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Modelling dispersal of eggs and quantifying connectivity among Norwegian coastal cod subpopulations

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The Norwegian coast is populated by two cod populations: Northeast Arctic cod and Norwegian Coastal cod. In this paper, we use a further division based on life history: oceanic cod, coastal cod, and fjord cod. A numerical ocean model was implemented for the northern Norwegian coast where all these populations have spawning areas. The model results were used to simulate connectivity and retention of cod eggs from the different subpopulations. The model reproduced the observed variability and mesoscale activity in the Norwegian Coastal Current. Eggs released at an oceanic spawning area were transported northwards along the coastline. Coastal cod eggs had intermediate connectivity with each other and fjord cod eggs had high local retention. Although the high retention of eggs in fjord areas is mainly caused by a subsurface distribution of eggs, the intermediate retention of eggs from coastal spawning areas is caused by small-scale eddies in-between many small islands. The high-resolution ocean model made it possible to reveal these specific dispersal patterns. The high retention of early life stages in fjords combined with strong homing to spawning areas indicates that fjord subpopulations may be described as a metapopulation.

Keywords: eddy activity, egg buoyancy, Gadus morhua L., metapopulation, Norwegian Coastal Current, particle tracking.

Introduction

The Norwegian coast is populated by two main cod populations (*Gadus morhua* L.), which are managed as two separate stocks, the Northeast Arctic cod (NEAC) and the Norwegian coastal cod (NCC). The NEAC is a large oceanic stock with spawning area in Vestfjorden (VE), in addition to several areas along the coast from 60 to 71°N (Sundby and Nakken, 2008). The eggs and larvae are transported northwards with the Norwegian Coastal Current, to the juvenile feeding and nursery areas in the Barents Sea, travelling a distance of up to 1200 km (Bergstad et al., 1987). The NCC has a very different life history, with both spawning and nursery areas at the coast. Several studies have indicated that the NCC consists of several subpopulations with separated life histories. NCC can be categorized into two major components: stationary NCC and migratory NCC. Stationary NCC spawns and feeds inside the fjords and does not migrate

far from their local habitat. Jakobsen (1987) even claimed that each fjord has its own cod population. Migratory NCC spawns at the coast and migrates short distances along the coast for feeding at coastal banks and bays. Altogether, there are three cod populations with different life histories spawning near VE: oceanic cod (NEAC), coastal cod (migratory NCC), and fjord cod (stationary NCC). Several authors have reported genetic differences between NEAC and NCC (e.g. Fevolden and Pogson, 1997; Pogson and Fevolden, 2003). Recently, also genetically separated subpopulations within NCC are recognized (Dahle et al., 2006; Jorde et al., 2007). Dispersal and mixing among early life stages from different spawning areas could counteract the build-up of genetic differentiation. This implies that the maintenance of this differentiation is depending on the retention of early life stages and/or strong homing of juveniles and adults (Knutsen et al., 2007). Retention mechanisms of cod eggs within

the fjords have been investigated, showing a large degree of isolation during the early life stages (Ciannelli et al., 2010; Myksvoll et al., 2011). Also the transport of NEAC eggs and larvae from Lofoten into the Barents Sea is well known by observations (Bergstad et al., 1987) and by modelling (Ådlandsvik and Sundby, 1994; Vikebø et al., 2005). However, the transport of early life stages from coastal spawning areas is not well characterized. Specifically, we want to investigate the potential for retention at the coast and quantify the connectivity among subpopulations spawning in coastal areas and among subpopulations spawning in fjords and coastal areas.

Smedbol and Wroblewski (2002) discussed the subpopulation structure of northern cod in a metapopulation perspective. Metapopulation means a "population of populations", where individual populations are connected through migration, extinction, and recolonization events (Smedbol et al., 2002). The theory was introduced by Levins (1970) consisting of three assumptions: (i) subpopulations have the same geographic extent and degree of isolation, (ii) each subpopulation has separate local population dynamics, and (iii) the rate of exchange of individuals among subpopulations is too low to affect local population dynamics (Smedbol and Wroblewski, 2002). The subpopulations are not necessarily genetically different, but an observed difference would indicate low exchange rates among subpopulations. Smedbol et al. (2002) emphasize that metapopulations have to be a set of semi-independent subpopulations where at least one must have a non-zero probability of extinction, not caused by anthropogenic influence such as fishing. One issue addressed when applying the metapopulation theory to marine populations is connectivity. Many species, such as cod, have pelagic eggs and larvae with potential for long-distance dispersal. Because of this, marine populations have traditionally been considered "open". However, Cowen et al. (2000) showed that larval behaviour might enhance retention and that coastal marine populations were not as "open" as previously assumed.

The objective of this paper is to investigate the degree of isolation among several coastal spawning areas by analysing the dispersal pattern during the pelagic egg stages. Biological data will be used as input to an individual-based model coupled to a circulation model covering Helgeland county in northern Norway. The results will be used to evaluate connectivity among fjord cod and coastal cod populations and will be discussed within a metapopulation framework. The focus in this paper will be on the egg stage, although the larval dispersal may also have a significant impact. Available knowledge regarding the vertical distribution of cod larvae state that the larvae avoid the upper 5–10 m of the water column (Ellertsen et al., 1984, 1989; Sundby and Fossum, 1990). The consequence of a subsurface larval distribution is a considerable reduction in spatial dispersion. It is therefore likely that the distribution pattern described for cod eggs will continue also for cod larvae. Dispersing eggs will continue to disperse, whereas eggs that are retained will continue to be retained as larvae.

Material and methods
The study area
The area of interest is shown in Figure 1, mainly covering the coastal areas of Nordland County in northern Norway from ~64.5 to 70.0°N. The coloured area shows the model domain with bathymetry, in relation to the Norwegian Costal Current and the Norwegian Atlantic Current. The Norwegian Coastal Current originates from the outflow of brackish water from the

Baltic Sea through Kattegat, the North Sea coastal water, and freshwater run-off from Norwegian rivers and follows the entire Norwegian coast (Sætre, 2007b). The low-saline current mixes initially with North Sea water and subsequently with Atlantic water northwards, becoming more saline. The Norwegian Coastal Current is mainly driven by the wind pattern and the density structure and forms a wedge-shaped current bordered by the Norwegian coast. The Norwegian Atlantic Current is located offshore of the coastal current and is characterized by warm saline water (Orvik and Niiler, 2002).

The model area was divided into seven subareas, called zones, representing different spawning areas and geographical regions as shown in Figure 2. The names of the zones with corresponding abbreviation are shown in Table 1, including geographical information and spawning population. Vikna (VI) is a known spawning area for NEAC (Sundby and Nakken, 2008) and is located offshore. The three coastal zones, Rørvik-Vega (RV), Vega-Træna (VT), and Træna-Bodø (TB), are known spawning areas for the NCC and
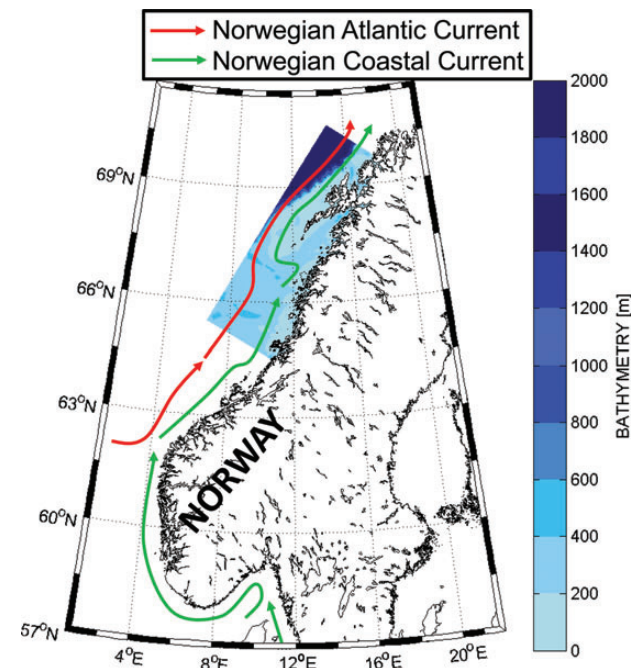

Figure 1. The location of the study area in Nordland County in northern Norway, in relation to the Norwegian Atlantic Current and the Norwegian Coastal Current.
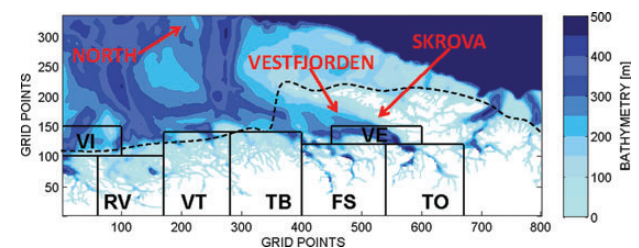

Figure 2. The model area with bathymetry and subdivision into seven zones representing different spawning areas and geographical regions: VI, RV, VT, TB, FS, TO, and VE. The location of VE, the main spawning area of NEAC, and the coastal station Skrova are shown on the map, and the dashed line is the baseline.

Table 1. Names of zones including information about the geographical region, spawning population by oceanic cod (NEAC), coastal cod (migratory NCC), or fjord cod (stationary NCC), and colour scheme used in Figure 7.

Abb.	Name	Region	Spawning population	Colour
VI	Vikna	Oceanic	Oceanic cod	Red
RV	Rørvik-Vega	Coastal	Coastal cod	Blue
VT	Vega-Træna	Coastal	Coastal cod	Green
TB	Træna-Bodø	Coastal	Coastal cod	Magenta
FS	Folda-Skjerstadfjord	Fjordic	Fjord cod	Cyan
TO	Tysfjord-Ofotfjord	Fjordic	Fjord cod	Blue (- -)
VE	Vestfjorden	Coastal	Oceanic/coastal cod	Red (- -)

Figure 3. Point measurements. Frequencies of the egg specific gravity at the morula stage measured from Tysfjord and Helgeland populations during spawning season (March to April). The egg specific gravity was expressed by the salinity of neutral buoyancy at $6°C$. Then total number of egg batches per population was ten for Tysfjord and eight for Helgeland. The total number of eggs per batch was ~50.

named Helgeland stock in Dahle *et al.* (2006) and Otterå *et al.* (2006). The two fjordic zones, Folda-Skjerstadfjord (FS) and Tysfjord-Ofotfjord (TO), are inhabited by the stationary component of NCC and are genetically separated from the Helgeland population (Dahle *et al.*, 2006). Myksvoll *et al.* (2011) showed how spawning in a fjord system enhance retention and therefore contribute to sustain the subpopulations within fjords. VE is the most important spawning area for NEAC, in addition to substantial spawning by NCC (Nordeide, 1998).

The transport of cod eggs is discussed in relation to the zones. The degree of retention is hereby defined as the percentage of eggs that hatch in the zone they were released. Connectivity is used to describe the degree of transport of cod eggs from one zone to another.

Egg specific gravity measurements

The egg specific gravity is one of the input parameters for the model of egg vertical distribution. Hence, we obtained the experimental data of the egg specific gravity examined by Jung *et al.* (2012) with Tysfjord and Helgeland origin cod populations, assuming that Tysfjord and Helgeland populations represent typical fjord-spawning cod and coastal-spawning cod, respectively. Eggs were naturally spawned during 2 months (March and April), and they were collected from seven and three different female cod for Tysfjord and Helgeland, respectively. See the study of Jung *et al.* (2012) for the detailed information of raised broodfish, egg collection, and the determination of the egg specific gravity.

Experiments for the measurements of the egg specific gravity were designed for two purposes: one was "point measurements" to obtain all possible phenotypes of the egg specific gravity only at the morula stage (2-d old; Fridgeirsson, 1978), and the other was "continuous measurements" to track ontogenetic changes in the egg specific gravity during development. (i) For the point measurements, up to four egg batches per broodfish were used. The total number of egg batches was ten for Tysfjord and eight for Helgeland, using ~50 eggs per batch. As there was no significant difference between Tysfjord and Helgeland (*t*-test, $P = 0.12$, Figure 3), all the measured values of specific gravities were merged to generate a normal distribution of the egg specific gravity at the morula stage (the mean egg specific gravity expressed in salinity units: 30.57; 1 s.d.: 1.27). (ii) Continuous measurements used a single egg batch for each population. About 50 eggs at the morula stage were used, and the eggs were monitored for 2 weeks until hatching. The positions of eggs and glass floats were noted every day. As seen in Figure 4, fertilized eggs showed a slight
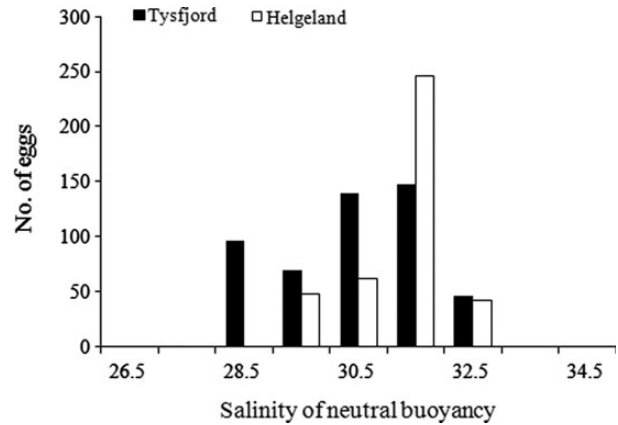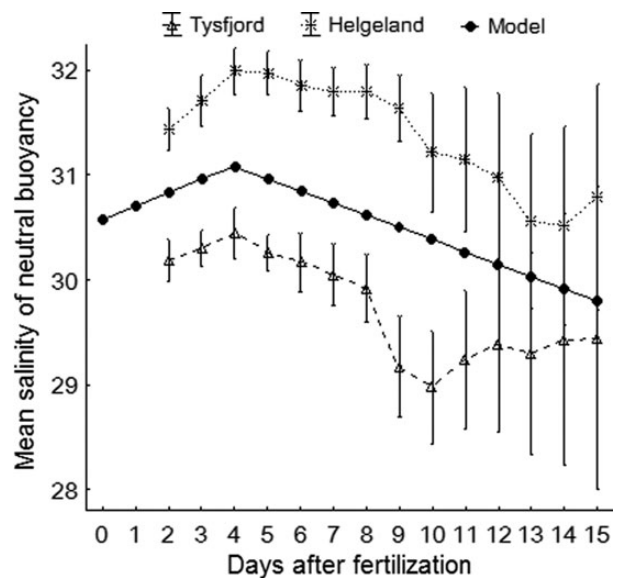

Figure 4. Continuous measurements. Ontogenetic changes in the mean salinity of neutral buoyancy for Tysfjord and Helgeland populations during development. Three transition points (i.e. morula stage, day 4, and day 15) were used to develop a simplified linear model in the present study. Vertical bars denote 1 s.d.

increase in their specific gravity until day 4, then a gradual decrease during the rest of the incubation time. To develop a simplified linear model during development, the specific gravity at the morula stage is assumed as the value at fertilization. The values on days 4 and 15 are assumed as maximum and minimum specific gravities, respectively. The ontogenetic variability was larger among individual eggs, but the degree of changes were limited between the maximum and minimum (Jung *et al.* 2012). Hence, we chose the trend of Helgeland because Helgeland showed much smoother changes in the egg specific gravity throughout the development.

Circulation model

The model used for the ocean current simulation is the Regional Ocean Modeling System (ROMS) version 3.4, algorithms described by Shchepetkin and McWilliams (2005). This is a free-surface, hydrostatic, primitive equation ocean model that uses stretched terrain-following s-coordinates in the vertical and curvilinear coordinates in the horizontal (Haidvogel et al., 2008). The primitive equations are solved by the finite differences method on an Arakawa C-grid, including a generic length scale turbulence closure scheme (Umlauf and Burchard, 2003) using the special case of Mellor-Yamada 2.5. Vikebø et al. (2010) used the ROMS model to simulate the transport of herring larvae and found that the ocean model reproduced observed variability within the Norwegian Coastal Current and the Norwegian Atlantic Current.

The model domain covers the Norwegian coast from 64.5 to 70°N (Figure 1; Albretsen et al., 2011). The Norwegian Mapping Authority, the hydrographic service, provided the bathymetric data. To avoid model instabilities, the bathymetry was smoothed to a maximum r factor of 0.33. The grid resolution is 800 m with 801 points in the ξ direction and 335 points in the η direction. In the vertical, there are 35 sigma layers, stacked together at the surface with a reduced resolution towards the bottom. The atmospheric forcing was extracted from the ERA-Interim reanalysis with 75-km resolution prepared at European Centre for Medium Range Weather Forecasts, including wind, temperature, pressure, cloud cover, humidity, and precipitation. Initial and boundary conditions were collected from the operational model Meteorological Institute's Princeton Ocean Model, operated by the Norwegian Meteorological Institute, covering the Nordic Seas with 4-km resolution. The input is updated with daily averaged currents, salinity, and temperature at ten vertical levels. A global barotropic model of ocean tides, TPXO7.2, provides eight primary harmonic constituents (M_2, S_2, N_2, K_1, K_2, O_1, P_1, and Q_1). The river input is provided by NVE (Norwegian Water Resources and Energy Directorate) and based on the Hydrologiska ByrûËns Vattenbalanssektions model hydrological model with 1-km horizontal resolution. Details about the model setup and external forcing may be found in Albretsen et al. (2011).

Individual-based cod egg model

The cod egg model is a simple individual-based model included to the particle-tracking routines of ROMS as described by Narvaez et al. (2012) and based on Sundby (1983, 1991). The input parameters are egg diameter (1.4 mm) and mean egg neutral buoyancy (30.57) with s.d.(1.27), in terms of salinity. Each egg is assigned a specific gravity based on a normally distributed random number generator with zero mean and unit variance. The eggs attain a vertical velocity depending on the egg size and the density difference between the egg and the surrounding water. Stokes' formula is used to calculate the terminal velocity:

$$w = \frac{1}{18} \frac{g d^2 \Delta \rho}{\mu}, \tag{1}$$

where g is the acceleration due to gravity, d the diameter of the egg, $\Delta \rho = \rho_w - \rho_e$ the density difference between the surrounding water and the egg, and μ the molecular viscosity. Stokes' formula is only valid when the Reynolds number is low, Re < 0.5:

$$Re = \frac{\rho_w d w}{\mu}, \tag{2}$$

When combining Equations (1) and (2), an expression for the maximum diameter D within Stokes' regime appears:

$$D^3 = \frac{9\mu^2}{\rho_w g \Delta \rho}, \tag{3}$$

For larger Reynolds numbers, Dallavalle's formula is used:

$$w = K_I (d - \zeta D) \Delta \rho^{2/3} \mu^{-1/3}, \tag{4}$$

where $\zeta = 0.4$ for a sphere. The coefficient K_I is derived by combining the two equations inserting Re = 0.5 and $d = D$.

$$K_I = \frac{5}{54} 9^{1/3} g^{2/3} \rho^{-1/3} = 0.0875\,\mathrm{kg}^{-1/3} m^{5/3} s^{-4/3}. \tag{5}$$

Both Stokes' and Dallavalle's formulae are included in the simulation, and for every time-step, the maximum diameter D is calculated to determine which regime the egg is within. The dynamic molecular viscosity of seawater is computed by the equation (Ådlandsvik, 2000):

$$\mu = 10^{-3} (1.7915 - 0.0538\,T + 0.0007\,T^2 + 0.0023\,S)\,\mathrm{kg\,m}^{-1}\,\mathrm{s}^{-1}. \tag{6}$$

The incubation time of the eggs is calculated as a function of temperature and integrated as degree-days until hatching. The relationship is assumed to have the shape of a power-curve, as showed by Page and Frank (1989):

$$DS = a(T + 2)^b, \tag{7}$$

where DS is the days and T the temperature. The parameters chosen here are reported in Table 9 for stage IV in Page and Frank (1989), $\log(a) = 1.88$ and $b = -0.85$.

$$DS(T + 2)^{0.85} = a \times \mathrm{const} = C. \tag{8}$$

A controlled experiment showed that the eggs hatch after 16 d at a constant temperature of 6°C. By using this information, we can adjust the right-hand side of Equation (8) and calculate a new constant $C = 93.70$.

The measurements described in "Egg specific gravity measurements" showed that the egg specific gravity increases just after spawning, reaching a maximum after 4 d (at 6°C) then declining to a minimum just before hatching as shown in Figure 4. The maximum specific gravity was 0.515 salinity units higher than the initial value resulting in an increase of 0.103 units per day until degree-days is 29.28. The difference between maximum and minimum specific gravities was 1.29 salinity units occurring from day 4 until day 16, causing a decrease of 0.117 units/day until degree-days is 93.70. This simplified linear approach was included in the individual-based model to include the variations in the egg specific gravity, as seen in Figure 4.

In total, 183 427 cod eggs were released into the model domain during the whole model simulation. Eggs were released in every fifth ocean grid cell reaching as far out as grid cell 150 in the y-direction (westwards, see Figure 2) all at 20-m depth, once every day through March and April 2009. Initial depth does not affect the horizontal distribution of eggs when the model calculates

the vertical distribution internally (Sundby, 1991; Myksvoll *et al.*, 2011). The egg specific gravity was equal for all the spawning areas, since Jung *et al.* (2012) found no significant population difference between NCC and NEAC.

Results

Hydrography and model evaluation

Hydrographic data are collected by the Institute of Marine Research at the coastal station at Skrova (Figure 2) in VE. Temperature and salinity are sampled irregularly, usually 2–4 times per month, at 12 fixed depths between 1 and 250 m. The frequency distributions of the temperature and salinity measurements are plotted in Figure 5 from eight profiles taken during March and April 2009. Model results from the approximate location are retrieved at the corresponding dates.

The temperature variations are reproduced well in the model compared with the observations. Temperatures between 3 and 4°C are most frequent both in the observations and in the model results. However, the highest observed temperatures (above 6°C) are not present in the model output, meaning that the temperatures are slightly underestimated. The distribution of salinity values in the model also deviates from the observations. The observations show two peak abundances, at 32.8 and 33.3, whereas the model shows only one peak at 33.5. The largest offset between the peaks is therefore 0.7, which is then an estimate of the maximum salinity error in the model. The salinity range in the model is narrower (33.2–34.1) than the range covered by the observations (32.3–34.6).

Figure 6 shows the surface temperature on 5 March and 25 March 2009. The Norwegian Coastal Current enters the model domain in the south, follows the shelf break and turns westward just south of VE. A small branch of the coastal current enters VE, seen as a tongue of warm water close to the coast. A temperature front between Atlantic and coastal water is positioned at the baseline on 5 March, where the outermost islands are located. Several mesoscale meanders characterize the flow pattern in the coastal current, enhancing the production of eddies. On 25 March, the front between Norwegian Atlantic Current and Norwegian Coastal Current is shifted offshore compared with 5 March.

Retention within and connectivity between areas

Trajectories from a selection of cod eggs released on 31 March and 20 April are shown in Figure 7, where colours correspond to different zones (Table 1). The drift pathways from the spawning area at VI, located offshore to the south, are clearly distinguished from the others due to the long and more offshore transport route. The eggs are caught in the Norwegian Coastal Current, follow the shelf break, and flow around the Lofoten archipelago. Most of the eggs released in the coastal area (RV–VT–TB) stay inside of the baseline and have a weak northwards component. Within the fjords (FS–TO), the retention is large and only a small number of eggs are transported out into VE. A large part of the eggs spawned in VE stay within the area, whereas a few is transported through the small straits towards north.

Figure 8 shows the retention of cod eggs within each of the zones, meaning percentage of eggs that hatch within the zone they were released, through the spawning season. The spatial variability between the locations is large, varying from 0% at VI to 90% at TO. The oceanic zone at VI has zero retention during the whole spawning period, as these eggs are captured by the coastal current jet (Saetre, 1999) and transported rapidly northwards. The highest retention is found in the fjordic zones. TO has high retention during the whole period (70–90%), whereas FS experience some temporal variability (50–90%). Regarding the coastal zones (RV–VT–TB), RV always has highest retention for all days through March and April followed by TB and VT with the lowest percentage. All three show similar temporal variability during the 2 months and the difference between them stays constant through the whole period. There is no obvious trend through the spawning season or any specific time that is specifically favourable for retention. VE has large variability in the retention, between 15 and 65%, and is occasionally negatively correlated with the other zones.

Transport of cod eggs between zones is illustrated in Figure 9 for eggs released at six different times during the spawning
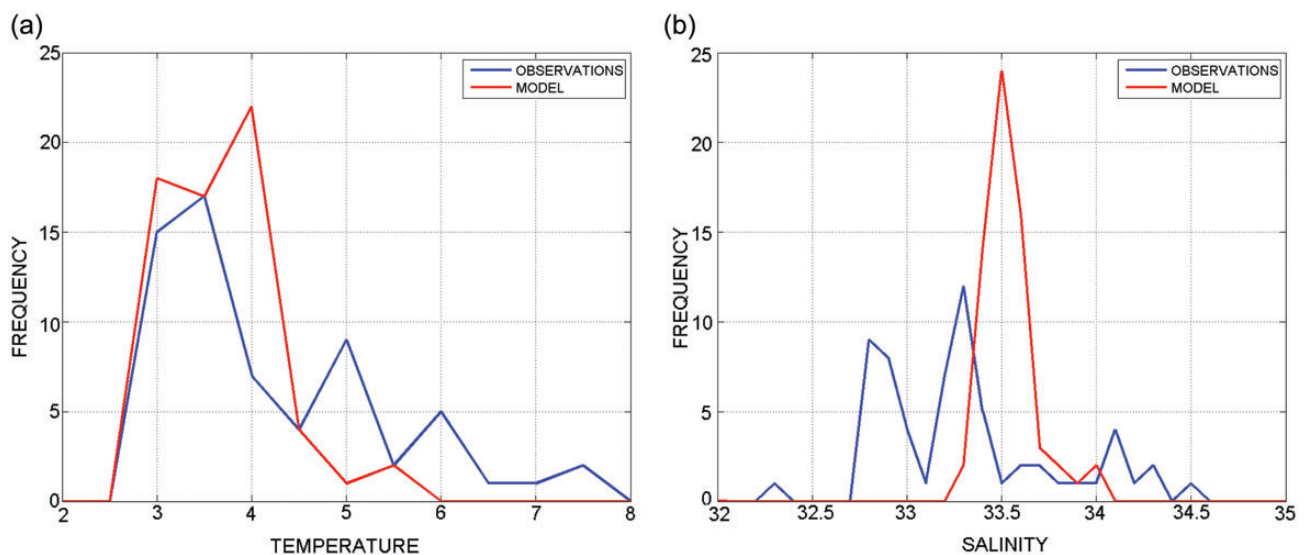

Figure 5. Eight observed (blue) profiles of temperature (a) and salinity (b) was compared with the model (red) results at the coastal station Skrova (Figure 1) during March and April 2009.
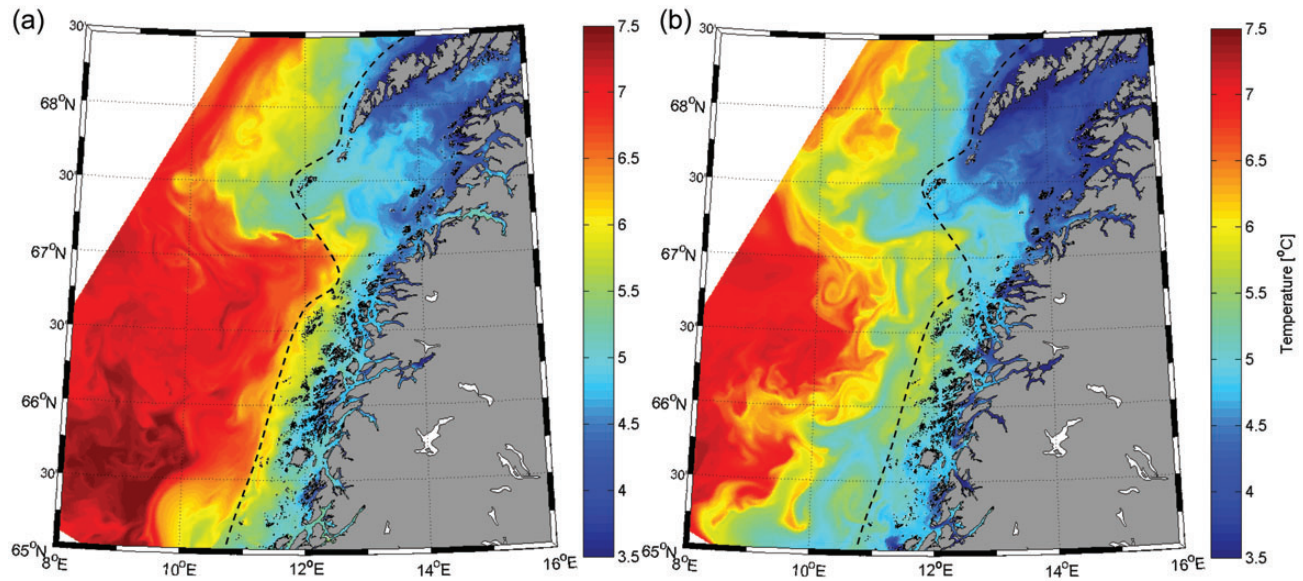
Figure 6. The daily mean sea surface temperature on two specific days in 2009. (a) 5 March and (b) 25 March.

season: 11 March, 21 March, 31 March, 10 April, 20 April, and 30 April. The *x*-axes represents the initial zone where the eggs were released at spawning and the *y*-axes shows the zones where the eggs are located at hatching time, starting from south moving northwards. The diagonal shows retention within the respective zones, the same values that was shown in the time-series in Figure 8. All numbers are the percentage of the initial number of eggs within this spawning zone.

The results show that the transport of eggs is directed northwards following the Norwegian Coastal Current, only a small number of eggs is transported southwards (values below the diagonal). The spawning area VI has low retention and highest connectivity with VT; otherwise most of the eggs have been transported offshore. The two following coastal zones (RV–VT) have medium retention within the zone, in addition to comparable transport into the neighbouring zone to the north (VT–TB). The third coastal-zone TB shows only small transport into the neighbouring fjord zone (FS) and VE. The two fjord zones (FS–TO) have little connectivity with the other zones, few eggs leave the spawning areas inside the fjords and those that do will most probably enter VE. Eggs spawned inside VE have medium retention during March, whereas in April, a considerable amount of eggs are transported into TO. Considering the whole period through March and April, the connectivity pattern is similar but the magnitude of transport varies, consistent with the variable mesoscale activity and the strength of the Norwegian Coastal Current.

Physical–biological interactions

The temperature experienced by the cod eggs was recorded from spawning to hatching, and a mean representing the entire egg stage in each zone was calculated (Figure 10a). Calculated hatching time, as a function of spawning date and temperature starting on 1 March continuing until 30 April, is shown in Figure 10b. The highest temperatures (5.5–6.5°C) were experienced by cod eggs spawned at VI, ∼0.5–1°C warmer than the coastal area. The decrease in temperature at the beginning of the period is associated with the offshore shift of the coastal current, as seen in Figure 6. All

the coastal zones (RV–VT–TB) are similar to each other, from 5 to 6°C, whereas VT is the warmest of these during the last part of March. The northern fjordic areas are coldest (below 4°C) during the whole period, ∼1°C colder than the coastal areas further south. All the areas experience small fluctuations in temperature initially, followed by the seasonal warming in mid-April. The fjordic regions have strongest warming, starting around 4°C increasing above 5°C during 20 d. The two southernmost zones, VI and RV, are geographically close together but a temperature difference of ∼1° is seen for the major part of the spawning period. The same difference is seen between TB and FS, which are neighbouring areas but represent coastal and fjordic regions.

Hatching time for cod eggs is a function of temperature experienced by the eggs along their trajectories [Equation (8)] and, therefore, depends on spawning zones and time (Figure 10b). The hatching time stays constant during the main part of the spawning period and decreasing towards the end of April when the seasonal warming starts. The fjord zones (FS and TO) show similar variability and are staying at ∼21 d during March while decreasing below 18 d in the end of April. The coastal areas further south have shorter hatching times starting at ∼18 d and decreasing towards 16 d. VI has the lowest hatching time during the whole spawning period, with a minimum of 15.5 d. The variability between the zones is largest at the beginning of the season and is reduced towards the end of April.

The mean transport depth of eggs released at VT on 31 March is shown in Figure 11a, in the upper panel, together with the temperature experienced by the eggs. The lower panel shows the salinity together with egg neutral buoyancy as a function of degree-days. The eggs in this figure represent the mean neutral buoyancy range from 29.62 to 31.52 and are surrounded by water with salinity of ∼33.5. This large salinity difference causes all the eggs to float towards the surface, being pelagically distributed. The eggs are confined to the surface through the whole egg stage with only small variations due to changes in water elevation. The temperature stays at around 5°C through egg development.

Figure 11b shows the eggs released at RV on 31 March and with neutral buoyancy ranging from 31.52 to 33.1. The salinity in this
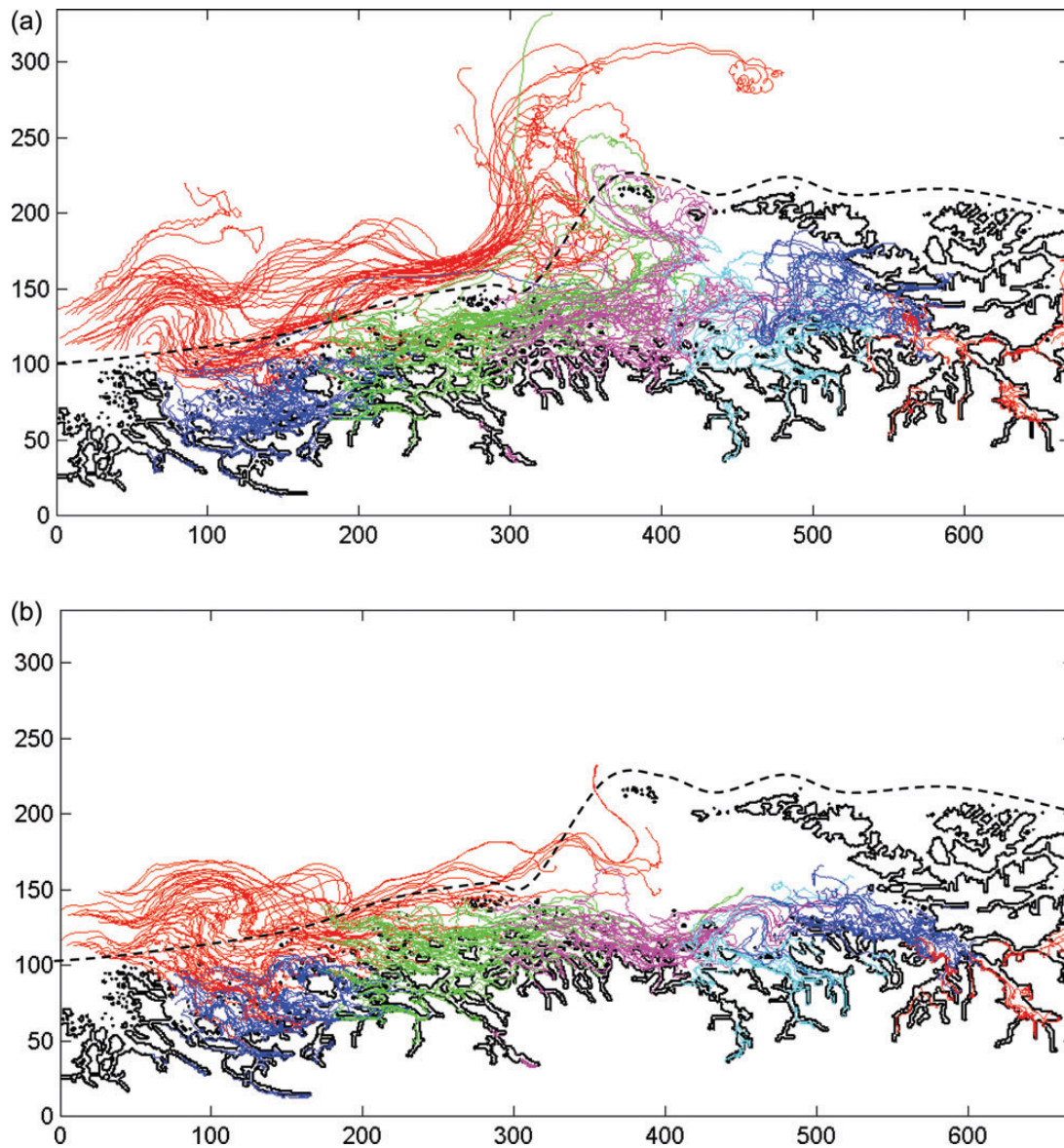
Figure 7. Trajectories of cod eggs from all spawning areas, colour coding is based on the zonal subdivision as seen in Table 1. All eggs are released simultaneously and advected for ∼18 d, which is the time when 50% of the eggs are hatched. The two dates, (a) 31 March and (b) 20 April, are examples of different dispersal patterns.

region is slightly lower than VT. For a short period, around degree-days 30, the neutral buoyancy approaches the surface salinity and the eggs become negatively buoyant. The corresponding impact on vertical distribution is seen in the upper panel, where the eggs sink to ∼13-m depth between degree-days 30 and 40. A small negative salinity difference between the egg and the surrounding water results in a weak descending speed [Equation (1)], this causes a delay in maximum depth related to the minimum salinity difference.

Discussion
Hydrography and model evaluation
The model reproduced the observed temperature distribution well, but the salinity to a lesser degree. The temperature variations within this region are basically controlled by the local air-sea exchange, whereas salinity variations are controlled by water masses advected by the Norwegian Coastal Current (Mork, 1981). The model domain is of limited geographical extent and upstream variations can only be included through the boundary conditions. A 4-km model provides the external forcing on the southern boundary where the coastal current enters the domain. The outer model includes the whole Norwegian coast and the input of low-saline water from the Baltic Sea, which is the most important freshwater source influencing hydrography (Røed and Albretsen, 2007). It is therefore likely that the 800-m model in this study is limited by low-resolution boundary conditions, which is not resolving the mesoscale structure of the coastal current. Albretsen and Røed (2010) showed that an eddy-resolving model is required to capture the mesoscale circulation along the southern Norwegian coast due to improved representation of the topography.

Higher salinity in the model than in the observations during winter can be caused by limitations in the river run-off to the model. Many hydroelectric power stations along the coast affect the seasonal cycle of river run-off through regulations (Pytte Asvall, 1976). The major difference is increased run-off during
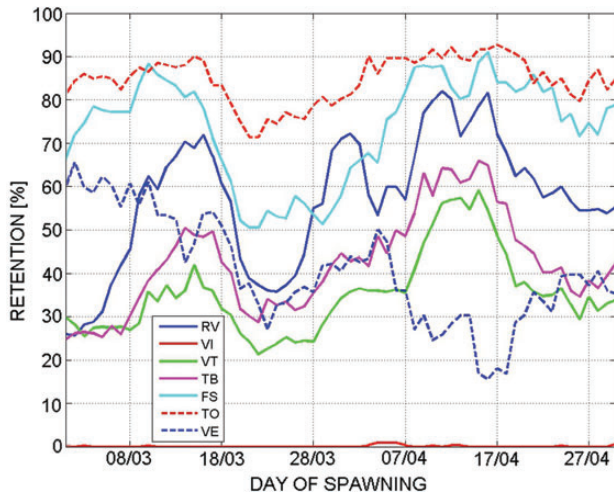

Figure 8. Retention of cod eggs, meaning the percentage that hatch within the zone they were spawned, in each of the zones; V), RV, VT, TB, Folda-Sagfjord (FS), TO, and VE through spawning season. The same number of eggs is released every day through March and April.

winter compared with naturally low discharge. The modelled run-off is not corrected for this shift, which might contribute to the difference in salinity between model and observations. Skarðhamar and Svendsen (2005) also acknowledged the importance of accurate freshwater discharge, as the strength of stratification controls the influence of wind, tides, and topography on surface circulation. However, Albretsen (2007) showed for the Skagerrak that realistic river run-off is not required when the focus is on modelling mesoscale activity, meaning that the current pattern may be simulated realistically despite an offset in the modelled density or salinity.

The salinity was higher in the model compared with the observations, on the same order as the spatial differences between the zones in the model. The specific gravity of cod eggs used in this study was significantly lower than spatial density variations in the model, which means that most of the eggs have a pelagic vertical distribution and is only affected by the model error to a limited degree. However, the heaviest portions of eggs located in regions of low salinity are very near their level of equilibrium. These are more influenced by the salinity discrepancy in the model and might attain a subsurface distribution in a realistic physical environment (Sundby, 1991). The effect of this discrepancy is largest in the fjord regions, since this is where the salinity is lowest. A subsurface distribution of cod eggs here would further reduce offshore transport and increase retention. This would therefore support the main connectivity pattern already described here.
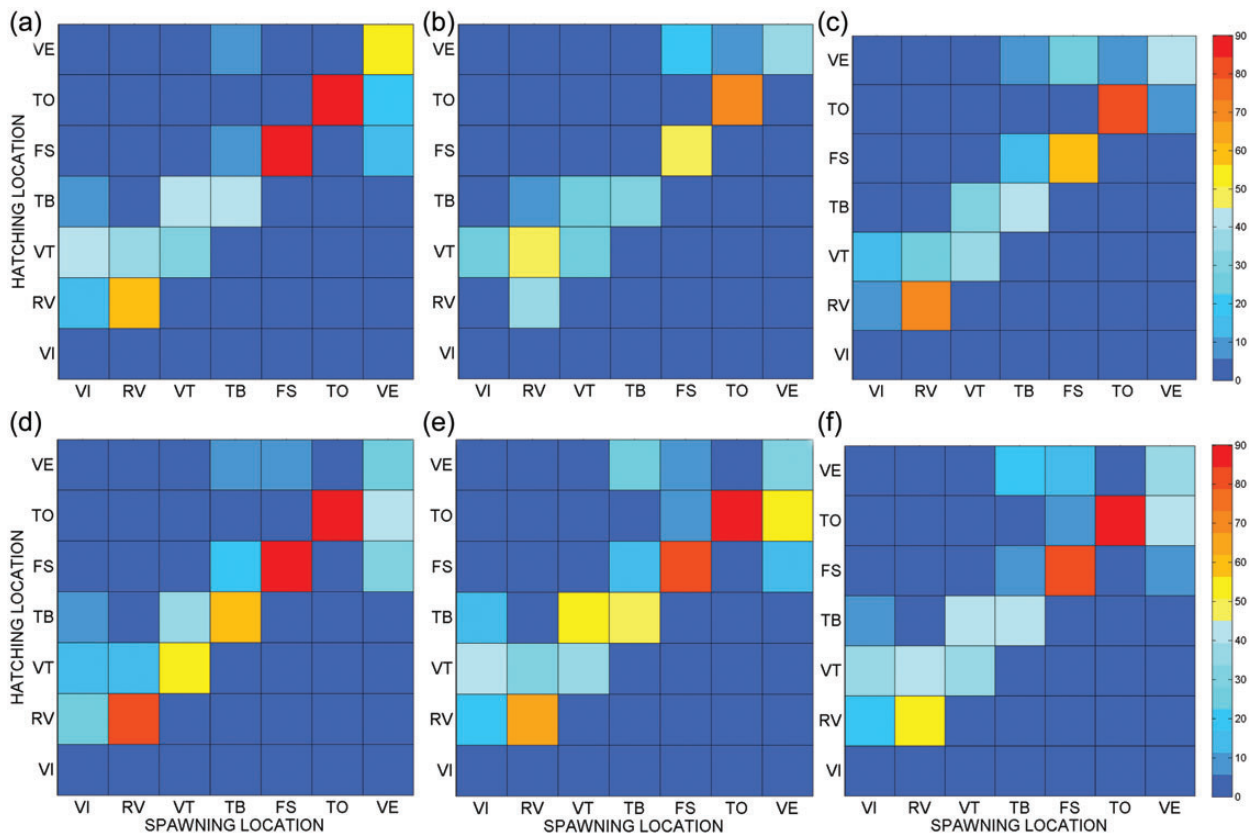
Figure 9. Connectivity matrices showing transport from spawning location (*x*-axes) to hatching location (*y*-axes), colour coding showing the percentage of the initial number of eggs released in the spawning zone. The diagonal shows retention within the respective zones. (a) 11 March, (b) 21 March, (c) 31 March, (d) 10 April, (e) 20 April, and (f) 30 April.
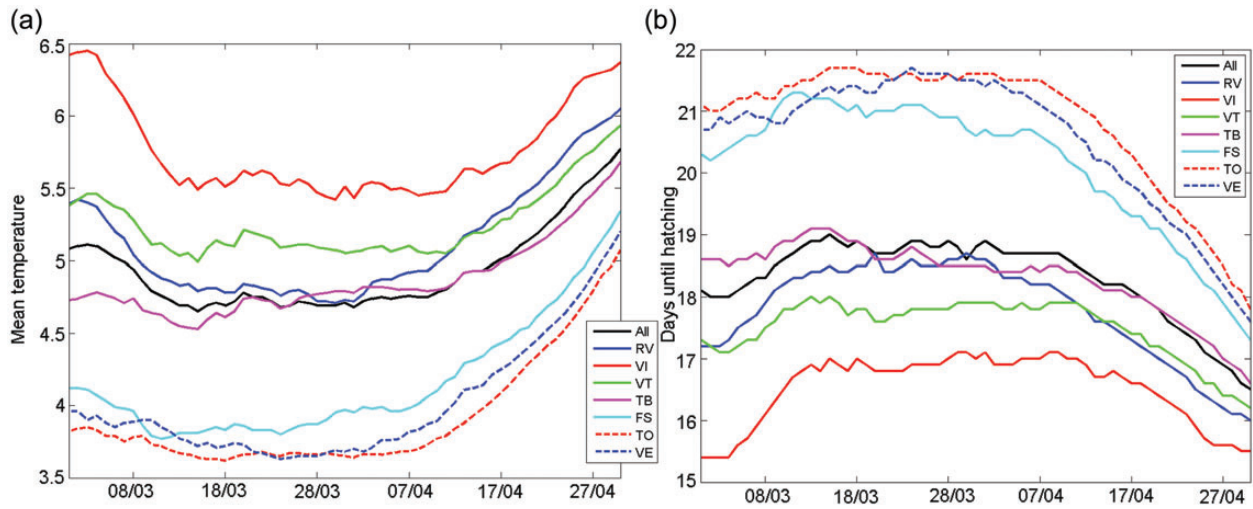
Figure 10. The mean temperature (a) experienced by cod eggs during development and calculated hatching time (b), as a function of spawning time, for all areas (black) and in each of the zones; VI, RV, VT, TB, Folda-Sagfjord (FS), TO, and VE. (a) Mean temperature and (b) days until hatching.
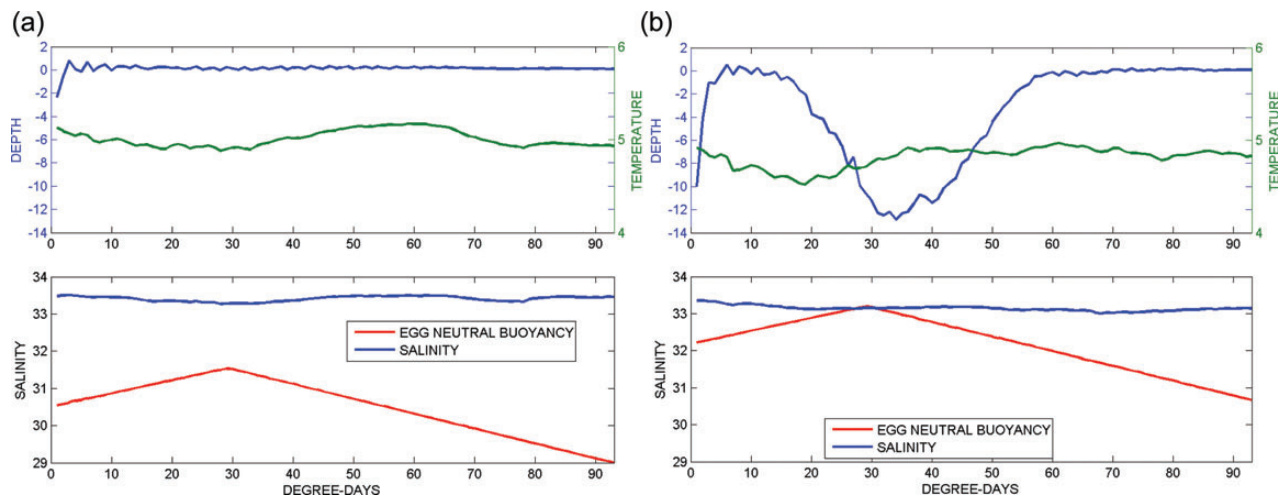

Figure 11. Evolution of the mean depth (blue, upper panel), temperature (green, upper panel), salinity (blue, lower panel), and egg neutral buoyancy (red, lower panel) through egg development as a function of degree-days for two specific zones, both released 31 March 2009. (a) VT, average for eggs with neutral buoyancy: 29.62–31.52, (b) RV, average for eggs with neutral buoyancy: 31.52–33.1.

The model used in these simulations is not well suited for detailed studies on fjord dynamics, because of the 800-m horizontal resolution and the regionally scaled run-off used in the model. The river run-off is an important mechanism controlling the estuarine circulation (Saelen, 1967), but is not realistically represented within each fjord in this model setup resulting in higher salinities within the fjords. However, river input is scaled to match the total freshwater contribution to the coastal current. Myksvoll *et al.* (2011) showed strong retention mechanisms inside the fjord system of Folda. The model simulations shown here focus more on possible transport pathways between coastal and fjord populations, showing that the connectivity is very low. This was hypothesized by Myksvoll *et al.* (2011) and confirmed by the present paper.

Observed seasonal variations in the horizontal extent of the coastal current were well reproduced by the model. It is well known that the width of the coastal current is affected

by monsoon like wind variations (Saere *et al.*, 1988; Mitchelson-Jacob and Sundby, 2001; Saetre, 2007a). North/north-westerly winds during summer typically advect the low salinity water offshore and the coastal current broadens. Southerly winds during winter push the coastal wedge towards the coast and cause a narrowing of the current. The model recreates this seasonal pattern, as illustrated in Figure 6, where the coastal current is broadening towards summer.

Retention within and connectivity between areas

The eggs spawned at VI are captured by the coastal current jet and dispersed rapidly northwards which favours transport into the Barents Sea. NEAC occupies several offshore spawning areas along the coast of Helgeland (Bergstad *et al.*, 1987; Sundby and Nakken, 2008), including VI and Vega. Opdal *et al.* (2008) showed that larval trajectories from these two spawning grounds

spread northwards along the Norwegian coast just offshore of the baseline. The model results show that spawning at VI results in a significantly different dispersal pattern than all the other spawning areas in this study, mainly due to persistent zero retention. This is consistent with being populated by another cod stock than the inshore spawning areas, which has a different life history.

There is no trend in retention during the spawning season; the variability is high but consistent between the zones. The exception is VE, which is occasionally negatively correlated with the others, probably influenced by wind interacting with local topography (Ellertsen et al., 1981; Furnes and Sundby, 1981). The spawning areas can be classified into different retention regimes: large retention in fjords, medium retention at the coast, and no retention offshore. The transition from zero to medium retention occurs at the baseline, which is marked by the outermost islands. The complex bathymetry of the Norwegian coast causes persistent mesoscale meanders and eddies along the path of the coastal current (Oey and Chen, 1992; Mitchelson-Jacob and Sundby, 2001). This might explain the persistent connectivity pattern through the spawning season, as retention is mainly caused by topographic features (Moseidjord et al., 1999; Saetre, 1999). Retention of cod eggs inshore of the baseline is mainly caused by interaction with small islands. High horizontal resolution is needed in such regions to model dispersion of particles, where strong tidal flow interacts with topographic features (Lynge et al., 2010). It is also important to emphasize that the conclusions made here are only based on simulations from 2009. However, the respective period in 2009 covers the seasonal transition from winter to spring and corresponding offshore shift in the coastal front. The connectivity pattern is stable through these seasonal shifts (Figure 8). The topographic features in the region controls the transport and the system is less sensitive to seasonal and interannual variability.

Transport from a coastal zone into the neighbouring zone to the north is of comparable magnitude as retention within the zone. Further northwards beyond the neighbouring zone, the connectivity is significantly lower. Saetre et al. (2002) studied larval transport from Norwegian spring-spawning herring in the same area. They found that larvae was temporarily retained due to topographically trapped eddies and good recruitment coincided with slow northwards drift.

Physical–biological interactions

Differences in temperature between the zones reflect the different dynamic regions and distance from the coast. The temperature gradient from inshore to offshore is larger than from north to south (Haakstad et al., 1994), at least within this part of the Norwegian coast. The highest temperatures are seen at the offshore spawning ground at VI, which was also shown in Opdal et al. (2008), whereas the lowest temperatures are seen inside the fjords. The coastal banks experience intermediate temperatures as an average between the open ocean and the fjords. The temperature differences are also reflected in the differences in hatching time, clearly showing a geographic pattern. It is therefore interesting that the pattern in hatching time is opposite of the connectivity pattern, meaning that fjord zones have long hatching time and high retention and at the same time VI has short hatching time and low retention. This illustrates the persistence of the connectivity pattern described in "Retention within and connectivity between areas", since it is working against the indirect effect of temperature on transport.

The egg specific gravities used in these calculations, relative to the coastal density structure, result in a pelagic vertical distribution with highest concentration at the surface and exponentially decreasing downwards (Sundby, 1991). Only the proportion with the highest specific gravity located in specific areas with low salinities attain a subsurface distribution. The cod eggs only experience these low salinities inside the fjords (Myksvoll et al., 2011), meaning that there is no difference in vertical distribution between oceanic and coastal cod in the coastal region. And the difference in vertical distribution between fjord cod and coastal cod is caused by the local salinity profile. Variations in the vertical distribution of cod eggs have two causes: (i) variations in the local salinity profile determined by the ocean physics and (ii) variations in the egg specific gravity determined by the phenotypic and genotypic characteristics of the spawners. Since the average specific gravity of eggs in a population appears to be remarkably constant through time, it is likely to assume that it is a long-term ecological adaptation to the average ambient environmental factors. But also the variation in the specific gravity around the mean value, expressed as, for example, by the s.d., must be considered to be a long-term ecological adaptation to the variation in the ambient environmental factor. However, variability, in general, caused by biotic as well as abiotic factors is a source to connectivity among populations, and variability in biotic factors is a source to the potential for adaptation to a variable and changing environment.

The observed variations in the egg specific gravity through development (Figure 4) affect the vertical distribution only for a limited period and are therefore not important for horizontal distribution. The only effect is for eggs that are situated in waters with approximately the same density as the egg, but for pelagic eggs the effect is negligible.

The connectivity matrices (Figure 9) show that offspring from different areas remain physically separated during the egg stages, and hence this result is not contradicting investigations, showing that coastal cod populations are genetically separated (Pogson and Fevolden, 2003). Myksvoll et al. (2011) showed high retention within a fjord system and here we show that transport from coastal areas into fjords is negligible. As larvae are known to obtain a subsurface distribution (Ellertsen et al., 1984), the described connectivity pattern is also representative for the larval stages. This means that fjord populations with stationary individuals are partly isolated and have low genetic connectivity (Jorde et al., 2007). The largest possibility for the exchange of genes is when juveniles and subsequently adults migrate into or out of the fjord and spawn together with another population.

Metapopulation perspective

We provide new knowledge of the degree of connectivity during egg stages among different cod habitats. Eggs spawned in typical fjords with a narrow entrance (FS and TO) were likely to be retained in their birth places until hatching (50–90% retention). Once hatched in the fjords, larvae would keep staying inside the fjords by active vertical movement against outflowing currents (Ellertsen et al., 1984). The hypothesis of larval retention has been confirmed by the study of Øresland and André (2008) showing genetic differences in cod larvae between inside and outside fjord. Besides, fjord cod had very low mixing rates with eggs originating from neighbouring coastal and fjord areas (Figure 9), indicating low connectivity of egg/larval stages to neighbouring areas. Recently, one study demonstrates that adult

cod have strong tendency of homing to their nursery fjord to spawn (Skjæraasen *et al.*, 2011). Hence, with the evidence of egg/larval retention and spawning site fidelity, it is conceivable that each single fjord cod population may evolve a disparate subpopulation. On the contrary, the egg retention in successive coastal areas (RV, VT, and TB) varied from 20 up to 80%. The remaining eggs were transported to the north by the Norwegian Coastal Current. Under this condition, the RV, VT, and TB might share a common larval pool so that self-recruitment occurs regionally on a larger geographical scale than the fjord population. Therefore, dispersal patterns of early life-history stages are clearly different between fjords and coastal areas, and hence this difference can enhance substructuring among cod populations along the Norwegian coast.

Levins (1970) postulated that subpopulations within a metapopulation would have the same geographic extent and a degree of isolation. The Norwegian coast consists of many fjords, which are all possible habitats for local cod populations, but the fjords do not have the same geographical extent. Some common features exist in many fjords, like large depth, small width, seasonal river run-off, and a sill near the mouth (Wassmann *et al.*, 1996). Large variations occur within these categories, e.g. differences in sill depth will affect the water exchange and correspondingly the habitat suitability. Large differences in cod abundance between neighbouring fjords (Berg and Albert, 2003) suggest uncorrelated recruitment mechanisms and potentially one subpopulation could go extinct, while another subpopulation nearby is sustained. For the coastal regions, the habitats are not as well delimited as in the fjords. While spawning inshore of the baseline increase the residence time of eggs, the retention is intermediate and mainly caused by small-scale eddies between the many islands.

Each subpopulation in a metapopulation should have its own dynamics, meaning that individuals spend their entire life cycle within the local habitat. Tagging experiments of cod show only short migrations mainly within the respective fjord (Karlsson and Mork, 2003; Knutsen *et al.*, 2011). Strong homing has also been detected for local populations in Skagerrak (Svedäng *et al.*, 2007) and several other places in the North Atlantic (Robichaud and Rose, 2004). This supports the assumption that fjord populations can have their own population dynamics. A study from Trondheimsfjorden in the middle of Norway shows that only 1.5% of tagged fish was recaptured outside of the fjord 5 years after the release (Karlsson and Mork, 2003). Migration on this scale is too low to affect the local dynamics and genetic structure, but is sufficient to allow a rescue or recolonization event in a neighbouring fjord following the so-called stepping-stone dispersal model.

Another important aspect of the metapopulation theory is that at least one subpopulation must have a non-zero probability of extinction (non-anthropogenic), followed by a recolonization event. Low abundance of cod in some fjords has been reported (Berg and Albert, 2003), but it is difficult to distinguish between natural and anthropogenic influence as they may occur at the same time. Extinctions have occurred in several subpopulations, but recolonizing is more seldom and possibly hard to detect. The large volume of a fjord makes it hard to know for sure that a population has gone extinct. It is also likely that the population is too low to be detected by fisheries and scientific surveys and might apparently recolonize itself in the absence of fishing.

Our study is the first report of egg connectivity among different cod habitats. Demographic exchanges by egg dispersal could be low not only between fjords and coastal areas but also among neighbouring fjords. With the evidence of resident behaviour in fjord populations, we argue that a fjord might have its own cod subpopulation. Regarding the coastal spawning populations it is not as clear due to less available knowledge and the weaker retention mechanism operating at the coast. Retention of early life stages within fjords, stationary juveniles, and spawning site fidelity indicate the existence of subpopulations in fjords similar to what is described as a metapopulation. And as the exchange of individuals between local habitats is low, the time-scale for natural recolonization events may be very long. This is very important to consider in fisheries management, as the growth and harvest potential could be overestimated, and for a collapse the recovery will be slow (Sterner, 2007).

Acknowledgements

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