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Comparison of various potential fecundity models for north-east Arctic cod *Gadus morhua*, L. using oocyte diameter as a standardizing factor

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To build a better data foundation for recruitment models of north-east Arctic cod *Gadus morhua* the construction of fecundity models reflecting variation in the nutritional status of the fish was attempted. The models were based on fecundity time series covering 9 years within the period 1986–2004 and included both general and year-specific approaches. Initial data analysis revealed that the potential fecundity (F_P) (standing stock of vitellogenic oocytes) was significantly reduced as the vitellogenic oocytes increased in size towards the start of spawning. Histological examination strongly indicated that this seasonal reduction was caused by atresia. Regression analysis showed that the F_P was positively correlated to fish total length (L_T) and the Fulton's condition factor (K). A multiple regression including data for all years using fish L_T, K and mean oocyte diameter (D_O) as independent predictors described the F_P with an $r^2 = 0{\cdot}94$. This was considerably higher than comparable univariate L_T or mass-based regressions. These univariate regressions had fairly high r^2 values when split by years, but not as high as found for year-specific multiple regressions. An important application for individual-based fecundity models may be to generate outputs that can be fed into stock level fecundity and recruitment models. Overall, the multivariate models seemed to be the most accurate. The multivariate model including mean D_O, however, also had the potential to correct for maturity and thus provide unbiased fecundity comparisons between years, stocks and locations.

Key words: Atlantic cod; condition; fecundity; north-east Arctic cod; oocyte diameter.

INTRODUCTION

Recruitment to a fish stock starts with the stock reproductive potential and then the early life-history numbers are modified by environmental and ecological factors such as temperature, food availability and predation. The stock reproductive potential can be considered as the stock fecundity, *i.e.* the sum of the fecundities of all its individual mature females. In many fish recruitment studies, the reproductive potential and spawner biomass are synonymous (Myers *et al.*, 1996; Francis, 1997; Gilbert, 1997; Hilborn, 1997; Myers, 1997;

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Barrowman & Myers, 2000; Fogarty *et al.*, 2001), which assumes that the relative fecundity (F_{RP}) [number of eggs per unit body mass (M)] of spawning females is constant. Some recent studies have questioned this approach and argued that the F_{RP} varies with size and condition of the fish (Kjesbu *et al.*, 1998; Marteinsdottir & Begg, 2002; Yoneda & Wright, 2004). This variability can lead to large year-to-year variation in egg production, both at the individual and at the stock level (Marshall *et al.*, 1998). For most species, however, there is a scarcity of data on variations in fecundity with these factors. This is partly because it is only recently that more time efficient methodologies for working up fecundity samples have become available (Witthames & Greer Walker, 1987; Thorsen & Kjesbu, 2001; Murua *et al.*, 2003) and so more fecundity data have accumulated. Therefore, only now is it possible to develop more sophisticated and accurate fecundity models.

For studies dealing with fecundity, there are two important distinctions: potential fecundity (F_P) and 'realized' fecundity. F_P is usually regarded as the number of maturing oocytes present in the prespawning ovary whilst 'realized' fecundity is the number of eggs that are actually spawned (Murua *et al.*, 2003). In some studies, the 'realized' fecundity has been estimated from the F_P by subtracting the detected level of atresia (resorption of maturing oocytes) in the ovary (Greer Walker *et al.*, 1994; Ma *et al.*, 1998; Armstrong *et al.*, 2001; Óskarsson *et al.*, 2002; Witthames *et al.*, 2003) This is difficult, however, because it is necessary to utilize accurate information on the duration of the atretic stages (Murua *et al.*, 2003). In some species, those classified as indeterminate spawners; this is further complicated by a continuous recruitment of mature oocytes well into the spawning period (Murua *et al.*, 2003). 'Realized' fecundity is sometimes investigated by collecting spawned eggs from captive fishes in tanks (Kjesbu, 1989; Kjesbu *et al.*, 1991; Trippel, 1998; Fordham & Trippel, 1999; Thorsen *et al.*, 2003).

Oocytes of Atlantic cod *Gadus morhua* L. enter the vitellogenic phase at a size of *c.* 250 μm (Sivertsen, 1935) and once started the fish will spawn in the coming season (Kjesbu & Kryvi, 1993). After *c.* 4–5 months of continuous vitellogenesis the largest oocytes (G1) have reached their maximum size of *c.* 900 μm before final maturation and start of spawning. At this stage the mean oocyte diameter (D_O) is typically 600–800 μm (Kjesbu *et al.*, 1990; Kjesbu & Kryvi, 1993; Thorsen & Kjesbu, 2001). This growth pattern seems to be rather consistent and D_O has therefore been used as an indicator of maturity and time to start of spawning (Kjesbu, 1994).

Size of spawned eggs seems to a large degree being decided during the very late oocyte development during the spawning season, up to one-third of the egg yolk is included during final maturation in the 2–3 days before the release of a batch (Wallace & Selman, 1985; Kjesbu & Kryvi, 1993). Prespawning mean D_O should therefore not be considered to be proportional to spawned egg size.

Atlantic cod is classified as a determinate batch-spawner, which typically produces 10–20 batches over the course of a single spawning season (Kjesbu, 1989). At present, the estimation of 'realized' fecundity of wild Atlantic cod is complicated and cannot be undertaken with high accuracy and precision because there are few data on atresia and the duration of the atretic stages.

Therefore, this study concentrated on the F_P as measured in the period before spawning, although some atresia data were also collected. In essence, this work is an extension of the study undertaken by Kjesbu *et al.* (1998).

Recently, Kurita *et al.* (2003) have demonstrated for Norwegian spring-spawning herring *Clupea harengus* L. that there is a steep decline in the standing stock of vitellogenic oocytes as maturation advances. This down-regulation was also investigated for Atlantic cod using mean vitellogenic D_O to reflect stage of maturity.

For the F_P models, total length (L_T) was used as the key independent predictor even though prespawning M in some situations may show a better correlation (Kjesbu *et al.*, 1998; McIntyre & Hutchings, 2003; Koops *et al.*, 2004). This choice was made because M, in contrast to L_T, is expected to fluctuate strongly within a year cycle, *e.g.* during the long spawning migration of north-east Arctic cod.

To improve the simple L_T-based model, however, Fulton's condition factor (K) and mean D_O were used as additional moderating predictors. K has been shown to correlate well with available lipid and protein reserves in *G. morhua* (Lambert & Dutil, 1997). Mean D_O was used to standardize for stage of maturity so that different levels of maturity in the sampled fish would not bias the models.

MATERIAL AND METHODS

The majority of fish used for this investigation were taken in the Vesterålen area (northern Norway; see Fig. 1) by commercial fishing vessels using a Danish seine. The fish were immediately landed locally at Andenes or Myre and fecundity samples were taken the same day. To ensure that the full range of vitellogenic oocyte development stages were represented in the material, some samples (Fig. 1 and Table I) were also collected by trawl in the Barents Sea during the Institute of Marine Research (IMR), Norway winter cruises. For all years the fish were measured (L_T to nearest 0·5 cm), weighed (nearest g for total mass, M, and nearest 0·1g for ovaries M_G). K was calculated from $K = 100ML_T^{-3}$. Sagittal otoliths were removed from all fish for stock separation (coastal cod, north-east Arctic cod or Svalbard cod) (Rollefsen, 1934). Only fish that were characterized as north-east Arctic cod were used in this investigation. Selection of fish was not totally random as there was positive selection for larger fish to ensure that large fish were represented in the sample.

For 1999–2004, all ovary samples (1–2 g) were taken from the middle part of the right ovary lobe and immediately fixed in at least 18 ml of 3·6% buffered formaldehyde (29·5 mM $NaH_2PO_4H_2O$ and 460 mM $Na_2HPO_42H_2O$). An earlier investigation (Kjesbu & Holm, 1994) has shown that oocyte distribution is homogenous in *G. morhua* ovaries.

F_P was defined as the number of vitellogenic oocytes present in the ovary at the time of sampling, whilst F_{RP} was defined as F_P per unit M (g). In the period from 1986 to 1989, the fecundity samples were frozen and analysed using a gravimetric method. The samples from 1991 were analysed using a stereometric method and a particle counter. Details of the sampling scheme and fecundity analyses for the period 1986–1991 are given in Kjesbu *et al.* (1998). For the material from 1986 to 1991, mean vitellogenic D_O were calculated from the number of oocytes g^{-1} ovary (as given by gravimetric counting; Thorsen & Kjesbu, 2001).

For the 1999–2004 material, vitellogenic D_O was measured using an image analyser as detailed in Thorsen & Kjesbu (2001). The auto-diametric fecundity method (Thorsen & Kjesbu, 2001) was used to estimate F_P using the mean D_O and M_G. The three different fecundity methods were carefully intercalibrated as outlined in Kjesbu *et al.* (1998) and Thorsen & Kjesbu (2001).

The level of atresia was analysed for the year 1999–2000 using stereological techniques, more precisely the Disector principle (Mayhew, 1992; Andersen, 2003). This was considered an improvement over the Weibel method used in Kjesbu *et al.*

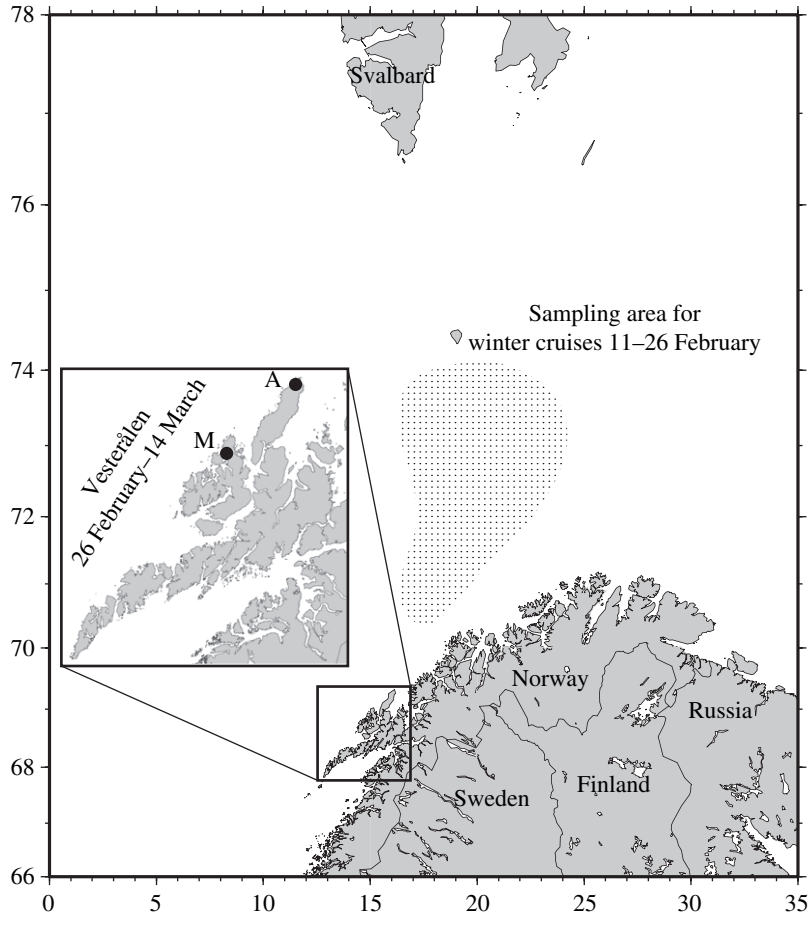

FIG. 1. Sampling areas: A, Andenes; M, Myre (see Table I).

(1998), as no cell shape factors needed to be included in the estimation and all cells, independent of size, had the same chance of being counted. Small pieces of fixed ovary material were dehydrated in increasing concentrations of ethanol (70–96%) and embedded in Technovit methyl methacrylate. Each block was then sectioned at 4 μm, stained with toluidine blue, and thereafter dried and mounted on glass slides. Only early (α-stage) atretic oocytes (Hunter & Macewicz, 1985; Witthames, 2003) were counted. To, as far as possible, exclude size-specific bias when estimating the number of atretic oocytes, the cells were counted following sectioning of pairs in parallel planes with a distance of *c.* 160 μm. This corresponded to *c.* 0·33–0·25 of the minimum cell (vitellogenic oocyte) D_O, according to standard procedure (Mayhew, 1992). Using a three-dimensional model (Mayhew, 1992), the oocytes were counted when found on the slide being analysed (the 'reference') but not on the next slide (the 'look-up'). The counting was performed using a stereomicroscope at ×4–20 magnifications. To be able to compare the 'look-up' with the 'reference' slide, video pictures were printed on transparencies and paper copies, respectively. The transparency was placed on top of the paper and placed next to the counting microscope so that the cells seen in the microscope were also present in the 'look-up' could be confirmed. For each sample an average of 156 (range: 150–190) oocytes were counted corresponding to an average of nine (range: four to 12) slides. In the subsequent estimation of atresia, the intensity of atresia (I_A) was

TABLE I. Samples of north-east Arctic cod collected. Samples from Vesterålen were landed in Andenes or Myre and processed the same day. Lofoten is the main spawning area of north-east Arctic cod and is located just south-east of Vesterålen

Year	Date	Sampling area	Vessel	Number of samples
1986	6–7 March	Vesterålen	Commercial landings	50
1987	6–7 March	Vesterålen	Commercial landings	44
1988	6–7 March	Vesterålen	Commercial landings	49
1989	6–7 March	Vesterålen	Commercial landings	111
1991	6–7 March	Lofoten	Commercial landings	8
1999	10–11 March	Vesterålen	Commercial landings	98
1999	11–26 February	Barents Sea	G. O. Sars	56
1999	17–18 February	Barents Sea	J. Hjort	2
2000	14 March	Vesterålen	Commercial landings	91
2001	28 January to 6 March	Barents Sea	G. O. Sars	79
2001	24–25 January	Barents Sea	J. Hjort	55
2003	3–4 March	Vesterålen	Commercial landings	55
2004	26–27 February	Vesterålen	Commercial landings	57
				Total = 755

calculated as: $I_A = 100\ N_{AVO}\ (N_{AO} + N_{VO})^{-1}$, where N_{AVO} is the number of atretic vitellogenic oocytes, N_{AO} is the number of atretic oocytes and N_{VO} is the number of vitellogenic oocytes. Prevalence of atresia was defined as the number of fish with atresia divided by the total number of fish.

All statistical analyses were undertaken using StatView 5.01. All data were ln transformed before regression analyses; the one exception was the D_O and F_{RP} regression. Only simple or multiple linear regressions were used. Year effects were analysed using ANCOVA.

RESULTS

ATRESIA AND RELATIVE FECUNDITY V. MATURITY

At the outset, the objective was to indicate the influence atresia levels have on the standing stock of vitellogenic oocytes (F_P) during maturation. Differing levels of maturity could make comparisons of fecundity between years and fish suspect since such differences might possibly cause a bias in the perception of fecundity. Mean D_O was chosen to represent the maturity status of the fish and this was presented against the F_{RP} (F_P per unit M). F_{RP} removed a major variation in F_P caused by differences in fish size that might else have obscured any relationship between mean D_O and F_P.

There was a significant relationship ($r^2 = 0{\cdot}17$, $n = 611$, $P < 0{\cdot}001$) between F_{RP} and mean D_O [Fig. 2(a)] for the combined material from the winter cruises and Andenes and Myre. On average (from the regression line), the F_{RP} decreased from 565 to 354 g^{-1} between 400 and 800 μm diameter oocytes. For mean $D_O < 600$ μm some F_{RP} values were much higher than found among fish with larger oocyte sizes. The decrease in F_{RP} overlapped with a period of high intensity of atresia [Fig. 2(b)], ranging from 0 to 19% (mean 2·54%, prevalence 0·36). Both the level of atresia and F_{RP} were highly variable, however, during the vitellogenic growth period that started at *c.* 250 μm (Kjesbu, 1991).

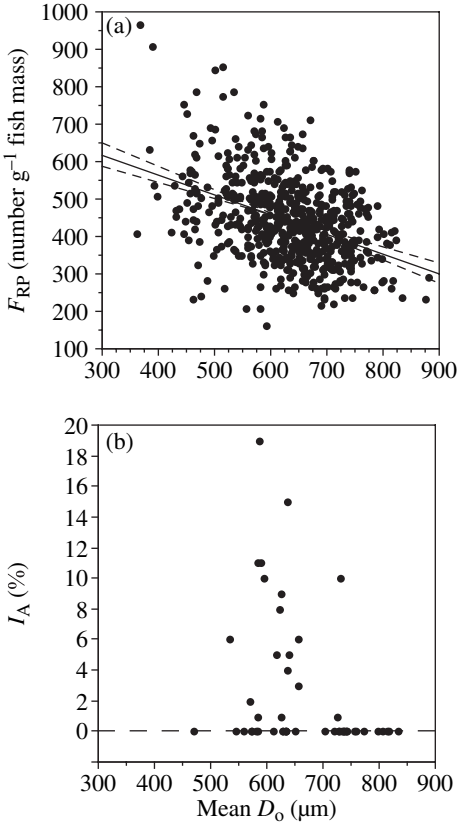

FIG. 2. (a) Relative fecundity and (b) intensity of atresia and mean oocyte diameter. The curve in (a) was fitted by: $y = 777 - 0{\cdot}527x$ (- - -, 95% CL for the slope of the regression line).

There was a weak but significant positive relationship between F_{RP} and L_T ($r^2 = 0{\cdot}09$, $P < 0{\cdot}001$), M ($r^2 = 0{\cdot}08$, $P < 0{\cdot}001$) and K ($r^2 = 0{\cdot}09$, $P < 0{\cdot}001$). The relationships between L_T and F_{RP} should, however, not significantly influence the D_O and F_{RP} relationship since mean D_O was not related to L_T ($r^2 = 0{\cdot}005$, $P > 0{\cdot}05$) and only very weakly to M ($r^2 = 0{\cdot}01$, $P = 0{\cdot}01$).

Because of the large variance in F_{RP} among the early maturing fish, early maturing fish were not included in the fecundity models. In practice, the criterion set for all later statistical analysis was that the oocytes should have a mean D_O of at least 500 μm and collected at Andenes or Myre in the period 26 February to 14 March. Spawning was expected to start *c.* 15 March with a peak in egg production close to 1 April (Pedersen, 1984).

BASIC CHARACTERISTICS OF FISH SAMPLED AT ANDENES AND MYRE

Mass and L_T (Table II) were the only body characteristics that were consistently reported for all years and as such are the core measurements for the

TABLE II. Basic statistics for total length (L_T), mass (M), condition (K), mean oocyte diameter (D_O) and relative fecundity (F_{RP}) for the years investigated between 1986 and 2004. Only fish with mean $D_O \geq 500$ μm were included

Variable	Year	Mean ± S.D.	Count	Minimum	Maximum
L_T (cm)	Total	83·4 ± 16·8	502	50	135
	1986	91·1 ± 18·3	49	55	135
	1987	64·6 ± 8·4	24	52	86
	1988	79·6 ± 19·4	49	50	122
	1989	84·2 ± 22·3	107	50	126
	1991	82·5 ± 14·5	8	57	101
	1999	85·3 ± 9·6	89	67·5	121
	2000	80·8 ± 9·4	79	57	101
	2003	85·3 ± 14·9	46	58·5	117
	2004	86·1 ± 16·1	51	63	121
K	Total	0·89 ± 0·1	496	0·62	1·29
	1986	0·92 ± 0·14	47	0·67	1·29
	1987	0·76 ± 0·1	21	0·62	0·92
	1988	0·89 ± 0·09	49	0·73	1·21
	1989	0·9 ± 0·08	106	0·64	1·14
	1991	1 ± 0·06	8	0·91	1·09
	1999	0·87 ± 0·07	89	0·71	1·04
	2000	0·89 ± 0·08	79	0·75	1·16
	2003	0·95 ± 0·09	46	0·78	1·17
	2004	0·87 ± 0·11	51	0·68	1·09
Mean D_O (μm)	Total	658 ± 68	502	502	880
	1986	692 ± 83	49	541	880
	1987	686 ± 47	24	598	784
	1988	681 ± 64	49	532	799
	1989	625 ± 56	107	506	763
	1991	740 ± 49	8	671	821
	1999	650 ± 59	89	521	813
	2000	692 ± 62	79	548	832
	2003	635 ± 66	46	515	773
	2004	627 ± 51	51	502	744
F_{RP} (number g^{-1})	Total	436 ± 106	498	216	854
	1986	428 ± 104	49	234	692
	1987	339 ± 64	21	233	434
	1988	377 ± 108	49	220	716
	1989	440 ± 99	106	216	789
	1991	451 ± 114	8	365	714
	1999	439 ± 90	89	262	684
	2000	426 ± 93	79	236	684
	2003	517 ± 121	46	283	854
	2004	465 ± 103	51	250	662

TABLE II. Continued

Variable	Year	Mean ± S.D.	Count	Minimum	Maximum
M (g)	Total	5986 ± 4068	498	900	30 000
	1986	8271 ± 5924	49	1400	30 000
	1987	2181 ± 1117	21	900	5600
	1988	5486 ± 4409	49	1100	16 100
	1989	6553 ± 4981	106	1120	19 140
	1991	5994 ± 2590	8	1800	9400
	1999	5662 ± 2281	89	2700	16 160
	2000	4897 ± 1867	79	1595	11 900
	2003	6542 ± 3731	46	1680	16 920
	2004	6409 ± 4101	51	2040	17 520

models. For the Andenes and Myre samples, the mean L_T for all years combined was 83 cm (Table II), with a minimum mean L_T of 65 cm in 1987 and a maximum of 91 cm in 1986. These 2 years also had the lowest and highest mean *M*, 2181 and 8271 g, respectively. When comparing *K* (Table II), 1987 was the lowest with 0·76 and 1991 was the highest with 1·00. Mean *K* for the whole time series period was 0·89 (Table II). Mean D_O for the different years varied from 625 μm in 1989 to 740 μm in 1991 with an overall mean for all years of 658 μm. Mean F_{RP} varied from 339 g^{-1} in 1987 to 517 g^{-1} in 2003, *i.e.* by a factor of 1·53, the overall was 436 g^{-1}.

In each year, *M* was strongly related to L_T with r^2 ranging from 0·94 to 0·99. There was, however, a significant year effect (ANCOVA, $P < 0{\cdot}001$) on the slope of the L_T and *M* relationship. When applying the different year-specific regression equations to estimate *M* and *K* at different L_T, the largest differences between years were found for the smallest fish (60 cm). In 1987, a 60 cm fish had an estimated *M* of 1573 g resulting in a *K* of 0·73, while in 1991 the corresponding values were 2208 g and 1·02. In contrast, the minimum and maximum *K* that were found for an 80 cm fish was 0·85 in 2004 and 1·00 in 1991.

POTENTIAL FECUNDITY DESCRIBED BY UNIVARIATE REGRESSION

The F_P at Andenes and Myre was related to L_T and *M* (Fig. 3 and Table III) with an r^2 for all years combined of 0·88 and 0·92, respectively. Over the years, r^2 for F_P and L_T and *M* ranged from 0·75 to 0·92 and 0·83–0·96, respectively. There was a year effect on slopes of the L_T and F_P, and *M* and F_P relationships (ANCOVA, $P < 0{\cdot}001$). The largest between year variations in F_P and F_{RP} at L_T were found among the small- and medium-sized fish [Table IV(a), (b)]. A 60 cm fish from 1991 had an estimated F_P that was approximately double that found for 1987 and 1988. An 80 cm fish from 1991 had a F_P that was 52% higher than in 1987. Among the larger fish (100 and 120 cm), the F_P values were much less variable. For a 100 cm fish a maximum difference of 23% was found between the years 1988 and 2003. F_P and F_{RP} at different *M* followed the same trends as for F_P and F_{RP} at L_T, although less variable [Table IV(c), (d)].

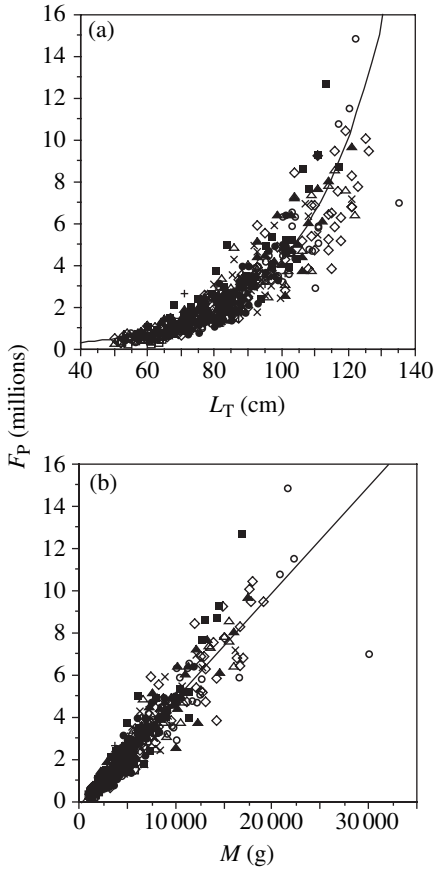

FIG. 3. Potential fecundity and (a) total body length and (b) mass split by years. 1986 (○), 1987 (□), 1988 (△), 1989 (◇), 1991 (+), 1999 (×), 2000 (●), 2003 (▲), 2004 (■) (see Table III).

POTENTIAL FECUNDITY DESCRIBED BY MULTIVARIATE REGRESSION

Length or M alone was considered unsatisfactory as independent variables in a general (year-independent) F_P model because the F_P at L_T or M varied strongly between years. Part of this variability seemed to be due to variation in K. To investigate this further, K was included as an additional independent variable in the F_P model together with L_T (Table V). L_T was preferred to M as the default descriptor of fecundity. Including K with L_T increased r^2 for the year-independent model significantly compared to using L_T alone (from 0·88 to 0·92). Compared to using M alone, the improvement was only marginal.

To further improve the model based on L_T and K, mean D_O was included as an additional independent variable. All three independent variables had P values $<0{\cdot}001$ and the adjusted r^2 was as high as 0·94 (Table VI). As expected from the above, both L_T and K had a positive contribution (Table VI) to F_P, while this was the opposite for mean D_O. The standard coefficients (Table VI)

TABLE III. Coefficients for the regressions ($y = e^a x^b$) of potential fecundity and (a) mass and (b) total length for the years investigated

Year	a	b	r^2	Count
(a)				
1986	−8·8497	1·12187	0·925	49
1987	−8·31068	1·04005	0·859	21
1988	−9·90533	1·23867	0·955	49
1989	−8·71379	1·11314	0·950	106
1991	−7·19689	0·93828	0·855	8
1999	−9·42858	1·19546	0·828	89
2000	−9·99618	1·26239	0·842	79
2003	−8·16666	1·06625	0·872	46
2004	−8·49827	1·09316	0·875	51
Total	−9·08531	1·15517	0·919	498
(b)				
1986	−16·168	3·822	0·892	49
1987	−15·542	3·637	0·787	24
1988	−16·580	3·904	0·917	49
1989	−14·018	3·352	0·925	107
1991	−11·003	2·697	0·819	8
1999	−15·523	3·682	0·751	89
2000	−15·802	3·751	0·770	79
2003	−14·077	3·411	0·854	46
2004	−15·290	3·641	0·872	51
Total	−15·361	3·651	0·879	502

showed that among the three independent variables L_T was the variable that influenced F_P the most. K and mean D_O had less influence and could therefore be considered as additional moderators to the major predictor L_T. As emphasized above, however, the present analysis only included samples with mean $D_O > 500$ μm.

Fish size and K are normally considered to be independent variables and were used as such in the present multivariate fecundity model. In the present material, however, K was related to L_T and M ($P < 0{\cdot}001$) although with very low r^2 (0·08 and 0·2 respectively). This relationship was therefore not considered to be problematic in the model. Analysis of the residuals (Fig. 4) indicated no serious deviation from the 'constant width pattern'. Thus, the ln transformation used seemed to be justified. This conclusion was supported by the clear linear relationship between the fitted F_P values and the observed F_P values (Fig. 4).

ANCOVA showed that even though K and mean D_O could explain a significant part of the variation in F_P the year effect was still present ($P < 0{\cdot}001$). The multiple regression model was therefore also split by years (Table VII) resulting in r^2 values from 0·842 in 1991 to 0·964 in 1988. This was in general higher than found for F_P and M [Table III(a)] or L_T in univariate regressions [Table III(b)].

TABLE IV. (a) Potential (F_P) and (b) relative (F_{RP}) fecundity at total length (L_T) and (c) F_P and (d) F_{RP} at mass (M) for the years investigated. Fecundity values at L_T were calculated from the regression coefficients given in Table III(b). The M used for calculating F_{RP} at L_T were taken from L_T and M regressions. F_P (c) and F_{RP} (d) at M were calculated from the regression coefficients given in Table III(a). F_P is in millions

(a)

L_T (cm) Year	60	80	100	120
		F_P ($\times 10^6$)		
1986	0·59	1·79	4·19	8·41
1987	0·52	1·49		
1988	0·55	1·70	4·05	8·26
1989	0·75	1·96	4·13	7·62
1991	1·04	2·26	4·13	6·75
1999		1·84	4·18	8·18
2000	0·64	1·88	4·35	8·61
2003	0·90	2·39	5·11	9·53
2004	0·68	1·94	4·37	8·50
Total	0·66	1·89	4·27	8·31

(b)

L_T (cm) Year	60	80	100	120
		F_{RP} (number g^{-1})		
1986	351	397	436	472
1987	332	327		
1988	303	372	436	496
1989	390	428	460	488
1991	472	442	421	404
1999		417	468	514
2000	323	409	491	570
2003	467	498	523	544
2004	409	445	476	502
Total	366	418	464	505

(c)

M (g) Year	2000	4000	8000	16 000
		F_P ($\times 10^6$)		
1986	0·72	1·58	3·43	7·47
1987	0·67	1·37		
1988	0·61	1·45	3·41	8·05
1989	0·78	1·68	3·63	7·86
1991	0·94	1·80	3·44	6·59
1999		1·63	3·73	8·53
2000	0·67	1·61	3·85	9·25
2003	0·94	1·97	4·12	8·63
2004		1·77	3·77	8·04
Total	0·74	1·64	3·66	8·14

TABLE IV. Continued

(d)

M (g) Year	2000	4000	8000	16 000
		F_{RP} (number g^{-1})		
1986	362	394	429	467
1987	333	343		
1988	306	361	426	503
1989	388	420	454	491
1991	468	449	430	412
1999		407	466	533
2000	335	402	482	578
2003	470	492	515	539
2004		441	471	502
Total	369	410	457	509

COMPARING OUTPUT FROM DIFFERENT FECUNDITY MODELS

To evaluate how the different year-independent univariate and multivariate regression models compared, their output for an 80 cm fish was plotted with K on the x-axis (Fig. 5). Since the univariate L_T-based model had no input for K, the fecundity output was constant. In contrast, F_P from the univariate M-based model increased linearly with K. The two multivariate models were slightly curved and parallel. Compared to the univariate M-based model the multivariate model using L_T and K gave approximately similar results for the most typical conditions (0·8–1·0), but became more and more different towards the extremes. It should be noted that the univariate M-based model overestimated the egg production at low K. The number of fish that had K-values $<0{\cdot}7$ and $>1{\cdot}1$ was limited to 11 and 12, respectively. Thus, the outputs from the models at these extremes will therefore have more uncertainty than for the more common K-values.

TABLE V. Year-specific and general multiple regressions on ln potential fecundity (F_P) and ln total length (L_T) (cm) and ln Fulton's condition factor (K) ($F_P = e^a L_T^b K^c$)

Year	a	b	c	r^2	n
1986	−13·571	3·267	1·340	0·930	47
1987	−10·208	2·473	1·786	0·867	21
1988	−14·355	3·458	2·310	0·964	49
1989	−13·623	3·304	1·639	0·952	106
1991	−11·778	2·875	2·217	0·822	8
1999	−13·804	3·356	1·960	0·839	89
2000	−15·474	3·720	1·601	0·842	79
2003	−13·210	3·227	0·963	0·867	46
2004	−13·146	3·198	1·280	0·900	51
Total	−13·835	3·348	1·588	0·920	496

TABLE VI. General multiple regression of ln potential fecundity (F_P) and ln total length (L_T), ln mean oocyte diameter (D_O) and ln Fulton's condition factor (K)

Regression summary					
Count	496				
r	0·968				
r^2	0·937				
Adjusted r^2	0·937				
RMS residual	0·197				
Regression coefficients					
	Coefficient	S.E.	Standard regression coefficient	t-value	P-value
Intercept	−7·628	0·606	−7·628	−12·592	<0·001
In L_T	3·323	0·047	0·856	71·265	<0·001
In K	1·610	0·086	0·224	18·639	<0·001
In D_O	−0·940	0·086	−0·123	−10·918	<0·001

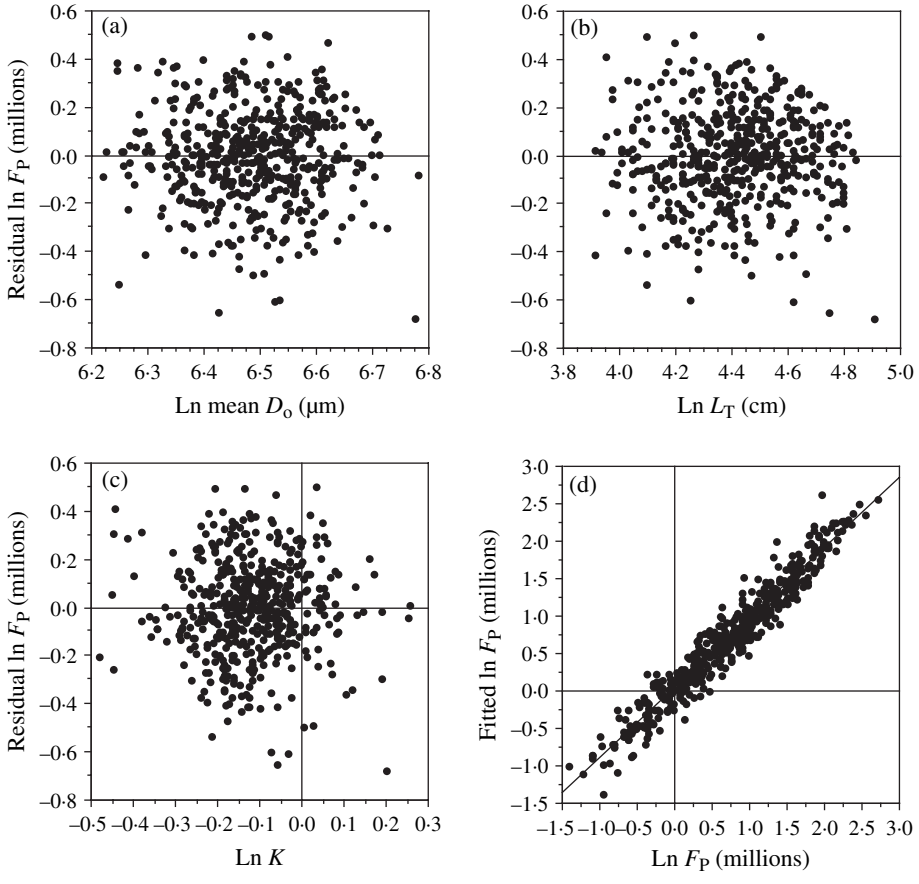

FIG. 4. Residual ln fecundity and (a) ln mean oocyte diameter (D_O), (b) ln total length (L_T), and (c) ln Fulton's condition factor (K). (d) ln measured potential fecundity (F_P) and fitted ln F_P from the multiple regression model.

TABLE VII. Year-specific and general multiple regressions of ln potential fecundity (F_P) and ln total length (L_T, cm), ln mean oocyte diameter (D_O, μm) and ln Fulton's condition factor (K) ($F_P = e^a L_T^b D_O^c K^d$)

Year	a	b	c	d	r^2	n
1986	−9·427	3·598	−0·863	1·243	0·936	47
1987	−5·335	2·498	−0·770	1·596	0·870	21
1988	−12·834	3·440	−0·222	2·264	0·964	49
1989	−6·800	3·277	−1·042	1·655	0·961	106
1991	−0·598	3·062	−1·818	1·678	0·842	8
1999	−8·504	3·327	−0·799	1·955	0·862	89
2000	−8·503	3·618	−0·998	1·618	0·873	79
2003	−4·290	2·978	−1·209	1·213	0·900	46
2004	−3·772	3·241	−1·483	1·412	0·926	51
Total	−7·628	3·323	−0·940	1·610	0·937	496

The model based on L_T and K gave values *c.* 6–8% higher than the model that also included mean D_O. The reason for this was that in the latter model the mean D_O was set at a constant of 700 μm. Typically, the mean D_O in a fish at the start of spawning is between 600 and 800 μm. In this study, the average mean D_O was 658 μm (Table II, excluding fish with mean $D_O < 500$ μm).

Using the year-independent multivariate model (L_T, K and mean D_O), it was possible to demonstrate the isolated effect of each of the independent variables separately (Table VIII). This was done by changing the three independents one at the time while the two other independents were held at standard settings (L_T 80 cm, K 0·9 and mean D_O 700 μm). When changing L_T from 60 to

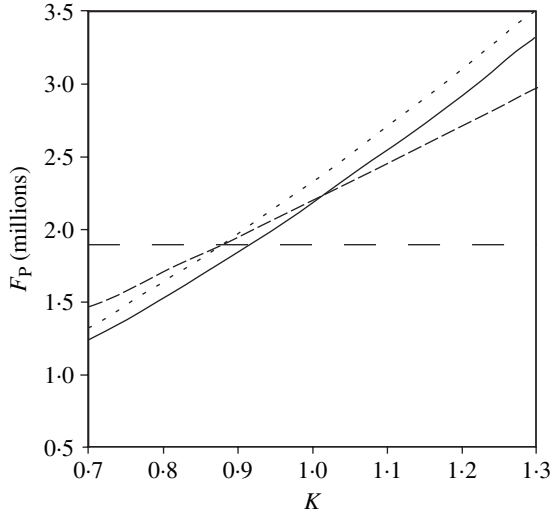

FIG. 5. Output from the different year-independent potential fecundity (F_P) regression models. Legends show independents: total length (L_T) (– –); mass (- - -); L_T and condition (K) (·····); L_T, K and oocyte diameter (700 μm) (——).

120 cm the F_P rose from 0·62 million to 6·21 million [Table VIII(a)]. Changing the K of a 80 cm fish from 0·7 to 1·3 increased the F_P from 1·08 to 2·92 million [Table VIII(b)], while changing the mean D_O of the same 80 cm fish from 500 to 800 μm reduced the F_P from 2·51 to 1·62 million [Table VIII(c)].

DISCUSSION

According to the often-cited paper by Hunter *et al.* (1992), oocytes of Dover sole *Microstomus pacificus* (Lockington) continue to recruit into the advanced vitellogenic stock until rather late in vitellogenesis [Fig. 6(a)]. In their study, the F_P continued to increase until the mean advanced D_O reached 860 μm but then stabilized until the beginning of spawning when this diameter reached *c.* 1100 μm. Thus, just as Atlantic cod the Dover sole can be considered to be a determinate spawner.

In contrast to the case described by Hunter *et al.* (1992), however, the present study on Atlantic cod indicates that the stock of vitellogenic oocytes is highest during early vitellogenesis, followed by rapid reduction before it reaches a more stable level just prior to spawning [Figs 2 and 6(b)]. A similar mechanism has been observed for Norwegian spring-spawning herring *Clupea harengus* L. (Kurita *et al.*, 2003). In that study, the number of vitellogenic oocytes was highest in early autumn, but then reduced by atresia in October and November. From January until spawning in March the number of oocytes seemed to be only slightly lowered. Similarly for sole *Solea solea* L. an 'atretic window' during early vitellogenesis has been found (Witthames & Greer Walker, 1995).

The present data [Table VIII(c)] indicated that cod sampled in the middle of vitellogenesis (mean diameter 500 μm) had F_P *c.* 27% higher than a cod caught late in vitellogenesis (mean diameter 700 μm). This difference was even larger if cod in late vitellogenesis were compared with these in early vitellogenesis (diameter 300–400 μm). The peak of the spawning period of north-east Arctic cod is usually rather constant from year to year, varying only by a few days around 1 April (Pedersen, 1984). From *c.* 1930 until the present, however, there has probably been a long time trend that has delayed spawning by *c.* 1–2 weeks

TABLE VIII. Potential fecundity (F_P) as a function of variable (a) total length (L_T), (b) Fulton's condition factor (K) and (c) mean oocyte diameter (D_O) using the year independent model (total) given in Table V. One variable was changed at a time while the others were held at the standard settings. The standard settings used were: $L_T = 80$ cm, $D_O = 700$ μm and $K = 0{\cdot}9$

(a)		(b)		(c)	
L_T	F_P	K	F_P	D_O	F_P
60	0·62	0·7	1·08	500	2·51
80	1·62	0·9	1·62	600	2·12
100	3·39	1·1	2·23	700	1·83
120	6·21	1·3	2·92	800	1·62

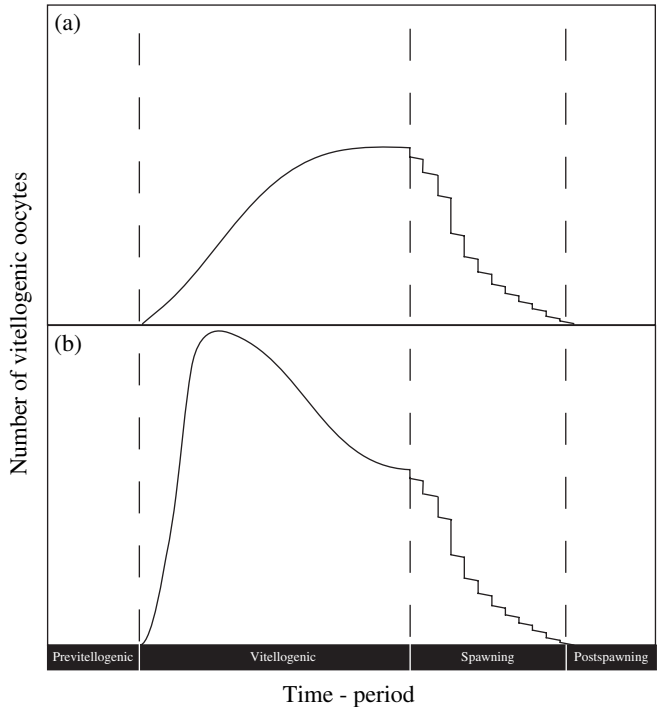

FIG. 6. Number of vitellogenic oocytes in the ovary with time (maturation). (a) Model for *Microstomus pacificus* (Hunter *et al.*, 1992) and (b) *Gadus morhua* (present study).

(Pedersen, 1984). In the present investigation, sampling was fairly consistent both in time and space over a limited time period of 18 years. This is probably the reason for the small difference found in average mean D_O between the years in this study, the major differences in mean D_O being observed at the individual level. Hence, the yearly differences in mean D_O changed the yearly fecundity estimates by only a small percentage. In spite of this it is important to consider the stage of maturity when making fecundity comparisons since such differences have the potential to bias the results considerably [Table VIII(c)]. Such differences may arise from inconsistent sampling in time or by yearly differences in the timing of maturation and spawning. When comparing fecundity data of geographically separated *G. morhua* stocks it is likely that the sampled material will be biased with regards to maturity. As already mentioned, the peak of spawning of north-east Arctic cod is *c.* 1 April, while *e.g.* for Baltic cod the major spawning is at the end of July (Wieland *et al.*, 2000).

Among individual *G. morhua* within a stock, the present study clearly shows that large differences in maturity status exist at the same time and that this may significantly influence individual fecundity estimates. This implies that also in studies comparing fecundities of individuals, *e.g.* large *v.* small individuals, correction for maturity is fundamental.

In this study measured mean D_Os were used to represent maturity, but in many cases, *e.g.* for the traditional gravimetric fecundity method, such data

are not available. Using oocyte density (number of oocytes g^{-1} ovary) as a maturity indicator, however, will probably work just as well, since mean D_O and oocyte density are highly correlated (Thorsen & Kjesbu, 2001). Oocyte density can be calculated simply by dividing the estimated F_P by M_G. Mean D_O can be calculated from oocyte density as described in Thorsen & Kjesbu (2001).

Since vitellogenic atresia seems to be a widespread phenomenon in fishes, the maturation stage should probably be taken into account also when studying the fecundity of many other fish species. Since the down-regulation [Fig. 6(b)] of the stock of vitellogenic oocytes seems to be most intense during early vitellogenesis, F_P should normally be measured as close to spawning as possible and the maturity stage (D_O) of the individual fish should be accounted for.

In the F_P model K was included to represent the nutritional status of the fish. In previous studies also the liver index has been used for this purpose (Marteinsdottir & Begg, 2002; Yoneda & Wright, 2004). This might be especially interesting for north-east Arctic cod where Russian time series on liver mass go back to 1927 (Yaragina & Marshall, 2000), while comparable data to calculate K are available only from 1988 (Marshall *et al.*, 1998). Preliminary work, however, indicated that using the prespawning liver index was unsatisfactory (unpubl. data). This might be explained by a possible inverse relationship between liver and M_G during maturation. It is known (Kjesbu *et al.*, 1991; Yaragina & Marshall, 2000) that much of the lipid that the fish need during vitellogenesis are taken from the liver.

Using K and L_T combined as variables to describe F_P has been tried in several studies. Both Marteinsdottir & Begg (2002) and Yoneda & Wright (2004) found that K contributed significantly to explain the variance in fecundity. McIntyre & Hutchings (2003), however, criticized the use of K and argued that it was relatively unimportant as a predictor for F_P compared to L_T or M. Koops *et al.* (2004) further argued that among L_T and M, M had better predictive power than L_T. When using the combination of L_T and K, K only seemed to explain the variation in fecundity that were already explainable by M alone.

In the present study M was also found to have a significantly better predictive power than L_T in univariate regressions. L_T was used, however, as the default predictor of F_P. M is known to fluctuate strongly during a yearly cycle (Hansen *et al.*, 2001). Sampled M may therefore be unreliable as the main predictor of fecundity. Furthermore, the application of univariate M-based regressions overestimated the F_P at low K, which would be in conflict with general precautionary principles. Finally, the combination of L_T and K had a slightly better predictive power than M alone.

The 'trigger' and regulation of atresia is poorly understood, but the nutritional status of the fish is probably one of the factors. In the present study, no correlation was found between atresia and K (unpubl. obs.), possibly due to the limited amount of data and large variation. Rideout *et al.* (2000), however, found a high frequency of mass atresia and possibly skipped spawning in low condition *G. morhua* in the Smith Sound, Newfoundland. In this case the atresia occurred at the cortical alveoli stage, which is somewhat earlier compared to the more commonly observed form of vitellogenic atresia. Also for Icelandic cod (Hardardottir *et al.*, 2003) atresia has been observed to be related to the condition of the fish and mainly restricted to $K < 1{\cdot}1$. Among those that

had high levels of atresia most of them were of low condition. The reported atresia occurred during the vitellogenic stage and the atresia seemed to relate to the mean D_O in a similar manner as found in this study.

For fish spawning multiple batches it is known (Kjesbu *et al.*, 1991; Greer Walker *et al.*, 1994) that atresia occurs also during the spawning period. Thus, 'realized' fecundity is likely to be somewhat lower than the F_P as measured or estimated just prior to spawning. The multiple fecundity model for *G. morhua* can simulate the number of vitellogenic oocytes at any stage before spawning. Because there are no satisfactory data about atresia during the spawning period, a good 'realized' fecundity model cannot be constructed. To estimate 'realized' fecundity from data on F_P and atresia, it is necessary to know the duration of the observed atretic stage, usually the α-stage (Hunter & Macewicz, 1985). At present there are no accurate data available, but the numbers available indicate that the α-atretic stage in *G. morhua* last for somewhere between 5 (unpubl. data) and 12·5 days (Kjesbu *et al.*, 1991). For a given period of time (T) the following expression (Kurita *et al.*, 2003) can be used to estimate 'realized' fecundity (F_R) from F_P, relative intensity of atresia (I_A), and the duration of the atretic stage (T_A): $F_R = F_P(1 - I_A)^{TT_A^{-1}}$. Using this expression when the $I_A = 0{\cdot}1$, the period of time is 30 days and the duration of the atretic stage is 5 days the fecundity will be reduced by 47%. If the duration of the atretic stage is 10 days, however, the reduction will be 27%. To calculate 'realized' fecundity it is also necessary to know how the I_A varies during the remaining period until the end of spawning, and also how the standing stock of vitellogenic oocytes is reduced as egg batches are released during spawning. Thus, to make good estimates of 'realized' fecundity from F_P and atresia demands rather detailed data not only about atresia but also on the spawning biology.

Spawning experiments with *G. morhua* in tanks has been conducted to study 'realized' fecundity (Kjesbu, 1989; Kjesbu *et al.*, 1991; Trippel, 1998; Fordham & Trippel, 1999). For Norwegian coastal cod (Kjesbu *et al.*, 1991), the level of atresia seemed to increase as spawning progressed and was on average 7·5%. By comparing the prespawning F_P with the 'realized' fecundity the average reduction by atresia was estimated to 36%. It is uncertain, however, whether 'realized' fecundity on captive fish is similar to 'realized' fecundity on wild fish. In addition, it is not unlikely that there are differences between stocks.

The intensity of atresia of prespawning *G. morhua* in this investigation [Fig. 2(b)] was in the range 0–19% and the average (including zero values) was 2·54%. According to Kjesbu (1994) the time from early vitellogenesis to start of spawning is *c.* 4 months. If then assuming a duration of the atretic stage of 10 days, and an average I_A of 2·54% the reduction in the standing stock of vitellogenic oocytes during vitellogenesis would be 27%. This theoretical decrease in fecundity is in the same region as that observed [Fig. 2(a)]. The present data on atresia, especially during early vitellogenesis, however, are sparse. Thus, although the data suggests that vitellogenic atresia is the major cause of the observed reduction in the standing stock of vitellogenic oocytes, further investigation on this topic is still needed.

The multivariate fecundity models presented in this study are, as far as is known, the first attempt to incorporate maturity status (D_O) as one of the independent variables. The combination of using both L_T, K and maturity status seems to

give relatively high r^2 compared to simpler models. With reference to models based solely on L_T or M, the present multiple regression model is more year independent, although some unexplained year-specific variation still exists. The multivariate model can also predict the F_P just before spawning even though sampling may have taken place at an earlier stage. Thus, F_P data for different years and stocks can be compared without being biased by different maturity.

Overall, the multiple regression model is probably accurate enough to be useful as input into larger recruitment models. In such cases the oocyte size could be set to a constant value typical of a fish just prior to spawning (*e.g.* 700 μm). This can be done without reduction in precision since the oocyte size is used solely to get a better fit with sampled data from fish with different maturity status and has no relevance when producing output of this kind. Thus, for such purposes the multiple regression model are based solely on variation in pre-spawning L_T and K. This type of data are available for north-east Arctic cod from 1988 (Marshall *et al.*, 1998) until today. In addition there has recently also been published a reconstructed 56 years long (1946–2001) L_T and M time series for the same stock (Marshall *et al.*, 2004). This work indicates that the scope of L_T and M variation found between years in the present study is sometimes surpassed. Thus, it is likely that the year-to-year variations in fecundity estimated in the present study will be exceeded in some years.

An obvious weakness in using F_P data as input to recruitment models is that what is really asked for is 'realized' fecundity. To estimate total egg production at the stock level using a multivariate F_P model as presented in this study, however, is a significant improvement compared to using spawning stock biomass.

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