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Spawning stock biomass modulation of environment - recruitment relationship in a marginal spring spawning herring (*Clupea harengus membras*) population

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Abstract

Scientific interest in the dynamics of fish recruitment dates back to the beginning of the 20th century. Since then, several studies have shown that the environment may have a stronger effect on recruitment (R) compared to that of the spawning stock biomass (SSB). By combining a suite of methods designed to detect the non-linear, non-stationary and interactive relationships, we have re-evaluated the potential drivers and their interactions responsible for the multiannual dynamics of the recruitment dynamics of the Gulf of Riga (Baltic Sea) spring spawning herring population at the longest time-span to date (1958-2015) allowing coverage of variable ecosystem conditions. R was affected significantly by prey density and the severity of the first winter. Although SSB was not a good predictor of R, adding interaction with SSB significantly improved the model, hence the effect of the two environmental variables on R was modulated by SSB. While temporal changes in the environment-R relationship were generally gradual, several abrupt changes were evident in the strength of these relationships. In addition, non-stationary, linear and non-linear relationships were observed.

Keywords: Baltic Sea, copepod abundance, long-term dynamics, linear and non-linear non-stationary relationships, winter severity

Introduction

Scientific interest in the dynamics of the fish recruitment dates back to at least the beginning of the 20th century, when it was understood that variations in catches are related to variations in recruitment: “...*These results naturally lead us to enquire into the causes, or better, the natural phenomena which occasion these peculiar fluctuations in the renewal of the stock; the hydrographical or biological conditions which give rise to the occurrence of rich or poor year*

classes of fish. The problem is one of unquestionable difficulty, embracing as it does all the conditions which in any way affect the fish from the egg stage to the time when they are caught. It will therefore appear most probable that the renewal of the fish stock, as in the case of any stock on land, is dependent upon many factors, all necessary, and all more or less variable (Hjort 1914).

There is a strong theoretical and empirical basis for links between the biomass of spawning adults and the number of young fish entering a population. For example, Myers and Barrowman (1996) showed in meta-analyses that stocks with below - average spawning stock biomass (SSB) tended to have lower-than-average recruitment (R) and vice versa. However, the effect of SSB on R weakens as SSB increases in size, with R varying only weakly with SSB at large stock sizes (Ricker 1954; Beverton and Holt 1957), indicating that other factors, including environmental conditions in the ecosystem, are key drivers for R at high stock size. The strong influence of environmental conditions on R has been documented in several recent studies. For example, SSB explained only up to 15% of the variability in R (Cury et al. 2014), and R and SSB were not positively related in 61% of 224 stocks in the global RAM Legacy Stock Assessment Database (Szuwalski et al. 2015). Factors affecting R include parental effects (SSB size and age structure, fecundity, skipped spawning, maternal effects), environmental factors (predation, starvation, oceanographic condition) and direct human intervention – fishing (Bailey et al. 2005, and references therein). Moreover, there are studies to demonstrate that interactions between SSB and environmental conditions can affect R (e.g., Brander 2010; Perry et al. 2010). Thus, both biotic and abiotic factors and their interaction need to be investigated when attempting to understand the causes of R variability (Myers 1998; Perry et al. 2010).

Several studies have shown that inclusion of environmental variables significantly contributed to improved predictability of R (e.g., Stige et al. 2013) and that the dynamics of exploited stocks can be described better if environmental or climatic variability is incorporated in the recruitment models (Keyl and Wolff 2008). The ability to detect the effect of environmental forcing on R inevitably increases with the length of the time series, especially when already encompassing multiple cycles of an environmental index (Haltuch and Punt 2011). However, the environment- R relationships of a given stock may change over time (Myers 1998), due to several reasons, such as non-stationarity (Stige et al. 2006; Ottersen et al. 2013), non-linearity (Beggs et al. 2014), changes in population age structure, reproductive potential or spatial heterogeneity of the underlying processes (Keyl and Wolff 2008). As a result, empirical case studies often result in increasingly unclear relationships the longer the time series become. Therefore, despite the assumed virtue, longer time series also pose new methodological challenges to the ability to predict R from environmental factors, including the incorporation of temporal changes itself into the models.

Evidence of temporal changes in environment- R relationship spans over different species/stocks and ecosystems. For example, the positive correlation between the recruitment of Northeast Arctic haddock and cod, and North Atlantic Oscillation index in 1973-1996 disappeared when extending the time-series back in time to 1945 (Solow 2002). Also, the strength of correlations of the environment- R relationship of several fish stocks in the Barents Sea, Gulf of Alaska and Bering Sea evidenced substantial variations over multidecadal scales with the relationship in some stocks reversing sign (Stige et al. 2013).

Herring populations commonly experience collapses and recoveries, which directly influence herring fisheries and have direct implications for national economies (e.g., Sigurdsson 2006).

Investigations of 64 herring populations detected the importance of local drivers in formation of R and suggested that generally complex and uncertain processes are responsible for the relationship between SSB and R (Trochta et al. 2020). One of the important drivers behind herring dynamics is climate change/warming, operating *via* modifications in ecosystem conditions, which may affect larval drift or cause changes in growth rates and recruitment survival (Drinkwater and Kristiansen 2018; Tiedemann et al. 2020).

Herring has been one of the most important commercial fish species in the Baltic Sea for centuries. Investigations in the environmental effects on spring spawning herring (*Clupea harengus membras*) were initiated in the Baltic Sea already at the end of the 1940s with the ultimate objective to identify environmental factors suitable for forecasting R (Rannak 1971, and references therein). These early and following investigations have identified several abiotic and biotic environmental factors, together with suggested processes/mechanisms responsible, that influence spring spawning herring R during different time-periods facing different ecosystem conditions. Also, these investigations have formed a base for establishment and maintaining continuous long-term time-series on several hydroclimate and environmental parameters. The aim of the current paper was to re-evaluate these potential drivers and their interactions responsible for the multiannual dynamics of the Gulf of Riga (GoR) spring spawning herring R . We used the data covering the longest time span to date (1958-2015), and a suite of methods designed to detect the non-linear, non-stationary and state-dependent links between R and its drivers, and more realistic criteria for model performance than simple explanatory power (e.g., out of sample prediction skill).

Material and Methods

The study area and the population

The GoR is a shallow (mean depth 27 m) partly landlocked sub-basin in the Baltic Sea, separated from the Baltic Proper by the shallow and narrow Irbé Strait. In most parts, salinity ranges between 5.0 and 6.5 PSU with the absence of a permanent halocline (Kotta et al. 2008). Due to its shallowness, the changes in air temperature have a direct influence on the dynamics of the temperature regime of the GoR (Kotta et al. 2009). Due to strong vertical mixing, dissolved oxygen concentration is in most areas higher than 5 mL L⁻¹, while below 2 mL L⁻¹ values have occasionally been found in the deepest part of the GoR (> 45 m; Kotta et al. 2008).

The GoR spring spawning herring represents a small population with a current stock size of ca. 160-190 thousand tons and annual landings around 26-33 thousand tons (ICES 2020). The fish does not undergo major migrations into the open Baltic Sea (only a minor component of the older herring may leave the GoR during summer/autumn), and constitutes thus a local resident population managed as a separate stock (ICES 2020). Compared to the other spring spawning herring stocks of the Baltic Sea, the GoR spring spawning herring is characterized by the lowest mean weight-at-age values: the mean individual weight of age groups 1-8 of the GoR herring and other herring stocks of the Baltic Sea in 2019 were 19.9 and 22.4-31.1 g, respectively (ICES 2020).

Data sources and preparation of time series

Annual data on R and SSB of the GoR spring spawning herring originate from Ojaveer et al. (2004) and ICES (2020), data from 1958 to 2015 was used. R is reported for the year when fish are already one year old. However, the first year of life is the most critical for survival of herring (i.e., determines the recruitment abundance) and the key processes may actually occur during the first months of life (e.g., Oeberst et al. 2009; Payne et al. 2009). Therefore, for the purpose of current

analysis, we shifted the time series of R by one year earlier, to align it with the environmental conditions and SSB values corresponding to the first year of life.

Daily air temperatures, measured at Kihnu weather station (58.09861 N, 23.97028 E), were provided by Estonian Environment Agency. Winter severity was calculated as a sum of negative daily mean air temperatures from November to March (e.g., Radziejewska and Chabior 2004; Livdane et al. 2016), and assigned to the year of spring (e.g., 1990 winter severity describes the period from November 1989 - April 1990). Winter severity was included in analyses in two versions: original and lagged. Original series describes the winter before hatching (WS0) and the lagged series the first winter these individuals survived (WS1).

The mean water temperature of 0-20 m water layer in May has previously been identified as a reasonably good predictor of the GoR spring spawning herring R dynamics (ICES 2020). Unfortunately, the *in situ* temperature measurements have been available only since 1963. As there is empirical evidence on the close correlation between the sea surface temperature (SST) in the GoR and the air temperature measured in a nearby hydrometeorological station ($r^2 > 0.90$; Kotta et al. 2009), we used the mean daily air temperatures in May instead. We hereby also argue that consistently and frequently (hourly) recorded air temperature data is likely a more reliable proxy of long-term (interannual) variability of the temperature conditions than irregularly sampled *in situ* water temperatures.

Diet of various life stages of the GoR spring spawning herring has been extensively studied, with the evidence originating from different decades. From these studies, the copepod *Eurytemora affinis* clearly appears the preferred and dominating prey for larvae (Arula et al. 2012), and juveniles and adults (Ojaveer et al. 2017 and references therein). Therefore, density of *E. affinis*

was used as a proxy for describing the prey availability. Abundance data of *E. affinis* was extracted from the Baltic Sea zooplankton database (Klais et al. 2016), obtained from the Institute of Food and Safety, Animal Health and Environment (BIOR, Latvia) and Estonian Marine Institute, University of Tartu (Estonia). From the open GoR, samples were collected during spring (May) monitoring cruises covering the entire basin, with vertical tows of a Juday net (mesh size 160 μm , opening diameter of upper ring 36 cm) and fixed in 4% formaldehyde solution. From Pärnu Bay, sampling was seasonally more frequent, and we used the data from the samples collected in May and June. Sample collection and analysis procedure was based on UNESCO (1968) and remained the same throughout the survey period.

From the *E. affinis* abundance data, three annual time series were calculated for both open GoR and Pärnu Bay, aggregating three different stages: 1) copepodites I-III, 2) copepodites IV-V, and 3) adult copepods. The abundances were converted from the volumetric unit ($\text{ind.} \times \text{m}^{-3}$) to area units ($\text{ind.} \times \text{m}^{-2}$), using the depth of the sampled profile. Since the spatio-temporal coverage of zooplankton data was not exactly the same every year, the annual values were estimated with the generalized additive model (GAM) (Wood 2017), where the sampling year was included as a categorical variable, in addition to the smooth functions of day of year (to account for the differences in exact timing of the cruise), and latitude and longitude as tensor product (two-dimensional smooth, to account for variations in exact locations of samples between years). Annual values were predicted by this model at the mid-points of latitude and longitude and the mean day of year, thereby assuring the comparability of annual values in spite of variations in the actual sampling scheme.

Statistical modelling

We first used GAM in a forward selection procedure to find the combination of variables that explain best the variability in R , while also testing for the non-linear links between R and the selected variables. Akaike's Information Criterion (AIC), adjusted R^2 , and significance (p-value) of added terms was used to guide the forward selection procedure. Two types of models were used: in the first model, all variables (except SSB) were included as individual smooth terms, in the second model, all variables (except SSB) were included as tensor products (two-dimensional smooth functions), where the second axis was always SSB.

Out of sample prediction skill was used as an additional measure of the model performance, and it was estimated for all GAM models that were fitted in the previous step, including all steps of the forward selection procedure. Due to small sample volume, a leave-one-out cross-validation (2011) approach was selected, i.e., the same model was fitted 55 times, excluding each year once, and predicting with the model the R to the year excluded from the model training data. The skill is measured as the adjusted R^2 of a linear model: observed $R \sim$ predicted R . This method can be used to evaluate which model has the most potential to predict "future" R .

The most optimal degrees of freedom for the smooth terms were estimated by varying k values between 3...6, and choosing the k that yielded the lowest GCV (Generalized Cross Validation) score. Concurvity (generalization of collinearity) between explanatory variables, where some smooth term in a model could be approximated by one or more of the other smooth terms in the model, is also a potential issue for GAM models, and can make the estimates unstable. Therefore, a concurvity test was applied to the final models and reported.

Temporal changes in the environment - recruitment relationship

Temporal behavior of the links between R and the explanatory variables from final GAMs (M1 and M2) were also analysed individually using two approaches: a growing window analysis, and sliding window analysis. In the growing window analysis, univariate GAMs were fitted to the gradually growing subsets of data, starting with the first 20 years, and then adding 1 year at each step. Goal of this approach was to mimic the real-world situation where time series are gradually growing, and often the links observed at first, disappear or change. Sliding window analysis was used to detect and visualize the non-stationarity in the links between R and the selected explanatory variables, similar to Kirby and Beaugrand (2009). This approach calculates the linear model parameters (slope, and p-value) for moving time periods (15 years window) with an increment of one year.

All analyses and visualisations were done in *RStudio* (version 1.3.1056, using *R* 4.0.2), GAM models were fitted using the library *mgcv* (1.8-31). Aim of the analysis is brought out in Table 1.

Results

The multi-decadal dynamics of herring stock characteristics, and of the variables that were determined as significant drivers of the R in later steps of analysis: the copepodites IV-V in open GoR, and the severity of the first winter the fish survived, are displayed in Fig. 1. Dynamics of all other explanatory variables used in the modelling, which didn't qualify as significant drivers (mean May air temperature; abundance of *E. affinis* copepodites stages I-III and adult copepodites in the open GoR; and abundance of *E. affinis* copepodites stages I-III, IV-V and adult copepodites in Pärnu Bay) are shown in supplementary Fig. S1. Herring R and SSB show generally similar patterns over the whole study period by exhibiting notably higher values since the early 1990s. SSB remained generally below 50 thousand tons before the late 1980s, but often exceeded 100

tons level since then. Increase in R was less pronounced than that of SSB, but R became more variable after the early 1990s (Fig. 1a). Except for a few years, the abundance of *E. affinis* copepodites stages IV-V in the open GoR remained below 200 000 ind. m⁻², but exhibited a few peaks with values above 500 000 ind. m⁻² (Fig. 1b). Abundance of *E. affinis* has generally shown an increase since the end of the 1970s and has remained at a higher level starting from 1990. In general, winters have become milder over time. The period until the mid 1980s is characterised with high variability in winter severity and several extremely low values. In contrast, many consecutive very mild winters have been observed since the end 1980 with the coldest winters being always warmer than until the mid-1980s (Fig. 1c).

The final model of GAM without interaction to SSB included the open GoR prey abundance (*E. affinis*; copepodite stages IV-V) and winter severity of the first year of life (WS1) (adjusted R²: 0.52, $p < 0.05$; Table 2, M1) as the best predictors of interannual variability in R. While R increased with prey abundance linearly (Fig. 2a), the relationship with winter severity was unimodal, with a peak at average winter temperatures and lower R for both, very mild and harsh winters (Fig. 2b). Concurvity index was 0.12 for prey and 0.11 for winter severity, indicating that both terms contributed to the model orthogonally.

The final model of GAM with interaction to SSB included the same variables as the previous model, but the overall explanatory power of the model was higher (adjusted R²: 0.62, $p < 0.001$; Table 2, M2). Highest values of R coincided with high levels of SSB combined with high prey abundance (Fig. 3a). In addition, elevated levels of R were detected in combination with low SSB and average winter temperatures (Fig. 3b). Concurvity tests indicated relatively high correlation

between the terms (0.44-0.51), which was expected given that the SSB was included in both interactions.

Out of the sample prediction skill test evaluated the potential of different GAM model candidates (steps 1 and 2 of M1 and M2; Table 2) to predict the future R values, and the results of this analysis allowed us to make two main observations. First, all M2 model steps where explanatory variables included an interaction with SSB, showed higher prediction skill than any of the M1 model steps. Second, winter severity improved the models' prediction skill only when it was in interaction with SSB (i.e., M1 step 1, the prey alone had as high adjusted R^2 as the step 2, but in M2, the adjusted R^2 increased still notably when adding the $\text{te}(\text{SSB}, \text{winter severity (WS1)})$ to the model; Table 2; Fig. 4). The improved prediction skill of M2 over M1 is visually evident from better match between the observed and predicted values, particularly for the period since the early 1990s, characterised by higher variability of R (Fig. 4).

Growing window analysis was applied to test if the shape of the link, direction or the strength of it between R and the investigated variables changes in relation to the length of the time-series. The relationship between R and SSB appeared to be unimodal during about the first 25 years peaking at around 30-40 thousand tons of SSB. When the time series was further extended, the unimodal relationship was quite abruptly replaced with a more linear and positive relationship between R and SSB (Fig. 5a), coinciding with about two-fold increase in the adjusted R^2 (from around 0.15 to 0.30, Fig. 5b). Addition of the last 5 years to the time series (i.e., 2010-2015), revealed a new maximum of R at high SSB level (ca. 90 thousand tons). The relationship between R and the prey abundance becomes more linear and more positive with every added year, adjusted R^2 value was low during the first three decades, but much higher since then, exceeding 0.45 mostly (Fig. 5c, d).

Winter severity, in contrast, has only a very marginal effect on R , at least when it is considered as a single variable in the model (Fig. 5e, f).

The sliding window analysis was applied to test the changes in strength and direction of the linear relationship between R and the investigated variables over time, while looking at the moving fixed length (15 year) time window. With exception in the 1970s, the relationship with SSB was positive from the beginning of the time-series until the mid-1990s, with a few most positive and significant relationships recorded for the mid/second-half of the 1980s. The relationship gradually declined since the peak values and remained negative until recently (Fig. 6a, b). The relationship between R and prey abundance has been always positive, and in most cases also significant, with gradual increase of the slope since the 1980s (Fig. 6c, d). The relationship between R and winter severity (WS1) has been mostly negative and insignificant throughout the entire period, except the 1980s, followed by a gradual sharp decrease to the early 2010s (Fig. 6e, f).

Discussion

What affects the R dynamics of commercial fish has a long history of research, but still remains as one of the most prominent questions in contemporary fisheries science (e.g., Somarakis et al. 2019). Myers and Barrowman (1996) showed that low SSB results in low R . However, low SSB and low R can be explained equally well by low R generating low SSB (Szuwalski et al. 2015). Extension of the length of time-series, into ecosystem conditions likely not met before, offers new avenues, including incorporation of environmental effects. While R dynamics is regulated by the interaction of multiple drivers (e.g., Wilson et al. 2018), and are therefore generally challenging to assess or predict because of the variation in their relevance over time and space, combining different data analysis techniques can be useful in improving our understanding in this matter

(Zimmermann et al. 2019). Through the utilization of different numerical and data visualization tools, we were able to identify the most likely drivers behind the long-term R dynamics of the GoR spring spawning herring population, together with specifying the patterns and types of the links between the suggested drivers and R.

Factors affecting GoR spring spawning herring R have been investigated since the 1950s. These investigations have been performed at shorter time-periods with applying simpler and fewer methodological approaches simultaneously than in the current work. In previous studies, variables identified as significant predictors of R included the abundance of food during the larval seasonal maximum in coastal areas (during 1961-1973; Rannak and Simm 1979), Fulton condition factor of age groups 2-5 (1977-2010; Putnis et al. 2011), strength of westerly winds in winter, winter air temperature and SST in April (1952-1970; Ojaveer 1974), Baltic Sea Index in winter, SST and SSB (1977-2004; Cardinale et al. 2009; Margonski et al. 2010), larval abundance in coastal areas, winter air temperature, and SSB during the mild winters (1951-2004; Ojaveer et al. 2011). Re-evaluation of all driver candidates from this list was impossible due to methodological constraints to data availability, but some comparisons of earlier results can be made. From the range of drivers analysed, R appeared to be driven most consistently by prey density in the open GoR, and the severity of the first winter the individuals survived. This finding corroborates the previous general suggestion by Raid et al. (2010) that the environment may be the key in defining R abundance, now substantiated with data. Although SSB itself was not a good predictor of R, adding interaction with SSB to other significant terms improved the overall model power significantly, hence their effect was modulated by the level of SSB. The significantly stronger link between R and the open GoR prey, compared to the effect of prey in coastal areas, corrects earlier studies stressing the key role of coastal nursery areas for the survival of larvae (Rannak and Simm 1979), and implies even

stronger role of larger scale processes affecting the R abundance. SSB no longer qualified as a significant driver for R dynamics during the period of mild winters, as suggested previously by Ojaveer et al. (2011). Several mild winters have occurred since the ecosystem regime shift during 1988/1989. The impact of SSB on R during this period was only marginal, with SSB being very often negatively linked to R.

Stock-recruitment relationships fail to capture the variation in R, due to the multiple drivers of R dynamics, including predation on early life stages (Zimmermann et al. 2021) which is a major factor controlling R success of marine fish stocks (e.g., Bailey and Houde 1989). For example, the top-down control of the herring larval stage by Atlantic mackerel (*Scomber scombrus*) has been most recently identified as one of the two main processes to control the R of the Norwegian spring spawning herring (Garcia et al. 2021). There is also evidence of intense predation on cod eggs by herring and sprat in the Baltic Sea which may affect R of the eastern Baltic cod stock (Köster et al. 2017, and references therein). However, based on the evidence so far, predation on early life stages has not been identified as a likely driver affecting herring R in the GoR, as the share of herring eggs and larvae in stomachs of most abundant local species (such as pikeperch *Sander lucioperca*, three spined stickleback *Gasterosteus aculeatus*, smelt *Osmerus eperlanus* and sprat *Sprattus sprattus*) is either low or negligible (Ojaveer et al. 1997).

It has been suggested that SSB may not be a good indicator of reproductive potential of a stock (Walters and Ludwig 1981), and the spawning potential of the repeat spawners should be used instead (Oskarsson and Taggart 2010). In addition, skipped spawning (Bucholz et al. 2013), size-dependent fecundity (Le Bris et al. 2015), size-dependent total reproductive-energy output of females (Barneche et al. 2018) and fish condition-dependent fecundity (Marshall et al. 1998; dos

Santos Schmidt et al. 2017) need to be considered in reproductive potential estimates. Although we do possess some information and knowledge on these issues for the GoR spring spawning herring (e.g., Fulton condition factor, size-dependent individual fecundity and population fecundity), relevant time series at the scale of the current study are lacking (Raid et al. 2010; Putnis et al. 2011). As a result, failure in incorporating this information weakens the 'power' of SSB as an accurate predictor of the reproductive potential.

Non-stationary and non-linear effects in GoR herring recruitment dynamics

The number of studies have shown that the relationships in natural ecosystems are often non-linear and non-stationary, due to simultaneous changes in multiple relevant drivers, and that exploited species are more likely to display abrupt changes than unexploited species (Glaser et al. 2014). For example, in variation of the relationship between R, SSB and temperature of the 38 commercially harvested fish stocks in the northern North Atlantic stocks, threshold models performed better than the linear or non-linear stationary models for 27 stocks, suggesting that abrupt changes are common (Ottersen et al. 2013). Another example is decoupling of herring growth from hydro-climatic factors above a certain threshold abundance of sprat in the Baltic Sea (Casini et al. 2010). The transient nature of the drivers of GoR spring spawning herring R was manifested in several observations in this study, including sudden changes in the strength of the effects over time, gradual changes in the type of the links, and the state dependence.

Extending the time-series may not only result in changes in the links of the R - explanatory variables relationship (Ottersen et al. 2013), but also the strength of the relationship (Stige et al. 2013). While the relationships between R and environment changed generally gradually, rapid changes were observed in the strength of these relationships in both, the growing and sliding

341 window analyses (adj. R^2 of each step). Most dramatic changes, in the form of sudden increase in
342 explanatory power in sliding window analysis, were found in the beginning of 1980s, in the effect
343 of SSB and prey density on R . These changes coincided with a gradual (in case of prey density) or
344 more rapid (SSB) increase in the relationship with R (i.e., slope of the linear model).

345 Also, the type of the relationships between R and the investigated three explanatory variables
346 changed throughout the time-series, most prominently in the case of R vs SSB: from unimodal to
347 linear to a new unimodal, but with a shifted optimum. In the models of R vs winter severity, the
348 result of a growing time series was a change of the link from unimodal to linear, while significantly
349 losing the explanatory power at the same time. At least some of the observed patterns (from the
350 growing window and sliding window analysis) can be clearly related to climate-driven ecosystem
351 regime shift at the end of the 1980s, to a warmer and less saline conditions, which amongst others,
352 resulted in elevated abundances of small-size brackish copepods and very high clupeid biomasses
353 (e.g., Möllmann et al. 2000). The notable improvement of model performance when the interaction
354 with SSB was included in the effects of prey and winter severity is additional proof of the state-
355 dependence, in this case, depending on the level of SSB.

356 Another, less obvious example of a non-stationary (or even state-dependent) process was the type
357 of prey that seems to be critical for R . Evidence supporting the early life-stage regulation of year-
358 class strength in herring is common (e.g., Nash and Dickey-Collas 2005), possibly happening
359 already during the early larval stages (Oeberst et al. 2009), when prey availability plays a key
360 factor in the survival (e.g., Rannak and Simm 1979; Alvarez-Fernandez et al. 2015). The most
361 significant explanatory variable explaining the multiannual dynamics of GoR spring spawning
362 herring R was the abundance of the late copepodite stages (IV-V) of *E. affinis*, which used to be

the main prey of large larvae (Arula et al. 2012), at least in the 1970s. This finding would imply that critical regulation of spring spawning herring R occurs rather during the late larvae in the GoR. However, the situation has probably changed over time. Water transparency in the GoR is very low and has decreased even more during the past decades due to excessive eutrophication. Reduced visibility can cause shifts in prey composition of larval herring, and force already medium-sized larvae to feed on late copepodites (stages IV-V) in the 2000s, but not in the 1970s (Arula et al. 2012). Thus, it is possible that some of the mechanisms responsible for the regulation of herring R abundance are dependent on the change of habitat conditions over time.

Somewhat surprisingly, considering that herring in the Baltic Sea is situated at the limit of the species' geographical range, and also in contrast to several previous studies, the climate signal appeared to be relatively weak and mostly insignificant, manifested mainly *via* the winter severity of the first year of life. Inclusion of winter severity increased the predictive power of the model, but only in case the interaction with the food resource was introduced to the model before. The unimodal link between R and winter severity further pointed to the existence of an optimum range of winter severity for the recruitment success of GoR herring population. Nevertheless, it must be noted that climate (winter air temperature and spring SST) significantly affects the dynamics of the main prey of herring - *E. affinis* - *via* modulation of timing of annual reproductive processes and abundance levels in the GoR (Kornilovs et al. 2004; Klais et al. 2017). Thus, climate is indirectly affecting interannual abundance dynamics of R through food-web dynamics.

Overall, our results point to a dynamic nature of the relationship between R and explanatory variables, and at minimum, call for caution in selecting either explanatory variables, time-periods

or analytical methods for investigations in multiannual dynamics or recruitment abundance, and interpreting and generalising the obtained results.

Relevance of time scale in the functional understanding

Time series of sufficient length are a prerequisite for unravelling the relative roles of different factors affecting R and evaluating whether the same factors remain dominant over longer periods (Hjort 1914). Ideally, the observation period should cover at least one prominent environmental cycle, to allow the detection of non-linear or non-stationary links. Longer time series that encompass multiple environmental cycles reduce the risk of finding spurious correlations (Haltuch and Punt 2011). Thus, shorter time series can bias the identification of most important drivers of R.

Many previous attempts to identify parameters affecting GoR spring spawning herring R dynamics were based on relatively short time series (2-3 decades), and applying mostly linear or parametric methods. Such studies were not even designed to detect non-stationary and non-linear links, like the ones that were found here and also often suggested to be the most common kind in any ecosystem. Current study was also based on the longest time series of GoR herring R to date. As expected, we gained several new insights that contrast at least some of the earlier observations (see above), and allow us to better understand the complexity of driving forces affecting the dynamics of herring R at different ecosystem states. Despite covering time-period over five decades, the evidence suggests that we haven't seen the entire cycle neither for environmental variables nor for the herring population (i.e., closing the loop) yet. Therefore, continuation of data collection (not only just for those parameters which appeared significant in the current work) would be required, to re-evaluate the relationships again in the future.

Our results further support the statement made in previous studies that multiple factors, rather than a single driver, interact in the regulation of the herring year-class abundance. Failure to document the significant relationship between the suggested drivers and R abundance may point to either inappropriate sampling schemes or knowledge gaps in relevant drivers (Wilson et al. 2018). The landscape of continuous improvement of our process-based knowledge, appearance of new analytical methods, and modification of sampling schemes and data collection methodologies poses challenges for identification of relevant drivers and selection of appropriate parameters to be incorporated into the long-term studies at the temporal scale comparable to the current one. While shorter time-scales allow analyses of higher numbers of different parameters, and so offer new insights in the process-based relationships applicable for particular ecosystem states, conclusions derived from the longer time series analyses, incorporating various ecosystem states, are more robust. One of such relevant outcomes of the current study is the importance of SSB in the modulation of the R vs winter severity relationship, where the effect of winter severity was observed only at low levels of SSB.

Relevance for stock assessment and predictions

Although the ecosystem approach to fisheries management has formally been widely adopted at least conceptually about 25 years ago, fish stock assessment and tactical management takes still very little account of ecosystem processes, implicitly ignoring that fish stock production depends on the physical and biological conditions of the ecosystem (Skern-Mauritzen et al. 2016). One of the reasons lies in the limited ability to predict R from environmental factors even if the principal mechanisms are understood (Myers 1998; Dickey-Collas et al. 2010). Thus, even if an

environmental variable is important, it does not mean that it is key to the management of the fishery.

Mean water temperature of 0-20 m water layer and the biomass of the main prey (the copepod *E. affinis*) in May have in the past been good predictors of the R, and were used in the GoR herring assessments and forecasts until 2011 (ICES 2020). When only the data after 2000 was used, biomass of *E. affinis* in May, and Fulton's condition factor for ages 2–5 proved to be good predictors of R, however, incorporating these variables into the herring assessment models also failed due to high variation ratio (ICES 2020). Thus, despite over 60 years of investigations, environment-based forecasts are still less reliable than other approaches for the GoR spring spawning herring assessment on regular basis, and the short-term forecast is currently based on the geometric mean of year classes from 1989 corresponding to a period of improved reproduction conditions and prevalence of mild winters (ICES 2020). The sliding window analysis in the current study implies that the abundance of copepodite stages IV-V of *E. affinis* described fairly well (small standard error) R dynamics until 1994 (incorporating years 1987-2011), but the standard error of the relationship increased sharply since then and has remained high until the end of the time-series. This increase is associated with the ecosystem-level regime shift which took place at the end 1980s (Möllmann et al. 2000). Thus, the current ecosystem regime is characterised by a still significant, but variable relationship between herring R and abundance of critical prey, which might not be satisfactory for assessment purposes on a regular basis.

Future work

Shallow littoral habitat plays a key role for early life-stages of herring in the Baltic Sea (Polte et al. 2017), supported by significant relationship between the larval abundance in the shallow coastal

area in the GoR (Pärnu Bay) and spring spawning herring R, found for shorter time-periods than considered in the current work (Ojaveer et al. 2011; Arula et al. 2016). Unfortunately, these extensive high-frequency larval time-series did not meet the requirements to be incorporated into the current analysis, because they are missing data for several years due to lack of surveys. Future investigations should utilise alternative analytical approaches to quantify the importance of larval abundance (by different developmental stages) on the GoR spring spawning herring population R. Also, feasibility of applying the larval growth index approach, which takes into account the non-linear relationship between water temperature and larval growth rate (Xing et al. 2021), should be considered. Larval index might be a better proxy than other environmental parameters (temperature or prey density) to study R dynamics and might allow incorporation of temporally patchy data on herring larvae in R predictions. Overall, this may lead to new possibilities for predicting R for routine assessment purposes.

Further progress in explaining R can also be achieved by using more sensitive measures of the true reproductive potential of the stock than the SSB. To increase our understanding of the stock's dynamics, consideration should be given to adaptive changes in the reproductive investment in relation to the effects of environment and exploitation (Claireaux et al. 2020). There is rather good data and information available for the stock (e.g., Raid et al. 2010, and references therein; ICES 2020), however, at a shorter time-period than covered by the current study (generally since the end 1970s).

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471 Competing interests

472 The authors declare there are no competing interests.

473 Contributors' statement

474 HO: Conceptualization, Funding acquisition, Investigation, Project administration, Supervision,
475 Writing – Original draft. RKP: Conceptualization, Data curation, Formal analysis, Investigation,
476 Methodology, Resources, Supervision, Writing – Original draft. HE: Data curation, Formal
477 analysis, Investigation, Visualization, Writing – Original draft. GR: Data curation, Investigation,
478 Writing - Review & Editing.

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484 Data availability statement

485 The data underpinning the work are available upon request.

486 References

487 Alvarez-Fernandez, S., Licandro, P., van Damme, C.J.G., and Hufnagl, M. 2015. Effect of
488 zooplankton on fish larval abundance and distribution: a long-term study of North Sea herring
489 (*Clupea harengus*). ICES J. Mar. Sci. **72**(9): 2569-2577. doi:10.1093/icesjms/fsv140.

- 490 Arula, T., Kotta, J., Lankov, A., Simm, M., and Põlme, S. 2012. Diet composition and feeding
491 activity of larval spring-spawning herring: importance of environmental variability. J. Sea Res.
492 **68**: 33–40. doi:10.1016/j.seares.2011.12.003.
- 493 Arula, T., Raid, T., Simm, M., and Ojaveer, H. 2016. Temperature-driven changes in early life-
494 history stages influence the Gulf of Riga spring spawning herring (*Clupea harengus m.*)
495 recruitment abundance. Hydrobiologia **767**(1): 125–135. doi:10.1007/s10750-015-2486-8.
- 496 Bailey, K.M., Ciannelli, L., Bond, N.A., Belgrano, A., and Stenseth, N.C. 2005. Recruitment of
497 walleye pollock in a physically and biologically complex ecosystem: A new perspective. Prog.
498 Oceanogr. **67**(1-2): 24–42. doi:10.1016/j.pocean.2005.06.001.
- 499 Bailey, K. M., and Houde, E. D. 1989. Predation on eggs and larvae of marine fishes and the
500 recruitment problem. Adv. Mar. **25**: 1–83.
- 501 Barneche, D. R., Robertson, D. R., White, C. R., and Marshall, D. J. 2018 Fish reproductive-
502 energy output increases disproportionately with body size. Science. **360**(6389): 642–645.
503 doi:10.1126/science.aao6868.
- 504 Beggs, S.E., Cardinale, M., Gowen, R.J., and Bartolino, V. 2014. Linking cod (*Gadus morhua*)
505 and climate: investigating variability in Irish Sea cod recruitment. Fish Oceanogr. **23**: 54–64.
506 doi:10.1111/fog.12043.
- 507 Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. Great
508 Britain. Ministry of Agriculture, Fisheries and Food. Fishery investigations, Series 2, v.19. Her
509 Majesty's Stationery Office, London. 533 pp.

- 510 Brander, K.M. 2010. Impacts of climate change on fisheries. J. Mar. Syst. **79**(3): 389–402. doi:
511 10.1016/j.jmarsys.2008.12.015.
- 512 Bucholz, R.H., Tomkiewicz, J., Nyengaard, J.R., and Andersen, J.B. 2013. Oogenesis, fecundity
513 and condition of Baltic herring (*Clupea harengus* L.): A stereological study. Fish. Res. **145**: 100–
514 113. doi:10.1016/j.fishres.2013.02.003.
- 515 Cardinale, M., Möllmann, C., Bartolino, V., Casini, B., Kornilovs, G., Raid, T., Margonski, P.,
516 Grzyb, A., Raitaniemi, J., Gröhsler, T., and Flinkman, J. 2009. Effect of environmental
517 variability of Baltic herring *Clupea harengus* populations. Mar. Ecol.:Prog. Ser. **388**: 221–234.
518 doi:10.2495/ECO110061.
- 519 Casini, M., Bartolino, V., Molinero, J.C., and Kornilovs, G. 2010. Linking fisheries, trophic
520 interactions and climate: threshold dynamics drive herring *Clupea harengus* growth in the central
521 Baltic Sea. Mar. Ecol. Prog. Ser. **413**: 241–252. doi:10.3354/meps08592.
- 522 Claireaux, M., dos Santos Schmidt, T. C., Olsen, E. M., Slotte, A., Varpe, Ø., Heino, M., and
523 Enberg, K. 2020. Eight decades of adaptive changes in herring reproductive investment: the joint
524 effect of environment and exploitation. ICES J. Mar. Sci. doi:10.1093/icesjms/fsaa123.
- 525 Cury, P.M., Fromentin, J.M. Figuet, S., and Bonhommeau, S. 2014. Resolving Hjort's dilemma:
526 How is recruitment related to spawning stock biomass in marine fish? Oceanography **27**(4): 42–
527 47. doi:10.5670/oceanog.2014.85.
- 528 Dickey-Collas, M., Nash, R.D.M., Brunel, T., van Damme, C.J.G., Marshall, C.T., Payne, M.R.,
529 Corten, A., Geffen, A.J., Peck, M.A., Hatfield, E.M.C., Hintzen, N.T., Enberg, K., Kell, L.T.,

- 530 and Simmonds, E.J. 2010. Lessons learned from stock collapse and recovery of North Sea
531 herring: a review. ICES J. Mar. Sci. **67**(9): 1875–1886. doi:10.1093/icesjms/fsq033.
- 532 dos Santos Schmidt, T. C., Slotte, A., Kennedy, J., Sundby, S., Johannessen, A., Óskarsson, G.
533 J., Kurita, Y., Stenseth, N. C., and Kjesbu, O. S. 2017. Oogenesis and reproductive investment of
534 Atlantic herring are functions of not only present but long-ago environmental influences as well.
535 Proc. Natl. Acad. Sci. **114**(10): 2634–2639. doi:101073/pnas.1700349114.
- 536 Drinkwater, K. F., and Kristiansen, T. 2018. A synthesis of the ecosystem responses to the late
537 20th century cold period in the northern North Atlantic. ICES J. Mar. Sci. **75**(7): 2325–2341.
538 doi:10.1093/icesjms/fsy077.
- 539 Glaser, S.M., Fogarty, M.J., Liu, H., Altman, I., Hsieh, C.H., Kaufman, L., MacCall, A.,
540 Rosenberg, A., Ye, H., and Sugihara, G. 2014. Complex dynamics may limit prediction in
541 marine fisheries. Fish Fish. **15**: 616–633. doi:10.1111/faf.12037.
- 542 Garcia, T., Planque, B., Arneberg, P., Bogstad, B., Skagseth, O., and Tiedemann, M. 2021. An
543 appraisal of the drivers of Norwegian spring-spawning herring (*Clupea harengus*) recruitment.
544 Fish. Oceanogr. **30**:159–173. doi:10.1111/fog.12510.
- 545 Haltuch, M.A., and Punt, A.E. 2011. The promises and pitfalls of including decadal scale climate
546 forcing of recruitment in groundfish stock assessment. Can. J. Fish. Aquat. Sci. **68**(5): 912–926.
547 doi:10.1139/f2011-030.

- 548 Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe: viewed in the light of
549 scientific research. *Rapports et Procès-Verbaux Conseil Permanent International pour*
550 *l'Exploration de la Mer* **20**: 1–228.
- 551 ICES. 2020. Baltic Fisheries Assessment Working Group (WGBFAS). *ICES Sci. Rep.* 2:45. 632
552 pp. doi:10.17895/ices.pub.6024.
- 553 Keyl, F., and Wolff, M. 2008. Environmental variability and fisheries: what can models do? *Rev.*
554 *Fish Biol. Fish.* **18**(3): 273–299. doi:10.1007/s11160-007-9075-5.
- 555 Kirby, R., and Beaugrand, G. 2009 Trophic amplifications of climate warming. *Proc. R. Soc. B.*
556 **276**(1676): 4095–103. doi:10.1098/rspb.2009.1320.
- 557 Klais, R., Lehtiniemi, M., Rubene, G., Semenova, A., Margonski, P., Ikauniece, A., Simm, A.,
558 Põllumäe, A., Grinienė, E., Mäkinen, K., and Ojaveer, H. 2016. Spatial and temporal variability
559 of zooplankton in a temperate semi-enclosed sea: implications for monitoring design and long-
560 term studies. *J. Plankton Res.* **38**(3): 652–661. doi:10.1093/plankt/fbw022.
- 561 Klais, R., Otto, S., Teder, M., Simm, M., and Ojaveer, H. 2017. Winter-spring climate effects on
562 small-sized copepods in the coastal Baltic Sea. *ICES J. Mar. Sci.* **74**(7): 1855–1864.
563 doi:10.1093/icesjms/fsx036.
- 564 Kornilovs, G., Möllmann, C., Sidrevics, L., and Berzinsh, V. 2004. Fish predation modified
565 climate-induced long-term trends of mesozooplankton in a semi-enclosed coastal gulf. *ICES CM*
566 *2004/L:13*. Copenhagen, Denmark. 26 pp.

- 567 Kotta, J., Kotta, I., Simm, M., and Põllupüü, M. 2009. Separate and interactive effects of
568 eutrophication and climate variables on the ecosystem elements of the Gulf of Riga. *Estuar.*
569 *Coast. Shelf Sci.* **84**(4): 509–518. doi:10.1016/j.ecss.2009.07.014.
- 570 Kotta, J., Lauringson, V., Martin, G., Simm, M., Kotta, I., Herkül, K., and Ojaveer, H. 2008.
571 Gulf of Riga and Pärnu Bay. *In Ecology of Baltic Coastal Waters: Ecological Studies* 197.
572 *Edited by* U, Schiewer. Springer, Berlin, pp. 217–243.
- 573 Köster, F. W., Huwer, B., Hinrichsen, H.-H., Neumann, V., Makarchouk, A., Eero, M., Dewitz,
574 B. V., Hüsey, K., Tomkiewicz, J., Margonski, P., Temming, A., Hermann, J.-P., Oesterwind, D.,
575 Dierking, J., Kotterba, P., and Plikshs, M. Eastern Baltic cod recruitment revisited-dynamics and
576 impacting factors. *ICES J. Mar. Sci.* **74**: 3–19. doi:10.1093/icesjms/fsw172.
- 577 Le Bris, A., Pershing, A.J., Hernandez, C.M., Mills, K.E., and Sherwood, G.D. 2015. Modelling
578 the effects of variation in reproductive traits on fish population resilience. *ICES J. Mar. Sci.* **72**:
579 2590–2599. doi:10.1093/icesjms/fsv154.
- 580 Leave-One-Out Cross-Validation. 2011. *In Encyclopedia of Machine Learning. Edited by* C.
581 Sammut and G.I. Webb. Springer, Boston, MA. doi:10.1007/978-0-387-30164-8_469.
- 582 Livdane, L., Putnis, I., Rubene, G., Elferts, D., and Ikauniece, A. 2016. Baltic herring prey
583 selectively on older copepodites of *Eurytemora affinis* and *Limnocalanus macrurus* in the Gulf
584 of Riga. *Oceanologia* **58**(1): 46–53. doi:10.1016/j.oceano.2015.09.001.

- 585 Margonski, P., Hansson, S., Tomczak, M.T., and Grzebielec, R. 2010. Climate influence on
586 Baltic cod, sprat, and herring stock–recruitment relationships. *Prog. Oceanography* **87**(1-4): 277–
587 288. doi:10.1016/j.pocean.2010.08.003.
- 588 Marshall, C. T., Kjesbu, O. S., Yaragina, N. A., Solemdal, P., and Ulltang, O. 1998. Is spawner
589 biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic
590 cod? *Can. J. Fish. Aquat. Sci.* **55**(7): 1766–1783. doi:10.1139/f98-062.
- 591 Möllman, C., Kornilovs, G., and Sildrevics, L. 2000. Long-term dynamics of main
592 mesozooplankton species in the central Baltic Sea. *J. Plank. Res.* **22**(11): 2015–2038.
593 doi:10.1093/plankt/22.11.2015.
- 594 Myers, R.A. 1998. When do environment-recruitment correlations work? *Rev. Fish Biol. Fish.* **8**:
595 285–305.
- 596 Myers, R.A., and Barrowman, N.J. 1996. Is fish recruitment related to spawner abundance? *Fish.*
597 *Bull.* **94**: 707–724.
- 598 Nash, R.D.M., and Dickey-Collas, M. 2005. The influence of life history dynamics and
599 environment on the determination of year class strength in North Sea herring (*Clupea harengus*
600 L.). *Fish. Oceanogr.* **14**(4): 279–291. doi:10.1111/j.1365-2419.2005.00336.x.
- 601 Oeberst, R., Klenz, B., Gröhsler, T., Dickey-Collas, M., Nash, R.D.M, and Zimmermann, C.
602 2009. When is year-class strength determined in western Baltic herring? *ICES J. Mar. Sci.* **66**:
603 1667–1672.

- 604 Ojaveer, E. 1974. On the conditions determining the abundance of the Gulf of Riga spring and
605 autumn herring. *Limnologisymposion* 105–117.
- 606 Ojaveer, E., Arula, T., Lankov, A., and Shipilev, H. 2011. Impact of environmental deviations on
607 the larval and year-class abundances in the spring spawning herring (*Clupea harengus membras*
608 L.) of the Gulf of Riga (Baltic Sea) in 1947-2004. *Fish. Res.* **107**: 159–168.
609 doi:10.1016/j.fishres.2010.11.001.
- 610 Ojaveer, H., Lankov, A., Lumberg, A., and Turovski, A. 1997. Forage fishes in the brackish Gulf
611 of Riga ecosystem (Baltic Sea). *In* Forage Fishes in Marine Ecosystems. Proceedings of the
612 International Symposium on the Role of Forage Fishes in Marine Ecosystems. University of
613 Alaska Fairbanks. Fairbanks, AK: 293–309.
- 614 Ojaveer, H., Lankov, A., Teder, M., Simm, M., and Klais, R. 2017. Feeding patterns of
615 dominating small pelagic fish in the Gulf of Riga, Baltic Sea. *Hydrobiologia.* **792**: 331–344.
616 doi:10.1007/s10750-016-3071-5.
- 617 Ojaveer, E., Raid, T., and Suursaar, Ü. 2004. On the assessment and management of local
618 herring stocks in the Baltic Sea. *In* Management of shared fish stocks. *Edited by* A. Payne, C.
619 O'Brien, and S. Rogers. Blackwell Publishing, Oxford. pp. 240–250.
- 620 Oskarsson, G.J., and Taggart, C.T. 2010. Variation in reproductive potential and influence on
621 Icelandic herring recruitment. *Fish. Oceanogr.* **19**: 412–426. doi:10.1111/j.1365-
622 2419.2010.00554.x.

- 623 Ottersen, G., Stige, L.C., Durant, J.M., Chan, K.S., Rouyer, T.A., Drinkwater, K.F., and
624 Stenseth, N.C. 2013. Temporal shifts in recruitment dynamics of North Atlantic fish stocks:
625 effects of spawning stock and temperature. *Mar. Ecol.: Prog. Ser.* **480**: 205–225.
626 doi:10.3354/meps10249.
- 627 Payne, M. R., Hatfield, E. M. C., Dickey-Collas, M., Falkenhaus, T., Gallego, A., Gröger, J.,
628 Licandro, P., Llope, M., Munk, P., Röckmann, C., Schmidt, J. O., and Nash, R. D. M. 2009.
629 Recruitment in a changing environment: the 2000s North Sea herring recruitment failure. *ICES J.*
630 *Mar. Sci.* **66**: 272–277. doi:10.1093/icesjms/fsn211.
- 631 Perry, R.I., Cury, P., Brander, K., Jennings, S., Möllmann, C., and Planque, B. 2010. Sensitivity
632 of marine systems to climate and fishing: Concepts, issues and management responses. *J. Mar.*
633 *Syst.* **79**(3-4): 427–435. doi:10.1016/j.jmarsys.2008.12.017.
- 634 Polte, P., Kotterba, P., Moll, D, and von Nordheim, L. 2017. Ontogenetic loops in habitat use
635 highlight the importance of littoral habitats for early life-stages of oceanic fishes in temperate
636 waters. *Sci. Rep.* **7**: 42709. doi:10.1038/srep42709.
- 637 Putnis, I., Müller-Karulis, B., and Kornilovs, G. 2011. Changes in the reproductive success of the
638 Gulf of Riga herring. *ICES Document CM 2011/H:13*. 4 pp.
- 639 Radziejewska, T., and Chabior, M. 2004. Climatic and hydrological controls over the zoobenthos
640 in a southern Baltic coastal lagoon. *Hydrobiologia* **514**(1): 171–181.
641 doi:10.1023/B:hydr.0000018217.38809.48.

- 642 Raid, T., Kornilovs, G., Lankov, A., Nisumaa, A M., Shpilev, H., and Järvik, A. 2010.
643 Recruitment dynamics of the Gulf of Riga herring stock: density-dependent and environmental
644 effects. *ICES J. Mar. Sci.* **67**: 1914–1920.
- 645 Rannak, L. 1971. On recruitment to the stock of spring herring in the northern Baltic. *Rapports et*
646 *Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **160**: 76–82.
- 647 Rannak, L., and Simm, M. 1979. Dependence of abundance of the Gulf of Riga spring herring
648 year-classes on the supply of larval food. *ICES Baltic Fish Committee, C.M.*, J9. 1–10.
- 649 Ricker, W.E. 1954. Stock and recruitment. *J. Fish. Res. Board Can.* **11**: 559–623.
- 650 Sigurdsson, T. 2006. The collapse of the Atlanto-Scandian herring fishery: Effects on the
651 Icelandic economy. *In* 13th International Institute of Fisheries Economics and Trade (IIFET)
652 Conference, July 11–14, Rebuilding Fisheries in an Uncertain Environment, Portsmouth, UK.
- 653 Skern-Mauritzen, M., Ottersen, G., Handegard, N.O., Huse, G., Dingsør, G.E., Stenseth, N.C.,
654 and Kjesbu, O.S. 2016. Ecosystem processes are rarely included in tactical fisheries
655 management. *Fish Fish.* **17**: 165–175. doi:10.1111/faf.12111.
- 656 Solow, A. R. 2002 Fisheries recruitment and the North Atlantic Oscillation. *Fish. Res.* **54**(2):
657 295–297. doi:10.1016/S0165-7836(00)00308-8.
- 658 Somarakis, S., Tsoukali, S., Giannoulaki, M., Schismenou, E., and Nikolioudakis, N. 2019.
659 Spawning stock, egg production and larval survival in relation to small pelagic fish recruitment.
660 *Mar. Ecol.: Prog. Ser.* **617-618**: 113–136. doi:10.3354/meps12642.

- 661 Stige, L.C., Hunsicker, M.E., Bailey, K.M., Yaragina, N.A., and Hunt, G.L. Jr. 2013. Predicting
662 fish recruitment from juvenile abundance and environmental indices. *Mar. Ecol.: Prog. Ser.* **480**:
663 245–261. doi:10.3354/meps10246.
- 664 Stige, L.C., Ottersen, G., Brander, K., Chan, K.S., and Stenseth, N.C. 2006. Cod and climate:
665 effect of the North Atlantic Oscillation on recruitment in the North Atlantic. *Mar. Ecol.:Prog.*
666 *Ser.* **325**: 227–241.
- 667 Szuwalski, C.S., Vert-Pre, K.A., Punt, A.E., Branch, T.A., and Hilborn, R. 2015. Examining
668 common assumptions about recruitment: a meta-analysis of recruitment dynamics for worldwide
669 marine fisheries. *Fish Fish.* **16**(4): 633–648. doi:10.1111/faf.12083.
- 670 Tiedemann, M., Nash, R. D. M., Stenevik, E. K., Stiasny, M. H., Slotte, A., and Kjesbu, O. S.
671 2020. Environmental influences on Norwegian spring-spawning herring (*Clupea harengus* L.)
672 larvae reveal recent constraints in recruitment success. *ICES J. Mar. Sci.*
673 doi:10.1093/icesjms/fsaa072.
- 674 Trochta, J. T., Branch, T. A., Shelton, A. O., and Hay, D. E. 2020 The highs and lows of herring:
675 A meta-analysis of patterns and factors in herring collapse and recovery. *Fish Fish.* **21**(3):639–
676 662. doi:10.1111/faf.12452.
- 677 UNESCO. 1968. Zooplankton Sampling. Monographs on Oceanographic Methodology, vol. 2.
678 UNESCO Press, New York. 174 pp.
- 679 Walters, C.J., and Ludwig, D. 1981. Effects of measurement errors on the assessment of stock-
680 recruitment relationships. *Can. J. Fish. Aquat. Sci.* **38**: 704–710. doi:10.1139/f81-093.

- 681 Wilson, C.J., Murphy, H.M., Bourne, C., Pepin, P., and Robert, D. 2018. Feeding ecology of
682 autumn-spawned Atlantic herring (*Clupea harengus*) larvae in Trinity Bay, Newfoundland: is
683 recruitment linked to main prey availability? J. Plank. Res. **40**(3): 255–258.
684 doi:10.1093/plankt/fby003.
- 685 Wood, S.N. 2017. Generalized Additive Models: An Introduction with R (2nd edition). Chapman
686 and Hall/CRC. 496 pp.
- 687 Xing, Q., Yu, H., Ito, S.-I., Ma, S., Yu, H., Wang, H., Tian, Y., Sun, P., Liu, Y., Li, J., and Ye, Z.
688 2021. Using a larval growth index to detect the environment-recruitment relationships and its
689 linkage with basin-scale climate variability: A case study for Japanese anchovy (*Engraulis*
690 *japonicus*) in the Yellow Sea. Ecol. Indic. **122**: 107301. doi:10.1016/j.ecolind.2020.107301.
- 691 Zimmermann, F., Claireaux, M., and Enberg, K. 2019. Common trends in recruitment dynamics
692 of north-east Atlantic fish stocks and their links to environment, ecology and management. Fish
693 Fish. **20**(3): 518–536. doi:10.1111/faf.12360.
- 694 Zimmermann, F., Enberg, K., and Mangel, M. 2021. Density-independent mortality at early life
695 stages increases the probability of overlooking an underlying stock–recruitment relationship.
696 ICES J. Mar. Sci. doi:10.1093/icesjms/fsaa246.

698 **Figure captions**

699 **Fig. 1.** Time-series of (a) Gulf of Riga herring recruitment (R, shifted one year earlier, 10^6
 700 individuals) and spawning stock biomass (SSB, thousand tons) (ICES 2020, Ojaveer *et al.* 2004),
 701 (b) abundance of *E. affinis* copepodites stages IV-V in open GoR; logarithmic ($\ln(\text{ind. m}^{-2})$) and
 702 absolute value ($1000 \times \text{ind. m}^{-2}$), and (c) winter severity, lagged time-series describing the first
 703 winter these individuals survived (WS1, sum of negative daily temperatures, °C).

704 **Fig. 2.** Generalized additive model (GAM) output without spawning stock biomass (SSB)
 705 interaction to describe (a) partial effect of abundance of *E. affinis* in open GoR (copepodites stages
 706 IV-V, $\ln(\text{ind. m}^{-2})$), and (b) partial effect of winter severity (WS1, sum of negative daily
 707 temperatures, °C) on the Gulf of Riga herring recruitment (R, 10^6 individuals) during 1958-2015
 708 (M1, see Table 2). Black dotted lines are 95% confidence intervals of the predicted lines (i.e., $\pm$
 709 SE).

710 **Fig. 3.** Generalized additive model (GAM) output with spawning stock biomass (SSB) interaction
 711 to describe (a) partial effect of the interaction of SSB and abundance of *E. affinis* in open GoR
 712 (copepodites stages IV-V, $\ln(\text{ind. m}^{-2})$), and (b) partial effect of the interaction of SSB and winter
 713 severity (WS1, sum of negative daily temperatures, °C) on the Gulf of Riga herring recruitment
 714 (R, 10^6 individuals) during 1958-2015. Color scale and contour lines indicate the R values
 715 predicted by the model (M2, see Table 2).

716 **Fig. 4.** Out of sample prediction for the Gulf of Riga herring recruitment abundance (R, 10^6
 717 individuals) during 1958-2015. For models and steps see Table 2. Black lines: observed R value;
 718 grey lines: R value predicted with the given model.

Fig. 5. Growing window analysis to test the changes in type (linear or non-linear), direction (positive or negative) and strength (R^2) of the relationship between the Gulf of Riga spring spawning herring recruitment abundance (R) and (a-b) spawning stock biomass (SSB, thousand tons), (c-d) abundance of *E. affinis* in open GoR (copepodites stages IV-V, $\ln(\text{ind. m}^{-2})$), and (e-f) winter severity (WS1, sum of negative daily temperatures, °C). Left panel: type and the direction of the relationships between R and the respective explanatory variable over increasing observation period. Coloring of the lines indicates the number of years included in each step, corresponding to the legend in panel c. Right panel: adjusted R^2 values for each time-step, filled points denote values where the step model was significant at $p < 0.05$.

Fig. 6. Sliding window analysis to test the stepwise changes in direction (positive or negative) and strength (R^2) of the linear relationship between the Gulf of Riga spring spawning herring recruitment abundance (R) and: (a-b) spawning stock biomass (SSB, thousand tons), (c-d) abundance of *E. affinis* in open GoR (copepodites stages IV-V, $\ln(\text{ind. m}^{-2})$), and (e-f) winter severity (WS1, sum of negative daily temperatures, °C). Left panel: slope of the linear model (points) and mean value of the respective explanatory variable (grey line), fitted to each 15 year subset of data. Error bars show the standard error of the slope for subsets where the slope was significant at $p < 0.05$. Right panel: adjusted R^2 of the linear model fitted in every step. Filled points show steps where the model was significant at $p < 0.05$.

Table 1. Statistical methods used in the study.

Method	Aim of the analysis
GAM without interaction to SSB (with forward selection)	Identify the set of variables that explain R the best, while excluding SSB from the variables. Although R is expected to depend on SSB, both R and SSB are recalculated and corrected for several years after the observation year, hence the model that includes SSB as predictor is less reliable in the operational prediction of the R for current year. GAM was chosen to test for the non-linearity of the relationships.
GAM including the interaction to SSB (with forward selection)	Identifying the set of variables that most likely affect R. SSB was only included as an interaction with other variables due to the hypothesis that links between R and environment are state-dependent, and the state itself is defined by the level of SSB. GAM was chosen to test for the non-linearity of the links.
Out of sample prediction skill	Evaluate the future R prediction skill of different model versions resulting from previous two analyses. Out of sample prediction skill is a generic validation procedure which provides more realistic evaluation of models' performance than the adjusted R ² of the model, and is often used as performance criteria for time series forecasts.
Growing window analysis	Test if the shape of the link, direction or the strength of it

changes when the longer period is analysed. The method is not common, i.e., we could not find any other study that would use a similar approach.

Sliding window analysis

Test the changes in strength and direction of the links over time, while keeping the length of period fixed. Inspired by Kirby and Beaugrand (2009).

Table 2. Results of the Generalized Additive Modelling of GoR herring recruitment abundance (R , 10^6 individuals) in 1958-2015, and the out of sample prediction skill of each model step. Explanatory variables tested in the analysis are SSB (thousand tons), winter severity (WS0, WS1; sum of negative daily temperatures, °C), mean May air temperature (°C), and abundance of *E. affinis* (copepodites stages I-III, IV-V, and adult copepods; $\ln(\text{ind. m}^{-2})$) in the open GoR and Pärnu Bay, $n = 55$.

Model	Adjusted R^2	P-value (for the first and second variable, respectively)	Out of sample prediction skill, adjusted R^2
Model 1 (M1; terms included individually without interaction to SSB)			
Step 1: $R \sim s(E. affinis \text{ (IV-V, GoR), } k=4)$	0.46	<0.001	0.40
Step 2 (final model): $R \sim s(E. affinis \text{ (IV-V, GoR), } k=4) + s(\text{winter severity (WS1), } k=4)$	0.52	<0.001 0.043	0.40
Model 2 (M2; all terms included in interaction with SSB)			
Step 1: $R \sim te(SSB, E. affinis \text{ (IV-V, GoR), } k=4)$	0.53	<0.001	0.49
Step 2 (final model): $R \sim te(SSB, E. affinis \text{ (IV-V, GoR), } k=4) +$	0.62	<0.001 <0.001	0.53

te(SSB, winter severity
(WS1), k=4)