ICES CM 2008/L:16
Theme session on Coupled physical and biological models: parametrization, validation and applications

Mechanisms affecting the transport of early stages of Norwegian Coastal Cod - a fjord study

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Abstract

An increasing concern in fisheries management in Norway is how the Arcto-Norwegian Cod (ANC), with its feeding habitat in the Barents Sea, is separated from or mixed with the local populations of Norwegian Coastal Cod (CC) in the fjords and along the Norwegian coast.

The fjord system of Sørfolda and Nordfolda in northern Norway is one of the spawning sites for the CC. The two fjords have a joint opening towards the ocean bay Vestfjorden, one of the main spawning sites for the ANC. The ANC eggs are lighter than the surrounding water masses in Vestfjorden resulting in a pelagic distribution, with exponentially increasing concentration towards the surface. The vertical distribution is sensitive to variations in wind-induced mixing. The CC eggs in Sørfolda and Nordfolda are heavier than the ANC eggs and within the low salinity water inside the fjord system they become mesopelagically distributed. A numerical model is used to investigate how the vertical distribution affects the transport of eggs. The result enlightens the mechanisms separating ANC and CC.

The simulation was set up for 1960 and 1989, representing a cold and dry year and a warm and wet year. The major difference in forcing between the simulations of the two years is the fresh water input, which causes variations in the estuarine circulation. Changes in salinity structure affect the vertical distribution of CC eggs, and might cause them to be transported out of the fjord system and being mixed with ANC eggs. A strong stratification causes the eggs to be concentrated lower in the water column, and gives retention inside the fjord. The retention of CC eggs is subjected to variations within a season and between years.

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1 Introduction

Vestfjorden (see Figure 1) is one of the main spawning sites for the Arcto-Norwegian Cod (ANC), *Gadus morhua* L. The larvae and pelagic juvenile of ANC are known to drift over long distances (600-1200 km) (Bergstad *et al.*, 1987) from the spawning areas along the Norwegian coast to the nursery and feeding areas in the Barents Sea. Reaching maturity the ANC migrate back to the Norwegian coast to spawn. In contrast to the migratory ANC is the stationary Norwegian Coastal Cod (CC). The CC both spawn at a number of locations along the Norwegian coast and inside the fjords.

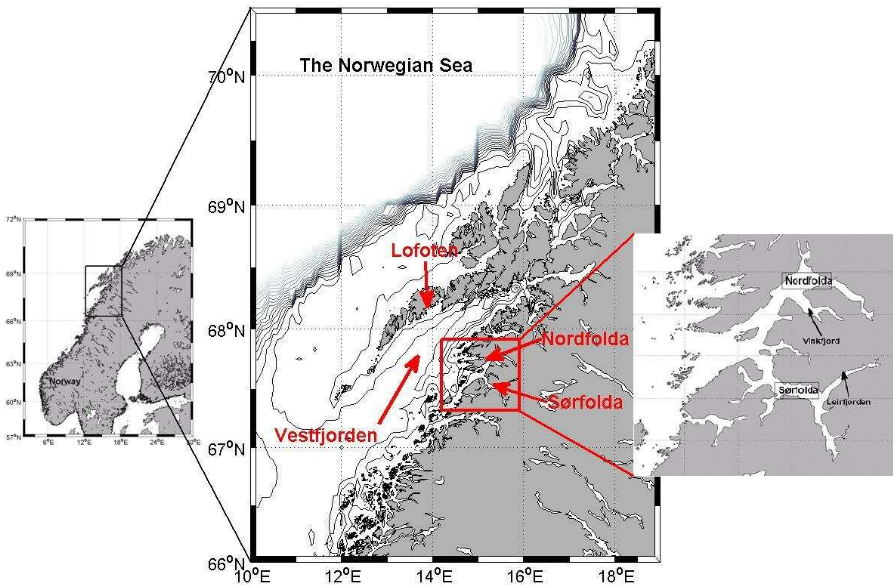


Figure 1: Lofoten and Vestfjorden in the northern part of Norway, with the area of study inside the red square.

A small difference between ANC and CC eggs is observed in the area, with the ANC eggs more buoyant (Kjesbu *et al.*, 1992). Sundby and Godø (1994) hypothesized that this difference in buoyancy could cause the eggs to follow different pathways during the pelagic drift and result in more onshore distribution of the heavier CC eggs. The pelagic[1] ANC eggs, spawned in the saline coastal waters, have maximum concentration at the surface and decrease with depth, and

[1]Pelagic eggs have a specific density lower than the mixed layer, Sundby (1991)

they are very sensitive to variations in wind-induced mixing (Sundby, 1983). The mesopelagic[2] CC eggs, spawned in the fjords with low-saline surface water, are concentrated lower in the water column, being more dependent on the stratification and hydrography (Sundby, 1991). Stenevik *et al.* (2008) showed that the specific gravity of CC eggs at different locations along the Norwegian coast did not vary much, but concluded that the local salinity structure determined whether the eggs were pelagically or mesopelagically distributed.

In the present study the fjord system of Sørfolda and Nordfolda (Figure 1), a CC spawning area adjacent to the ANC spawning areas in Vestfjorden (Sundby & Bratland, 1987), is selected to explore the mechanisms behind the separation in distribution and drift pattern between ANC and CC eggs. These are two separate fjords with a joint opening towards Vestfjorden, located in the northern part of Norway at 67.5°N. Moreover, we will explore how climate variability might influence separation or mixing of eggs from the two stocks. A regional ocean model is used to simulate the circulation within the fjord system during two different years. The first year, 1960, represents a cold and dry year with low runoff to the coast, and the second year, 1989, represents a warm and wet year with high runoff to the coast. Drift patterns of eggs are calculated with a particle tracking model utilizing the modelled velocity fields. The particle tracking model includes a model component resolving the dynamical vertical distribution. Our main objective is to study the transport of eggs in the fjord system in relation to interannual variation in the physical forcing. More specifically; is the interannual variation in the freshwater runoff from land sufficient to significantly affect the proportion of eggs advected out of the fjord system?

1.1 The vertical distribution of eggs

Solemdal and Sundby (1981) collected ANC eggs in Lofoten from 1968 to 1972. They found the neutral buoyancy of the eggs, equivalent to salinity to be between 29.5 and 33.0 (see Figure 2). Within Vestfjorden such eggs are lighter than the ambient water, resulting in a pelagic distribution. The spawning starts early March, and continues until early May with a peak concentration around the first days of April (Ellertsen *et al.*, 1989).

Stenevik *et al.* (2008) measured specific gravity of eggs from the CC at several places along the Norwegian coast. They confirmed the earlier observations by Kjesbu *et al.* (1992) that the CC eggs are slightly heavier than the ANC eggs. The specific gravity of eggs did not vary much between the locations, except for the northern most one, which is thought to be influenced by the ANC. In Tysfjord,

[2]Mesopelagic eggs have a specific density higher than the mixed layer and lower than the bottom layer, named bathypelagic eggs by Sundby (1991)

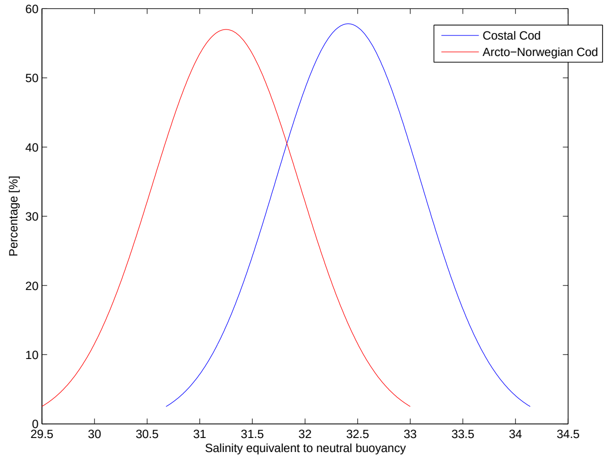


Figure 2: Neutral buoyancy of Arcto-Norwegian Cod (Solemdal and Sundby, 1981) and Norwegian Coastal Cod eggs (Stenevik *et al.*, 2008).

at the inner part of Vestfjorden, the neutral buoyancy equivalent to salinity was ranging from 30.6 to 34.1 (see Figure 2). This is slightly higher than the ANC eggs, causing a fraction of the CC eggs to be heavier than the surrounding water and therefore mesopelagically distributed. The CC spawn during a longer time period than ANC, with a peak concentration delayed by 3-4 weeks compared to ANC (Kjesbu, 1988).

The vertical distribution of eggs is a function of ascending speed and downward mixing. The vertical velocity is given by Stokes' formula:

$$w = \frac{1}{18}\frac{gd^2\triangle\rho}{\mu} \tag{1}$$

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

$$Re = \frac{\rho_w dw}{\mu} \tag{2}$$

Mixing can be supported by winds, tides and velocity shear. The pelagic eggs are mainly situated in the mixed layer and highly affected by wind-induced mixing (Sundby, 1983). Strong winds result in reduced concentrations at the surface and calm winds increase the surface concentration. The mesopelagic eggs are less affected by the winds and the vertical distribution has stronger dependency on buoyancy variations and stratification (Sundby, 1991).

2 Model and methods

2.1 Fresh water discharge

Fresh water runoff is the major driving mechanism in fjords, controlling both the circulation and the hydrography (Sælen, 1967). The Norwegian Water Resources and Energy Directorate (NVE) provided data from four rivers discharging into the fjord system. The river discharge depends on the drainage area. The location of the drainage area, specifically the elevation above sea level and distance from the coast, controls the seasonal cycle of the river runoff. The four rivers have different seasonal variations and are chosen to represent different areas surrounding the fjord system.

Figure 3 shows the interannual variability of the four rivers discharging into the fjord system. The annual mean discharge is standardized for comparison. The

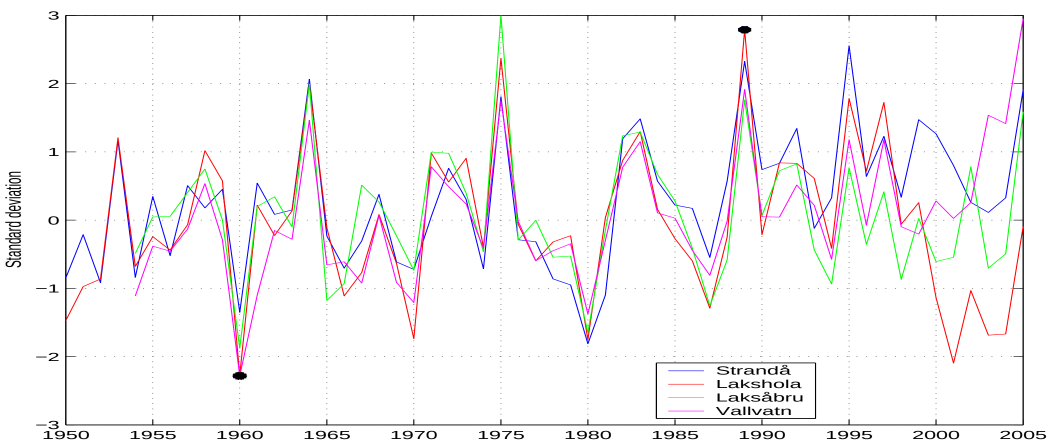


Figure 3: The annual mean discharge from four rivers in the model area, standardized for comparison. The two selected years are marked with black dots.

rivers show similar interannual variability, except after 1999 when one river was regulated and water was guided away from the river. From this data the two years, 1960 and 1989, were chosen. Both years are more than two standard deviations away from the mean, in opposite directions.

2.2 The circulation model

The circulation model used in these simulations is the Regional Ocean Modeling System (ROMS) version 3.0 (Shchepetkin & McWilliams, 2005; Haidvogel *et al.*, 2007). This is a free-surface, hydrostatic, primitive equation ocean model using stretched terrain-following s-coordinates in the vertical. The primitive equations are solved on an Arakawa C-grid, including a Generic Length Scale (GLS) turbulence closure scheme.

2.3 Model setup

The model domain includes high resolution bathymetry where the largest depth was set to 300 m. The horizontal grid length is 200 m, while the vertical is spanned by 35 vertical sigma layers, close together near the surface and reduced resolution towards the bottom.

The initial field was calculated from data collected in the fjord system November 1993. The atmospheric forcing was extracted from the ERA-40 archive, with a horizontal resolution of 1 degree and a temporal resolution of six hours. The lateral boundary conditions are taken from a dataset covering the Nordic Sea (Engedahl *et al.*, 1998), containing salinity, temperature, currents and surface elevation. The lateral forcing is included along the open boundaries together with four tidal components.

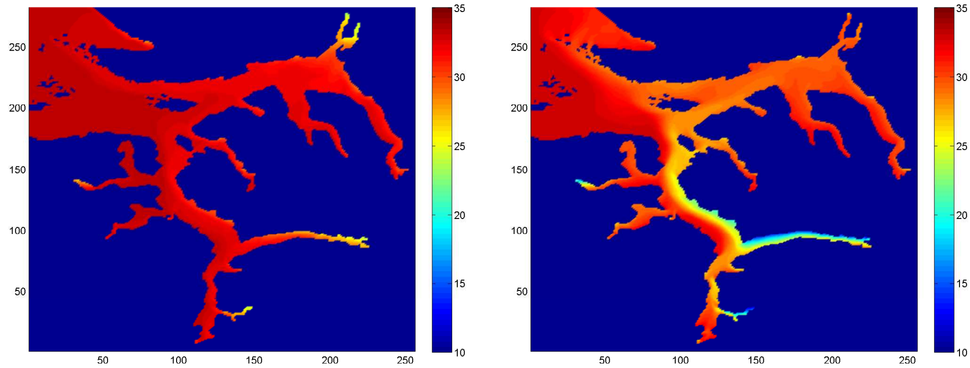
2.4 The particle tracking model

A Lagrangian Advection and DIffusion Model (LADIM) is used to simulate transport of eggs inside the fjord system (Ådlandsvik & Sundby, 1994). The model utilizes the hourly averaged output from ROMS to advect the eggs in an off-line mode. Each egg has its own specific gravity and a vertical velocity is calculated depending on the density difference between the egg and the surrounding water. The vertical displacement is computed based on the vertical velocity and the eddy diffusivity coefficient, as described in Thygesen and Ådlandsvik (2007).

3 Results

3.1 Model results

Figure 4 shows the salinity at 1 m depth in Sørfolda and Nordfolda. The date is 10^{th} April, and results are shown from both 1960 and 1989. This is about the time of peak spawning, and the time of increasing fresh water discharge. The freshest areas in 1960 are at the inner end of the fjord. The salinity is slightly lower in Nordfolda ($\sim$32) than in Sørfolda ($\sim$33), but generally the horizontal variations are small. Leirfjorden is the freshest fjord area in 1989, however a few other branches show very low salinity at the head. There are very small cross-fjord variations inside the narrow Leirfjorden, but in Sørfolda the fresh surface layer is constricted



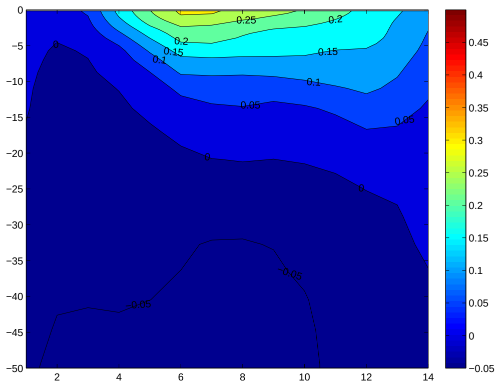
(a) 10^{th} April 1960

(b) 10^{th} April 1989

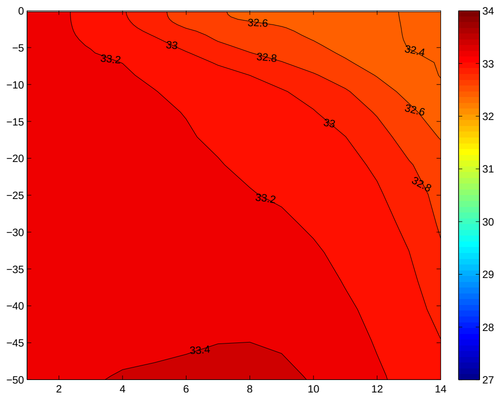
Figure 4: Salinity at 1 m depth.

to the right hand side, in relation to the flow directions, causing strong cross-fjord variance. In Nordfolda the salinity is quite constant in the whole fjord. Brackish water leave the fjord on the northern side of the mouth area. The main difference between the two extreme years is the distinct low-saline water in 1989 located in Leirfjorden and Sørfolda. The salinity is in general lower during 1989 than 1960 for the whole fjord system.

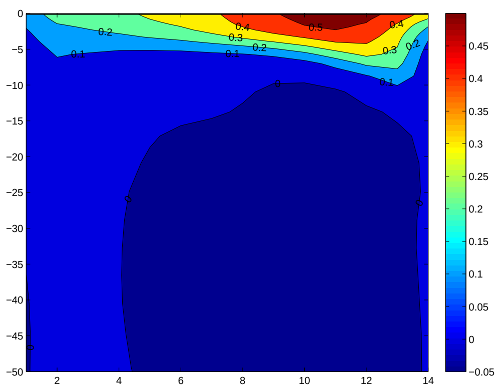
Figure 5 shows cross-sections at the sill in Sørfolda on April 10^{th} 1960 (upper panel) and 1989 (lower panel), including both current speed and salinity structure. Positive current velocity is directed out of the fjord. In 1960 the strongest current speed is observed in the surface layer. The depth of no motion is lower on the eastern side than on the western side. Below 25 m depth the current is directed the opposite way, going into the fjord. The salinity structure shows freshest water in the upper layers on the eastern side. On 10^{th} April 1989 the strongest surface current is seen in the upper layer, constricted to the upper 5 m. The strength of the current is greater in 1989 than compared to 1960. In 1989 the salinity profile shows lower salinities in the surface layer on eastern side than was observed in 1960. The stratification is weaker on the western side of the fjord compared to the eastern side.



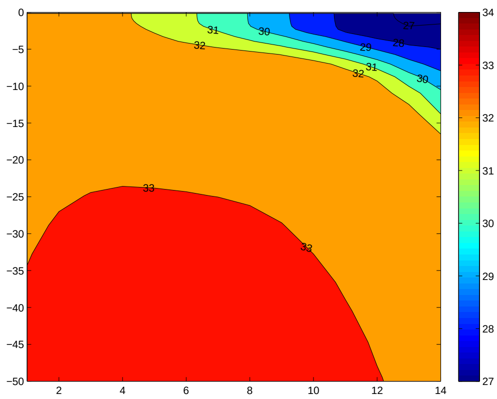
(a) Current speed 1960



(b) Salinity 1960



(c) Current speed 1989



(d) Salinity 1989

Figure 5: Cross-sections at the sill in Sørfolda 10^{th} April, from west to east. Positive current velocity is directed out of the fjord and the x-axis is number of grid points.

3.2 Transport of eggs

The Norwegian Coastal Cod (CC) eggs are advected by the modelled currents inside the fjord system. A model component of LADIM ensures a dynamical vertical distribution of eggs. Each egg obtains a specific level of neutral buoyancy according to the distribution in Figure 6, for easier interpretation of the results the eggs are divided into five buoyancy groups. Their individual vertical velocity is then calculated according to the density difference between the eggs and the surrounding water. The simulations are continued for 21 days, being close to the

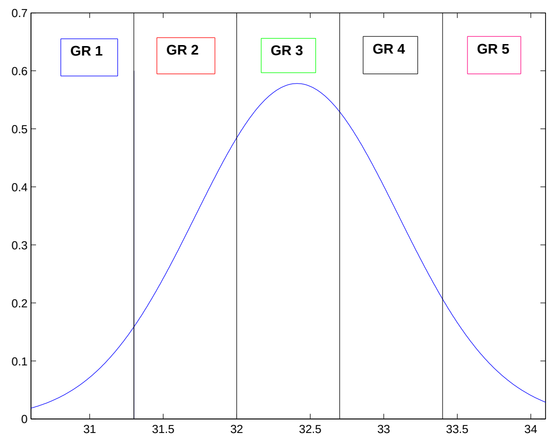
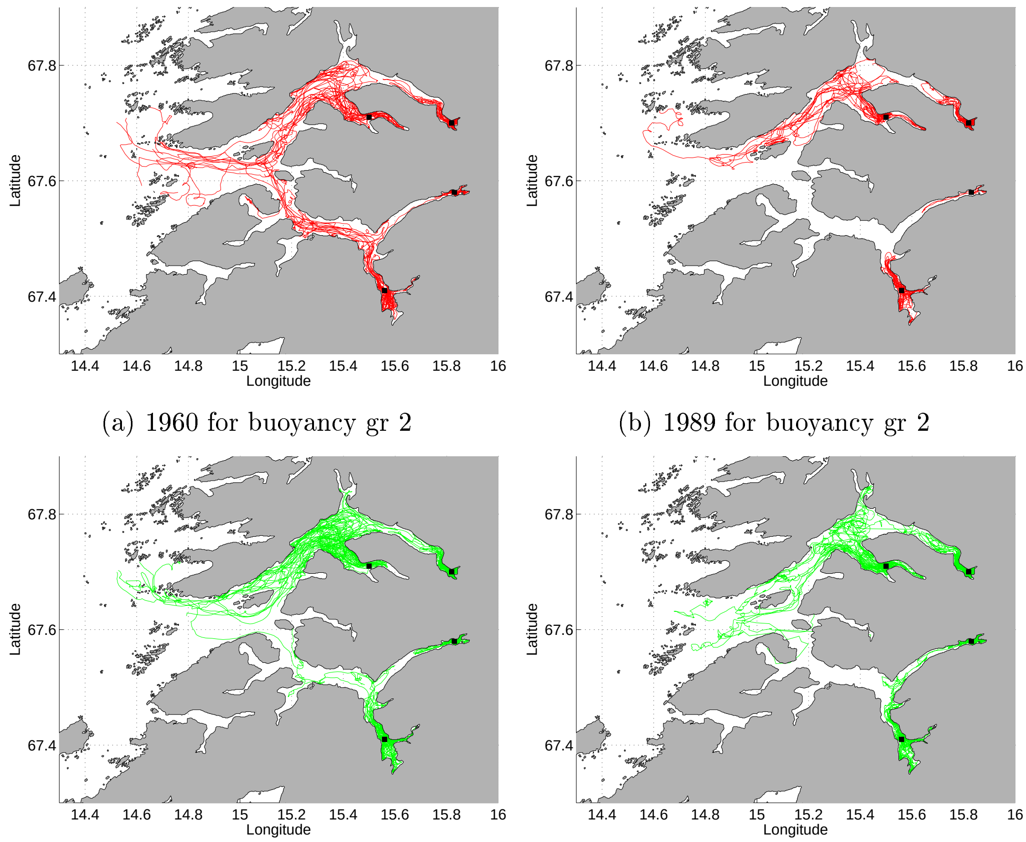


Figure 6: Neutral buoyancy of Norwegian Coastal Cod (Stenevik *et al.*, 2008), divided into five buoyancy groups for easier comparison of results.

incubation time for cod eggs at this latitude. Four different release times where used; 15^{th} March, 1^{st} April, 15^{th} April and 1^{st} May. In every setup approximately 15000 eggs are included with a diameter of 1.4 mm. All are released at 20 m depth and equally distributed at four spawning grounds; Sørfolda, Leirfjorden, Nordfolda and Vinkfjord.

Trajectories from a selection of eggs in buoyancy group 2 and 3 are shown in Figure 7. The figure shows the path covered during 21 days of advection by eggs released 15^{th} April 1960 and 1989. The spreading of eggs in buoyancy group 2 are shown in Figures 7(a) and 7(b). The trajectories from 1960 covers the whole fjord system. All spawning grounds show a large dispersal of eggs, both within the fjord branches and out through the mouth. In 1989 only eggs from Vinkfjord show large dispersion, all other spawning areas have a strong degree of retention.

Figures 7(c) and 7(d) show the paths covered by buoyancy group 3. The eggs spawned in 1960 have been subjected to large spreading. Especially in Nordfolda the eggs are situated within the whole fjord. The majority of these eggs are



(a) 1960 for buoyancy gr 2

(b) 1989 for buoyancy gr 2

(c) 1960 for buoyancy gr 3

(d) 1989 for buoyancy gr 3

Figure 7: Trajectories from eggs released on 15^{th} April and transported for 21 days in 1960 and 1989, black boxes indicate spawning grounds.

coming from Vinkfjord, some are also leaving the fjord system. From Sørfolda a small portion of eggs are located in the main part of the fjord. All eggs released in Leirfjorden are retained there. In general, there is less dispersal of eggs in the fjord system in 1989. Eggs from Vinkfjord are transported out into Nordfolda and towards the mouth area. Most particles from Nordfolda, Sørfolda and Leirfjorden remain close to their origin.

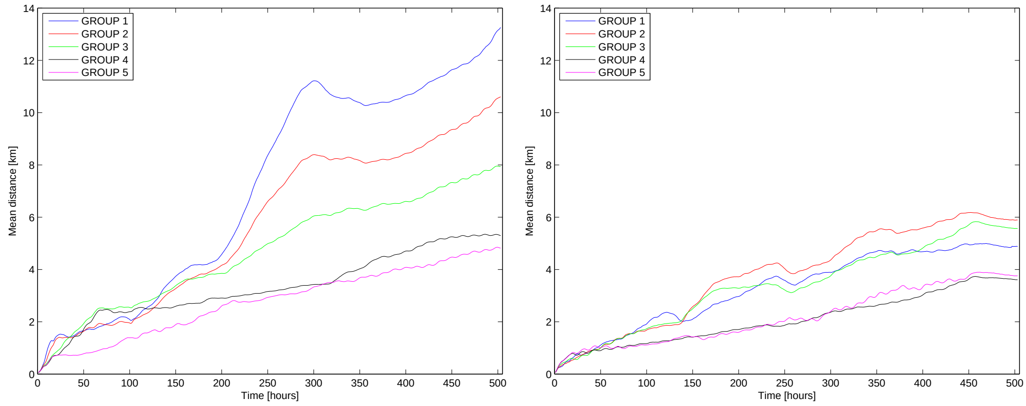
Table 1 shows the percentage of eggs leaving the fjord system after 21 days of advection. For 1960 the percent is largest for the lightest buoyancy groups, and increasing with time. For the other buoyancy groups the number of eggs lost is lower. In 1989 mainly eggs in buoyancy group 1 and 2 are transported out of the region, and this occurs mostly on 15^{th} March and 1^{st} April. From 15^{th} April and onwards the percentage of eggs leaving the fjord system is small in all buoyancy

Table 1: Percentage of eggs that have left the fjord system.

		15thMarch	**1stApril**	**15thApril**	**1stMay**
1960	gr 1	0	3,4	11,5	13,6
	gr 2	0,3	4,2	9,8	3,0
	gr 3	0,7	4,1	6,4	0,3
	gr 4	0,6	0,8	1,8	0
	gr 5	0	0,1	0	0
1989	gr 1	10,0	13,9	1,2	1,8
	gr 2	5,7	13,0	2,2	1,2
	gr 3	2,2	7,6	1,2	0,9
	gr 4	0,1	0	0	0,1
	gr 5	0	0	0	0

groups. The major difference between 1960 and 1989 is in buoyancy group 1 (the lightest one). This group has largest dispersion late in spring 1960 and early in spring 1989.

Mean distance travelled from spawning grounds by each buoyancy group is shown in Figure 8, from 15th April and 21 days onwards. All buoyancy groups show



(a) 1960

(b) 1989

Figure 8: Mean distance versus time travelled from spawning grounds, released 15th April and 21 days ahead.

similar patterns in the beginning of the simulation during 1960. After approximately 10 days the paths separate, with the lightest buoyancy groups travelling the largest distance. After 21 days of advection the mean distance varies between 5 km and 13 km, from heavier to lighter buoyancy groups. During the simulation for the year 1989 all curves stay close together throughout the whole run. The two heaviest buoyancy groups remain within 4 km after 21 days, the others do not exceed more than 6 km from the spawning ground. The major difference between 1960 and 1989 is found in the three lightest buoyancy groups, where they travel about twice as long in 1960 compared to 1989.

Figure 9 illustrates the vertical profile of Norwegian Coastal Cod (CC) eggs according to the corresponding salinity profile for April 1960 and 1989. The salinity

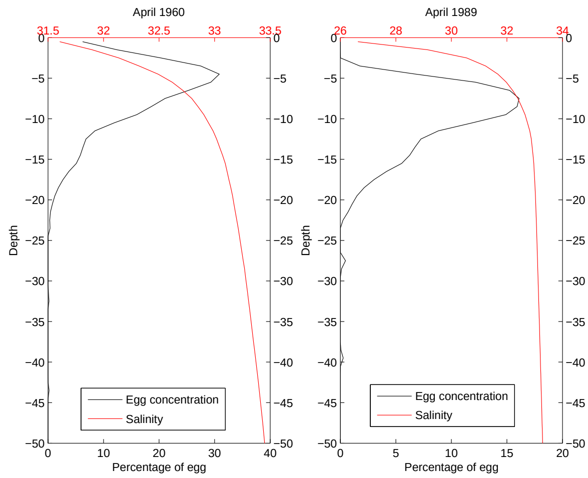


Figure 9: The vertical distribution of eggs according to the local salinity profile from April 1960 (left) and 1989 (right).

profile is a monthly mean for April and the eggs have the buoyancy distribution as shown in Figure 6. The concentration of eggs is a function of the density difference and the eddy diffusivity coefficient (Sundby, 1983), calculated with VertEgg toolbox (Ådlandsvik, 2000).

The major difference between 1960 and 1989 is the surface salinity, being close to 31.8 in 1960 and 26.6 in 1989. With this difference in salinity the concentration of eggs near the surface has changed. In 1960 some eggs are situated close to the surface and the maximum is around 5 m depth. However, in 1989 all the eggs are positioned below 2.5 m depth, with highest concentration around 7.5 m depth. When the surface layer is thin, as in 1989, this difference in vertical distribution is important. When the eggs are at a lower level of the water column, the possibility of being transported away from the spawning site is much smaller and the degree of retention is larger.

The same vertical profile of eggs is show in Figure 10 together with the corresponding along-fjord current profile, where positive currents are directed out of the fjord. The maximum current speed is observed at the surface in both years, but with different scales. In 1960 the outflowing surface current is close to 0.15 m/s,

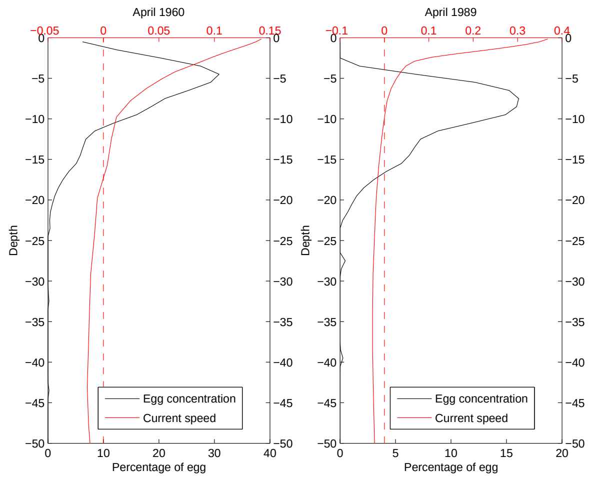


Figure 10: The vertical distribution of eggs together with the local along-fjord current speed from April 1960 (left) and 1989 (right). Positive direction is out of the fjord.

and approximately 0.36 m/s in 1989. The depth of the surface layer is largest in 1960, in the same way as with the salinity profile. This results in a greater portion of eggs situated within the outgoing surface layer in 1960, than in 1989. In 1989, only a small percentage of eggs are confined to the outflowing water, while the rest of the eggs are in a location with no currents or inward currents. This explains the results showing larger degree of retention towards the end of April 1989 compared to 1960.

4 Discussion

The results show that the model simulate the main features related to the estuarine circulation. The salinity is lowest at the inner end of the fjord branches, and increasing towards the mouth. A strong outflow is restricted within the surface layer and weaker inflow is observed below, corresponding to the estuarine circulation. A cross-fjord variance is observed in Sørfolda, verifying the influence of rotation causing motion to be deflected towards right.

4.1 Separation and mixing of ANC and CC eggs

When discussing the separation and mixing between Arcto-Norwegian Cod (ANC) and Norwegian Coastal Cod (CC) it is assumed that when CC eggs are transported out of the fjord, the probability of mixing with ANC eggs is high. Whenever the CC eggs are retained within the fjord system the two populations are kept separated.

4.1.1 Importance of buoyancy

The neutral buoyancy of CC eggs is the only variable used in these simulations to evaluate the separation between ANC and CC. However, the results show that the buoyancy of eggs are an important factor determining the spreading of eggs. When the estuarine circulation is established, the outgoing surface currents are strong. Pelagic eggs in this fjord system, situated close to the surface, would then be transported out of the fjord. However, since the mesopelagic CC eggs are heavier then the surface layer, they avoid offshore transport and mixing with ANC outside the fjord. There is also a variability in the transport within the buoyancy distribution of CC eggs. The lightest buoyancy group has the highest probability (6.9%) of being advected out of the fjord and being mixed with ANC eggs. The three heaviest buoyancy groups, containing 66% of the eggs, have minor leakage at all times and are separated from ANC eggs. Modeling studies in a fjord on the western coast of Norway done by Asplin *et al.* (1999) also acknowledged the possibility for eggs and larvae to be advected out of fjord in the surface layer. They indicated that species have adapted the depth of spawning and the buoyancy of eggs to reduce dispersal of younger stages. The results shown here (Figure 9) indicate that CC have adapted their spawning behavior to increase the retention of eggs inside a fjord system.

4.1.2 Spawning grounds

A significant difference between ANC and CC is the different spawning grounds. The ANC spawn in Vestfjorden, where the eggs are lighter than the mixed layer, while the CC spawn inside the fjord where the eggs are heavier than the mixed layer. The CC eggs will mainly be mesopelagically distributed inside Folda, but mostly pelagically distributed in Vestfjorden where the surface salinity is normally around 33. This is a major factor maintaining the separation between ANC and CC.

The selection of stratified water masses as spawning grounds to prevent dispersion of eggs stages was discussed by Salvanes *et al.* (2004), which in turn causes the CC to develop into different coastal and fjord sub-populations adapted to the local environment.

4.1.3 Seasonal and interannual variations

The results show that the retention of CC eggs within Folda depends on the spawning time. In 1960 the spreading of eggs is highest in late spring, compared to 1989 when the spreading was highest in early spring. The main causes of this is assumed to be different onset of the estuarine circulation and thereby changed surface salinity.

The peak spawning time for CC is towards the end of April, while the ANC reach a spawning maximum at the beginning of April. From Table 1 a distinct difference in transport of eggs spawned on 1^{st} and 15^{th} April is seen. For early spawners the retention is largest in 1960, causing separation between ANC and CC in 1960 but more mixing in 1989. For late spawners the retention is strongest in 1989, resulting in mixing in 1960 and separation in 1989. This illustrates that the seasonal variations are on the same scale as the interannual variations. The time of spawning is therefore an important variable, a shift in the timing might have a large impact on the final distribution of eggs.

A clear difference between 1960 and 1989 is seen as well. The main difference is seen in the fresh water input, being about twice as large in 1989. The fresh water discharge causes changes in the estuarine circulation and in the salinity of the brackish layer. Despite of this difference between the years the total amount of eggs leaving the fjord is 2.7% during both 1960 and 1989, when including all buoyancy groups and all spawning times. Hence the total amount of mixing between ANC and CC eggs do not change between the years, but the time of mixing is different. In March and the beginning of April the separation is stronger in 1960 than in 1989, contrary to the end of April and May when the separation is more pronounced in 1989 than in 1960. The favorable time for spawning to achieve separation is changing between the years. However, these two years show that the mixing between ANC and CC is limited and constant between years, when considering all release times.

The two last spawning times, 15^{th} April and 1^{st} May, are closest to the time of maximized spawning concentration of CC. Only considering these two release times, there is a significant difference between 1960 and 1989. The amount of eggs leaving the fjord is 3.7% in 1960 and 0.9% in 1989. Hence the mixing between CC and ANC is largest in 1960, and 1989 shows a strong separation between the populations.

4.1.4 The impact of climate change

The climate is not constant and varies on different time scales. A global warming is observed on top of these natural variations, caused by anthropogenic emissions of greenhouse gases. This warming is expected to continue in the future, which may have large impacts on the climate. Downscaling of climate models show a temperature increase of 1.6° in northern Norway in 50 years (Alfsen, 2001). The precipitation is expected to increase, up to a seasonal average of 7.8%. Even warmer and wetter years are probable to occur more often, being similar to 1989.

Meaning that the situation observed in 1989 is likely to occur more frequently in the future.

In 1989 the mixing between ANC and CC occurred in early spring, and separation was stronger late in spring. With late April as the time of maximized spawning, this pattern favors separation. If years like 1989 occur more often and might even be warmer and wetter, these results show increased separation between ANC and CC eggs. The amount of mixing occurring early in 1989 was caused by early onset of estuarine circulation, but weaker stratification than later. Hence separation is depending on a strong stratification, which might increase due to climate change. Therefore the climate change is expected to increase the separation between ANC and CC during early life stages, caused by the retention of CC eggs.

4.1.5 Conclusion

These results confirm that the CC in Folda is separated geographically from the ANC in Vestfjorden during the egg stage and the mixing between them is limited. Earlier work on cod recruitment in northern Norway also acknowledged different early life history of ANC and CC (Løken *et al.*, 1994). Furthermore, they discussed juvenile segregation due to different bottom settling strategies. Knutsen *et al.* (2007) sampled eggs from CC in 20 Norwegian fjords throughout a large geographical area. The results revealed a pattern with higher density of pelagic eggs inside sheltered fjord habitats along the Norwegian coast. Jorde *et al.* (2007) found indications of local coastal cod populations within a geographical extent of 30 km, on the scale of local fjords. All these results confirms the existence of separated CC populations inside different fjords, being highly self-recruiting. This is a major challenge for managing the stocks. Overfishing in a fjord might cause the stock to suffer severe damage and it will have difficulties to recover, while at the same time stocks in the neighboring fjord might be sustainable and suffer no depletion. Weak interaction between local populations demands local administration of fish quotas.

The present results indicate that CC has developed robust mechanisms to keep their eggs separated from the adjacent spawning population of ANC. However, a small fraction of the CC eggs has the potential to leave the fjord and mix with the ANC eggs. It is likely that this escaping fraction will vary with the runoff, and hence with climate variability. On the other hand, the probability for ANC eggs to be advected into habitat of the CC eggs in the fjord system is much smaller. Hence, we conclude that the a potential gene flow must occur from the CC to the ANC and not vice versa. The question whether such a gene flow would be higher under a cool and dry climate needs further exploration. More specifically, we need then to extend the model simulations from the two extreme year to a time series of years.

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