

Climate change and condition of herring (*Clupea harengus*) explain long-term trends in extent of skipped reproduction

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Abstract It is commonly assumed that iteroparous fish, once mature, normally reproduce in all consecutive seasons. Recent work has suggested, however, that in Norwegian spring-spawning herring—a population that undertakes extensive spawning migrations—almost one in two adults may skip their second spawning migration. Why should herring not return to spawn the year after first spawning, but instead wait an extra year? For herring, participation in distant, energetically costly, and risky spawning migrations will only pay off in terms of fitness if individuals are sufficiently large, and in sufficient condition, to both successfully migrate and spawn. Changes in the environment and individual condition should therefore affect the likelihood of skipped spawning. This paper describes long-term changes in the extent to which the second reproductive season is

skipped in this herring population. These are shown to be linked to the size and condition of herring as first-time spawners, and to climatic factors possibly related to food availability. The findings corroborate the hypothesis that skipped reproduction results from trade-offs between current and future reproduction, growth and survival.

Keywords Skipping reproduction · Size and condition · Climate · Current and future reproduction · Spawning migration costs and risks

Introduction

The reproductive potential and hence future biomass of animal populations are directly influenced by the fraction of individuals involved in reproduction. For iteroparous (i.e. repeatedly reproducing) species, this fraction is not only dependent on growth and maturity—two aspects that have been widely investigated—but also on the extent to which adult individuals may skip reproductive seasons. Remarkably, the possibility of skipped reproduction has received relatively little attention in research on fish, including species of high commercial significance (for some notable exceptions, see Rijnsdorp 1990; Oganessian 1993; Burton et al. 1997; Rideout et al. 2000, 2005; Fiksen and MacKenzie 2001; Jørgensen et al. 2006). In fact, it is often assumed that adult fish, once matured, normally return to spawn annually. Recent evidence suggests, however, that skipping of reproductive seasons by adult fish may occur more commonly than usually believed (reviewed by Rideout et al. 2005). For a number of commercially important

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stocks, there are indications of fairly extensive skipping of reproductive seasons (e.g. Oganessian 1993; Rideout et al. 2000; Engelhard and Heino 2005).

Norwegian spring-spawning herring, the world's largest stock of Atlantic herring *Clupea harengus*, occur in the Norwegian and Barents Seas. In this population, individuals mature at ages of 3–9 years; the maximum life-span is over 20 years. Adults undertake long annual migrations between productive summer-feeding areas in the Norwegian Sea, overwintering areas off northwestern Norway, and spawning areas off western and southwestern Norway, where the ripe herring arrive from midwinter to early spring. Analysis of extensive historical data on scales suggested, however, that individual herring do not necessarily spawn annually (Engelhard and Heino 2005). In samples collected in the spawning areas from 1935 to 1974, second-time spawners were strongly underrepresented in comparison to both first-time spawners and older repeat spawners. Statistical analysis revealed that, on average, about 47% of potential second-time spawners were absent from the spawning grounds. It is currently impossible to entirely discount the possibility that scale-reading errors account for this finding. If biologically real, however, this would suggest that almost one in two first-time spawners did not participate in the spawning migration the year after, but instead waited an extra year before recommencing reproduction (Engelhard and Heino 2005). On the stock level this would imply that, on average, about 10% of mature individuals do not spawn in any given year.

Why should herring not return to spawn the year after first spawning? This paper examines the hypothesis that skipping of reproduction relates to trade-offs between current and future reproduction, growth and survival (Roff 2002). For herring, such trade-offs may imply that participation in distant, energetically costly, and risky spawning migrations will only pay off in terms of fitness if individuals are sufficiently large, and in sufficient condition, to both successfully migrate and spawn. We previously hypothesised (Engelhard and Heino 2005) that first-time spawning herring, due to their small size compared to older, repeat spawners, may often need an extra year to regain the energy stores needed to migrate and spawn. Here we examine the following predictions: (1) that cohort-level variability in size and condition of young adult herring will be mirrored in variations in the extent of skipped reproduction; and (2) that climatic changes related to herring condition will moreover be linked to the extent of skipped reproduction.

Materials and methods

The data

Age, age at maturation (here, age at first spawning), and number of post-maturation years (i.e. years completed since the first spawning event) were obtained from scales of 84,116 adult Norwegian spring-spawning herring, sampled randomly in the spawning areas by the Institute of Marine Research (see Engelhard et al. 2003). All samples were collected during January–March of 1935–1973 (see Table 1 for annual sample sizes). Experienced scale readers, following methods established in the 1920s (Lea 1928; Runnström 1936) and applied consistently until the 1970s, distinguished between three types of growth layers. These were (1) “coastal” rings corresponding to the juvenile stage (rather narrow to very wide summer zones divided by either diffuse or sharp winter lines), (2) “oceanic” rings corresponding with the late immature stage when the animals live in the Norwegian Sea (wide summer zones divided by diffuse winter lines), and (3) “spawning” rings corresponding to the mature or adult stage (narrow to very narrow outer summer zones divided by sharp winter lines: Runnström 1936; Engelhard et al. 2003). For adult herring, the number of coastal and oceanic rings thus equals age at maturation, and the number of spawning rings equals the number of post-maturation years. In addition, body length (cm) and weight (g) were measured in all samples; an index of body condition was defined as weight length⁻³ (g cm⁻³; cf. Slotte 1999b).

Table 1 Total annual numbers of observations (N_y) on age at maturation and post-maturation years in Norwegian spring-spawning herring, collected in the spawning areas by the Institute of Marine Research, 1935–1973

Year	N_y	Year	N_y	Year	N_y
1935	2,578	1948	2,584	1961	2,048
1936	2,818	1949	3,281	1962	9
1937	2,568	1950	3,257	1963	3
1938	1,974	1951	4,337	1964	13
1939	1,681	1952	0	1965	1,999
1940	5,641	1953	0	1966	2,270
1941	3,881	1954	4,258	1967	2,271
1942	159	1955	5,161	1968	1,946
1943	1,852	1956	44	1969	1,898
1944	2,423	1957	51	1970	1
1945	2,322	1958	5,154	1971	2,438
1946	4,681	1959	3,841	1972	419
1947	3,889	1960	8	1973	357

Note that analyses on skipped reproductive seasons require decent sample sizes in at least two consecutive years. Years where $N_y < 100$ were excluded from analyses

As a description of interannual environmental variability, we used (1) the Kola temperature and (2) the North Atlantic Oscillation (NAO) winter index. The Kola temperature is defined here as the mean annual temperature in the Kola Section of the Barents Sea, averaged over the 0–200 m depth layer; it is correlated with sea temperatures in the Norwegian Sea (Bochkov 1982). Information on the Kola temperature was extracted from databases of the Institute of Marine Research. The NAO winter index was defined as the December–March average difference of normalised sea level pressure between Lisbon, Portugal, and Stykkisholmur/Reykjavik, Iceland (Hurrell et al. 2003). Information on the NAO index was extracted from <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>.

Statistical modelling

Modelling survival and skipped reproduction

In this paper, a maturation cohort is defined as all individuals of a year-class sharing the same age at maturation, i.e. that first spawned in the same year (e.g. Beverton et al. 2004). We previously tested the assumption that after maturation, herring return annually to the spawning areas (Engelhard and Heino 2005). This assumption predicts that the numbers of males and females of each maturation cohort present in the spawning area in consecutive spawning seasons should decrease solely as a function of mortality. Post-maturation survival was modelled, based on the sampled numbers (*n*) of fish of a given maturation cohort for each sex, sampled in consecutive years *y* and *y*+1 and with respectively *p* and *p*+1 post-maturation years (cf. Fig. 1a). Log-transformation permits the following linear model to be used:

$$\log(n_{p+1,y+1}) \sim \log(n_{p,y}) + \log(N_{y+1}/N_y) + \log(S_y/S_{y+1}) + c_p \tag{1}$$

where *n_{p,y}* and *n_{p+1,y+1}* are the sampled numbers of either males or females of a given maturation cohort with *p* and *p*+1 post-maturation years, respectively, and *c_p* is a vector of survival coefficients, corresponding to the logarithm of change in numbers from *p* to *p*+1 post-maturation years. *N_y* and *N_{y+1}* are the total numbers of fish for all maturation cohorts sampled in the same years (Table 1), included to account for the effects of annual variations in sampling effort on capture probability. *S_y* and *S_{y+1}* are estimates of the numbers of fish in the spawning stock in years *y* and *y*+1, respectively,

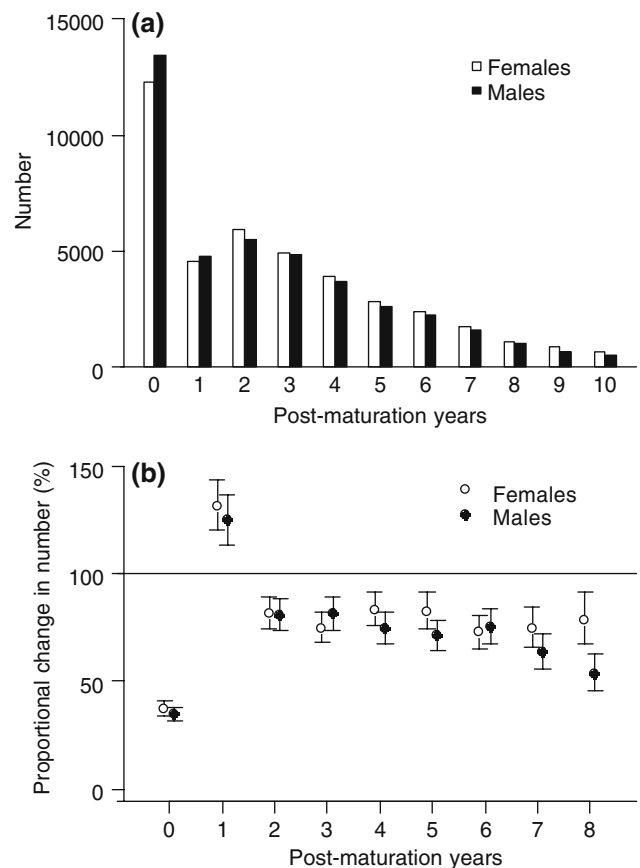


Fig. 1a–b **a** Numbers of male and female herring sampled in the spawning area during the spawning seasons of 1935–1973 at different numbers of post-maturation years. First-time spawners have zero post-maturation years. Note the strong underrepresentation of second-time spawners (one post-maturation year). **b** Proportional change (with SE) in numbers of male and female herring present in the spawning area from *p* to *p*+1 post-maturation years (estimated with model 1)

obtained from the official stock assessment (ICES 2002) based on virtual population analysis (VPA). These were included to account for annual variations in capture probability due to major fluctuations in spawning stock over the period examined (i.e., increase from ~26×10⁹ spawners in 1935 to ~54×10⁹ spawners in 1944, followed by a dramatic decrease to ~9×10⁶ spawners in 1972).

Survival coefficients (*c_p*) estimated with model (1) were similar for most transitions, except for the transitions from 0 → 1 and 1 → 2 post-maturation years (Fig. 1b). This suggested constant annual survival and underrepresentation of fish with 1 post-maturation year in samples. We interpret this as evidence that Norwegian spring-spawning herring frequently skip the second reproductive season (Engelhard and Heino 2005). The extent to which the second spawning season is skipped can be modelled as follows:

$$\log(n_{p+1,y+1}) \sim \log(n_{p,y}) + \log(N_{y+1}/N_y) + \log(S_y/S_{y+1}) + c_0 + c_1 I_p \quad (2)$$

where c_0 is a mean survival coefficient, c_1 is a coefficient of underrepresentation in the second spawning season, and I_p is an indicator variable with

$$I_p = 1 \quad \text{if } p = 0 \text{ post-maturation years, and} \\ I_p = -1 \quad \text{if } p = 1 \text{ post-maturation year, and} \\ I_p = 0 \quad \text{otherwise.}$$

Mean annual post-maturation survival is thus estimated as e^{c_0} , and the fraction of fish skipping the second spawning season as $1 - e^{c_1}$.

Note that possible skipped reproduction after the second potential spawning season may confound the survival estimate. Indeed, for other fish species there is evidence that older adult fish can also skip spawning seasons (Ivanov 1971; Rideout and Rose 2006).

Year-class variability

We examined for year-class variability in the extent to which the second spawning season was skipped by herring, by including year-class Y as a factor in model (1):

$$\log(n_{p+1,y+1}) \sim \log(n_{p,y}) + \log(N_{y+1}/N_y) + \log(S_y/S_{y+1}) + c_{0,Y} + c_{1,Y} I_p \quad (3)$$

where $e^{c_{0,Y}}$ and $1 - e^{c_{1,Y}}$ provide estimates of adult survival and the fraction of fish skipping the second spawning season, respectively, for year-class Y . Note that the ratio S_y/S_{y+1} is assumed to be accurately known; errors in this ratio will confound the estimates of annual survival and skipped spawning.

Effects of fish size, sex and environmental variables

We modelled effects of fish sex, size (length or weight), condition and environmental variables (Kola temperature and NAO winter index) on survival and the extent to which the second spawning season may be skipped. Size and condition were calculated as mean values, by year, for each maturation cohort separately. Model (2) was therefore extended, as follows:

$$\log(n_{p+1,y+1}) \sim \log(n_{p,y}) + \log(N_{y+1}/N_y) + \log(S_y/S_{y+1}) + c_0 + c_1 I_p + c_2 V_y + c_3 I_p V_y - F \quad (4)$$

where the parameters c_2 and c_3 describe the effects of variable V (size, sex or environmental variable) on

survival and skipped reproduction, respectively. The offset F [fishing mortality (year^{-1}): annual averages over ages 2–13 years; ICES 2002] was added to account for annual losses of fish due to fishing mortality (allowing us to focus on how fish size and environmental variables may affect “natural mortality”). It should be noted that over the study period important changes in fishing mortality took place, remaining low in the 1930s–1940s, increasing steadily in the 1950s, and becoming excessively high in the late 1960s–early 1970s (e.g. Toresen and Østvedt 2000). Data for 1966–1973, when the spawning stock was virtually fished out and collapsed, were excluded from this part of the analysis.

For statistical testing, fish size and environmental variables were analysed as variates. For graphical purposes only, fish size variables were discretised and analysed as factors. In modelling the effects of fish size and environmental variables on skipped reproduction, the transition from 1 → 2 post-maturation years was not included, as it refers to fish returning to spawn after having potentially skipped the second spawning season.

Notice that with the available data, probabilities of survival and skipped reproduction can only be estimated for maturation cohorts. The models used here thus cannot directly reveal how the variables considered affect survival and skipped reproduction at the individual level.

Data selection criteria

The results of the analyses were, to a moderate extent, affected by the available sample sizes, which were very small for some years (N_y ; Table 1) and for some maturation cohorts, especially with higher numbers of post-maturation years ($n_{p,y}$). Excluded from analyses were any years with $N_y < 100$ and any combinations of maturation cohort and post-maturation years where $(n_{p,y} + n_{p+1,y+1}) < 20$ or $n_{p,y} < 5$. Finally, Beverton et al. (2004) provided evidence that after about eight spawnings, Norwegian spring-spawning herring suffer increased mortality through senescence; reliable ageing of very old herring is moreover problematic. We therefore excluded any combinations of maturation cohort and eight or more post-maturation years ($n_{p>7,y}$).

Results

Survival and skipped reproduction in male and female herring

Both sexes show a similar pattern of exponentially declining numbers of spawners with increasing post-

maturation years, indicating constant annual survival (Fig. 1a), and both sexes show underrepresentation of fish with one post-maturation year (second-time spawners), suggesting that the second spawning season was skipped by a fraction of potential spawners. When proportional change in numbers of male and female spawners between consecutive post-maturation years is plotted (Fig. 1b), the discrepancy in the transitions from 0 → 1 and 1 → 2 post-maturation years, compared with later transitions, suggests that the second spawning season may often be skipped in both sexes.

Applying model (2) to the sexes separately, it was found that about 47% of potential second-time spawners were missing from the samples and likely skipped reproduction in both males and females ($c_{I,F}=-0.63$, $SE=0.06$; $c_{I,M}=-0.64$, $SE=0.07$). Mean post-maturation survival was estimated at 76% for females and 71% for males ($c_{0,F}=-0.27$, $SE=0.03$; $c_{0,M}=-0.34$, $SE=0.03$). Applying model (4) revealed no significant difference between the sexes, either in skipped reproduction ($P=0.967$) or in post-maturation survival ($P=0.300$).

Year-class variability in survival and skipped reproduction

Annual survival of spawners was high for all year-classes from 1935 to 1953 (estimates mostly above 60%; Fig. 2a). In subsequent year-classes, annual survival dropped substantially to below 30%, reaching a minimum of only 7% in the 1963 year-class. It is well known that year-classes of the late 1950s and 1960s suffered (very) high fishing mortality, contributing to population collapse in the late 1960s (e.g. Toresen and Østvedt 2000; Engelhard and Heino 2004b). Annual survival appeared higher again in year-classes of the late 1960s, although the estimates are less reliable due to small sample sizes.

Fractions of fish skipping the second spawning season (Fig. 2b) were estimated to be high in the year-classes 1930–1934 and 1936 (~50–80%), but low in most year-classes from 1937 to 1953 (~0–40%); in fact, for some of these (1941, 1951) there was no significant evidence of skipped spawning. Estimates were unavailable for those year-classes from 1954 to 1970 that were weak, or for the moderately strong but rapidly fished-out year-class of 1963, owing to small sample sizes (Table 1). In the strong or moderate year-classes of the later period (1959–1961, 1964, 1966), estimated fractions of fish skipping the second spawning season were again fairly high (~50–60%).

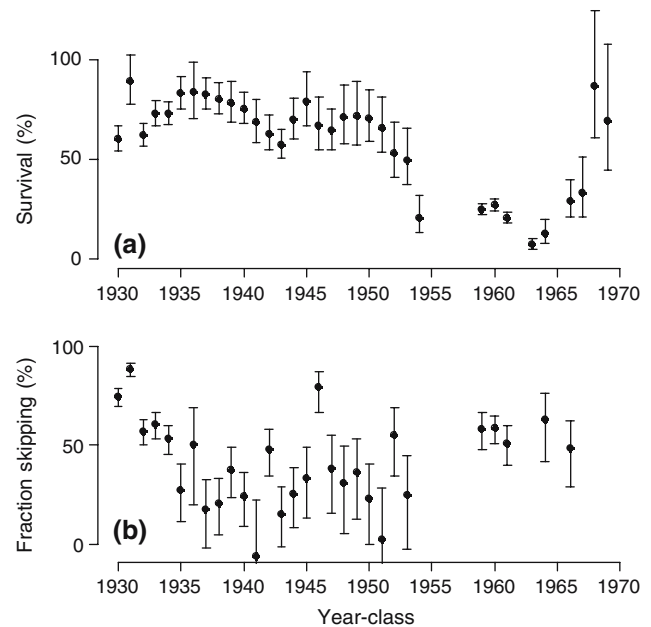


Fig. 2a–b Year-class variability in (a) estimated annual survival (with SE) of adult herring, and (b) the estimated fraction (with SE) of potential second-time spawners skipping reproduction, derived from Eq. 3. Estimates were not available for some year-classes where sample sizes were insufficient. Survival estimates are potentially confounded by errors in the stock assessment-based estimates of annual changes in stock numbers. Note that observation errors may cause survival estimates to be larger than one and skipping estimates to be negative. In particular, the negative skipped spawning estimate for the 1941 year-class is explained by marginally more (not fewer) observations of second-time spawners than expected from mortality alone

Length, weight and condition

Over the year-classes 1930–1970 there were generally increasing trends in the mean length, weight and condition index of spawners (Fig. 3). These were approximately linear for length and weight (Fig. 3a, b), but less so for condition index, which peaked in year-classes 1945–1955 (Fig. 3c). In first-time spawners and “third-time” spawners (strictly, spawners with two post-maturation years), trends were significant ($P<0.05$) for each of the three size variables. In second-time spawners (strictly, spawners with one post-maturation year), only the trend in condition index was significant ($P<0.005$); there was no trend in mean length ($P=0.897$) while a possible trend in mean weight approached statistical significance ($P=0.090$).

The mean length, weight, and condition index of first-time spawners had significant effects on the fractions of fish skipping reproduction the year after (Fig. 4a–c, based on Eq. 4). If first-time spawners had larger body lengths ($P<0.01$), higher body weights ($P<0.0005$), or higher condition indices ($P<0.005$),

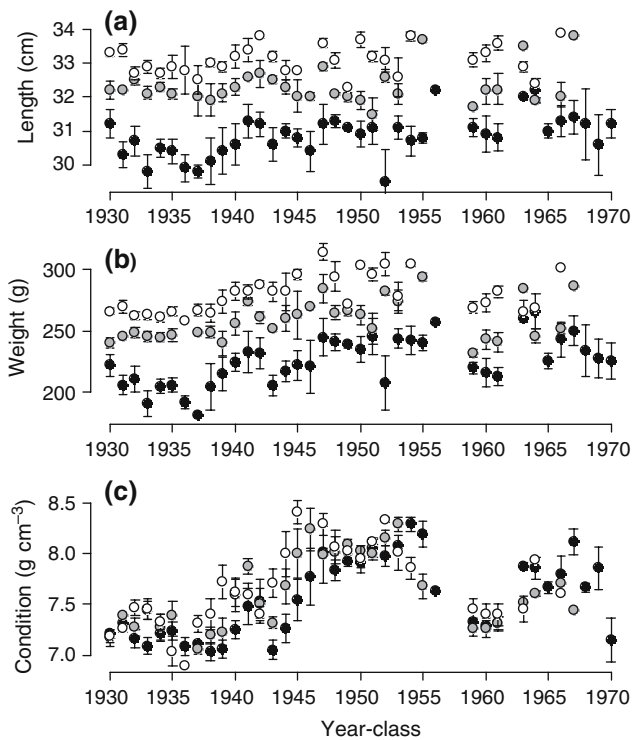


Fig. 3a–c Year-class variability for 1930–1970 in (a) mean length, (b) weight, and (c) condition index for first-time spawners (black symbols), second-time spawners (grey), and third-time spawners (white; strictly, spawners with two post-maturation years). Note that the figures only include fish actually present in the spawning areas. Symbols show the grand means (with SE) of the means for maturation cohorts-at-age

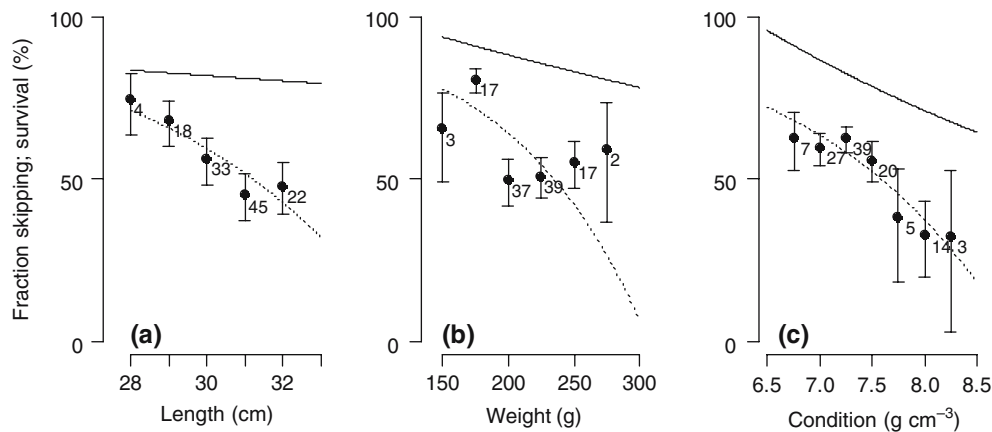


Fig. 4a–c Symbols: Relationships between the mean length (a), weight (b), and condition index (c) of maturation cohorts as first-time spawners in year y , and the estimated fraction of fish skipping reproduction in year $y+1$ (Eq. 4, but size variables analysed as factors). Vertical bars indicate SE of estimates; numbers indicate sample sizes (i.e. number of maturation cohorts by sex in each size bin). Dotted lines: Modelled relationships between length, weight and condition of first-time spawners and

then skipping of reproduction was less likely to occur in the following year.

Unexpectedly, an inverse relationship of the condition index of spawners in year y with the fraction surviving to year $y+1$ was found ($P < 0.005$; Fig. 4c). There were no significant effects of body length ($P = 0.743$) or weight ($P = 0.209$) on survival (Fig. 4a, b).

There was no evidence ($P > 0.3$) that relationships of length, weight or condition of spawners with survival and skipped spawning differed significantly between male and female herring.

Environmental variables

Over the period 1935–1974, the annual temperature in the Kola Section of the Barents Sea varied between 2.84 and 4.78 °C, and the North Atlantic Oscillation (NAO) winter index varied between -4.89 and $+2.52$ (Fig. 5). The NAO index was significantly and positively correlated with the Kola temperature in the same year ($r = 0.44$, $P < 0.005$) as well as in the following year ($r = 0.38$, $P < 0.05$), but not for later or earlier years. The Kola temperature and NAO were characterised by annual fluctuations overlaying long-term (interdecadal) variability (cf. smoothed indices in Fig. 5). Values tended to be high or fairly high from the 1930s through 1950s, but decreased to anomalously low levels in the 1960s and early 1970s.

The Kola temperature averaged over year y was negatively correlated with the mean length of first-time spawners at the beginning of year $y+1$ ($r = -0.48$,

the fraction of fish skipping reproduction the year after (Eq. 4; size variables analysed as variates). Solid lines: Overall survival from year y to year $y+1$ as a function of length, weight, and condition in year y , as modelled for all spawners (both first-time and repeat spawners, excluding second-time spawners). Analysis excludes data from 1966 to 1973 (period of extremely high fishing mortality and resulting stock collapse)

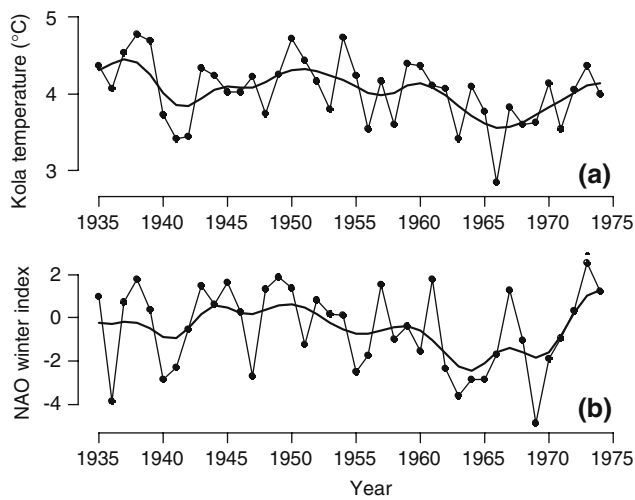


Fig. 5a–b Interannual variability for 1935–1974 in (a) the mean annual temperature in the Kola Section of the Barents Sea and (b) the NAO winter index. Long-term variability is illustrated by heavy solid lines, representing values smoothed with a low-pass filter with seven weights (1, 3, 5, 6, 5, 3, 1) to remove fluctuations with periods of less than four years (following Hurrell 1995)

$P=0.008$; Table 2); a negative correlation with first-time spawners’ weight approached statistical significance ($r=-0.36$, $P=0.060$), but there was no correlation with condition index ($P=0.878$). There were no further correlations between the Kola temperature, or NAO winter index, and the mean length, weight or condition of spawners at the beginning of year $y+1$. Nor were there any lagged correlations with these indices at the beginning of year $y+2$ (Table 2).

Table 2 Pearson correlation coefficients between environmental variables (Kola temperature and NAO winter index) and the mean length (cm), weight (g) and condition (g cm^{-3}) for first-, second- and third-time spawners (strictly, spawners with zero, one and two post-maturation years, respectively) sampled the winter immediately after and with a delay of one year

	Kola temperature (°C)		NAO winter index	
	Year $y+1$	Year $y+2$	Year $y+1$	Year $y+2$
<i>First-time spawners</i>				
Length	-0.48*	0.14	-0.27	0.03
Weight	-0.36	0.04	-0.03	0.13
Condition	-0.03	0.13	0.18	0.15
<i>Second-time spawners</i>				
Length	-0.28	0.13	-0.16	0.14
Weight	-0.08	0.09	0.08	0.33
Condition	0.16	0.04	0.21	0.27
<i>Third-time spawners</i>				
Length	-0.22	0.20	-0.13	0.24
Weight	-0.10	0.10	0.04	0.27
Condition	0.05	0.00	0.11	0.10

*Correlation significant at the 0.01 level

Using general linear models, we examined how the Kola temperature, NAO winter index, and condition of herring may be related to adult survival and the fraction of fish skipping the second spawning season (see Table 3 for a selection of models). There was strong evidence that the Kola temperature in year y was significantly but inversely related with both survival and participation in the second spawning season (Table 3: Model K1, confirmed by Models K2 and C2; note sharp decreases in AIC compared to the null model). This suggested that colder temperatures lead to better adult survival and less frequent skipping of spawning. Moreover, a lagged relationship between the Kola temperature and skipped spawning, but not survival, after two years was found, again suggesting that colder temperatures lead to a decrease in skipped spawning (Model K2). These direct and lagged relationships were also significant if Model K2 was extended to include herring condition (Model C2; significant drop in AIC by 4.4).

There was no clear evidence of a relationship of the NAO with adult herring survival or skipped spawning. Models including the NAO only (Model N1) or extended to also include a lagged NAO effect (Model N2) had higher AIC values compared to the null model, and did not reveal significant relationships. However, some models that also included the Kola temperature (e.g. Model C3, “best model” with lowest AIC) did suggest a possible relationship of the NAO with skipped spawning, although interpretation requires caution given the possibility of a spurious relationship, as the two environmental variables are correlated. In all models examined, the Kola temperature was tightly related to both survival and skipped spawning, whereas the relationship of the NAO with skipped spawning was only found in some models.

Discussion

This study enhances our understanding of why a significant fraction of adult Norwegian spring-spawning herring may not spawn annually, but instead skip the second reproductive season (Engelhard and Heino 2005). First, it describes long-term changes in the frequency of skipped reproduction. Second, it shows that the size and condition of first-time spawners, as well as environmental variables, are linked with the extent to which these fish skip reproduction the year after, although there are no differences between the sexes. Third, relationships are revealed between condition, environmental variables and survival of adult herring.

Table 3 Summary of selected general linear models examining effects of the Kola temperature (°C), NAO winter index and condition of herring (g cm⁻³) in year *y* on survival from year *y* → *y*+1 and on the fraction of fish skipping the second spawning season in year *y*+1

Model	Variable	Survival			Participation in 2nd spawning			AIC	Δ_i	w_i
		Coefficient	SE	P	Coefficient	SE	P			
Null model	Excludes condition or environmental variables							1,025.0	80.1	0
Model K1	Kola temperature, year <i>y</i>	-0.331	0.073	<0.0001	-0.425	0.152	<0.01	978.5	33.6	0
Model K2	Kola temperature, year <i>y</i> Kola temperature, year <i>y</i> -1	-0.333 -0.021	0.072 0.090	<0.0001 0.815	-0.395 -0.746	0.149 0.175	<0.01 <0.0001	956.6	11.7	0.003
Model N1	NAO, year <i>y</i>	-0.022	0.017	0.187	0.035	0.035	0.321	1,027.1	82.2	0
Model N2	NAO, year <i>y</i> NAO, year <i>y</i> -1	-0.021 -0.024	0.017 0.020	0.215 0.234	0.041 -0.042	0.035 0.038	0.247 0.275	1,025.6	80.7	0
Model C1	Condition, year <i>y</i>	-0.198	0.065	<0.005	0.538	0.169	<0.005	1,015.1	70.2	0
Model C2	Condition, year <i>y</i> Kola temperature, year <i>y</i> Kola temperature, year <i>y</i> -1	-0.172 -0.312 -0.061	0.062 0.072 0.091	<0.01 <0.0001 0.504	0.294 -0.405 -0.686	0.162 0.149 0.176	0.070 <0.01 <0.0005	952.2	7.3	0.025
Model C3 (final model)	Condition, year <i>y</i> Kola temperature, year <i>y</i> Kola temperature, year <i>y</i> -1 NAO, year <i>y</i>	-0.196 -0.281 -0.083 -0.015	0.069 0.082 0.095 0.020	<0.005 <0.001 0.382 0.449	0.446 -0.739 -0.467 0.138	0.168 0.179 0.187 0.043	<0.01 <0.0001 <0.05 <0.005	944.9	0.0	0.972

Bold type indicates coefficients (shown with SE) that are significantly different from zero ($P < 0.05$). Note that a positive coefficient implies that a variable is positively related to either survival (see left columns) or participation in the second spawning season (right); the latter is equivalent to fewer fish skipping reproduction. Models K1–2 (including Kola temperature), N1–2 (including NAO) and C1–3 (including both herring condition and environmental variables) were selected based on biological significance and the Akaike information criterion (AIC). Delta AIC (Δ_i) and Akaike weights (w_i) are shown as a measure of the strength of each model relative to the “best” model (i.e., Model C3)

There are two caveats in interpreting our results. First, these are based on indirect evidence of skipped reproduction—underrepresentation of second-time spawners. Direct evidence of skipped reproduction in Atlantic herring is still lacking. An alternative hypothesis that could be used to explain the data is that lack of second-time spawners is due to frequent scale-reading errors. However, the ring widths in scales appear consistent between individuals that matured at the same age but were sampled in different years following maturation (Engelhard and Heino 2005). While we maintain that skipped reproduction is the most parsimonious explanation for the observed patterns, the possibility of scale-reading errors producing artificial patterns cannot be fully discounted (see Engelhard and Heino 2005 for discussion).

Second, we observe skipped reproduction only probabilistically at the aggregate level of maturation cohorts. Therefore, for further analyses, individual-level biological data (fish size and condition) need to be aggregated to the corresponding degree; environmental data are only available at yearly resolution from the onset. It should not be taken for granted that aggregated data accurately reflect individual-level processes affecting skipped reproduction. Furthermore, our perception

of the dynamics of these maturation cohorts, and the frequency of skipped reproduction, is influenced by the input from the VPA-based stock assessment (ICES 2002): estimated stock numbers, and for some analyses fishing mortality. Such errors are expected to add noise, but not bias, to the estimates of skipped reproduction. Survival estimates, however, may potentially be biased: if, for some period, stock assessment suggests a shallower decrease or steeper increase in stock numbers than in reality, then survival will be overestimated in the models used here, and vice versa.

The absence of sex differences in skipped reproduction is in line with previous work showing no sex differences in age or size at maturation (Engelhard et al. 2003) or body fat content (Slotte 1999a) in this stock, suggesting similar reproductive investment in males and females. The similarities may well relate to the collective behaviour in herring schools (Fernö et al. 1998; Axelsen et al. 2000), which typically consist of about equal numbers of both sexes; when “deciding” whether to participate in spawning migration, individuals are strongly dependent on the decisions of surrounding individuals (Huse et al. 2002).

Overall, the results corroborate well with life-history theory predicting that adult individuals are expected to

skip reproduction when the loss in reproductive output this season is more than balanced by an increase in expected reproductive output over the entire future lifespan, discounted by the probability of surviving until later reproductive seasons (Roff 2002; Rideout et al. 2005). Investment in reproductive activity implies costs and risks, such as reduction in growth and survival and hence expected future reproductive success (Stearns 1992). In Norwegian spring-spawning herring, a high cost of reproduction is evidenced by a strong decrease in growth rate after maturation (Runnström 1936; Engelhard et al. 2003). Trade-offs between current and future reproduction, growth and survival imply that participation in spawning will only pay off in terms of fitness when herring are sufficiently large and in sufficiently good condition. Indeed, this study shows that mean length, weight and condition in cohorts of first-time spawners are significantly and positively related to participation in spawning the year after (Fig. 4a–c). Thus, strong support is provided for the hypothesis (Engelhard and Heino 2005) that young adult herring, which owing to their small size rely heavily on condition, often need an extra year after first reproduction to regain the energy stores required for reproduction, in contrast to older adult herring, which are advantaged by larger size (compare with Fig. 3). Correspondingly, inverse relationships between condition and the likelihood of skipped reproduction have also been found for several other species (fish: Rijnsdorp 1990; Oganessian 1993; Burton et al. 1997; Rideout et al. 2000, reptiles: Broderick et al. 2003).

It is not surprising that first-time spawning herring are more likely to skip an entire reproductive season when of smaller size and/or in reduced condition. The extensive spawning migrations incur a high energetic cost even before actual spawning can be commenced; since herring do not feed while migrating, only fish with sufficient energy stores can successfully migrate and spawn (e.g. Slotte and Fiksen 2000). Moreover, smaller fish have an additional disadvantage due to the positive relationship of fish length with swimming speed (Ware 1978). Finally, predation risk is likely to be particularly high for spawning herring; they are preyed upon by a range of coastal predators including fishes, marine mammals and seabirds (Fernö et al. 1998; Høines and Bergstad 1999; Axelsen et al. 2000). Under the given conditions, skipping the second season, rather than exacerbating already low energy stores, is likely to be an optimal life-history strategy leading to improved lifetime reproductive success (cf. Jørgensen et al. 2006). It has been suggested that by skipping spawning in a year of poor condition (and hence high potential mortality), Atlantic cod *Gadus*

morhua may increase lifetime reproductive output by greater than 40% (Rideout et al. 2005).

The inverse relationship between condition and survival was opposite to that expected (Fig. 4c). This may be due to errors in relative stock numbers that confound the survival estimates, given that VPA may lead to a bias in stock numbers for several years in a row. However, this relationship may also be real. If so, reduced condition and increased survival may not have cause–effect relationships, but rather be the result of common underlying causes. First, favourable conditions early in life can result in high survival but reduced growth and condition due to reduced per capita food intake, as a density-dependent effect (Barros and Toresen 1998). Second, strong year-classes, characterised by reduced growth and condition indices (Toresen 1990; Holst 1996) may suffer less predation and exploitation mortality due to the dilution effect (Axelsen et al. 2001). Alternatively, if skipped reproduction is not restricted to the second spawning season but also occurs in older spawners—as has been reported for other fish species (Ivanov 1971; Rideout and Rose 2006)—then the inverse relationship between condition and survival might even be the result of skipped reproduction per se. In a strict sense, the survival estimates presented here indicate annual changes in fish numbers present in the spawning area. In a year of low body condition, a larger proportion of the adult population might skip spawning and thus be under-represented in the spawning area: if the same fish return to spawn the year after, this will lead to an inverse condition–survival relationship in data collected from the spawning area. Unfortunately, if skipping of reproduction becomes unsynchronised after the second spawning season, it becomes particularly hard to study with the data available to us, as it is not possible to separate absence of spawners due to skipping from absence due to mortality (Engelhard and Heino 2005).

The extent to which herring may skip reproduction was found to be not only related to fish size and condition but also to climatic factors. The mean temperature in the Kola section of the Barents Sea for a given year was significantly and inversely related to adult survival, and to participation in the second spawning season in the following two years (Table 3). There was no clear link with the North Atlantic Oscillation. Although some models that also included the Kola temperature did suggest this possibility, there was clearly, by and large, a considerably tighter link with the Kola temperature than with the NAO. Notably, colder sea temperatures (possibly associated with a negative NAO index) favoured both adult survival and participation in the second spawning season (Table 3). Prey

availability is a possible mechanism for this. The copepod *Calanus finmarchicus*, a key species in the Norwegian Sea ecosystem, is the most important prey species for adult herring during the summer feeding season (Dalpadado et al. 2000). There is an inverse relationship of *C. finmarchicus* abundance with the NAO and sea surface temperatures (Fromentin and Planque 1996). In colder years, better feeding conditions for herring during summer are likely to improve survival, and lead to higher participation in reproduction during the winter immediately after, and with a delay of one year. The lagged effect on reproduction is unsurprising given that herring are capital spawners fully relying on energy stored for reproduction (Varpe et al. 2005); it may in addition relate to a possible lagged effect of temperature on *C. finmarchicus* abundance. However, it is important to note that the favourable impact of cold temperature on reproduction does have a limit; in fact, skipped spawning in some fishes has been attributed to water temperatures too cold to allow proper oocyte development (Fedorov 1971; Pawson et al. 2000).

In contrast, the Kola temperature is also positively associated with overall stock abundance of Norwegian spring-spawning herring, through a positive effect on year-class strength (Toresen and Østvedt 2000). The prime nursery areas for this stock, however, are in the Barents Sea, which is widely distant from the feeding areas for adult herring in the Norwegian Sea. In the Barents Sea, *Calanus* abundance is thought to be positively related to the Kola temperature, as warmer temperatures are associated with an increased influx of copepod-rich waters from the Atlantic (Aksnes and Blindheim 1996). The possibility of contrasting climate effects on juvenile and adult herring has interesting population implications. Usually, variations in survival early in life far exceed those in adults, so that the relationship of overall stock abundance with temperature will still follow that of juveniles (in agreement with Toresen and Østvedt 2000). Despite this, the inverse temperature effect on adult herring survival and skipped reproduction remains relevant, as it is directly linked to the population's reproductive potential, and refers to the part of the stock relevant to commercial fisheries.

In conclusion, interannual variability in the Norwegian Sea environment and variations in the size and condition of spawning herring (Figs. 4, 5) may explain the dynamics in the frequency of skipped reproduction in Norwegian spring-spawning herring (Fig. 2). The decrease in frequency of skipped reproduction in year-classes from the 1930s to 1950s may have resulted from a gradual increase in herring condition (Fig. 3c; cf.

Holst 1996), combined with particularly warm temperatures at the beginning of the time-series followed by colder years (Fig. 5). High frequency of skipped reproduction in year-classes 1959–1961 was likely related to particularly low weight and condition (Fig. 3). When the stock was at extremely low levels in the two decades following stock collapse in the late 1960s, growth and condition indices were particularly high (Toresen 1990; Engelhard and Heino 2004a); we may postulate that infrequent skipping of reproduction contributed to stock recovery. On the other hand, a year of poor environmental conditions, by affecting growth and condition, can have a threefold negative effect on reproductive potential: (1) by increasing mortality, (2) by reducing the mean fecundity per individual spawner (Marshall et al. 1998; Blanchard et al. 2003), and (3) by increasing the fraction of adults skipping reproduction. The very strong annual fluctuations in year-class strength in Norwegian spring-spawning herring (ICES 2002) may thus partly, among other factors, be explained by variations in skipped spawning. The major implications of skipped reproduction for population dynamics and reproductive potential highlight the need for critical re-evaluation of a common presumption in fish stock assessments—that adult fish spawn strictly annually.

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