Cod egg characteristics and viability in relation to low temperature and maternal nutritional condition

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In 1995 and 1996, groups of female cod (*Gadus morhua*) of varying nutritional condition and maturing at different temperatures were used to investigate relationships between female condition, egg production, egg characteristics, and viability. Over the two years, egg samples from every batch spawned by 34 females were analyzed for egg diameter, dry mass, and energy content. In addition, 51 egg batches from 24 females (ca. 2 egg batches female^{-1} yr^{-1}) were used to monitor development rate and hatching success. The weighted mean egg dry mass was positively correlated ($p<0.05$) to the females' pre-spawning condition in 1996. In 1995 this positive correlation was not observed for females at $\sim 2°C$ during maturation. For both years, the decline in the mean egg dry mass per batch throughout spawning was correlated ($p<0.05$) with the females' post-spawning energy reserves. However, no trend in the total egg dry mass per batch during the sequence of spawning was observed. Thus, the total energy investment per batch remained stable throughout spawning and was not influenced by the depletion of the females' energy reserves. In 1996, high hatching successes were observed only for egg batches from females in high pre-spawning condition. However, egg size and dry mass showed no correlation with survival rate or hatching success in either year.

Key words: female cod, nutritional condition, egg size, egg survival, hatching success.

Introduction

Most cod (*Gadus morhua* L.) stocks in the northwest Atlantic are currently at their lowest historical abundances (FRCC, 1999). In addition, the age and size structure of the spawners' biomass is strongly biased towards smaller and younger fish (reviewed in Trippel *et al*., 1997). Reproduction is then largely dependent on recruit spawners (first-time spawners) of small sizes and could result in the production of eggs of poorer quality and lower viability (Trippel, 1998). It has been argued that considering egg quality and viability as well as quantity with spawning stock abundance could improve our understanding of the stock recruitment relationships (e.g. Hislop, 1988; Solemdal, 1997; Trippel *et al*., 1997a; Marshall *et al*., 1998; Marteinsdottir and Steinarsson, 1998; Trippel, 1999). The potential of this approach rests on the existence of relatively strong (i.e. with high predictive values) statistical relationships between egg quality and viability and maternal characteristics. However, a review of recent literature offers many different examples of maternal effects on cod eggs characteristics. For example, Kjesbu (1989) reported a relationship between female size and egg size in the first batch of eggs while Chambers and Waiwood (1996) did not observe such a relationship. Mean egg size was related to female condition in some studies (Chambers and Waiwood, 1996; Marteindottir and Steinarsson, 1998) but not in others, e.g. where pre-spawning condition exceeded 1 for all females (Kjesbu *et al*., 1996). Lower fertilization rates and hatching success (i.e. viability) were observed in the eggs of first-time vs. second-time spawners by Solemdal *et al*. (1995) and Trippel (1998). On the other hand, Kjesbu *et al*. (1996) observed fertilization rates >90% in first-time spawners. Moreover, Marteinsdottir and Steinarsson (1998) did not observe any relatonship between hatching success and characteristics of females or eggs. Differences in methods might partly explain the discrepancies between studies. Fish were caught in the wild then acclimated to laboratory conditions (Chambers and Waiwood, 1996; Trippel, 1998), reared from eggs to adult stages in the laboratory (Kjesbu *et al*.,

1996), or eggs were sampled by stripping females at sea (Marteinsdottir and Steinarsson, 1998). Nonetheless, although there is evidence of maternal effects on cod egg size or weight, there has been no unequivocal demonstration of maternal effects on cod egg viability and hatching success.

The examination of historical data has revealed a recent shift to lower age and size at maturity for cod in the northern Gulf of St Lawrence (Trippel *et al*., 1997b; Dutil *et al*., 1999). Lower nutritional condition also accompanied the sharp decline in the stock biomass observed in the early 1990s (Lambert and Dutil, 1997a). Our study was initiated under the hypothesis that female cod in situations of lower nutritional condition would produce eggs of poorer quality and lower viability.

Two different laboratory experiments conducted in successive years (1995 and 1996) were designed to investigate the relations between female condition, egg production, and egg characteristics and viability. Females were conditioned with different feeding regimes to obtain a range of nutritional condition, from fish in a very good nutritional state to fish with exhausted energy reserves. In 1995, the fish were conditioned at two different temperature regimes during maturation and spawning whereas in 1996 the temperature was kept constant throughout maturation and spawning. The influence of a lower condition on reproductive investment, somatic energy losses, and post-spawning condition of these female cod has been presented elsewhere (Lambert and Dutil, 2000). These experiments revealed that fecundity and total egg dry weight were significantly lower in poor-condition females (Lambert and Dutil, 2000). It was also demonstrated that female cod with high pre-spawning condition factors ended reproduction in better condition and lost a lower proportion of their somatic mass and energy reserves than poor-condition females. In the present paper, variations in egg characteristics, egg viability, and hatching success accompanying the variability in fecundity and total egg dry weight for these females are presented. Individual females monitored for the entire duration of their spawning cycle were used to examine the relationships between a female's nutritional condition and different measures of egg quality and viability. The results from 1995 and 1996 are presented independently as the temperature regimes were different between the years.

Materials and methods

Brood stock conditioning

Cod used in these experiments were caught by trawl at the same location in the St Lawrence Estuary in June 1994 and 1995 (Lambert and Dutil, 2000). Prior to experiments, fish were kept under natural photoperiod and temperature in 7.5 m³ tanks and were fed to satiation three times weekly with frozen capelin (*Mallotus villosus*). Both experiments began the following September. Each year, 400 cod were divided into four groups of 100 fish and transferred to separate 7.5 m³ tanks. During the first experiment (hereafter referred to as the 1995 experiment), two temperature regimes were applied. In the first regime, cod were acclimated to 10°C and the temperature was gradually decreased to a minimum of 6°C in January 1995. The temperature was then kept constant throughout spawning, which began in April. In the second regime, cod were acclimated to 6°C and temperatures were subsequently decreased to 2°C in January; temperature was kept constant throughout spawning. While most cod populations reside at higher temperature during maturation, groups of cod can be found in coastal habitat all year round where maturation is probably occurring at low (e.g. 2°C or less) temperature (Green and Wroblewski, 2000). During the second experiment (hereafter referred to as the 1996 experiment), temperature was kept at 4–5°C all the time. For both years, groups of cod received a high or a low ration. Feeding regimes in each experiment were adjusted to take into consideration the variations in temperature and to ensure that female cod of different pre-spawning condition would be obtained. Exact feeding levels are given in Lambert and Dutil (2000). In the 1995 experiment, female cod were randomly selected for different feeding regimes with respect to size. In the 1996 experiment, female cod were divided into two size classes (<55 cm; 51.2 ± 1.19 cm and >55 cm; 60.9 ± 2.99 cm) to insure that the size of the fish would be more evenly distributed over the size range observed for cod in the northern Gulf of St Lawrence. Within each size class, one group of females was fed on a low ration and another on a high ration.

The condition factor (Fulton's K), expressed as the ratio between total weight (g) and length³ (fork length in cm) times 100, was used as an index of condition for pre-spawning females (Lambert and Dutil, 1997a). The condition factor in cod is a very good indicator of nutritional condition and energy reserves (Lambert and Dutil, 1997a, b).

Spawning and egg characteristics

During each experiment, females were paired with males in 1.2 m³ circular tanks to individually monitor egg production of the females for the entire duration of their spawning cycle. Collectors placed on the outflow of the central drain of each tank were used to retain eggs, hence to collect every batch of eggs released by each female. A complete description of the holding conditions and methods of egg collection and sampling is given in Lambert and Dutil (2000). The spawning activity of 17

females in the 1995 experiment and 21 females in the 1996 experiment was monitored by recording and sampling all egg batches produced [Table 1(a) and (b)]. For each spawning event, the volume (ml) of eggs released was measured. The number of eggs per unit of volume in three subsamples (2 ml) of eggs was used to estimate the total number of eggs per batch. Mean egg diameter (± 0.01 mm) for each batch was estimated with a sample of 25–50 eggs using an image analysis system (Leica Q500MC, Cambridge). Two subsamples (10–20 ml) of eggs were also weighed and frozen for the estimation of mean egg dry mass and energy content. Egg dry mass (μg egg^{-1}) was determined by drying the subsamples to constant weight at 65°C and egg energy content (J egg^{-1}) by combusting the dry samples in an oxygen bomb calorimeter (Parr, model 1261). Benzoic acid with an energy equivalence of 26.453 kJ g^{-1} was used as a standard for the determination of energy content. In the 1995 experiment, total lipid and total yolk protein content of eggs were quantified for each egg batch. A complete description of the protocols for the lipid and protein determinations is presented in Ouellet (1997). Finally, estimates of weighted mean egg diameter and dry mass were calculated for each female by weighting the means for each batch by the number of eggs in the batch.

Females were sacrificed 15 d after the production of their last egg batch. Fork length (± 0.1 cm), total weight (± 1 g), and gutted, liver, and gonad weight (± 0.1 g) were also noted. Subsamples of muscle, liver, and gonads were individually frozen at -20°C and used for the determination of water and energy content. Methods used to determine tissue composition and somatic energy content are presented in Lambert and Dutil (1997a).

Egg development and survival

A total of 53 egg batches from the two experiments (31 in 1995 and 22 in 1996) were used to monitor egg development and hatching success at two temperatures (0°C and 4°C). These temperatures reflect normal spring developmental conditions for cod eggs in mid-water column [cold intermediate layer (CIL); ~ 0°C] and near the surface (~ 4°C) in the northeastern Gulf of St Lawrence (Ouellet *et al*., 1997). For each batch, the eggs were first acclimated to a constant salinity (28‰) and placed in 10% Aquidyne® solution for 10 min. For each egg batch, duplicate samples of fertilized eggs (300–500 eggs) were isolated in incubation chambers (500 ml) at the two temperatures. The jars were examined daily to remove and count dead eggs and/or larvae and to renew ca. 50% of the water. In 1995, different egg batches ranging from batch number one through eight were used for the experiments. In 1996, only eggs from the third and the sixth batches were incubated. To

minimize the variance associated with the selection of different egg batches for the analysis, the various egg batches were coded to represent eggs from the first third (1), the second third (2), and the last third (3) of the spawning sequence of the females.

Statistical analysis

A Pearson parametric correlation was used to examine relationships between female size, pre-spawning condition, and egg characteristics. The decline in total egg dry mass and mean egg dry mass per batch throughout spawning was examined in relation to post-spawning energy reserves for individual females. The slopes of linear regressions between total egg dry mass per batch and mean egg dry mass per batch vs. batch number were used as indices to describe the declining trends in these variables over the spawning season of an individual female. Indices of available energy reserves for post-spawning females were calculated as ratios between observed energy reserve levels (K_O) and those corresponding to a complete exhaustion of energy reserves (K_E) for a female of the same size. Female cod showing complete exhaustion of energy reserves are characterized by a mean condition factor of 0.54, a mean liver index of 1.1, and muscle and liver water contents of 86 (2.81 kJ) and 74% (7.74 kJ), respectively (Dutil and Lambert, 2000). Thus, females with mean energy indices K_O/K_E of 1 have completely exhausted their energy reserves.

Egg batches were incubated in duplicate only. To assess the validity of the results, the mean difference and the 95% confidence interval (CI) between all replicates were calculated. The specific data on egg survival and hatching success for an egg batch were discarded if the absolute difference between the duplicates exceeded the 95% upper confidence interval of the overall mean. This test resulted in the rejection of the data for seven out of 31 egg batches in 1995 and for six out of 22 egg batches in 1996. Analysis of the egg incubation data proceeded in two steps. First, daily survival estimates were obtained from the daily count of dead and live eggs by "Life-table" methods: a non-parametric approach that does not require any *a priori* assumption about the functional form of the survival distribution (Cox and Oakes, 1984). Second, non-linear models were fitted to survival distributions by the least-squares method (SYSTAT® 7.0, non-linear regression). Three typical patterns of response were observed during the egg incubation experiments (see the Appendix). Three functions were used to model the different survival distributions, but these equations share the same parameters: the ρ parameter has the dimension of the reciprocal of time and is interpreted as a rate whereas the κ parameters are dimensionless (shape) parameters (Cox and Oakes, 1984; see the Appendix).

Table 1. Summary data for female cod used in (A) the 1995 spawning experiments; and (B) the 1996 spawning experiments. (—)=missing data.

Female	Length (cm)	Weight (g)	Pre-spawning K	Post-spawning K	Post-spawning muscle energy (kJ)	Post-spawning liver energy (kJ)	Post-spawning somatic energy (kJ)	Maturation T°C	No. of egg batches	Mean batch interval (d)	Fecundity × 10^5	No. of egg batches incubated at 4°C	No. of egg batches incubated at 0°C
A
1	56.3	1 566	0.878	0.638	2 837	156	4 063	2.42	10	3.2	6.02	4	4
2	57.9	1 770	0.912	0.642	3 097	101	4 365	2.42	6	7.2	9.37	0	0
3	56.4	1 447	0.807	0.630	2 869	98	4 070	2.42	6	2.9	5.31	2	2
4	55.5	1 896	1.109	0.820	3 790	1 035	6 294	2.42	9	3.1	10.01	3	2
5	54.3	1 527	0.954	0.830	3 956	1 234	6 645	2.14	3	7.7	2.94	1	1
6	61.4	2 586	1.117	0.730	4 476	2 716	8 937	2.01	13	4.0	14.64	2	0
7	53.5	1 646	1.075	0.704	2 179	505	3 556	2.05	7	9.4	5.88	2	2
9	46.6	1 037	1.025	0.742	2 511	409	3 779	2.50	4	6.3	3.74	3	3
8	58.9	2 082	1.019	(—)	(—)	(—)	(—)	2.55	9	6.3	3.62	3	3
11	64.1	3 079	1.169	0.891	6 249	2 113	10 767	5.80	10	3.9	19.02	2	2
12	58.9	2 534	1.240	0.830	4 992	2 017	8 838	5.80	10	5.8	16.16	2	2
13	59.0	2 426	1.181	0.795	4 926	410	6 700	5.90	13	5.1	13.36	2	0
15	60.2	2 472	1.133	0.777	4 946	292	7 020	5.90	10	5.0	11.95	2	2
17	57.2	2 252	1.203	0.753	3 480	673	5 484	5.70	9	3.7	13.08	2	2
18	51.6	1 706	1.242	0.922	4 010	1 207	6 649	5.70	10	4.4	11.7	1	1
19	59.4	2 195	1.047	0.772	3 971	837	6 302	5.80	10	4.2	12.5	2	2
22	50.1	961	0.764	0.508	745	31	1 160	5.80	3	5.9	2.36	0	0
B
3	49.1	990	0.836	0.604	801	18	1 242	4.64	11	3.5	3.56	3	1
4	52.3	1 080	0.755	0.536	874	22	1 346	4.9	4	5.2	0.28	0	0
5	61.2	2 965	1.294	0.746	(—)	(—)	(—)	4.83	9	5.4	(—)	2	1
6	61.2	2 954	1.289	0.777	4 233	3 207	9 197	4.69	8	5.9	16.7	2	0
7	50.6	1 230	0.949	0.641	1 893	65	2 687	4.72	13	3.7	5.04	0	0
8	50.4	1 047	0.818	0.615	1 368	51	1 994	4.69	4	7.4	3.14	1	0
10	58.6	2 085	1.036	0.697	2 719	289	1 985	4.64	9	6.7	7.01	0	0
11	52.1	1 238	0.875	0.578	962	44	1 510	4.64	8	5.6	5.99	0	0
12	49.6	1 145	0.938	0.607	1 012	43	1 534	4.91	3	9.0	0.3	0	0
13	52.3	1 506	1.053	0.682	2 118	414	3 367	4.73	8	4.2	7.16	3	1
14	60.9	2 365	1.047	0.713	2 226	77	3 385	4.73	10	6.7	5.82	0	0
15	55.1	(—)	(—)	0.883	4 168	1 893	7 620	4.76	12	5.8	8.85	0	0
16	59.8	2 152	1.006	0.659	2 532	122	3 753	4.8	10	4.5	9.66	2	0
17	52.2	1 698	1.194	0.820	3 012	1 606	5 787	4.71	13	7.0	7.08	4	0
18	50.5	1 418	1.101	0.712	2 083	619	3 508	4.83	15	3.2	8.19	0	0
19	64.0	2 704	1.031	0.732	4 260	1 348	7 331	4.68	11	6.4	10.72	0	0
20	65.8	2 511	0.881	0.617	2 654	61	3 981	4.63	8	7.4	8.63	2	1
21	52.2	1 668	1.173	0.717	2 669	1 217	4 904	4.74	9	5.5	5.06	1	0
22	52.0	1 419	1.009	0.637	1 777	48	2 562	4.73	11	4.3	6.74	0	0
23	63.0	2 664	1.065	0.744	2 973	100	4 444	4.72	6	5.5	9.9	0	0
24	59.3	1 579	0.757	0.481	1 319	29	1 991	4.72	7	6.2	4.95	2	1

Differences in hatching success, i.e. total number of live larvae compared to the total number of eggs incubated, relative to the position of the eggs in the spawning sequence for each year and for each maturation temperature in 1995 were assessed by the non-parametric Kruskal–Wallis one-way ANOVA.

Results

Egg production and female size and condition

Even though cod were divided in two distinct size classes in 1996 (<55 cm and >55 cm) overall size range and average length of pre-spawning females were not different between the two experiments [1995: 56.6 ± 4.2 cm, CV=7.5%; 1996: 55.8 ± 5.4 cm, CV=9.7%; Table 1(a) and (b)]. In both experiments, female pre-spawning and post-spawning condition (Fulton's K) ranged from 0.657–1.242 and 0.481–0.923, respectively [Table 1(a) and (b)]. However, post-spawning condition differed between years (t test; t=2.97, p=0.006), with the mean post-spawning condition being slightly lower in 1996 (0.66 ± 0.084) relative to 1995 (0.76 ± 0.11). Smaller fish and fish in lower condition were better represented in the 1996 experiment. Female length and pre- or post-spawning condition were not correlated in either year. Mean number of egg batches, realized fecundity (i.e. mean total number of eggs spawned), and mean batch interval were not statistically different between years [Table 1(a) and (b)]. However, in 1995 the range of condition values was narrower and females with high pre-spawning condition were better represented in the group of fish maintained at the higher maturation temperature. Results are presented separately for each maturation temperature in 1995 to ascertain the possible influence of maturation temperature, pre-spawning condition and/or the possible interaction between the two on egg characteristics.

Egg characteristics and female condition in 1995

Weighted mean egg diameter, dry mass, and energy content were positively correlated (r=0.89, p=0.003; r=0.93, p=0.001; r=0.87, p=0.004) with pre-spawning condition for females maturing at 6°C (Figure 1). No such correlation was observed for females maturing at 2°C except for a negative correlation between energy content and female pre-spawning condition (r= − 0.68, p=0.03). However, the correlation at 6°C was no longer significant when the only female with a low condition factor [female 22, Table 1(a)] was excluded from the analysis as the range in nutritional condition was much narrower. No length effects on weighted mean egg diameter, weighted mean egg dry mass, and energy content were detected (p>0.05) in either temperature regime (Figure 1).

The batch number in the spawning sequence had a significant effect on cod egg diameter and dry mass (Figure 2). Cod eggs were larger and heavier at 2°C than at 6°C, but the declining trends in egg characteristics with the spawning sequence were not different between the maturation temperatures (Test of homogeneity of slopes: diameter, F=1.627, p=0.204; dry mass, F=0.428, p=0.51). Moreover, mean overall egg diameter was larger for females kept at the lower temperature (2°C compared to 6°C; t test, t=4.55, p<0.001) (Figure 3).

No detectable trends in total lipid/protein ratios with the spawning sequence were observed in cod eggs in 1995 at either maturation temperature (Figure 4). Moreover, female pre-spawning condition had no effect on overall mean total lipid/protein ratios of the spawned eggs at either maturation temperature (Figure 4).

While mean egg dry mass per batch showed negative trends (i.e. negative slopes) over the spawning sequence of individual females (Figure 2), no definite trends in total egg dry mass per batch were observed over the spawning sequence at either maturation temperature. The decline in mean egg dry mass per batch during spawning was related to somatic (r=0.62, p=0.02) and muscle (r=0.67, p=0.008) but not to liver (p=0.23) reserve indices (Figure 5). These significant relations were driven by the value observed for one individual female (slope of 2.5 for the mean egg dry mass per batch; Figure 5); none of these relationships is significant (p>0.18) if the value for that female is excluded. For the majority of females (78%), no significant relationships (p>0.05) were observed between total egg dry mass per batch and batch number. Thus, total egg dry mass per batch of individual females during spawning was not related to post-spawning somatic (somatic reserve index), protein (muscle reserve index), or lipid (liver reserve index) reserves.

Egg characteristics and female condition in 1996

Weighted mean egg dry mass and energy content were correlated (r=0.52, p=0.022 and r=0.55, p=0.02, respectively) with female pre-spawning condition in 1996 while weighted mean egg diameter was not correlated with pre-spawning condition (Figure 1). As in 1995, no length effects on weighted mean egg dry mass, egg diameter, and energy content were detected (p>0.1). Again as in 1995, the batch number in the spawning sequence had a significant negative effect on cod egg diameter and dry mass (Figure 2).

While mean egg dry mass per batch showed negative trends (i.e. negative slopes) over the spawning sequence of individual females, no definite trends in total egg dry mass per batch were observed over the spawning
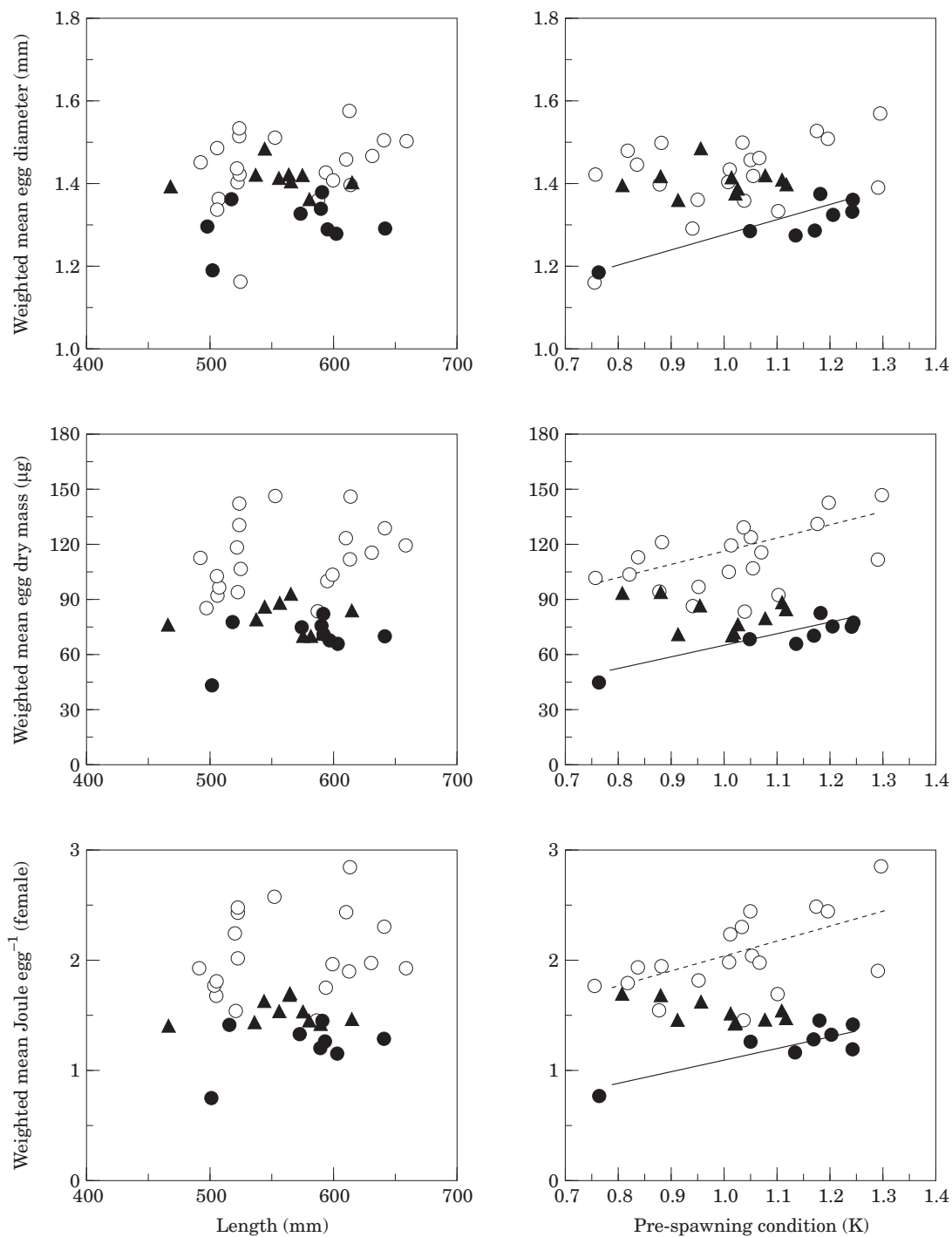
Figure 1. Weighted mean egg diameter, dry mass, and energy content in relation to length (left) and pre-spawning condition (right) for individual female cod in 1995 and 1996. Data for each maturation temperature in 1995 are presented separately. ●, 1995; 6°C; ▲, 1995, 2°C; ○, 1996.

sequence. The decline in mean egg dry mass per batch during spawning was not related to somatic ($p = 0.28$), muscle ($p = 0.30$), or liver ($p = 0.15$) reserve indices (Figure 5). Thus, total egg dry mass per batch of individual females during spawning was not related to post-spawning somatic, protein, or lipid reserves.
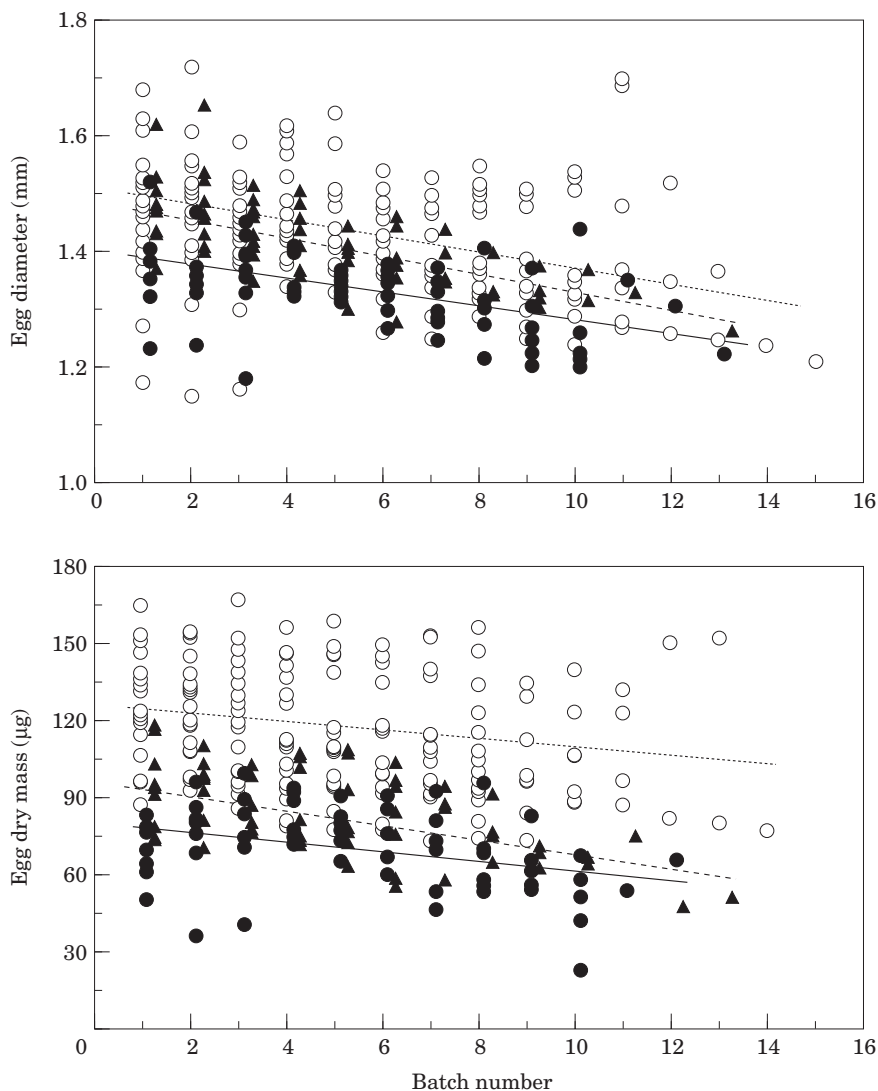
Figure 2. Mean egg diameter and dry mass per batch in relation to the spawning sequence (batch number) for individual females in each experiment. Data for each maturation temperature in 1995 are presented separately. ●, 1995, 6°C; ▲, 1995, 2°C; ○, 1996.

Egg viability and hatching success

For each year, eggs incubated at 4°C took on average 21.3 ± 1.91 d to hatch (50% hatching) whereas 44.8 ± 7.4 d were needed to reach 50% hatching at 0°C. The rate and shape parameters of the fitted survival functions were not correlated with egg characteristics such as mean diameter and dry mass in either year. However, high mortality was observed during hatching in most cases. For each egg batch, cumulative survival until first hatch (hatch-t_0) and mortality during hatching, calculated by subtracting the cumulative survival to hatch-t_0 from the final cumulative survival, were estimated. For both years and temperature regimes, although the range of pre-spawning condition was very

narrow in cod maturing at 6°C in 1995, there was no correlation ($p>0.05$) between egg survival to hatch-t_0 and female pre-spawning condition (Figure 6). However, high mortality at hatching was recorded in two of the three egg batches from females with condition factor <0.9, maturing at 2°C in 1995, despite their producing larger and heavier eggs (Figure 6). Hence, it would seem that late embryos and larvae hatching from eggs produced by poor-condition females were less viable.

Hatching success was highly variable for both years. At 0°C, the mean proportion of eggs hatching was $2.9 \pm 6.4\%$ (1995) and $1.6 \pm 2.5\%$ (1996). At 4°C, hatching success ranged from 0–74% (mean=34.8 ± 22.2) in 1995 (both maturation temperatures) and from 1–82% (mean=26.3 ± 24.8) in 1996. In 1995, when all egg
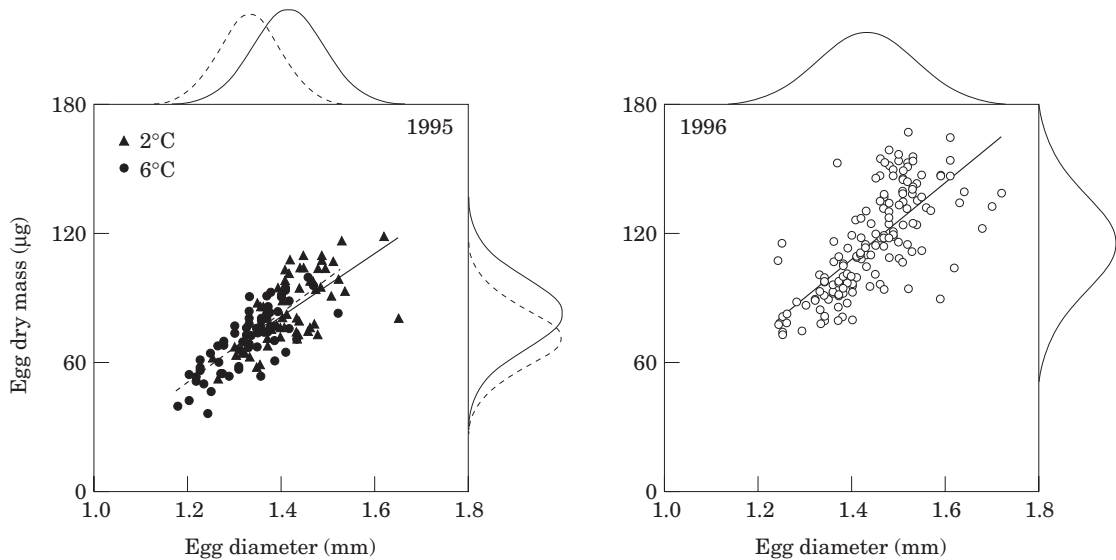
Figure 3. Mean egg dry mass per batch in relation to mean egg diameter per batch for each year and for each maturation temperature used in the 1995 experiment. The normal curves from the frequency distribution of both variables are illustrated on the upper x-axis and the right y-axis, respectively.

batches were incubated at both temperatures, hatching success at 0°C was positively correlated (r=0.49, p=0.017) with hatching at 4°C. Hatching success was independent of batch number (Kruskal–Wallis one-way ANOVA: 1995 (both maturation temperatures), p=0.84; 1996, p=0.53; Figure 7) and was not related to egg diameter or dry mass in either experiment (Table 2). Female pre- and post-spawning condition and hatching success were also not correlated in either year (Table 2). However, in 1996, high hatching successes were observed only in egg batches spawned by females with high (>1.0) pre-spawning condition factor, whereas hatching success was always very low for females with pre-spawning condition factor below 1.0 (Figure 6).

Discussion

The spawning performance of the fish was similar in both years, and the mean realized fecundity, mean number of egg batches, and number of days between batches all indicate that the fish were at least second time spawners (e.g. Trippel, 1998). Even though realized fecundity was strongly influenced by female size and nutritional condition during the experiments (Lambert and Dutil, 2000), only limited effects of maternal nutritional condition on egg survival and hatching success were observed.

There was a significant difference in egg size between the 1995 and 1996 experiments and between maturation temperatures in 1995: smaller eggs were observed from the females kept at the higher maturation temperature. Nonetheless, the same general variability in hatching

success among batches and females was observed each year. Therefore, these results suggest a limited impact of the egg characteristics on their viability and hatching success. The results are also consistent with the findings of many recent studies that investigated the correlation between egg characteristics and hatching success in fish (Table 3).

Maternal influence on egg characteristics

In recent studies, divergent observations have been made on the relationships between female cod condition and the phenotypic characteristics of the eggs and larvae. Chambers and Waiwood (1996) concluded that egg size was correlated to the female's condition rather than the female's size. Females in their study had a restricted size range (54–68 cm), but Trippel (1998), using repeat spawners, showed a narrow size range for eggs between 1.51–1.54 mm from female cod between 45–83 cm. Kjesbu *et al.* (1996) found a correlation between weighted mean egg size and female weight but no correlation between egg size and female condition. However, pre-spawning K was greater than 1 for all females. From eggs obtained from running-ripe females at sea, Marteinsdottir and Steinarsson (1998) concluded that egg size (diameter) was influenced by female length and condition but that condition explained more of the variability in egg size than length. However, these results may not be directly comparable since condition was not measured in pre-spawning females as in the other studies. Differences in egg size have also been related to the female's age rather than size (Kjesbu *et al.*, 1996;
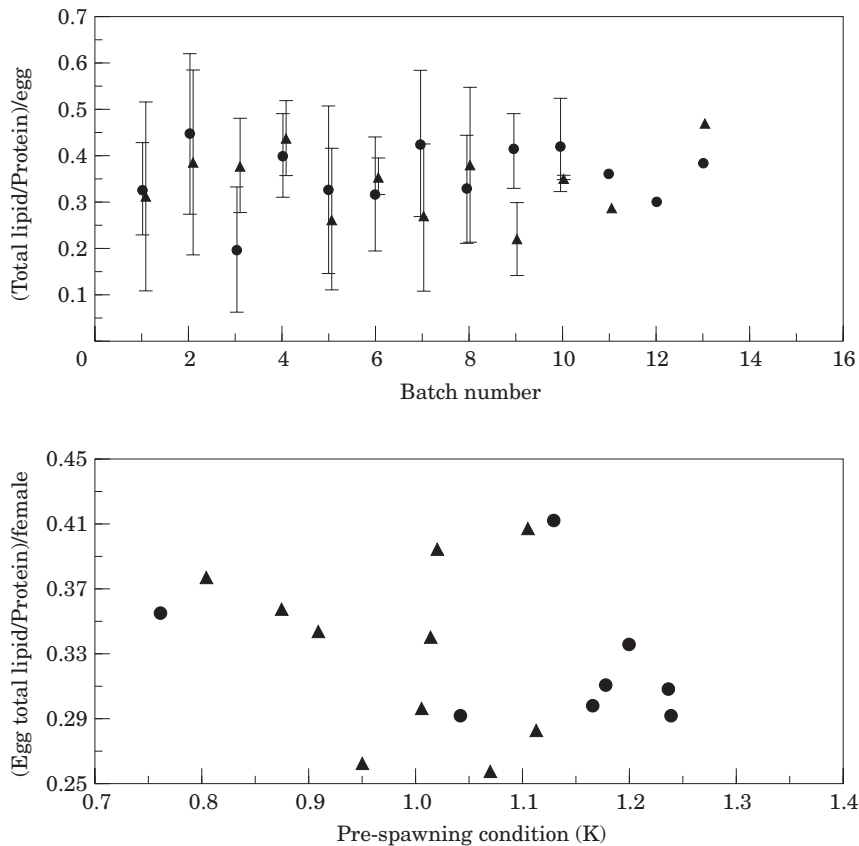
Figure 4. Total lipid and yolk protein ratios (mean ± s.d.) in cod eggs in relation to the batch number (upper panel), and mean overall total lipid/yolk protein ratios in relation to female pre-spawning condition. Total lipid and yolk protein were determined in 1995 only and the results are presented for each maturation temperature separately. ●, 1995, 6°C; ▲, 1995, 2°C.

Trippel, 1998; Hislop, 1988 with *Melanogrammus aeglefinus*). Moreover, significant relationships between egg size and female size were found when comparing selected egg batches (e.g. first egg batch only; Kjesbu, 1989). However, the first egg batch is often of low abundance (Kjesbu *et al.*, 1996) and/or the eggs are of poor quality (Chambers and Waiwood, 1996). Hence, a weighted mean should be a better way to express the overall impact of female status on the mass of eggs spawned over a season (Kjesbu *et al.*, 1996; Trippel, 1998; this study).

The size range of the females in the present study, although typical of size distribution of cod in the northern Gulf of St Lawrence (Ouellet *et al.*, 1997), may have restricted the possibility to detect female size effect. However, the absence of female size effect reduces the number of factors that could have affected the egg characteristics, hence a greater possibility to detect the female's condition effect on egg quality.

Significant correlations were observed between mean egg dry mass and pre-spawning condition for females

maturing at 6°C in 1995 (if we include the low condition female) and in 1996. However, females with high condition indices ($K > 1.05$) produced heavier eggs in 1996 than in 1995. For cod, it has been suggested that past reproductive investments influence future investments (Kjesbu *et al.*, 1996). In the first experiment, female cod were caught in early summer 1994, which was a year of very low cod nutritional condition in the Gulf of St Lawrence; females in the second experiment were caught in early summer 1995, when cod nutritional condition had significantly improved relative to the previous year (Lambert and Dutil, 1997b, 2000). We can speculate that long-term feeding history and growth can somehow influence the quality of the eggs to be produced during a given season. However, the females captured in June were kept for two to three months under high feeding ration which resulted in fish with comparable nutritional condition in September of both years before the onset of maturity ($K = 0.85$ and 0.89 in September 1994 and 1995, respectively). Nevertheless, very little is understood about the interannual variability
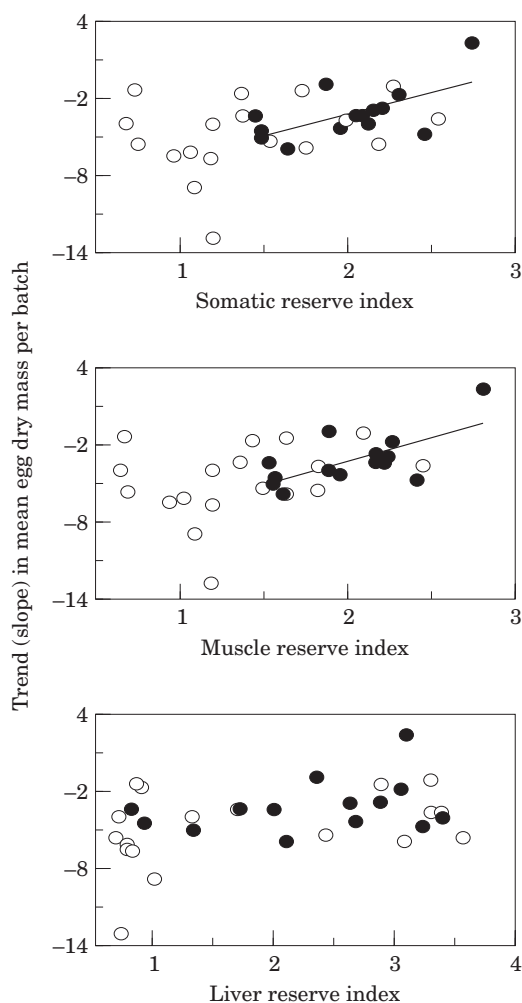
Figure 5. Relations between indices of changes in mean egg dry mass per batch during the sequence of spawning and female post-spawning indices of energy reserves. The somatic reserve index represents the total available energy reserves while muscle and liver reserve indices are indicators of available protein and lipid reserves, respectively. ●, 1995; ○, 1996.

in fish fecundity and egg characteristics in relation to the past history of female growth, condition, and feeding conditions in wild populations.

Other factors may affect the strength of relationships between female status on egg size and quality. Female cod can respond to unfavorable conditions by reducing realized fecundity. Kjesbu *et al*. (1991) observed that actual fecundity was between 20% and 80% of the potential fecundity depending on the females' nutritional condition. Lambert and Dutil (2000) also observed a significantly lower realized fecundity for individual females in this study that were in poorer condition. Thus, oocyte atresia resulting in lower realized fecundity could explain the relatively weak maternal

effects observed on egg size, with the females resorbing eggs of poorer quality.

As in other studies, a general decline in mean egg size (diameter and dry mass) was observed through the spawning sequence. Such trends in cod and in other batch spawners have often been attributed to the progressive depletion of the female's energy reserves as the spawning season progresses. This interpretation has been doubted by Kjesbu *et al*. (1996) and Trippel (1998). The absence of negative relationships between total egg dry mass per batch and batch number as well as the stable total lipid/yolk protein ratios observed during the spawning sequence of the females support the hyphthesis that the decreasing egg size is not due to depletion of the female's energy reserves.

Egg viability and hatching success

Egg incubation at low temperature was examined as previous work in the northern Gulf of St Lawrence had revealed that a high proportion of cod eggs were located in the mid water column at very low water temperatures (Ouellet, 1997). The low hatching success observed for eggs incubated at 0°C would suggest that only 2–5% of all eggs found in the cold intermediate layer (CIL) in the spring of 1993 and 1994 (Ouellet, 1997) would have hatched normally. Moreover, in the laboratory experiments, the few larvae that hatched at 0°C were small and often abnormal, indicating that survival rates for cod eggs located in the CIL would be very low. Negative effects of cold incubation temperatures on larvae size have also been reported in cod (Pepin *et al*., 1997) and flounder (*Pleuronectes ferrugineus*) (Benoît and Pepin, 1999).

Given the low hatching success for the majority of egg batches at the 0°C incubation temperature, the discussion will focus on the results at 4°C. Maternal influences on the characteristics of the progeny have been a common subject in the recent literature (citations above). There is, however, much less evidence that maternal status (condition, size) significantly affects survival and hatching success of the eggs (Table 3). However, fish age or spawning experience seem to play a role in explaining differential hatching success (Solemdal *et al*., 1995; Trippel, 1998).

The survival pattern that we observed over the two years was not different from that described in other reports: high mortality in the few days (up to complete gastrulation) and often again during hatching (Laurence and Rogers, 1976; Nissling and Westin, 1991; Keckeis *et al*., 2000). Moreover, the correlation between hatching rates at 0°C and 4°C supports the validity of our methods as it shows that same batch of eggs have relatively high hatching success at both temperatures. Although no relationships between the females' condition and measures of hatching success were statistically
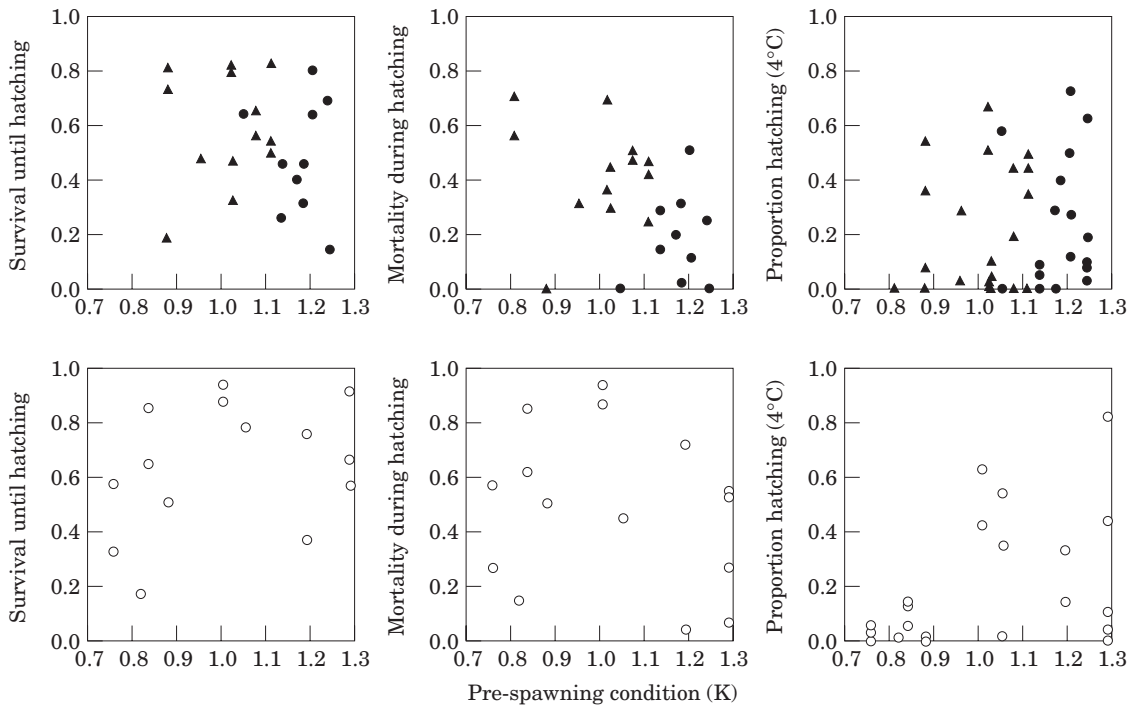
Figure 6. Cumulative survival until hatching, mortality during hatching, and hatching success at 4°C in relation to female pre-spawning condition in 1995 (upper panels) and 1996 (lower panels). For the 1995 experiment, results for each maturation temperature are presented separately. ▲, 2°C; ●, 6°C.

significant, survival of newly hatched larvae seems reduced for females in poor condition (mainly females at 2°C during maturation) in 1995. Moreover, the only high values of hatching successes recorded in 1996 were for egg batches spawned by females with pre-spawning

condition factors greater than 1.0. Overall, these observations suggest some effects of female condition on egg survival. But the large variability in the results between years and the absence of statistically significant correlations call for caution in the interpretation of these observations. Finally, batch number was not a factor in egg survival for either year. Nissling *et al.* (1998)
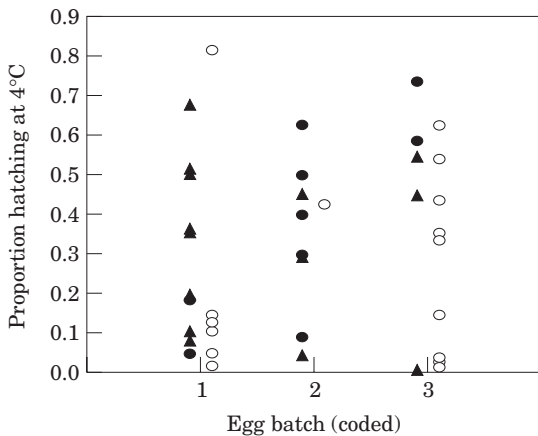

Figure 7. Effect of the relative position of the egg batch (first third (1), second third (2), and last third (3) of the female's spawning sequence) on hatching success at 4°C. For the 1995 experiment, results for each maturation temperature are presented separately. ●, 1995, 6°C; ▲, 1995, 2°C; ○, 1996.

Table 2. Pearson correlation coefficients (r) between hatching success at 4°C and the female's condition and mean diameter and dry mass of the egg batch. No coefficients were statistically significant at $p = 0.05$.

	Proportion hatching (4°C)
1995	
Pre-spawning K	0.135
Post-spawning K	0.047
Mean egg diameter (batch)	0.029
Mean egg dry mass (batch)	0.165
1996	
Pre-spawning K	0.444
Post-spawning K	0.430
Mean egg diameter (batch)	− 0.359
Mean egg dry mass (batch)	− 0.137

Table 3. Summary table of published studies examining correlation between fish eggs or female attributes and hatching success and/or larvae survival potential. NS=not significant; YES=graphical or statistical evidence of a positive relationship between female/egg size and larval size/survival.

Variable tested	Egg survival/ hatching success	Larvae survival potential	Species	Reference
Pre-spawning K	NS	No data		
Post-spawning K	NS	No data	Cod (*Gadus morhua*)	Our study (1995)
Egg size (diameter)	NS	No data		
Egg dry weight	NS	No data		
Pre-spawning K	NS*	No data		
Post-spawning K	NS*	No data	Cod (*Gadus morhua*)	Our study (1996)
Egg size (diameter)	NS	No data		
Egg dry-weight	NS	No data		
Female length	NS	NS		
Female weight	NS	NS		
Female age	NS	NS	Cod (*Gadus morhua*)	Marteinsdottir and Steinarsson (1998)
K (pre-spawning?)	NS	YES		
Egg size (diameter)	NS	YES		
Egg dry-weight	NS	YES		
Egg size (diameter)	NS**	No data	Yellowtail flounder (*Pleuronectes ferrugineus*)	Benoît and Pepin (1999)
Egg size (diameter)	NS	YES	Cod (*Gadus morhua*)	Pepin *et al.* (1997)
Egg size (diameter)	NS	YES	Cod (*Gadus morhua*)	Nissling *et al.* (1998)
Egg size***	YES	YES	Cod (*Gadus morhua*)	Trippel (1998)
Female length and weight	YES	NS	Winter flounder (*Pseudopleuronectes americanus*)	Buckley *et al.* (1991)
Female condition	NS	NS		
Egg size (diameter)	NS	NS		
Egg composition	NS	NS		
Egg weight	NS	YES	*Chondrostoma nasus*	Keckeis *et al.* (2000)
Egg energy content	NS	YES		

*In 1996, high hatching success was observed in egg batches from females with high condition factor but no correlation was statistically significant.

**From an interpretation of their Figures 2 and 3.

***Comparing mean egg size and hatching success of first-time vs. second-time spawners.

and Manning and Crim (1998) also reported that egg hatching success was not related to the spawning stage (i.e. batch number) of the females in cod or yellowtail flounder (*Pleuronectes ferrugineus*). Solemdal *et al.* (1995) reported an effect of batch number on hatching success but not in a more recent series of experiments (Solemdal *et al.*, 1998).

The average percentage of hatching eggs in our study was lower than in other studies (ca. 30% vs. ca. 60% in Laurence and Rogers, 1976; Marteinsdottir and Steinarsson, 1998, and for second time spawners in Trippel, 1998). This could reflect the fact that we have a greater proportion of female cod in relatively low nutritional condition (K<1.0) compared to other studies. On the other hand, it is possible that we did not consider some indicators of egg quality that might be significant in the determination of egg viability. The egg is a very complex entity (e.g. Brooks, 1997), and egg diameter and dry mass are only gross descriptors of quality. For example, cell morphology in early development was not evaluated in our study but it has been shown to be a predictor of egg survival (Kjørsvik, 1994; Pickova *et al.*, 1997). Many molecular substances (essential fatty acids, growth hormones, etc.) that pass from the female to the egg during oocyte formation are not distinguished in total lipid or protein estimates. For example, McCormick (1998) demonstrated a link between maternal levels of the stress-associated hormone cortisol, egg cortisol level and egg viability in the fish *Pomacentrus amboinensis*. Although there was a higher incidence of abnormal larvae hatching from eggs of stressed females, Morgan *et al.* (1999) were not able to show significant differences between hatching success of cod eggs from stressed vs. control females. Future investigations to establish the role of female status on progeny characteristics and viability should be designed to go beyond simple descriptors such as egg size, mass, and energy content.

Studies that did not find a direct maternal influence on egg hatching success present some evidence of maternal

effects on larval viability parameters (e.g. hatching size, growth rates) that are usually linked to the fact that larger eggs give larger larvae at hatching (Marteinsdottir and Steinarsson, 1998). A positive relationship was observed between egg diameter and larval length each year (unpublished data). However, preliminary analysis showed no effects of female or egg characteristics on larvae-specific growth rates in 1995 (Dutil *et al.*, 1998).

Conclusion

In exploited stocks, interannual variability in recruitment levels and selective fishing pressure can create important changes in the spawning stock biomass and in the age and size structure of the spawning population. These changes can potentially affect total egg production and/or egg quality (Kjesbu *et al.*, 1996; Trippel *et al.*, 1997; Marshall *et al.*, 1998). The ability to include such changes in estimating the production potential of a stock would be a real advantage in the study of stock-recruitment relationships (Trippel, 1999). To do so, however, strong relationships must exist between egg and/or larval viability and parental attributes. Although female length and nutritional condition of cod have a strong influence on realized fecundity (Lambert and Dutil, 2000), this study presents less conclusive data concerning maternal effects on egg viability. Survival through development and egg hatching success were not related to egg characteristics such as size or dry mass. These results would indicate that stock-recruitment relationships should account for changes in fish fecundity in relation to the reduction in size and condition, but more empirical studies are required to describe quantitatively the relationships between female or egg characteristics and egg viability or hatching success.

Acknowledgements

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Appendix

In view of the variety of survival distributions derived from the incubation experiments over the two years, an empirical approach was chosen to quantify the time course of egg survival in each incubation. The method is based on estimating daily survival and standard error by Life-tables methods, i.e. non-parametric procedures that do not depend on the assumption of specific distributions, following an empirical estimation of the survivor functions (Lawless, 1982). Survival $[S(t_i)]$ was estimated by the product-limit or Kaplan–Meier estimator for interval censored data (Cox and Oakes, 1984; Steinberg *et al.*, 1997):

$$S(t_i) = \Pi(1 - d_j/r_j), \text{ for } t_j < t_i,$$

where d_j is the number of deaths at time t_j and r_j is the number at risk (those that have not failed, i.e. died or been removed, immediately before t_j. The variance is defined by:
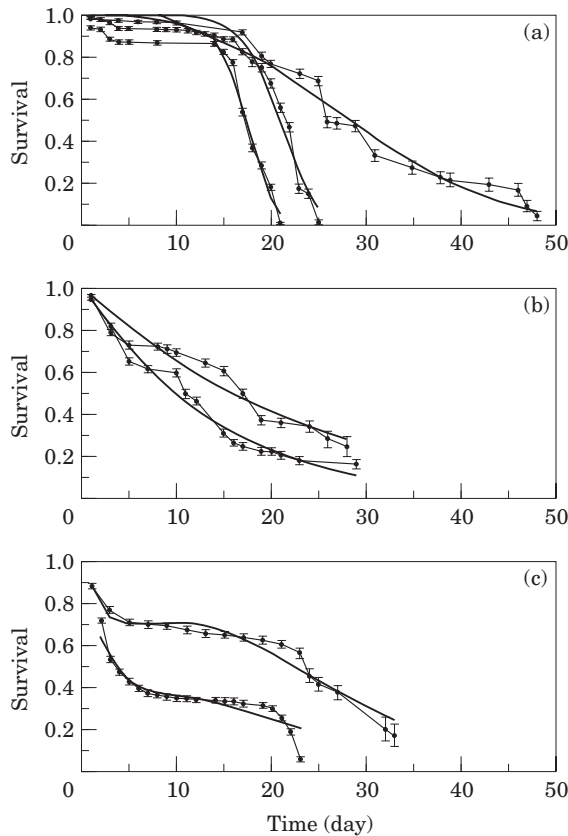
Figure A1. Illustration of the three different types of survival distribution for the incubation experiments of 1995 and 1996 at 4°C. For each case, the estimated survival values with their standard errors and the fitted function (continuous heavy lines) are presented.

$$var[S(t_i)] = [S(t_i)]^2 \Sigma d_j / r_j(r_j - d_j)$$

The illustration of the different survival distributions obtained are presented in Figure A1. The first pattern (Type A; about $\sim 40\%$ of cases) of survival distribution was best fitted by the Weibull survivor distribution:

$$S(t_i) = \exp[-(\rho \text{ time})^\kappa]$$

where the hazard is itself a function of time, increasing if $\kappa > 1$ and decreasing if $\kappa < 1$. In most cases the values of κ were rather high, hence the observed increase in mortality during hatching (Figure A1).

Much less frequence (about 5% of all cases) was the Type B distribution (Figure A1), a special case of the Weibull distribution where $\kappa = 1$:

$$S(t_i) = \exp[-\rho \text{ time}]$$

i.e. the hazard (mortality) was constant through time.

Lastly, a more complex form of survival distribution (Type C) was encountered most of the time ($\sim 50\%$ of all cases). The pattern of fluctuation indicates that the rate of death changed over time (increasing, decreasing, and increasing again) during development. One way of representing distributions close to a particular simple form is via an expansion in terms of orthogonal polynomials associated with the simple form (Cox and Oakes, 1984):

$$S(t_i) = \exp[-\rho \text{ time}]$$
$$[1 + \kappa_1 \rho \text{ time} + \kappa_2 \rho \text{ time} (\rho \text{ time} - 2)]$$

Note that after the initial period of high mortality the shape of this distribution is similar graphically to Type A, or the normal Weibull distribution (Figure A1).