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Cod at drift in the North Sea

M.B.O. Huserbråten^{a,b,*}, E. Moland^{a,b}, J. Albretsen^b^a Centre for Coastal Research, Department of Natural Sciences, University of Agder, N-4604 Kristiansand, Norway^b Institute of Marine Research, Nye Flødevigveien 20, N-4817 His, Norway

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ABSTRACT

There has been a large-scale geographical re-distribution of the North Sea cod stock over the past century, and recent surveys indicate a north-eastern modal distribution. Here we assess the consequences of the contemporary distribution of North Sea cod (*Gadus morhua*) spawning biomass to inter-ocean recruitment potential. By simulations of drifting cod eggs and larvae spawned in the northern North Sea over 16 spawning seasons (in the period 1995–2016), we show that a large portion of the North Sea produced pelagic juveniles most likely settle along the Norwegian Sea shelf. For example during the early 2000s when the North Sea cod spawning biomass was at its lowest, 20% to 27% of larvae produced in the northern North Sea most likely settled along the Norwegian Sea shelf, while as few as 8% and 10% were retained within the North Sea in some years. We hypothesise the spillover of North Sea cod into nursery habitat along the Norwegian north-western coast to be beneficial to the stock, as larvae would encounter far higher abundances of their favoured prey, the copepod *Calanus finmarchicus*. Looking back at a century of overfishing, warming, and variable nursery conditions for cod in the North Sea, getting entrained in the Norwegian coastal current seems like a viable “back-door exit” strategy, allowing the north-eastern spawning cod to thrive even in seemingly adverse climatic periods.

1. Introduction

There has been a large scale change in the distribution of the North Sea fish assemblage the past decades, with a general northward, deepened distribution of both exploited and unexploited species (Perry et al., 2005; Dulvy et al., 2008). This observed change has been accompanied by a dramatic decline in abundance of many commercially important species in the North Sea. The most famous example is perhaps the decline of the North Sea cod (*Gadus morhua*)—boasting a spawning stock biomass (SSB) of 300.000 t in the 1970s, plummeting down to an all time low of 50.000 t in the mid 2000s (ICES, 2015). As fishing mortality almost mirrored the cod SSB in this period, the immediate and perhaps natural explanation for the observed decline is that fishing curtailed the abundance of cod (Engelhard et al., 2014). However, throughout the modern record there has been large inter-annual as well as decadal variation in the recruitment of cod, and the single variable that explains the most of this variation is the abundance of copepod *Calanus finmarchicus* (Beaugrand and Kirby, 2010), a fundamental prey for early life stages of cod (Heath and Lough, 2007). For example, in the 1970s there was a succession of exceptional years for recruitment of cod in the middle of the North Sea correlated with high abundance of *C. finmarchicus*, a period later known as the ‘gadoid

outburst’ (Cushing, 1984; Rothschild, 1998); whereas throughout the 1990s the abundance of *C. finmarchicus* diminished in the south, leading to cod recruitment collapse (Beaugrand and Kirby, 2010). Although the SSB of cod in the North Sea as a whole has almost doubled since the collapse of the early 2000s, most of this biomass is concentrated in the northern and north-eastern North Sea (Engelhard et al., 2014; Holmes, 2014).

Whether driven by bottom-up or top-down/socio-economic processes, the spatial abundance of North Sea cod seems to have constantly been changing over the last century. And in the past decades a large part of the North Sea SSB has been found along the western slopes of the Norwegian Trench in spring, most likely congregating there to spawn (Fox et al., 2008; Hjermann et al., 2013; Engelhard et al., 2014). Coincidentally, sweeping along the northern slope of the European continental shelf and into the Norwegian Trench (i.e. on the border between the North Sea and the Norwegian Sea) we find the main entry point of *C. finmarchicus* to the shelf-system in spring, transported with the Continental Slope Jet that also supplies the North Sea with most of its Atlantic water (Heath et al., 1999; Winther and Johannessen, 2006; Hjøllø et al., 2009). However, the majority of this inflowing Atlantic water gets retroflected and eject underneath the Norwegian Coastal Current (NCC) on the eastern side of the Trench before reaching 59°N,

* Corresponding author at: Institute of Marine Research, Nye Flødevigveien 20, N-4817 His, Norway.

E-mail address: mats.huserbraaten@hi.no (M.B.O. Huserbråten).

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or mixes with the northward propagating eddies that represents the Norwegian Coastal Current (Sætre, 2007). It may thus be deduced from the circulation patterns in the area and the distribution of mature cod along the Trench that a large portion of the North Sea produced eggs and larvae will get entrained with the outbound Atlantic water at depth, or with the NCC upon floating towards the surface layers (note that cod eggs are slightly buoyant within the Atlantic water masses, Sundby, 1997)—either way a sortie from the North Sea is highly likely (cf. Figs. 1 and 2). Now, “spillover” of recruits from one perceived stock to the next is not a new phenomenon (as discussed by Frank, 1992), and it has either been directly observed or modelled all along the European range of cod reflecting the advective nature of the pelagic habitat that most cod is spawned into (Storr-Paulsen et al., 2004; Stenseth et al., 2006; Svedäng et al., 2007; Strand et al., 2017). Yet to date surprisingly little attention have been directed towards the possibility of a large scale spillover of cod production from the North Sea into the Norwegian Sea, given the high concentration of SSB along the Trench and the dominant circulation patterns in the area. Thus, herein we aim to address the question of leakage of North Sea cod recruits out of the North Sea. More specifically we wanted to: (1) describe the main dispersal pathways of cod spawned in the north-eastern North Sea and Skagerrak, as no studies have addressed this question in sufficient detail; (2) quantify the potential for settlement into the nursing grounds available to pelagic juveniles in drift in the greater northern North Sea area; and (3) expose the possibility of spillover of spawning products from the North Sea and into to the Norwegian Sea—analogueous to the hypothesis

put forward for saithe (*Pollachius virens*) spawned along the slopes of the Norwegian Trench (e.g. Furnes et al., 1986; Bjørke and Sætre, 1994). This was addressed by applying a coupled hydrodynamic/particle trajectory model with sub-routines for vertical egg and larval behaviour, and using SSB data from the ICES international bottom trawl survey (IBTS) aggregated per sub-area as tentative release points. Simulations were done for 16 spawning seasons in the period between 1995 and 2016.

Given the unfavourable nursing conditions for cod in the North Sea in the contemporary ocean climate (as shown by Beaugrand and Kirby, 2010), getting entrained within this *C. finmarchicus* highway of the Nordic Seas we predict to be highly beneficial. The rationale being that the pelagic juveniles that potentially settle along the coastal margins of the Norwegian Sea may experience far superior nursing habitat both in terms of higher food abundance and a colder, more stable temperature regime than in the North Sea proper (Beaugrand and Kirby, 2010; Melle et al., 2014). In accordance with life history theory a subsequent back-migration of the expatriates to spawn is then a prerequisite for this spawning strategy to be maintained in the long run, which is plausible as variations of this life history strategy can be found across the entire geographical range of cod (Robichaud and Rose, 2004); for example, cod spawned in the central North Sea may drift westward and settle into Swedish coastal waters and migrate back to spawn when mature (Svedäng et al., 2007); cod spawned in Iceland have been shown to recruit to nursery areas in Eastern Greenland and later showing up in Icelandic catches upon reaching maturity (Storr-paulsen et al., 2004);

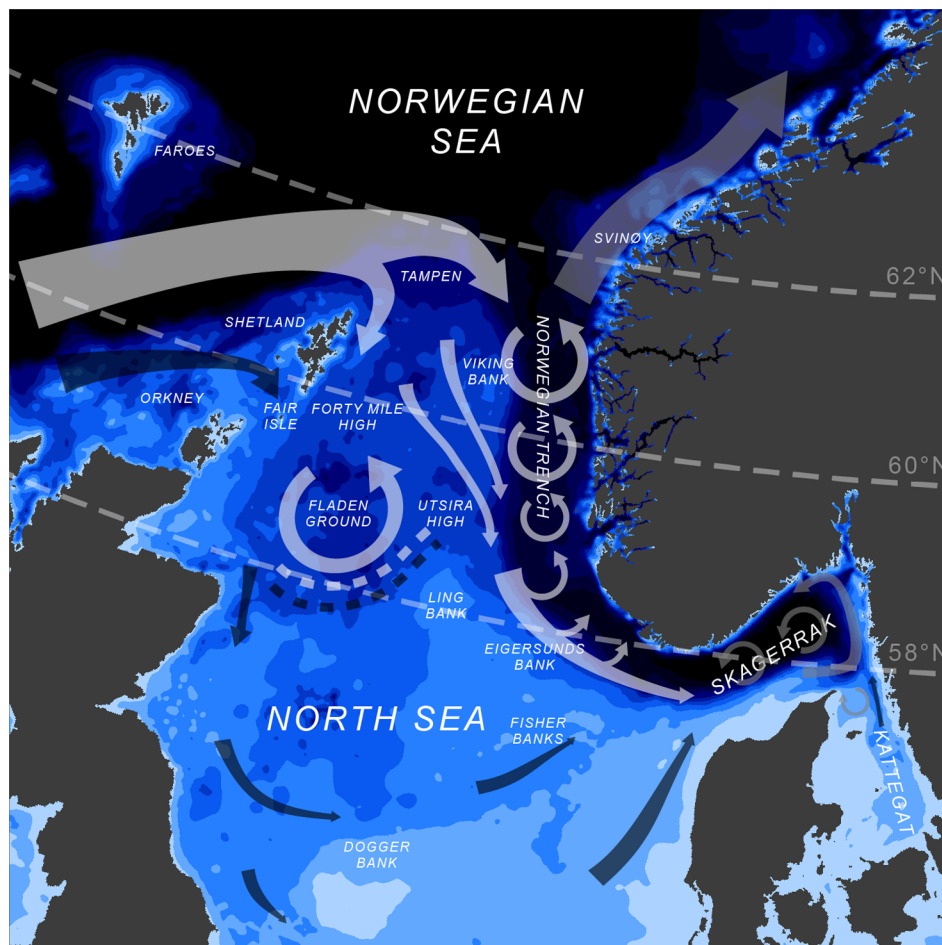


Fig. 1. Idealised large-scale circulation patterns in the northern North Sea (width of arrows roughly scaled to transport), names of areas referred to in the text, and bathymetry of the study area where blue surfaces represent the depth contours of (from light blue to black) 25, 50, 75, 100, 125, 250, 200, 250, 300, and 400 m.

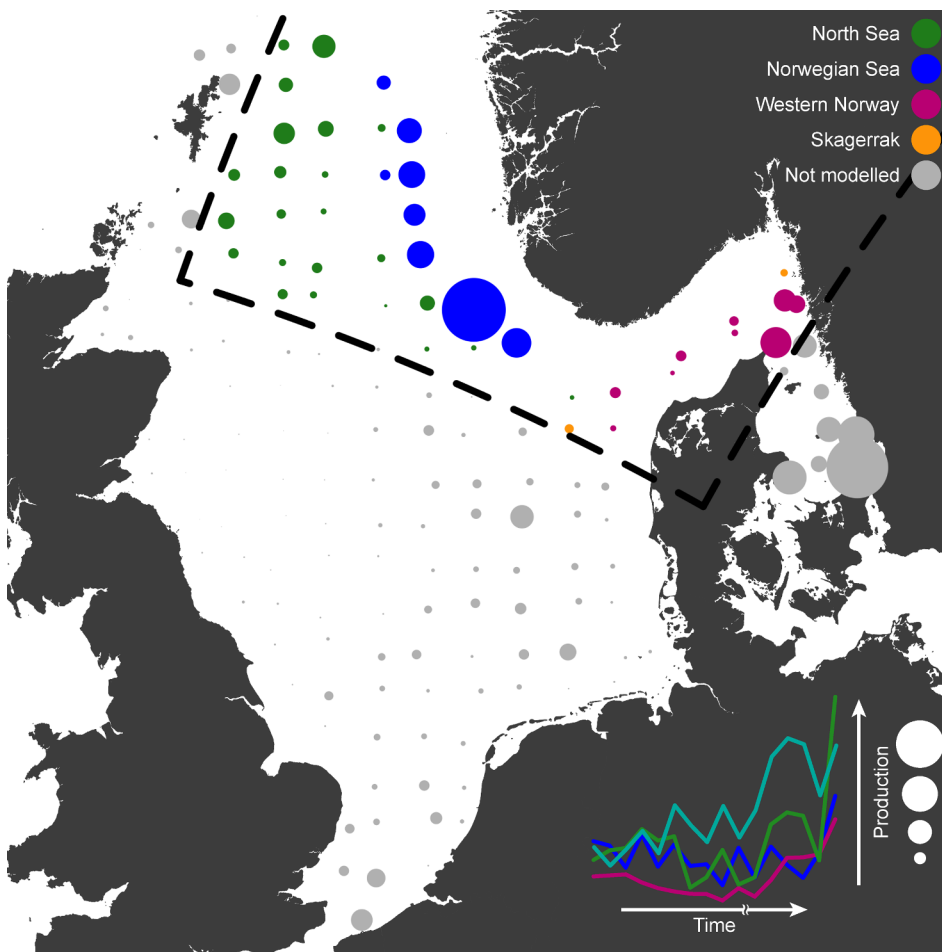


Fig. 2. Estimated average annual egg production per ICES sub-area within study period (1995–2016, omitting years 2005–2010). Here sizes of circles represent relative magnitude of production, and colours represent the hypothesised nursing area that the majority of larval trajectories eventually settled into (cf. Fig. 4A). Grey circles represents sub-areas for which egg production was estimated, but drift was not modelled. Inset graph (lower right corner) represents the temporal development in relative production among the spawning units identified in this study, while cyan line represents the proportion of total North Sea produced eggs within study area ranging from 32% to 69% (see Section 2).

and not to mention the well described spawning migrations undertaken by the north-east Arctic cod spawned off Lofoten, settling as juveniles in the Barents Sea, and eventually coming back to spawn off the coast of northern Norway (e.g. Hjort, 1914).

2. Materials and methods

2.1. Estimated egg production in north-eastern North Sea and Skagerrak

To derive an estimate of the spatial distribution of egg production in the North Sea we extrapolated potential egg production from the annual ICES international bottom trawl survey (IBTS, quarter 1). This survey is run between January and March every year, and is mainly designed to assess the SSB of cod. We used the average coordinates of the survey trawl-hauls per ICES sub-area per year as release points in our drift simulations (usually three to four hauls per sub-area), and the number of eggs released at each coordinate was calculated from the number of fish of different size classes caught in that sub-area standardised by haul duration/area trawled. For simplicity, the egg production in each year at each sub-area was calculated using the following equation for estimation of potential fecundity of Atlantic cod: $F = 5.4 \times L^3 - 13,000$ (Eq. [3] in Oosthuizen and Daan, 1974), where F is number of eggs, and L is length class of cod binned into 10 cm intervals (see Fig. 2 for the average egg production estimates over the 16 spawning seasons). We assumed a 50% sex ratio in the trawl-hauls and fish below 40 cm were considered immature, and thus did not contribute to egg production. For an exhaustive analysis of the SSB we refer to ICES (2015). The average fraction of estimated North Sea egg production that was within our model's domain was 48% for the study period (1995–2016), ranging from 32% in 1996 and 69% in 2013

(Fig. 2). A portion of the total estimated egg production in a sub-area in a given year was then released in the ocean model each day of the spawning season, where the magnitude released followed a normal distribution from February 2nd to May 9th with a peak spawning activity on March 3rd (Brander, 1994; Heath et al., 2008). To simulate spawning behaviour observed in the wild (e.g. as described in Rose, 1993), the eggs were released uniformly from one meter above the sea bottom, up to 40% of bottom depth (e.g. 20 m above sea bottom when total depth was 50 m) at each release site. The average number of particles released per spawning season was around 30,000, minimum was 16,000 in 2001, and maximum was 78,000 in 2016; totalling 490,000 particles over the 16 spawning seasons modelled.

2.2. The ocean circulation model

The circulation model used was the Regional Ocean Modelling System (ROMS, <http://myroms.org>), a free-surface, hydrostatic, primitive equation ocean model (e.g. Shchepetkin and McWilliams, 2005; Haidvogel et al., 2008). The circulation model was run with 800 m resolution in the horizontal and was forced over a time period of 16 years (1995–2016, without years 2005–2010), using daily averages of currents and hydrography along the open boundaries from a large-scale model covering the Nordic Seas (Lien et al., 2013), high-resolution wind fields (Weather Research and Forecasting model, WRF, using 3 km horizontal resolution, see Skamarock et al., 2008) and realistic freshwater discharge from all rivers in the model domain (provided by the Norwegian Water Resources and Energy Directorate, see Beldring et al., 2003). The time-varying arrays from the ROMS contained velocity fields and physical variables with a temporal resolution of one hour (i.e. allowing tidal motion to be properly resolved), 35 terrain following

depth layers, and covering a total area of 2602×902 grid points giving a total model area of approximately $2080 \text{ km} \times 720 \text{ km}$ (see inset in Fig. 4A). More technical details on the ROMS simulation can be found in Albretsen et al. (2011). To validate the ocean model we compared its physical output variables (salinity and temperature) with hydrographical data routinely sampled within the model domain. Overall, the model compared well with observations, with no significant biases in predicted salinity or temperature, equivalent to former and more comprehensive validation analysis of the same modelling system shown in e.g. Myksvoll et al. (2013) and Strand et al. (2017).

2.3. The individual based model for eggs and larvae

At the initiation of each drift simulation, eggs were assigned an individual buoyancy value measured in practical salinity units. As no studies have quantified buoyancy of North Sea cod eggs, we used values typical of Arcto-Norwegian cod, around 32 psu (Sundby, 1997). Density of eggs was then calculated as a function of its pre-set salinity equivalent and the ambient sea temperature (Sundby and Kristiansen, 2015). At each time step of ten minutes, the egg was then pushed either upwards or downwards depending on the hydrostatic pressure acting on it. Egg incubation time was calculated as a function of temperature (Peterson et al., 2004), and upon hatching larvae experienced temperature dependant growth (Folkvord, 2005). In the wild, young cod larvae are generally found within or immediately below the pycnocline (Munk, 2014), while older larvae are found deeper (Lough and Potter, 1993). Cod larvae are also known to display a vertical movement of up to 10 m over the course of 24 h (Höffle et al., 2013; Munk, 2014), indicating some active movement in the water column. However, during episodes of high wind-induced turbulence, smaller larvae have been shown to be mixed homogeneously in the water column (Ellertsen et al., 1984). Thus, from hatching until time of first feeding our modelled larva had little swimming capability (max 10 cm per 10 min), vertical position was mainly regulated their density (here we used the same density as the egg stage), and they were programmed to attract towards the pycnocline. Maximum vertical swimming speed of feeding larva smaller than 10 mm was set to 0.2 m per 10 min, while bigger larvae could swim up to 0.8 m per 10 min time step. The potential integrated vertical swimming distances used in the model was well below critical swimming speeds observed in laboratory experiments (Guan et al., 2008), however, there are no empirical evidence for extensive swimming activity in the wild. After the time of first feeding, we hypothesised that vertical position was regulated by larva's behaviour in response to light. The rationale is that a certain amount of light is needed to feed, while too much light would increase predator exposure. Thus, the feeding larvae were programmed to swim upwards if situated below the isolume of 1 W/m^2 , downwards if above the isolume of 10 W/m^2 , and remain still at onset of total darkness (see Fig. 3 for a sample of the vertical movement profile of eggs, larvae, and pelagic juveniles). To

account for vertical mixing experienced by eggs and larvae, a pre-set vertical perturbation component was added at each time step (up to 0.5 m per 10 min). If mixed into the transition layer and when situated below the upper mixing layer, one tenth of the mixing coefficient was used. The mixing layer depth was calculated as the depth where the vertical gradient in water density was highest. Particle advection in the horizontal plane was modelled using a fourth-order Runge-Kutta scheme with the velocity field arrays from the hydrodynamic model. We included no horizontal swimming behaviour to larvae in our model.

When larvae reached a size between 25 mm and 35 mm they were defined as ready to settle (larvae within this size range is hereby referred to as pelagic juvenile), as this is the size range of newly settled larvae observed along the Skagerrak coast and in the north-western part of the North Sea (Bastrikin et al., 2014; Johannessen, 2014). To quantify the spatial distribution of settlement in the model area, we integrated the number of days spent by pelagic juveniles in proximity of each $800 \text{ m} \times 800 \text{ m}$ grid cell of our hydrodynamical model that was shallower than 200 m. To quantify the relative importance of the hypothesized settlement areas, we divided the area shallower than 200 m into specific nursery areas we termed: the northern North Sea, Skagerrak, Kattegat, western Norwegian coast, Norwegian Sea coast, and Barents Sea (see insert in Fig. 4A). Note that although the western Norwegian coast nursery area technically is a part of the North Sea, we distinguished the two areas because they stood out as two geographically separate entities separated by the deep Norwegian Trench. To determine how sensitive the observed settlement patterns were to the vertical behaviour included in the individual based model, we ran a separate set of simulations for selected years (1995, 2004, 2011, and 2016) with a fixed depth in the upper water column distributed uniformly from 1 to 30 m, from release to settlement.

3. Results

As hypothesised in the introduction, the cod spawned along the western slope of the Norwegian Trench had indeed a high chance of settling along the shelf habitat along of the Norwegian Sea coast. The probability of settling there integrated over all 16 years varied between 14% and 31% among the eight ICES sub-areas situated along the western slope of the Trench, with a median around 25%. For example, a cod larvae spawned in the ICES sub-area with the highest average estimated egg production (close to the Eigersunds Bank, cf. Fig. 1) had a 2.2 times higher probability of settling along the Norwegian Sea coast than within the North Sea. At the same time, there was a high degree of retention of cod spawned over the northern North Sea plateau (i.e. the area east of the Norwegian Trench, Fig. 4A). Most of the particles released along the southern slopes of the trench, over the Fisher Banks, and in the Skagerrak followed a characteristic 'Skagerrak loop' with a counter-clockwise trajectory along the Danish, Swedish, and Norwegian Skagerrak coasts. The majority of these particles eventually settled into

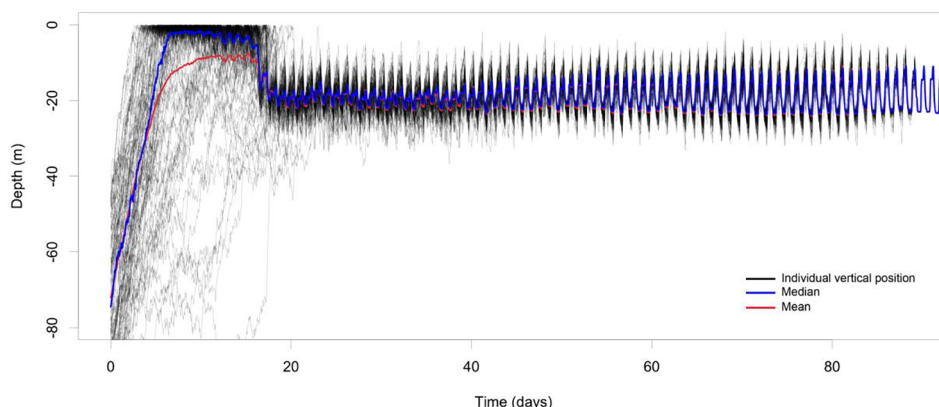


Fig. 3. Vertical distribution through development of 100 eggs, larvae, and pelagic juveniles spawned over the western slopes of the Norwegian Trench. Here majority of hatching occurs \approx day 16 after initiation, the yolk-sac stage ends some days later, and when larvae starts feeding the characteristic diel vertical movement starts. At days 80+ the larvae have reached 25 mm and control of vertical position is assumed to be total (i.e. more or less following the isolume of 1 W/m^2). Blue line represents the median depth, while red represents mean depth.

the North Sea along the western coast of Norway (see purple lines in Fig. 4A). However, the ‘affinity’ for settling into a particular area was not as clear as on the plateau or along the western slopes of the trench, as the probability was almost equal for settling in the Skagerrak, western Norway, the North Sea plateau, or the Norwegian Sea coast. Moreover, integrated over all the years of simulations, the most important settlement area was on the northern North Sea plateau between the Viking Bank, the Fladen Ground, and Utsira High, and secondly the shelf margin along the north-western coast of Norway (Fig. 4B). There was also a high variation in the alongshore distribution of the settlement along the coastal margin of the Norwegian Sea among the years. For example, the year when the “spillover” from the North Sea reached the furthest, in 2011, the median of the distribution was 155 km further downstream than in 2000 when the pelagic juveniles settling into the area drifted the shortest. Comparing the quarter of the distribution that drifted the furthest (i.e. the 3rd quartile of the distribution) in these two years (2011 and 2000) the difference was 325 km (Fig. 4C). Note that the probability of being advected into unsuitable settlement habitat (> 200 m) was more than two times higher if spawned along the Trench than on the northern North Sea plateau, with a median probability of 0.34 among the eight trench areas compared to a median of

0.16 among the shelf areas.

Looking at drift trajectories within individual spawning seasons in more detail; although many of the particles released in the North Sea were retained over the northern North Sea plateau, there was a linear decline of particles retained there over time in most of the spawning seasons, where the slope of the decline varied little among years. This linear decline of particles retained on the northern North Sea plateau was mirrored in an almost equal increase in particles flowing into the Norwegian Sea (Fig. 5A). Depending on year, everything from 28% to 66% (median = 33%) of the cod spawned in the North Sea part of the model domain entered Skagerrak at some point in time (i.e. did some variation of the ‘Skagerrak loop’). The remainder of the particles was either advected into the model boundaries (and subsequently removed from the study), advected into Kattegat, or the Barents Sea, which did happen in most years but the proportion was always less than 0.01 of total production before the pelagic phase of larvae was over.

There was also some variation in progression of the settlement phase among years (i.e. the onset of the time interval when larvae where between 25 and 35 mm), where the mid-point of the settlement phase (i.e. when 50% of all potential settlement days had accrued) varied between the 10th of June in the warmest years and 6th of July in

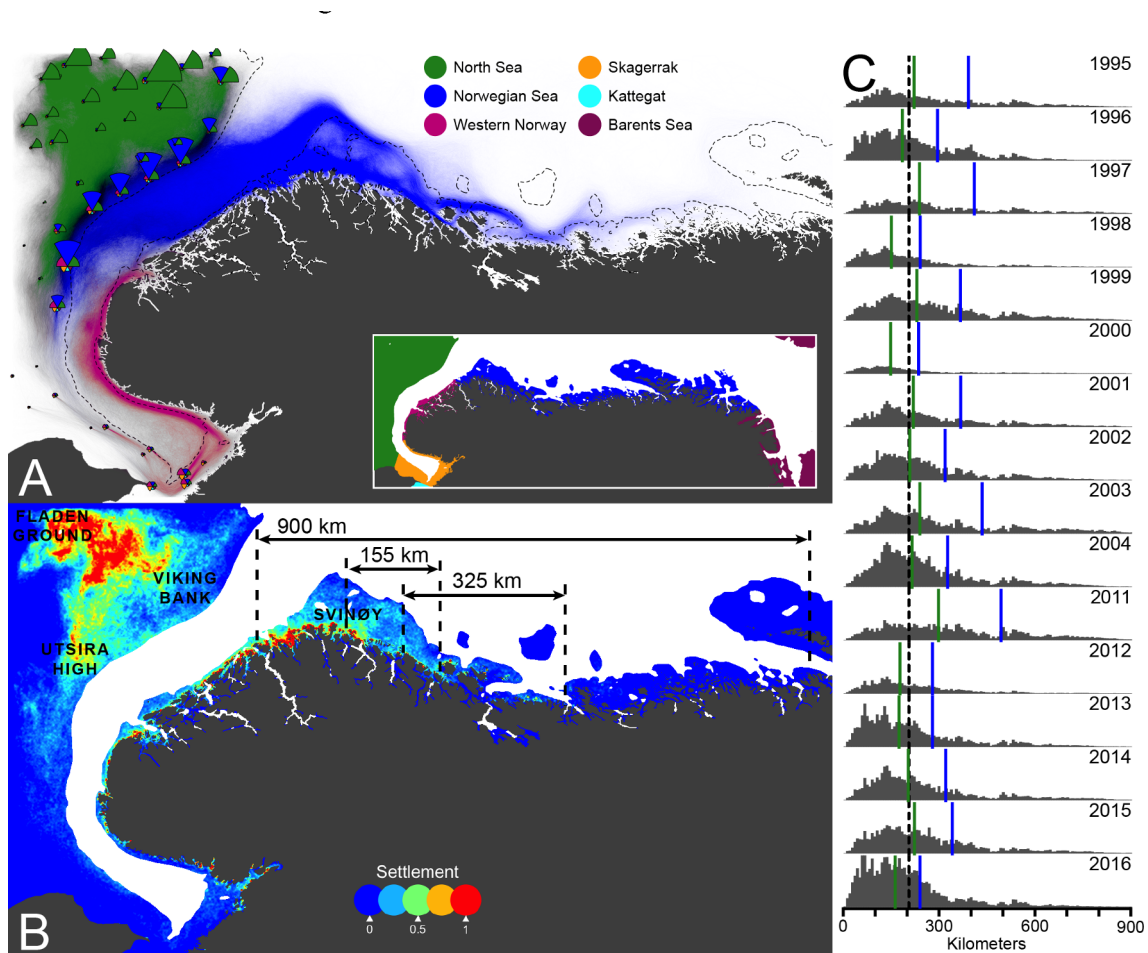


Fig. 4. Fate of cod spawned within the ICES sub-areas integrated over 16 spawning seasons between 1995 and 2016. (A) Here the area of the pie-slices represent the relative probability of cod spawned within a given ICES sub-area to settle into one of the hypothesised nursery areas (as they appear in the insert, note that the juveniles that settled in unsuitable habitat was factored out) scaled by the average production of eggs in the ICES sub-area. Coloured lines represents trajectories of individual larvae that successfully settled into the nursing ground that the majority of larvae from that location settled into. (B) Density distribution of the integrated number of settlement days received per grid cell of the ocean model shallower than 200 m. (C) Alongshore distribution of settlement days received by the nursery area along the Norwegian Sea coastal margin (i.e. along the horizontal axis of the blue area in the A insert). Green and blue vertical lines represent the median and 3rd quartile of the distribution in the given year; stippled line represents the median among all the 16 years.

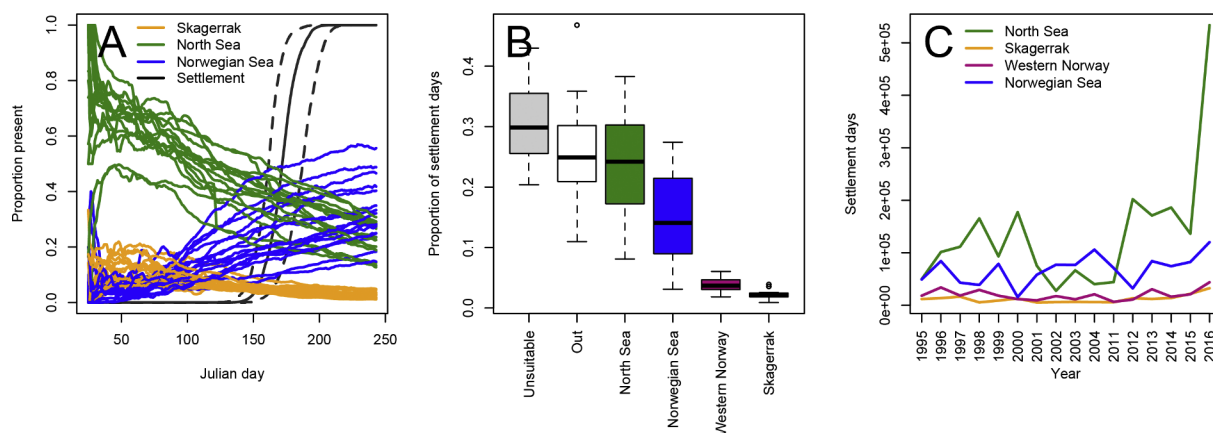


Fig. 5. (A) Proportion of particles present in the North Sea (green), Norwegian Sea (blue), or Skagerrak (yellow) during each year of simulations. Black curve represents the progression of the settlement phase in a ‘normal’ year, with extreme values indicated by the stippled lines. (B) Boxplot of proportion of settlement days received by the respective nursing grounds, see insert in Fig. 4A for extent of nursing grounds available to pelagic juveniles in drift. (C) Absolute number of settlement days received by nursing grounds in all the years of simulations.

the coldest years, with an overall median among the simulations at 21st of June. When integrating the number of settlement days spent within the hypothesised nursing habitats situated within the respective oceans, the most important settlement area was the northern North Sea plateau, which received 24% of the settlers in a ‘normal’ year, although with considerable variation among years. The proportion of settlers received by the shelf habitat along the coast of the Norwegian Sea in a normal year was 14%; also here there was considerable variation among years (Fig. 5B). The proportion of settlers received by the coast off western Norway and Skagerrak in a normal year was 3% and 2%. The absolute number of settlement days received by the northern North Sea plateau was almost always higher than the number received by the Norwegian Sea shelf habitat – although interestingly, in the beginning of the 2000s, the Norwegian Sea shelf habitat received the majority of settlers (Fig. 5C).

Based on the sensitivity analyses run for four of the years (namely 1995, 2004, 2011, and 2016) there was a negligible difference in the number of settlement days received by the nursing areas when vertical position was fixed at a depth between 1 and 30 m. The average difference among 32 comparisons was less than one 1%, with a standard deviation of ≈ 1 , where the highest difference was between the proportions that were advected onto the model boundary in 1995, where the model with a fixed depth lost 4% less of the particles. On closer inspection, the simulation of 1995 was affected by what appeared to be an episode of strong easterly winds between 21st of April and 1st of May, pushing the surface layer of the northern North Sea plateau out of the model area, taking with it many of the particles.

4. Discussion

Here we show that during the past two decades of cod spawning in the north-eastern North Sea and Skagerrak, around 24% of pelagic juveniles produced there settled onto the northern North Sea plateau while 14% settled along the coastline of the Norwegian Sea in a ‘normal’ spawning season; the numbers presented here being representative for an average of 48% of the total North Sea SSB (including Skagerrak and Kattegat) in the study period. However, in the period 2001–2004 there were strong anomalies in the spatial settlement patterns, when between 20% and 27% of the pelagic juveniles settled to the Norwegian Sea coastal margin; while at the same time in 2002 and 2004 only 8% and 10% was retained in the North Sea (cf. Fig. 5C). Interestingly, this low point in retention of production on the northern North Sea plateau coincided with the period when the SSB in the North Sea was at its lowest since the beginning of the modern record (i.e. since

the 1950s). Also, in line with the observed “comeback” of SSB on the northern North Sea plateau in recent years (which caused the huge increase in egg production there in 2016) we also observed a high retention on the plateau, culminating with a high point in 2016 when 38% of benthic recruits settled onto the plateau. There was also a high chance (median of 30% among the years) of being advected into unfavourable habitat, which transposes directly to *Hjort’s second hypothesis* (1914) that names advection into unfavourable habitat as one of the major causes of mortality in fish larvae. Although no spatially explicit mortality field was included in the model due to a lack of data, we hypothesise that this would only reinforce the observed asymmetry in the spatial recruitment patterns observed during the climatically adverse period of the 2000s, as will be addressed in the discussion below (see Section 4.2).

4.1. A synoptic outline of cod dispersal units in the northern North Sea

Earlier studies that have modelled the drift of cod eggs and larvae in the North Sea have suggested a substantial downstream transport of cod propagules from the spawning grounds along the western and north-western margin of the North Sea to the southern nursing areas (e.g. Dogger bank). At the same time the retention of eggs spawned over historically important spawning grounds in the southern North Sea, for example around Dogger bank, the Southern Bight, and the German bight appears almost total, although with a leakage up to 35% from the north-eastern extreme of Dogger bank into Skagerrak in some years. By contrast, less than 5% of pelagic juveniles spawned within the north-eastern North Sea are advected into nursing areas in the western and southern parts of the North Sea (Heath et al., 2008; Jonsson et al., 2016). The north-eastern spawning assemblage of cod also constitutes a genetic unit, in distinction to the cod in the Celtic Seas, or cod spawning along the north-western, western and southern margin of the North Sea (Heath et al., 2014). This genetic heterogeneity is highly parsimonious with the large-scale circulation pattern of water masses in the northern North Sea, where several more or less defined currents effectively divide the northern North Sea cod stock into two or more “dispersal units”.

The first unit, the Dogger dispersal unit, extends downstream of the Fair Isle current that enters the North Sea between Orkney and Shetland, and this current transports coastal water originating from west of the British Isles into the North Sea (cf. Fig. 1). Its path continues south past the Scottish coast, and before reaching 57°N it turns east in an anti-clockwise fashion, while deflecting parts of its mass south along the English coast (in some sources referred to as the ‘Fulton drift’, e.g. in

Fransz et al., 1991) and onto the shallower central/southern North Sea (e.g. the Dogger bank). Cod spawned into the water masses along this path may potentially settle all along the route sketched out above, namely as the genetic data suggest, along the north-western, western and southern margin of the North Sea (Heath et al., 2014). In the contemporary ocean climate, and especially during the early 2000s, the survival of older cod larvae within this flow regime is/was probably low, considering the low amount of *C. finmarchicus* that was/is advected with the coastal water originating from west of the British Isles in spring (Beare and McKenzie, 1999; Gallego et al., 1999; Greene et al., 2003).

The second tentative dispersal unit is the Viking dispersal unit, which roughly coincides with the northern North Sea plateau spawning assemblage/nursery area described in this study. The Viking dispersal unit is separated from the Dogger unit by the East Shetland current, which transports Atlantic water into the North Sea in a southern direction along the eastern side of Shetland. Before reaching 58°N, the East Shetland current also turns east and aligns with the Fair Isle current in a double-entrainment, and together they form an anti-clockwise gyre over the Fladen ground (cf. Fig. 1). A branch of this double Fair Isle/East Shetland current (together referred to as the 'Dooley current') turns around the Ling bank and into Skagerrak (Svendsen et al., 1991; Turrell et al., 1996), effectively dividing the North Sea into two oceanographically and biogeographically decoupled parts (Otto et al., 1990; Fransz et al., 1991). As highlighted in this study, the cod spawned into the water masses on the northern North Sea plateau most likely settle somewhere between the Viking Bank, the Fladen Ground, and the Utsira High. The survival of cod larvae spawned into this area is expected to be variable among years, given the high variation in advection of *C. finmarchicus* with the East Shetland current (Gallego et al., 1999; Harms et al., 2000), but the increase in cod SSB during the 2010s in the area suggest a clear improvement in nursing conditions compared to the 1990s–2000s.

4.2. The Norwegian Trench as a spawning refuge in climatically adverse periods?

Because of the novelty of our results, there is to date no clear answer to whether the cod that spawns along the western slopes of the Norwegian Trench should be considered a separate dispersal unit (i.e. a Trench-Norwegian Sea dispersal unit, spawning in the North Sea with nursery area along the Norwegian north-western coast). Heath et al. (2014) did discover significant genetic heterogeneity within the entities named in previous section (although subtle), but further genetic studies are needed to quantify the potential reproductive isolation between the Viking dispersal unit and the tentative Trench dispersal unit. Nevertheless, an interesting aspect of this study was the coincidental timing of a high proportion of North Sea SSB concentrated along the western slopes of the Trench with a high export to the Norwegian Sea during the seemingly adverse climatic period of the yearly 2000s. Given the highly correlated relationship between geographical distribution of cod and the fluctuating bio-geographical distribution of *C. finmarchicus* (Sundby, 2000; Beaugrand and Kirby, 2010), we find it necessary to briefly review the ecology of *C. finmarchicus* in the Norwegian Trench circulation system. The closest upstream overwintering ground of *C. finmarchicus* in the region is situated in the Faroe-Shetland channel (Heath and Jonasdottir, 1999), and the overwintering copepodites' least variable entry point to the highly productive NCC is through the mouth of the Norwegian Trench (Gallego et al., 1999; Harms et al., 2000). After the brief visit in the Trench mouth the outflowing Atlantic water aligns with the NCC and at $\approx 63^\circ\text{N}$ offshore off Svinøy, which coincidentally is 'spot on' the long-term median of the alongshore distribution of the cod larvae settling in the Norwegian Sea (cf. Fig. 4B and C), the highest abundances of *C. finmarchicus* across the entire northern hemisphere is found (Melle et al., 2014).

Spawning at a location that ensures larvae and pelagic juveniles are advected into this *C. finmarchicus* hot spot seems to be a successful

spawning strategy for the North Sea gadoids. For example, the main spawning ground used by the North Sea saithe is over the far northern, deep end of the North Sea/European continental shelf (in the Tampen area, cf. Fig. 1). Most of the saithe eggs and larvae spawned there most likely follow a similar path as the cod spawned along the slopes of the Norwegian Trench highlighted in this study, as shown by Furnes et al. (1986) and Bjørke and Sætre (1994). The comparably vast SSB of North Sea saithe since the 1990s of between 100.000 and 300.000 tonnes bears witness to the recruitment potential that lies in this spawning strategy even in the seemingly unfavourable climatic period since the start of the 90s (ICES, 2015). It thus appears that despite the declining trends of *C. finmarchicus* in the North Sea proper (Beare and McKenzie, 1999), the Trench inflow regime facilitates more stable nursery conditions to the cod larvae spawned there (Beaugrand and Kirby, 2010). On the other hand, because of the affinity of cod juveniles to the benthic habitat, in contrast to for example the more pelagic saithe juveniles, the narrowness of the shelf margin along the Norwegian Sea makes the probability of attaining suitable nursery habitat lower, reducing overall production potential of this spawning strategy for cod (as compared to saithe). Ultimately the two spawning strategies (shelf vs. trench slope) represent a trade-off in potential fitness, with better food conditions for larvae spawned in the trench vs. a higher probability of settling into preferred habitat if spawned on the North Sea shelf.

In a longer time perspective, the ocean-climate of the North Atlantic and the Nordic Seas have followed a quasi-periodic cycle of around 65 years (i.e. the Atlantic Multidecadal Oscillation, Knight et al., 2005)—where the two latest cold periods coincided with the strong recruitment years for cod in the North Sea of the 20s and 60s–70s. But because of the general warming of the ocean-climate of the North Atlantic and Nordic Seas, the sub-arctic zooplankton assemblage (of which *C. finmarchicus* contributes the highest biomass) is projected to continue their northward retreat into the foreseeable future (Beaugrand et al., 2008). However, there are aspects of the northern North Sea-Skagerrak circulation that gives the system a certain resilience. For example, as long as there will be a compensatory return flow of the Norwegian Sea deep water into the Faroe-Shetland Channel, that is, as long as the meridional overturning circulation continues in its present mode (Rahmstorf, 2002; Kuhlbrodt et al., 2007), the integrity of the Faroe-Shetland Channel as overwintering habitat to *C. finmarchicus* will probably be maintained (Wilson et al., 2016).

Thus in essence, due to the inherent flow dynamics between the northern North Sea and Norwegian Sea and the upstream position of the Faroe-Shetland Channel containing overwintering *C. finmarchicus*, even in climatically unfavourable periods the Norwegian Trench inflow regime can facilitate favourable nursing conditions to the spring spawning gadoids spawning there. Whether spawning along the western slope of the Norwegian Trench is a behavioural response of the Viking spawning unit to adverse ocean climate, or if the cod that spawns there constitute a separate entity within the North Sea cod population complex, further studies have to show.

4.3. Model evaluation and caveats

The individual based model seemed to represent the development stages of cod well, with the modelled pelagic juvenile settlement window coinciding well with timing of settlement observed in the wild (Bastrikin et al., 2014; Johannessen, 2014). At the same time, the assumptions made on the vertical movement of larvae appeared to have a negligible effect on the potential settlement patterns. The high probability of larvae entering the Skagerrak, represented by the large fraction of particles doing a variation of the 'Skagerrak loop' compare well with field observations done in the front north of the Danish Jutland coast (Munk, 2007, 2014), and the few data points that are available for the abundance of cod larvae along the western Norwegian coast indicates some agreement with our model (Riley and Parnell, 1984; Nedreaas et al., 2008). Moreover, an issue with the model was that

roughly 25% of particles drifted onto the model boundary. For example, among the particles released over the Fisher Banks and in the southern parts of Skagerrak the portion that was advected onto the model boundary to Kattegat was especially high, with an overall median of 39% among these areas (as opposed to a median of 19% among all the other areas). Since the model boundary intersected parts of the dispersal paths taken by many of the particles doing the ‘Skagerrak loop’ (most notably those that were advected into Kattegat), this may cause a bias in results and downplay the importance of Skagerrak/Kattegat, and to some degree the south-western Norwegian coast, as nursery areas. This bias should be considered when looking at the overall settlement patterns, as more larvae may potentially settle in Kattegat and Skagerrak than presented here. However, considering the narrow area of suitable habitat along for example the Norwegian and Swedish Skagerrak coasts, the overall importance of these areas is still expected to be substantially lower than for example the Norwegian Sea coast. Regarding estimation of potential fecundity, we duly note that the simple equation used herein was unable to account for any population specific changes in size at maturity, or maturity ogives, that might have occurred in the study area throughout the period spanning the study – or any differences in the same between the modelled sub-areas.

4.4. Conclusions and implications

Here we showed that a large proportion of pelagic juveniles produced in the North Sea might settle along the shelf margin of the Norwegian Sea. The spillover of North Sea cod into nursery habitat along the Norwegian north-western coast we hypothesise to be beneficial to the stock, as pelagic- and recently settled juveniles would encounter far higher abundances of their favoured prey. However, a trade-off in fitness is to be expected between spawning along the Trench, that favours spillover into the Norwegian Sea – as opposed to spawning on the northern North Sea shelf, as spawning products originating from the Trench had a markedly higher chance of being advected into unfavorable habitat. An obvious implication of the modelled spillover of production from the North Sea into nursery areas along the Norwegian north-western coast is that the identified nursery areas should be surveyed during the ICES IBTS, in an endeavour to obtain a more holistic picture of the vital rates of the North Sea cod stock. This advice should be accentuated in periods of adverse climatic conditions, during which this nursery habitat become even more important to the North Sea cod population complex.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.pocean.2018.07.005>.

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