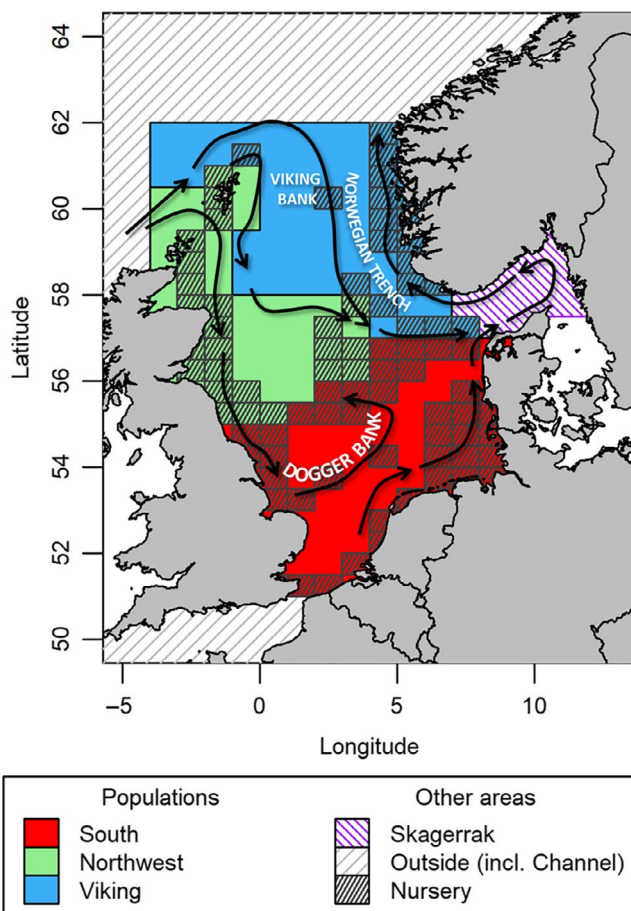


FIGURE 1 Study area showing distribution of populations (following ICES, 2015) and other potential sink areas for simulated cod larvae in our study. Nursery areas are overlaid to the population of appartenance [Colour figure can be viewed at wileyonlinelibrary.com]

(hereafter, ELS dispersal model) for the time period 1971–2014 and included the model output in statistical stock–recruitment models for the same years. The individual-based model (IBM) simulates development and transport of cod eggs and larvae based on earlier studies of larval cod (Kristiansen, Lough, Werner, Broughton, & Buckley, 2009; Kristiansen, Stock, Drinkwater, & Curchitser, 2014; Kristiansen, Vikebø, Sundby, Huse, & Fiksen, 2009). The IBM is integrated as a module in the open source Lagrangian particle tracking framework OpenDrift (github.com/opendrift; Dagestad, Röhrs, Breivik, & Ådlandsvik, 2018; Kvile et al., 2018), and the code for the cod eggs and larvae module is available on github.com/trondkr/KINO-ROMS/tree/master/Romagnoni-2019-OpenDrift. To simulate transport with ocean currents and temperature-dependent development, the IBM was coupled offline to a reanalysis of the regional ocean circulation model ROMS (Shchepetkin & McWilliams, 2005) configured for ocean regions covering the Nordic Seas (including the North Sea) and parts of the Arctic Ocean, with 4 km horizontal resolution, 32 vertical layers and output stored daily (Lien, Gusdal, Albretsen, & Melsom, 2013). For downloading options, see http://thredds.met.no/thredds/nansen_daily.html. Further details on the characteristics and limitations of the ELS dispersal model are available in Kvile et al. (2018).

Due to long-term and interannual variation in the relative importance of spawning grounds (González-Irusta & Wright, 2016; Sundby et al., 2017) and the uncertainty in spawning ground locations early in the time series, we released particles representing cod eggs uniformly within the three populations' spatial extent (Figure 1). Although this could reduce the precision of connectivity estimates in some years, we considered this approach as more conservative when modelling larval transport over a long time period including years with unknown spawning ground distribution. To obtain uniform spatial distribution (0.12–0.14 eggs/km²), we set the number of eggs released based on the sizes of the population areas: ~32,400 in the South (~270,000 km²), ~22,950 in the Northwest (~170,000 km²) and ~27,000 in the Viking area (~200,000 km²), for a total of ~91,500 eggs.

We defined the timing of egg release using prior knowledge of the population spawning periods (Brander, 1994, 2005; Fox et al., 2008): between December 15th and April 15th for the South population, between January 1st and May 1st for the Northwest population and between February 1st and May 15th for the Viking population (Figure 2a). The number of eggs released per day followed a Gaussian distribution, $N(\mu, \sigma^2)$, where $\mu = 1$ and $\sigma = 0.25$, scaled to the length of the spawning season and the total number of particles defined per population area and with peaks that approximately matched the spawning peak described by Brander (1994). Setting a broader spawning season than observed in recent years accounts for uncertainty in the spawning season early in the time series. For example, spawning was allowed to start in December for the South population to account for the fact that the Southern Bight component, which spawns earlier than the German Bight and Central-west (Brander, 1994), was more abundant in the past.

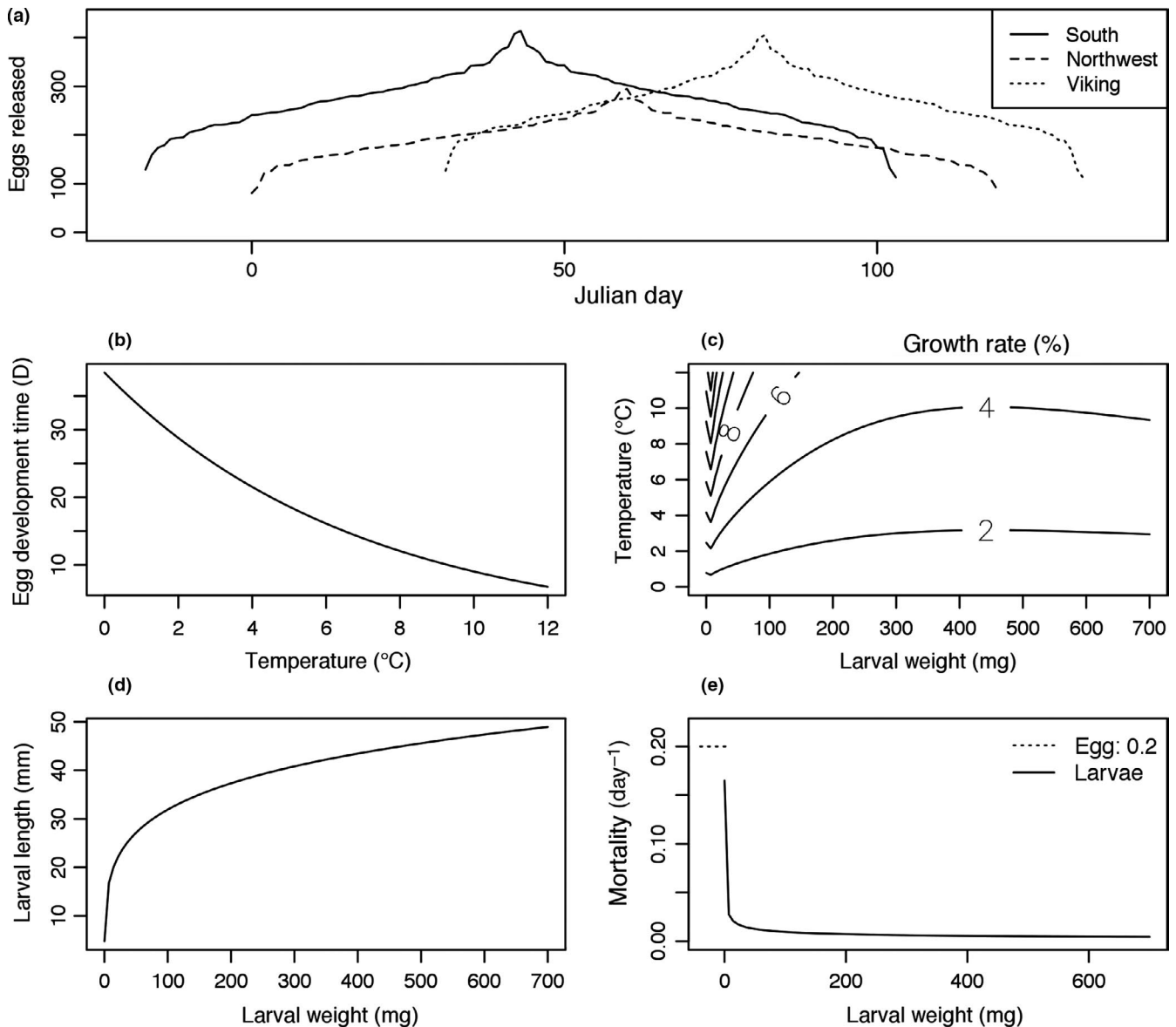


FIGURE 2 Cod egg and larvae IBM functions. (a) Number of eggs released per Julian day (counting from January 1st) per spawning ground; (b) egg development time (d) as a function of temperature; (c) growth rate of larvae day⁻¹ (GR, contours) as a function of larval weight and temperature; (d) larval length (L) as a function of weight; and (e) mortality rate (m, day⁻¹) for eggs (fixed at 0.2) and larvae as a function of larval weight

Eggs were released in equal numbers at 10 m depth intervals between 0 and 50 m (i.e. for a given population, an equal number of eggs was uniformly released at 0, 10, 20, 30, 40 and 50 m). After release, eggs and larvae were advected horizontally at fixed depths using an Euler interpolation scheme without horizontal diffusion and a 1-hr time step. The Euler scheme differed minimally compared to a more computationally costly Runge–Kutta scheme (Kvile et al., 2018). We used different drift depths to represent vertical movement within the depth range typically available in the North Sea, based on the finding that incorporating a more computationally costly vertical movement behaviour had limited effect on connectivity and retention of cod ELS at settlement in the North Sea (Kvile et al., 2018). Development time of planktonic eggs (d , days) was a function of the ambient sea water temperature (T , °C) according to

the ocean model reanalyses, parameterised based on observations for cod eggs (Langangen, Stige, Yaragina, Vikebø, et al., 2014, based on data in Ellertsen, Fossum, Solemdal, Sundby, & Tilseth, 1987, Figure 2b):

$$\ln d = 3.65 - 0.145 \times T \quad (1)$$

After completing the egg stage, the simulated individuals hatch into cod larvae. The simulated cod larvae grew with a growth rate (GR, percentage of larval weight/day) depending on larval weight (W , mg) and ambient temperature (T), as estimated experimentally for Atlantic cod larvae (Folkvord, 2005) (Figure 2c):

$$GR = 1.08 + 1.79 \times T - 0.074 \times T \times \ln W - 0.0965 \times T \times \ln W^2 + 0.0112 \times T \times \ln W^3 \quad (2)$$

Larvae were assumed to feed ad libitum, and their initial weight was set at 0.08 mg. Larval length (L , mm) was a function of weight (Folkvord, 2005) (Figure 2d):

$$L = e^{2.296 + 0.277 \times \ln W - 0.005128 \times \ln W^2} \quad (3)$$

We assumed that cod larvae had no directional horizontal (swimming) movement. During the simulation, eggs were subject to a fixed daily mortality rate (m) of 0.2, which is within the range of mean values estimated in studies of cod eggs (0.1–0.32, Rijnsdorp & Jaworski, 1990; see Table 2 in Langangen, Stige, Yaragina, Vikebø, et al., 2014). For larvae, we set the mortality rate to decrease with weight (Figure 2e) as parameterised for North Sea cod larvae in

Akimova, Hufnagl, Kreuz, and Peck (2016), based on the size-spectrum theory (Peterson & Wroblewski, 1984):

$$m = 0.06 \times W^{-0.4} \quad (4)$$

The survival probability of each individual was updated throughout the simulation according to the mortality rate (i.e. individuals were not removed from the simulation), following a super-individual approach (Scheffer, Baveco, DeAngelis, Rose, & van Nes, 1995).

Larvae settled when reaching a length >49 mm (Bastrikin, Gallego, Millar, Priede, & Jones, 2014). Only larvae settling within known nursery areas for North Sea cod (based on Heath et al., 2014; see Figure 1) were considered to successfully settle and survive; larvae that reached settlement length outside nursery areas were considered dead (hereafter “not settling”). Larvae not reaching settlement length by the end of the simulation (set to 15th August for South and 29th September for Northwest and Viking) were considered dead (amounting to $<1\%$ of larvae, not included in the analysis). The juvenile stage was not simulated since cod adopt a demersal life-style upon reaching settlement length.

For each population, we estimated the proportion of larvae (a) retained in a nursery area for the given population of origin; (b) drifting into the nursery area of another population; (c) drifting out of the study area (to the Skagerrak or “outside”) and (d) reaching settlement size within any population area, but not within a nursery area (“not settling”). Annual values (1971–2014) for these metrics were included in the stock–recruitment analysis (see below). To test the robustness of the results of the stock–recruitment analysis to key assumptions in the larval dispersal model, we performed additional simulations where the mortality rate (for eggs and larvae) was adjusted by $\pm 20\%$ and separate simulations where settlement size was adjusted by $\pm 20\%$. We ran these additional simulations for 1990 and 2010, two years with different climatic conditions (high and low NAO phase, respectively; Figure 3) and contrasting results of larval dispersal. Parameters included in the ELS model are summarised in Table 1.

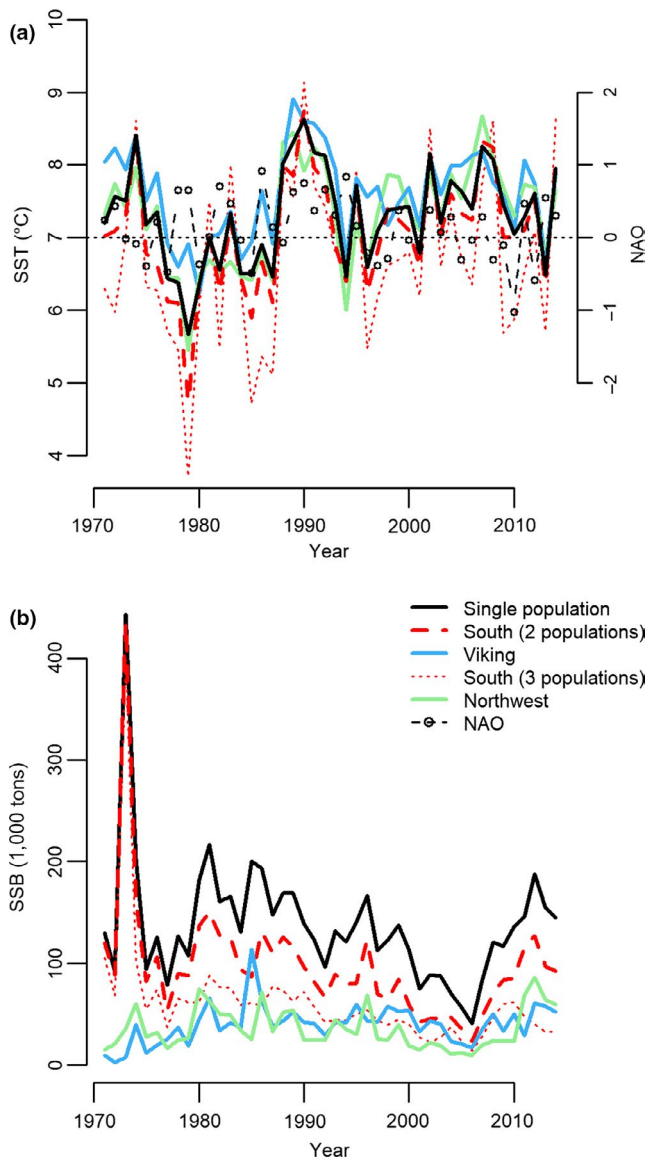


FIGURE 3 (a) Sea surface temperature (SST) by population area across the three, two and single populations cases, and the NAO index. (b) Spawning stock biomass (SSB) by population area across the three, two and single populations cases [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Parameters used in the ELS model

| Parameter | Unit | Meaning |
|-----------|------------------------|--|
| μ | | Mean of the Gaussian distribution of eggs spawned per day (1) |
| σ | | Standard deviation of the Gaussian distribution of eggs spawned per day (0.25) |
| d | days | Development time of planktonic eggs |
| T | °C | Ambient sea water temperature |
| GR | % of larval weight/day | Larval growth rate |
| W | mg | Larval weight |
| L | mm | Larval length |
| m | day ⁻¹ | Mortality rate |

2.4 | Observational data

We calculated population-specific estimates of SSB and recruitment (age 1) based on abundance data (1971–2014) obtained from the ICES North Sea International Bottom Trawl Survey (NS-IBTS) as catch per unit of effort per ICES statistical sub-rectangle (ICES, 2018a; Figure 3). Although more accurate abundance estimates could be obtained by using standardised indices instead of raw data, these are only available from 1983. We instead used raw data to include a longer time series, spanning years when SSB was higher, to provide robustness to the stock–recruitment estimates. We generated annual data of age-specific abundance to match the ICES statistical sub-rectangle using Catch-Per-Unit-Effort (CPUE) adjusted for swept area and gear catchability, assuming that the sample is representative of fish abundance. The swept area is a function of standardised tow length and net width during towing, which in turn is a function of tow depth (ICES, 2012). Average depth per sub-rectangle (NGDC, 1995) was used as a proxy for tow depth. Catchability coefficient for the survey gear by age (Fraser, Greenstreet, & Piet, 2007) was multiplied by the ratio of the swept area to the whole ICES rectangle area. SSB was calculated as abundance per age multiplied by maturity and weight per age and year, assumed homogeneous between populations lacking population-specific data (ICES, 2017). The recruitment index was estimated by back-calculating abundance of age 1 from averaged age 2 and 3 abundances scaled by the age- and year-specific natural mortality (ICES, 2015). As climate variables, we included sea surface temperature (SST) mean monthly values (ICES, 2018b) for the period February to June (the period of highest sensitivity of cod larvae to temperature in this area, Nicolas et al., 2014), resolved at ICES sub-rectangles and averaged per population area; and monthly means of NAO data (NOAA, 2018) averaged per year (Figure 3).

2.5 | Stock–recruitment models

We used the Cushing parametric stock–recruitment model formulation, following recent literature on North Sea cod (Akimova, Núñez-Riboni, et al., 2016). We considered model formulations with (a) drift anomaly included as a covariate or using (b) retention-only SSB (rSSB) or (c) net drift plus retention of SSB (ndSSB) as an alternative predictor for recruitment to SSB. Conceptually, the SSB effectively contributing to recruitment is a fraction of total SSB: rSSB accounts for the proportion of larvae retained within the population of origin after settlement. ndSSB accounts both for the proportion retained and for the number of larvae settling into a population from other populations, quantified as the fraction of other populations' SSB drifted into the population of interest:

$$rSSB_p = SSB_p \times D_{p,p} \quad (5)$$

$$ndSSB_p = SSB_p \times D_{p,p} + \sum_{p \neq p'} SSB_{p'} \times D_{p,p'} \quad (6)$$

For any population p in the pool of all populations P , rSSB was calculated as the product of its SSB and the retention proportion $D_{p,p}$. ndSSB was the sum of rSSB and the summed product of the biomass and drift proportion into p for all other populations in P ($D_{p,p'}$).

Similarly to the SSB-based models, models with ndSSB and rSSB were fitted with or without climate variables as covariates (Table 2). The models thus took the form (Akimova, Núñez-Riboni, et al., 2016):

$$R = \alpha S^\gamma \quad (7)$$

Where recruitment R was calculated as a function of the generic S (either SSB, rSSB or ndSSB). This was extended for inclusion of climate variable E as:

$$R = \alpha S^{(\gamma + \theta E)} \quad (8)$$

E was any climate variable (SST, NAO or retention anomaly, RA). RA was calculated as the annual deviation from the mean larval retention over the whole time series for a given population, determined from the ELS dispersal model.

The linear forms of the models (see Appendix S1) were tested for residuals assumptions, and outliers were removed from the analysis. Commonly used model comparison methods such as AIC and likelihood-based approaches could not be used since models with SSB, ndSSB or rSSB included different data in the predictor variable. Models were therefore compared through their absolute fit to data using adjusted R^2 , with significance threshold set at .05. Adjusted R^2 allows highlighting the combinations of predictor and covariates with highest explanatory power, that is those that improve the model more than expected by chance, with penalisation of additional parameters.

3 | RESULTS

We compared the performance of stock–recruitment models for North Sea cod across the three population levels and model formulations (SSB, rSSB, ndSSB, Table 3). At the three populations scale, models including SST as a covariate (models 2, 6 and 9) have

TABLE 2 Models used in analyses with their predictors and climate variables

| Model | Predictor | Covariate |
|-------|-----------|-----------|
| 1 | SSB | None |
| 2 | SSB | SST |
| 3 | SSB | NAO |
| 4 | SSB | RA |
| 5 | rSSB | None |
| 6 | rSSB | SST |
| 7 | rSSB | NAO |
| 8 | ndSSB | None |
| 9 | ndSSB | SST |
| 10 | ndSSB | NAO |

highest fit to data for the South and Northwest populations. In the Northwest population, models with ndSSB have higher fit than their counterparts with SSB when including no covariate or NAO (but not with SST). Model performance is generally low for the Viking population, with only models replacing SSB with ndSSB with or without SST as covariate (models 8 and 9) showing significant fit ($p < .05$). At the two populations scale, results for the South (including Northwest) unit are similar to the three populations scale,

but with higher overall fit. In the Viking population, models 1–4 and 5–7 in the two and three population cases are fitted to the same data and models 8–10 (with ndSSB) give similar results to the three populations scale. Combining the Northwest and South populations result in slight changes in connectivity values for the Viking population. At the single population scale, model 4 using retention anomaly as covariate shows highest fit, followed by model 2 with SST.

TABLE 3 Adjusted R^2 and p -values for each model (Table 2) and population across the three cases of population scale

| | Predictor | Covariate | South | | Viking | | Northwest | |
|----|-----------|-----------|-------------------|------|------------|------|------------|------|
| | | | Adj. R^2 | p | Adj. R^2 | p | Adj. R^2 | p |
| 1 | SSB | None | .22 | .001 | .04 | .106 | .23 | .001 |
| 2 | SSB | SST | .31 | .001 | .03 | .233 | .35 | .000 |
| 3 | SSB | NAO | .20 | .008 | .05 | .171 | .19 | .011 |
| 4 | SSB | D | .22 | .005 | -.01 | .445 | .19 | .009 |
| 5 | rSSB | None | .21 | .001 | .03 | .121 | .22 | .001 |
| 6 | rSSB | SST | .29 | .001 | .05 | .185 | .33 | .000 |
| 7 | rSSB | NAO | .23 | .005 | .04 | .218 | .18 | .012 |
| 8 | ndSSB | None | .18 | .003 | .11 | .016 | .27 | .000 |
| 9 | ndSSB | SST | .27 | .001 | .15 | .027 | .34 | .000 |
| 10 | ndSSB | NAO | .19 | .010 | .09 | .090 | .25 | .003 |
| | | | South + Northwest | | Viking | | | |
| | Predictor | Covariate | Adj. R^2 | p | Adj. R^2 | p | | |
| 1 | SSB | None | .26 | .000 | .04 | .106 | | |
| 2 | SSB | SST | .36 | .000 | .03 | .233 | | |
| 3 | SSB | NAO | .24 | .003 | .05 | .171 | | |
| 4 | SSB | D | .23 | .004 | -.01 | .445 | | |
| 5 | rSSB | None | .25 | .000 | .03 | .121 | | |
| 6 | rSSB | SST | .34 | .000 | .05 | .185 | | |
| 7 | rSSB | NAO | .24 | .003 | .04 | .218 | | |
| 8 | ndSSB | None | .25 | .000 | .13 | .010 | | |
| 9 | ndSSB | SST | .32 | .000 | .17 | .018 | | |
| 10 | ndSSB | NAO | .23 | .004 | .10 | .068 | | |
| | | | Single population | | | | | |
| | Predictor | Covariate | Adj. R^2 | p | | | | |
| 1 | SSB | None | .24 | .001 | | | | |
| 2 | SSB | SST | .28 | .001 | | | | |
| 3 | SSB | NAO | .21 | .006 | | | | |
| 4 | SSB | D | .32 | .000 | | | | |
| 5 | rSSB | None | .15 | .005 | | | | |
| 6 | rSSB | SST | .21 | .007 | | | | |
| 7 | rSSB | NAO | .14 | .031 | | | | |
| 8 | ndSSB | None | - | - | | | | |
| 9 | ndSSB | SST | - | - | | | | |
| 10 | ndSSB | NAO | - | - | | | | |

Note: Darker shades of grey indicate higher adjusted R^2 (higher model fit and better model performance). In the single population case, ndSSB is not calculated.

The interannual variation in SSB, rSSB and ndSSB is largest for the Viking and Northwest units (Figure 4). The three indices show similar interannual patterns (but for example the peak around 1985 in Viking SSB Figure missing in rSSB and ndSSB), but can still result in different fit to data (Figure 5b), with, for example, higher fit using ndSSB than rSSB in Viking and Northwest populations (Table 3). Using traditional SSB with retention anomaly (model 4, Table 3), the effect of retention is captured at the single population scale but not at the two or three populations scale. In this case, the effect has a similar magnitude and effect as the inclusion of SST as covariate (Figure 5a,c).

The interannual variation in retention and connectivity is relatively low (Figure 6). Retention is higher in South (0.39 ± 0.08) and Northwest (0.31 ± 0.06) populations compared to the Viking population (0.14 ± 0.04). Connectivity among the three populations is always low. The drift from South to Northwest and Viking populations is comparable (0.02 ± 0.03 and 0.03 ± 0.03 , respectively). The drift from the Northwest to South population is slightly higher than to the Viking population (0.07 ± 0.04 and 0.04 ± 0.03 , respectively),

while drift from the Viking population is low or close to zero to the Northwest and South populations (0.03 ± 0.05 and 0.01 ± 0.01 , respectively). The proportion of larvae drifting to the Skagerrak from the South and Viking populations is similar (0.07 ± 0.07 and 0.07 ± 0.06 , respectively) while drift from the Northwest population is lower (0.02 ± 0.03). The proportion of larvae drifting outside of the study area is low for the South (0.03 ± 0.03) and Northwest (0.07 ± 0.05) populations. In contrast, for the Viking population, drift to the outside area is higher than the retention rate (0.39 ± 0.13). The proportion of larvae remaining within the study area but not settling within a nursery area is high for all populations (0.46 ± 0.08 , 0.48 ± 0.09 and 0.36 ± 0.08 for South, Northwest and Viking populations, respectively). Only drift from the South to the Viking population and to the Skagerrak and from South to Northwest populations significantly increase or decrease, respectively, in time (Table 4).

The NAO and SST indices are significantly correlated with drift anomalies across population scales (Table 4). SST is positively correlated with drift to the Skagerrak at the single population scale

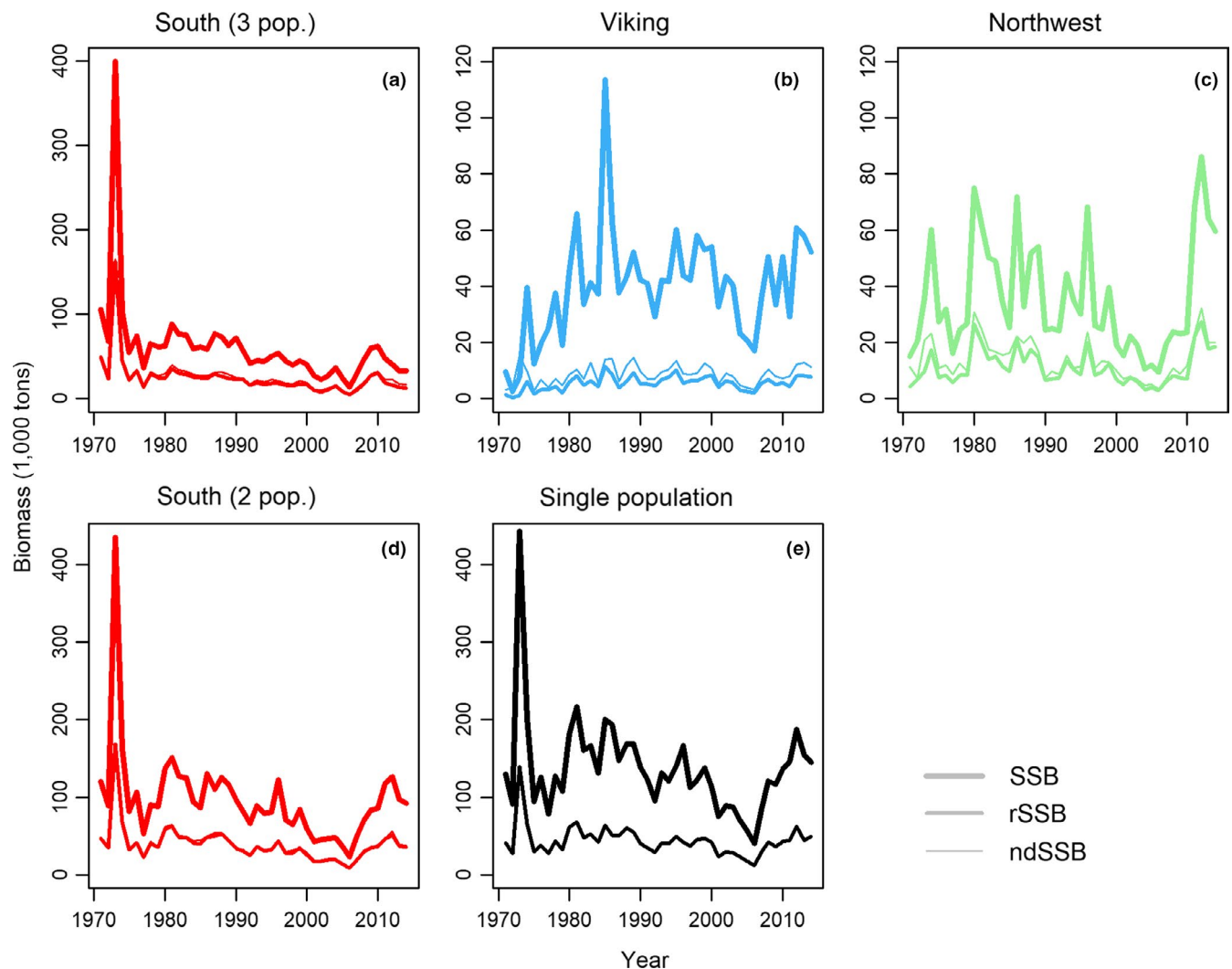


FIGURE 4 Interannual variation in SSB, rSSB and ndSSB (thick, medium and thin lines, respectively) across populations for the three, two and single population cases. Note that rSSB and ndSSB are close, but not identical, for the South population. For the single population case, ndSSB is not calculated [Colour figure can be viewed at wileyonlinelibrary.com]

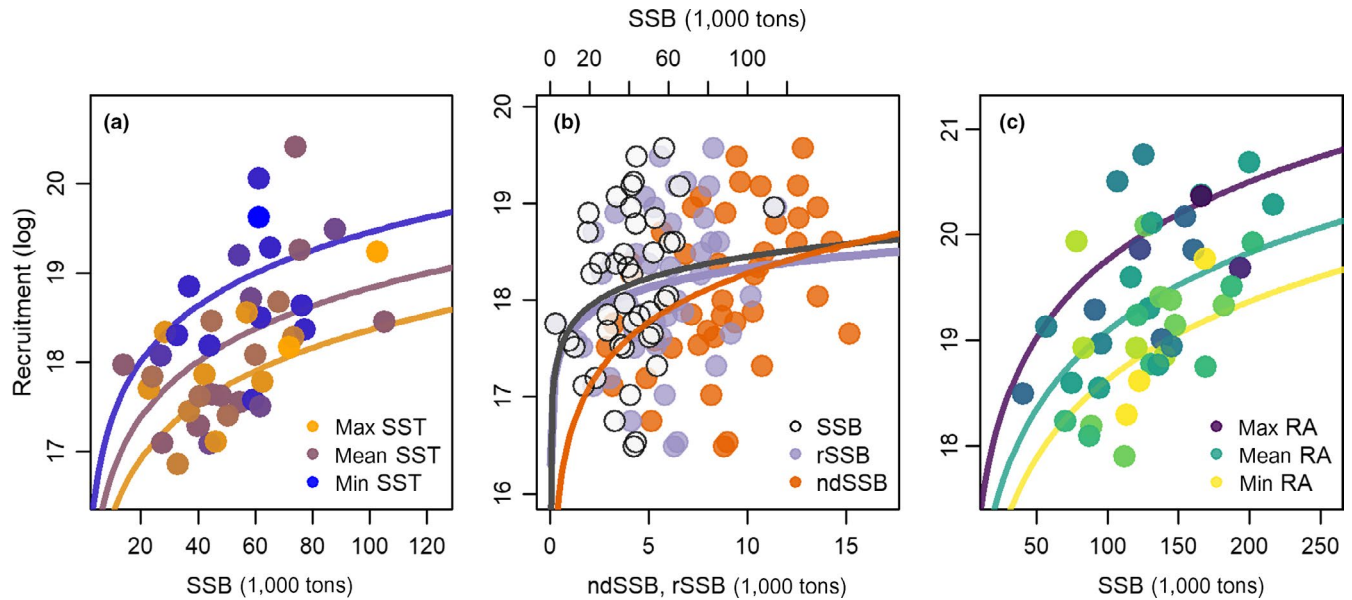


FIGURE 5 Effects of inclusion of covariates and alternative SSB predictors across populations, spatial scale and predictor variables. Data (dots) and predicted stock–recruitment relationships (lines) for the following: (a) inclusion of SST as covariate (model 2) for the South unit at the three populations scale; (b) three alternative predictor variables with no covariates (models 1, 5, 8) for the Viking unit at the three populations scale; and (c) inclusion of retention anomaly (model 4) in the single population case. In (a) and (c), dots colour scale indicates the covariate anomaly, line colour indicates the model prediction at corresponding maximum, mean and minimum value of the covariate. In (b), SSB scaled by 10^{-1} (open dots, dark grey line) is compared to rSSB (purple dots and line) and ndSSB (orange dots and line) [Colour figure can be viewed at wileyonlinelibrary.com]

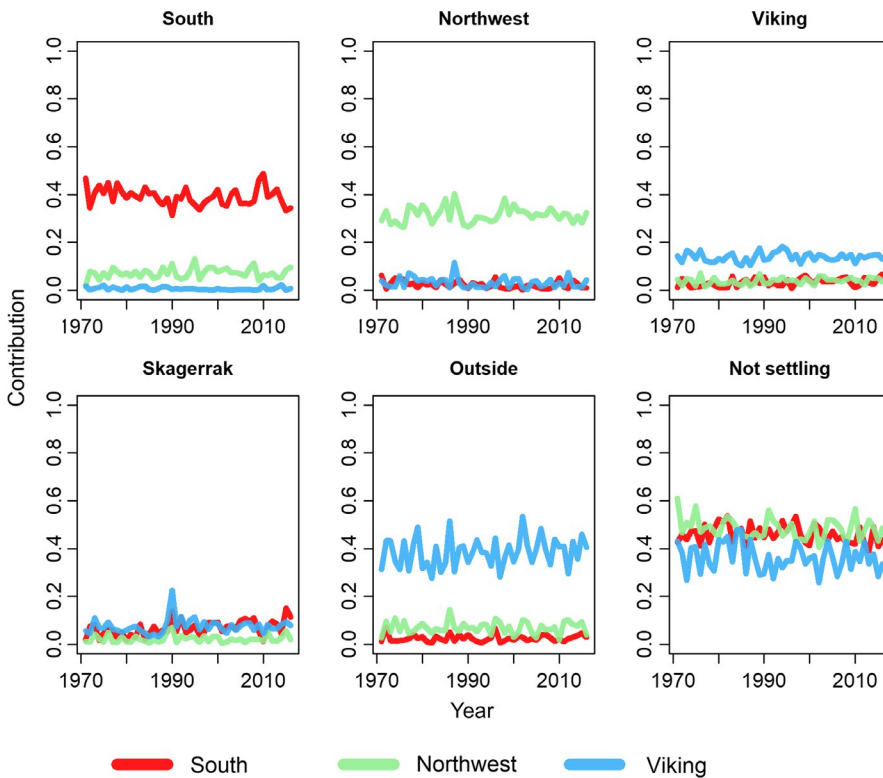


FIGURE 6 Contribution (retention and proportion of larvae drifted to other areas) from each of the three populations (South in red; Northwest in green; Viking in blue) and numbers of individuals not settled. (Drift to Kattegat is not shown as it was always close to 0). “Not settling” includes larvae that reach settlement length outside of nursery areas, and “outside” includes particles drifting out of the study area (see Figure 1) [Colour figure can be viewed at wileyonlinelibrary.com]

and with drift to the Skagerrak and to the Viking unit from all populations at two and three population scales. SST is negatively correlated with drift from Viking to South populations (at two populations scale) and with retention in South population (also at two populations scale). A high NAO phase corresponds to reduced drift

from the Viking to the South populations, reduced retention in the South population at the two populations scale, reduced drift from Viking to Northwest populations and reduced retention in the Northwest population at the three populations scale. The number of individuals not settling in the Viking population is associated

TABLE 4 Pearson correlation coefficients between indices of drift, climate and year

| | Source | Sink | Years | NAO | SST South | SST Viking | SST Northwest | | | | | |
|-------------------|-----------|--------------|-------|-----|-----------|------------|---------------|------|-------|-------|-------|----|
| 3 populations | South | South | | | | | | | | | | |
| | | Northwest | -0.4 | ** | | | | | | | | |
| | | Viking | 0.42 | ** | | 0.43 | ** | 0.43 | ** | | | |
| | | Skagerrak | 0.48 | *** | | 0.43 | ** | 0.37 | * | 0.42 | ** | |
| | | Outside | | | | | | | | | | |
| | Viking | Not settling | | | | | | | | -0.33 | * | |
| | | South | | | | | | | | | | |
| | | Northwest | | | -0.42 | ** | -0.39 | ** | -0.46 | ** | -0.33 | * |
| | | Viking | | | 0.37 | * | 0.38 | ** | 0.39 | ** | | |
| | | Skagerrak | | | 0.32 | * | 0.46 | ** | 0.44 | ** | 0.33 | * |
| | Northwest | Outside | | | 0.39 | ** | | | | | | |
| | | Not settling | | | -0.52 | *** | -0.29 | * | -0.4 | ** | | |
| | | South | | | | | | | | | | |
| | | Northwest | | | -0.37 | * | -0.3 | * | -0.43 | ** | | |
| | | Viking | | | 0.34 | * | | | 0.3 | * | | |
| 2 populations | South | Skagerrak | | | 0.45 | ** | 0.33 | * | 0.41 | ** | | |
| | | Outside | | | 0.31 | * | | | | | | |
| | | Not settling | | | | | | | | | | |
| | | South | | | -0.48 | *** | -0.32 | * | -0.53 | *** | | |
| | | Viking | | | 0.44 | ** | 0.33 | * | 0.4 | ** | 0.41 | ** |
| | Viking | Skagerrak | | | 0.39 | ** | 0.37 | * | 0.48 | *** | 0.44 | ** |
| | | Outside | | | 0.3 | * | | | | | | |
| | | Not settling | | | -0.37 | * | | | | | | |
| | | South | | | -0.44 | ** | -0.32 | * | -0.45 | ** | | |
| | | Viking | | | 0.37 | * | 0.33 | * | 0.39 | ** | | |
| | Northwest | Skagerrak | | | 0.32 | * | 0.45 | ** | 0.44 | ** | | |
| | | Outside | | | 0.39 | ** | | | | | | |
| | | Not settling | | | -0.52 | *** | | | -0.4 | ** | | |
| | | South | | | | | | | | | | |
| | | Viking | | | | | | | | | | |
| Single population | North Sea | North Sea | | | -0.31 | * | | | | | | |
| | | Skagerrak | | | 0.38 | ** | 0.5 | *** | | | | |
| | | Outside | | | 0.36 | * | | | | | | |
| | | Not settling | | | -0.46 | ** | | | | | | |

Note: "Not settling" represents the proportion of particles that do not reach settlement size within a nursery area and are lost.

Positive correlations are represented in light grey, negative correlation in dark grey.

Asterisks indicate the significance level (***<0.001<**<0.01<*<0.05).

White cells indicate non-significant values at the 0.05 level.

with high NAO. A high NAO is also positively correlated with high drift into the Skagerrak and outside the study area for all populations scales except the South population at the three populations scale.

4 | DISCUSSION

In this study, we combined long-term observational data with modelled estimates of larval transport to quantitatively assess the

effect of transport on recruitment across spatial scales of observation, and we propose a novel approach for measuring effective biomass contributing to recruitment. While the effect of transport on recruitment has previously been explored using coupled biological-oceanographic models (e.g. Daewel et al., 2015; Hinrichsen et al., 2016), direct inclusion of ELS dispersal model output in stock-recruitment models is less common (but see Hidalgo et al., 2019). Some studies have used proxies for larval transport such as wind speed (e.g. Hare et al., 2015; Köster et al., 2003), water circulation indices (Zimmermann et al., 2019) or cumulative average depth of

modelled particles (Baumann et al., 2006). We instead incorporate estimates of the proportion of cod larvae retained within a population and the influx of larvae from neighbouring populations, that is a more direct proxy for the effect of larval transport (Hidalgo et al., 2019), and apply this approach to the North Sea cod.

Our results suggest that although larval drift appears to play a minor role in the recruitment dynamics of North Sea cod, the effect is comparable in magnitude to the well-established effect of SST on cod recruitment (Beaugrand & Kirby, 2010; Nicolas et al., 2014). Similarly, Daewel et al. (2015) found that although correlations between modelled larval survival and observed recruitment of North Sea cod were variable and periodically low, effects of transport processes and temperature on larval survival were of comparable importance. Comparing different model formulations and population scales, our analysis captures the interplay between oceanographic drift and temperature on recruitment patterns across spatial scales of observation (Figure 7). Specifically, the importance of considering larval drift depends on the spatial scale of analyses. At the population scale, larval transport between populations and larval loss due to transport affect the recruitment in Viking and Northwest populations. When aggregating all populations at the basin scale these effects are diluted, but not dissipated, and are captured through the retention anomaly (Figure 7).

4.1 | Effective biomass

Estimating effective biomass is a novel approach to account for larval transport compared to using SSB with additive covariates. In traditional stock–recruitment models, a covariate allows higher (lower) asymptotic value, that is higher (lower) expected recruitment at a

given SSB value, while maintaining the shape of the curve (Figure 5a, c). Incorporating retention anomaly as a covariate, the interpretation is that a positive anomaly (higher than usual retention) results in higher level of recruitment compared to the same level of SSB with a lower drift anomaly. Subbey et al. (2014) point out that model forms with environmental covariates are generally linear approximations of non-linear environmental effects, approximations that might be unreliable or inaccurate. In our case, the linear approximation at the single population scale captures an overall effect that encompasses multiple mechanisms operating at finer scale. Conversely, the inclusion of drift as effective biomass allows estimating the contributing biomass to an observed recruit value and re-designing the curve altogether (Figure 5b), permitting higher flexibility to data compared to the traditional SSB.

Spawning stock biomass is a suboptimal variable for predicting recruitment, since it does not capture biological aspects such as age and size structure, sex ratio, total egg production, skipped spawning or interannual variability in fecundity or condition (Köster et al., 2003; Marshall et al., 2003; Marshall, Needle, Thorsen, Kjesbu, & Yaragina, 2006; Marteinsdottir & Begg, 2002; Mintervera et al., 2019). Marshall et al. (2006) and Köster et al. (2003) show that female-only spawner biomass and predicted potential egg production are better predictors of realised egg production than SSB in Northeast Arctic and Baltic cod stocks. Similarly, our study shows that effective SSB might be a better predictor at population scale for some populations, such as the Viking unit, characterised by large drift to other areas and low retention rate. A similar result was observed by Hidalgo et al. (2019) who found that retention influenced recruitment in European Hake populations characterised by high drift to and from other areas in the northwest Mediterranean.

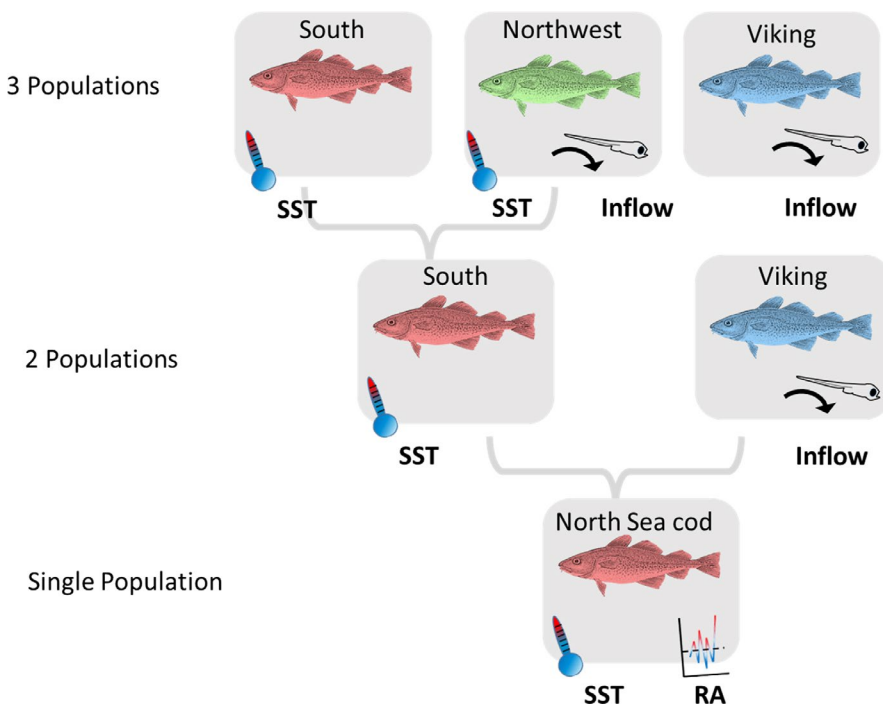


FIGURE 7 Graphical scheme summarising the key factors influencing recruitment of the different populations across spatial scales: sea surface temperature (SST), larval inflow (through connectivity with other populations) and retention anomaly (RA) [Colour figure can be viewed at wileyonlinelibrary.com]

4.2 | Effects of drift and climate variables on recruitment

We investigated the emergent relationships between climate variables (SST and NAO), connectivity and retention metrics and recruitment. High SST can influence recruitment through faster development and thus increased retention and survival to settlement (Heath, Kunzlik, Gallego, Holmes, & Wright, 2008). Additionally, both SST and NAO could be proxies for other phenomena acting at local scales, such as food availability (Capuzzo et al., 2018; Nicolas et al., 2014) and flow regimes (Henriksen et al., 2018). NAO and SST can furthermore be correlated to connectivity and retention (Table 4). However, these relationships do not necessarily affect recruitment dynamics. For example, NAO is correlated with retention and connectivity across populations and scales, but including NAO as a covariate in the stock–recruitment model does generally not improve model fit (Table 3). NAO as a proxy thus captures the phenomena influencing circulation patterns, but not those affecting actual survival to recruitment.

Sea surface temperature interacts with each population in different ways. For the South population, increased SST is correlated with increased outflow to the Viking and Skagerrak populations; however, accounting for drift does not improve the stock–recruitment model fit. This might be due to the limited outflow and high retention in the South population. The observed effect of SST on recruitment could therefore be due to other mechanisms: for example food availability (Nicolas et al., 2014), physiological constraints (Butzin & Pörtner, 2016; Nunez-Riboni, Taylor, Kempf, Pu, & Mathis, 2019) and predation by warm-water predators (Akimova, Hufnagl, et al., 2016). For the Viking population, our results suggest that SST could influence recruitment through drift both positively and negatively. In fact, higher SST is associated with increased retention and inflow, but also increased outflow to Skagerrak. At present, the two effects seem to counterbalance each other: SST does not influence recruitment according to our model results. However, with increasing SST this equilibrium, which currently masks the underlying relationships, might break down with unforeseeable outcomes in terms of magnitude and direction. Recruitment in the Northwest population is negatively associated with increased SST via reduced drift from the Viking population. The effects of both SST and inflow on recruitment are strong but not additive (indicated by similar fit of model 2 and of model 8 and 9), and likely reflect the same phenomenon: increasing temperature corresponds to decreasing inflow, resulting in lower recruitment for the Northwest population.

For the South population, the importance of SST for recruitment and its correlation with drift patterns are similar in the three- and two population scales, indicating that effects of SST (but not of NAO) on the dynamics of retention, connectivity and recruitment are dominated by the South component in the combined unit. At the single population scale, the association between SST and drift is reduced: SST is correlated with flow into the Skagerrak but not with retention. At this scale, however, recruitment is affected by SST and, importantly, by drift. Here the retention anomaly (model 4), but

not rSSB, improves the stock–recruitment model fit. The two models involve the same variable (retention), but differing mechanisms, as described in the section “Effective biomass” above.

Overall, our results indicate that the key mechanisms affecting recruitment (summarised in Figure 7) include: SST in the South population through processes unrelated to larval transport, SST and transport through the same underlying phenomenon in the Northwest population, with inflow from the Viking population and retention being higher in low SST years, and inflow from other populations into the Viking population (Figure 5b; Table 3).

4.3 | Drift patterns, retention and population connectivity

The retention and connectivity patterns estimated here broadly reflect known patterns for the area. The southern North Sea is characterised by a generally retentive system (Henriksen et al., 2018), while in the northern area there is a strong flow to the Skagerrak and the Norwegian Sea (Huserbråten et al., 2018). Consequently, the South and North populations are generally isolated, with limited connectivity (Heath et al., 2008). According to our results, connectivity between the Northwest and South units is higher, but declined from the 1970s to present, while connectivity between South and Viking units increased.

Drifting into a suitable nursery area, however, is not enough for granting survival to recruitment, as density dependence and predation after settlement might influence successful recruitment into the new populations (Akimova, Hufnagl, et al., 2016; Heath et al., 2014). Some studies discriminate potential connectivity (estimated from modelled particle drift) from effective connectivity using genetic methods (e.g. Bode et al., 2019; Jahnke et al., 2017). In our study, effective connectivity is an emerging result of fitting stock–recruitment models to data after inclusion of drift anomaly. Our results highlight that effective connectivity only affects the Viking and Northwest populations.

Notably, we assess how larval drift influences recruitment, irrespective of whether individuals merge with the host population or return to the natal population after being accounted as recruits. For example, our results indicate that larvae from the South unit enter the Viking area and survive until being accounted as recruitment of the Viking population (shown by higher fit with ndSSB than rSSB or SSB). However, the Viking and South units show genetic differences, generally considered incompatible with interbreeding between populations (Heath et al., 2014). We therefore speculate that juveniles from the South unit settle in the Viking area and survive until age 1, to then return to the population of origin. This mechanism, known as homing behaviour and site fidelity, is known for cod in the North Sea (Neat et al., 2014) and between the North Sea and Skagerrak (André et al., 2016; Jonsson, Corell, André, Svedäng, & Moksnes, 2016), and is suggested for larvae drifting from the Norwegian Trench (within our Viking area) to the Norwegian Sea (Huserbråten et al., 2018).

Although drift between the North Sea and Skagerrak is well known (Jonsson et al., 2016), we show here for the first time, to our knowledge, that larval drift from the Viking and South units into the Skagerrak is potentially of the same order of magnitude, showing an increasing trend in time and positive correlation with SST (Table 4). Although the effective contribution cannot be determined in this study, trends in larval influx from the North Sea might have implications for management and recovery of cod in offshore and coastal areas of the Skagerrak.

Our results are influenced by the assumptions and simplifications of the ELS dispersal model. However, in a previous study, Kvile et al. (2018) showed that the present model configuration yields comparable results to a more realistic but computationally costly alternative. Specifically, both the inclusion of vertical swimming behaviour and the use of a higher resolution ocean model that resolves tidal circulation had limited effects on larval drift patterns compared to interannual variations in ocean dynamics. Since our aim here was to quantify long-term interannual variation in population connectivity, we opted for a less computationally costly representation of vertical movement using fixed drift depths, and applied the coarser ocean model that was available for 44 years. Additionally, sensitivity analyses of the parameterisation of ELS mortality and settlement size, the latter related to temperature-dependent growth, confirmed the robustness of the results to these key parameters (Tables A2 and A3 in the Appendix S1). Finally, factors such as spatially explicit predation pressure and prey fields, variability in fecundity, juvenile mortality through predation and density dependence upon settlement might all affect recruitment dynamics, but are not accounted for in this study. These caveats need to be considered in the interpretation of results.

4.4 | Implications for management

Despite the relatively low prediction power and major assumptions (Subbey et al., 2014), stock-recruitment models are routinely applied in management for short-term advice (e.g. Punt, 2019), and there is increasing interest in including spatial structure in recruitment dynamics in stock assessment (Cadrin et al., 2019; Hidalgo et al., 2019; Punt, 2019). Although reliable ocean current forecasts are not available in advance, estimates of larval drift can be useful to inform short-term forecasts (Henriksen et al., 2018; Hidalgo et al., 2019). This effort is however constrained by the availability and rapid applicability of ocean models in the context of operational fisheries oceanography (Hidalgo et al., 2019).

We find relatively low fit to data in the stock-recruitment models for North Sea cod, and inclusion of indices for larval drift results in relatively small improvements. Considering the computational cost of running ELS dispersal models, one must therefore carefully consider the benefits of this approach for the specific case at hand. Regardless, our study highlights a novel approach for accounting for connectivity in stock-recruitment dynamics, with potential applications for fisheries assessment and management in

stocks characterised by highly dynamic oceanographic conditions. Adopting spawning output metrics that account for effective connectivity, for example, could affect the determination of biological reference points (Minte-vera et al., 2019), with direct implications for management. For example, relationships between drift, temperature and recruitment across populations (Figure 7) have implications for management of the North Sea cod population complex in the context of a changing climate (Nunez-Riboni et al., 2019).

Future research should focus on how climate change can influence larval transport, survival of larvae drifting between units and homing behaviour. Understanding these aspects, and developing operational fisheries oceanography and its application to management, will improve our capacity to tailor management to the population structure in the context of a changing climate.

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CONFLICT OF INTERESTS

The authors declare to have no conflict of interest.

AUTHOR CONTRIBUTIONS

GR, KK, ØL and AME conceived the research idea; GR and KK ran data analyses and wrote the manuscript; KFD, TK, ØL, AME and NCS participated in discussions of the results and critically reviewed the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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