Ecology, 91(10), 2010, pp. 2918–2930

Small-scale genetic structure in a marine population in relation to water circulation and egg characteristics

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Abstract. Until the last decade it was assumed that most marine species have pronounced gene flow over vast areas, largely because of their potential for dispersal during early life stages. However, recent genetic, modeling, and field studies have shown that marine populations may be structured at scales that are inconsistent with extensive dispersal of eggs and larvae. Such findings have stimulated the birth of new studies explaining the mechanisms that promote population structure and isolation in the oceans, in the face of high potential for dispersal. Here we study the vertical and horizontal distribution of cod (*Gadus morhua*) eggs in relation to small-scale circulation and water column hydrography in a coastal location of southern Norway. Previous studies conducted in this region have shown that cod populations inhabiting fjord locations, which are on average 30 km apart, are genetically differentiated, a remarkable outcome considering that Atlantic cod have pelagic egg stages and long pelagic larval duration. We document that cod eggs are found in greater abundance in shallow water layers, which on average are flowing up the fjord (away from the open ocean), and in the inner portion of the fjord, which is subject to lower current speeds compared to the outer or mouth of the fjord. Eggs were found to be neutrally buoyant at shallow depths, a trait that also favors local retention, given the local circulation. The same patterns held during two environmentally contrasting years. These results strongly suggest that population structure of Atlantic cod is favored and maintained by a balance between water circulation and egg characteristics.

Key words: Atlantic cod; connectivity; early life history; Gadus morhua; *population structure; Tvedestrand fjord, Skagerrak coast, southern Norway.*

INTRODUCTION

Marine populations were generally assumed to be open systems due to dispersal during pelagic early life stages (for review, see Caley et al. 1996). Recent studies, however, have questioned the generality of this assumption. There is increasing evidence that some marine species are subject to a high degree of self-recruitment (Jones et al. 1999, 2005, Miller and Shanks 2004, Cowen et al. 2006, Almany et al. 2007, Planes et al. 2009), a feature leading to fine-scale genetic structure (Miller et al. 2005, Jorde et al. 2007) and local adaptations (Conover and Present 1990, Bricelj et al. 2005, Olsen et al. 2008). This lack of correspondence between expectations and observations over a wide range of species (Perez-Losada et al. 2002, Taylor and Hellberg 2003, Kenchington et al. 2006, McCairns and Bernatchez 2008) has given rise to a physical and biological conundrum: How can marine organisms maintain their genetic structure in the face of a high dispersal potential? There are many unsolved issues regarding the mechanisms promoting and maintaining self-recruitment and the spatial scales at which it occurs. For instance, Pineda et al. (2007) pointed out that knowledge to date of how early pelagic life stages are transported in coastal waters is very limited and that major drawbacks include a lack of understanding of the manner in which local-scale physical mechanisms, such as tidal currents, along- and cross-shore winds, and water column hydrography, affect egg and larval transport.

In higher latitude seas the patterns of genetic differentiation among different populations is even more puzzling. For example, it has been shown that dispersal distances and potential for genetic similarity are directly proportional to the pelagic larval duration (PLD) (Bradbury et al. 2008*b*). In turn, PLD tends to increase in fish residing at higher latitudes and lower temperatures (O'Connor et al. 2007, Bradbury et al. 2008*b*). Therefore, the expectation is that higher

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Manuscript received 1 September 2009; revised 19 February 2010; accepted 1 March 2010. Corresponding Editor: S. G. Morgan.

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latitude fish have lower genetic diversity (Bradbury et al. 2008*b*). However, the scientific evidence accumulated so far also questions the generality of this expectation, indicating that a high degree of genetic structure exists in high-latitude and cold-water-adapted fish, such as Atlantic cod (*Gadus morhua*; e.g., Ruzzante et al. 1999, Knutsen et al. 2003, Bradbury et al. 2008*a*). Particularly for temperate and subarctic species, the mechanisms behind this structuring are still a matter of scientific debate (e.g., Bradbury and Laurel 2007, Svedäng et al. 2007, Knutsen et al. 2009). Indeed, retention during early life history stages (e.g., Taylor and Hellberg 2003) in combination with natal homing and reproductive behavior are key processes that contribute to genetic isolation (Thorrold et al. 2001, Almany et al. 2007).

Coastal Atlantic cod of the Skagerrak Coast in the northeastern North Sea represent a promising case study for elucidating mechanisms of population structuring in high-latitude fish species. In this region there is strong evidence for spatially structured populations (Knutsen et al. 2003), where samples separated by as little as 30 km are genetically and thus reproductively isolated (Jorde et al. 2007). This population structure is also mirrored in spatially structured adaptive traits, indicative of local adaptive evolution (Olsen et al. 2008). Spawning in sheltered fjord basins (Knutsen et al. 2007) in combination with high site fidelity of older life stages (Espeland et al. 2008) are potential behavioral adaptations favoring population structuring. Fjord circulation in the Skagerrak system can be spatially and temporally variable, hence cod eggs would have to occupy water layers that favor local retention in spite of seasonal, spatial, and interannual variability in circulation patterns. Aure et al. (1996) have shown that for fjords at the Skagerrak coast, circulation below an outflowing layer of freshwater-driven flow is remotely controlled by density differences in the water column of the coastal current and winds over larger scales. These governing processes have been described from numerical simulations in Asplin et al. (1999). However, for these regions small-scale patterns of within-fjord water circulation during the period in which fish eggs are present are still undescribed. This is a critical knowledge gap in the understanding of mechanisms of cod egg distribution and ultimately population connectivity in this fjord system.

The objective of this study is to analyze the vertical and horizontal distribution of cod eggs in relation to the small-scale circulation and hydrography in a Norwegian fjord in the Skagerrak coast. In doing so we bring together data from a variety of sources. We use the coastal Atlantic cod and the fjords of Skagerrak coast in southern Norway as a model species and system in order to study the mechanisms behind small-scale genetic structure in fish with relatively long PLD residing in high-latitude seas.

Material and Methods

Study site

The study site, Tvedestrand fjord in southern Norway, is 8 km long, with a maximum depth of 85 m (Fig. 1). The Tvedestrand fjord was chosen because several inshore spawning sites for coastal cod occur there (Knutsen et al. 2007). Also, the topography of the Tvedestrand fjord is representative of the fjord systems along the Skagerrak coast. For example, the length of the fjord is about average for the Skagerrak area and thus well suited for a detailed study linking ocean currents with egg distribution. The fjord is also narrow enough to gain feasible and representative current measurements. As a narrow fjord, the water dynamics at Tvedestrand are unaffected by the rotation of the Earth, which in wide fjords (e.g., typically wider than a few kilometers) would maintain circulation balanced by across-fjord water density gradients and in principle lead to a higher exchange of water with the coastal ocean (Asplin et al. 1999).

Current and hydrography measures

We measured currents during two consecutive years, 2006–2007, using moored acoustic doppler current profilers (Nortek Aquadopp, Rud, Norway) at two locations along the fjord, one inner (T2) and one outer (T4; Fig. 1). The instruments were positioned above the bottom at depths between 35 and 40 m. The currents are averaged vertically in 1 m deep cells. The first cell starts 0.5 m above the instrument. From the surface and down to a depth of ∼10% of the instrument depth, the measurements are noisy and in principle lost due to side lobe effects from the slightly angled sound beams. Each instrument measured constantly for 15 min, with a resting period of 45 min. The mean values of three-dimensional current components for these 15-min periods are stored internally in the instrument, thus representing hourly values. Also stored are a variety of other parameters such as water pressure and temperature at the instrument location. In 2006, T2 and T4 current moorings were deployed on 14 February and retrieved on 23 and 9 May, respectively, and in 2007 they were deployed on 11 February and retrieved on 26 April.

Water column hydrography (i.e., salinity and temperature) down to ∼2 m above the bottom was measured employing a compact conductivity/temperature/depth (CTD) sensor (model 204; SAIV Environmental Sensors and Systems, Bergen, Norway) at each egg survey station. Vertical profiles of salinity and temperature were also measured at the current mooring positions T2 and T4 (Fig. 1).

Wind observations at the coast

Data on wind along the coast is taken from observations at the Lyngør lighthouse, ∼10 km northeast of the Tvedestrand fjord and were made available

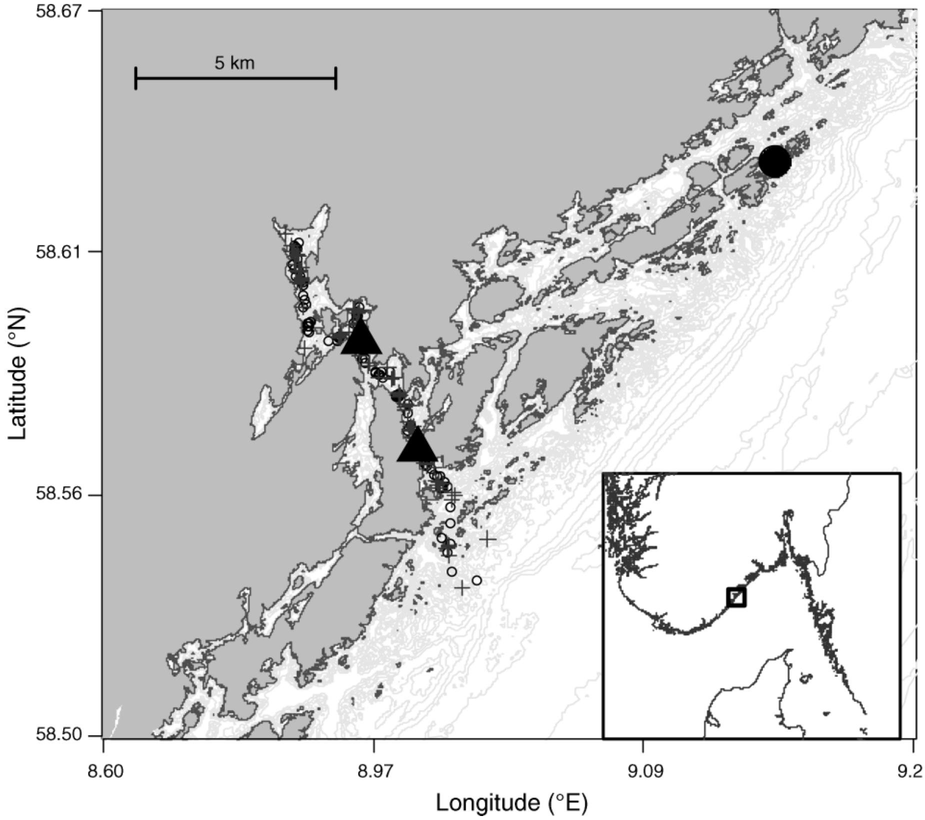

FIG. 1. Map of the Tvedestrand fjord at the Norwegian Skagerrak coast, with the locations of current meters (triangles; T2, inner fjord; T4, outer fjord) and cod (*Gadus morhua*) egg stations sampled in 2006 (crosses) and 2007 (open circles). Also shown as a solid circle is the location of the Lyngør light house, located ~10 km northeast of the Tvedestrand fjord.

by the Norwegian Meteorological Institute. Average wind speed and directions for 6-h periods were decomposed into the along-coast direction (i.e., rotated 40° clockwise).

Field sampling of cod eggs and measure of egg buoyancy

Cod eggs were sampled weekly in 2006 and 2007 during the peak spawning period of February to April. Stations were distributed along an inshore–offshore transect, at a spacing of <1 km, whenever ice conditions allowed (Fig. 1). During most occasions, eggs were sampled from a small open boat. On some occasions, however, part of the fjord was covered with sea ice. In these cases, eggs were sampled from the inshore by walking on the ice cover where it was safe to do so, and also from the offshore with a small vessel. Sometimes, due to unsafe conditions in the proximity of the ice edge, the distance between the offshore-most and inshore-most stations sampled by land and sea, respectively, was greater than 1 km. Eggs were sampled with a 500-µm vertical plankton ring net (Fraser 1968) deployed and pulled by hand. The mouth diameter of the net at the inner edge of the frame was 56 cm, resulting in a mouth area of 0.246 m^2. Vertically stratified samples from 50 to 30 m, 30 to 15 m, 15 to 5 m, and 5 m to the surface were taken whenever depth allowed. For stations with depth <50 m, the deepest samples were taken from 5 m off the bottom to the shallower corresponding level. Egg density was measured as the number of eggs per meter hauled, which can be promptly converted to volumetric density (e.g., number of egg per cubic meter) by taking the product with the inverse of the net mouth area. We use the term "sample" when referring to cod eggs collected at each water layer sampled, i.e., a specific plankton net haul. Because we conducted depth-stratified hauls, there can be more than one sample per station. During 2006 and 2007 we obtained 702 samples of cod eggs over 220 stations sampled.

Sampling for egg buoyancy measures occurred in 2006 only, in the proximity of the T2 (26 and 27 March) and T4 (25 March) current meters. Eggs for buoyancy measurements were randomly taken from the entire water column samples (50 m to surface). Prior to the analysis, eggs were staged as: 1, no visible larvae inside, or 2, visible larva inside, indicating that the egg was ready to hatch. Egg buoyancy was measured according to Coombs (1981), employing a density gradient column. Each density gradient was calibrated with 2–3 glass spheres of known density (Martin Instrument Company, Wednesbury, UK). The buoyancy was measured at 18°C and recalculated to ambient temperature according to Fofonoff and Millard (1983). The final buoyancy measure was expressed as "equivalent salinity" (Ådlandsvik et al. 2001).

Statistical analysis

Measures of egg buoyancy were analyzed with a two-way ANOVA, in which sampling location/time (four levels: inner 1, inner 2, outer 1, and outer 2) and stage (two levels: 1 and 2) and their interaction were the explanatory variables. Tukey's honestly significant difference test was used for post hoc pairwise comparisons.

Cod egg distribution was analyzed using generalized additive models (GAM; Wood 2006). Prior to that, several samples had to be removed from the analysis. Specifically, 34 samples had clear error in recording information (e.g., missing or clearly wrong positioning). Also, samples within 30–50 m depth ($n = 83$) were removed from the statistical analysis (although they are retained in the descriptive Figs. 3 and 5) because this depth interval could not be consistently sampled at all stations, even when enough bottom depth was available. Most of this fieldwork was conducted during short winter days, and we gave first priority to sampling the entire length of the fjord, from the innermost areas out toward the open ocean. As shown in the results, the abundance of cod eggs below 30 m was negligible and its inclusion did not affect the results, but its removal stabilized the residual patterns of the GAM model. This initial screening of the data left 583 samples for statistical analysis.

We were primarily interested in (1) testing whether the distribution of cod eggs along the fjord changed according to the depth strata from which they were sampled and the year (2006 and 2007) of egg collection and (2) what the relationship was between cod egg distribution and water current velocity. These two objectives could not be addressed in the same model formulation because measures of water current velocity were available only for a limited fraction of all our egg samples, namely those closest to the current moorings. Therefore two GAMs were implemented.

To address our first objective the following GAM model formulation was applied:

$$y_{i,t,z} = a_{z,t} I_{z,t} + O_i + s(d_i) I_{z,t} + \mathrm{offset}\Big(\ln(w_i)\Big) + \varepsilon_{i,z,t} \quad (1)$$

where y is the egg number, a is an intercept term specific to year (t) and depth strata (z), d is distance (in meters) from a fixed inshore location, I is an indicator variable equal to 0 or 1, depending on the value of the depth strata and year of egg collection, $\ln(w)$ is the natural logarithm of length (in meters) towed by the net, ε is the residual error, and s is a smoothing function, in this particular case, natural cubic spline. In order to achieve a workable sample size, egg collections were combined in only two depth strata, above and below 15 m, even though they were collected at more refined depth intervals. Also, we made no distinction in relation to egg development stage. Because we had two years and two depth strata sampled there was a total of four indicator variables (I): (1) $\leq$15 m, 2006; (2) $>$15 m, 2006; (3) $\leq$15 m, 2007; (4) $>$15 m, 2007. We note that the GAM model presented in (1) includes a combination of both parametric and nonparametric terms. The parametric terms are the indicator variables (I), with linear coefficients (a). The nonparametric terms are the continuous variables (d), and their effect is estimated through the use of cubic splines (s). Given the relatively high count of tows with zero or very small egg numbers, we employed a quasi-Poisson distribution family, with over-dispersed residual errors and a log link (Wood 2006). The offset term, $\ln(w)$, is treated as a variable with coefficient equal to 1. Therefore, in this case the offset term is needed to standardize egg number by the vertical distance in meters of the net path. It is natural log-transformed due to the natural log-link of the Poisson distribution. The use of an offset term is necessary in Poisson-distributed models, which only accept integers as input variables (in our case egg number). We also analyzed the same data set using a binomial (presence/absence) and a negative binomial distribution family and obtained similar results to the quasi-Poisson. However, residuals were better distributed in the quasi-Poisson case.

During the 2006 collections we had a single tow with a very large number of cod eggs caught in the proximity of the T4 current meter. While such a large egg count is realistic and should not be removed from the analysis, its inclusion destabilizes the residual pattern. Therefore we opted to leave the high egg count but flag it with an "outlier" effect (O). The exclusion of this term did not affect the model results or the study conclusion; however, it stabilized the residual pattern and therefore we opted to retain it in the model.

To address our second objective, of linking cod egg density with water current velocity, the following GAM model formulation was applied:

$$y_{i,t,z} = a_t I_t + s(d_i) + s(c_{i,z}) + \mathrm{offset}\Big(\ln(w_i)\Big) + \varepsilon_{i,t,z} \quad (2)$$

where a is the year intercept (2006 or 2007) and c is the water current speed (in meters per second) measured from the current meters as an average throughout the depth layer at which the egg sample was caught (i.e., 5–15 m and 15–30 m). The uppermost depth layer (0–5 m) was excluded from this analysis since the current measurements were noisy near the surface. All other model terms are identical to those described for Eq. 1. Mean current velocities (c) were derived over three different time spans: (1) during the same day in which the egg sample was obtained, representative of the current speed to which eggs were exposed during the day on which they were caught; (2) three days before and five days after the day on which the egg sample was obtained, representative of

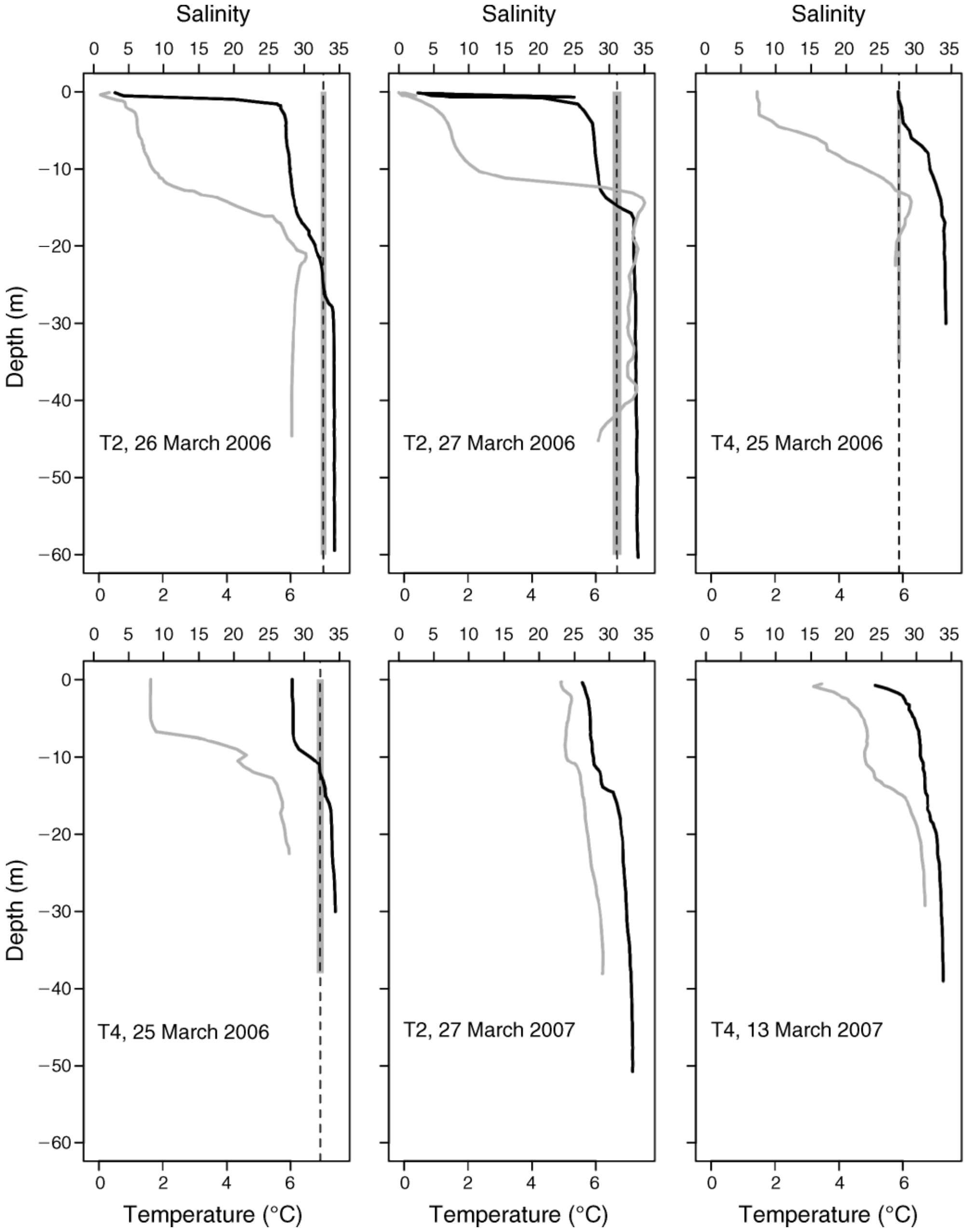

FIG. 2. Water column temperature (gray line) and salinity (black line) in the vicinity of current meters T2 and T4 in 2006 and in 2007. In 2006 only casts in which cod (*Gadus morhua*) egg buoyancy was measured are shown (Table 2). In 2007 corresponding casts by time of year and location are shown; however, egg buoyancy was only measured in 2006. Note that in 2006 there were two separate sampling events occurring at the T4 location, and both on 25 March 2006. The vertical dashed line indicates the estimated mean equivalent salinity of cod eggs from similar stations in which the water column profiles were obtained. The shaded regions along the dashed lines indicate the 95% confidence intervals around the mean. See Table 2 for results of the egg equivalent salinity.

the current speed that eggs would experience throughout most of their developmental stage; (3) throughout the entire cod egg season, obtained at the first and last day of the year in which cod eggs were present in our sampling activities. This last metric is representative of the current that eggs would experience throughout the entire spawning season. The analysis was repeated for all three current metrics, and the results were very similar. Here we only report results from the middle metric (2). In this particular case the analysis was limited to egg samples that were <1000 m away from either the T2 or T4 current mooring, which resulted in a total sample size of 186.

All statistical analyzes were run in R, version 2.7.2 (R Foundation for Statistical Computing, Vienna, Austria).

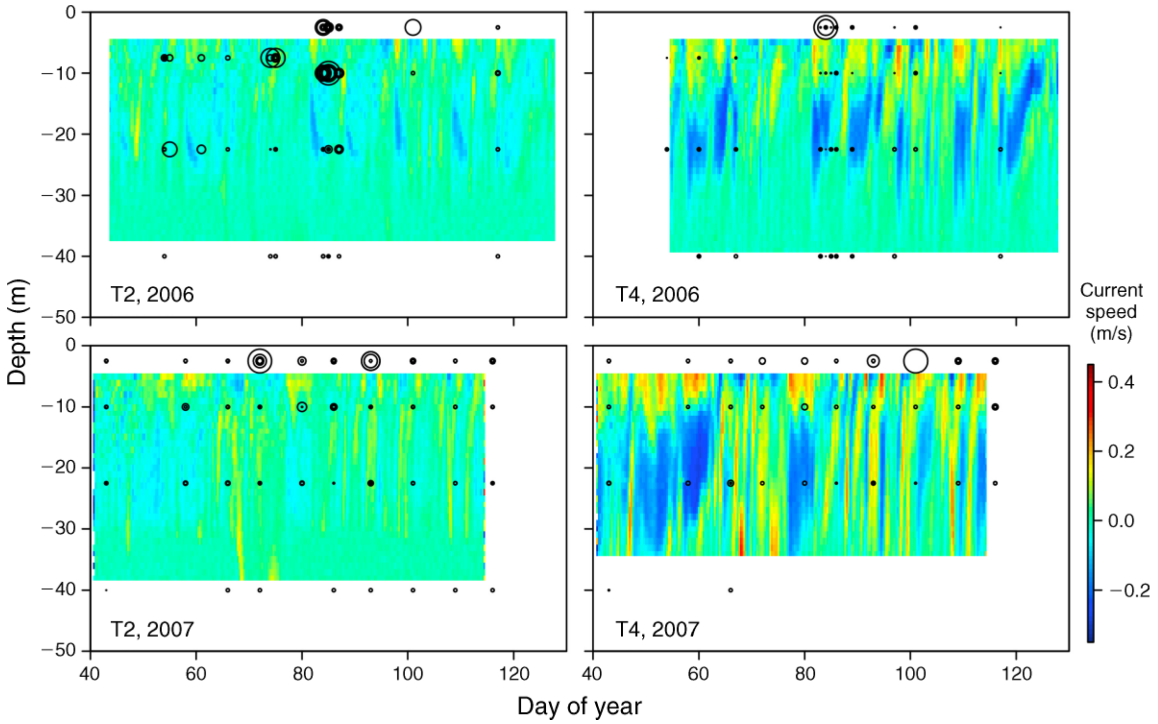

FIG. 3. Images of along-fjord current speed at various depths during the sampling season (day of the year) of 2006 and 2007 at current meter locations T2 and T4. Positive values are up-fjord (away from the ocean). Open circles overlaid on top of the image plot show the mean cod egg density (number/m) in correspondence with the day of the year and depth at which the sampling occurred. Only egg stations within 1000 m of the current meter stations (T2 and T4) are shown in the egg density plots. The sizes of the circles are not standardized and thus should not be compared across panels, but rather only within each panel.

RESULTS

Currents, winds, and hydrography

The hydrography profiles taken in 2006 in the proximity of the current meters reveal the typical two-layer structure of the fjord (Fig. 2). In the inner zone there is a thin surface freshwater layer (~1 m). Below that, water temperature and salinity rapidly increase with depth up to ~30 m. At lower depths, there is little variation in water column hydrography. In the outer zone, there is no freshwater layer at the top, and the lower extreme of the thermocline and halocline depth is found at ~20 m. With the exception of the thin surface freshwater layer at the inner station, similar patterns were observed in 2007 for corresponding locations and time of the year (Fig. 2).

Observations of the vertical current structures at the T2 and T4 positions during spring of 2006 and 2007 show a two-layer flow system. The along-fjord flow has an upper layer flowing up-fjord (away from the ocean) down to ~10–15 m depth (disregarding the possible shallow surface layer forced by river runoff) accompanied by a lower layer of reversed flow (Fig. 3). The flow pattern is characterized by episodes of up to several days with reversed flow (down-fjord at the surface and up-fjord at the bottom) of shorter duration. Clear examples of such flow reversal for both locations (T2 and T4) occurred in 2006 on the 82nd, 90th, 98th, 110th days of the year, and in 2007 during the 60th and 80th days of the year (Fig. 3). We also find the current speed to be stronger in the outer part of the fjord (at T4) compared to further into the fjord (at T2). Qualitatively the flow was similar between 2006 and 2007; however, the mean strength of the upper-layer, up-fjord flow was higher in 2007 than in 2006.

The winds along the Skagerrak coast were compared to the along-fjord flow (Fig. 4). We found a tight match between the winds and currents at 7 m (upper layer) and 20 m (lower layer) as expected from the results of Aure et al. (1996). Winds along the coast from the northeast cause up-fjord flow in the upper layer and down-fjord flow in the lower layer, while the reverse flow pattern occurs when winds are from the southwest.

Vertical and horizontal egg distribution

From inspection of distribution patterns, cod eggs were consistently more abundant in the top 15 m than below. Occasionally, high egg densities were also found between 15 and 30 m, particularly around T2 in 2006 (Fig. 5). Horizontally, the pattern of egg distribution along the fjord changed according to depth layer considered. Shallower than 15 m, cod eggs were more

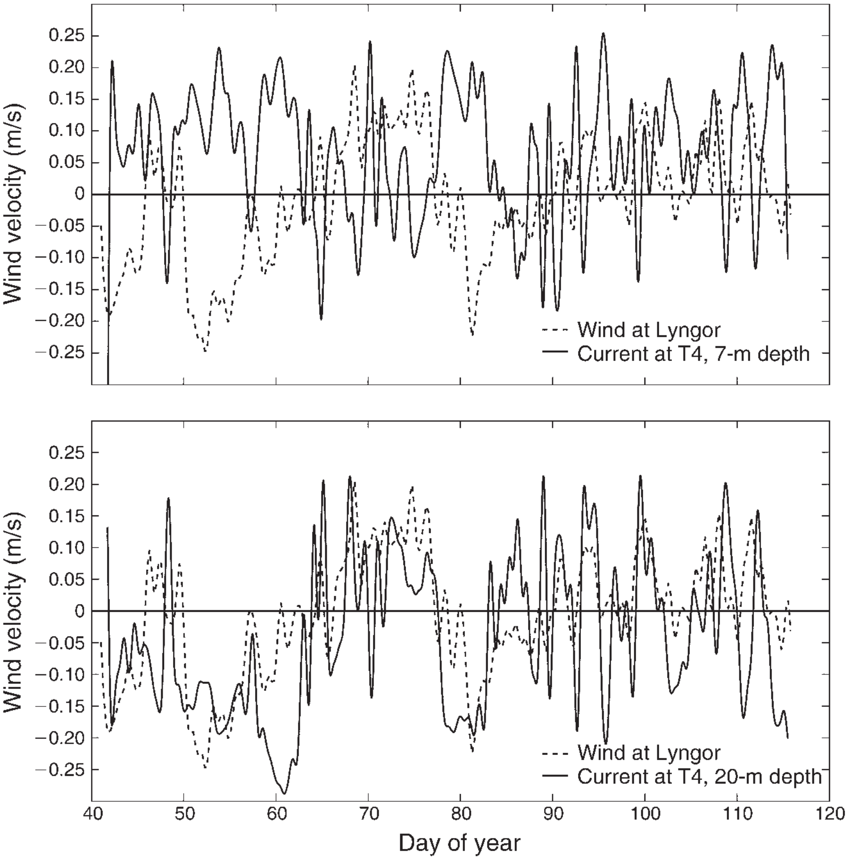

FIG. 4. Along-coast wind at Lyngør lighthouse (dashed line) and along-fjord current (solid line) at current meter position T4 for 2007. Wind values are reduced by a factor of 50 to fit within the axis. The upper panel shows the current at 7-m depth, and the lower panel shows the current at 20-m depth. Positive currents are up-fjord. Positive wind values are to the northeast (i.e., creating an offshore volume transport of surface coastal water and inshore of deeper water).

numerous inshore than offshore of the fjord, inside of the T2 and T4 locations. However, below 15 m there was no clear pattern of egg distribution along the inshore–offshore gradient (Fig. 6).

Results from the GAM analysis gave statistical significance to these visually inspected trends of egg distribution. In both years we found that distance from the inshore location had a significant decreasing effect on egg abundance above 15 m but not below (Fig. 7). The GAM analysis also confirmed that eggs were more numerous above 15 m than below and that eggs were more numerous in 2006 than in 2007, particularly above the 15-m depth threshold (Table 1). The described effects explained 67.6% of the total variance of the examined egg data. From the restricted data set in the vicinity of the two current meters, we found that cod eggs were more abundant in slower and up-fjord flowing water masses (Fig. 8).

Egg buoyancy and estimate of equivalent salinity

The results of the egg buoyancy measures are expressed in equivalent salinity units, after applying temperature corrections (Table 2). Mean egg salinity values within each examined station ranged from 26.97 (outer, stage 1) to 32.78 (inner, stage 1). The inner fjord locations appeared to have higher egg salinity than the outer fjord locations; however, this main effect was subordinate to the fact that the interaction between egg stage (1 vs. 2) and sampling location (inner vs. outer) was significant ($F = 45.70$, df = 2, 184, $P \ll 0.001$), indicating that the variability of egg salinity measures cannot be clearly attributed to either of these two factors alone. Water column salinity values, comparable to those of the eggs, were found from ~2 to 30 m depth (Fig. 2). In the absence of turbulence, the egg would be neutrally buoyant at similar depth ranges. Given that most of the sampled stations were under ice, the effect of local wind-driven turbulence should be minimal, although there can still be turbulence driven by shear offshore in the ice-free areas. Nonetheless, the estimates of egg vertical distribution from vertical profiles of salinity closely match those obtained from the field at the same location and time. For example, the lowest egg equivalent salinity of the outer location stage 1 was consistent with the high catch of cod eggs in the top 5 m during 2006 (Fig. 2).

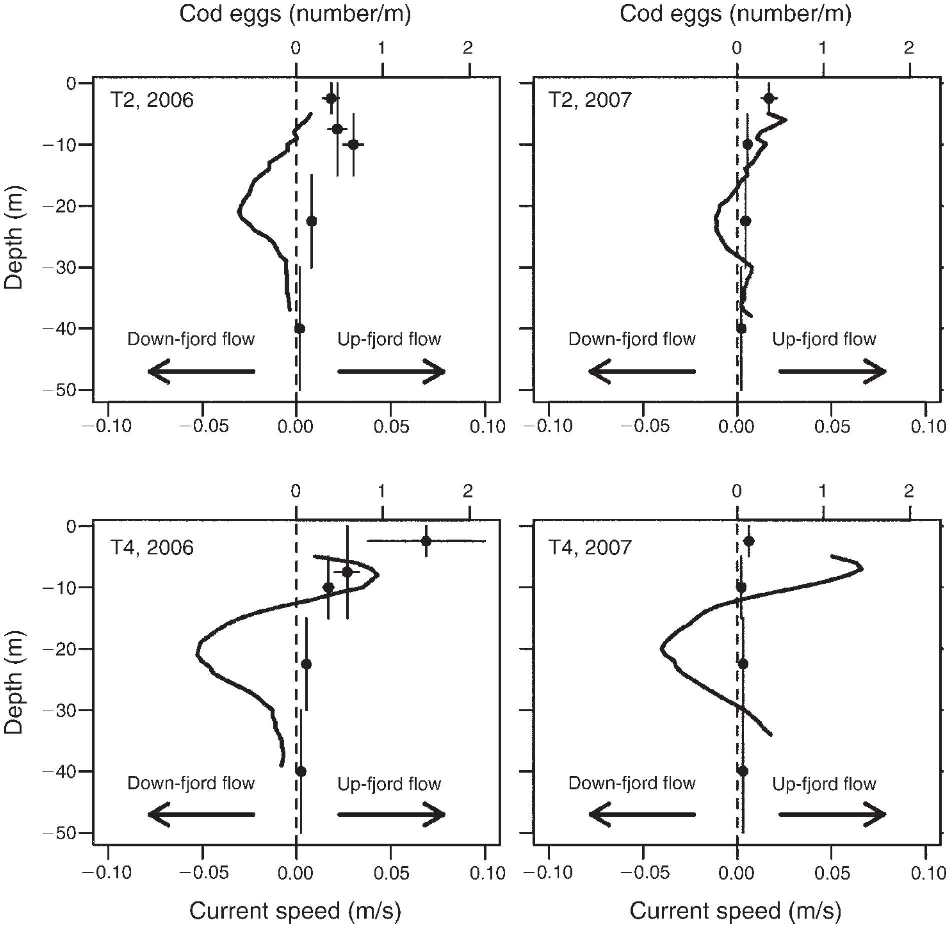

FIG. 5. Cod egg density (solid circles) in relation to mean current speed (line plot) at current meter positions T2 and T4 during 2006 and 2007. The mean current was calculated by only considering days on which egg sampling occurred. Only egg samples collected within 1000 m of the current stations are included in the calculation of mean egg density. The very high density of eggs in the top 5 m near T4 in 2006 was mostly driven by a single sample with an exceptionally high abundance of cod eggs. Horizontal lines indicate ±SD; vertical lines indicate the extent of the vertical egg sampling.

DISCUSSION

By linking detailed field data on biology and hydrography, our study reveals a mechanism for explaining fine-scale retention of pelagic eggs in fjord populations of pelagic spawners such as the Atlantic cod. We show that cod eggs are found in greater abundance in the top (15 m) of the water column, where water masses are on average flowing toward the inner parts of the fjord and where water currents are gradually dampened. Those fewer eggs that are found at greater depths have a nearly homogeneous distribution along the fjord. However, circulation reversal events occur, in which water exchange in the entire fjord takes place. Therefore, a clear evolutionary advantage to spawn in the inner part of the fjord is expected, where reversal events are less likely to flush eggs out of the fjord and where current speed is lower and the local topography of the fjord most likely inhibits the water exchange with the outer parts of the fjord and the coast. From typical current speeds in the outer part of the fjord (0.1–0.2 m/s) we must expect exchange of the water masses in each layer within a few days.

We contend that small-scale egg retention is the key mechanism in the explanation of the consistent high density of eggs inside the fjord (Knutsen et al. 2007) and ultimately the maintenance of local population structure over time. Our study does not include the larval stage, and egg retention mechanisms cannot be representative of patterns occurring later during the early life cycle (i.e., larval stage). However, a complete retention throughout the entire duration of the early life stages is not necessary to guarantee genetic isolation of the adult stocks, as long as older individuals have strong homing behavior at any stage of their life (Svedäng et al. 2007). In the particular case of these coastal cod populations, evidence from other studies strongly points to the fact that individuals complete their entire life cycle within the fjord. For example, there is a marked difference in macroparasite fauna between newly settled juveniles captured within and outside the fjord habitats (Schulze

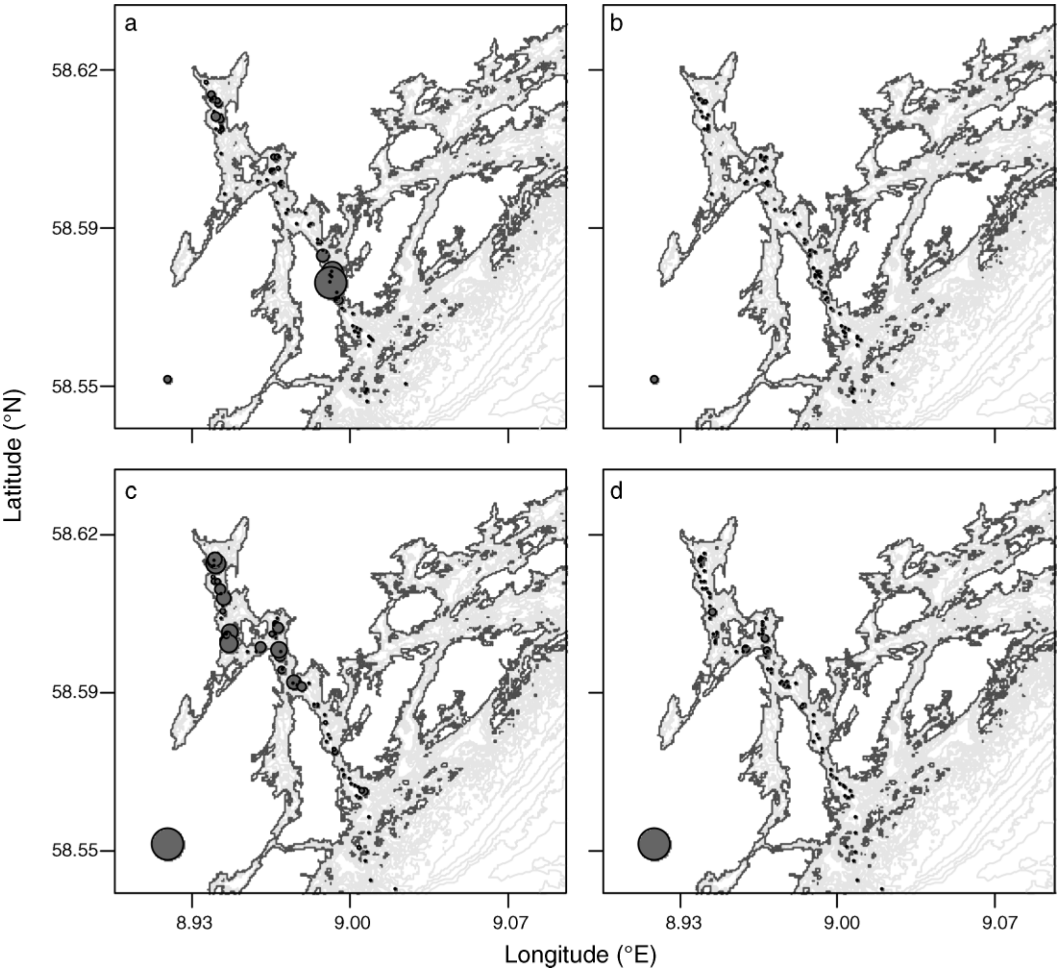

FIG. 6. Distribution of cod eggs during (a, b) 2006 and (c, d) 2007. (a, c) The distribution of eggs caught in the upper 0–15 m of the water column; (b, d) eggs caught below 15 m. The size of the circle is proportional to the standardized number of eggs caught within each year. A reference circle (lower left corner), equal to 20 eggs/m, is added to each panel for reference. All egg developmental stages are included in the plots.

2006). Tagging studies have indicated that there is high site fidelity of older life stages captured within a fjord (Espeland et al. 2008). Finally, genetic studies of juvenile cod from the Gulmar fjord on the Swedish Skagerrak coast also show significant differences between inner and outer fjord areas (Øresland and André 2008).

We found large variability of cod egg buoyancy among locations/hauls. The statistically strong effect that the interaction term between stage and location had in explaining the observed patterns of egg buoyancy indicates that the within-sample variability (i.e., egg-to-egg differences) was subordinate to the among-sample variability (i.e., due to stage or location). The apparent correspondence between egg distribution predicted from the salinity and observed in the field suggests that the among-sample variability is of a biological nature as opposed to measurement errors. If the variability is of a biological nature, it is likely that at each sampling event we capture eggs originating from a single or very few spawning individuals. Possible factors contributing to changes of egg buoyancy are maternal effects as well as egg quality differences among different batches. In the Baltic Sea, for example, eggs spawned by large and older females are less dense and more buoyant than those from young females (Vallin and Nissling 2000). Also, batch number can influence the egg size and its buoyancy, generally with smaller and denser eggs in later batches (Vallin and Nissling 2000).

The genetic analysis on mature cod from the Skagerrak system indicates that there is a limited amount of gene flow among different fjord populations and that genetic isolation among fjords separated by more than 30 km is not related to distance (i.e., fjord populations that are 30 km apart are just as different from one another as fjord populations that are $\gg$30 km apart; Knutsen et al. 2003, Jorde et al. 2007). In the present analysis we found a high variability of both circulation patterns and vertical egg distribution, sug-

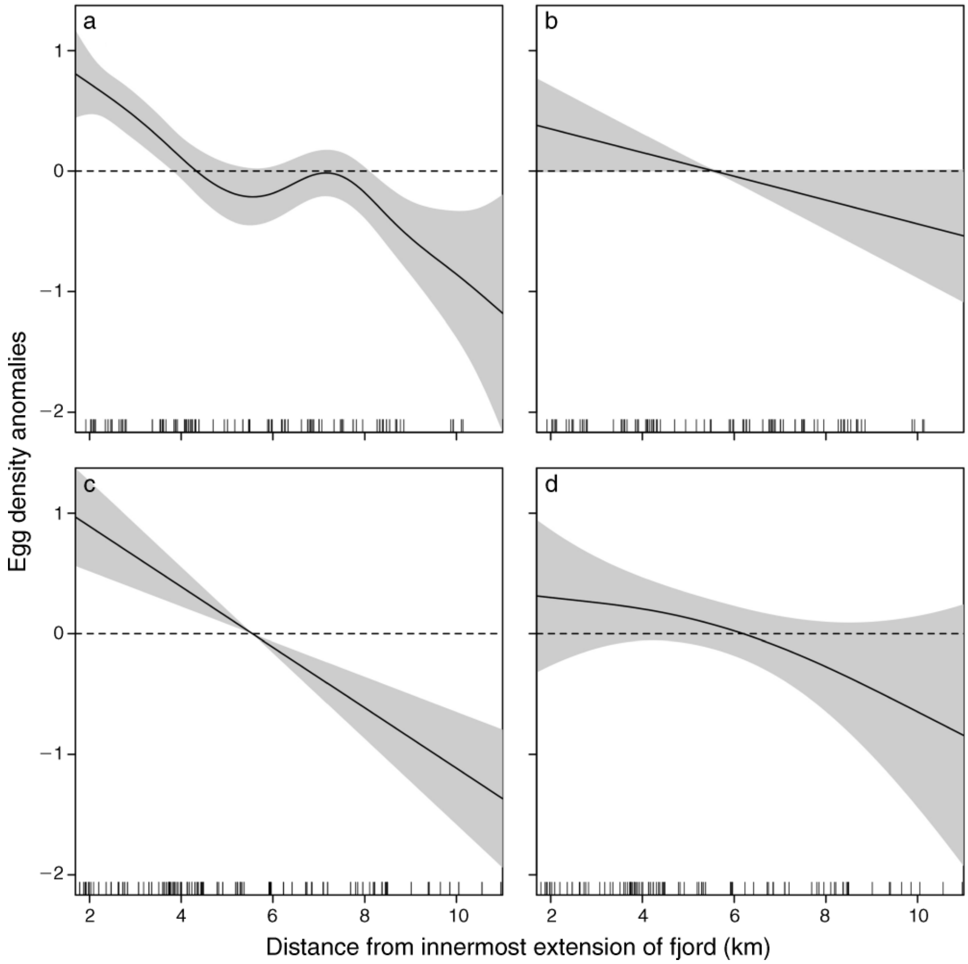

FIG. 7. Anomalies of egg densities as a function of distance from a fixed inshore location as predicted from a generalized additive model (GAM). Four different functions were fitted within a single model; (a) 2006, ≤15 m ($P \ll 0.001$); (b) 2006, >15 m ($P = 0.123$); (c) 2007, ≤15 m ($P \ll 0.001$); (d) 2007, >15 m ($P = 0.193$). The solid lines are estimated mean effects, the gray areas are 95% point-wise confidence intervals, the horizontal dashed lines are references for a null effect (0), and ticks along the *x*-axes are points at which observations were obtained.

gesting that the within-fjord retention mechanisms are not perfect. Some confined levels of egg "leaking" are therefore expected. This also conforms to genetic findings concluding that the very limited gene flow was unrelated to distance and therefore more likely to occur at the early pelagic stage than during older life stages known to be stationary (cf. Knutsen et al. 2003). However, we contend that these vagrant individuals

TABLE 1. Results of the parametric portion of the cod (*Gadus morhua*) egg generalized additive model (GAM) for Tvedestrand fjord, southern Norway.

Intercept terms	Estimate value	SE	*F*	*P*
≤15 m, 2006	−0.743	0.059	160.3	≪0.001
>15 m, 2006	−2.152	0.117	337.7	≪0.001
≤15 m, 2007	−1.942	0.125	241.8	≪0.001
>15 m, 2007	−2.645	0.165	257.2	≪0.001
Outlier	3.129	0.162	373.6	≪0.001

Notes: The model assumed a Poisson distribution of the egg count with log-link function. It contained four intercept terms, specific to each pairwise combination of year (2006, 2007) and depth strata (≤15 m, >15 m) sampled. It also had an outlier effect in correspondence of the 2006 high egg density observed near the T4 current meter. *P* values refer to the null hypothesis that the estimated value of each intercept term is equal to zero. The 95% CI for each intercept estimate can be obtained by subtracting and adding 1.96 times the respective SE estimates. The smooth function of distance from shore is shown in Fig. 7.

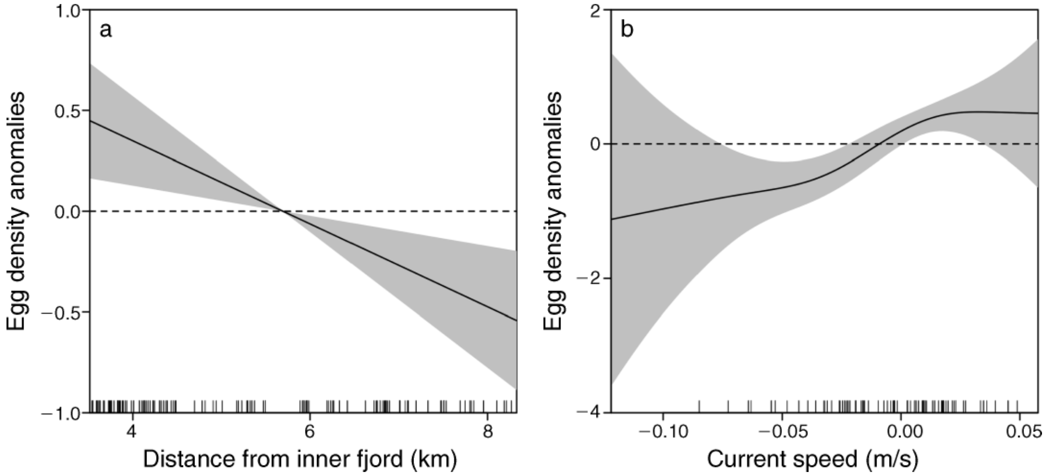

FIG. 8. Anomalies of egg densities as a function of (a) distance from a fixed inshore location and (b) current speed in the water layer in which the eggs were found, as predicted from a generalized additive model (GAM). Positive currents indicate up-fjord flow (toward the inner fjord), while negative currents indicate down-fjord flow (toward the open ocean). See Fig. 7 for an explanation of graph features.

would encounter a limited chance of successful survival. In fact, eggs leaking out the fjord have very little chance of reentering another fjord, as they would have to enter a very narrow opening while drifting within a highly variable flow pattern.

Considering the observed current patterns, the fjord flow seems to be mostly controlled by the large-scale coastal winds and the subsequent change in water mass density structure outside the fjord as previously described by Aure et al. (1996). The coupling with the along-coast wind and the along-fjord flow in the shallow and deep layers of the water column is relatively strong. Southwesterly winds at the coast will push surface water offshore (due to classical Ekman transport) and create a coastal upwelling. This again produces heavy water at depth outside the fjord mouth and inflow to the fjord in the lower layer and outflow in the upper layer. For northeasterly winds the mechanism is opposite, with onshore Ekman transport and coastal downwelling, with inflow to the fjord in the upper layer and outflow in the lower. Thus, this two-layer circulation does not originate inside the Tvedestrand fjord but offshore in the Norwegian Coastal Current. This described pattern contrasts with the classic estuarine circulation in which up-fjord flow in the upper layer can be mistakenly thought to be compensation current due to entrainment of water in the brackish surface layer. This is an unlikely scenario for these fjords since there is no major freshwater runoff at this time of year. Variability that cannot be related to along-coast winds might stem from variability in the coastal ocean hydrography due to internal waves or effect of the local wind fields and local topography.

TABLE 2. Equivalent cod (*Gadus morhua*) egg salinities in 2006 for Tvedestrand fjord, southern Norway.

Location	Date	Latitude (°N)	Longitude (°E)	Stage	*N*	Salinity Mean	Salinity SD
Inner	26 Mar	58.61	8.94	1	37	32.78 (a)	1.18
Inner	26 Mar	58.61	8.94	2	18	32.63 (a)	1.64
Inner	27 Mar	58.60	8.97	1	26	32.60 (a)	1.30
Inner	27 Mar	58.60	8.97	2	27	29.55 (b)	1.62
Outer	25 Mar	58.57	8.99	1	33	26.97 (c)	0.14
Outer	25 Mar	58.57	8.99	2	17	28.52 (b)	0.61
Outer	25 Mar	58.56	9.00	1	33	32.29 (a)	1.32

Notes: The letter index in parenthesis after the mean values indicates the results of a Tukey honestly significant difference test. Mean pairs with similar indices are not statistically different from one another ($\alpha = 0.05$). *N* is the number of eggs used in buoyancy measures (expressed as equivalent salinity). "Inner" refers to the inshore region of the fjord, in the proximity of the T2 current meter; "outer" refers to the offshore region of the fjord, in the proximity of the T4 current meter (see Fig. 1). Eggs were staged as: 1, no visible larvae inside; or 2, visible larva inside, indicating that the egg was ready to hatch.

An intriguing question is why such a local population structure, involving retention of early life stages and site fidelity of older life stages, has evolved. What is the fitness advantage of fjord-specific home ranges? Clearly, other cod stocks such as the northeast Arctic cod are doing fine by spawning in more exposed coastal areas, allowing the offspring to be transported by ocean currents to fairly remote offshore nursery areas (Bergstad et al. 1987). It could be argued that this is all about adaptations being scaled to the opportunities and challenges offered by specific environments. Darwin (1872:72) pointed out that animals "do not needlessly wander about," but tend to have fairly restricted movement patterns. One possible scenario is that retention mechanisms are favored through coevolution with other traits exposed to local selection regimes, i.e., retention of early life stages may involve a fitness advantage when other advantages accrue through local adaptation (Conover et al. 2006). There is indeed evidence for such local adaptations in life history traits in Skagerrak coastal cod (Olsen et al. 2008). Furthermore, since the parental (fjord) habitat is demonstrably of sufficient quality for survival and reproduction (Espeland et al. 2007, Olsen et al. 2009), there is a strong argument in favor of retention, especially if the probability of encountering superior adult habitat by dispersal is low (Strathmann et al. 2002, Almany et al. 2007).

In summary, we have provided evidence that a balance between egg characteristics and small-scale water circulation patterns favors the retention of cod eggs within the fjord system. Ultimately, this retention allows the formation and maintenance of a fine-scale population structure of coastal cod in the Skagerrak fjord system. Our study adds to the growing understanding that marine fish, although found in a relatively open environment, can form local populations by taking advantage of small-scale circulation and hydrography features to which they are well adapted. This study also underscores the importance of preserving spawning and nursery areas at a local scale in order to preserve the genetic diversity and ultimately the resilience (sensu Hilborn et al. 2006) of the Skagerrak coastal cod.

ACKNOWLEDGMENTS

This work was funded by the Norwegian Research Council and the Norwegian Ministry of Fishery and Coastal Affairs. We thank Øivind Østensen, Hanne Sannæs, Kate Enersen, Svein E. Enersen, Jan Erik Stiensen, and Jan Henrik Simonsen for assisting during field and laboratory work. Valerio Bartolino and two anonymous reviewers provided valuable comments on an earlier draft of the manuscript. L. Ciannelli acknowledges partial support from the NSF (CMG-0620789) and the OSU International Programs Faculty Grants and Awards.

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