Individual fecundity of the autumn spawning Baltic herring *Clupea harengus membras* L.

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Abstract. Variability in reproductive investment is an important factor behind recruitment and population dynamics of fish. We investigated absolute individual fecundity (AF) of the currently depleted population of autumn spawning herring in the northern Baltic Sea over three sequential years (2008–2010). Fecundity of fish in relation to changes in individual body mass, individual body length, body condition factor, age, and gonadosomatic index was investigated. AF varied between 11 838 and 108 093 oocytes per fish and, as an average, varied insignificantly between years. AF was positively significantly related to fish length and weight, but not to age. In general, individuals with a higher condition factor (K) had a higher AF. However, the correlation with K was weak or non-significant in some cases. Relative fecundity of the fish was found to vary 24–33% between years, being significantly different in all three years. In addition, the obtained results on AF were compared with historical findings from 1959–1970, when the population was at a high level. Notable differences were found in the AF between the two time periods by age groups, while by weights AF remained the same. The results of the present study, together with ongoing additional biological and ecological investigations, will help to identify mechanisms that configure the fecundity and recruitment processes.

Key words: fecundity, *Clupea harengus*, Fulton's K, gonadosomatic index, interannual variability.

INTRODUCTION

Advanced understanding in the dynamics of fish fecundity is of fundamental importance in fish and fisheries ecology and also has strong practical significance. It has been empirically shown that individual fecundity of fish is directly related to fish stock recruitment variation, suggesting thereby that fecundity is an important component of fish stock dynamics (Rickmann et al., 2000). More specifically, fecundity of individual fish is required for the assessment of the reproduction potential of fish stocks (Bleil & Oeberst, 2005). Stock reproductive potential is, in turn, subject to interannual fluctuations due to environmental changes influencing maturation, growth, and condition of fish (e.g., Morgan & Rideout, 2008). As a response to the changing environment, different sub-species of fish have evolved with intriguing reproductive strategies that reflect spatially small-scale adaptation to surrounding environmental conditions and ecological niches (Murua & Saborido-Rey, 2003).

Herring, unlike most other clupeoids, are total spawners with a group-synchronous ovarian organization (Murua & Saborido-Rey, 2003). However, at a population level, they may be considered serial spawners, similar to most other Clupeiformes. They accomplish this by spawning in waves over a protracted spawning season, the older herring usually spawning first, with the younger herring and recruits spawning in subsequent weeks (Ware & Tanasichuk, 1989). Thus multiple intra-annual spawning (in this case wave spawning) can be considered as 'intraseasonal iteroparity' (Jennings & Beverton, 1991).

Several life history parameters of fish related to reproductive biology may change over time and space. Amongst others, these include: reproductive rate (size-specific fecundity), age or size at maturation, quality or size of gametes, timing of maturation and spawning (Bailey & Almatar, 1989). Specifically, fecundity-at-length variability in autumn spawning herring in the Gulf of Maine (Kelly & Stevenson, 1985), spring and autumn spawning herring in the Gulf of St Lawrence (Lambert, 1987), the Clyde spring spawning herring (Bailey & Almatar, 1989), but also in a range of other fish species (Bagenal, 1973) has been suggested and has been related to density dependent effects. In addition, interannual differences in length-specific fecundity of the Norwegian spring spawning herring were explained by variation in weight-at-length, that is higher fecundity of spawners in better condition (Oskarsson et al., 2002).

Baltic Sea fish populations have fluctuated over time, and an increasing amount of historical evidence is becoming available for several commercial fish species on the magnitude and direction of these fluctuations, together with identification of the drivers responsible (e.g., Eero et al., 2011). Studies on Baltic herring started already in the late 19th century, when on the basis of morphometric and meristic characters, two races – spring and autumn spawners – were distinguished (Heincke, 1898). While spring spawning herring generally constitute most of the herring landings in the Baltic Sea, the importance of the autumn spawners has varied over time. For instance, about a century ago autumn spawners constituted the main part of the herring catches in the Baltic Sea, which was often based on a few strong year-classes (Hessle, 1931, and references therein). Unfortunately, information on the Baltic autumn spawning herring is relatively fragmental and almost lacking during the past decades.

In the northern Baltic Sea, at the border of its distribution area, autumn herring finds favourable conditions only during the periods of relatively warm winters and high salinity with abundant year-classes being formed only after mild winters (Ojaveer, 2003). Autumn spawning herring made a substantial contribution of herring landings in the Gulf of Riga until the mid-1970s accounting for up to 47% in some years, but the fish fell into deep depression since then and has not recovered yet (Ojaveer, 2003). In addition, annual catches of autumn herring in the coastal gillnet fishery reached about 3000 tonnes in the Gulf of Riga in the late 1950s (Ojaveer, 1962), but are now about two orders of magnitude lower (T. Arula, unpublished data). Further, proof of the low abundance of this species currently lies in the fact that its share in the total herring landings in the Gulf of Riga, assessed by otolith appearance and fish maturity ogives, does not exceed 1% (H. Shpilev, unpublished data).

We have started investigations of a relatively small autumn herring population in the northern Baltic Sea. This population is called Saaremaa–Ventspils autumn herring. Most of the population is located west of the Irbe Sound, but also within the sound and in the western part of the Gulf of Riga (Ojaveer, 1974). Here we report results on reproductive indices as potential proxies for annual fecundity variations of this herring population. In addition, we test the hypothesis that individual fish condition is the primary factor responsible for the variability observed in the fecundity of autumn herring. And finally, we put the obtained results from the most recent years into historical perspective and compare the absolute individual fecundity data with those several decades ago when the fish was very abundant.

MATERIAL AND METHODS

Study area and data collection

Fish samples were taken from commercial gillnet catches on spawning grounds of a distinct autumn herring population, called Saaremaa–Ventspils population (Ojaveer, 1974), during 2008–2010. The targeted fishery on autumn herring is performed with gillnets; their material and mesh size have nowadays remained the same as historically. Although gillnets are known to be selective, this should pose no restrictions for annual-scale comparisons within the current study as the same nets were used in all years.

In general, potential fecundity estimates taken very close to spawning are considered to closely reflect the realized fecundity (Kurita et al., 2003). Therefore, we sampled fish just prior to spawning when a potential down-regulation by atresia had been completed.

Earlier studies have shown that the latitudinal range may have some effect on the fish condition factor (e.g. Slotte, 1999). Therefore, we included in fecundity analyses only herring originating from the same spawning grounds. The total number of fish analysed from the respective location is shown in Table 1.

Table 1. Sampling coordinates of Saaremaa–Ventspils autumn spawning herring, together with annual information on the number of individuals (N) analysed, individual total length (TL), individual total weight (TW), age, and Fulton's body condition factor (K) (mean±SD)

Year	Sampling coordinates	N	TL, cm	TW, g	Age, years	K
2008	N 58′15″352 E 23′01″981	74	18.7±1.1	47.3±7.4	5.0±1.2	0.7±0.1
2009	N 58′15″421 E 23′01″343	43	18.6±1.1	45.0±9.1*	5.0±1.7	0.7±0.0
2010	N 58′15″517 E 23′01″747	44	19.1±1.5	50.9±10.9*	5.0±1.7	0.7±0.1

* Marks morphological values statistically different between years (RMA, Bonferroni post hoc test; $p < 0.05$).

For each fish, standard morphometric measurements were taken: total length (TL, measured to the nearest 0.1 cm), total body weight (TW, measured to the nearest 0.1 g), and gonad weight (GW, measurement precision 0.001 g). Fish age was determined from otoliths. The herring included in the fecundity analysis were characterized as 'spawning (prepared)'. Fish in this stage contain ovaries with clearly visiable hydrated oocytes, but are not running or have hydrated oocytes in their terminal oviduct. Ovaries fill most of the body cavity. Their colour is translucent to mother of pearl (ICES, 2012). Fish that showed indications of ovulation (eggs released by pressure on the belly) or signs on atresia were not considered. Ovaries were removed by careful dissection, weighed fresh, and preserved in 90% ethanol.

Fecundity samples

Two about 0.5 g samples were weighed fresh (precision 0.001 g) and also after preservation in ethanol. The total number of oocytes from about a 0.2 g sub-sample was counted. Absolute individual fecundity (AF) was calculated as the ratio of the total gonad weight to the weight of the respective sub-sample, multiplied by the number of oocytes counted in a sub-sample. Samples where the difference between sub-sample counts exceeded 5% were excluded from further analysis. Estimates of AF of each female were obtained from the average of the raised sub-sample counts:

$$\mathrm{AF} = \frac{\sum C_n O / W_n}{N},\qquad(1)$$

where C_n is the counted number of eggs in sub-sample n, O is the ovary weight, W_n is the sub-sample weight, and N is the number of subsamples.

Gonadosomatic index (GSI) gives the proportion of the ovary weight to the total fish weight. Condition factor shows how much of the individual energy reserves has been invested to weight growth, and the relative fecundity indicates how many eggs per gram body weight were produced.

Condition factor (K), relative fecundity (RF), and GSI were calculated for each fish using the following equations:

$$\mathrm{K} = 100 \times \mathrm{TW} / \mathrm{TL}^3,\qquad(2)$$

$$\mathrm{GSI} = 100 \times \mathrm{GW} / \mathrm{TW},\qquad(3)$$

$$\mathrm{RF} = \mathrm{AF} / \mathrm{TW}.\qquad(4)$$

A common criticism of K is that this variable shows a length dependency with larger fish tending to have a higher value of K. This was examined using common

Pearson correlation analysis in the current data sets for all years independently. There was no significant correlation (i.e., $p > 0.05$) between TL and K. According to Slotte (1999), relative weight loss during overwintering and migration is inversely related to length in North Sea spring herring and the weak positive correlation between TL and K is a result of greater weight loss, relative to body size, from feeding to spawning rather than a statistical artefact.

Earlier studies have shown that the share of individuals from other autumn herring populations than the Saaremaa–Ventspils population in the current study area (see Table 1) is negligible (Ojaveer, 1974). Therefore, we also performed comparative evaluation between the fecundity estimates obtained during the two time periods: the most recent period of 2008–2010 and the 'historical period' of 1959–1970 (for details, see also below).

Statistical analysis

To compare AF between 1959–1970 and 2008–2010, and because only the pooled regression formula for the 'historical period' was available, we used this pooled regression formula to plot the linear curve and to assess visually differences in AF between 1959–1970 and 2008–2010. The formula for the 'historical period' was taken from Ojaveer (1974): $AF = 890 \times TW - 12\,360$; $r = 0.8$, $p < 0.05$, $n = 382$.

Statistical treatments were conducted using the STATISTICA 10 software (Statsoft Inc., Tulsa, Oklahoma). In regression analyses for 2008–2010 we first examined if the assumption of normally distributed errors and constant variance was met. The assumption of linearity, normal distribution, and homogeneity of variance between years (2008–2010 only) was studied with linear regression used for each year. Predictive models for AF (as dependent factor) were analysed by univariate linear regressions where TL, TW, age, K, and GSI were covariates. A relationship was considered statistically significant when $p < 0.05$. Further, multiple regressions were applied to assess the major predictors of fecundity. The model, based on the lowest residual sum of squares, was run stepwise with subsequently excluding non-significant variables ($p > 0.05$, starting with the highest) until only significant predictors were included in the respective model (see also Rideout & Morgan, 2010; Skjaeraasen et al., 2011).

The significance of differences in the studied characteristics between years was estimated by the Bonferroni post hoc test in repeated measures analysis of variance (RM ANOVA). Repeated measures analysis of covariance (RM ANCOVA) was used to analyse the time effect (levels: years) on AF. Sampling time was considered as repeated measure with TL, TW, and age included into the analysis as time-varying covariates. Repeated measures ANCOVA tests whether time factor has an effect on AF after removing the variance for which covariates account. Thus, the inclusion of covariates can increase statistical power of the model because it takes into account covariance. To avoid methodological errors independent predictive factors such as TL, TW, and age were critically assessed for equal variances from annual mean value (Table 1).

RESULTS

Interannual variability

The mean age of the analysed fish was 5 years with insignificant interannual variability (RM ANOVA, Bonferroni post hoc test, $p < 0.05$, Table 1). While the mean TL was similar in all studied years (RM ANOVA, Bonferroni post hoc test, $p > 0.05$), TW was significantly higher in 2010 than in 2009 (RM ANOVA, Bonferroni post hoc test, $p < 0.05$). No other significant interannual differences in TW occurred (RM ANOVA, Bonferroni post hoc test, $p > 0.05$, Table 1). Interannual variability of K was non-significant with the highest value in 2009 and similar values for the other two years (RM ANOVA, Bonferroni post hoc test, $p > 0.05$, Table 1).

During 2008–2010 AF varied between 11 838 and 108 093 oocytes per fish with insignificant interannual differences in mean value, when considering TW, TL, and age as time-varying covariates (RM ANCOVA, $n = 161$, $p > 0.05$). Also year effect was non-significant in the model (RM ANCOVA, $n = 161$, $p > 0.05$). The highest average AF was observed in 2008 (Fig. 1). RF of the fish was found to vary from 24% to 33% between years. Like AF, RF was highest in 2008. Unlike in AF, highly significant differences in RF occurred between all the years (RM ANOVA, Bonferroni post hoc test, $p < 0.05$) while annual variability in GSI did not reach significance level between any of the years (RM ANOVA, Bonferroni post hoc test, $p > 0.05$). The highest GSI was also observed in 2008, followed by the years 2010 and 2009 (Table 2).
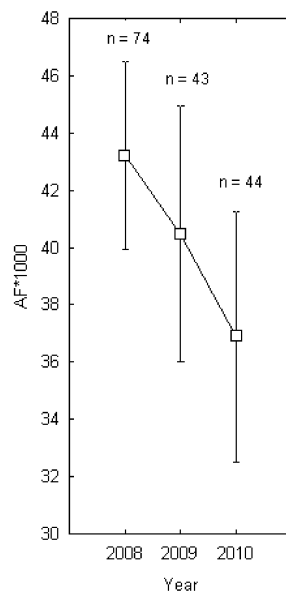
Fig. 1. Annual adjusted mean from ANCOVA analyses of absolute individual fecundity (AF × 1000) of Saaremaa–Ventspils autumn spawning herring. Repeated measure ANCOVA with individual total length, total weight, and age as covariates was used. The vertical lines give approximation for the 95% confidence interval of repeated measures test of ANCOVA with covariates.

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Table 2. Annual-scale variation (mean±SD) of the relative fecundity (RF) and gonadosomatic index (GSI) of Saaremaa–Ventspils autumn spawning herring

Year	RF	GSI
2008	1171.2±479.2*	26.5±5.0
2009	902.5±548.1*	22.9±12.9
2010	788.6±193.9*	25.5±4.8

* Marks morphological values statistically different between years (RMA, Bonferroni post hoc test; $p < 0.05$).

Importance of single predictors of fecundity

The relationship between AF and TL during 2008–2010 was highly significant by all years separately as well as when all the data were pooled together (linear regression, $p < 0.05$). However, the strength of the relationship varied between years (Table 3). In general, larger individuals had higher AF (Fig. 2). TW appeared to be a considerably better predictor for AF than TL (linear regression, $p < 0.05$, Table 3). Plotting the TW–AF data revealed large scattering, potentially caused by different life histories of individuals with similar weight but different age. However, age as a single predictor had no significant effects either on AF, RF, GSI, K, or GW (linear regression, $p > 0.05$).

A significant correlation between AF and K occurred for one year (2009) only but also for pooled data (linear regression, $p < 0.05$, Table 3). Similarly, GSI explained a substantial amount of variation in AF in 2009 (linear regression, $p < 0.05$). Remaining still significant, GSI explained much less variability in AF during the other study years as well as when annual data were pooled together (Table 3). Nevertheless, compared to TL or TW, GSI was a less stable predictor for AF. Differently from GSI, fish age remained an insignificant factor for determining AF at both annual scale and for the pooled data (linear regression, $p > 0.05$). Importantly, individuals with similar age had a very variable AF. For instance, AF for 3-years old fish varied from 11 122 to 73 324 eggs.

Table 3. Annual correlation coefficents between the absolute individul fecundity (dependent) and several independent predictors (for abbreviations see Tables 1 and 2) of Saaremaa–Ventspils autumn spawning herring

Year	TL	TW	K	GSI	Age
2008	0.3*	0.5*	0.3	0.4*	0.1
2009	0.6*	0.8*	0.5*	0.8*	0.2
2010	0.6*	0.7*	0.2	0.4*	0.4
All years	**0.5***	**0.6***	**0.4***	**0.4***	**0.2**

* Marks highly significant ($p < 0.05$) correlations.
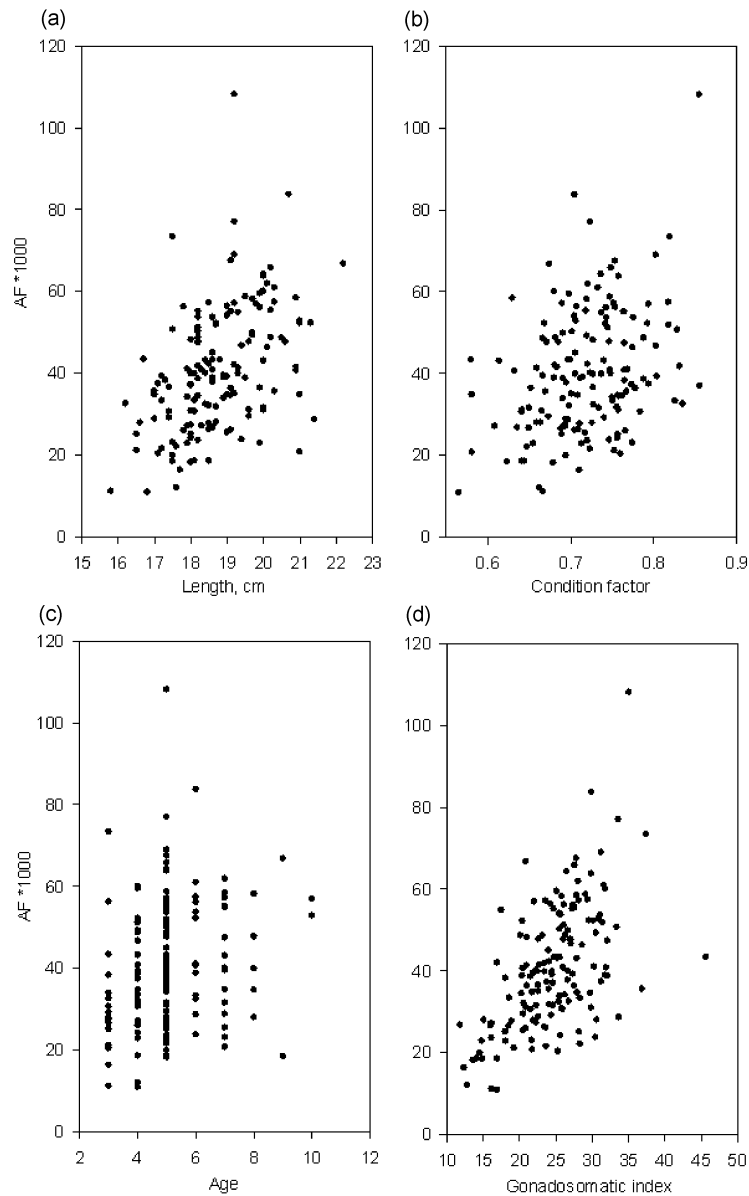
Fig. 2. Scatterplots of the absolute individual fecundity and total length (a), condition factor (b), age (c), and gonadosomatic index (d) of Saaremaa–Ventspils autumn spawning herring during 2008–2010.

Multiple regression analysis

When analysing the data for the multivariate effect to describe variation in AF, three out of the five studied variables appeared to be significant (Stepwise multiple regression; $n = 161$, $p < 0.05$; for statistics see Table 4). Significant variables that

Table 4. Multiple regression results for the dependent variable absolute individual fecundity (2008–2010) of Saaremaa–Ventspils autumn spawning herring. All significant ($p < 0.05$) factors were considered for the final model (for abbreviations see Tables 1 and 2)

| Model factor	Effect	
	Independent variable	SE
Intercept	−158.3	21.5
TL	5.8	0.8
K	88.9	17.1
GSI	1.1	0.2
Model $r = 0.7$		

were included in the model were TL, GSI, and K, but not TW. Similarly to the univariate model, fish age did not exceed significance level in the multivariate model ($p > 0.05$). Predictions from the above-mentioned variables described 71% of the variance in AF. The observed AF was smaller at the lowest values and higher amongst the highest values than the predicted values (Fig. 3).
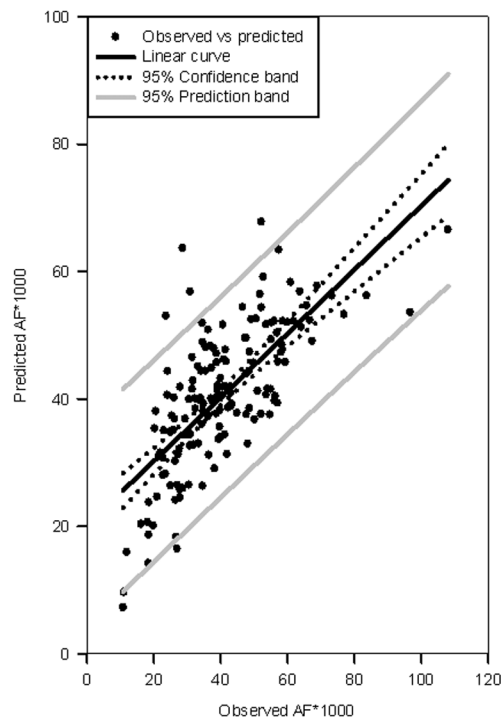

Fig. 3. Scatterplot of multivariate regression between observed and predicted values of absolute individual fecundity (AF × 1000) of Saaremaa–Ventspils autumn spawning herring. Significant predictors in the model are total length, gonadosomatic index, and condition factor. Regression was fitted to scatterplot $AF_{predicted} = 20.2355 + 0.5007x$ (see statistics from Table 4).

Comparison of AF with historical data

Comparison of the linear regression between AF and TW from 1959–1970 with the regression line drawn on the observational data for 2008–2010 (Fig. 4) does not reveal any obvious differences between the 'historical' and 'new' regression lines. We added fish age as a third dimension into the figure to visualize the relationship between fish age and TW. It appears that individuals have very different weights by age groups: in several occasions 3- and 8-year old fish have similar TW and AF (Fig. 4). This explains why there is no relationship between age and AF. Unfortunately, statistical analyses could not be provided between the two periods, and only mean values in AF by TW calculated from the regression formula can be displayed for the years 1959–1970. However, when comparing mean AF by age groups during different time periods, it appears that younger fish (3–4 years old) had substantially higher mean fecundity in 2008–2010 than during 1959–1970, while the opposite pattern is valid for older, 5–8 years old fish (Fig. 5).
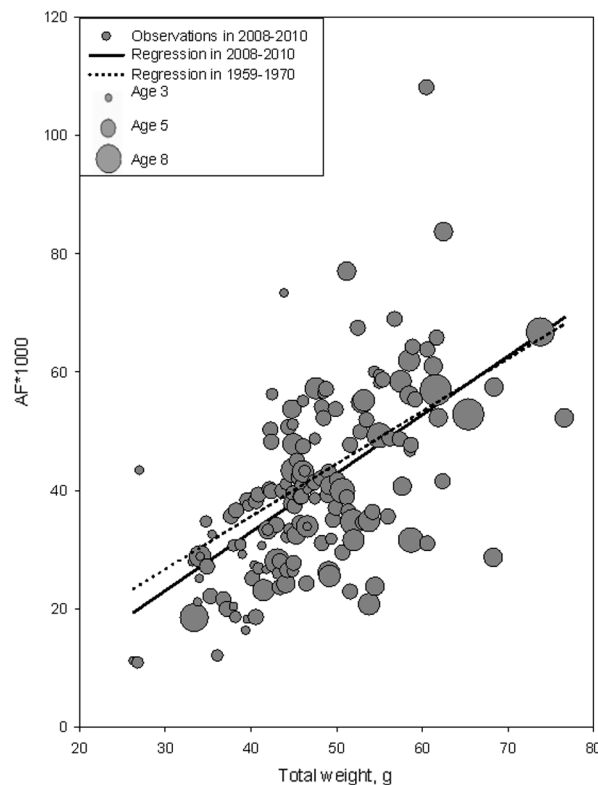
Fig. 4. Absolute individual fecundity (AF × 1000) of Saaremaa–Ventspils autumn spawning herring by individual total weight (TW) during 1959–1970 (regression line; AF = 890 × TW – 12 360, $n = 382$, $r = 0.8$; $p < 0.05$; from Ojaveer, 1974) and 2008–2010 (observations and regression line). Regression was fitted to scatterplot AF = 670 × TW + 8510, $n = 161$, $r = 0.6$, $p < 0.05$). Larger dots indicate older individuals.
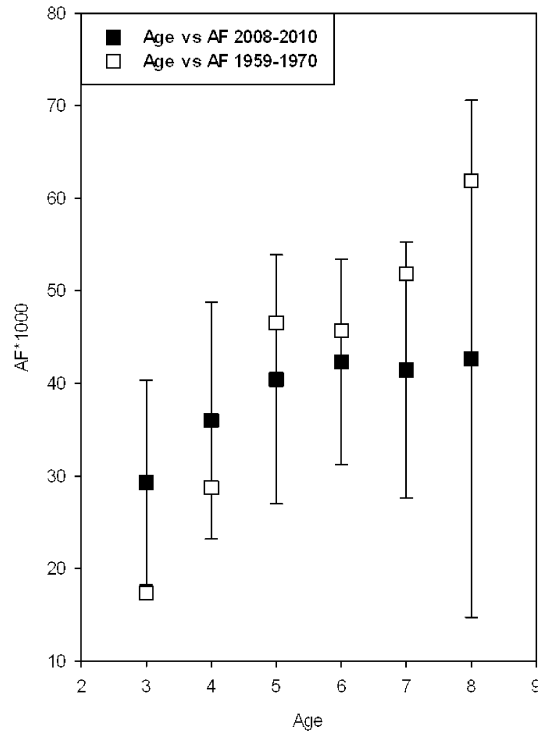
Fig. 5. Mean absolute individual fecundity of Saaremaa–Ventspils autumn spawning herring by age groups in 2008–2010 (mean±SD) and 1959–1970. Data for 1959–1970 were taken from Ojaveer, 1974.

DISCUSSION

The focus of the present study was on describing and analysing the interannual variability of individual fecundity parameters of the autumn spawning herring in the Baltic Sea. The annual-scale variability in fecundity parameters was analysed against the selected individual characteristics of the fish: total body weight, body length, condition factor, age, and gonadosomatic index. Further, we compared the recent absolute individual fecundity values with similar data from the same region at the time when autumn spawning herring was very abundant and the ecosystem had a different configuration (HELCOM, 2009). This aspect adds valuable temporal context to the current study, by enabling to expand our knowledge to the status of fish species and populations at historical time-scale (e.g., MacKenzie et al., 2011).

Large and significant interannual differences were observed in the relative fecundity of the fish in the present study. These might be related to seasonally varying prey availability between years during the maturation process in May–July and associated energy allocations for reproductive growth. For instance Kennedy et al. (2011) found that because of fluctuations in prey field, annual

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values in fecundity for Norwegian spring spawning herring differ by up to 18%. In addition to fish length and individual body mass, which both show strong relationships with individual fecundity (Oskarsson et al., 2002), body condition factor is also very often used in fish fecundity studies (Stares et al., 2007). Fish condition may be dependent on several, often interconnected, factors such as density dependence (Casini et al., 2011), hydro-climatic conditions, and selective fishing (Vainikka et al., 2009). However, because of the seasonal pattern of gamete growth and concurrent changes in the condition factor, the timing and method of sampling can impact the potential relationship between fish fecundity and condition factor (Stares et al., 2007). Therefore, the condition of the fish at the time of capture may not reflect the condition at the time fecundity was actually set, as down regulation by atresia might occur as a result of unfavourable environment after initial determination of fecundity (Kennedy et al., 2007).

Our results confirmed that condition factor measured just prior to spawning did not vary significantly between the years, while relative fecundity values did, indicating that the sampling time and method used in the current study were appropriate. We suggest that the condition factor of individual fish just prior to spawning might be a more precise predictor for fecundity. In fact, body condition factor of the adult autumn herring in the NE Baltic Sea undergoes substantial seasonal variaton being 0.8 in April–May and 1.3 in July (Ojaveer, 1988). This calls for the need, within fish fecundity investigations, to perform additional sampling of fish several months before the spawning actually takes place. However, as evidenced by the results of the current study, body condition factor might still be highly significantly related to absolute fecundity. Therefore, in addition to the recently suggested energy reserves in liver (Davidson & Marshall, 2010), body condition factor might still be of use for fish fecundity studies, but with clearer and more specific focus on the timing of fish sampling and proper interpretations.

Absolute individual fecundity of fish is known to vary over time and space (Kennedy et al., 2007; Morgan & Rideout, 2008). In many cases, these variations have been linked to food availability, which affects energy reserves, both at the individual and stock level (Kjesbu et al., 1991). Major environmental changes in the Baltic Sea during the past decades include excessively high eutrophication, which has resulted in an increase of biological production (HELCOM, 2009) and a decrease in salinity. This has caused, amongst others, substantial changes in zooplankton community composition and abundance/biomass in various taxonomic groups: large-sized copepods (e.g., *Pseudocalanus acuspes*, *Limnocalanus grimaldii*), which are the preferred food for herring, have been replaced by small-sized and energetically less profitable taxa (like *Eurytemora affinis*, *Acartia* spp.) (Sidrevics et al., 1993; Möllmann et al., 2008). Those changes are manifested in reduced individual growth of spring spawning herring and a general increase in its abundance (e.g., Rönkkönen et al., 2004). Thus, prey field, both species composition and abundance/biomass, for especially older autumn herring should be considered currently undoubtedly less favourable than in the 1960s while younger herring should benefit nowadays from elevated production of small-sized copepods.

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Our observations in the individual fecundity estimates of the autumn herring, where younger age-groups have nowadays higher and older fish substantially lower absolute fecundity than historically, might simply mirror the availability and abundance of the food resource for the fish. In other words, younger age-classes are currently favoured by abundantly occurring prey items while older age classes are probably forced to eat an energetically less profitable diet as the preferred large-bodied copepods have nowadays very low abundance values. These trophic changes might have caused period- and age-specific shifts in individual growth of fish with measurable differences in individual absolute fecundities. However, the potential food-web effect on the weight-at-age of the fish needs future studies and the proposed link with individual fecundity should be evaluated afterwards.

Very recent findings for spring spawning herring suggest that, contrary to historical findings, the diet of the young and old herring in the Gulf of Riga overlaps nowadays significantly, probably because of changed prey availability associated with very low abundance of large-bodied copepods (Lankov et al., 2010). This suggests that prey availability may play a crucial role in pelagic fish performance dynamics. This aspect deserves further attention.

The study area, that is the NE Baltic Sea, is also inhabited by very abundant two other clupeoid species: spring herring and sprat, which both can induce density-dependent effects (Casini et al., 2011). Unfortunately, we lack estimates of the spring herring or sprat abundance/biomass in the Saaremaa–Ventspils autumn herring distribution area for 1959–1970. In general, pelagic fish abundance is currently high and they strongly dominate in the Baltic main basin. Therefore, both these clupeoid species can potentially cause density effects on the growth and fecundity of autumn herring via food competition. From purely autumn herring perspective, the potential negative effect of food shortage on fish fecundity may be compensated for by proportionally decreased fish abundance. However, quantification of these effects remains a challenge for future studies.

The stability of marine fish populations can conceptually be due to density-dependent regulation during the adult phase (Bailey & Almatar, 1989) and there are examples evidencing such regulation (e.g., Wright, 2005; Casini et al., 2011). However, there are also examples that failed to find support for such a relationship (Stares et al., 2007 and references therein). Signs of the density-dependent relationship in herring are supported by the most recent findings in a nearby herring population, the spring spawning herring of the Gulf of Riga. Under the conditions of high population abundance and spawning stock biomass, their individual-level fecundity has shown substantially lower values, associated with reductions in individual growth and body condition of the fish (Raid et al., 2010).

At the present stage we lack information on the potential changes in the individual growth and body condition of the autumn herring. This will be a subject for further investigations. However, the observed differences in individual fecundity by different age groups between 1959–1970 and 2008–2010 may indicate that the potential density-dependent regulation is probably also a function of the availability of prey.

In summary, the most variable parameter related to fecundity of the Baltic autumn spawning herring at the interannual scale was relative fecundity, while absolute fecundity and gonadosomatic index were not significantly different. These interannual variations did not fully match with the variability of the somatic growth of the fish. Absolute fecundity was found to be primarily dependent on the total body length and weight, while the body condition factor had less importance and fish age was a non-significant factor both in univariate and multivariate models. Therefore, the length, body condition, and gonadosomatic index of spawners appear to be the primary determinants of the total egg production for this fish. Comparison between 1959–1970 and 2008–2010 suggests that moderate changes have occurred in the individual absolute fecundity by age groups, with younger herring having nowadays higher and older fish lower fecundity. This may be an outcome of changed prey composition and density, resulting from the altered hydro-climatic environment.

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REFERENCES

Bagenal, T. B. 1973. Fish fecundity and its relations with stock and recruitment. *Rapp. P.-v. Reun. Cons. int. Explor. Mer*, **164**, 186–198.

Bailey, R. S. & Almatar, S. M. 1989. Variation in the fecundity and egg weight of herring *(Clupea harengus* L.). Part II. Implications for hypotheses on the stability of marine fish populations. *J. Cons. int. Explor. Mer*, **45**, 125–130.

Bleil, M. & Oeberst, R. 2005. The potential fecundity of cod in the Baltic Sea from 1993 to 1999. *J. Appl. Ichthyol.*, **21**, 19–27.

Casini, M., Kornilovs, G., Cardinale, M., Möllmann, C., Grygiel, W., Jonsson, P., Flinkman, J., Raid, T. & Feldman, V. 2011. Spatial and temporal density dependence regulates the condition of central Baltic Sea clupeids: compelling evidence using an extensive international acoustic survey. *Pop. Ecol.*, **53**(4), 511–523.

Davidson, D. & Marshall, C. T. 2010. Are morphometric indices accurate indicators of stored energy in herring *Clupea harengus*? *J. Fish Biol.*, **76**, 913–929.

Eero, M., MacKenzie, B. R., Köster, F. W. & Gislason, H. 2011. Multi-decadal responses of a cod (*Gadus morhua*) population to human-induced trophic changes, fishing, and climate. *Ecol. Appl.*, **21**(1), 214–226.

Heincke, F. 1898. Naturgeschichte des Herings. *Abh. Dtsh. Seefisch. Ver.*, **2**(1).

HELCOM. 2009. Eutrophication in the Baltic Sea – an integrated thematic assessment of the effects of nutrient enrichment and eutrophication in the Baltic Sea region. *Balt. Sea Environ. Proc.*, No. 115B. HELCOM, Helsinki.

Hessle, H. 1931. Biological statistics regarding the herrings along the Baltic coast of Sweden. *Publ. Circ. Conc. Int. Explor. Mer.*

ICES. 2012. Standardized European female herring maturity scale. Workshop on Sexual Maturity Staging of Herring and Sprat (WKMSHS). In prep.

Jennings, S. & Beverton, R. J. H. 1991. Intraspecific variation in the life history tactics of Atlantic herring (*Clupea harengus* L.) stocks. *ICES J. Mar. Sci.*, **48**, 117–125.

Kelly, K. H. & Stevenson, D. K. 1985. Fecundity of Atlantic herring (*Clupea harengus*) from three spawning areas in the western Gulf of Maine, 1969 and 1982. *J. Northw. Atl. Fish. Sci.*, **6**, 149–155.

Kennedy, J., Witthames, P. R. & Nash, R. D. M. 2007. The concept of fecundity regulation in plaice *Pleuronectes platessa* L. tested on three Irish Sea spawning populations. *Can. J. Fish. Aqua. Sci.*, **64**, 587–601.

Kennedy, J., Nash, D. M., Slotte, A. & Kjesbu, O. S. 2011. The role of fecundity regulation and abortive maturation in the reproductive strategy of Norwegian spring-spawning herring (*Clupea harengus*). *Mar. Biol.*, **158**, 1287–1299.

Kjesbu, O. S., Klungsyr, J., Kryvi, H., Witthames, P. R. & Greer-Walker, M. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. *Can. J. Fish. Aqua. Sci.*, **48**, 2333–2343.

Kurita, Y., Meier, S. & Kjesbu, O. S. 2003. Oocyte growth and fecundity regulation by atresia of Atlantic herring (*Clupea harengus*) in relation to body condition throughout the maturation cycle. *J. Sea Res.*, **49**, 203–219.

Lambert, T. C. 1987. Duration and intensity of spawning in herring (*Clupea harengus)* as related to the age structure of the mature population. *Mar. Ecol. Prog. Ser.*, **39**, 209–220.

Lankov, A., Ojaveer, H., Simm, M., Põllupüü, M. & Möllmann, C. 2010. Feeding ecology of pelagic fish species in the Gulf of Riga (Baltic Sea): the importance of changes in the zooplankton community. *J. Fish Biol.*, **77**(10), 2268–2284.

MacKenzie, B. R., Eero, M. & Ojaveer, H. 2011. Historical ecology provides new insights for ecosystem management: eastern Baltic cod case study. *Mar. Pol.*, **35**, 266–270.

Möllmann, C., Müller-Karulis, B., Kornilovs, G. & St John, M. A. 2008. Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem. *ICES J. Mar. Sci.*, **65**, 302–310.

Morgan, M. J. & Rideout, R. M. 2008. The impact of intrapopulation variability in reproductive traits on population reproductive potential of Grand Bank American plaice (*Hippoglossoides platessoides*) and yellowtail flounder (*Limanda ferruginea*). *J. Sea Res.*, **59**(3), 186–197.

Murua, H. & Saborido-Rey, F. 2003. Female reproductive strategies of marine fish species of the North Atlantic. *J. North Atl. Fish Sci.*, **33**, 23–31.

Ojaveer, E. 1962. Sügiskudu räim Liivi lahes. PhD dissertation.

Ojaveer, E. 1974. Fecundity of autumn herring (*Clupea harengus m.*) populations in NE of the Baltic Sea. *Voprosy ikhtiologii*, **4**(87), 645–653 (in Russian).

Ojaveer, E. 1988. *The Baltic Herrings (Biology and Fishery)*. Agropromizdat, Moscow (in Russian).

Ojaveer, E. 2003. Baltic herring. In *Fishes of Estonia* (Ojaveer, E., Pihu, E. & Saat, T., eds), pp. 60–78. Estonian Academy Publishers, Tallinn.

Oskarsson, G. J., Kjesbu, O. S. & Slotte, A. 2002. Predictions of realised fecundity and spawning time in Norwegian spring-spawning herring (*Clupea harengus*). *J. Sea Res.*, **48**(1), 59–79.

Raid, T., Kornilovs, G., Lankov, A., Nisumaa, A.-M., Shpilev, H. & Järvik, A. 2010. Recruitment dynamics of the Gulf of Riga herring stock: density-dependent and environmental effects. *ICES J. Mar. Sci.*, **67**, 1914–1920.

Rickmann, S. J., Dulvy, N. K., Jennings, S. & Reynolds, J. D. 2000. Recruitment variation related to fecundity in marine fishes. *Can. J. Fish. Aquat. Sci.*, **57**, 116–124.

Rideout, M. R. & Morgan, J. M. 2010. Relationships between maternal body size, condition and potential fecundity of four north-west Atlantic demersal fishes. *J. Fish Biol.*, **76**, 1379–1395.

Rönkkönen, S., Ojaveer, E., Raid, T. & Viitasalo, M. 2004. Long-term changes in Baltic herring (*Clupea harengus membras*) growth in the Gulf of Finland. *Can. J. Fish Aquat. Sci.*, **61**, 219–229.

Sidrevics, L., Line, V., Berzinsh, V. & Kornilovs, G. 1993. Long-term changes in zooplankton abundance in the Gulf of Riga. *ICES CM*, **L: 15**.

Skjaeraasen, J. E., Nash, D. M., Kennedy, J., Thorsen, A., Nilsen, T. & Kjesbu, O. S. 2011. Liver energy, atresia and oocyte stage influence fecundity regulation in Northeast Arctic cod. *Mar. Ecol. Prog. Ser.*, **404**, 173–183.

Slotte, A. 1999. Differential utilization of energy during wintering and spawning migration in Norwegian spring-spawning herring. *J. Fish Biol.*, **54**, 338–355.

Stares, J. C., Rideout, R. M., Morgan, M. J. & Brattey, J. 2007. Did population collapse influence individual fecundity of Northwest Atlantic cod? *ICES J. Mar. Sci.*, **64**, 1338–1347.

Vainikka, A., Mollet, F., Casini, M. & Gardmark, A. 2009. Spatial variation in growth, condition and maturation reaction norms of the Baltic herring *Clupea harengus membras*. *Mar. Ecol. Progr. Ser.*, **383**, 285–294.

Ware, D. M. & Tanasichuk, R. W. 1989. Biological basis of maturation and spawning waves in Pacific herring *Clupea harengus pallasi*. *Can. J. Fish. Aquat. Sci.*, **46**, 1776–1784.

Wright, P. J. 2005. Temporal and spatial variation in reproductive investment of haddock in the North Sea. *ICES CM*, **Q: 07**.

Sügiskuderäime (*Clupea harengus membras* L.) individuaalne viljakus

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Kalade reproduktiivne potentsiaal on oluline tegur, mis määrab noorkalade arvukuse ja populatsiooni suuruse dünaamika. Käesolevas töös analüüsisime kolmel järjestikusel aastal (2008–2010) sügiskuderäime absoluutset individuaalset viljakust (AF) Läänemere kirdeosas. AF seostati järgmiste somaatiliste parameetritega: kala individuaalne kehamass ja pikkus, konditsioonifaktor, vanus ning gonadosomaatiline indeks. AF varieerus vahemikus 11 838 ja 108 093 ootsüüti ning selle keskmine erinevus aastate vahel ei olnud statistiliselt oluline. AF seostus statistiliselt oluliselt ja positiivselt kala kehamassi ning pikkusega, kuid mitte vanusega. Üldjoontes oli kõrgema konditsioonifaktoriga isendite AF suurem. Siiski väljendus korrelatsioon nõrgalt ja oli kahel aastal statistiliselt ebaoluline. Erinevus kalade suhtelises viljakuses oli kõigi kolme aasta vahel statistiliselt oluline, varieerudes vahemikus 24–33%. Lisaks eelnevale võrdlesime käesoleva töö tulemusi varasematega ajaperioodist 1959–1970, kui sügiskuderäime varu oli märkimisväärselt suurem. Ilmnes, et vanuserühmade lõikes erines sügisräime AF kahel uuritaval perioodil (1959–1970 ja 2008–2010) märkimisväärselt, samas kui kehamassi kaupa AF-is erinevust ei leitud. Käesolevad tulemused koos muude käimasolevate bioloogiliste ja ökoloogiliste uuringutega aitavad meil mõista põhjuslikke seoseid, mis mõjutavad selle kalaliigi individuaalset viljakust ning noorkalade arvukust.