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Differences in spawning time of captive Atlantic cod from four regions of Norway, kept under identical conditions

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Several hundred Atlantic cod (*Gadus morhua* L.) were collected from selected spawning grounds along the Norwegian coast in March 2002. Four areas or regions that represent a wide range of environmental conditions were chosen for our breeding experiments: Porsangerfjord, Tysfjord, Helgeland, and Øygarden. Cod were transported to Øygarden near Bergen, individually tagged, and kept in sea cages. In both 2003 and 2004, a total of 40 family groups (adult pairs) representing the four regions were monitored for their spawning performance in separate tanks. During the spawning period, the quantity and diameter of eggs were recorded. During 2003, the time of peak spawning differed among groups. It was evident that the broodstock from the Øygarden region spawned about one month earlier than the broodstock collected from the Helgeland region. This also occurred in 2004, two years after the cod were collected, suggesting that the difference has a genetic component. Differences in life history parameters between cod populations, such as spawning cycles as described here, could be adaptive and under genetic control. This must be taken into consideration when assessing precautionary means of overcoming the problem with escapees from future cod mariculture.

Keywords: cod, *Gadus morhua*, genetic influence, local populations, mariculture, spawning time.

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Introduction

Knowledge of the genetic structure of wild cod populations is a prerequisite to understanding a wide range of issues dealing with cod mariculture. From an industrial perspective, it is important to select a wild broodstock that produces offspring with high performance in a farming situation, and that is adapted to the local mariculture conditions. For society in general, knowledge of the genetic structure of the species is essential in enabling us to evaluate potential environmental effects of cod farming. Escapees from net cages as well as natural spawning in pens can both contribute to the undesirable spread of farmed cod to the environment. These issues are highly relevant since cod mariculture is a rapidly growing industry. In Norway, annual juvenile production is about five million (2004) and is expected to increase rapidly. Cod mariculture is also developing in several other European countries and North America (Rosenlund and Skretting, 2006).

It is well established that there is genetic differentiation among Atlantic cod stocks in the northern Atlantic. The early studies of Møller (1966, 1968) demonstrated genetic differences among the migratory stocks of northeast Arctic cod or "skrei" and various groups of non-migratory coastal cod. Later allozyme studies revealed less differentiation, resulting in different interpretations of the geographic variation observed (Jørstad, 1984; Mork *et al.*, 1985; Jørstad and Nævdal, 1989; Mork and Giæver, 1999). Recent studies using various DNA techniques, however, have revealed large genetic differences in the *Pan I* locus among cod populations in northern Norway (Fevolden and Pogson, 1995, 1997; Sarvas, 2005). In general, studies based on microsatellite analyses have documented a detailed and complex population structure of Atlantic cod in both the western (Bentzen *et al.*, 1996; Ruzzante *et al.*, 1998) and eastern Atlantic (Hutchinson *et al.*, 2001; Nielsen *et al.*, 2001; Imsland and Jonsdottir, 2002; Jonsdottir *et al.*, 2002; Knutsen *et al.*, 2003).

The biological consequences of genetic differentiation are understood more poorly. Imsland and Jonsdottir (2002) reviewed the stock-specific effects on growth in cod, but this is only one potential trait. Spawning behaviour

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in cod may also have a genetic component (Nordeide, 1998) and, thus, may be of importance to the genetic structure of populations (Bekkevold *et al.*, 2002). Time of spawning may also be determined genetically in part, as has been shown in several other species (e.g. Pacific salmon species; Ricker, 1972). For Atlantic herring (*Clupea harengus*), both location and time of spawning are among the most important factors for maintaining the complex population structure (Iles and Sinclair, 1982; Sinclair, 1988; Stephenson *et al.*, 2001). In a review of population structure of Atlantic cod in the western Atlantic, Ruzzante *et al.* (1999) summarized the genetic information available as well as biological parameters including spawning information (location and time) and natural hydrographic systems, and thus provided an overall explanation for the existence of genetic differentiation in the area.

In fish species with a pelagic egg stage, time of spawning is probably important for recruitment, as Cushing (1969) suggested in the "match–mismatch" hypothesis. Spawning that takes place too early or too late may mean that the start-feeding larvae will miss the zooplankton bloom, which is very important for successful first-feeding (e.g. Ellertsen *et al.*, 1981; Taggart and Frank, 1990; Pepin and Myers, 1991; Sundby, 2000). Brander (1994) found a clear, but not conclusive, correlation between time of spawning and onset of primary production for cod spawning around the British Isles.

Many experiments have focused on the relationship between maternal characteristics and egg quality and viability. Factors such as female age, spawning experience, size, or condition can often be related to egg viability characteristics such as size, energy content, hatching success, etc., and to fecundity (e.g. Kjesbu, 1994; Trippel, 1998; Ouellet *et al.*, 2001). Clemmesen *et al.* (2003) were even able to find indications that maternal characteristics influence the size of larvae several weeks after hatching.

The present contribution is part of a larger project, in which the spawning and life history attributes of progeny of coastal cod collected from four regions in Norway are being compared. Herein, we focus on the overall success and time of spawning of cod sampled from different regions, while the performance (growth and survival) of the offspring from the experiments will be reported elsewhere.

Material and methods

Four groups of wild coastal cod were collected, transferred to sea cages, and the natural spawning success of pairs of cod was monitored during two subsequent spawning seasons.

Collection of broodstock

The broodstocks used in the present experiment were collected from Porsangerfjord, Tysfjord, Helgeland, and Øygarden. The localities are spread along the Norwegian coast and represent a broad range of environmental conditions (Figure 1a, b). Broodstock collection was mainly carried out in cooperation with local fishers. Most of these fish were caught by Danish seine, cod traps, or hand gear (for details see Dahle *et al.*, 2006). Fish were transported in tanks with running seawater to the Institute of Marine Research's Parisvatnet field station in Øygarden, west of Bergen, for spawning experiments. Most of the fish were collected in 2002, during the respective spawning seasons of each location, but an additional 40 fish from Tysfjord were collected in spring 2003. Collection of coastal cod from Porsangerfjord was decided upon biological (Jakobsen, 1987) and genetic (Jørstad, 1984) knowledge of the cod in this fjord.

The broodstock from each region was kept separately in net pens. Mortality was high during the first period of adaptation to farming conditions, mainly as a result of high summer temperature in combination with inadequate weaning to commercial feeds. In November 2002, after the period of cage adaptation, all surviving fish were measured (length and weight), individually tagged (PIT tags), and samples of blood, white muscle, and a fin clip were taken for genetic analysis (Dahle *et al.*, 2006). After weaning to commercial dry feed (DanFeed, 1562) and tagging, the potential broodstock from all four groups was kept in a common net pen (100 m^3) until individuals of each group were taken for use in the comparative spawning experiments.

Because of the high initial mortality, handling of the fish was minimized during the first period, and the spawning status for 2002 was not recorded. However, based on the broodstock size in November 2002 (Table 1) and otolith readings of similar sized fish from the same areas (Porsanger, Tysfjord, and Helgeland: Knut Jørstad, unpublished data; Øygarden: Otterå *et al.*, 1999), it can be concluded that the fish were aged four to six years (Porsangerfjord four to eight years) and were mainly first- and second-time spawners during the first experiment. The Porsangerfjord group had the greatest proportion of second-time spawners, while few of the Tysfjord group were mature the first year.

Spawning experiment

Forty outdoor spawning tanks were used for the experiment. Each tank contained approximately 1.8 m^3 water (diameter = 1.5 m, height = 1.2 m) and was made of glass fibre-reinforced polyester. The tanks were green inside and had a conical bottom. The water inlet and outlet were at the top of the tanks. The drained water was filtered through a fine-mesh net (500 μm), and placed in a water bath outside each tank so that spawned eggs could be collected and measured (see below). The water to the spawning tanks was taken from the sea at a depth of 20 m and filtered (300 μm) before it entered the tanks. Flow rate was approximately 20 l min^{-1} $tank^{-1}$. The temperature during the spawning season was relatively stable, from 5 to 6 °C in both years, and salinity varied from 32 to 34. The spawning tanks were covered by a black fine-mesh net, which reduced the light level by about 70%.

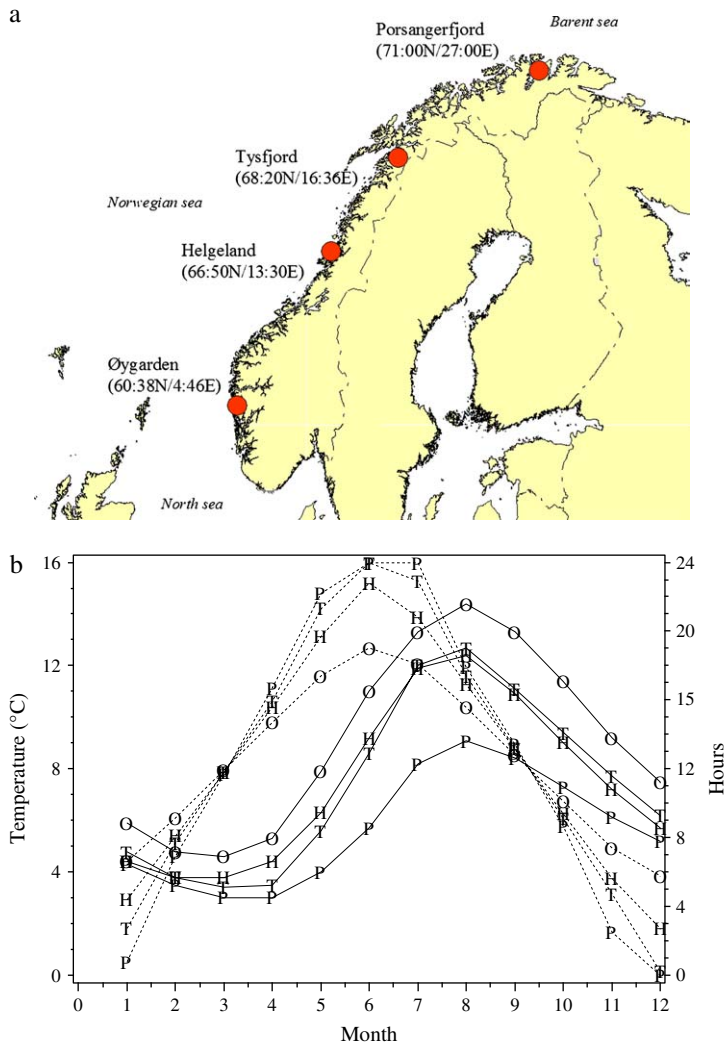

Figure 1. (a) The origins of the four groups of broodstock are indicated by circles. The spawning experiment was performed at the Øygarden site. (b) Monthly averages of temperature (left axis, continuous lines) and hours of light (right axis, stippled lines) for the four areas. The letters, P, T, H, and O, indicate the respective areas (Porsangerfjord, Tysfjord, Helgeland, and Øygarden). Temperature data are given as monthly averages (1936–1989) at 4-m depth from fixed coastal monitoring stations close to the actual capture area (Aure and Strand, 2001). Hours of light are given as those between sunrise and sunset at the actual latitude.

Before each spawning season, all available broodstock was measured and their maturation status evaluated. From each group (locality), we selected fish that were healthy and mature. Male–female pairs were transferred to individual spawning tanks in February, presumably before spawning had started. We tried to select males and females of similar size, but the limited quantity of broodstock made that difficult for some of the pairs. Few of the Tysfjord group were mature in the first spawning season; therefore, we chose not to include this group in the 2003 spawning set-up. Nine of the pairs used in 2003 were also used in the 2004 experiment.

The spawning success of the 40 pairs in the tanks was monitored during the spawning season. Monitoring lasted from 22 February to 9 April in 2003 and from 14 February to 3 May in 2004. Eggs were collected from the water-bath filters placed outside each tank every morning. The quantity of eggs was recorded, and the eggs were examined under a binocular microscope. Egg diameter, fertilization rate, cleavage status, and percentage of dead eggs were recorded (only egg diameter is reported here). Some of the egg batches were incubated and hatched for further evaluation of larval and juvenile quality in relation to egg quality and genetic background (results not reported here).

Several of the pairs did not spawn easily, even though the females were mature and ready for spawning. In such cases, we replaced either the female or the male with another from the holding cage, if available, or switched males between

Table 1. The number and size (average, with range in brackets) of the broodstock used in the spawning experiment. Only pairs that could be observed throughout the whole monitoring period are included. Measurements of body characteristics for the 2003 experiment were made in November 2002 and for the 2004 experiment in December 2003. Condition factor (CF) was calculated as 100(weight (g)/length (cm)^3).

Region		2003				2004			
		n	TL (cm)	*W* (g)	CF	*n*	TL (cm)	*W* (g)	CF
Porsangerfjord	Male	11	67 (56–75)	3 076 (2 020–4 230)	1.0 (0.7–1.2)	9	73 (65–77)	5 040 (4 000–6 200)	1.3 (0.9–1.6)
	Female	11	70 (58–80)	3 556 (1 950–6 000)	1.0 (0.6–1.2)	9	70 (63–77)	5 544 (4 300–6 900)	1.6 (1.4–1.8)
Tysfjord	Male	—	—	—	—	6	70 (61–80)	5 022 (3 230–6 400)	1.5 (1.2–1.9)
	Female	—	—	—	—	6	77 (69–87)	5 591 (4 700–6 400)	1.3 (0.9–1.6)
Helgeland	Male	12	67 (59–75)	3 460 (1 790–5 235)	1.1 (0.9–1.2)	9	69 (61–82)	4 423 (3 500–7 400)	1.4 (1.1–1.6)
	Female	12	67 (62–73)	3 864 (2 020–6 225)	1.3 (0.8–1.6)	9	77 (74–82)	6 677 (5 500–7 220)	1.5 (1.2–1.6)
Øygarden	Male	11	62 (54–67)	2 816 (1 120–3 703)	1.2 (0.7–1.5)	8	74 (70–79)	6 350 (4 500–7 900)	1.5 (1.3–1.9)
	Female	11	67 (55–80)	4 216 (2 241–8 290)	1.3 (1.2–1.6)	8	74 (59–86)	6 124 (3 060–8 500)	1.5 (1.2–1.6)

spawning tanks. All changes were made within each group. Where one of the partners died or was exchanged during the spawning period, the pair concerned was omitted from the analysis reported here. Table 1 gives an overview of the broodstock used in the experiment. Thorsen *et al.* (2003) give a general overview of methods related to experimental spawning of cod.

Results

From the 40 couples of cod that participated in the experiment each year, we managed to obtain eggs from, and to follow through the spawning period, 34 pairs in 2003 and 32 pairs in 2004. Most of the remaining pairs also produced some eggs, but were omitted from the analysis owing to death and/or replacement.

Spawning was very regular for some of the pairs, with spawning every third day accompanied by a decrease in egg diameter during the season (Figure 2). Many of the pairs, however, displayed less regular spawning, with longer and more variable intervals between each batch. Average batch size was 556 ml in 2003 and 599 ml in 2004, and 65% of the batches were between 200 and 1200 ml. Overall, there was a decrease in egg diameter through the spawning period, from around 1.4 mm in mid-February to around 1.2–1.3 mm towards the end of the spawning period (Figure 3). The Porsangerfjord group had the largest mean egg size in both years (2003: mean = 1.36, s.d. = 0.06; 2004: mean = 1.37, s.d. = 0.08), followed by Øygarden (2003: mean = 1.34, s.d. = 0.07; 2004: mean = 1.35, s.d. = 0.08), Helgeland (2003: mean = 1.30, s.d. = 0.06; 2004: mean = 1.31, s.d. = 0.06), and Tysfjord (2004: mean = 1.31, s.d. = 0.09).

There were differences in time of peak spawning between groups in both 2003 and 2004. In both years, the Øygarden group, followed by Porsangerfjord, spawned earliest and Helgeland latest. In terms of volume of collected eggs,

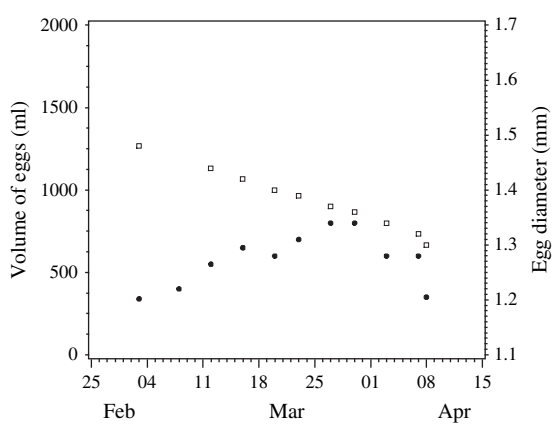

Figure 2. Example of spawning performance from one of the pairs. Egg quantity is symbolized by open squares (left *y*-axis) and egg diameter by filled squares (right *y*-axis).

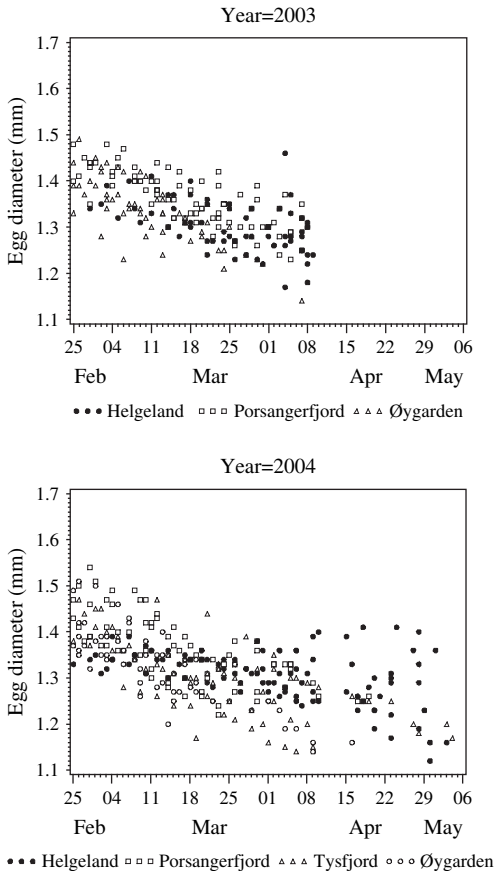

Figure 3. Egg diameter through the spawning season in 2003 and 2004. The observation period was 22 February–9 April in 2003 and 14 February–3 May in 2004.

the Øygarden group had spawned 50% of the eggs by 9 March in 2003 and 4 March in 2004 (Figure 4). The corresponding dates are 17 March and 11 March for Porsangerfjord, 23 March for Tysfjord (2004 only), and 26 March and 30 March for Helgeland. In 2003 and possibly also in 2004, the Øygarden group had started spawning before data collection started, which means that some records are missing on the leftmost bar in Figure 4. Furthermore in 2003, monitoring was stopped before all groups had finished spawning, so that the latest batches from the Helgeland group are missing in Figure 4. As a result, the differences in spawning time among groups are underestimated. Despite the incomplete data presented, it is quite clear that peak spawning in the Øygarden group occurred at least one month before the Helgeland group, and this persisted even in the second year.

Discussion

The most interesting observation from this experiment was that time of peak spawning differed between the broodstocks originating from different regions along the Norwegian coast. These broodstocks were held in the same environment from July of the year before the first spawning experiment. The fact that the differences persisted even during the second spawning season after capture suggests that spawning time in cod is genetically determined to some extent.

Concurrent with the collection of broodstock, genetic screening of the cod populations in the four areas was performed. Both the actual broodstock and additional samples were analysed for a number of gene markers (haemoglobin *Hb1*, allozymes, *Pan I*, and microsatellites). The results are reported in detail in Dahle *et al.* (2006). Overall, the results demonstrated significant genetic differences among cod from the four areas (all 17 loci, $F_{st} = 0.015$). The Tysfjord and Helgeland groups were estimated to be closest. The largest values of F_{st} were found for the *Pan I*, *Hb1*, and *Gmo132* loci. As opposed to the migratory northeast Arctic cod, Norwegian coastal cod used in the current experiment are believed to be relatively stationary (Bergstad *et al.*, 1987).

The broodstock used in this experiment originated in regions with different temperature and light regimes. In laboratory experiments, Hansen *et al.* (2001) observed that manipulating photoperiod changed the incidence of sexual maturation, spawning time, fecundity, and egg size in captive cod. Temperature has a strong effect on growth (e.g. Otterlei *et al.*, 1999), and also, indirectly, on size at maturity. It is likely, therefore, that subpopulations of cod are adapted to local environmental conditions, as is suggested by our results. The differences in spawning time shown in the present experiment, however, are not related directly to a north–south gradient, or temperature or light regime (Figure 1b). In Norwegian coastal cod, spawning time may differ by several weeks in spawning groups only a few kilometres from one another (Knut Jørstad, unpublished data). Therefore, the mechanisms for control of spawning time are probably influenced by a number of genetic, environmental, and maternal factors. Quantitative trait loci (QTL) are likely to be involved in the genetic factors, and this should be studied in greater detail through experimental manipulations. Recently, such studies have been carried out in rainbow trout (*Oncorhynchus mykiss*) using a large number of DNA markers. In these studies, QTLs associated with spawning time (Sakamoto *et al.*, 1999) as well as upper temperature tolerance (Danzmann *et al.*, 1999) were demonstrated.

The experimental set-up used in the present study, where broodstocks are reared under identical conditions prior to spawning, should eliminate most of the direct environmental influence on spawning time between the groups. Maturation of oocytes starts about six months prior to spawning (Anders Thorsen, Institute of Marine Research, pers. comm.), while the broodstock was transferred to a common environment at least seven months before spawning. Therefore, even for the 2003 experiment, females should have had an identical environment through the maturation

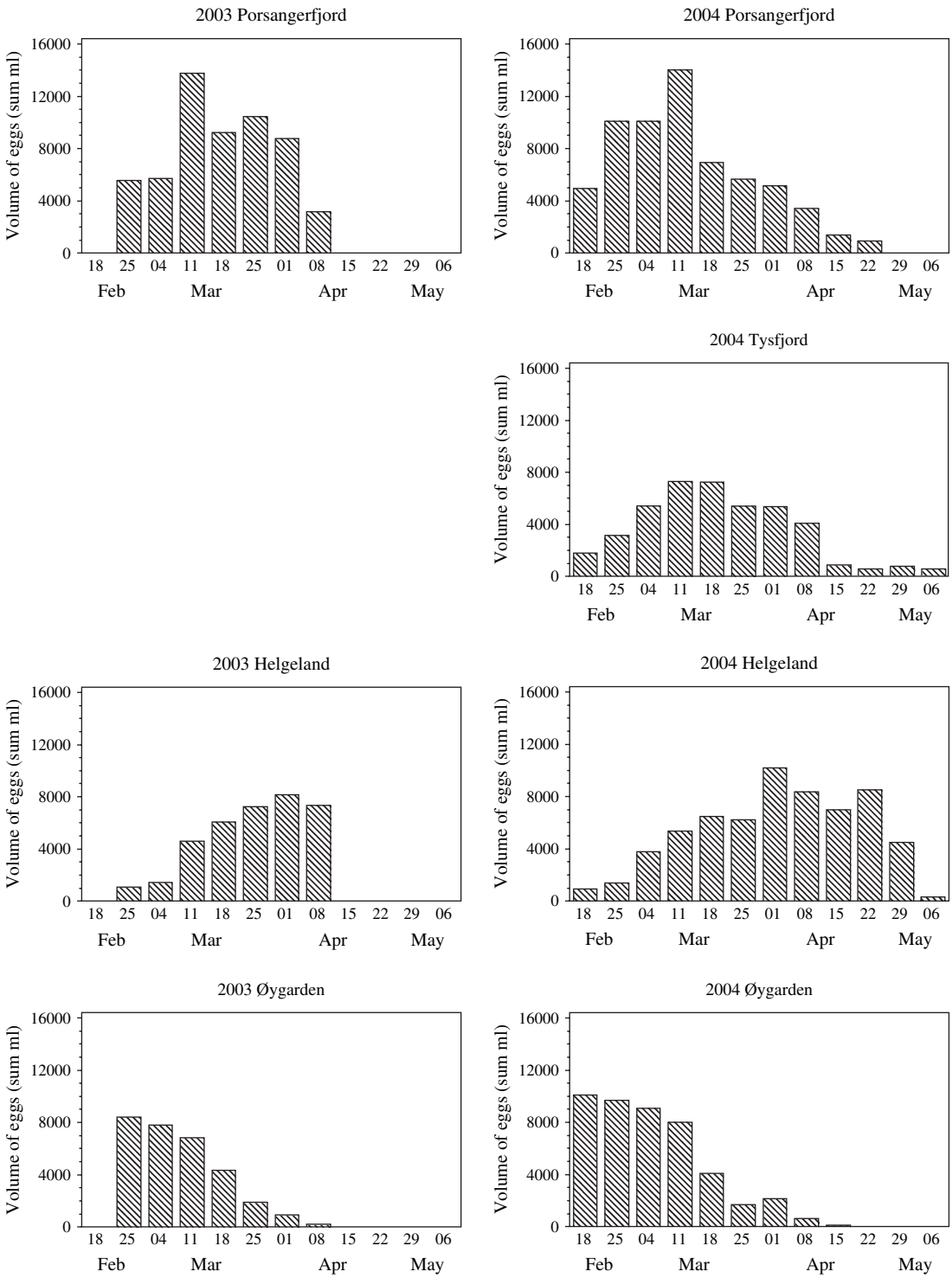

Figure 4. Sum of eggs spawned per week by each group in 2003 (left panel) and 2004 (right panel). Note there are different numbers of spawners per group. The observation period was 22 February–9 April in 2003 and 14 February–3 May in 2004.

cycle. Maternal factors like female size and spawning experience are also believed to be important in determining spawning success in cod (Trippel *et al.*, 1997). However, Kjesbu (1994) found no clear relation between fish length and start of spawning for wild Arcto-Norwegian cod, while fecundity increased with female size (Kjesbu *et al.*, 1996). Our broodstock groups were relatively similar in size and age structure, suggesting that maternal effects were of minor importance to the results.

The expected large increase in cod mariculture in Norway and other countries around the North Atlantic may have ecological and genetic consequences for the wild population of cod. The preliminary results presented in the current paper suggest that the selection of broodstock should be carefully considered. The use of a non-native broodstock followed by escapement from sea cages could have a detrimental influence on local stocks. Probably most important, as has been demonstrated in Atlantic salmon (McGinnity *et al.*, 2004), is the possible interbreeding between farmed and wild populations resulting in a decrease in overall fitness. Therefore, further research on the performance of cod related to their genetic origin and its potential influence on wild populations is highly recommended.

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