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**Evidence from the past: exploitation as cause of commercial
extinction of autumn spawning herring in the Gulf of Riga,
Baltic Sea**

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Abstract:

Historical marine ecology has shown that many exploited animal populations declined before their abundance was quantified by scientists. This situation applies for autumn spawning herring in the Baltic Sea. This stock used to be the dominant spawning group of herring in the early decades of the 1900s and supported several commercially important fisheries, including in the Gulf of Riga (GoR). However, the GoR stock declined during the 1960s–1970s and has not recovered. Neither the former biomass nor reasons for decline are known. Here we recover and analyse historical fishery and biological data and conduct population development simulations to evaluate the hypothesis that exploitation may have been sufficient to lead the stock towards commercial extinction. We found that the estimated exploitation pattern, including exploitation of juveniles,

was unsustainable and led to stock decline. The pattern of exploitation of this stock was consistent with that which caused collapses of other herring stocks, which have since recovered. If autumn spawning herring in the GoR recovers, our findings indicate that this stock could support sustainable annual yields of ca. 4000 t and diversify the fishery resource base which is presently restricted to a relatively small number of species for essentially local coastal inhabitants.

Keywords: Historical marine ecology, herring, catch reconstruction, fishing mortality, immature catch, population modeling, Gulf of Riga

Introduction

Small pelagic fish populations, such as herring *Clupea harengus*, undergo large abundance and biomass fluctuations over time (Dickey-Collas *et al.*, 2010; Harma *et al.*, 2012; Schweigert *et al.*, 2010). Factors responsible for stock dynamics are known for several herring stocks in different marine ecosystems, and suggest that the long-term inter-annual dynamics are driven by a combination of different factors and processes related to both externalities and internalities of marine ecosystems (Dickey-Collas *et al.*, 2010; Schweigert *et al.*, 2010; Toresen and Jakobsson, 2002).

Herring has been one of the most ecologically and commercially important species in European northern seas. The species has a complicated and dynamic population and racial/ecotype (i.e. autumn and spring spawners) sub-structure, which has received attention at least since the end of the 19th century (Heincke, 1898; Zijlstra, 1969). In European waters, there are local populations which spawn at different times of year (e. g., spring, summer, fall and winter), and sometimes populations in the same geographic region spawn at different times (Sinclair and Tremblay, 1984). Within the Baltic Sea, there are historically both spring and fall spawning groups, as well as

48 spatially-distinct groups within each spawning season (Ojaveer, 1988). Presently the dominant
 49 seasonal group of spawners are the spring spawners, which are furthermore recognized to belong to
 50 several different populations which are subject to stock-specific fishery regulations (ICES, 2017).
 51
 52 Autumn spawning herring in the Baltic Sea are presently rare, compared to spring-spawners, and
 53 support no directed fisheries (ICES, 2017; Parmanne *et al.*, 1994). However they were formerly
 54 common or even dominant in the western Baltic-Rugen area, central Baltic Sea and Gulf of Riga
 55 (GoR), and historically made an important contribution to the Baltic Sea herring landings
 56 (Parmanne *et al.*, 1994). For example, they contributed over 90% of the landings from the central
 57 Baltic Sea in 1925–1927 (Hessle, 1931); in the Gulf of Riga, the catches of spring and autumn
 58 spawning herring are shown together in official statistics, but autumn spawning herring made up to
 59 47 % of the total herring catches on feeding grounds in the 1970s (Ojaveer, 2003). Also, it was
 60 hypothesized that autumn spawning herring was an important target fish in the Gulf of Riga fishery
 61 in the late 17th century (Gaumiga *et al.*, 2007). The spring and autumn spawning herring ecotypes
 62 in the Baltic Sea differ genetically and hence support full reproductive isolation (Bekkevold *et al.*,
 63 2016). Some of the key characteristics of the autumn spawning herring, relative to the spring
 64 spawning herring, specifically in the Gulf of Riga, include spatio-temporally differentiated
 65 spawning (autumn spawners reproduce in more offshore areas and at greater depths in late summer
 66 – fall period while spring herring reproduces in shallow coastal areas in spring), harsher
 67 environment during the larval retention period (fall-winter for autumn spawners vs. spring-early
 68 summer for spring spawners) with poorer larval feeding conditions for autumn spawners, later
 69 maturation (age 3 or 4 for autumn spawners vs. age 2 for spring spawners) and bigger weight-at-
 70 age ($T_{w_{inf}}$ 85.0 and 65.1 g for autumn and spring spawners, respectively) (Ojaveer, 1988, 2003).
 71 Many of these traits, in particular, the last two, make the autumn herring more vulnerable than

spring spawning herring to fishery exploitation because some fishing regulations (e.g. mesh sizes) are presently set according to the dominating spring spawning herring growth and maturation rates.

The diversity of herring stocks in general, and in the Baltic Sea and GoR in particular, may have positive benefits for commercial fisheries. The potential beneficial effects of a rich and diverse population base on which fisheries can depend has been evident for nearly 60 years (Ricker, 1958), and has gained increased attention in the past 1-2 decades. Modelling studies show that mixed-stock fisheries can be more productive if each stock is managed according to its productivity, rather than applying the same regulations to all stocks in the stock assemblage (Hutchinson, 2008; Ricker, 1958; Schindler *et al.*, 2010). This multi-stock effect is also believed to have parallels at the species level in communities, with communities having more species believed to be more stable because of complementarities among species in their ecosystem functions and life histories (Figge, 2004; Lindegren *et al.*, 2018). These effects of multiple stocks within a species or multiple species within communities are known as portfolio effects (Figge, 2004; Hilborn *et al.*, 2003; Schindler *et al.*, 2010). In the case of herring in the Baltic Sea, multiple stocks, including the autumn and spring spawning ecotypes, are often captured together (ICES, 2016a). As noted by Ricker (1958), exploitation of the more productive stocks at their maximal levels could lead to the local extermination of less productive stocks in mixed-stock fisheries. This situation may have happened to some of the autumn spawning herring stocks in the Baltic Sea, including that inhabiting GoR. In contrast, in some other areas where only one ecotype dominates the herring biomass, commercial extinctions of those ecotypes could not be offset by alternative ecotypes. This situation characterizes the North Sea and Norwegian Sea, whose autumn- and spring-spring spawning stocks respectively were overexploited (including high exploitation of juveniles) and eventually collapsed during the 1960s-early 1980s (partly due also to poor environmental conditions); these stocks have

since recovered to high levels during the 1990s-2010s (Dickey-Collas *et al.*, 2010; ICES, 2015; Toresen and Jakobsson, 2002).

The factors which have caused the near total collapse of autumn spawning herring spawners in the Baltic Sea are not known as little modern investigation has been done since the 1990s, mostly due to lack of fish to investigate. Most knowledge is therefore based on older material but has not yet been interpreted in ways which could identify reasons for the decline. We re-examine much of the historical material for this stock and track the magnitude of the autumn-spawning herring fishery in one sub-basin of the Baltic Sea (GoR) for almost one century (since the 1920s). In addition, we apply quantitative fishery population methods to investigate the potential that fishing, both on adults and juveniles, was a contributing factor to the decline, and estimate the historical spawning stock biomass (SSB).

Material and methods

Description of the study area and herring fishery

The GoR (area 16 330 km², volume 424 km³) is situated in the north-east part of the Baltic Sea (Figure 1). It is connected to the Baltic Proper *via* two shallow straits in the west and receives most of the riverine freshwater input in the south. The shallow depth of the GoR (mean 26 m, maximum > 60 m) results in a complete vertical mixing during the winter (Berzinsh, 1995). Salinity varies from almost freshwater (< 1 PSU) in coastal surface layers in spring to > 7 PSU at the bottom close to Irbe Sound (Berzinsh, 1995) without any vertical stratification. The GoR is covered by ice in winter. The seasonal thermocline occurs from May until September and separates the relatively

120 stable deep water (temperature ca. 3°C) and the highly variable surface layers (temperature up to
121 20°C) (Raudsepp, 2001).

122

123 The GoR is inhabited by permanent local spring and autumn spawning herring populations, with
124 temporal occurrence, mostly during the spawning season, of herring originating from one or more
125 populations from the Baltic Proper (Ojaveer, 1988). In the current work, we assume that the autumn
126 spawning herring stock was exploited at a high level from the mid-1950s–1970s, due to the specific
127 circumstances of fishery at that time: these included the Soviet planned economy, an already-
128 established bottom trawl fishery and basically unregulated fishery before the International Baltic
129 Sea Fisheries Commission was established (in 1974) ((Ojaveer, 1988) and E. Ojaveer, pers.
130 comm.). There are no direct quantitative estimates of fishing effort (e. g. numbers of fishers, boats,
131 nets, fishing days per year) for the time period, which limits the type of analyses that are possible.
132 However, given the nature of the fishery as outlined above and in earlier literature (Ojaveer, 1962,
133 1988), there is a good reason to assume that fishing effort was already high in the mid 1950s.
134 While market demand remained principally the same throughout the years (due to the Soviet
135 planned economy) and the fishery was oriented at maximizing landings, some technological
136 advancements in trawling occurred: bigger and more efficient pelagic pair trawls started to be used
137 in the first half of the 1960s (Ojaveer, 1988). However, the impact of this gear development on
138 autumn spawning herring is impossible to quantify. These circumstances facilitate use of the catch
139 data for estimating approximate fishing mortality (F) rates and biomass in ways which are described
140 below and in the classical fisheries literature (Hilborn and Walters, 2001; Quinn II and Deriso,
141 1999).

142

143 *Historical data availability and sources*

144 As a basis for the population analyses, our initial objective has been to compile and digitize the
 145 available data from historical sources and organize them in ways that could facilitate quantitative
 146 analysis. All available information and data for the coastal fishery for two fishing districts in the
 147 northern GoR (Pärnu and Saaremaa; Figure 1), which were historically the most important autumn
 148 spawning herring fishery regions in the area, were retrieved from different sources for the following
 149 three periods:

- 150 i. For the period of 1920s–1930s, the data was extracted from Estonian national fishery
 151 journals *Kalandus*, and *Laevandus ja Kalandus*. The reliability of data is unknown but
 152 presumably similar to that for other national fishery agencies around the Baltic at the same
 153 time; however, the underlying raw data are unavailable.
- 154 ii. Original summary notes, often on handwritten sheets, from primary sources during the
 155 Soviet time (1945–1989) were obtained from archives of the Estonian Marine Institute,
 156 University of Tartu. The sources of these data were the local state-owned fishing companies
 157 (called in the former USSR fishing kolhoses). The reliability of these data is considered
 158 relatively high, as data often originate from ‘local correspondents’ who were in close contact
 159 with scientific staff of the governmental research institute at that time (the Tallinn
 160 Department of the Baltic Sea Fisheries Research Institute: BALTNII RH) receiving the
 161 reporting.
- 162 iii. Official catch statistics from the most recent period was obtained from the Ministry of
 163 Environment (1992–2005) and Ministry of Rural Affairs (since 2006) of Estonia. The
 164 reliability and accuracy of data is similar to reporting of all other of fish catches, incl. of
 165 internationally assessed and managed species.

166

The months when fishing occurred (August–November) were assumed to be similar across all years. While detailed quantitative effort data were only sporadically available, the background qualitative information on fishing gear types and practices used are relatively well known for all three periods both from the same sources of quantitative catch data availability as well as personal communication with local fishermen (by H. Ojaveer).

Information for both offshore trawl and coastal fishery on the number of fish caught by age-cohorts formed in years 1951–1971 was available for the entire GoR from archives of Estonian Marine Institute, University of Tartu. The data represent the landings made by the former USSR and therefore landings made by the present-day countries of Estonia and Latvia. Autumn- and spring-spawning herring were distinguished using otolith characteristics (Ojaveer, 1962, 2003). We used mean maturity ogive data available for 1964–1977 ((Ojaveer, 1988); Supplementary Table T3) to calculate the percentage of immature fish by numbers in the catch. The various datasets were then used to develop estimates of F and SSB (Figure 2 flow chart of data flows), as described in following sections.

Data analyses and population modelling (see also Supplementary material):

One of the objectives of our investigation was to evaluate whether F would have been sufficient to cause a large decline of the SSB . Evaluating this objective requires estimates of F , which can then be compared with estimates of F_{msy} for other herring stocks, including those in the Baltic Sea.

We first estimated total mortality rates (Z) and F for the GoR autumn spawning herring using the

190 available numbers-at-age in the catch data for 1954–1976. We used “catch curve analysis”
191 (Hilborn and Walters, 2001; Quinn II and Deriso, 1999) to derive estimates of total and fishing
192 mortality for each year during this time period. Details are provided in the Supplementary Material.
193
194 There are and never have been fishery or biomass reference points for the autumn spawning herring
195 stock in the GoR. Consequently, it is not possible to compare our historical F estimates with those
196 that are estimated to lead to sustainable exploitation for this specific stock. Instead, and to estimate
197 approximately whether the fishing may have been unsustainable, we use information from other fish
198 stocks with similar life-histories and experiencing similar ecosystem conditions. These include
199 other Baltic herring stocks, such as the GoR spring spawning stock, the central Baltic Sea herring
200 stock, the western Baltic herring stock and the Gulf of Bothnia herring stock. In addition, we also
201 compared our F with those which preceded major collapses and local extinctions of other herring
202 populations to determine whether F were similar to those which were associated with major herring
203 declines elsewhere. In combination, these two comparisons can indicate approximately whether
204 exploitation of the autumn spawning GoR herring was sustainable.

205

206 *Estimation of spawning stock biomass:*

207

208 We used the estimated F to derive estimates of SSB. Such estimates can potentially be used as
209 approximate indices of the level of biomass that may have been present, and the potential carrying
210 capacity for autumn spawning herring in this region. As F is instantaneous value, it can be
211 converted algebraically to total annual removal rates (Dick and MacCall, 2011), which are measures
212 of the exploitation rate (i.e. yield/biomass or yield/SSB (MacCall, 2009; Rosenberg *et al.*, 2014;
213 Walters *et al.*, 2006; Worm *et al.*, 2009):

214

215
$$E_{SSB} = Y/SSB$$

216

217 where E_{SSB} is annual exploitation rate for SSB, and Y = yield in tonnes (t). Rearrangement of this
218 equation enables estimation of SSB for each year in the time series, given age composition data and
219 maturity-at-age probabilities (Supplementary Tables 1, 2). We used these data to estimate annual
220 SSB.

221

222 We were also able to derive additional SSB estimates for a limited number of years (1957–1961)
223 based on a different approach involving different assumptions. These estimates are based on the
224 relative share of autumn and spring spawning herring in scientifically monitored commercial trawl
225 catches in the GoR throughout the entire ice-free season (March–November); this sampling
226 extended over a relatively long period of the year to obtain as full seasonal coverage as possible and
227 beyond that associated with only the specifically targeted fishery in coastal areas during spawning
228 time (Ojaveer, 1962). The years when these samples were collected correspond to those when
229 catches of autumn spawning herring were at their highest during our 80+ year time series (See
230 Results: Figure 3). The proportion of autumn spawning herring in the monitored trawl catches was
231 applied to earlier-derived estimates of the SSB of the spring-spawning stock (Ojaveer *et al.*, 2004),
232 assuming that the relative share of autumn spawning herring in the monitored trawl catches was
233 similar to their relative share in the ecosystem during the whole ice-free season. These estimates of
234 SSB, based on fewer data and other assumptions, were compared with those derived above from
235 age-based catch-curve analyses.

236

237 *Stock dynamics modeling:*

238

239 We investigated the potential role of fishing on the decline of autumn spawning herring in the GoR
240 by simulating the stock dynamics using the derived estimates of SSB and F. The simulation used a
241 standard single-species age-structured model of fish population dynamics (Quinn II and Deriso,
242 1999). Stock simulations with this model allowed us to investigate whether the estimated F (see
243 above) were sufficiently high to have caused collapse, or whether additional factors would also
244 need to be present to cause collapse (e.g. higher M, reduced stock productivity due for example to
245 lower recruit production per spawner, etc.). Our objectives with these simulations were to evaluate
246 whether fishing could have been the main factor to reduce SSB and Y by the levels observed
247 between 1954–1976, and whether the timing and rates of these declines *in situ* could be reproduced
248 by applying the estimated F. Our simulation time period starts when estimated SSB and recorded
249 commercial catches were near their maxima (1960) and extends forward for a period of 31 years.

250

251 The model requires several inputs of biological data (weights, maturation probability and M-at-age;
252 numbers at age in the population) and relationships (i.e., SSB-R) associated with herring life-history
253 to enable population calculations. Most of these inputs were available from historical fisheries
254 literature for this stock.

255

256 However, there is no SSB-R relationship for the autumn spawning herring in the GoR. A
257 reasonable alternative model for a SSB-R relationship is a downscaled version of the relationship
258 (Ricker, 1954) for the spring spawning stock in the central Baltic Sea (i.e. ICES Subdivisions 25–
259 27, 28.2, 29 and 32), where ecological conditions are similar to those in the GoR. The downscaling
260 process preserves the shape of the relationship but adjusts parameter magnitudes to observed levels
261 of SSB derived from the historical data (See results below). Further details of the downscaling and

parameterisation of the SSB-R relationship are available in the Supplementary Material. Our use of the central Baltic stock to represent stock-recruit dynamics is only intended to represent a reasonable first-order estimate of the shape of the relationship; a true parameterisation, which does not yet exist for this stock, could differ somewhat depending on local conditions and stock biology, and could indicate a different vulnerability to exploitation and recovery rate than estimated using the central Baltic herring relationship. However, given the uncertainty of stock-recruitment relationships, including that for the central Baltic spring spawning, such differences between the two stocks probably have little ecological importance.

The uncertainty of the recruit estimates from the downscaled stock-recruitment relationship was used together with the derived estimates of age-specific F and other biological inputs in simulations of the population dynamics of the autumn spawning herring stock. Modelling scenarios are described below.

Modelling scenarios:

We conducted a modest number of scenarios to address whether observed levels of exploitation could have led to a major decline in biomass and how exploitation of juveniles contributed to the decline. Model scenarios addressed how population biomass would have been influenced by levels of exploitation corresponding to status quo F (F_{sq}), including and excluding exploitation of juveniles (ages 1 and 2).

An additional scenario was conducted to explore the combined consequences of a large increase in F during 1973–1976 (see Results below) and an increase in M due to increased predation by cod in

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1979–1983 following an increase in cod abundance and subsequent trophic cascade effects in the GoR (Casini *et al.*, 2012). For these years, M was increased by 25% from 0.15 to 0.1875, as also assumed by the ICES stock assessment working group for the GoR spring spawning herring stock (ICES, 2016a). The scenarios and their input settings are detailed in Table 1.

Table 1. Summary of settings used and key assumptions for simulation scenarios of autumn spawning herring stock dynamics in the Gulf of Riga, Baltic Sea. The stock dynamics were simulated using an age-structured model including a stock-recruitment model, parameterized and downscaled for the central Baltic Sea spring spawning herring stock. Scenarios 1-3 were conducted to explore effects of fishing at historical levels on stock dynamics. Scenarios 4-9 were conducted to estimate spawning stock biomass under six combinations of assumed fishing and natural mortality rates. See Methods for details.

Scenario	Fishing mortality for ages 3-8	Fishing mortality for ages 1 and 2	Natural mortality (all ages)	Stock-recruit model	Comments
1	0.58	0.02; 0.31 (time series medians)	0.15	Ricker	The fishing mortalities assumed in this scenario correspond to those estimated from catch-at-age and catch-curve analyses (i. e., "observed")

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					fishing mortality pattern).
2	0.58	0	0.15	Ricker	Exploitation pattern as in Scenario 1, but with no juvenile F.
3	0.58; 1.16 for 1973-1976	0.02; 0.31 and 0.04; 0.62 for 1973-1976	0.15; 0.1875 for 1979-1983	Ricker	Exploitation pattern as in Scenario 1, except that it was increased in some years. In addition, this scenario assumes a higher M for some years due to higher cod predation.
4	F_{msy} (0.22) for central Baltic spring spawners	0; 0.22	0.15	Ricker	Sensitivity scenario for F, M.
5	F_{msy} (0.22) for central Baltic spring spawners	0; 0.22	0.20	Ricker	Sensitivity scenario for F, M.
6	F_{msy} (0.22) for central	0; 0.22	0.25	Ricker	Sensitivity scenario for F, M.

	Baltic spring spawners				
7	F_{msy} (0.32) for G. Riga spring spawners	0; 0.32	0.15	Ricker	Sensitivity scenario for F, M.
8	F_{msy} (0.32) for G. Riga spring spawners	0; 0.32	0.20	Ricker	Sensitivity scenario for F, M.
9	F_{msy} (0.32) for G. Riga spring spawners	0; 0.32	0.25	Ricker	Sensitivity scenario for F, M.

299

300

301 *Model exploration of candidate F_{msy} and B_{msy} reference points:*

302

303 We used our population model to simulate how two potential F_{msy} values could affect the stock
 304 dynamics and potential fishery Y. The F_{msy} values we considered were those for the GoR spring
 305 spawning herring and the central Baltic spring spawning herring. We note that the assumed levels
 306 of M, for the three stocks differ somewhat: 0.15 for autumn spawning herring in the GoR (Ojaveer,
 307 1988), 0.2 for spring spawning herring in the GoR (ICES, 2016a) and 0.21–0.33 for central Baltic
 308 spring spawning herring (1990–2015; (ICES, 2016a)). Because differences in M can potentially

allow different levels of sustainable exploitation, we also included simulations for three different M (0.15, 0.20, 0.25) at each F_{msy} level. We calculated the final median SSB and fishery Y after 30 years of population simulation; these SSB levels can be considered to be estimates of the SSB likely to be present under a sustainable level of exploitation, i.e., B_{msy} . For these six scenarios we assumed exploitation of age 2 herring to be the same level as for older ages (3–8), and exploitation of age 1 herring was zero (See Table 1).

315

316 **Results**

317

318 *Dynamics of landings:*

319

320 In the coastal fishery, landings data for autumn spawning herring are available in Pärnu and
321 Saaremaa regions since the late 1920s and for the entire GoR during 1945–1989 (Figure 3;
322 Supplementary Table T3). Saaremaa landings were often much higher in the 1920s–1930s than in
323 the 1940s and first years of the 1950s. Afterwards, coastal landings both in Pärnu and Saaremaa
324 regions and the entire GoR increased exponentially and reached a peak by the end of the 1950s–
325 early 1960s (ca. 1 500 and 3 000 t in the Pärnu/Saaremaa region and the GoR, respectively).
326 Subsequently the landings declined steeply and continued to fall more slowly from the mid-1960s
327 until the end of the 1980s. During the 1990s, there were almost no landing records. In the more
328 recent years (since 2006), landings rarely exceeded the level of 15 t (Figure 3). The decrease in
329 landings since the 1960s has led to a reduction in the number of harbours where autumn spawning
330 herring were landed in the northern GoR: 28 harbours in the 1950s–1960s compared to only 4 at
331 present (Figure 1).

332

333 Comparing the period means for 1945–1971 and 2006–2014, coastal landings in the Pärnu area in
 334 the earlier period exceeded those in the more recent period by 109 times (539.8 ± 82.3 , 4.9 ± 2.4 ;
 335 mean $\pm$ SE, respectively). Similarly, landings around Saaremaa were 60 times higher in the earlier
 336 period than recently (567.4 ± 77.0 , 9.4 ± 3.6 ; mean $\pm$ SE, respectively). The age composition of the
 337 commercial catches is known during 1954–1976. In this period, approximately half of the total
 338 annual catches were juveniles (mean = 42%; range: 17–79%; Figure 4).

339

340 *Evaluation of F and SSB:*

341

342 The catch-curve analyses of the decline in numbers-at-age were usually highly significant for each
 343 year in our time series (Supplementary Table T4). Based on the slopes of these relationships, F for
 344 ages 3–8 during 1954–1976, averaged 0.58 (range 0.08–1.42; SD = 0.32; Figure 4). Mean F during
 345 this period was therefore almost twice as high as F_{msy} (0.32) for the GoR spring spawning herring
 346 and 2–3 fold higher than for some other Baltic herring stocks (Table 2 – list of F_{msy} for different
 347 herring stocks). Given the estimates of F and the catch data, the estimated annual SSB ranged
 348 between ca. 8 000–27 000 t during the time period (Figure 4).

349

350 Table 2. Estimates of F_{msy} for several Baltic and other herring stocks.

351

Stock	F_{msy}	Reference
Gulf of Riga spring spawning herring	0.32	(ICES, 2016a)
Central Baltic Sea spring spawning herring (ICES Subdivisions 25–27, 28.2, 29 and 32)	0.22	(ICES, 2016a)
Gulf of Bothnia, Northern Baltic Sea spring spawning herring	0.15	(ICES, 2016a)

(ICES Subdivision 30)		
Western Baltic Sea spring spawning herring (Division IIIA and ICES Subdivisions 22-24)	0.33	(ICES, 2016b)
North Sea autumn spawning herring	0.33	(ICES, 2016b)
Norwegian Sea spring spawning herring	0.15	(ICES, 2015)

352

353

354 SSB estimates for the years 1957–1961 based on the scientifically monitored catches, the relative
 355 proportions of spring and autumn spawning herring in these catches and estimates of spring
 356 spawning herring SSB indicated that SSB during these years averaged 21 000 t with a peak of 26
 357 000 t (Table 3). These estimates compared favorably with those derived analytically for the same
 358 years using catch age composition and catch-curve analysis methods (Figure 4).

359

360 Table 3. Estimates of spawner biomass for autumn spawning herring derived from direct
 361 measurements using scientifically monitored catches during ice-free seasons in 1957-1961 in the
 362 Gulf of Riga (Ojaveer, 1962). The spawning stock biomass of autumn spawning herring was
 363 assumed equal to spring spawning herring spawner biomass * (% autumn spawners in catches / 100
 364 - % autumn spawners in catches).

365

Year	Spring spawning herring spawner biomass (thousand tons)	% autumn spawning herring in scientifically monitored commercial catch during ice-free seasons	Autumn spawning herring spawner biomass (thousand tons)
------	---	--	---

1957	28.4	44.1	22.4
1958	19.4	49.7	19.2
1959	30.8	41.0	21.4
1960	23.2	53.0	26.1
1961	34.8	30.9	15.6
Avg.	27.3	43.7	21.2

366

367

368 *Simulated population development:*

369

370 The initial SSB of ca. 25 000 t declined within ca. 15 years to ca. 7 500 t and to 5 000 t after 30
371 years, for an exploitation scenario corresponding to the long-term mean F observed from our catch-
372 curve analysis and including exploitation of juveniles (ages 1 and 2; Figure 4). The likely
373 uncertainty due to the S-R relationship and the initial stock numbers indicated that the 10th – 90th
374 percentile range for SSB at the end of the 30-year period is 2 800–7 100 t (Supplementary Figure
375 2).

376

377 A simulation having identical settings, but with no juvenile exploitation allowed the stock to remain
378 at a higher level (ca. 11 000 t) after 30 years (Figure 5, upper panel). Final expected annual Y
379 associated with these two exploitation scenarios were ca. 3 000 and 6 000 t respectively (Figure 5,
380 lower panel).). As a result, the expected yield could have been nearly doubled had juvenile
381 exploitation been kept near zero (i. e., a fishing gear selection pattern having $F = 0$ for juveniles).

382

383 The simulation involving high adult exploitation during the mid-late 1970s and increased M during
384 1979–1983 led to a rapid drop in SSB and a corresponding short-term gain in Y. In the years
385 which followed, exploitation level was lower and the biomass recovered slightly. The impact of
386 higher M on SSB was relatively small in this simulation.

387

388 The range of simulated SSB and Y after 30 years of simulation using 6 combinations of F and M
389 was 6 800–23 000 t of SSB and 2 700–5 800 t of Y (Figure 6). Within each F scenario, the range in
390 M resulted in a ca. 2–fold range in final SSB (Figure 6).

391

392 **Discussion**

393

394 *Historical ecology for insight to past dynamics of autumn spawning herring in GoR:*

395

396 We have recovered and analysed historical fishery and biological data to derive a new picture of the
397 magnitude of biomass and variability of this stock which declined several decades ago, and for
398 which the reasons have previously not been investigated. Our original calculations indicate that the
399 stock experienced unsustainably high fishery exploitation. This pattern included overall high levels
400 of exploitation which exceeded ca. 2–4 times those now considered to be sustainable for other
401 neighboring herring stocks, including a stock living in the same region. In addition, the exploitation
402 included a high rate of juvenile removals, on average accounting for 40–50% of all the herring
403 landed by number. In combination these factors likely led to a rapid drawdown of stock biomass.

404

405 We have also been able to derive a new time series of SSB. This time series compares well with
406 SSB estimates available from limited survey data in a few years in the late 1950s–early 1960s.

407 These two methods for SSB estimation are based on vastly different datasets and assumptions.

408 However, their consistency indicates that they both likely provide reasonable estimates of the

409 historical biomass of autumn spawning herring that once lived in the GoR. As such, they provide

410 useful historical ecological knowledge of the magnitude of past biomass levels, as well as targets

411 for future stock recovery actions.

412

413 As noted by others recently (Engelhard *et al.*, 2016; Lotze, 2014; Schwerdtner Máñez *et al.*, 2014),

414 historical marine ecological information can potentially inform present-day decision-makers about

415 past and future stock and ecosystem dynamics. Such inferences are often made based on data

416 material which is fragmented or averaged over time – space scales which do not easily fit into many

417 routine stock assessment methods. This situation also applies to our case study. As a result, the

418 findings (e.g. F and SSB time series) should be considered indicative of likely levels and trends

419 applicable over long time periods, rather than precise estimates for specific years. This is partly

420 because many of the input data were averages over different time periods, or not available for this

421 stock, and also because there is limited fishery-independent or effort data available for calibration

422 (“tuning”) or comparison. However, the consistency of the different SSB estimates, and the general

423 correspondence between the simulated biomass dynamics and the development of the fishery,

424 suggest that the approaches and conclusions are reasonable.

425

426 Methodologically, our work and methods could be considered to lie approximately in the middle of

427 an “information gradient” available for doing stock assessments and hindcasts. This gradient could

428 be considered to span a range from more extensive, data-resourced assessments such as those done

429 for many of the largest and commercially most important stocks in Europe and North America

430 where available datasets include detailed catch sampling and monitoring (e. g., sizes, ages,

431 maturities), effort indices, research vessel surveys for estimating pre-recruit, recruit and adult
432 abundances, and standardized CPUE time series for assessment tuning, to smaller stocks where only
433 catch and some species-specific lifehistory (e. g., maximum body size, age and size at maturity)
434 data are available (e. g., in many multi-species fisheries around the world). There are now methods
435 becoming increasingly available for assessing the ecological status of data-limited stocks and
436 historical dynamics (Costello *et al.*, 2012; Pauly, 2013; Rosenberg *et al.*, 2014; Walters *et al.*,
437 2006), and these also include many assumptions about fishing effort and stock productivity. Our
438 investigation, given its reliance on incomplete historical data, includes some methodological
439 approaches and concepts from both data-rich and data-poor stock assessment and reconstruction
440 methods. It has, however, developed some reasonable estimates of the past dynamics and relative
441 roles of fishing and environmental factors on this stock.

442

443 In general, estimating the dynamics of fish stocks and diagnosing causes for past fluctuations is a
444 challenge even with the most data-resourced stocks, and this challenge is even more difficult with
445 historical data due to various limitations (Rosenberg *et al.*, 2014). In future, the consequence of
446 such data limitations on perception of stock dynamics and their causes could be addressed, via
447 simulation and sensitivity analysis using a data-rich stock such as, for example, North Sea herring,
448 whose long-term dynamics are relatively well-known, as a case study. Various data or entire
449 datasets could be removed to create gaps, exclude years, etc., to turn effectively a data-rich stock
450 into a data-poor one; different stock assessment and reconstruction methods now available (see
451 citations above) could then be applied to the stock for various levels of data availability, and the
452 derived estimates of SSB, recruitment, and exploitation rate (and their temporal variability) could
453 be compared with the same variables from the full data-rich assessment.

454

455 Such an analysis and comparison would quantify how much deterioration in outputs occurs with
456 data loss (or limitation), and illustrate which data inputs have biggest impacts on the uncertainty of
457 key stock and fishery-related variables. The analysis would have the added advantage of
458 illustrating how much “better” (as judged by different criteria) the assessment or reconstruction
459 becomes as new kinds of data are included. Furthermore, given the cost of acquiring that data (e.
460 g., age composition monitoring of commercial catches; fishing effort data), the analysis could reveal
461 how much more (less) reliable the results become as the financial cost associated with data
462 acquisition and availability increases (decreases).

463

464 *Exploitation as likely driver of stock decline:*

465

466 Our population simulations showed that the observed level and pattern of exploitation led to a rapid
467 decline in SSB and Y. Additional simulation showed that a short period of even higher
468 exploitation, similar to that observed in the mid-late 1970s, depressed the stock even further. These
469 simulated declines occurred at approximately the same time and with same magnitude as those
470 observed in nature, i.e., the simulated biomass declined by ca. 70% (from 25 000 to 75 00 t) within
471 ca. 15 years, corresponding closely to the changes observed in the available catch data. The
472 similarities of the dynamics further suggest that the simulation model setup and its underlying data
473 and assumptions represent most of the key processes (e.g. mortality, reproduction, growth) affecting
474 the stock. Moreover, the estimated magnitude of exploitation which led to these declines (0.58), as
475 noted above, exceeds typical estimates for F_{msy} for Baltic and other herring populations (Table 2).
476 Consistent with an unsustainable level of exploitation, the simulated population also declined to a
477 low level within a short time.

478

479 The F estimates and population simulations indicate that fishing alone can explain most of the
480 observed decline in SSB in the 1960s–1970s. That is, if exploitation levels did exceed F_{msy} to this
481 degree, and juvenile exploitation also was as high as estimated here, it is likely that exploitation was
482 the main factor which brought the stock to a low level by the end of the 1980s. Similar
483 combinations of overexploitation of adults together with high exploitation of juveniles have led to
484 collapses of several other herring stocks, including those in the North Sea, Norwegian Sea and
485 Georges Bank (Dickey-Collas *et al.*, 2010; Melvin and Stephenson, 2007; Toresen and Jakobsson,
486 2002). For example, F for adults and juveniles in the years leading up to the collapse of the North
487 Sea herring was 0.6–1.4 and 0.1–0.4 respectively (Dickey-Collas *et al.*, 2010). Similarly, F for
488 adults in the pre-collapse and collapsing period for the Norwegian spring-spawning herring in the
489 late 1960s was 0.4–1.4 and was frequently even higher for juveniles during most of the 1950s–
490 1960s (Dragesund *et al.*, 1980). Given that our estimates of F (Figure 4) are within these ranges,
491 the decline of the autumn spawning herring in GoR is consistent with the consequences of similarly
492 high levels of herring exploitation elsewhere.

493
494 Moreover our calculations of the impact of exploitation may have underestimated the impact of
495 fishing. Due to lack of quantitative information about fishing effort and the fishing technology
496 used, we followed the assumption that fishing effort was high and remained high during the time
497 period of our study. Given the nature of the fishery management and the Soviet planned economy
498 in place at the time (see Methods), it is evident that fishing effort was high already at the start of the
499 time period and remained so during at least until the stock had declined to low levels. Increases in
500 fishing effort due, for example, to technological creep or other factors, would therefore represent an
501 increased influence of exploitation on the stock, which is not accounted for in our analyses due to
502 lack of quantitative information.

503

504 The high level of adult and juvenile exploitation apparently dominated the direct potential impacts
505 of a variety of environmental factors that could also have influenced population dynamics. For
506 example, winter severity and autumn-winter wind strength have been shown to influence year-class
507 strength (Ojaveer, 1988), and warm ($> 15^{\circ}\text{C}$) water temperatures in late summer may cause female
508 reproduction failure in autumn spawning herring (Ojaveer *et al.*, 2015). In addition, given that
509 spawning habitat for autumn spawning herring is deeper than that for spring spawning herring
510 (Ojaveer, 1988), the autumn stock may be more vulnerable to eutrophication-related anoxia events.
511 Human-induced eutrophication, first observed in the Baltic Sea in the 1950s–1960s (Elmgren,
512 1989), may therefore have played some role in egg survival and larval hatching success for both
513 stocks, and is believed to have caused very high (up to around 90%) average annual embryonic
514 mortality of the spring spawning herring in the GoR during 1985-1991 (Kornilovs, 2006).

515

516 Some of these factors, including the temperature-related reproductive impairment which was also
517 observed in the 1960s-1970s (E. Ojaveer, pers. comm.), and possible interactions of exploitation on
518 stock biology that increase stock vulnerability to detrimental environmental conditions (Anderson *et al.*,
519 2008; Planque *et al.*, 2010) via for example altered age or size composition effects on stock
520 reproductive potential and success (Lambert, 1990; Marshall *et al.*, 2003), may have also
521 contributed to the overall decline. However, our population simulations showed that the estimated
522 levels of exploitation, despite assuming no environmentally – structured variation in the recruitment
523 or stock productivity, were sufficient to cause a decline comparable in magnitude and timing as that
524 observed from the available data. Had environmental factors or their interaction with stock biology
525 been important for stock dynamics over a sufficiently long period, the stock would have declined
526 faster and/or earlier than it did and than was estimated from our population simulations. For these

527 reasons, we believe that the environmental variables were secondary drivers of stock dynamics
528 during this time-period, including affecting some year-to-year variations, and that direct effects of
529 exploitation was likely the main reason for the decline.

530

531 Our finding that exploitation was sufficiently high to cause the stock decline is another example of
532 how overexploitation has led to major declines, and in some cases, commercial extinctions of
533 herring stocks. As noted earlier, some major herring stocks collapsed in the 1960s-early 1980s
534 following prolonged periods of high exploitation (e. g., $F > F_{msy}$) of both adults and juveniles.
535 Following these declines, exploitation was reduced and the stocks eventually recovered. These
536 declines and recoveries demonstrate the potential consequences of extended overexploitation of
537 both adults and juveniles on stock dynamics and fishery yields, and the benefits of ensuring
538 exploitation is at sustainable levels.

539

540 Our simulations can potentially identify candidate levels for fishery and biological reference points
541 for this stock. Such reference points will be needed, should the stock recover to commercially
542 exploitable levels. In general, and according to theoretical models of fishing impacts on fish
543 population dynamics, an approximate level of F_{msy} is an F value that results in a long-term reduction
544 of SSB by ca. 50% from a maximal or unexploited level (MacCall, 2009; Rosenberg *et al.*, 2014).
545 Our sensitivity analyses of the combined effects of two levels of F and three levels of M indicate
546 that SSB would be reduced by 5–73% for these combinations of F and M . These results suggest
547 that, if $M = 0.15$ and a reduction of SSB by ca. 50% is a desirable management policy objective,
548 F_{msy} could be > 0.32 (the current F_{msy} for the spring spawning herring in the GoR) and consequently
549 somewhat higher than F_{msy} for both the central Baltic stock and the spring spawning herring stock in
550 the GoR. However as illustrated by the sensitivity analysis, any estimated F_{msy} will depend on the

551 assumed level of M (as well as many other variables), so new studies of M may be needed to
 552 improve a future estimate of F_{msy} (and B_{msy}). Moreover, the estimated reference points will be
 553 sensitive to the underlying dynamics (and resulting parameters) of the S-R relationship. A dedicated
 554 autumn spawning S-R relationship should be derived to support estimation of reference points.
 555 However, given that only one new observation becomes available per year, such a relationship
 556 cannot be quantified before many years. Given the various uncertainties associated with, for
 557 example, the estimate of M and the absence of a stock-recruit relationship for the autumn spawning
 558 GoR herring, it may be more prudent to adopt a more pre-cautionary (i. e., lower) value of F_{msy} such
 559 as that used for the central Baltic herring (0.22) or the northern Baltic herring (0.15; Table 2).

560

561 Decline of the autumn spawning herring represents a reduction of the portfolio effect of having a
 562 diverse range of stocks and species on which local fishing industries can depend (Schindler *et al.*,
 563 2010); in principle, such a reduction increases the vulnerability of the fishing industry to collapses
 564 of the remaining stocks or species. Given that the Baltic Sea, and the GoR in particular, has a low
 565 number of species and functional groups in its fish community (Ojaveer *et al.*, 2010), a reduction in
 566 their abundance must be considered as a decline in the potential resources for fishery exploitation.

567

568 *Future prospects for autumn spawning herring in the GoR*

569

570 The future status of autumn spawning herring in the GoR is unclear. The strong recoveries of
 571 previously collapsed large herring stocks elsewhere demonstrate that herring stocks can and do
 572 recover under some circumstances. In the case of the autumn spawning herring in the GoR, it is
 573 very difficult to forecast when the stock might rebuild to commercially exploitable levels: there is
 574 presently very little direct knowledge of its R or (essentially egg and larval) mortality processes, or

575 other stock knowledge during the past 30 years on which sound fishery management advice could
576 be based.

577

578 In general, however, recovery would be promoted by strong year-classes and low exploitation of
579 existing autumn spawning herring, either via targeted fishing or as bycatch in other fisheries (e.g.,
580 for spring-spawning herring, which presently dominates herring catches in the GoR). Reducing
581 exploitation of autumn spawning herring could be achieved by restricting fishing effort for spring-
582 spawning herring to times and places where the chances of catching autumn-spawning herring are
583 minimal. In addition, because the size at maturation of autumn herring is much bigger than for
584 spring spawning herring and because autumn spawning herring have been caught together with
585 spring spawning herring (Ojaveer, 1988), an increase in mesh size used in spring spawning herring
586 fisheries in some seasons or areas could reduce the catch of juvenile autumn spawning herring; this
587 would allow more juveniles to survive and reproduce.

588

589 Recovery could also be influenced by oceanographic and climatic conditions that influence stock
590 biology and productivity (also see above). Fish stocks undergo multi-annual periods of varying
591 productivities which are large enough to drive major fluctuations in population dynamics (Britten *et*
592 *al.*, 2017). For example, the current combination of increasing summer temperatures (which may
593 cause female reproduction failure in the GoR autumn spawning herring; Ojaveer *et al.* 2015),
594 continued eutrophication, and increasing abundance of a herring predator (grey seal, *Halichoerus*
595 *grypus* (HELCOM, 2015; Lundström *et al.*, 2010)), together with potential bycatch in spring-
596 spawning herring fisheries could be sufficient to keep the stock at low abundance. In addition,
597 given past and expected future warming of the Baltic Sea in the coming decades (BACC, 2007;
598 MacKenzie and Schiedek, 2007; Meier *et al.*, 2012), the reproductive success of the remaining

599 autumn spawning herring may decline, thereby delaying recovery even longer than under an
600 average or colder temperature regime.

601

602 However, if the stock does recover to, for example, a biomass associated with some of our B_{msy}
603 estimates, then it could support small localized fisheries of ca. 4 000-t annually. Such fisheries
604 could support and diversify local sea-based economies in coastal regions of Estonia and Latvia.
605 Our findings therefore provide a quantified historical context against which future stock
606 developments may be compared and interpreted. More generally we have illustrated how historical
607 but incomplete fishery records can be combined and used to develop new quantitative insight into
608 the dynamics of a former commercially-exploited fish stock, which can potentially contribute to
609 new fishery and ecosystem management plans (Engelhard *et al.*, 2016). There are likely many other
610 similar opportunities for historical reconstruction and insight for exploited animal stocks in other
611 parts of the global ocean. The recovery and analysis of such data would broaden the current
612 knowledge base of how human activities have affected marine populations and ecosystems.

613

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624

625 **Figure captions:**

626 Figure 1. Map of the study area showing the Gulf of Riga in the eastern Baltic Sea, and currently
 627 and formerly operational fishing harbours in the Estonian part of the Gulf of Riga.

628

629 Figure 2. Flow chart illustrating steps and datasets used for estimating fishing mortality and total
 630 and spawning stock biomass for autumn spawning herring in the Gulf of Riga during 1954-1976.
 631 SSB, TB, F are spawning stock biomass, total biomass, and fishing mortality.

632

633 Figure 3. A. Coastal fishery catches of autumn-spawning herring in the Pärnu Bay area and near
 634 Saaremaa Island during 1928-2014. B. Catches of autumn-spawning herring in the Gulf of Riga
 635 during 1928-2015. Shown are the sum of catches in two local coastal areas (Pärnu Bay area and
 636 near Saaremaa) during 1928-2015, and for the entire Gulf of Riga in offshore trawl and coastal
 637 fishery by all gears during 1951-1976 according to data availability. Note that the catch in tonnes
 638 for the entire Gulf of Riga offshore + coastal fishery is calculated from annual catch numbers-at-age
 639 and a mean weight-at-age from the catch for the period 1960-1969 (Kostrichkina and Ojaveer,
 640 1982).

641

642 Figure 4. A. Proportion of immature fish in autumn spawning herring coastal fishery catches in the Gulf of
 643 Riga during 1954-1976. B. Instantaneous fishing mortality estimates for ages 3-8 autumn spawning
 644 herring in the Gulf of Riga as estimated from catch-curve analyses applied to annual catch age
 645 composition data. F_{msy} is for the central Baltic herring stock (ICES, 2016b). See Methods for details

646 of calculations. C. Time series of estimated spawning stock biomass for Gulf of Riga autumn
 647 spawning herring during 1954-1976. Fishing mortality rates used as inputs were estimated based on
 648 catch-at-age data and catch curve analyses; see Methods for details.

649

650 Figure 5. Simulated trajectories of spawner biomass (A) and yield (B) for three scenarios of
 651 exploitation of autumn spawning herring in the Gulf of Riga. Scenarios 1 and 2 only differ in the
 652 levels of juvenile exploitation (i. e., 0 or 0.31). Scenarios 2 and 3 differ in levels of exploitation
 653 (increased in 1973-1976) and natural mortality (increased during 1979-1983). See methods for
 654 details and Table 1 for scenario setting descriptions.

655

656 Figure 6. Simulated spawning stock biomass (A) and fishery yield (B) for autumn spawning
 657 herring in the Gulf of Riga under two levels of fishing mortality (0.22, 0.32) and three assumptions
 658 of natural mortality (0.15, 0.20, 0.25). The results correspond to scenarios 4-9 in Table 1. Spawner
 659 biomass and yield are estimated as the medians of the final year of a 30-year simulation (200
 660 realisations per year) using an age-structured model incorporating uncertainty in the initial stock
 661 numbers and the stock-recruitment relationship. See Methods for details and Table 1 for scenario
 662 settings.

663

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665

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843

**Evidence from the past: exploitation as cause of commercial
extinction of autumn spawning herring in the Gulf of Riga,
Baltic Sea**

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Supplementary Materials:

Text (Methods)

Figures

Tables

Supplementary Methods:

The following text is an extended version of sections of the Methods in the main text:

21 Data analyses and population modelling:

22

23 One of the objectives of our investigation was to evaluate whether F would have been sufficient to
24 cause a large decline in the autumn spawning stock. Evaluating this objective requires estimates of
25 F , which can then be compared with estimates of F_{msy} for other herring stocks, including those in
26 the Baltic Sea.

27

28 We first estimated total and fishing mortality rates for GoR autumn spawning herring using the
29 available numbers-at-age in the catch data for 1954–1976. We used “catch curve analysis”
30 (Hilborn and Walters, 2001; Quinn II and Deriso, 1999) to derive estimates of total and fishing
31 mortality for each year during this time period. For this analysis, we assumed that ages 1–2,
32 although captured in high numbers in some years (Supplementary Table T1, Supplementary Figure
33 1) were not fully recruited to the fishery, as is the case with present herring fisheries in the GoR and
34 other parts of the Baltic Sea. This assumption was supported by visual inspection of the natural
35 logarithm ($\ln$) of numbers-at-age vs. age scatterplots which showed that these age groups tended to
36 be outliers from linear regression models applied to older age groups (Supplementary Figure F1 –
37 age composition plot for ages 1–14). The catch curve analysis used all age-groups 3 years and
38 older.

39

40 According to this method of analysis, the slope of the linear regression of $\ln$ numbers-at-age vs. age
41 corresponds to the total mortality rate experienced on average during the period of the study
42 (Hilborn and Walters, 2001; Quinn II and Deriso, 1999). To derive F by age for each year for the
43 fully – recruited age groups (i.e. 3+), we used an earlier-derived estimate of natural mortality (M)

44 rate for this time period ($M = 0.15$; (Ojaveer, 1988)). This rate is somewhat lower than M estimated
45 for GoR spring spawning herring (0.2 or 0.25 for all age-groups since 1977; (ICES, 2016)).

46

47 The catch curve method for estimating F assumes that recruitment (R) is constant or varies
48 randomly among years (Hilborn and Walters, 2001). Real inter-annual variations in recruitment
49 (and also other variables such as natural mortality, M) will therefore lead to variations and
50 uncertainties in the estimated slope of the catch-curve analysis. It is difficult with the data at hand
51 to estimate how large an effect this has on the estimated F values. We note however that in general,
52 the uncertainty of the F estimates can be expressed in different ways, including the root-mean-
53 square-error (RMSE) of the fitted regression model, and the standard error of the slope term. We
54 calculated and displayed both metrics of uncertainty in the Results (Supplementary Table 4).
55 Because the method for estimating F is uncertain for individual or specific years, we avoid
56 making comparisons of F between years and give most emphasis in our investigation to the overall
57 mean value derived from the time series. In this way, the potential effects of inter-annual variations
58 in recruitment are integrated over time, thereby allowing above- and below-average recruitment
59 years to balance each other, and reducing potential uncertainties in time-averaged F as much as
60 possible.

61

62 To derive approximate estimates of F for the ages which were not fully recruited (i.e. ages 1 and 2),
63 we used the long-term mean relative age composition of the stock based on the experimental
64 catches (1964–1972), the known catch numbers.-at-age for all age groups (including ages 1 and 2),
65 the maturity probabilities, weights-at-age (Supplementary Table 2) and the estimated SSB (see
66 below). These data allowed us to estimate the numbers in the stock at ages 1 and 2. Given the

67 catch numbers at age for these ages in each year, it is possible to derive the annual exploitation
68 (removal) rate for these age groups:

69

70 $E = \text{total numbers removed} / \text{total number in stock}$

71

72 The annual exploitation rate can then be used to estimate the instantaneous F according to

73

74 $N_t = N_0 e^{-Ft}$

75

76 $N_t / N_0 = e^{-Ft}$

77

78 $F = -\ln(N_t / N_0)$, assuming $t = 1$ year (Hilborn and Walters, 2001).

79

80 As there are and never have been fishery or biomass reference points for the autumn spawning
81 herring stock in the GoR, it is not possible to compare the F with those that are estimated to lead to
82 sustainable exploitation for this specific stock. Instead, and to estimate approximately whether the
83 fishing may have been unsustainable, we use information from other fish stocks with similar life-
84 histories and experiencing similar ecosystem conditions; these include other Baltic herring stocks,
85 such as the GoR spring spawning stock, the central Baltic Sea herring stock, the western Baltic
86 herring stock and the Gulf of Finland herring stock. In addition, we also compared our F with those
87 which preceded major collapses and local extinctions of other herring populations to determine
88 whether F were similar to those which were associated with major herring declines elsewhere. In
89 combination, these two comparisons can indicate approximately whether exploitation of the autumn
90 spawning GoR herring was sustainable.

91

92 *Stock dynamics modeling*

93

94 We investigated the potential role of fishing on the decline of autumn spawning herring in the GoR
95 by simulating the stock dynamics using the derived estimates of SSB and F. The simulation used a
96 standard single-species age-structured model of fish population dynamics (MacKenzie *et al.*, 2009;
97 Quinn II and Deriso, 1999). Stock simulations with this model allowed us to investigate whether
98 the estimated F (see above) were sufficiently high to have caused collapse, or whether additional
99 factors would also need to be present to cause collapse (e.g. higher M, reduced stock productivity
100 due to for example lower recruit production per spawner, etc.). Our objectives with these
101 simulations were to evaluate whether fishing could have been the main factor to reduce SSB and Y
102 by the levels observed between 1954–1976, and whether the timing and rates of these declines *in*
103 *situ* could be reproduced by applying the estimated F. Our simulation time period starts when
104 estimated SSB and recorded commercial catches were near their maxima (1960) and extends
105 forward for a period of 31 years.

106

107 The model requires several inputs of biological data (weights, maturation probability and M-at-age;
108 numbers at age in the population) and relationships (i.e., stock-recruitment) associated with herring
109 life-history to enable population calculations. We used age 8+ as the final age group in these
110 simulations because numbers of older ages were usually low or absent in many years from the
111 commercial data available (Supplementary Table 1 showing the catch numbers-at-age time series).
112 Weight-at-age for ages 1–6 are available as long-term means from gillnet catches in coastal areas
113 during spawning time (Ojaveer, 1988). For weights-at-age of ages 7 and 8, we calculated the mean
114 % weight increment between ages 3–4, 4–5, 5–6, applied this increment to age 6 to derive the

weight increment to age 7. We repeated this process for age 8 which was the oldest age group used in our simulations; the data used in our simulations are shown in Supplementary Table T2. M and maturity-at-age were also available from Ojaveer (1988). The initial stock numbers were based on the relative age composition of experimental fishery catches (Ojaveer, 1988), averaged for the period 1964–1972, and applied to our estimate of SSB present in the late 1950s–early 1960s when catches were maximal and accommodating observed maturity-at-age data (Supplementary Table T2). We incorporated uncertainty in the initial stock numbers-at-age estimates assuming levels of uncertainty corresponding to those associated with the stock number estimates from the stock assessment for the GoR spring spawning stock (ICES, 2016).

The population dynamics model requires a stock-recruitment (S-R) model, which is not available for the autumn spawning herring in the GoR. We assumed that a reasonable alternative model for a S-R relationship would be that for the spring spawning stock in the central Baltic Sea (i.e. ICES Subdivisions 25–27, 28.2, 29 and 32), where ecological conditions are quite similar to those in the GoR. The S-R relationship for the central Baltic herring stock was parameterised using a Ricker (Ricker, 1954) model and explains significant variation in R ($R_{adj.}^2 = 0.15$; $P = 0.009$). The shape of the relationship covers a wide range of stock dynamics, including at low stock levels where the rate of recruit production increases sharply with SSB and at high levels of SSB where R per spawner is relatively low and independent of SSB due to density-dependent effects. We considered using the S-R relationship for the GoR spring-spawning herring stock but this relationship does not exhibit strong density – dependence at high SSB and could yield unrealistic results when performing population dynamics simulations (e.g. predicting levels of SSB higher than those observed in our historical time series).

139 The central Baltic spring herring SSB is much larger than either of the GoR stocks (spring or fall).
 140 Application of its S-R model directly to the fall spawning stock would therefore lead to unrealistic
 141 levels of stock size and dynamics. We therefore downscaled the stock-recruit model from the
 142 central Baltic stock to allow estimation of stock-recruit dynamics for the autumn stock. The time
 143 series of SSB for the central Baltic was downscaled to match the range estimated historically for the
 144 GoR autumn spawning stock (shown below). The downscaling was accomplished by scaling the
 145 largest observed SSB for the central Baltic stock to the approximate maximum SSB observed
 146 historically for the autumn stock. The downscaling factor was 60 and preserves the *shape* of the
 147 relationship for application to the autumn stock. We downscaled both the stock and R data for the
 148 central Baltic stock by this factor, and re-fitted the resulting Ricker stock-recruit model ($R =$
 149 $40.1 * S * e^{-0.000045S}$) to these downscaled time series. The fitted downscaled model is based on the
 150 time series of SSB and R data available from ICES (i.e. year-classes 1974–2014; (ICES, 2016)) and
 151 was used in simulations. The uncertainty of the recruit estimates (i.e. root mean square error = 93
 152 425) of the fitted downscaled Ricker model was used in simulations of the population dynamics of
 153 the autumn herring stock.

154

155 We recognize that the GoR and central Baltic populations/stocks have different ecologies (e.g.
 156 exposure of eggs and larvae to different abiotic conditions that could affect survival; (Ojaveer,
 157 1974)) and potentially different recruit production dynamics that need further investigation and
 158 parameterisation. However, our use of the central Baltic stock to represent stock-recruit dynamics
 159 is only intended to represent a reasonable first-order estimate of the shape of the relationship; a true
 160 parameterisation, which does not yet exist for this stock, could differ somewhat depending on local
 161 conditions and stock biology.

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163 We used the derived estimates of age-specific F to simulate the effects of fishing on the dynamics.
164 F for all ages were assumed constant through the simulation period for most scenarios. F for ages
165 3–8 were the time series means of those derived from historical analyses (see above) and those for
166 ages 1–2 were time series medians due to their higher variability.

167

168 We conducted our simulations for a period of 31 years; each year was simulated 200 times using the
169 random variation associated with the S-R relationship and initial stock numbers-at-age. Output data
170 are the time series of SSB, R and Y , including user-defined percentiles to display model uncertainty
171 and the estimated risks of stock declines. We saved and visualized the 10th, 50th and 90th
172 percentiles of the distributions for each of these output variables.

173

174 The modelling scenarios conducted are described in the main text and summarized in Table 1.

175

176

177

178 **Supplementary Figures:**

179

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182

183 Supplementary Figure F1. Age composition of commercial catches for autumn spawning herring
 184 during 1954-1976 in the Gulf of Riga, Baltic Sea. Ages 3-8 were used for subsequent catch-curve
 185 analyses to estimate total and fishing mortality rates. See methods for data sources.

186

187

188

189

190 Supplementary Figure F2. Range of uncertainty of modelled spawner biomass (A) and fishery
 191 yields (B) of autumn spawning herring in the Gulf of Riga, based on an age-structured model
 192 incorporating uncertainties associated with the stock-recruitment relationship and the initial stock
 193 numbers at age. The figure shows the 10th, 50th and 90th percentiles of the distributions, based on
 194 200 simulations and assuming random variability due to the uncertainties. The scenario for this
 195 illustration is scenario 1 (i. e., $F = 0.58$, including juvenile fishing mortality).

196

197

198 **Supplementary tables:**

199

200 Supplementary Table T1. Total catch-at-age in numbers (in 100,000s) for autumn spawning herring
 201 in the Gulf of Riga during 1954-1976. See Methods for data sources.

Age\ year	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965
1	77	329	53	764	75	325	29	536	91	19	49	413
2	1276	278	1186	188	1722	452	599	210	792	1720	118	309
3	582	1458	318	1355	253	3475	445	1005	85	748	1987	177
4	371	416	1043	227	1033	135	2081	470	898	45	589	1115
5	171	171	192	481	128	459	74	1248	227	481	20	380
6	164	74	74	83	284	58	271	25	748	105	255	6
7	25	88	68	40	67	148	15	44	10	318	17	198
8		20		31	89	12	45	2	20	3	256	1
9				24	33	61	15	1	0	7	0	147
10					3	6	4	2	4	0	6	0
11					25	6	25		1	9	0	6
12												
13												
14												

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1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976
57	23	60	10	48	242	40	17	147	28	14
2421	1113	563	164	47	148	896	1174	1007	886	296
371	3495	858	558	117	12	34	1257	1581	1584	1284
55	149	1001	451	504	34	1	15	958	934	894
332	22	49	489	246	120	4	11	15	561	351
100	154	5	27	330	37	72	2	5	7	240
1	43	76	2	3	104	36	7	2	2	1
165	0	35	67	0	0	32	8	13	1	1
1	41	0	35	11	0	0	9	0	0	0
118	0	26	0	3	9	0	0	0	0	0
0	22	0	27	0	15	4	0	0		
	0	14	0	0	0	0	0	0		
	0	9		0	0					
		3								

203

204 Supplementary Table T2. Mean weight-at-age (Ojaveer 1988; data are presented in source as long-
205 term average for 1960-1969) and the probability of maturity (Ojaveer 1988; data are presented in
206 source as long-term average for 1964-1977) for autumn spawning herring in the Gulf of Riga, as
207 estimated from commercial samples.

Age	Wt. (kg)	Prob. mature
1	0.0145	0.000
2	0.0213	0.073

3	0.0275	0.701
4	0.0349	0.842
5	0.0412	0.941
6	0.0503	1.000
7	0.0568	1.000
8+	0.0642	1.000

208

209 Supplementary Table T3. Catches of autumn-spawning herring in the Gulf of Riga during 1928-
 210 2014. Shown are the catches by gillnets in spawning areas in coastal waters for the entire Gulf of
 211 Riga, by the same gear in two local coastal areas (Pärnu Bay area and near Saaremaa), and for the
 212 entire Gulf of Riga by all gears. See methods for data sources.

Year	Gulf of Riga total gillnets in coastal spawning areas	Pärnu	Saaremaa	Total Gulf of Riga (all gears, areas)
1928			999.6	
1929		92.4	844.0	
1930		131	771.4	
1931		115	850.0	
1932		107	1004.4	
1933		115.6	722.7	
1934		151	1090.3	
1935		117	867.3	
1936		69.2	964.4	

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1937		63.7	889.6	
1938		51.4	577.1	
1939		22.7	739.6	
1940				
1941				
1942				
1943				
1944				
1945	218	25.7	46.3	
1946	170	21.6	84.6	
1947	410	32.1	75	
1948	377	70.1	222.9	
1949	779	166.6	465.4	
1950	638	80.1	382.7	
1951	601	59.7	433.4	
1952	744	98.1	504.7	
1953	930	229.7	617.6	
1954	695	246.9	321.8	4567
1955	1531	677.5	700.2	7167
1956	1934	796.5	925.7	6064
1957	2864	968.8	1770	7518
1958	2848	1394.6	1218	7652
1959	2582	1362.5	1003.2	13658

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1960	1681	828.6	630.7	10848
1961	1360	857.6	871	9956
1962	2003	887.1	828.8	8287
1963	1739	598.2	797.8	6667
1964	2194	997.8	686.2	10669
1965	1765	775	567.6	8216
1966	1009	437.4	417.1	5012
1967	1574	792.3	468.1	11698
1968	923	332.7	162.8	6925
1969	860	372.9	113.4	6151
1970	1765	742.1	436.8	4873
1971	970			1597
1972	1040		567.4	915
1973	1004	364.6		3721
1974	1085	559.9		7873
1975	1237	604.3		9980
1976	1066	417		9316
1977	1155	406		
1978	800	513.4		
1979	417	297		
1980	400	168		
1981	220			
1982	200			

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1983	120			
1984	140			
1985	180			
1986	180			
1987	150			
1988	120			
1989	40			
1990				
1991				
1992				
1993		1.2		
1994		2.1		
1995				
1996				
1997				
1998				
1999				
2000		52.3	14.3	
2001		107.5	26.4	
2002		27	10.1	
2003		115.9	10.1	
2004		27.6	9.1	
2005		32.5	10.5	

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2006		0.6	4.5	
2007		0.6	1.8	
2008		1.1	3.3	
2009		0.2	3.3	
2010		4.7	11.8	
2011		0.0	18.6	
2012		25.2	15.4	
2013		7.3	14.3	
2014		5.0	11.7	
2015		4.0		

213

214

215 Supplementary Table T4. Results of catch curve regression analyses (ln nos.-at-age vs. age for each
 216 year during 1954-1976) for autumn spawning herring in the Gulf of Riga. SE = standard error;
 217 RMSE = root mean square error.

Year	Intercept; SE	Slope; SE	$R^2_{adj.}$	RMSE	P value
1954	8.676; 0.799	-0.703; 0.154	0.833	0.486	0.0196
1955	9.244; 0.571	-0.762; 0.099	0.921	0.414	0.0015
1956	8.154; 1.273	-0.570; 0.245	0.524	0.775	0.1026
1957	8.744; 0.688	-0.656; 0.109	0.855	0.576	0.0018
1958	7.885; 0.900	-0.493; 0.121	0.663	0.934	0.0046
1959	8.898; 1.001	-0.654; 0.134	0.740	1.040	0.0018

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1960	8.217; 1.129	-0.572; 0.151	0.625	1.172	0.0069
1961	10.390; 1.172	-1.019; 0.170	0.833	1.102	0.0010
1962	8.706; 1.480	-0.751; 0.198	0.625	1.537	0.0069
1963	8.340; 1.479	-0.670; 0.198	0.566	1.535	0.0117
1964	9.271; 1.904	-0.793; 0.276	0.508	1.791	0.0285
1965	8.002; 1.938	-0.619; 0.260	0.369	2.012	0.0487
1966	7.150; 1.953	-0.519; 0.262	0.268	2.027	0.0877
1967	8.102; 1.854	-0.649; 0.249	0.421	1.925	0.0348
1968	8.521; 1.560	-0.732; 0.209	0.584	1.620	0.0100
1969	7.843; 1.622	-0.578; 0.217	0.431	1.684	0.0326
1970	8.365; 1.488	-0.757; 0.199	0.627	1.544	0.0067
1971	4.583; 1.638	-0.269; 0.219	0.059	1.700	0.2595
1972	3.715; 1.596	-0.231; 0.214	0.021	1.657	0.3155
1973	6.309; 1.978	-0.574; 0.313	0.283	1.655	0.1261
1974	10.343; 2.256	-1.198; 0.392	0.626	1.638	0.0377
1975	12.689; 1.520	-1.567; 0.264	0.873	1.104	0.0040
1976	12.465; 1.816	-1.458; 0.315	0.803	1.319	0.0099

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