ICES Journal of Marine Science

ICES Journal of Marine Science (2012), 69(10), 1722–1728. doi:10.1093/icesjms/fss135

Is spawning time of marine fish imprinted in the genes? A two-generation experiment on local Atlantic cod (*Gadus morhua* L.) populations from different geographical regions

H. Otterå*, A-L. Agnalt, A. Thorsen, O.S. Kjesbu, G. Dahle, and K. Jørstad

Institute of Marine Research, POB 1870 Nordnes, N-5817 Bergen, Norway

**Corresponding Author: tel: +47 55238500; fax: +47 55238531; e-mail: haakon@imr.no*

Otterå*, H., Agnalt, A-L., Thorsen, A., Kjesbu, O.S., Dahle, G., and Jørstad, K. 2012. Is spawning time of marine fish imprinted in the genes? A two-generation experiment on local Atlantic cod (*Gadus morhua* L.) populations from different geographical regions. – ICES Journal of Marine Science, 69: 1722 – 1728.

Received 14 February 2012; accepted 27 June 2012; advance access publication 27 July 2012.

Spawning time (onset of spawning) in Atlantic cod (*Gadus morhua* L.) was monitored in an experimental setup and combined with modelled spawning time estimates from the wild. The experiment broodstock were collected from several geographical areas and kept in a common environment. Their spawning times in 2004 were compared with the spawning times of their daughters in 2009 and 2010. Daughter spawning time was highly correlated with that of the mother, indicating genetic regulation of spawning time. However, large individual variation in spawning time was observed. The modelling data suggests a north-south gradient in onset of spawning along the Norwegian coast, driven by differences in temperature, i.e. later dates of spawning in the north.

Keywords: Atlantic cod, Gadus morhua, heritability, local adaptations, spawning time, temperature.

Introduction

Temporal differences in spawning time between different fish populations of the same species, including the Atlantic cod (*Gadus morhua*), are well documented (Brander, 1993; Brander, 2005). For many species, spawning at the right time is crucial for the survival of their offspring. Larval feeding conditions may vary considerably throughout the year, so it will be of great importance for the survival of the larvae and juveniles to be born at a time when plankton conditions are favourable (Cushing, 1969; Wright and Trippel, 2009; Kristiansen *et al.*, 2011). Hence, the ability to change spawning time according to what is optimal for the offspring is vital if the environment changes unexpectedly, for instance due to a rapid climate change.

Whether this local flexibility in spawning time is a result of phenotypic plasticity of the individuals or genetic divergence of the population is much less documented. Knowledge about the genetic control of spawning time and its influence on population structure in marine fish is very limited, although some studies have been performed on salmonids (eg. Hendry and Troy, 2005). Photoperiod and temperature are believed to be the main operational factors for synchronizing spawning time in temperate fishes (Wang *et al.*, 2010), and it can therefore be hypothesized that such environmental cues may very well induce genetic divergence in populations living along a latitudinal gradient.

Cod aquaculture is in its infancy, with a total annual production of a few thousand ton. This species is, however, the key object in the traditional demersal fishery on both sides of the North Atlantic Ocean. This fishery typically targets both resident (coastal/local) and long-migratory (oceanic) populations showing different levels of productivity and thereby maximum sustainable yield. The varying quantity of fish landed throughout the year has stimulated interests in successful rearing techniques for delivery of high price farmed cod to the market. For cod in aquaculture, on-growing is carried out in sea cages as for Atlantic salmon (*Salmo salar*) farming. This means that escapes may occur, and in addition mature cod will spawn naturally in the cages and spread fertilized eggs to the surroundings (Jørstad *et al.*, 2008). The selection of broodstock is therefore of concern not only for the fish farmer, but also for the fishermen and the rest of the community. The possible genetic interaction between small and vulnerable local cod populations and escapees from farmed cod is a major issue in the debate of how to make the cod aquaculture industry sustainable and profitable (Bekkevold *et al.*, 2006).

In a previous experimental study on cod, Otterå *et al.* (2006) found indications of genetic control of spawning time for specimens originating from four regions in Norway. Spawning time remained different between the groups even at their second spawning after the broodfish had been translocated to a common environment. In the present paper we utilize these spawning data further and include similar data for their offspring in order to possibly reveal further evidence of genetic control of spawning time in cod. In addition, we also include some modelling of spawning time in the wild.

Material and Methods

Wild broodstock collection and spawning

During spring 2002, several hundred adult Atlantic cod (*Gadus morhua* L.) specimens were collected from selected spawning grounds along the Norwegian coast (Figure 1). Four regions (Porsangerfjord, Tysfjord, Helgeland and Øygarden) representing a wide range of environmental conditions were chosen for the subsequent spawning experiment. The fish were kept in the same sea cage until the spawning experiment started in spring 2003. The spawning performance (including spawning time) of 40 selected pairs of naturally spawning cod was monitored in 2003 and 2004. Further details about the broodstock collection and spawning of the F0 generation are given in Otterå *et al.* (2006) and Dahle *et al.* (2006).

Production of F1 generation

A subset of the spawned egg batches in the 2004 spawning was hatched and start-fed in a communal setup. In order to minimize size differences of the larvae during start-feeding, larval groups that hatched almost simultaneously (within three days) were specifically selected. By this restriction we were able to hatch sufficient numbers of 13 full-sib crosses that could be used in an experiment (four from Porsangerfjord, two from Helgeland, five from Tysfjord and two from Øygarden). These larval groups were mixed and reared further in a common garden setup. At the juvenile stage, these fish were identified to family of origin by microsatellite analysis (Dahle *et al.*, 2006), being individually tagged using Passive Integrated Transponder (PIT) tags, and kept together in the same cages for the rest of the experiment (not reported here).

Spawning F1

By spring 2009 we had access to 254 individuals from the original population of several thousand produced in 2004. The reduction in numbers from 2004 to 2009 was due to natural mortality, use in other experiments, and thinning of the biomass. No deliberately biased removal of fish was undertaken at any step in this period. In spring 2009 all the offspring had become well-established spawners (Svåsand *et al.*, 1996), and the available broodstock was represented by females from 11 out of the 13 families present at hatch in 2004. However, some of the F1 families were represented in low numbers (Table 1).

In spring 2009 a subset of 30 pairs representing different families/regions were used in a spawning experiment in the same way as their parents were in 2004 (Table 1). Each female was placed together with a male from the same region (but not a sibling), with the exception of the females from Øygarden that were placed with males from Porsangerfjord since all Øygarden broodfish were siblings.

The pairs were placed in separate compartments (1.8 m^3), allowing natural spawning. The number of eggs spawned each day, egg diameter, fertilization rate, and egg malformation rate was monitored in the same way as for their parents (Otterå *et al.*, 2006). In addition to the monitoring of the entire spawning season for these 30 pairs, date for start of spawning was estimated in advance using ovary "biopsy" (see below) on all females. Complete observation of spawning activity was not performed in 2010, but ovary biopsy was performed on all females in order to indicate start of spawning. These estimates were validated by stripping the fish during the spawning season. Thus, we have a two-year spawning record of these fish, as well as of their parents.

Oocyte development measurements

By measuring the growth of developing oocytes the start of spawning in cod can be predicted (Kjesbu, 1994; Kjesbu *et al.*, 2010) from the average diameter of the most advanced oocytes, commonly named as the leading cohort (LC). The broodstock was anaesthetized and an ovarian sample (~0.5 ml) removed by a specially designed plastic tube (Pipelle de Cornier®) inserted through the genital pore. The samples were stored for at least two weeks in 3.6% buffered formaldehyde before the oocytes were photographed digitally and size subsequently measured by automatic particle analysis (Thorsen and Kjesbu, 2001). In addition to LC diameter (95 percentile), the mean diameter of all the 200 measured oocytes per sample was extracted from the data produced.

Prior to the 2010 spawning season we took four biopsy samples from each of the females (at 16 Dec, 12 Jan, 4 Feb and 18 Feb). Date of first spawning could then be estimated either directly from the linear regression of LC diameter vs. calendar date established for individual fish, or from each of the four oocyte measurement points separately by applying Equation (1) (see next section for method details). In both cases the day of the year that corresponds to an LC value of 875 μm was defined as the first spawning day for that fish (Kjesbu *et al.*, 2010). In 2009 start of spawning was estimated from the one and only gonadal biopsy taken just before spawning (3 Feb). An ambient temperature of 5°C was used both for 2009 and 2010, which gives an oocyte growth rate of 3.56 μm day^{-1} according to Equation (1).

Spawning time in the wild

In order to compare spawning time in the experiments with spawning time at different field locations we utilized a temperature-based oocyte growth model and recorded temperature data from the Norwegian coast. The typical calendar day of spawning commencement was estimated from temperature-dependent LC oocyte growth rates (R, $\mu m \cdot d^{-1}$) given in Kjesbu *et al.* (2010). These were determined from studies on both local fish held in tanks (Bergen) as well as fish landed in connection with the traditional Lofoten fishery (Andenes). The applied environmental temperature data (accuracy: ±0.01°C) were extracted from the IMR database (1–2 measurements per month for the period 1935/44–1993). Seven out of eight fixed oceanographic stations considered in the series (two stations are located very closely to each other) were selected for analysis. Hence, virtually the entire coast of Norway was covered (Figure 1). The mean temperature per station for this time series (T_{new}) was calculated, restricting the analysis to the period from 1 October to 1 March, i.e. to the main part of vitellogenesis (Kjesbu *et al.*, 2010), and the depths 50 and 100 m. Thereafter oocyte growth rate (R_{new})

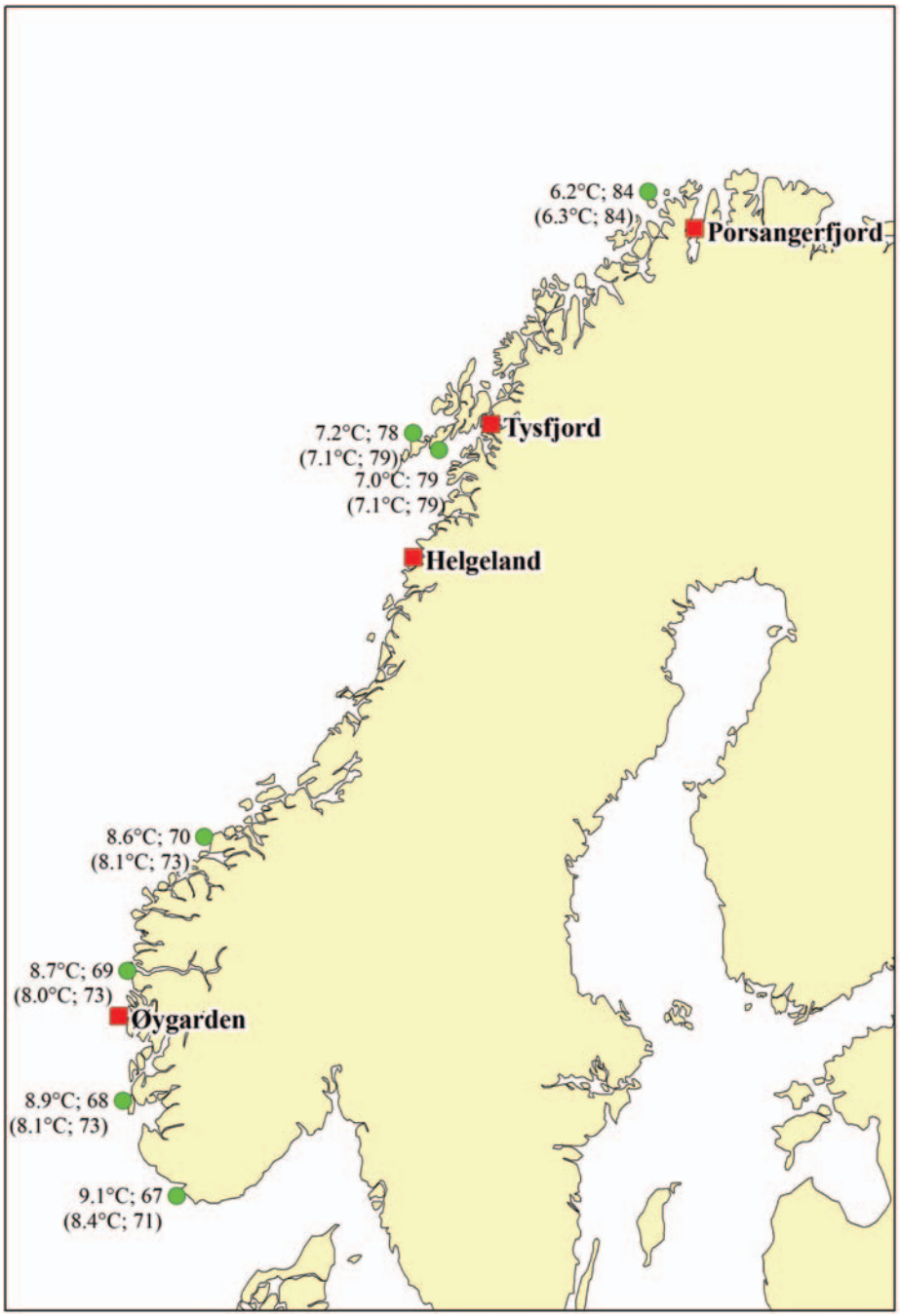

Figure 1. Collection of broodstock (red squares). For each of the seven locations where start of spawning was modelled (green circles), average sea temperature from 1 October to 1 March at 50 m depth, and the corresponding estimated spawning date (day of the year) is given. Values for 100 m depth are given in parentheses.

at T_{new} was found by application of the Q_{10}-law (setting the Q_{10}-value to 1.44 and the initial R (9.60°C) to 4.21 μm·d^{-1}) (cf. Equation 8 in Kjesbu *et al.*, 2010):

$$R_{new} = 4.21 \times 1.44^{(T_{new}-9.60)/10}$$

Finally, calendar day of start of spawning (ED_{vit}) was given by (see Kjesbu *et al.*, 2010):

$$ED_{vit} = (625/R_{new}) - 84$$

where ED_{vit} is elapsed days since 8 October (first microscopic manifestation of yolk granules in cytoplasm) but subtracting the number of days up to 31 December, i.e. 84, to get the calendar day in the new year. Furthermore, vitellogenesis was assumed, as for the experimental material described above, to start at an LC diameter of 250 μm and end at 875 μm (spawning), i.e. covering an increase in vitellogenic oocyte diameter of 625 μm. This estimation of date of spawning should be considered adequate at the population level (provided the females stay in the assumed temperatures) while individual figures may deviate by ±1

Table 1. Overview of the broodstock (females only) used in the experiment.

		F0 (mothers)											
		P10	**P17**	**P8**	**P9**	**H1**	**H33**	**T2**	**T29**	**T37**	**T40**	**Ø11**	**Total**
F1 (daughters)	2009-tank	4	1	5	0	1	4	3	2	2	3	5	30
	2009-oocyte	6	23	7	14	1	4	21	6	8	15	16	121
	2010-oocyte	1	18	5	12	0	3	13	4	6	13	12	87

The top row shows the name of the mothers that spawned in 2004, and gave birth to the F1 generation whose spawning was monitored in 2009 and 2010. The mothers are named according to origin of the actual mother (P = Porsangerfjord, H = Helgeland, T = Tysfjord, Ø = Øygarden) and spawning tank in 2004. The number of daughters from each mother used in the tank experiment in 2009, as well as number examined for oocyte growth in 2009 and 2010 is given in the following rows.

month around this predicted date, mainly due to differences in start of vitellogenesis (Kjesbu *et al.*, 2010).

Statistics

All calculations, plots and statistics were done with the statistical package R, version 2.12.1 (R Development Core Team, 2010). Spawning times of the daughters were compared with the spawning times of their mothers using a linear mixed model with family (mother) as a random term and spawning time of the mother and year of spawning (2009 or 2010) as fixed effects. Possible violations of the underlying assumptions in the linear regression models were assessed by inspection of residuals. Region was not included in any of the statistical tests reported here, due to the low number of families per region.

Results

Experimental spawning time

For eleven of the mothers that spawned in 2004 we have corresponding spawning data for their daughters in 2009 and 2010 (Figure 2, [mothers' spawning dates are partly overlapping]). These data indicate that mothers that started spawning early in the spawning season had daughters that also, on average, start spawning early, and vice versa for late spawners (Figure 2, linear mixed model, slope = 1.02, s.e. = 0.4, $p = 0.02$). However, the variation within each mother (family) was large. The established regression lines indicated that predicted offspring spawning time in 2009 was on average 34 days later than actually observed for their respective parents. The corresponding number in 2010 was 42 days later.

In 2010 we had four separate measurements of oocyte size that presumably should have given a more precise prediction of oocyte growth rate and thereby start of spawning than the single point used in 2009. However, combining all four points into a common oocyte growth rate, which was the original intention, or using each point separately in Equation (1), gave approximately the same result. Thus only the result from the measurement taken on 4 February, which is most comparable with the 2009 sampling in Figure 2, is presented. The other three regression lines based on Equation (1) give slope estimates between 0.96 and 1.01 d^{-1}, all being significant ($p < 0.05$). The first set of points on the x-axis may seem to have a high leverage on the regression (Figure 2), but removal of this early spawning mother only slightly influenced the regression. The length or weight of the daughters did not contribute significantly when included as a covariate in the regression model.

In 2009 we had observations from the 30 pairs that spawned naturally in the tanks, as well as estimates of start of spawning from all females based on oocyte size as reported on 3 February 2009 (Figure 2, left panel). The correlation between observed spawning and oocyte-estimated spawning in 2009 was high ($r^2 = 0.68$) but the apparently high slope indicates that the latter estimates give unrealistically late start of spawning (Figure 3). The relationship between start of spawning in 2009 and 2010 for the same individuals, using the same methodology, appeared to be highly correlated (Figure 4).

Field predictions of spawning time

The outputs from the modelling of spawning time in the wild showed that there would be a gradual northward delay in start of spawning of stationary cod along the Norwegian coast (Figure 1). The maximum observed delay was around two weeks: 17 d at 50 m depth and 13 d at 100 m depth, associated with a difference in vitellogenic temperature of 2.9 and 2.1°C, respectively. All estimates showed initiation of spawning in March, but from early to late in the month. In Southern Norway specimens staying in the upper water masses apparently start to spawn a few days earlier than those potentially staying deeper, but such an effect was absent in Northern Norway. This was related to a temperature difference of 0.5–0.9 and 0.1°C, respectively.

Discussion

The positive and significant correlation between mother and daughter spawning time provides evidence for a genetic component in spawning time for Atlantic cod. This is in accordance with the sparing literature on spawning time in fish, which mainly comes from studies on salmonids. High heritability values are reported ($h^2 \sim 0.5$–0.9, pooled 0.65) along with a daughter–mother regression coefficient for spawning date of 0.35 for pooled data in three experimental lines of rainbow trout (*Oncorhynchus mykiss*) (Su *et al.*, 1999). O'Malley *et al.* (2003) found several quantitative trait loci (QTL) in rainbow trout for spawning date. In a selection program for spawning date in rainbow trout Siitonen and Gall (1989) observed a heritability value of 0.54. Quinton *et al.* (2004) found, when crossing different strains of rainbow trout, that hybrids generally had an intermediate spawning date compared to their pure strain combinations, suggesting a largely additive inheritance of spawning time. Heritability has been investigated for several morpho-physiological traits in Atlantic cod (Kolstad *et al.*, 2006; Garber *et al.*, 2010), but to our knowledge not for spawning time heritability.

A comparison of estimated start of spawning between the 2009 and 2010 spawning season for the same individuals shows that specimens that tend to start spawning early in the season one year tend to do the same the next year, and, correspondingly, for late

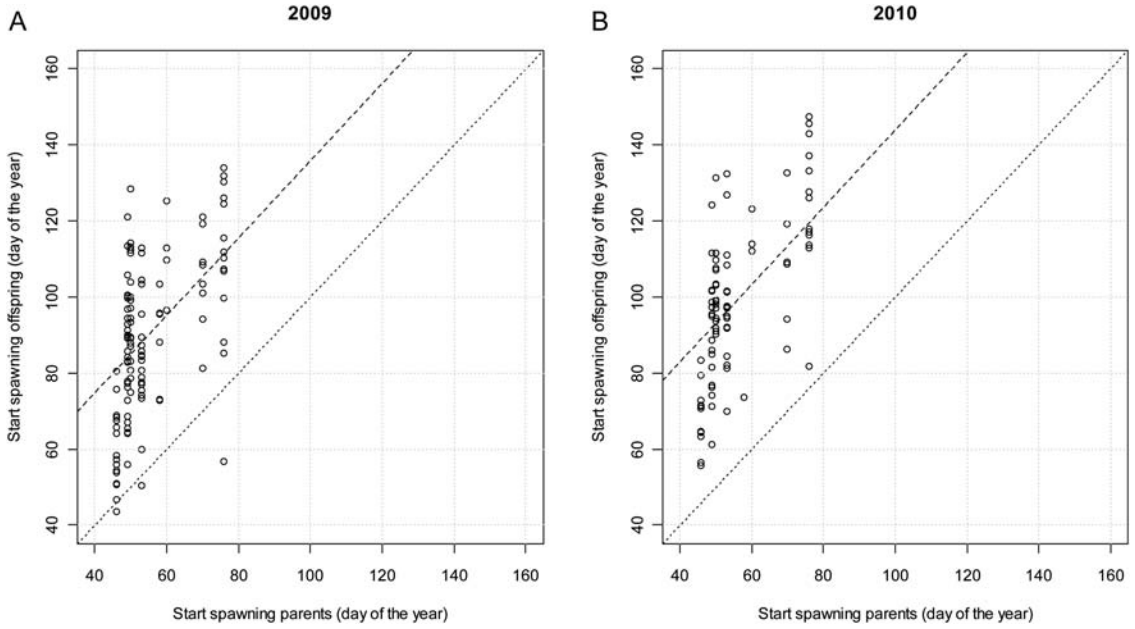

Figure 2. Start of spawning for the mothers in 2004 on the *x*-axis plotted against start of spawning of their daughters in 2009 and 2010 on the *y*-axis. The mother spawning time was observed from natural spawning, while the daughter spawning time was estimated by applying Equation (1) on the oocyte size at 3 February 2009 (2009 spawning, left panel), and 4 February 2010 (2010 spawning, right panel) (see text for details). Linear regression lines were estimated from a linear mixed model.

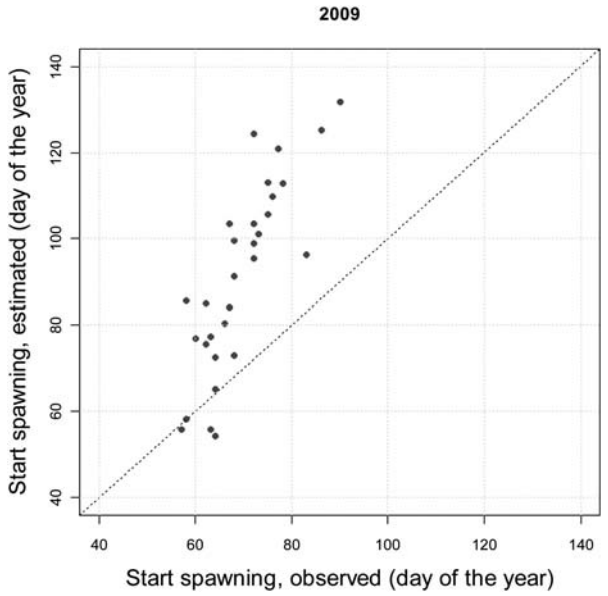

Figure 3. Comparison of observed start of spawning in 2009 from the 30 spawning tanks (*x*-axis) versus estimated start of spawning from the oocyte measurements (*y*-axis). Pearson's product moment correlation, $r = 0.83$, $p < 0.01$).

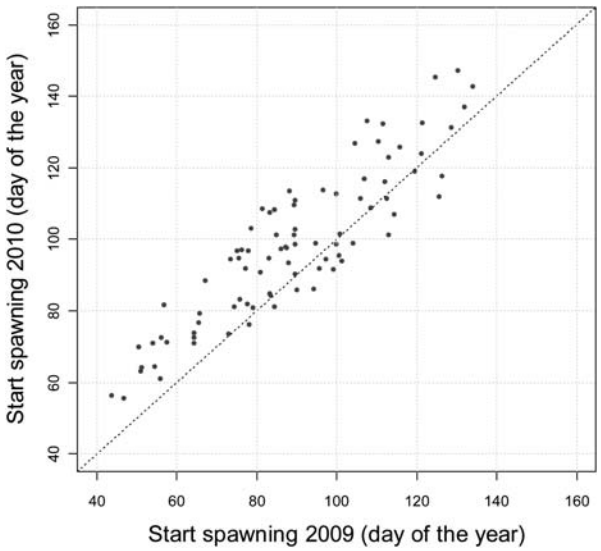

Figure 4. Start of spawning for the same individuals in 2009 and 2010. Spawning day was estimated by applying Equation (1) on oocyte measurements from respectively 3 February 2009 and 4 February 2010 (Pearson's product moment correlation, $r = 0.90$, $p < 0.01$).

spawners (Figure 3). This was also indicated in an earlier, similar type of tracking study, but temperature and fecundity variation apparently act in different directions (Kjesbu, 1994) complicating a direct comparison. However, Quinton *et al.* (2004) made similar observations on rainbow trout, with repeatability estimates of 0.72. Even though the correlation between years is quite strong, the very late estimated start of spawning in 2010 suggests that there are methodological issues to consider. First of all, Equation (1) as used here is said to give realistic estimates when applied to wild specimens (Kjesbu *et al.*, 2010). Our along-the-coast analysis of spawning time variation gives reason to believe that this statement is correct; estimated onset of spawning time in Lofoten matches closely with earlier reports based on egg surveys and gonad maturity sampling programmes (Pedersen,

1984), although one should not exclude the possibility that there has been changes in the spawning pattern in this area since then. So why does Equation (1) currently *de facto* underestimate the time of onset of spawning? Here the gonad growth is apparently characterized by being slow for a long period of time followed by a fast acceleration close to initiation of spawning. This in contrast to the more stable linear oocyte growth seen in those females which were originally used to establish these sets of equation, referring to individuals maintained either at stable deep-water temperatures in tanks or sampled randomly in the field. Further studies are needed to investigate these seemingly irregular patterns. One particularly interesting candidate factor is summer temperature. In the present study, using net pens floating in the surface layer meant that the females were exposed to high temperatures (Otterå *et al.*, 2006), probably slowing down, among other aspects, cytoplasmic preparation of sex cells for subsequent maturation (see McPherson and Kjesbu, 2012 and references therein).

Results from the modelling analysis suggest a north-south gradient for the start of spawning along the Norwegian coast, driven by differences in temperature. This is generally supported by previously published data obtained from the experimental spawning in 2003 and 2004; it was demonstrated that the broodstock from the four different regions had different peaks in spawning time, even though they had been held in the same cages since captured in 2002 (Otterå *et al.*, 2006). It was evident that broodstock from the Øygarden region, western Norway spawned about one month earlier, compared with broodstock originating from the Helgeland region, northern Norway. However, cod from the northernmost region, Porsangerfjord had a peak spawning in between, making the picture more confusing (Otterå *et al.*, 2006). Monitoring of the spawning performance of their offspring in 2009 tended to reveal a similar pattern, an early peak spawning for the Øygarden group, a late peak spawning for the Helgeland group, and the other two regions in between (data not shown). Due to the low number of families per geographical group we cannot generalize regarding spawning time between these regions. However, the data enable us to contrast spawning time between two generations of closely-related individuals, mothers and their daughters, and therefore advance the understanding of the strength of the genetic regulation of spawning time in cod, irrespective of geographic origin.

So even though the data clearly point to an important genetic component in the regulation of spawning time in cod, they also give a clear impression of the large variation in spawning time between siblings. Thus, cod is a species with great plasticity regarding spawning time and ability to live in various ecosystems. Further, individual cod spawn over a long period of time (Kjesbu, 1989), contrary to most salmonids, and should therefore be well-adapted to varying environmental conditions. However, this plasticity in spawning time may very well be significantly reduced after some generations of breeding. In such case, escapees from aquaculture may have reduced fitness in the wild compared to native specimens. The consequences this would have on the local population of cod are unclear at the moment, but great care should be taken when using non-native cod in aquaculture systems that could be subject to escapes.

Acknowledgements

We appreciate the skilled technical assistance provided by Bjørnar Skjold and Jan Pedersen during the spawning experiments, and by Bente Njøs Strand for oocyte measurements. Also thanks to Drs Terje Svåsand and Mikko Heino for valuable comments on an earlier draft of the paper.

Funding

This study was financed by the Norwegian Ministry of Fisheries and Coastal Affairs and The Research Council of Norway.

References

Bekkevold, D., Hansen, M. M., and Nielsen, E. E. 2006. Genetic impact of gadoid culture on wild fish populations: predictions, lessons from salmonids, and possibilities for minimizing adverse effects. ICES Journal of Marine Science, 63: 198–208.

Brander, K. 1993. Comparison of spawning characteristics of cod (*Gadus morhua*) stocks in the North Atlantic. Northwest Atlantic Fisheries Organization Scientific Council Studies, 18: 13–20.

Brander, K. (Ed). 2005. Spawning and life history information for North Atlantic cod stocks. *In* ICES Cooperative Research Report 274. 152 pp.

Cushing, D. H. 1969. The regularity of the spawning season of some fishes. Journal du Conseil International pour l'Exploration de la Mer, 33: 81–92.

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.

Garber, A. F., Tosh, J. J., Fordham, S. E., Hubert, S., Simpson, G., Symonds, J. E., Robinson, J. A. B., *et al.* 2010. Survival and growth traits at harvest of communally reared families of Atlantic cod (*Gadus morhua*). Aquaculture, 307: 12–19.

Hendry, A. P., and Troy, D. A. Y. 2005. Population structure attributable to reproductive time: isolation by time and adaptation by time. Molecular Ecology, 14: 901–916.

Jørstad, K., van der Meeren, T., Paulsen, O. I., Thomsen, T., Thorsen, A., and Svåsand, T. 2008. Escapes of eggs from farmed cod spawning in net pens: recruitment to wild stocks. Reviews in Fisheries Science, 16: 285–295.

Kjesbu, O. S. 1989. The spawning activity of cod, *Gadus morhua* L. Journal of Fish Biology, 34: 195–206.

Kjesbu, O. S. 1994. Time of start of spawning in Atlantic cod (*Gadus morhua*) females in relation to vitellogenic oocyte diameter, temperature, fish length and condition. Journal of Fish Biology, 45: 719–735.

Kjesbu, O. S., Righton, D., Krüger-Johnsen, M., Thorsen, A., Michalsen, K., Fonn, M., and Witthames, P. R. 2010. Thermal dynamics of ovarian maturation in Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 67: 605–625.

Kolstad, K., Thorland, I., Refstie, T., and Gjerde, B. 2006. Body weight, sexual maturity, and spinal deformity in strains and families of Atlantic cod (*Gadus morhua*) at two years of age at different locations along the Norwegian coast. ICES Journal of Marine Science, 63: 246–252.

Kristiansen, T., Drinkwater, K. F., Lough, R. G., and Sundby, S. 2011. Recruitment variability in North Atlantic cod and match-mismatch dynamics. PLoS ONE, 6: e17456. [doi:10.1371/journal.pone.0017456]

McPherson, L.R., and Kjesbu, O.S. 2012. Emergence of an oocytic circumnuclear ring in response to increasing day length in Atlantic herring (*Clupea harengus*). Marine Biology, 159: 341–353.

O'Malley, K. G., Sakamoto, T., Danzmann, R. G., and Ferguson, M. M. 2003. Quantitative trait loci for spawning date and body weight in rainbow trout: testing for conserved effects across ancestrally duplicated chromosomes. Journal of Heredity, 94: 273–284.

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.

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. *In* The Propagation of Cod Gadus morhua L. An International Symposium, Arendal, 14-17 June 1983. Ed. by E. Dahl, D.S. Danielssen, E. Moksness, and P. Solemdal. Flødevigen rapportser 1, Institute of Marine Research, Flødevigen Biological Station, Arendal, Norway. pp. 301–316.

Quinton, C. D., McKay, L. R., and McMillan, I. 2004. Strain and maturation effects on female spawning time in diallel crosses of three strains of rainbow trout (*Oncorhynchus mykiss*). Aquaculture, 234: 99–110.

R Development Core Team 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org/.

Siitonen, L., and Gall, G. A. E. 1989. Response to selection for early spawn date in rainbow trout, *Salmo gairdneri.* Aquaculture, 78: 153–161.

Su, G-S., Liljedahl, L-E., and Gall, G. A. E. 1999. Estimates of phenotypic and genetic parameters for within-season date and age at spawning of female rainbow trout. Aquaculture, 171: 209–220.

Svåsand, T., Jørstad, K. E., Otterå, H., and Kjesbu, O. S. 1996. Differences in growth performance between Arcto-Norwegian and Norwegian coastal cod reared under identical conditions. Journal of Fish Biology, 49: 108–119.

Thorsen, A., and Kjesbu, O. S. 2001. A rapid method for estimation of oocyte size and potential fecundity in Atlantic cod using a computer-aided particle analysis system. Journal of Sea Research, 46: 295–308.

Wang, N., Teletchea, F., Kestemont, P., Milla, S., and Fontaine, P. 2010. Photothermal control of the reproductive cycle in temperate fishes. Reviews in Aquaculture, 2: 209–222.

Wright, P. J., and Trippel, E. A.. 2009. Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. Fish and Fisheries, 10: 283–304.

Handling editor: Francis Juanes