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Maternal influence on the size and viability of Iceland cod *Gadus morhua* eggs and larvae

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Size, condition, and age of female-Icelandic cod *Gadus morhua* were correlated to the size of their eggs and newly hatched larvae. A positive relationship was detected between egg size and some larval viability parameters, including the age at first feeding, successful development of a swimbladder, and specific growth rates during the first 15 days after hatching. These results reveal that the viability of cod larvae is related to attributes of the spawning females and that this information is important to our understanding of stock–recruitment relationships.

Key words: Icelandic cod; egg quality; egg size; female effects; maternal effects; larval feeding; larval growth; swimbladder.

INTRODUCTION

Although relationships between egg size and larval characteristics that may influence survival, such as larval size, feeding activity, resistance to starvation and predator avoidance, are well documented (Blaxter & Hempel, 1963; Blaxter, 1969; Knutsen & Tilseth, 1985; Miller *et al.*, 1988; Hinckley, 1990; Marteinsdottir & Able, 1992; Baynes & Howell, 1996; Chambers & Leggett, 1996; Chambers, 1997), the role of maternal attributes in determining survival is less obvious. This is due largely to a lack of information on the relationship between female characteristics (size, age, and condition) and egg size or viability on one hand and survival of the subsequent larvae on the other hand. Some studies have not detected any relationship between egg size and female size (Marsh, 1984; Townshend & Wootton, 1984; Hinckley, 1990), whereas, others have reported a positive relationship between egg size and female size, in, for example, the Atlantic herring *Clupea harengus* (Blaxter & Hempel, 1963); the common carp *Cyprinus carpio* L. (Zonova, 1973; Hulata *et al.*, 1974); the Atlantic salmon *Salmo salar* L. (Kazakov, 1981); the chum salmon *Oncorhynchus keta* (Walbaum) (Beacham & Murray, 1985); the dace *Leuciscus leuciscus* L. (Mann & Mills, 1985); the mummichog *Fundulus heteroclitus* L. (Marteinsdottir & Able, 1988); the Queenfish *Seriphus politus* Ayres (DeMartini, 1991); and cod, *Gadus morhua* L. (Kjesbu, 1989; Tripple *et al.*, 1997). There is also a review by Chambers (1997).

The relationships between female characteristics and those of eggs and larvae are especially difficult to detect in multiple batch spawners. In cod, which spawns several batches of eggs over a prolonged spawning season, egg size

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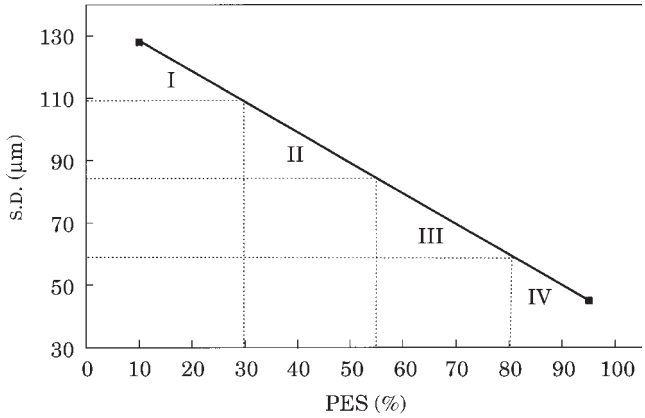

FIG. 1. Grouping of females into spawning stages I–IV, based on the standard deviation of vitellogenic oocytes (S.D.) in relation to the estimated proportion of total number of eggs spawned per season (PES, as demonstrated in Kjesbu *et al.*, 1990). See text (Material and Methods) for further explanation.

decreases during the course of the spawning season (Kjesbu *et al.*, 1992; Chambers & Waiwood, 1996). Detecting these relationships is even more difficult when the timing and duration of spawning among size and age classes of cod are asynchronous (Hutchings & Myers, 1993; Chambers & Waiwood, 1996; Marteinsdottir & Petursdottir, unpubl.).

The main objective of this paper is to determine if maternal characteristics are related to the status and viability of eggs and larvae. The first task is to identify variables that can serve as indicators of egg or larval viability. Second, the relationship between these variables and female age, size, and condition is investigated. These details should enhance estimates of the quantity and quality of egg production, which, once incorporated into models of relationships between stock size and recruitment, could extend our understanding of the role of the reproductive processes in the level of recruitment.

MATERIALS AND METHODS

FEMALE CHARACTERISTICS

Sexually mature cod were collected with a bottom trawl during three cruises in April–May 1994, on the main spawning grounds at Selvogsbanki and nearby coastal areas of Iceland. Eggs were stripped from 79 females with freely running eggs and fertilized *in vitro* on board the research vessels. Eggs of each female were fertilized by sperm of different males picked at random from the catch. Fertilized eggs were stored on board in 1-l containers at 6°–7° C, changing the water every 6 h, and transported to the laboratory within 2–3 days of sampling. All females were classified into four spawning stages based on the relationship between the standard deviation (S.D.) of the vitellogenic oocytes present in the ovary at stripping and the portion of the total number of eggs spawned in a season (PES; according to a method in Kjesbu *et al.*, 1990). Oocyte diameters were measured from ovary samples stored in Gilson's fluid (Bagenal, 1978) during the first 3 months and 4% formalin thereafter. The maximum S.D. value ($\pm$ 128 μm), obtained by measuring vitellogenic oocytes from an ovary sampled at the beginning of spawning (characterized by the presence of many, very small, brownish vitellogenic oocytes), was assumed to represent a female that had spawned *c.* 10% or less of the total eggs (Fig. 1). The minimum S.D. ($\pm$ 45 μm), obtained from a ovary sampled

at the end of the spawning season (characterized by very few numbers of vitellogenic oocytes in relation to the number of hyaline oocytes/eggs), was assumed to represent a female that had spawned >80% of the total eggs present in the ovary during the season (Fig. 1). Spawning stages (S) were defined as follows: I, <30% of eggs spawned; II, 30–55% of eggs spawned; III, 55–80% spawned; and IV, >80% spawned (Fig. 1). Females were classified into these spawning stages based on the S.D. value where S.D. >110 μm represented spawning stage I, S.D. between 85 and 110 represented spawning stage II, S.D. between 60 and 85 represented spawning stage III and S.D. <60 represented spawning stage IV (Fig. 1). Otoliths were removed from all stripped females and their lengths, weights (gutted/ungutted), liver weights and gonad weights were recorded.

EGG CHARACTERISTICS

Hatching success was based on two replicates from each female batch. On board the ship, the first 21–22 batches collected and fertilized during each cruise were selected for the hatching success study (a total of 64 batches). At 12–16 h after fertilization, *c.* 2 × 200 eggs were picked from the floating portion of each batch, disinfected in 1% Buffodine for 10 min, placed in 1-l plastic containers (transparent polystyrene) and maintained at 7° C, gently aerated, in a temperature-controlled chamber on board the ship. All sea water used in the experiment was UV-irradiated and filtered through 30- and 5-μm serial filters. Experimental batches were transported in coolers to the laboratory (transport time 1·5 h) within 2–3 days from the start of the experiment and maintained in their initial sea water gently aerated at 7° C until the completion of the experiment. Dead eggs and newly hatched larvae (if present) were removed every day. Hatching success was based on the number of dead eggs/total number of eggs in the experiment. The total number of eggs was obtained by adding the number of dead eggs and newly hatched larvae recorded during the experiment.

Eggs for rearing were transported in a similar way, 30–40 ml of eggs from each female in 1-l containers. In the laboratory, all egg batches were reared in duplicate. After disinfection in 1% Buffodine for 10 min, two samples of 10 ml each from each batch were transferred into 3-l glass bowls filled with UV-irradiated sea water filtered through 30- and 5-μm serial filters. Since the sea water at the laboratory was 31–32‰, 6 g of dissolved laboratory salt (NaCl) were added to each bowl in order to raise the salinity by 2‰ and thus make the eggs positively buoyant. The bowls were stored at 7° C on open shelves in the laboratory and aerated gently by using submerged Pasteur pipettes. The light regime was fixed at 18 L : 6 D with a light intensity of 10–30 lx on the shelves. Dead eggs were removed daily by siphoning.

Egg diameters, dry and wet weights, were obtained on arrival at the laboratory. Total diameters of 30 eggs from each batch were measured to the nearest 0·01 mm. Duplicate samples of 25 eggs were taken from each batch for measurements of wet weight and dry weight. The eggs were counted onto a 350-μm mesh and the excess sea water was removed by wiping the back of the mesh for 30 s. With the timer still running the eggs were transferred into a preweighed aluminium cup and placed on a pretared scale (Cahn Microbalance, C-33). At 60 s the weight of the 25 eggs was taken to 1·0 μg precision. After 48 h at 68° C and 24 h in a desiccator the dry weight of each sample was measured similarly to 1·0 μg precision.

LARVAL CHARACTERISTICS

All size measurements were made on larvae collected within a few hours of first hatch (day 0). Images of 20 larvae from each batch were recorded at 25 × magnification with an image analyser (Leica 500Q) attached to a binocular microscope from which larval lengths were estimated. After immersion in ionized water, duplicate samples of 20 larvae were taken from each batch for measurements of wet weight and dry weight in the same way as described for the eggs.

Larvae used for the feeding and growth experiments were transferred to the rearing and experimental containers on day 1 when hatching among all batches had attained 50%. For the feeding experiments, 17, 18 and 16 batches (or a total of 51 batches) were

selected randomly from all female batches collected in the first, second and third cruise. Due to the process of random selection, nine of these batches had not been included in the hatching success study. A total of 400 larvae, picked randomly from both hatching bowls, was transferred to black, 20-l buckets filled to 19 l with aerated sea water. The temperature was controlled at 7° C and the light regime was fixed at 18 L : 6 D with a light intensity of 100 lx at the surface of each bucket. Feeding with rotifers started on day 2 and an inital density of 500 rotifers l^{-1} was adjusted daily. Each day, 3 h after feeding, a sample of 20 larvae was taken for the estimation of gut fullness. Daily sampling was continued until 60% of the larvae from each batch had started feeding.

Larvae from 45 egg batches (15 from each cruise) were used for the growth experiments. These batches were selected at random from the population of 51 batches used in the feeding study. The number of experimental batches was restricted by the number of available rearing containers each time. At 50% hatching (day 1), 1200 larvae from each batch were counted into 1-l plastic boxes (transparent polystyrene with the sides covered by a black plastic bag) and stored without aeration in the laboratory for 2 days. Dead larvae were removed daily and replaced by live ones. On day 3, larvae were transferred to black cylindro-conical silos (140 l) for rearing. Sea water was fed into the silos through a pipe attached to four submerged glass rods that reached to different depths in the water column (from 10 cm above the bottom to 10 cm below the surface). Formation of a surface film was avoided by maintaining a constant dripping on the surface. The outlet was through a central standpipe covered with a 188-μm mesh and attached to an external telescope. The water flow was set at $1{\cdot}0 \pm 0{\cdot}1$ l min^{-1}. The temperature of the inflow was constant at 7° C but due to external heating the temperature in the silos was $8{\cdot}0 \pm 0{\cdot}5$° C. The sea water in the silos was not aerated. The light regime was fixed at 18 L : 6 D with fluorescent lamps providing a light intensity of 150–200 lx at the surface in each silo.

A mixture of microalgae (*Isochrysis galbana*, *Tetraselmis suecia* and *Rhodomonas baltica*) was added to each silo every morning for the first 3 days at an original density of approximately 50 000 cells ml^{-1}. Rotifers (*Brachionus plicatilis*) were added twice a day at an original density of 1 rotifer ml^{-1}.

Samples were taken 5, 10, 15 and 20 days after hatching. Dry weights were measured from duplicate samples of 10 larvae in the same way as described for the eggs. Images of 20 larvae from each batch were recorded at 25 ×, 18 ×, 12 × and 9 × magnification to estimate total length, myotome height, tail length and the presence of a swimbladder. The larvae were immobilized in a bath of ice water to which had been added a few drops of sparkling water containing CO_2. Growth rates were calculated according to Otterå (1993): daily growth rate, $g = (\ln W_{t_2} - \ln W_{t_1})(t_2 - t_1)^{-1}$; specific growth rate, $G = 100(e^g - 1)$.

STATISTICAL ANALYSIS

Differences in egg size among females of different spawning stages were compared using analysis of variance (ANOVA) on log transformed data. Differences in hatching success (percentage hatched) were compared using ANOVA on arcsine transformed data.

The influence of female age, length, eviscerated weight, condition (Fulton's K = eviscerated weight/length^3) and liver index (liver weight/eviscerated weight) and seasonal effects (S = stage of spawning) on egg diameter (D) were analysed by entering the stage of spawning as a class variable and testing first for the homogeneity of the slopes (see Table II; SAS, 1988):

$$D = \alpha + \beta_1 X_i + \beta_2 S + \beta_3 X_i S + \varepsilon_i.$$

If the interaction term did not contribute significantly to the model the influence of female characteristics (X_i) on egg size were evaluated with an analysis of covariance (ANCOVA) without interaction:

$$D = \alpha + \beta_1 X_i + \beta_2 S + \varepsilon_i.$$

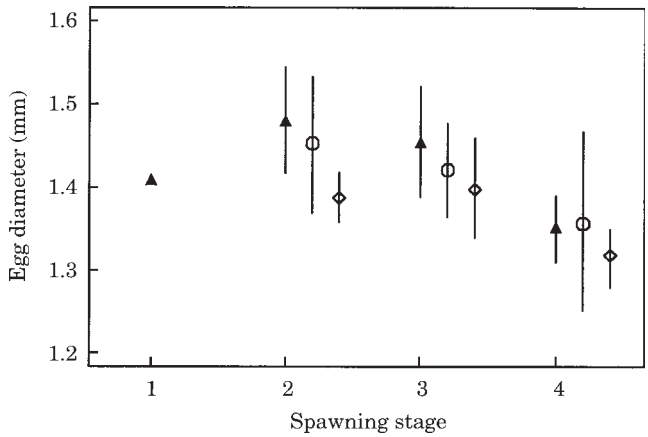

FIG. 2. Mean egg size (± S.D., vertical lines) of females classified into three length groups and four spawning stages at the time of capture. See text (Material and Methods) for definition of spawning stages. ▲, Females >100 cm; ○, females 76–100 cm; ◇, females <76 cm.

The relationships between egg diameters and the characteristics of larval viability were explored in three different ways. The differences in larval percentage of feeding with respect to egg diameters were tested with χ^2. The relationship between egg diameters and specific growth rates of larvae were analysed with a linear regression. Due to the binary nature of swimbladder occurrence (larvae with or without swimbladders), the relationship between egg diameters and frequency of larvae with swimbladders was explored by fitting a logistic model (generalized linear models in Splus, version 3.4, as demonstrated in Venable & Ripley, 1994):

$$\log_e[Y(1-Y)^{-1}] = \alpha + \beta_1 X.$$

RESULTS

SEASONAL AND MATERNAL VARIATIONS IN EGG SIZE

Egg size declined as the spawning season progressed (Table I, Fig. 2). Only one female was classified into spawning stage I. The relatively small egg size displayed by this female may be explained by the fact that the size of eggs at the beginning of spawning are often smaller than the size of eggs from the following batches (Kjesbu *et al.*, 1991). In general, eggs produced by females early in the spawning period (spawning stage II, Table I) were significantly larger than the eggs produced by females towards the end of the spawning season (spawning stage IV; $P<0{\cdot}001$). Eggs of females <76 cm and females >100 cm long decreased significantly during the season (Fig. 2; $P<0{\cdot}001$), while the decrease in egg size among females between 76–100 cm long was not significant ($P>0{\cdot}05$). However, the large standard deviation of the mean egg size among these females (76–100 cm) in spawning stage IV (Fig. 2) may account for the deviation from the general trend of decline. Variations in egg diameters within females were generally low where coefficients of variation (CV) ranged from 0·7 to 2·3% with an average of 1·3%. No trends were detected in CVs of egg diameters within females of different spawning stages, which averaged 1·32, 1·32 and 1·36 at spawning stages II, III and IV, respectively.

TABLE I. Means (± S.D.) and numbers (*n*) of all female, egg and larval age and size variables grouped by female spawning stages

	Spawning stages							
	I	*n*	II	*n*	III	*n*	IV	*n*
Female length (cm)	127	1	102·0 ± 21·3	30	90·4 ± 22·6	33	94·3 ± 25·4	15
Age (years)	8	1	8 ± 2·1	30	7·3 ± 2·3	33	7·5 ± 2·5	15
Eviscerated weight (kg)	17·8	1	10·86 ± 5·9	30	7·0 ± 5·1	33	7·7 ± 5·8	15
Liver index (%)	15·7	1	10·2 ± 3·4	30	8·4 ± 2·6	33	7·0 ± 2·4	15
Condition (*K*)	0·87	1	0·86 ± 0·13	30	0·76 ± 0·10	33	0·74 ± 0·10	15
Egg diameter (mm)	1·41	1	1·46 ± 0·07	30	1·43 ± 0·06	33	1·34 ± 0·05	15
Egg dry weight (mg)	0·12	1	0·14 ± 0·02	30	0·13 ± 0·02	33	1·12 ± 0·01	15
Egg wet weight (mg)	1·474	1	1·71 ± 0·26	30	1·57 ± 0·25	33	1·30 ± 0·14	15
Larval length at hatching (mm)	4·7	1	4·63 ± 0·16	30	4·59 ± 0·18	32	4·42 ± 0·17	14
Larval dry weight at hatching (mg)	0·069	1	0·074 ± 0·01	30	0·073 ± 0·01	32	0·063 ± 0·01	14
Larval wet weight at hatching (mg)	0·93	1	1·02 ± 0·13	30	1·01 ± 0·15	32	0·95 ± 0·13	14

Female condition (K) = (eviscerated weight/length^3) × 100. Liver index = (liver weight/eviscerated weight) × 100. See Material and Methods for the number of measurements on eggs and larvae from each female.

TABLE II. Analysis of the effects of female parameters (condition, length, weight, age and liver index = liver weight/eviscerated weight) and the stage of spawning (*S*) on egg size

Model	Source of variation	Sums of squares	*F*	*P*>*F*	r^2
1	Total model	0·202	15·1	0·0001	0·45
	S	0·082	19·0	0·0001	
	Condition (*K*)	0·063	8·2	0·0001	
2	Total model	0·186	13·1	0·0001	0·41
	S	0·124	13·3	0·0005	
	Length	0·047	11·6	0·0001	
3	Total model	0·195	14·2	0·0001	0·43
	S	0·114	11·1	0·0001	
	log-weight	0·056	16·6	0·0001	
4	Total model	0·175	11·8	0·0001	0·39
	S	0·125	11·2	0·0001	
	Age	0·036	9·8	0·0025	
5	Total model	0·153	9·5	0·0001	0·34
	S	0·098	8·2	0·0001	
	Liver index	0·014	3·5	0·064	

Condition (*K*) = eviscerated weight/length^3. See text for the definition of spawning stages. Results from the ANCOVA model include sums of squares for the model, type III (marginal) sum of squares for each of the parameters, results of the *F* statistics (*F*), the probability levels and the proportion of variation in egg size explained by the model (r^2)

Egg size was influenced by stage of spawning as well as age, size and condition of females (Table II). The analysis of the relative influence of the female age, size and condition, regarding the spawning stages as a covariate, demonstrated that the interaction between the female characteristics and the spawning stages were in all cases non-significant with normal distribution of the residuals. The slopes derived from the relationships between egg diameters and each of the female parameters were, therefore, the same for each spawning stage. Of the five female characteristics (length, weight, age, condition and the liver index), tested with ANCOVA, female condition in connection with the stage of spawning appeared to explain slightly more of the variation in egg size ($r^2 = 0{\cdot}45$) than did either female age ($r^2 = 0{\cdot}39$), length ($r^2 = 0{\cdot}41$) or weight ($r^2 = 0{\cdot}43$) (Table II). In contrast, the liver index did not have a significant effect on egg size ($P = 0{\cdot}064$). Egg size was influenced in all cases more by the stage of spawning than by each of the female characteristics (Table II). However, the effects of female condition on egg size (Fig. 3) were nearly as large as the effects of seasonal decline due to female spawning stages. This can be seen by comparing the marginal sums of squares where the increase in the model's error sums of squares would equal 0·082 if the spawning stage effects were removed and 0·063 if the effects of female condition were removed from the model.

EGG AND LARVAL VIABILITIES

Except for larval dry weight, hatching success was not influenced by egg size or any other female or larval attributes (Table IV). Hatching success decreased with increasing larval dry weight, however, only 8% of the variation was

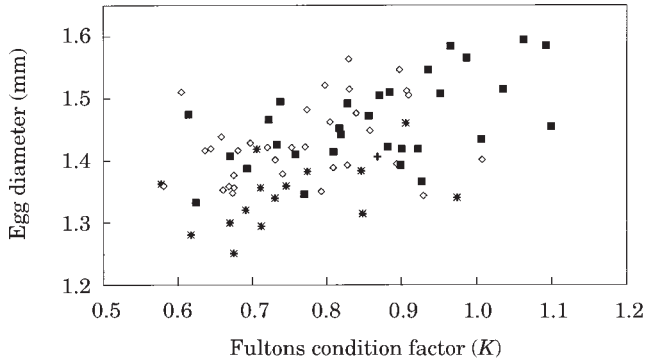

FIG. 3. The relationship between mean egg size and female condition (K = eviscerated weight length^{-3}) for cod of different spawning stages (S). See text (Material and Methods) for definition of spawning stages. Thirty eggs were measured from each female. +, $S=1$; ■, $S=2$; ◇, $S=3$; *, $S=4$. $r^2=0{\cdot}45$, $F_{4,78}=15{\cdot}1$, $P<0{\cdot}01$.

explained by this relationship ($P=0{\cdot}04$). Hatching success varied from 0 to 100% with an average of 61·3% among female batches. It did not change as the season progressed because average hatching successes (64·5, 57·8 and 64·3%) of females in spawning stages II, III, and IV were not significantly different (ANOVA on arcsin transformed data, $P<0{\cdot}01$).

Larval size at hatching increased with egg size ($r^2=0{\cdot}58$; Table III). Three of the larval viability characteristics (feeding success on day 5, swimbladder occurrence and specific growth rates on day 15) were related positively to all of the egg and larval size variables (Table IV). Feeding success on day 3 also increased with egg size and larval length although its relationship with larval weight at hatching was not significant (Table IV). Specific growth rate at day 20 was related positively to larval length and wet weight at hatching but not significantly to any of the other female, egg or larval variables (Table IV). Correlations between the female characteristics and those of larval viability were less pronounced. However, larval feeding success was correlated positively with female condition (Fulton's K and the liver index) and larval specific growth rate at day 15 increased with female age and length.

Larval feeding success increased with egg size (Figs 4 and 5). The null hypothesis that feeding success was the same for larvae derived from eggs of different sizes was rejected ($\chi^2=18{\cdot}7$, d.f. = 5, $P<0{\cdot}01$, Fig. 4). Larvae from the largest egg started to feed earlier than larvae from the smaller eggs (Fig. 5). All larval batches from eggs >1·5 mm had achieved 50% feeding success by the age of 4 days while larvae from the smaller eggs had not achieved similar success until day 6 or 7 (Fig. 5). Similarly, the frequency of larvae that were feeding on day 5 (Fig. 4) shows that larvae from eggs >1·5 mm had a feeding success of more than 60% on this day while larvae from smaller eggs expressed lower feeding success. The larval feeding success was influenced only partially by the female's stage of spawning. As an example, eggs from females in the second spawning stage hatched into larvae that expressed both high and low feeding success. However, all of the eggs from females in the fourth and the final spawning stage hatched into larvae that expressed low (<50%) feeding success.

TABLE III. Parameter estimates for linear regressions relating egg diameters (D) (mean = 1·42 mm, range 1·25–1·59 mm) to egg dry weight, egg wet weight, larval dry weight at hatching and larval wet weight at hatching ($y_i = \alpha + \beta D + \varepsilon_i$)

Response variables (Y)	n	Mean (range)	Intercept α	Slope β	r^2	F	P
Egg dry weight	79	0·131 mg (0·090-0·190)	1·044	2·906	0·56	99·3	<0·0001
Egg wet weight	79	1·571 mg (1·99–2·300)	1·052	0·237	0·75	235·8	<0·0001
Hatch length	77	4·58 mm (4·20–4·98)	− 0·020	0·316	0·58	104·6	<0·0001
Hatch dry weight	77	0·071 mg (0·052–0·098)	1·110	4·428	0·38	45·9	<0·0001
Hatch wet weight	77	1·0 mg (0·613–1·320)	1·181	0·245	0·21	19·7	<0·0001

Eggs were measured from 79 females (n = number stripped). Two egg batches did not survive through hatching. Therefore, only 77 batches were used for the estimation of larval sizes. See Material and Methods for the number of measurements on eggs and larvae from each female batch.

TABLE IV. Pearsons correlations (*n*) between attributes of females, eggs and larvae

	Hatching success	Feeding (day 3)	Feeding (day 5)	Swimbladder (day 10)	*G* (day 15)	*G* (day 20)
Female length	0·217	0·185	0·197	0·017	0·33*	0·086
	(64)	(51)	(51)	(45)	(38)	(20)
Female weight	0·163	0·258	0·264	0·024	0·299	0·124
	(64)	(51)	(51)	(45)	(38)	(20)
Female age	0·095	0·141	0·1884	0·106	0·382*	0·111
	(64)	(51)	(51)	(45)	(38)	(20)
Female condition (*K*)	0·152	0·349*	0·366**	0·073	0·153	0·023
	(64)	(51)	(51)	(45)	(38)	(20)
Female liver index	0·032	0·415**	0·364**	0·266	0·496**	0·218
	(64)	(51)	(51)	(45)	(38)	(20)
Egg diameter	−0·108	0·462**	0·559**	0·593**	0·535**	0·414
	(64)	(51)	(51)	(45)	(38)	(20)
Egg dry weight	−0·067	0·238	0·484**	0·487**	0·474**	0·333
	(64)	(51)	(51)	(45)	(38)	(20)
Egg wet weight	−0·116	0·425**	0·638**	0·381**	0·593**	0·431
	(64)	(51)	(51)	(45)	(38)	(20)
Larval hatch length	−0·219	0·385**	0·521**	0·587**	0·509**	0·531**
	(62)	(50)	(50)	(44)	(38)	(20)
Larval dry weight	−0·278*	0·068	0·387**	0·478**	0·186	0·246
	(62)	(51)	(51)	(45)	(38)	(20)
Larval wet weight	−0·146	0·237	0·320*	0·381**	0·446**	0·499*
	(62)	(51)	(51)	(45)	(38)	(20)

Egg and larval viability parameters include hatching success (%); percentage of larvae feeding on day 3 and 5 from hatching; percentage of larvae that had developed a swimbladder at the age of 10 days; and specific growth rates (*G*) at the age of 15 and 20 days.

*$P<0{\cdot}05$; **$P<0{\cdot}01$.

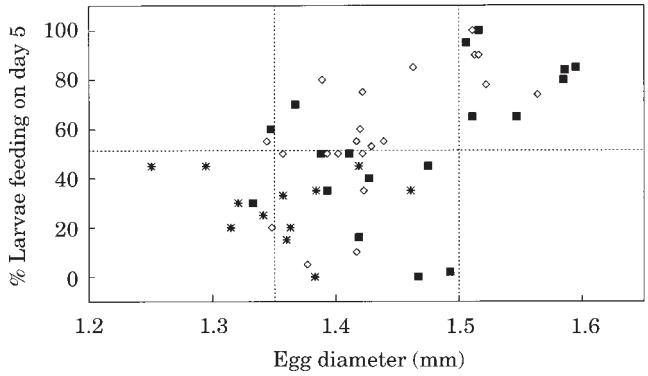

FIG. 4. Mean size of eggs and the frequency of larvae that had initiated feeding on day 5 post-hatch. Each data point is marked according to the spawning state of the stripped females (*S*). Significant differences in feeding frequencies (divided at 50%) occurred among the three size classes of eggs indicated by the dotted lines ($\chi^2 = 18{\cdot}7$, $P < 0.01$). See text (Material and Methods) for definition of spawning stages. ■, $S = 2$; ◇, $S = 3$; *, $S = 4$.

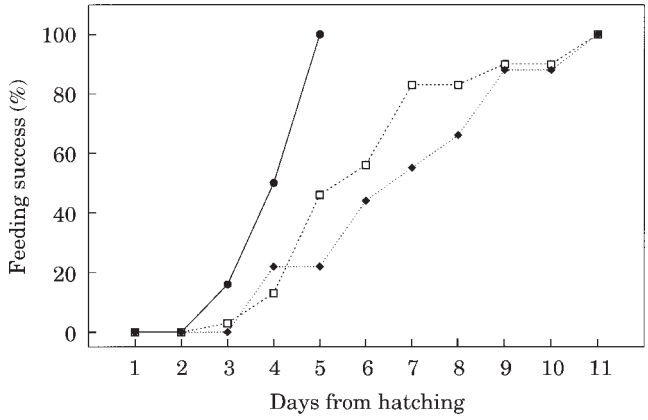

FIG. 5. Cumulative frequency of larval batches that had attained 50% feeding success during the first 11 days from hatching. Larval batches were divided into three groups based on egg size. The numbers of batches in each group were 16, 30 and 9 for eggs >1·5 mm (—●—), 1·35–1·5 mm (– –□– –) and <1·35 mm (—◆—), respectively.

The percentage of larvae that had developed a swimbladder on day 10 increased with egg size ($\chi^2 = 19{\cdot}23$, d.f. = 43, $P < 0{\cdot}01$, Fig. 6). Most of the larvae that had not developed a swimbladder at this age were from eggs that were on average <1·43 mm in diameter. In contrast, larvae from larger eggs, especially eggs >1·5 mm showed high frequencies of swimbladder occurrence. Swimbladder occurrence did not appear to be influenced by female spawning stage. Eggs from females in all spawning stages hatched into larvae that expressed either high or low swimbladder occurrence.

It appears that larvae from larger eggs may have a better start due to faster initial growth. Specific growth rates of 15-day-old larvae were higher for larvae derived from larger eggs ($r^2 = 0{\cdot}27$; $P < 0{\cdot}001$, Fig. 7). Negative growth was detected among the larvae from the smaller eggs both at the age of 5 days and the age of 10 days (Fig. 8). In contrast, larvae from the largest eggs had already

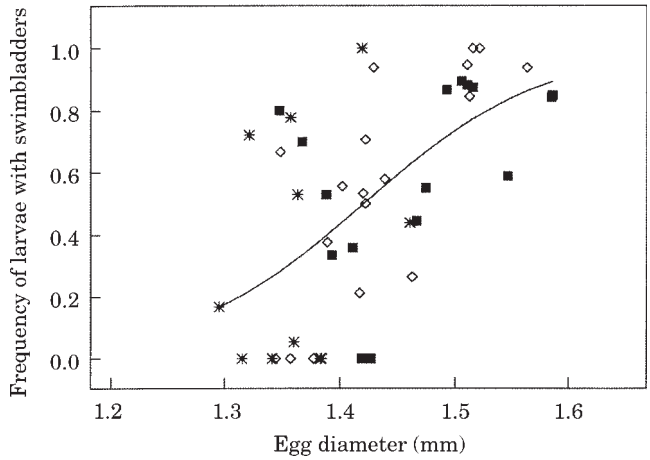

FIG. 6. Mean size of eggs and the frequency of larvae that had developed swimbladders by day 10 post-hatch. Each data point is marked according to the spawning state of the stripped females (*S*). See text for definition of spawning stages. The curve was fitted with a logistic regression model ($\chi^2 = 19{\cdot}2$; $P < 0{\cdot}01$): $\log_e[y(1-y)^{-1}] = -18{\cdot}278 + 12{\cdot}866\ x$. ■, $S = 2$; ◇, $S = 3$; *, $S = 4$.

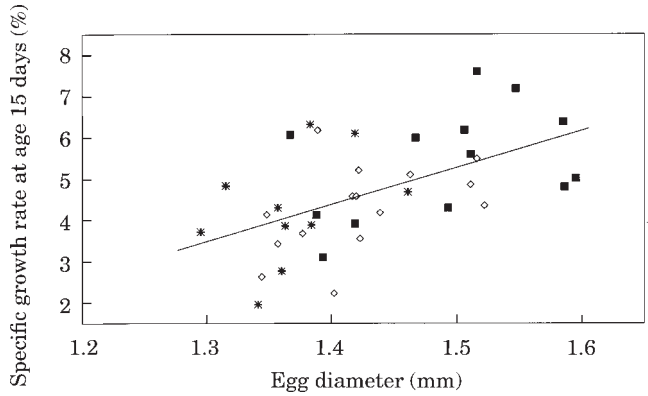

FIG. 7. The relationship between size of eggs and the average specific growth rate of larvae on day 15 post-hatch described with a simple linear regression: $y = -10{\cdot}1 + 10{\cdot}2\ x$, $r^2 = 0{\cdot}27$, $P = 0{\cdot}001$. Each data point is marked according to the spawning state of the stripped females (*S*). See text (Material and Methods) for definition of spawning stages. ■, $S = 2$; ◇, $S = 3$; *, $S = 4$.

gained some weight by the age of 5 days and were 40–60% heavier than the larvae from the two smaller size groups by the age of 10 days.

Only 38 of the 45 larval batches used for the growth experiment survived the first 15 days. However, all of the batches survived through the first 10 days. Differences in survival between days 10 and 15 did not appear to be related to egg size (average size of eggs from batches that did not survive to day 15 ranged from 1·35 to 1·56 mm; mean = 1·43) or female size (size of females that produced those egg batches ranged from 57 to 131 cm; mean = 86 cm). In contrast, the differences in survival of larval batches after 15 days were related clearly to egg size since no larvae from the smallest eggs survived past 15 days. As a result, differences in growth rates among larval batches at the age of 20 days were less

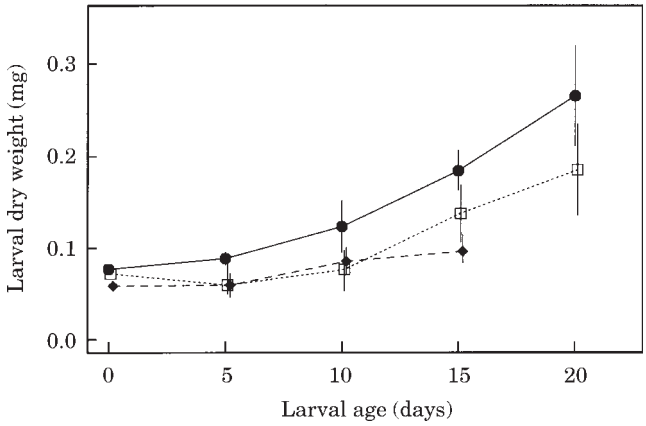

FIG. 8. Mean (± S.D.) observed size at age (mg dry weight) of larvae from eggs of three size classes. Each mean represents batches of larvae from several females. Number of batches were: 12, 12, 10 and 8 for eggs >1.5 mm (●) at the age of 5, 10, 15 and 20 days post-hatch. For eggs in the size range 1·35–1·5 (□), the number of batches were: 26, 26, 23 and 12 and for eggs <1·35 (◆) the number of batches were 7, 7, 5 and 0.

pronounced than the growth differences at the age of 15 days and the relationship between egg size and growth rate at this age was not significant (Table IV).

In general, larvae that rated high with respect to one viability characteristic expressed also high ratings in other measures of viability (Table V). For example, larvae that showed greater feeding activity developed swimbladders in higher frequencies. Similarly, those larvae that expressed faster growth rates during the first 15 days had initiated feeding earlier ($r = 0{\cdot}626$, specific growth rates on day 15 *v.* feeding on day 3; Table V) and developed swimbladders in greater numbers.

DISCUSSION

EGG AND LARVAL SIZE AS A MEASURE OF VIABILITY

Hatching success, was not influenced by egg size, larval size, or by female age, size and condition. However, although hatching success was not correlated significantly with the age of the females, the lowest values obtained were derived from the youngest females (0–19% hatching success among eggs of the 4-year-olds). Other studies have shown that compared with second or third time spawners, hatching success appears to be significantly lower among eggs of first time spawners (Tripple *et al.*, 1997; Solemdal *et al.*, unpubl.).

The positive relationship between egg size and larval size (Table III) confirms reports on cod larvae by Knutsen & Tilseth (1985). Additionally, positive relationships were detected between egg and larval size characteristics and some larval viability characteristics such as age at first feeding, feeding success, swimbladder occurrence and growth. Age at first feeding and feeding success may be important indicators of larval viability. In the present study, compared with larvae that hatched from smaller eggs, those larvae that hatched from the largest eggs initiated feeding earlier and expressed higher incidence of feeding during the first days of feeding (Figs 4 and 5). The period during which first feeding can occur is important as fish larvae must start feeding shortly after yolk

TABLE V. Pearson's correlations (n) among egg and larval viability parameters (see Table IV for definitions)

	Hatching success	Feeding (day 3)	Feeding (day %)	Swimbladder (day 10)	G (day 15)	G (day 20)
Hatching success	1·000 (64)	− 0·103 (42)	− 0·075 (42)	− 0·134 (36)	− 0·009 (31)	− 0·286 (15)
Feeding (day 3)		1·000 (51)	0·463** (51)	0·330* (45)	0·626** (38)	0·181 (20)
Feeding (day 5)			1·000 (51)	0·572** (45)	0·371* (38)	0·391 (20)
Swimbladder (day 10)				1·000 (45)	0·457** (36)	0·114 (18)
G (day 15)					1·000 (38)	0·521* (20)
G (day 20)						1·000 (20)

*P<0·05; **P<0·01.

exhaustion (Yin & Blaxter, 1987; Miller *et al.*, 1988; Brown & Taylor, 1992). As the yolk-sac energy of cod larvae is exhausted by 7–9 days after hatching (Ellertsen *et al.*, 1980; Fossum, 1986), the potential first feeding period of the larvae that hatch from the smallest eggs (Fig. 5) is very short.

The development of a functional swimbladder may be an important indicator of larval viability. High larval mortality and low growth rates in hatcheries have been connected with the lack of a functional swimbladder (Chatain & Dewavrin, 1989). High mortality is thought to result from higher energy requirement and lower feeding efficiency where swimbladders have failed to become functional (Chatain & Dewavrin, 1989). Furthermore, larvae that do not develop a functional swimbladder develop spinal deformities to compensate for the lack of swimbladder functions (Daoulas *et al.*, 1991, reviewed in Boglione *et al.*, 1995). Based on the strong correlations between swimbladder occurrence and egg/larval size parameters, failure to attain a functional swimbladder may be predicted by egg and larval sizes.

The positive relationship between larval growth rates and egg/larval size characteristics (Table IV, Fig. 7) indicates that size at hatching may influence the growth of larvae, at least during the first 2 weeks. Most of the larvae from the smallest eggs had died by the age of 20 days. Therefore, correlations between egg/larval size characteristics and growth at the age of 20 days are irrelevant and do not describe the potential differences among larval batches. The specific growth rates of larvae at age 15 days in the present study ranged from 2 to 8%. These growth rates are similar to specific growth rates reported for cod in a seawater pond in Norway (Blom *et al.*, 1991) and for captive cod in small tanks (Gamble & Houde, 1984) but less than growth rates reported for cod larvae in plastic bags or enclosures (Gamble & Houde, 1984; van der Meeren *et al.*, 1994). The advantage of large size at hatching and fast growth during the first weeks of life has been related to the larva's ability to cope with a wider range of prey sizes

as well as greater feeding efficiency, competitive ability and predator avoidance (Blaxter & Hempel, 1963; Hempel & Blaxter, 1967; Hunter, 1981, 1984; Knutsen & Tilseth, 1985; Miller *et al.*, 1988; Goto, 1990; Hinckley, 1990; Tripple *et al.*, 1997).

EFFECTS OF FEMALE CHARACTERISTICS ON EGGS AND LARVAE

An important objective of the present study was to identify and evaluate maternal influences on the quality and viability of eggs and larvae. Significant correlations were detected between several female and larval viability characteristics, including a positive relationships between Fulton's condition factor and larval feeding success, the liver index and larval feeding success, and the liver index and the specific growth rates of larvae at day 15 (Table IV). Additional, though less significant, correlations were detected between the age and length of females and the specific growth rates of larvae at day 15 (Table IV). Furthermore, all female characteristics were significantly related to egg size, which in turn, was correlated highly with all of the larval viability components (Fig. 3, Table IV).

The larval viability characteristics (feeding success, swimbladder occurrence, and growth rates) were influenced only partially by the seasonal component represented by the female's stage of spawning (Figs 4, 6 and 7). However, eggs >1·5 mm appeared to hatch into larvae that had the highest feeding success, greatest swimbladder occurrence, and relatively high growth rates. These eggs tended to be produced by the largest females and, in general, by the older females: eggs >1·5 mm on the average were produced by 12 females >100 cm (8–11 years old); three females between 75–100 cm (6–10 years old) and only one female <71 cm (a 5-year-old), respectively. All of these eggs were from females in the second or the third spawning stage.

The present study demonstrates that maternal characteristics are associated with, and may influence the quality and viability of cod larvae. The relative production of large, good quality eggs by females of different sizes and conditions is likely to be an important component in the total production of viable offspring by the stock. Therefore, in any future appraisal of stock–recruitment relationships it is important to include information on stock composition and account for size and condition related features of the spawning stock.

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