

Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*)

O.S. Kjesbu, P. Solemdal, P. Bratland, and M. Fonn

Abstract: Variability in the annual egg production of hatchery-reared Atlantic cod (*Gadus morhua*) was determined under stable experimental conditions. Egg size increased with fish age as an approximate step function. Comparing first- and second-time spawners, the variance in egg dry weight was 32% within individuals (i.e., the seasonal effect, the cod being a multiple-batch spawner), 55% between years, and 12% between individuals. In several repeat spawners, the curvature of the seasonal egg size curves showed little difference between years. The seasonal decrease in egg size was typically smaller in recruit spawners than in repeat spawners. There was no empirical evidence to suggest that environmental temperature regulates seasonal variations in egg size. The extent of egg swelling (i.e., the egg dry weight/diameter ratio) indicated a strong genetic component. Investment in ovarian growth was influenced by previous allocations as exemplified by annual, sinusoidal fecundity oscillations. Larger fish showed significantly longer spawning periods. The combined influence of maternal factors and the annual temperature variations noticed in the field during early stages suggests that larger larvae at the onset of feeding are more likely to survive.

Résumé : On a déterminé la variabilité de la production annuelle d'oeufs chez des morues de l'Atlantique (*Gadus morhua*) et élevage dans des conditions expérimentales stables. La taille des oeufs augmentait avec l'âge des poissons en suivant approximativement une fonction en escalier. On a comparé le poids sec des oeufs chez des géniteurs à la première et à la deuxième ponte, ce qui a donné une variance de 32% chez les individus (ce qui correspond à l'effet saisonnier, la morue ayant plusieurs pontes pendant la saison), de 55% entre les années et de 12% entre les individus. Chez plusieurs géniteurs ayant frayé plusieurs fois, la forme des courbes saisonnières de la taille des oeufs n'indiquait que peu de différences d'une année à l'autre. La diminution saisonnière de la taille de ceux-ci était typiquement plus faible chez les nouveaux géniteurs que chez les anciens. Rien ne permet de croire que la température du milieu régule les variations saisonnières de la taille des oeufs. L'importance du gonflement des oeufs (c.-à-d. le rapport poids sec/diamètre de l'oeuf) semblait indiquer l'existence d'un important facteur génétique. L'investissement dans la croissance des ovaires était influencé par des investissements antérieurs similaires, comme le montrent les oscillations annuelles sinusoïdales de la fécondité. Les poissons de plus grande taille présentaient des périodes de ponte significativement plus longues. L'influence combinée de facteurs maternels et des variations de la température annuelle notées sur le terrain au cours des premiers stades indique que les larves qui sont les plus grosses au début de la période d'alimentation ont les plus grandes chances de survie.

[Traduit par la Rédaction]

Introduction

Although the relevance of individually based egg production time series relates both to aquaculture (i.e., fry mass production) (Kjørsvik et al. 1990; Kjørsvik and Holmefjord 1995) and fisheries conservation (i.e., stock recruitment programmes) (Rothschild 1986), egg production studies using individual marine fish over a number of years are absent from the literature. Precise information on changes in egg production with age, size, and condition of iteroparous fish is best obtained in the laboratory through careful monitoring of individuals over several spawning seasons. Studies based on single annual estimates are complicated by important between-female variation (Kamler 1992), especially in multiple-batch spawners such as the Atlantic cod (*Gadus morhua*) (Chambers

1993). Examination of the maternal effects began in the former Soviet Union in the 1930s on freshwater fish (Nikolskii 1962). Similar studies have recently been initiated on wild marine fish (Chambers et al. 1989; Buckley et al. 1991a, 1991b; Marteinsdottir et al. 1993; Solemdal et al. 1993). It is important that a long-term study should involve fish of a similar history and employ stable stress-free environmental conditions. Stress responses were noted by Bromley et al. (1986) using a group of naturally spawning turbot (*Scophthalmus maximus*) over 4 consecutive years. The egg production increased substantially over the years, but unknown numbers of nonviable eggs settled on the bottom of the tank. There are, however, several examples of spawning marine roundfish that have yielded useful data (Hislop 1975; Hislop et al. 1978; Foscarini 1988; Kjesbu 1989; Hinckley 1990; Kjesbu et al. 1991; Sakurai 1993). Typically, flatfish have to be hand stripped for eggs (McEvoy and McEvoy 1991; Norberg et al. 1991) and some of the resulting data might be more difficult to relate to natural conditions.

An alternative assessment model for Arcto-Norwegian cod is presently being developed wherein biological data, including quantification of annual variations in egg and larval production, play a role in predicting recruitment (Ulltang 1993).

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Our present work is part of this programme but is also part of a larger study on Atlantic cod in general. The current objectives were to examine the influence of age, size, and condition of individual females monitored over several seasons on the variability in egg production. Changes in egg size and actual (realized) fecundity, length of spawning interval (time between successive batches), and spawning period (time between first and last batch) with increasing female age were tested for importance. Efforts were also made to relate the seasonal pattern in egg size to water temperature and fish nutritional status. The results are discussed in relation to possible effects of stock composition on recruitment.

Materials and methods

Experimental protocol and fish

We used fish reared from eggs of local, Norwegian coastal cod in a mass rearing programme at the Austevoll Aquaculture Research Station, Norway (Naas 1990; van der Meeren 1993). Individual fish tagged for later identification were transported to the laboratory at Bergen either as 1 year olds (>200 g) that were expected to be first-time (recruit) spawners the following year (Karlsen et al. 1995) or as ≥ 2 year olds that had already spawned. Fish of the same age were stocked in outdoor seawater tanks of 30 m³ and fed moderately on wet pellets (0.5% wet body weight-day⁻¹), except for a subgroup of the 1 year old fish, which were temporarily separated from the others by a net in the tank and held on low ration ($\approx 0.25\%$ wet body weight-day⁻¹) for 3 months prior to the first spawning season. The latter procedure was done to test for any effect of variation in daily food consumption on egg production in recruit spawners (Kjesbu et al. 1991). No food was given to the fish during spawning as they do not normally feed at this time (Kjesbu et al. 1991).

The sex of the fish was identified in prespawning specimens that were anaesthetized by means of benzocaine or, more recently, metomidate (Mattson and Rippe 1989; Thomas and Robertson 1991) and catheterized (McEvoy 1984; Kjesbu 1989). The ovarian biopsy samples were placed under a binocular microscope and the mean diameter of the most advanced vitellogenic oocytes was measured to forecast the calendar day of first spawning (Kjesbu 1994).

Immediately before spawning, pairs of selected females and males were moved to 1 of 10 single chambers in an indoor circular seawater tank of 200 m³ with a natural light cycle. The criteria for the selection of a pair of fish included the feeding history, sex, health status, and the predicted date for the start of spawning. Priority was given to females that were to be observed over a number of spawning seasons. These females were placed in the same chamber each year. Fish that after the first introduction to the chamber stayed permanently in corners (Kjesbu 1989) and had an abnormal, patchy skin colouring were taken out as this indicated chronically frightened fish (Pawson 1977). At the end of the experiment, which comprised the spawning seasons of 1989–1992, the egg production of 10 females had been monitored for 2–4 consecutive seasons. Egg samples were obtained for every female in each spawning season following the procedures described in Kjesbu et al. (1991). After egg production ceased, fish of each pair were transported back to the outdoor feeding tank.

For each fish, whole wet body weight was determined to the nearest 1 g. Total length was measured to the nearest 0.5 cm for fish <40 cm, otherwise to the nearest 1 cm. Fish length and weight were, with few exceptions, recorded monthly from August in the first year. All fish were weighed just prior to the spawning season and immediately after.

The ambient water temperature was measured on a weekly basis throughout the whole experiment but every day during spawning. The temperature variation in the 6 months prior to spawning was $\pm 0.5^\circ\text{C}$. An increase of the order of 1°C occurred at the time of

replacement from the outdoor tank to the indoor spawning chamber. Mean water temperature for each female during spawning was calculated. Salinity was measured once a week during spawning and ranged between 34.0 and 34.8‰.

Egg characterization and measurements

The following variables were measured in each batch of eggs: diameter, dry weight, percent fertilization, stage of development (i.e., number of cells in blastodisc), and total volume of eggs spawned. The mean egg diameter was based on measurements (± 0.01 mm) of 50 healthy eggs in the 2- to 128-cell stage. In a very few instances, less than 50 eggs became fertilized. In that situation, either 50 unactivated or 50 activated, unfertilized eggs were taken, and their mean diameter was subsequently multiplied by 1.03 and 1.01, respectively, to give mean fertilized egg diameter. These correction factors were determined from studies on eight separate batches of eggs comprising all three categories of eggs using measurements of 50 eggs from each category. Triplicate samples of 50 fertilized eggs from five batches of different females were used to calculate the coefficient of variation ($\text{CV} = (100 \times \text{SD})/\text{mean}$) of egg diameter within a batch. The mean diameter varied by no more than 0.005 mm, while the grand mean CV was 0.2%. To measure the mean egg dry weight, 50 eggs were rinsed in distilled water, dried for at least 3 days at 70°C , and weighed (± 1 μg). The precision of mean dry weight recordings was tested on triplicate samples of 50 eggs from eight separate batches. The record of mean dry weight within a batch varied by up to 3 μg with a grand mean CV of 1.0%. Examination for any change in egg dry weight during the period of incubation at the time of sampling (4–20 h) was conducted by repeatedly sampling triplicates of 50 eggs from three batches over the first 2 days. Any loss in weight was hardly measurable. As a low number of samples included unfertilized eggs only, we compared the mean egg dry weight of unfertilized and fertilized eggs from the same batch and found no significant differences ($P = 0.681$, $n = 6$, paired samples t test). Weighted estimates of mean egg diameter and dry weight were obtained by weighting the mean for each batch by the number of eggs spawned in that batch. The latter figure was calculated by dividing the volume of eggs by the estimated number of eggs per millilitre (Kjesbu 1989). The total number of eggs spawned was found by summing over all batches shed by the female in one season. The total egg dry weight was estimated by multiplying the total egg number by the weighted mean egg dry weight.

Egg dry weight/diameter ratios were calculated for each female to test for seasonal trends among and within females. The expected egg dry weight was found by entering the observed diameter in a power regression equation valid for both wild and captive specimens (Knutsen and Tilseth 1985; Kjesbu 1989). Residual egg dry weight was subsequently calculated as the difference between observed and expected dry weight.

Estimation of spawning times

The time of shedding of a particular batch of eggs was back calculated from the recorded egg stage at the time of collection and the rate of egg development (Kjesbu 1989). A pilot test on eggs sampled from two females during the course of spawning gave no indications of any size dependency in development rates. The time intervals between successive batches (spawning intervals) were calculated, and the spawning period was defined as the time between the first and last batches.

Results

Interannual variation in egg production

First-time (recruit) spawners produced significantly smaller and, typically, a lower number of eggs at shorter spawning intervals than did repeat spawners (Table 1). The fertilization

Table 1. Data on the spawning activity of the 10 females held in captivity for several years.

Fish No.	Year	Age	Ration	Prespawning			Spawning					
				W (g)	L (cm)	K	No. of batches shed	Mean water temp. (°C)	Spawning period (days)	Mean spawning interval (h)	Actual fecundity	
											Absolute (millions)	Relative (eggs/g)
1	1990	2	Moderate	571	37.5	1.08	16	8.9	28	45.0	0.20	344
	1991	3	Moderate	1177	48.0	1.06	17	9.3	34	50.8	0.40	338
	1992	4	Moderate	2436	58.0	1.25	18	9.2	45	56.3	2.19	901
2	1990	2	Moderate	656	38.5	1.15	20	8.9	38	47.0	0.58	878
	1991	3	Moderate	1804	52.0	1.28	21	9.4	48	52.7	1.44	799
	1992	4	Moderate	3327	62.0	1.40	16*	9.1	>40	—	1.95*	586*
3	1990	2	Moderate	733	40.0	1.15	14	9.0	27	47.5	0.38	525
	1991	3	Moderate	1730	53.0	1.16	4	9.4	6	—	0.05	30
4	1990	2	Low	428	35.0	1.00	12	9.1	22	45.7	0.33	768
	1991	3	Moderate	1388	48.0	1.26	19*	9.3	41	51.8	0.96	693
	1992	4	Moderate	3302	63.0	1.32	21	9.2	45	54.1	3.01	910
5	1990	2	Low	534	36.5	1.10	13	9.1	22	45.7	0.36	668
	1991	3	Moderate	1524	49.0	1.30	19	9.3	41	54.9	1.37	897
6	1990	2	Low	508	37.0	1.00	15	8.9	29	51.0	0.36	709
	1991	3	Moderate	1292	50.0	1.03	11	9.4	33	60.9	0.48	369
7	1991	3	Moderate	1955	57.0	1.06	8*	9.4	—	53*	0.25*	128*
	1992	4	Moderate	4065	68.0	1.29	20	9.2	48	—	1.52	373
8	1989	4	Moderate	3750	64.0	1.43	16	8.8	30	48.2	3.22	860
	1990	5	Moderate	3710	68.0	1.18	15	9.0	27	46.6	2.21	595
	1991	6	Moderate	5064	72.0	1.36	18	9.4	37	52.2	2.87	567
	1992	7	Moderate	4554	72.0	1.22	14	9.1	36	60.0	1.93	425
9	1989	4	Moderate	4800	67.0	1.60	19	8.9	41	54.1	2.87	597
	1990	5	Moderate	5240	72.0	1.40	10	9.2	22	57.6	0.15	28
	1991	6	Moderate	7001	79.0	1.42	6*	9.3	—	68.2*	0.13*	19*
10	1989	4	Low	1500	50.0	1.20	15	8.7	36	54.9	0.69	457
	1991	6	Moderate	3525	63.0	1.41	21	9.4	>44	56.0	1.83	519

Note: Year of study and fish age refer to the forthcoming spawning season. W, whole body weight; L, total length; K, Fulton's condition factor, $(W/L^3) \times 100$; spawning period, time period from first to last batch; spawning interval, time period between subsequent batches of eggs; actual fecundity, number of eggs shed; relative actual fecundity, number of eggs per gram prespawning body weight; residual, observed egg dry weight – estimated egg dry weight; ΔW , weight loss during spawning; *, an incomplete data set; —, missing value.

rate was normally higher than 90%, indicating that the fish were generally well acclimatized. An initial analysis included females monitored from the time as recruit (2 year old) spawners only, i.e., fish Nos. 1–6. The change in weighted egg diameter noted between first- and second-time spawning is equal to an increase in the corresponding egg volume of about 25% but this declines to about 20% when first- and third-time spawners are compared (Fig. 1). The concurrent change in weighted egg dry weight was about 20% in both cases (Fig. 1). The relationship between actual fecundity and fish weight was very similar to that between total dry weight of spawned eggs and fish weight (Fig. 1). There was no sign of any trade-off between egg size and egg number between first- and second-time spawning, although it may have been present between second- and third-time spawning. Mean spawning interval was found to be positively correlated with fish weight (Fig. 1). No consistent trend existed between interval length and egg size. The mean spawning interval rate was on average 11.5% lower at age 3 than at age 2. Excluding the effect of the 0.5°C higher water temperature at age 3 (Kjesbu 1989), the Q_{10} dropped by 15% between first- and second-time spawning.

The calculation of the egg dry weight/diameter ratio (i.e., weighted egg dry weight residual) revealed that individual

females tended to produce consistent mean departures from year to year relative to the general relationship between diameter and dry weight for cod eggs (Table 1). The residual was lower when the fish was a second-time spawner than when it was first- or third-time spawner.

Within-year variation in egg production

The within-year effect of variation in female size on egg production was similar to the interannual variability discussed earlier. Maternal weight was positively, significantly correlated with the number of batches shed, the length of the spawning period, the total number and dry weight of spawned eggs, and the weighted egg size (Table 2). The condition of the fish did not significantly influence the weighted egg size but did influence the other variables tested. Previously published data (Kjesbu 1989; Kjesbu et al. 1991) were included in these analyses using an allometric model, i.e., according to the general formula $y = aW^bL^c$, where W is whole body weight and L is total length. Addition of age as the third independent variable was in no case warranted statistically ($P > 0.05$).

Grouping the individual fish data according to the number of spawning seasons and the feeding regime experienced over the last 6 months prior to spawning, we found no significant

Spawning				Spent	
Weighted mean egg size			Total egg dry weight (g)	ΔW (%)	K
Diameter (mm)	Dry weight (μg)	Residual (μg)			
1.230	77.0	4.7	15	-24	0.83
1.315	90.7	1.2	36	-31	0.73
1.293	89.8	5.2	197	41	0.74
1.362	76.5	-23.5	44	-36	0.74
1.454	91.7	-31.4	132	-39	0.78
1.419*	92.5*	-21.3*	180*	-47	0.73
1.370	81.6	-20.1	31	-26	0.85
1.479	97.1	-32.7	5	-12	1.02
1.212	75.9	6.9	25	-22	0.78
1.312	89.8	1.1	86	-29	0.89
1.293	93.5	8.8	281	-32	0.90
1.274	88.0	7.2	31	-31	0.76
1.351	97.3	-0.1	133	-41	0.76
1.162	63.8	3.5	23	-28	0.72
1.288	85.5	1.9	41	-29	0.74
1.375*	—	—	—	-15	0.89
1.395	98.6	-9.2	149	-26	0.96
1.289	85.6	1.7	276	-35	0.93
1.276	83.8	2.7	185	-29	0.84
1.336	95.6	1.8	275	-33	0.92
1.327	98.3	6.3	190	-26	0.90
1.342	93.0	-2.3	267	-26	1.18
1.341	88.0	-7.1	13	-7	1.31
1.362*	91.4*	-8.5*	12*	-8	1.30
1.348	79.9	-16.6	55	-20	0.96
1.397	84.6	-23.8	155	-35	0.92

effect of food ration size on weighted mean egg dry weight in recruit spawners, although repeat spawners produced significantly larger eggs (ANOVA: low-ration ($n = 6$) versus moderate-ration first-time spawners ($n = 4$), $P = 0.960$; second-time ($n = 7$) versus third-time spawners ($n = 7$), $P = 0.359$; recruit ($n = 10$) versus repeat spawners ($n = 14$), $P = 0.002$).

Single egg batch production

Egg dry weight/diameter ratio and estimation of water content

There was a large variation in the egg dry weight/diameter ratio (residuals) among females but high consistency in residuals within an individual among batches and year (Fig. 2). When relevant data on egg buoyancy were included (Kjesbu et al. 1992), the water content was found to range from 91.7 to 94.4%. As a consequence of this, the study of egg size focused on egg dry weight rather than egg diameter or egg volume.

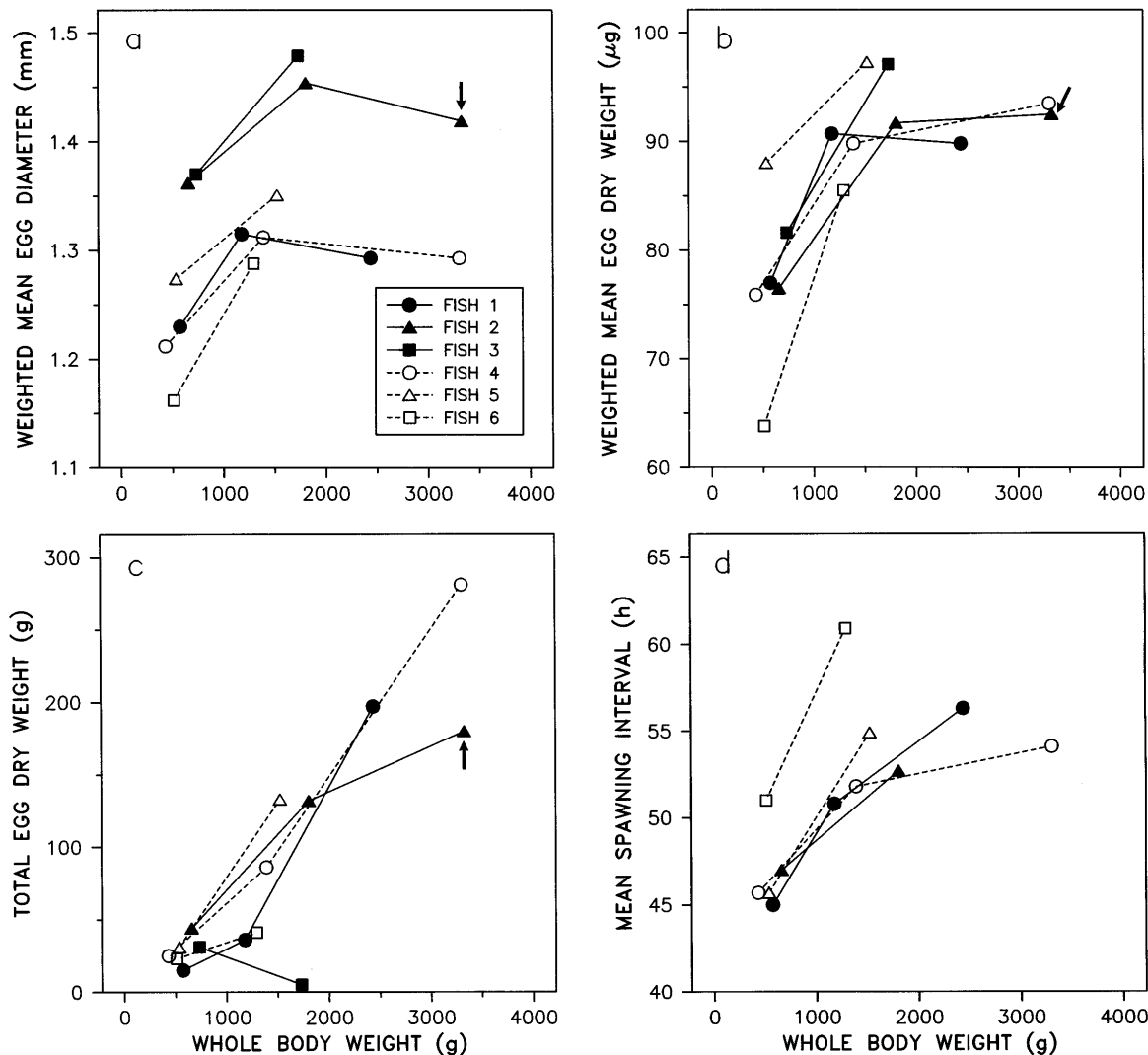
Seasonal change in egg size

Neither ambient water temperature nor time interval between batches could explain the seasonal patterns in egg size. Within each of the six 3-year-old moderate-ration specimens exam-

ined, mean egg dry weight varied by 17–47 μg during the whole spawning period, spawning interval varied by 20–49 h, and water temperature varied by 0.2–0.45°C. A multiple regression analysis showed no significant contribution of inter-batch temperature to subsequent mean egg dry weight ($P \geq 0.09$). Only three females showed a significant contribution of spawning interval length ($P \leq 0.03$). These females, however, had high losses in spawning body weights ($\Delta W < -35\%$); subsequent tests showed that spawning intervals were significantly correlated with ΔW ($r = 0.939$, $P = 0.005$) representing the former by its slope taken from a linear regression of batch number versus spawning interval (Fig. 3).

The seasonal change in egg size varied considerably both between females and within females among years, although egg size generally decreased during the course of spawning (Fig. 4). Two fish, Nos. 12 and 18, were observed only during one spawning period but they were included in the analysis because they were of particular interest: No. 12 was the smallest sexually mature female cod recorded (26 cm, 180 g (prespawning data)) (E. Lied, Institute of Nutrition, Directorate of Fisheries, N-5002 Bergen, Norway, unpublished data) and No. 18 (64 cm) was in extremely good condition

Fig. 1. Weighted mean egg diameter (a), dry weight (b), total egg dry weight (c), and mean spawning interval (d) in relation to the whole body weight for six individual female cod monitored over two to three spawning seasons. Prespawning body weights of <1000, 1000–2000, and >2000 g indicate that the fish are first-, second-, and third-time spawners, respectively. Solid symbols represent fish fed moderately; open symbols represent fish fed on a low ration for 6 months prior to the first spawning, then on moderate ration. A downward-pointing arrow indicates an overestimated value (the fish retained a number of small, late season eggs that were not measured); an upward pointing arrow indicates an underestimated value (excludes a number of retained eggs).



($K = 1.75$) but had the highest absolute change in ΔW (–50.9%) (fish data taken from Table 3 in Kjesbu et al. 1992). Several repeat spawners showed little difference in the curvature of the egg size curve over years. Some fish showed a decline in the egg size from the beginning of spawning, although it would seem unlikely that energy reserves would be depleted at this time. Normally, however, egg size rose to a maximum after a few batches and then declined.

Differences in egg size between first- and second-time spawners were detected, in descending order of importance, between years, within seasons, and between fish. For mean dry weight, the variance component of a two-level nested ANOVA (Sokal and Rohlf 1981) for the within-fish level was 32.3%, for the between-year level 55.3%, and for the between-fish level 12.4%. Data from low- and moderate-ratio recruit

spawning fish were not treated separately. The respective figures for mean egg diameter were 20.4, 51.8, and 27.8%.

Batch number and size

The changes in the number of eggs per batch (i.e., batch size) throughout the spawning period followed a dome-shaped curve (Kjesbu 1989). This curve could, however, be skewed towards either early or late batches (Fig. 5). Fecundity was regulated by varying both the number of batches (up to 21) and their size. It would appear that the latter is the more important. There were indications that the batch size curve was skewed towards late-season eggs at times of high egg productivity.

Discussion

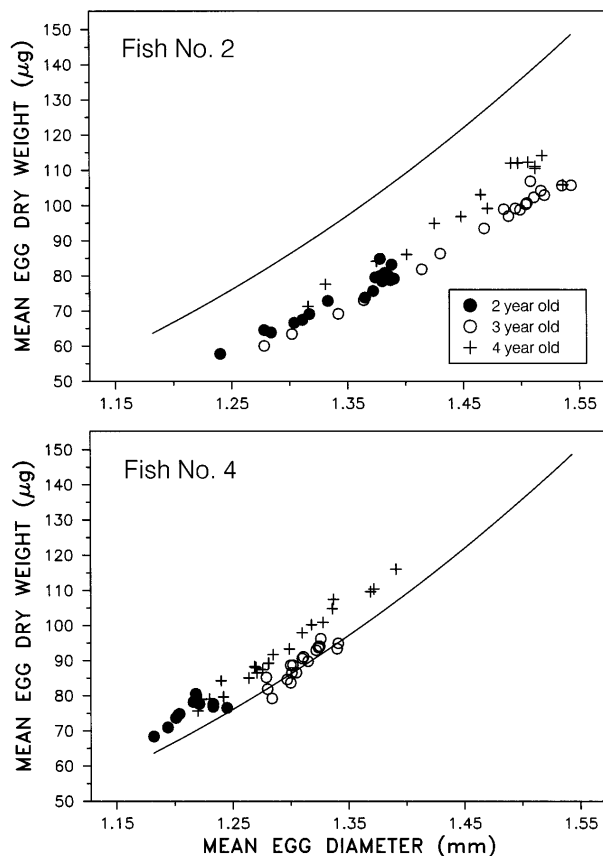
This longitudinal study demonstrates that egg size, actual

Table 2. Spawning activity variables (y) as a function of the prespawning whole body weight (W , in g) and total length (L , in cm) according to the formula $y = 3 aW^bL^c$.

Spawning activity	a	b	c	n	r^2	P
No. of batches shed	3.29×10^4	1.475	-4.720	20	0.782	<0.001
Spawning period (days)	2.33×10^4	1.461	-4.414	18	0.699	<0.001
Actual fecundity (millions)	1.66	2.739	-5.318	23	0.897	<0.001
Weighted mean egg diameter (mm)	1.08	0.026	—	23	0.260	0.013
Weighted mean egg dry weight (μg)	5.23×10^1	0.065	—	23	0.370	0.002
Total egg dry weight (g)	1.03×10^2	2.836	-5.427	23	0.921	<0.001

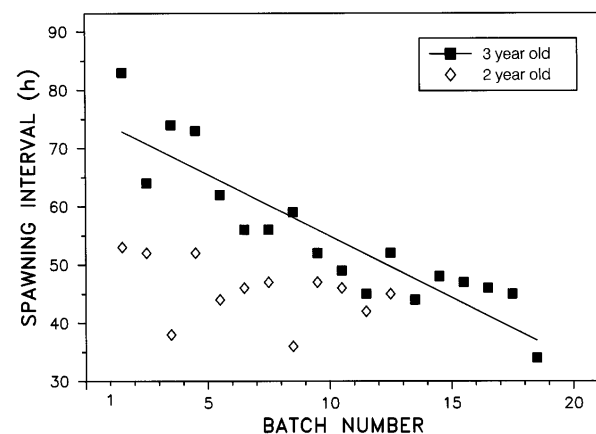
Note: Where L did not contribute significantly it is indicated by —. For the calculation of the spawning period, only fish experiencing similar water temperatures ($8.8 \pm 0.6^\circ\text{C}$) were considered. n = number of females.

Fig. 2. Relationship between mean diameter and dry weight in single batches of eggs produced by fish Nos. 2 and 4 over three consecutive spawning seasons. The general regression curve for cod (Kjesbu 1989) is given as a reference.



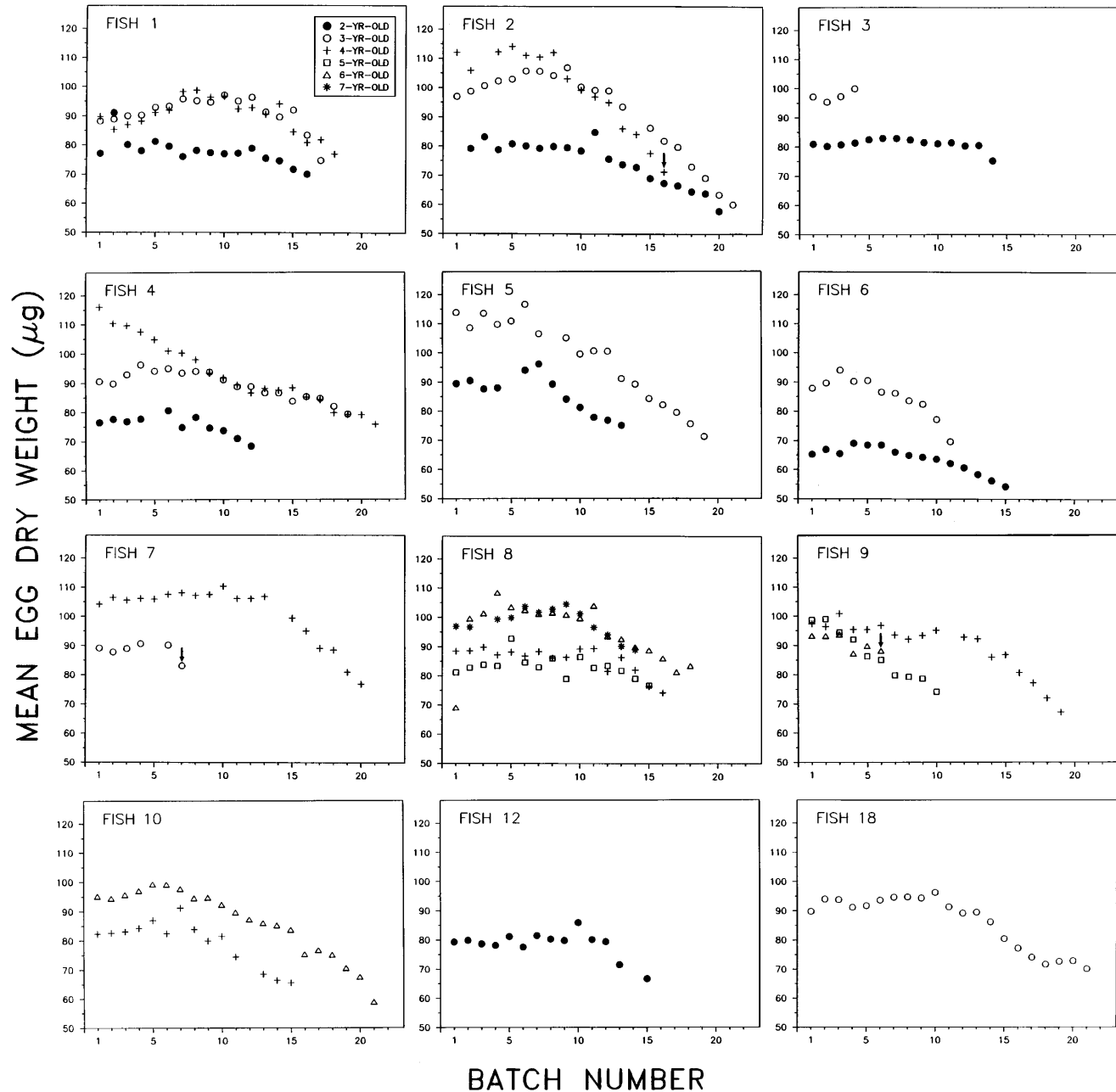
(realized) fecundity, and spawning period in the Atlantic cod generally increase with maternal size. However, in a manner similar to the viviparous guppy (*Poecilia reticulata*) (Reznick and Yang 1993), past investments in reproduction influenced future investments: there were indications that a high actual fecundity in one season negatively affected both the next seasonal production of eggs and the fish body weight. Several examples in the present study support the idea that maternal size at age produces a stepwise increase in egg size from the years immediately following recruitment to the spawning fish population, the overall picture being one of an increase in egg size between the 1st and 2nd year of spawning, arrest in the

Fig. 3. Spawning intervals of fish No. 5 as a first- and second-time spawner, the least-squares regression line applying to the latter situation.



subsequent year, and then an increase again, and so on. This strategy not only points to an inherent, hormonal trait but also suggests that egg size takes priority over the actual fecundity. The within-individual stability in the egg dry weight/diameter ratio also suggests a strong genetic component, persisting through to the formation of the egg. Although there are several conflicting results for gadoids on the relationship between egg size and fish size (Hinckley 1990), this study confirms the statement of Pepin and Miller (1993) that the level of aggregation of data may significantly influence the conclusions drawn. In his study on hand-stripped, wild haddock (*Melanogrammus aeglefinus*), Hislop (1988) also described a substantial increase in egg size between 2- and 3-year-old specimens but about two-thirds of the 3 year olds were probably recruit spawners. Although the 2-year-old cod in our study produced small eggs too, they were within the normal size range for this stock (Knutzen and Tilseth 1985). However, for the Arcto-Norwegian cod and other cod stocks where recruitment to the spawning stock shifts to older fish, the egg size increase between first- and second-time spawners might not be similar to that presently observed. We found no significant influences of the condition of prespawning fish on subsequent weighted egg size, which agrees with the results of Hislop et al. (1978), who compared haddock held on high and low ration over a period of 1–2 months before the start of spawning. By contrast, this and previous studies on cod (Kjesbu et al. 1991) show that fecundity may be very susceptible

Fig. 4. Relationship between mean egg dry weight and batch number for 12 females observed over one or more spawning seasons. Arrows indicate that spawning was incomplete.



to regulation. Nevertheless, the combination of more batches and longer spawning intervals in the larger, more fecund females led to a considerably lengthened spawning period, the ecological implications of which are discussed below.

The underlying reason for the seasonal decrease in egg size in individual Atlantic cod is still unclear. Physiological explanations for the seasonal pattern in egg size noted for marine multiple batch spawners include variations in environmental temperature, fish nutritional status, and size-specific spawning times (McEvoy and McEvoy 1991; Rijnsdorp and Vingerhoed 1994). Ecological explanations include temporal and spatial changes in food particle size and availability to larvae and

predation. We will consider physiological explanations for the first two topics. There are several examples of a significant negative relationship between egg size and temperature in the literature (Hinckley 1990). These correlations are, however, unsatisfactory as they do not refer to the individual fish level or do not take into account a sharp increase in temperature towards the end of the season. In contrast, McEvoy and McEvoy (1991) stripped individual turbot females at a stable water temperature and noticed a significant reduction in egg diameter from the first to the last batch. Similarly, we found no data to support the hypothesis that temperature during spawning regulates egg size, though the temperature was well

Fig. 5. The relationship between batch size and batch number in three fish. Fish No. 4 is recorded as a first-, second-, and third-time spawner, Fish No. 18 is recorded in a single year as an extremely well fed fish, and fish No. 8 is recorded over 4 years as a fully adult fish. Arrows indicate where an approximation has been made either because eggs were lost (fish No. 4, age 2) or because they were stripped by hand (fish No. 4, age 3).

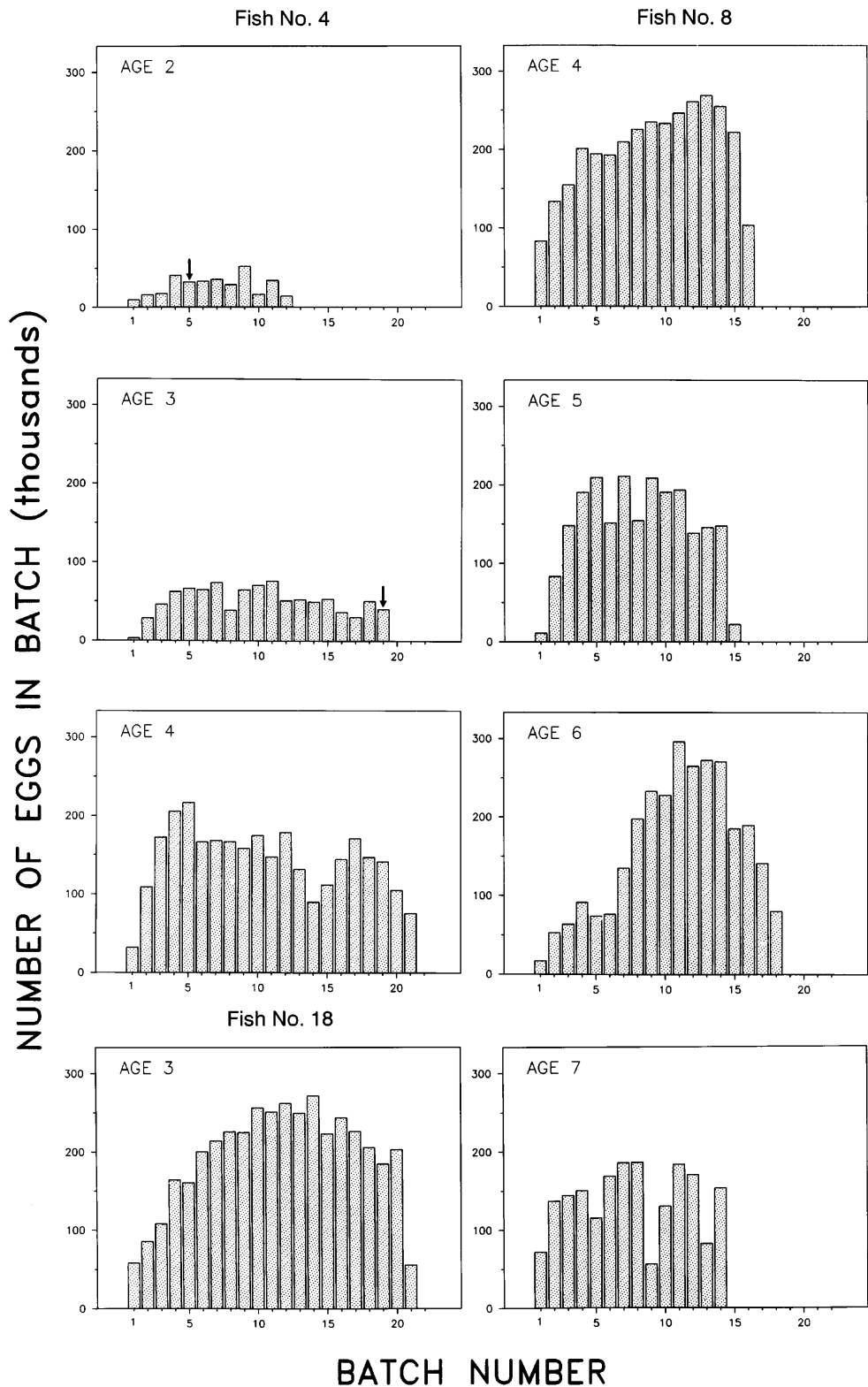
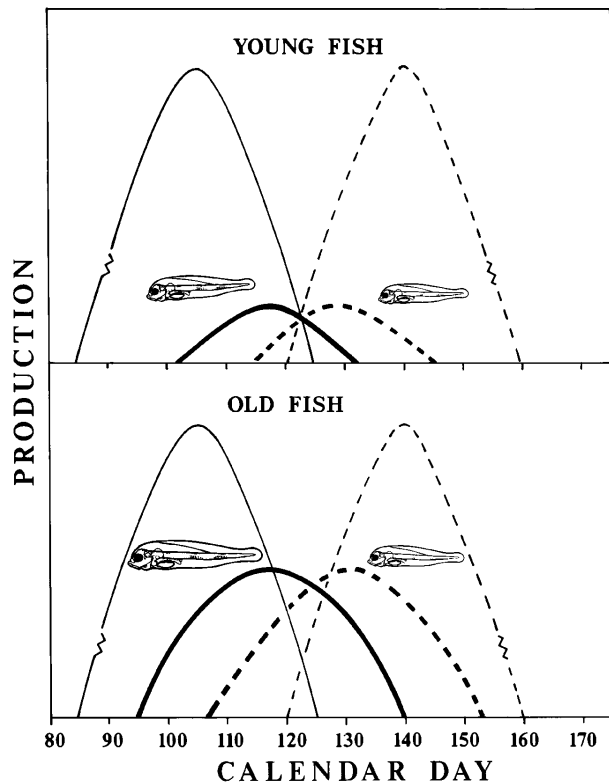


Fig. 6. The temporal production of first feeding larvae (thick line) by a single young (recruit) and an old (repeat) female cod spawner and of their most important prey, the *Calanus* nauplii (thin line), in Lofoten, Norway, in a cold (2.1°C) (broken line) and warm (4.1°C) (solid line) year. Temperatures refer to the coastal water. Points on the x axis are based on empirical data sets whereas the y axis scale is arbitrary but showing relative curve heights that are in agreement with existing observations. The higher number of larvae from the old fish than from the young fish is assumed to relate directly to present noted differences in the egg production. The production of nauplii and the temporal aspects of the cod larval production were based on Ellertsen et al. (1989) and Solemdal and Kjesbu (1992). The average length of the spawning period of a typical old and young fish as demonstrated in this study was used in subsequent analyses. The length of cod larvae as illustrated represents estimated larval dry weight (day 5 post-hatch) from a linear regression (Knutsen and Tilseth 1985) using present typical egg dry weight data. Larval appearance is from Fridgerisson (1978).



within accepted tolerance limits (Jobling 1988). Nor could the seasonal egg size pattern be explained by variations in the ambient seawater salinity (Davenport et al. 1981). The spawning cod ovary is very active in terms of vitellogenesis (Kjesbu et al. 1991). Despite this, we were not able to demonstrate that the length of the spawning interval or depletion of body reserves are important physiological explanations for the individual decline in egg size. On the other hand, several female cod showed little differences in the curvature of the egg size curves between years but, as discussed above, there were variations in the elevation of the curves. The former information

points to genetically influenced hormonal profiles, relevant profiles of which are shown in Kjorsvik and Holmefjord (1995). Taken together, it seems reasonable to believe that the seasonal decrease in egg size is not due to environmental factors but arises from an innate rhythm under hormonal control.

The importance of differences in progeny size, fecundity, and spawning period between young and old cod for subsequent year-class formation may be discussed in relation to annual temperature variations during early stages and the production of zooplankton (Fig. 6). As noticed, one important assumption is that large cod eggs result in large cod larvae. Our interest in this topic arose from the fact that a high temperature during the early life stages is a necessary but not sufficient requirement for good recruitment of the Arcto-Norwegian cod stock (Ellertsen et al. 1989; Nilssen et al. 1994; Ottersen et al. 1994). A full presentation of other recruitment mechanisms (Rothschild 1986; Leggett and Deblois 1994) was considered to be beyond the scope of this study. The latter recent review gives, however, reasons to believe that the so-called match-mismatch hypothesis is still relevant in recruitment studies. On the other hand, the "bigger is better" concept should be treated with caution as larger larvae might be more vulnerable to size-selective predation but, speaking physiologically, they should be in a better situation to survive (e.g., the lengthened period to point of no return; see review by Miller et al. 1988). When evaluating Fig. 6, the perfect temporal symmetry between the predator (first-feeding cod larvae) and prey (*Calanus* nauplii) curves is obvious under the two different sets of environmental conditions. More important in the present context is, however, the finding that the cod larvae showing the dominant overlap with the nauplii curve are of larger size in the warm year and of smaller size in the cold year. Also, the degree of overlap is enlarged in the older fish as compared with in the younger fish. This nauplii production may, in simplified terms, be characterized as unimodal and monocultural and is strongly influenced by the temperature in the coastal water overlying the warmer, more temperature-stable and saline Atlantic water, with the cod spawning in the 4–6°C thermocline (Ellertsen et al. 1989; Sundby 1994). In summary, the data presented in this paper suggest that the larger cod larvae for both physiological and ecological (food availability) reasons should be in a better survival situation than the smaller larvae. The existence of a rich variety of age-classes in the spawning stock should therefore help to increase the probability of successful recruitment.

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