Short Communication

Buoyancy and vertical distribution of Norwegian coastal cod (*Gadus morhua*) eggs from different areas along the coast

Erling Kåre Stenevik, Svein Sundby, and Ann Lisbeth Agnalt

Stenevik, E. K., Sundby, S., and Agnalt, A. L. 2008. Buoyancy and vertical distribution of Norwegian coastal cod (*Gadus morhua*) eggs from different areas along the coast. – ICES Journal of Marine Science, 65: 1198–1202.

There are significant genetic differences in coastal cod (*Gadus morhua*) along the Norwegian coast, and in order to maintain these differences, there must be mechanisms that ensure local retention of eggs and larvae in the spawning areas. The buoyancy of eggs from four different areas along the Norwegian coast was measured using a density gradient column, and the results from modelling experiments showed that in three of the groups (Tysfjord, Helgeland, and Øygarden), the buoyancy in combination with local hydrography would place the eggs in subsurface waters where retention is greater than in surface waters.

Keywords: buoyancy, eggs, *Gadus morhua*, retention.

Received 16 January 2008; accepted 25 May 2008; advance access publication 17 June 2008.

E. K. Stenevik, S. Sundby and A. L. Agnalt: Institute of Marine Research, PO Box 1870, Nordnes, 5817 Bergen, Norway. Correspondence to E. K. Stenevik: tel: +47 55 23 84 86; fax: +47 55 23 85 31; e-mail: erling.stenevik@imr.no.

Introduction

Norwegian coastal cod (*Gadus morhua*) differs morphometrically (Løken and Pedersen, 1996), genetically (Knutsen *et al.*, 2003; Dahle *et al.*, 2006), and behaviourally (Salvanes *et al.*, 2004) among areas of the Norwegian coast. Pogson and Fevolden (2003) suggested that there was a greater degree of similarity between Northeast Arctic and coastal cod from the Porsangen fjord in northern Norway than among coastal cod sampled from different populations along the coast, suggesting a recent exchange of genes between cod from Porsangen and from the Northeast Arctic population.

The evolution of genetically differentiated subpopulations in a species is likely as long as there are mechanisms ensuring local retention of early life stages (Asplin *et al.*, 1999; Cowen *et al.*, 2000; Knutsen *et al.*, 2007). Vertical distribution of the eggs is one factor which will affect their transport. Eggs from Northeast Arctic cod are spawned at the coast in water with higher salinity than in the fjords, and they are buoyant relative to surface layers (Solemdal and Sundby, 1981). As a result, their concentration increases towards the surface and their vertical distribution can be modelled from the observed egg buoyancy and the vertical turbulent mixing (Sundby, 1983). Eggs spawned by coastal cod in fjords have the potential of being heavier than the low-saline surface water of the fjords and consequently they might float subsurface and could be modelled using Sundby's (1991) approach. Because of the often strong vertical current shear caused by the estuarine circulation in fjords, eggs in the upper water column will be subject to different currents and transport than those deeper in the water column. Transport in surface waters will favour advection away from spawning areas close to shore and inside fjords, whereas eggs distributed deeper will have a greater degree of retention in the spawning area (Sundby, 1994). The duration of the egg stage of cod in northern Norwegian waters is relatively long (∼3 weeks in March/April) because of the low temperature at spawning. Simulation studies have shown that frequent shifts in northerly and southerly winds may cause exchange of surface-dwelling fish eggs and larvae between neighbouring fjords (Asplin *et al.*, 1999) and hence counteract genetic isolation. Asplin *et al.* (1999) suggested that the spawning depth and buoyancy of fish eggs might have evolved to reduce dispersal of the younger stages. This is in accordance with Sundby (1991), who outlined the importance of egg buoyancy on horizontal transport of early life-history stages from spawning areas to nursery grounds. The buoyancy of pelagic eggs is determined by their specific gravity, the salinity structure of the ambient water, and wind-mixing (Sundby, 1991), and all three factors are important when investigating the vertical distribution of eggs.

Here, we measured the buoyancy of eggs from four groups of coastal cod, and simulated the vertical distribution of the eggs using field data on vertical salinity structure from the respective spawning areas. The eggs were collected from a larger experiment comparing the life history of coastal cod from four different sites along the Norwegian coast (Dahle *et al.*, 2006; Otterå *et al.*, 2006).

Material and methods

The broodstock used in the experiments were collected in 2002 at four spawning sites along the Norwegian coast, Porsangen, Tysfjord, Helgeland, and Øygarden (Figure 1). Detailed descriptions of the sampling and the spawning experiments are given by Dahle *et al.* (2006) and Otterå *et al.* (2006). The spawning of separate pairs was monitored in 40 outdoor spawning tanks, each with one female and one male from the same spawning group. The water temperature in the tanks varied from 5 to 6°C, and the salinity from 32 to 34. The experiments were run at the Institute of Marine Research (IMR) Parisvatnet field station in Øygarden, west of Bergen (Figure 1). The number of eggs spawned was recorded daily. Generally, spawning took place late at night or in the early morning, and eggs were collected later, within 24 h.

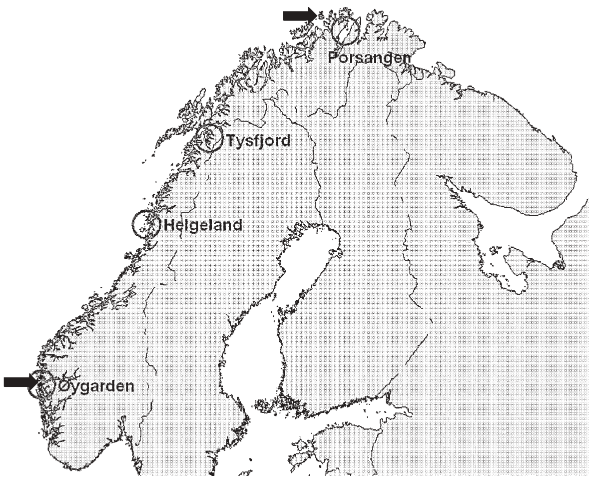

Figure 1. The geographic locations of the four cod broodstocks used in the study. The arrows indicate the position of the coastal monitoring stations at Sognesjøen in the south and Ingøy in the north.

Eggs used in the buoyancy measurements were collected three times during the spawning season in 2004 (17, 21, and 23 March), and transported to the laboratory in Bergen for analysis. Eggs were placed into incubators with circulating water, and buoyancy measurements were carried out the next day when the eggs were in the lens stage (Fridgeirsson, 1978). Egg buoyancy was measured with a unit from Martin Instrument Co. Ltd. Methods for setting up and operating the unit follow Coombs (1981). The unit contains three salinity gradient columns submersed in a 6.0°C water bath held in a rectangular transparent container. The salinity gradient was constructed by preparing two stock solutions from diluted natural seawater and salt-added natural seawater. The salinity gradients were calibrated with four spherical glass floats (accurate to ± 0.0002 g cm^{-3}) placed in each column.

Eggs were gently introduced into the columns just below the water surface using a pipette, and allowed to settle for 1 h before reading their vertical position in the column. Neutral buoyancy of the eggs was expressed in salinity units by calculating the salinity gradient in the column from the absolute densities of the floats and the temperature in the columns. In all, 22 buoyancy experiments were completed, and ca. 30 eggs were measured in each experiment. Precision in this method is relatively high, and differences in density may be resolved to better than 1×10^{-4} g cm^{-3}.

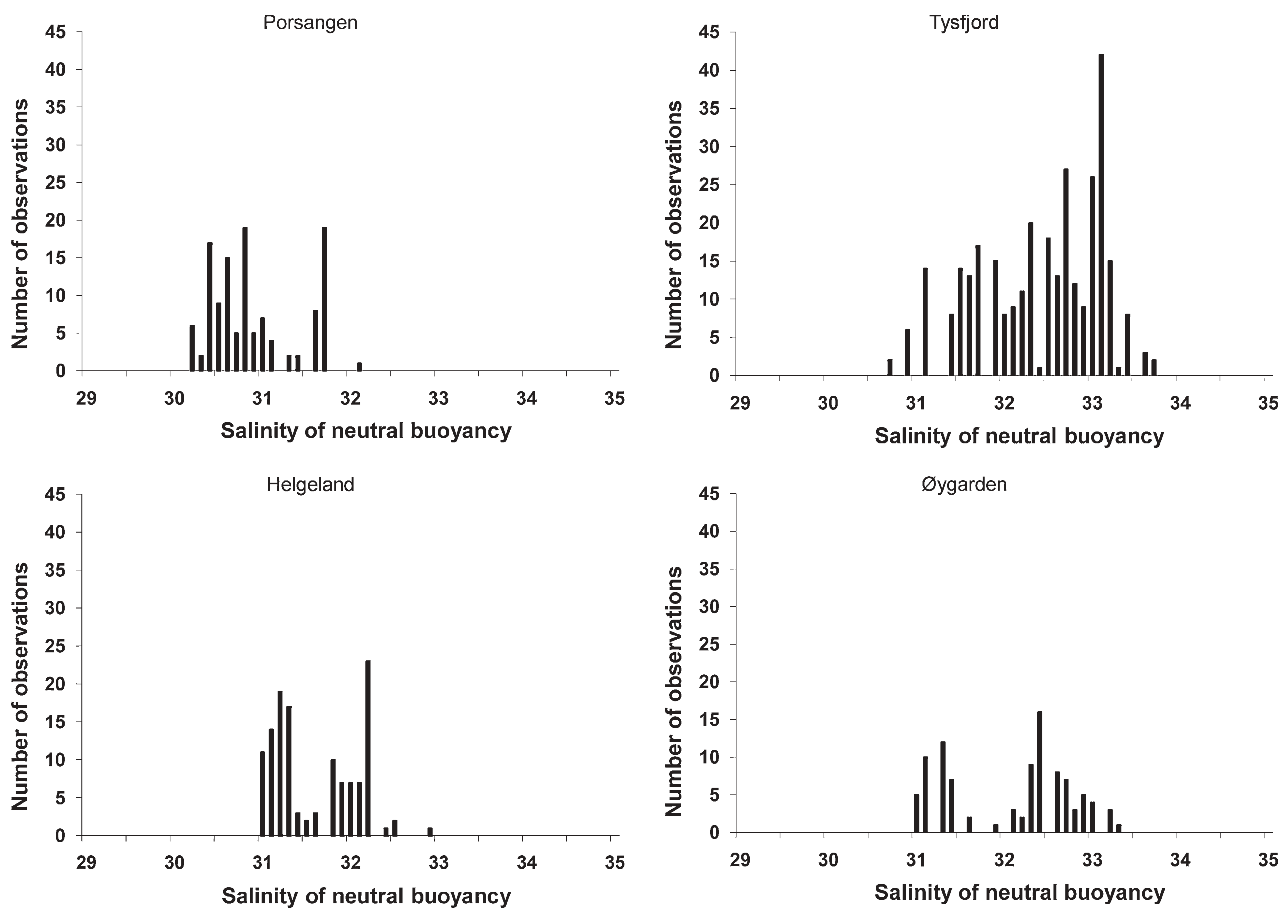

Figure 2. Salinity of neutral buoyancy of eggs from Porsangen (upper left), Tysfjord (upper right), Helgeland (lower left), and Øygarden (lower right).

The predicted vertical distribution of the cod eggs is based on models developed for pelagic (Sundby, 1983) and bathypelagic eggs (Sundby, 1991), based on the fraction of eggs with a density lower and higher than that of surface waters, respectively. A general numerical model for the vertical distribution of fish eggs was developed by Ådlandsvik *et al.* (2001). This numerical

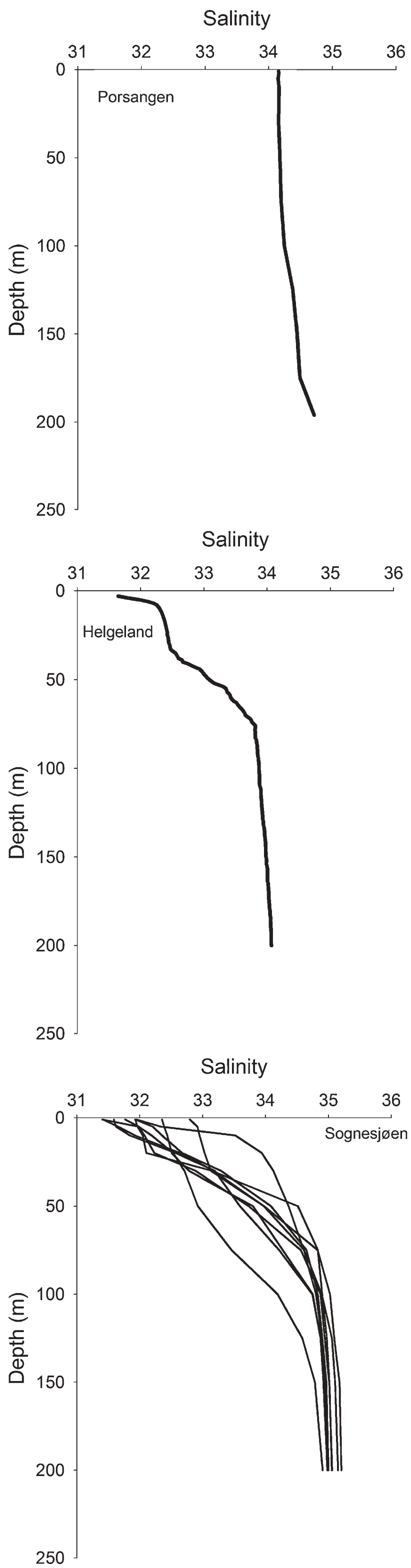

Figure 3. Salinity profiles in Porsangen (upper left), Tysfjord (upper right), Helgeland (middle left), and Øygarden (middle right) during the spawning period. Also shown is the average salinity structure in April for the years 2000–2008 for the coastal monitoring stations at Sognesjøen (lower left) and Ingøy (lower right).

model can be applied for stationary, steady-state (equilibrium between buoyancy forces and vertical turbulent forced), and non-stationary distributions of fish eggs. It was based on earlier work by Sundby (1983, 1991), who derived analytical models for stationary distributions of pelagic and bathypelagic eggs, respectively. As we are limiting our evaluation to stationary vertical distributions, the original models developed by Sundby (1983, 1991) can be applied.

Because the variation in buoyancy distribution of the bathypelagic egg fraction is the major cause of vertical spreading of the eggs, and not vertical mixing (Sundby, 1991), the vertical distribution of the bathypelagic egg fraction is determined by the buoyancy distribution and is negligibly affected by variation in vertical mixing of the halocline, where they are neutrally buoyant. The pelagic fraction, however, is strongly influenced by changes in vertical mixing. A constant vertical windmixing comparable to mixing at a windspeed of 6 m s^{-1} is applied for the modelled profiles of pelagic eggs for each of the four fjords, following Sundby (1983).

Results

The mean salinity of neutral buoyancy varied among groups (Figure 2). Differences were significant between all groups (Kruskal–Wallis test, $H = 265.3$, $p < 0.05$), with Tysfjord eggs having the lowest buoyancy (mean neutral buoyancy at a salinity of 32.52), and Porsangen eggs the highest buoyancy (mean neutral buoyancy at a salinity of 31.0).

Salinity profiles taken from surveys conducted by IMR on the spawning grounds where the fish originated demonstrate that, in Porsangen, the water column was well mixed, with high salinities, varying from 34.17 at the surface to 34.71 at 200 m deep (Figure 3). The vertical salinity structure in Porsangen is similar to that of northern Norwegian coastal waters, where Northeast Arctic cod spawn. In the other three areas, the water columns were similar to those of stratified estuarine conditions, with a halocline around 40–50 m deep (Figure 3). The salinity profiles used in the simulations were taken from just one station because we wanted to use observations as close as possible to the location where the fish had been sampled. To demonstrate interannual variation in salinity profiles, average salinity profiles during April of 2000–2008 from two of IMRs coastal monitoring stations were used as examples (Figure 3). Sognesjøen is a station close to Øygarden, and representative of the three areas influenced by coastal water (Øygarden, Helgeland, and Tysfjord). Ingøy is a station in northern Norway and representative of areas less influenced by coastal water (Porsangen). From these profiles, it is clear that, although there are interannual variations, the pattern of stratification in the southern areas is influenced by coastal water, while there is no stratification in areas not influenced by coastal water.

Model simulations demonstrate that the eggs from all four sites were distributed in the upper 60–70 m (Figure 4). In all groups except Porsangen, egg concentration peaked at depths of 40–50 m. The Porsangen eggs had a pelagic vertical distribution similar to eggs of Northeast Arctic cod adjacent to where they spawn, as described by Sundby (1983), with greatest concentration at the surface and decreasing exponentially with depth.

Discussion

Spawning areas of coastal cod are partly along the coast, and partly in fjords (Jakobsen, 1987). The typical Norwegian fjord has an estuarine circulation characterized by an upper brackish/low-saline layer flowing out of the fjord and a saltier compensation current flowing up the fjord at depth (Klinck *et al.*, 1981). Therefore, the vertical distribution modelled here will most likely result in retention of the eggs close to the spawning areas inside the fjord and lead to a subsurface accumulation at the head of the fjord. In a study of 20 Norwegian fjords, Knutsen

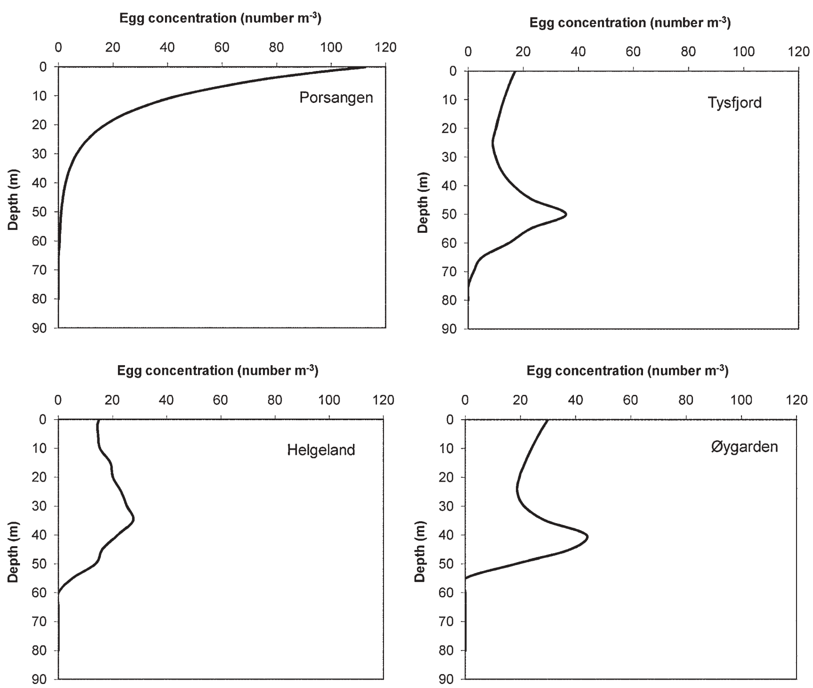

Figure 4. Modelled vertical distribution of cod eggs from Porsangen (upper left), Tysfjord (upper right), Helgeland (lower left), and Øygarden (lower right).

et al. (2007) found the greatest concentrations of eggs inside the fjords, and concentrations decreasing offshore. They suggested that eggs were retained within the fjords, although they had no data to support this suggestion in terms of a possible mechanism behind the retention. Our data on buoyancy and the modelled vertical distributions, together with the general estuarine circulation in fjords, suggest that concentration of the eggs at the head of a fjord is a possible mechanism for retaining the eggs within the fjord spawning areas. This can also provide a physical mechanism for genetic separation between the cod populations spawning at the coast and cod populations spawning in the fjords. Moreover, it provides an explanatory mechanism for the genetic separation of cod spawning in different fjords (Knutsen *et al*., 2003; Dahle *et al*., 2006). Although concentrations of cod eggs peak well below the surface, there is variability in buoyancy within groups, and simulations show that some eggs are found also in the surface water and are hence susceptible to offshore transport. This may explain why Knutsen *et al*. (2007) found low concentrations of eggs offshore.

The Porsangen eggs had greater buoyancy, and the model results suggest that the highest concentrations would likely be at the surface, making them more susceptible to offshore transport. In Porsangen, the salinity is relatively high throughout the water column, and there is no strong stratification. Therefore, there is no halocline where the eggs could concentrate. The cod eggs would therefore either ascend towards the surface or sink towards the bottom if their buoyancy is positive or negative (Sundby, 1991).

The buoyancy of cod eggs may change during development (Mangor-Jensen, 1987). Typically, eggs get heavier as they approach hatching. We did not follow any of the egg batches through their development. However, if we assume that the eggs became heavier through development, retention in the three southern areas would increase, but the change in buoyancy would have to be relatively large to alter the vertical distribution of the eggs in Porsangen because the salinity there was relatively high throughout the water column.

Acknowledgements

The study was partly funded by the Norwegian Research Council, project number 155930/700.

References

Ådlandsvik, B., Coombs, S., Sundby, S., and Temple, G. 2001. Buoyancy and vertical distribution of eggs and larvae of blue whiting (*Micromesistius poutassou*): observations and modeling. Fisheries Research, 50: 59–72.

Asplin, L., Salvanes, A. G. V., and Kristoffersen, J. B. 1999. Nonlocal wind-driven fjord-coast advection and its potential effect on plankton and fish recruitment. Fisheries Oceanography, 8: 255–263.

Coombs, S. H. 1981. A density-gradient column for determining the specific gravity of fish eggs, with particular reference to eggs of the mackerel *Scomber scombrus*.. Marine Biology, 63: 101–106.

Cowen, R. K., Lwiza, K. M. M., Sponaugle, S., Paris, C. B., and Olson, D. B. 2000. Connectivity of marine populations: open or closed. Science, 287: 857–859.

Dahle, G., Jørstad, K. E., Rusaas, H. E., and Otterå, H. 2006. Genetic characteristics of broodstock collected from four Norwegian coastal cod (*Gadus morhua*) populations. ICES Journal of Marine Science, 63: 209–215.

Fridgeirsson, E. 1978. Embryonic development of five species of gadoid fishes in Icelandic waters. Rit Fiskideildar, 5(6). 68 pp.

Jakobsen, T. 1987. Coastal cod in northern Norway. Fisheries Research, 5: 223–234.

Klinck, J., O'Brien, J., and Svendsen, H. 1981. A simple model of fjord and coastal circulation interaction. Journal of Physical Oceanography, 11: 1612–1626.

Knutsen, H., Jorde, P. E., André, C., and Stenseth, N. C. 2003. Fine-scaled geographic population structuring in a highly mobile marine species. Molecular Ecology, 12: 385–394.

Knutsen, H., Olsen, E. M., Cianelli, L., Espeland, S. H., Knutsen, J. A., Simonsen, J. H., Skreslet, S., *et al.* 2007. Egg distribution, bottom topography and small-scale cod population structure in a coastal marine system. Marine Ecology Progress Series, 333: 249–255.

Løken, S., and Pedersen, T. 1996. Effect of parent type and temperature on vertebrae number in juvenile cod, *Gadus morhua* L., in northern Norway. Sarsia, 80: 293–298.

Mangor-Jensen, A. 1987. Water balance in developing eggs of the cod *Gadus morhua* L. Fish Physiology and Biochemistry, 3: 17–24.

Otterå, H., Agnalt, A. L., and Jørstad, K. E. 2006. Differences in spawning time of captive Atlantic cod from four regions of Norway, kept under identical conditions. ICES Journal of Marine Science, 63: 216–223.

Pogson, G. H., and Fevolden, S. E. 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 (*Pan*I) locus. Molecular Ecology, 12: 63–74.

Salvanes, A. G. V., Skjæraasen, J. E., and Nilsen, T. 2004. Sub-populations of coastal cod with different behaviour and life-history strategies. Marine Ecology Progress Series, 267: 241–251.

Solemdal, P., and Sundby, S. 1981. Vertical distribution of pelagic fish eggs in relation to species, spawning behaviour and wind conditions. ICES Document CM 1981/G: 77. 26 pp.

Sundby, S. 1983. A one-dimensional model for the vertical distribution of pelagic fish eggs in the mixed layer. Deep-Sea Research, 30: 645–661.

Sundby, S. 1991. Factors affecting the vertical distribution of eggs. ICES Marine Science Symposia, 192: 33–38.

Sundby, S. 1994. The influence of bio-physical processes on fish recruitment in an Arctic-boreal ecosystem. PhD thesis, University of Bergen, Norway. 189 pp.

doi:10.1093/icesjms/fsn101