

The effects of spatial and temporal variations in spawning on offspring survival in Northeast Arctic cod

C. A. K. Endo ^{1,2,*}, M. D. Skogen¹, L. C. Stige ^{2,3}, S. S. Hjøllø¹ and F. B. Vikebø ^{1,4}

¹Institute of Marine Research, P.O. Box 1870 Nordnes, NO-5817 Bergen, Norway

²Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biosciences, University of Oslo, P.O. Box 1066 Blindern, N-0316 Oslo, Norway

³Norwegian Veterinary Institute, P.O. Box 64, N-1431 Ås, Norway

⁴Geophysical Institute, University of Bergen, P.O. Box 7803, NO-5020 Bergen, Norway

*Corresponding author. tel: +47 901 27 893; e-mail: clarissa.endo@hi.no.

Climate change and harvesting result in temporal and spatial changes and variability in spawning, and thus in offspring ambient drift conditions. As a result, variable survival of offspring and thereby in recruitment are expected. This is especially true for species with long reproduction migration as is the case for some Atlantic cod stocks. We utilize biophysical model simulations to analyze survival from spawning until age 1 resulting from different scenarios of spatial and temporal changes in spawning. We find that survival is 1.5–2 times higher when spawning is shifted southwards as compared to northerly shifts. In general, survival is more sensitive to shifts in spawning location than in spawning time. Early spawning is only favourable if spawning is concurrently shifted farther north. A future spawning scenario with a northward shift in spawning grounds beyond what has been observed historically suggests reduced offspring survival and increased sensitivity to the timing of spawning.

Keywords: Barents Sea cod, climate change, fish population demography, individual-based model (IBM).

Introduction

Global climate change and ocean variability act on ecosystem components at a wide range of spatial and temporal scales, and operate through diverse mechanisms, including changes in temperature, stratification, sea ice, turbulence, advection, and trophic interactions (Drinkwater *et al.*, 2010; Cheung *et al.*, 2013; Kjesbu *et al.*, 2021). This comes in addition to anthropogenic pressures such as fisheries, which in concert result in changes in phenology, age, and size of the spawners, species distribution, and productivity in ocean ecosystems. Climate change and fisheries are identified as the main causes for modifications in fish population dispersal, abundance, and population dynamics (Perry *et al.*, 2010; Kjesbu *et al.*, 2014). Environmental changes are expected to affect marine organisms through all life stages, but especially the early life stages, with consequences for populations, communities, and the structure and functioning of whole ecosystems (Perry *et al.*, 2010). For example, changes in temperature, primary and secondary production, prey distribution, and hydrodynamic conditions are observed and projected as the main causes for distribution shifts of fish and other marine species (Perry *et al.*, 2005; Ottersen *et al.*, 2010; Dalpadado *et al.*, 2012). With higher temperatures, fish populations are expected to shift their distributions to higher latitudes and have smaller body sizes (Perry *et al.*, 2005; Cheung *et al.*, 2013).

Fisheries directly affect the abundance and demographic structure of the spawning stock. By reducing the chance of individuals to reach older age, the demographic structure changes, which in turn affects life-history traits, thereby reducing the buffering capacity of the population against pressures including climate change. Older and larger individuals

tend to have longer (time) and larger (space) spawning distribution than younger and smaller individuals (Opdal, 2010). Fisheries pressure also affects the spatial distribution of the adult population (Engelhard *et al.*, 2014). Therefore, fishing pressure can potentially have unforeseen consequences for offspring growth and survival, which depends on the spatial and temporal distribution of the spawning adults (Ottersen *et al.*, 2006). Fisheries may in addition to short-term effects on the biomass, demographic composition and spatial distribution of the stock, result in long-term responses, e.g. evolutionary changes in growth and maturation (Heino and Godø, 2002; Jørgensen *et al.*, 2008). Changes in biomass and demographic structure may take years to decades to rebuild after strong harvesting depending on factors such as the generation time and recruitment pattern of the fish species in question as well as on interactions with other species. For example, in the Northwest Atlantic several cod stocks collapsed following heavy fishing in the 1990s and have yet not rebuilt despite bans on fishing (Frank *et al.*, 2011; Hutchings and Rangeley, 2011).

The Northeast Atlantic (NEA) stock of Atlantic cod (*Gadus morhua*), or the Barents Sea cod, spawns at banks from 63°N to 71°N along the Norwegian coast (Figure 1). The spawning activity is highest around the Lofoten region at 69°N and more variable among the spawning sites (SS) in the Finnmark region towards the north and the Møre region towards the south (Sundby and Nakken, 2008). The use of spawning locations by the adult stock has been found to vary between warm and cold decadal to inter-decadal periods, but also according to the demographic composition of the spawning stock, possibly shaped by fishing pressure (Langangen *et al.*, 2018). The relative roles of climate and fishing in driving the changes

Received: June 27, 2022. Revised: February 3, 2023. Accepted: February 17, 2023

© The Author(s) 2023. Published by Oxford University Press on behalf of International Council for the Exploration of the Sea. This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

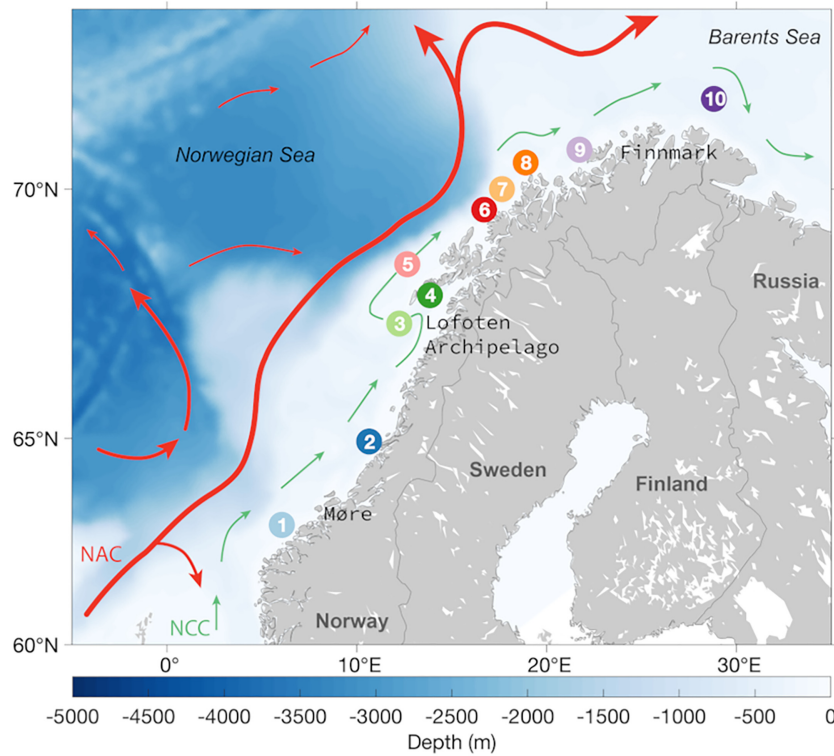


Figure 1. Study area and spawning sites (and particle origin) used by Northeast Arctic cod along the Norwegian coast. (1) Møre, (2) Vikna, (3) Røst, (4) Lofoten, (5) Moskenesgrunnen, (6) Senja, (7) Malangsgrunnen, (8) Torsvåg, (9) Breivikbotn, and (10) East Finnmark. Main ocean surface circulation pattern in the Barents Sea and Norwegian Sea is represented by the Norwegian Coastal Current (green arrows) and the Norwegian Atlantic Current (red arrows).

in spawning location remain, however, controversial (Sundby and Nakken, 2008; Opdal, 2010; Opdal and Jørgensen, 2015; Sundby, 2015; Langangen *et al.*, 2018). Both the Norwegian Sea and the Barents Sea are expected to warm in a future climate (Skogen *et al.*, 2018). By identifying physical conditions at preferred SS utilized under present climate conditions, Sandø *et al.* (2020) analyzed the results from a regional climate model simulation that used initial and boundary condition variables derived from the Intergovernmental Panel on Climate Change Representative Concentration Pathway scenario RCP4.5 (IPCC, 2013), and identified suitable spawning grounds in a future warmer climate. When limiting spawning to water-masses with temperature (T) and salinity (S) in the range $4^{\circ}\text{C} < T < 6^{\circ}\text{C}$ and $34.0 < S < 34.9$, they found that over the next 50 years the spawning grounds may shift towards the northeast. At the traditional SS from Lofoten and southwards, temperature was a limiting factor, and these grounds lost their suitability as spawning habitats (Sandø *et al.*, 2020).

As both climate change and harvesting pressure result in temporal and spatial changes and variability in spawning and in adult spawning condition, variability in survival of offspring and thereby in recruitment are expected. After spawning, the eggs and subsequently larvae drift northeast towards the Barents Sea. Depending on the location and time of spawning, each individual experiences a unique drift route, with variable biotic and abiotic conditions, which influence individual survival (Vikebø *et al.*, 2007; Putman *et al.*, 2016). Individuals spawned at the southern SS will experience higher temperatures and more favourable retention (mainly late in the season), and consequently higher growth rates, compared to the ones spawned farther north (Opdal *et al.*, 2008, 2011). Vari-

able spawning intensity over the SS along the Norwegian coast may, therefore, potentially be more relevant than interannual variability of environmental conditions in determining recruitment success (Opdal *et al.*, 2011). When also accounting for other influences on survival, the benefit of spawning around Lofoten compared to northern spawning has, however, been found to be small (Langangen *et al.*, 2016). According to these results, interannual variations in biotic and abiotic conditions appear to have more pronounced effects on the early life stages survival than variation in SS (Langangen *et al.*, 2016).

Factors besides temperature that are likely to influence offspring survival include, e.g. predation and feeding conditions, which also vary spatially and temporally and may cause corresponding variability in natural mortality rates (Ciannelli *et al.*, 2007; Langangen *et al.*, 2016). Differences in daylight length have been reported to be one of the most limiting factors to NEA cod larval growth and survival, but other environmental variables such as adequate prey and turbulence also affect growth, especially for the early spawned individuals in the northern SS with the sun low on the horizon (Kristiansen *et al.*, 2009). Because of the many interacting processes that influence growth and survival, it remains unclear how spatial and temporal shifts in spawning influence early life-stage dynamics and ultimately recruitment.

Here, we consider different scenarios of spatial and temporal changes in spawning patterns, simulating climate change and fishery-induced changes in the population, and analyze the corresponding resulting survival of the offspring from spawning until the 1-age group. In contrast to most previous studies on the topic (e.g. Opdal *et al.*, 2011; Langangen *et al.*, 2016; Langangen and Stige, 2021; but see Vikebø *et al.*, 2021), we use a coupled physical-biological model that sim-

Table 1. Summary of the models used in the study.

Model	Description	Reference
SVIM archive	Nordic Seas numerical ocean model hindcast using the Regional Ocean Modelling System with 4 km horizontal resolution and 32 sigma coordinates.	Lien <i>et al.</i> (2013, 2016), Shchepetkin and McWilliams (2005)
NORWECOM	NORWegian ECOlogical Model is a coupled physical, chemical, and biological model system. Including a nutrient-phytoplankton-zooplankton-detritus model and an IBM for <i>Calanus finmarchicus</i> .	Skogen <i>et al.</i> (1995), Hjøllo <i>et al.</i> (2012)
IBM <i>Calanus finmarchicus</i>	IBM that simulates the entire life-cycle of the copepod <i>Calanus finmarchicus</i> including a genetic algorithm.	Hjøllo <i>et al.</i> (2012), Huse <i>et al.</i> (2018).
IBM cod eggs and larvae	Lagrangian dispersal model. Includes several biological characteristics for the development and growth of the individuals based on ambient variables.	Vikebø <i>et al.</i> (2005, 2007), Kristiansen <i>et al.</i> (2007)

ulates the dynamics of NEA cod eggs and larvae as well as the dynamics of the zooplankton prey of the cod larvae (Endo *et al.*, 2022). Coupled models can shed light into processes that cannot be fully understood based solely on *in situ* sampled data. In this context, models represent a framework in which available information can be integrated and tested. On the other hand, there are many poorly understood processes that cannot be completely parameterized in the model simulations, due to for example, lack of precise information. This should be kept in mind while interpreting the results. Previous coupled modelling of the dynamics of NEA cod and their prey have identified spatial and temporal differences in the mechanisms that regulate dispersal, growth, and survival of the early life stages of the cod larvae (Vikebø *et al.*, 2021; Endo *et al.*, 2022), which forms a good basis for investigating the effects of spatial and temporal shifts in spawning.

Four hypotheses are proposed: (i) a more northern spawning distribution within the historic range of variation results in lower survival of NEA cod offspring until age 1 because of relatively low temperatures, and thereby reduced growth potential and prolonged stage duration (Opdal *et al.*, 2011); (ii) survival to age 1 decreases if the current peak spawning date (SD) of 1st April shifts to either earlier or later dates because of mismatch with suitable prey resulting in reduced growth and prolonged stage duration (Cushing, 1990); (iii) a possible climate change-induced northward shift in spawning distribution beyond the historic range of variation will result in reduced survival because of a potential mismatch with adequate prey; and (iv) interannual variability in survival increases if spawning becomes more constrained to the northern spawning grounds or if the peak SD shifts away from the current peak, because the combination of prey availability and physical conditions become sub-optimal (Murphy, 1967; Solemdal, 1997; Wright and Trippel, 2009).

Material and methods

We investigate consequences of shifts in spawning site (SS) and spawning date (SD) for early life-stage survival of NEA cod until 1-year age. To do this, we combine the ocean model ROMS/SVIM archive with the nutrient-phytoplankton-zooplankton-detritus (NPZD) model NORWECOM and an individual-based (IBM) early life-stage model for NEA cod (Table 1 and supporting information).

The ocean model SVIM archive has been validated by Lien *et al.* (2013, 2016), who found the modelled temperature variability in the near-shore waters to be in close agree-

ment with observations. The biological model systems have been validated by comparison with field data in the North Sea/Skagerrak (Skogen *et al.*, 1997, 2004, 2007; Søiland and Skogen, 2000; Hjøllo *et al.*, 2009; Gao *et al.*, 2021), as well as in the Nordic Seas and Barents Sea (Hjøllo *et al.*, 2012, 2021; Skaret *et al.*, 2014; Dalpadado *et al.*, 2014).

IBM for cod eggs and larvae

A total of 18 experiments, representing years with different hydrographic conditions, were simulated with the IBM for cod eggs and larvae (Table 2). Each individual egg/larva is represented by a super-individual that experiences unique biotic and abiotic conditions during the pelagic drift (for further details, see Supporting Information and Endo *et al.*, 2022). Moreover, each larva experiences individual feeding conditions from the *Calanus finmarchicus* and meso-zooplankton fields. Density-dependent mechanisms between cod larvae and their prey are not included in the model set up.

The super-individual approach (Grimm *et al.*, 2020) means that each particle represents multiple individuals with similar attributes (SS, SD, egg density, stage, stomach fullness, size—weight and length, 3D positions, and prey catch). This approach allows the quantification of super-individual survival probabilities as a function of SS and SD. The eggs spawned in spring develop according to ambient temperatures and then hatch into larvae. The larvae grow according to temperature and food availability. In addition, growth in the IBM is dependent on a mechanistic feeding module. After drifting back to the Barents Sea, the individuals settle for a demersal life at nursery grounds. The subsequent winter is the least productive season and lasts until the spring bloom the year after, when the individuals reach the age of 1 year and have surpassed the vulnerable early life stages.

Eggs, larvae, and juveniles have stage-specific mortality rates reported in the literature (Langangen *et al.*, 2014a; Bogstad *et al.*, 2016), which were used here as per the approach in Endo *et al.* (2022). In addition, we add mortality as a function of successful hatching, feeding, and reaching the Barents Sea as well as size-dependent mortality to age-1 during the overwintering in the Barents Sea. Survival for each super-individual from the 30th of September to late winter (the time of an age-1 survey in the Barents Sea) is calculated following the equation:

$$N_{1age_{x,d,y}} = N_{0age}^{c_1} \left[\ln(L_{0age}) - \ln(L_{mean}) \right],$$

Table 2. Experimental setup and initial characteristics for IBM for cod eggs and larvae.

Experimental set up	
Variable	Description
Simulated years	2000–2017
Simulation period	15th January–30th September
Spawning date (SD)	Daily from 15th February until 15th May
Spawning site (SS)	Ten areas from 63°N to 71°N (Figure 1)
Number of super-individuals	1 000 per combination of SD and SS
Super-individual initial characteristics	
Variable	Value
Egg buoyancy	31.25 ± 0.69*
Larvae weight at hatching	45 µg
Larvae length at hatching	4 mm

* Quantified as the density difference between the eggs and the ambient water (number drawn from a normally distributed salinity equivalent).

where survival N_{1age} scales with the proportion of eggs surviving to age 1, x is SS, d is spawning day, y is year, N_{0age} is the proportion surviving to age 0, L_{0age} is mean length at age 0, L_{mean} is the mean length at the end of the simulation, and $c_1 = 9.78$ as estimated in Stige *et al.* (2019). Note that N_{0age} excludes the individuals that have starved to death in the model, those that did not hatch until the 30th of September or those that did not reach the Barents Sea, and hence accounts for the effects of these factors on survival (Endo *et al.*, 2022).

Assessment metrics

Combining the various factors accounting for survival until age 1 enables the quantification of the *mean survival* (MS) of individuals from spawning until age 1 as a function of SS and SD and for each of the years 2000–2017 (Endo *et al.*, 2022). Further, the *Grand mean survival* (GMS) is also a function of SS and SD and is calculated as the mean of MS across all years (2000–2017). Finally, the *integrated population-level survival* (IPS) at the population level is defined as the mean of the GMS-matrix weighted by the assumed use of each SS and SD by the spawners. The weights given to different SS and SD depend on scenarios representing spatial and temporal shifts in spawning. Specifically, the following equations were used:

$$GMS_{x,d} = \text{mean}(N_{1age_{x,d,y}}),$$

$$IPS_{X,D} = \text{mean}(GMS_{x,d} * w_{x,d}(X, D)).$$

Here, GMS is the grand mean survival, x is spawning site, d is spawning day, y is year from 2000 until 2017, IPS is integrated population-level survival, $w(X, D)$ are weights for scenarios with variable location X and peak day D . $N_{1age_{x,d,y}}$ is the survival as previously described.

A coefficient of variation (CV) of the interannual variability in IPS was calculated according to the following equation:

$$CV_{X,D} = SD(N_{1age_{x,d,y}} * w_{x,d,y}(X, D)) / IPS_{X,D}.$$

Here, the numerator is the between-years standard deviation (SD) and the denominator the mean offspring survival (IPS) for a given spawning scenario.

Scaling of the various spawning grounds and peak spawning times

Based on the GMS, we may manipulate spatio-temporal spawning intensity according to reported impacts of climate and fisheries from scientific literature to assess the effects of

combined shifts in space and time on survival probabilities. Adding scaling weights simply means that we manipulate the relative importance of different combinations of SS and SD. The total number of offspring remains the same independent of the scaling weights. The long-term average spawning intensity is composed of a spatial distribution in spawning intensity with most of the spawning taking place in Lofoten (Figure 2), and a temporal normal distribution of SD with a peak on 1st April, a standard deviation of 2 weeks and a total duration of 8 weeks.

Spatial scaling: we use a long time series (1959–2017) of observed NEA cod spawning intensity in different locations along the Norwegian coast (Strand *et al.*, 2017) as a basis for spatially varying spawning intensity. To find scaling weights for the use of each SS (Figure 1) in a northern and a southern scenario within the historical range, we use the mean SS distribution for the 5 years with, respectively, the northernmost and the southernmost centre of gravity for spawning (Figure 2—north/south). We also consider intermediate scenarios by varying the scaling of spawning intensity from the southernmost to the northernmost years by linear increments according to the south/north difference within each SS using 50 steps. Climate change may result in spatial shifts beyond historic records. We, therefore, also include a northward shift in SS preference according to the projection proposed in Sandø *et al.* (2020). This is done by moving additional 50 linear steps from the northernmost centre of gravity and towards the projected SS. The environment (temperature, prey availability, and currents) is as for the rest of the scenarios.

Temporal scaling: there are studies that report a difference of up to a month in peak SD between cod populations from different regions (Otterå *et al.*, 2006). Moreover, changes in the length of the spawning period (up to 4 weeks difference) and in the date of the spawning peak (2 weeks shift) were observed due to selective fisheries truncating the age distribution of the population resulting in a lower mean age of the spawning stock (Pedersen, 1984; Scott *et al.*, 2006). Temporal shifts in SD are included by adding temporal scaling weights to move the peak SD from 15th March until 15th April in 30 steps while maintaining the original normal distribution in SD. The spawning duration is set to 8 weeks (from 4 weeks before to 4 weeks after the peak), which ensures that the entire spawning period is simulated for all scenarios.

The various scaling scenarios of spawning shifts in space and time are applied individually to the GMS matrix in Figure 3. Mean GMS for each scaling scenario (a total of 100 times 30 combinations of changes in scaling weights of SSs and SDs)

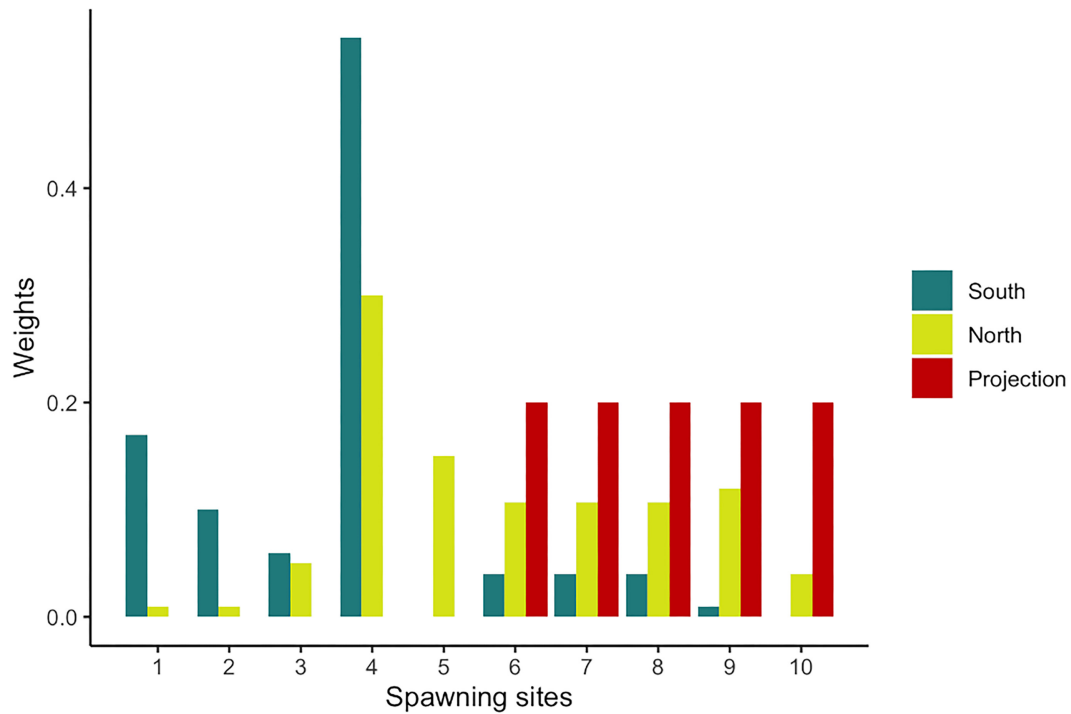


Figure 2. Scaling weights for SS use in the northernmost (light green) and southernmost (dark green) scenario. For the scenarios in between these two extremes, linear interpolation is used, totalling 50 spatial scenarios.

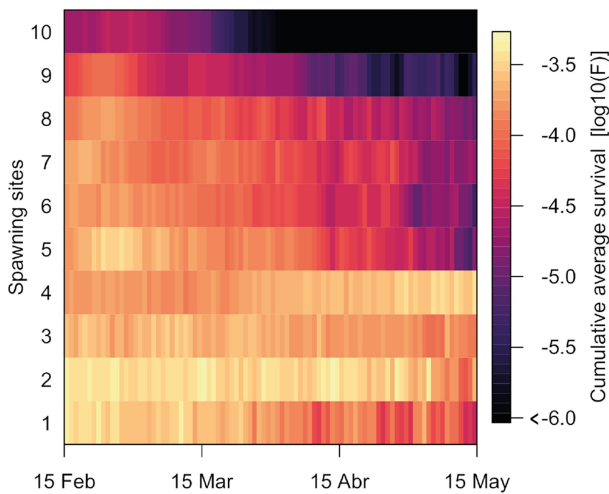


Figure 3. GMS to age 1 [$\log_{10}(F)$] (F_x, d —fraction of surviving eggs spawned at SS x , day d) averaged over the period 2000–2017 by SS and SD. Not scaled by different SS-weights or peak SD-weights.

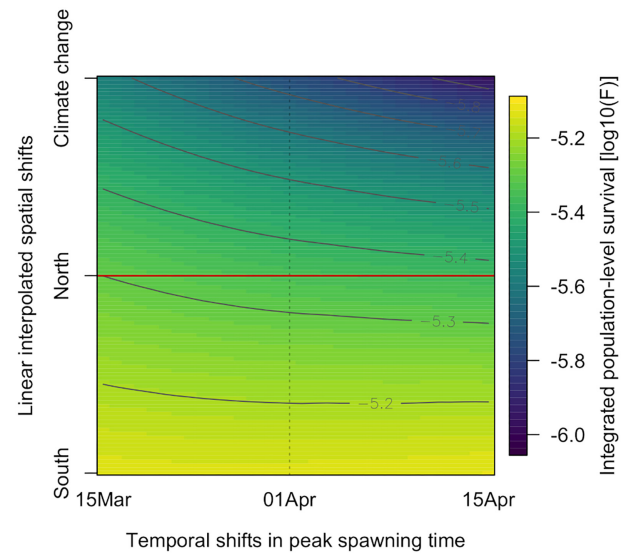


Figure 4. IPS to age 1 [$\log_{10}(F)$] (F —fraction). Spawning location importance shifted gradually between southern (South) to northern (North), and from northern to a future climate change projected spawning distribution. Temporal shifts in peak spawning time were calculated daily for the period 15th of March until the 15th of April. Each grid cell in the figure is composed by the mean of the GMS-matrix (Figure 3) and the spatial and temporal scaling weights.

is further used to compose the IPS-matrix that illustrates in which scenarios survival is high or low. In other words, each grid cell in Figure 4 is the IPS of a scaled GMS using the different weights according to shifts in space (Figure 2) and/or in peak SD. Lastly, the CV of the interannual variability in population-level survival was calculated for each scenario.

Results

Survival analysis—unscaled spawning

GMS until age 1 is a function of SS and SD and a product of several factors included in the IBM. In this study, it includes

successful hatching, non-starving until mid-summer, successfully entering the Barents Sea nursery areas, stage-dependent natural mortality, and size-dependent mortality from the 0-group stage until age 1 (Figure 4).

Elevated GMS is seen for early and southern spawning, most notably for SS 1, 2, and 3 in the first half of the spawning period, it is also elevated for the second half of April for

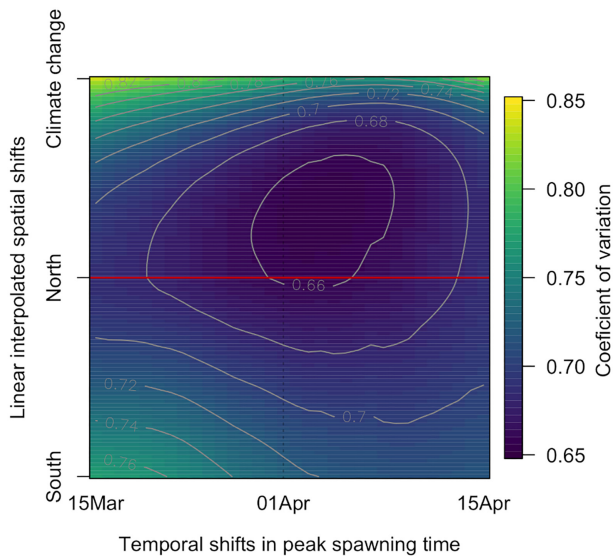


Figure 5. CV of population-level survival to age 1. Spawning location importance shifted gradually between southern (south) to northern (north), and from northern to a future climate change projected spawning distribution. Temporal shifts in peak spawning time were calculated daily for the period 15th of March until the 15th of April. Each grid cell in the figure is composed of the standard deviation (for the period from 2000 until 2017) of annual population-level survival (Supplementary Figure S1) using the different weights from Figure 2 and the temporal scaling weights.

SS 2 only. Similarly high levels of survival are found for the late-spawned individuals from SS 4. Low levels of GMS are found throughout the spawning period for SS 9 and 10, and for the second half of the SDs at SS 5–8. The lowest GMS results indicate nearly three orders of magnitude lower survivor numbers at age 1 compared to the highest.

Survival analysis—spatiotemporal shifts in spawning intensity

IPS until age 1 for the period from 2000 to 2017 as a function of combined northward or southward shift in SS and early or late shift in peak SD are shown in Figure 4. As a general feature, results indicate that spatial shifts have larger effects on IPS than temporal shifts. IPS is three times higher in the southern spawning scenario compared to the projection for early spawning and seven times higher for late spawning (Figure 4). Temporal shifts in peak SD become increasingly important with northward shifts in SS, especially for projected SS under the climate change spawning scenario. A southward shift in SS results in 1.5–2 times higher survival than a corresponding northward shift in SS within the observed spatiotemporal variation in spawning intensity. A northward shift in SS under a projected climate change scenario results in an IPS to age 1 that is 2.5 times higher for early compared to late peak spawned individuals.

The CV for interannual variation in population-level survival for the period 2000–2017 (Figure 5) shows that the variation is at its minimum (CV around 0.65) for peak SD near 1st April with a northward shift in SS. Variation is higher (CV up to around 0.8) when peak SD are shifted earlier in the year with a shift in SS either southwards or northwards. Also, variation in survival between years increases for the projected northernmost shift in SS for most shifts in peak SD.

Survival is in general high in the southern spawning scenarios for all temporal shifts (Figure 4), but if peak day is before approximately 25 March, the interannual survival is somewhat more variable (CV around 0.75, Figure 5) than for peak days later in the season (CV around 0.7). These variations in survival for southern and early shifts in spawning are visible in the yearly population-level survival matrices (Supplementary Figure S1). By observing the orientation of the contour lines, in some years, e.g. 2007, 2012, 2014, 2015, and 2016, there is a change from the average pattern of survival being sensitive to spatial shifts (horizontal contour lines in Supplementary Figure S1) to higher importance of temporal shifts (vertical contour lines).

Discussion

Key findings

The combined results of 18 years of coupled biophysical modelling—including an ocean circulation model, a NPZD model, an IBM for *C. finmarchicus* and an IBM for NEA cod early life stages, were used to analyze the effects of shifts in SS and SD on survival of NEA cod to age 1. Survival of individuals in nature and in our analysis depends on many factors, including where and when the individuals were spawned and their full advective history including the experienced environmental conditions and prey availability.

Our results show higher GMS for individuals spawned earlier in the season. GMS decreases from the southernmost to the northernmost SS. Various scenarios regarding changes in spawning of NEA cod adults along the Norwegian coast were chosen based on literature considering both possible climate- and fisheries-induced changes. Overall, IPS is higher for the southern spawning with early peak spawning day, i.e. 15th March, and it decreases as peak spawning shifts towards April, reaching its minimum in the spawning scenario corresponding to a climate change projection with peak spawning day late in the spawning season. Note however, that this is not because cod reaches its thermal tolerance level as is the case for climate warming scenarios in the North Sea (Brander, 2019; Kjesbu *et al.*, 2021, 2023). Kjesbu *et al.* (2023) show that a key underlying mechanism that may come into play under global warming is distressed ovulation above 9.6°C and, consequently, a significant decrease in reproduction.

Our results support the proposed first hypothesis that IPS is higher when the spatial spawning distribution is in its southernmost configuration and decreases if the spawning distribution shifts towards the northern configuration. Survival is thought to be lower in a northern spawning scenario because individuals spawned in the north experience in general lower temperatures than the ones spawned further south (Endo *et al.*, 2022). The northern low temperatures result in reduced growth and extended stage durations, which reduces survival because of the higher mortality rates of the earliest life stages (the “stage duration hypothesis”; Houde, 1987). Prey availability has the potential to eliminate these differences if insufficient to support high growth rates in the south, but our model indicates that this circumstance is unlikely. Similarly, Endo *et al.* (2022) found that even though more cod larvae were food limited in warm years, recruitment was higher than in cold years because of the positive effects of temperature on survival through enhanced development and growth. Differently to this pattern, Daewel *et al.* (2011, 2015) showed

that North Sea cod match poorly with prey during warm periods and have reduced survival, potentially due to changes in the match-mismatch dynamics, since developmental rates and feeding requirements are temperature dependent while the timing of secondary production is not. Furthermore, a mismatch in space between cod larvae and their key prey, *C. finmarchicus*, has been observed in warm periods, particularly in the southern areas of the North Sea (Kjesbu *et al.*, 2023). A possible reason for this difference between the warmer North Sea and the colder Barents Sea is that cod larval survival is more likely to be limited by food at high temperatures due to higher metabolic needs (Daewel *et al.*, 2011) whilst at low temperatures it is more influenced by direct temperature effects on growth at low temperatures due to long stage durations.

The proposed second hypothesis that peak spawning around 1st April provides highest offspring survival cannot be entirely confirmed. IPS is high for the southern spawning scenarios through all temporal peak spawning shifts, but for the northern and the climate change projection scenario, IPS tends to be highest on 15th March and to gradually decrease until 15th April. Although the benefit of early spawning for survival is most pronounced for northerly shifts in spawning distribution, the early spawned individuals from northern spawning grounds are also prone to slower development due to lower ambient temperatures (Endo *et al.*, 2022). Sundby and Bratland (1987) report a delay of about 14 days in peak spawning at the northernmost spawning grounds compared to spawning grounds in Lofoten. A similar pattern is found at a larger scale, where for example Northern cod of Newfoundland and Labrador experience colder temperatures and have later SD than Irish and North Sea cod (Wright, 2013). Our results suggest that delayed spawning is not providing offspring survival benefits for NEA cod through the mechanisms included in our model. Hence, other factors (e.g. predation or maternal constraints) are likely to play a defining role for the delayed spawning at northern spawning grounds (e.g. temperature constraints on maturation; Kjesbu *et al.* 2010).

The third hypothesis of lower survival due to a climate-induced shift towards an even more northern spawning is supported by our results. Even with increased temperatures in the climate change scenario, northerly spawning is likely to cause prolonged stage duration due to the lower temperatures. Climate changes in the order of 1°C do not raise northern temperatures enough to reach the levels at current southern spawning grounds (Skogen *et al.*, 2018). Changes in temperature may also result in potential mismatch with adequate prey. Furthermore, a constrained use of the spawning grounds may increase the risk of reproductive failure and reduce the resilience of the stocks (Wright and Rowe, 2019). Similarly, Greenland cod occupying cold waters expanded its distribution and doubled its stock biomass during a 1°C temperature increase between 1920 and 1930 (Brander, 2019).

Lastly, the fourth hypothesis is partly confirmed, as we do observe higher interannual variability in survival if spawning is shifted northwards, if only for the largest spatial changes. However, the magnitude of the difference between scenarios is small. The observed higher variation can be a consequence of slow growth (Figure 5), to the point that individuals fail to reach a large enough size to survive the winter (Endo *et al.*, 2022). Slower individual growth might also result in mismatch with appropriate prey, though this is not observed in our results, possibly because prey fields were not adapted to a

climate change scenario (see further explanation under “Study limitations” below).

Reduced survival compared to the interannual variation in population-level survival

By comparing GMS in the various SS, we find that there is, on average, a difference of two orders of magnitude between SS 1 and SS 10. Similarly, Opdal *et al.* (2011), found survival for the southern-spawned individuals to be 3–4 orders of magnitude higher than northern-spawned individuals. Changes in IPS between the northernmost and southernmost scenarios within the historic range are generally moderate compared to the interannual variation in recruitment (JRN-AFWG, 2022), suggesting that interannual variation in the geographic distribution of spawning only accounts for a moderate part of recruitment variation. The typical magnitude of the CV of around 0.7 implies roughly an 8-fold difference in survival between a “good” and a “bad” year, here calculated as the 95 and 5 percentiles of a lognormal distribution. This difference is larger than the 1.5–2-fold difference in survival between southern and northern spawning scenarios seen in this study. These findings differ from the proposal by Opdal *et al.* (2011) that interannual variation in the latitude of spawning has a larger effect on recruitment than interannual variation in environmental conditions.

The 1.5–2-fold survival differences between southern and northern spawning scenarios are on the same order of magnitude as found for differences between low and high mean weight of the spawners based on a different model for NEA cod (Langangen and Stige, 2021). The changes in MS have implications for the long-term reproductive potential of the population, which can be compared to the implications of corresponding changes in the spawning stock biomass. Climate- or fisheries-induced spatial shifts in recruitment may, therefore, have consequences for population dynamics. Furthermore, variations in survival in the climate change scenario are on the same order of magnitude as the interannual variations that have been estimated for juvenile survival of NEA cod (Ohlberger *et al.*, 2014).

Fisheries-induced changes

Fisheries have throughout history caused changes in the demography of a wide range of exploited fish stocks, including the NEA cod population (Law, 2000). Historical data on maturity-at-age of NEA cod shows that from 1946 up until the 1980s when fishing mortality was at its peak, maturation age decreased from 11 to around 7–8 years (Ottersen, 2008). This trend changed after the 1990s, since which maturation age has increased (Kjesbu *et al.*, 2014). Demographic changes in the size distribution of the spawning stock have been hypothesized to cause differences in use of spawning areas over time (Opdal, 2010; Opdal and Jørgensen, 2015). The southern spawning grounds have been proposed to be energetically more costly for the spawners to reach but to provide higher offspring survival. These mechanisms combined with different fitness trade-offs for large and small spawners have been evoked to explain reduced use of the southern spawning areas in periods with low mean size of the spawning adults (Opdal, 2010). Our findings support higher survival of southern spawned offspring. However, the hypothesis that demographic changes in the spawning stock is the main driver of changes in spawning ground use has been questioned (Sundby,

2015), and in contrast to the expectations from the hypothesis, empirical data suggest that the southernmost spawning areas are mostly used by the smaller individuals in the adult spawning stock (Langangen *et al.*, 2019). We note that if smaller adults tend to spawn in southern SS (Langangen *et al.*, 2019), our findings suggest that higher offspring survival can compensate for the lower egg abundance and quality from these smaller adults.

Fisheries-induced demographic changes can also influence recruitment through other mechanisms than changes in spawning ground use. Maternal characteristics affect egg quality, which in turn can impact larval susceptibility to starvation (Marteinsdottir and Steinarsson, 1998) and have direct effects on survival. Larger adults produce more eggs and spawn more batches within a season, generally producing larger and more viable eggs than smaller and younger fish (Kjesbu *et al.*, 1991; Marteinsdottir and Begg, 2002). Higher egg and larvae abundances have been observed when there are bigger individuals in the spawning stock (Stige *et al.*, 2017; Endo *et al.*, 2020). Furthermore, recruitment at age 3 has recently been found to correlate with a high proportion of large and old individuals in the spawning stock (Ohlberger *et al.*, 2022), in contrast to the findings of an earlier study (Ottersen, 2008). The mechanism for the positive association between high mean age of the spawners and good recruitment appears to be the high abundance rather than the large distributional extent of eggs and larvae (Stige *et al.*, 2017; Endo *et al.*, 2020), as the wide distribution leads to a higher proportion of the larvae in unsuitable areas for survival (Langangen and Stige, 2021).

Climate-induced changes

The NEA cod stock abundance has been in synchrony with multidecadal climate oscillations, e.g. the Atlantic Multidecadal Oscillation, as have its distribution and spawning habitats (Sundby and Nakken, 2008; Drinkwater and Kristiansen, 2018). Previous studies have shown that the NEA cod stock distribution expands northeast in the feeding habitat in the Barents Sea with increased temperatures and a corresponding smaller ice coverage (Ottersen *et al.*, 1998; Kjesbu *et al.*, 2014). Consequently, NEA cod spawning areas also tend to be shifted northeast along the Norwegian coast (Sundby and Nakken, 2008; Langangen *et al.*, 2019). Changes in the areas used for spawning and in the size of the spawning aggregation have also been reported in the North Sea and Kattegat regions (Wright and Rowe, 2019).

Adult NEA cod benefit from the northern extension of its habitat due to the warming Barents Sea (Kjesbu *et al.*, 2014). Yet, Opdal *et al.* (2011) found that offspring survival is favoured by a southern spawning distribution, contrary to the observed northward shift in spawning distribution. Moreover, the survival of northern spawned larvae may increase in the future if the temperature increases. The volume of warmer Atlantic water entering the Barents Sea has increased (Skagseth *et al.*, 2020). Higher temperatures can provide better food conditions for the early life stages of cod, which can result in higher survival rates (Ellertsen *et al.*, 1989). Sandø *et al.* (2021) showed, however, only a small increase (4%) in gross secondary production for a projected temperature increase of 0.7°C, for the Barents Sea. On the other hand, higher temperatures are also likely to increase the metabolic needs and energetic costs of the young individuals, as found for the North Sea

cod stock (Beaugrand and Kirby, 2010), and the better food conditions might not be enough to provide energy for maintenance of base metabolism and growth (Fouzai *et al.*, 2015). The survival benefits of fast development at high temperatures appear, however, to be larger than the potential higher starvation rates for the NEA cod (Endo *et al.*, 2022).

The NEA cod stock is in the northern part of the distribution range of Atlantic cod, where climate warming has been associated with good recruitment and population growth (Planque and Frédou, 1999; Drinkwater, 2005). On the other hand, for stocks in the warm end of the cod distribution, as for example the North Sea, Irish and Celtic Sea, and West of Scotland, warming temperatures have likely contributed to the decline of the stocks (Brander, 2019).

Altogether, our results suggest that variations in offspring survival resulting from climate–fisheries-driven changes in spawning ground use have tended to dampen rather than enhance the climate–recruitment association in the past, as more northern spawning in warm periods have contributed to reduced rather than increased offspring survival. Whether the net effect of warming will be positive or negative in the future depends on the balance between the multiple direct and indirect effects of temperature along with other environmental variables.

Study limitations

Analyses of empirical distributions of NEA cod larvae and juveniles suggest that natural mortality rates are highest in the central parts of the distribution area (Ciannelli *et al.*, 2007; Langangen *et al.*, 2014b). When accounting for these geographic patterns in natural mortality in a coupled biophysical IBM, survival of NEA cod eggs to age 1 was similar for central and northern spawning grounds and for early and late spawning (Langangen *et al.*, 2016). Our model accounts for spatiotemporal variations in food conditions, which is one possible cause of variations in natural mortality. However, spatiotemporal variations in natural mortality due to, predation for example, are not accounted for.

Larval survival in a future warmer climate was modelled by applying the northernmost present day spawning grounds only, mimicking the results from Sandø *et al.* (2020). It should be noted that both the spatial and the interannual variability in survival in nature may be different than modelled, as we do not model all processes that influence survival. The approach used here is not fully incorporating the complexity of climate change, as the prey and temperature field and the ocean current field transporting the larvae are still representative for present-day climate. Gross primary and secondary production are expected to have a small increase with high interannual variability, in the Barents Sea inflow area and further northwards but with no clear changes between the present and future climate scenarios (Sandø *et al.*, 2021). In addition, the scenario we used from Sandø *et al.* (2020) has an upper temperature limit of 6°C for the area being identified as spawning grounds but spawning at temperatures up to 9.6°C has been reported (Kjesbu *et al.*, 2010). Using an upper temperature limit of 8°C would allow spawning also at SS 3–5 in addition to SS 6–10. Temperatures in the Barents Sea are expected to rise by 0.5–1°C, which is likely to result in sea-ice loss in some regions (Sandø *et al.*, 2021).

Our results also did not observe differences in survival due to mismatch with appropriate prey. However, this is possibly

because prey fields were not adapted to a climate change scenario. Kjesbu *et al.* (2023), for example, have shown that a northwards retraction of *C. finmarchicus* is indeed projected to limit feeding opportunities for cod larvae in the North Sea. In this scenario, feeding opportunities will not be supplemented by increases in other species of copepods due to a mismatch in the time of peak abundances, resulting in lower survival.

Models enable the study of the dispersal of early-life stages, and thereby also a full investigation of system-wide cause–effect relationships, which is impossible if based purely on observations (Skogen *et al.*, 2021). Model results should be interpreted with caution as it is not possible to include all biological variables and interactions at the fine-scale resolution necessary to resolve such complex processes due to computational limitations. In addition, some ecosystem and biological processes have been simplified due to lack of information or lack of data for parameterization.

Nevertheless, the results presented here contribute to the understanding of the complex biological processes related to offspring survival under varying spawning conditions, including a scenario of climate change.

Concluding remarks and future studies

Compared to other influences on recruitment, variations in spawning ground use appears to play a minor role in explaining the interannual variability of offspring survival. Long-term changes in spawning ground use may nonetheless have significant consequences for population dynamics. Especially a climate-change induced northward shift in spawning beyond the historic range may reduce offspring survival and make survival more sensitive to the timing of spawning. Moreover, it is important to recall that there are other processes and non-linear interactions not included in this study that might significantly affect survival. Future work of extending the model period backwards in time to include earlier cold periods combined with modelled prey availability under climate projections rather than assuming they remain unchanged would further strengthen the basis for analysis and conclusions.

Acknowledgements

This work was supported by the Research Council of Norway (project number 280468) under the project “Drivers and effects of Spatial shifts in early life stages of marine fish (SpaceShift).” The simulations were performed on resources provided by UNINETT Sigma2—the National Infrastructure for High-Performance Computing and Data Storage in Norway under grant NN2984K. Significant improvements to the manuscript were provided by the comments from the anonymous reviewers

Supplementary data

[Supplementary material](#) is available at the *ICESJMS* online version of the manuscript.

Conflict of interest

The authors declare no competing or conflicting interests.

Authors' contributions

CE contributed with evaluation of model, model analyses, and writing of the manuscript. MS contributed with model runs, model analysis, and feedback on the manuscript writing. LS, SH, and FV contributed with constructive discussions, suggestions for model analysis, and feedback on the manuscript writing. All authors contributed to the work and the discussion of hypothesis, methods, and results. All authors reviewed the manuscript.

Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

References

- Beaugrand, G., and Kirby, R. R. 2010. Climate, plankton and cod. *Global Change Biology*, 16: 1268–1280.
- Bogstad, B., Yaragina, N. A., and Nash, R. D. M. 2016. The early life-history dynamics of Northeast Arctic cod: levels of natural mortality and abundance during the first 3 years of life. *Canadian Journal of Fisheries and Aquatic Sciences*, 73: 246–256.
- Brander, K. 2019. Cod and climate change. *In Atlantic Cod: The Bio-Ecology of the Fish*, pp. 87–132. Ed. by G Rose. John Wiley & Sons Ltd., London.
- Cheung, W. W. L., Sarmiento, J. L., Dunne, J., Frölicher, T. L., Lam, V. W. Y., Palomares, M. L. D., Watson, R *et al.* 2013. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, 3: 254–258.
- Ciannelli, L., Fauchald, P., Chan, K. S., Agostini, V. N., and Dingsør, G. E. 2008. Spatial fisheries ecology: recent progress and future prospects. *Journal of Marine Systems*, 71: 223–236.
- Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology*, 26: 249–293.
- Daewel, U., Peck, M., and Schrum, C. 2011. Life history strategy and impacts of environmental variability on early life stages of two marine fishes in the North Sea: and individual-based modelling approach. *Canadian Journal of Fisheries and Aquatic Sciences*, 68: 426–443.
- Daewel, U., Schrum, C., and Gupta, A. K. (2015). The predictive potential of early life stage individual-based models (IBMs): an example for Atlantic cod *Gadus morhua* in the North Sea. *Marine Ecology Progress Series*, 534: 199–219.
- Dalpadado, P., Arrigo, K.R., Hjøllø, S.S., Rey, F., Randi, B.I., Sperfeld, E., Gert, L. van D., *et al.* 2014. Productivity in the Barents Sea – response to recent climate variability. *PLoS ONE*, 9: e95273
- Dalpadado, P., Ingvaldsen, R. B., Stige, L. C., Bogstad, B., Knutsen, T., Ottersen, G., and Ellertsen, B. 2012. Climate effects on Barents Sea ecosystem dynamics. *ICES Journal of Marine Science*, 69: 1303–1316.
- Drinkwater, K. F. 2005. The response of Atlantic cod (*Gadus morhua*) to future climate change. *ICES Journal of Marine Science*, 62: 1327–1337.
- Drinkwater, K. F., Beaugrand, G., Kaeriyama, M., Kim, S., Ottersen, G., Perry, R. I., Pörtner, H. O *et al.* 2010. On the processes linking climate to ecosystem changes. *Journal of Marine Systems*, 79: 374–388.
- Drinkwater, K. F., and Kristiansen, T. 2018. A synthesis of the ecosystem responses to the late 20th century cold period in the northern North Atlantic. *ICES Journal of Marine Science*, 75: 2325–2341.
- Ellertsen, B., Fossum, P., Solemdal, P., and Sundby, S. 1989. Relation between temperature and survival of eggs and first-feeding larvae of northeast Arctic cod (*Gadus morhua* L.). *Journal du Conseil Permanent International pour l'Exploration de la Mer*, 191: 209–219.
- Endo, C. A. K., Vikebø, F. B., Yaragina, N. A., Hjøllø, S. S., and Stige, L. C.. 2020. Effects of climate and spawning stock structure on the

- spatial distribution of Northeast Arctic cod larvae. *ICES Journal of Marine Science*, 78(2): 666–679.
- Endo, C. A. K., Stige, L. C., Skogen, M. D., Ciannelli, L., and Vikebø, F. B. 2022. Two decades of match-mismatch in Northeast Arctic cod – feeding conditions and survival, *Frontiers in Marine Science*, 9: 1–14.
- Engelhard, G. H., Righton, D. A., and Pinnegar, J. K. 2014. Climate change and fishing: a century of shifting distribution in North Sea cod. *Global Change Biology*, 20: 2473–2483.
- Fouzai, N., Opdal, A. F., Jørgensen, C., and Fiksen, Ø. 2015. Effects of temperature and food availability on larval cod survival: a model for behaviour in vertical gradients. *Marine Ecology Progress Series*, 529: 199–212.
- Frank, K. T., Petrie, B., Fisher, J. A. D., and Leggett, W. C. 2011. Transient dynamics of an altered large marine ecosystem. *Nature*, 477: 86–89.
- Gao, S., Hjøllø, S.S., Falkenhaus, T., Strand, E., Edwards, M., and Skogen, M.D. 2021. Overwintering distribution, inflow patterns and sustainability of *Calanus finmarchicus* in the North Sea. *Progress in Oceanography*, 194: 102567
- Grimm, V., Railsback, S. F., Vincenot, C. E., Uta, B., Gallagher, C., Angelis, D. L. De, Edmonds, B., et al. 2020. The ODD protocol for describing agent-based and other simulation models: a second update to improve clarity, replication, and structural realism. *Journal of Artificial Societies and Social Simulation*, 23: 7.
- Heino, M., and Godø, O. R. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. *Bulletin of Marine Science*, 70: 639–656.
- Hjøllø, S. S., Huse, G., Skogen, M. D., and Melle, W. 2012. Modelling secondary production in the Norwegian Sea with a fully coupled physical/primary production/individual-based *Calanus finmarchicus* model system. *Marine Biology Research*, 8: 508–526.
- Hjøllø, S.S., Hansen, C., and Skogen, M.D. 2021. Assessing the importance of zooplankton sampling patterns with an ecosystem model. *Marine Ecology Progress Series*, 680: 163–176.
- Hjøllø, S.S., Skogen, M.D., and Svendsen, E. 2009. Exploring currents and heat within the North Sea using a numerical model. *Journal of Marine Systems*, 78: 180
- Houde, E. D. 1987. Fish early life dynamics recruitment variability. *American Fisheries Society Symposium*, 2: 17–29.
- Huse, G., Melle, W., Skogen, M. D., Hjøllø, S. S., Svendsen, E., and Budgell, W. P. 2018. Modeling emergent life histories of copepods. *Frontiers in Ecology and Evolution*, 6: 23.
- Hutchings, J. A., and Rangeley, R. W. 2011. Correlates of recovery for Canadian Atlantic cod (*Gadus morhua*). *Canadian Journal of Zoology*, 89: 386–400.
- IPCC, 2013. Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC.
- Jørgensen, C., Dunlop, E. S., Opdal, A. F., and Fiksen, Ø. 2008. The evolution of spawning migrations: state dependence and fishing-induced changes. *Ecology*, 89: 3436–3448.
- Kjesbu, O. S., Alix, M., Sandø, A. B., Strand, E., Wright, P. J., Johns, D. G., Thorsen, A et al. 2023. Latitudinally distinct stocks of Atlantic cod face fundamentally different biophysical challenges under ongoing climate change. *Fish and Fisheries*, 00: 1–24.
- Kjesbu, O. S., Bogstad, B., Devine, J. A., Gjøsaeter, H., Howell, D., Ingvaldsen, R. B., Nash, R. D. M et al. 2014. Synergies between climate and management for Atlantic cod fisheries at high latitudes. *Proceedings of the National Academy of Sciences of the United States of America*, 111: 3478–3483.
- Kjesbu, O. S., Klungsoy, J., Kryvi, H., Witthames, P. R., and Greer Walker, M. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. *Canadian Journal of Fisheries and Aquatic Sciences*, 48: 12.
- Kjesbu, O. S., Righton, D., Krüger-Johnsen, M., Thorsen, A., Michalsen, K., Fonn, M., and Witthames, P. R. 2010. Thermal dynamics of ovarian maturation in Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 67: 605–625.
- Kjesbu, O. S., Svein, S., Sandø, A. B., Maud, A., Hjøllø, S. S., Tiedemann, M., Skern-Mauritzen, M et al. 2022. Highly mixed impacts of near-future climate change on stock productivity proxies in the North East Atlantic. *Fish and Fisheries*, 23: 601–615.
- Kristiansen, T., Fiksen, Ø, and Folkvord, A.. 2007. Modelling feeding, growth, and habitat selection in larval Atlantic cod (*Gadus morhua*): observations and model predictions in a macrocosm environment. *Canadian Journal of Fisheries and Aquatic Sciences*, 64: 136–151.
- Kristiansen, T., Vikebø, F., Sundby, S., Huse, G., and Fiksen, Ø. 2009. Modeling growth of larval cod (*Gadus morhua*) in large-scale seasonal and latitudinal environmental gradients. *Deep Sea Research Part II: Topical Studies in Oceanography*, 56: 2001–2011.
- Langangen, Ø., Färber, L., Stige, L. C., Diekert, F. K., Barth, J. M. I., Matschiner, M., Berg, P. R et al. 2019. Ticket to spawn: combining economic and genetic data to evaluate the effect of climate and demographic structure on spawning distribution in Atlantic cod. *Global Change Biology*, 25: 134–143.
- Langangen, Ø., Ottersen, G., Ciannelli, L., Vikebø, F. B., and Stige, L. C. 2016. Reproductive strategy of a migratory fish stock: implications of spatial variations in natural mortality. *Canadian Journal of Fisheries and Aquatic Sciences*, 73: 1742–1749.
- Langangen, Ø., and Stige, L. C. 2021. Shedding light on the link between the spatial distribution of eggs and survival in Northeast Arctic cod. *Fisheries Oceanography*, 30: 429–436.
- Langangen, Ø., Stige, L. C., Kvile, K., Yaragina, N. A., Skjæraasen, J. E., Vikebø, F. B., and Ottersen, G. 2018. Multi-decadal variations in spawning ground use in Northeast Arctic haddock (*Melanogrammus aeglefinus*). *Fisheries Oceanography*, 27: 435–444.
- Langangen, Ø., Stige, L. C., Yaragina, N. A., Ottersen, G., Vikebø, F. B., and Stenseth, N. C. 2014a. Spatial variations in mortality in pelagic early life stages of a marine fish (*Gadus morhua*). *Progress in Oceanography*, 127: 96–107.
- Langangen, Ø., Stige, L. C., Yaragina, N. A., Vikebø, F. B., Bogstad, B., and Gusdal, Y. 2014b. Egg mortality of northeast Arctic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). *ICES Journal of Marine Science*, 71: 1129–1136.
- Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*, 57: 659–668.
- Lien, V. S., Gusdal, Y., Albretsen, J., Melsom, A., and Vikebø, F. B. 2013. Evaluation of a Nordic Seas 4 km numerical ocean model hind-cast archive (SVIM), 1960–2011. *In Fisker og Havet*. 7, Havforskningsinstituttet, Bergen.
- Lien, V. S., Hjøllø, S. S., Skogen, M. D., Svendsen, E., Wehde, H., Bertino, L et al. 2016. An assessment of the added value from data assimilation on modelled Nordic Seas hydrography and ocean transports. *Ocean Modelling*, 99: 43–59.
- Marteinsdottir, G., and Begg, G. A. 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series*, 235: 235–256.
- Marteinsdottir, G., and Steinarsson, A. 1998. Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae. *Journal of Fish Biology*, 52: 1241–1258.
- Murphy, G. I. 1967. Vital statistics of the Pacific sardine (*Sardinops Caerulea*) and the population consequences. *Ecological Society of America*, 48: 731–736.
- Ohlberger, J., Langangen, Ø., and Stige, L. C. 2022. Age structure affects population productivity in an exploited fish species. *Ecological Applications*, 32: e2614.
- Ohlberger, J., Rogers, L. A., and Stenseth, N. C. 2014. Stochasticity and determinism: how density-independent and density-dependent processes affect population variability. *PLoS ONE*, 9: e98940.
- Opdal, A. F. 2010. Fisheries change the spawning ground distribution of northeast Arctic cod. *Biology Letters*, 6: 261–264.
- Opdal, A. F., and Jørgensen, C. 2015. Long-term change in a behavioural trait: truncated spawning distribution and demography in Northeast Arctic cod. *Global Change Biology*, 21: 1521–1530.

- Opdal, A. F., Vikebø, F. B., and Ø. 2008. Relationships between spawning ground identity, latitude and early life thermal exposure in Northeast Arctic cod. *Journal of Northwest Atlantic Fishery Science*, 41: 13–22.
- Opdal, A. F., Vikebø, F. B., and Fiksen, Ø. 2011. Parental migration, climate and thermal exposure of larvae: spawning in southern regions gives Northeast Arctic cod a warm start. *Marine Ecology Progress Series*, 439: 255–262.
- Otterå, H., Agnalt, A. L., and Jørstad, K. E. 2006. Differences in spawning time of captive Atlantic cod from four regions of Norway, kept under identical conditions. *ICES Journal of Marine Science*, 63: 216–223.
- Ottersen, G. 2008. Pronounced long-term juvenation in the spawning stock of Arcto-Norwegian cod (*Gadus morhua*) and possible consequences for recruitment. *Canadian Journal of Fisheries and Aquatic Sciences*, 65: 523–534.
- Ottersen, G., Hjermann, D. O., and Stenseth, N. C. 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fisheries Oceanography*, 15: 230–243.
- Ottersen, G., Kim, S., Huse, G., Polovina, J. J., and Stenseth, N. C. 2010. Major pathways by which climate may force marine fish populations. *Journal of Marine Systems*, 79: 343–360.
- Ottersen, G., Michalsen, K., and Nakken, O. 1998. Ambient temperature and distribution of North-East Arctic cod. *ICES Journal of Marine Science*, 55: 67–85.
- Pedersen, T. 1984. Variation of peak spawning of Arcto-Norwegian cod (*Gadus morhua* L.) during the time period 1929–1982 based on indices estimated from fishery statistics. In *Flødevigen Rapportserie*. Havforskningsinstituttet, Bergen. 301–316pp.
- Perry, A. L., Low, P. J., Ellis, J. R., and Reynolds, J. D. 2005. Ecology: climate change and distribution shifts in marine fishes. *Science*, 308: 1912–1915.
- Perry, R. I., Cury, P., Brander, K., Jennings, S., Möllmann, C., and Planque, B. 2010. Sensitivity of marine systems to climate and fishing: concepts, issues and management responses. *Journal of Marine Systems*, 79: 427–435.
- Planque, B., and Frédou, T. 1999. Temperature and the recruitment of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 2069–2077.
- Putman, N. F., Lumpkin, R., Sacco, A. E., and Mansfield, K. L. 2016. Passive drift or active swimming in marine organisms?. *Proceedings of the Royal Society B: Biological Sciences*, 283: 20161689.
- Sandø, A. B., Johansen, G. O., Aglen, A., Stiansen, J. E., and Renner, A. H. H. 2020. Climate change and new potential spawning sites for Northeast Arctic cod. *Frontiers in Marine Science*, 7: 1–13.
- Sandø, A. B., Mousing, E. A., Budgell, W. P., Hjøllø, S. S., Skogen, M. D., and Ådlandsvik, B. 2021. Barents Sea plankton production and controlling factors in a fluctuating climate. *ICES Journal of Marine Science*, 78: 1999–2016.
- Scott, B. E., Marteinsdottir, G., Begg, G. A., Wright, P. J., and Kjesbu, O. S. 2006. Effects of population size/age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*). *Ecological Modelling*, 191: 383–415.
- Schepetkin, A. F., and McWilliams, J. C. 2005. The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Modelling*, 9: 347–404.
- Skagseth, Ø., Eldevik, T., Årthun, M., Asbjørnsen, H., Lien, V. S., and Smedsrud, L. H. 2020. Reduced efficiency of the Barents Sea cooling machine. *Nature Climate Change*, 10: 661–666.
- Skaret, G., Dalpadado, P., Hjøllø, S. S., Skogen, M. D., and Strand, E. 2014. Calanus finmarchicus abundance, production and population dynamics in the Barents Sea in a future climate. *Progress in Oceanography*, 125: 26.
- Skogen, M. D., Hjøllø, S. S., Sandø, A. B., and Tjiputra, J. 2018. Future ecosystem changes in the Northeast Atlantic: a comparison between a global and a regional model system. *ICES Journal of Marine Science*, 75: 2355–2369.
- Skogen, M. D., Svendsen, E., Berntsen, J., Aksnes, D., and Ulvestad, K. B. 1995. Modelling the primary production in the North Sea using a coupled three dimensional physical–chemical–biological ocean model. *Estuarine, Coastal and Shelf Science*, 41: 545–565.
- Skogen, M., Ji, R., Akimova, A., Daewel, U., Hansen, C., Hjøllø, S., van Leeuwen, S *et al.* 2021. Disclosing the truth: are models better than observations?. *Marine Ecology Progress Series*, 680: 1–7.
- Skogen, M. D., Budgell, W. P., and Rey, F. 2007. Interannual variability in Nordic seas primary production. *ICES Journal of Marine Science*, 64: 889.
- Skogen, M. D., Søiland, H., and Svendsen, E. 2004. Effects of changing nutrient loads to the North Sea. *Journal of Marine Systems*, 46: 23.
- Skogen, M. D., Svendsen, E., and Ostrowski, M. 1997. Quantifying volume transports during SKAGEX with the Norwegian Ecological Model system. *Continental Shelf Research*, 17: 1817.
- Søiland, H., and Skogen, M. D. 2000. Validation of a three-dimensional biophysical model using nutrient observations in the North Sea. *ICES Journal of Marine Science*, 57: 816.
- Solemdal, P. 1997. Maternal effects – a link between the past and the future. *Journal of Sea Research*, 37: 213–227.
- Stige, L. C., Rogers, L. A., Neuheimer, A. B., Hunsicker, M. E., Yaragina, N. A., Ottersen, G., Ciannelli, L *et al.* 2019. Density- and size-dependent mortality in fish early life stages. *Fish and Fisheries*, 20: 962–976.
- Stige, L. C., Yaragina, N. A., Langangen, Ø., Bogstad, B., Stenseth, N. C., and Ottersen, G. 2017. Effect of a fish stock's demographic structure on offspring survival and sensitivity to climate. *Proceedings of the National Academy of Sciences*, 114: 1347–1352.
- Strand, K. O., Sundby, S., Albretsen, J., and Vikebø, F. B. 2017. The Northeast Greenland shelf as a potential habitat for the Northeast Arctic Cod. *Frontiers in Marine Science*, 4: 1–14.
- Sundby, S. 2015. Erratum: comment to long-term change in a behavioural trait: truncated spawning distribution and demography in Northeast Arctic cod. *Global Change Biology*, 21: 2465–2466.
- Sundby, S., and Bratland, P. 1987. Kartlegging av gyterfeltene for Norsk-Arktisk torsk i Nord-Norge og Beregning av eggproduksjonen i årene 1983-1985. *Fisken Havet*, 1: 1–58.
- Sundby, S., and Nakken, O. 2008. Spatial shifts in spawning habitats of Arcto-Norwegian cod related to multidecadal climate oscillations and climate change. *ICES Journal of Marine Science*, 65: 953–962.
- Vikebø, F. B., Broch, O. J., Endo, C. A. K., Frøysa, H. G., Carroll, J., Juselius, J., and Langangen, Ø. 2021. Northeast Arctic cod and prey match-mismatch in a high-latitude spring-bloom system. *Frontiers in Marine Science*, 8: 1–13.
- Vikebø, F., Jørgensen, C., Kristiansen, T., and Fiksen, Ø. 2007. Drift, growth, and survival of larval Northeast Arctic cod with simple rules of behaviour. *Marine Ecology Progress Series*, 347: 207–219.
- Vikebø, F., Sundby, S., Ådlandsvik, B., and Fiksen, Ø. 2005. The combined effect of transport and temperature on distribution and growth of larvae and pelagic juveniles of Arcto-Norwegian cod. *ICES Journal of Marine Science*, 62: 1375–1386.
- Wright, P. J. 2013. Methodological challenges to examining the causes of variation in stock reproductive potential. *Fisheries Research*, 138: 14–22.
- Wright, P. J., and Rowe, S. 2019. Reproduction and spawning. In *Atlantic Cod: The Bio-Ecology of the Fish*, pp. 87–132. Ed. by G Rose. John Wiley & Sons Ltd., London.
- Wright, P. J., and Trippel, E. A. 2009. Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. *Fish and Fisheries*, 10: 283–304.