



Modelling drift of pelagic offspring: the importance of egg surveys in providing a realistic model initialization

Sigurd Heiberg Espeland^{1*}, Jon Albretsen¹, Esben Moland Olsen^{1,2,3}, and Torjan Bodvin¹

¹Institute of Marine Research Flødevigen, 4817 His, Norway

²Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066, Blindern, 0316 Oslo, Norway

³Department of Natural Sciences, University of Agder, 4604 Kristiansand, Norway

*Corresponding author: tel: + 47 55 23 85 00; fax: +47 37 05 90 01; e-mail: sigurd.heiberg.espeland@imr.no

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Having valid information about the location and dynamics of biological processes is important for coastal management. In this context modelling, the pelagic drift of early life stages has been shown to be an important tool for understanding the spatial scale of population dynamics in marine systems. Often simulated particles are released in hypothetical quantities at assumed spawning grounds with no or few field data to guide the model parametrization. In this study, we combine high-resolution field data and state-of-the-art oceanographic modelling and use a probabilistic approach to construct kernel density distributions of the dispersal of pelagic fish eggs. Specifically, the potential drift of pelagic offspring of cod (*Gadus morhua*) was investigated in a large, open fjord system in northern Norway by combining field observations of newly spawned cod eggs with simulations of particle movement using a semi-Lagrangian trajectory model with inputs from high-resolution hydrodynamic simulations. The larger part of the distribution of eggs after drift was located in the fjord, suggesting fjord scale recruitment dynamics. Finally, we also examined the drift of eggs released in a uniform distribution and found that lack of egg survey data gave an unrealistically large spread of egg particles within this fjord system.

Keywords: coastal cod, early life stages, particle drift modelling, retention, ROMS, spawning areas.

Introduction

Sound management requires valid data on location and nature of the biological processes taking place in the coastal zone. For instance, spawning in coastal areas may be subject to different degrees of pelagic drift. This pelagic dispersal of early life stages is a widespread mechanism influencing population structure and dynamics in marine systems (Bohonak, 1999; Cowen *et al.*, 2000; Hastings and Botsford, 2006). Understanding the scale and variability of dispersal from spawning areas is essential for a range of fields, such as, for example, the design of marine protected area networks (Shanks *et al.*, 2003; Botsford *et al.*, 2009) and other trade-offs in conflicts of interest in the coastal zone. The use of oceanographic modelling has gained increased attention in predicting dispersal (Werner *et al.*, 2001; Myksvoll *et al.*, 2011; Bauer *et al.*, 2013; LaCroix *et al.*, 2013; Øresland and Ulmestrand, 2013). However, the fate of the virtual pelagic offspring depends on the resolution and parameterization of the oceanographic model (Lyngé *et al.*,

2010; Myksvoll *et al.*, 2012). Model outcomes can also be affected by variations in time, unresolved subgrid turbulence, inclusion of mortality and behaviour (Cowen *et al.*, 2000; Paris *et al.*, 2007), and other discrepancies between models and real life (Watson *et al.*, 2012). In addition, if similar uncertainties apply to the locations of where eggs are released in the model, the results obtained may not be representative of the real dispersal of pelagic offspring. Pelagic eggs may either be dispersed or retained in the area depending on ocean currents in location they are released (Myksvoll *et al.*, 2014a, b), while the overall biological outcome is also dependent on the numbers of eggs released in the different locations. A focus on equal number of trajectories of drift from different locations may give the impression that the endpoints are equally likely unless the model is parametrized with realistic initial data.

Dispersal of pelagic offspring has been most extensively studied for teleost fish associated with tropical coral reefs (Cowen *et al.*, 2006; Shanks, 2009; Buston *et al.*, 2012). These are characterized

by relatively short pelagic phases, short dispersal distances, and a high degree of self-recruitment (Jones *et al.*, 1999; Cowen *et al.*, 2006; Almany *et al.*, 2007; Planes *et al.*, 2009), but do not represent the global pattern of dispersal and connectivity (Bradbury *et al.*, 2008). Pelagic duration and egg development time increase when moving poleward (increasing latitude) towards colder waters, and comparatively, the genetic differentiation (F_{st}) has been found to decrease (Bradbury *et al.*, 2008). Thus, there is a negative correlation between pelagic duration and the degree of population differentiation. This decrease in genetic differentiation may be due to the physiology of the species in relation to latitudinal gradients in, for instance, temperature, but oceanography, bottom topography, and other external physical properties without latitudinal gradients may also significantly affect dispersal distances.

The Atlantic cod (*Gadus morhua*) has a development time of 20–24 d from spawning to hatching at 4°C water temperature, and in colder water (near 0°C) the development time may extend beyond 40 d (Westernhagen, 1970). During this long pelagic period, the eggs may potentially be subject to a large variation in oceanographic processes and advected far from the spawning area. When spawning in enclosed fjord basins sheltered from major and persistent current systems, the Atlantic cod can display significant retention of pelagic eggs in the area of release (Knutson *et al.*, 2007; Ciannelli *et al.*, 2010; Knickle and Rose, 2010; Myksvoll *et al.*, 2012). However, there is less knowledge of the fate of pelagic eggs (from cod and other marine species) spawned in more open fjord and coastal habitats.

In this study, we evaluate the dispersal of pelagic offspring of cod in a large open fjord system in northern Norway by a probabilistic interpretation of a dispersal kernel. High-resolution egg sampling surveys of the horizontal and vertical distribution of cod eggs in a spawning area were used to calibrate the number of particles released in variations of an oceanographic model. Simulations of the drift of eggs were also performed on eggs released in a horizontal uniform distribution, with equal amounts of eggs released on all stations, throughout the area.

Material and methods

Eggs were sampled in two consecutive years, 16 April–20 April in 2009 and 24 and 25 April in 2010. The sampling was performed in the Storfjorden—Lyngen area, Northern Norway (69.25°–70.10°N, 20.50°E, Figure 1). This fjord system is relatively open, lacking a defined sill or any bottom topography that might promote retention of pelagic early life stages. A grid net of 75 stations was designed to cover both potential spawning areas and the rest of the fjord system. From an interview survey performed by the Directorate of Fisheries, spawning areas for cod were located at several places in the fjord system. However, the spawning areas were not verified scientifically. A mature cod may release eggs due to inflation of the swimbladder when hauled from large depths, even when not spawning, so some reported spawning areas may rather be good fishing areas for mature fish. The average distance between the stations was 1863 m. For logistic reasons, stations were more closely spaced in the inner part of the fjord than in the outer part (Figure 1).

Stations were sampled by vertical hauls (0.5 m s⁻¹) with a WP2 plankton net (diameter = 0.6 m, mesh size = 500 μm). The net could be closed by releasing a weight attached to the rope that would spring a closing mechanism. In 2009, two depth-stratified hauls were taken at each station, where the first haul sampled the deeper 50–20 m depth interval, and the second haul from 20 m depth to the surface. In 2010, a single haul from 50 m depth to the surface was taken at all stations. When analysing the data, the depth-

stratified hauls from 2009 were pooled to allow for a direct comparison with the data from 2010. All fish eggs were extracted from the sample and identified to species level. On some occasions, the sample was first sieved through a 2000-μm mesh plankton gauze to remove phytoplankton and copepods, and to ease the visual identification of eggs. Early-stage cod eggs were identified by their size (1.2–1.5 mm) while older stages were identified by their pigmentation (Hiemstra, 1962). Cod eggs were staged according to a five-point scale (Thompson and Riley, 1981). We note that while early-stage eggs of haddock may be misidentified as cod, only a single older stage haddock egg was found in 2010 and none in 2009. In contrast, we found several older stage cod eggs, suggesting that most of the eggs were indeed cod and not haddock.

The circulation model used is the Regional Ocean Modeling System (ROMS; Shchepetkin and McWilliams, 2005; Haidvogel *et al.*, 2008). This is a three-dimensional free-surface, hydrostatic, primitive equation ocean model using terrain-following s -coordinates in the vertical. The model was run with a third-order upwind scheme for solving the advection equations, and the generic length scale turbulence closure scheme was used for subgrid-scale mixing (Warner *et al.*, 2005). Due to the varying width of the Storfjord—Lyngen study system, we found it necessary to decrease the horizontal grid resolution to 200 m. The 200-m model covered several of the adjacent fjords and some of the offshore area. A coarser model with a horizontal resolution of 800 m [explained in Albretsen *et al.* (2011)] provided nesting conditions (hourly fields of sea level, hydrography, and currents) for the fine resolution model. The open boundaries in the 800-m model applied daily averaged fields provided from the operational model system (4 km resolution) at the Norwegian Meteorological Institute. The eight most dominant tidal constituents (four diurnal and four semi-diurnal) were included, based on the global tidal solution TPXO (Egbert and Erofeeva, 2002). High-resolution coastal bathymetric data (originally 50 × 50 m horizontal resolution) were retrieved from the Norwegian Mapping Authority (the Norwegian Hydrographic Service) and merged with offshore data from the ETOPO database (from the National Geophysical Data Centre). An atmospheric model WRF (non-hydrostatic Advanced Weather Research and Forecasting Model AR-WRF version 3.0.1) was run with 3 km horizontal resolution to provide high-resolution wind, air pressure, precipitation, and thermodynamical surface variables for the ocean models. Freshwater discharges from rivers were estimated by a hydrological model (Beldring *et al.*, 2003) and provided by the Norwegian Water Resources and Energy Directorate (NVE). More details on the circulation model can be found in Albretsen *et al.* (2011).

To evaluate the reliability of the numerical circulation model, three current profilers (Recording Doppler Current Profiler 600 from Aanderaa Instruments) were deployed at 50 m depth and recorded current speed and direction for ~1 month (15 April–14 May 2009). The instruments profiled currents upwards, then recorded currents from 50 to 5 m depth with a vertical spacing of 2 m. The locations of the RDCP sites were all distributed in the Storfjord (Figure 1). In addition, 13 CTD profiles (SAIV SD204, <http://www.saivas.no>) were taken along the entire fjord at both sides and used for model validation purposes. Modelled hydrography and currents were used at the corresponding observational depths. Currents were extracted every hour, while daily averages of modelled salinity were used in our comparison.

The egg drift simulations were based on hourly currents from the finest resolution ROMS simulation (200 m). A standard semi-Lagrangian trajectory model with random-walk diffusion

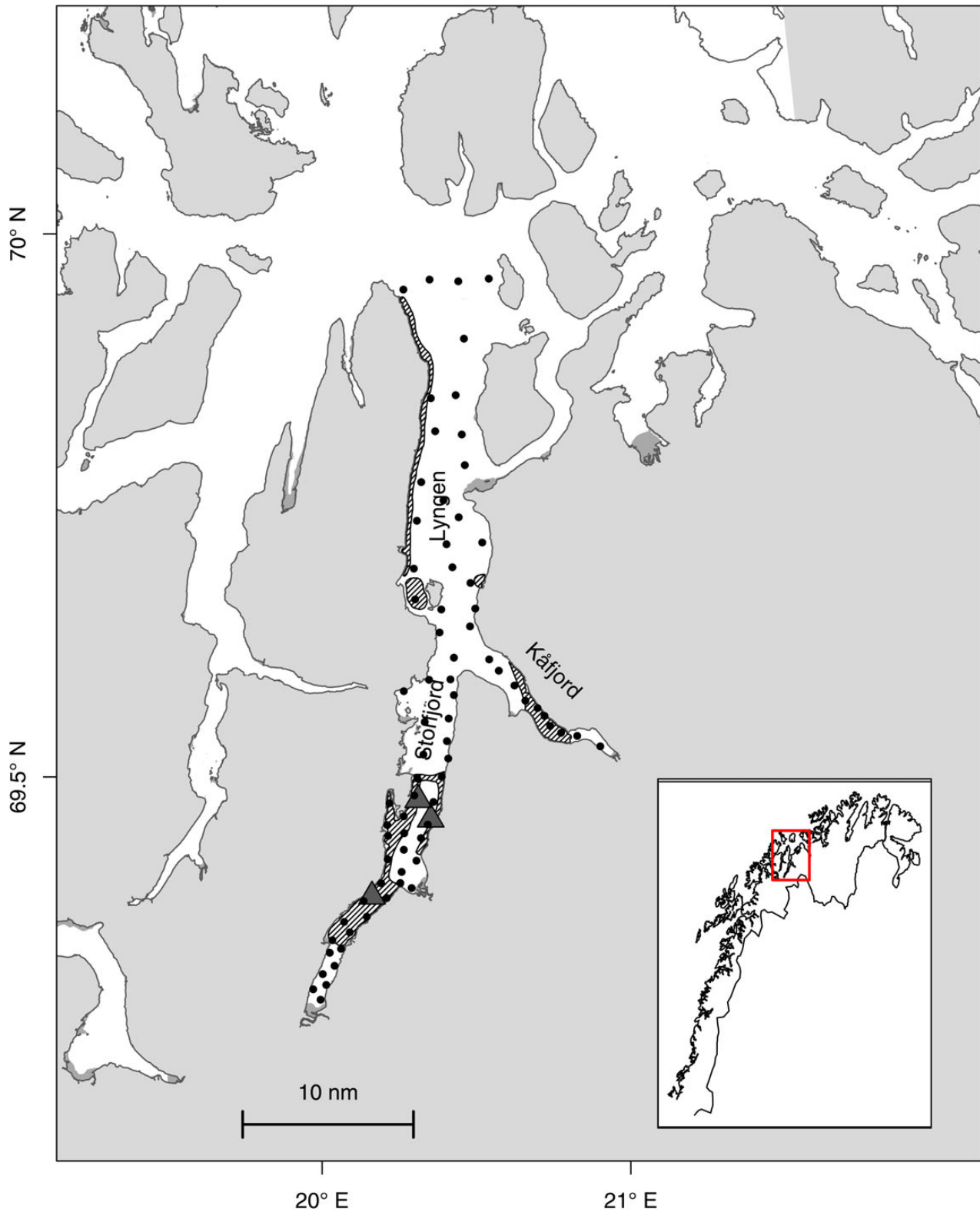


Figure 1. The study area of the fjords Lyngen branching into Kåfjord and Storfjord. The black dots represent stations where eggs were sampled in both 2009 and 2010. The triangles denote the three RCDP stations. The shaded areas are reported spawning areas according to local fishers. The insert shows where the geographical location of the study area is located in northern Norway.

was applied [e.g. Ådlandsvik and Sundby, 1994 or a similar version of the model investigating salmon lice in Norwegian fjords in Asplin *et al.* (2013)]. To compensate for natural variability in the

circulation pattern that was not resolved by the ocean model, a random diffusion term was added to the particles velocity. This random walk was modelled as a Gaussian distributed diffusion with

a coefficient of $1 \text{ m}^2 \text{ s}^{-1}$ (corresponding to a velocity limited by -2 and $+2 \text{ cm s}^{-1}$). Eggs were initially distributed at several fixed depths between 2 and 50 m according to a Gaussian distribution with an average of 15 m and a standard deviation of 10 m. This gave a depth distribution of eggs that approximately corresponded to the ratio of eggs found in the two different depth intervals examined in 2009.

Release of the modelled eggs closely followed the empirical egg sampling dates. Specifically, the sampling in 2009 took place during 16–20 April where the simulations were started at 16, 18, and 20 April. Sampling in 2010 took place during 24 and 25 April, while the simulated eggs were released on 22, 24, and 26 April. The number of simulated eggs released per station was scaled according to the number of first- and second-stage eggs found at each station each year during the field study. Each egg was scaled with 20 particles, implying that a total of 35 020 and 11 740 particles were released in each simulation for 2009 and 2010, respectively. When released in the model, eggs were allowed to drift in their respective predefined depths determined by ocean currents for 30 d. Finally, a simulation where 100 particles were released from all 75 egg survey stations into the 2010 current regime was conducted (7500 particles in total). This was done to evaluate the hypothetical approach in lack of field data where all registered spawning areas were given equal importance.

To visualize the dispersal kernels of eggs after drift and to construct a geographic dispersal probability distribution, kernel density distributions (Epanechnikov, 1969; Samiuddin and Elsayyad, 1990) of the eggs at the end of day 30 were created for the total combined drift from both years (all particles released) as well as for each release date, at each of four depth intervals (2–5, 5–10, 10–20, and >20 m) for each year for comparison. A distribution was also created from the uniform release of particles in the fjord. The kernel density distributions were evaluated on a 250×250 m matrix.

Results

Egg surveys

In both years, hauls taken in the fjord were dominated by cod eggs, but contained some other fish species as well (Table 1). In 2010, a large number of small gadoid eggs ($N = 233$, 1.1–1.2 mm in diameter) were found. Based on the known size range of cod eggs (Hiemstra, 1962), these smaller eggs were unlikely to be cod and therefore were not included in the analysis. The total number of cod eggs sampled was considerably higher in 2009 (total of 1868) than in 2010 (total of 703). In 2009, a large proportion of the eggs were in the earliest developmental stage. In 2010, a larger proportion of the eggs were older, and a considerable number of larvae were also found (Table 1). In 2009, the average density of cod eggs was $68.32 \text{ eggs m}^{-2}$ surface (range: 0–2592, s.d.: 303.32). In 2010, the

average density was $35.04 \text{ eggs m}^{-2}$ surface (range: 0–293, s.d.: 58.51). The results in 2009 were heavily influenced by one station containing 733 eggs. When omitting this station, the 2009 mean was $34.19 \text{ eggs m}^{-2}$ surface (s.d.: 68.65).

The highest densities of cod eggs were found in the inner parts of the fjord (Figure 2). To test for spatial autocorrelation, the differences in ln number of eggs were calculated between all pairs of stations. The average difference was calculated for groups based on the average distance between stations (1863 m). The group containing pairs of stations separated by less than the average distance between stations had the lowest average spatial autocorrelation. In 2010, the semi-variance (Rossi et al., 1992; Perry et al., 2002) in this group was 0.7 compared with an average of 1.3 for all other groups (0.9–2.0). There was no linear trend in the semi-variance. In 2009, the spatial autocorrelation was not as apparent, but this was due to the one station containing 42% of the eggs. When omitting this station, the pattern in 2009 resembled the distribution found in 2010. The vertically separated hauls taken in 2009 also showed that most of the eggs (77%) were found in the upper 20 m of the water column. Excluding the single station where 42% of all eggs were found, we found that 36% of the eggs were located between 20 and 50 m depth.

Model validation

The modelled currents in the Storfjord showed, in general, a surface current direction dominated by the winds, typically in an along-fjord direction. In periods with calm winds, the modelled surface circulation displayed a complex pattern with small-scale eddies and meanders. The freshwater discharge from rivers was too small to establish a well-defined surface boundary layer during April, implying that the upper 50 m was well mixed with typical salinities at 33.8 and temperatures between 3 and 3.5°C (Figure 3). In May, however, seasonal warming of the fjord and inland melting of snow leading to increased river run-off created a surface layer of 10–15 m thickness (Figure 3). Such dynamical features typical for Norwegian fjords are explained in more detail in, for example, Aure et al. (2007).

The implication of a well-defined surface layer was that the wind forces had less impact on the ocean currents below this mixed surface layer. Besides the local rivers and the seasonal warming in May, the density stratification in the Storfjord was mainly influenced by exchange of coastal and offshore water through the Lyngenfjord. During winter and spring, water density is mainly determined by salinity in Norwegian waters, and all the salinity measurements have been compared with corresponding model values, separated between 15 April and 14 May (Figure 4). The model indicated no significant bias in salinity, except for the lowest values in mid-May close to the surface. The relatively homogeneous conditions in mid-April are well reproduced in the model, and due to enhanced river run-off initiated by the melting of snow, the model builds up a surface layer in May as seen in the measurements.

Table 1. Results from egg surveys.

Stage	Non-cod	Stage I	Stage II	Stage III	Stage IV	Stage V	Larvae
2009 Number	341	1709	42	103	5	9	0
2009 Ratio		0.91	0.02	0.06	0.00	0.00	
2009 0–20 m	177	1328	37	75	3	5	
2009 20–50 m	164	381	5	28	2	4	
2010 Number	500	502	85	67	12	37	42
2010 Ratio		0.71	0.12	0.10	0.02	0.05	

Number of eggs and proportion of total according to the stage. Samples from 2009 and 2010 are samples from an identical set of 75 stations. Numbers from 2009 are pooled numbers from an upper and a lower haul given by the depth intervals 2–20 and 20–50 m, respectively.

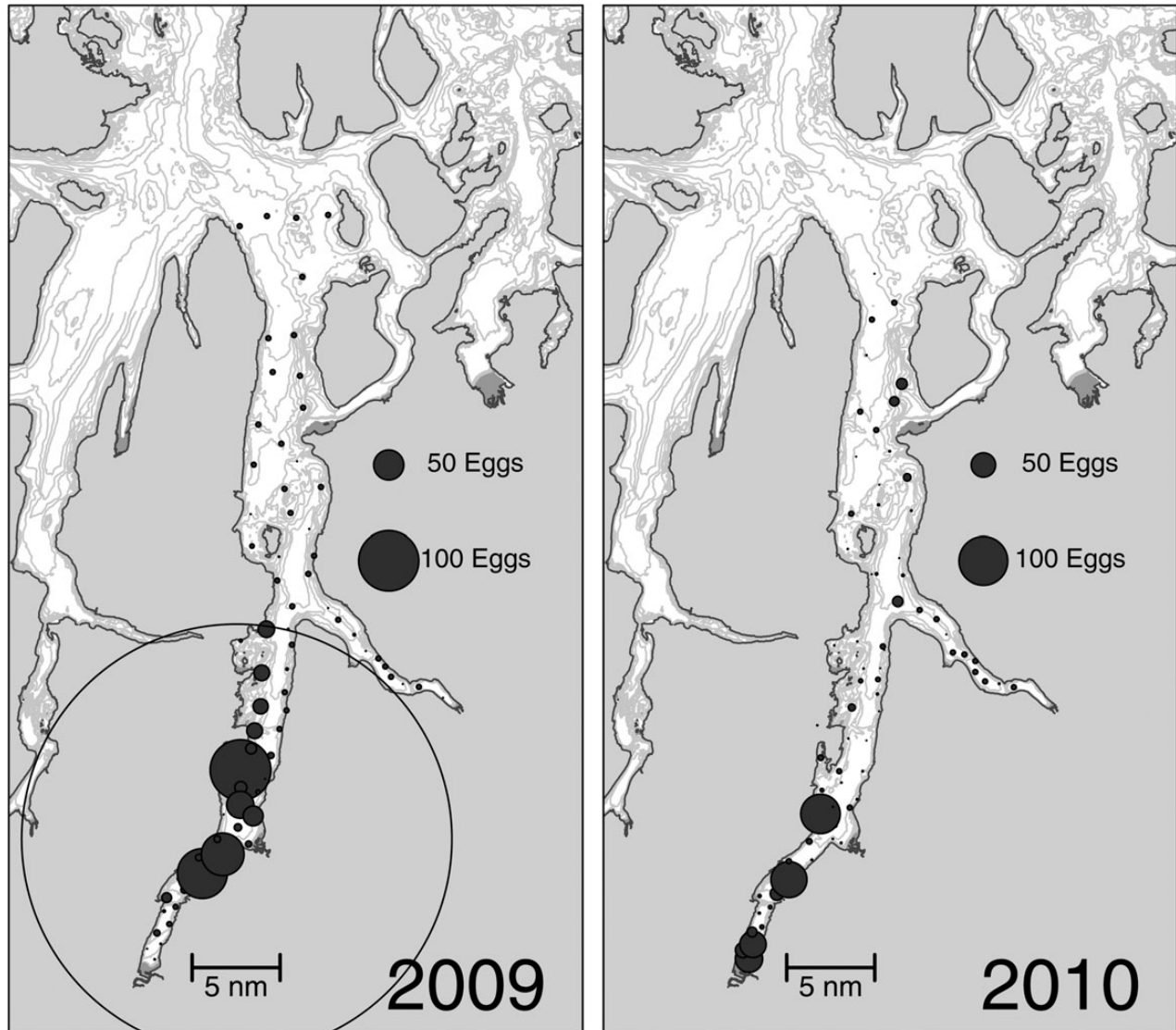


Figure 2. Distribution of newly spawned cod eggs from the years 2009 and 2010. Filled circles are scaled to the number of cod eggs of stages 1 and 2 at each station sampled. Zero count stations are marked as small dots. Left panel: Distributions from 2009. One circle is left unfilled so to make the other circles visible. Right panel: distributions from 2010.

The capability of reproducing ocean currents well is vital in our effort of estimating realistic drift patterns for the cod eggs. The drifting phase for the eggs is assumed to be 3–4 weeks, and it must be emphasized to validate the model's ability to reproduce the observed currents, in particular in a statistical sense. The main portion of the particles in the drift model was released between 10 and 20 m, and ocean currents at 20 m depth were used to demonstrate the differences between observed and modelled currents. First, the measured and modelled current speeds are plotted in scatter and quantile diagrams for all stations (Figure 5). In the quantile diagram, first all percentiles from 1 to 99 are found in the observed and modelled time-series individually, then these are compared with each other. A perfect model would then reproduce the diagonal line starting in the origin. As demonstrated by the scatterplots, the model is not able to reproduce the correct current speed at the correct time, but as shown by the quantile diagrams, the statistical values for the observational period of 1 month are more realistic. The model overestimates

the strongest currents; however, these represent only a few events. Second, both observed and modelled currents at 20 m depth are presented in a progressive vector diagram (PVD; Figure 6). PVDs alternatively display the particle path based on current vectors from fixed locations. The PVD from RDCP station 1 shows that the main current direction was inward. The model reproduces the direction of the currents well, but the drift speed is overestimated. The RDCP stations 2 and 3 are located east and west, respectively, and measurements show a typical inflow at the western side and an outflow at the opposite side. As for station 1, the model exaggerates the inflow drift speed at station 3. At station 2, the model reproduces the outflow well in the first third of the observational period while observed currents indicate a persistent flow from this location towards land to the east. These onshore currents are not seen in the model results and may be attributed to restrictions and deficiencies due to the spatial resolution, e.g. how well the bathymetry is represented and the resolution of the external forcing.

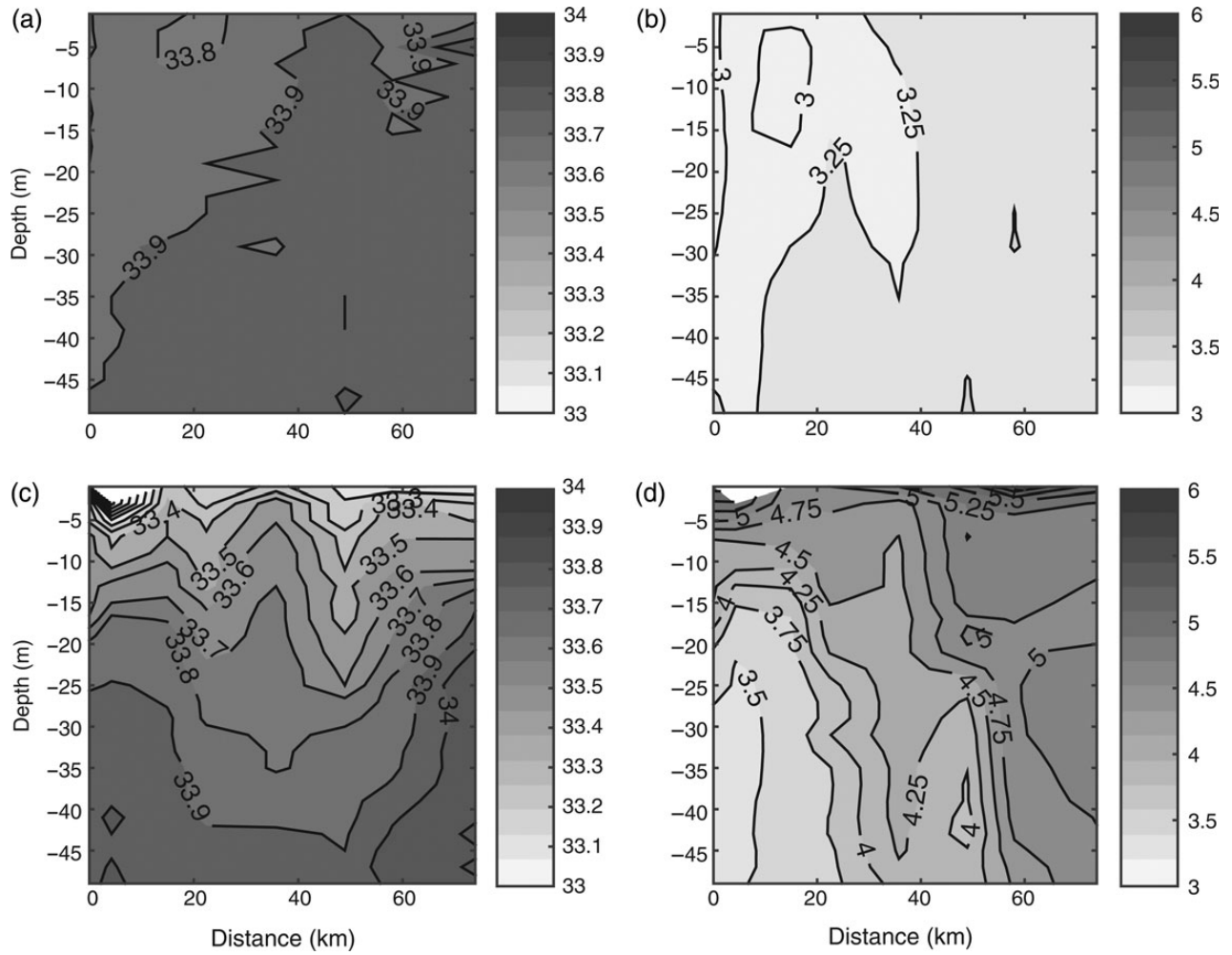


Figure 3. Hydrographic profiles measured 15 April 2009 (a) and (b), and May 14th 2009 (c) and (d) along the entire Storfjord between the surface and 50 m depth. The panels to the left (a) and (c) show salinity and temperatures are displayed to the right (b) and (d).

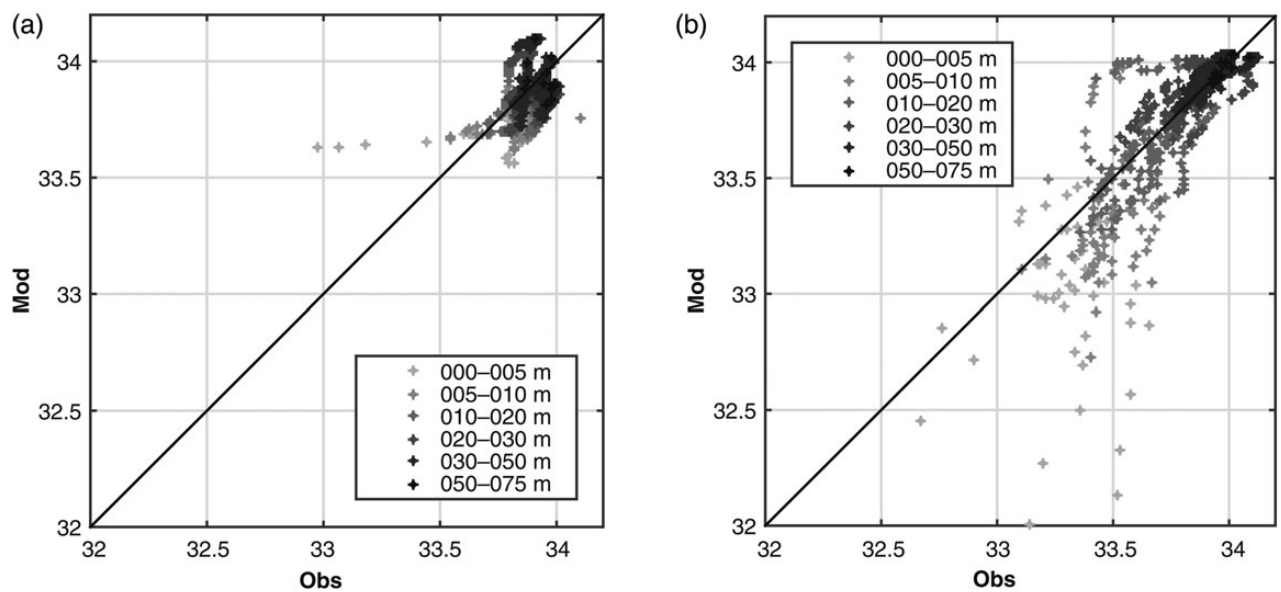


Figure 4. Model validation. Scatter diagrams where observed salinity (along horizontal axis) is plotted against modelled values (vertical axis) for April 15th (a) and May 14th (b) 2009. The grey colours denote depth levels where lighter grey dots represent measurements closer to the surface.

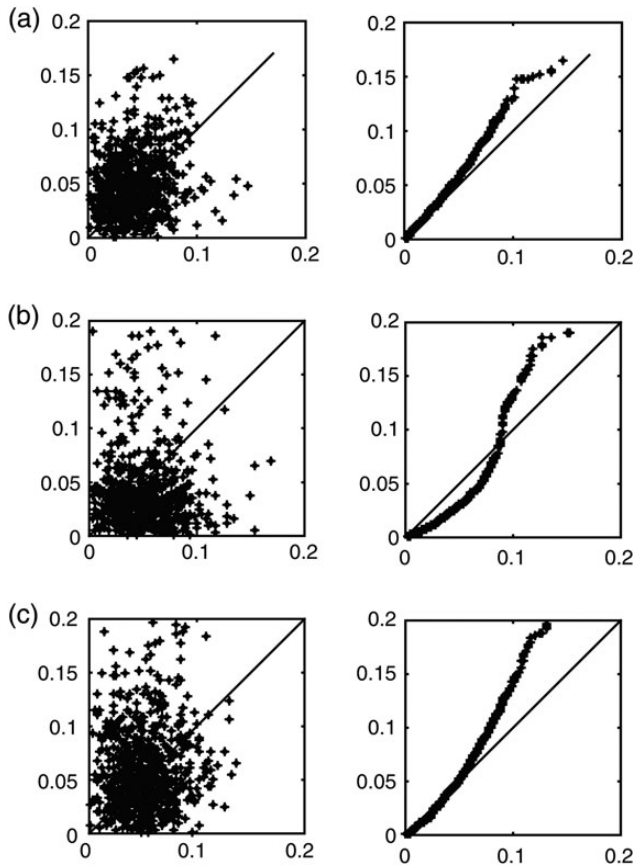


Figure 5. Scatter (left panels) and quantile plots (right panels) for current speed at 20 m depth from RDCP locations 1 (a), 2 (b), and 3 (c) based on hourly currents from 15 April to 14 May 2009. Observed and modelled values are displayed along the horizontal and vertical axes, respectively.

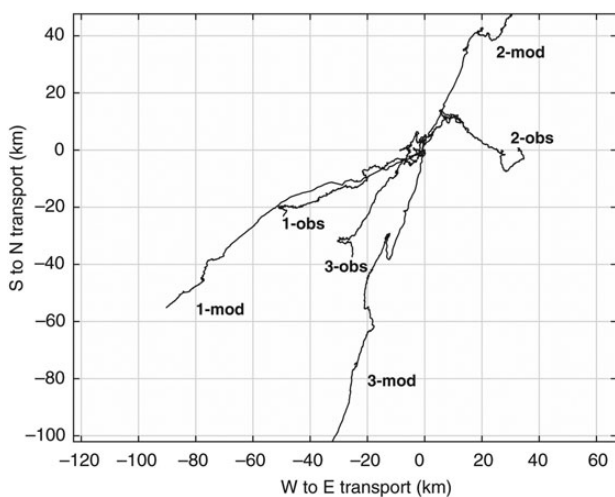


Figure 6. PVD displaying the observed and modelled currents at 20 m depth based on RDCP stations 1, 2, and 3 (see tags in the diagram). All vectors start 15 April 2009 in the origin and end after 30 d. The horizontal and vertical axes denote the hypothetical drift distance (in km) for a passive particle in the West – East and South – North direction, respectively.

Particle drift and retention

After 30-d drift in the particle-tracking model with input of ocean currents and even if the model domain was extended far from the egg-haul stations, 14.71% of the particles ended up outside the model domain and were excluded in the analysis. The average drift distance for the egg particles was 20.0 and 15.8 km in 2009 and 2010, respectively. The probability distribution of eggs after drift portrayed a concentration of eggs in the inner parts of the Storfjord, with the 75% border of the density distribution on the inside of the Kåfjord, Storfjord branch (Figure 7). Some eggs, shown by the extended 95% border, were transported longer distances eastward (~100 km) and ended up in the neighbouring fjord (Nordreisa). The overall highest concentrations were found in the innermost part of the Storfjord across all years and release dates (Figure 7). Overall, the eggs located in the deepest levels below 10 m experienced much less dispersal with more concentrated distributions towards the fjord end for both years and for different release dates (Figure 8). The upper 5 m demonstrated the highest degree of dispersal, and

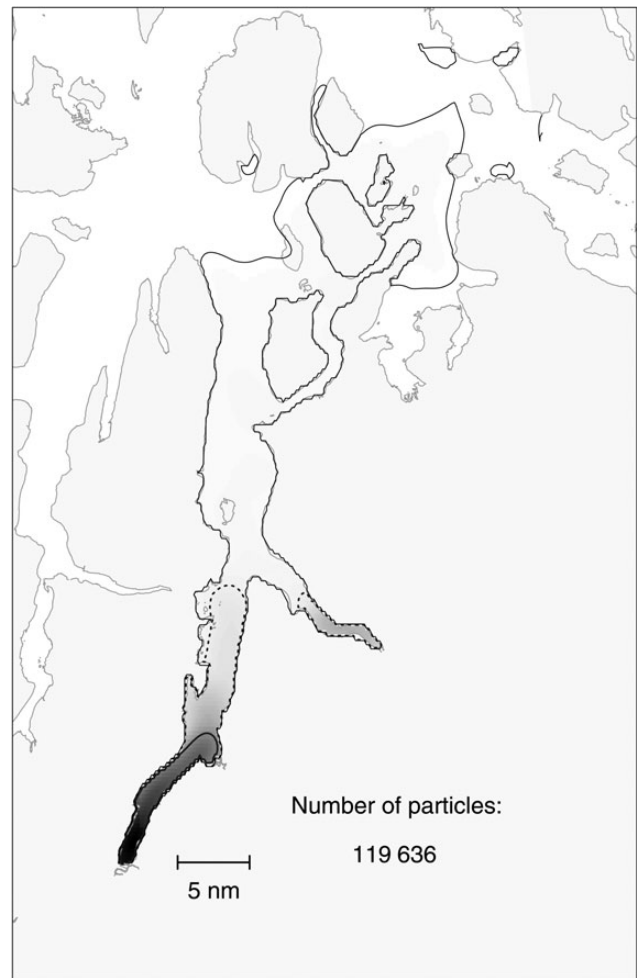


Figure 7. Map of where a cod may expect the offspring to end up. The combined probability distribution of all particles released in the 2 years 2009 and 2010. The colour scale of black to white indicates going from a high to low probability of finding an egg after 30 d of drift. The thick line indicates the area where the probability is 50% or higher, the thick dotted line indicates the 75% area, and the thin black line indicates the 95% area.

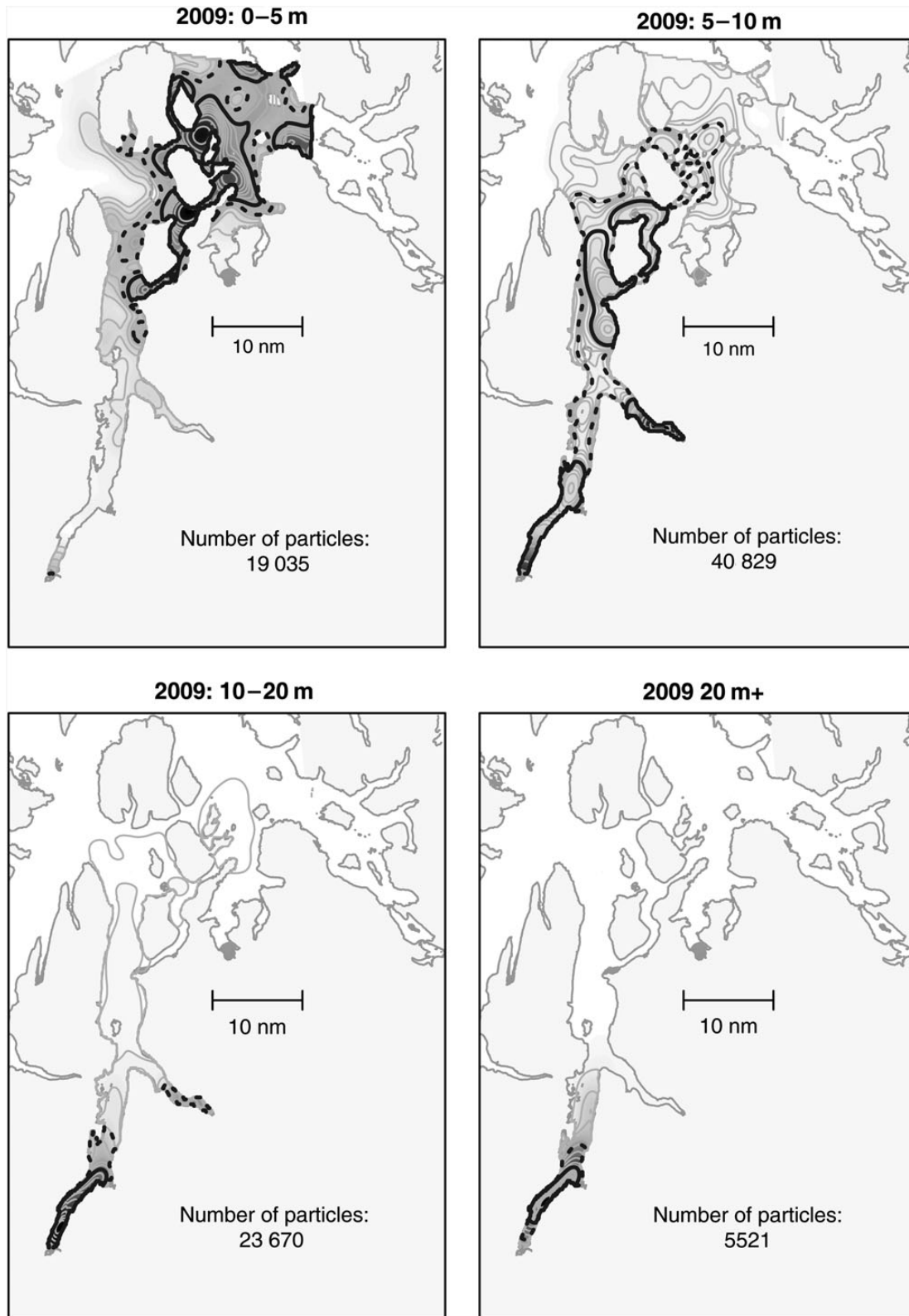


Figure 8. Probability density distributions for eggs released at different depths. Upper left: 0–5 m, upper right: 5–10 m, lower left: 10–20 m, and lower right: > 20 m. Grey lines are isolines connecting parts of the distribution with equal probability of finding a cod egg 30 d after spawning, so the distribution inside sums up to a given percentage of the entire distribution. One line is drawn for every 5% of the distribution. The thick line indicates the 75% line and the thick dotted line indicates the 50% area.

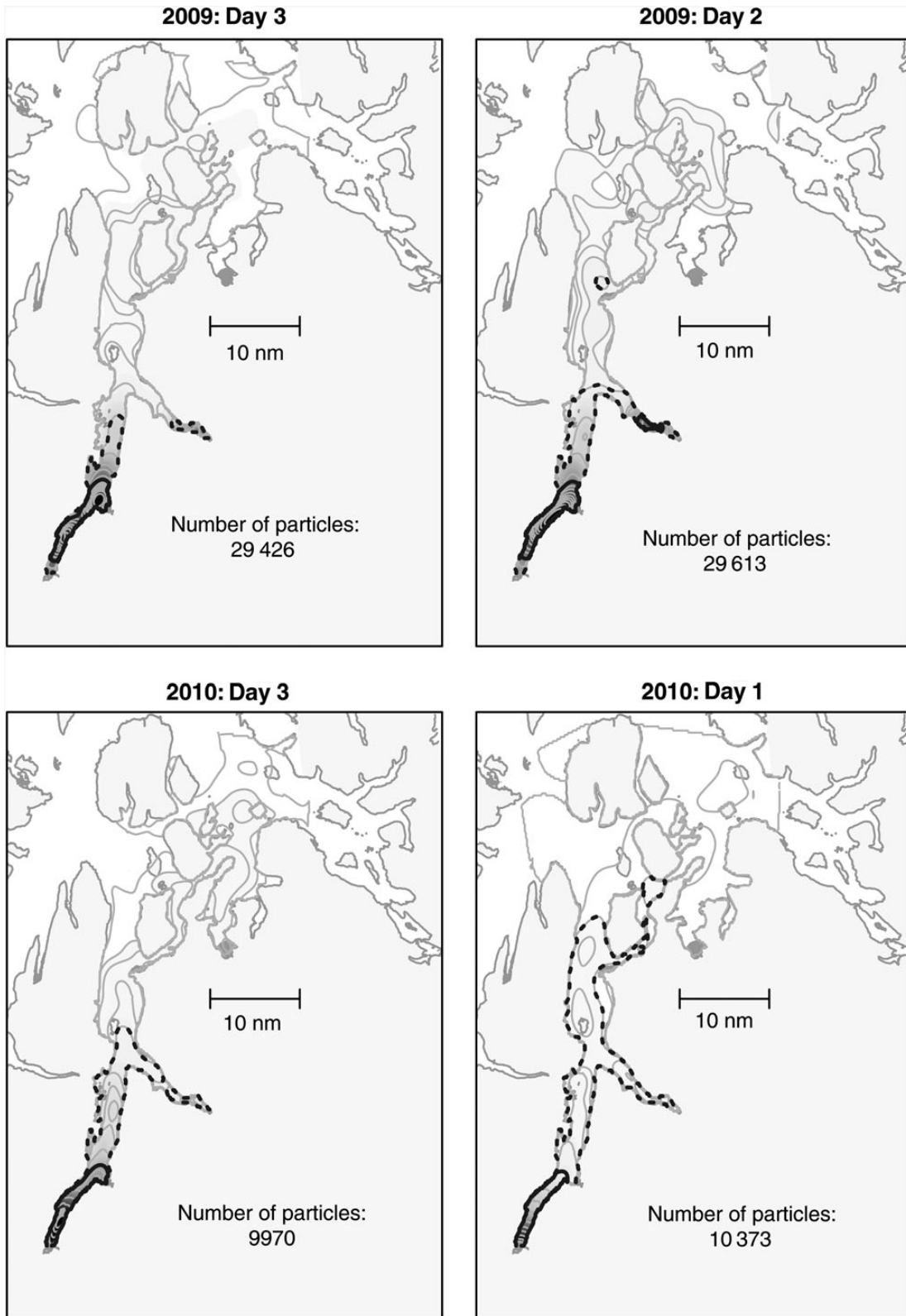


Figure 9. Probability distributions for all eggs released at a given day for a given year. Grey lines are isolines connecting parts of the distribution with equal probability of finding a cod egg 30 d after spawning so the distribution inside sums up to a given percentage of the entire distribution. One line is drawn for every 5% of the distribution. The thick line indicates the 75% area and the thick dotted line indicates the 50% area. Every year particles were released on three different dates. The upper row is for two different dates from 2009, with the one showing the least dispersal on the left and the one showing the most dispersal on the right. The lower equals the upper but are for particles released in 2010.

the variation in dispersal between different depths was far greater than between different release dates and years (Figure 9). In the simulation, a total of 21% of the eggs were released in the upper 5 m. Releasing egg particles in a uniform distribution, i.e. with an equal number of eggs at each station, gave the overall largest areas and thus the greatest dispersal of eggs (Figure 10).

Discussion

In this study, we used a probabilistic approach to investigate the dispersal of pelagic eggs of Atlantic cod spawned within an open Arctic fjord and how these dispersal distributions would be affected by model initialization. Based on empirical observations of the spatial distribution of newly spawned cod eggs, the oceanographic model could be initialized properly, and by applying time-variant ocean currents, we predicted that most offspring will indeed remain within the fjord system throughout the early pelagic phase. In particular, eggs found at depths below 10 m will often be transported up the fjord (away from the open ocean), leading to an aggregation of offspring in the inner parts of the fjord system. In comparison, eggs that were found closer to the surface had a higher probability of being transported out the fjord. Finally, releasing eggs in proportions as found in the field described the initial data more realistically and therefore a more probable retention than releasing eggs in a uniform distribution throughout the fjord,

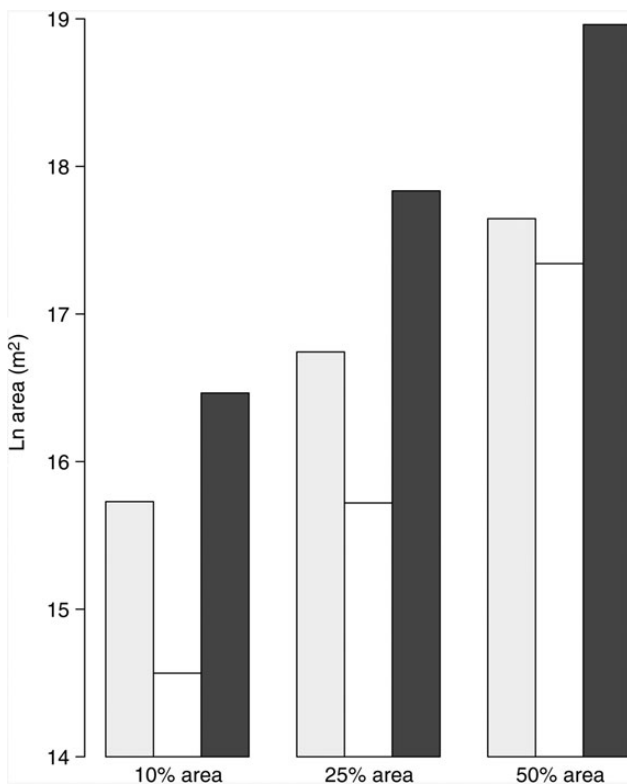


Figure 10. Areas covered by drift under different release scenarios. Height of bars corresponds to the \ln of the area (m^2) containing 10, 25, and 50% of the density of distributions. Each colour denotes a different release scenario. The leftmost bars show the areas after drift where eggs were released in the same proportions as they were found in 2009, the next show areas from 2010, and the rightmost bars denote the areas after drift when a uniform distribution of eggs, i.e. same number of particles at every egg station, were released in the 2010 current regime.

although the latter also described the concentration of eggs in the inner part of the fjord. The main reason for this potential exaggeration of the spread of cod larvae was that eggs were not observed at many of the outermost egg stations, although this part of the fjord system was previously marked as a spawning area based on catches only. Below we discuss the methodological and ecological implications of these findings.

Knutsen *et al.* (2007) reported a possible retention in relation to sills in fjords based on high egg concentrations near sills. Here, we demonstrated that eggs may be retained even in the absence of sills or bottom topographical features limiting dispersal. We showed that ocean currents in the intermediate layer (below the 10–15 m deep surface layer developing in May), and the probable vertical location of the spawned eggs, had a dominating current inflow at the western side of the fjord and mainly current outflow along the eastern side, leaving no clear sign of whether the Storfjord is a retention area or not. By modelling the release of particles, we demonstrated that the main portion of the spawning products remained in the fjord.

Ocean circulation models are certainly not perfect, but the validation results for the Storfjord have shown that ROMS reproduced current statistics and hydrography satisfactorily. The discrepancies shown in the ocean current validation may indicate that particle drift speed was overestimated, implying that larvae end their drifting phase closer to the spawning sites than shown by the model. Releasing 20 times more egg particles than eggs observed allowed statistically significant evaluation of the different particle trajectories within the model, and to some degree, we compensated for deficiencies in the modelled currents by additional random-walk diffusion of each particle. It is then important that our particle drift results are treated in a probabilistic sense, meaning that conclusions based on individual particles are meaningless.

Our particle-tracking simulations were conducted by releasing all egg particles at multiple fixed levels below the surface, i.e. between 2 and 50 m with the main portion released between 10 and 20 m depth. In the ocean, cod eggs do not float at a fixed level below the surface, but find their vertical position dependent on their buoyancy (Stenevik *et al.*, 2008). As we pointed out in the results, we found that the hydrography in Storfjord was quite homogeneous during spawning season in April. In addition, we always find discrepancies and biases between observed and modelled hydrography, i.e. model errors in density. We performed initial particle-tracking simulations where the eggs were released at 15 and 30 m depth initially, and were all allowed to drift freely. Measurements of egg density from Stenevik *et al.* (2008) were applied for the egg particles (denoted with a mean salinity and a standard deviation), and salinity, temperature, and vertical diffusion estimates were used in addition to currents as input from the ocean model to the particle-tracking model. The drift results then showed an upwards drift immediately after release causing an unrealistically high density of particle eggs in the upper 2 m and a subsequent massive drift out of the fjord (as seen in Figure 8, upper left panel). The upwards drift was mainly explained by insertion of eggs in a too dense environment. Due to the homogeneous water in April, very small errors in the modelled density field will have a major impact on the buoyancy of the eggs, either causing them to sink deeper or rise higher than what is realistic. In addition, the applied density of the eggs [from Stenevik *et al.* (2008)] were retrieved from experiments where adult cod were caught in a fjord representing the area of interest in northern Norway and released in a test cage at the west coast of Norway for spawning. One must assume that cod adjust the internal density of their spawning mass with respect to the oceanic environment.

The uncertainties regarding the modelled density fields of the fjord and the density of the cod eggs forced us to simulate drift at fixed vertical levels where we have confidence in the horizontally modelled currents. Our choice of the fixed depths, however, was based on observations of egg density, implying that fjord cod eggs are located below the typical surface mixed layer (Ciannelli *et al.*, 2010; Myksvoll *et al.*, 2011). In addition, choosing deployment of egg particles at all depths at all stations left us with broad drift scenarios where all potential spawning levels were represented.

Retention was much clearer in the deep layers than in the surface layers. Field observations showed that about one-third of the eggs were found deeper than 20 m in the water column. Our model showed that if the real vertical distribution of eggs was not taken into account, it overestimated dispersal, implying that retention could easily be affected by the vertical distribution of eggs. This result is in agreement with other studies also demonstrating an important effect of vertical distribution of eggs (Knickle and Rose, 2010; Pacariz *et al.*, 2014). In 2010, we found fewer eggs than the previous year, and in addition a larger proportion of the eggs were located closer to the fjord end. As a result, retention was higher in 2010 than the year before, but combining an observed egg distribution with the drift model simulated a distribution spread over a much smaller area than when eggs were released using a uniform distribution. In conclusion, our study underscores the value of having accurate empirical data on pelagic early life stages to feed into simulation models. By doing this, we revealed that the classical spawning strategy of marine fish might involve retention of early pelagic stages even in fairly open habitats with no obvious barriers to dispersal. Therefore, a more constrained spatial scale of population dynamics may be more widespread than previously thought.

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