



Original Article

A model approach to identify the spawning grounds and describing the early life history of Northeast Arctic haddock (*Melanogrammus aeglefinus*)

Rocío Castaño-Primo^{1*}, Frode Bendiksen Vikebø², and Svein Sundby²

¹Geophysical Institute, University of Bergen, PO Box 7803, NO-5020 Bergen, Norway

²Institute of Marine Research, Norway and Hjort Centre for Marine Ecosystem Dynamics, PO Box 1870, N-5817 Bergen, Norway

*Corresponding author: e-mail: rocio.primo@gf.uib.no

Castaño-Primo, R., Vikebø, F. B., and Sundby, S. A model approach to identify the spawning grounds and describing the early life history of Northeast Arctic haddock (*Melanogrammus aeglefinus*). – ICES Journal of Marine Science, 71: 2505–2514.

Received 7 November 2012; revised 4 April 2014; accepted 4 April 2014; advance access publication 9 June 2014.

The time-series of recruitment of Northeast Arctic (NEA) haddock (*Melanogrammus aeglefinus*) reveals larger interannual fluctuations than other gadoid species of the region. The position of spawning sites and the subsequent drift pattern of the offspring may contribute to the large transport variability, and hence, to the large variation in recruitment. A mechanistic individual-based biophysical model covering the egg stage to presettling juveniles, together with observations of 0-group distribution in the Barents Sea and time-series of abundance estimates are used to analyse these factors. The model indicates that spawning north of 67°N is favourable for offspring transport into the nursery grounds in the Barents Sea. The effect of latitude is stronger than across-shelf position for both growth and transport to the nursery grounds. The model predicts 0-group haddock outside the standard sampling area of the annual 0-group survey in the Barents Sea, which could partially explain the occasional occurrence of increase in cohort abundance from the 0-group to 1-year stage.

Keywords: Barents Sea, 0-group distribution, individual-based model, larval loss, mortality, Northeast Arctic haddock, shelf edge, spawning grounds.

Introduction

The reported landings of Northeast Arctic (NEA) haddock in 2011 were ~310 000 t, a record-high number since 1973. The Norwegian catches alone had a market value of nearly 1 billion Norwegian kroner in 2010 and 2011 (Norwegian Statistisk Sentralbyrå, <http://statbank.ssb.no>). This is the result of exceptionally strong recruitment during the years of 2004–2006. These three consecutive strong year classes have resulted in a total-stock biomass currently at historical records since 1950, with over a million tonnes (ICES, 2012). Despite its major role in the Barents Sea ecosystem, the literature about NEA haddock is relatively scarce. Most of the information about the species is found in internal reports, working papers, and other non-peer-reviewed documents (see Olsen *et al.*, 2010).

The recruitment of NEA haddock is characterized by a larger variability in year-class strength than for other gadoids in the area (Bergstad *et al.*, 1987). Very strong year classes appear with no clear periodicity and sustain the stock for several years, although strong year classes prevail in warm periods (Landa, 2012). These

exceptional year classes are several-fold the size of previous or subsequent year classes (ICES, 2012). The large interannual fluctuations also appear in other stocks of haddock, e.g. at the Georges Bank (Lough *et al.*, 2006) and in the North Sea (Pope and Macer, 1996). In contrast to the NEA cod, the recruitment into the fishery (3 years old) cannot be predicted from the abundance of 0-group (5–7 months old) juveniles (Bergstad *et al.*, 1987). Although there is a general feature that strong year classes at the 0-group stage also remain strong at later stages (Bogstad *et al.*, 2010), some year classes turn out stronger at later stages than they appeared as 0-group (SJØMIL database, IMR, Norway). This is potentially due to inaccuracies in sampling and poses a major problem for the management of the stock.

Disentangling the causes of recruitment variability in fish is challenging, as it is a result of interactions between multiple processes through the prerecruit stages. Recruitment cannot simply be predicted from the spawning-stock biomass (Mackenzie *et al.*, 2003) or egg abundance. Larval stages have the highest mortality rates (Houde, 1997), and perturbations in these rates have a relative

larger impact on future recruitment compared with later stages. The causes of this large variability in offspring survival have been an enigma in fisheries biology over the past century and have resulted in many recruitment hypotheses since Hjort (1914). Most recruitment hypotheses involve physical processes directly or indirectly. In some of them, the physical aspect is even the key issue, as in Hjort's (1914, 1926) second hypothesis on "variable advection", the "member-vagrant" hypothesis (Iles and Sinclair, 1982) considering transport of larvae out of its natural nursery habitats, and in the "optimal environmental window" hypothesis (Cury and Roy, 1989) where recruitment variability is explained by changes in upwelling winds.

For NEA haddock, spawning adults migrate from downstream overwintering grounds in the Barents Sea to upstream spawning grounds along the shelf edge of the Norwegian Coast. Solemdal *et al.* (1989) investigated the spawning grounds and spawning season of NEA haddock. Mature females have been found at the bottom, mostly in depths between 300 and 600 m. The main spawning areas seem to be the slope from Tromsøflaket to Lofoten, in addition to Vestfjorden. Spawning south of these areas is believed to be scarce and the spawning component at Møre (62°N) is hypothesized to be part of a local population. Russian investigations set the northern limit for spawning at 74°N. The spawning season of NEA haddock extends from mid-March to early June, and peaks between late April and early May. The offspring need to reach the nursery grounds in the Barents Sea between August and October, when the juveniles leave the pelagic and settle. Larvae have limited swimming capabilities and therefore they largely rely on the ambient currents to transport them. The fact that NEA haddock spawns along the continental shelf break, i.e. on the edge between the continental shelf and the deep Norwegian Sea, makes the variable advection of the pelagic offspring a highly relevant factor in exploring recruitment variability.

This work describes a first mechanistic attempt to model the growth, survival, and dispersal of early life stages of NEA haddock, combining field observations and numerical models. Individual-based models (IBMs) coupled to hydrodynamical models have been widely used in the last decades to study the early life stages of marine fish (see Peck and Hufnagl, 2012, for a review). Here, an IBM that has been previously used for Norwegian Spring-spawning (NSS) herring (Vikebø *et al.*, 2010) and NEA cod (Vikebø *et al.*, 2007; Opdal *et al.*, 2011) has been adapted to NEA haddock behaviour and physiology where information was available. Supplementary data for parameterization were taken from other stocks of haddock (e.g. Georges Bank) or similar species (NEA cod). By quantifying the individual growth, survival, and dispersal and comparing observations with estimated pelagic juvenile distributions, the following research questions are addressed: How sensitive is the larval/juvenile growth, transport, and spatial distribution of pelagic 0-group to the localization of spawning grounds? Which spawning grounds result in better match between observations and estimations? Are transport and growth enough to explain the observed pelagic 0-group distributions? Is the current 0-group survey appropriately designed for fully covering the distribution of pelagic 0-group haddock?

Material and methods

Biophysical model

Ocean model

The hydrodynamical model was a 4-km horizontal resolution ROMS (Haidvogel *et al.*, 2008) of the Nordic seas with 30 terrain-

following s-levels in the vertical direction (Vikebø *et al.*, 2010). The lateral boundary conditions were monthly mean values of sea surface height, three-dimensional velocities, temperature, and salinity from a global 20-km ROMS of the North Atlantic and the Arctic oceans, and eight tidal constituents from the TOPEX/Poseidon Global Inverse Solution. Vertical boundary conditions were taken from the ERA40 interim: 6-hourly data of sea level pressure, windstress, and heat fluxes. The model reproduces well the hydrography and circulation across a section located off the coast of Norway, at 63°N. The seasonal volume fluxes are captured and the model resolves the non-persistent eddy structures in the Norwegian Slope Atlantic Current along the shelf break (Vikebø *et al.*, 2010). The hydrodynamical model provided daily average three-dimensional fields of temperature, salinity, turbulence, and current direction and speed. They were fed into the particle-tracking model LADIM (Lagrangian Advection and Diffusion Model, Ådlandsvik and Sundby 1994). It uses the fourth-order Runge–Kutta advection schemes and bilinear three-dimensional interpolation of daily mean velocity and temperature fields. The high spatial resolution of the model reduces the need for a parameterized horizontal diffusion (Vikebø *et al.*, 2007). This means that horizontal diffusion as a result of subgrid scale is neglected in the present model. Hydrodynamic numerical models, in general, introduce numerical diffusion by discretization of the basic equations. Therefore, no horizontal random walk was added, because of the combined effects of high grid resolution and implicit model diffusion.

Stage duration and growth

The model for the egg stage duration and larval length at hatch was derived from data of Bay of Fundy haddock eggs reared at different temperatures (Martell *et al.*, 2005). The larval weight at each time-step was calculated from two temperature-dependent growth models formulated for NEA and Icelandic cod. That is, Folkvord (2005) for larvae up to 400 mg dry weight, and Björnsson *et al.* (2007) for the subsequent stages. Although the first growth model was developed for larvae between 0.03 and 50 mg dry weight, the author indicates that it can be extrapolated up to 400–600 mg larvae (Folkvord, 2005). The Folkvord (2005) model has been used together in an earlier version of the Björnsson model (Björnsson and Steinarsson, 2002) in an IBM for NEA cod (Vikebø *et al.*, 2005). The transition between these models is smooth. The change of model is only noticeable as a slight change in the slope at temperatures below 5°C. The choice of cod growth models to simulate haddock larvae was based on the lack of an appropriate temperature-dependent growth model for haddock, the taxonomic proximity of the species, and the similar environmental conditions they face during their early life stages. This approach has also been taken, for example, by Petrik *et al.* (2009), who used an almost identical bioenergetic model for cod and haddock in Georges Bank.

Egg and larval vertical distribution

The vertical position of eggs was calculated from their size, buoyancy, and the ambient turbulence, modelled using a binned random walk scheme (Thygesen and Ådlandsvik, 2007). The specific gravity of the NEA haddock eggs was assumed to be similar to NEA cod eggs. This assumption has recently been confirmed by a survey conducted during spring 2012, where the specific gravity in NEA haddock eggs was measured (IMR, unpublished data). Larvae and juveniles were allowed to perform diel vertical migrations. They ascended during the day and descended during the night, within

depth ranges from 5–30 to 10–40 m as the larvae grew. There are no direct measurements of the NEA haddock larvae vertical distribution, but observations made in Georges Bank (Lough and Potter, 1993; Lough et al., 1996) indicate that haddock larvae from 6 to 8 mm concentrated deeper at night, and very few juveniles could be caught in the upper 10 m. The swimming speed increases with

size and is set to 0.1 body lengths (BL) s^{-1} . Maximum sustainable swimming speed of haddock is lower than for other gadoids (Breen et al., 2004), and therefore, we have chosen a conservative value of 0.1 BL s^{-1} . In addition, there is a random movement term added to the active swimming to simulate the effect of turbulence.

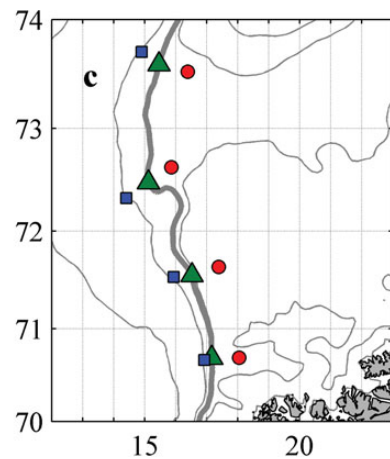
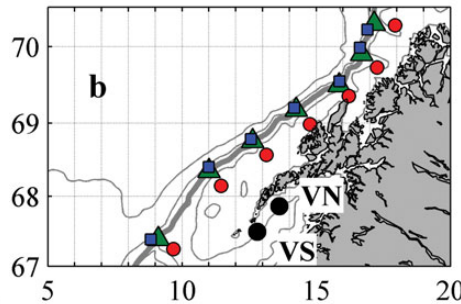
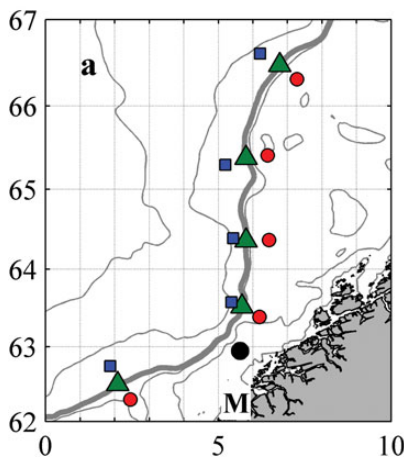
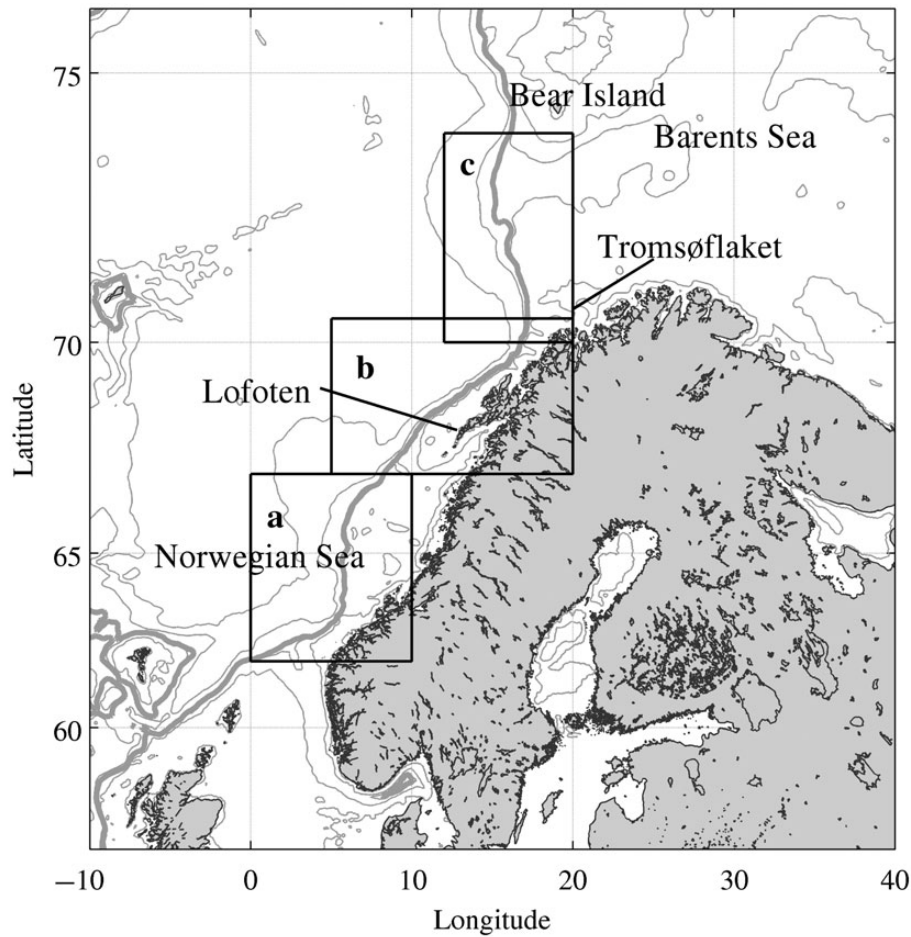


Figure 1. Area where the particles were initialized. The symbols and colour code indicate the position of the release points respect to the shelf break: off-shelf as squares, shelf break as triangles, and on-shelf as red circles. The black dots indicate the coastal locations: one in Møre (M) and two in Vestfjorden, north (VN) and south (VS). 50, 200, 400, 500, 1000, and 2000 m isobaths are drawn. The thicker line corresponds to the 500 m isobath.

Natural mortality

Two mortality models were used. One of them only accounted for the growth in the early stages (M1) and the other integrated size-dependent mortality rates during the entire simulation (M2). In the M1 model, the 20% of the particles that first reached 30 mm were designated as survivors each year. Note that 30 mm is the lower end of the size range observed in the 0-group NEA haddock (Olsen *et al.*, 2010). In the M2 model, a daily size-dependent larval mortality rate Z_t was computed with $Z_t = 1.5 \times W_t^{-0.5} W_t^{-0.5} (\text{day}^{-1})$, where W_t is the larval dry weight in microgrammes at day t . Egg mortality was set constant to 0.225 day^{-1} . These mortality rates have previously been applied in an IBM for North Sea haddock (Heath and Gallego, 1998), where the rationale behind the choice of the mortality model parameters is given. The particles with accumulated survival over the percentile 80 were chosen as survivors. The choice of the 20% level does not have any biological or ecological meaning, but was picked to ensure enough particles to perform statistical analysis. An exploration of different values of threshold mortality reveals that the main patterns remain insensitive. The results from the mortality model M2 are particularly resilient to the changes in survival percentage.

Spawning grounds

To evaluate the effect of the latitude of spawning, release points were first chosen at every degree latitude from 62° to 74°N , covering the whole potential spawning area of NEA haddock. In all, 130 050 particles were released each year. The particles were initialized at each spawning ground as random distributions in $20 \times 20 \text{ km}^2$ squares centred in the sites showed in the lower panels of Figure 1. Three sites were included per latitude: at the shelf break (defined as the 500 m isobath), on the shelf 30 km from the break, and off shelf in waters shallower than 1000 m, at a maximum distance of 30 km. Where the release sites were too close together, the particles were initialized in smaller squares of $8 \times 8 \text{ km}^2$. A preliminary model run indicated that the area from 67° to 70°N required a finer latitudinal resolution (Figure 1b). Three additional coastal sites were therefore chosen; one at Møre, and two in Vestfjorden. When comparing modelled and observed distributions, only the particles from the main observed spawning areas were analysed. That is, the shelf break from 67.5° to 71.5°N (Lofoten to Tromsøflaket) and Vestfjorden.

Time of spawning

The spawning season was set from 15 March to 3 June corresponding to NEA haddock (Bergstad *et al.*, 1987). The releases were made every fifth day. The spawning intensity curve was simplified to a 5-bin histogram, depicted in Figure 2. The model was run for 200 days from 15 March to 30 September, as juvenile haddock settle to the bottom between August and October (Bergstad *et al.*, 1987). The results presented and discussed in this work are based on the model output at the end of the simulation. We focus on long-term trends and effects. The averages, standard deviations, and other calculations are therefore done for the period 1989–2006 based on annual means. The annual geographical centres of mass are the simple arithmetic mean latitude and longitude of all the particles modelled.

Survey data

Pelagic 0-group haddock data were obtained in annual multispecies 0-group surveys in the Barents Sea and the Svalbard region. These surveys are conducted jointly by IMR (Norway) and PINRO

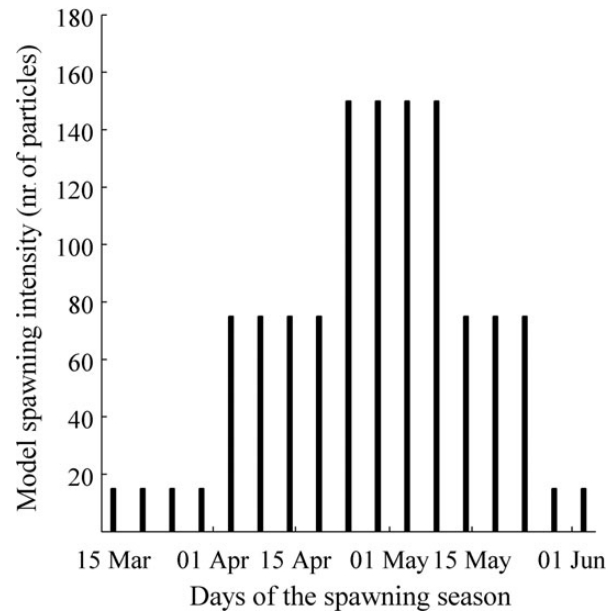


Figure 2. Spawning intensity distribution used in the model. The bars indicate the particular dates the releases were made, every fifth day.

(Russia), in August–September, following a standard trawling procedure since 1980 (Eriksen and Prozorkevich, 2011). At each station, three tows of half a nautical mile each were performed at three depths (0, 20, and 40 m). If the echosounder revealed the presence of 0-group below 40 m, additional tows at 60 and 80 m were performed. A 0-group index for abundance was calculated as logarithmic means per nautical mile and stored in a 25-by-25 km grid. In our analysis, the observations are given in terms of abundance with their centres of mass calculated as weighted mean latitude and longitude. Time-series of estimated abundances per age are public accessible from the SJØMIL database (<http://www.imr.no/sjomil/index.html>), maintained by IMR. These estimates are based on the aforementioned 0-group surveys and bottom trawl winter surveys for age 1 and older (Pennington *et al.* 2011).

Results

Effect of initial latitude and position across-shelf on transport and growth

The effects of initial position are analysed with respect to initial latitude and position across the shelf. The particles originating south of 67°N reach a larger size for both mortality models (Figure 3). There is no significant latitudinal gradient among individuals originating south of 67°N . North of 67°N , the trends are different depending on the mortality models. The average length resulting of the M1 is consistently lower, following an abrupt transition around 67°N . In contrast, the M2 individuals do not show such a variation in final length with latitude. In general, their average length is in the higher end of the length range. There is an apparent minimum around 68°N , but it is not statistically significant as its standard deviation is too large.

On average, between 80 and 90% of the survivors reach the Barents Sea if they are released north of 67°N (Figure 3). In comparison, $\sim 50\%$ of the individuals reach the Barents Sea on average, if the releases were made south of 67°N . The variation of this fraction with latitude is a near-mirrored image of the M1 length variation, again

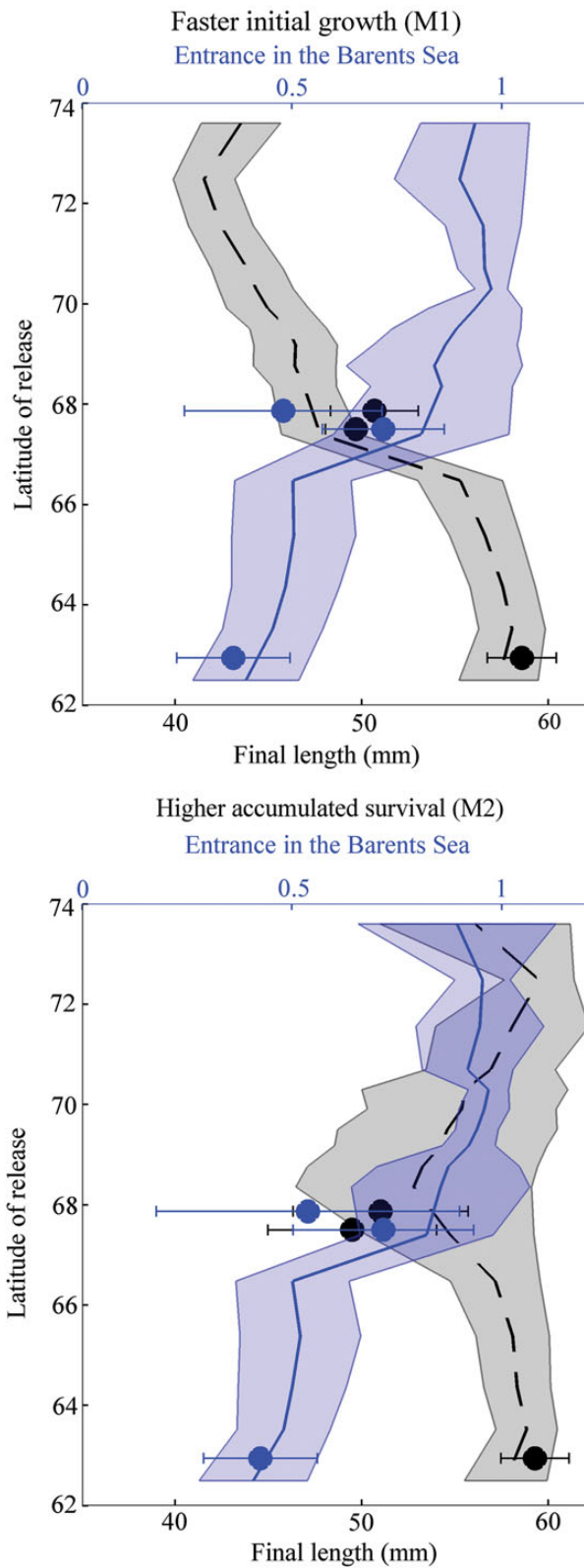


Figure 3. Modelled average length (dashed line) and the fraction of particles that entered the Barents Sea (solid line) by the end of the simulations, for the mortality schemes used (M1, M2). 1989–2006 averages ± 1 standard deviation, calculated from annual means. The dots represent the coastal releases in Møre and Vestfjorden at their corresponding latitudes.

with a sharp transition around 67°N and relatively homogeneous values north and south of this transition.

The closer to the coast the particles were released, the larger their average length is (Figure 4). This difference is statistically significant (ANOVA, p -value < 0.05) for both mortality models: the off-shelf particles were significantly smaller than the shelf break and on-shelf particles. The fraction that reached the Barents Sea did not change with across-shelf position for M1. For the M2 particles, the off-shelf releases produced a significantly smaller fraction. In general, on-shelf and shelf break particles were no different.

Figure 5 shows the areas that comprise the annual centres of mass of the final geographical distributions of individuals from 1989 to 2006, split by latitude range (“South”, “Central”, and “North” based on Figure 1 lower panels) and across-shelf position (off-shelf, shelf break, and on-shelf) where they were initially released. The centres of mass from “South” locations do not vary remarkably with the mortality model chosen. They are consistently outside the shelf, southwest of the Barents Sea. The farther from the coast the particles were initialized, the more dispersed the centres of mass are, as reflected by the bigger size of the polygons. These “South” centres of mass clearly differ from the “Central” and

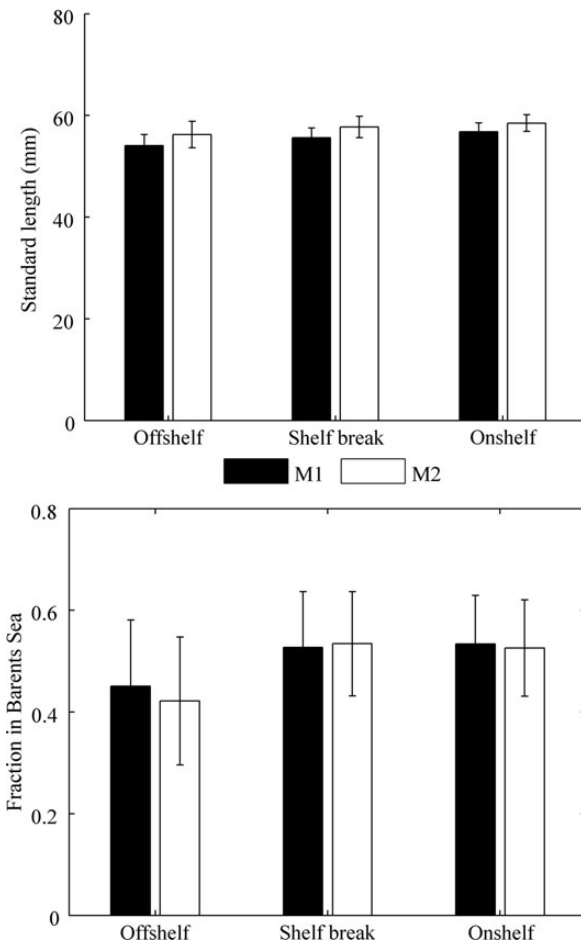


Figure 4. Average standard lengths (upper panel) and fraction in the Barents Sea (lower panel) by the end of the simulations for the mortality models used (M1, M2). The means were calculated annually, per across-shelf position, integrating all the latitudes. The coastal releases were excluded. The error bars indicate ± 1 s.d.

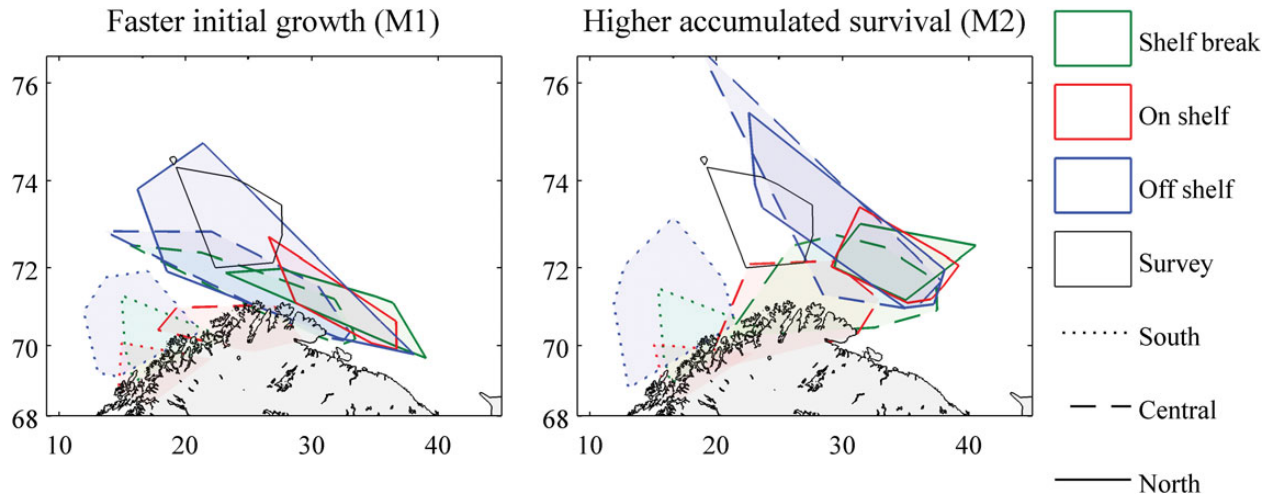


Figure 5. Areas covering all the annual centres of mass (defined as *convex hull*) for different combinations of latitudinal zones and across-shelf positions. The “South” releases are from 62.5° to 66.5°N including Møre (Figure 1a), “Central” from 66.5° to 70.3°N including Vestfjorden (Figure 1b), “North” from 70.5° to 73.5°N (Figure 1c). The “Survey” area covers the annual centres of mass calculated from observations of pelagic 0-group haddock for the same period as the simulations (1989–2006).

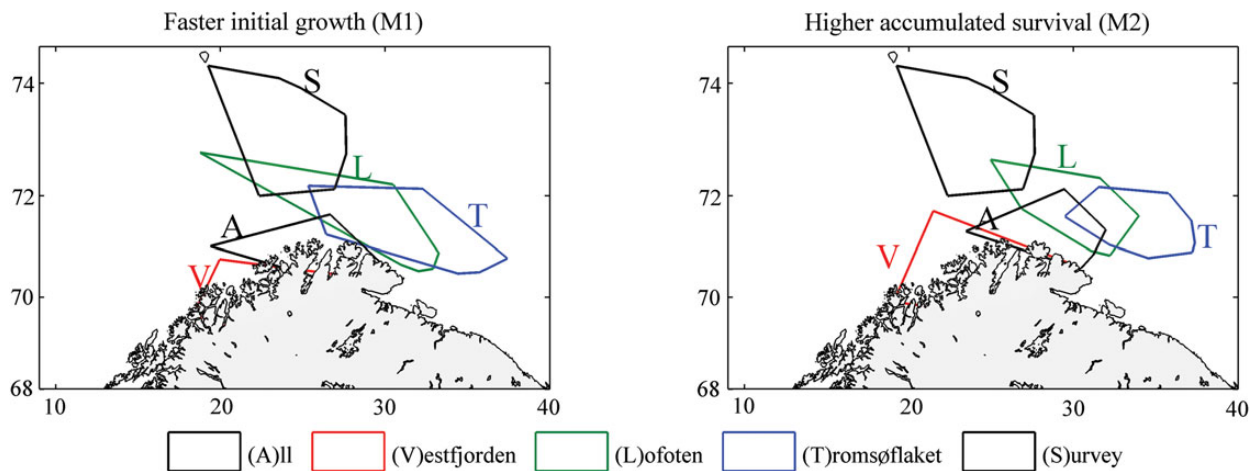


Figure 6. Areas covering all the annual centres of mass (defined as *convex hull*) of individuals initialized at the shelf break in the “Lofoten” area (six southernmost sites in Figure 1b), western “Tromsøflaket” (northernmost site in Figure 1b and two southernmost sites in Figure 1c), and the coastal releases in “Vestfjorden” (VN and VS). It is also shown the distribution for “All” the particles extracted for this analysis. The “Survey” area is the same as shown in Figure 5.

“North” centres of mass. The “Central” centres of mass are indeed sensitive to the mortality model chosen. Using the M1 model, the shelf break and the off-shelf centres of mass are distributed similarly, with an overlap off the coast of northern Norway, following a north-west to southeast axis. Contrary, the on-shelf centres of mass are closer to the coast. The M2 model gives a higher dispersion of the “Central” centres of mass. In this case, the shelf break distribution of centres of mass is more similar to the on-shelf’s, close to the Norwegian coast. The off-shelf distribution is located along a north-west to southeast axis farther northeast than the corresponding M1 distributions. The “North” centres of mass are all in the Barents Sea. They largely overlap towards the southeast end of their distribution areas, specially the shelf break and on-shelf centres of mass, as the off-shelf are the most spread.

Comparing the model with the surveys

Figure 6 also shows distributions of annual centres of mass similar to Figure 5. But now, the results are based on release/spawning sites in closer agreement with the literature: all the particles originating south of Lofoten were removed, and we distinguish between particles originating from Vestfjorden, Lofoten, and Tromsøflaket.

The main difference between the distributions of centres of mass resulting from the two mortality models resides in their shapes. M1 distributions are elongated, while in M2, the centres of mass are closer together. The centres of mass of releases from Vestfjorden are close to the coast. The centres of mass from Lofoten and Tromsøflaket are progressively towards the northeastern Barents Sea. In general, the modelled centres of mass are consistently located south or southeast of the observed “Survey” centres of

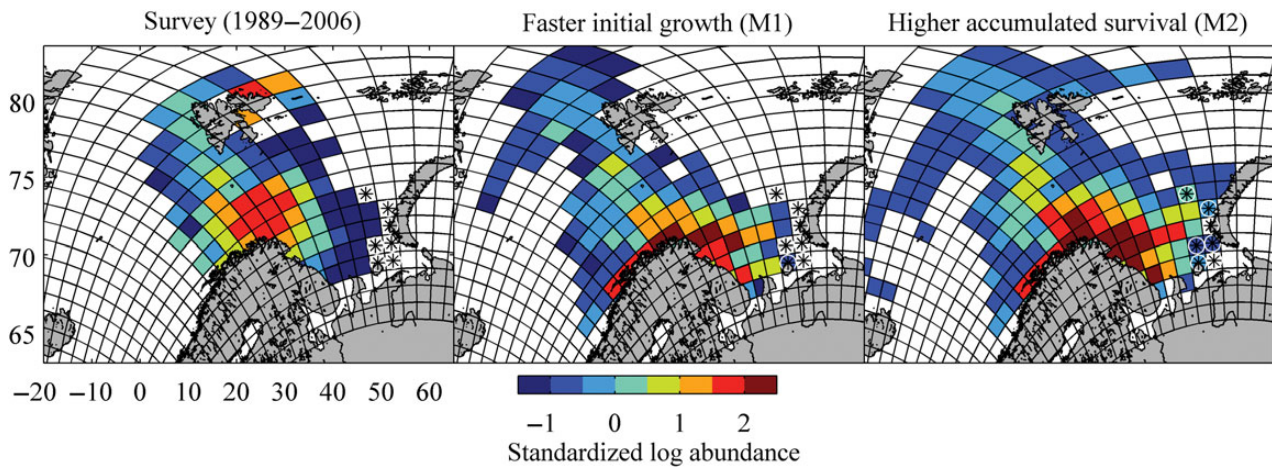


Figure 7. Spatial distribution of the standardized 1989–2006 mean of observed (left panel) and modelled 0-group abundance in logarithmic scale. The grid cells with an encircled star indicate areas surveyed where no pelagic 0-group haddock was found in any year. The observations are typically carried out between August and September, while the model distributions are taken at 30 September. The observations and the model data were recalculated in a common grid of 120 by 120 km. The observed high values northeast of Svalbard are due to stations sampled only one or two times in the whole period, which distorts the mean.

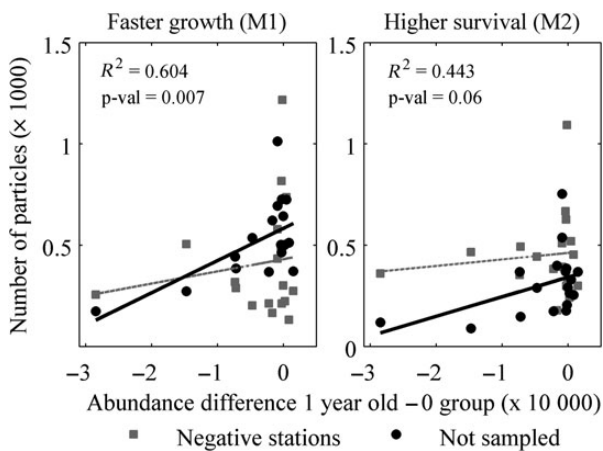


Figure 8. Correlation between the abundance difference from 0-group to 1-year olds and the number of individuals predicted by the model to be out of the sampling area (dots, solid line). The dashed line indicates the correlation with the amount of individuals predicted in areas covered by the surveys where 0-group haddock was not found. Linear correlations calculated for the mortality models M1 and M2. The R^2 and p -value shown correspond only to the significant correlations with $\alpha = 0.1$, in both cases with the not sampled areas (dots, solid line).

mass. Only a small area of the Lofoten distribution overlaps with the distribution obtained from the observations.

Figure 7 shows the geographical abundance distributions as standardized means for the period 1989–2006, based on surveys (left panel) and the IBM with mortality scheme M1 (mid-panel) and M2 (right panel). The modelled abundance maxima are consistently closer to the coast and farther into the Barents Sea than the observations indicate. On the other hand, the modelled distributions also extend farther north and west than the observations. In the eastern Barents Sea, the model predicts particles in areas that have been sampled, but no 0-group haddock was found during the period considered (star cells in Figure 5), especially using the M2 mortality model. The areas where occurrence of 0-group was

predicted by the model, but not found in the survey (here defined “Negative stations”) are larger in single year distributions (not shown).

The abundances of 1-year olds are in some years higher than the abundance of 0-group fish. The correlation between this difference (1-year–0-group fish abundance) and the amount of particles that the model predicts to be outside the sampled area was found positive and significant (p -value < 0.1; Figure 8). However, there is not such a correlation with the particles predicted in “Negative stations”.

Discussion

The model results indicate that individuals originating from spawning grounds north of 67°N have higher probability of successful transport into the Barents Sea than for the individuals originating farther south. Also, their distribution at the time of settlement is more similar to the observed distribution. The effect of latitude is stronger than across-shelf position for both growth and transport to the nursery grounds. However, this is sensitive to the choice of mortality scheme. In the case where only the 20% of the individuals that reached 30 mm first were considered to survive, the length of the 0-group fish dropped for individuals originating north of 67°N. Contrary, if only the 20% of the largest individuals at the settlement stage were considered to survive, the length of the 0-group fish was independent of the latitude of their origin. Furthermore, the observed 0-group distribution is consistently farther north than the modelled distributions, independent of mortality schemes used, when limiting the spawning grounds to the ones consistent with the literature. Finally, it is shown that the observed discrepancy between 0-group and 1-year old fish abundances is correlated with modelled distributions outside the survey area. That is, in years when observed 0-group fish abundance is higher than the corresponding abundance of 1-year-old fish, the model predicts that more of the individuals are located outside the area covered by the survey.

The transport and the temperature exposure (and hence the temperature-dependent growth) of NEA haddock larvae change as a function of the time and location of spawning. Spawning grounds south of 67°N provide warmer environments that would

enhance initial growth rates, if food were unlimited. This effect is very clear when the M1 mortality model was applied. Southern spawning grounds have been suggested to be beneficial for NEA cod larvae (Opdal *et al.*, 2011) with respect to temperature exposure, and the difference in temperature exposure of individuals from southern compared with northern spawning grounds is shown to exceed the effect of interannual environmental variability in the larval temperature exposure. However, southern spawning grounds are detrimental for the transport of the offspring to the nursery grounds. Eggs and larvae would have to cover a larger distance, and pass by the shallow banks of the Mid Norway shelf with retention times of up to 10–50 d (Sætre, 2007). Therefore, large amounts of juveniles may remain outside the nursery grounds during the time of settlement in September. As such, the Møre spawning component has been suggested to be part of a coastal population, and not part of the NEA stock (Solemdal *et al.*, 1989). Our results support this hypothesis. Contrary, the spawning grounds north of 67°N, have the advantage of a shorter route into the Barents Sea and, hence, a lower risk of transport off-the-shelf nursery grounds.

While the model indicates that spawning north of 67°N is favourable for the successful transport to the Barents Sea, the effect on growth is inconclusive and sensitive to the mortality scheme chosen. The exact location of the spawning grounds of NEA haddock is not known as of yet. However, considering that Solemdal *et al.* (1989) observed spawning areas north of 67°N in Vestfjorden, off Lofoten, and at Tromsøflaket, the model and observations jointly suggest that the transport of the offspring is more important than temperature exposure for adult spawning strategies. It must be emphasized that the model only accounts for the offspring early life history, but spawning strategies are essentially the result of a trade-off between parental costs and offspring survival (Williams, 1966). The adult habitat of NEA haddock is the Barents Sea, and a shorter spawning migration would result in a higher fraction of energy available for reproduction. Spawning north of 67°N would clearly be beneficial for spawning adults and the offspring in terms of transport to the nursery grounds.

The effect of the across-shelf positioning of spawning grounds on growth and transport is not as strong as the corresponding effect of latitude. Furthermore, there is little to none effect on the transport into the Barents Sea. Hence, the model used here is unable to explain that NEA haddock is observed to spawn at the shelf break, between 300 and 600 m (Olsen *et al.*, 2010). On-shelf spawning would result in as many and as big juveniles in the nursery grounds as the ones originating at the shelf break, while off-shelf spawning seems to produce juvenile distributions more similar to the observations. There are additional factors that have not been accounted for here that could partially explain why NEA haddock prefer to spawn at the shelf break. It seems that mature female haddock prefer a certain thermal window of 4–6°C to spawn (Olsen *et al.*, 2010). The prey availability for first-feeding larvae is another important factor. The general picture is that the abundance of *Calanus finmarchicus*, the main prey of NEA haddock larvae (and NEA cod) is higher off shelf and at the shelf break than in the coastal waters (Sundby, 2000). Growth rates of pelagic juvenile NEA cod are found to be larger for the juveniles in the western part of the Barents Sea, close to the shelf break, than for the juveniles farther east (Suthers and Sundby, 1993). This is partially because *C. finmarchicus* was more abundant near the shelf break and because temperature is higher. Spawning at the shelf break would also reduce food competition between NEA haddock and NEA

cod, which spawns in coastal waters. Cod spawning season partially overlaps with haddock and it has been hypothesized that larval haddock is a less efficient predator than cod when competing for prey (Campana and Hurley, 1989). Other variables like predation pressure might also play a role, but this is not yet supported by data.

It is challenging to estimate larval mortality, and the choice of a particular mortality scheme is a mere attempt of quantifying it. Currently, we cannot say which of the schemes are more adequate for NEA haddock. The M1 scheme captures the idea that the early larval stages are the most critical for further survival and the resulting Barents Sea distribution is more consistent with observations. On the other hand, the M2 scheme accounts for the whole drift period and favours the transport of individuals released at the shelf break rather than the on- or off-shelf spawning locations, in agreement with existing knowledge of NEA haddock spawning preferences. Both approaches can be found in the literature. Accumulated daily mortality rates like M2 have been widely applied, for example, to North Sea haddock (Heath and Gallego, 1998) or Icelandic cod (Brickman *et al.*, 2007). A concept similar to M1 is found in Opdal *et al.* (2011), where the larval mortality rate for cod was set constant, and the accumulated mortality calculated until the larvae reached 18 mm length. In nature, haddock larval mortality might be a combination of both approaches and/or vary in space and time. However, the two main results of this study, that spawning north of 67°N is favourable for successful transport into the Barents Sea and that a significant part of the 0-group juveniles are transported out of the sampling area, are insensitive to the choice of mortality scheme. Another aspect to consider is the choice of the mortality threshold. It was set that 20% of the particles released each year were considered survivors. We repeated the analyses for 15 and 25% thresholds and the figures, results, and conclusions expressed in this work remained valid for all three cases.

Survey-based estimated abundances indicate erroneously that cohorts of 1-year-old haddock are occasionally more abundant at the 0-group stage. Undersampling and subsequent underestimation of 0-group haddock are likely behind these anomalies. There are two potential sources of undersampling: poor horizontal coverage and early settling. Distribution maps from 0-group surveys reveal that significant amounts of 0-group haddock have been found in the western limit of the sampling area several years (Eriksen and Prozorkevich, 2011). It is reasonable to assume that there are juveniles further west, not sampled. The model results reinforce the idea that the sampling area of the 0-group surveys does not completely capture the distribution of 0-group haddock. The model consistently predicts individuals in areas not sampled, mostly in the deep-sea areas west of the Barents Sea, though the numbers vary widely from year to year. There is also a significant correlation between the modelled abundance outside the sampling areas and the abundance difference from 0 to 1 year olds. The correlation is positive, which means that observed year classes with very low losses or even gains of individuals at year 1 occur in years when the model predicts larger amounts of individuals outside the sampling areas. For these “outsiders” to contribute to the stock, we need to assume that they can delay their settling until they reach the nursery grounds in the Barents Sea. The magnitude of this effect in the underestimation of 0-group is uncertain. However, it is, at least, a factor that cannot be completely excluded at this stage of knowledge, and its importance may well vary from year to year. Early settling is probably another source of underestimation. In the 0-group surveys, haddock is assumed to be in their pelagic phase and the samples are representative of the first 50 m of the water column

(Eriksen and Prozorkevich, 2011). However, there are indications of 0-group haddock already settled by the time of the surveys (Anon., 2009) and the magnitude of this settling is not yet assessed. It is worth to note that juvenile haddock may settle progressively. Bolz and Lough (1988) did not find any settling check in the otolith microstructure of Georges Bank haddock. Therefore, juveniles absent from the surface might be at the bottom and/or elsewhere in the water column, which poses an additional difficulty to the sampling design. The amount of 0-group haddock below 80 m might make an important fraction of the total abundance, and change from year to year. If the settling is not geographically homogeneous and starts earlier in certain areas, it might also distort the abundance distribution. The mechanisms and triggers of settling need to be further investigated to evaluate its actual impact in survey estimations.

References

- Ådlandsvik, B., and Sundby, S. 1994. Modelling the transport of cod larvae from the Lofoten area. ICES Marine Science Symposia, 198: 379–392.
- Anon. 2009. Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea August–October 2009. IMR/PINRO Joint Report Series, No. 2/2010. 118 pp.
- Bergstad, O. A., Jorgensen, T., and Dragesund, O. 1987. Life history and ecology of the gadoid resources of the Barents Sea. Fisheries Research, 5: 119–161.
- Björnsson, B., and Steinarsson, A. 2002. The food-unlimited growth rate of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 59: 494–502.
- Björnsson, B., Steinarsson, A., and Árnason, T. 2007. Growth model for Atlantic cod (*Gadus morhua*): effects of temperature and body weight on growth rate. Aquaculture, 271: 216–226.
- Bogstad, B., Nakken, O., Eriksen, E., and Marshall, C. T. 2010. Abundance and mortality of Northeast Arctic cod and haddock during their first years of life. ICES Document CM 2010/C:04. 17 pp.
- Bolz, G. R., and Lough, R. G. 1988. Growth through the first six months of Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*, based on daily otolith increments. Fishery Bulletin, 86: 223–235.
- Breen, M., Dyson, J., Finbarr, G. O., Jones, E., and Haigh, M. 2004. Swimming endurance of haddock (*Melanogrammus aeglefinus*, L.) at prolonged and sustained swimming speeds, and its role in their capture by towed fishing gears. ICES Journal of Marine Science, 61: 1071–1079.
- Brickman, D., Taylor, L., Gudmundsdóttir, Á., and Marteinsdóttir, G. 2007. Optimized biophysical model for Icelandic cod (*Gadus morhua*) larvae. Fisheries Oceanography, 16: 448–458.
- Campana, S. E., and Hurley, P. C. F. 1989. An age and temperature-mediated growth model for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae in the Gulf of Maine. Canadian Journal of Fisheries and Aquatic Sciences, 46: 603–613.
- Cury, P., and Roy, C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Canadian Journal of Fisheries and Aquatic Sciences, 46: 670–680.
- Eriksen, E., and Prozorkevich, D. 2011. 0-group survey. In The Barents Sea Ecosystem, Resources, Management. Half a Century of Russian–Norwegian Cooperation, pp. 557–569. Ed. by T. Jakobsen, and V. Ozhigin. Tapir Academic Press, Trondheim.
- Folkvord, A. 2005. Comparison of size-at-age of larval Atlantic cod (*Gadus morhua*) from different populations based on size- and temperature-dependent growth models. Canadian Journal of Fisheries and Aquatic Sciences, 62: 1037–1052.
- Haidvogel, D., Arango, H., Budgell, W., Cornuelle, B., Curchitser, E., Di Lorenzo, E., Fennel, K., et al. 2008. Ocean forecasting in terrain-following coordinates: formulation and skill assessment of the Regional Ocean Modelling System. Journal of Computational Physics, 227: 3595–3624.
- Heath, M., and Gallego, A. 1998. Bio-physical modelling of the early life stages of haddock, *Melanogrammus aeglefinus*, in the North Sea. Fisheries Oceanography, 7: 110–125.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapports et Procès-Verbaux des Réunions du Conseil Permanent International pour l'Exploration de la Mer, 22: 1–236.
- Hjort, J. 1926. Fluctuations in the year classes of important food fishes. Journal du Conseil International pour l'Exploration de la Mer, 1: 5–38.
- Houde, E. D. 1997. Patterns and trends in larval-stage growth and mortality of teleost fish. Journal of Fish Biology, 51: 52–83.
- ICES. 2012. Report of the Arctic Fisheries Working Group (AFWG). 20–26 April 2012. ICES Document CM 2012/ACOM: 05. 663 pp.
- Iles, T. D., and Sinclair, M. 1982. Atlantic herring: stock discreteness and abundance. Science, 215: 627–633.
- Landa, C. S. 2012. Geographical distribution and abundance of Northeast Arctic haddock (*Melanogrammus aeglefinus*) in a fluctuating climate. MSc thesis. University of Bergen.
- Lough, R. G., Caldarone, E. M., Rotunno, T. K., Broughton, E. A., and Burns, B. R. 1996. Vertical distribution of cod and haddock eggs and larvae, feeding and condition in stratified and mixed waters on southern Georges Bank. Deep Sea Research II: Topical Studies in Oceanography, 43: 1875–1904.
- Lough, R. G., Hannah, C. G., Berrien, P., Brickman, D., Loder, J. W., and Quinlan, J. A. 2006. Spawning pattern variability and its effect on retention, larval growth and recruitment in Georges Bank cod and haddock. Marine Ecology Progress Series, 310: 193–212.
- Lough, R. G., and Potter, D. C. 1993. Vertical distribution patterns and diel vertical migrations of larval and juvenile haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* on Georges Bank. Fishery Bulletin, 91: 281–303.
- Mackenzie, B. R., Myers, R., and Bowen, K. 2003. Spawner–recruit relationships and fish stock carrying capacity in aquatic ecosystems. Marine Ecology Progress Series, 248: 209–220.
- Martell, D. J., Kieffer, J. D., and Trippel, E. A. 2005. Effects of temperature during early life history on embryonic and larval development and growth in haddock. Journal of Fish Biology, 66: 1558–1575.
- Olsen, E., Aanes, S., Mehl, S., Holst, J. C., Aglen, A., and Gjosæter, H. 2010. Cod, haddock, saithe, herring, and capelin in the Barents Sea and adjacent waters: a review of the biological value of the area. ICES Journal of Marine Science, 67: 87–101.
- 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.
- Petrik, C. M., Kristiansen, T., Lough, G. R., and Davis, C. S. 2009. Prey selection by larval haddock and cod on copepods with species-specific behavior: an individual-based model analysis. Marine Ecology Progress Series, 396: 123–143.
- Peck, M. A., and Hufnagl, M. 2012. Can IBMs tell us why most larvae die in the sea? Model sensitivities and scenarios reveal research needs. Journal of Marine Systems, 93: 77–93.
- Pennington, M., Shevlev, M. S., Vølstad, J. H., and Nakken, O. 2011. Bottom trawl surveys. In The Barents Sea Ecosystem, Resources, Management. Half a Century of Russian–Norwegian Cooperation, pp. 557–569. Ed. by T. Jakobsen, and V. Ozhigin. Tapir Academic Press, Trondheim.
- Pope, J. G., and Macer, C. T. 1996. An evaluation of the stock structure of North Sea cod, haddock, and whiting since 1920, together with a consideration of the impacts of fisheries and predation effects on their biomass and recruitment. ICES Journal of Marine Science, 53: 1157–1169.
- Sette, R. (Ed.) 2007 The Norwegian Coastal Current—Oceanography and Climate. Tapir Academic Press, Trondheim, Ch. 7, 159 pp.

- Solemdal, P., Knutsen, T., and Bjørke, H. 1989. Spawning areas and spawning period of the North-east Arctic haddock (*Melanogrammus aeglefinus* L.). Havforskningsinstituttets egg- og larveprogram (HELP) 25/1989, 43.
- Sundby, S. 2000. Recruitment of Atlantic cod stocks in relation to temperature and advection of copepod populations. *Sarsia*, 85: 277–298.
- Suthers, I. M., and Sundby, S. 1993. Dispersal and growth of pelagic juvenile Arcto-Norwegian cod (*Gadus morhua*), inferred from otolith microstructure and water temperature. *ICES Journal of Marine Science*, 50: 261–270.
- Thygesen, U. H., and Ådlandsvik, B. 2007. Simulating vertical turbulent dispersal with finite volumes and binned random walks. *Marine Ecology Progress Series*, 347: 145–153.
- Vikebø, F. B., Ådlandsvik, B., Sundby, S., and Fiksen, Ø. 2005. The combined effect of transport and temperature distribution and growth of larvae and pelagic juveniles of Arcto-Norwegian cod. *ICES Marine Science Symposia*, 62: 1375–1386.
- Vikebø, F. B., 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. B., Husebø, Å., Slotte, A., Stenevik, E. K., and Lien, V. S. 2010. Effect of hatching date, vertical distribution, and interannual variation in physical forcing on northward displacement and temperature conditions of Norwegian spring-spawning herring larvae. *ICES Journal of Marine Science*, 67: 1948–1956.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist*, 100: 687–690.

Handling editor: Claire Paris