



## Eight decades of adaptive changes in herring reproductive investment: the joint effect of environment and exploitation

Marion Claireaux <sup>1,2</sup>, Thassya C. dos Santos Schmidt<sup>1</sup>, Esben Moland Olsen<sup>3,4,5</sup>, Aril Slotte<sup>1</sup>, Øystein Varpe <sup>2,6</sup>, Mikko Heino <sup>1,2,7</sup>, and Katja Enberg <sup>2\*</sup>

<sup>1</sup>Institute of Marine Research, PO Box 1870 Nordnes, Bergen N-5817, Norway

<sup>2</sup>Department of Biological Sciences, University of Bergen, PO Box 7803, Bergen N-5020, Norway

<sup>3</sup>Center for Coastal Research (CCR), Department of Natural Sciences, University of Agder, PO Box 422, Kristiansand N-4604, Norway

<sup>4</sup>Institute of Marine Research Flødevigen, Nye Flødevigvei 20, His N-4817, Norway

<sup>5</sup>Department of Biosciences, University of Oslo Centre for Ecological and Evolutionary Synthesis, Oslo, Norway

<sup>6</sup>Norwegian Institute for Nature Research, Bergen N-5006, Norway

<sup>7</sup>Evolution and Ecology Program, International Institute for Applied Systems Analysis (IIASA), Laxenburg A-2361, Austria

\*Corresponding author: tel: +47 55 58 44 14; e-mail: [katja.enberg@uib.no](mailto:katja.enberg@uib.no).

Claireaux, M., dos Santos Schmidt, T. C., Olsen, E. M., Slotte, A., Varpe, Ø., Heino, M., and Enberg, K. Eight decades of adaptive changes in herring reproductive investment: the joint effect of environment and exploitation. – ICES Journal of Marine Science, 78: 631–639.

Received 15 October 2019; revised 10 June 2020; accepted 21 June 2020; advance access publication 4 September 2020.

Reproductive investment is a central trait for population dynamics and productivity. Fishing and environmental variations are major drivers affecting population structure, dynamics, and adaptation of life-history and behavioural traits. However, those factors are often considered independently, and few studies take into account their joint effect. In this study, we investigate the contribution of environment, fishing pressure, and intra-specific competition to variation in the reproductive investment of the Norwegian spring-spawning herring (*Clupea harengus*), a stock that has been fished for centuries, and monitored for decades. Reproductive investment and post-spawning weight were affected differently by growth rate (measured as mean age-at-length), sea surface temperature, North Atlantic Oscillation, and spawning stock biomass in periods with no fishing, unselective fishing, and low but size-selective fishing. We hypothesize that those changes can be explained by direct effects of exploitation such as age truncation and changes in migration patterns. Our results highlight how fishing, by affecting population-level dynamics, can modify the impact of environmental variations on life-history traits.

**Keywords:** *Clupea harengus*, environmental variation, fishing, Norwegian spring-spawning herring, trade-offs

### Introduction

Investment into reproduction is a major life-history trait directly contributing to fitness. It is constrained by important trade-offs (e.g. between growth and reproduction or between current and future reproduction) shaped by the total energy available, the survival landscape, and the environmental conditions (McBride *et al.*, 2015). These trade-offs and the optimal strategies arising

from them have been extensively observed (e.g. Reznick and Endler, 1982; Reznick *et al.*, 1990, 1996) and investigated by theoretical models (e.g. Roff, 1992; Stearns, 1992; Charlesworth, 1994). The main expectations from theory are that (i) reproductive investment increases with age due to the trade-off between current and future reproduction; (ii) an increase in mortality in all age-classes will lead to an increased reproductive investment

earlier in life; and (iii) similarly, if mortality increases after a certain age (or in one specific age class), reproductive investment increases before and decreases after that age (Fabian and Flatt, 2012).

Fisheries are an important source of mortality in exploited stocks and have the capacity to induce changes in life-history traits of wild populations through two major mechanisms (Rijnsdorp and van Leeuwen, 1992; Reznick and Yang, 1993; Law, 2000): first, by removing individuals, fishing can induce compensatory changes in density-dependent traits such as growth. Those changes are plastic, usually occur fast, and are easily reversible, at least in principle. Second, by changing the selection landscape and introducing an additional source of mortality, fishing can induce more durable, evolutionary changes in traits important for a stock's dynamics and productivity (Trippel, 1995; Rochet, 1998; Law, 2000). Such fishing-induced evolution has been widely documented, most frequently as a decrease in age and size at maturation (Ernande et al., 2004; Jorgensen et al., 2007; Heino et al., 2015).

Another, often overlooked, effect of exploitation is its joint effect with environment [see Planque et al. (2010) for a review]. At the population level, the removal of individuals can alter the age-structure, biocomplexity (Hilborn et al., 2003), and spatial range of a population (Corten, 2001), which, in turn, can decrease its buffering capacity (Field and Francis, 2002) and tighten the link between recruitment and environmental conditions (Brander, 2005). At the individual level, Morrongiello et al. (2019) showed that exploitation affects the expression of growth thermal reaction norms in the purple wrasse and, therefore, modifies the adaptive capacity of the species to deal with climate change. To our knowledge, very limited number of studies have considered the joint effect of exploitation and environmental variation on reproductive investment (Hidalgo et al., 2012).

Norwegian spring-spawning herring (NSS herring; *Clupea harengus*) is a widely distributed and very abundant pelagic fish, with a current stock size of ~4 million tons (ICES, 2018). It can live up to 25 years and reach a body length of 40 cm. It presents an indeterminate, density-dependent growth and reproduces annually after maturation (i.e. iteroparity). A very specific characteristic of NSS herring is its extensive migrations between spawning, feeding, and overwintering grounds (Dragesund et al., 1997; Varpe et al., 2005). The amount of energy allocated to its basic needs (e.g. growth, reproduction) largely depends on the amount of resources acquired during the short feeding season (Slotte, 1999a, b; Stephens et al., 2009; Kennedy et al., 2011), when it preys mainly on *Calanus* sp. Around September, NSS herring migrates to the overwintering grounds, currently located along the northern part of the Norwegian coast. In January, it starts swimming southwards and spawns between February and April, mainly off the coast of Møre in central Norway (Slotte and Fiksen, 2000). This capital breeder type of strategy (Jönsson, 1997) makes NSS herring a particularly interesting study species to investigate relationships between environmental conditions, resource acquisition, and trade-off between growth and reproduction.

NSS herring has been exploited for centuries. Catches increased steadily from the 1920s onwards. Modernization of the fleet in the early-1960s kept the numbers increasing, with the highest annual catch recorded in 1966, reaching almost two million tonnes. However, catches rapidly dropped and, in the late-1960s, over-harvesting caused the stock to collapse, leading to the

closing of the fishery (Toresen and Østvedt, 2000; Sandberg, 2010). Almost 15 years later, the strong 1983 year-class allowed the stock to recover. During the decades preceding the collapse, no minimum landing size existed and the average catch size in the last two decades before the collapse was 22 cm, and large amounts of immature fish were caught (calculated from ICES, 2019). This fishery on small herring has been suggested to have led to growth overfishing and, together with overall too high catch rates and resultant recruitment overfishing, contributed to the collapse (Sandberg, 2010). Iceland and USSR established a minimum landing size limit of 25 and 26 cm in 1970, respectively, and Norway established a minimum landing size limit at 20 cm in 1970 and further increased it to 25 cm in 1977 (Sandberg, 2010). Consequently, during the collapse period (here defined as 1970–1989) the average size in catch was 29 cm (calculated from ICES (2019), although strict restrictions were in place and catches were only a fraction of those before and after this period. In the last period (1990–2015), the average catch size was 34 cm (calculated from ICES, 2019).

Given the long and, at times, heavy exploitation history of this stock, it is surprising that so far only two papers have attempted to disentangle the effects of exploitation and environment for the NSS herring life-history traits. Focusing on size and age at maturation, Engelhard and Heino (2004a, b) detected weak changes attributable to fisheries-induced evolution and could not conclude on the presence of evolutionary changes. Adaptation to fishing in NSS herring might be occurring through other life-history traits, but these have so far been mainly studied in the light of environmental and internal drivers [body growth and trade-off between number and size of oocytes (dos Santos Schmidt et al., 2020), gametogenesis (dos Santos Schmidt et al., 2017), spawning migration (Slotte, 1999a, b), and timing of maturation (Slotte and Fiksen, 2000)]. Because reproductive investment together with survival and recruitment success forms the basis of stock productivity and resilience, investigating the long-term changes in reproductive investment and the joint effects of environment and exploitation on this trait is necessary to increase our understanding of the stock's dynamics.

In this study, we use multivariate regression analyses to investigate changes in the reproductive investment and the post-spawning weight of NSS herring in a time period ranging from 1935 to 2015 and spanning from open access fishery via a collapse to a well-managed fishery. We set out to investigate the joint effect of fishing and environmental variations on reproductive investment by comparing the relationship between a proxy of gonad weight and environmental variables at different periods, corresponding to different exploitation patterns and population states.

## Material and methods

### Data description and selection

Our dataset consists of a combination of survey and catch data collected by the Institute of Marine Research (Norway) from 1935 to 2015. Data were first visually inspected and clearly false outliers removed. Only data sampled in the geographical limits determined for the NSS herring stock, in the Norwegian Sea (above 58 N), were used.

Until the mid-1970s, purse seine was the main gear used for the sampling, while both purse seine and pelagic trawl dominated afterwards (Supplementary Figure S1). A comparison of the

samples taken by these two main gear types in the same period revealed that pelagic trawls caught lighter individuals compared to seines (Supplementary Figure S2 and Table S1). We therefore excluded individuals sampled with pelagic trawls from further data analysis to avoid any bias due to changes in sampling gear. There were no statistical differences between females and males, and we therefore pooled both sexes together (Supplementary Figure S3 and Table S2).

The selected data contained 126 664 sexually mature individuals (99 808 maturing/mature and 23 920 spent), sampled along the Norwegian coast between January and April (Supplementary Figure S4). For each individual, the following parameters were considered: whole body weight (g), total length (cm), sex, maturity stage and age (years; read from scales) (Mjanger *et al.*, 2006).

Gonad weight measured directly was available only from 1994 onwards. We therefore needed a proxy of reproductive investment available through the whole time series. In capital breeders such as Atlantic herring, reproductive investment can reliably be estimated from the energy loss during spawning (Rijnsdorp *et al.*, 2005). Because each individual could only be observed once, the reproductive investment  $R$  at year  $i$  was estimated at the population level as the difference between the mean weight before spawning  $W_{pre}$  and the mean weight after spawning  $W_{post}$  at year  $i$  (1)

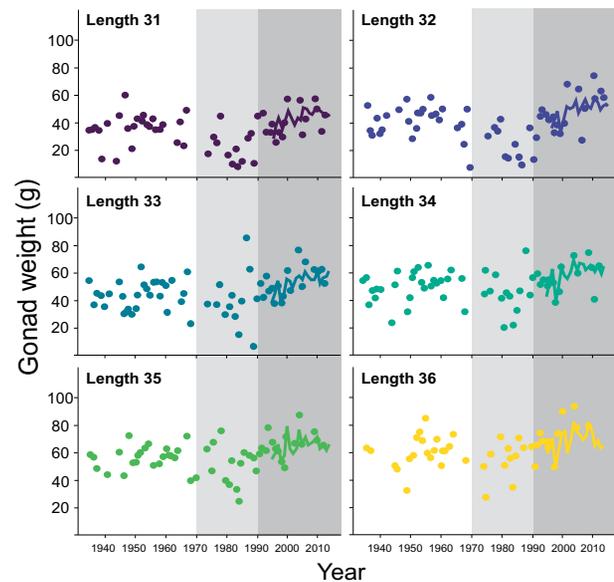
$$R_i = W_{pre,i} - W_{post,i} \quad (1)$$

This measurement was obtained by first aggregating individuals of similar length (1-cm bins) and maturity stage. Even though it would have been desirable to aggregate the data also by age class, this was not possible due to the limited number of observations per year. However, age plays a smaller role than length and condition in NSS herring (Slotte 1999a, b; Slotte and Fiksen, 2000), and age distribution is relatively similar between sampled pre-spawning and spent individuals both across (Supplementary Figures S8 and S9) and within (Supplementary Figure S10) years, increasing the confidence in our proxy of reproductive investment.

The annual pre-spawning weight-at-length was calculated as the mean weight of maturing and mature fish (maturity stages 4 and 5), and the post-spawning weight-at-length as the mean weight of the spent individuals (maturity stages 7 and 8) (Mjanger *et al.*, 2006). Weight measurement up until April was considered to exclude as much as possible the weight gained during the feeding season starting around May. Note that males and females were pooled together as weight-at-length data were not affected by sex (Supplementary Figure S3; Engelhard and Heino, 2004a).

NSS herring usually first reproduces at a length between 29 and 30 cm but can start maturing from sizes as small as 27 cm (Torensen, 1990; Engelhard and Heino, 2004a). In our analyses, we focused on the most abundant length classes—from 31 to 36 cm—and excluded any year and length class combination with <5 pre- or post-spawning individuals.

To confirm our choice of reproductive investment index, we compared it to gonad weight data available from 1994 onwards. We regressed the mean annual gonad weight against our index for each length class, to evaluate the significance of the relationship between the two datasets. In addition, we estimated the correlation between the gonad data and our index using the Pearson's correlation coefficient. Slopes for length classes 33 cm



**Figure 1.** Time series of the mean annual gonad weight (plain line) and of our proxy for reproductive investment (dots) for length classes 31–36 cm. The shaded areas represent different time periods: before the collapse where fishing was unselective (white, 1935–1969), during the collapse where fishing was anecdotal and regulated with minimum landing size (light grey, 1970–1989), and after the collapse where fishing was regulated with minimum landing size and a harvest control rule (dark grey, 1990–2015).

and above were significantly positive but not for length classes 31 and 32 cm (although close to significance for size 32 cm, Supplementary Table S2). The  $R$ -squared and Pearson's correlation coefficient showed reasonable values for length classes 33–36 cm ( $R^2$  between 0.53 and 0.75; Pearson's coefficient from 0.73 to 0.87). However, it seems that our index is weakly correlated to gonad weight for length class 31 (Supplementary Table S2). Nevertheless, we consider our proxy to acceptably reflect reproductive investment (Figure 1).

### Selection of explanatory variables

The choice of explanatory variable was limited by collinearity and time coverage of potential time series. Many potentially important variables such as zooplankton density, competitor abundance, and detailed oceanographic information had to be ignored because the available time series were too short. As our interest in this study lies in the long-term patterns, we chose to focus on explanatory variables for which time series covering the whole period of our dataset (1930–2015) were available.

Temperature is an important driver of many physiological processes and can also affect resource availability and allocation (Clarke and Johnston, 1999; Pörtner *et al.*, 2008). This was accounted for by the averaged Norwegian Sea surface temperature (SST) (National Center for Atmospheric Research, 2017) during the feeding season (May to August, Supplementary Figure S11).

The North Atlantic Oscillation (NAO) (National Center for Atmospheric Research, 2017) describes the large-scale fluctuations in the difference of atmospheric pressure between the Icelandic low-pressure centre and the Azores high-pressure ridge. It is associated with the strength of the westerly winds across the Nordic Seas and governs the circulation's strength of Atlantic and

Arctic waters in the area. Plankton abundance in a given year is shown to be correlated to the spring NAO the year before (Skjoldal, 2004). The averaged NAO in spring (March to May) 2 years before spawning was therefore used as a proxy for feeding conditions (Supplementary Figure S12).

We selected the spawning stock biomass (SSB) as an estimate of intra-specific competition (Olsen *et al.*, 2007; Huse *et al.*, 2012). We used the log-transformed SSB in the analyses to linearize the relationship between SSB and our explanatory variable. The stock assessment used for advisory purposes only spans from 1988 onwards (ICES, 2017), but for the reference point estimation purposes a stock assessment with a longer time perspective has been conducted (ICES, 2018; Aanes, pers. comm., see Supplementary Figure S12 for SSB).

To account for potential trade-offs between growth and reproduction, the mean age-at-length (referred to as Age (at length) in the rest of the manuscript) was included as it reflects differences in growth rates—high age-at-length corresponds to slow somatic growth, and vice versa.

Finally, human activities have the potential to induce changes in the life-history traits of wild populations. As the fishery's selectivity and activity changed during the last 80 years, and as there was no other measurement of selectivity, the data were divided into three periods: (i) where fishing was non-selective and intense in the last part of the period (1935–1969), (ii) collapse period when there was very little targeted fishing (1970–1989), and (iii) after the collapse period when fishing has been kept low and a minimum landing size of 25 cm has been in effect (1990–2015).

The reproductive investment at any given year can be assumed to be affected by environmental factors experienced by NSS herring the year before the spawning season (e.g. down-regulation through atresia; Kurita *et al.*, 2003), but also up to 4 years before the spawning event considered (e.g. reduction in oögonia production through apoptosis; dos Santos Schmidt *et al.*, 2020). However, due to the nature of our data, individuals of different ages were aggregated and it becomes difficult to determine which lag is the most appropriate. To account for this effect, each covariate, except Age (at length), was averaged over 3 years before the spawning season.

### Statistical analyses

To explain the variation in the reproductive effort and the post-spawning weight, we used multivariate linear models. As Age (at length) and SSB were collinear, we used two separate models (2 and 3, respectively) to study their respective effect

$$\text{Weight}\alpha_{ij} + \beta_{1j}\text{SST} + \beta_{2j}\text{Age} + \beta_{3j}\text{NAO} + \varepsilon, \quad (2)$$

$$\text{Weight}\alpha_{ij} + \beta_{1j}\text{SST} + \beta_{2j}\text{SSB} + \beta_{3j}\text{NAO} + \varepsilon, \quad (3)$$

where weight is the reproductive investment or the post-spawning weight,  $\alpha_{ij}$  is the intercept associated to length class  $i$  and period  $j$ ,  $\beta_{1j}$  to  $\beta_{3j}$  are the slopes corresponding to the different covariates for each length class  $i$  and period  $j$ , and  $\varepsilon$  is the remaining variation.

Our goal being to find the simplest model explaining the variations in reproductive investment and post-spawning weight, selection of the environmental variables was made using the backward selection, i.e. starting with the full model and sequentially

removing variables until we reached the most parsimonious models (as measured by the AIC). All the analyses were performed with R (R Core Team, 2019). Goodness of fit and potential autocorrelation were assessed by visual inspection of the residuals (Supplementary Figures S13–S20).

## Results

### Reproductive investment

The most parsimonious models for describing the long-term variations in NSS herring reproductive investment included all the covariates, but not all interactions with length  $i$  and period  $j$  (4 and 5), and are summarized in Supplementary Tables S3 and S4

$$R_{ij}\alpha_{ij} + \beta_{1j}\text{SST} + \beta_{2j}\text{Age} + \beta_{3j}\text{NAO} + \varepsilon; R^2 = 0.52, \quad (4)$$

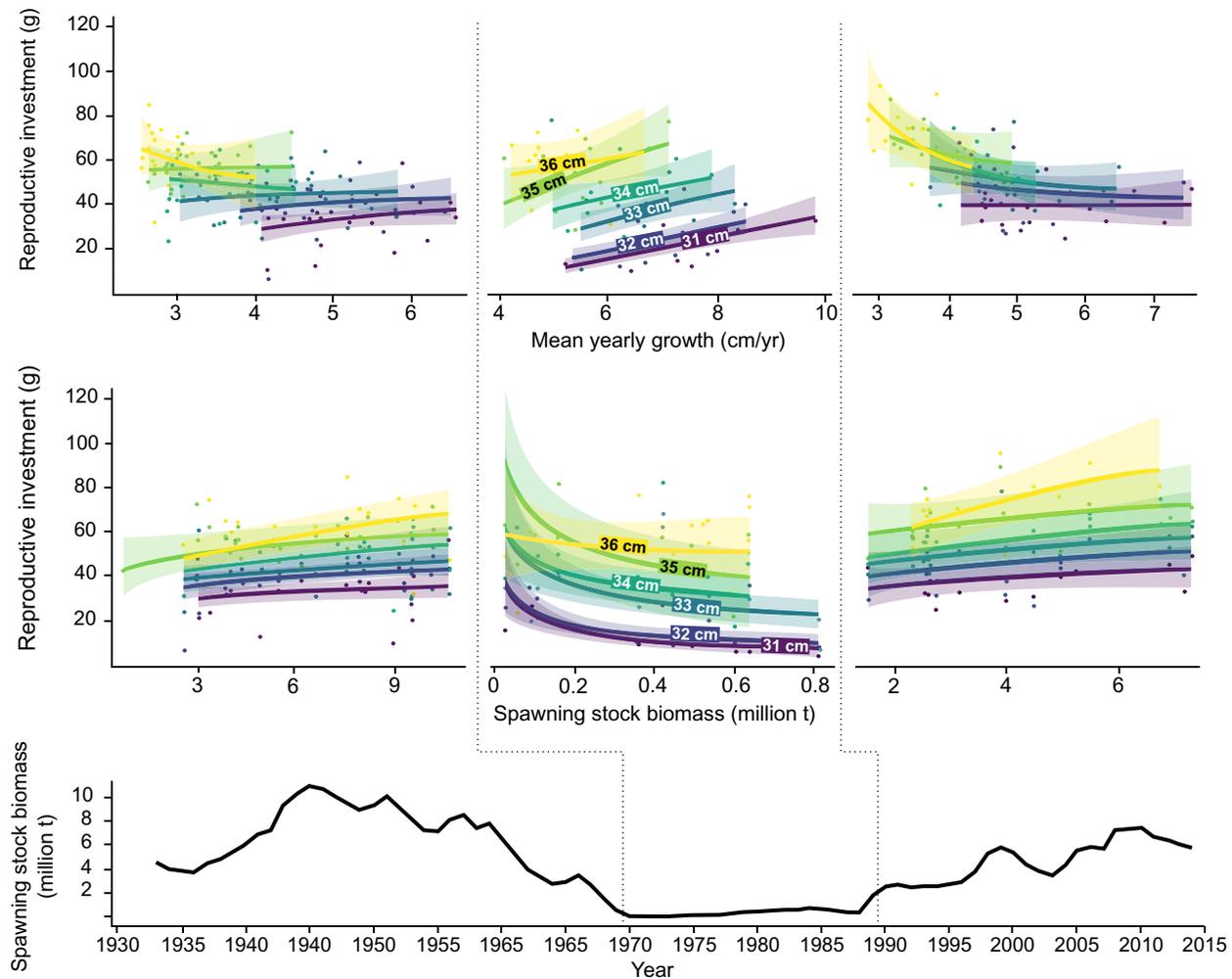
$$R_{ij}\alpha_{ij} + \beta_{1j}\text{SST} + \beta_{4j}\text{SSB} + \beta_{3j}\text{NAO} + \varepsilon; R^2 = 0.55. \quad (5)$$

As expected, the reproductive investment was, in general, higher for larger individuals (Figure 2). For all length classes, gonad weight was the lowest during the collapse (period 2, 1970–1989) and relatively similar between periods 1 and 3 (1935–1969; 1990–2015).

The effect of SST and NAO on the reproductive investment was dependent on the period, but not on the length class (Supplementary Table S3). Before the collapse (period 1), the gonad weight seemed hardly influenced by SST, while it decreased with an increasing NAO. This last relationship got reversed during the collapse period (period 2), as gonad weight increased with NAO but became non-significant after the collapse (period 3). The effect of SST switched from being non-significant to positive during and after the collapse. However, the significance of this relationship varied between the model including SSB or including Age (at length) (Supplementary Tables S3 and S4). It should therefore be interpreted with caution.

The effect of Age (at length) changed between length and period (Figure 2 and Supplementary Table S3). Note that Figure 2 illustrates mean annual growth rate instead of Age (at length), and as high Age (at length) corresponds to slow mean annual growth rate, the slopes in Figure 2 have the opposite direction than what is described below. Before the collapse (period 1), the relationship between Age (at length) and gonad weight was not significant, even though it shifted progressively from negative (31-cm length class) to positive (36-cm length class). During the collapse (period 2), Age (at length) had a significant negative effect for all length classes, at the exception of length class 36 cm, for which it was non-significant. On the opposite, after the collapse (period 3), the slope between Age (at length) and reproductive investment started as non-significant for length class 31 cm and progressively increased, to become significantly positive for length class 36 cm.

Before the collapse, the reproductive investment was positively correlated with SSB in all length classes (Figure 2 and Supplementary Table S4). This relationship changed to significantly negative during the collapse period, at the exception of length class 36 cm, for which it became non-significant. After the collapse, the effect of SSB on the reproductive investment became non-significant, at the exception of length class 36 cm, for which it became positive.



**Figure 2.** Effect of mean age-at-length (upper row) and SSB (middle row, note that the x-axes use different scales) on the reproductive investment of NSS herring for each length class and period. For the sake of visualization and interpretation, we used the mean yearly growth (size divided by mean age-at-length) to represent the trade-off between growth and gonads rather than mean age-at-length directly. The bottom row shows how the SSB varied since 1930. Until 1970, there were no minimum size limits, and both adult and juvenile herring were caught. The fishing pressure intensified in the early-1960s and the stock collapsed a few years later. The stock started to recover with the exceptionally abundant 1983 length class and was considered fully recovered by 1989. Since its recovery, the stock has been closely monitored and managed with harvest control rule and minimum size limit has been in effect.

**Post-spawning weight**

The final models to study the long-term variations in NSS herring post-spawning weight included all the covariates except SSB, but not all interactions with length *i* and period *j* (6 and 7). Some auto-correlation was detected in the residuals and was dealt with by adding a first-order autoregressive structure to the model, using the “gls()” function in R from the nlme package (R Core Team, 2019). As *R*<sup>2</sup> is not computed for these models, we calculated a pseudo *R*<sup>2</sup> (*p.R*<sup>2</sup>) as the correlation between raw and fitted data

$$W_{\text{post}_j} \alpha_{ij} + \beta_1 \text{SST} + \beta_2 \text{Age} + \beta_3 \text{NAO}; p.R^2 = 0.88. \quad (6)$$

$$W_{\text{post}_j} \alpha_{ij} + \beta_1 \text{SST} + \beta_3 \text{NAO}; p.R^2 = 0.87. \quad (7)$$

As expected, bigger individuals also had a heavier post-spawning weight (Supplementary Tables S5 and S6). Post-

spawning weight was relatively similar before (period 1) and after the collapse (period 3) but higher during the collapse (period 2). SST had a negative effect on post-spawning weight before and during the collapse, but became positive, after the collapse (Supplementary Tables S5 and S6). The significance of this relationship was different depending on whether Age (at length) or SSB was used in the model. It should therefore be interpreted with caution. The effect of NAO on post-spawning weight switched from negative before and during the collapse to positive after the collapse.

The effect of Age (at length) on post-spawning weight was the same before (period 1) and during the collapse (period 2) but varied between length classes (Supplementary Table S5): it switched progressively from significantly positive for the 31-cm length class to non-significant for the 36-cm length class. After the collapse (period 3), the post-spawning weight was positively correlated to Age (at length) for length classes 31–33 cm, but this

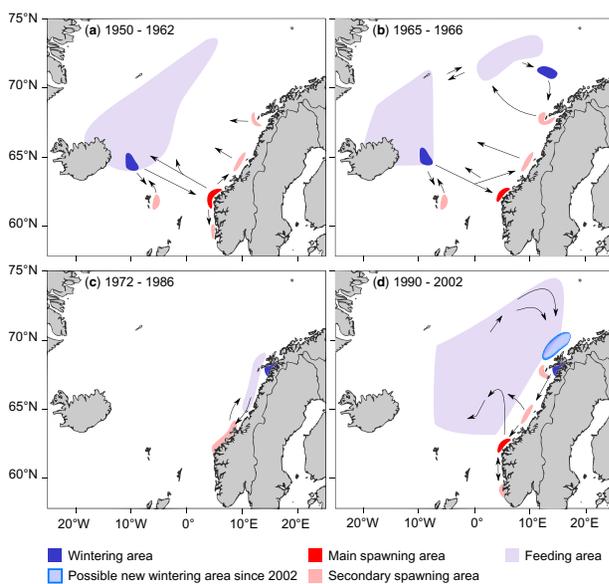
relationship was not significant for the others. Our analysis showed no statistical relationship between SSB and post-spawning weight.

## Discussion

Disentangling the effects of environment and fishing pressure on exploited fish stocks is a complex but major task to increase our understanding of population- and ecosystem-level processes observed and can hopefully help build sustainable management plans. However, only a few studies have explored the joint effect of exploitation and environmental variation [reviewed by Planque *et al.* (2010)] and focused mainly on population-level dynamics such as recruitment (Brander, 2005; Ottersen *et al.*, 2006), migration patterns (Petitgas *et al.*, 2006), and stock's resilience and productivity (Hilborn *et al.*, 2003; Kjesbu *et al.*, 2014; Le Bris *et al.*, 2018). To our knowledge, only one study investigated the combined effect of exploitation and environment at the individual level (on growth; Morrongiello *et al.*, 2019). Our study brings insight into how population size, status, and exploitation can change the relationship between a population's reproductive investment and environmental factors.

## Before and after the collapse

The effects of NAO and SST on the reproductive investment and the post-spawning condition during the post-collapse period (1990–2015) correspond to expectations (Jennings and Beverton, 1991; Skjoldal, 2004) and can emerge through several, mutually non-exclusive, processes: (i) better feeding conditions (i.e. number and quality of food items; Skjoldal, 2004), (ii) increased physiological rates and metabolism, influencing processes related to energy acquisition and allocation (Blaxter and Holliday, 1963; Bailey, 1982), and (iii) increased gonad development rates through hormone synthesis, secretion, metabolism, and gametogenesis (Wood and McDonald, 1997; dos Santos Schmidt *et al.*, 2017).



**Figure 3.** NSS herring migration before (a and b), during (c), and after (d) the collapse [inspired from Skjoldal (2004)]. The oceanic feeding migration pattern has continued into present time (ICES, 2019).

The unexpected patterns we observe during the collapse (i.e. negative effect of NAO and SST on reproductive investment) could be explained by changes in NSS herring migration and distribution between the two periods. Between 1950 and 1965, the stock's feeding grounds were located between the North of Iceland and the middle of the Norwegian Sea, while they covered most of the Norwegian Sea going from the Faroe Islands to Bear Island in the North of Norway in the 1990s (Figure 3; Skjoldal, 2004). Espinasse *et al.* (2017) showed that different *Calanus* species, at different locations over the Nordic Seas, are not impacted the same way by the hydrographic conditions induced by NAO. For example, a positive NAO is linked to a high abundance of *Calanus finmarchicus* on the coast of Northern Norway but to a low abundance of *Calanus hyperboreus* in Northern Iceland. Our assumption that a positive NAO reflects good feeding conditions was based on data gathered after 1990, linking the biomass of *C. finmarchicus* in Atlantic waters of the Norwegian Sea to herring condition (Skjoldal, 2004). The relationship between NAO and feeding conditions for NSS herring could therefore have changed with the feeding grounds location, thus changing the correlation between NAO and gonad weight.

Before the collapse, we could see a trade-off in energy allocation in the 31-cm length class, as years of slow growth were associated with a higher post-spawning condition and vice versa, while the reproductive investment stayed the same. Reaching a large size early pays off later in terms of lifetime reproductive output as bigger individuals have a lower metabolic rate (Winberg, 1956, 1961), higher survival (Gislason *et al.*, 2008, 2010), higher optimal swimming speed (Ware, 1975, 1978), and lower relative cost of migration (Slotte, 1999a, b; Slotte and Fiksen, 2000; Slotte *et al.*, 2000; Jørgensen *et al.*, 2008). However, condition seems to play an important role in migration distance and spawning time, thus influencing egg and larvae development and survival (Slotte *et al.*, 2000). Even though our data do not allow us to conclude why some years have a high growth and low condition and not others, this trade-off only affected the smallest size class (31 cm), probably because this length class is dominated by first-time spawners, which are particularly vulnerable to variations in their energetic status (Slotte, 1999b).

After the collapse, slower growth was associated with higher condition for length classes 31–33 cm, as well as to higher gonad weight, even though the latter relationship was significant only for the 36-cm length class. Such changes in energy allocation between the two periods are difficult to explain, and we can only draw hypotheses in an attempt to understand them. One possible explanation could be the changes in mortality patterns, induced by fishing, predation, or starvation (e.g. through low-resource availability or high inter-specific competition) as theory predicts an increase in reproductive investment with higher mortality (Reznick *et al.*, 1990; Roff, 1992; Stearns, 1992; Jørgensen and Holt, 2013). Fishing mortality seems an unlikely cause for this, as it has been kept relatively low since the stock's recovery. In addition, it targets individuals above 25 cm in this period and this type of selectivity, targeting mostly mature individuals, typically induces little evolutionary pressure on life-history traits (Ernande *et al.*, 2004). Some studies suggest intensification of inter-specific competition for shared food resources between the main pelagic stocks (NSS herring, blue whiting, and mackerel) of the area in the last decade (Huse *et al.*, 2012; Bachiller *et al.*, 2018) that could contribute to the results observed. However, as data on zooplankton and other pelagic stocks are temporally limited compared to

our time series, a more mechanistic approach is necessary to confirm or dismiss this hypothesis.

### During the collapse

The positive relationship between mean annual growth rate and reproductive investment observed during the collapse period lends support to [Reznick \*et al.\*'s \(2000\)](#) hypothesis that challenged the then (and maybe still) dominating view where higher investment into reproduction would automatically mean lower investment into somatic growth, and there would be a clear trade-off between these two costs where the amount of available energy would be divided between the two. However, it is not only the allocation that is flexible but also the acquisition can be changing. This would mean that individuals can vary in their energy acquisition capacities, and those with high energy acquisition rate would have both high somatic growth rates and high reproductive investment, while the individuals with low-energy acquisition capacity would both grow slowly and reproduce less ([Enberg \*et al.\*, 2012](#)). This is exactly what we observe in the collapse period, and to some extent in the period before the collapse ([Figure 2](#)), but why this pattern is reversed in the post-collapse period is not immediately clear to us.

Intra-specific competition could be assumed to have been low when the stock was in the collapsed state, and we do indeed observe higher mean yearly growth rates and size at age during the collapse, supporting the studies suggesting that intra-specific competition was low during this period ([Engelhard and Heino, 2004a](#); [Torensen, 1990](#)). However, reproductive investment and post-spawning weight show a negative relationship with the spawning stock size, implying potentially some other mechanisms of intra-specific competition, for example due to the stock having been restricted to a small area on the Norwegian coast ([Figure 3](#)).

### Do the observed changes have a genetic basis?

One issue that is often raised when investigating the effects of exploitation on life-history traits ([Heino \*et al.\*, 2015](#)), and that we could not address because of the nature of our data, is the contribution of genetic changes to the patterns observed. For example, are the differences in energy allocation (i.e. the relationship between mean age-at-length and gonad weight) observed before and after the collapse only phenotypic or do they have a genetic basis? First, the population collapse induced a potential bottleneck, meaning a loss of allelic diversity that may, in turn, affect phenotypic traits ([Maruyama and Fuerst, 1985](#)). However, this hypothesis is not supported for NSS herring and it is not likely that the stock collapse durably affected the genetic pool of the population ([Gaggiotti \*et al.\*, 2009](#)). Second, recent studies demonstrate that fishing can affect the allelic variation in a population while inducing no changes at the phenotypic level ([Giske \*et al.\*, 2014](#); [Therkildsen \*et al.\*, 2019](#)). In addition, [Therkildsen \*et al.\* \(2019\)](#) showed that size-selective fishing caused greater loss of genetic diversity compared with size-independent fishing. These findings suggest that the loss of genetic diversity in NSS herring due to fishing may be stronger in the current period rather than before the collapse. As we could not investigate those questions in this article, we suggest the genetic analysis of historical NSS herring samples as an essential follow-up of this work.

Understanding how anthropogenic activities can directly or indirectly influence the relationship between life-history traits and environmental factors at the population level is important to

ensure the correct use and interpretation of the data. This is especially true when relationships between traits or between traits and environment are extracted from observational data and then plugged into simulation models. We believe the findings presented in our article can help, for example in parameterizing models for management strategy evaluations, which often lack information about the effects of environment and intra-specific competition on central processes such as growth and recruitment, which are directly linked to reproductive investment and energy allocation.

### Data availability

The data is available upon request through the Norwegian Marine Data Centre ([datahjelp@hi.no](mailto:datahjelp@hi.no)).

### Supplementary data

[Supplementary material](#) is available at the *ICESJMS* online version of the manuscript.

### Acknowledgements

The authors are thankful to Kjell Arne Mork for providing Sea Surface Temperature and NAO data and several reviewers for their constructive comments.

### Funding

MC, KE, and MH acknowledge the Research Council of Norway for funding (ConEvolHer project, number 243735). TCdSS was supported by the National Council of Scientific and Technological Development (CNPq), Brazil (240467/2012-4).

### Author contributions

MC: formal analysis, writing—original draft. TCdSS: writing—review and editing. EMO, AS, ØV: preliminary data analysis, writing—review and editing. . MH and KE: supervision, writing—review and editing.

### References

- Bachiller, E., Utne, K. R., Jansen, T., and Huse, G. 2018. Bioenergetics modeling of the annual consumption of zooplankton by pelagic fish feeding in the Northeast Atlantic. *PLoS One*, 13: e0190345.
- Bailey, R. S. 1982. The population biology of blue whiting in the North Atlantic. *Advances in Marine Biology*, 19: 257–355.
- Blaxter, J. H. S., and Holliday, F. G. T. 1963. The behaviour and physiology of herring and other clupeids. *Advances in Marine Biology*, 1: 261–394.
- Brander, K. M. 2005. Cod recruitment is strongly affected by climate when stock biomass is low. *ICES Journal of Marine Science*, 62: 339–343.
- Charlesworth, B. 1994. Evolutionary genetics: the nature and origin of mating types. *Current Biology*, 4: 739–741.
- Clarke, A., and Johnston, N. M. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, 68: 893–905.
- Corten, A. 2001. The role of “conservatism” in herring migrations. *Reviews in Fish Biology and Fisheries*, 11: 339–361.
- dos Santos Schmidt, T. C., Devine, J. A., Slotte, A., Claireaux, M., Johannessen, A., Enberg, K., Óskarsson, G. J., *et al.* 2020. Environmental stressors may cause unpredicted, notably lagged life-history responses in adults of the planktivorous Atlantic herring. *Progress in Oceanography*, 181: 102257.
- dos Santos Schmidt, T. C., Slotte, A., Kennedy, J., Sundby, S., Johannessen, A., Óskarsson, G. J., Kurita, Y., *et al.* 2017. Oogenesis and reproductive investment of Atlantic herring are

- functions of not only present but long-ago environmental influences as well. Proceedings of the National Academy of Sciences of the United States of America, 114: 2634–2639.
- Dragesund, O., Johannessen, A., and Ulltang, Ø. 1997. Variation in migration and abundance of Norwegian spring spawning herring (*Clupea harengus* L.). Sarsia, 82: 97–105.
- Enberg, K., Jørgensen, C., Dunlop, E. S., Varpe, Ø., Boukal, D. S., Baulier, L., Eliassen, S., et al. 2012. Fishing-induced evolution of growth: concepts, mechanisms, and the empirical evidence. Marine Ecology, 33: 1–25.
- Engelhard, G. H., and Heino, M. 2004a. Maturity changes in Norwegian spring-spawning herring before, during, and after a major population collapse. Fisheries Research, 66: 299–310.
- Engelhard, G. H., and Heino, M. 2004b. Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary responses? Marine Ecology, 272: 245–256.
- Ernande, B., Dieckmann, U., and Heino, M. 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. Proceedings of the Royal Society of London. Series B: Biological Sciences, 271: 415–423.
- Espinasse, M., Halsband, C., Varpe, Ø., Gislason, A., Gudmundsson, K., Falk-Petersen, S., and Eiane, K. 2017. The role of local and regional environmental factors for *Calanus finmarchicus* and *C. hyperboreus* abundances in the Nordic Seas. Polar Biology, 40: 2363–2380.
- Fabian, D., and Flatt, T. 2012. Life history evolution. Nature Education Knowledge, 3: 24.
- Field, J. C., and Francis, R. C. 2002. Cooperating with the environment: case studies of climate and fisheries in the Northern California current. American Fisheries Society Symposium, 32: 245–260.
- Gaggiotti, O. E., Bekkevold, D., Jørgensen, H. B., Foll, M., Carvalho, G. R., Andre, C., and Ruzzante, D. E. 2009. Disentangling the effects of evolutionary, demographic, and environmental factors influencing genetic structure of natural populations: Atlantic herring as a case study. Evolution: An International Journal of Organic Evolution 63: 2939–2951.
- Giske, J., Eliassen, S., Fiksen, Ø., Jakobsen, P. J., Aksnes, D. L., Mangel, M., and Jørgensen, C. 2014. The emotion system promotes diversity and evolvability. Proceedings of the Royal Society B: Biological Sciences, 281: 20141096.
- Gislason, H., Daan, N., Rice, J. C., and Pope, J. G. 2010. Size, growth, temperature and the natural mortality of marine fish. Fish and Fisheries, 11: 149–158.
- Gislason, H., Pope, J. G., Rice, J. C., and Daan, N. 2008. Coexistence in North Sea fish communities: implications for growth and natural mortality. ICES Journal of Marine Science, 65: 514–530.
- Heino, M., Pauli, B. D., and Dieckmann, U. 2015. Fisheries-induced evolution. Annual Review of Ecology, Evolution, and Systematics, 46: 461–480.
- Hidalgo, M., Rouyer, T., Bartolino, V., Cerviño, S., Ciannelli, L., Massutí, E., Jadaud, A., et al. 2012. Context-dependent interplays between truncated demographies and climate variation shape the population growth rate of a harvested species. Ecography, 35: 637–649.
- Hilborn, R., Quinn, T. P., Schindler, D. E., and Rogers, D. E. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences of the United States of America, 100: 6564–6568.
- Huse, G., Holst, J. C., Utne, K., Nottestad, L., Melle, W., Slotte, A., Ottersen, G., et al. 2012. Effects of interactions between fish populations on ecosystem dynamics in the Norwegian Sea—results of the INFERNO project preface. Marine Biology Research, 8: 415–419.
- ICES. 2019. Working Group on Widely Distributed Stocks (WGWIDE). ICES Scientific Reports. 1:36. 948 pp, doi: 10.17895/ices.pub.5574.
- ICES. 2017. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 30 August–5 September 2017, ICES Headquarters, Copenhagen, Denmark. ICES CM 2017/ACOM: 23. 1111 pp.
- ICES. 2018. Report of the Workshop on the Determination of Reference Points for Norwegian Spring Spawning Herring (WKNSSHREF), 10–11 April 2018, ICES Headquarters, Copenhagen, Denmark. ICES CM 2018/ACOM: 45. 83 pp.
- Jennings, S., and Beverton, R. J. H. 1991. Intraspecific variation in the life history tactics of Atlantic herring (*Clupea harengus* L.) stocks. ICES Journal of Marine Science, 48: 117–125.
- Jönsson, K. I. 1997. Capital and income breeding as alternative tactics of resource use in reproduction. Oikos, 78: 57–66.
- Jørgensen, C., Enberg, K., Dunlop, E. S., Arlinghaus, R., Boukal, D. S., Brander, K., Ernande, B., et al. 2007. Ecology: Managing Evolving Fish Stocks. Science, 318: 1247–1248.
- Jørgensen, C., Dunlop, E. S., Opdal, A. F., and Fiksen, Ø. 2008. The evolution of spawning migrations: state dependence and fishing-induced changes. Ecology, 89: 3436–3448.
- Jørgensen, C., and Holt, R. E. 2013. Natural mortality: its ecology, how it shapes fish life histories, and why it may be increased by fishing. Journal of Sea Research, 75: 8–18.
- Kennedy, J., Skjæraasen, J. E., Nash, R. D. M., Slotte, A., Geffen, A. J., and Kjesbu, O. S. 2011. Evaluation of the frequency of skipped spawning in Norwegian spring-spawning herring. Journal of Sea Research, 65: 327–332.
- Kjesbu, O. S., Bogstad, B., Devine, J. A., Gjosæter, H., Howell, D., Ingvaldsen, R. B., Nash, R. D., et al. 2014. Synergies between climate and management for Atlantic cod fisheries at high latitudes. Proceedings of the National Academy of Sciences of the United States of America, 111: 3478–3483.
- Kurita, Y., Meier, S., and Kjesbu, O. S. 2003. Oocyte growth and fecundity regulation by atresia of Atlantic herring (*Clupea harengus*) in relation to body condition throughout the maturation cycle. Journal of Sea Research, 49: 203–219.
- Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES Journal of Marine Science, 57: 659–668.
- Le Bris, A., Mills, K. E., Wahle, R. A., Chen, Y., Alexander, M. A., Allyn, A. J., Schuetz, J. G., et al. 2018. Climate vulnerability and resilience in the most valuable North American fishery. Proceedings of the National Academy of Sciences of the United States of America, 115: 1831–1836.
- Maruyama, T., and Fuerst, P. A. 1985. Population bottlenecks and nonequilibrium models in population genetics. II. Number of alleles in a small population that was formed by a recent bottleneck. Genetics, 111: 675–689.
- McBride, R. S., Somarakis, S., Fitzhugh, G. R., Albert, A., Yaragina, N. A., Wuenschel, M. J., Alonso-Fernández, A., et al. 2015. Energy acquisition and allocation to egg production in relation to fish reproductive strategies. Fish and Fisheries, 16: 23–57.
- Mjanger, H., Hestenes, K., Olsen, E., Svendsen, B. V., and de Lange Wenneck, T. 2006. Manual for Sampling of Fish and Crustaceans. Version 1.0. Institute of Marine Research, Bergen, Norway. <http://84.89.132.1/~michael/barecore/Handbook-fish-December-2006.pdf>
- Morrongiello, J., Sweetman, P., and Thresher, R. 2019. Fishing constrains phenotypic responses of marine fish to climate variability. Journal of Animal Ecology, 88: 1645–1656.
- National Center for Atmospheric Research Staff (Eds). Last modified 22 May 2020. "The Climate Data Guide: Hurrell North Atlantic Oscillation (NAO) Index (PC-based)." Retrieved from <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-pc-based>.
- Olsen, E. M., Melle, W., Kaartvedt, S., Holst, J. C., and Mork, K. A. 2007. Spatially structured interactions between a migratory pelagic predator, the Norwegian spring-spawning herring *Clupea*

- harengus* L., and its zooplankton prey. *Journal of Fish Biology*, 70: 799–815.
- Ottersen, G., Hjermann, D. Ø., and Stenseth, N. C. 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fisheries Oceanography*, 15: 230–243.
- Petitgas, P., Reid, D., Planque, B., Nogueira, E., O’Hea, B., and Cotano, U. 2006. The Entrainment Hypothesis: An Explanation for the Persistence and Innovation in Spawning Migrations and Life Cycle Spatial Patterns. ICES Document CM 2006/B: 07. 9pp.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Core Team 2019. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-141. <https://CRAN.R-project.org/package=nlme> (last accessed 9 December 2019).
- Planque, B., Fromentin, J. M., Cury, P., Drinkwater, K. F., Jennings, S., Perry, R. I., and Kifani, S. 2010. How does fishing alter marine populations and ecosystems sensitivity to climate? *Journal of Marine Systems*, 79: 403–417.
- Pörtner, H. O., Bock, C., Knust, R., Lannig, G., Lucassen, M., Mark, F. C., and Sartoris, F. J. 2008. Cod and climate in a latitudinal cline: physiological analyses of climate effects in marine fishes. *Climate Research*, 37: 253–270.
- R Core Team 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/> (last accessed 9 December 2019).
- Reznick, D., and Endler, J. A. 1982. The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution*, 36: 160–177.
- Reznick, D., and Yang, A. P. 1993. The influence of fluctuating resources on life-history—patterns of allocation and plasticity in female guppies. *Ecology*, 74: 2011–2019.
- Reznick, D. A., Bryga, H., and Endler, J. A. 1990. Experimentally induced life-history evolution in a natural population. *Nature*, 346: 357–359.
- Reznick, D. A., Nunney, L., and Tessier, A. 2000. Big houses, big cars, superfleas and the costs of reproduction. *Trends in Ecology & Evolution*, 15: 421–425.
- Reznick, D. N., Butler, M. J. IV, Rodd, F. H., and Ross, P. 1996. Life-history evolution in guppies (*Poecilia reticulata*) 6. Differential mortality as a mechanism for natural selection. *Evolution*, 50: 1651–1660.
- Rijnsdorp, A. D., Grift, R. E., and Kraak, S. B. M. 2005. Fisheries-induced adaptive change in reproductive investment in North Sea plaice (*Pleuronectes platessa*)? *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 833–843.
- Rijnsdorp, A. D., and van Leeuwen, P. I. 1992. Density-dependent and independent changes in somatic growth of female North-Sea plaice *Pleuronectes platessa* between 1930 and 1985 as revealed by back-calculation of otoliths. *Marine Ecology*, 88: 19–32.
- Rochet, M. J. 1998. Short-term effects of fishing on life history traits of fishes. *ICES Journal of Marine Science*, 55: 371–391.
- Roff, D. A. 1992. *The Evolution of Life Histories: Theory and Analyses*. Chapman & Hall, New York.
- Sandberg, P. 2010. Rebuilding the stock of Norwegian spring spawning herring: lessons learned. In *OECD 2010, The Economics of Rebuilding Fisheries: Workshop Proceedings*, pp. 219–234. OECD Publishing, Paris.
- Skjoldal, H. R. (Ed.) 2004. *The Norwegian Sea Ecosystem*. Tapir Academic Press, Trondheim.
- Slotte, A. 1999a. Differential utilization of energy during wintering and spawning migration in Norwegian spring-spawning herring. *Journal of Fish Biology*, 54: 338–355.
- Slotte, A. 1999b. Effects of fish length and condition on spawning migration in Norwegian spring spawning herring (*Clupea harengus* L.). *Sarsia*, 84: 111–127.
- Slotte, A., and Fiksen, Ø. 2000. State-dependent spawning migration in Norwegian spring-spawning herring. *Journal of Fish Biology*, 56: 138–162.
- Slotte, A., Johannessen, A., and Kjesbu, O. 2000. Effects of fish size on spawning time in Norwegian spring-spawning herring. *Journal of Fish Biology*, 56: 295–310.
- Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Stephens, P. A., Boyd, I. L., McNamara, J. M., and Houston, A. I. 2009. Capital breeding and income breeding: their meaning, measurement, and worth. *Ecology*, 90: 2057–2067.
- Therkildsen, N. O., Wilder, A. P., Conover, D. O., Munch, S. B., Baumann, H., and Palumbi, S. R. 2019. Contrasting genomic shifts underlie parallel phenotypic evolution in response to fishing. *Science*, 365: 487–490.
- Toresen, R. 1990. Long-term changes in growth of Norwegian spring-spawning herring. *ICES Journal of Marine Science*, 47: 48–56.
- Toresen, R., and Østvedt, O. J. 2000. Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. *Fish and Fisheries*, 1: 231–256.
- Trippel, E. A. 1995. Age at maturity as a stress indicator in fisheries. *Bioscience*, 45: 759–771.
- Varpe, Ø., Fiksen, Ø., and Slotte, A. 2005. Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. *Oecologia*, 146: 443–451.
- Ware, D. M. 1975. Growth, metabolism, and optimal swimming speed of a pelagic fish. *Journal of the Fisheries Research Board of Canada*, 32: 33–41.
- Ware, D. M. 1978. Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. *Journal of the Fisheries Research Board of Canada*, 35: 220–228.
- Winberg, G. 1956. Rate of metabolism and food requirements of fish. *Fisheries Research Board of Canada. Translations Series*, 194: 1–253.
- Winberg, G. G. 1961. New information on metabolic rate in fishes. *Fisheries Research Board of Canada. Translations Series*, 362: 1–11.
- Wood, C. M., and McDonald, D. G. 1997. *Global Warming: Implications for Freshwater and Marine Fish*. Cambridge University Press, Cambridge.

Handling editor: Valerio Bartolino