Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod *Gadus morhua*

Gudrun Marteinsdottir[1,2,*], Gavin A. Begg[2,**]

[1]University of Iceland, Institute of Biology, and [2]Marine Research Institute; Skulagata 4, PO Box 1390, 121 Reykjavik, Iceland

ABSTRACT: Evidence accumulated over the last decade indicates that reproductive potential of marine fish stocks is not correctly represented by spawning stock biomass. Fundamental variables that affect reproductive potential of fish stocks (i.e. proportion mature at age, fecundity, and offspring size and viability) have found to vary with age, size, and condition of spawning fish, and/or spawning experience. Modeling initiatives that attempt to describe reproductive potential by incorporating all available information on reproductive variables require extensive, high quality data of a temporal and spatial origin. In this study, we explored the influence of female age, size, and condition on several reproductive variables for the cod *Gadus morhua*, including maturity, fecundity, egg density and size, and larval size and growth. In addition, we described the potential for annual variation in these relationships to increase our knowledge of temporal stability for fundamental variables that influence reproductive potential.

KEY WORDS: Cod · Maturity · Fecundity · Egg size · Larval size · Stock-recruitment · Population dynamics · Fisheries management

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INTRODUCTION

Reproductive potential represents the ability of a fish stock to produce viable offspring that may recruit to the adult population or fishery (Trippel 1999), incorporating individual and stock effects of its spawning components. Traditionally, spawning stock biomass (SSB) has been used in stock-recruitment models as a proxy for reproductive potential, with the implicit assumption of proportionality between total egg production (i.e. reproductive potential) and SSB (Trippel et al. 1997a, Marshall et al. 1998). However, during the past decade an increasing number of studies have demonstrated that SSB is not an accurate measure of reproductive potential, with serious flaws in the assumed proportionality between the 2 measures (Trippel et al. 1997a, Marshall et al. 1998, Marteinsdottir & Thorarinsson 1998, Scott et al. 1999). Fundamental variables that affect reproductive potential of fish stocks (i.e. proportion mature at age, fecundity, and offspring size and viability) have found to vary with age, size, and condition of spawning fish, and/or spawning experience (Stearns & Crandall 1984, Jørgensen 1990, Kjesbu et al. 1991, Solemdal et al. 1995, MacKenzie et al. 1998, Marshall et al. 1998, Marteinsdottir & Steinarsson 1998, Trippel 1998). Moreover, accumulating information on maternal effects has stimulated modelers to re-estimate reproductive potential by incorporating reproductive variables that influence total egg production (Marshall et al. 1998, 1999, Murawski et al. 1999, Scott et al. 1999, Cardinale & Arrhenius 2000a,b, Marteinsdottir et al. 2000a). Based on these modeling

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*E-mail: runa@hafro.is
**Present address: CRC Reef Research Centre, James Cook University, Townsville, Queensland 4811, Australia

initiatives, re-examination of stock-recruitment relationships may provide new information on how the composition of a spawning stock influences recruitment (Marteinsdottir & Thorarinsson 1998). However, to create new biological reference points based on stock-recruitment relationships, such modeling initiatives require extensive data on the influence of maternal effects on reproductive potential (Trippel 1999), particularly time series data on age, size and condition of spawners (Marshall et al. 2000).

In Atlantic cod *Gadus morhua*, relationships between some fundamental reproductive variables and age, size and condition of spawners have been well documented. For example, the maternal effects of age, size and condition on size, growth and viability of eggs and larvae have been widely studied (Knutsen & Tilseth 1985, Kjesbu 1989, Solemdal et al. 1992, 1995, Chambers & Waiwood 1996, Chambers 1997, Solemdal 1997, Trippel et al. 1997a, Marteinsdottir & Steinarsson 1998). Furthermore, relationships between potential fecundity and female age and/or size have been documented for many cod populations (May 1967, Schopka 1971, Pinhorn 1984, Kjesbu et al. 1998, Marteinsdottir et al. 2000a). However, fewer studies have attempted to document the influence of spawners' condition on fecundity, and relationships based on relative fecundity of cod populations are scarce (Kjesbu et al. 1998). Considering the great importance of these relationships and the influence they have on final estimates of total egg production, and hence reproductive potential, there is an obvious need for more data and a greater understanding of the spatial and temporal variation in potential and relative fecundity. Similarly, while information on age and/or length at maturity is routinely collected for stock assessment purposes, fundamental relationships on the effects of condition on maturity are also scarce.

Data that exist on the influence of maternal effects on reproductive variables are often based on observations from restricted time-series that do not allow analysis of temporal stability of these variables. Kjesbu et al. (1998) have questioned the underlying assumption of constant relative fecundity that is presently used in recruitment studies, after demonstrating environmentally induced variation in both potential and relative fecundity of Arcto-Norwegian cod due to annual changes in its food source. Similarly, environmental conditions are likely to influence not only the amplitude of egg production, but also the time of maturation, and the quality of production reflected in egg and larval sizes and survival (Cardinale & Arrhenius 2000a, Vallin & Nissling 2000). However, uncoupling the influence of environmental and biotic conditions on reproductive life history characteristics is difficult, particularly given the magnitude of fishery-induced

changes that have typically occurred on most exploited cod stocks (Serchuk et al. 1994).

In this study, we explored the influence of age, size and condition of cod on reproductive variables, including maturity, fecundity, egg density and size, and larval size and growth. Essential relationships based on these variables were derived to provide modellers with the necessary information required for re-estimation of more accurate measures of reproductive potential. In addition, we described the potential for annual variation in these relationships to increase our knowledge of temporal stability for the fundamental variables that influence reproductive potential. These relationships were placed in the context of those for other cod populations in the north Atlantic to determine their spatial consistency, while providing a comprehensive basis for future modeling initiatives re-examining stock-recruitment relationships.

MATERIALS AND METHODS

Maturity. Data on age and size at maturity of cod were obtained from the annual (1985 to 1999) Icelandic spring groundfish surveys. These surveys were conducted each year for 2 to 3 wk in March coinciding with the beginning of the spawning season for cod (Pálsson et al. 1989). More than 250 stations were sampled each year, providing a complete coverage of the geographical area (Fig. 1) occupied by cod on the continental shelf around Iceland (Pálsson et al. 1989). At each station, most cod were measured (cm), and sex and maturity stage (1: immature; 2: ripening; 3: spawning; or 4: spent) determined macroscopically (following the stages defined in Powles 1958). Otoliths were removed from all weighted fish, and in the laboratory, 1 otolith from each pair was sectioned and assigned an age following standard methods (Pentilla & Dery 1988).

A total of 52243 cod were included in the maturity data analysis, of which 34 608 were immature and 17 635 mature (Table 1). The data were divided geographically into northern and southern statistical

Table 1. Number of mature and immature cod sampled during the Icelandic spring groundfish surveys (1985 to 1999) in the northern and southern statistical regions used in the maturity analysis

| Region	Immature	Mature females	Mature males	Total mature	Total
North	26757	3200	3378	6578	33335
South	7851	4838	6219	11057	18908
Total	34608	8038	9597	17635	52243
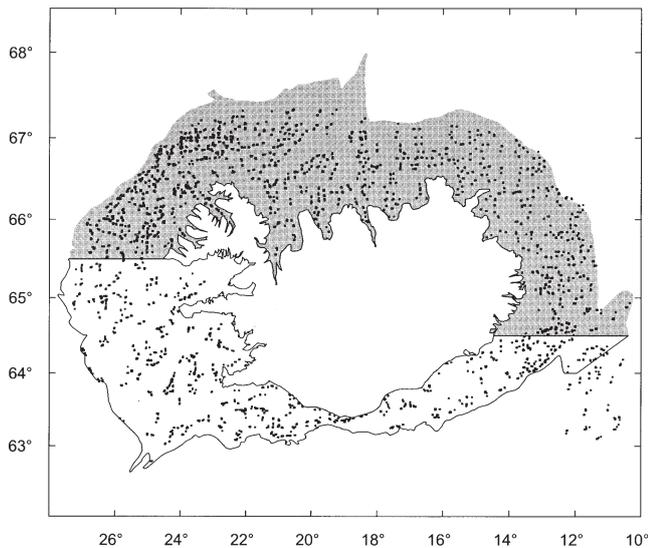
Fig. 1. Station locations of Icelandic spring groundfish surveys (1985 to 1999) for the northern and southern statistical regions. The outer boundary designates the 500 m depth contour

regions based on hydrographical and ecological differences (Begg & Marteinsdottir 2002a; their Fig. 1), where the waters in the northern region were generally colder and more variable than those in the southern region (Malmberg & Kristmannsson 1992).

Fecundity. Potential fecundity (PF) and relative fecundity (RF) were estimated for cod females collected each year (1995 to 2000) several weeks (January to February) prior to the spawning season (March to May) from the main spawning grounds off the southwest coast of Iceland (Fig. 1). Potential fecundity is the total number of developing (or vitellogenic) oocytes in the ovary that can potentially be released, while relative fecundity is a measure of potential fecundity per unit of body weight (Kjesbu et al. 1998, Marshall et al. 1998). Total length, whole body weight and gonad and liver weights of each female were measured and used to calculate indices of Somatic condition (K) and hepatosomatic condition (H). In order to maintain consistency with other studies (i.e. Kjesbu et al. 1991, 1998), estimates of K were based on whole body weight and H on ovarian free body weight according to the following equations:

$$K = \frac{W}{L^3} \times 100 \qquad (1)$$

$$H = \frac{LW}{(W - OW)} \times 100 \qquad (2)$$

where W = whole body weight (g); L = total length (cm); LW = liver weight (g); and OW = ovary weight (g).

Potential fecundity estimates were then determined gravimetrically from counts of oocytes in weighed portions (0.3 g) of ovary tissue. A total of 869 female cod were analyzed during this period, where different methods of oocyte preservation were used. In 1995, ovary sections were digested in Gilson fluid for 3 mo and then transferred to 4% buffered formalin. In 1996 and 1997, ovary sections were digested in 2 ml of buffered enzyme solution (2 mg Collagenase D from Boehringer Cat.#:1088866 dissolved in 2 ml 0.1 M Tris/5 mM CaCl$_2$, pH 7.6 for 120 min, which dissolved the collagen in the connective tissue but left the oocytes intact; G. Steingrimsdottir & G. Petursdottir unpubl.) and then transferred to 4% formaldehyde. In 1998, 1999 and 2000, oocytes were separated from ovary sections by rapid shaking (Thermolyne Vortex Shaker E-51805-00, Cole Parmer Instumental) in 4% buffered formalin for 1 to 2 min. If the ovary section could not be treated immediately after sampling, the sections were stored in their ovarian fluid in a refrigerator (~4°C) for no more than 12 h. Following all methods of preservation, a sub-sample of vitellogenic oocytes from each section was then counted with the aid of an image analyzer (Optimas 5.2 or Leica Q500) attached to a dissecting microscope, using 6× magnification. Each image was compared visually with the sub-sample under the microscope and checked for accuracy of oocyte detection. RF of each cod was then estimated according to the following equation:

$$RF = \frac{PF}{W} \qquad (3)$$

where PF = potential fecundity (millions vitellogenic oocytes).

Batch fecundity (BF) was estimated for 200 spawning cod collected in 1999 during the spawning season from the main spawning grounds off the southwest coast of Iceland. Batch fecundity is the number of hyaline or ovulated oocytes in the ovary due to be spawned in the immediate future (Kjesbu et al. 1998). Batch fecundity estimates were determined from weighed sub-samples (0.16 to 0.18 g) of ovarian tissue, preserved in 4% phosphate buffered formalin. Batch size estimates were then determined from the total number of hydrated oocytes counted in the ovary sub-sample. The total number of vitellogenic oocytes was also counted and compared to the estimated potential fecundity (EPF) for each sample to provide an indication of spawning status (proportion of oocytes left in the ovary in relation to EPF). EPF was derived from the 1999 relationship between PF and L.

Egg and larvae. During the spawning season of 1994, 1995 and 1996, freely running eggs were stripped from a total of 79, 86 and 69 female cod, respectively, on the main spawning grounds off the SW coast of Iceland.

Eggs were stripped from female cod during several cruises throughout the spawning season and fertilized *in vitro*. L and W, LW and ovary weight of each female were also measured, and their otoliths removed. Eggs were maintained at 6 to 7°C, and transported to the laboratory within 2 to 3 d of sampling. In 1994 and 1996, females were classified into 4 spawning stages (SPS), based on mean and standard deviation of vitellogenic oocytes present in the ovary at each time (Kjesbu et al. 1990, Marteinsdottir & Steinarsson 1998): I: <30%; II: 30 to 50%; III: 55 to 80%; and IV: >80% of eggs spawned. In the laboratory, egg diameters (ED), and egg dry and wet weights were obtained following the methods in Marteinsdottir & Steinarsson (1998). Egg batches were reared in individual containers at 7°C. In 1996, absolute density (g cm^{-3}) of 20 eggs from each batch were sampled 5 d after fertilization and measured in a density gradient column (Martin Instruments) following the methods in Coombs (1981). A fresh salinity gradient was prepared each day using UV-filtered sea water, de-ionized fresh water and NaCl. Temperature was held constant at 7 to 7.3°C during all density measurements and all density data were converted to 7°C.

At hatching, larvae were sampled for initial length measurements within a few hours of first hatch (Marteinsdottir & Steinarsson 1998). Length measurements (mm) were obtained for 20 larvae from each batch, with the aid of an image analyzer (Leica Q500) attached to a binocular microscope, using 25× magnification. Additional samples of 20 larvae were taken from each batch for measurements of wet weight (only in 1994) and dry weight (all years). Larvae from 45, 35 and 60 egg batches in 1994, 1995 and 1996, respectively, were retained for rearing and growth experiments. Experiments were terminated after 20 d. Daily (DGR, mg d^{-1}) and specific growth rates (SGR, % d^{-1}) of each larvae were then estimated according to the following equations:

$$DGR = \frac{\log_e W_{t_2} - \log_e W_{t_1}}{t_2 - t_1} \qquad (4)$$

$$SGR = (e^{DGR} - 1) \times 100 \qquad (5)$$

where W = body weight (mg); t_1 = time at hatching (Day 0) and t_2 = time when the experiment was terminated (Day 20). For further details see Marteinsdottir & Steinarsson (1998).

Statistical analysis. Logistic regression analysis (Sokal & Rohlf 1995) was used to estimate maturity ogives (immature: Stage 1; mature: Stages 2 to 4) to determine length (L_{50}) and age (A_{50}) at 50% maturity for female and male cod in each statistical region (North, South) and year (1985 to 1999). Scheffé multiple comparison tests (MathSoft 1998) were used to compare maturity

ogives between sexes, and condition groups of each sex in each region. Generalized linear models (GLM, binomial distribution) were then used to examine the influence of length, age and condition on maturity. An additional measure of model fit was based on a pseudo-coefficient of determination (R^2), which was the fraction of the total 'variation' explained by the model

$$R^2 = 1 - \left\lfloor \frac{\text{Residual deviance}}{\text{Null deviance}} \right\rfloor$$

where deviance was analagous to the residual sums of squares (Swartzman et al. 1995). Analysis of variance (ANOVA) on $\log_e$-transformed data was used to compare length and condition among age groups of each sex in each region.

Fecundity relationships were compared with analysis of covariance (ANCOVA), while the influence of length and condition on relative fecundity was evaluated with a multiple regression.

Similarly, the effects of year, spawning stage and length on egg diameters were examined with multiple regression models. The same procedures were used to examine the relative influence of spawning stage, egg diameter, female size and condition on egg density.

RESULTS

Maturity

Sexual maturity (L_{50} and A_{50}) was found to differ on a spatial and temporal basis, both among and between female and male cod (Fig. 2, Table 2). Overall, throughout the survey period (1985 to 1999), 50% of female cod reached maturity at the mean length of 75.6 cm and mean age of 6.6 yr (Table 2). In contrast, 50% of male cod reached maturity at 67.2 cm and 5.8 yr (Table 2). Significant differences in maturity were found between cod in waters off the north and south coasts (Scheffé *F*-test, $p < 0.05$), as well as between sexes in each region (Scheffé *F*-test, $p < 0.05$; Fig. 2, Table 2). In the north, 50% of female cod reached maturity at 80.2 cm and 7.3 yr, while in the south L_{50} and A_{50} were 71.0 cm and 5.9 yr, respectively (Table 2). In contrast, 50% of male cod in the north reached maturity at 72.8 cm and 6.6 yr, while in the south L_{50} and A_{50} were 61.5 cm and 5.0 yr, respectively (Table 2).

The size and age at sexual maturity were also found to differ between years for cod in waters off the north and south coasts, with a general decline in both length and age at maturity observed throughout the survey period (Fig. 2). Sexual maturity of female cod in the north declined from 87.3 cm and 8.3 yr in 1985 to 76.5 cm and 6.7 yr in 1999 (Linear regressions, L_{50}: $r^2 =$

0.61, p < 0.001, A_{50}: r^2 = 0.57, p < 0.001) and in the south from 77.4 cm and 6.5 yr to 69.2 cm and 5.8 yr (linear regressions omitting 1990 to 1991, L_{50}: r^2 = 0.48, p < 0.05, A_{50}: r^2 = 0.34, p < 0.05; Fig. 2). Similarly, although not as consistent, sexual maturity of male cod in the north declined from 73.5 cm and 6.8 yr in 1985 to 70.0 cm and 6.4 yr in 1999 (linear regressions, L_{50}: r^2 = 0.34, p < 0.05, A_{50}: r^2 = 0.29, p < 0.05), and in the south from 66.9 to 59.4 cm (linear regression omitting 1990 to 1991, r_2 = 0.45, p < 0.05), while decline in A_{50} from 5.4 to 4.8 yr was not significant (linear regression omitting 1990 to 1991, r^2 = 0.15, p = 0.198; Fig. 2). The spatial disparity in maturity between cod in waters off the north and south coasts, where those in the north reached maturity at greater lengths and ages than those in the south, was most likely reflective of slower growth rate, influenced by colder water temperatures in the north (Fig. 3).

Size of mature and immature cod overlapped greatly (combined data 1985 to 1999), although generally within an age group the mean total length of mature cod was significantly greater than that of immature cod (ANOVA on ln-transformed total length, p < 0.05; Fig. 4). This was true for age groups 4 to 9 among sexes and regions, except 4 and 5 yr old males in the north. Similarly, somatic condition (K) of mature and immature cod overlapped greatly, although within an age group the mean K of mature cod was significantly

greater than that of immature cod, except for 3 yr old females and males in both regions and for 4 yr old females in the north (ANOVA, p < 0.05; Fig. 4). Low sample sizes within the respective age, region, sex and maturity-stage were most likely responsible for the non-significant results detected in these analyses. Small sample sizes prevented the analysis of these data on an annual basis.

Both length and condition (K) affected maturity when analysed within the same model (p < 0.01, Table 3). Moreover, on average, length accounted for a 16-fold greater amount of the variation than that accounted for by K (Table 3). Similar results were found for the effects of age and K on maturity, where on average, age accounted for an 8-fold greater amount of variation than that accounted for by K (Tables 2 & 3). Differences in L_{50} of cod in the different condition classes (low: $K < 0.8$; medium: $K = 0.8$ to 1.0; high: $K > 1.0$) were less distinct in the south than in the north (Fig. 5, Table 2). L_{50} differed significantly between all condition classes of female and male cod in the north (Scheffé F-test, p < 0.05), while only low-condition cod differed significantly from high- and medium-condition cod in the south (Scheffé F-test, p < 0.05; Fig. 5, Table 2). In contrast, A_{50} differed significantly between all condition classes of female and male cod both in the north and in the south (Scheffé F-test, p < 0.05; Fig. 5, Table 2).

Table 2. Length L_{50} (cm ± SE) and age A_{50} (yr ± SE) at 50% maturity for female and male cod in 3 condition (K) classes $(K > 1.0$; $K = 0.8$ to 1.0; $K < 0.8)$ in waters off the north and south coasts of Iceland $(L_{50}$ and A_{50} for all cod were obtained from the combined data 1983 to 1999; L_{50} and A_{50} for condition groups were obtained from the combined data from 1985 to 1999)

| Sex | Region | L_{50} all cod | Condition (K) | | |
			<0.8	0.8–1.0	>1.0
Females	North	80.2 ± 0.31	90.0 ± 2.43	77.0 ± 0.52	67.8 ± 0.75
	South	71.0 ± 0.25	75.5 ± 0.84	69.6 ± 0.43	68.7 ± 0.83
	Total	75.6 ± 0.18	79.8 ± 0.74	73.4 ± 0.35	68.0 ± 0.54
Males	North	72.8 ± 0.29	89.1 ± 2.49	69.8 ± 0.43	60.4 ± 0.68
	South	61.5 ± 0.26	69.1 ± 0.77	60.6 ± 0.44	57.9 ± 0.98
	Total	67.2 ± 0.16	75.5 ± 0.69	65.7 ± 0.25	59.6 ± 0.54
Both	North	77.0 ± 0.22	89.9 ± 1.78	73.7 ± 0.31	64.2 ± 0.53
	South	65.9 ± 0.18	72.4 ± 0.59	64.8 ± 0.31	62.8 ± 0.66
	Total	71.4 ± 0.12	77.8 ± 0.52	69.5 ± 0.20	63.6 ± 0.39

| Sex | Region | A_{50} all cod | Condition (K) | | |
			<0.8	0.8–1.0	>1.0
Females	North	7.3 ± 0.04	9.7 ± 0.45	6.8 ± 0.05	5.8 ± 0.07
	South	5.9 ± 0.02	6.5 ± 0.11	5.7 ± 0.03	5.1 ± 0.08
	Total	6.6 ± 0.03	7.6 ± 0.13	6.3 ± 0.03	5.5 ± 0.05
Males	North	6.6 ± 0.02	9.6 ± 0.47	6.2 ± 0.05	5.1 ± 0.07
	South	5.0 ± 0.03	5.8 ± 0.11	5.0 ± 0.05	4.5 ± 0.09
	Total	5.8 ± 0.03	7.2 ± 0.12	5.7 ± 0.05	4.9 ± 0.05
Both	North	7.0 ± 0.02	9.6 ± 0.33	6.5 ± 0.04	5.5 ± 0.05
	South	5.4 ± 0.02	6.2 ± 0.07	5.4 ± 0.03	4.8 ± 0.06
	Total	6.2 ± 0.01	7.4 ± 0.09	6.0 ± 0.02	5.2 ± 0.03
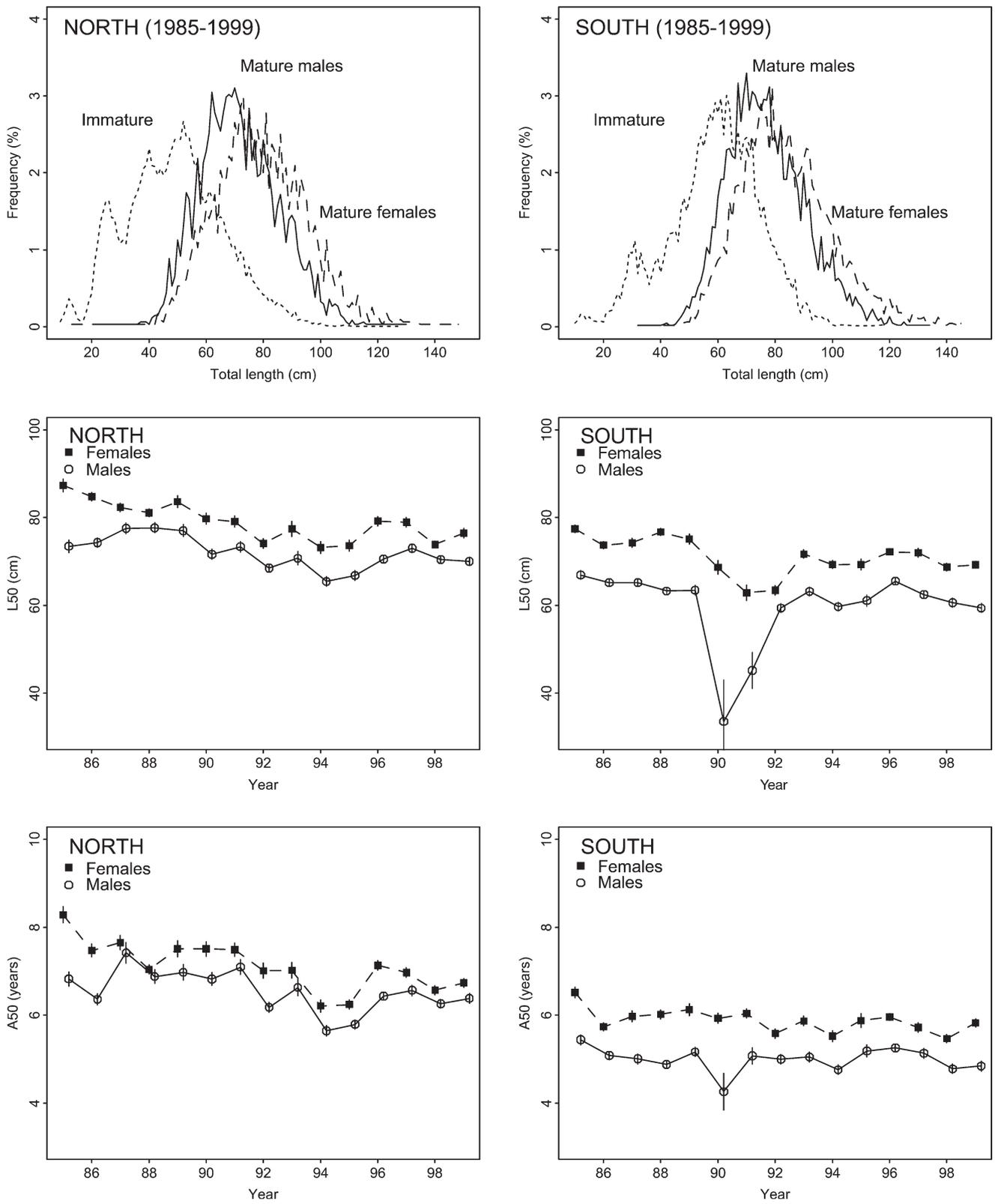
Fig. 2. Length frequency distributions for mature and immature cod (combined data 1985 to 1999), and annual mean lengths (L_{50}) and ages (A_{50}) at 50% maturity (±SE) for female and male cod in waters off the north and south coasts of Iceland
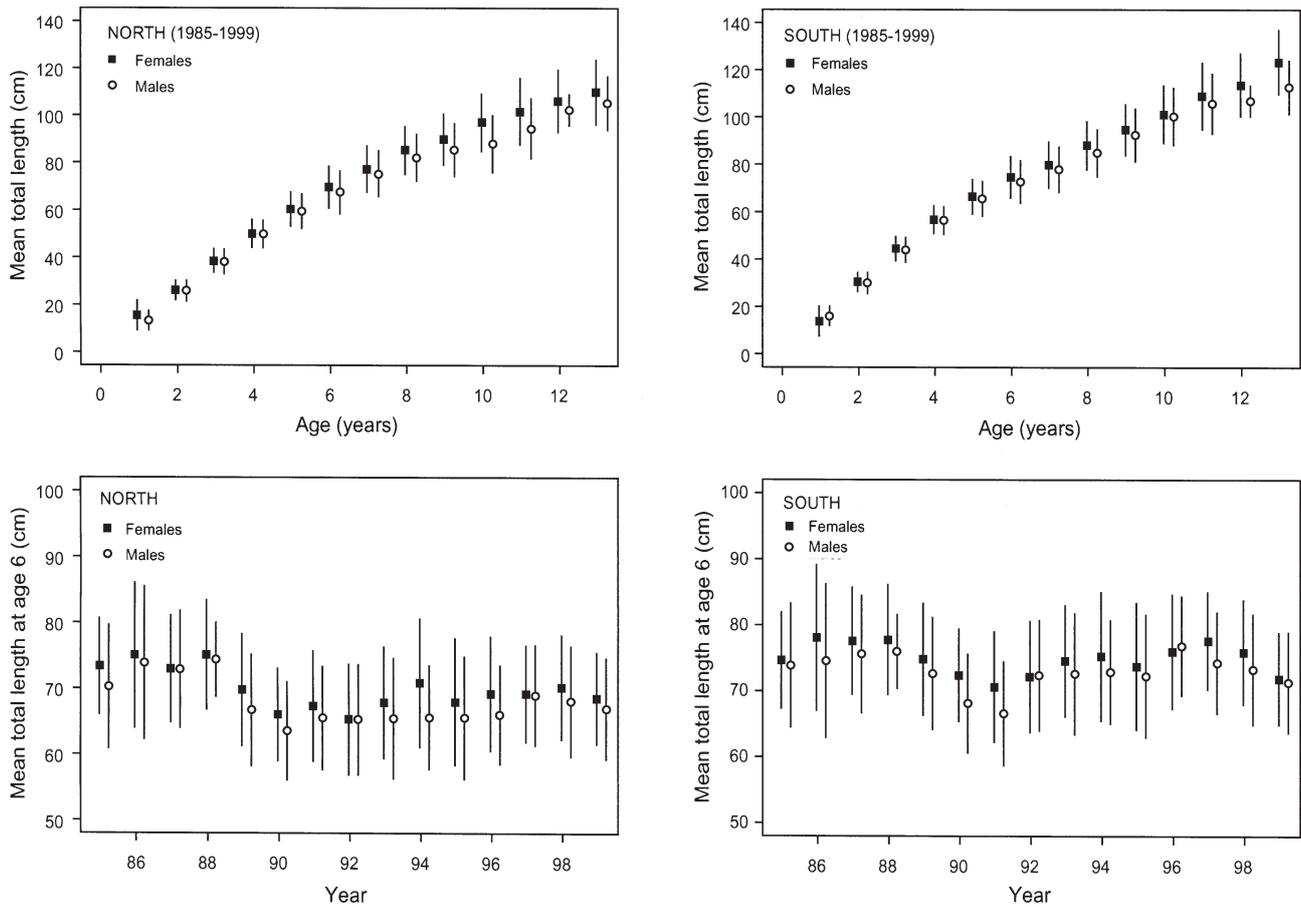
Fig. 3. Mean total length (cm) at age (yr) for cod (combined data 1985 to 1999), and annual mean total length at age 6 (±SD) for female and male cod in waters off the north and south coasts of Iceland

Fecundity

PF of Icelandic cod ranged from 0.23 to 31.7 million vitellogenic oocytes (Fig. 6). As expected, PF increased significantly with female length (Table 4; p < 0.001 for each of the 6 yr, 1999 to 2000) and weight (p < 0.001 for each of the 6 yr, 1999 to 2000). The relationship between PF and TL for the entire data (1995 to 2000) was best described with a power equation (PF = $0.0118 \times TL^{4.372}$, $r^2 = 0.81$, n = 869), while the relationship between PF and W was linear (PF = $-1491732 + 778 \times W(g)$, $r^2 = 0.85$, n = 869). The relationship between PF and TL varied annually (ANCOVA, p < 0.001; Fig. 6). The greatest slopes were obtained in 1997 and 1998, and the smallest in 1996 and 1999 (Table 4). PF varied between years from 836×10^3 to 1726×10^3 for a standard fish of 70 cm length, 3294×10^3 to 4835×10^3 for 90 cm fish and 13850×10^3 to 15822×10^3 for a 120 cm fish (Table 4). The mean differences amounted to 106, 46 and 14%, respectively, between years.

PF was influenced by female condition. Including either W or K in a model describing the relationship between PF and TL increased the amount of variation explained in all years ($r^2 = 0.87$, 0.93, 0.73, 0.85, 0.92, 0.89 in 1995 to 2000, respectively). However, addition of K to a model describing the relationship between fecundity and W did not improve the variation explained. In contrast, addition of H to such a model had a significant effect in all years except 1996 and 1999 (p < 0.01).

RF ranged from 51 to 1327 oocytes g^{-1} of whole body weight and was significantly related to TL in all years (Fig. 7, Table 5, $r^2 = 0.14$ to 0.38). RF was also influenced by K and and H (Table 6). The influence of K was significant in 1995 and 1997, while H was significant in all years except 1996 and 1998 (p < 0.05). Generally, more variation was explained by H than by K, and in some years (1997, 2000), H explained more variation in RF than TL (Table 6).

RF of a standard fish, 70 cm long, varied from 376 in 1997 to 573 eggs g^{-1} in 1999 (Table 5). Similar trends of
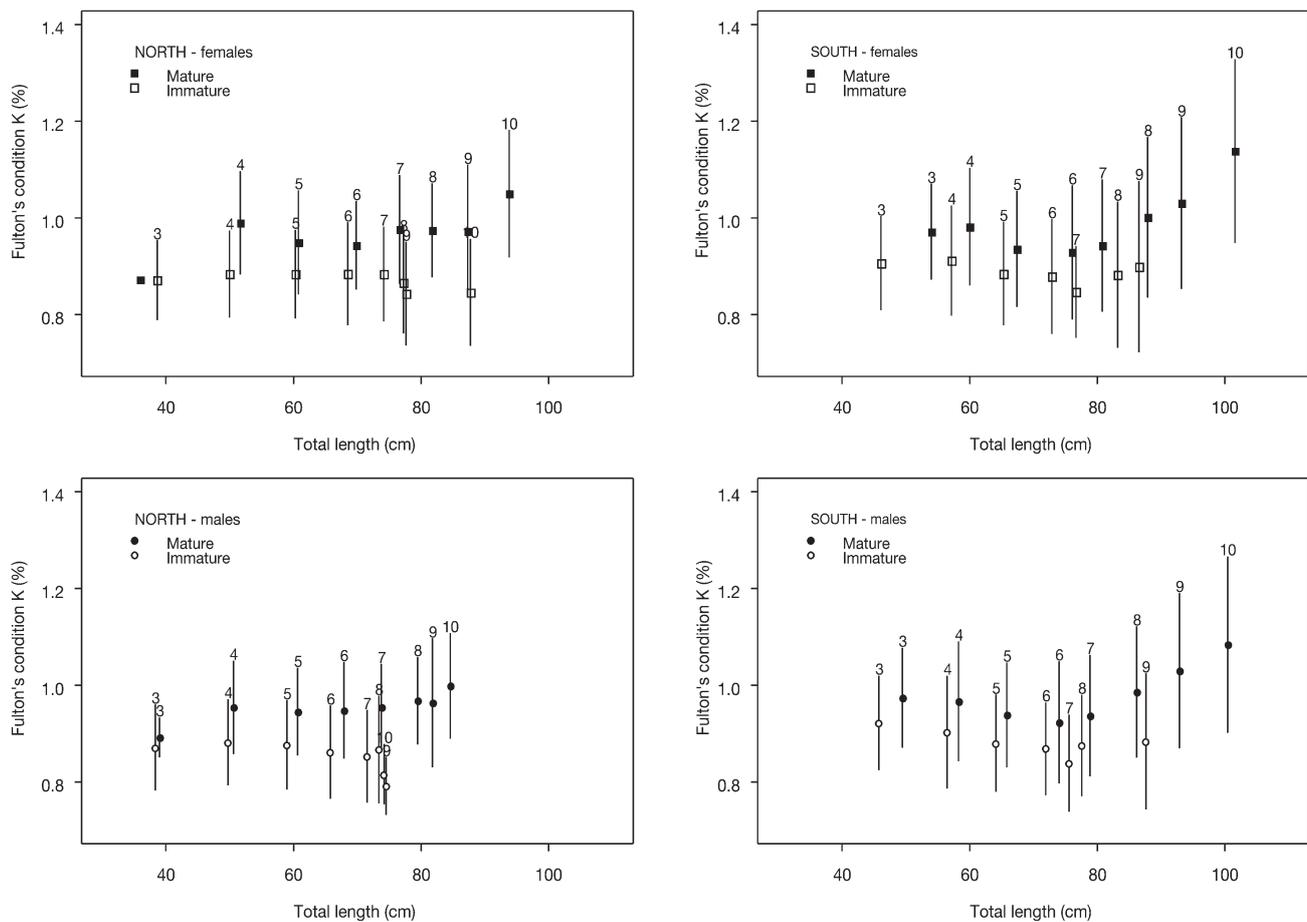
Fig. 4. Age-specific total length (cm) and Fulton's condition index (*K*) (mean ± SD) for mature and immature female and male cod in waters off the north and south coasts of Iceland (combined data 1985 to 1999)

lowest RF in 1997 and highest in 1999 were also observed for standard fish of 90 and 120 cm length (Table 5).

Batch fecundity (BF) ranged from 0.014 to 2.325 million hydrated oocytes present in the ovary at any given time during the spawning season (Fig. 8). Batch size appeared to be positively related to female total length ($r^2 = 0.234$, $p < 0.001$; Fig. 8), where the smallest females (50 to 80 cm) did not produce batches greater than 0.5 million eggs and only females >100 cm produced batches greater than 1.0 million eggs. However, for each female size class, batch size oscillated from close to 0 (presumably immediately after spawning) to a larger number (presumably when the size of the batch had been established). Batch size was also influenced by somatic condition, where an increased proportion of the variation was explained by including *K* in the analysis (BF = $-1116501 + 11811 \times L + 380166 \times K$; $r^2 = 0.256$, $p < 0.0001$). In contrast, the addition of *H* did not have a significant effect on batch size ($p > 0.80$), nor did SPS ($p > 0.88$; Fig. 8).

Eggs and larvae

ED was significantly influenced by all variables including year, spawning stage and female total length ($p < 0.05$; Fig. 9, Table 7). However, within each spawning stage, significant results were only obtained for Stage II in 1994 (ED = $1.27 + 0.0018 \times L$, $r^2 = 0.31$, $p < 0.05$, n = 29) and 1996 (ED = $1.24 + 0.0019 \times L$, $r^2 = 0.23$, $p = 0.06$, n = 15), and Stage III in 1996 (ED = $1.28 + 0.0011 \times L$, $r^2 = 0.14$, $p < 0.05$, n = 35). Consistent with other reports (e.g. Solemdal et al. 1993), the regression relationships between ED and female *L* in 1994 and 1996 for combined SPS II and III were also significant (Table 8). Analysis of the data for females in SPS II and III in 1994 and 1996, revealed that the slopes of the 2 fitted lines were not significantly different (ANCOVA, $p > 0.711$). However, the intercepts were significantly different (ANCOVA, $p < 0.001$). Including *K* in the models had little influence on the amount of variation explained ($r^2 = 0.243$ [1994]; $r^2 = 0.282$ [1996]) and the effects of *K* were not significant at $\alpha = 0.05$

Table 3. GLM results (null and residual deviance, pseudo-R^2) and coefficients of maturity ogives incorporating the effects of length (TL), age (A) and condition (K) that were used to estimate proportion mature (M) of female and male cod in waters off the north and south coasts of Iceland (combined data 1985–1999). $M = 1/1+e^{-(-a + b \times X + c \times K)}$, where X = TL or A. Dev = residual deviance (analogous to sums of squares)

Sex	Region	Coefficients			Null dev	Res dev	R^2	Dev TL	Dev K
		a	b	c					
Females	North	−14.296	0.104	6.845	8252.9	5104.4	0.38	2737.7	410.7
	South	−9.525	0.108	2.110	6330.7	4326.1	0.32	1962.3	42.3
	Total	−12.056	0.112	4.227	16168.4	9705.4	0.40	6129.0	334.0
Males	North	−15.082	0.109	8.164	8889.5	5569.2	0.37	2740.1	580.2
	South	−9.910	0.106	3.769	6543.0	4642.6	0.29	1779.5	120.8
	Total	−13.070	0.117	5.864	17840.5	10668.0	0.40	6554.8	617.6
Both	North	−14.317	0.103	7.373	17185.6	10896.7	0.37	5322.7	966.2
	South	−9.279	0.101	2.913	13033.1	9315.4	0.29	3558.4	159.3
	Total	−12.170	0.110	4.942	34211.1	20975.8	0.39	12314.5	920.8

Sex	Region	Coefficients			Null dev	Res dev	R^2	Dev A	Dev K
		a	b	c					
Females	North	−14.135	1.061	7.528	7021.3	4206.5	0.40	2424.5	390.3
	South	−10.704	1.187	4.263	4949.9	3018.0	0.39	1799.1	132.8
	Total	−12.454	1.149	5.684	13163.6	7636.3	0.42	5043.1	484.2
Males	North	−14.528	1.023	8.902	7725.9	4812.9	0.38	2318.8	594.1
	South	−10.150	1.107	5.053	5052.9	3257.0	0.36	1625.2	170.8
	Total	−12.780	1.109	7.072	14400.4	8666.3	0.40	4968.7	765.4
Both	North	−14.081	1.016	8.109	14794.8	9180.1	0.38	4655.7	959.0
	South	−10.173	1.109	4.623	10096.6	6459.2	0.36	3331.9	305.5
	Total	−12.370	1.100	6.297	27703.3	16655.4	0.40	9826.7	1221.3

(p = 0.095 [1994]; p = 0.079 [1996]). A similar amount of variation was explained by including only female W in the models (ED = $1.1510 \times W^{0.0248}$, r^2 = 0.246, p < 0.0001 [1994]; ED = $1.0637 \times W^{0.0299}$, r^2 = 0.28, p < 0.0001 [1996]). In addition to L, neither H (p > 0.371 [1994]; p > 0.785 [1996]) nor age (p > 0.865 [1994]; p > 0.242 [1996]) contributed significantly to the variation explained by the models.

Absolute density of eggs (ρ) varied from 1.02256 to 1.02657 g cm^{-3}. Egg density was significantly related to both female total length and egg diameter (p < 0.0001), indicating that larger females produced larger eggs of a greater density than did smaller females (Fig. 10). An analysis of the relative influence of female L, SPS and ED on egg density demonstrated that SPS did not have a significant effect on egg density (p = 0.587), while both total length and egg diameter contributed to the variation in egg density (r^2 = 0.46; p < 0.05). A model describing the influence of total body weight and ED on egg density explained only slightly more of the variation (r^2 = 0.49). Similarly, K, in addition to female L and ED, did not have a significant effect on egg density (p = 0.529). In contrast, H had highly significant effects on egg density where 3 times more of the explained variation could be attributed to H than to total length

(ρ = 1.0208 + 0.0000153 × L + 0.00328 × HSI, r^2 = 0.51, p < 0.0001)

Variation in egg density (ρ_{SD} = standard deviation of 20 egg density measurements within each female batch) was also significantly related to female TL and ED (p < 0.001; Fig. 10). More than 50% of the explained variation was attributed to L (ln-transformed; p < 0.039) in comparison to the variation explained by the ED (p = 0.073). Similarly, spawning stage had no effect on variation in egg density (p = 0.582). However, both K and H had a significant effect on the variation in egg density. Influence of H was much greater than both K and L, and in a model exploring the combined effects of L and H (r^2 = 0.32), most of the variation in egg density was attributed to H (p < 0.001), while the effect of L was not significant (p > 0.45).

In all years, both L and W of larvae increased with ED (Table 8, Fig. 11). Moreover, better model fits were observed between ED and larval dry weight than ED and L (Fig. 11; Table 8). Larval length at 20 d was also shown to increase significantly with ED (Fig. 11; Table 8). However, only in 1994 was the SGR found to increase significantly with ED (SGR = −7.649 + 8.744 × SGR, r^2 = 0.18, p < 0.05). The range of SGR was similar among years (1994: 2.8 to 7.5%; 1995: 4.4 to 9.1%; 1996: 3.1 to 8.4).
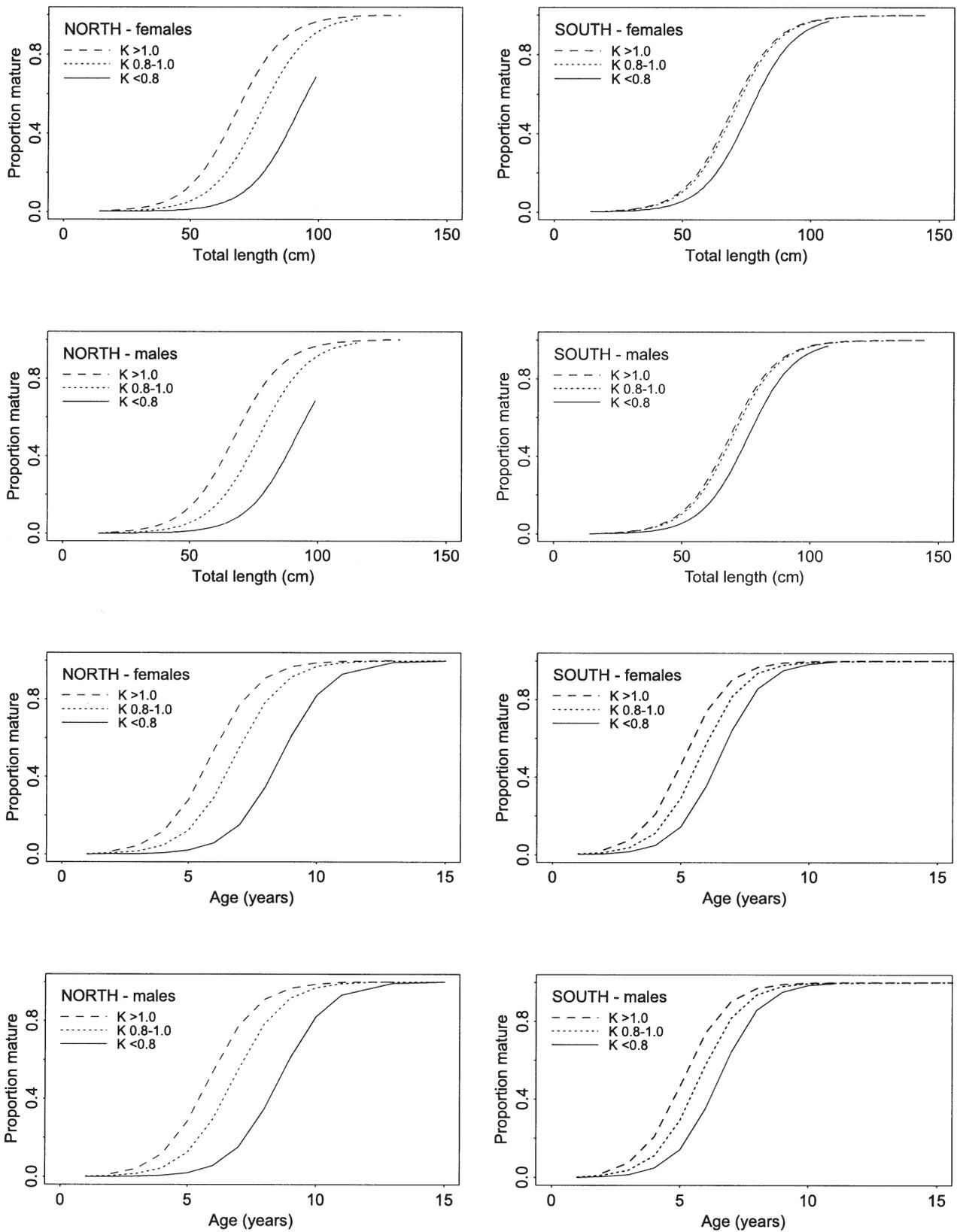
Fig. 5. Maturity ogives for female and male cod in waters off the north and south coasts of Iceland that were used to estimate the proportion of mature cod at each length for 3 condition (K) classes ($K < 0.8$; $K = 0.8$ to 1.0; $K > 1.0$) (combined data 1985 to 1999)
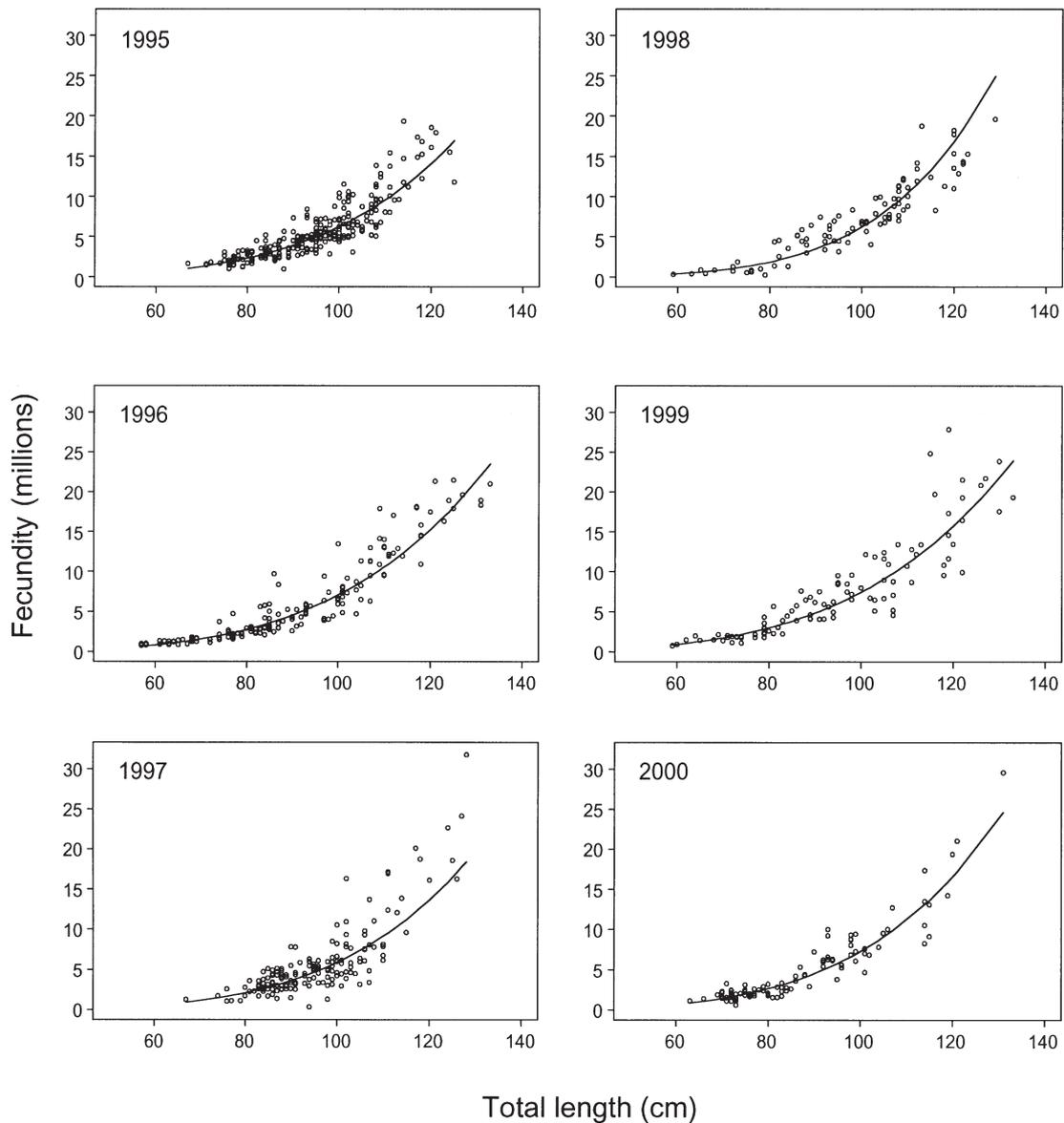
Fig. 6. Potential fecundity (PF) of cod in Icelandic waters, 1995 to 2000

DISCUSSION

Reproductive potentials of cod stocks throughout the north Atlantic are undoubtedly influenced by a multitude of factors interacting at both the individual and stock levels (Trippel et al. 1997a, Marshall et al. 1998, Marteinsdottir & Thorarinsson 1998). We found reproductive potential in the Icelandic cod stock to be strongly influenced by the age, size and condition of individual spawning fish as well as the population demographics and life history characteristics of the spawning stock. Results from this study will provide fishery modelers with a set of fundamental relationships that will aid the estimation of reproductive

potential in cod stocks throughout the north Atlantic, which, in turn, will support the re-examination of stock-recruitment relationships for these stocks. Based on these relationships, more accurate biological reference points can then be formulated for the development of more realistic fishery harvesting strategies (Marshall et al. 1998, Scott et al. 1999).

Age and size at sexual maturity are fundamental variables that influence the reproductive potential of a fish stock (Jørgensen 1990, Rijinsdorp et al. 1991, Trippel et al. 1997a). Often in fisheries stock assessments these variables are assumed to be constant over extensive spatial and temporal scales (Rijinsdorp et al. 1991, Marshall et al. 1999), with little regard for the plasticity

Table 4. Potential fecundity relationships (PF = $a \times$ length^b) and potential fecundity of a standard fish, 70, 90 and 120 cm length cod from different areas in the North Atlantic, the Baltic and the North Sea

Geographical area	Time period	n	Length range	a	b	r²	Fec-70 cm	Fec-90 cm	Fec-120 cm	Source
Gulf St. Lawrence	1955–1956	43	51–140	0.38	3.5	0.83	1.090	2.628	7.192	Powles (1958)[a]
Labrador and Newfoundland	1964	130	50–130	0.5	3.42	0.72–0.93	1.021	2.412	6.453	May (1967)
Gulf St. Lawrence	1980	30	47–103	1.1	3.28	0.81	1.239	2.827	7.262	Buzeta & Waiwood (1982)
Newfoundland (Bonavista Bay)	1967–1968	58	65–109	0.3548	3.5	0.77	1.018	2.454	6.716	Pinhorn (1984)
Newfoundland (Trinity Bay)	1967–1968	78	60–108	1.7783	3.13	0.78	1.060	2.327	5.726	Pinhorn (1984)
Newfoundland (St. Pierre Bank)	1970,1967, 1969	103	51–128	0.4168	3.37	0.82	0.688	1.606	4.235	Pinhorn (1984)
Newfoundland (St. John's)	1966,1968	62	61–118	2630.267	1.41	0.38	1.050	1.498	2.247	Pinhorn (1984)
Newfoundland (Placenta Bay)	1966	96	64–113	53.703	2.42	0.72	1.567	2.879	5.776	Pinhorn (1984)
Gulf St. Lawrence	1995	53	37–65	0.065	3.964	0.70	1.339	NA	NA	Lambert & Dutil (2000)
Iceland	1960	42	58–94	3.42	3.071	0.525	1.586	3.432	NA	Joakimsson (1969)
Iceland	1967	49	54–125	0.5678	3.457	0.835	1.357	3.236	8.748	Schopka (1971)
Iceland	1995	264	67–125	0.0076	4.457	0.81	1.272	3.898	14.051	Present study
Iceland	1996	160	57–133	0.0252	4.223	0.9	1.562	4.516	15.220	Present study
Iceland	1997	160	67–128	0.0034	4.622	0.62	1.146	3.664	13.850	Present study
Iceland	1998	88	59–129	0.000072	5.455	0.83	0.836	3.294	15.822	Present study
Iceland	1999	102	59–133	0.0472	4.099	0.88	1.726	4.835	15.722	Present study
Iceland	2000	96	63–131	0.0063	4.535	0.86	1.468	4.590	16.921	Present study
Baltic[b]	1987	64	32–104	49.76	2.51	0.76	2.126	3.995	8.224	Kraus et al. (2000)
Baltic	1996	37	40–100	185.56	2.28	0.79	2.987	5.298	10.209	Kraus et al. (2000)
NE Arcto-Norwegian	1986	50	50–120	0.123	3.764	0.89	1.083	2.790	8.240	Kjesbu et al. (1998)
NE Arcto-Norwegian	1987	46	50–90	0.261	3.541	0.79	0.891	2.171	NA	Kjesbu et al. (1998)
NE Arcto-Norwegian	1988	49	50–125	0.0614	3.909	0.92	1.001	2.675	8.235	Kjesbu et al. (1998)
NE Arcto-Norwegian	1989	111	50–130	0.804	3.357	0.92	1.257	2.922	7.675	Kjesbu et al. (1998)
NE Arcto-Norwegian	1991	8	50–130	16.8	2.693	0.82	1.564	3.077	6.676	Kjesbu et al. (1998)
North Sea	1971–1972	92	60–110	1.29	3.29	0.82	1.517	3.468	8.935	Oosthuzien & Daan (1974)

[a] Regression coefficients obtained from Buzeta & Waiwood (1982)
[b] In the Baltic, years containing large females were selected from Kraus et al. (2000)
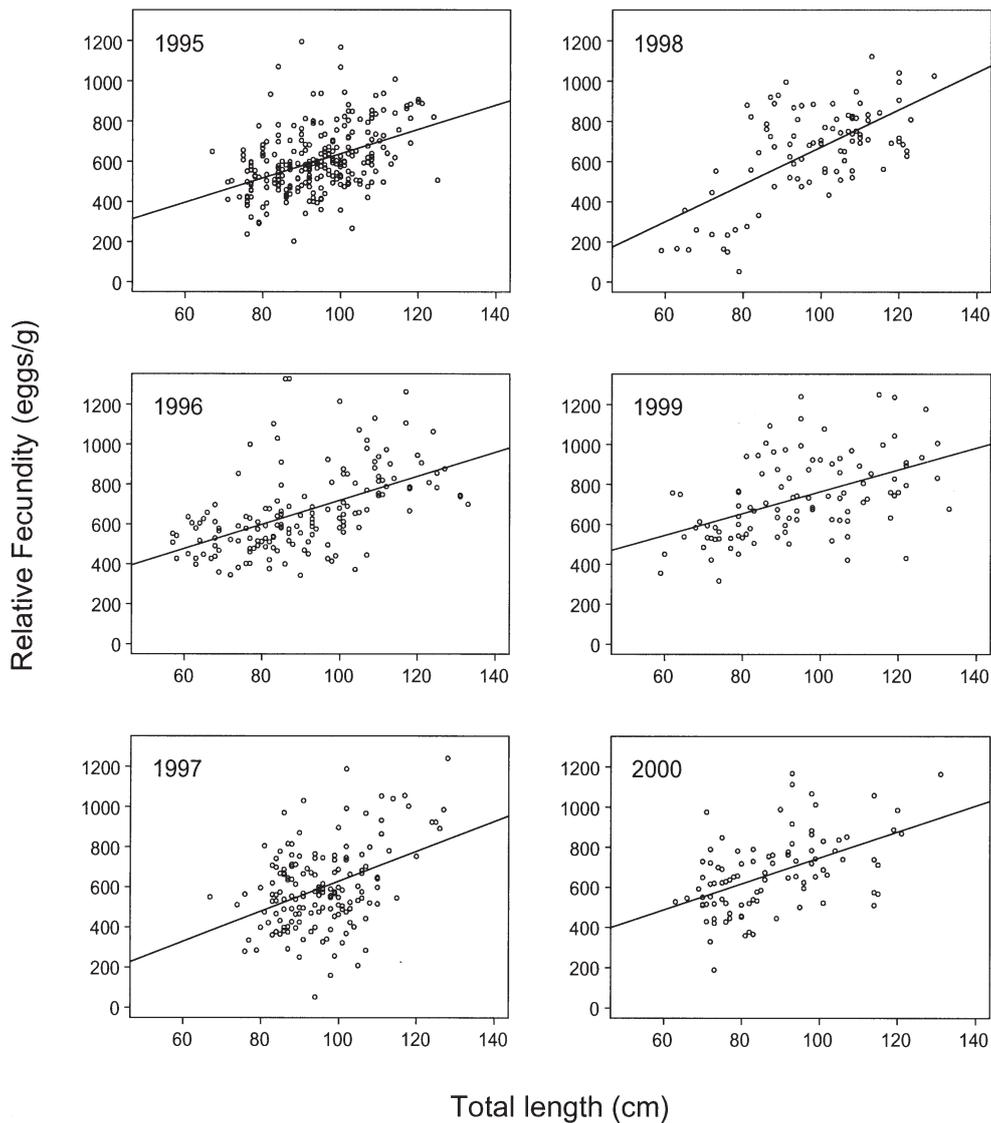
Fig. 7. Relative fecundity (RF) of cod in Icelandic waters, 1995 to 2000

in these flexible life history characteristics to fishing exploitation and environmental perturbations (Stearns & Crandall 1984). Indeed, similar to other cod stocks throughout the north Atlantic (Holdway & Beamish 1985, Godø & Moksness 1987, Trippel et al. 1997b, Begg et al. 1999, Cardinale & Modin 1999, O'Brien 1999), the Icelandic cod stock demonstrated significant sexual, spatial and temporal variation in age and size at maturity (Fig. 2) that were strongly affected by growth and condition (Fig. 5). Faster-growing cod in waters off the south coast of Iceland attained sexual maturity at a smaller size and younger age than slower-

growing cod off the north coast. Moreover, the influence of condition on maturity was more apparent for cod in waters off the north coast, particularly for size at

Table 5. Regression equations for relative fecundity (RF: g^{-1} whole body weight) on female length (L) in 1995 to 2000. Estimated relative fecundity for a standard fish, 70 and 90 cm long

Year	Regression	r^2	p	RF-70	RF-90	RF-120
1995	RF = 91.2 + 4.8 × L	0.2	<0.001	427	523	667
1996	RF = 184.7 + 4.6 × L	0.23	<0.001	507	599	737
1997	RF = −8.4 + 5.5 × L	0.14	<0.001	377	486	652
1998	RF = -200.2 + 8.3 × L	0.38	<0.001	381	547	796
1999	RF = 258.6 + 4.5 × L	0.19	<0.001	574	664	799
2000	RF = 168.6 + 5.1 × L	0.21	<0.001	525	628	781

Table 6. Analysis of the effects of length, somatic condition (K) and liver condition (H) on relative fecundity of cod (number of eggs g^{-1} total body weight). Results include the range of values for each source of variation in the model, coefficients (the intercepts listed in the top line for each year), marginal sums of squares (Type III in thousands), results of the F statistics (rounded to a whole number), the probability levels and proportion of variation explained by the model

Year	Source of variation	Range of values	Coefficients	Sums of squares	F	p > F	r^2
1995	Total model		−96.15	1213	29	<0.0001	0.26
	Length	67–125	4.35	479	35	<0.001	
	K	0.46–1.49	115.87	63	5	0.031	
	H	2.7–15.8	13.57	266	20	<0.001	
1996	Total model		127.45	4701	22	<0.001	0.26
	Length	57–133	3.55	299	13	<0.001	
	K	0.73–1.59	84.79	17	1	0.374	
	H	1.7–14.4	9.42	73	3	0.071	
1997	Total model		−188.12	4183	21	<0.001	0.29
	Length	67–128	2.86	114	6	0.016	
	K	0.73–1.59	194.85	141	7	0.008	
	H	3.0–12.6	27.64	359	18	<0.001	
1998	Total model		−391.80	3999	19	<0.001	0.41
	Length	59–129	8.36	820	29	<0.001	
	K	0.68–1.35	73.26	4	1	0.678	
	H	2.1–13.5	15.18	67	3	0.125	
1999	Total model		67.51	3456	12	<0.001	0.27
	Length	59–133	2.69	156	6	0.016	
	K	0.75–1.46	233.26	100	4	0.053	
	H	2.7–18.9	15.82	128	5	0.028	
2000	Total model		−41.51	2734	15	<0.001	0.33
	Length	63–131	4.47	179	9	0.004	
	K	0.72–1.57	60.82	4	1	0.643	
	H	1.8–13.4	27.60	288	14	<0.001	

Table 7. Mean (mm) and standard deviation of egg diameters in 1994 and 1996 grouped by spawning stages and female size groups

Female size groups	SPS-I			SPS-II			SPS-III			SPS-IV		
	n	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD
1994												
>100 cm	1	–	–	19	1.48	0.06	12	1.46	0.06	8	1.35	0.04
75–100 cm	–	–	–	7	1.45	0.08	7	1.42	0.07	1	–	–
<75 cm	–	–	–	4	1.39	0.03	14	1.41	0.05	6	1.31	0.04
1996												
>100 cm	4	1.42	0.06	9	1.44	0.07	9	1.41	0.05	1	–	–
75–100 cm	–	–	–	5	1.43	0.04	21	1.36	0.04	6	1.33	0.06
<75 cm	–	–	–	1	–	–	5	1.36	0.04	6	1.33	0.06

maturity, where distinct differences were detected between cod of variable condition. The influence of condition may be more significant for cod in the north, where waters are cooler and more variable, and hence less conducive to growth and survival than waters in the south, which tend to be on average at least 4°C warmer (Malmberg & Kristmannsson 1992, Begg & Marteinsdottir 2000). The more variable environment in the north may exacerbate life history differences between fish in good and poor condition, as has been found in other studies where poor condition was correlated with slow growth (Lambert & Dutil 1997a,b). Alternatively, the disparity in age and size at maturity between cod in waters off the north and south coasts may be due to variable fishing pressure, where greater exploitation of spawning fish exists on the main spawning grounds off the south coast (Begg & Marteinsdottir 2002a,b).
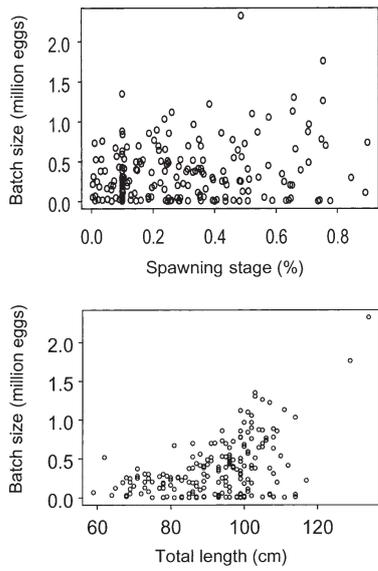
Fig. 8. Batch size vs female total length (cm) and spawning stage
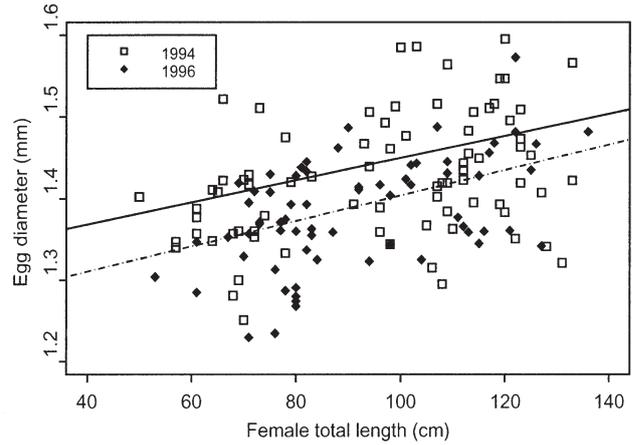
Fig. 9. Linear relationships between female total length (cm) and egg diameter (ED), 1994 to 1996. Shown are fitted regression lines for female cod in Spawning Stages II and III in 1994 (solid line) and 1996 (dashed line). Regression equations are listed in Table 8
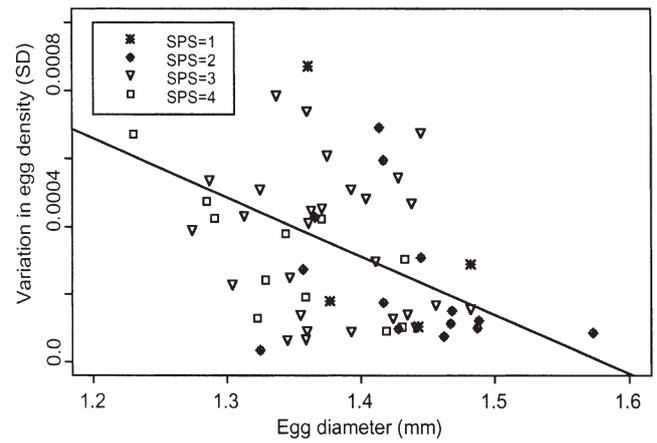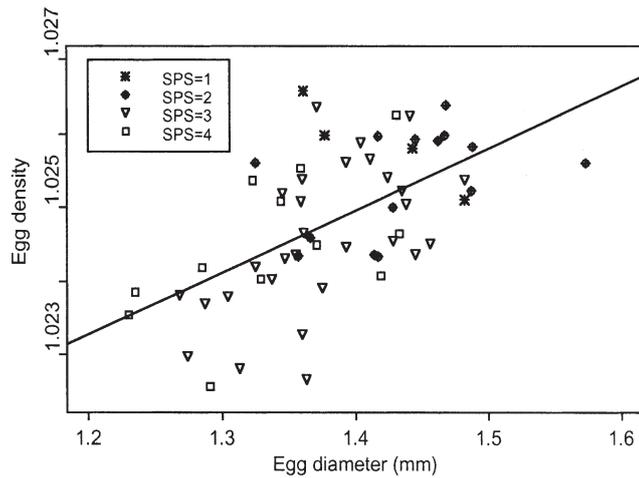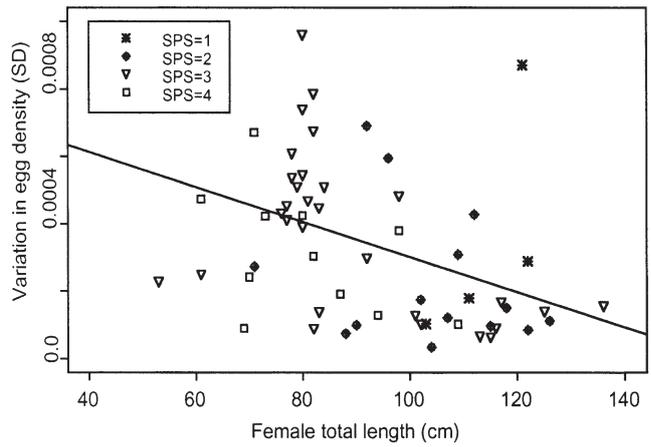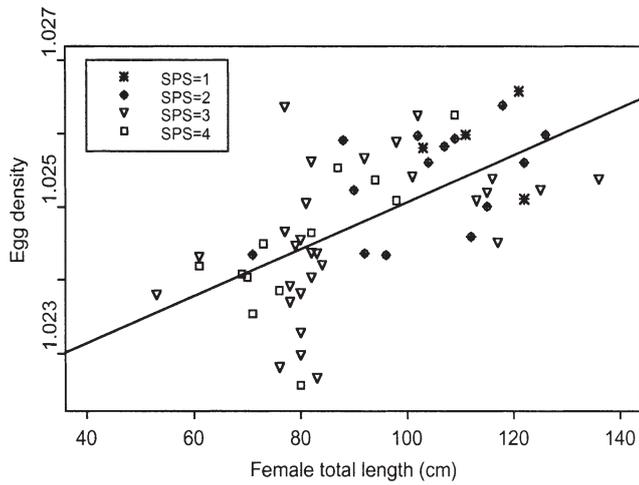

Fig. 10. Linear relationships between female total length, egg diameters (ED), egg density (ρ) and the variation in egg density in 1996

Table 8. Relationships between cod egg size and female length (TL, cm) as well as egg and larval sizes measured as egg diameters (ED, mm), egg dry weight (EDW, mg), egg wet weight (EWW, mg), larval length at hatching (LTLH, mm), larval dry weight at hatching (LDWH, mg) larval dry weight at 5 d post-hatch (LDW5, mg) and larval dry weight at 20 d post hatch (LDW20, mg) among the different cod stocks in the North Atlantic (Norway: captive, NCC = Norwegian coastal cod, NAC = Norwegian Arctic cod, Baltic, North Sea, Iceland and Scotian Shelf and Northwest Atlantic cod). Predicted values based on the relationships are given for females 70 and 120 cm long, eggs diameters 1.2 and 1.5 mm and egg dry weight 0.08 and 0.18 mg

Size range of indepent variable	Fixation	Year of analysis	Regression equation	n	r^2	p	Predicted values	Predicted values	Cod stock	Source
FL and ED							TL = 70 cm	TL = 120 cm		
55–75 cm	Fresh	1986	ED = 0.8964 + 0.0076 × TL[e]	12	0.471	<0.05	1.43	1.81	Norway-Captive	Kjesbu (1989)
46–91 cm	Fresh	1993–1997	ED = 1.3773 + 0.00393 × TL[d]	47	0.424	<0.001	1.65	NA	Baltic	Vallin & Nissling (2000)
70–120 cm	Fresh	1993	ED = 1.227 + 0.002 × TL[f]	26	0.243	<0.05	1.37	1.47	NAC	Solemdal et al. (1993)
55–135 cm	Fresh	1994	ED = 1.312 + 0.0014 × TL[f]	28	0.324	<0.001	1.41	1.50	Iceland	Present study
55–135 cm	Fresh	1996	ED = 1.248 + 0.0016 × TL[f]	14	0.235	<0.001	1.37	1.46	Iceland	Present study
ED and egg dry weight							ED = 1.2 mm	ED = 1.5 mm		
1.3–1.5 mm	Fresh	1986	EDW = −0.206 + 0.255 × ED	146	0.821	<0.001	0.1255	0.1765	Captive	Kjesbu (1989)
1.16–1.6 mm	Fresh	1985–1986	EDW = 0.04 × ED[2.837]	16	0.928	<0.001	0.0842	0.12637	North Sea/West Scotland	Hislop & Bell (1987)
1.16–1.60 mm	Fresh/preserve[a]	1985–1986	EDW = 0.057 × ED[2.138]	11	0.595	NS	0.0999	0.1356	North Sea/West Scotland	Hislop & Bell (1987)
1.25–1.6 mm	Fresh	1994	EDW = −0.1385 + 0.1892 × ED	76	0.563	<0.0001	0.1075	0.1453	Iceland	Present study[h]
1.23–1.53mm	Fresh	1995	EDW = −0.1273 + 0.1810 × ED	84	0.733	<0.0001	0.1080	0.1442	Iceland	Present study
1.23–1.57 mm	Fresh	1996	EDW = −0.215 + 0.2442 × ED	66	0.936	<0.0001	0.1025	0.1513	Iceland	Present study
1.15–1.41 mm	Fresh	?	EDW = −0.202 + 0.222 × ED[c]	12	0.86	<0.05	0.0866	0.1310	NCC	Knutsen & Tilseth (1985)
ED and EDW							ED = 1.2 mm	ED = 1.5 mm		
1.25–1.6 mm	Fresh	1994	EW = −2.956 + 3.177 × ED	78	0.754	<0.0001	1.1741	1.8095	Iceland	Present study
1.23–1.53 mm	Fresh	1995	EW = −2.638 + 2.969 × ED	84	0.907	<0.0001	1.2217	1.8155	Iceland	Present study
1.23–1.57 mm	Fresh	1996	EW = −2.9844 + 3.225 × ED	67	0.969	<0.0001	1.2081	1.8531	Iceland	Present study
ED and LL							ED = 1.2 mm	ED = 1.5 mm		
1.2–1.8 mm	Fresh	1992	LTLH = 0.112 + 2.84 ED	282	0.372	<0.001	3.52	4.65	Scotian Shelf	Miller et al. (1995)
1.2–1.6 mm[b]	Fresh	1993–1997	LTLH = 1.2711 + 2.1351 ED	37	0.715	<0.0001	4.05	4.47	Skagerrak	Nissling et al. (1998)
1.15–1.65 mm	Fresh	1993–1997	LTLH = 2.0425 + 1.3613 ED	35	0.467	<0.0001	3.81	4.08	Baltic	Nissling et al. (1998)
1.25–1.5 mm	Fresh	1992	LTL5 = 1.0801 + 2.9407 × ED	15	0.638	<0.001	4.90	5.49	NAC	Solemdal et al. (1992)
1.25–1.6 mm	Fresh	1994	LTLH = 1.935 + 1.8537 × ED	75	0.586	<0.0001	4.34	4.71	Iceland	Present study[h]
1.23–1.53 mm	Fresh	1995	LTLH = 3.672 + 0.662 × ED	65	0.064	<0.05	4.53	4.66	Iceland	Present study
1.23–1.57 mm	Fresh	1996	LTLH = 3.355 + 0.813 × ED	64	0.09	<0.05	4.41	4.57	Iceland	Present study
ED and LDW							ED = 1.2 mm	ED = 1.5 mm		
1.33–1.63 mm	Fresh/preserved	1991–1992	LDWH = −0.1042 + 0.112 × ED	34	0.83	<0.001	0.04179	0.06425	Bay of Fundi	Trippel (1998)
1.25–1.45 mm	Fresh	1992–1993	LDWH = 0.23562 × ED/2[4.04239]	59	0.978	<0.001	0.04130	0.07365	NCC	Van der Meerren et al. (1994)
1.3–1.53 mm	Fresh	1992–1993	LDWH = 0.14969 × ED/2[2.78861]	54	0.966	<0.001	0.04503	0.06711	NAC	Van der Meerren et al. (1994)
1.25–1.6 mm	Fresh	1994	LSWH = −0.0508 + 0.0858 × ED	76	0.394	<0.001	0.06074	0.07790	Iceland	Present study
1.23–1.53 mm	Fresh	1995	LDWH = −0.0876 + 0.1114 × ED	84	0.361	<0.001	0.05722	0.07950	Iceland	Present study
1.23–1.57 mm	Fresh	1996	LDWH = −0.0934 + 0.1148 × ED	66	0.559	<0.001	0.05584	0.07880	Iceland	Present study
ED and LWW							ED = 1.2 mm	ED = 1.5 mm		
1.25–1.6 mm	Fresh	1994	LWWH = −2.086 + 0.8469 × ED	76	0.208	<0.001	0.89197	1.06135	Iceland	Present study

Table 8 (continued)

Size range of indepent variable	Fixation	Year of analysis	Regression equation	n	r^2	p	Predicted values	Predicted values	Cod stock	Source
ED and LDW at 20 d post hatch							ED = 1.2 mm	ED = 1.5 mm		
1.25–1.6 mm	Fresh	1994	LDW20 = −0.6042 + 0.5589 × ED	20	0.355	<0.001	0.12237	0.23415	Iceland	Present paper
1.23–1.53 mm	Fresh	1995	LDW20 = −0.3022 + 0.3721 × ED	28	0.136	<0.001	0.18153	0.25595	Iceland	Present paper
1.23–1.57 mm	Fresh	1996	LDW20 = −0.3502 + 0.4082 × ED	60	0.335	<0.001	0.18036	0.26200	Iceland	Present paper
EDW and LL							EDW = 0.08 mg	EDW = 0.18 mg		
0.055–0.110	Fresh	?	LTL5 = 3.22 + 0.015 × EDW	12	0.8	<0.0001	4.42	5.92[i]	South Norway	Knutsen & Tilseth (1985)
0.089–0.190 mg	Fresh	1994	LTL = 3.935 + 4.905 × EDW	74	0.272	<0.001	4.327	4.818	Iceland	Present paper
0.094–0.203 mg	Fresh	1995	LTL = 4.434 + 1.313EDW	65	0.016	<0.001	4.539	4.670	Iceland	Present paper
0.090–0.178 mg	Fresh	1996	LTL = 3.949 + 4.337 × EDW	65	0.171	<0.001	4.296	4.729	Iceland	Present paper
EDW and LDW							EDW = 0.08 mg	EDW = 0.18 mg		
0.055–0.110	Fresh	?	LDW5 = 0.00319 + 0.53 × EDW	12	0.87	<0.0001	0.07430	0.12730	South Norway	Knutsen & Tilseth (1985)
0.080–0.135	Fresh	1992	LDW5 = 0.00837 + 0.5138 EDW	12	0.95	<0.001	0.04111	0.10080	NAC	Solemdal (1992)
0.090–0.190	Fresh	1994	LDW = 0.0406 + 0.2353 × EDW	76	0.189	<0.001	0.05942	0.08295	Iceland	Present paper
0.090–0.203	Fresh	1995	LDW = −0.0069 + 0.6006 × EDW	81	0.422	<0.001	0.04115	0.10121	Iceland	Present paper
0.090–0.178	Fresh	1996	LDW = 0.0069 + 0.4774 × EDW	65	0.604	<0.001	0.04509	0.09283	Iceland	Present paper

[a]Egg diameters estimated on preserved samples (size corrected for fixation); Egg dry weight measured on fresh samples
[b]Larvae measured at 50% hatching
[c]Modified from ED = 0.91 + 0.0045 EDW (µg)
[d]Egg size of first batch
[e]Egg size of first batch, indoor females only
[f]Egg size of females in spawning stages 2 and 3
[g]Similar relationship from another year of sampling for females in all stages of spawning was not significant
[h]Corrected values to replace previously published erroneous values due to typographical errors in Marteinsdottir & Steinarsson (1998)
[i]Survival to Day 10 post hatch
[j]5 d old larvae
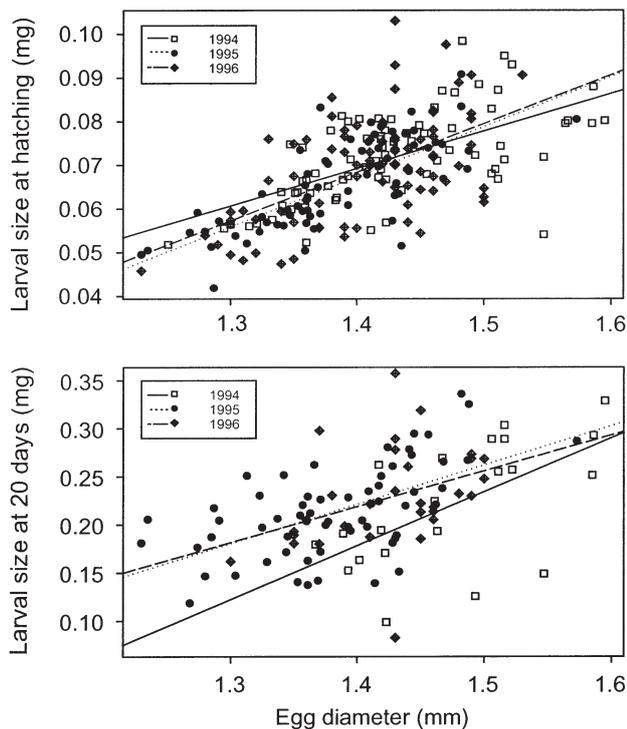
Fig. 11. Linear relationship between egg diameters (ED) and larval length at hatching and at age 20 d in 1994, 1995 and 1996

During the past few decades cod stocks across the entire north Atlantic have experienced declines in size and age at maturity, associated with severe declines in abundance and selective removal of older and larger spawners as a result of increased exploitation (Holdway & Beamish 1985, Jørgensen 1990, Rijinsdorp et al. 1991, Trippel et al. 1997b, Begg et al. 1999). Similarly, the Icelandic cod stock has experienced changes in age and size composition, as well as abundance (Marteinsdottir & Thorarinsson 1998), resulting in significant reductions in age and size at maturity of 2.8 yr and 24 cm during the survey period (excluding 1990 to 1991; Fig. 2). Notably, reductions in sexual maturity have been linked to compensatory responses in total egg production, where Trippel et al. (1997a) estimated a 16% increase in egg production when age at maturity was reduced by 1 yr compared to what it would have been with no reduction. However, more significant is that increased exploitation rates have resulted in cod stocks being comprised largely of recruit spawners due to the disproportionate loss of older and larger repeat spawners (Trippel et al. 1997b, Murawski et al. 1999), adversely affecting both the quantity and quality of total egg production (Marshall et al. 1998, Scott et al. 1999). In the Icelandic cod stock, periods of narrow age distributions have become more frequent and fewer

fish now survive beyond 7 or 8 yr of age (Marteinsdottir & Thorarinsson 1998). Consequently, accounting for variability in rates of sexual maturity, including the rarely addressed influence of condition, is important in modelling reproductive potential, as shifts in maturity can significantly affect the composition of a spawning stock and its subsequent reproductive outputs. Furthermore, accurate differentiation of recruit and repeat spawners is an area that requires greater research, particularly owing to the assumed contribution of spawning experience to reproductive potential.

While fecundity does not give information on offspring viability, it does provide the starting number of potential offspring that can be produced and is therefore one of the essential components for estimating an individual's reproductive potential. As in other studies on cod (Table 4 in Kjesbu et al. 1998), we found that fecundity was strongly influenced by size and condition of the female. The influence of condition and especially the liver index on potential and relative fecundity has, however, not been confirmed so clearly before (Oosthuzien & Daan 1974, Kjesbu et al. 1998). The proportionally stronger influence of liver condition on relative fecundity compared to length in the present study underscores the need for thorough monitoring of spawner condition levels, as well as all factors that influence condition and growth of indviduals within a stock. Similarly, accumulating evidence has demonstrated that substantial differences exist in size-specific RF (39 to 73% increase in RF between standard fish of 70 and 120 cm length in the present study and 32 to 86% increase for 50 to 120 cm North Arctic cod in Kjesbu et al. [1998]). This result alone undermines the simplistic use of spawning stock biomass to estimate reproductive potential.

The potential utility of realistic spawner-fecundity relationships to more accurately model reproductive potential also emphasizes the need for more information on temporal and spatial variation in these relationships. In the present study, coefficients of fecundity-length relationships varied significantly from one year to another. Temporal variations in length-specific fecundity relationships may have many causes, including variable growth rates and condition levels among different size classes, changes in environmental factors that explain residual variation in fecundity (Buzeta & Waiwood 1982, Kjesbu et al. 1998, Lambert & Dutil 2000) and biased sampling resulting in unequal representation of different stock units of genetically diverse origin.

Comparisons of potential fecundity revealed a considerable spatial variation among different stocks of cod in the north Atlantic. Fecundity of the Icelandic cod appeared to be higher than fecundity of Arcto-Norwegian cod and the NW Atlantic cod. Fecundity for large Icelandic cod was also higher than that for Baltic

and North Sea cod of a similar size. The slopes for the Icelandic relationships obtained in the present study (4th to 5th power) were higher than any of the other stocks (closer to 2nd to 3rd power; Table 4). Furthermore, the slopes of the fecundity-length relationships were higher for cod in the present study than for cod of a similar size sampled in 1967 (Schopka 1971, Table 4; fecundity estimated gravimetrically as in the present study). The relatively low fecundity of large female cod in 1967 may reflect the unfavorable environmental conditions in the Icelandic waters during 1965 to 1971, often referred to as the 'ice-years'. This period (the beginning of the 'Great Salinity Anomaly of 1970') was characterized by an extension of sea ice, exceptionally low sea temperatures north and east of the country, and low populations levels of *Calanus finmarchius* (Astthorsson et al. 1983, Jakobsson 1992, Astthorsson & Gislason 1995). These environmental conditions were shown to influence the herring *Clupea harengus* stocks (Jakobsson 1992) and are likely to have also influenced the capelin *Mallotus villosus* stock, the main diet of cod in Icelandic waters.

Such pronounced spatial and temporal variation in fecundity emphasizes that caution is needed when attempting to generalize from 1 year or 1 stock to another. A difference in potential fecundity of 1 to 2 million eggs female^{-1} will lead to very large differences at the population level. It also highlights the need for annual monitoring of fecundity from all the main spawning components of the stocks.

An important question concerns the influence of female age, size and condition on offspring viability and survival. In addition to our study, a number of others have demonstrated significant relationships between maternal effects and offspring size (Kjesbu 1989, Solemdal et al. 1993, Trippel 1998, Chambers & Waiwood 1996, Marteinsdottir & Steinarsson 1998, Vallin & Nissling 2000). However, only 2 have demonstrated a direct connection between egg size and larval survival (Marteinsdottir & Steinarsson 1998, Nissling et al. 1998). Several studies have, however, shown that the smaller eggs of recruit spawners exhibit lower fertilization rates and greater mortality during incubation (Solemdal 1997, Trippel 1998, Trippel et al. 1999) and that initial larval size, condition and growth are related to egg size (Knutsen & Tilseth 1985, Miller et al. 1995, Pepin et al. 1997, Marteinsdottir & Steinarsson 1998, Nissling et al. 2000).

The pattern and magnitude of variation in female size-egg size relationships at the inter- and intra-stock level remains a perplexing problem. The measurements for Icelandic cod from 1994 and 1996 showed that the slopes of the relationships were similar but the intercepts were significantly different, due to a generally greater egg size in 1994. Similarly, the slopes of

the relationships of North Arctic cod (NAC; Solemdal et al. 1993) and Icelandic cod appeared to be remarkably similar (Table 8), while the intercept of the NAC was lower than the intercepts for the Icelandic relationships. In contrast, the female-egg size relationship for Baltic cod has a much steeper slope due to production of much larger eggs (1.45 to 1.8 mm), especially by the larger females (Vallin & Nissling 2000).

Egg diameters, egg dry weights and larval sizes were in all cases significantly correlated (Table 8). However, comparisons of weights and lengths between individual studies are difficult, because different techniques are used for size estimation of eggs and larvae. Regardless, considerable variation appears to exist in these relationships both at the inter- and intrastock level. Therefore, comparative studies using standardized techniques to estimate size of eggs and larvae, as well as growth and viability, are needed. Such studies would undoubtedly reveal stock-specific differences that may reflect adaptations to local conditions.

The present study also shows that there is considerable variation in egg density, both with respect to female and egg sizes and within female egg batches. In general, density of eggs increased with female size, liver condition and egg size. This is in contrast to other studies on cod by Kjesbu et al. (1992), Nissling et al. (1994) and Vallin & Nissling (2000), which have shown a significant negative correlation between egg size and specific gravity. It should be noted, however, that the observations made by Kjesbu et al. (1992) represent a seasonal decline in density, as well as, being based on relatively few and much smaller females (26 to 74 cm) than those examined here (55 to 135 cm). Furthermore, density of eggs produced by second-time spawners were initially greater than density of eggs produced by the same females the year before (Kjesbu et al. 1992), indicating that the relationship between egg density and size among the Norwegian coastal cod may actually be similar to the one for Icelandic cod.

Egg density and vertical distribution of eggs and larvae are likely to reflect adaptation to local environmental condition and transport scenarios. For example, egg density plays a major role in determining survival of eggs and larvae in the Baltic, where greater buoyancy is needed to keep the eggs above the low oxygen and high salinity layer (Vallin & Nissling 2000). In Iceland, on the main spawning grounds along the SW coast, large cod are known to spawn close to the shore (Marteinsdottir et al. 2000a) and their eggs are likely to be distributed relatively deeper in the water column (at salinity of neutral buoyancy 32 to 34.5 psu), but over a narrower range of depths than eggs of smaller fish that spawn in deeper water on the Selvogsbanki and along the continental edge. This distribution may well represent an adaptation to differential current and transport

mechanisms. Drift of eggs in the area close to shore is thought to be governed by the westward-flowing coastal current induced by the freshwater runoff of the large glacial rivers on the south shore of Iceland (Olafsson 1985, Thordardottir 1986, Marteinsdottir et al. 2000b, Begg & Marteinsdottir 2002c). The neutral buoyancy of the larger eggs would position them within the lower range of the upper density layer. Much less is known about the currents and transport mechanism from the regions further away from the shore. The smaller cod that characteristically spawn in this area (Marteinsdottir et al. 2000a) produce smaller eggs on average. The neutral buoyancy of these eggs (29 to 32 psu) will position them close to the surface or well within the upper stratification layer.

Conclusion

Our results show that not only size, but also condition of spawners may have significant effects on reproductive potential. Condition, measured both as somatic condition and relative liver weight, influence the time of maturation, as well as quality and magnitude of egg production. Fish respond to fisheries and environmental perturbations in complex ways. Consequently, we can no longer ignore the plasticity of life history traits in assessment and management. The effects of female size and condition on reproductive potential underscore the importance of maintaining wide age distributions and relatively high numbers of spawners in the older year classes. Furthermore, implications of potential loss of genetic components of larger, older spawners has not been considered at all. In Icelandic waters, distinct differences in growth and condition are observed between adjacent spawning areas within the main spawning region (Marteinsdottir et al. 2000a), indicating that the population structure of cod may be a complex mosaic of groups that grow at different rates and vary with respect to relative contribution to recruitment of the total management unit.

It would be highly remiss of scientists working under the guise of the precautionary approach to overlook these complex yet tractable features.

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