

Variation in egg mass within two Atlantic herring *Clupea harengus* stocks

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The main objective of this study was to investigate if egg size (mass) at spawning is invariant for Scotia-Fundy summer and autumn (SFSH) and Icelandic summer (ISSH) spawning herring *Clupea harengus*. Oocyte dry mass measurements for SFSH females collected in 2001 and ISSH females collected in 1999 and 2000 showed a large variation. Difference in egg dry mass among fish was found to vary by as much as twofold in each stock. For ISSH, variation in egg mass was also apparent from oocyte volume measurements made jointly with a histological examination of the ovaries. Approximately 20% of the variation in egg mass could be explained by maternal whole-body mass or total length, indicating that length or age composition in the stocks can potentially influence the recruitment success. This implies that fisheries management strategies should aim to maintain a broad range in age composition.

KEYWORDS

body condition, *Clupea harengus*, egg size, herring, oocyte size, repeat spawners

1 | INTRODUCTION

Species-specific or stock-specific average egg size is thought to be evolutionarily determined and thus to reflect a heritable trait that presumably increases the survival potential of offspring (Jones, 1978). However, there is variation around this average egg size within a stock, which is consistent with evolutionary arguments. Several authors have addressed this variation and while some can explain as much as 72% of the egg size variation using maternal factors, others found maternal factors unable to explain the variation (Table 1). These maternal factors include fish length, whole body mass, body condition and spawning history. For example, in controlled feeding experiments with serial-spawning Atlantic cod *Gadus morhua* L. 1758, the food ration had a limited influence on egg size but, egg size increased systematically with the spawning experience (Kjesbu *et al.*, 1996). Similar findings have been observed in several stocks of herring *Clupea harengus* L. 1758 (Blaxter & Hempel, 1963) and haddock *Melanogrammus aeglefinus* (L. 1758) (Hislop, 1988; Hislop *et al.*, 1978) where the average egg size is to some extent dependent on fish length, age, or spawning experience. Furthermore, the general impression is that first time (recruit) spawners are not as reproductively fit as

repeat spawners (Buckley *et al.*, 1991; Chambers *et al.*, 1989; Hislop, 1988; Knutsen & Tilseth, 1985; Trippel *et al.*, 1997; Vallin & Nissling, 2000) and this has been used to explain why the exclusion of the recruit spawners from spawning stock biomass estimates provides a stronger stock–recruitment relationship; *e.g.*, Georges Bank haddock (Wigley, 1999). Although some authors have not found significant relationships between egg size and maternal factors (Bengtson *et al.*, 1987; Green & Chambers, 2007; Hinckley, 1990; Leal *et al.*, 2009; Marsh, 1984; Townshend & Wootton, 1984), there is a general acceptance in the literature (Carter *et al.*, 2015; Johnston & Leggett, 2002; Kamler, 2005; Kennedy *et al.*, 2007; Marshall *et al.*, 2003; Marteinsdóttir & Begg, 2002; Trippel, 1998; Trippel & Neil, 2004; Vallin & Nissling, 2000) that egg size increases as some function (linear, exponential, *etc.*) of spawner size; or age.

These earlier findings provided the motivation for this paper that was designed to determine if egg size (mass) of Scotia-Fundy summer and autumn-spawning (SFSH) and Icelandic summer-spawning *C. harengus* (ISSH), at spawning, is invariant or alternatively, is egg mass some function (multivariate or otherwise) of maternal state, including length, Fulton's condition factor *K* (Fulton, 1904), or spawning experience. The egg mass variation was explored in two

TABLE 1 Summary of literature where maternal factors including length (L), mass (M), age (A), body condition (K), and lipid content in various marine fish species have been shown to account for some percentage of the variation in egg–oocyte size measured as dry mass (M_{OD}), mass (M_O), volume (V_O), diameter (D_O), or egg yolk volume (V_Y)

| Common name | Species Scientific name | Reference | Maternal | Egg measures | Explained variance (%) |
|---------------------|----------------------------------|---------------------------------------|------------------|---------------|-------------------------------------|
| Atlantic herring | <i>Clupea harengus</i> | Blaxter and Hempel (1963) | L | M_{OD} | 11–49; NS in all cases ^a |
| Baltic herring | <i>C. harengus membras</i> | Parmanne and Kuittinen (1990) | L | M_{OD} | 14–42; NS in all cases ^b |
| Pacific herring | <i>C. harengus pallasi</i> | Hay and Brett (1988) | L, M | M_O | 13–23 |
| Anchoveta | <i>Engraulis ringens</i> | Leal <i>et al.</i> (2009) | L, M | V_O | NS |
| Capelin | <i>Mallotus villosus</i> | Chambers <i>et al.</i> (1989) | K, lipid content | V_Y | 42, 72 |
| Atlantic cod | <i>Gadus morhua</i> ^c | Chambers and Waiwood (1996) | K | D_O | 42, 55 ^d |
| | <i>G. morhua</i> | Solemdal <i>et al.</i> (1993) | W, K | D_O | 34, 38 |
| | <i>G. morhua</i> | Marteinsdóttir and Steinarsson (1998) | L, K | D_O | 41, 45 |
| | <i>G. morhua</i> | Vallin and Nissling (2000) | L | OD | 42 |
| | <i>G. morhua</i> ^e | Marteinsdóttir and Begg (2002) | L | D_O | 32 and 24 |
| Haddock | <i>Melanogrammus aeglefinus</i> | Hislop (1988) | L | D_O, M_{OD} | 22, 20 |
| | <i>M. aeglefinus</i> | Trippel and Neil (2004) | L, K, M | D_O | 22, 17, 32; (M independently) |
| Walleye pollock | <i>Theragra chalcogramma</i> | Hinckley (1990) | L, A, K | D_O, M_{OD} | NS |
| Atlantic tomcod | <i>Microgadus tomcod</i> | Green and Chambers (2007) | L | D_O | NS |
| Yellowtail flounder | <i>Pleuronectes ferrugineus</i> | Manning and Crim (1998) | | D_O, M_{OD} | NS ^f |
| Atlantic plaice | <i>Pleuronectes platessa</i> | Kennedy <i>et al.</i> (2007) | M | M_{OD} | 44 |
| Atlantic silverside | <i>Menida menida</i> | Bengtson <i>et al.</i> (1987) | L | D_O | NS |
| Argentine hake | <i>Merluccius hubbsi</i> | Macchi <i>et al.</i> (2013) | L, M, A, K | M_{OD} | 5–18 |

NS, Not significant.

^aSeveral stocks, where significant relationships were observed in six cases but not significant in seven.

^bFour spawning components at two different maturity stages where significant relationships were observed in five cases but not significant in two.

^cCaptive.

^dFirst and the last batch of eggs, respectively. Fish length was not significant.

^eTwo different years, 1994 and 1996.

^fNot significant with any measure of maternal size.

different ways, by analyses of egg dry mass from fully mature gonads (SFSH and ISSH) and by histological analyses of oocyte volume following a verification about the developmental status (ISSH).

The relevance of this research is twofold. These two *C. harengus* stocks have historically shown large fluctuations in abundance and consequently a large variation in size and age composition (Óskarsson *et al.*, 2016; Óskarsson & Taggart, 2010). If egg mass in the stocks varies with maternal state, it may be reflected in recruitment potential and thus help explain the large variations in recruitment (Óskarsson, 2005; Óskarsson & Taggart, 2010). Moreover, results demonstrating that variation in egg mass is a function of maternal factors may have implications for fishery management strategies in terms of maintaining a healthy stock composition and thereby maximise the reproductive potential.

2 | MATERIALS AND METHODS

The simplest way to explore the variation in egg mass at spawning was to assess oocyte dry mass from fully mature ovaries of fish from both stocks. However, access to fully mature ovaries of ISSH was limited due to both the lack of active fishery at that time and limitations

on dedicated surveys, so average oocyte diameter of pre-spawning *C. harengus*, about 2 weeks prior to the main spawning wave (Óskarsson & Taggart, 2009), was also analysed. This latter approach required a histological examination of the oocytes to assess how representative oocyte diameter is of egg mass and thus if it may be suitable as an index of energy content at spawning, or if, alternatively, it simply represents oocytes maturation difference.

2.1 | Scotia-Fundy summer and autumn-spawning *C. harengus*

Ovaries from 100 SFSH were collected by purse seining a spawning aggregation on German Bank (Figure 1) during the spawning season (19 September 2001). Total length (L_T ; 0.1 cm), whole body mass (M_T ; 0.1 g) and maturity (stage 1–8; Anon., 1962) were recorded for each fish and the ovaries were removed, weighed (M_O ; 0.1 g) and preserved in 4.8% buffered formalin. The same standardised international maturity scale was used for both SFSH and ISSH. The scale relies on macroscopic examination of external characteristic of the fresh ovaries, which was the norm at that time. Histological examination of the

ovaries for staging the maturity, comparable to Brown-Peterson *et al.* (2011) was not applied.

Oocyte dry mass was determined for all fish at maturity stage 5 (fully mature with some transparent oocytes) and 6 (ovulating with running gonads) which included all the SFSH ovaries collected ($n = 100$). For each ovary, three subsamples of 10 oocytes were withdrawn, rinsed with distilled water and oven dried on pre-weighed aluminium foil at 62°C for 48 h and then placed in a desiccator for 24 h. The above is standard procedure (Hislop & Bell, 1987; Marteinisdóttir & Steinarsson, 1998; Thorsen *et al.*, 1996) and drying at temperatures up to 90°C does not adversely affect dry mass estimates (Hislop & Bell, 1987). Oocyte dry mass (M_{OD}) was recorded ($\pm 1 \mu\text{g}$) for the 10 oocytes (*n.b.*, in the results section M_{OD} refers to the average mass across the three subsamples for a single oocyte). To overcome subjectivity in maturity stage designation, all the stage 5 ovaries were either classified under a binocular to fish containing transparent oocytes (all or part of them) and thus assumed to be hydrated, or to fish containing easily distinguishable non-transparent oocytes, which had presumably not started to hydrate and were possibly not fully mature (*i.e.*, at stage 4). A statistical comparison was made between the classes of ovaries with the different optical properties of the eggs to determine if they could be pooled in further analyses. The relationship between oocyte dry mass and a gonado-somatic index ($I_{GS} = 100M_O(M_T - M_O)^{-1}$, was also examined.

2.2 | Icelandic summer-spawning *C. harengus*

ISSH samples were collected from the known spawning locations (Friðriksson & Timmermann, 1950; Figure 1) prior to spawning in 1999 and 2000 to provide an estimate of inter-annual variation in the

different measures (*e.g.*, egg mass and fecundity; Óskarsson & Taggart, 2006). During the period 9–24 June (Julian day 161–176) in 1999, the 165 samples were collected as commercial bycatch from nets and trawls (Table 2) and they represented all the known spawning locations. A further 15 samples from the commercial bycatch were collected on 13 July 2000 (Julian day 196). The ovaries were removed, weighed ($\pm 0.1 \text{ g}$) and preserved in buffered formalin and later processed for oocyte size determinations. The L_T ($\pm 0.5 \text{ cm}$), M_T ($\pm 0.1 \text{ g}$) and maturation stage were recorded for each individual.

During the period 27 June–5 July 2000 (Julian day 179–187) and again 4–11 July 2009, ISSH samples were collected during research surveys on all the spawning locations (Figure 1) using research bottom and pelagic trawls. The processing of the 283 ovaries collected in 2000 and the 79 ovaries from 2009 was as described above for 1999 (Table 2).

Oocyte dry mass of ISSH was determined as for SFSH (§ 2.1) except that only a small number ($n = 23$) of ISSH ovaries from 1999 and 2000 were at maturity stage 5 or 6. Therefore, ovaries from 79 females at either maturity stage 5 or 6 were secured in the beginning of July 2009 from a survey comparable to the one conducted in 2000.

An alternative method was also applied to explore the egg mass variation and general biology of the stock. The dry mass of oocytes from 38 ISSH ovaries at stage 4 (maturing gonads with no evidence of hydration) were used for comparison with the stage 5 and 6 ovaries, to provide an estimate of maximum and minimum oocyte size prior to ovulation and to serve in exploring the relation between M_{OD} (g) and oocyte volume (mm^3 ; see below).

Histological examinations followed the Óskarsson *et al.* (2002) approach, except performed only a few weeks prior to spawning in

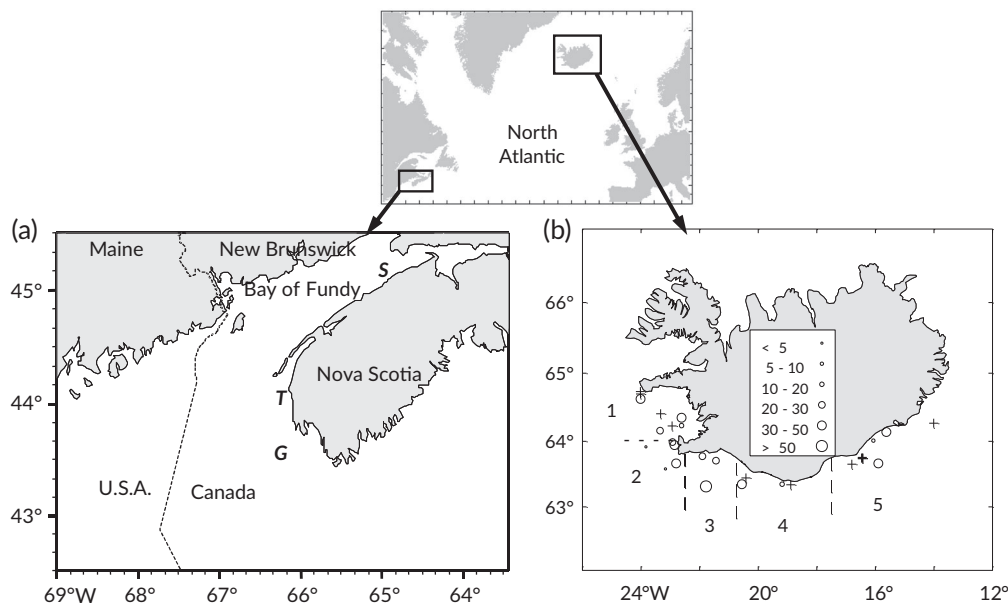


FIGURE 1 Chart showing the locations of the *Clupea harengus* ovary sampling. (a) The main spawning areas of the Scotia-Fundy summer and autumn-spawning *C. harengus* (S, Scots Bay; T, Trinity Ledge; G, German Bank), where all the ovary samples were collected in 2001. (b) The sampling locations (O) shown among five known spawning grounds (areas 1–5) for Icelandic summer-spawning herring off south and south-west Iceland. The expanding symbols (O) reflect the number of individual pre-spawning females collected for fecundity and oocyte mass determinations during 1999 and 2000

TABLE 2 Summary of Icelandic summer-spawning herring female samples collected during the summers of 1999 and 2000 giving dates, locations, and number of samples taken for investigation for the different methods

| Year | Date | Julian day | Location ^a | Fecundity ^b and oocyte mass determination | Histological examination | Oocyte dry mass measurements | |
|-------------|-----------------|------------|-----------------------|--|--------------------------|------------------------------|------------------------|
| | | | | | | Maturity stage 5 and 6 | Maturity stage 3 and 4 |
| 1999 | | | | | | | |
| June | 21-23 | 173-175 | 1 | 12 | | | |
| - | 21-24 | 173-176 | 2 | 40 | | | |
| - | 22 | 174 | 3 | 51 | | | |
| - | 16-18 | 168-170 | 4 | 14 | | | |
| - | 09-11 | 161-163 | 5 | 51 | | | |
| July | 22 | 205 | 1 | 0 | | 3 | 1 |
| 2000 | | | | | | | |
| June & July | 27 & 05 | 179 & 187 | 1 | 70 | 9 | 2 | 1 |
| June | 28-29 | 180-181 | 2 | 90 | 19 | 3 | 17 |
| June & July | 30 June-01 July | 182-183 | 3 | 53 | | | 3 |
| July | 02 | 184 | 4 | 33 | | | 5 |
| | 04 | 186 | 5 | 37 | | 0 | 19 |
| | 13 | 196 | 1 | | | 15 | |
| 2009 | | | | | | | |
| July | 4-11 | 187-194 | 1-5 | | | 79 | |
| Total | | | | 451 | 28 | 102 | 46 |

^aLocations shown in Figure 1.

^bSee Óskarsson and Taggart (2006).

contrast with 3 months. The intent was to determine if the oocyte diameter at that time reflects the egg mass at spawning and not variation in apparent oocytes maturation 3 months prior to spawning (Óskarsson *et al.*, 2002). If oocyte size during the sampling period is representative of egg mass at spawning, the oocyte size of fixed ovaries can simply be analysed directly to explore the variation in egg mass at spawning. The diameter of the vitellogenic oocytes was measured using one subsample from each ISSH ovary. The diameter was determined from measurements made using Sigma Scan Plus 5.0 (www.sigmaplot.co.uk) and digital images taken using XCAP-Imaging (Epix Inc.; www.epixinc.com) and Leica QWin 2.3 (www.leica-micrystems.com) or using a charge-couple device video camera. Digital calibrations of all equipment allowed data aggregation. For each sample, individual area estimates for a total of 50 vitellogenic oocytes were collected. The validity of the sample size of 50 oocytes was determined through examination of the coefficient of variation (CV) as a function of replicates. Oocyte diameter (D_O ; μm) measurements were collected from 432 individuals (149 in 1999 and 283 in 2000). The oocyte volume (V_O ; mm^3) was then simply determined from D_O as: $V_O = \frac{4}{3}(0.5D_O \times 10^{-3})^3$.

Developmental status of vitellogenic oocytes was estimated using ovaries from 28 ISSH collected during the summer of 2000. The samples used covered the range of vitellogenic oocytes average diameters measured using a binocular microscope. Preserved ovaries were dehydrated in increasing concentrations of ethanol (70–95%),

embedded in Histo-resin (Leica) and sectioned (2 μm thick) using a microtome. The sections were stained with toluidine blue, dried and mounted (Mountex, Histolab Products AB; www.histolab.se). At least two sections were made from each sample.

If vitellogenic oocyte nuclei were recognised within sections (*i.e.*, the section revealed the core of an oocyte), then oocyte diameter was estimated using the digital image. Three different measures were recorded for each of these oocytes: area of the 10 largest yolk-granules, thickness of the chorion (at three different locations within the section) and volume of yolk-granules expressed as a percentage of the egg volume where the per cent volume was estimated using the stereological method based on the principle that the volume fraction, V_i , equals areal fraction, A_i (Emerson *et al.*, 1990; Gundersen *et al.*, 1988). A grid constructed with arbitrarily chosen reference points (P_i) was placed on the analyser screen and the yolk-granules intersecting the upper right corner of the reference points were counted (P_h). The per cent volume of yolk granules within single vitellogenic oocyte was calculated:

$$A_i = V_i\% = (P_h P_i^{-1}) 100 \quad (1)$$

These three estimates (A_i , $V_i\%$ and chorion thickness) are all assumed to increase with oocyte development to a relatively constant quantity (Óskarsson *et al.*, 2002). Therefore, they can be used to determine if oocyte size variation is representing oocyte maturation

difference or different sizes at spawning. The results were compared to those provided for Norwegian spring-spawning *C. harengus* (NSSH) (Óskarsson *et al.*, 2002) and analysed together for illustrative purpose and to cover longer period of the oocytes development. Furthermore, it makes it possible to analyse the growth curve and to obtain a functional relation of these three estimates throughout the main developmental phase of the oocytes. To be directly comparable with diameter measurements of preserved oocytes (due to shrinkage related embedding) all measurements of vitellogenic oocyte diameter made using digital images were corrected using measurements made under the binocular microscope (Ma *et al.*, 1998).

For assessing variation in M_{OD} and D_O , simple and multiple linear regression models were used with appropriate data transformations. Standardised residuals examined in relation to regression estimates were used to identify outliers and assess homogeneity of the variance. Quantile-plots of the residuals were used to test the assumption of normal distribution (S-Plus 6.0, 2000). Analysis of variance (ANOVA) was applied to the oocyte volume measurements to determine the source of the variation, as well as where there was a need to assess differences among population averages. As with linear regression, homogeneity of variance and normal distributions were assessed prior to ANOVA.

3 | RESULTS

3.1 | Scotia-Fundy summer and autumn-spawning *C. harengus*

Fifty-five of the 100 ovaries had transparent (hydrated) oocytes. Forty-five ovaries had opaque oocytes. Average M_{OD} was the same (146 μg) for the two transparency classes (ANOVA; $P > 0.05$) and the range from 97 to 187 μg and 90 to 190 μg , respectively. Thus, the data were aggregated for further analyses as the fish from which the eggs were taken can be considered fully mature regardless of egg transparency. M_{OD} increased with fish length (Figure 2a; $r^2 = 0.152$;

$n = 100$; $P < 0.001$) and although noisy, neither the addition of M_T nor Fulton's condition factor K made significant contributions to the explained variance through stepwise multivariate regression. M_{OD} also increased with whole body mass in a similar manner ($r^2 = 0.161$; $n = 100$; $P < 0.001$). There were several fish with anomalously low M_{OD} . Five of the eight fish with $M_{OD} < 120 \mu\text{g}$ had non-transparent oocytes while three individuals had transparent oocytes (L_T estimated at 23.6, 25.3 and 25.6 cm, respectively). Exclusion of these five ovaries with non-transparent oocytes resulted in L_T explaining 23% of the variation in M_{OD} ($n = 95$; $P < 0.001$). M_{OD} was also found to be semi-log function of the gonado-somatic index (\log_{10} -transformed: $n = 100$; $r^2 = 0.363$; $P < 0.0001$; Figure 2b) and the product of F_P and M_{OD} (μg) correlated strongly with the ovary wet mass (\log_{10} - \log_{10} transformed: $r = 0.957$).

3.2 | Icelandic summer-spawning *C. harengus*

3.2.1 | Oocyte dry mass measurements

There was a wide range in oocyte dry mass for ISSH collected in 1999, 2000 and 2009 just prior to spawning (maturity stage 5) and at spawning (stage 6); 113–230 and 108–237 μg , respectively. Values of M_{OD} were higher in 2009 (mean = 176 μg) than in 1999 and 2000 (mean = 163 μg) with ($P < 0.05$; ANCOVA) or without L_T as covariate (ANOVA $P < 0.05$), which prevented aggregating the data (Figure 3a). In 1999 and 2000, M_{OD} increased with whole body mass ($r^2 = 0.206$; $n = 23$; $P < 0.05$) but not with total length (Figure 3a; $P > 0.05$; \log_{10} -transformed) or K ($P > 0.05$). The M_{OD} in 2009 was best explained by total length (5.5%) in addition to K (additional 10.0%; $n = 79$; $P < 0.01$) according to model selection based on Cp-statistic (Mallows, 1973), even if the dry mass was also significantly related to L_T alone (Figure 3a) and M_T ($r^2 = 0.141$; $n = 79$; $P < 0.001$). M_{OD} of stage 3 ovaries (early maturing with visible oocyte yolk) and 4 ranged from 13 to 235 μg and there was a strong relationship between their

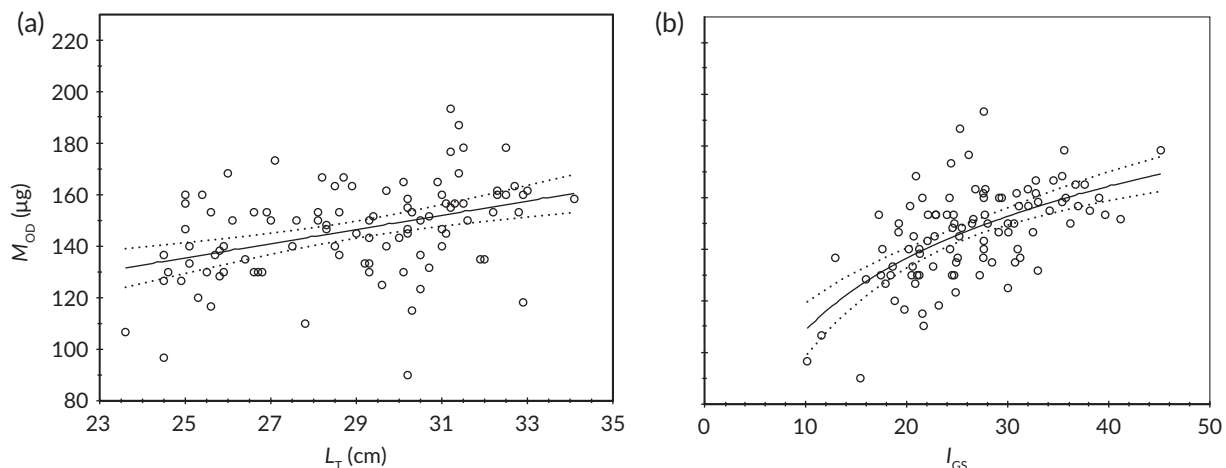


FIGURE 2 (a) Linear least-squares relationship between Scotia-Fundy summer and autumn spawning *Clupea harengus* (fully mature, stage 5) average oocyte dry mass (M_{OD}) and total length (L_T) in 2001 ($y = 2.76x + 66.4$, $r^2 = 0.159$, $n = 100$, $P < 0.001$) and (b) the semi-log increase of gonado-somatic index (I_{GS} ; $y = 92.4\log_{10}x + 16.37$; r^2 between fitted and observed estimates = 0.363, $n = 100$, $P < 0.001$). O, Observations; —, fitted regression curves; ···, 95% confidence intervals

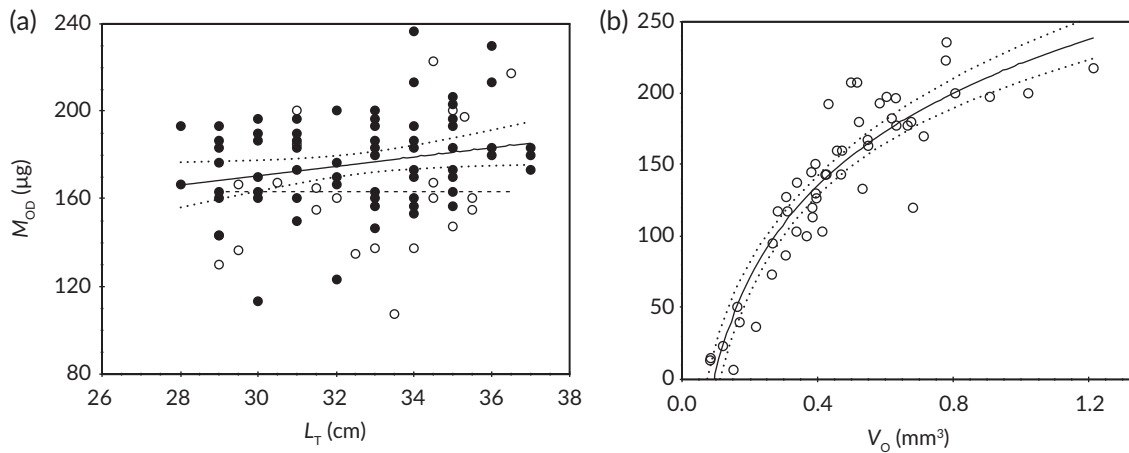


FIGURE 3 (a) Linear least-squares relationship between Scotia-Fundy summer and autumn spawning (fully mature, stage 5 and ovulating, stage 6) *Clupea harengus* average oocyte dry mass (M_{OD}) and total length (L_T) in 1999–2000 [O; mean M_{OD} (---) = 163.2 μm , $r^2 = 0.055$, $n = 79$, $P > 0.05$;] and 2009 (●, $y = 2.13x + 107$, $r^2 = 0.055$, $n = 79$; $P < 0.05$). --, Fitted regression curves; ---, 95% confidence intervals

M_{OD} and the average V_O ($r^2 = 0.836$; $n = 50$; $P < 0.001$; Figure 3b). The range of M_{OD} for fish at maturity stage 5 or 6 (Figure 3a) corresponds to V_O of c. 0.30–1.05 mm^3 (Figure 3b) indicating that the minimum egg size at spawning is at least 0.30 mm^3 (diameter of 830 μm). M_{OD} for fish at maturity stage 5 or 6 was related (semi-log) to I_{GS} (\log_{10} -transformed; $r^2 = 0.342$; $n = 23$; $P < 0.01$).

3.2.2 | Oocyte diameter and histological investigations

Examination of 100 randomly chosen individual female *C. harengus* from the year 2000 samples revealed that the overall variation in V_O was mostly explained by differences among females (92.3%), while the remaining 7.7% was explained by variation in V_O within each female ovary (ANOVA, $F_{1,5148} = 430$; $P < 0.001$). Thus, this analysis revealed that the oocyte size variation within ovaries could be omitted allowing average oocyte size to represent each ovary in the remaining analyses.

The oocyte size data were analysed separately according to the Julian day of sampling as the oocytes generally increase in size over the whole period (Figure 4). The samples collected after day 178 were from different locations. The apparent decrease in V_O during the period from day 178 to 186 (ANOVA, $F_{7,274} = 3.39$; $P < 0.01$) was considered to reflect differences among locations in maturity stage at length and date of spawning. In other words, this decrease was not considered to reflect the overall pattern in V_O development for the stock and therefore all these samples from 2000 were combined in further analyses. While there was no relation between V_O and total length of the spawner at Julian day 161–170 in 1999 (Figure 5a; $P > 0.05$), there was a weak relation as spawning time was approached; at the Julian day 173–176 ($r^2 = 0.096$; $n = 98$; $P < 0.01$; all at maturity stage 3–4). In year 2000 (day 179–187), V_O of fish at maturity stage 3–4 showed a stronger increasing semi-log relation with L_T ($r^2 = 0.282$; $n = 274$, $P < 0.001$; Figure 5b). The samples from 2000 were classified into two groups; assumed to be recruit spawners (< 30 cm) and repeat spawners (≥ 30 cm), consistent with Jakobsson

et al. (1993) and results presented in Óskarsson and Taggart (2009), where 2000 repeat spawners were shown to spawn c. 17 days later than 1999 repeat spawners. There was no relationship between V_O and L_T for repeat spawners ($P > 0.05$; Figure 5b), though there was a relatively (to those above) strong relation for recruit spawners ($r^2 = 0.380$; $n = 76$; $P < 0.001$). For the repeat spawners V_O appeared more or less constant at c. 0.5 mm^3 (Figure 5b). V_O was also related (semi-log linear relationship) with I_{GS} (\log_{10} -transformed) at Julian day 173–176 in 1999 ($r^2 = 0.609$; $n = 98$; $P < 0.001$; Figure 6a) and day 179–187 in 2000 ($r^2 = 0.536$; $n = 277$; $P < 0.001$; Figure 6b).

In addressing the question of whether oocyte size a few weeks prior to spawning represents the maturation stage or egg mass at spawning (the motivation for the histological examination), the

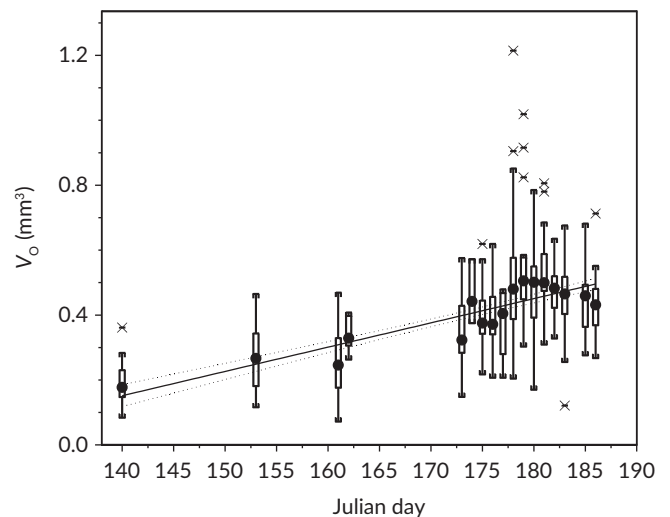


FIGURE 4 Box plots (●, median; □, 25th and 75th percentiles; T, 1.5 interquartile range; X, outliers) of Icelandic summer-spawning *Clupea harengus* (total length ≥ 30 cm) oocyte volume (V_O) as a function of Julian day in 1999 (Julian days 140–175) and 2000 (Julian day >175): $y = 6.90 \times 10^{-3}x - 0.793$; $r^2 = 0.364$, $n = 409$, $P < 0.001$. --, Fitted regression curves; ---, 95% confidence intervals

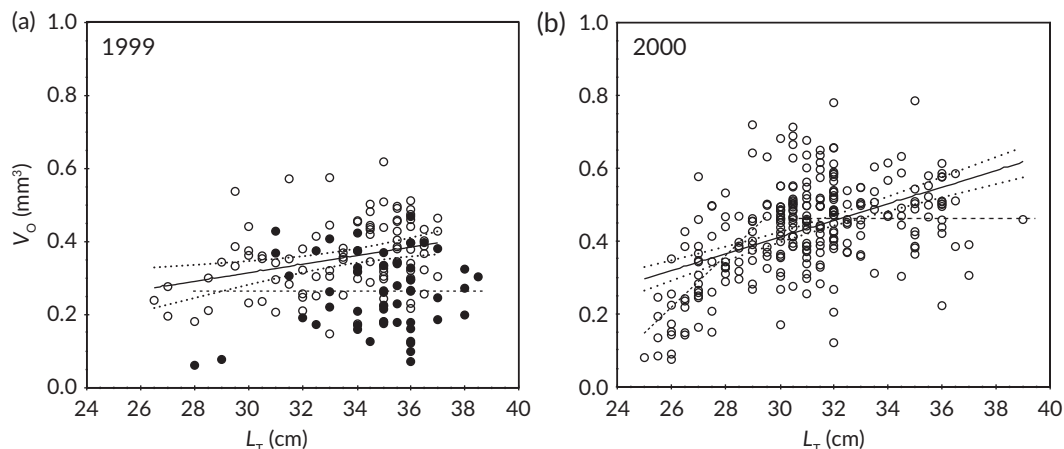
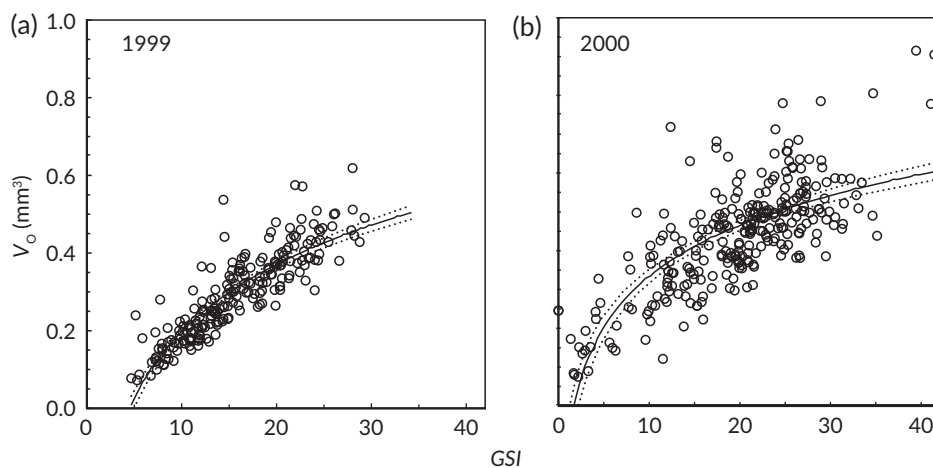


FIGURE 5 (a) Relationship of average oocyte volume (V_O) with total length (L_T) of Icelandic summer-spawning *Clupea harengus* at maturity stage 3 or 4 (period of oocyte growth) at (a) Julian days 161–170 (●; ---, mean $V_O = 0.26 \text{ mm}^3$, SD = 0.10; $n = 51$) and days 173–176 (○; $y = 0.879 \log_{10} x - 0.984$, $r^2 = 0.096$, $n = 98$, $P < 0.01$). (b) The semi-log relationship at Julian day 179 and 187 in 2000 ($y = 2.05 \log_{10} x - 2.62$, $r^2 = 0.282$, $n = 277$, $P < 0.001$) and average V_O of repeat spawners or herring ≥ 30 -cm L_T (---; mean $V_O = 0.478$, SD = 0.114, $n = 198$) and recruit spawners (· · ·, $y = 7.03 \cdot 10^{-2} x - 1.60$, $r^2 = 0.380$, $n = 76$, $P < 0.001$). —, Fitted regression curves; · · ·, 95% confidence intervals

analyses revealed no relationships between V_O and volume fraction of yolk-granule for ISSH; the average volume fraction being 50.5% ($n = 26$, SD = 4.07; Figure 7a). Corresponding analyses of pooled ISSH and NSSH (Óskarsson *et al.*, 2002) data, with comparable oocyte size, indicated a semi-log relationship between yolk volume fraction and V_O (\log_{10} -transformed) which approached an asymptote of *c.* 50% ($r^2 = 0.328$; $n = 52$; $P < 0.001$; Figure 7a). Apparently, the asymptotic volume fraction in NSSH is approached as oocyte volume reaches 0.2 mm^3 with an average volume fraction of 45% ($n = 11$, SD = 3.88). Given that the yolk volume fraction increases during the oocyte growth to a constant level, as indicated by NSSH (Figure 7a), the observed range in ISSH V_O apparently does not represent a difference in maturation stage. In other words, all the ISSH oocytes had reached the yolk volume fraction limit typical of fully mature ovaries; around 50% and significantly higher than NSSH with $V_O > 0.2 \text{ mm}^3$ ($F_{1,35} = 15.0$; $P < 0.001$). No relationship was found between V_O and volume of the 10 largest yolk granules for ISSH ($P > 0.05$; Figure 7b), while aggregating the ISSH and NSSH data showed a significant relationship ($r^2 = 0.448$; $n = 67$; $P < 0.001$). The aggregation of the data was necessary to obtain a functional relation as none of the collected

ISSH had the small V_O . However, there are indications that yolk granule volume in NSSH did not reach an asymptote as did the ISSH, suggesting that the V_O of NSSH represents the maturation stage (still increasing) while not for ISSH. Chorion thickness was found to increase (semi-log linear relationship) with V_O (\log -transformed) for ISSH (Figure 7c; $r^2 = 0.550$; $n = 26$; $P < 0.001$), as well as for the aggregated ISSH and NSSH data ($r^2 = 0.716$; $n = 67$; $P < 0.001$). The relationship for the aggregated data indicates asymptotic behaviour and chorion thickness of fully mature eggs reaching 15–20 μm , although there is a suggestion that the chorion in ISSH eggs may be slightly thicker than in NSSH oocytes of similar size. Among the three oocyte measures of maturation stage, only chorion thickness and yolk-granule volume showed a marginal correlation ($r^2 = 0.14$; $P < 0.05$) in ISSH. Considering the objective of the analyses of these three measures of oocyte maturation stage, the results for ISSH can be summarised as: yolk volume fraction and volume of the 10 largest yolk granules suggest that the oocyte volume represents egg mass at spawning (not the maturation stage); chorion thickness suggests that the oocyte volume represents maturation stage.

FIGURE 6 Semi-log Relationship of average oocyte volume (V_O) with gonado somatic index (L_{GS}) of Icelandic summer-spawning *Clupea harengus* in (a) 1999 ($y = 0.512 \log_{10} x - 0.0280$, r^2 between fitted and observed estimates = 0.609, $n = 98$, $P < 0.001$) and (b) 2000 ($y = 0.414 \log_{10} y - 0.078$, $r^2 = 0.536$, $n = 277$, $P < 0.001$). ○, Observations; —, fitted regression curves; · · ·, 95% confidence intervals



4 | DISCUSSION

These results allow us to conclude that there is a variation in oocyte mass at spawning for both Scotia-Fundy summer and autumn-spawning and Icelandic summer-spawning *C. harengus*. This conclusion is new for ISSH but in part consistent with Messieh (1976) for SFSH who noted a variation in egg mass in the stock but did not analyse the variation with

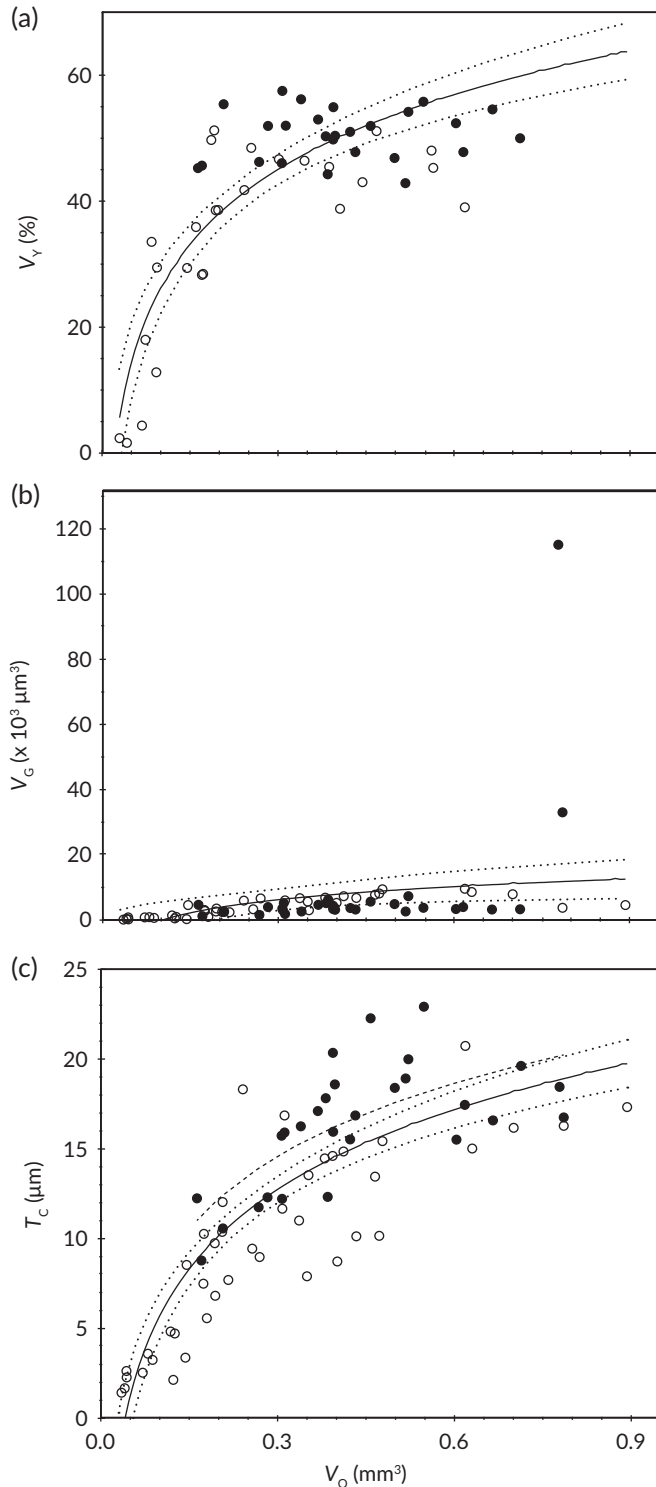


FIGURE 7 Legend on next column.

respect to maternal factors. This conclusion is based on M_{OD} measurements for both stocks and on analyses of V_O in ISSH. The M_{OD} at spawning can be as low as $110 \mu\text{g}$ (corresponding to V_O of 0.3 mm^3 for unhydrated eggs and D_O of c. $830 \mu\text{m}$; Figure 3b) for both stocks according to the M_{OD} measurements (Figures 2a and 3a). The upper limit of the egg mass is less clear; being c. $190 \mu\text{g}$ M_{OD} ($V_O \approx 0.72 \text{ mm}^3$; $D_O \approx 1110 \mu\text{m}$) for SFSH and $225 \mu\text{g}$ M_{OD} ($V_O \approx 0.905 \text{ mm}^3$; $D_O \approx 1200 \mu\text{m}$) for ISSH. This means that the stock-related differences between the largest and the smallest eggs are at least twofold in terms of M_{OD} and around threefold in terms of volume of hydrated eggs.

Maternal factors, including M_T and L_T , made significant contributions to explained variance in the egg mass of both stocks. Total length explained 16% of the variation in M_{OD} of SFSH (Figure 2a) and as much as 23% when five individuals with anomalously small oocytes were excluded. For ISSH, maternal factors explained variation in two unrelated measures of egg mass at spawning; M_{OD} and V_O . Whole M_T was found to explain 20.6% of the variation in M_{OD} in 1999–2000, while L_T and K explained 15.5% of the variation in 2009 (Figure 3a). The analyses of the V_O were based on the interpretation, drawn from the histological analyses, that the volume determinations of the wet oocytes a few weeks prior to spawning reflect egg mass at spawning. On Julian day 173–176 in 1999 (Figure 5a) and in 2000 (Figure 5b), L_T explained 10 and 28%, respectively, of the variation in V_O . The difference between the years (1999 and 2000) is thought to reflect different length distributions where only a few presumed recruit spawners (11) were collected in 1999 (Figure 5a). The fact that no relationship was found between V_O and various maternal factors (L_T , M_T , or K) for repeat spawners in 2000, in contrast with significant relationship for recruit spawners (Figure 5b), indicates that the amount of variation in egg mass explained with the maternal factors (see above) is due to a smaller egg mass for recruit spawners. Moreover, of all the maternal factors examined, the l_{GS} showed the strongest relationship to the M_{OD} of SFSH (Figure 2b) and ISSH and to the oocyte volume for ISSH (Figure 6), with the CV ranging from 0.342 to 0.609. Comparable results were found for NSSH on less developed oocytes (Óskarsson *et al.*, 2002). The relationships between l_{GS} and egg mass is proposed to indicate that the fish investing most in reproduction, relative to

FIGURE 7 Comparisons of Icelandic summer-spawning *Clupea harengus* (ISSH; ●) at Julian day 180 and 186 in 2000 (c. 2 weeks pre-spawning) with Norwegian spring-spawning *C. harengus* (O) in December 1996 (at least 3 months prior to spawning; data from Óskarsson *et al.*, 2002) oocyte volume (V_O) relationships with: (a) yolk volume fraction of granule (V_F), where for pooled data $y = 35.8 \log_{10} x + 62.8$, r^2 between fitted and observed estimates = 0.328, $n = 52$, $P < 0.001$, but for the ISSH stock alone V_F was not a function of V_O ($P > 0.05$) but was on average 50–5% ($n = 26$, $SD = 4.07$); (b) the average volume of ten largest yolk granule (V_G), where for pooled data $y = 5.04 \log_{10} x + 6.71$, $r^2 = 0.448$; $n = 67$, $P < 0.001$, but for the ISSH stock alone V_G was not a function of V_O ($P > 0.05$), but was on average $3.80 \mu\text{m}^3$ ($n = 26$, $SD = 1.42$); (c) the chorion thickness (T_C) where for the pooled data $y = 14.9 \log_{10} x + 20.6$, $r^2 = 0.716$, $n = 67$; $P < 0.001$, but for ISSH stock alone $y = 15.8 \log_{10} x + 22.8$, $r^2 = 0.550$, $n = 26$, $P < 0.001$. --, Fitted regression curves; ---, 95% confidence intervals

their body mass (highest I_{GS}), spawn the largest eggs. For both stocks, these findings show that the degree of egg-mass variation explained by the conventional maternal factors (*i.e.*, L_T and M_T ; *c.* 20%), though statistically significant, is generally lower than that observed for many other fish species (Table 1). The question becomes, what is the biological significance from a stock reproduction and recruitment perspective?

It can be argued for both SFSH and ISSH that the size, or age-composition and average body condition will affect the quality (through the egg mass variation) and quantity (Óskarsson *et al.*, 2016; Óskarsson & Taggart, 2006, 2010) of reproductive output. During years when the proportion of larger repeat spawners, relative to recruit spawners, is high, the viability of the larvae can be expected to be higher and thereby also the recruitment potential and subsequent year-class strength. Thus, the results of Óskarsson and Taggart (2010) showing that the inter-annual variation in total egg production of recruit spawners is not significantly related to the recruitment variation of the ISSH stock is suggested to be a least partly related to their smaller egg mass. However, the unexplained variation in egg mass is considerable and presumably related to heritable factors, trade-offs between fecundity and egg mass (Óskarsson & Taggart, 2006) and temporal (*e.g.*, annual) variation in the environment. Moreover, egg quality has been considered in the simplest manner; egg mass and yolk mass and this neglects other factors such as free amino-acids, lipids and protein content (Berkeley *et al.*, 2004; Carter *et al.*, 2015; Halfyard & Parrish, 2002; Maarstoel *et al.*, 1993; McEvoy *et al.*, 1993; Moodie *et al.*, 1989; Riveiro *et al.*, 2000). It is not clear that studies of these factors would provide more informative evaluations of the influences of maternal factors on the reproductive potential of *C. harengus*.

Egg size variation in *C. harengus* was observed decades ago by Blaxter and Hempel (1963) who demonstrated that the ratio between the smallest and largest egg diameter for *C. harengus* was 1:1.5, equivalent to the results above for ISSH (1:1.4; 850:1200 μm). Furthermore, the yolk dry mass (M_{YD}) can be estimated using M_{OD} and the strictly empirical relation employed by Morley *et al.* (1999) derived from Blaxter and Hempel (1966): $M_{YD} = 0.88(0.012M_{OD})$. When applied to the minimum (90 μg) and maximum (190 μg) observed M_{OD} for SFSH, the yolk mass is 78 and 166 μg , respectively. Corresponding values of M_Y for ISSH are 100 and 197 μg , respectively. The difference in M_Y among *C. harengus* can therefore vary by twofold, indicating that the nutritional status of larvae hatching from large eggs would be superior to that for larvae from relatively small eggs. This, in turn, is thought to translate to differences in larval survival, which is consistent with a positive relationship between egg size and their larval size among various fish stocks (Blaxter & Hempel, 1963; Knutsen & Tilseth, 1985; Chambers *et al.*, 1989; Hinckley, 1990; Buckley *et al.*, 1991; Marteinsdóttir & Able, 1992; Miller *et al.*, 1995 (not in all cases); Pepin *et al.*, 1997; Nissling *et al.*, 1998; Trippel, 1998; Zhao *et al.*, 2001; Marteinsdóttir & Begg, 2002; Kennedy *et al.*, 2007) and larvae from large eggs within various fish species having greater viability and survival than those from small eggs (Blaxter & Hempel, 1963; Buckley *et al.*, 1991; Duarte & Alcaraz, 1989; Kjesbu *et al.*, 1996;

Marteinsdóttir & Steinarsson, 1998; Rijnsdorp & Vingerhoed, 1994). Even if in some cases no relationships were found between maternal factors and egg survival or hatching success (Marteinsdóttir & Steinarsson, 1998; Ouellet *et al.*, 2001) or larvae survival (Buckley *et al.*, 1991; Ouellet *et al.*, 2001) the claim by Solemdal *et al.* (1991; page 9) that “small eggs having a high mortality producing inferior larvae” is consistent with the majority of studies.

The M_{OD} in SFSH can be compared with Messieh (1976) who recorded the oocyte dry mass, in the same stock, earlier in the year (July to August) and prior to spawning (earlier than in the present study) and the results were different. The dry mass of 100 oocytes weighed in 1970 corresponds to an average M_O of 91 μg (upper 2 SE \approx 10 μg). In 2001 the mass of 10 oocytes corresponded to average M_O of 146 μg (upper 2 SE \approx 14.2 μg ; Figure 2a). The methods used differed in that Messieh's (1976) drying process was shorter (overnight) and at lower temperature (50°C) relative to the method used in this study (48 h at 62°C). However, there is no basis to argue that the applied method can explain the difference as equivalent eggs dried at a lower temperature over a shorter period would not be expected to weigh less. The most reasonable explanation is that the *C. harengus* studies in 1970 were further from spawning and thus the oocytes had not reached their ultimate mass or size, as illustrated in Figure 4 for ISSH. This is consistent with the Messieh (1976) study that used *C. harengus* at maturity stage 4 or 5, while all the SFSH collected in 2001 were at stage 5. Sampling in 1970 took place earlier or mainly in July and August while the 2001 fish used here were collected in September. However, it does not necessarily indicate less developed ovaries as SFSH spawning occurs over a protracted period, starting as early as June (Óskarsson, 2005), but might indicate that the egg mass within the stock is also a function of the spawning time. Yet another difference is that Messieh (1976) collected *C. harengus* samples from several spawning grounds and aggregated the data in his analyses while the present collection was from a single spawning aggregation.

There was a fundamental difference in the sampling procedure for the two stocks examined here. The SFSH was collected on a single spawning ground while the ISSH was collected across all the spawning grounds of the stock. The difference is partly due to access to samples during the time of the study and focus of the study. However, the sampling procedure reflects also ideas about stock structure where the former is considered to consist of several sub-units represented by the different spawning grounds (Stephenson *et al.*, 1999) while no such indications or theories exists for complexity of the ISSH stock. At the time of this study, each of these stocks were however, assessed as single stocks across all spawning grounds, even if there were in effect restrictions in the fishery on the different spawning complexes within the SFSH stock (Stephenson *et al.*, 1999). Considering that the sampling approach followed the ideas about the stocks structure, its implications on the results are negligible. Thus, for SFSH the results are at least applicable to the spawning complex at German Bank, though applicable to the whole ISSH stock.

The results from the analyses of the three histological characteristics within the ovaries of ISSH are not entirely consistent.

Determination of the volume fraction of yolk granule and volume of the 10 largest yolk granules suggest that the oocyte volume represents the oocyte mass variation at spawning rather than oocyte maturity phase (Figures 7a and 7b, respectively) as the values approach an asymptote. It means that the volume fraction and the yolk granules size have apparently reached their maximum size for ISSH or that the oocytes are fully mature. The chorion thickness suggests the opposite, that V_O represents the variation in oocytes maturation because the chorion thickness was found to increase with V_O for ISSH and for NSSH aggregated with ISSH (Figure 7c). This interpretation of chorion thickness is presumably true for NSSH as concluded by Óskarsson *et al.* (2002). However, it is probably not the case for ISSH exclusively, this close to spawning, which implies that that chorion thickness must increase with egg mass. Blaxter and Hempel (1966) observed that the chorion varies from 21 to 33% of total egg dry mass in *C. harengus* and the chorion is thicker in heavier eggs, consistent with the interpretation here. Thus, it can be concluded that the V_O measurements on ISSH primarily reflect egg mass variation at spawning; an interpretation consistent with analyses of the V_O variation and the analyses of the variation in fully mature M_{OD} where c. 20% of the variation was explained by maternal factors.

Despite the conclusion above concerning the results of the histological examinations of ISSH, there are some features that need further consideration. The lowest V_O in the histological examination was c. 0.2 mm^3 , which might suggest that oocytes $<0.2 \text{ mm}^3$ (Figure 5b) are smaller because they are less developed than the larger oocytes and are, therefore, not representative for the egg mass at spawning. These small oocytes are mainly observed in the presumed recruit spawners (Figure 5b) and their occurrence is consistent with the results of Óskarsson and Taggart (2009) where recruit spawners were found to spawn on average 17 days later than repeat spawners. However, as histological examinations of the maturation phase of these oocytes $<0.2 \text{ mm}^3$ do not exist, the conclusion remains that the V_O determinations of ISSH reflects the egg-mass variation at spawning. Other considerations relate to NSSH eggs that typically exhibit twice the mass of ISSH eggs (Blaxter & Hempel, 1963: c. $300 \mu\text{g}$ eggs v. c. $150 \mu\text{g}$ eggs) and, therefore, correspondingly lower fecundity at size (Óskarsson *et al.*, 2002; Óskarsson & Taggart, 2006). Thus, the oocytes of NSSH (collected c. 3 months prior to spawning; Óskarsson *et al.*, 2002; Figure 7a–c) are less developed than those of ISSH (collected <1 month prior to spawning). In contrast, the asymptote in yolk volume fraction is similar for NSSH and ISSH, suggesting that fully mature and unhydrated oocytes have 40 to 50% of their total volume as yolk. However, there are some indications that yolk granule volume may approach a higher asymptote in fully mature oocytes in NSSH than in ISSH (Figure 7b); possibly related to greater egg mass at spawning for NSSH.

The variation in egg mass in ISSH and SFSH documented in this study has substantial implications for management. There is at least a twofold difference in oocyte dry mass and a threefold difference in volume of wet oocytes within each of these stocks. While maternal factors, *i.e.*, length and mass, explain only c. 20% of this variation in egg dry mass and oocyte volume, the observation that egg mass is

positively related to fish size combined with the indication that egg mass is related to viability of offspring, means that the eggs of larger (older) spawners will contribute disproportionately more to recruitment. Thus, management strategies should aim for keeping a broad range in the size and age composition of the stocks and maintain a suitable portion of larger fish to improve the prospect for recruitment success of the stocks. While the management plan for SFSH has an explicit objective of maintaining a balanced age (size) composition, the desirable fraction of older fish has not been determined to this point and there have been discussion about the fact that the age range has been narrow and that there was a need to rebuild the older segment of the population (Power *et al.*, 2007).

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