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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 spatially-distinct groups within each spawning season (Ojaveer, 1988). Presently the dominant seasonal group of spawners are the spring spawners, which are furthermore recognized to belong to several different populations which are subject to stock-specific fishery regulations (ICES, 2017).

Autumn spawning herring in the Baltic Sea are presently rare, compared to spring-spawners, and support no directed fisheries (ICES, 2017; Parmanne *et al.*, 1994). However they were formerly common or even dominant in the western Baltic-Rugen area, central Baltic Sea and Gulf of Riga (GoR), and historically made an important contribution to the Baltic Sea herring landings (Parmanne *et al.*, 1994). For example, they contributed over 90% of the landings from the central Baltic Sea in 1925–1927 (Hessle, 1931); in the Gulf of Riga, the catches of spring and autumn spawning herring are shown together in official statistics, but autumn spawning herring made up to 47 % of the total herring ctaches on feeding grounds in the 1970s (Ojaveer, 2003). Also, it was hypothesized that autumn spawning herring was an important target fish in the Gulf of Riga fishery in the late 17th century (Gaumiga *et al.*, 2007). The spring and autumn spawning herring ecotypes in the Baltic Sea differ genetically and hence support full reproductive isolation (Bekkevold *et al.*, 2016). Some of the key characteristics of the autumn spawning herring, relative to the spring spawning herring, specifically in the Gulf of Riga, include spatio-temporally differentiated spawning (autumn spawners reproduce in more offshore areas and at greater depths in late summer – fall period while spring herring reproduces in shallow coastal areas in spring), harsher environment during the larval retention period (fall-winter for autumn spawners vs. spring-early summer for spring spawners) with poorer larval feeding conditions for autumn spawners, later maturation (age 3 or 4 for autumn spawners vs. age 2 for spring spawners) and bigger weight-at-age (Tw_{inf} 85.0 and 65.1 g for autumn and spring spawners, respectively) (Ojaveer, 1988, 2003). 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 km^2, volume 424 km^3) 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 stable deep water (temperature ca. 3°C) and the highly variable surface layers (temperature up to 20°C) (Raudsepp, 2001).

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

Historical data availability and sources

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

i. For the period of 1920s–1930s, the data was extracted from Estonian national fishery journals *Kalandus*, and *Laevandus ja Kalandus*. The reliability of data is unknown but presumably similar to that for other national fishery agencies around the Baltic at the saame time; however, the underlying raw data are unavailable.

ii. Original summary notes, often on handwritten sheets, from primary sources during the Soviet time (1945–1989) were obtained from archives of the Estonian Marine Institute, University of Tartu. The sources of these data were the local state-owned fishing companies (called in the former USSR fishing kolhoses). The reliability of these data is considered relatively high, as data often originate from ‘local correspondents’ who were in close contact with scientific staff of the governmental research institute at that time (the Tallinn Department of the Baltic Sea Fisheries Research Institute: BALTNIIRH) receiving the reporting.

iii. Official catch statistics from the most recent period was obtained from the Ministry of Environment (1992–2005) and Ministry of Rural Affairs (since 2006) of Estonia. The reliability and accuracy of data is similar to reporting of all other of fish catches, incl. of internationally assessed and managed species.

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 available numbers-at-age in the catch data for 1954–1976. We used “catch curve analysis” (Hilborn and Walters, 2001; Quinn II and Deriso, 1999) to derive estimates of total and fishing mortality for each year during this time period. Details are provided in the Supplementary Material.

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

Estimation of spawning stock biomass:

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

$E_{SSB} = Y/SSB$

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

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

Stock dynamics modeling:

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

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

However, there is no SSB-R relationship for the autumn spawning herring in the GoR. A reasonable alternative model for a SSB-R relationship is a downscaled version of the relationship (Ricker, 1954) 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 similar to those in the GoR. The downscaling process preserves the shape of the relationship but adjusts parameter magnitudes to observed levels 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

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”

					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.

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

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

Results

Dynamics of landings:

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

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

Evaluation of F and SSB:

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

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

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 Subdivsions 22-24)	0.33	(ICES, 2016b)
North Sea autumn spawning herring	0.33	(ICES, 2016b)
Norwegian Sea spring spawning herring	0.15	(ICES, 2015)

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

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

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

Simulated population development:

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

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

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

The range of simulated SSB and Y after 30 years of simulation using 6 combinations of F and M 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 M resulted in a ca. 2–fold range in final SSB (Figure 6).

Discussion

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

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

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

These two methods for SSB estimation are based on vastly different datasets and assumptions. However, their consistency indicates that they both likely provide reasonable estimates of the historical biomass of autumn spawning herring that once lived in the GoR. As such, they provide useful historical ecological knowledge of the magnitude of past biomass levels, as well as targets for future stock recovery actions.

As noted by others recently (Engelhard *et al.*, 2016; Lotze, 2014; Schwerdtner Máñez *et al.*, 2014), historical marine ecological information can potentially inform present-day decision-makers about past and future stock and ecosystem dynamics. Such inferences are often made based on data material which is fragmented or averaged over time – space scales which do not easily fit into many routine stock assessment methods. This situation also applies to our case study. As a result, the findings (e.g. F and SSB time series) should be considered indicative of likely levels and trends applicable over long time periods, rather than precise estimates for specific years. This is partly because many of the input data were averages over different time periods, or not available for this stock, and also because there is limited fishery-independent or effort data available for calibration ("tuning") or comparison. However, the consistency of the different SSB estimates, and the general correspondence between the simulated biomass dynamics and the development of the fishery, suggest that the approaches and conclusions are reasonable.

Methodologically, our work and methods could be considered to lie approximately in the middle of an "information gradient" available for doing stock assessments and hindcasts. This gradient could be considered to span a range from more extensive, data-resourced assessments such as those done for many of the largest and commercially most important stocks in Europe and North America where available datasets include detailed catch sampling and monitoring (e. g., sizes, ages, maturities), effort indices, research vessel surveys for estimating pre-recruit, recruit and adult abundances, and standardized CPUE time series for assessment tuning, to smaller stocks where only catch and some species-specific lifehistory (e. g., maximum body size, age and size at maturity) data are available (e. g., in many multi-species fisheries around the world). There are now methods becoming increasingly available for assessing the ecological status of data-limited stocks and historical dynamics (Costello *et al.*, 2012; Pauly, 2013; Rosenberg *et al.*, 2014; Walters *et al.*, 2006), and these also include many assumptions about fishing effort and stock productivity. Our investigation, given its reliance on incomplete historical data, includes some methodological approaches and concepts from both data-rich and data-poor stock assessment and reconstruction methods. It has, however, developed some reasonable estimates of the past dynamics and relative roles of fishing and environmental factors on this stock.

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

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

Exploitation as likely driver of stock decline:

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

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

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

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

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

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

Our simulations can potentially identify candidate levels for fishery and biological reference points for this stock. Such reference points will be needed, should the stock recover to commercially exploitable levels. In general, and according to theoretical models of fishing impacts on fish population dynamics, an approximate level of F_{msy} is an F value that results in a long-term reduction of SSB by ca. 50% from a maximal or unexploited level (MacCall, 2009; Rosenberg *et al.*, 2014). Our sensitivity analyses of the combined effects of two levels of F and three levels of M indicate that SSB would be reduced by 5–73% for these combinations of F and M. These results suggest that, if $M = 0.15$ and a reduction of SSB by ca. 50% is a desirable management policy objective, F_{msy} could be > 0.32 (the current F_{msy} for the spring spawning herring in the GoR) and consequently somewhat higher than F_{msy} for both the central Baltic stock and the spring spawning herring stock in the GoR. However as illustrated by the sensitivity analysis, any estimated F_{msy} will depend on the assumed level of M (as well as many other variables), so new studies of M may be needed to improve a future estimate of F_{msy} (and B_{msy}). Moreover, the estimated reference points will be sensitive to the underlying dynamics (and resulting parameters) of the S-R relationship. A dedicated autumn spawning S-R relationship should be derived to support estimation of reference points. However, given that only one new observation becomes available per year, such a relationship cannot be quantified before many years. Given the various uncertainties associated with, for example, the estimate of M and the absence of a stock-recruit relationship for the autumn spawning GoR herring, it may be more prudent to adopt a more pre-cautionary (i. e., lower) value of F_{msy} such as that used for the central Baltic herring (0.22) or the northern Baltic herring (0.15; Table 2).

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

Future prospects for autumn spawning herring in the GoR

The future status of autumn spawning herring in the GoR is unclear. The strong recoveries of previously collapsed large herring stocks elsewhere demonstrate that herring stocks can and do recover under some circumstances. In the case of the autumn spawning herring in the GoR, it is very difficult to forecast when the stock might rebuild to commercially exploitable levels: there is presently very little direct knowledge of its R or (essentially egg and larval) mortality processes, or other stock knowledge during the past 30 years on which sound fishery management advice could be based.

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

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

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

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Figure captions:

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

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

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

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

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

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

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

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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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Supplementary Materials:

Text (Methods)

Figures

Tables

Supplementary Methods:

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

Data analyses and population modelling:

One of the objectives of our investigation was to evaluate whether F would have been sufficient to cause a large decline in the autumn spawning stock. 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 and fishing mortality rates for GoR autumn spawning herring using the available numbers-at-age in the catch data for 1954–1976. We used “catch curve analysis” (Hilborn and Walters, 2001; Quinn II and Deriso, 1999) to derive estimates of total and fishing mortality for each year during this time period. For this analysis, we assumed that ages 1–2, although captured in high numbers in some years (Supplementary Table T1, Supplementary Figure 1) were not fully recruited to the fishery, as is the case with present herring fisheries in the GoR and other parts of the Baltic Sea. This assumption was supported by visual inspection of the natural logarithm (ln) of numbers-at-age vs. age scatterplots which showed that these age groups tended to be outliers from linear regression models applied to older age groups (Supplementary Figure F1 – age composition plot for ages 1–14). The catch curve analysis used all age-groups 3 years and older.

According to this method of analysis, the slope of the linear regression of ln numbers-at-age vs. age corresponds to the total mortality rate experienced on average during the period of the study (Hilborn and Walters, 2001; Quinn II and Deriso, 1999). To derive F by age for each year for the fully – recruited age groups (i.e. 3+), we used an earlier-derived estimate of natural mortality (M) rate for this time period (M = 0.15; (Ojaveer, 1988)). This rate is somewhat lower than M estimated for GoR spring spawning herring (0.2 or 0.25 for all age-groups since 1977; (ICES, 2016)).

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

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

E = total numbers removed/ total number in stock

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

$N_t = N_0e^{-Ft}$

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

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

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

Stock dynamics modeling

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

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

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

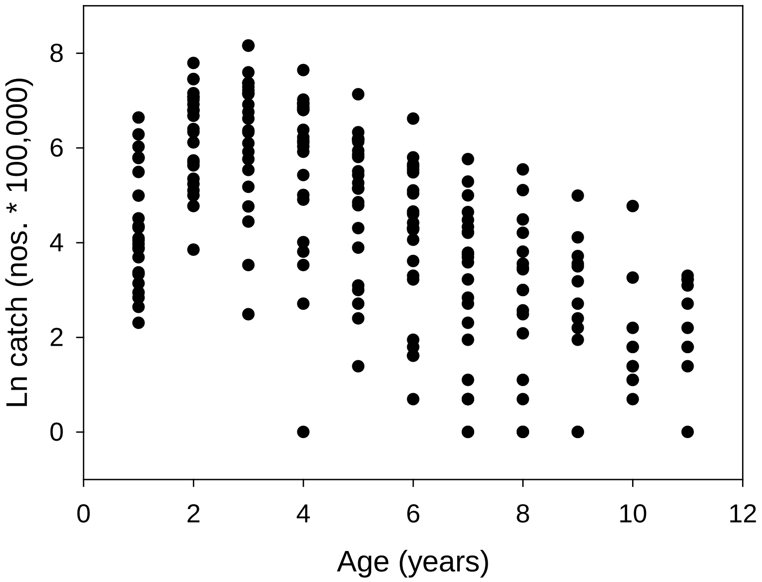
We recognize that the GoR and central Baltic populations/stocks have different ecologies (e.g. exposure of eggs and larvae to different abiotic conditions that could affect survival; (Ojaveer, 1974)) and potentially different recruit production dynamics that need further investigation and parameterisation. However, 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.

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

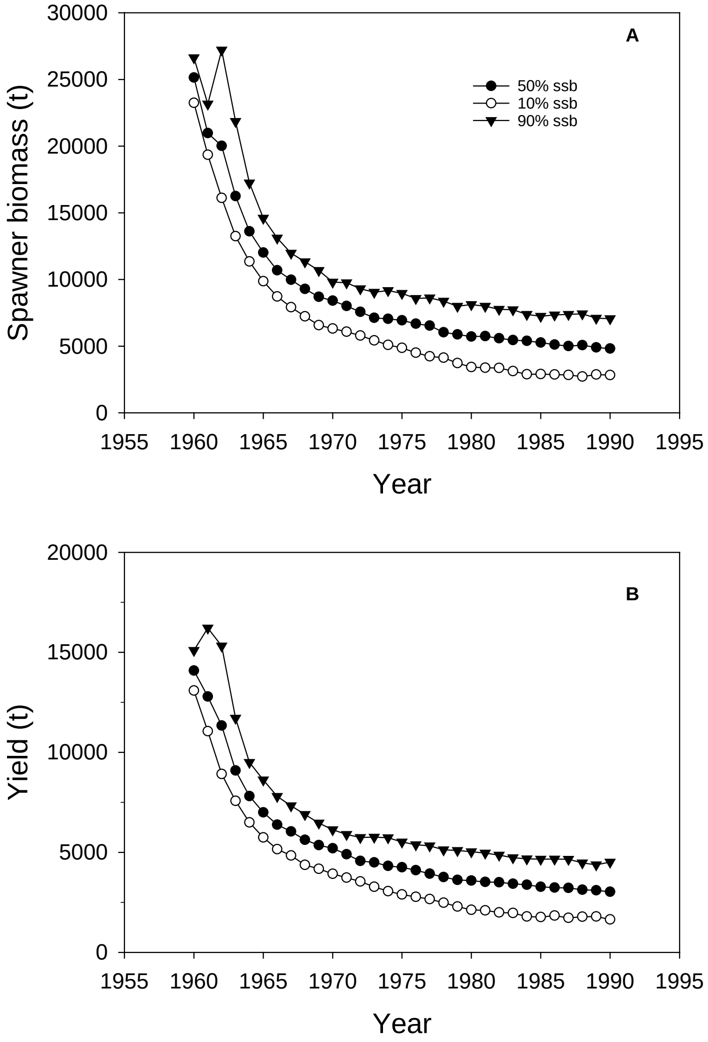
We conducted our simulations for a period of 31 years; each year was simulated 200 times using the random variation associated with the S-R relationship and initial stock numbers-at-age. Output data are the time series of SSB, R and Y, including user-defined percentiles to display model uncertainty and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

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

Supplementary Figures:



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



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

Supplementary tables:

Supplementary Table T1. Total catch-at-age in numbers (in 100,000s) for autumn spawning herring 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												

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								

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

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

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

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			

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	

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		

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

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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