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An appraisal of the drivers of Norwegian spring-spawning herring (*Clupea harengus*) recruitment

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Abstract

Norwegian spring-spawning herring (NSSH, *Clupea harengus*) is a key species in the food-web and for fisheries in the north-east Atlantic. NSSH has been the focus of many ecological and fisheries studies over decades and several hypotheses have been put forward to explain variations in its recruitment. We conducted an extensive literature review of the processes that have been hypothesized to control recruitment at age-2 years. From this review, we constructed a conceptual model to represent how these processes are inter-connected. We then evaluated several of these hypothesized processes using quantile regression modelling and the most recent available data series as input. Most of the hypotheses were not supported by our analyses. Only two hypotheses were supported: the top-down control of herring larval stage by Atlantic mackerel (*Scomber scombrus*) and the positive effect of temperature on recruitment. For the latter the interpretation of the results is nevertheless ambiguous when the latest years (1998–2018) of observations are included, as the correlation then changes from positive to negative. Furthermore, when retesting the hypotheses on age-2 years estimates, we observe a benefitting effect of a consistent strong forcing of the Norwegian Coastal Current and a possible positive effect of the NSSH spawning stock on recruitment. How much these hypotheses can be used to make predictions about future recruitment of herring remains to be tested but based on our results, the relatively short time series available and the dispersion of the observations around the regression models, we can anticipate that such predictions would have limited use for the purpose of fisheries assessment and management.

KEYWORDS
early-life stage, environmental conditions, herring, multiple hypothesis testing, Norwegian and Barents Sea, Pelagic fish recruitment, replicability studies

1 | INTRODUCTION

Determining the drivers of fish recruitment to predict stock dynamics has been an endeavour of fisheries research for over a century. Some of the fundamental mechanisms of recruitment control, related to early-life stage survival—the critical period—food availability, predation and transport have been described in the early years of fisheries research (Hjort, 1914). There is a long history of refining the early hypotheses which include among others, the match–mismatch hypothesis (Cushing, 1990), the member–vagrant hypothesis (Sinclair & Iles, 1989) and the triad of production, concentration and retention (Bakun, 1996). Although stock–recruitment relationships are widely used in fisheries management, meta-analyses have shown that the link between stock biomass and subsequent abundance of recruits is generally weak (Cury et al., 2014; Szuwalski et al., 2015), in particular for small pelagic fish species. In their comprehensive analysis of fish recruitment in the world's oceans, Cury et al. (2014) showed that only 4% of the variance in small pelagic fish recruitment could be explained by variations in spawning stock biomass alone.

The recruitment of pelagic fish is known to be highly variable and often assumed to be primarily driven by environmental conditions. In their review of pelagic fish ecology, Trenkel et al. (2014) summarized the hypothesized controlling factors for the recruitment of pelagic fishes. These include the effect of temperature, large scale oceanic patterns (such as the North Atlantic subpolar gyre), predation pressure and body condition/prey availability. A similar set of controlling factors were identified in a subsequent analysis of recruitment drivers in the north-east Atlantic by Zimmermann et al. (2019). From these reviews, there appears to be some degree of generality in the controls and mechanisms that connect environmental variations to recruitment, but the specifics are often context dependent and may vary between populations, regions and time periods (see, e.g., Bailey, 2000; Cushing, 1990; Planque & Frédou, 1999; van der Sleen et al., 2018). If one wants to anticipate possible future year-class strength of a fish population, it is therefore of primary importance to resolve the details of the physical and biological processes that affect recruitment for that particular population.

For fisheries purpose, recruitment is usually considered at the population level and on an annual time scale. This process is spatialized over large geographical areas (spawning grounds, corridors of larval drift, nursery areas) and can extend in time from weeks to years, between egg and recruit stages. Consequently, it is nearly impossible to directly test recruitment hypotheses in an experimental setup. Rather, recruitment studies rely on observations collected over multi-annual time periods and wide geographical areas. In an ecosystem, many controlling factors can interact and may be confounded, so one can never be certain that the connections between controlling factors and recruitment are interpreted correctly. The exact list of detailed controlling mechanisms is generally unknown, and observations in the ocean are limited and prone to observational errors. These elements make the recruitment problem a particularly difficult one to address.

Correlation and regression type analyses have long been central to the study of recruitment control (Myers, 1998). These must be considered with caution, since regressions or correlations that appear to be significant can sometimes emerge between time series that are not related, for example when analysing autocorrelated time series, or because of effects of unmeasured confounding variables. The opposite problem, that is, non-significant regressions or correlations between time series that are causally related, may also occur because of low statistical power, non-linear relationships or complex interactions.

Developments in statistical modelling in recent decades have helped in dealing with the issues mentioned above. Non-linear relationships can be addressed using, for example, generalized additive models (Hastie & Tibshirani, 1990). Robust inference in the case of short autocorrelated time series can be performed through revised statistics (Pyper & Peterman, 1998) or data simulation (Planque & Buffaz, 2008). The study of incomplete sets of limiting factors can be approached using quantile regressions (Cade & Noon, 2003) both for linear and non-linear relationships with quantile generalized additive models (QGAM, Fasiolo et al., 2020). Although these methods cannot solve all the limitations of recruitment studies, they offer new, and hopefully more powerful, ways to explore data and test recruitment hypotheses.

Despite the accumulation of environmental and biological time series data, it remains challenging to robustly and exhaustively identify and quantify the processes involved in determining recruitment. The mechanisms that control recruitment are often hypothesized from limited sets of observations, rather than being directly observed. Environment–recruitment relationships remain elusive and can break down after re-examination (Myers, 1998; Solow, 2002) or be replaced by new hypotheses (Bailey, 2000). Results from different statistical analyses may also appear to be inconsistent because they rely on different assumptions about causal mechanisms or functional relationships between environmental controls and recruitment response (Megrey et al., 2005).

In this context, it is critical to retest past hypotheses and investigate mechanisms behind reported correlations and regressions, as new data and statistical approaches become available (Huse, 2016). This is part of a general process to promote robustness of ecological results through reproducibility and transparency (Powers & Hampton, 2019). In the present study, our purpose is to re-examine existing hypotheses about the control of recruitment for Norwegian spring-spawning herring (NSSH, *Clupea harengus*). We first review the main hypotheses that have been formulated about the control of NSSH recruitment. We then restrict this set of hypotheses to those for which time series data are available to perform quantitative re-evaluation. For each hypothesis, we specify the corresponding expected relationships between data series. We test these expectations using QGAMs (Fasiolo et al., 2020) and classify the results as either inconclusive, supporting or refuting the original hypothesis. Finally, we discuss the possible reasons for the lack of support of previously proposed hypotheses and possible approaches for investigating these further, as well as the potential for NSSH recruitment predictions.
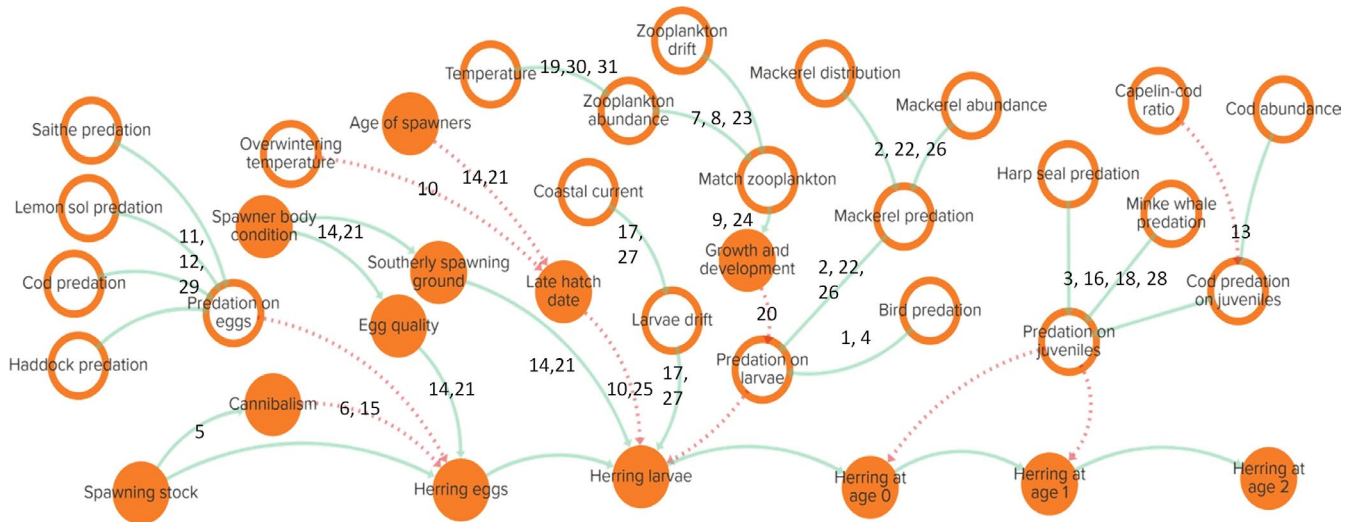
FIGURE 1 Conceptual model of NSSH recruitment. Filled and empty circles represent respectively the relevant intrinsic and extrinsic factors affecting herring recruitment through causal links (arrows). Dashed red arrows mean negative effect and full green arrows a positive effect. Numbers correspond to the references of the review (see Table 1). An online interactive version of the conceptual diagram is available (https://embed.kumu.io/21a64421484dc364eaccf9e95a5e21ca)

2 | MATERIAL & METHODS

2.1 | Case study of the Norwegian spring-spawning herring

The NSSH stock is the most abundant stock of Atlantic herring (*Clupea harengus)*, with an estimated spawning stock biomass (SSB) of 3.8 million tonnes in 2018 (ICES, 2018a). *C. harengus* is a key species for the fishing industry of several northern European countries (Bjørndal et al., 2004; Hamre, 1994; Sandberg et al., 1998). The NSSH plays an ecological key role in the Norwegian and Barents Sea both as a predator of planktonic resources and as a forage species for higher trophic levels (Bogstad et al., 2015; Haug et al., 2002; Wassmann et al., 2006). NSSH spawns along the Norwegian coast in February–March. The larvae drift northward along the coast, and juveniles reach the main nursery area in the Barents Sea. During summer, adults are feeding in the Norwegian Sea (Huse, 2016). During the last century, the NSSH stock underwent great variations in abundance and geographical distribution (Huse et al., 2002; ICES, 2018d). The NSSH stock collapse in the 1960s was assigned to overfishing, particularly on immature individuals (Dragesund, 1970). However, the causes for the observed variations in herring abundance are still not fully resolved, and several biotic and abiotic factors are proposed to play an important role in controlling recruitment (Loeng & Drinkwater, 2007; Røttingen, 1990; Toresen & Østvedt, 2000). In this study, we mainly focus on recruitment of NSSH at age-2 years and on the processes that can explain past variations in recruitment and possibly be used for prediction purposes in the future. The number of age-2 years recruits is a key variable in stock assessments supporting advisory processes through, for example, the ICES working groups on Widely Distributed Stocks (WGWIDE, ICES, 2018c) and Integrated Ecosystem Assessment for the Norwegian Sea (WGINOR, ICES, 2018b).

Historically, a number of hypotheses related to processes occurring during the first year of life of herring were tested using abundance estimates derived from stock assessments (Toresen & Østvedt, 2000; Toresen et al., 2019). Because they were derived from cohort analysis (VPA), these estimations of abundance are based on observed abundances at a later age and are estimated by assuming constant mortality at young ages ($M = 0.9$ for age 0–2, $M = 0.15$ for age 3 and older). As a result, these numbers do not directly reflect observations of young fish (0-1-2 years) in the ocean. Rather they express the expected number of young fish that would have led to the observed numbers of older fish, given assumed mortality rates. For the purpose of retesting previously published analyses, we used the age-0 abundance indices from the Barents Sea ecosystem survey in August/September (Eriksen et al., 2009, values for recent years in ICES, 2018b). Survey data for ages 1–2 also exist from surveys in May/June (ICES, 2018d, Table 4.4.7.2) and August/September (Meeren & Prozorkevitch, 2019, Table 7.3.2.2), but they were found to be very noisy and not internally consistent and were therefore not used in this study.

2.2 | Elaboration of the conceptual model and data set conception

The first step of the analysis was to compile and synthesize available information about various hypothesized drivers of NSSH recruitment and formalize these into a common framework. For this purpose, an extensive bibliographic review was conducted (Supplementary Material S1), in which hypotheses about the ecological processes involved in controlling recruitment were compiled. The set of hypotheses was mapped into a conceptual diagram that represents variables, processes, biological responses and the connections between them (Figure 1, Table 1).

TABLE 1 List of the references used in the conceptual model of NSSH recruitment and their corresponding index according to Figure 1

Index (Figure 1)	References
1	Anker-Nilssen & Barrett, (1991)
2	Astthorsson et al., (2012)
3	Bogstad et al., (2015)
4	Barrett et al., (2002)
5	Fiksen & Slotte, (2002)
6	Fromentin et al., (2001)
7	Fossum & Moksness, (1993)
8	Fossum, (1996)
9	Fiksen & Folkvord, (1999)
10	Husebø et al., (2009)
11	Høines & Bergstad, (1999)
12	Høines & Bergstad, (2002)
13	Hamre, (1988)
14	Heath & Gallego, (1997)
15	Holst, (1992)
16	Haug et al., (2002)
17	Loeng & Drinkwater, (2007)
18	Lindstrøm et al., (2002)
19	Megrey et al., (2005)
20	Ottersen & Loeng, (2000)
21	Óskarsson et al., (2002)
22	Olafsdottir et al., (2019)
23	Prokopchuk & Sentyabov, (2006)
24	Rice et al., (1993)
25	Slotte et al., (2019)
26	Skaret et al., (2015)
27	Skagseth et al., (2015)
28	Tjelmeland & Lindstrøm, (2005)
29	Toresen, (1991)
30	Toresen & Østvedt, (2000)
31	Toresen et al., (2019)

The intention of this study is to retest most of the hypotheses illustrated in Figure 1 using time series of biological and environmental observations. Since multi-annual time series are only available for a subset of the variables presented in the complete conceptual model, a revised and simplified conceptual model was constructed. This model includes components and processes for which there are observational data available to perform the data analyses needed to retest the hypotheses. Observational time series were taken from the literature, when available. Otherwise, they were re-calculated following the methodological information provided by the authors of the original studies.

Finally, the conceptual model selected to perform the numerical analyses was structured around seven major hypotheses:

(i) Spawning stock does not determine the strength of herring recruitment at age-0, except when SSB reaches extremely low levels (Fiksen & Slotte, 2002).

(ii) Early hatching positively affects larval survival (Husebø et al., 2009; Slotte et al., 2019). Older and larger adults reach southernmost grounds where they can spawn eggs of higher quality early in the year (Heath & Gallego, 1997; Óskarsson et al., 2002).

(iii) Mackerel predation reduces larval survival (Skaret et al., 2015).

(iv) The strength of the Norwegian Coastal Current (NCC) controls the northward larval drift towards Barents Sea nursery areas (Loeng & Drinkwater, 2007; Skagseth et al., 2015). A strong NCC implies that the proportion of larvae reaching the nurseries in the Barents Sea is high. NCC is driven mainly by two mechanisms (Skagseth et al., 2015): the density difference between the coastal and Atlantic water (represented by a salinity anomalies index), and a wind-driven part (represented by an along coast wind index, ACW).

(v) Cod predation reduces juvenile survival in the nursery area (Hamre, 1988). Johansen (2003) showed that cod predation on herring is dependent on cod size. The highest predation rates on herring juveniles were determined for cod between 25 and 75 cm, which corresponds approximately to 3–8 years old cod. de Barros et al. (1998) demonstrated that cod predation on herring is dependent on the abundance ratio of capelin to cod.

(vi) Increase in water temperature affects larval survival positively (Toresen & Østvedt, 2000) below a certain threshold and negatively above that threshold (Toresen et al., 2019).

(vii) Zooplankton has a bottom-up controlling effect on recruitment. In recent years (after 2005), a reduction of the zooplankton biomass has been observed and has been associated with weak NSSH recruitment (Toresen et al., 2019).

The selected variables and data sets are summarized in Table 2. An explanation of the selection or re-calculation of the proxies is provided in Supplementary Material S2. When time series of biotic and abiotic data are linked to processes affecting NSSH at other ages than age-2 years, the time series have been lagged (Table 2). This allowed to study the mechanisms that affect a given cohort. For example, when exploring the relationship between salinity and age-2 years recruits, the recruitment time series is compared to the salinity measurements in the year of birth, that is, 2 years earlier.

2.3 | Data analysis

Two types of relationships between factors and responses were considered: limiting relationships and controlling relationships. The notion of limiting factor was developed by Sprengel and Liebig in agronomy in the early 19th century (van der Ploeg et al., 1999). The law's main principle is that "only one element limits the growth of organisms at any given time." The concept has been commonly applied in ecology (Danger et al., 2008), where a factor is considered as limiting if the response cannot exceed an upper limit and this limit is conditional on the value of the factor. Cade and Noon (2003)

TABLE 2 List of the data series and brief descriptions of their characteristics and origin

Variable	Code	Measure of… (Orange circles in Figure 1)	Lag	Time range (not lagged)	Source
Herring abundance at age-2 years (XSAM estimation in millions)	H_R2	Recruitment at age 2	Not lagged	1988–2018	ICES, (2018d) (Table 4.5.1.4)
Herring abundance at age-0 (survey estimation in millions)	H_0	Recruitment at age 0	−2	1980–2017	ICES, (2018b) (Table 1.2)
Spawning stock biomass (XSAM estimation, 1,000 tonnes)	SSB_H	Spawning stock	−2	1988–2018	ICES, (2018d) (Table 4.5.1.4)
Consumption of age-0 and age-1 herring by cod (in millions)	Cc_H	Cod predation	−1	1984–2018	Based on ICES, (2018b) (Table 1.3)
Cod abundance (3–8 years old, in thousands)	Cod	Cod population size	−1	1947–2018	ICES, (2018b) (Table 3.16)
Capelin-cod ratio	Cap_cod_rat	Capelin-cod ratio	−1	1973–2018	ICES, (2018b) (Table 3.16 & 9.5)
Mackerel abundance (in thousands)	Mack	Mackerel predation	−2	1980–2018	ICES, (2018d) (Table 8.7.3.2.)
Along coast wind stress (N.m^{-2})	ACW_stress	Norwegian Coastal Current (strength)	−2	1948–2018	Calculated with data from NCEP-NCAR database
Salinity anomalies	Sal_I2	Norwegian Coastal Current (strength)	−2	1936–2018	Skagseth et al., (2015)
Mean hatching date (in days)	mean_hatch	Hatch timing	−2	1987–2016	Calculated with data from larvae surveys (data provision and curation IMR Kjell Bakkeplass)
Average spawners age	Age_index1	Population structure	−2	1988–2018	ICES, (2018c) (Table 4.4.4.2., 4.4.5.1, 4.5.1.2)
% of recruit spawners	Age_index2	Population structure	−2	1989–2018	ICES, (2018c) (Table 4.4.5.1, 4.5.1.2)
Dry weight of zooplankton along Norwegian coast in (g/m^2)	plank	Zooplankton biomass	−2	1995–2013 (except 2003 & 2007)	Toresen et al., (2019)
Juvenile mortality rate due to cod	Zcod	-	Not lagged	1990–2018	Calculations (S2-c)
Juvenile mortality rate	Ztot	-	Not lagged	1990–2018	Calculations (S2-b)
Kola section water temperature in winter [0–200 m], smoothed over 5 years	Smooth_temp_kola	Water temperature	−1	1935–2015	Calculated with PINRO data as Toresen et al., (2000)

justified the utilization of quantiles near the maximum response to model limiting factors with quantile regression.

In contrast to limiting factors, a controlling factor can drive the response (i.e., causing it to increase or decrease) rather than limit the maximum response. The response to a controlling factor is often modelled by estimating the mean response conditional to the level of the controlling factor. When using quantile regressions, at quantile $\tau = 0.5$, the median response is modelled. This provides results that are similar to those obtained with conventional regression (that estimate the mean rather than the median) but the method is non-parametric and more robust to outliers (Marrie et al., 2009). It is therefore

possible to model the effects of controlling and limiting factors within the single framework of quantile regressions. Quantile GAMs (Fasiolo et al., 2020) offer a powerful statistical modelling technique in cases when the relationships are not expected to be linear.

2.3.1 | Evaluation of earlier hypotheses

Based on the simplified conceptual model, quantile GAMs (Fasiolo et al., 2020) were used to model each controlling and limiting effect. Regressions were performed using a fixed low degree of

freedom ($df_{max} = 3$) to avoid shapes too complex to be meaningfully interpreted as ecological relationships. Controlling effects ($\tau = 0.5$) were tested for all processes, and limiting effects ($\tau = 0.9$) were assessed for predation, temperature and density-dependent processes. This explicitly reflects assumptions from earlier work (S1) that the latter factors may act as limiting factors on recruitment.

The hypotheses structuring the simplified conceptual model can be translated into 13 relationships between pairs of variables. The number of years used for each relationship depends on the lengths of available time series.

For all the 13 relationships, controlling effects were assessed (i.e., by performing quantile regressions with $\tau = 0.5$). Six relationships were additionally considered in the framework of limiting factors (i.e., modelled with quantile $\tau = 0.9$).

To investigate the effects of SSB on abundance of age-0, a Ricker type model was fitted using the linearized form of the model:

$$\ln\left(\frac{N_0}{SSB}\right) = \ln(\alpha) - \beta \times SSB \tag{1}$$

where N_0 is the number of recruits at age-0; SSB the spawning stock biomass; $\ln(\alpha)$ and $-\beta$ are the intercept and slope of the regression, respectively. These parameters were subsequently back-transformed to fit the conventional Ricker model:

$$N_0 = \alpha \times SSB e^{-\beta \times SSB} \tag{2}$$

Using the linearized form of the Ricker equation, instead of using the standard non-linear form, was motivated by the poor performance of the non-linear quantile model fitting (i.e., poor convergence and unstable results). One side effect of the linear transformation is that the independent and dependent variables are correlated, since they both contain the term "SSB." As a result, the model inference must be considered with caution, in particular when the parameter estimates appear to be statistically significant.

Based on the results of the numerical analyses, the hypotheses were categorized in four groups:

1. Hypotheses were considered as "supported" when the quantile regression analysis displayed a significant response to a factor in the same direction as given in the literature.
2. Hypotheses were considered as "refuted" when the quantile regression analysis displayed significant response but in the direction opposite from that reported in the literature.
3. Hypotheses were considered as "inconclusive" when the analyses resulted in non-significant relationships between the factor and the response.
4. For complex cases (i.e., with multiple hypotheses for only one mechanism), hypotheses were considered as "partly supported" when at least one regression was in line with the prior hypotheses while others were not.

2.3.2 | Relationship between age-0 and age-2 years

To be able to compare our results with earlier studies that have used VPA estimates of age-0 abundance, hypotheses from these studies were reassessed using abundance estimates at age-2 years from the most recent assessment (i.e., XSAM, see Supplementary Material, Aanes, 2016a, 2016b, Aanes, 2016c), serving as a proxy for the age-0 VPA abundance estimate for 2 years previously. For this purpose, 11 additional regressions were performed, summing the total number of regressions to 30.

When time series are positively autocorrelated, the number of independent observations is less than expected from the number of actual observations. This tends to bias the inference towards higher rejection rates of the null hypothesis. In cases where the null hypothesis is rejected, it is therefore relevant to consider autocorrelation as a possible source of bias. On the other hand, in cases where the null hypothesis is not rejected, one can ignore the autocorrelation bias, since correcting for autocorrelation would not change the result of the inference test.

The statistical analyses were computed using the R software (R Development Core Team, 2020). The R scripts and the data set are available in the following repository: https://github.com/theogarcia/SEM_Herring

3 | RESULTS

3.1 | Evaluation of earlier hypotheses

Of the 30 quantile regressions modelled in this study, 11 yielded significant results (rejecting the null hypothesis at $p < .05$), indicating controlling or limiting effects. One regression model was close to significance ($p = .050$, Table 3).

The Ricker stock–recruitment models (i.e., quantile regressions of the linearized Ricker models, Figure 2a) were not significant, and results were classified as inconclusive. Analyses of larval drift (i.e., through ACW index and salinity anomalies) showed non-significant relationships and thus led to inconclusive results (Figure 2b and c). The hypothesis that eggs hatch earlier with higher mean age of spawners was supported by the regression analysis (Figure 2d), but no significant controlling effect of percentage of first-time spawners on hatching date was seen (Figure 2e). No evidence of the controlling effect of the timing of hatching on the number of age-0 herring was observed (Figure 2f). Water temperature had no apparent limiting effect on age-0 herring, but a controlling effect was partly supported (the warmer, the more recruits, Figure 2g). Mackerel abundance, on the other hand, appeared to act as limiting factor to the abundance of 0-group herring, but no controlling effect was observed (Figure 2h). No evidence of the bottom-up control of zooplankton biomass on NSSH abundance at age-0 was observed (Figure 2i). The related hypothesis was therefore classified as inconclusive.

The hypothesis that cod predation negatively affects herring recruitment was refuted, as the regression model displays a significant positive

TABLE 3 Summary of the quantile regressions

Model name	Formula	Years	Quantile	Degree of freedom of the smoothed explanatory variable	p-value (in bold < .05)	Autocorrelation in residuals (lag in years)
M1	$\ln(H\_0/SSB) \sim \ln \alpha - \beta \times SSB$	1988–2017	0.5	1	.652	No
M1'	$\ln(H\_R2/SSB) \sim \ln \alpha - \beta \times SSB$	1988–2018	0.5	1	**.026**	Yes (3)
M2	$\ln(H\_0/SSB) \sim \ln \alpha - \beta \times SSB$	1988–2017	0.9	1	.777	No
M2'	$\ln(H\_R2/SSB) \sim \ln \alpha - \beta \times SSB$	1988–2018	0.9	1	**<.001**	Yes (3)
M3	H_0 ~ ACW_stress	1980–2017	0.5	1.124	.390	No
M3'	H_ R2 ~ ACW_stress	1988–2018	0.5	1.001	.110	No
M4	H_0 ~ Sal_I2	1980–2017	0.5	1.038	.737	No
M4'	H_R2 ~ Sal_I2	1988–2018	0.5	1.916	**<.001**	No
M5	mean_hatch ~ Age_index1	1988–2016	0.5	1.65	**.006**	Yes (1)
M6	mean_hatch ~ Age_index2	1989–2016	0.5	1.337	.219	Yes (1)
M7	H_0 ~ mean_hatch	1987–2016	0.5	1.368	.784	No
M7'	H_R2 ~ mean_hatch	1988–2016	0.5	1.004	.379	Yes (10)
M8	H_0 ~ smooth_temp_kola	1980–2015	0.5	1.456	**.002**	No
M8'	H_R2 ~ smooth_temp_kola	1988–2015	0.5	1.904	**.006**	Yes (10)
M9	H_0 ~ smooth_temp_kola	1980–2015	0.9	1.3	.710	No
M9'	H_R2 ~ smooth_temp_kola	1988–2015	0.9	1.98	**<.001**	No
M10	H_0 ~ Mack	1980–2017	0.5	1.594	.427	No
M10'	H_R2 ~ Mack	1988–2018	0.5	1	.217	Yes (10)
M11	H_0 ~ Mack	1980–2017	0.9	1.439	**.004**	No
M11'	H_R2 ~ Mack	1988–2018	0.9	1.33	**.023**	Yes (1)
M12	H_0 ~ plank	1995–2013	0.5	1.311	.78	No
M12'	H_R2 ~ plank	1995–2013	0.5	1.687	.389	No
M13	H_0 ~ plank	1995–2013	0.9	1	.777	No
M13'	H_R2 ~ plank	1995–2013	0.9	1.002	.868	No
M14	H_R2 ~ Cc_H	1984–2017	0.5	1	**.011**	No
M15	H_R2 ~ Cc_H	1984–2017	0.9	1.784	**<.001**	No
M16	Cc_H ~ Cap_cod_rat	1984–2018	0.5	1.362	.171	Yes (8)
M17	Cc_H ~ Cod	1984–2018	0.5	1	.757	No
M18	H_R2 ~ H_0	1988–2017	0.5	1.039	.050	No
M19	H_R2 ~ H_0	1988–2017	0.9	1	.862	No

Note: For every model, the formula and the time period covered are indicated. The controlling effects were modelled using quantile 0.5, whereas limiting effects modelled using quantile 0.9. The statistics of the models are summarized and the results of the examination of the autocorrelation are given with indication of the autocorrelation time-lag. In the case of the Ricker models (i.e., M1, M1', M2 and M2'), the p-value refers to the β parameter. For all others relationship, the *p*-value refers to the smoother of the explanatory variable.

relationship between cod predation and the abundance of age-2 years herring (both controlling and limiting, Figure 2j). Additionally, we compared the mortality rate of herring between age-0 and age-2 years due to cod predation to the total herring mortality rate for this age range. It appeared that mortality due to cod predation only represents a small fraction of the mortality experienced by herring between age-0 and age-2 years (see Figure S2.1 in S2). The hypotheses of the modulation of the predation by cod were inconclusive both for the capelin:cod ratio and for the 3–8 years cod abundance (Figure 2k and l). No clear evidence of a controlling or limiting relationship between the number of 0-group and recruitment at age-2 years was observed (Figure 2m), although the controlling relationship was close to significance (p = .050) (M18, Table 3).

The results from the regression analyses described above and shown in Figure 2 are summarized in Table 3.

3.2 | Recruitment (abundance) at age-2 years *versus* abundance at age-0

Figure 2m shows that the estimates derived from survey (age-0) and stock assessment (age-2 years) are only weakly related. Some results of the relationships modelled in Figure 2 (i.e., mechanisms related to age-0 estimates) differed when the age-2 years estimate was used as response variable instead of age-0 estimates (Figure 3). The linearized
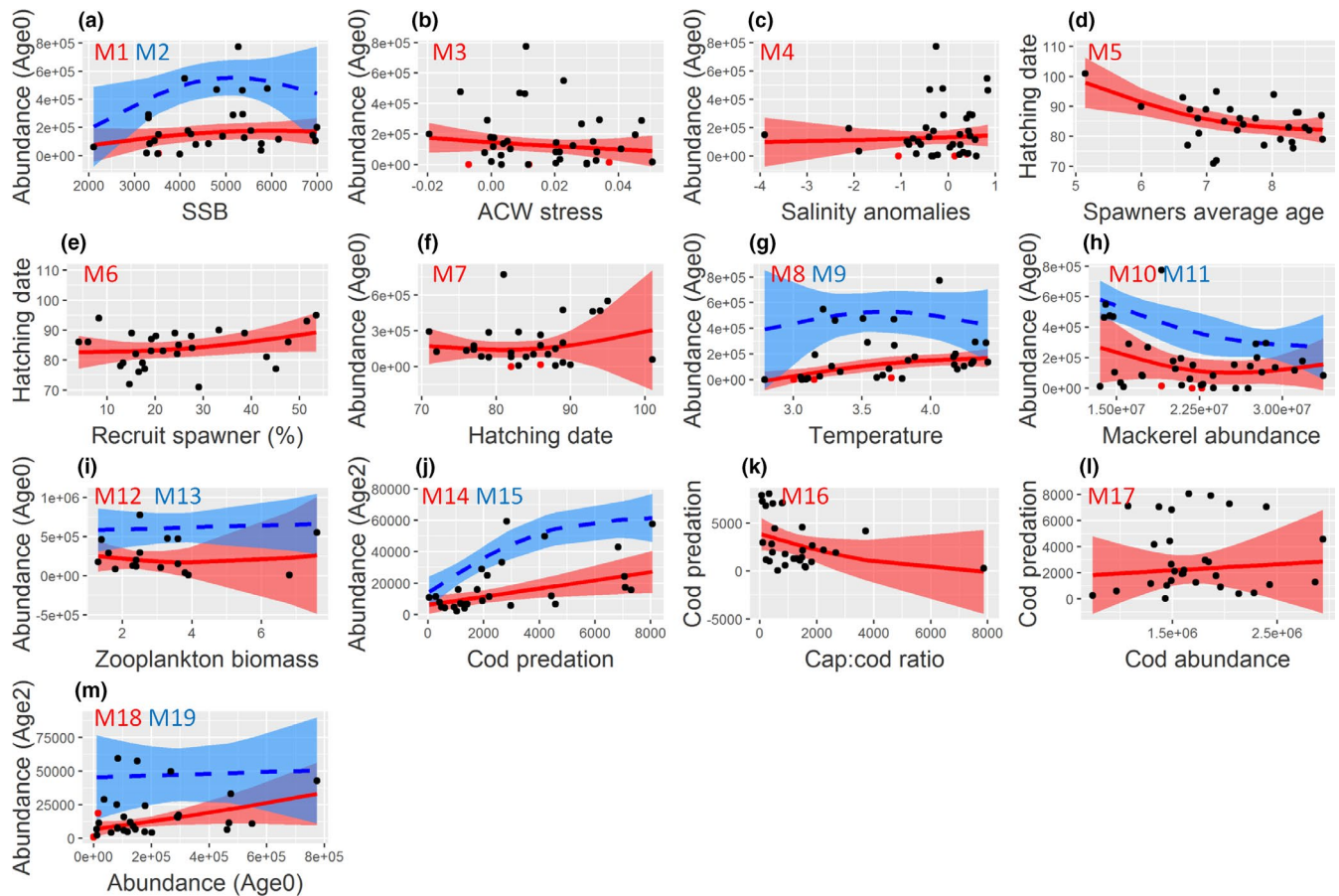
FIGURE 2 Bivariate plots of the quantile regressions performed: at quantiles τ = 0.5 (red line) for controlling relationships and τ = 0.9 (dashed blue line) for limiting relationships. Confidence intervals (CI at 95%) are represented by coloured shadows. Black dots are observations used when fitting the model, and red dots are observations excluded from the model fitting (number of 0-group fish larger than the subsequent number of age-2 years fish in the same cohort, see S2). Model numbers in red (controlling) and blue (limiting)

Ricker model appeared significant for both the limiting and controlling stock–recruitment relationship (Figure 3a), although estimates of the Ricker model parameters were highly uncertain. Given that the linearization of the Ricker function tends to bias the inference towards higher rejection rates (more significant relationships), it is reasonable to assume that unbiased estimates of the model parameters could have yielded non-significant results. The relationship between ACW stress and the abundance of herring at age-2 years appears positive (Figure 3b) while it was negative when recruits at age-0 were considered (Figure 2b), although the two models are not significant. The relationship between abundance at age-2 years and salinity anomalies (Figure 3c) appears significant, although this is primarily driven by two observations with extreme low salinity anomalies. The effects of the date of hatching (Figure 3d), mackerel abundance (Figure 3f) and zooplankton biomass (Figure 3g) remained comparable to those found in the analyses of the 0-age group (Figure 2f, h and i). Both controlling and limiting effects of age-2 years abundance by temperature are dome-shaped (Figure 3e) suggesting a limiting effect on the number of age-2 years for the lowest and highest temperatures.

The results of the hypotheses testing in this subsection are summarized in Figure 4. The hypothesis that early hatching benefits recruitment remains inconclusive, because no significant

relationships were observed. The results support the hypotheses about negative effects of mackerel abundance and positive effects of water temperature on the abundance of age-2 years herring. The positive effect of SSB on the number of age-2 years recruits is classified as partly supported. Although a statistically significant relationship was found, large confidence intervals prevent any conclusion of the SSB effect on recruitment. Of the two hypotheses related to larval drift, only the hydrographic component was significant (i.e., represented by salinity index, M4'). The atmospheric component remained insignificant (i.e., represented by ACW index, M3'). Thus, the results partly supported the hypotheses related to larval drift.

4 | DISCUSSION

We have synthesized a large amount of existing literature about NSSH recruitment dynamics. Many of the reported hypotheses are based on classic fish recruitment theories (Bakun, 1996; Cushing, 1990; Hjort, 1914; Sinclair & Iles, 1989). The graphical representation of the conceptual models (Figure 1) enabled a simplified visualization of how diverse processes can contribute to variations
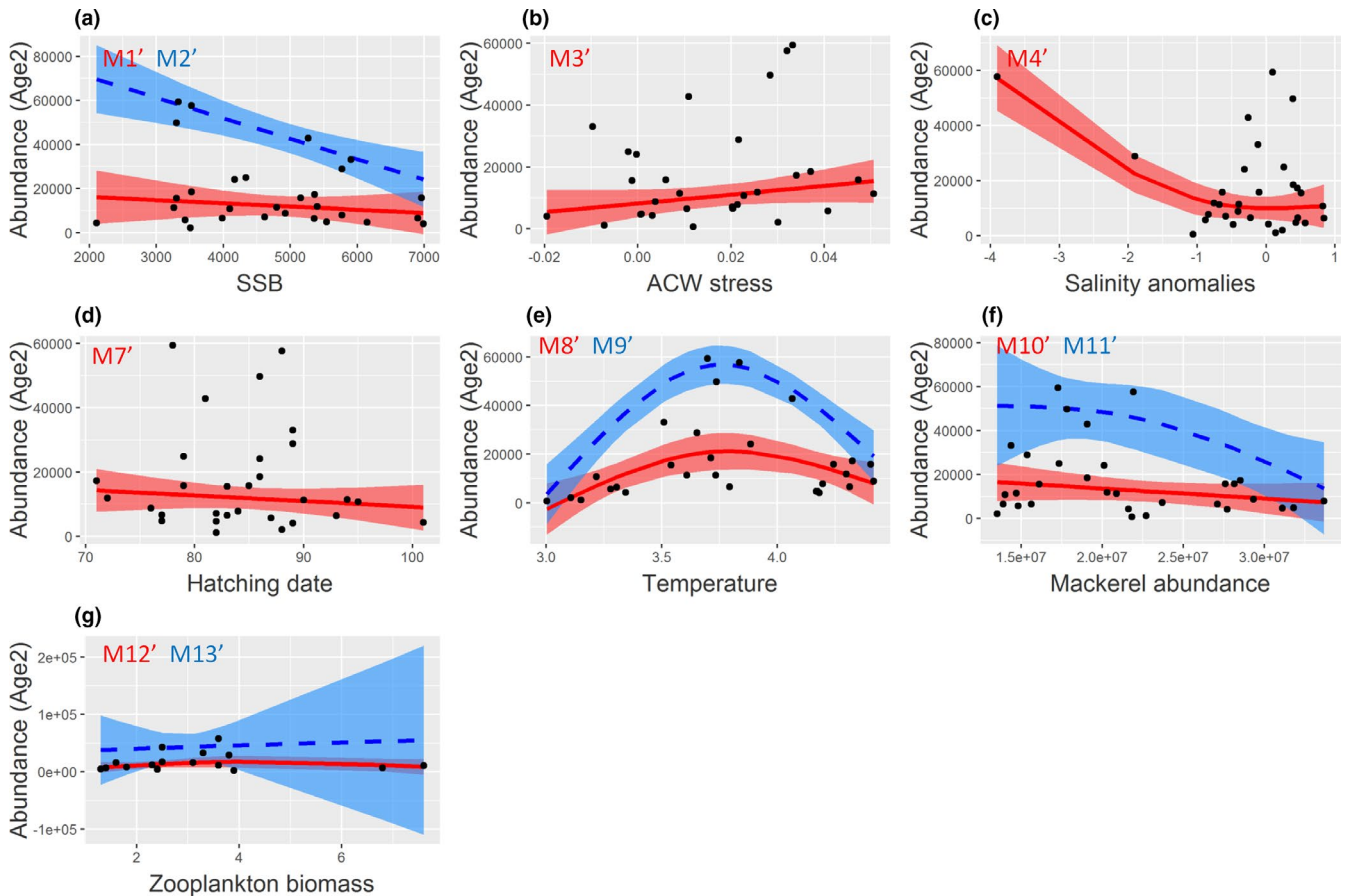
FIGURE 3 Bivariate plots of the quantile regressions for the re-analysis of selected hypotheses using age-2 years estimates (XSAM) as a proxy for age-0 abundance two years previously: at quantiles $\tau = 0.5$ (red line) for controlling relationships and $\tau = 0.9$ (dashed blue line) for limiting relationships. Confidence intervals (CI at 95%) are represented by coloured shadow. Model numbers in red (controlling) and blue (limiting)

in herring early-life stage abundances and how these processes are connected. Based on this, the different steps in the processes can be addressed in the analyses and the most appropriate time series identified. This approach is in a way comparable and complementary to using Paulik diagrams (Brooks et al., 2019) to resolve mechanisms operating at different life stages when establishing stock–recruitment relationships. NSSH has been a model species for some of the prominent earlier hypotheses on fish recruitment (e.g., Cushing, 1990; Hjort, 1914). Nonetheless, in a number of earlier studies, hypotheses about recruitment control have been inferred from empirical observations without a clear understanding of the underlying mechanism (e.g., warm years are associated with higher recruitment at age-2 years). Despite our effort to construct a comprehensive compilation of factors affecting NSSH recruitment, some processes inevitably remain unaddressed. For example, it has been shown in the North Sea that herring larvae may be affected by parasites (Heath & Nicoll, 1991). In the case of NSSH, possible effects of parasitism have not yet been addressed. This illustrates the need to update the conceptual syntheses presented as the results of new studies become available.

The numerical analyses support the hypothesis of a limiting effect of Atlantic mackerel predation on the number of herring larvae,

consistent with the study of Skaret et al. (2015). The geographical expansion of mackerel in the Norwegian Sea during the last decades (Astthorsson et al., 2012; Berge et al., 2015; Olafsdottir et al., 2019; Utne et al., 2012) is hypothesized to have increased a spatial and temporal overlap between mackerel distribution and the drift routes of NSSH larvae (Skaret et al., 2015). Our results also confirm the weak relationship between SSB and age-0 herring abundance (see Figure 2a). In Fiksen and Slotte (2002), the stock–recruitment (at age-0) model prevents making strong predictions of recruitment based on SSB, due to great uncertainties in the Ricker model coefficients. In the data set used in the present work, the stock–recruitment relationship is poorly informed for low values of SSB, which further limits our ability to robustly estimate the Ricker model parameters. We also found relationships between temperature and the number of juveniles, but while some regressions (Figure 2g) tend to support the earlier work of Toresen and Østvedt (2000) indicating a positive link between temperature and age-0 abundance, other regressions (Figure 3e) are more in line with the recent study of Toresen et al. (2019) assuming a dome-shaped relationship with a negative effect of temperature on recruitment in recent warm years. This latter result is similar to the dome-shaped relationship established for cod recruitment and temperature in the north Atlantic
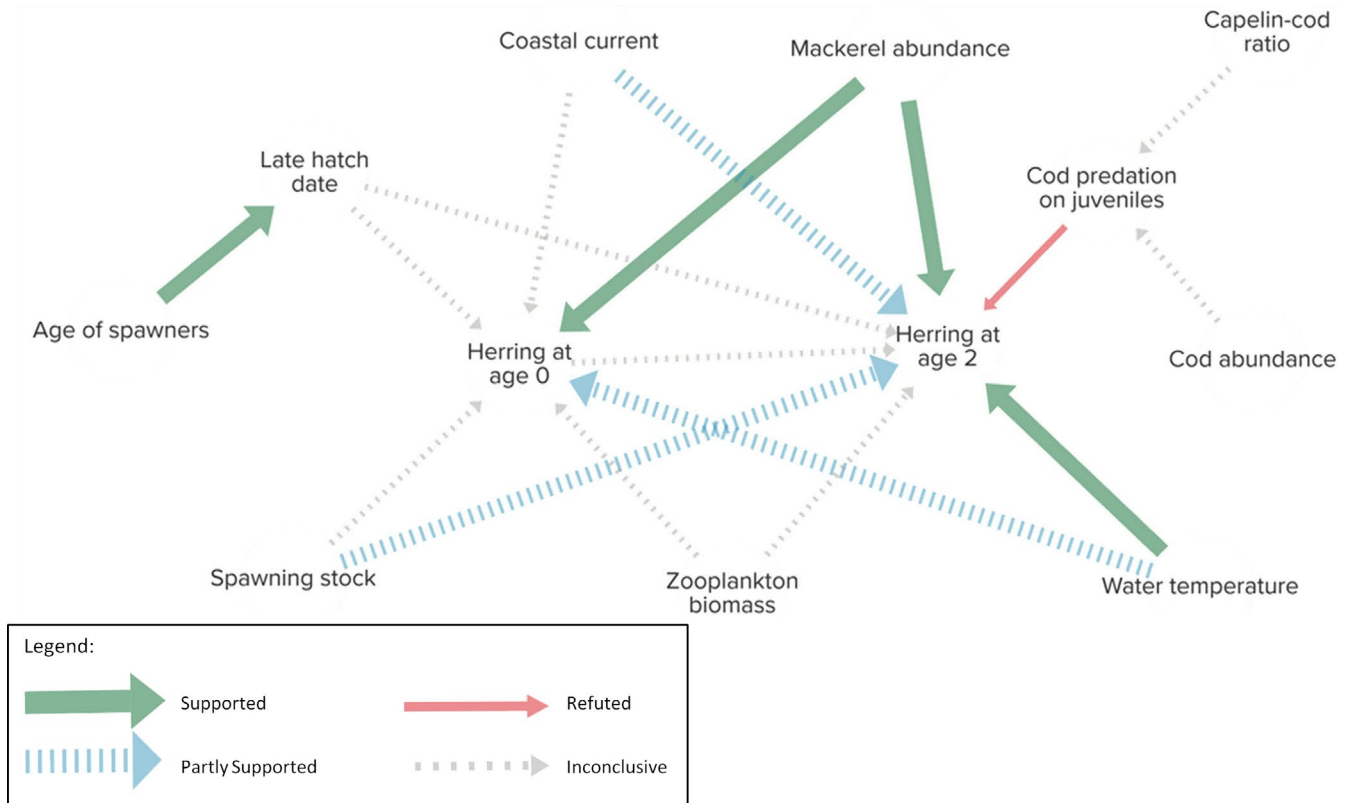
FIGURE 4 Graphical summary of the quantile regression results. Arrows between every component represent the hypothesized mechanism. The colour of the arrows shows the result of the hypothesis testing with quantile regressions ("supported hypotheses" in solid thick green lines, "partly supported hypotheses" in dashed thick blue lines, "inconclusive hypotheses" in dashed thin grey lines and "refuted hypotheses" in solid thin red lines)

(Drinkwater, 2005; Planque & Frédou, 1999). Unprecedented high temperatures since 2002, exceeding previous periods of warm phases in the North Atlantic, suggest that the Norwegian Sea approached temperature conditions outside optimal regimes for herring recruitment. Since 2004, strong changes in environmental regimes have been observed during the early transitions from yolk sac to preflexion NSSH larval stages and were also associated with weak recruitment (Tiedemann et al., 2020). Although the limiting effect of temperature on recruitment is clear at age-2 years (Figure 3e), it is not significant when age-0 abundance is considered (Figure 2g). Toresen and Østvedt (2000) highlighted that the Kola section, where the temperature data were taken from, can often be influenced by Arctic waters which does not adequately reflect the temperature of the water masses that NSSH larvae are experiencing while drifting. This questions the Kola section temperature time series data as a reasonable proxy to examine the ecological link between number of larvae and water temperature. The use of the time series of vertically resolved measurements along the Norwegian coast may constitute a better proxy especially for larval regimes (Skagseth et al., 2015; Slotte & Fiksen, 2000). In this context, evaluating and updating this index further is required. Temperature may affect many ecological processes simultaneously, such as zooplankton phenology and production (Prokopchuk & Sentyabov, 2006), or larval growth (Ottersen & Loeng, 2000). Thus, temperature alone influences

mechanistic relationships that are difficult to assess when only assessing one factor to explain a complex process like recruitment.

Our result revealed an unexpected positive relationship between herring recruitment and cod predation. The hypothesis that cod predation should have a negative impact on the number of age-2 years recruits was refuted; both by the quantile regression analysis and by the contrast between NSSH mortality rate through cod predation and the overall mortality rate of juvenile herring. A positive link between cod predation and the number of recruits would suggest that a third unmeasured variable may be responsible for the perceived positive relationship. Either high predation rates that could limit NSSH recruitment were not adequately measured during the short time series investigated or the observed predation rates are representative, and they never exceed a sufficient threshold to limit herring abundance at age-2 years. Also, the mortality on herring from age 0 to 2 years is partly due to predation by minke whales (Tjelmeland & Lindstrøm, 2005). Trophic cascades in cod dominated ecosystems have been observed (Frank et al., 2005; Hjermann et al., 2007, 2010), and nevertheless, our results do not highlight major top-down control on herring juveniles by cod predation.

For most of the hypotheses retested, results were statistically non-significant leading to inconclusive results. Some of the original hypotheses were based on only a few years of observation (e.g., investigating 5 years of size-dependent cod predation,

Johansen, 2003; or nine years of the variability of cod predation by the capelin–cod ratio, de Barros et al., 1998). In these cases, the original results indicated significant relationships for the period investigated but are likely not robust enough to be considered for longer periods. The statistical analyses of short ecological time series are prone to artefactual results (Siple et al., 2020) and, as environmental–recruitment relationships may change over time, it is an asset to periodically re-evaluate these relationships with updated and longer time series. The bottom-up effect of zooplankton was retested with a time series of 17 years. The analyses led to inconclusive results for limiting and controlling effects both on age-0 and age-2 years NSSH abundance. It seems that quantile GAM failed at fitting the relationship due to two extreme zooplankton biomass values (for years 1997 and 2001). The analyses of the effect of the NCC on recruitment at age-0 were inconclusive whereas the same effects on recruitment at age-2 years led to partly supported results. Such observation can be explained by the inconsistency between age-0 and age-2 years estimates or by the difficulty to describe complex mechanisms such as larval drift. As highlighted by different authors (Cury & Roy, 1989; Skagseth et al., 2015), the advection hypothesis captures complex mechanisms. Wind conditions and bathymetry drive the strength and the direction of the NCC and thus the larval drift. However, such mechanisms might modify also abiotic (e.g., water turbulence, turbidity, salinity) and biotic conditions (e.g., primary production, predation pressure, availability of prey, Fiksen & Slotte, 2002). Thus, as in the case of temperature, it remains difficult to interpret the effects of larval transport on recruitment without considering a collection of interacting mechanisms.

In some of the earlier studies, estimates of 0-group abundances were taken from stock assessment results (VPA and XSAM, Fiksen & Slotte, 2002; Husebø et al., 2009; Skagseth et al., 2015; Toresen & Østvedt, 2000). When using cohort models such as VPA and XSAM, the abundance of young year classes is partly derived from abundances of the same cohort observed in later years while assuming that the mortality of early stages is known. As a result, this implies that estimated 0-group abundance is proportional to the abundance of older fish observed in later years (as illustrated in Figure S2.1). Using such procedure, the age-0 estimate is also prone to errors due to uncertainties in age determination of the older fish (Bogstad et al., 2016). In this study, we have used direct observations of abundance at age-0 from surveys (Dingsør, 2005; Eriksen et al., 2009) and found that there was no direct relationship between survey abundance estimates at age-0 (i.e., Barents Sea survey) and modelled abundance estimates at age-2 years (i.e., XSAM) 2 years later. Hypotheses about ecological control of the 0-group abundance were retested using the age-2 years abundance estimates in order to investigate the possible consequence of the discrepancy between age-2 years and age-0 estimates. In the cases of testing NCC, SSB and temperature the results of the two analyses were not in line. At this point, it remains unclear whether the differences in the results obtained using the age-0 or age-2 years time series arise from high uncertainties in the age-0 abundances estimates or from processes occurring during the first 1.5 year of life which affect NSSH survival

but are not explicitly considered when using age-2 years time series (e.g., minke whale predation, Tjelmeland & Lindstrøm, 2005). This observation questions the reliability of the age-0 abundance estimates. Although the indices might be considered to be reliable for strong year classes (Eriksen et al., 2009), they might be biased for weak year classes (Aanes, 2016a) or for low catchability (i.e., mostly due to small and young fish not fully recruited or by low sampling effort, Aanes, 2016c).

Our re-analysis of earlier hypotheses about the control of herring recruitment was conducted in the spirit of "replicability studies" which aim at evaluating the robustness of prior results (Powers & Hampton, 2019). We could not follow a strict replication protocol, as can be done in biomedical sciences, given that the study is not conducted in an experimental setup. Rather, we compiled data series that best correspond to the processes investigated in earlier studies and used these data series to retest earlier hypotheses. The hypotheses were tested in a simple way using a series of regressions between one dependent and one independent variable. Some of the resulting models had a few extreme values on the x-axis (e.g., M4, M4', M5, M7, M16) or were constrained by a low number of statistical units for some ranges of the explanatory response (e.g., low values of SSB were not available in M1, M2, M1' and M2'). Such data set compositions may lead to problems with interpretation of results from statistical analyses (e.g., difficulties with making inferences for ranges without data on the x-axis) or to biased results (e.g., when significant relationships are mainly driven by outliers, Rousseeuw & Leroy, 2005). Additionally, regression residuals were autocorrelated for nine of the 30 models performed (M1', M2', M5, M6, M7', M8', M10', M11'; see Table 3). Procedures for correcting for autocorrelation have so far not been implemented for quantile GAMs and could not be done directly here. Alternative approaches that include transformation of the time series before model fitting using, for example, prewhitening or first-differencing (Pyper & Peterman, 1998) were not used since they modify the hypothesis that is tested (e.g., testing for effect of year-to-year change in temperature on year-to-year change in recruitment is not equivalent to testing for the effect of temperature on recruitment). Temporal autocorrelation in residuals is known to bias the significance of the tested relationships in the direction of increasing the rejection rate (Bence, 1995). The issue of temporal autocorrelation is therefore only of concern for the models that appear to be statistically significant (M1' and M2': SSB-Recruitment, M5: age-hatching date, M8': temperature–recruitment and M11': mackerel–recruitment). The statistical significance of these models must therefore be taken with caution.

In summary, of the 30 regressions performed, 11 appeared statistically significant. Of these, two were in contradiction with the original hypothesis (M14 and M15), five are potentially biased due to data transformation (M1', M2') and/or autocorrelation (M5, M8' and M11') and one is mostly driven by two outliers (M4'). Residuals in remaining regressions M8 and M9' are not autocorrelated but the time series of Kola temperature used in these models are strongly autocorrelated by construction (5 years running average) which is

also expected to bias the inference. The remaining regression M11 supports the original hypothesis (Mackerel abundance limiting age-0 recruits) without likely statistical bias. How much these hypotheses can be used to make predictions about future recruitment of herring remains to be tested but based on these results, the relatively short time series available and the dispersion of the observations around the regression models we can anticipate that such predictions will have limited use for the purpose of fisheries assessment and management.

Following Huse (2016), we evaluated a set of scientific hypotheses about NSSH recruitment within a common analytical framework. We assembled a collection of observational time series which was used to retest existing hypotheses about processes influencing NSSH recruitment. Based on these results, we conclude that only few of the original hypotheses find empirical support from multidecadal observations. We anticipate that the current set of hypotheses and data is not currently sufficient to perform robust predictions of herring recruitment one or several years into the future.

CONFLICT OF INTEREST
The authors declare to have not conflict of interest.

AUTHOR CONTRIBUTION
TG, BP and PA conceived the research idea; TG ran data analyses; TG and BP wrote the manuscript; PA, BB, ØS and MT provided some data series and participated in discussions of the results and critically reviewed the manuscript.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are available on the online repository https://github.com/theogarcia/SEM_Herring.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.