Home range and elevated egg densities within an inshore spawning ground of coastal cod

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Atlantic cod (Gadus morhua) along the Norwegian Skagerrak coast are structured into genetically distinct local populations. Mechanisms contributing to this genetic structure may include spawning site fidelity of adult cod as well as retention of pelagic early life stages close to the spawning grounds. Spawning in sheltered inshore localities is likely to favour retention of eggs and larvae, the opposite situation to offshore spawning. A combined study was made of area utilization by adult cod and the distribution of cod eggs within an inshore locality of the Norwegian Skagerrak coast. The behaviour of adult cod was studied using acoustic telemetry and kernel modelling, and eggs were sampled throughout the spawning season. Generalized additive models were applied to test hypotheses about the spatial dynamics of the eggs, and the best model described a central spawning area that retained its integrity through time. Adult cod were confined to small parts of the study area and remained there throughout the spawning season. The average home range of the adult cod was 27 ha. Overall, the study demonstrated two mechanisms by which coastal (i.e. inshore) cod maintain their population structure: spawning site fidelity and the spatial dynamics of their eggs.

Keywords: Atlantic cod, egg retention, Gadus morhua, home range, local populations, spawning, stock structure.

Introduction

Marine species display a great variation in population structure (Ward, 2006). Hence, knowledge of population structure is important both for understanding biological processes and for implementing sustainable management. Different mechanisms may either enhance or erode population structure. These mechanisms may include lifelong behavioural effects such as year-round site fidelity or accurate homing to the natal spawning area (Robichaud and Rose, 2004), but also short-term mechanisms operating within a specific spawning season. Retention of planktonic life stages close to the spawning area may promote population structure. Advection of pelagic early life stages (eggs and larvae) by ocean currents will tend to break down local population structure, if the dispersers survive and spawn in non-natal areas (Waples, 1998). Spawning in inshore areas sheltered from strong currents could reduce such passive drift of eggs and larvae and help to maintain local self-reproducing units (Hastings and Botsford, 2006).

The Norwegian Skagerrak coast holds a complex of genetically distinct populations of Atlantic cod (Gadus morhua), with small but significant neutral genetic differentiation at a scale of only a few tens of kilometres (Knutsen et al., 2003, 2004). Many of these populations also differ in adaptive traits (Olsen et al., 2004). It is already known that the cod spawn inshore, perhaps to minimize the advection of eggs. The spawning grounds are typically separated by just a few tens of kilometres (Knutsen et al., 2007). On a year-round basis, there is evidence that the Skagerrak coastal cod are fairly stationary, most (>90%) marked fish being recaptured less than 20 km from their point of release (Danielssen and Gjøsaeter, 1994) and indicating a high degree of site fidelity between spawning events. However, with the distance between spawning areas being short, cod would also need to show good site fidelity throughout the spawning season.

We used hydro-acoustic equipment to monitor movements of mature fish on a fine spatial and temporal scale. Such methodology has been widely used to track various gadoid species (Hawkins et al., 1974; Clark and Green, 1990; Robichaud and Rose, 2001; Cote et al., 2004). Next, we use generalized additive models (GAMs) to describe the spatio-temporal dynamics of cod eggs in the same region, so adding to current knowledge by estimating the home range of adult cod throughout the season, and at the same time investigating the spatio-temporal dynamics of their eggs.

Material and methods

The study was conducted in the strait between the island of Tromøya and the mainland (58°29′N 8°51′E) on the Norwegian Skagerrak coast (Figure 1). The strait is open to the sea at both
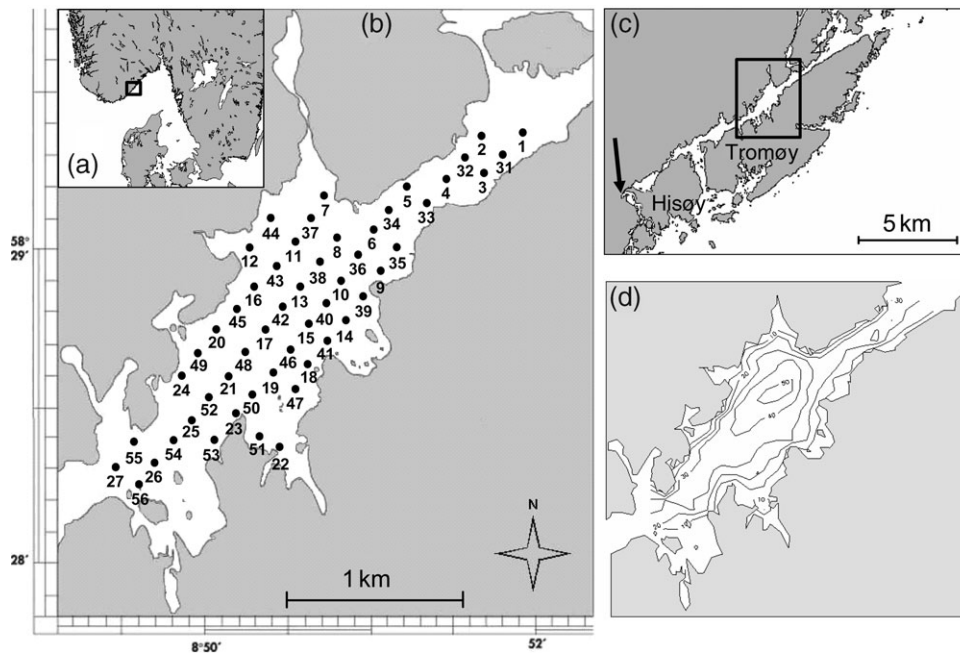
Figure 1. (a) Location of the study area in Norway. (b) Egg sampling stations throughout the study area; sampling alternated between stations 1–27 and 31–56. Buoys for tracking ultrasonic transmitters were located at stations 49, 19, and 16. (c) The region around the study area, showing the Tromøysund strait and the islands of Tromøya and Hisøya to the south; the arrow indicates the outflow of the River Nidelva. The island of Buøya, referred to by Olsen *et al.* (2004), is located in the top right corner of (b). (d) Depth contours.

ends, and the distance to open water is 9 km (in a southwest direction) and 7 km (to the northeast). The average water depth is 30 m, but deeper areas extend down to 50–60 m. Within the study area, there are sills at both ends 25 m deep. There is considerable water replacement of surface water of the strait, but the water is stagnant at deeper levels (Dahl and Danielssen, 1986). Coastal cod from the Tromøy strait are genetically different from cod in neighbouring fjords, and form part of a network of local populations typically separated by only a few tens of kilometres (Knutsen *et al.*, 2003). The study took place during 64 d from 8 February to 12 April 2001, of which ultrasonic tracking was conducted from 8 February to 22 March and sampling of eggs from 23 February to 12 April. Eggs were sampled 18 times during the 48-d period, with vertical tows made with a WP2 net of diameter 0.46 m and mesh size 320 μm. The tows were usually made from 30 m deep to the surface, meaning that in shallow water the tows covered the whole water column. The tows were conducted on 53 stations arranged in a square grid covering the target area. Because of limited daylight, not all stations were sampled in a single day, so sampling effort was divided between two sets of stations (Figure 1). Every second station in the grid (1–27) belonged to set A and the rest (30–56) to set B, and both sets covered the entire geographical extent of the target area. Eggs were preserved in 4% formalin. On 28 March, four hauls were made from the bottom to the surface and three from 10 m to the surface at stations 1 and 21. The results of these hauls indicated that most eggs (>88%) were collected deeper than 10 m.

The number of eggs in each sample was enumerated, but because of the large number of eggs found, the diameters of only 20% from each sample were measured and identified; the raised numbers of cod eggs in the subsamples were used in subsequent analyses. The eggs were identified to species by combining diameter and pigmentation

pattern of eggs in late stages of development. The cod eggs were at a variety of developmental stages, but these were not recorded for each egg individually. In the later part of the study period, several larvae were also caught. The diameters of eggs were measured taking into account a shrinkage of formalin-preserved eggs of ∼7% (Hiemstra, 1962). Eggs with an original diameter from 1.11 (Hiemstra, 1962) to 1.67 mm (Ehrenbaum, 1905) were defined as cod eggs. In all, 3343 eggs were measured and 2377 were identified as cod eggs. The number of cod eggs from each subsample was divided by the station depth and plotted against depth, latitude and longitude of the station, and day sampled (Figure 2). Those eggs not identified by this method as cod had size distribution peaks of 1.02, 1.87, and 2.3 mm and were presumed to be of *Platichthys flesus*, *Trisopterus minutus*, *Merlangius merlangus*, *Microstomus kitt*, and *Pleuronectes platessa*. It is easy to misclassify early stages of cod and haddock eggs (Hurley and Campana, 1989; Lough *et al.*, 1996; Bradbury *et al.*, 2000), but information from local fishers is that the area does not hold adult haddock.

Ten cod were tagged with ultrasonic transmitters and tracked using a stationary positioning system (VRAP, Vemco Ltd, Shad Bay, Nova Scotia, Canada) capable of discriminating up to ten different transmitters. The system consisted of three hydrophone buoys arranged in a triangle 600–900 m apart. Positions were calculated based on the relative delay of pulse arrivals at the hydrophones and could be calculated up to 1 km outside the buoy triangle, depending on ambient conditions. Environmental noise and echoes may contribute to error in position calculation, so a stationary transmitter was used to assess the precision of the positioning system. For a transmitter held stationary within the triangle for 1 h, all calculated positions fell within a 5 m^2 area. When the transmitter was held 370 m outside the triangle, the positions calculated had a wider margin of error (34 m^2).
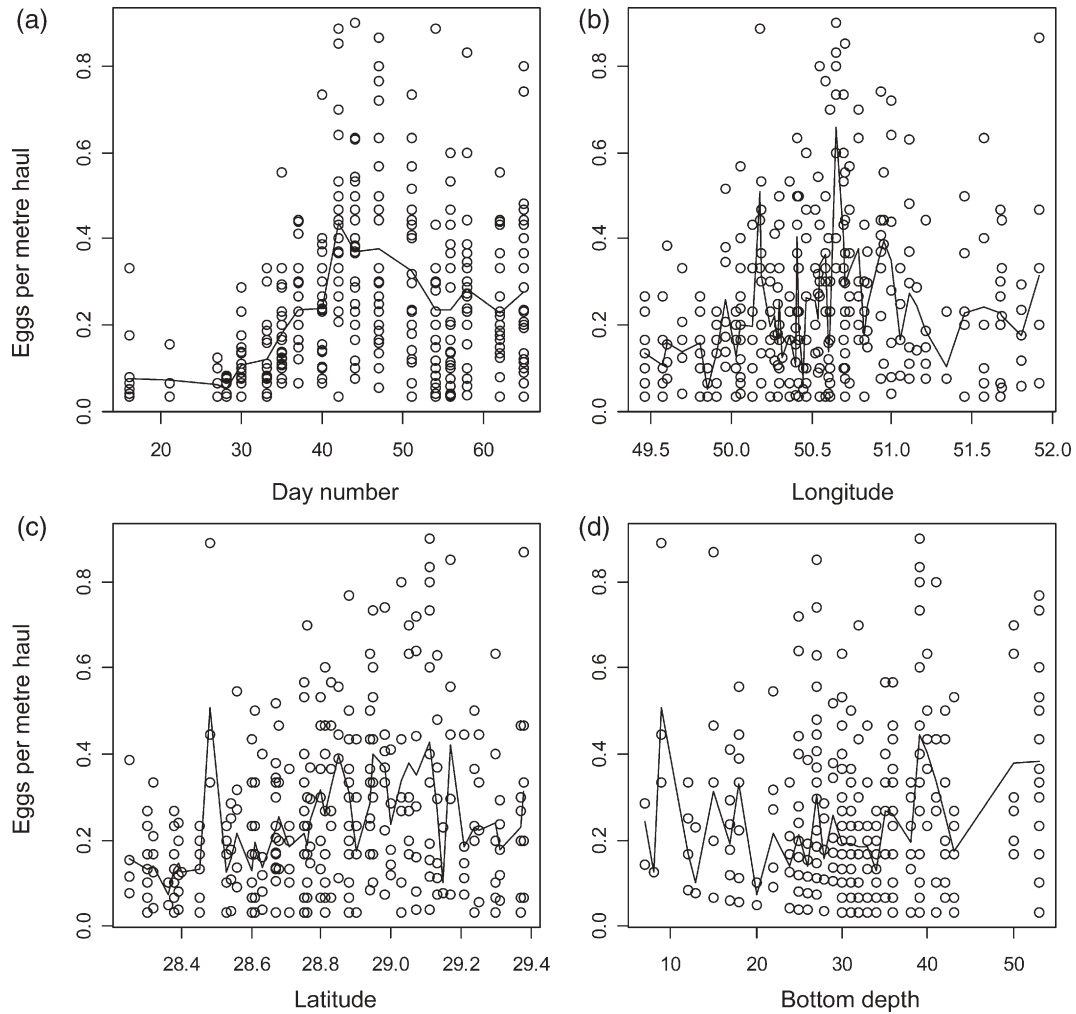
Figure 2. The number of eggs per metre as a function of four variables. Eggs per metre haul is the number of cod eggs in the 20% subsamples, divided by the depth of the station. The solid lines connect the average number of eggs per metre for each variable. The four variables are (a) day number, (b) longitude and (c) latitude at the sampling stations, and (d) bottom depth at the sampling station.

Therefore, home ranges extending far beyond the triangle may be somewhat overestimated.

A local fisher deploying eel pots caught all ten cod used for this study, over a period of time and in several locations within the study area. Cod ranged in size from 55 to 79 cm, and based on this relatively large body size, all were assumed to be sexually mature (Olsen *et al.*, 2004). Cod were tagged with surgically implanted ultrasonic transmitters (Vemco, continuous V16-6L). measuring 90 × 16 mm, weighing 37 g (14 g in water), and consti- tuting 0.8−2% of the fish body weight. Fish were anaesthetized in a 7:20 000 solution of quinaldine, and after surgery, kept in tanks for 2−3 d to ensure that they had recovered fully. They were then released. Recent studies have shown that such transmitters can be used effectively on marine fish, inserted gastrically (Lucas and Johnstone, 1990; Winger and Walsh, 2001; Winger *et al.*, 2002) or surgically (Comeau *et al.*, 2002; Bridger and Booth, 2003; Cote *et al.*, 2004). Our surgical procedures were also tested for any effect on behaviour prior to the study (Espeland, 2002); no behavioural effects were found.

During tracking, formation and break-up of ice occasionally moved the hydrophone buoys. Positions recorded during such

Table 1. Home range estimates for the ten fish released in the strait.

Fish number	$\alpha = 0.50$ area	$\alpha = 0.90$ area	Ratio of logged signals	Number of positions
1	20.88	77.33	0.17	179
2	5.90	17.62	0.80	561
3	0.74	3.38	0.92	1679
4	2.03	6.72	0.43	24
5	3.63	10.38	0.92	1035
6	19.01	59.32	0.92	22
7	–	–	0.29	1
8	1.17	3.05	0.49	423
9	0.77	3.44	0.82	1569
10	13.12	62.13	0.93	365

Fish number is the identity of the fish. The column $\alpha = 0.50$ area is the area in ha covered by 50% of the utilization distribution (UD), and $\alpha = 0.90$ area is the area covered by the home range, or 90% of the distribution. Ratio of logged signals is the number of times a transmitter was searched for, and any buoy recorded a signal (all three buoys had to record the same signal to calculate a position fix). Number of positions is the number of fixes used to calculate each home range.
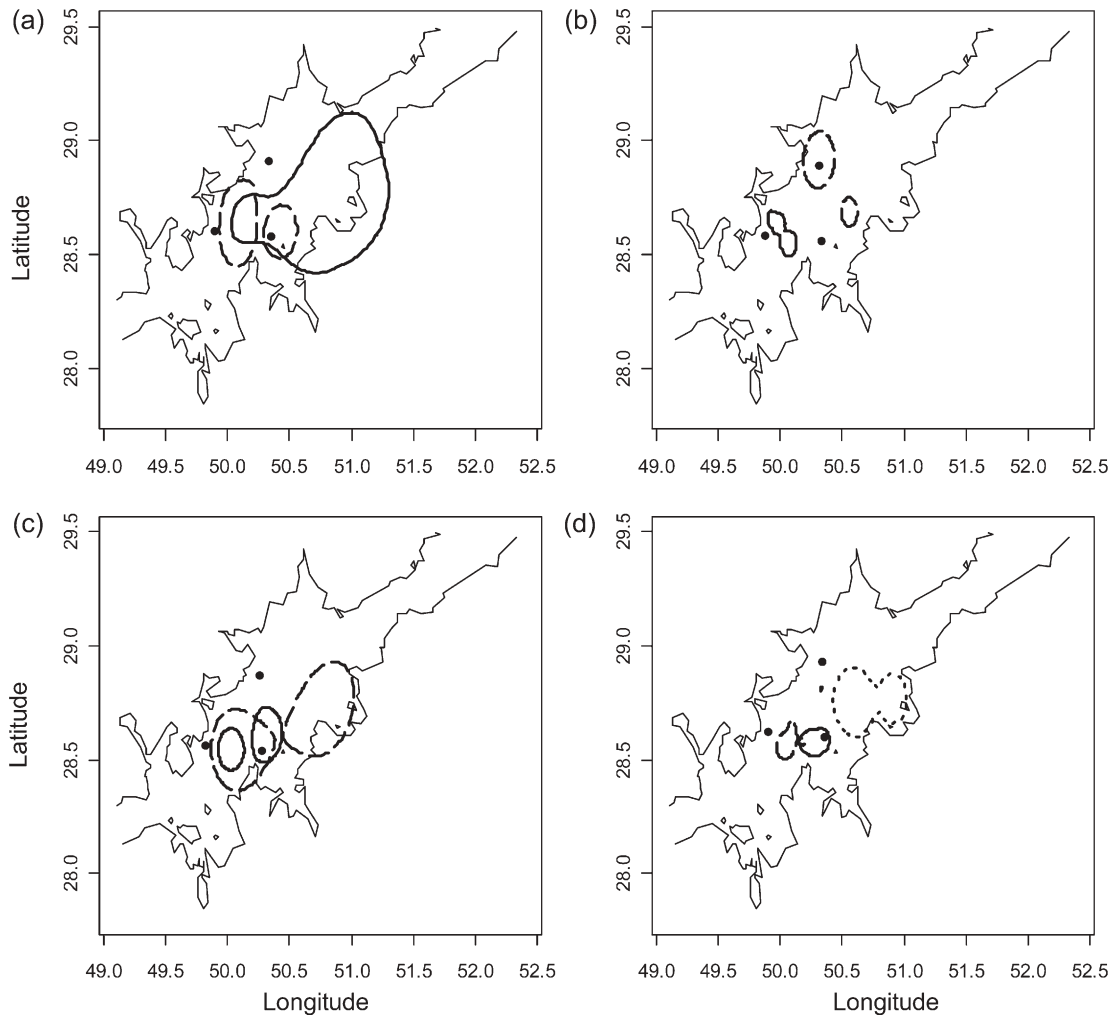
Figure 3. Home ranges for nine fish tracked in the strait from 12 February to 22 March 2001. (a) Cod numbers 1 and 2, (b) cod numbers 3 and 4, (c) cod numbers 5 and 6, (d) cod numbers 7–9. The solid dotted and dashed lines delimit the home ranges for each fish. Dots indicate the locations of the buoys in the VRAP system.

periods, as well as immediately after release (1–4 d) and obviously false positions, were excluded from the analyses. Rocks and rough ground can easily reduce the accuracy of a position fix, so the number of fixes for each fish varied (22–1679 for nine fish, and one fix for one fish). The three buoys had to be hit by the same signal for a position to be calculated. The number of positive signal detections by each buoy was compared with the total number of possible detections to give the ratio of time a transmitter was detected (Table 1). Manual tracking was conducted on several occasions to locate fish that could not be detected with the VRAP system, intensively throughout June and occasionally thereafter (when tracking with the VRAP system had ended).

Studies of home range and area utilization are well developed within the field of terrestrial biology (Mohr, 1947; Jennrich and Turner, 1969), and development of various statistical tools has facilitated the concept of utilization distribution (UD). It can be defined as "the two-dimensional relative frequency distribution for the points of location of an animal over a period of time" (Winkel, 1975). Methods to estimate the UD of an animal include a non-parametric method of kernel density estimation, introduced by Worton (1989), a method consisting of placing a

kernel (a symmetrical density function) above each position in the sample. Then, by superimposing a grid on the data, the sum of the kernel density distributions can be identified at each grid intersection, and the overall frequency distribution of the sample can be deduced.

A kernel UD was estimated for each fish (Kenward and Hodder, 1996), using the formula below to give the frequency distribution:

$$f(x,y) = \left(\frac{1}{nh^2}\right) \sum_{t=1}^{n} K\left\{\frac{1}{n}[K(x) - x_t, E(y) - y_t]\right\}, \quad (1)$$

where n is the number of observations and x and y the coordinates of the position fixes. $E(x)$ and $E(y)$ are the expected average positions calculated as arithmetic means of the sample. The kernel K is a unimodal symmetrical bivariate probability density function, and h is the smoothing parameter (describing the weight of the tails of kernel K). In this study, a fixed kernel distribution was estimated for each individual range with the smoothing parameter set at $h_{ref} = n^{-1/6} \sigma$, where σ is the standard deviation of the coordinates of the positions. We did not choose h based on least
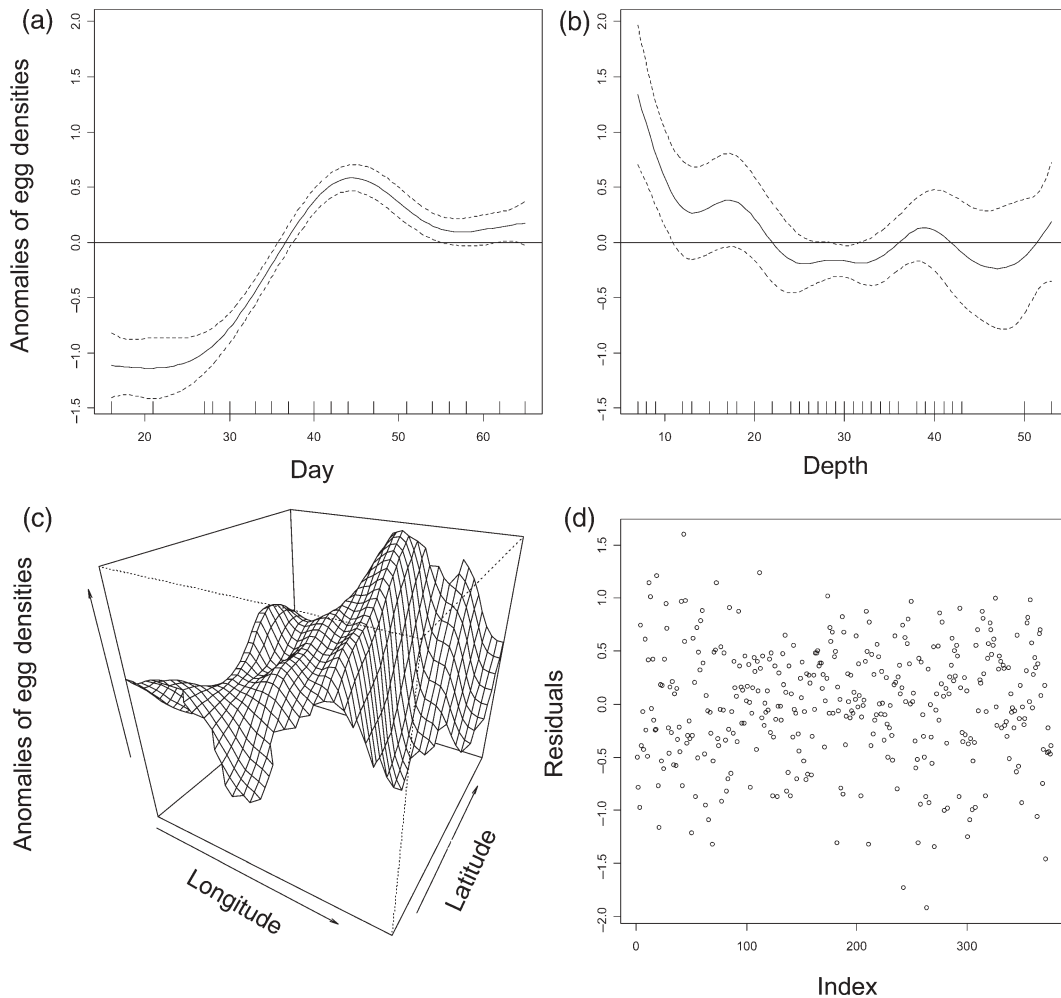
Figure 4. Results from the basic GAM model (2). Effect of (a) day and (b) bottom depth on the anomalies of egg densities. The horizontal lines give value zero, or no significant deviance. (c) The effect of geography on anomalies of egg density modelled as a smooth surface. (d) Plot of residuals of the model.

square cross validation (LSCV) because it may create an over-fragmented distribution (Blundell et al., 2001; Hemson et al., 2005).

Different values of α may be used to describe different percentages of the mass of the distribution. $\alpha = 0.90$ was considered as containing the home range area. Autocorrelation can cause an underestimation of home range (Swihart and Slade, 1985), but reducing the number of positions to achieve independence may cause bias because of small samples (Hansteen et al., 1997; Rooney et al., 1998; De Solla et al., 1999). Therefore, we did not attempt to reduce the autocorrelation. Here, we included all the distributions we calculated, but those based on samples with fewer than 30–50 position fixes may be biased compared with true distributions (Seaman and Powell, 1996; Seaman et al., 1999).

The spatial and temporal distribution of cod eggs was modelled with GAMs (Hastie and Tibshirani, 1990). The response variable (y) was the natural logarithm of egg density, standardized by volume filtered (eggs per metre hauled). Hauls containing zero eggs and hauls not sampled because of ice presence (100) were excluded from the analyses. The models were also tested using null data with no major differences. Predictor variables were the

bottom depth at each sampling station (d), day (t), longitude (x), and latitude (z). Model selection was based on the generalized cross validation (GCV) criterion (Wood, 2000). Residual plots were used for checking the fit of the models.

Results

Home ranges ($\alpha = 0.90$) of mature fish were estimated from the positions observed for nine fish (Table 1, Figure 3). The average home range size was 27.04 ha (3.05–77.33 ha). One fish did not yield sufficient positions to calculate a UD, but manual tracking confirmed that the fish was present throughout the study period. After removal of the buoys in late March, three fish (numbers 2, 3, and 6) disappeared altogether (i.e. moved >10 km from the release point), and two (8 and 9) moved intermediate distances (5 and 7.5 km); the other four stayed in the study area. Three stopped moving totally during summer (1, 4, and 7) and were therefore classified as dead. Two of the fish originally released (5 and 9) were taken by fishers during summer, and the other two fish remained in the area until the next spawning season (February/March 2002).

Our general model [formulation (2) below] describing the spatial and temporal distribution of cod eggs had bottom depth
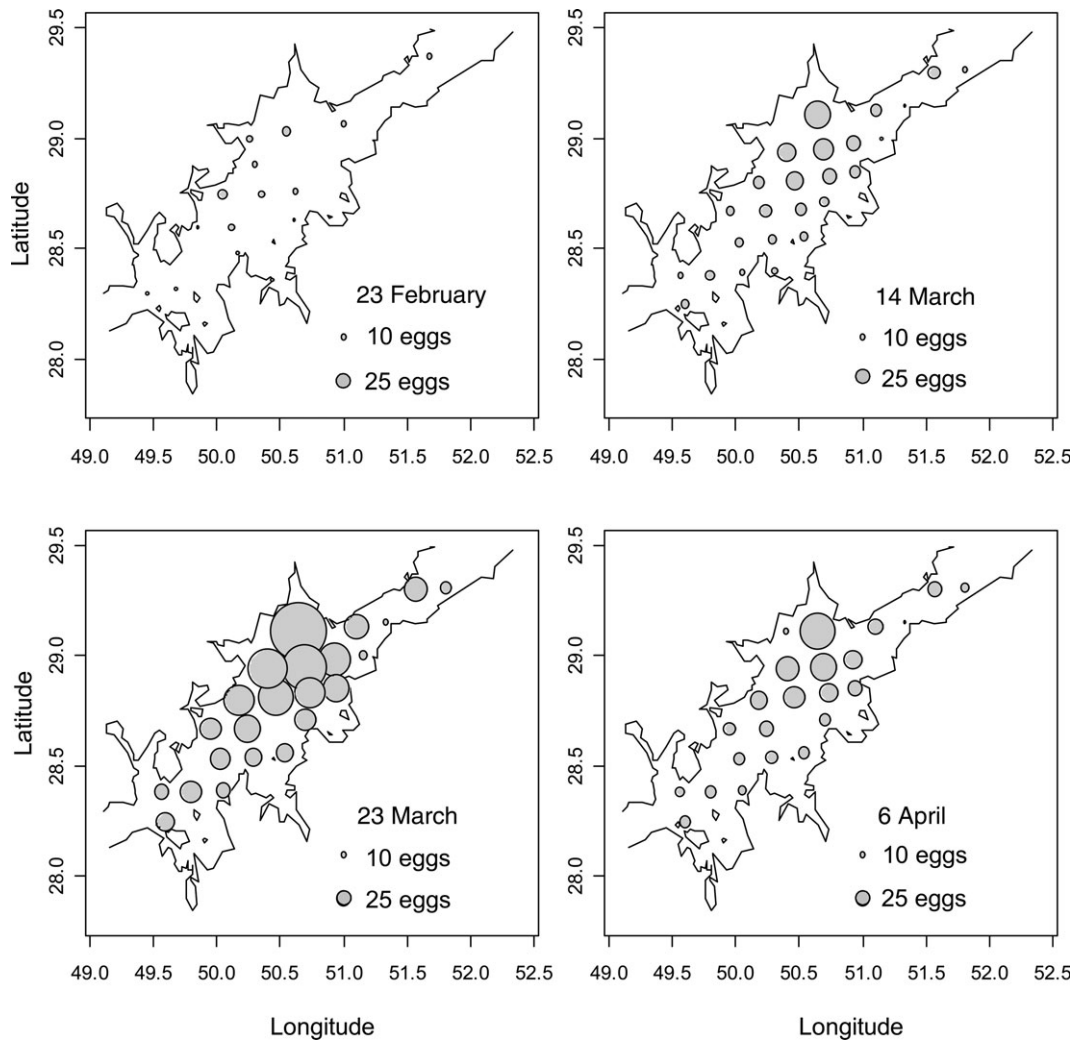
Figure 5. Predictions of egg densities from the basic model (2) for four different dates in the study period. The scale of the circles is the number of eggs in the total sample, backcalculated from the subsamples.

and day number as additive effects, and latitude and longitude modelled as a smoothed surface (Figure 4):

$$y = k + g_1(d) + g_2(t) + g_3(x,z) + \varepsilon, \quad (2)$$

where k is the intercept, g_n the smoothing functions, and ε the error term. The model had a GCV of 0.38, and was superior to more constrained models that exclude one or more covariates (GCV > 0.41). Egg density increased throughout the spawning season, peaked, then declined to a more moderate level (Figure 4). The effect of bottom depth on egg density was less clear, but egg densities tended to be high in the shallower areas (Figure 4). Densities peaked in the central northern region of the study area and dropped towards the east and were moderate south and southwest of the northern peak (Figures 4 and 5).

Our general starting model (2) considered the temporal dynamics to have the same effect anywhere, indicating no shift in the distribution of cod eggs. To test the stability of the density patterns through time, we built a more complex model (3), in which day (t) was considered to interact with depth (d), latitude

(z), and longitude (x):

$$y = k + g_1(t) + g_2(d,t) + g_3(x,t) + g_4(z,t) + \varepsilon. \quad (3)$$

In model (3), neither the stand-alone effect of day nor the interaction between day and longitude were significant, so they were removed. The interaction effects did not improve the fit over the basic model (2), and the alternative model (3) had a slightly higher GCV (0.39). The difference in the two models is not only through the interaction effect of time, but also through a lesser performance in modelling the geographical effect as additive rather than as a smooth surface, as in the basic model. This can be seen when comparing basic model (2) with a GCV of 0.38 with a model with a purely additive effect (GCV 0.41), so model (3) may have some support. When considering the terms of the interaction model (Figure 6), most variation in the day–latitude interaction seemed to be derived from increasing egg densities over time. Early in the period, there seemed to be equal numbers of eggs in the north and the south (for a given day, there was little difference between northern and southern locations). Moving through time, the density increase in the
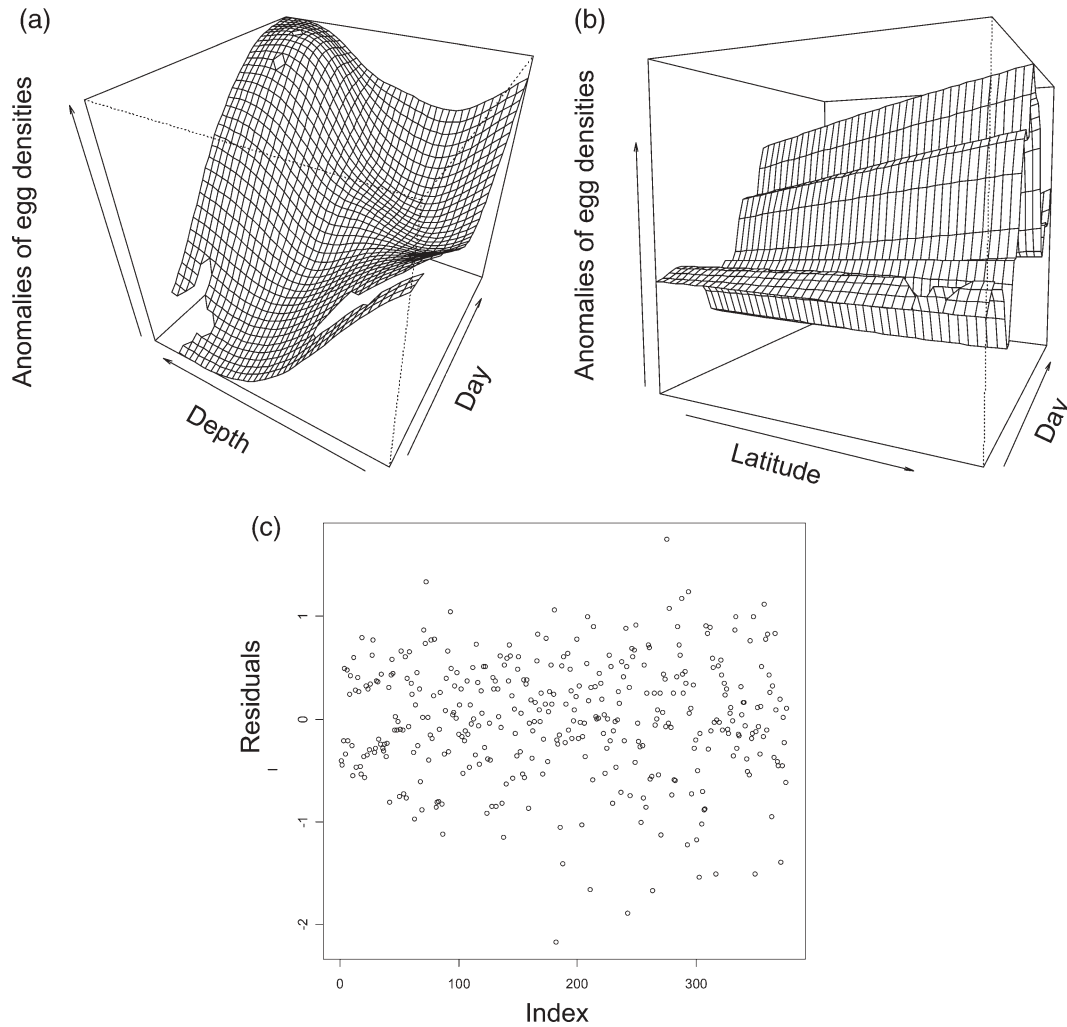
Figure 6. Results of the model describing day as interacting with depth and latitude. The upper panels show the effect of the two interactions: (a) day with depth and (b) day with latitude. (c) Plot of residuals of the model.

northern area was greater than in the south, resulting in relatively more eggs in the northern locations when spawning peaked. The interaction effect between day and depth revealed an increase in the number of eggs in the deeper locations as spawning progressed.

Discussion

Several mechanisms may work to enhance or erode small-scale population structure in marine species. Here, we highlight two mechanisms working within the spawning season that may help to explain why local populations of coastal cod are able to persist along the Norwegian Skagerrak coast (Knutsen *et al.*, 2003). First, the inshore distribution of eggs suggests inshore spawning activity, and the stability of the distribution throughout the spawning season is indicative of inshore retention of the early life stages. Second, we found a high degree of site fidelity of adult cod in the area during the spawning season, evidenced by acoustic tracking.

On the spawning ground, the greatest egg densities were in a central basin, with no significant shift in location of egg densities through time. We found evidence for a temporal peak in egg densities, likely to describe the peak of the spawning season (Kjesbu, 1989). Absence of a clear drop in egg density after the peak

suggests that cod eggs are being retained within the basin. These results are consistent with previous findings (Knutsen *et al.*, 2007). In fjords, where physical structures such as a sill influence the concentration of eggs and the topography of the basin, the same structures may also influence water circulation and prevent dispersal of eggs and larvae.

There was some evidence for a weak shift in egg densities northwards through the strait over time. This temporal effect could be a weak current taking the eggs north, or perhaps a shift in the main spawning area. From comparing home ranges of cod with predictions of their egg density, we conclude that mature cod utilize areas slightly south of the highest densities. This can be an effect of the same weak current taking the eggs from the major spawning site north to the main hatching basin, or that the tagged cod were slightly unrepresentative of the population, implying that several untagged cod spawned slightly north of the study area.

The sample of mature fish that we tracked had a high degree of site fidelity. Not only did they confine themselves to the strait, but also to certain areas within the strait, utilizing areas much smaller than the total area available (160 ha). The home ranges were close to areas with high egg densities, although just south of the "hotspot". Manual tracking confirmed that the fish stayed in the

strait throughout the spawning season. Through spawning years, fish need to show either year-round site fidelity or accurate homing to their natal spawning area. However, our few adult fish precludes us drawing strong conclusions about homing tendencies in the population.

A sedentary behaviour of spawning fish and an indication of local retention of eggs is clear from our analysis. Local populations of coastal cod may spawn inshore to prevent advection of eggs and larva (Wroblewski *et al.*, 2005), and the results of this study demonstrate the effects of both mechanisms on a much smaller scale then previously documented (Bradbury *et al.*, 2000, 2003; Green and Wroblewski, 2000), in accordance with the observed geographic scale of earlier studies on population structure.

Acknowledgements

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