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1 **Long-term changes in the total egg production of Norwegian**
2 **spring-spawning herring *Clupea harengus* (L.) –**
3 **implications of variations in population structure and**
4 **condition factor**

5

6 Hilkka O.N. Ndjaula^{a,b,*}, Richard D.M. Nash^b, Aril Slotte^b, Arne Johannessen^a, Olav
7 Sigurd Kjesbu^b

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9

10 ^a*Department of Biology, University of Bergen, P.O. Box 7800, 5020 Bergen, Norway*

11 ^b*Institute of Marine Research, P.O. Box 1870 Nordnes, 5817 Bergen, Norway*

12

13 *Corresponding author. Marine Research Institute, Zoology Department, University
14 of Cape Town, Private Bag X3, Rondebosch 7701, Cape Town, South Africa

15 Tel: +27216503613; fax: +27216504988. *E-mail address:* hilkka.ndjaula@uct.ac.za

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17

18 **ABSTRACT**

19 The reproductive potential of Norwegian spring-spawning herring (*Clupea harengus*)
20 was estimated in terms of total egg production (TEP) for the period 1935-2005, using
21 a model where spawning stock numbers (SSN)-, weight- and length-at-age were
22 combined with fecundity-weight relationships. In general, the modelled TEP was
23 closely related to SSN. However, larger positive and negative deviations from this
24 relationship were found in periods with high SSN in combination with increasing
25 proportions of either recruit or repeat spawners and condition factor (K) below 0.73 or
26 above 0.8. When relating the current estimated TEP to similar type of figures based
27 on earlier data (including fecundity observations in 1951-1983), deviations were less
28 pronounced, but they still tended to occur in periods of high SSN. These results
29 suggest that at stable high stock levels, the population structure of the stock and its
30 condition in terms of K, can have implications for the reproductive output. Hence,
31 quantification of the reproductive potential as TEP has the potential to strengthen the
32 stock-recruitment models, because it captures both the stock population structure and
33 reproductive dynamics.

34

35

36 **Keywords:** Norwegian spring-spawning herring, Fecundity, Total egg production,
37 Reproductive potential, Stock recovery

38

39

40 **1. Introduction**

41

42 The Norwegian spring-spawning (NSS) herring (*Clupea harengus*) stock is
43 distributed in both the Norwegian and Barents Sea (Holst et al., 2004). Over the past
44 century this commercially valuable stock has undergone substantial fluctuations in
45 abundance and recruitment (Dragesund et al., 1997; Toresen and Østvedt, 2000;
46 Nakken, 2008). In the 1940s the spawning stock was 10 to 16 million tonnes, but it
47 then declined and collapsed in the late 1960s (ICES, 1999; Toresen and Østvedt,
48 2000, 2002). The lowest estimated spawning stock biomass (SSB) of a few thousand
49 tonnes occurred in 1972, remaining extremely low throughout the 1970s. After
50 implementation of very strict management regulations and a strong year-class in 1983,

51 the biomass increased, and by 1986, the SSB started recovering, with the current SSB
52 between 8 and 10 million tonnes (ICES, 2007).

53 SSB has often been used as a proxy for the egg production of a fish population
54 (Trippel, 1999). However, it has become apparent that other factors such as stock age
55 or size structure and individual fish condition can have a considerable influence on the
56 stock reproductive potential (SRP) and this in turn could contribute to the recruitment
57 variability (Marshall et al., 1998, 2000; Trippel, 1998, 1999).

58 The estimation of SRP is generally undertaken by scaling up from individual level
59 characteristics to population level. Therefore, information is needed on factors
60 influencing the reproductive investment of each fish. Fecundity of NSS herring has
61 been studied both experimentally and in the field, and condition factor was found to
62 have a significant positive effect on oocyte production (Ma et al., 1998; Óskarsson et
63 al., 2002; Kurita et al., 2003; González-Vasallo, 2006). This has also been noted in
64 both marine and freshwater fish species for example, cod (*Gadus morhua*) (Kjesbu et
65 al., 1991; Lambert and Dutil, 2000); haddock (*Melanogrammus aeglefinus*) (Hislop et
66 al., 1978); winter flounder (*Pseudopleuronectes americanus*) (Tyler and Dunn, 1976),
67 brown trout (*Salmo trutta*) (Bagenal, 1969) and rainbow trout (*Oncorhynchus mykiss*)
68 (Bromage et al., 1991). Age composition of the population and spawning experience
69 (recruit versus repeat spawners) can also influence oocyte production (Solemdal,
70 1997, Atlantic cod; Marshall et al., 1998, Northeast Arctic cod; Macchi et al., 2004,
71 Argentine hake (*Merluccius hubbsi*); Óskarsson and Taggart, 2006, Icelandic
72 summer-spawning herring; Marteinsdottir and Begg, 2002, Atlantic cod). Changes in
73 age and size at sexual maturation as reported in Baltic cod (Cardinale and Modin,
74 1999) and in the same herring stock as present (Engelhard and Heino, 2004) could
75 also alter the reproductive potential of the stock. The NSS herring stock showed
76 spatio-temporal segregation of early and delayed maturation individuals, both in the
77 Norwegian and Barents Sea (Devold, 1963; Dragesund et al., 1980, 1997; Toresen
78 and Østvedt, 2000; Engelhard and Heino, 2004).

79 It has been suggested that total egg production (TEP), rather than SSB, is a better
80 measure of reproductive potential when predicting recruitment (Marshall et al., 2003),
81 as it will account for variations in egg production as a result of fish condition, stock
82 composition, environmental and ecological factors. The dynamics of NSS herring

83 reproductive output with regard to its population composition (recruit and repeat
84 spawners abundance), structure (size and age) and condition factor have, however,
85 not been investigated up to now. Our objective is therefore to explore the impacts of
86 the stock structure and fish condition factor on TEP. This investigation is a
87 contribution toward an understanding of causes for variability in recruitment, as it
88 adds more insight to stock-recruitment relationship by incorporation of inter-annual
89 variability in the condition of individual fish, and the size structure of the population
90 on TEP.

91 The main objective is to link our knowledge of reproductive biology with stock
92 dynamics to improve our understanding of variability in SRP, which will ultimately
93 lead to a better understanding of processes affecting recruitment. More specifically, in
94 this study we explored short and long-term impacts of stock fluctuations in NSS
95 herring on perceived stock productivity, by examining total egg production at
96 different periods and for different fish condition factors.

97

98 **2. Materials and methods**

99

100 *2.1. Study area and data collection*

101

102 Fishery samples caught using different gear (drift nets, beach-seines, purse-seines and
103 trawls) and Institute of Marine Research (IMR) samples caught using research vessels
104 were taken from NSS spawning grounds (58°N to 70°N) from 1935 to 2005. Samples
105 of 100-200 herring per trawl station were regularly collected during the spawning
106 months from January to March along the Norwegian coast. The latitudinal range of
107 data may have some effect on the fish condition factor data, as condition factor may
108 vary with latitudes (Slotte, 1999) and the sampling coverage may vary inter-annually.
109 For each fish, standard morphometric measurements were taken: total length (TL,
110 measured to the nearest 0.5 cm), whole body weight (W, measured to the nearest 1
111 gram), sex, maturity stage, as recommended in Anon. (1962), and scales were
112 sampled for age reading. The herring included in the present analyses were all staged
113 as maturing, i.e., in a pre-spawning state. Spawning and spent individuals were
114 excluded from the analyses as this would have biased length weight relationships.

115

116 2.2. Total egg production (TEP) estimation

117

118 Input data for TEP estimation was taken from the ICES (2006) report. These data
119 were annual spawning stock biomass (SSB) and annual spawning stock numbers
120 (SSN) at age. Because we needed to have the data distributed over length rather than
121 age to get the numbers at length, with their associated weight for the purposes of
122 estimating oocyte production from the fecundity models, the total abundance was re-
123 distributed over length. The conversion of SSB and SSN per age to length was
124 undertaken by using the total numbers at age and then applying the length-at-age
125 proportions given for that year in order to re-distribute the total number at age into
126 length classes. SSN were therefore assigned to the observed proportions of 1 cm size
127 classes in the annually derived length-age keys of mature fish on the spawning
128 grounds. Finally, SSN by length was summed over all age groups by year, of which
129 50% were assumed to be females based on a relatively stable female to male ratio of
130 1:1 as we observed in the raw data over the whole study period to give female
131 spawning stock number (FSSN). The annual mean weight at length was calculated
132 using the raw data from the spawning grounds. Annual TEP was then estimated as the
133 sum of the number of eggs produced by spawning females in each size class
134 multiplied by their average fecundity, which was estimated from the fecundity-weight
135 relationship given by Óskarsson et al. (2002):

136

137
$$TEP_y = \sum_{x=i}^j F_x FSSN_x ,$$

138

139 where y is year, x is size (length in cm) ranging from i to j , F is average fecundity
140 (number of vitellogenic oocytes per female) and FSSN is female spawning stock
141 numbers. This method is similar to the approach used by Marshall et al. (1998). By
142 using annual length frequencies and the year-specific length-weight relationships we
143 were able to both utilise the fecundity-weight relationship and incorporate the effect
144 of variable condition into the analyses (see Marshall et al. 1998). The reasoning is that
145 fish at a given length at the onset of maturation that were heavier were in a better
146 condition. How we obtained the parameters used in the above equation is explained
147 in the next section.

148 Since we have calculated TEP from SSN, which is derived from SSB, and used the
149 same fecundity formula in every case, we needed to investigate and verify how our
150 modelled TEP compares with TEP estimations based on annual fecundity counts. The
151 estimated TEP (1951-1983) from Serebryakov (1990) were compared directly with
152 our estimates of TEP. In the case of Seliverstova (1990) fecundity at age data
153 available for the period 1954-1975 were multiplying by the assumed number of
154 females at age for the same years (ICES, 2006). Where fecundity data were missing
155 for an age class a linear interpolation was used between the adjacent younger and
156 older age classes. A further comparison was made of the annual TEP for the whole
157 time series by replacing the equation we used from Óskarsson et al. (2002) (see
158 above) with the weight related fecundity of Baxter (1959).

159

160 *2.3. Fecundity (F) estimation*

161

162 To estimate TEP of the stock it was necessary to choose an appropriate equation that
163 best describes fecundity-length or fecundity-weight relationship of individuals, an
164 important parameter in the TEP equation. Although there have been a number of
165 studies on the fecundity of NSS herring (Baxter, 1959; Lyamin 1966; Seliverstova,
166 1990; Serebryakov, 1990; Krysov et al., 1995; Belikov et al., 1996; Ma et al., 1998;
167 Óskarsson et al., 2002; Kurita et al., 2003; González-Vasallo, 2006), the results from
168 Óskarsson et al. (2002) were assumed to be the most appropriate because their
169 equation for potential fecundity was based on most recent field samples from January
170 1998. Their equation was $F = 224.3 \times W - 8883$ ($r^2=0.796$; $n=47$), where F is
171 fecundity and W is total body weight (g). However, it should, be noted that the fish
172 size distribution used to determine the fecundity relationship in the work by
173 Óskarsson et al. (2002) did not fully cover the same length and weight range as our
174 data. Another appropriate study on NSS herring fecundity by Baxter (1959) gave both
175 fecundity-length and fecundity-weight relationships and it was used together with that
176 of Óskarsson et al (2002). Results of Ma et al. (1998) and González-Vasallo (2006)
177 were based on laboratory studies and gave significantly higher relative fecundities
178 than the other studies. The study of Kurita et al. (2003) was more concerned with
179 atresia (resorption of oocytes) and does not give a formal equation for length or
180 weight and fecundity. Seliverstova (1990) reported fecundity by age class rather than

181 with a general formula incorporating length and weight and Serebryakov (1990)
182 reported the TEP with no fecundity formula given.

183

184 *2.4. Stock structure and composition*

185

186 Using the age based database, the age structure of this spawning stock was estimated
187 for the period 1935 to 2005 by calculating the Shannon age diversity index (see
188 Marteinsdottir and Thorarinsson, 1998 and reference therein). This index is
189 independent of stock size, and describes both the number of cohorts contributing to
190 the egg production and the evenness of the numbers of individuals across cohorts.

191 Studies on gonad development have demonstrated that length at 50% maturity in NSS
192 herring is relatively stable at 29-30 cm for both males and females, after which all
193 herring are repeat spawners (Østvedt, 1964; Toresen, 1986, 2001; Slotte, 1998, 1999;
194 Óskarsson et al., 2002; Kurita et al., 2003; Engelhard and Heino, 2004). Hence, a
195 length of 32 cm was used in the present study as a threshold between recruit (<32cm)
196 and repeat (≥ 32 cm) spawners, and it was assumed to be applicable for the whole time
197 series under consideration.

198

199 *2.5. Condition factor*

200

201 The stock well-being or fitness (Bolger and Connolly, 1989) was determined as the
202 weighted (by numbers in each length class) condition factor averaged over the 1 cm
203 size classes each year. In this study, we used both Fulton's condition factor (K_F) and
204 relative condition factor (K_R) (both referred to in Ricker, 1975). Fulton's condition
205 factor assumes isometric growth: $K_F = 100 \times W / TL^3$, where W is the total weight (g)
206 and TL is total length (cm). Relative condition factor relates the realised weight to the
207 expected (theoretical) weight calculated from the length-weight relationship, thus
208 $K_R = W_R / W_{TH}$, where W_R is realised weight in grams and W_{TH} is theoretical weight in
209 grams.

210 At the population level, the average K values indicate the overall 'state' of the
211 population's 'health'. It should be noted, however, that the condition factor of fish is
212 influenced by the development stage of its reproductive organs (Le Cren, 1951) and

213 might also be length-dependent (Scott et al., 2006). Consequently, variability might be
214 generated by individual gonad development or inter-annual variation in spawning
215 time. The information in the database came from a number of months around
216 spawning time; hence inter-annual variations in spawning time should not have any
217 dramatic effect at a population scale perspective. Samples were analysed fresh on
218 board the vessel, and therefore we assume that there were no significant effects from
219 handling. However, to test for the possible effect of inter-annual variability, monthly
220 average condition factor for each size class was analysed for significant differences
221 between years. Relationships between K_F and K_R were then analysed using a
222 continuous wavelet transform (CWT) (see Subbey et al., 2008). The wavelet approach
223 allows a scale-to-scale comparison of the two K approaches, to see if they are in
224 agreement. Periodicities in the condition data were analysed using Single Series
225 Fourier Analyses in STATISTICA.

226

227 **3. Results**

228

229 *3.1. Population structure*

230

231 Spawning stock size in biomass and in numbers as estimated by VPA indicated a
232 decline from above 15×10^6 tonnes or 50×10^9 fish in 1944 and 1945 to below $20 \times$
233 10^3 tonnes or 10×10^6 fish in 1972, and again above 8×10^6 tonnes or 40×10^9 fish in
234 1997 (data from ICES, 2006, Fig. 1a). Then it has been kept at around the level of
235 1997. Strong recruitment to the spawning stock was evident as a significant increase
236 in number of fish below 32 cm (Fig. 1b), with relative peaks visible during 1944,
237 1956, 1965, 1977, 1988, 1997 and 2004. Overall, the spawning stock was dominated
238 (above 90%) by repeat spawners (≥ 32 cm), but in the years 1943-1944, 1965-1966,
239 1973, 1976-1977, 1986-1989, 1996-1998 and 2003-2004 the recruit spawners were
240 most abundant (i.e. $> 50\%$ of the SSN) (Fig. 1b). The age structure as characterised by
241 age diversity (H) showed relatively large variations (Fig. 1b). Age diversity was
242 relatively high from 1935 to the early 1950s. From then onward, through the period of
243 stock collapse in the mid 1970s, age diversity declined. Age diversity showed a fairly
244 rapid increase through the late 1970s to mid 1980s even though there was not a major
245 increase in abundance. This was primarily due to an increase in number of age classes
246 and a more even spread of ages within the stock, as the stock recovered. Large year

247 classes tended to make the age structure less even across year classes and this was
248 reflected in the periodic ‘dips’ in the value of H . By the early 1990s to the present the
249 age diversity returned to a relatively high level but not to the levels seen prior to the
250 onset of the stock collapse.

251

252 3.2. Condition factor

253

254 Generally, condition variation was significant within sizes (Student t -test, $p < 0.001$,
255 $n = 149689$) and between sizes (Chi-square, $\chi^2 = 157.48$, $p < 0.001$, $n = 149689$), with
256 more variation observed among fish that were less than 28 cm (Fig. 2). Both K_F and
257 K_R oscillated (Fig. 3) over time, and a continuous wavelet transform showed that there
258 was considerable similarity in fluctuations in the two measures at a wide range of
259 inter-annual scales with the minimum correlation coefficient (r) being approximately
260 0.998. This indicates that the two measures of K are in agreement and therefore any
261 possible influence of gonad maturation did not change the condition dynamics. When
262 the data were pooled over a 5 year moving average it appeared there was a cyclical
263 pattern in the data (Fig. 3). Overall, the two dominant periodicities in both condition
264 indices were 23.3 and 17.5 years for K_F and K_R , respectively (single series Fourier
265 Analyses) (see Fig. 3). Herring reached high average conditions during the late 1950s
266 ($K_F = 0.85$), late 1970s ($K_F = 0.86$) and mid 1990s ($K_F = 0.84$). The lowest average K_F
267 was observed in 1945, while the highest was observed in 1956 and 1972. During the
268 periods toward the mid 1940s and late 1990s when abundance was at its highest (Fig.
269 1), there was a decrease in condition factor (Fig. 3), however, there was no significant
270 correlation between SSN and mean condition factor (K_F) ($r^2 = 0.07$; $P > 0.05$) (Fig. 4).

271

272 3.3. Fecundity

273

274 While fecundity estimates used here are based on a fecundity-weight relationship, Fig.
275 5 illustrates the potential variability in fecundity-at-length due to variability in weight-
276 at-length or condition of the fish. The highest variation in the estimated fecundity was
277 found among the biggest fish, possibly due to the fact that there is a tendency of more
278 weight variation among larger fish.

279 3.4. Long-term TEP

280 Estimated TEP for the full time series 1935-2005 followed the SSN trend closely (Fig.
281 6a), but the residuals in the TEP-SSN relationships (Fig. 6b) were related to changes
282 in proportion of recruit spawners and condition (Fig. 6c). Typically, larger deviations
283 from this relationship were found in periods with high SSN in combination with
284 increasing proportions of either recruit or repeat spawners and decreasing or
285 increasing condition factor (K). Deviations were positive when the stock comprised of
286 above 80% of repeat spawners and K_F above 0.8, and they were negative when the
287 stock was dominated by recruit spawners (repeat spawners less than 40%, Fig. 6c) and
288 K_F below 0.73.

289

290 *3.5. TEP comparisons with published data sets*

291 There existed only a few data to compare with our length-based estimate of TEP. Data
292 from Seliverstova (1990) and Serebryakov (1990) on inter-annual variations in TEP
293 indicate that similar levels of TEP are estimated using either Óskarsson et al.'s (2002)
294 model or the different annually varying fecundity relationships (Fig. 7). In addition
295 whilst there are some differences in the absolute level, especially at higher TEPs the
296 linear regressions between different TEP estimates are highly significant ($r^2 > 0.92$, p
297 $\ll 0.05$). The use of Baxter's (1959) fecundity relationship essentially provides the
298 same perspective as using Óskarsson et al.'s (2002) relationship (Fig. 7).

299 Although linear relationships between different TEP estimated were highly significant
300 (Fig. 8 a,b), the residual plots from both predictors (Fig. 8 c,d) showed that there were
301 systematic deviations between the fitted curves over time, with greater differences in
302 the 1950s, the time when the stock abundance was relatively high, and less in the
303 1970s, the time when the stock abundance was also decreasing substantially.
304 Similarly, residuals against predicted values indicated that deviations were greatest
305 during times of high predicted egg production (Fig. 8 e,f).

306

307 **4. Discussion**

308 In the present study, the TEP of NSS herring was estimated for the period 1935-2005
309 using data on population abundance and structure combined with published
310 relationships between length, weight and fecundity. Over this 70 year period, the TEP
311 fluctuated considerably, closely following the SSB or SSN. Residual analyses

312 demonstrated that positive variations in TEP that were not attributed to SSB or SSN,
313 occurred in periods of high abundance in combination with high K_F and high
314 proportions of repeat spawners. On the other hand, negative residuals are observed
315 when a period of high abundance had fish with low K_F and dominated by recruit
316 spawners. In the same periods systematic deviations were also found between the
317 estimated TEP and previous TEP estimates (Seliverstova, 1990). This is likely to be a
318 result of intra-annual variations in potential and relative potential fecundity in the
319 order of 35 – 55% (Óskarsson et al., 2002), which may be a result of variation in
320 condition factor or the composition of the stock.

321

322 The average K values should not be regarded as absolute because it is likely that intra-
323 annual variation is influenced by gonad development, as energy reserves decline with
324 gonad maturation (Kennedy et al., 2010). However this effect was considered minimal
325 at the inter-annual scale because there was no statistical difference between K_F and
326 K_R . Nevertheless, the fact that K_F and K_R indices showed similar dynamics indicates
327 our use of Fulton's K as a reliable proxy for this stock's condition status. Patterns of
328 changes in condition factor for the entire period could be indicating differences in
329 allocation of energy to growth and reproduction between recruit and repeat spawners
330 (Óskarsson et al., 2002; Engelhard and Heino, 2006). Although we have observed that
331 most of the time K_F of the population was above 0.75, other studies (Óskarsson et al.,
332 2002; Kennedy et al., 2010) have observed that atresia increases markedly when K_F is
333 less than 0.7. In this regard, the long term dynamics of the state of the stock measured
334 in condition factor would still be appropriate at the population level.

335 There has been variation in maturity at age and length over the years (Dragesund et
336 al., 1980; Engelhard and Heino, 2004). Although these changes in maturity at length
337 were relatively small, there were significant differences between year classes before,
338 during and after the collapse (Engelhard and Heino, 2004). The year classes after the
339 collapse (1986-2000) indicated that the stock is regaining characteristics (weight at
340 length, and size and length at maturity) similar to those before the collapse period
341 (1935-1968). The ICES data on age at maturity may not be accurate, because
342 Engelhard and Heino (2004) suggested variation in spawning age that differs from
343 that reported by in the ICES report. These changes could have led to differences in the

344 fecundity and productivity of the stock. In the view of the reproductive potential of
345 recruit and repeat spawners (Slotte, 1998), changes in sexual maturation could also
346 lead to recruitment variances when a bigger year class with early or delayed
347 maturation is recruited. This seemed to be the case during the years that had a more
348 skewed proportion of recruit and repeat spawners, because they correspond with the
349 years of higher residuals. This suggests that detailed stock structure parameters are
350 important for stock productivity and, hence, to be taken into account during
351 assessments. Other factors like atresia (Kurita et al., 2003; Kennedy et al., 2010) and
352 the skipped spawning (Engelhard and Heino, 2005) could also contribute to the TEP
353 variation, but more research on these topics is required to draw any further
354 conclusions.

355 The use of one weight-specific fecundity relationship to estimate TEP could have
356 resulted in increased residuals during periods that had experienced a change in
357 productivity due to differences in condition factors. However, the fecundity model
358 from Óskarsson et al. (2002) was not significantly different from that of Baxter
359 (1959), suggesting that fecundity-weight relationship in 1998 was similar to the one
360 observed in the late 1950s. Nonetheless, levels of variations in fecundity under
361 various conditions (González-Vasallo, 2006; Kennedy et al., 2010) can be significant,
362 and it is therefore still advisable that fecundity and maturation schedules (maturity
363 ogives) should be monitored frequently as there is the possibility they could change
364 over short or long time periods. Maturation at a young but bigger size, as observed
365 during the collapse period (Engelhard and Heino, 2005), is often associated with
366 decline in population size (Toresen, 1990; Trippel, 1995), and could include genetic
367 and phenotypic responses (Shin and Rochet, 1998; Olsen et al., 2004; Marshall and
368 McAdam, 2007).

369 In this study we have not investigated genetic responses, but their role in changes of
370 SRP should not be ignored. Similarly, we did not address the possibility that fecundity
371 may increase with age for a given length or weight, or that there may be a negative
372 effect of population cohort size on fecundity, as there is no unequivocal evidence for
373 these phenomena in NSS herring. However, we examined the data given in
374 Seliverstova (1990) and there was no clear trend in fecundity with age or abundance.
375 During the time period of their investigation, mean weights were changing as was the

376 thermal regime, which probably confounded any potential patterns. The observed
377 deviations between various TEPs indices illustrate other possible factors that could
378 lead to potential different perceptions of stock productivity, as measured by total egg
379 production. In this regard cohort based reproductive potential analyses should be
380 considered since there are cohort effects on life history (Sæther, 1997; Beckerman et
381 al., 2002), i.e., parental or inherited traits define individuals.

382 Clearly, depending on the year-specific condition factor (see e.g. Kennedy et al. 2010)
383 and the structure of the population, total egg production of the stock can vary
384 considerably, mostly at times of high stock abundance. For example, TEP in relation
385 to SSN was overestimated at times when the stock was dominated by recruit
386 spawners, and underestimated when the stock was dominated by repeat spawners. As
387 a result, reference points derived from spawning stock biomass only, may not account
388 for these year-specific variations and year-class structure differences. Not accounting
389 for these factors and dynamics could lead to varying recruitment rates, and more so
390 when coupled with environmental causes. If the egg production potential of the stock
391 is not accounted for in stock assessments and the management, this in turn may
392 impact on expectations for the recovery of the stock. Our work therefore suggests that
393 quantifying the reproductive potential as TEP will contribute to understanding stock-
394 recruitment dynamics because it captures both the population and reproductive
395 dynamics of the stock.

396

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398

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409

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595

596

597 **Fig. 1.** Norwegian spring-spawning herring population abundance and structure over
598 the period 1935 to 2005. (a) annual spawning stock size in numbers (SSN, bars) and
599 spawning stock biomass (SSB, line), (b) the stock structure per recruit (< 32 cm, black
600 bars) and repeat spawners (≥ 32 cm, grey bars) and Shannon age diversity index H
601 (line).

602

603 **Fig. 2.** The variability (mean \pm range) in Fulton's condition factor (K_F) and relative
604 condition factor (K_R) over the range of length classes in Norwegian spring-spawning
605 herring. Each data point represents the mean and standard deviation (SD) of observed
606 fish at each length over time.

607

608

609 **Fig. 3.** Annual variations of the Norwegian spring-spawning herring K_F and K_R (mean
610 ± 0.95 confidence limits) together with the weighted condition factor and a five years
611 moving average.

612

613 **Fig. 4.** Relationship between K_F and SSN for Norwegian spring-spawning herring.

614

615 **Fig. 5.** The variability in fecundity over the range of mature length classes in
616 Norwegian spring-spawning herring. Óskarsson et al. (2002) (open squares) and
617 Baxter (1959) (filled squares). Fecundity relationship of Óskarsson et al. (2002) is a
618 function of weight but transformed to length, using weight-length relationship. Each
619 data point represents the mean and standard deviation (SD) of observed fish at each
620 length over time.

621

622 **Fig. 6.** (a) annual TEP (solid line and dash-dotted line), SSB, (dashed line), and SSN
623 (dotted line), (b) TEP against SSN residuals over time and (c) the relationship
624 between the proportion of repeat spawners, K_F and the annual residuals from TEP-
625 SSN for the years corresponding to the residuals. Closed circles represent annual
626 residuals at their corresponding annual proportions of repeat spawners and each open
627 square represent average K_F .

628

629 **Fig. 7.** (a) total egg production over time as estimated by different authors (Óskarsson
630 et al, solid line: Baxter, dash-dotted line; Serebryakov, dotted line and Seliverstova,
631 mesh line)..

632

633 **Fig. 8.** Relationship between various TEP estimates (a, b) and the residuals by year (c,
634 d) or TEP (e, f), between this study (based on the fecundity curve of Óskarsson et al.
635 (2002)) and Seliverstova (1990) and Serebryakov (1990).

Figure 1

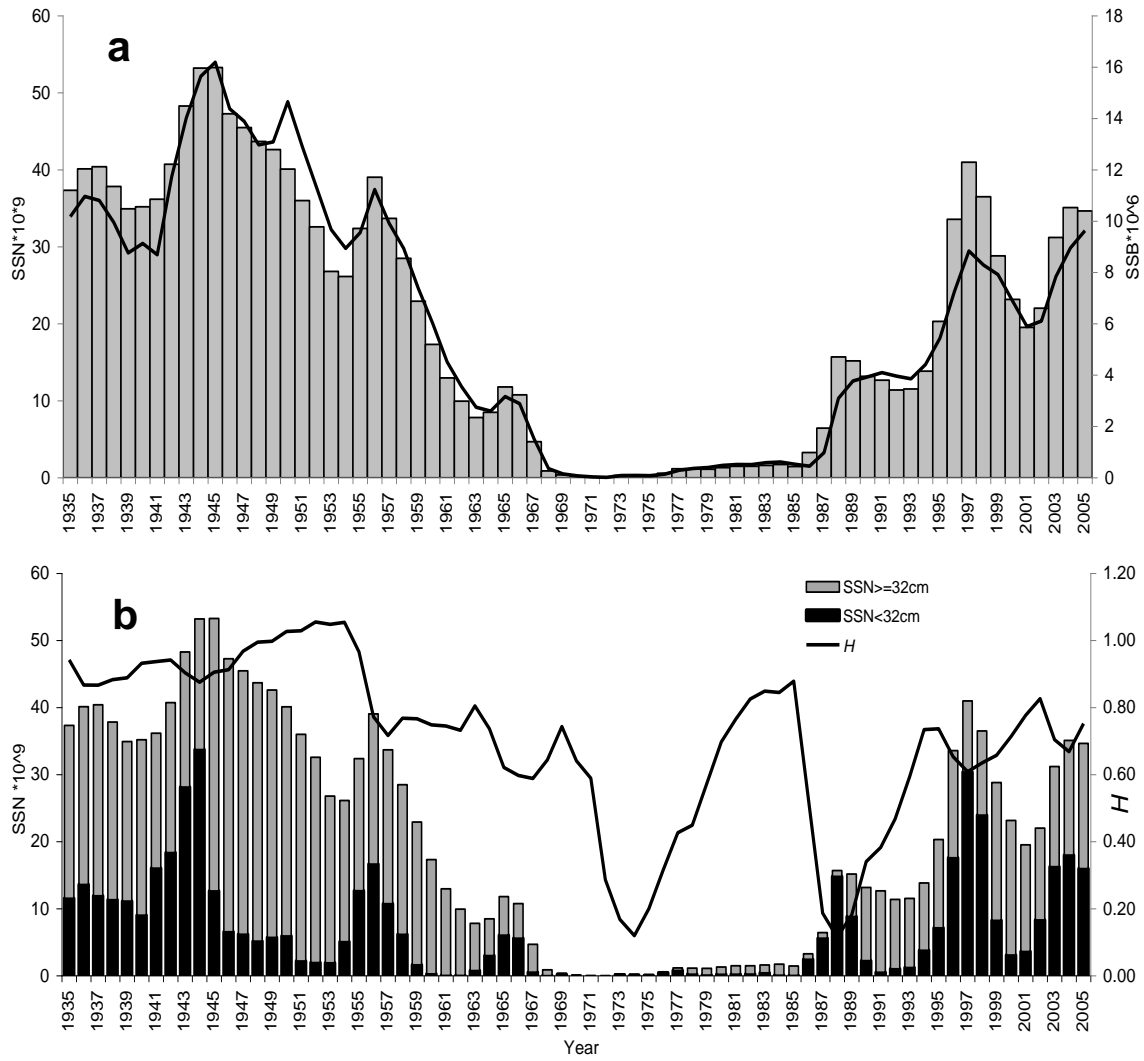


Figure 2

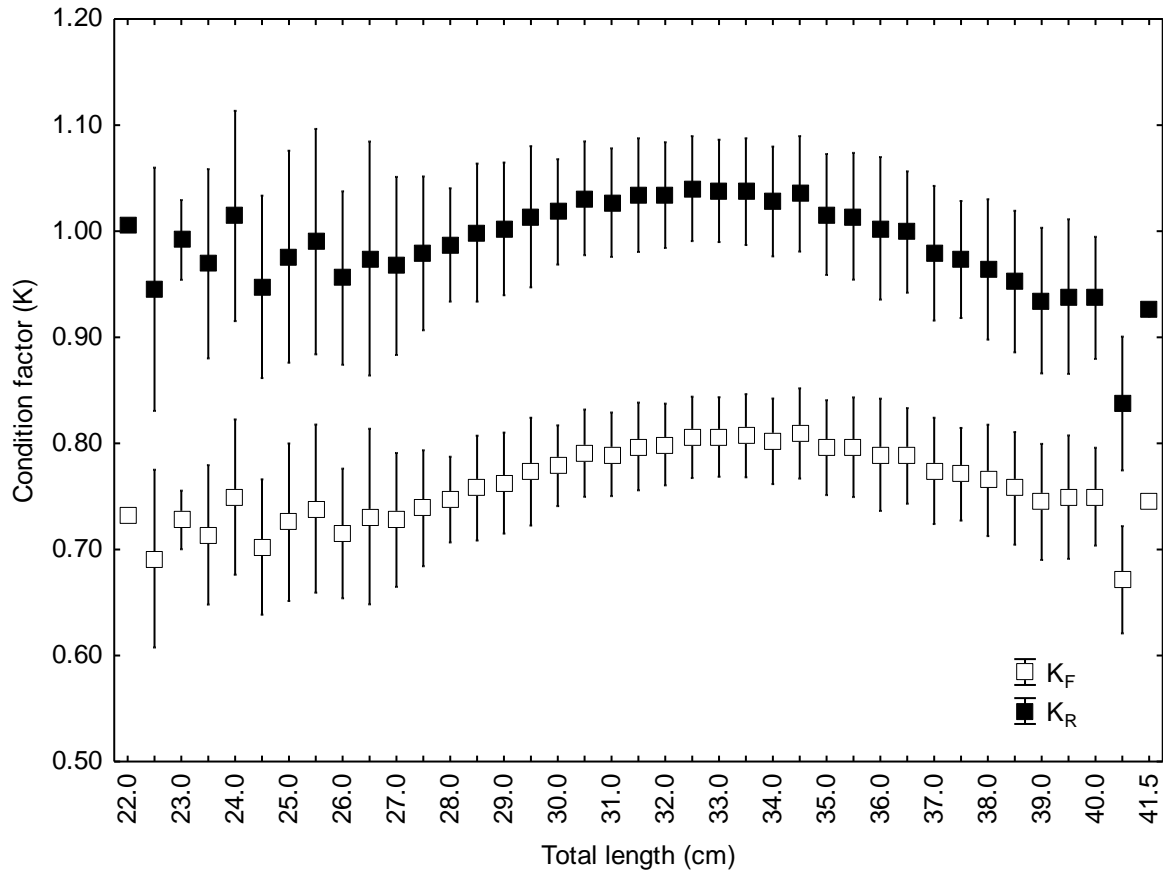


Figure 3

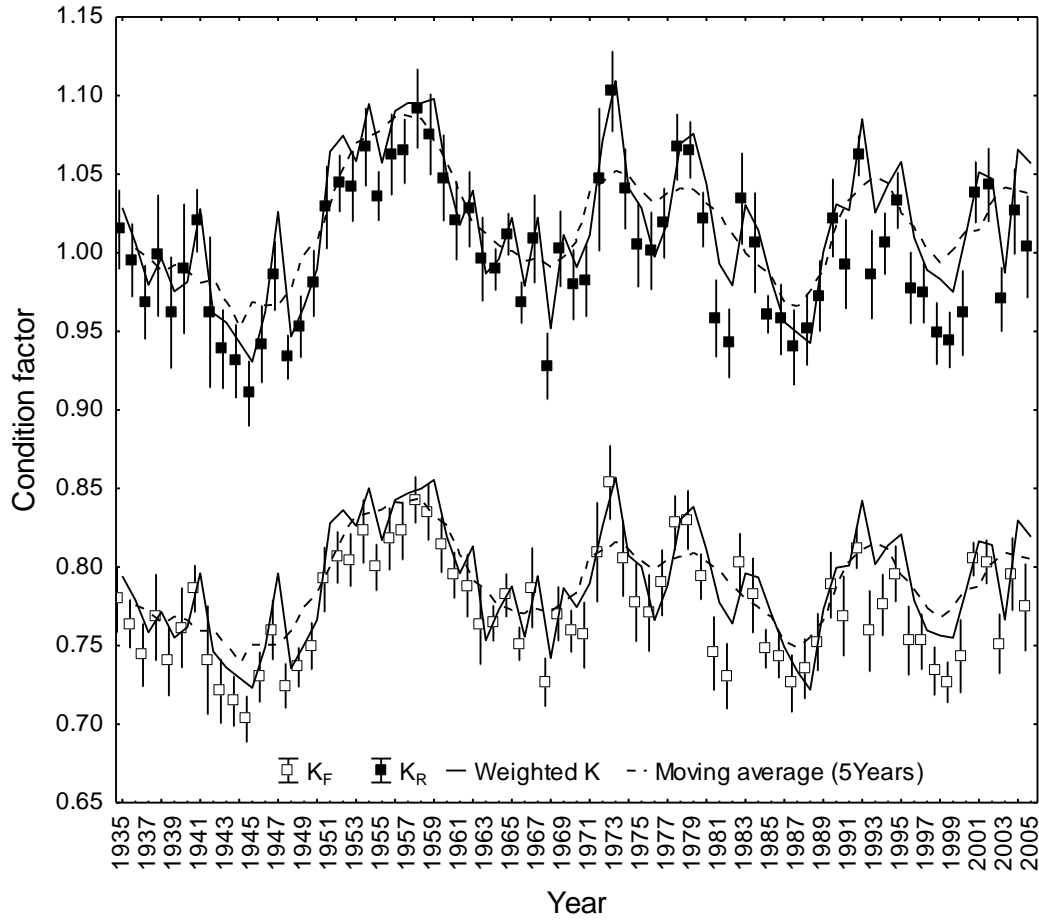


Figure 4

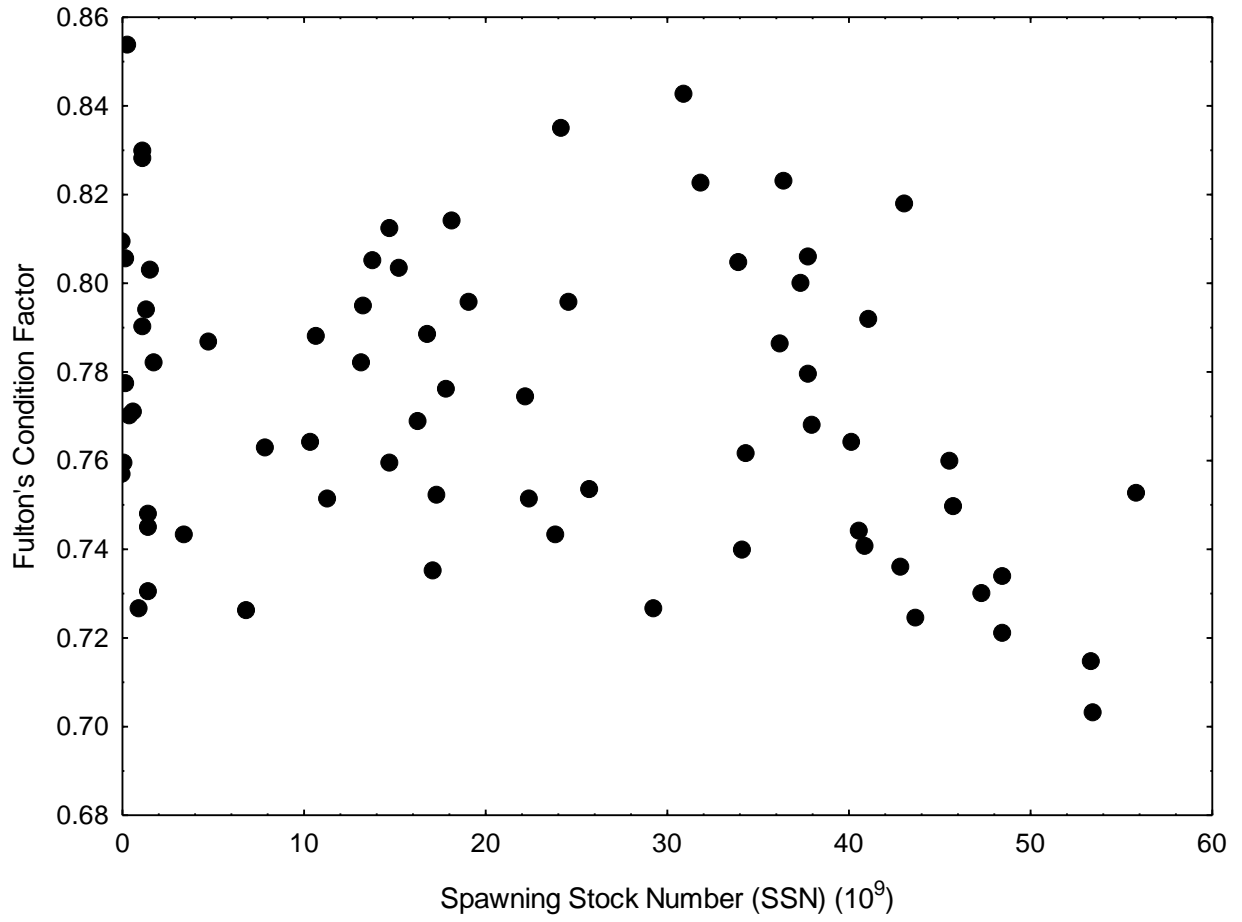


Figure 5.

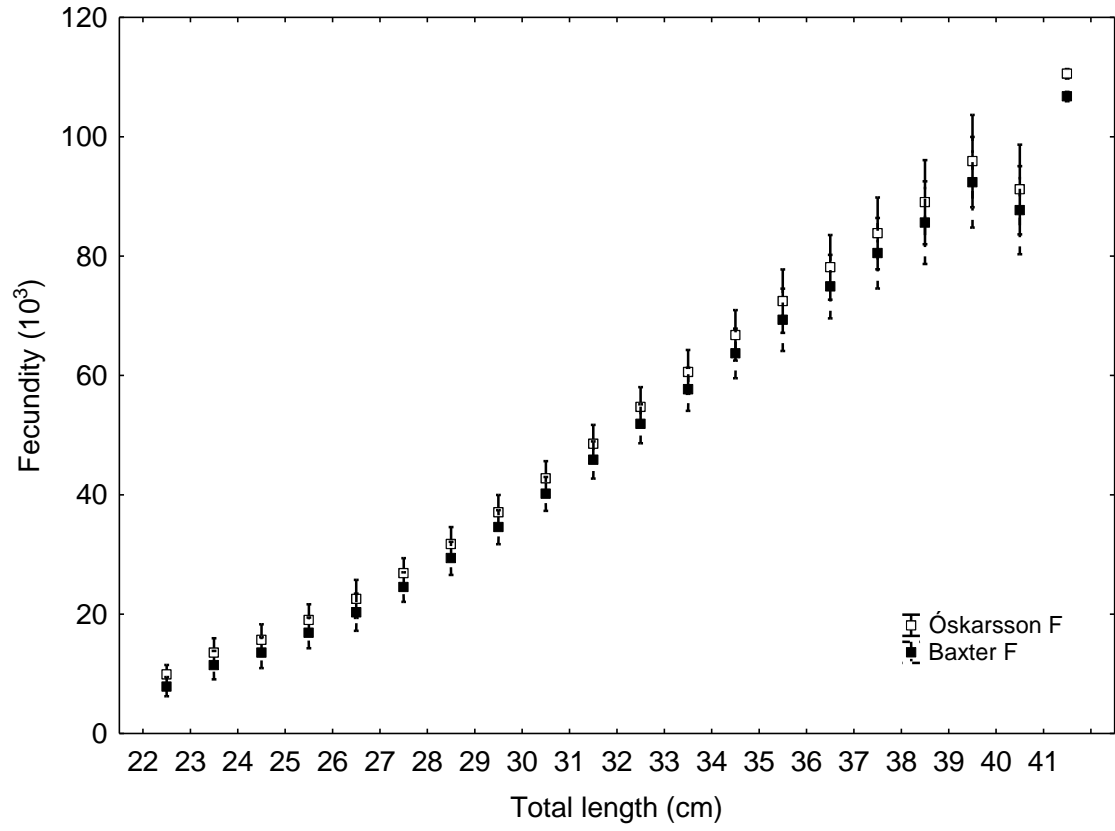


Figure 6.

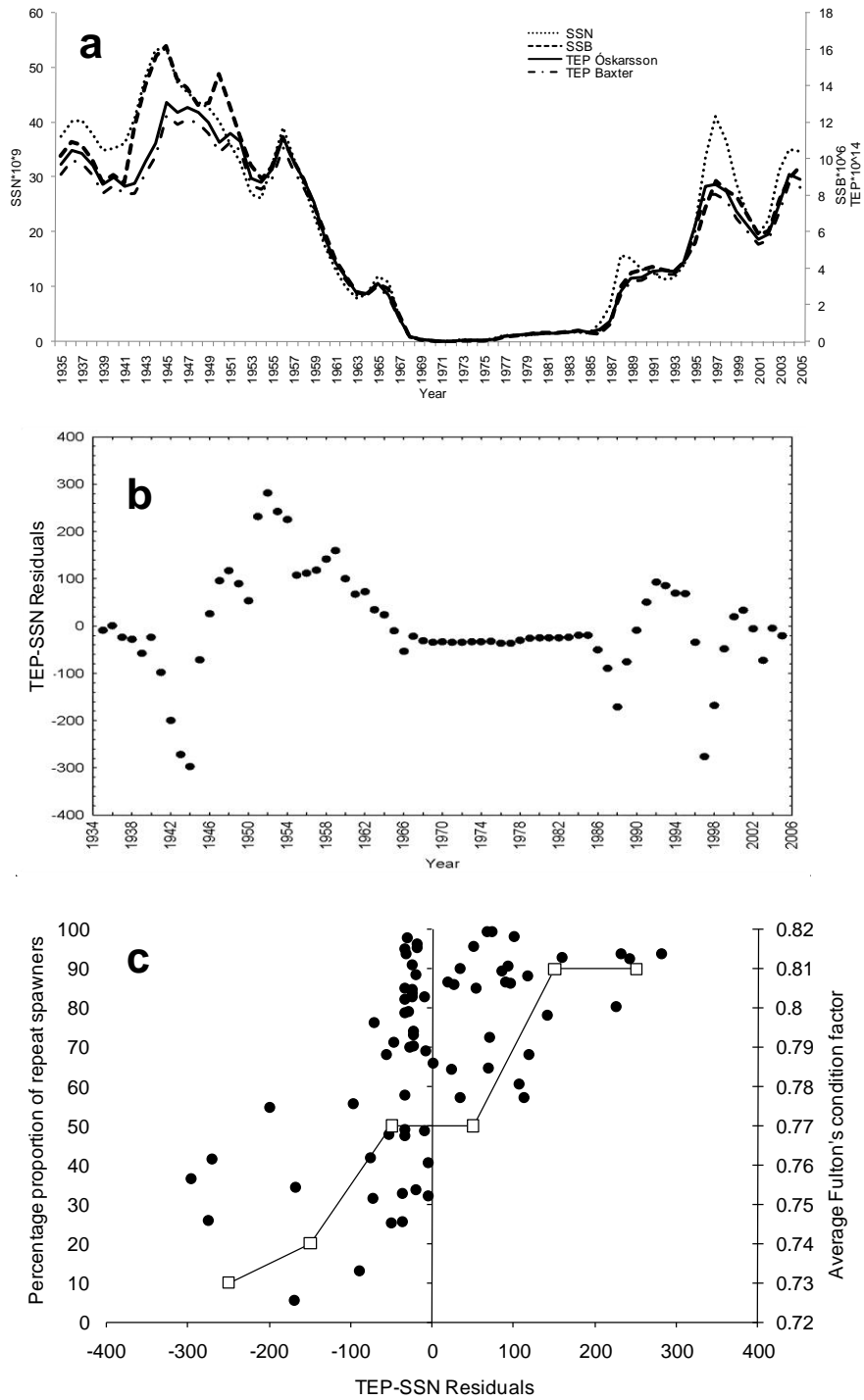


Figure 7.

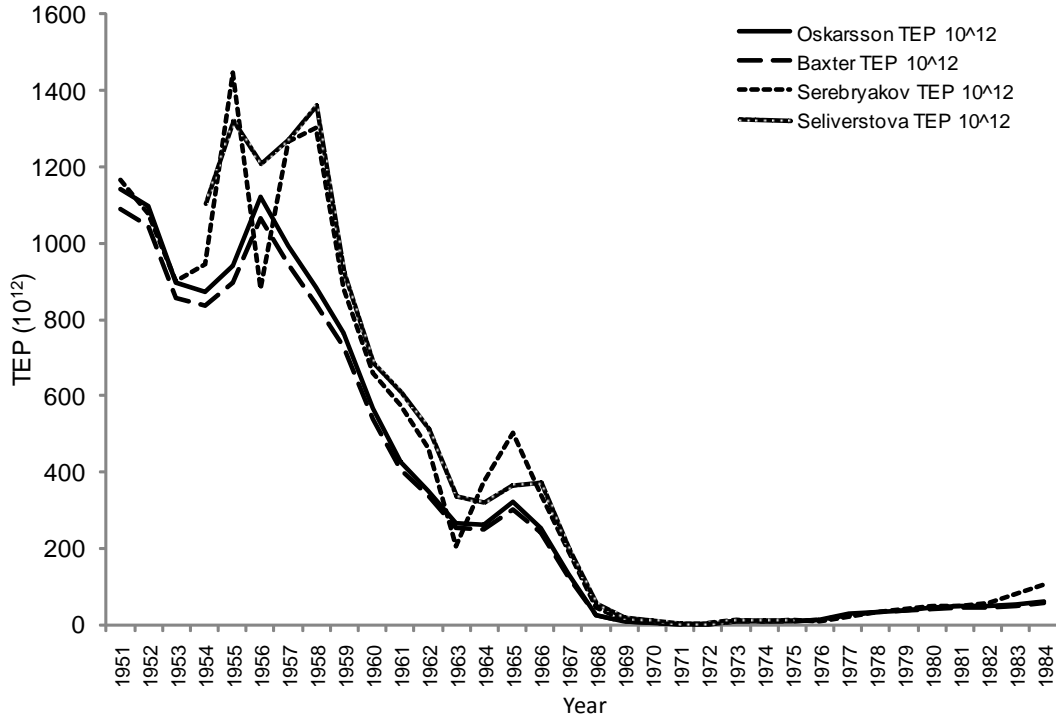


Figure 8.

