

# Fecundity variation in Icelandic summer-spawning herring and implications for reproductive potential

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An exploration of fish fecundity aimed at estimating the reproductive potential of a stock requires comprehensive and quantitative examinations of the influencing factors. Here, Icelandic summer-spawning herring (*Clupea harengus*) are used to quantify potential fecundity ( $F_p$ , number of eggs) and relative fecundity [ $RF_p = F_p (\text{body weight} - \text{ovary weight})^{-1}$ ] as functions of length ( $L$ ) and weight ( $W$ ) in mature prespawning herring. Using a coupled examination of atresia (oocyte degeneration in the ovary) and the maturation stage of oocytes as characterized by size, we show that atresia has no meaningful effect on fecundity estimates if determined near the spawning time. Among prespawning herring,  $F_p$  is a strong function of  $L$  or  $W$  ( $r^2 = 0.84$  in either case). Fulton's condition factor  $K (=100WL^{-3})$  explains a trivial (1.5%) but significant ( $p < 0.0001$ ) amount of the residual variation in  $F_p$ , and appears to have the greatest effect among smaller length classes.  $RF_p$  is also a function of  $L$  ( $r^2 = 0.56$ ), and oocyte diameter explains 36% of the residual variation ( $p < 0.001$ ). Therefore, stock-specific total egg production in herring can diverge from the assumed proportionality between total egg production and spawning-stock biomass through variations in the length structure of the stock, and to a lesser extent through the condition of prespawning herring.

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## Introduction

Quantitative information concerning factors that influence individual fish fecundity is fundamental to reliable estimation of the reproductive potential of a given stock. Various non-heritable maternal traits (i.e. dynamic phenotypic variation among females) that have been investigated in controlled experimental conditions and in nature appear to influence potential fecundity ( $F_p$ , the number of vitellogenic oocytes in a prespawning ovary). In controlled laboratory experiments, food ration has a positive influence on  $F_p$  for many fish species, including Atlantic herring (*Clupea harengus*; Ma *et al.*, 1998), Atlantic cod (*Gadus morhua*; Lambert and Dutil, 2000), haddock (*Melanogrammus aeglefinus*; Hislop *et al.*, 1978), winter flounder (*Pleuronectes americanus*; Tyler and Dunn, 1976), brown trout (*Salmo trutta*; Bagenal, 1969), and rainbow trout (*Oncorhynchus mykiss*; Bromage *et al.*, 1991). Positive relations between the ration-fed and species-specific measures of body condition (e.g. hepatosomatic index,

$HSI = 100 \times \text{liver weight} \times \text{whole body weight}^{-1}$ ; or Fulton's condition factor,  $K = 100 \times \text{whole body weight} \times \text{total length}^{-3}$ ) were observed in those studies. No relation between food quantity and fecundity was observed for Pacific herring (*C. harengus pallasi*; Hay and Brett, 1988) or Atlantic cod (Kjesbu *et al.*, 1991), because the fish that were fed a "reduced" ration maintained their potential fecundity at the same level as those fed a "normal" ration. The former were presumably able to maintain  $F_p$  via an energetic trade-off expressed as a decrease in somatic weight. Field studies provide results similar to those of most experimental studies. For example, Kjesbu *et al.* (1998) considered the reduction in  $F_p$  among wild Arcto-Norwegian cod to be a function of a decrease in the abundance of a primary prey species (capelin; *Mallotus villosus*). Fecundity in Icelandic cod (Marteinsdottir and Begg, 2002) and eastern Scotian Shelf haddock (Blanchard *et al.*, 2003) is a function of  $K$  and the hepatosomatic index.

Interannual variation in length-specific fecundity has been observed in several herring stocks *in situ*.

Fecundity-at-length variation in autumn-spawning herring in the Gulf of Maine is thought to be a function of stock-specific density-dependence (Kelly and Stevenson, 1985). Similar explanations for length-specific fecundity variation have been suggested for spring- and autumn-spawning herring in the Gulf of St Lawrence (Lambert, 1987), for the Clyde spring-spawning herring (Bailey and Almaraz, 1989), and for a range of other fish species (Bagenal, 1973). Interannual differences in length-specific fecundity for Norwegian spring-spawning herring could be explained by variation in weight-at-length (i.e. higher fecundity among spawners in better condition; Óskarsson *et al.*, 2002).

Fulton's  $K$ , a useful index of individual energetic status in herring (Kurita *et al.*, 2003), is inversely related to the intensity of atresia (oocyte degeneration; e.g. Óskarsson *et al.*, 2002). Somatic- and liver-condition indices also appear to be related to atresia (e.g. Rideout *et al.*, 2000; Atlantic cod) and therefore fecundity. Tyler and Sumpter (1996) consider atresia to be a primary factor influencing fish fecundity. If atresia is a function of condition, and if atresia reflects the process through which condition indirectly influences fecundity (i.e. fecundity as a function of atresia), then fecundity should be some function of body condition. However, the direct influence of  $K$  on potential fecundity in herring (i.e. length- and  $K$ -specific fecundity or length-specific fecundity for individuals classified according to  $K$ ) has, to date, only been inferred (Óskarsson *et al.*, 2002).

Typically, stock-specific total egg production ( $E$ ) is estimated using a generalized fecundity-at-length relation (e.g. Serebryakov, 1990; Johannsdottir and Vilhjalmsón, 1999). Accordingly, the effect of  $K$  (i.e. energy available for reproduction) on the fecundity-at-length relationship is often ignored despite the fact that residuals from fitted relations are frequently explained by variations in  $K$ , or some analogue (e.g. Bagenal, 1973; Hempel, 1979; Solemdal, 1997). Moreover, some authors (e.g. Rijnsdorp, 1994, for flatfish *Pleuronectes platessa* and *Solea solea*; and Marshall *et al.*, 1998, for Atlantic cod) have challenged the frequently employed assumption of proportionality between  $E$  and spawning-stock biomass (SSB), because maternal traits appear to compensate for a decrease in  $E$  that is normally attributed to a decrease in SSB. For example, fish fecundity can be influenced by the intensity and, from a stock-wide perspective, the frequency of atresia. However, the frequency (prevalence) of atresia declines with increasing seasonal maturity (Óskarsson *et al.*, 2002; Kurita *et al.*, 2003), such that atresia becomes undetectable as spawning approaches.

The observations and arguments above indicate that determining the amount of variation in size-specific fecundity, which can be explained by body condition or by year-specific fecundity-at-length relations, as in Marshall *et al.* (1998), or both, should provide improved stock-specific estimates of  $E$ . Accordingly, we set out to establish a fecundity relationship for Icelandic summer-spawning (ISS) herring that incorporates the relevant and easily measured

maternal traits as necessary. The goal is to determine if such a relationship can subsequently provide the essential information necessary for estimating annual reproduction potential (total female reproductive output expressed as the number of eggs) of the Icelandic summer-spawning herring stock. We then determine the relation between relative fecundity,  $RF_P$  (expressed as  $F_P$  per unit somatic body weight), and spawner size to determine the extent to which the stock-specific estimate of  $E$  at a given SSB will vary according to the size composition of the spawning stock. To achieve each objective, we first have to determine the manner by which atresia might influence the fecundity estimates.

## Material and methods

### Sample collection

Samples were collected from five known spawning grounds of ISS herring (Figure 1), as detailed by Fridriksson and Timmermann (1950). The fish were collected just prior to spawning in 1999 and 2000 to provide estimates of variation in maturation stage (Bowers and Holliday, 1961), age ( $\pm 1$  year), total length ( $L$ ,  $\pm 0.5$  cm), fresh wet whole body weight ( $W$ ,  $\pm 0.1$  g), ovary weight ( $OW$ ,  $\pm 0.1$  g), condition ( $K = 100WL^{-3}$ ), fecundity (oocytes per ovary), oocyte diameter ( $OD$ ,  $\pm 10$   $\mu$ m), and atresia ( $A$ , percentage of total eggs per ovary that are atretic). Sample size among collections varied with fish availability (Table 1). The 1999 samples were collected from commercial net and trawl bycatch and comprised  $\sim 50$  mature females from each of the spawning grounds. The length distribution of the 1999 samples is not considered representative of the mature stock because the fish were collected using a range of commercial

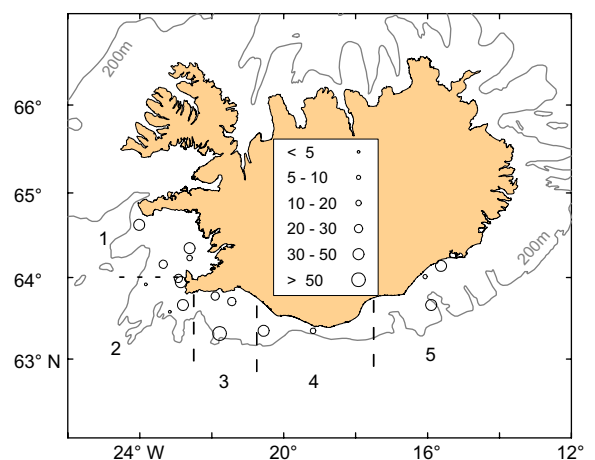


Figure 1. Chart of the known herring spawning Areas 1–5 (see Table 1) delimited by dashed lines, sampling locations, and number (expanding symbol) of prespawning Icelandic summer spawners collected at each location in 1999 and 2000 and used for fecundity determination.

Table 1. Summary of Icelandic summer-spawning herring ovaries collected during 1999 and 2000 by date, spawning area (see Figure 1), and ovary sample size ( $n$ ) among analysis categories.

Collection dates and range	Day-of-year and range	Area	Fecundity, egg size, whole-mount	Histological-profile atresia
			atresia ( $n$ )	( $n$ )
15–18 May 1999	139–140	1	38	19
01 Jun 1999	153	1	32	15
21–23 Jun 1999	173–175	1	12	12
21–24 Jun 1999	173–176	2	40	
22 Jun 1999	174	3	51	
16–18 Jun 1999	168–170	4	14	
09–11 Jun 1999	161–163	5	51	
27 Jun, 05 Jul 2000	179, 187	1	70	8
28–29 Jun 2000	180–181	2	90	17
30 Jun–01 Jul 2000	182–183	3	53	
02 Jul 2000	184	4	33	
04 Jul 2000	186	5	37	
Total			521	71

size-selective gear (20–22.5-cm-mesh cod nets, and bottom trawls fitted with 8–13.5-cm-mesh codends). The length distribution of the samples collected in 2000 is considered more representative of the mature stock because the fish were collected during a research survey that employed pelagic- and bottom-trawl gear with small mesh codends that are considered to be less size selective than commercial gear. In each year, for each fish, both total length and weight were recorded, the ovaries were removed, weighed, and preserved in buffered formaldehyde, and fish scales were removed for age determination.

### Atresia

Preserved ovaries were dehydrated in increasing concentrations of ethanol (70–95%), embedded in Histo-resin, microtome sectioned (4  $\mu$ m), stained with toluidine blue, dried, and mounted (Mountex<sup>®</sup>). At least two sections were made from each ovary before counting the number of  $\alpha$ -stage atretic (Hunter and Macewicz, 1985) and normal oocytes in a single section under a microscope – the histological-profile count method (Kurita *et al.*, 2003). Intensity of atresia is defined here as the number of atretic vitellogenic oocytes within a section relative to the sum of all vitellogenic oocytes, expressed as a percentage. The intensity of atresia was also estimated using whole-mount counting of  $\alpha$ -stage atretic and normal oocytes under a binocular microscope – the whole-mount stereometric method (Óskarsson *et al.*, 2002). The intensity of atresia from the whole-mount counts is defined and expressed as above for the profile count method. Atretic oocytes were distinguished from normal oocytes by irregularities in shape, relative size, and

opacity (atretic eggs are typically smaller and more transparent). The frequency or prevalence of atresia is defined as the number of ovaries containing at least one atretic oocyte relative to the number of all ovaries examined, expressed as a percentage.

### Fecundity and oocyte size

The weight of each preserved ovary (OW) was recorded, and three subsamples ( $s$ ) of 150–250 g were excised from each ovary, weighed ( $OW_s$ ,  $\pm 0.1$  g), and used for fecundity estimation. The validity of using three subsamples was determined through examination of the coefficient of variation (CV) as a function of replicates. The number ( $N$ ) of vitellogenic oocytes in each subsample was counted under a binocular microscope. Annual potential fecundity ( $F_p$ ) was then calculated using the gravimetric method:

$$F_p = \frac{OW}{OW_s} N. \quad (1)$$

Oocyte diameter is an indicator of spawning maturity stage when assessed through histological examination of ovaries collected three months prior to spawning (Óskarsson *et al.*, 2002). The diameter of vitellogenic oocytes was estimated using eggs from one subsample of each ovary measured using Sigma Scan Plus v5.0, and digital images were captured using XCAP<sup>®</sup>-Imaging and a Kodak Megaplus<sup>®</sup> 1.4I high-resolution digital camera. In all, 50 vitellogenic oocytes were measured for each ovary because analyses of that number of oocytes provided a sufficient estimate of mean oocyte size within an ovary, based on the CV as above (see also Ma *et al.*, 1998; Kurita *et al.*, 2003).

Annual herring collection data for the period 1962–2000 inclusive and archived at the Marine Research Institute (MRI), Reykjavík, Iceland, were used to determine the minimum length at first maturity.

### Statistical analyses

Potential and relative fecundity were each assessed using linear regression, the variables being appropriately transformed as required. Analysis of covariance (ANCOVA) was used to compare different variables (e.g. oocyte diameter, weight-at-length,  $F_p$ -at-length) among collection periods or years, and a subsequent parallelism test (partial multiple  $F$ -test; StatSoft Inc., 2004) was used to test for the equality of slopes. The examination of standardized residuals was used to identify outliers and to verify the assumption of variance homogeneity, and quantile plots of the residuals were used to assess assumptions of normality. Significance was nominally considered at  $\alpha = 0.05$ . The appropriateness of varying models describing  $F_p$  was determined using Mallows'  $C_p$  statistic (Neter *et al.*, 1996). The best model was assumed to be that with the lowest  $C_p$  statistic (relative to the full model) that is not improved

by eliminating any term (S-Plus 6.0, 2000). Improvements in model fit were also evaluated on the basis of approximate  $F$ -tests (Hastie and Tibshirani, 1990).

## Results

### Atresia

There was no difference (Wilcoxon matched pair test;  $p = 0.149$ ) between the two estimates of atresia intensity based on the histological-profile and whole-mount stereometric count methods. Analyses of the serial collections (May through June 1999) of ovaries from the same area demonstrated that the intensity of atresia, as indicated by the profile method, decreased with day of the year as spawning time (day-of-year  $200 \pm 20$  d; Óskarsson, 2005) approached (Figure 2a). This pattern was paralleled by the prevalence of atresia, where the number of ovaries containing atretic eggs decreased from  $\sim 50\%$  on day 140 to  $\sim 10\%$  on day 175 (Figure 2b). Inspection of whole-mount preparations demonstrated a low intensity of atresia: average  $0.54\%$  (s.d. = 1.2) with a range of 0–8.35% ( $n = 149$ ) just prior to spawning at day-of-year 161–176 in 1999.

To test the reliability of these low atresia estimates near spawning time, the intensity of atresia using the whole-mount stereometric method was examined in 25 randomly selected ovaries collected on days 180 and 186 in 2000. None had atretic oocytes. Overall, atresia was predominately associated with ovaries with the smallest mean oocyte size, and was not observed in ovaries where the mean oocyte diameter was  $>920 \mu\text{m}$  (Figure 3). Based on the low and declining (toward spawning time) intensity of atresia, the declining number of ovaries observed with atretic eggs, and considering the maturity stage (i.e. the oocyte size) of the fish examined (primarily from area 1; Figure 1), we conclude that potential fecundity, estimated using ovaries collected from around day-of-year 153 and later, provides a reliable approximation of realized fecundity because atresia becomes increasingly inconsequential as spawning approaches.

### Oocyte size

The average oocyte diameter in ISS herring ovaries increased at a rate of  $\sim 3.9 \mu\text{m d}^{-1}$  from day 140 to day 175 in 1999 (Figure 4; ANOVA;  $F_{2,165} = 43.7$ ,  $p < 0.001$ ; *a posteriori* test,  $p < 0.001$  in all cases). Oocyte diameter was independent of total length ( $p = 0.100$ ) of maturing fish. In 1999, there were differences ( $F_{3,144} = 17.66$ ,  $p < 0.001$ ; Figure 5) in oocyte diameter among areas; herring collected in Area 5 (Figure 1) over the period 9–11 June had smaller oocytes on average ( $773 \mu\text{m}$ , s.d. = 115) and a greater range in size than did those collected from other areas a week or more later ( $874 \mu\text{m}$ , s.d. = 81;

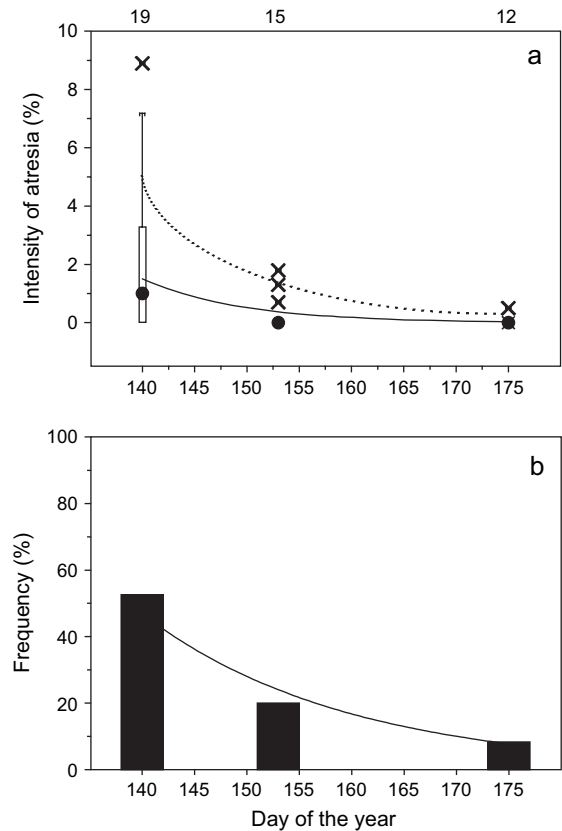


Figure 2. Decay, among Icelandic summer-spawning herring ovaries, as a function of day-of-year ( $D$ ) in 1999, in (a) intensity of atresia ( $A$ ), with a regression model  $A = 1.03 \times 10^6 e^{-0.095D}$  (solid line), 95% C.I. around the regression (dotted line), quartiles (box) around the median percentage (filled circle), non-outlier range (whiskers), and outliers  $>1.5$  interquartile range (crosses); and (b) the percentage ( $P$ ) frequency or prevalence of ovaries containing atretic eggs (solid bars), with a regression model  $P = 4.59 \times 10^6 e^{-0.107D}$  (solid line) equivalent to  $-1.2\% D^{-1}$ . The number of ovaries examined for each collection period is provided above panel (a).

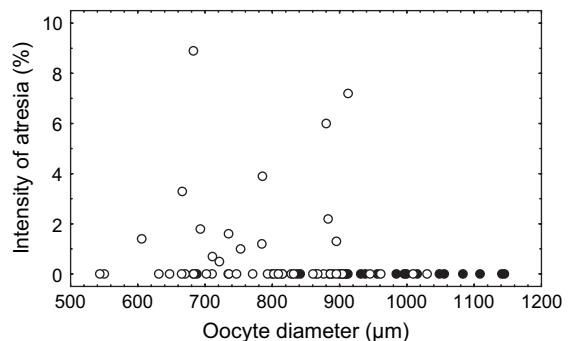


Figure 3. Intensity of atresia among Icelandic summer-spawning herring ovaries collected in 1999 (open symbols;  $n = 46$ ) and 2000 (filled symbols;  $n = 25$ ) in relation to ovary-averaged oocyte diameter.

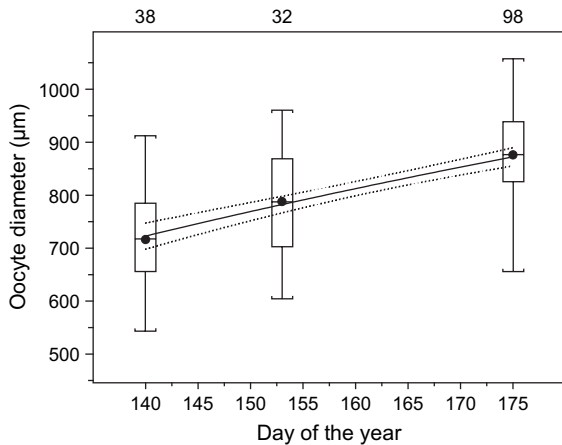


Figure 4. Increase in oocyte diameter (OD) as a function of day-of-year ( $D$ ) for Icelandic summer-spawning herring  $\geq 30$  cm total length for three collection periods in 1999 in Areas 1–3 (Figure 1), with a regression model  $OD = 1543 \log_{10} D - 2590$ ,  $n = 168$ ,  $r^2 = 0.346$ ,  $p < 0.0001$  (solid line), and the 95% C.I. around the regression (dotted line). Each collection shows the quartiles (box) around the median percentage (bar with solid circle), the non-outlier range (whiskers), and the number of samples examined for each period (above the figure).

*a posteriori*,  $p < 0.01$ ). However, there were no differences in average oocyte diameter among the other areas ( $p > 0.05$ ).

Estimates of atresia were limited to ovaries collected in areas 1 and 2, as stated above. Therefore, the appropriateness of including area 5 ovaries (with smaller oocytes) in subsequent analyses is questionable and requires explanation. Average oocyte diameter in area 5 ( $\sim$  day 160) was not different from that in area 1 on day 153 ( $F_{1,81} = 0.21$ ,  $p = 0.648$ ), but was different from that estimated in the same area on days 140 and 175 ( $F_{1,87} = 5.10$ ,  $p = 0.026$

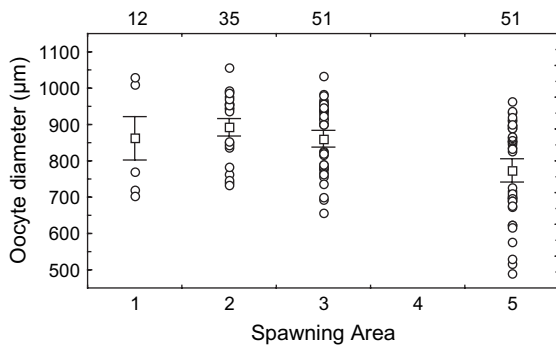


Figure 5. Average oocyte diameter (open circles) in 1999 among individual Icelandic summer-spawning herring ovaries collected during days-of-year 173–176 in spawning areas 1–3 and days 161–163 in area 5 (Figure 1). The grand mean diameter (open square)  $\pm 2$  s.e. (whiskers) and sample size (above graph) are shown for each area.

and  $F_{1,96} = 29.37$ ,  $p < 0.0001$ , respectively). Accordingly, oocyte size can be used reasonably to conclude that atresia should have no significant effect on fecundity estimates among fish in area 1 on day 153 or later, or on oocyte size from day 160 or later in area 5. Therefore, given both the level of atresia and the oocyte size, the data derived from area 5 on day 160 and later in 1999 were included in subsequent analyses.

In 2000, the ovary samples were collected over a relatively short period, and inspection of ovaries collected some 6 (area 5) and 8 (area 1) days subsequent to the last collection date (day 187; Table 1) showed that spawning had begun (92% and 45% of the fish spawning, respectively, in the two areas). Therefore, atresia should not significantly influence the fecundity estimates, at least according to the analyses and results provided above and those of Óskarsson *et al.* (2002). Consequently, all data collected in 2000 were used in subsequent analyses.

### Fecundity

At a population level, the weight of ISS herring among those collected in 1999 and 2000 clearly increases as the cube of length (Figure 6), and those herring collected in 1999 had less weight-at-length than those collected in 2000 (ANCOVA;  $F_{1,448} = 41.86$ ,  $p < 0.0001$ ; Figure 6). Although the slopes of the relations were the same in each year ( $p = 0.768$ ), the deviations from the overall mean between years appeared most notable for larger fish. The data from all five sampling locations in both 1999 and 2000 were pooled because there were no differences or marginal differences in  $F_P$  among locations when using either total length as a covariate (ANCOVA; 1999:  $p = 0.104$ ; 2000:

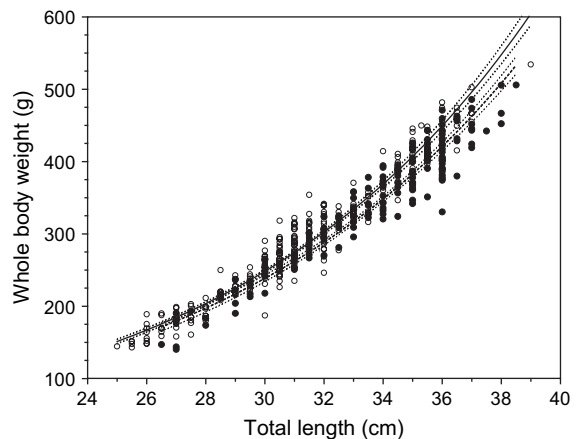


Figure 6. Whole body weight ( $W$ ) as a function of total length ( $L$ ) for Icelandic summer-spawning herring collected in five spawning areas (Figure 1) in 1999 (filled symbols, broken line;  $W = 1.03 \times 10^{-2} L^{2.96}$ ;  $n = 168$ ,  $r^2 = 0.915$ ,  $p < 0.0001$ ), and in 2000 (open symbols, solid line;  $W = 9.34 \times 10^{-3} L^{3.00}$ ;  $n = 283$ ,  $r^2 = 0.940$ ,  $p < 0.0001$ ). The dotted lines indicate the 95% C.I. around the regressions.

$F_{4,277} = 2.61$ ,  $p = 0.036$ ) or whole body weight as a covariate (ANCOVA; 1999:  $F_{4,163} = 7.65$ ,  $p < 0.001$ ; 2000:  $p = 0.063$ ). Potential fecundity increased linearly with total length over the length range 25–39 cm in both 1999 and 2000 (Figure 7). The slopes were the same ( $p = 0.363$ ) in each year, and although the elevations (length at  $F_P = 0$ ) in length-specific  $F_P$  were different between years (ANCOVA;  $F_{1,448} = 5.86$ ,  $p = 0.0159$ ), they both approached 24 cm (23.3 cm in 1999; 24.1 cm in 2000), which is, according to data in the central database at MRI (Óskarsson, 2005), the minimum length at first maturity for ISS herring.

Having both the weight-at-length relationship (Figure 6) for the aggregated 1999 and 2000 data ( $W = 1.38 \times 10^{-2} L^{2.88}$ ;  $n = 456$ ,  $r^2 = 0.935$ ,  $p < 0.0001$ ) and the aggregated  $F_P$ -at-length relationship (Figure 7), we can analytically derive the  $F_P$ -at-weight relationship directly (Figure 8) and compare it with the empirically determined  $F_P$ -at-weight relations based on (i) linear regression and (ii) semi-log-linear regression, and find that in each comparison the two are highly correlated ( $r^2 = 0.988$  and  $0.976$ , respectively; see also Figure 8). Although the last two regressions explain similar amounts of variation in  $F_P$  (Table 2), the log-linear model is preferred because the intercept better reflects weight at first maturation (i.e. 100–150 g at 24 cm; Figure 6; Óskarsson, 2005), and because it reflects the analytically derived  $F_P$ -at-weight function (Figure 8). As observed for the length-specific  $F_P$ , there was a difference between the years 1999 and 2000 for weight-specific  $F_P$  (Figure 8;  $F_{1,449} = 46.30$ ,  $p < 0.0001$ ), though the slopes were the same ( $p = 0.736$ ).

The above results clearly show that between 73% (1999, Figure 7) and 85% (2000, Figure 8) of the variation in  $F_P$  among Icelandic summer-spawning herring can be

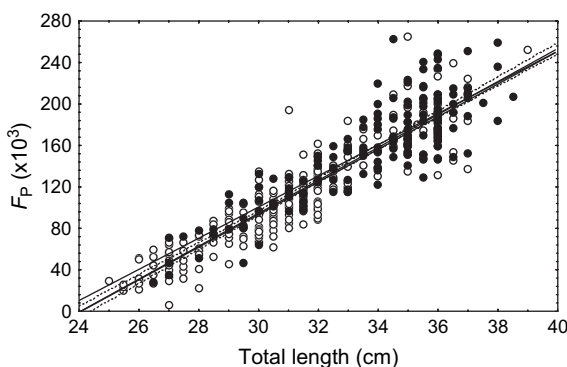


Figure 7. Potential fecundity ( $F_P \times 10^3$ ) as a function of total length ( $L$ ) for Icelandic summer-spawning herring collected in 1999 during day-of-year 161–176 (filled symbols, dashed line;  $F_P \times 10^3 = 15.04L - 350.6$ ;  $n = 168$ ,  $r^2 = 0.732$ ,  $p < 0.0001$ ), in 2000 during day-of-year 179–186 (open symbols, solid line;  $F_P \times 10^3 = 15.74L - 379.3$ ;  $n = 283$ ,  $r^2 = 0.837$ ,  $p < 0.0001$ ), and aggregated over both years (solid heavy line;  $F_P \times 10^3 = 15.90L - 382.2$ ;  $n = 451$ ,  $r^2 = 0.836$ ,  $p < 0.0001$ ) with 95% C.I. around the aggregated-data regression (dotted line).

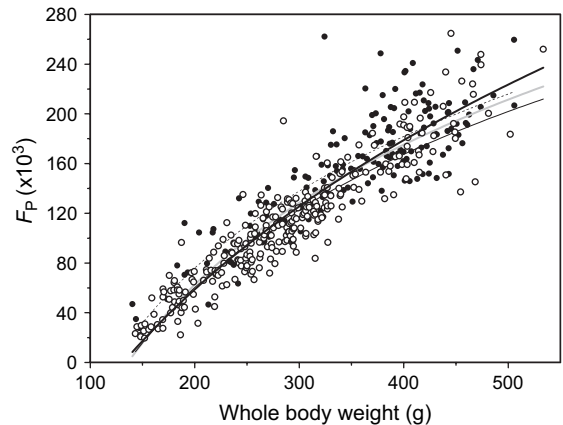


Figure 8. Potential fecundity ( $F_P \times 10^3$ ) as a function of whole body weight ( $W$ ) for Icelandic summer-spawning herring collected in 1999 during day-of-year 161–176 (filled symbols, dashed line;  $F_P \times 10^3 = 351.5 \log_{10} W - 732.9$ ;  $n = 168$ ,  $r^2 = 0.733$ ,  $p < 0.0001$ ), in 2000 during the day-of-year 179–186 (open symbols, solid line;  $F_P \times 10^3 = 357.4 \log_{10} W - 762.5$ ;  $n = 283$ ,  $r^2 = 0.847$ ,  $p < 0.0001$ ), aggregated over both years (solid heavy grey line;  $F_P \times 10^3 = 375.3 \log_{10} W - 801.4$ ;  $n = 451$ ,  $r^2 = 0.829$ ,  $p < 0.0001$ ), and as analytically derived from weight ( $W$ )-at-length ( $L$ ) shown in Figure 6 and  $F_P$ -at-length shown in Figure 7 for the aggregated data (solid thick line;  $F_P \times 10^3 = 70.29W^{0.3467} - 382.2$ ).

explained by either length or weight if measured immediately prior to spawning. Although weight alone explained marginally more variation in  $F_P$  than length alone in each year examined, length is considered the preferred independent variable for three reasons: it should be independent of condition (but see below), it is therefore relatively independent of seasonal variations in weight, and it is generally the more available metric. There were no differences in length-specific  $F_P$  among the three dates investigated in 1999 in area 1 (days 140, 153, and 175; ANCOVA,  $\log_{10}$ -transformed data,  $p = 0.435$ ), which is consistent with our earlier assumption concerning atresia that realized fecundity can be adequately estimated from around day-of-year 150 in area 1.

Figure 9 shows a positive relationship between the residuals in  $F_P$  estimated as a function of  $L$  and  $K$  in 1999 and 2000. There were no substantial differences between years in the residuals, with  $K$  as a co-factor, for the intercepts ( $p = 0.0629$ ) and slopes ( $p = 0.517$ ). Despite the statistical difference between 1999 and 2000 in  $F_P$ -at-length and  $F_P$ -at-weight (see above, and Figures 7 and 8), it appears that the differences are sufficiently small to allow aggregation of the 1999 and 2000 fecundity ( $F_P$ ) data for subsequent analyses.

$RF_P$ , as a function of  $L$ , was not different between years (ANCOVA;  $p = 0.675$ ) and, not surprisingly (based on Figures 7 and 8), using the aggregated 1999 and 2000 data,  $RF_P$  increased as an asymptotic function of length with an intercept ( $RF_P = 0$ ) near  $L = 24$  cm (Figure 10). Similar to  $F_P$ , 60% of the variation in  $RF_P$  can be explained by

Table 2. Comparative summary of bi- and multi-variate regression models and parameters determining  $F_P$  as a function of total length ( $L$ ), whole body weight ( $W$ ), and condition factor ( $K$ ) with the associated coefficient of determination ( $r^2$ ), lower and upper 95% confidence intervals of the parameters, and Mallows'  $C_P$  statistic for Icelandic summer-spawning herring based on aggregated (1999 and 2000) fish and associated ovary collections.  $p \leq 0.0001$  and  $n = 451$  in all cases.

Model	$r^2$	Parameters			95% Confidence intervals			$C_P$
		$\beta_0$	$\beta_1$	$\beta_2$	$\beta_0$	$\beta_1$	$\beta_2$	
$F_P = \beta_0 + \beta_1 L$	0.84	$-3.82 \times 10^5$	$1.59 \times 10^4$		$-4.03 \times 10^5$ $-3.61 \times 10^5$	$1.52 \times 10^4$ $1.65 \times 10^4$		$2.07 \times 10^5$
$F_P = \beta_0 L^{\beta_1}$	0.82	$1.33 \times 10^{-1}$	3.96		$4.10 \times 10^{-2}$ $2.25 \times 10^{-1}$	3.76 4.16		$2.30 \times 10^5$
$F_P = \beta_0 + \beta_1 W$	0.84	$-4.67 \times 10^4$	559.9		$-5.41 \times 10^4$ $-3.92 \times 10^4$	537 583		$2.07 \times 10^5$
$F_P = \beta_0 + \beta_1 \log_{10} W$	0.83	$-7.98 \times 10^5$	$3.74 \times 10^5$		$-8.38 \times 10^5$ $-7.58 \times 10^5$	$3.58 \times 10^5$ $3.90 \times 10^5$		$2.17 \times 10^5$
* $F_P = \beta_0 + \beta_1 L + \beta_2 W$	0.85	$-2.22 \times 10^5$	8 172	281	$-2.75 \times 10^5$ $-1.69 \times 10^5$	$5.73 \times 10^3$ $1.06 \times 10^4$	195 368	$1.90 \times 10^5$
$F_P = \beta_0 + \beta_1 L + \beta_2 K$	0.85	$-4.69 \times 10^5$	$1.60 \times 10^4$	$9.11 \times 10^4$	$-5.03 \times 10^5$ $-4.34 \times 10^5$	$1.54 \times 10^4$ $1.66 \times 10^4$	$6.15 \times 10^4$ $1.21 \times 10^5$	$1.92 \times 10^5$
$F_P = \beta_0 + \beta_1 W + \beta_2 K$	0.85	$2.59 \times 10^4$	570.7	$-8.27 \times 10^4$	$1.57 \times 10^3$ $5.35 \times 10^4$	548 594	$-1.13 \times 10^5$ $-5.24 \times 10^4$	$1.95 \times 10^5$

\*In this model  $L$  and  $W$  interaction made no significant contribution to explained variance ( $p = 0.201$ ).

length alone when measured immediately prior to spawning. The deviations from the regression model in Figure 10 appear to be a function of oocyte diameter (Figure 11).

The most appropriate models (based primarily on the  $C_P$  statistic) for estimating  $F_P$  for the aggregated 1999 and

2000 data appeared to be those that use length and weight and those that use length and  $K$  (Table 2). Ignoring either weight or  $K$  results in a significant decline in explained variation in  $F_P$  ( $F_{1,447} = 36.7$ ,  $p < 0.001$  and  $F_{1,447} = 41.9$ ,  $p < 0.001$ , respectively). However, it appears that the

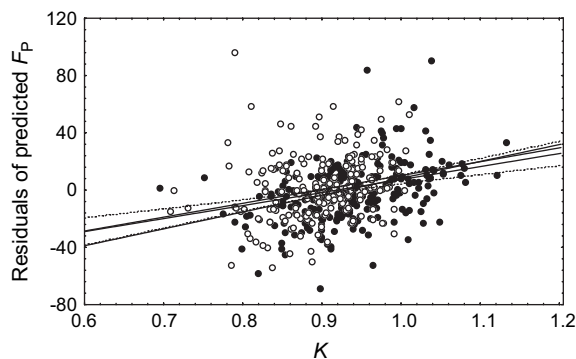


Figure 9. Residuals ( $R$ ) around potential fecundity ( $F_P \times 10^3$ ) fitted using total length  $L$  (see Figure 7) as a function of Fulton's condition index ( $K$ ) for Icelandic summer-spawning herring in 1999 during day-of-year 161–176 (filled symbols, dashed line;  $R = 96.82K - 86.70$ ;  $n = 168$ ,  $r^2 = 0.058$ ,  $p < 0.0017$ ), in 2000 during the day-of-year 179–186 (open symbols, solid line;  $R = 117.8K - 109.5$ ;  $n = 283$ ,  $r^2 = 0.148$ ,  $p < 0.0001$ ), and aggregated over both years (solid heavy line;  $R = 90.8K - 83.5$ ;  $n = 451$ ,  $r^2 = 0.076$ ,  $p < 0.0001$ ) with 95% C.I. around the aggregated-data regression (dotted line).

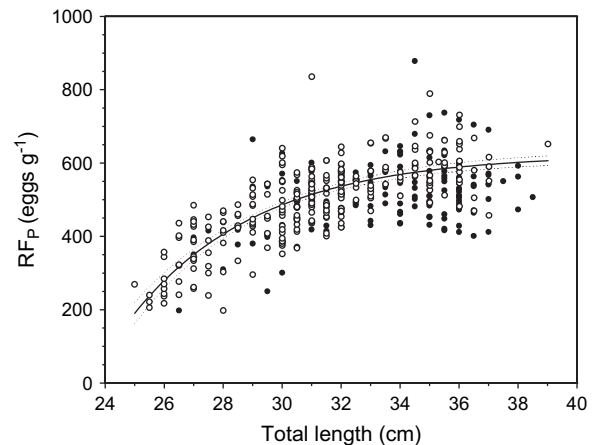


Figure 10. Relative fecundity ( $RF_P$ , number of eggs per unit somatic weight) in Icelandic summer-spawning herring collected in 1999 (filled symbols) and 2000 (open symbols) as a function of total length ( $L$ ) for day-of-year 161–186 and aggregated over both years for the regression (solid line)  $RF_P = 590.3 - e^{11.9 - 0.2295L}$ ;  $n = 451$ ,  $r^2 = 0.569$  (expected vs. observed), and  $p < 0.0001$  with 95% C.I. around the aggregated-data regression (dotted line).

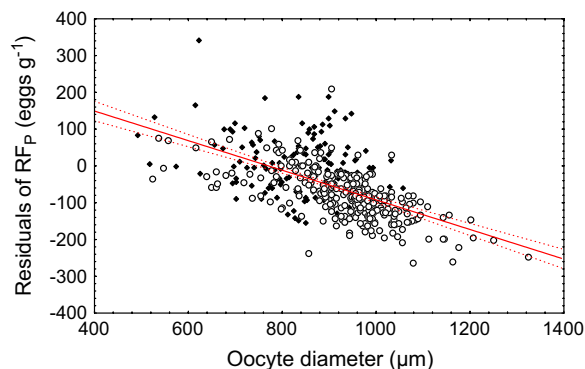


Figure 11. Residual around the length-specific relative fecundity ( $RF_p$ ; Figure 10) for Icelandic summer-spawning herring collected in 1999 (filled symbols) and 2000 (open symbols) as a function of total oocyte diameter (OD) for day-of-year 161–186 where  $RF_p = -0.402OD + 310.2$  (solid line),  $n = 432$ ,  $r^2 = 0.356$ , and  $p < 0.0001$  with 95% C.I. around the regression (dotted lines).

model incorporating length and  $K$  is preferred because  $K$  was statistically independent of length in 1999 ( $p = 0.143$ ), in 2000 ( $p = 0.112$ ) and when the year data are aggregated ( $p = 0.306$ ). Furthermore, length and  $K$  estimates (at least as averages among length classes) are frequently available in typical fisheries data collections. We acknowledge that  $K$  explains a very marginal (1.5%) but significant ( $p < 0.0001$ ) increase in the explained variance in  $F_p$  when used in concert with length.

## Discussion

Our analyses show that potential fecundity in Icelandic summer-spawning herring is a function of size; either length or weight if measured just prior to spawning. These results are consistent with those of Jakobsson *et al.* (1969), who studied the same stock, and with Hodder (1972), Zijlstra (1973), Messieh (1976), Hay and Brett (1988), Almatar and Bailey (1989), Ma *et al.* (1998), and Óskarsson *et al.* (2002), who studied different herring stocks. Therefore, it is clear that the contribution of individual spawners to total egg production in a herring stock increases systematically with spawner length. Relative fecundity,  $RF_p$ , in individual Icelandic summer-spawning herring is a function of length, as in Norwegian spring-spawning herring (Óskarsson *et al.*, 2002) and cod (Marshall *et al.*, 1998). Therefore, it becomes equally clear that the individual length (and possibly age) composition of a stock is a significant factor, in addition to the number of mature females-at-age, in estimating stock-specific total egg production or reproductive potential. Moreover,  $F_p$  increases with length with a larger exponent (i.e.  $\sim 4.0$ ; Table 2) than does whole body weight with length ( $\sim 3$ ; Figure 6), indicating that the average number of eggs per recruit will diverge from SSB per recruit, especially when a stock consists of

large spawners (Rothschild, 2000). Together, these results alone challenge the credibility of the frequently applied assumption in stock assessments of stock-specific total egg production ( $E$ ) being directly proportional to SSB (Rijnsdorp, 1994; Marshall *et al.*, 1998). However, a non-linear relation between  $F_p$  and whole body weight did as well (statistically) as a linear relation, where the latter would logically suggest a proportional relation between SSB and  $E$ . Therefore, the divergence from proportionality between SSB and  $E$  can be expected to be small unless the age structure for a given SSB is highly variable (i.e. disproportionate numbers of small to large spawners, or *vice versa*, for the same SSB).

In addition to length, the body condition factor ( $K$ ) explained a small but statistically significant amount of the variation in  $F_p$  in ISS herring in 1999 and 2000. Differences in length-specific fecundity in herring have been linked, but not as we have tested here, to  $K$  or similar indices in some stocks (Hay and Brett, 1988; Ma *et al.*, 1998; Óskarsson *et al.*, 2002; Kurita *et al.*, 2003), but not in others (Zijlstra, 1973). However, several fecundity-related studies ignore the influence of  $K$  or its analogues on variation in  $F_p$  (e.g. Jakobsson *et al.*, 1969; Hodder, 1972; Messieh, 1976; Almatar and Bailey, 1989). Studies of other species show that the inclusion of  $K$  (or some analogue) improves the degree of variation explained in fecundity-at-length relations (see Introduction), but the effects are often small, as in our study, and sometimes insignificant (McIntyre and Hutchings, 2003). Furthermore, Koops *et al.* (2004) found little empirical evidence that  $K$  affects  $F_p$  among several stocks of cod and brook trout (*Salvelinus fontinalis*) where  $W$  was normally preferred over  $L$  and  $K$  in estimating  $F_p$ .

Are there alternative explanations for the small effect of  $K$  on  $F_p$  as observed in ISS herring? It may be that herring with high values of  $K$  employ a different strategy in the trade-off between reproduction and somatic growth relative to that used by fish with lower values of  $K$ ; i.e. a higher proportion of available energy is used for reproduction and the fish are able to sustain a higher fecundity. Better condition (higher  $K$ ) would reflect more energy (protein and/or fat) extracted from the somatic reserves, and this would lead to more hydration of somatic tissues (an inverse relation between fat and water in somatic tissues of herring; Iles, 1984; Bradford, 1993; Slotte, 1999, and references therein), and the maintenance of an elevated  $K$ . If so, it is neither a size-specific difference in trade-off between reproduction and growth ( $K$  is independent of length), nor a result of spawning location (no difference in  $K$  among collection areas). Factors other than fish size and spawning location may influence possible trade-offs, and although we have no information with which to assess such alternatives, it may be sufficient to conclude that the effect of  $K$  on length-specific  $F_p$  in ISS herring is of energetic origin, and that the annual variation in average  $K$ , during and prior to spawning, may cause the relationship between total egg production and SSB to deviate from proportionality.



There are possible shortcomings in the methods used to determine the number of eggs actually spawned (i.e. not reduced through atresia) and to determine the time, relative to spawning, when atresia becomes undetectable (i.e. the time when observed potential fecundity would best reflect realized fecundity). The lifespan of  $\alpha$ -stage atretic oocytes directly influences any reduction in fecundity because a shorter turnover time implies a greater reduction as a consequence of the cumulative temporal effect of the intensity of atresia (e.g. Óskarsson *et al.*, 2002). For herring, the turnover time of  $\alpha$ -stage atretic oocytes is estimated to be about 10 days at a water temperature of 8°C (Ma *et al.*, 1998) and around 7 days at 7°C (Kurita *et al.*, 2003). Such temperatures approximate those encountered 50 m deep off south and southwest Iceland in May and June (7–8°C; Anon., 2001). Therefore, considering (i) the relatively low intensity and frequency of atresia observed in June and July (Figure 2), and (ii) the proximity to spawning as observed subsequent to the sampling period (i.e. days 194–196; see above) and its consistency with an extensive analysis of the spawning time (Óskarsson, 2005), atresia likely has limited effects on  $F_p$  from day 153 on. Therefore, we conclude that the effects of atresia are of no significance in estimating  $F_p$  for herring if  $F_p$  is estimated just prior to spawning, despite what is said in the Introduction that atresia is considered to be the primary factor influencing fish fecundity (Tyler and Sumpter, 1996). We caution that the same may not be true for delayed spawners, in which the effects of atresia might easily be underestimated.

It has been argued that the histological-profile method used to determine the intensity of atresia may provide underestimates relative to a histological stereometric method because atretic oocytes are smaller and have a lesser probability of being detected relative to “normal” oocytes; hence, the endorsement for the histological stereometric method (Hardardottir *et al.*, 2003; Kurita *et al.*, 2003). Those authors compared the two histological methods and showed that the mean level of atresia estimated from histological-profile counts was 79% (s.d. 17.1%), similar to estimates provided by histological stereometric counts. However, our conclusion that atresia will not affect fecundity determinations is not unduly jeopardized by the findings of Kurita *et al.* (2003) because the intensity of atresia in our samples was low (Figure 2), and we found no evidence of underestimation in our histological-profile counts relative to whole-mount stereometric counts, consistent with Óskarsson *et al.* (2002), although the latter is, at best, a weak analogue of the histological stereometric method.

In herring, an inverse relationship between fecundity and egg size within ovaries can occur among years (Tanasichuk and Ware, 1987) and individuals (Kurita *et al.*, 2003). Our results also indicate a negative relationship between the residuals of the  $F_p$  relation and oocyte diameter (Figure 11). Together, such observations might reflect a trade-off (per unit ovary) between egg size and egg number. Alternatively, fish

with small oocytes (i.e. positive residuals) may delay spawning (Óskarsson, 2005) and have a higher probability of developing atretic eggs (e.g. Óskarsson *et al.*, 2002), so their fecundity (relative to fish with larger oocytes) will decrease as spawning time approaches. However, the entirety of the results presented above concerning the low intensity and prevalence of atresia suggests that the first alternative is likely valid. Accordingly, it appears that although part of the variation in herring egg size can be explained by fish size and body condition (Óskarsson, 2005), a significant amount (36% of the variation in the residuals of length-specific  $RF_p$ ; Figure 11) of the variation appears to result from an individual (per unit ovary) trade-off between egg number and size.

The fecundity data from 1999 and 2000 were aggregated in all of the main analyses, despite some admittedly marginal differences between years in size-specific  $F_p$  (Figures 7 and 8). The resultant differences in  $F_p$  were small because of the small difference in weight-at-length (Figure 6). The differences may reflect “real” interannual differences, or conversely they may simply be a function of delayed (later) seasonal sampling in 2000 relative to 1999. The differences may also be related to the use of the more size-selective commercial fishing gear in 1999 relative to 2000, leading to a difference in the size distribution of samples between years (relatively few large fish in 2000 compared with 1999 and *vice versa* for smaller fish). In addition, interannual differences in length-specific  $F_p$  for a relatively long-lived species like herring are presumably only a function of differences in body condition (i.e. dynamic phenotype). The insignificant difference between years in the residuals of  $F_p$  as a function of  $K$  (Figure 9) is consistent with this argument. Therefore, aggregating data across years appears appropriately justified.

In summary, the observed fecundity of ISS herring near spawning time is a function of total length, or weight, and to a very limited extent body condition, and it is unlikely to be reduced by atresia. Therefore, the length structure of the spawning population and to a lesser extent its average body condition just prior to spawning appear to be the primary determinants of total egg production for the stock. Consequently, these metrics provide not only more accurate estimates of total egg production, but also their use should result in an improved approach to the examination of stock-recruitment relationships, where the stock is measured in terms of total egg production derived from the  $F_p$ - or  $RF_p$ -at-size relationships.

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