

Retention of Coastal Cod Eggs in a Fjord Caused by Interactions between Egg Buoyancy and Circulation Pattern

Authors: Myksvoll, Mari S., Sundby, Svein, Ådlandsvik, Bjørn, and Vikebø, Frode B.

Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 3(1) : 279-294

Published By: American Fisheries Society

URL: <https://doi.org/10.1080/19425120.2011.595258>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

ARTICLE

Retention of Coastal Cod Eggs in a Fjord Caused by Interactions between Egg Buoyancy and Circulation Pattern

Mari S. Myksvoll,* Svein Sundby, Bjørn Ådlandsvik, and Frode B. Vikebø

Institute of Marine Research, Post Office Box 1870 Nordnes, N-5817 Bergen, Norway;

and Bjerknæs Centre for Climate Research, Post Office Box 7810, N-5020 Bergen, Norway

Abstract

Norwegian coastal cod form a stationary population of Atlantic cod *Gadus morhua* consisting of several genetically separated subpopulations. A small-scale differentiation in marine populations with pelagic eggs and larvae is made possible by local retention of early life stages in coastal environments. A numerical model was used to simulate the circulation in a fjord system in northern Norway over 2 years with different river runoff patterns. The dispersal of cod eggs was calculated with a particle-tracking model that used three-dimensional currents. The observed thickness of the low-salinity surface layer was well reproduced by the model, but the surface salinity was generally lower in the model than in the observations. The cod eggs attained a subsurface vertical distribution, avoiding the surface and causing retention. Interannual variations in river runoff can cause small changes in the vertical distribution of cod eggs and larger changes in the vertical current structure. Retention in the fjord system was strong in both years, but some eggs were subjected to offshore transport over a limited time period. The timing of offshore transport depended on the precipitation and temperatures in adjacent drainage areas. A possible match between maximized spawning and offshore transport may have a negative effect on local recruitment.

Norwegian coastal cod consist of stationary populations of Atlantic cod *Gadus morhua* that spawn at several locations along the Norwegian coast, particularly in the fjords (Jakobsen 1987). The coastal cod offspring grow up close to their spawning site, in large contrast to the Arcto-Norwegian Atlantic cod stock, whose pelagic offspring are transported from their coastal spawning site in Vestfjorden (Figure 1) up to 1500 km into the Barents Sea (Bergstad et al. 1987). The Arcto-Norwegian cod and the Norwegian coastal cod are considered separate populations with respect to management and quotas, and the distinction between the two is supported by a genetic differentiation (Pogson and Fevolden 2003). Since the mid-1990s the Norwegian coastal cod north of 62°N have been declining (ICES 2009) from a large biomass in 1994 (300,000 tons) to a minimum in 2008 (90,000 metric tons), and in many local regions the coastal cod population is critically low. The neighboring Arcto-Norwegian cod stocks have remained in good condition during

the past two decades. The coastal cod have been managed as one stock unit, but recent studies have revealed a genetic structure between coastal broodstocks on small spatial scales (Knutsen et al. 2003; Salvanes et al. 2004; Dahle et al. 2006; Espeland et al. 2007). Jorde et al. (2007) found a population structure with a geographical range of 30 km, which suggested significant genetic differences between neighboring fjords. A small-scale genetic differentiation in marine populations with pelagic eggs and larvae is made possible by local retention of early life stages (Cowen et al. 2000). Knutsen et al. (2007) showed that retention of cod eggs is evident in a number of Norwegian fjords. Asplin et al. (1999) argued that species have adapted their spawning depth and the buoyancy of eggs to reduce the dispersal of young stages. To maintain the coastal cod offspring close to the spawning site, retention mechanisms of the planktonic stages and active return migration of the juveniles must occur.

Subject editor: Suam Kim, Pukyong National University, Busan, South Korea

*Corresponding author: mari.myksvoll@imr.no

Received April 20, 2010; accepted January 3, 2011

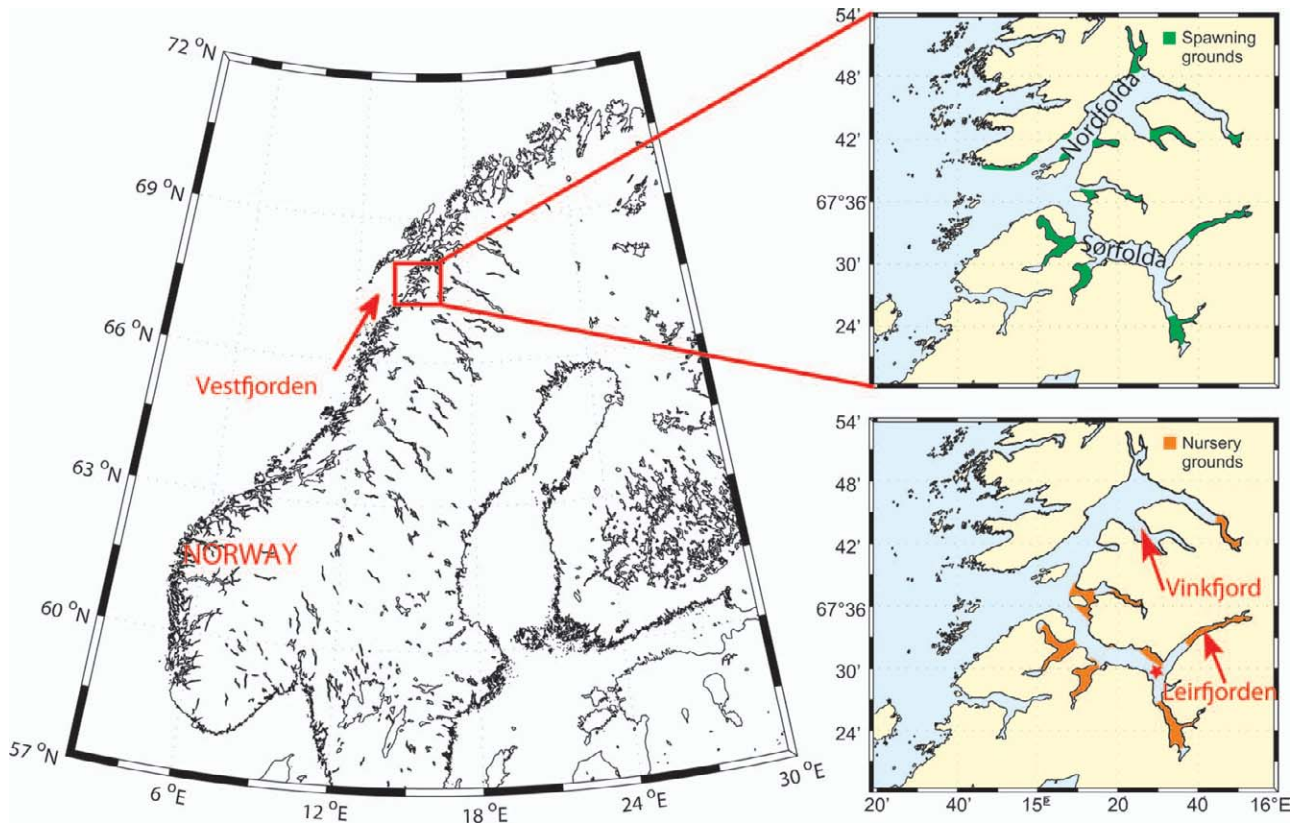


FIGURE 1. The fjord system of Nordfjolda and Sørfjolda located in the northern part of Norway, including the fjord branches of Vinkfjorden and Leirfjorden and known spawning areas (upper right panel) and nursery areas (lower right panel) of Norwegian coastal cod; the data were provided by Gyda Lorås at the Norwegian Directorate of Fisheries.

An estuary is a semi-enclosed body of water where freshwater from river runoff meets saline water from the ocean. The physical environment in an estuary is highly dependent on the balance between these two water masses. When river runoff dominates over tidal input, estuarine circulation develops, which is characterized by a strong stratification (Dyer 1997). A fjord is a special type of estuary that is carved out by a glacier. Many Norwegian fjords have a deep basin (up to 1,300 m) and a shallow sill near the mouth (10–200 m) (Svendsen 1995). Fjords are also characterized by a small width-to-depth ratio and can reach a length of 200 km (Dyer 1997). Estuarine circulation is a general feature observed in many fjords where the river runoff is large compared with the surface area of the fjord (Svendsen 1995). This circulation is characterized by strong outflowing currents at the surface and weak inflow in the lower layers. The surface outflowing layer is thin (<5 m) with low salinity. The deep water below the sill level is affected by another circulation system. This water mass can remain stagnant for longer periods and can only leave the fjord when lifted above the sill level. Vertical mixing and diffusion are important to control the deep-water circulation. The connection between the estuarine circulation and the deep-water circulation is weak in fjords with deep sills, and they are separated by an intermediate layer (Stigebrandt 1981).

While the spawning period of Arcto-Norwegian cod in Vestfjorden is well known (Pedersen 1984; Ellertsen et al. 1989), the exact time of spawning for coastal cod has been less investigated. Results by Kjesbu (1988) suggest that the spawning continues for several months during the spring, with a peak concentration toward the end of April. When the coastal cod spawn in the fjord environment, the horizontal transport of eggs and larvae is highly dependent on their vertical position. If the eggs are lighter than the surface layer, they will attain a pelagic distribution with the concentration occurring at the surface and then exponentially decreasing downward (Sundby 1983). Eggs that are heavier than the surface layer but lighter than the deeper layers will have a subsurface distribution with maximum concentration occurring at the pycnocline (Sundby 1991). Measurements from Tysfjord show that the neutral buoyancy of coastal cod eggs in terms of salinity varies between 30.6 and 34.1 (practical salinity scale; Stenevik et al. 2008). In a fjord with sufficient freshwater discharge, the surface salinity is low enough for the cod eggs to be submerged below the surface layer. The cod eggs will then not be affected by the strong currents at the surface, thus increasing their chances to be retained locally. Stenevik et al. (2008) showed that the specific gravity of coastal cod eggs did not vary much among different locations along the Norwegian

coast but concluded that the local salinity structure determined whether the eggs attained a pelagic or subsurface distribution.

The objective of this study was to quantify the importance of the vertical distribution of cod eggs for horizontal transport and retention within a fjord system and to evaluate how interannual variations in river runoff change the local retention. A regional ocean model was used to simulate the circulation in a fjord system during two different years, 1960 and 1989. The first year represented a cold, dry year with low river runoff, while the second year represented a warm, wet year with high river runoff. By studying two years having extreme conditions, the magnitude of interannual differences in dispersal of eggs could be quantified. Drift patterns of eggs were calculated with a particle-tracking model that used the modeled velocity fields. The particle-tracking model included a component that resolved the dynamical vertical distribution.

STUDY AREA

The fjord system of Sørfolda and Nordfolda (Figure 1) was selected to study the physical mechanisms causing local retention of cod eggs. These are two separate fjords with a joint opening toward Vestfjorden, located in the northern part of Norway at 67.5°N (Figure 1). The spawning and nursery areas inside the fjord system have been mapped by the Norwegian Directorate of Fisheries, as seen in Figure 1 (Gyda Lorås, personal communication). The spawning areas have been localized in the innermost ends of the branches in the fjord system, while the nursery areas are limited to the branches of Sørfolda, except for the head of Nordfolda. Sørfolda has a sill depth of 265 m, and the deepest part of the fjord is 574 m. The main part of the fjord is 3.5 km wide, narrowing to 1.6 km toward the head. The inner end of Sørfolda is divided into two main branches; the northern part is called Leirfjorden. The sill depth in Nordfolda is 225 m, and the deepest part of the fjord reaches 527 m. The fjord width ranges from 5.5 km in the central part to 2.4 km in the innermost part. Nordfolda is divided into several smaller branches, including Vinkfjord to the south. The whole fjord system is surrounded by steep mountains. Because both fjords have a large sill depth, there is no topographical feature limiting the water exchange with the continental shelf.

The Institute of Marine Research in Bergen has been monitoring the hydrography in Sørfolda and Nordfolda every year since 1975 (Aure and Pettersen 2004) but has only collected data during late fall (November–December) when the river runoff is low. These observations show a low-salinity surface layer with large interannual variability. Sørfolda has, in general, a fresher surface layer than Nordfolda, and both have the lowest salinity at the heads. In 2007, several salinity and temperature profiles were measured in Sørfolda, and these results formed a good basis for the validation of the ocean model. The main feature observed was a shallow surface layer less than 5 m deep with salinities as low as 25. This is characteristic for a fjord system with considerable river runoff compared with the surface area of the fjord (Svendsen 1995). The circulation patterns in

Sørfolda and Nordfolda have not been described in detail in earlier work, but knowledge from similar systems indicates that the estuarine circulation develops when the river runoff is high during the season of ice melt (Farmer and Freeland 1983). Mohus and Haakstad (1984) measured currents close to the head of Sørfolda in November 1978. The circulation pattern was complicated but was characterized by the estuarine circulation, with outflow in the upper layer and compensating inflow below. The surface current was also found to vary strongly with the local winds, having the potential to spin up the estuarine circulation or reverse the whole system. Under normal conditions in Sørfolda the surface current was observed to be 5% of the wind speed.

A cod egg survey was performed in Sørfolda and Nordfolda on April 4–5, 2007 (Magnus Johannessen, Institute of Marine Research, personal communication) by means of Juday nets with an 80-cm mouth diameter and a mesh size of 375 μm . Coastal cod eggs were collected at 10 stations with four vertical hauls at each station: 60–45 m, 45–30 m, 30–15 m, and 15–0 m. The eggs were divided into six different development stages as described by Fridgeirsson (1978). In total, 226 eggs were sampled, and the horizontal distribution is shown in Figure 2. For plotting purposes the eggs were divided into three groups according to their egg stage; the blue columns include egg stages 1 and 2 (0–5 d old), green columns egg include stages 3 and 4 (6–14 d old), and red columns include egg stages 5 and 6 (15–21 d old). The largest number of eggs were collected at the southernmost station in Sørfolda, with 67 cod eggs encompassing all stages. The red column at this station corresponds to 29 eggs; the other columns are scaled accordingly. The majority of eggs sampled, especially the oldest ones, were located in the inner part of the fjord system at the beginning of the spawning season (Figure 2). The survey was performed early in the spawning season, and at every station except one near the mouth of Sørfolda, the number of old eggs (6–21 d old) exceeded the number of young eggs (0–5 d), indicating eggs were retained rather than dispersed.

METHODS

Freshwater discharge.—In fjords with high river runoff compared with their surface area, the runoff is a major driving mechanism controlling both the circulation and the hydrography (Sælen 1967). The seasonal cycle of the river discharge depends on the drainage area. To calculate the annual mean discharge, the area was divided into 17 drainage areas. A planimeter was used on an isohydate map from The Norwegian Water Resources and Energy Directorate (NVE), as described by Sundby (1982). The drainage areas were classified into different regimes depending on elevation above sea level and distance from the coast. A coastal regime dominates near the mouth of the fjord system where the highest runoff occurs during autumn and winter and lowest during summer, which is directly correlated with the local precipitation. A mountain–glacier regime is located close to the head of the fjord, with high flows in summer and low flows in winter owing to precipitation accumulating as snow. Between these two is the inland–transition regime with high runoff during

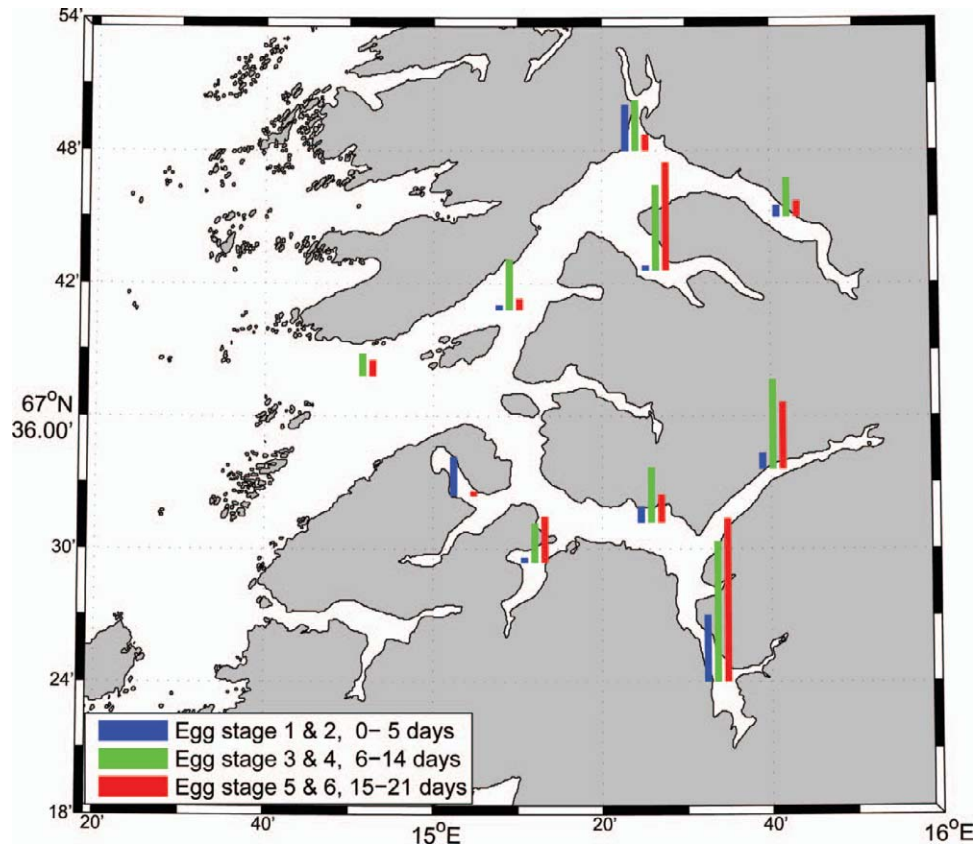


FIGURE 2. Sampled cod eggs at 10 stations in the study area during a survey on April 4–5, 2007, by egg stage.

spring and autumn and low flow during summer and winter. Most of the land surrounding Nordfolda is at intermediate altitude (100–600 m) and is considered a transition regime. The inner part of Sørfolda and Leirfjorden is surrounded by mountains and glaciers, dominated by high summer flows. The freshwater input into Nordfolda is much less than into Sørfolda, and has a different seasonal cycle. To include information about annual mean discharge and seasonal variations, a representative watermark had to be determined for every drainage area. The NVE (Ingeborg Kleivane, personal communication) provided data from four rivers in the area that were suitable to use as watermarks and represented each regime. The data were averaged over 5 d and released into the model domain as a freshwater source in the upper 10 sigma layers, linearly increasing toward the surface.

The interannual variability of the four chosen rivers discharging into the fjord system is shown in Figure 3. The annual mean discharge is standardized for comparison. The rivers showed similar interannual variability, except after 1999 when one river was regulated and water was guided away from the river. From these data 2 years, 1960 and 1989, were chosen. Both years are more than two standard deviations away from the mean, in opposite directions.

The seasonal cycle of freshwater discharge for the four rivers used in the simulation is shown in Figure 4. The upper panel

shows the data from the Lakshola River during 1960 and 1989, whereas the lower panel shows the mean from the Lakså Bridge, Strandå, and Vallvatn rivers (note different scales). The Lakshola River represents a mountain–glacier regime with a strong maximum discharge during summer and is approximately 10 times larger than the other rivers. The Lakså Bridge and Vallvatn River represent an inland–transition regime, while the Strandå River represents a coastal regime; all of these regimes have a similar seasonal cycle. The major difference between these watermarks and Lakshola is the enhanced discharge during fall (September and October) and winter (December and January), which is most pronounced in 1989. All the rivers had higher runoff during 1989 than in 1960 for every month.

The circulation model.—The circulation model used was the Regional Ocean Modeling System (ROMS), version 3.0 (Shchepetkin and McWilliams 2005; Haidvogel et al. 2008). This is a three-dimensional, free-surface, hydrostatic, primitive equation ocean model that uses terrain-following s -coordinates in the vertical. The primitive equations were solved on an Arakawa C-grid. A generic length scale (GLS) turbulence closure scheme was used for subgrid-scale mixing in these simulations with a modified form of the Mellor–Yamada 2.5 closure (Warner et al. 2005b). The ROMS has been successfully applied to various modeling problems on the continental shelf seas,

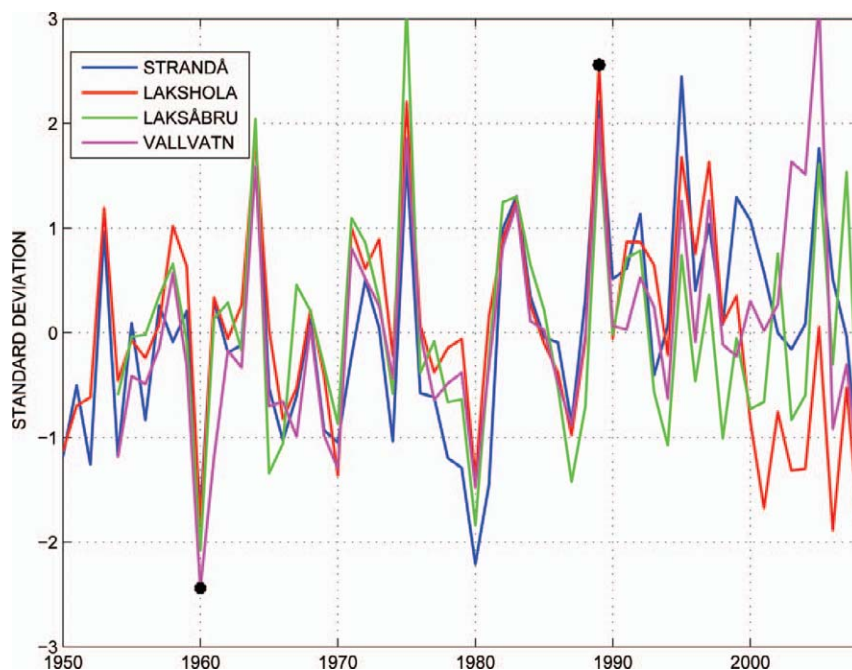


FIGURE 3. Annual mean discharge from four rivers in the model area, standardized for comparison. The two selected years are marked with black dots.

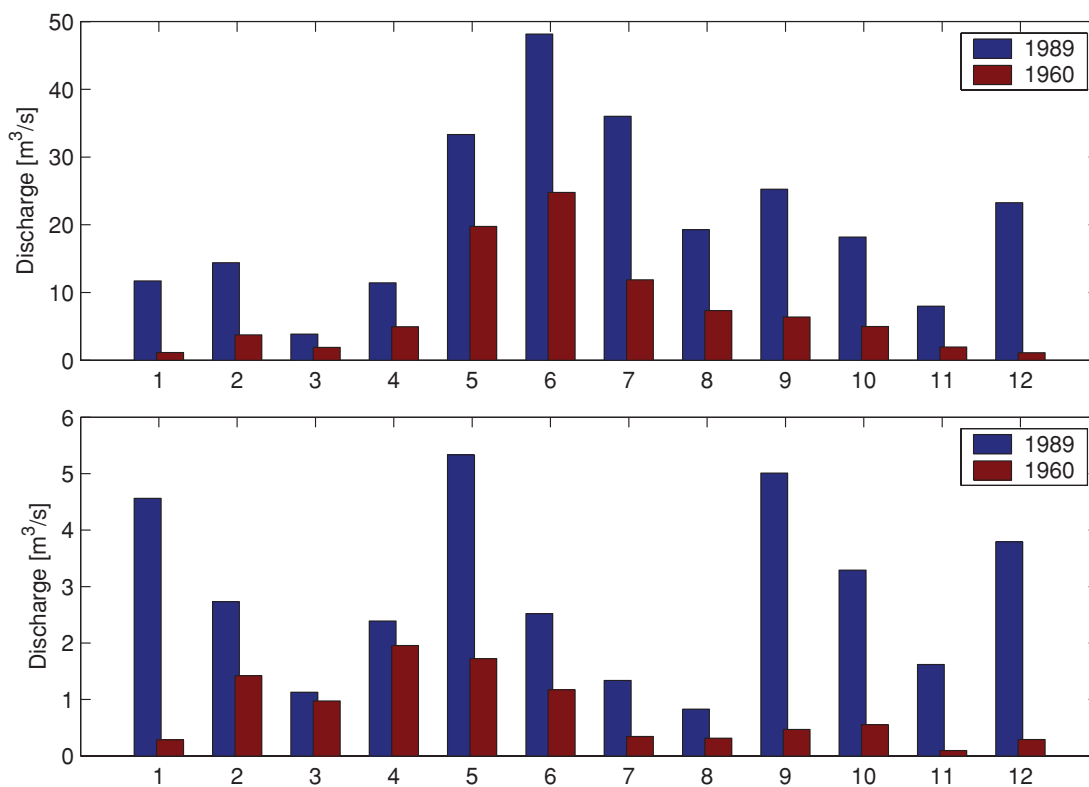


FIGURE 4. Monthly mean discharge from January until December for the years 1960 and 1989 in Lakshola River (upper panel) and an average of Lakså Bridge, Strandå, and Vallvatn rivers (lower panel); note the difference in scales.

including the Chukchi Sea (Winsor and Chapman 2004), the Norwegian coast (Vikebø et al. 2005), the Barents Sea (Budgell 2005; Gammelsrød et al. 2009), the Philippine Archipelago (Han et al. 2009), the coastal Gulf of Alaska (Hermann et al. 2009), Skagerrak and the North Sea (Albretsen and Røed 2010), and in coastal zones such as the southern Benguela Current (Mullon et al. 2003), Hudson River estuary (Warner et al. 2005a), Chesapeake Bay (Li et al. 2005), Storfjorden (Smedsrud et al. 2006), and the coast of Peru (Brochier et al. 2008).

The model domain includes high-resolution bathymetry in which the largest depth was set to 300 m to avoid overly steep gradients. The horizontal grid length was about 200 m, and the vertical was spanned by 35 sigma levels, with increased resolution near the surface and reduced resolution toward the bottom. The thickness of the upper layer varied from 29 to 33 cm.

The initial hydrography field was interpolated from data collected in the fjord system during November 1993. The model run started on November 1 the year before the year of interest. The atmospheric forcing was extracted from the ERA-40 archive, with a horizontal resolution of 1° and a temporal resolution of 6 h. The lateral boundary conditions were taken from a climatological data set covering the Nordic Seas (Engedahl et al. 1998) and containing the monthly mean salinity, temperature, currents, and surface elevation with 20 km resolution. The lateral forcing is included along the open boundary outside the fjord system along with four tidal constituents (M_2 , S_2 , N_2 , and K_1).

The particle-tracking model.—A Lagrangian advection and diffusion model (LADIM) was used to simulate the transport of cod eggs inside the fjord system with a fourth-order Runge–Kutta advection scheme (Ådlandsvik and Sundby 1994). The model applied the hourly mean output from ROMS to advect the eggs with a time step of 6 s in an off-line mode. Each egg had its own level of neutral buoyancy, and a vertical buoyant velocity was calculated depending on the density difference between the egg and the surrounding water. The vertical displacement was computed based on the buoyant velocity and the eddy diffusivity coefficient, as described in Thygesen and Ådlandsvik (2007).

Each egg was given a fixed specific level of neutral buoyancy according to the distribution in Figure 5. The data were taken from Stenevik et al. (2008) who showed that the specific gravity of cod eggs did not vary much among three coastal broodstocks, except for Porsanger, which is assumed to be influenced by the Arcto-Norwegian cod. The data from Tysfjord, a neighboring fjord of Sørfolda and Nordfolda, was used in this study. The buoyancy was held constant through the developmental stages. The coastal cod eggs have a tendency to get heavier halfway during their development and lighter again immediately before hatching. The corresponding buoyancy variations are small compared with the observed salinity variations in the fjord. Because the local salinity profile is most important for determining the vertical distribution, variations in buoyancy through developmental stages would not introduce large differences. For easier interpretation of the results, the eggs were

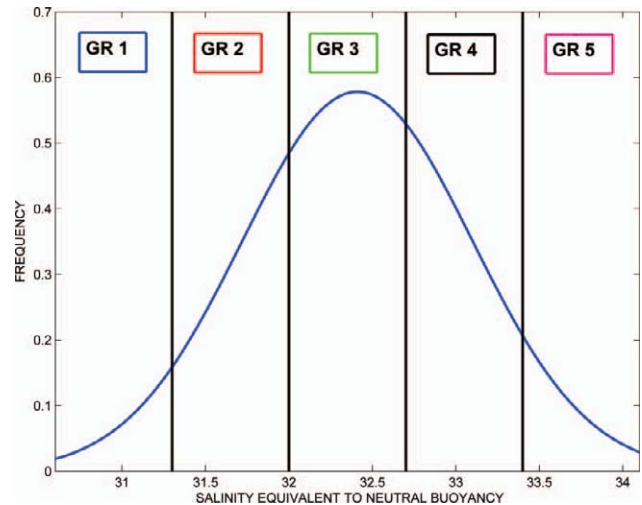


FIGURE 5. Neutral buoyancy of Norwegian coastal cod eggs (Stenevik et al. 2008), divided into five buoyancy groups for easier comparison of the model results.

divided into five buoyancy groups: Group 1: 30.5–31.3; group 2: 31.3–32.0; group 3: 32.0–32.7; group 4: 32.7–33.4; and group 5: 33.4–34.1 in which salinity is equivalent to neutral buoyancy (see Figure 5). All the buoyancy groups spanned a salinity range of 0.7. Because eggs attain the same temperature as the ambient water, the specific gravity and egg buoyancy is largely controlled by salinity alone. The simulations were continued for 21 d, close to the incubation time for cod eggs at this latitude with low temperatures (Page and Frank 1989). Four different release times were used: March 15, April 1, April 15, and May 1. In every drift experiment, approximately 15,000 eggs were released at a depth of 20 m. Initial depth does not affect horizontal distribution when buoyancy is included in the calculations (Parada et al. 2003; Brochier et al. 2008). Four spawning areas were chosen based on Figure 1 and represent different parts of the fjord system: the head of Sørfolda, Leirfjorden, the head of Nordfolda, and Vinkfjord, with respective distances of 50.0, 55.9, 39.6, and 55.9 km from the coast. The 15,000 particles were equally distributed among the four spawning areas. No background information has been available to make other assumptions. The diameter of coastal cod eggs ranges from 1.2 to 1.6 mm. The egg diameter used in the present modeling was the mean diameter of 1.4 mm. Data from Norwegian coastal cod showed no clear relationship between egg diameter and buoyancy. In Tysfjord the diameter stays constant while the buoyancy varies (Kyungmi Jung, Institute of Marine Research, personal communication).

The vertical distribution of cod eggs was calculated with a Matlab toolbox routine called VertEgg (Ådlandsvik 2000), which is based on the steady-state distribution developed by Sundby (1983). In all calculations, the egg diameter was set to 1.4 mm, wind speed to 6 m/s, mean buoyancy to 32.41 with SD of 0.69 (Stenevik et al. 2008), and maximum depth to 100 m. A case-specific salinity profile was included in each case, and

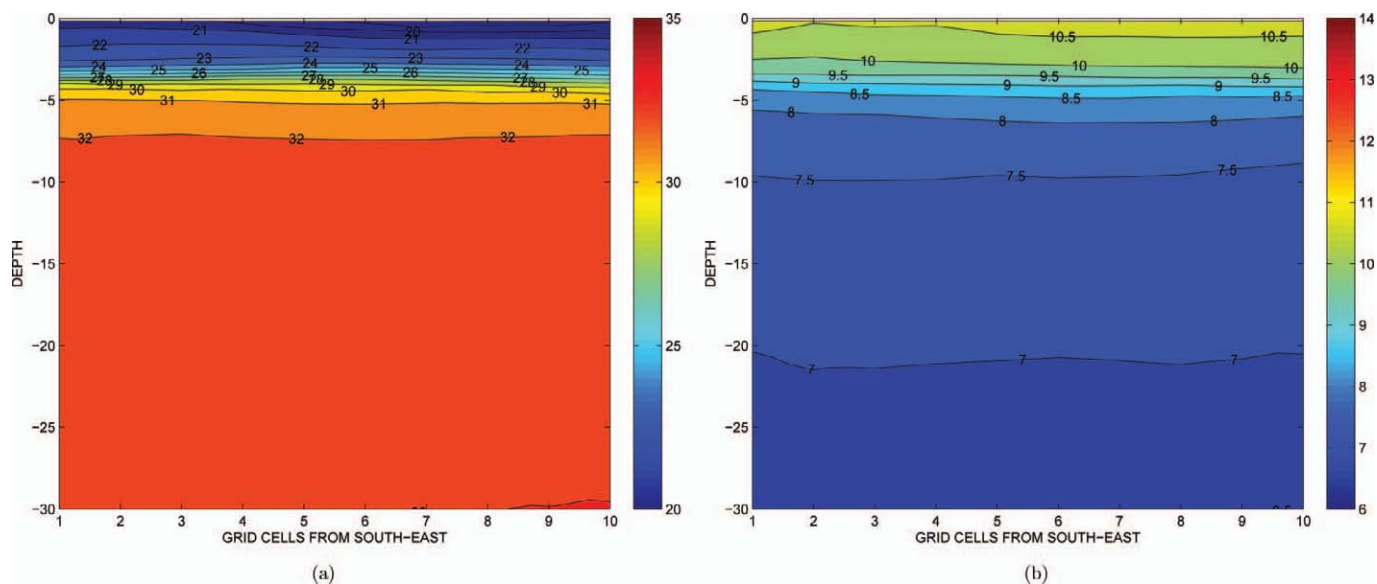


FIGURE 6. Modeled patterns of (a) salinity and (b) temperature with respect to depth across the mouth of Leirfjorden on July 14, 2007.

the terminal velocity was computed by Stokes' or Dallavalle's formula. Then, the exact stationary solution of the convection diffusion equation was calculated as a function of eddy diffusivity and terminal velocity. When model results were available, the modeled eddy diffusivity was used; otherwise, constant eddy diffusivity was computed from the wind speed.

RESULTS

Model Evaluation

In July 2007 a hydrographic survey was performed in Sørfolda, which consisted of 31 conductivity–temperature–

depth (CTD) stations, including several cross-sections. This is the only adequate mapping available from a season with relatively high river runoff, suitable for evaluating the hydrographic structure in the model. Therefore, the circulation model was run for 2007 to compare the model results against observations.

The salinity section from the model is shown in Figure 6a and that from observations in Figure 7a. The location of the cross-section was at the mouth of Leirfjorden where it enters the main part of Sørfolda. Both measurements and model indicated a low-salinity surface layer restricted to the upper 5 m. The surface salinity was lower in the model results (~ 20) compared

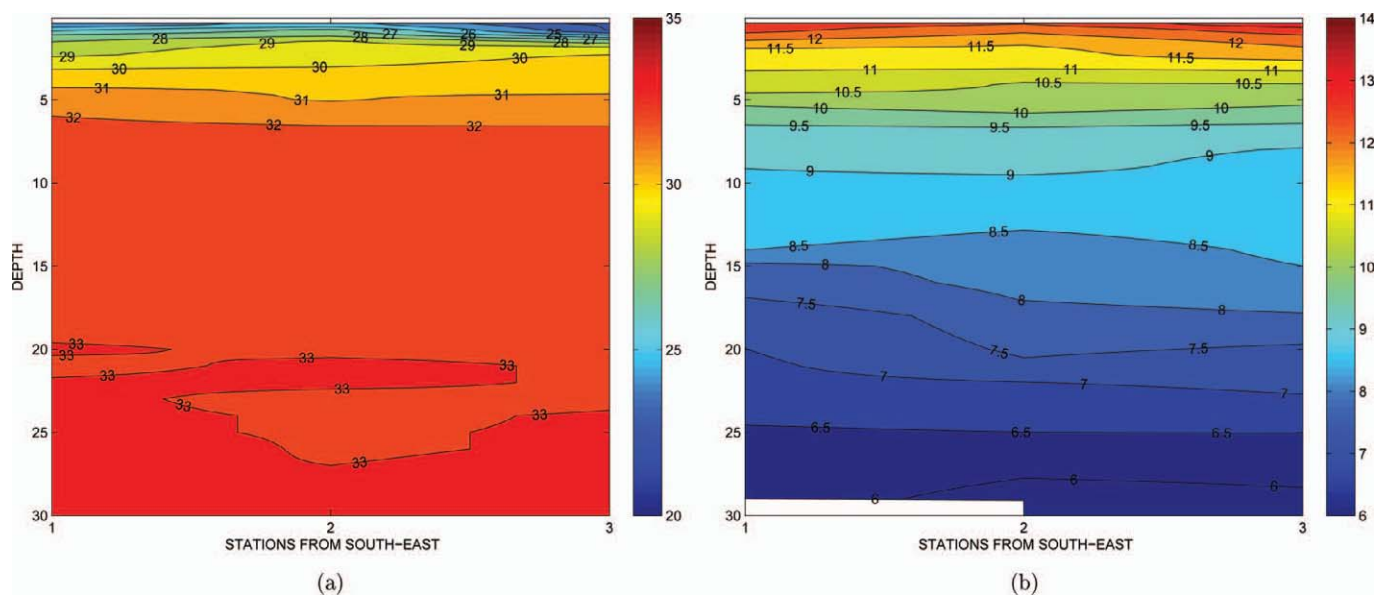


FIGURE 7. Observed patterns of (a) salinity and (b) temperature with respect to depth across the mouth of Leirfjorden on July 14, 2007.

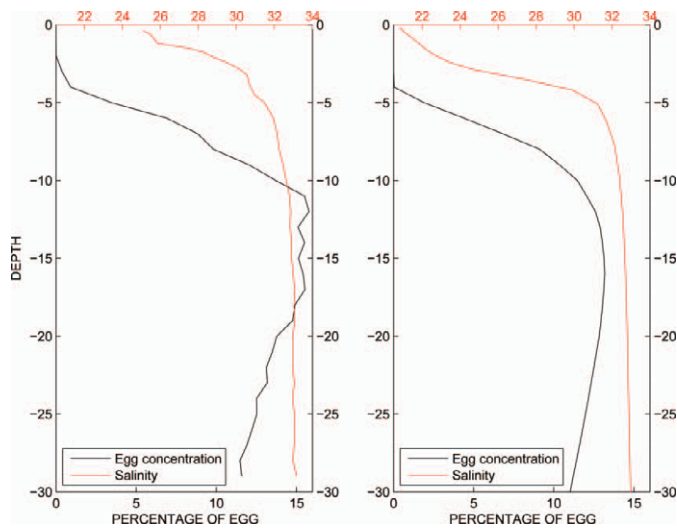


FIGURE 8. Observed (left panel) and modeled (right panel) salinity profiles on July 14, 2007, at the position marked with a red star in Figure 1, together with the egg concentrations calculated from those profiles.

with the observations (~ 25). The vertical positions of the 31 and 32 isohaline layers were similar between the cases, at about 4–5 m and 6–7 m depth, respectively. This observation implies that the thickness of the low-salinity layer was similar between the model and the observations. This pattern was present for all the cross-sections available from this survey. Figures 6b and 7b show the corresponding temperature section as viewed in Figures 6a and 7a. The model results showed a distinct thermocline at about 5 m depth, while the observations indicate a smoother transition from the warm surface toward the cold water

below. The surface temperature was higher in the observations ($\sim 14^\circ\text{C}$) than in the model ($\sim 11^\circ\text{C}$). The highest temperatures in the observations were restricted to the upper 2–3 m.

In Figure 8, one single salinity profile was chosen from the position in Sørfolda marked with a red star in Figure 1. The left panel shows the observed salinity profile, and the right panel shows the corresponding values from the model, both from July 14, 2007. The major difference between the profiles was again the surface salinity, being 21 in the model compared with 25 in the observations. The black lines in Figure 8 are the calculated vertical distributions of cod eggs based on the buoyancy distribution shown in Figure 5 and the observed and modeled salinity profiles, respectively. Both panels show strong similarities in the vertical distribution of the eggs. Almost no eggs were located above 5 m, and the maximum egg concentration was between 10 and 20 m, declining below 20 m for both cases. The pattern at this station was representative of all the stations sampled during this survey. It also demonstrated that the vertical distribution of eggs can be realistically reproduced by the model system.

Hydrography and Circulation

The daily mean salinity at 1 m depth on April 25 in 1960 and 1989 is shown in Figure 9. In late April, the river runoff is relatively high, and the period covers the main part of the cod spawning period. Both years show progressively increasing salinity from head to mouth in all fjord branches. The results showed a gradient across the fjord in Sørfolda, but to a much lesser degree in Nordfolda. The cross-fjord difference was more pronounced in 1989 than in 1960. The salinity was generally higher in 1960 compared with 1989. In April 1989, there was a pronounced difference between Sørfolda and Nordfolda, with

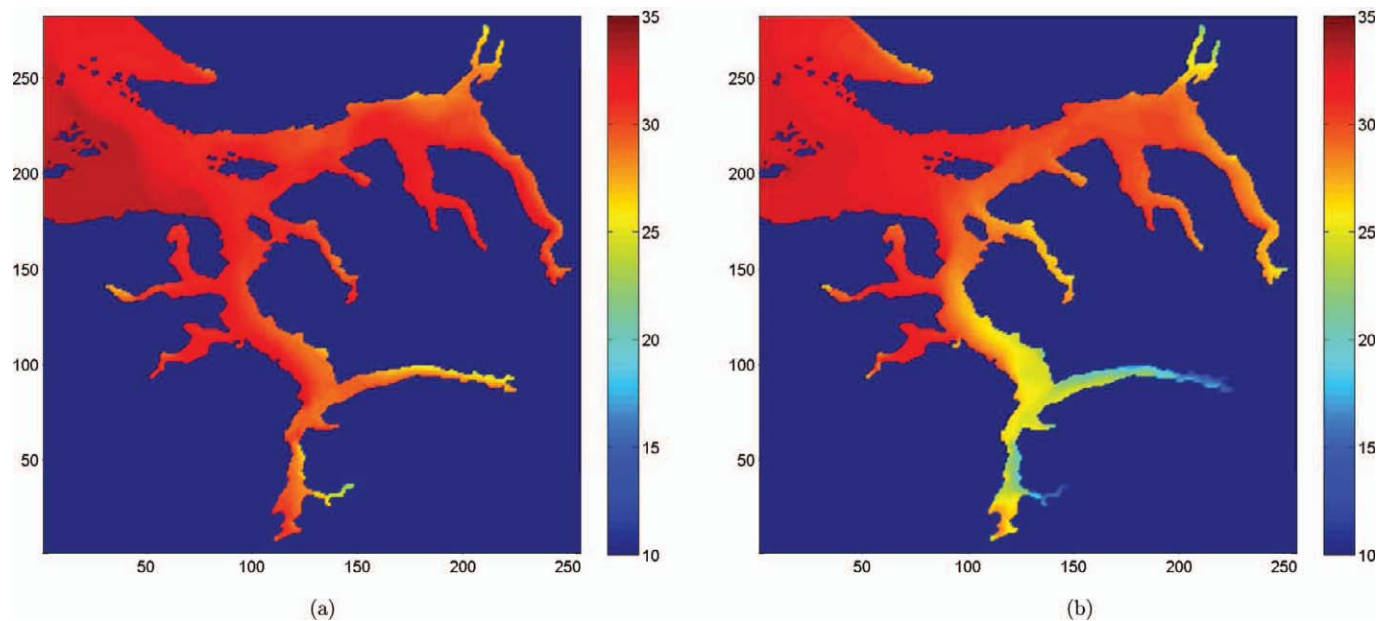


FIGURE 9. Modeled daily mean salinity at 1 m depth on April 25 in (a) 1960 and (b) 1989.

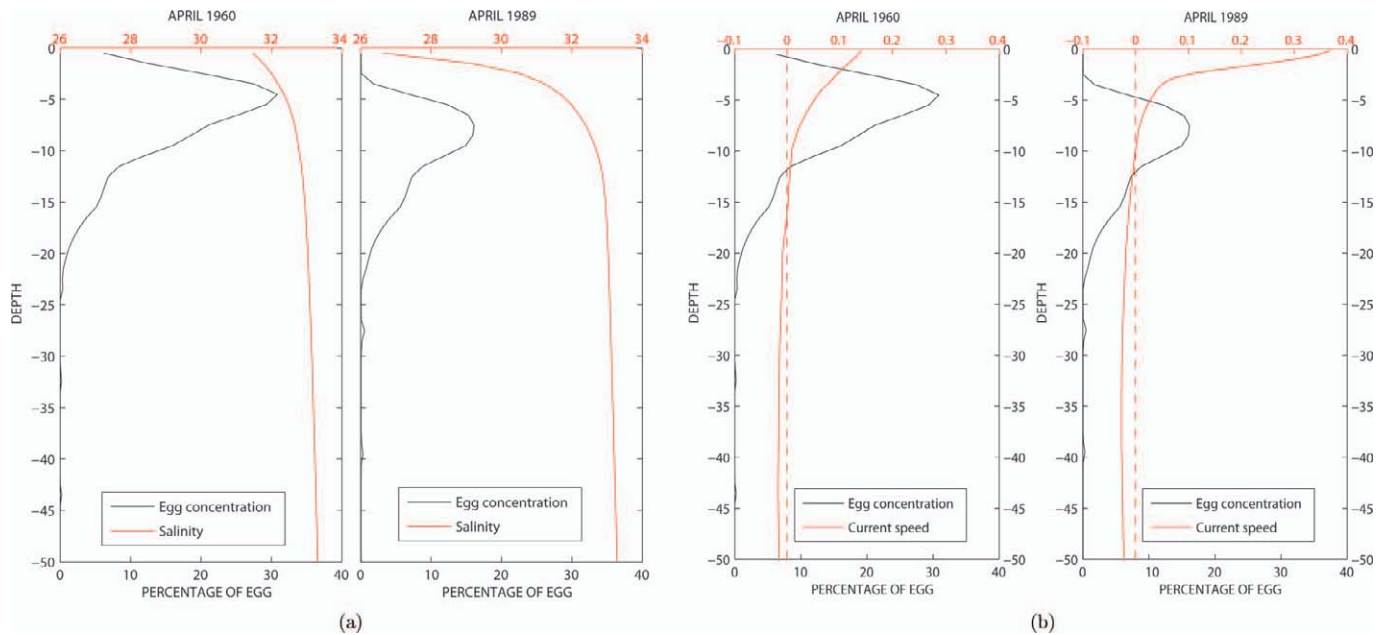


FIGURE 10. Vertical distributions of cod eggs according to (a) the modeled salinity profiles and (b) the modeled along-fjord current speeds (positive direction towards the ocean) in April 1960 and April 1989 at the position marked with a red star in Figure 1.

the lowest salinity present in Sørfolda, reflecting the large difference in freshwater input between Sørfolda and Nordfolda.

The low-salinity surface layer, which covers a large part of the fjord system, is accompanied by strong currents in the upper layer directed out of the fjord. These are characteristics of the estuarine circulation and describe the general pattern in the fjord system. When the river runoff is low at the beginning of the ice melt season, the difference between Sørfolda and Nordfolda is apparent but not very strong. As the freshwater discharge increases during spring, the difference becomes more pronounced and was always more distinct in 1989.

Transport of Eggs as a Function of Buoyancy

The vertical distribution of cod eggs according to the local salinity profile is shown in Figure 10a as monthly averages from April 1960 (left panel) and 1989 (right panel). The main difference between 1960 and 1989 was the surface salinity, which was highest in the cold and dry year of 1960. Some cod eggs were located at the surface in 1960, while the maximum concentration was at 5 m depth. However, in the warm and wet year of 1989, all the eggs were positioned below 2.5 m, with the highest concentration occurring around 7.5 m depth. The vertical egg distribution along with the current profile is shown in Figure 10b. The outflowing surface layer was about 20 m deep in 1960, compared with 10 m in 1989. A greater portion of eggs was thus situated within the outgoing surface layer in 1960 compared with 1989.

The trajectories from a random selection of eggs in buoyancy group 2 are shown in Figure 11. The eggs were released on

April 15 in 1960 and 1989 and advected for 21 d, and the black boxes indicate the four different release positions. The trajectories during 1960 covered the entire fjord system. The spawning areas of Vinkfjord and Sørfolda showed large dispersals of eggs, both within the fjord branches and out through the mouth. The eggs released in Leirfjorden and Nordfolda remained within a small radius from their initial position. In 1989, only eggs from Vinkfjord showed large dispersion; all other spawning areas had a high degree of retention (Figure 11b).

The main results are summarized in Tables 1 and 2, which show the mean distance traveled by cod eggs from spawning areas after 21 d of advection, with the SD values in parentheses. The results between 1960 and 1989 as a function of the buoyancy group, spawning time, and spawning area are compared in Table 1, while results are divided in Table 2 into spawning times as a function of the buoyancy group and spawning area. The results demonstrate that the SD was comparable to the mean value in all cases, indicating high variability. Buoyancy group 1, which included the lightest eggs, was subjected to the longest transport during both years and all spawning times. Heavier eggs were transported shorter distances. This pattern was evident during both 1960 and 1989 (Table 1). A two-way analysis of variance (ANOVA) method showed that the 2 years were significantly different at a 95% confidence level after accounting for buoyancy variations ($P = 0.0418$) but not significantly different when including spawning time ($P = 0.1153$) or spawning area ($P = 0.3895$). The results indicate that seasonal variations ($P = 0.0181$) in spawning were more important for the dispersal of cod eggs than were interannual variations. The largest

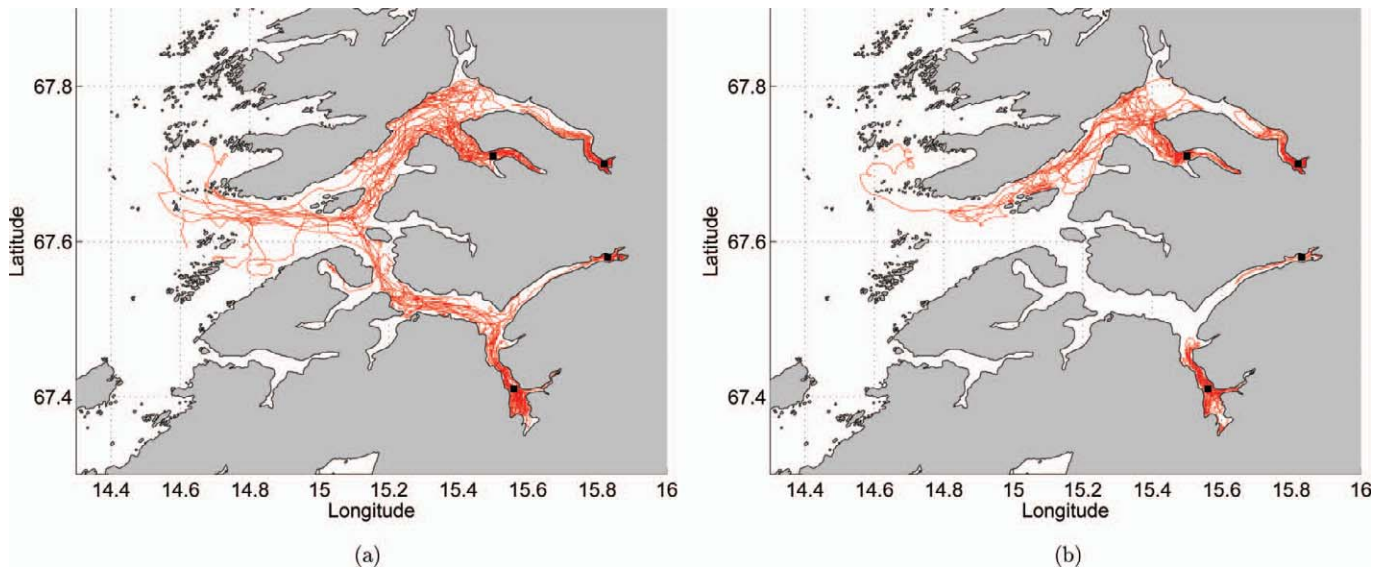


FIGURE 11. Trajectories of a random selection of eggs in buoyancy group 2 released on April 15 and transported for 21 d in (a) 1960 and (b) 1989. The black boxes indicate spawning areas.

change in transport occurred between April 1 and May 1. Also, the spawning area was an important variable controlling dispersal ($P = 0.0081$). In particular, spawning in Vinkfjord differed significantly from that in the other spawning areas.

The data in Table 2 are averages of those for 1960 and 1989 and focus on seasonal variations as a function of the buoyancy group and spawning area. The two-way ANOVA analyses show that both spawning time ($P = 0.0029$) and buoyancy ($P = 0.0002$) were important factors affecting the spreading of cod eggs. The two first spawning times showed a larger spread than the final two. All of the buoyancy groups except group 5 were significantly different from each other. When combining spawning time with spawning area, the sea-

sonality ($P = 0.1135$) was no longer important; only location remained important ($P = 0.0007$). The Vinkfjord spawning area significantly differed from all others. If Vinkfjord was removed from the analyses, seasonality was again important ($P = 0.0103$) together with location ($P = 0.015$). This indicates that changes during the spawning season were not important in Vinkfjord but were significant in Sørfolda, Leirfjorden, and Nordfolda. The seasonal changes were evident as differences between the two first spawning times and the last two. Without Vinkfjord, a significant difference was also apparent between the spawning areas in Sørfolda and Nordfolda.

DISCUSSION

Model Evaluation

The model reproduced the strong stratification characteristic of Norwegian fjords with considerable river runoff. The thickness of the low-salinity surface layer showed good correspondence between the model and observations. This suggests that the river forcing in the model setup was realistic and that the model captured the upper water circulation well. Warner et al. (2005b) used ROMS in a shallow (15 m) estuary and showed good agreement between the model results and observations.

The surface salinity was generally lower in the model than in the observations. Both unresolved vertical mixing and coarse boundary conditions might have contributed to this discrepancy. Small-scale mixing originating from internal waves and complex topography were not well represented and could have made a considerable contribution to the overall vertical salinity structure. The Mellor–Yamada 2.5 closure scheme was used in this study, but several earlier studies have shown that the

TABLE 1. Mean distance [km] travelled by cod eggs from spawning areas for 21 days, standard deviation in parenthesis, comparing 1960 and 1989.

	1960		1989	
Buoyancy Gr 1	13.01	(12.45)	10.12	(11.37)
Buoyancy Gr 2	10.31	(10.83)	9.24	(10.80)
Buoyancy Gr 3	7.82	(9.05)	6.46	(8.43)
Buoyancy Gr 4	4.74	(5.92)	3.71	(3.79)
Buoyancy Gr 5	5.01	(4.70)	4.83	(4.03)
15 March	7.69	(8.02)	7.56	(9.75)
1 April	10.25	(11.24)	8.73	(12.04)
15 April	7.90	(11.04)	5.89	(6.22)
1 May	4.81	(6.81)	4.47	(6.04)
Sørfolda	2.82	(7.29)	1.94	(5.49)
Leirfjorden	4.92	(6.27)	3.36	(4.33)
Nordfolda	4.27	(6.58)	5.27	(7.33)
Vinkfjord	10.19	(9.38)	9.44	(9.67)

TABLE 2. Mean distance [km] travelled by cod eggs from spawning areas for 21 days, standard deviation in parenthesis, as a function of spawning time.

	15 March		1 April		15 April		1 May	
Buoyancy Gr 1	13.46	(11.58)	15.08	(13.70)	9.07	(11.31)	8.65	(11.05)
Buoyancy Gr 2	10.85	(10.63)	14.62	(13.89)	8.25	(10.79)	5.38	(8.00)
Buoyancy Gr 3	7.15	(8.45)	10.08	(11.98)	6.76	(8.88)	4.57	(5.65)
Buoyancy Gr 4	4.48	(5.12)	4.40	(5.39)	4.46	(5.28)	3.58	(3.64)
Buoyancy Gr 5	6.92	(5.41)	5.24	(4.85)	4.29	(3.91)	3.23	(3.30)
Sørfolda	2.78	(7.21)	3.57	(9.40)	1.83	(5.17)	1.34	(3.77)
Leirfjorden	6.44	(8.46)	4.91	(6.34)	2.87	(4.07)	2.34	(2.32)
Nordfolda	5.63	(7.29)	7.23	(10.20)	3.28	(4.99)	3.30	(5.34)
Vinkfjord	7.48	(7.73)	11.78	(11.11)	12.36	(11.10)	7.64	(8.17)

results are insensitive to different closure schemes (Li et al. 2005; Warner et al. 2005a, 2005b). Coarse boundary conditions with low temporal resolution will probably affect the circulation in the intermediate layer. Nonlocal wind aligned with the coast creates upwelling and downwelling at the coast. Density variations at the coast can cause large volume fluxes out of or into the fjord (Asplin et al. 1999). Skogen et al. (2009) found that the exchange of water between the Hardangerfjord and the coast was the most important factor providing nutrients to the system. Instabilities and mixing will then be created at the interface between the intermediate layer and the upper layer. Li et al. (2005) also reported that ROMS was less accurate under conditions of strong stratification.

The difference between the observed temperature and the modeled temperature was linked to the strong model stratification. The model displayed a two-layer structure, while the observations continuously decrease from high temperatures at the surface downward. The strong halocline in the model prevented the heat input at the surface from penetrating deeper and distributed the heat equally in the surface layer.

The wind forcing from ERA-40, with 1° resolution, did not capture the complex wind structure in this fjord system. A comparison between wind from ERA-40 and from observations from the Norwegian Meteorological Institute (<http://met.no>) is shown in Figure 12. The observations are from Skrova, a coastal station located in Vestfjorden and Kobbelv, a fjord station located at the head of Leirfjorden. The figure shows the frequency of wind speed, ranging from 1 to 15 m/s, during the period from March 1 until May 31, 1989. The observations from Skrova were similar to ERA-40, indicating that the most common wind speeds were between 2 and 6 m/s for both data sets. Stronger winds (8–12 m/s) were also represented in both time series. At the fjord station the most common wind speeds were between 0 and 2 m/s, and no observations were above 7 m/s. The wind forcing from ERA-40 had no spatial variability between these two sites. This comparison illustrates that the wind forcing from ERA-40 represents the coastal area well, but performs poorly inside the fjord. Steep and complex topography surrounding the fjord causes local variations in both wind speed and direction, which are not resolved by the forcing field. The total effect of

these processes is not known. Some places will experience lee effects and others strong jet effects. Svendsen and Thompson (1978) recognized that the wind stress inside the fjord is not correlated with the wind stress at the coast. The steep mountain surrounding the fjord will steer the wind along the fjord axis, causing the wind to be directed straight into or out of the fjord (Svendsen 1995).

The difference in surface salinity between the model and the observations did not affect the vertical distribution of cod eggs (Figure 8) because the neutral buoyancy of the eggs was considerably higher than both the observed and modeled surface salinities. Although the model was not able to match the observed surface salinity exactly, the salinity structure below the surface layer corresponded well with the observations. The corresponding vertical distribution of cod eggs based on the observations was well reproduced by the model. This demonstrates that the model is suitable for studying the horizontal transport of cod eggs as a function of vertical distribution. Stenevik et al.

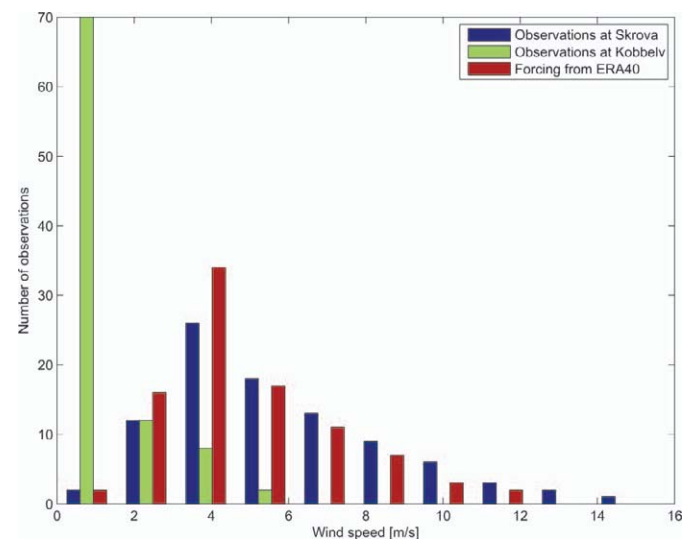


FIGURE 12. Wind speeds at Skrova and Kobbelv comparing observations from the Norwegian Meteorological Institute (<http://met.no>) and the forcing used in the model run from ERA-40.

(2008) showed that the local salinity profile is the most important factor controlling the vertical distribution of coastal cod eggs.

Hydrography and Circulation

The model results show that Nordfolda was generally more saline than Sørfolda (Figure 9). This difference is caused mainly by higher freshwater input to Sørfolda. When the total river runoff is low, this difference is present but not as pronounced. Aure and Pettersen (2004) also observed the difference between the fjords during the fall, showing that this is a general feature.

The surface layer was shallower and had lower salinity in 1989 than in 1960 (Figure 10a, b). The most significant change in the model forcing between the years is the river runoff. Much energy is needed to mix all of this freshwater downward, so it remains at the surface, forming a thin fresh layer. Wind stress is an important factor that provides energy for mixing at the surface (Klinck et al. 1981; Leth 1995; Gibbs et al. 2000). Svendsen and Thompson (1978) argue that strong stratification in a fjord can trap the wind-stress response at the near-surface layer. The wind forcing in the model had little variability between the years, implying that the modeled difference in surface layer thickness was caused by the river runoff.

Transport of Eggs as a Function of Buoyancy

Eggs from the Norwegian coastal cod spawned inside Sørfolda and Nordfolda attained a subsurface vertical distribution, avoiding the surface (Figure 10a, b). The vertical position of eggs is controlled by the specific gravity of eggs relative to the local salinity structure. By “choosing” to spawn in an estuarine environment with low surface salinity, the coastal cod affect the vertical distribution of their eggs. This spawning strategy causes local retention of eggs within the fjord system (Figure 11). If the coastal cod spawn outside the fjord in the marine environment with higher surface salinities, their eggs would attain a pelagic distribution and would be subjected to large dispersal with the Norwegian Coastal Current (Sundby 1983). Vestfjorden, just outside the fjord system, is the main spawning area for the Arcto-Norwegian cod that spread their eggs and larvae over large areas (Vikebø et al. 2005). These model results support the hypothesis by Asplin et al. (1999) that species can adapt their spawning depth and buoyancy of eggs to reduce dispersal of early life stages. Several studies have shown evidence for retention of cod eggs in Norwegian fjords (Salvanes et al. 2004; Espeland et al. 2007; Jorde et al. 2007; Knutsen et al. 2007) but few have explored the underlying physical mechanism. Genetic research has confirmed the existence of several genetically differentiated coastal cod broodstocks (Jørstad 1984; Pogson and Fevolden 2003; Dahle et al. 2006; Øresland and André 2008; Stransky et al. 2008). For species with long egg and larval stages the potential for offshore transport is large (Cowen et al. 2000), suggesting that persistent physical mechanisms that cause retention are necessary to maintain genetic separation.

Strong retention mechanisms for eggs within a fjord support the indications that the genetic difference between fjord populations is larger than the difference between a fjord population and a coastal population (Pogson and Fevolden 2003). The model results showed that most of the eggs were retained within the fjord, and a small portion was transported out, but no eggs were seen drifting back into the fjord. Only the lightest eggs situated in the low-salinity outflowing layer were transported out of the fjord. As long as they are transported at this depth, the currents are directed out of most fjords. This indicates a low connectivity between fjords during the egg stage. However, frequent shifts between northerly and southerly winds on the coast that cause up- and downwelling could counteract this mechanism and enhance genetic exchange between neighboring fjords (Asplin et al. 1999). Bucklin et al. (2000) found that the genetic structure of plankton between fjords depend on species behavior. Passively drifting species (e.g., the copepod *Calanus finmarchicus*) show no significant genetic differentiation between fjord populations, while resident species (e.g., the copepod *Acartia clausi*) show a marked difference.

Interannual variations in river runoff can cause small changes in the vertical distribution of cod eggs and larger changes in the vertical current structure (Figure 10b). The cod eggs attained subsurface distributions in both 1960 and 1989, which were shifted 2–3 m down in 1989. This change was mainly due to lower salinities in the surface layer in 1989. This difference was present toward the end of the spawning period (late April and May) when the ice melt season had started. The shift in the vertical distribution together with a shallower outflowing layer caused stronger retention during this period for the lightest buoyancy egg groups during 1989 (Figure 11). For the heavier fractions of eggs, retention occurred during both years. Early in the spawning season (late March and early April) the pattern of retention was the opposite, and the strongest retention occurred in 1960. One explanation for this difference is a shift in the onset of the ice melt season. Before ice melting starts, the potential for offshore transport is small; this explains the high egg retention that occurred during the early spawning season in 1960. When the melting starts and the estuarine circulation develops, the possibility for advection out of the fjord increases. Consequently, there was an increased loss of light eggs during the late part of the spawning season in 1960 and during the early part of the spawning season in 1989. The river runoff demonstrated that the melting started about 1 month earlier in the warm year, 1989, than it did in the cold year, 1960. High river runoff during the period of ice melt produces a thin surface layer with low salinities. Most of the eggs are then negatively buoyant in the surface layer and sink below the strong outflow. This is the reason for the increased retention at the end of the spawning period in 1989. These results indicate that there is a “window” of about 1 month during which a small portion of the lightest cod eggs is able to leave the fjord system. This “window” is open before the estuarine circulation is well established and coincided with relatively high surface salinities. The timing for

opening this “window” can change between years as a function of precipitation and temperature, which both contribute to the river runoff. The exact spawning time for coastal cod is not well known but probably continues for several months during spring (Kjesbu 1988). A possible match between maximized spawning and the “window” of leakage could have a negative effect on local recruitment. Otterå et al. (2006) showed differences in spawning time between cod broodstocks from four regions in Norway kept under identical conditions. This indicates that the subpopulations of cod might have adapted their spawning behavior to the local environment.

Though this study included two different and extreme years, the total difference in retention was not large. The major difference was the timing of the leakage. This suggests that the retention mechanism is robust within the observed range. The field data from 2007 (Figure 2), which was a year of medium river runoff, also indicate retention of cod eggs in the inner part of the fjord system. Unfortunately, the ship was not able to enter the inner part of Nordfolda where the model indicated retention of eggs. The model results show that the light eggs had a higher probability of being transported offshore than were the heavier eggs (Table 1). Progressively heavier eggs were transported decreasing distances until they reached buoyancy group 4 (32.7–33.4), after which increased buoyancy no longer had an effect. This might be the reason why the coastal cod have developed eggs that are heavier than those of the Arcto-Norwegian cod (Kjesbu et al. 1992), which spawn just outside of the fjord system. When the light eggs are transported out of the fjord system, they are probably lost from the local population unless the pelagic juvenile cod actively migrate back into the ecosystem where they were spawned. Only heavy eggs that remain inside the fjord, in the vicinity of the spawning ground, are likely to contribute to the local recruitment.

The cod eggs released in Vinkfjord were spread out and covered a larger area than those in all the other spawning grounds. This feature was evident for all buoyancy groups and at all times (Tables 1 and 2). In Figure 1, Vinkfjord is marked as a spawning area, but not as a nursery area. This background information supports the results provided by the model, implying that this was not an artifact created by the model. One reason for the strong dispersal from Vinkfjord might be the low river input to the fjord branch. As described earlier, the river runoff affects the vertical distribution of cod eggs and enhances retention. If this mechanism is not present in Vinkfjord, the dispersal is larger than elsewhere in the fjord system. After removing the Vinkfjord spawning area from the ANOVA analysis, a difference between Nordfolda and Sørfolda became evident. This difference was also related to the river runoff, which can be seen in Figure 4. The lower panel shows the smaller amount of freshwater entering Nordfolda than Sørfolda, and also starting earlier during the winter. This explains the weaker retention in Nordfolda and the large dispersal early in the spawning season.

Transport of anchovy *Engraulis capensis* eggs as a function of buoyancy has been studied in upwelling systems with both

ROMS and individual-based models by Parada et al. (2003) and Brochier et al. (2008). They show that the buoyancy of eggs, which affects the vertical distribution, is important for determining retention even though the egg stage only lasts 1–4 d. An upwelling system is similar to an estuarine system regarding the vertical current structure. Strong currents at the surface are directed away from the coast, and below the currents are directed toward the coast. The vertical positioning in relation to this strong vertical gradient is important for determining retention success (Sundby et al. 2001). North and Houde (2006) investigated retention of white perch *Morone americana* and striped bass *M. saxatilis* early life stages in Chesapeake Bay during 2 years of different freshwater discharge. In this system, the larval recruitment is strongly linked to the physics of the estuarine turbidity maximum (ETM) (North and Houde 2001). During a year with discharge below average, negative consequences were observed for fish early-stage retention and survival. This is an example of fish that take advantage of physical phenomena and increase local retention and recruitment. Most of the modeling simulations performed to explore retention mechanisms have been applied to fish with short egg-stage durations (1–4 d). Ouellet (1997) sampled cod eggs in the Gulf of St. Lawrence and found that egg development at 0°C lasted for approximately 40 d. Temperature strongly affects the cod egg stage duration (Page and Frank 1989) and causes egg stages to be long at high latitudes such as in northern Norway. Werner et al. (1993) investigated the retention of cod early life stages on Georges Bank with the egg-stage duration of 20 d. Their results indicate that larvae located within the surface Ekman layer were subjected to offshore transport and loss from Georges Bank. The retention increases strongly when spawning takes place at shallow waters northeast of the bank. The work by Werner et al. (1993) is similar to what has been presented here regarding specific spawning behavior that can enhance the retention of cod eggs with long egg-stage durations.

The interaction between egg buoyancy and the physical environment is an important mechanism determining the dispersal and local recruitment of Norwegian coastal cod. Observations show that the physical environment is changing, going from a cold and dry climate around 1960–1970 toward a warm and wet climate from about 1990 onwards. This trend is expected to continue as a result of the observed and predicted global warming. Regional downscaling of climate models together with hydrological models show an increase in the annual mean discharge between 10% and 20% for the period 2071–2100 compared with 1961–1990 for a specific river in Sørfolda (Roald et al. 2006). In particular, during the spring season, the increase reached 50–70%, varying with different projections of greenhouse gas emission and climate model used. The results from our study showed that the highest probability for leakage of cod eggs was during a limited time period linked to the onset of the melting season, which is dependent on precipitation and temperature in any particular year. In the warm and wet year of 1989, this “window” of leakage opened early in the spawning season.

Because the climate is continuing to get warmer and wetter this “window” is moving further into the early part of the spring season. Assuming that the spawning period for coastal cod stays constant, the “window” will have closed by the time the spawning starts, and the quantity of eggs transported out of the system will decrease. In this way, climate might enhance the genetic differentiation between coastal subpopulations. However, high temperatures are accompanied by enhanced low-pressure activity in northern Norway, and climate models predict stronger and more frequent passages of low-pressure systems. Strong winds along the coast will increase mixing and might enhance the frequency of upwelling events with the potential to transport the upper layer out of the fjord (Asplin et al. 1999). These processes might increase the offshore transport of early life stages, meaning that the total effect of climate change is not apparent.

Even though the retention of cod eggs within the fjord system is strong, some light eggs are subjected to offshore transport for a limited time period. The fate of these eggs is unknown. Will they survive and contribute to the Arcto-Norwegian cod population? Will they be transported to unfavorable areas and die? Or will they actively migrate back to their spawning habitats as pelagic juveniles or adults? If these eggs contribute to the recruitment of the Arcto-Norwegian cod population, this offshore transport will counteract the genetic differentiation between the fjord and the oceanic Atlantic cod stock. Moreover, it is important to emphasize that the transport of eggs from Arcto-Norwegian cod spawning areas into the Norwegian coastal cod areas is much less likely to occur. Therefore, a potential gene flow will be directed only one way, from the Norwegian coastal cod populations to the Arcto-Norwegian cod population. This gene flow might change in a future warmer climate and possibly enhance the genetic differentiation.

ACKNOWLEDGMENTS

We acknowledge Ingeborg Kleivane at The Norwegian Water Resources and Energy Directorate (NVE) for providing hydrological data, and Gyda Lorås at the Norwegian Directorate of Fisheries for local information about spawning and nursery areas. We also thank Karen Gjertsen for editing the figures and Lars Asplin for valuable discussion. This work received financial support from the Bjercknes Centre for Climate Research. We thank two anonymous reviewers for constructive comments that helped to significantly improve the manuscript.

REFERENCES

- Ådlandsvik, B. 2000. VertEgg: a toolbox for simulation of vertical distribution of fish eggs. Institute of Marine Research, Bergen, Norway.
- Ådlandsvik, B., and S. Sundby. 1994. Modeling the transport of cod larvae from the Lofoten area. ICES (International Council for the Exploration of the Sea) Marine Science Symposium 198:379–392.
- Albretsen, J., and L. P. Røed. 2010. Decadal long simulations of mesoscale structures in the northern North Sea/ Skagerrak using two ocean models. *Ocean Dynamics* 60:933–935.
- Asplin, L., A. G. V. Salvanes, and J. B. Kristoffersen. 1999. Nonlocal wind-driven fjord-coast advection and its potential effect on plankton and fish recruitment. *Fisheries Oceanography* 8:255–263.
- Aure, J., and R. Pettersen. 2004. Miljøundersøkelser i Norske fjorder 1975–2000. [Environmental investigations in Norwegian fjords 1975–2000.] *Fisken og Havet* 8:1–176. (In Norwegian).
- Bergstad, O. A., T. Jørgensen, and O. Dragesund. 1987. Life history and ecology of the gadoid resources of the Barents Sea. *Fisheries Research* 5:199–161.
- Brochier, T., C. Lett, J. Tam, P. Fréon, R. Colas, and P. Ayón. 2008. An individual-based model study of anchovy early life history in the northern Humboldt Current system. *Progress in Oceanography* 79:313–325.
- Bucklin, A., S. Kaartvedt, M. Guarneri, and U. Goswami. 2000. Population genetics of drifting (*Calanus* spp.) and resident (*Acartia clausi*) plankton in Norwegian fjords. *Journal of Plankton Research* 22:1237–1251.
- Budgell, W. P. 2005. Numerical simulation of ice-ocean variability in the Barents Sea region towards dynamical downscaling. *Ocean Dynamics* 55:370–387.
- Cowen, R. K., K. M. M. Lwiza, S. Sponaugle, C. B. Paris, and D. B. Olson. 2000. Connectivity of marine populations: open or closed? *Science (Washington, D.C.)* 287:857–859.
- Dahle, G., K. E. Jørstad, H. E. Rusaas, and H. Otterå. 2006. Genetic characteristics of broodstock collected from four Norwegian coastal cod (*Gadus morhua*) populations. *ICES (International Council for the Exploration of the Sea) Journal of Marine Science* 63:209–215.
- Dyer, K. R. 1997. *Estuaries: a physical introduction*, 2nd edition. Wiley, New York.
- Ellertsen, B., P. Fossum, P. Solemdal, and S. Sundby. 1989. Relation between temperature and survival of eggs and first-feeding larvae of northeast Arctic cod (*Gadus morhua* L.). *Rapports et Proces-Verbaux des Reunions Conseil International pour l'Exploration de la Mer* 191:209–219.
- Engedahl, E., B. Ådlandsvik, and E. A. Martinsen. 1998. Production of monthly mean climatology archives for the Nordic Seas. *Journal of Marine Systems* 14:1–26.
- Espeland, S. H., A. F. Gundersen, E. M. Olsen, H. Knutsen, J. Gjøsaeter, and N. C. Stenseth. 2007. Home range and elevated egg densities within an inshore spawning ground of coastal cod. *ICES (International Council for the Exploration of the Sea) Journal of Marine Science* 64:920–928.
- Farmer, D. M., and H. J. Freeland. 1983. The physical oceanography of fjords. *Progress in Oceanography* 12:147–220.
- Fridgeirsson, E. 1978. Embryonic development of five species of gadoid fishes in Icelandic waters. *Rit Fiskideildar* 5:1–68.
- Gammelsrød, T., Ø. Leikvin, V. Lien, W. P. Budgell, H. Loeng, and W. Malowski. 2009. Mass and heat transports in the NE Barents Sea: observations and models. *Journal of Marine Systems* 75:56–69.
- Gibbs, M. T., M. J. Bowman, and D. E. Dietrich. 2000. Maintenance of near-surface stratification in Doubtful Sound, a New Zealand fjord. *Estuarine, Coastal, and Shelf Science* 51:683–704.
- Haidvogel, D. B., H. Arango, W. P. Budgell, B. D. Cornuelle, E. Curchitser, E. Di Lorenzo, K. Fennel, W. R. Geyer, A. J. Hermann, L. Lanerolle, J. Levin, J. C. McWilliams, A. J. Miller, A. M. Moore, T. M. Powell, A. F. Shchepetkin, C. R. Sherwood, R. P. Signell, J. C. Warner, and J. Wilkin. 2008. Ocean forecasting in terrain-following coordinates: formulation and skill assessment of the regional ocean modeling system. *Journal of Computational Physics* 227:3595–3624.
- Han, W., A. M. Moore, J. Levin, B. Zhang, H. G. Arango, E. Curchitser, E. Di Lorenzo, A. L. Gordon, and J. Lin. 2009. Seasonal surface ocean circulation and dynamics in the Philippine Archipelago region during 2004–2008. *Dynamics of Atmospheres and Oceans* 47:114–137.
- Hermann, A. J., S. Hinckley, E. L. Dobbins, D. B. Haidvogel, N. A. Bond, C. Mordy, N. Kachel, and P. J. Stabeno. 2009. Quantifying cross-shelf and vertical nutrient flux in the Coastal Gulf of Alaska with a spatially nested, coupled biophysical model. *Deep-Sea Research Part II: Topical Studies in Oceanography* 56:2474–2486.
- ICES (International Council for the Exploration of the Sea). 2009. Report of the Arctic fisheries working group. ICES, C.M. 2009/ACOM:02, Copenhagen.

- Jakobsen, T. 1987. Coastal cod in northern Norway. *Fisheries Research* 5:223–234.
- Jorde, P. E., H. Knutsen, S. H. Espeland, and N. C. Stenseth. 2007. Spatial scale of genetic structuring in coastal cod *Gadus morhua* and geographic extent of local populations. *Marine Ecology Progress Series* 343:229–237.
- Jørstad, K. 1984. Genetic analyses of cod in northern Norway. Pages 745–760 in E. Dahl, D. S. Danielsen, E. Moksness, and P. Solemdal, editors. The propagation of cod (*Gadus morhua* L.). Institute of Marine Research Biological Station, Arendal, Norway.
- Kjesbu, O. S. 1988. Fecundity and maturity of cod. ICES (International Council for the Exploration of the Sea), C.M.1988/G:28, Copenhagen.
- Kjesbu, O. S., H. Kryvi, S. Sundby, and P. Solemdal. 1992. Buoyancy variations in eggs of Atlantic cod in relation to chorion thickness and egg size: theory and observations. *Journal of Fish Biology* 41:581–599.
- Klinck, J. M., J. J. O'Brien, and H. Svendsen. 1981. A simple model of fjord and coastal circulation interaction. *Journal of Physical Oceanography* 11:1612–1626.
- Knutsen, H., P. E. Jorde, C. Andre, and N. C. Stenseth. 2003. Fine-scaled geographical population structuring in a highly mobile marine species: the Atlantic cod. *Molecular Ecology* 12:385–394.
- Knutsen, H., E. M. Olsen, L. Ciannelli, S. H. Espeland, J. A. Knutsen, J. H. Simonsen, S. Skreslet, and N. C. Stenseth. 2007. Egg distribution, bottom topography and small-scale cod population structure in a coastal marine system. *Marine Ecology Progress Series* 333:249–255.
- Leth, O. K. 1995. A study on the effect of local wind on the dynamics of the upper layer in the inner part of Malangen. Pages 185–194 in H. R. Skjoldal, C. Hopkins, K. E. Erikstad, and H. P. Leinaas, editors. *Ecology of fjords and coastal waters*. Elsevier, Amsterdam.
- Li, M., L. Zhong, and W. C. Boicourt. 2005. Simulations of Chesapeake Bay estuary: sensitivity to turbulence mixing parameterizations and comparison with observations. *Journal of Geophysical Research* 110:C12004.
- Mohus, Å., and M. Haakstad. 1984. Straumbukta i Sørfold, en kortfattet hydrografisk og hydrokjemisk kartlegging. [Straumbukta in Sørfold a brief hydrographic and hydrochemical survey.] Nordland distriktshøgskole, Bodø, Norway. (In Norwegian).
- Mullon, C., P. Freon, C. Parada, C. van der Lingen, and J. Hugget. 2003. From particles to individuals: modelling the early stages of anchovy (*Engraulis capensis/encrasicolus*) in the southern Benguela. *Fisheries Oceanography* 12:396–406.
- North, E. W., and E. D. Houde. 2001. Retention of white perch and striped bass larvae: biological-physical interactions in Chesapeake Bay estuarine turbidity maximum. *Estuaries* 24:756–769.
- North, E. W., and E. D. Houde. 2006. Retention mechanisms of white perch (*Morone americana*) and striped bass (*Morone saxatilis*) early-life stages in an estuarine turbidity maximum: an integrative fixed-location and mapping approach. *Fisheries Oceanography* 15:429–450.
- Øresland, V., and C. André. 2008. Larval group differentiation in Atlantic cod (*Gadus morhua*) inside and outside the Gullmar Fjord. *Fisheries Research* 90:9–16.
- Otterå, H., A. L. Agnalt, and K. E. Jørstad. 2006. Differences in spawning time of captive Atlantic cod from four regions of Norway, kept under identical conditions. ICES (International Council for the Exploration of the Sea) *Journal of Marine Science* 63:216–223.
- Ouellet, P. 1997. Characteristics and vertical distribution of Atlantic cod (*Gadus morhua*) eggs in the northern Gulf of St. Lawrence, and the possible effect of cold water temperature on recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* 54:211–223.
- Page, F. H., and K. T. Frank. 1989. Spawning time and eggs stage duration in northwest Atlantic haddock (*Melanogrammus aeglefinus*) stocks with emphasis on Georges Bank and Browns Bank. *Canadian Journal of Fisheries and Aquatic Sciences* 46:68–81.
- Parada, C., C. D. van derLingen, C. Mullon, and P. Penven. 2003. Modelling the effect of buoyancy on the transport of anchovy (*Engraulis capensis*) eggs from spawning to nursery grounds in the southern Benguela: an IBM approach. *Fisheries Oceanography* 12:170–184.
- Pedersen, T. 1984. Variation of peak spawning of Arcto-Norwegian cod (*Gadus morhua* L.) during the time period 1929–1982 based on indices estimated from fishery statistics. Pages 301–316 in E. Dahl, D. S. Danielsen, E. Moksness, and P. Solemdal, editors. The propagation of cod (*Gadus morhua* L.). Institute of Marine Research Biological Station, Arendal, Norway.
- Pogson, G. H., and S. E. Fevolden. 2003. Natural selection and the genetic differentiation of coastal and Arctic populations of the Atlantic cod in northern Norway: a test involving nucleotide sequence variation at the pantophysin (PanI) locus. *Molecular Ecology* 12:63–74.
- Roald, L. A., S. Beldring, T. E. Skaugen, E. J. Førland, and R. Benestad. 2006. Climate change impacts on streamflow in Norway. Norwegian Water Resources and Energy Directorate, Consultancy Report A 1-2006, Oslo.
- Sælen, O. H. 1967. Some features of the hydrography of Norwegian fjords. Pages 63–70 in G. H. Lauff, editor. *Estuaries*. American Association for the Advancement of Science, Washington, D.C.
- Salvanes, A. G. V., J. E. Skjæraasen, and T. Nilsen. 2004. Sub-populations of coastal cod with different behavior and life history strategies. *Marine Ecology Progress Series* 267:241–251.
- Schepetkin, A. F., and J. C. McWilliams. 2005. The regional ocean modeling system (ROMS): a split-explicit, free-surface, topography following coordinate oceanic model. *Ocean Modelling* 9:347–404.
- Skogen, M. D., M. Eknes, L. C. Asplin, and A. D. Sandvik. 2009. Modelling the environmental effects of fish farming in a Norwegian fjord. *Aquaculture* 298:70–75.
- Smedsrud, L. H., W. P. Budgell, A. D. Jenkins, and B. Ådlandsvik. 2006. Fine-scale sea-ice modelling of the Storfjorden polynya, Svalbard. *Annals of Glaciology* 44:73–79.
- Stenevik, E. K., S. Sundby, and A. L. Agnalt. 2008. Buoyancy and vertical distribution of Norwegian coastal cod (*Gadus morhua*) eggs from different areas along the coast. ICES (International Council for the Exploration of the Sea) *Journal of Marine Science* 65:1198–1202.
- Stigebrandt, S. 1981. A mechanism governing the estuarine circulation in deep, strongly stratified fjords. *Estuarine, Coastal, and Shelf Science* 13:197–211.
- Stransky, C., H. Baumann, S. E. Fevolden, A. Harbitz, H. Høie, K. H. Nedreaas, A. B. Salberg, and T. H. Skarstein. 2008. Separation of Norwegian coastal cod and Northeast Arctic cod by outer otolith shape analysis. *Fisheries Research* 90:26–35.
- Sundby, S. 1982. [Investigations in Vestfjorden 1978: freshwater budget and wind conditions]. *Fisken og Havet* 1:1–30. (In Norwegian with English summary.)
- Sundby, S. 1983. A one-dimensional model for the vertical distribution of pelagic fish eggs in the mixed layer. *Deep-Sea Research Part A: Oceanographic Research Papers* 30:645–661.
- Sundby, S. 1991. Factors affecting the vertical distribution of eggs. ICES (International Council for the Exploration of the Sea) *Marine Science Symposia* 192:33–38.
- Sundby, S., A. J. Boyd, L. Hutchings, M. J. O'Toole, K. Thorisson, and A. Thorsen. 2001. Interaction between cape hake spawning and the circulation in the northern Benguela upwelling ecosystem. *South African Journal of Marine Science* 23:317–336.
- Svendsen, H. 1995. Physical oceanography of coupled fjord-coast systems in northern Norway with special focus on frontal dynamics and tides. Pages 149–164 in H. R. Skjoldal, C. Hopkins, K. E. Erikstad, and H. P. Leinaas, editors. *Ecology of fjords and coastal waters*. Elsevier, Amsterdam.
- Svendsen, H., and R.O.R.Y. Thompson. 1978. Wind-driven circulation in a fjord. *Journal of Physical Oceanography* 8:703–712.
- Thygesen, U. H., and B. Ådlandsvik. 2007. Simulating vertical turbulent dispersal with finite volumes and binned random walks. *Marine Ecology Progress Series* 347:145–153.
- Vikebø, F., S. Sundby, B. Ådlandsvik, and Ø. Fiksen. 2005. The combined effect of transport and temperature on distribution and growth of larvae and

- pelagic juveniles of Arcto-Norwegian cod. ICES (International Council for the Exploration of the Sea) *Journal of Marine Science* 62:1375–1386.
- Warner, J. C., W. R. Geyer, and J. A. Lerczak. 2005a. Numerical modeling of an estuary: a comprehensive assessment. *Journal of Geophysical Research* 110:C05001.
- Warner, J. C., C. R. Sherwood, H. G. Arango, and R. P. Signell. 2005b. Performance of four turbulence closure models implemented using a generic length scale method. *Ocean Modelling* 8:81–113.
- Werner, F. E., F. H. Page, D. R. Lynch, J. W. Loder, R. G. Lough, R. I. Perry, D. A. Greenberg, and M. M. Sinclair. 1993. Influence of mean advection and simple behavior on the distribution of cod and haddock early life stages on Georges Bank. *Fisheries Oceanography* 2: 43–64.
- Winsor, P., and D. C. Chapman. 2004. Pathways of Pacific water across the Chukchi Sea: a numerical model study. *Journal of Geophysical Research* 109:C03002.