Theme Session K

The Life History, Dynamics and Exploitation of Living Marine Resources:
Advances in Knowledge and Methodology

Dynamics in frequency of skipped reproduction
in Norwegian spring-spawning herring

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A common presumption in fisheries science is that adult iteroparous fish, once matured, typically spawn in all consecutive years. Recent evidence suggests, however, that skipping of reproduction occurs more commonly than is usually believed. Adult Norwegian spring-spawning herring (*Clupea harengus*) undertake long annual migrations between feeding, overwintering, and spawning areas. Analysis of extensive historical data on scales suggested that, on average, almost one in two herring may skip their second spawning migration. Moreover, the frequency of skipping may vary considerably from year to year. Based on annual variations in skipped reproduction, relationships are examined here between the mean weight and condition of spawning herring in a given year, and the fraction of fish skipping the second reproductive season in the following year. Environmental influences on skipping are examined based on indices of annual temperature and zooplankton abundance in the Norwegian Sea. The results corroborate with the hypothesis that skipped reproduction results from trade-offs between current and future reproduction, growth and survival: participation in distant, energetically costly and risky spawning migrations may only pay off in terms of fitness if individuals are sufficiently large and in sufficient condition to both successfully migrate and spawn.

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INTRODUCTION

The spawning stock biomass and reproductive potential of a population are directly influenced by the fraction of individuals involved in reproduction. For iteroparous (i.e. repeat-spawning) species, this fraction is not only dependent on growth and maturity—two aspects routinely investigated in many fish stocks—but also on the extent to which adult fish may skip reproductive seasons. Remarkably, the possibility of skipped reproduction has received little attention in fisheries science (for some notable exceptions, see Rijnsdorp 1990; Oganesyan 1993; Burton et al. 1997; Rideout et al. 2000; and Fiksen & MacKenzie 2001). In fact, it is commonly presumed that adult fish, once matured, normally return to spawn in all consecutive years of their life. Recent evidence suggests, however, that skipping of reproductive seasons by adult fish may occur more commonly than usually believed. For a number of commercially important stocks, there are now indications of fairly extensive skipping of reproductive seasons (e.g. Oganesyan 1993; Rideout et al. 2000; Engelhard & Heino submitted).

Norwegian spring-spawning herring, the world's largest stock of 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. The adult herring undertake long annual migrations between productive foraging areas in the Norwegian Sea, overwintering areas off northwestern Norway, and spawning areas off western and southwestern Norway, where the ripe herring arrive in mid-winter–early spring. Analysis of extensive historical data on scales suggested, however, that individual herring do not necessarily spawn strictly annually (Engelhard & Heino submitted). In samples, collected in the spawning areas from 1935–1974, second-time spawners were strongly under-represented in comparison to both first-time spawners and older repeat-spawners (Figure 1a). Statistical analysis revealed that on average, about 46% of potential second-time spawners were apparently absent from the spawning grounds (Figure 1b). This suggested that almost one in two first-time spawners did not return to spawn the year after, but instead waited an extra year before recommencing reproduction (Engelhard & Heino submitted).

Why should herring not return to spawn the year after first spawning? Obviously, reproduction implies costs and risks, affecting future reproduction and survival. This trade-off between current and future reproduction implies that participation in distant, energetically costly and risky spawning migrations may only pay off in terms of fitness if individuals are sufficiently large and in sufficient condition to both successfully migrate and spawn. This paper examines the hypothesis that first-time spawning herring, due to their small size, often need an extra year to re-gain the energy stores needed to reproduce (Engelhard & Heino submitted). First, it describes annual variations in the frequency of skipped reproduction. Second, relationships are examined between the size and condition of cohorts of first-time spawners in a given year, and the fraction of fish skipping reproduction in the following year. Third, environmental influences on skipping are examined based on indices of annual temperature and zooplankton abundance.
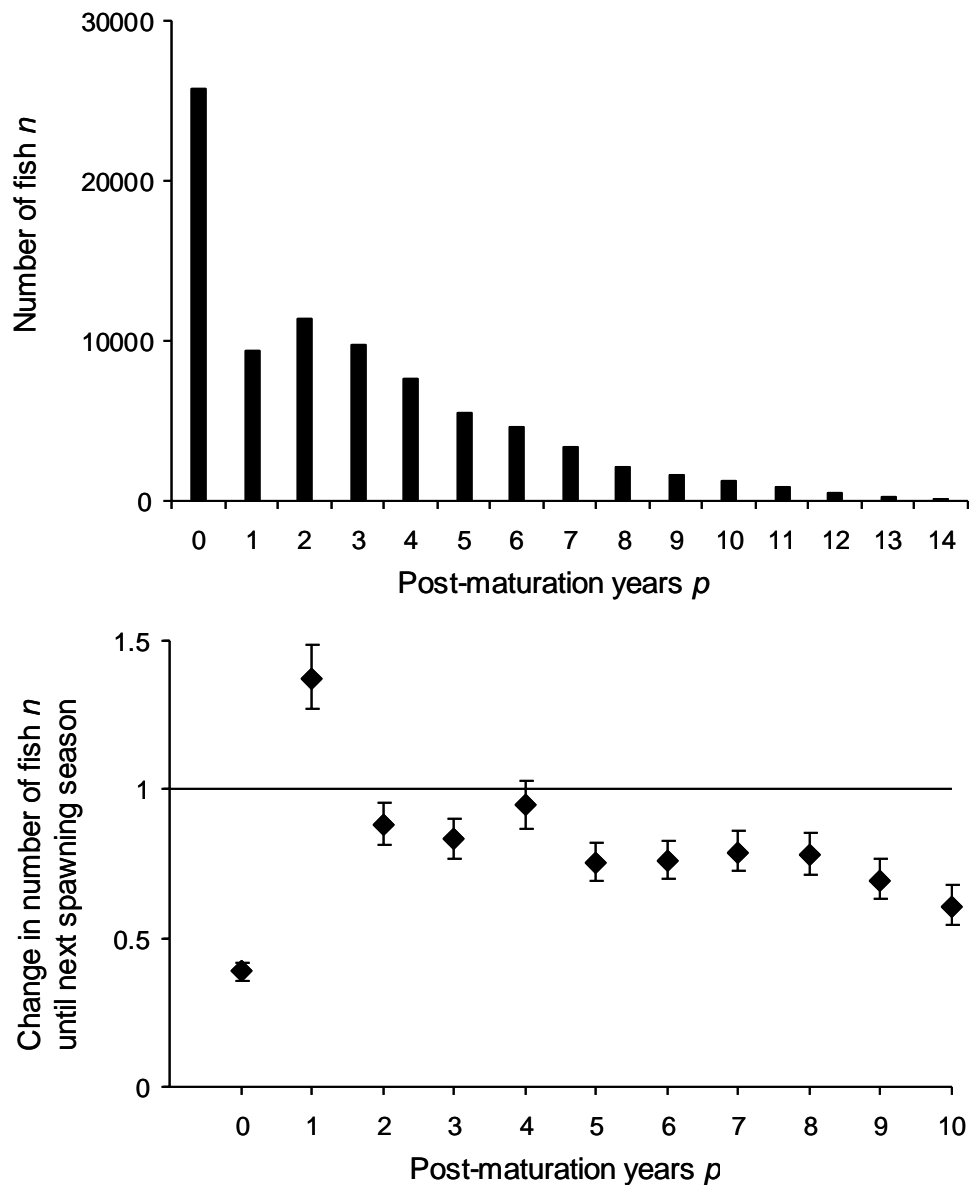
Figure 1. (a) Frequency distribution for herring, sampled in the spawning area during 1935–1973, at different numbers of post-maturation years. Note that 0, 1, ... post-maturation years correspond with first-time spawners, second-time spawners, and so forth. **(b)** Proportional change (with SE) in numbers of herring, present in the spawning area, from p to $p + 1$ post-maturation years, estimated with equation (2). Values below and above 1 indicate decrease and increase in numbers, respectively. In both graphs, note strong under-representation of second-time spawners ($p = 1$). From Engelhard & Heino (submitted).

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 distinguished between three types of growth layers: relatively wide 'coastal' and 'oceanic' rings, corresponding with the early and late immature stages, respectively; and narrow 'spawning' rings, corresponding with the mature stage (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 and weight were measured in all samples; an index of body condition was defined as weight length^{-3} (cf. Slotte 1999).

As a description of interannual environmental variability we used (1) the Kola temperature and (2) an index of zooplankton biomass in the Norwegian Sea based on the North Atlantic Oscillation (NAO) index (ICES 2002). 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). Norwegian Sea zooplankton biomass in May (g m^{-2}) was predicted from the NAO winter index (December–March) as in ICES (2002), as follows:

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. 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.

Year	N_y	Year	N_y	Year	N_y
1935	2578	1948	2584	1961	2048
1936	2818	1949	3281	1962	9
1937	2568	1950	3257	1963	3
1938	1974	1951	4337	1964	13
1939	1681	1952	0	1965	1999
1940	5641	1953	0	1966	2270
1941	3881	1954	4258	1967	2271
1942	159	1955	5161	1968	1946
1943	1852	1956	44	1969	1898
1944	2423	1957	51	1970	1
1945	2322	1958	5154	1971	2438
1946	4681	1959	3841	1972	419
1947	3889	1960	8	1973	357

$$B_y = 1.2 \, NAO_{y-1} + 0.93 \, NAO_y + 9.56 \qquad\qquad (R^2 = 0.84) \tag{1}$$

where B_y is zooplankton biomass in year y, and NAO_{y-1} and NAO_y are the winter NAO indices in years $y - 1$ and y, respectively. Notice that this relationship has not been calibrated for the period studied in this paper. Information on climatic variables was extracted from databases of the Institute of Marine Research.

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 & Heino submitted). Following this assumption, the numbers of a maturation cohort present in the spawning area in consecutive spawning seasons should solely decrease as a function of mortality. Post-maturation survival was modelled, based on the numbers of fish (n) for a given maturation cohort, sampled in consecutive years y and $y + 1$ and with respectively p and $p + 1$ post-maturation years. Log-transformation allows using the following linear model:

$$\log(n_{p+1,y+1}) \sim \log(n_{p,y}) + \log(N_{y+1} / N_y) + \log(S_y / S_{y+1}) + c_p \tag{2}$$

where $n_{p,y}$ and $n_{p+1,y+1}$ are the sampled numbers of fish 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 variations in sampling effort. S_y and S_{y+1} are estimates of the numbers of fish in the spawning stock in years y and $y + 1$, respectively, obtained from the official stock assessment (ICES 2002). These were included to account for major fluctuations in spawning stock over the period examined (i.e., increase from ~$26 \cdot 10^9$ spawners in 1935 to ~$54 \cdot 10^9$ spawners in 1944, followed by a dramatic decrease to ~$9 \cdot 10^6$ 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 (Figure 1b). This suggested constant annual survival and under-representation of fish with 1 post-maturation year in samples. We interpret this as evidence that Norwegian spring-spawners frequently skip the second reproductive season (Engelhard & Heino submitted). The extent to which the second spawning season is skipped can be modelled as follows:

$$\log(n_{p+1,y+1}) \sim \log(n_{p,y}) + \log(N_{y+1} / N_y) + \log(S_y / S_{y+1}) + c_0 + c_1 I_p \tag{3}$$

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

$I_p = 1$ if $p = 0$ post-maturation years, and

$I_p = -1$ if $p = 1$ post-maturation year, and

$I_p = 0$ otherwise.

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

Interannual variability in survival and skipped reproduction. We examined for interannual variability in the extent to which the second spawning season was skipped by herring, by including year Y as a factor in model (2):

$$\log (n_{p+1,y+1}) \sim \log (n_{p,y}) + \log (N_{y+1} / N_y) + \log (S_y / S_{y+1}) + c_{0,y} Y + c_{1,y} I_p Y \qquad (4)$$

where $e^{c_{0,y}}$ and $1 - e^{c_{1,y}}$ provide annual estimates of survival and the fraction of fish skipping the second spawning season, respectively. Note that the ratio S_y / S_{y+1} is assumed to be accurately known; errors in this ratio will affect the estimates of annual survival and skipping. The transition from 1→2 post-maturation years was not included in this and the following analyses.

Factors affecting frequency of skipped reproduction. We modelled effects of fish size and condition (mean length, weight, and condition index in maturation cohorts) and of environmental variables (Kola temperature and zooplankton biomass) on survival and the extent to which the second spawning season may be skipped. Model (3) was therefore extended, by adding fish size or environmental variables either as factors or variates, as follows:

$$\log (n_{p+1,y+1}) \sim \log (n_{p,y}) + \log (N_{y+1} / N_y) + \log (S_y / S_{y+1}) + c_0 + c_1 I_p + c_2 V + c_3 I_p V \qquad (5)$$

where the parameters c_2 and c_3 describe effects of variable V on survival and skipped reproduction, respectively. For statistical testing, fish size or environmental variables were analysed as variates. For graphical purposes only, fish size variables were discretised and analysed as discrete factors.

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; see 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 $(n_{p,y} + n_{p+1,y+1}) < 25$ or $n_{p,y} < 5$. Finally, Beverton et al. (2004) provided evidence that after about 8 spawnings, Norwegian spring-spawning herring suffer increased mortality through senescence. We therefore excluded any combinations of maturation cohort and 8 or more post-maturation years ($n_{p>7,y}$).

RESULTS

Interannual variability in survival and skipped reproduction

For the period 1935–1971, Figure 2 shows interannual variability in survival of adult herring and the fraction of fish skipping the second reproductive season, estimated with equation (4). Estimates were calculated for most years from 1935–1950, but only for a small number of years from 1954–1971. This was due to small sample sizes in the second half of the time-series (compare with Table 1).

      Estimated fractions of fish skipping the second spawning season (Figure 2a) were high in the mid- to late-1930s (~0.6–0.8). Hereafter they declined fairly gradually until around 1950 (~0.1–0.3). There was no clear temporal trend in skipped reproduction from the 1950s until the early 1970s, with quite variable annual estimates of skipped reproduction in this period (range ~0.2–0.8).
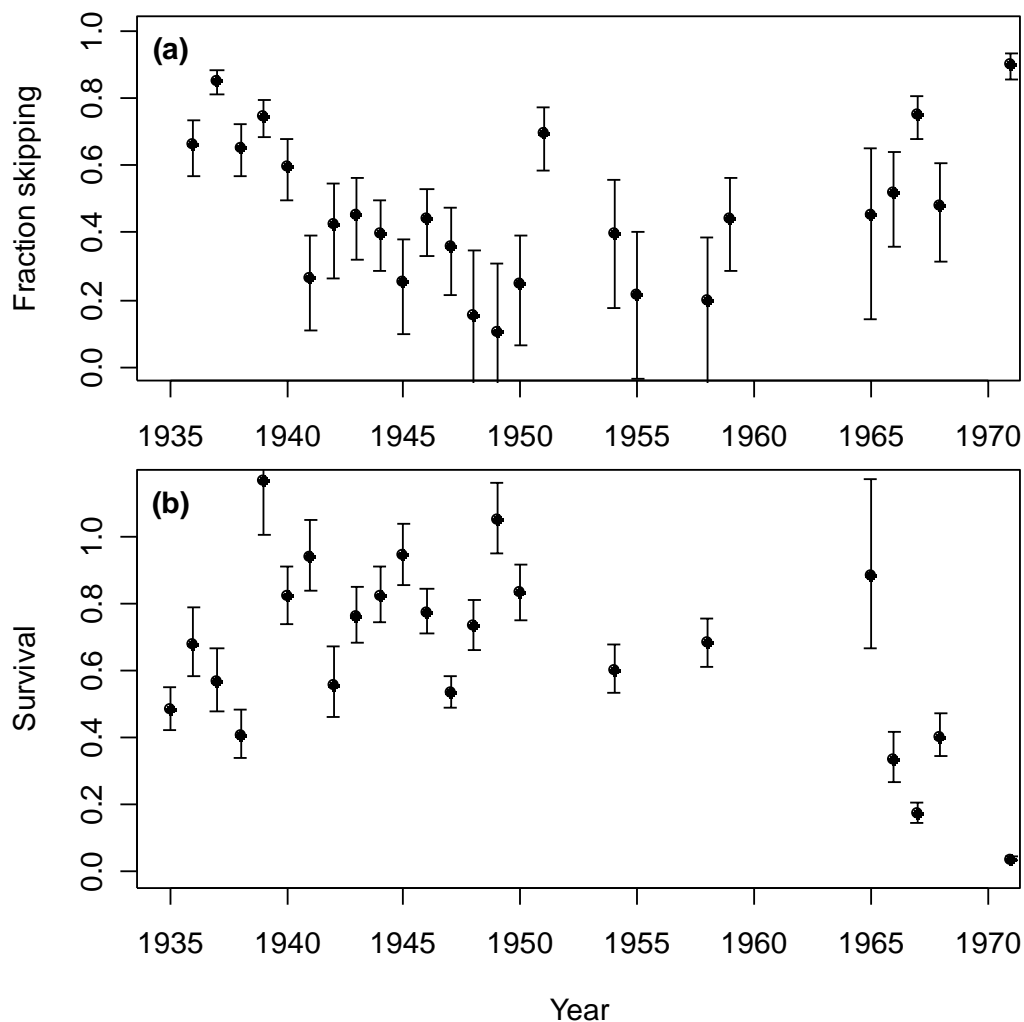

Figure 2. Interannual variability for 1935–1971 in **(a)** the estimated fraction (with SE) of herring skipping the second spawning season in year *y*, and **(b)** estimated survival (with SE) of adult herring from year *y* to year *y* + 1, derived from equation (4). Survival estimates are potentially confounded by errors in the stock-assessment based estimates of annual changes in stock numbers.

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During most of the period 1935–1965, adult survival was either high or moderately high (>0.6 in most years; Figure 2b). After 1965, adult survival dropped substantially to ~0.05–0.4. Unfortunately, the estimates of both survival and skipped reproduction for 1965–1971 may be unreliable, due to very high fishing mortality and population collapse in this period.
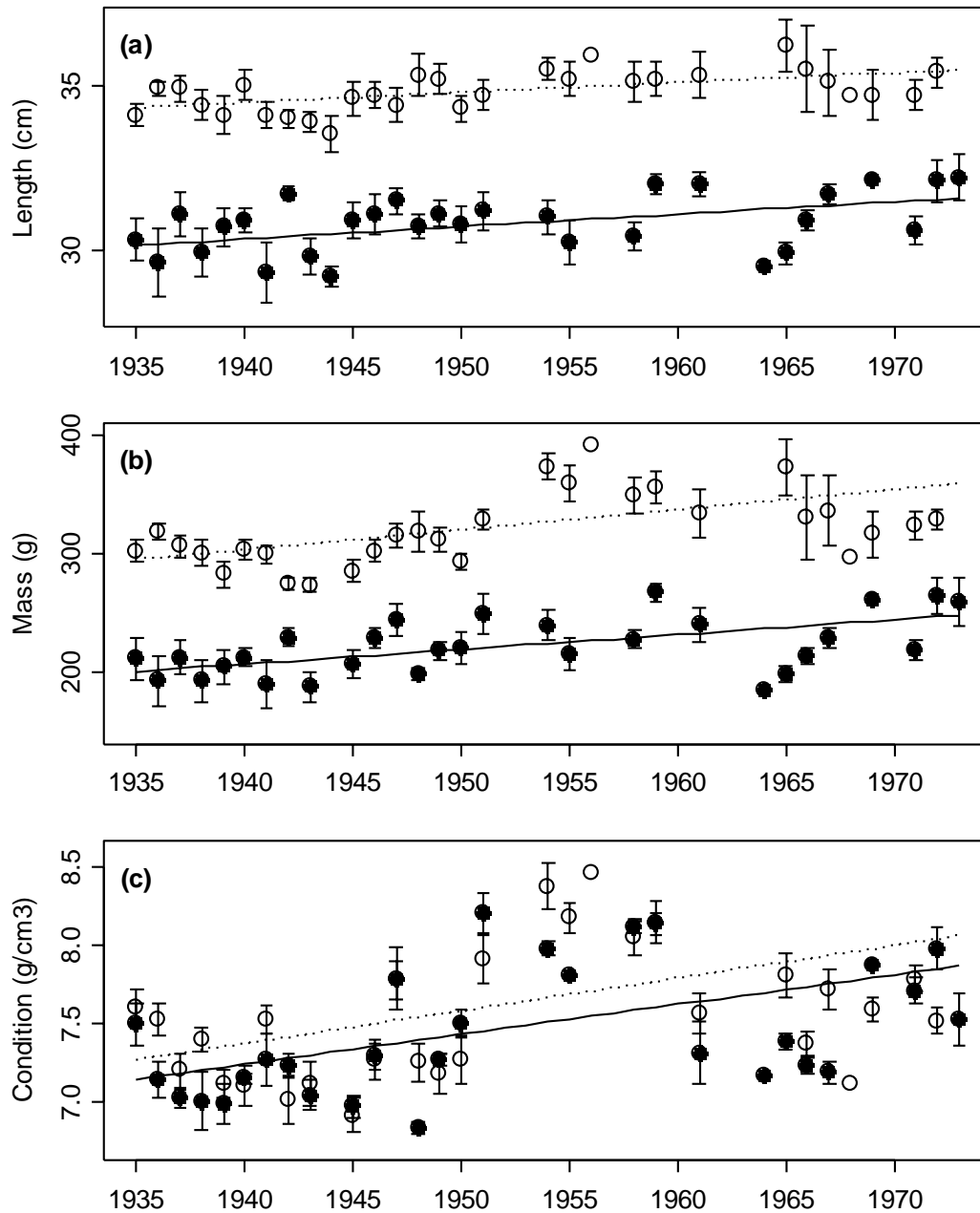

Figure 3. Interannual variability for 1935–1973 in **(a)** mean length, **(b)** mean weight, and **(c)** condition index for first-time spawners (closed symbols) and repeat spawners (open symbols; excluding second-time spawners). Symbols show the grand means (with SE) of the means for maturation cohorts-at-age. Solid and dotted lines indicate significant ($P < 0.0005$) positive temporal trends in length, weight, and condition for first-time and repeat spawners, respectively.
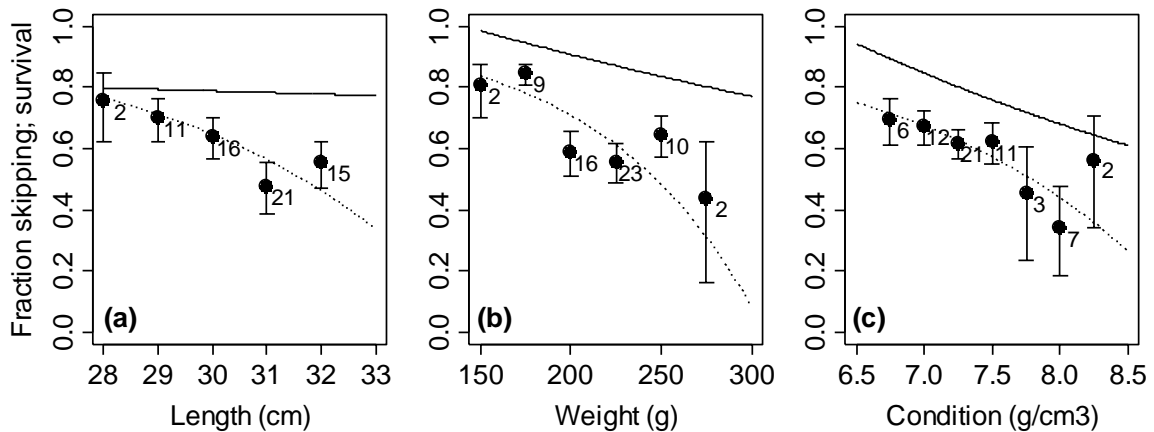
Figure 4. *Symbols:* Relationships between the mean length **(a)**, weight **(b)**, and condition index **(c)** of maturation cohorts as first-time spawners in year *y*, and the estimated fraction of fish skipping reproduction in year *y* + 1 (equation 4; size variables analysed as factors). Vertical bars indicate SE of estimates; numbers indicate sample sizes (i.e., number of maturation cohorts in each size bin). *Dotted lines:* modelled relationships between length, weight, and condition of first-time spawners and the fraction of fish skipping reproduction the year after (equation 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 1960s–early 1970s (period of extremely high fishing mortality and resulting stock collapse).

Length, weight, and condition

The mean length, weight, and condition index of spawning herring increased significantly over the period 1935–1973 (Figure 3). This was the case for both first-time spawners (length: 0.038 cm yr^{-1}, $P < 0.0005$; weight: 1.2 g yr^{-1}, $P < 0.0001$; condition: 0.019 g cm^{-3} yr^{-1}, $P < 0.0001$) and repeat spawners (length: 0.030 cm yr^{-1}, $P < 0.0001$; weight: 1.7 g yr^{-1}, $P < 0.0001$; condition: 0.021 g cm^{-3} yr^{-1}, $P < 0.0001$). The increasing trends were approximately linear for length and weight (Figure 3a-b), but less so for condition index; the latter peaked in the 1950s (Figure 3c).

The mean length, weight, and condition index of first-time spawners had significant effects on the fractions of fish skipping reproduction the year after (Figure 4a-c). If first-time spawners had larger body lengths ($P < 0.005$), higher body weights ($P < 0.0005$), or higher condition indices ($P < 0.01$), then skipping of reproduction was less likely to occur in the following year.

Unexpectedly, a negative relationship of the condition index of spawners in year *y* with the fraction surviving to year *y* + 1 was found ($P < 0.005$, first-time and repeat spawners combined; Figure 4c). There was suggestive evidence for a weak negative relationship between weight and survival ($P = 0.098$; Figure 4b). There was no effect of length on survival ($P = 0.825$; Figure 4a).
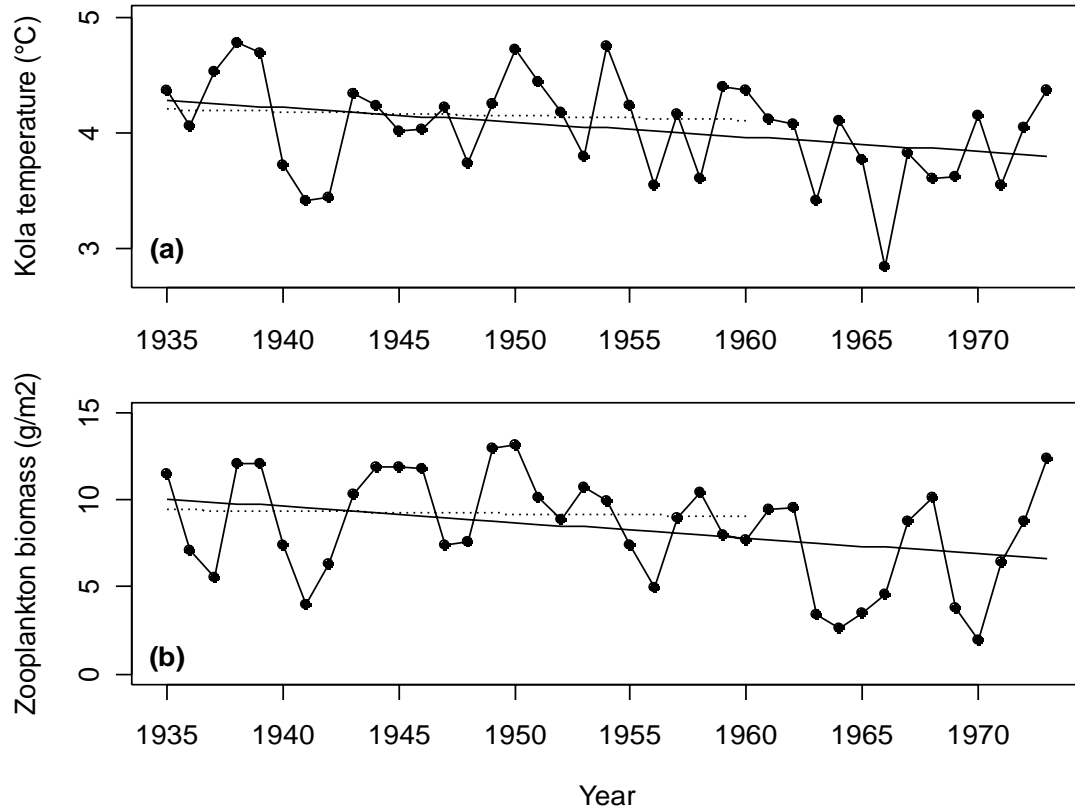
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Figure 5. Interannual variability for 1935–1973 in **(a)** the mean annual temperature in the Kola section and **(b)** estimates of zooplankton biomass derived from NAO winter indices using equation (1). Solid and dotted lines indicate trends, respectively, for the period 1935–1973 (significant) and 1935–1960 (not significant).

Environmental variables

Over the period 1935–1973, the mean annual Kola temperature varied from 2.84–4.78 °C and annual estimates of zooplankton biomass varied from 1.93–13.11 g m^{-2} (Figure 5). The two variables were significantly and positively correlated ($r = 0.538$, $P < 0.0005$). Over the entire time-series, significant negative trends were found in both Kola temperature ($P < 0.05$) and zooplankton biomass ($P < 0.05$). This was mainly due to low values in the 1960s and early 1970s; over the period 1935–1960 there were neither trends in the Kola temperature ($P = 0.73$) nor in zooplankton biomass ($P = 0.83$). Given that the 1960s and early 1970s also coincided with extremely high exploitation of Norwegian spring-spawning herring and stock collapse, complicating interpretation of results, further analyses were restricted to the period 1935–1960.

Using general linear models, we examined for possible relationships between the Kola temperature, zooplankton biomass and the condition of herring in a given year, and the fraction of fish surviving until the following year and skipping the second reproductive season the following year (see Table 2 for a selection of models). Models including only temperature (Model 1) or only zooplankton biomass (Model 2) did not reveal significant effects on survival, but did implicate that higher temperatures are related with more frequent skipping of

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reproduction ($P < 0.005$). However, a model including both temperature and plankton biomass (Model 3) suggested that survival was negatively affected by temperature ($P = 0.030$) but positively affected by plankton biomass ($P = 0.011$); higher temperatures would lead to more frequent skipping of reproduction ($P = 0.001$) but skipping was not affected by plankton biomass ($P = 0.185$).

These patterns were generally also found if condition was included (Models 4–6). A model including temperature, plankton biomass, and condition as main effects (Model 4) confirmed the negative relationships of condition with both survival ($P = 0.015$) and skipping of reproduction ($P = 0.063$), as reported above (see Figure 3c). However, the negative effect of condition on survival was related with negative interactions of condition with plankton biomass and temperature: accounting for these interactions (Models 5, 6) suggested that condition has a positive effect on survival ($P < 0.05$).

Table 2. Summary of selected general linear models examining the effects of Kola temperature, zooplankton biomass (based on indirect data), and condition of herring in year y on survival from year $y \rightarrow y + 1$ and on the fraction of fish skipping the second spawning season in year $y + 1$. Models were selected based on biological significance and the Akaike information criterion (AIC).

Model, variable	Survival			Skipped reproduction			AIC
	t	P	Effect	t	P	Effect	
Model 1							730
Temperature	−1.02	0.309	(−)	−0.545	< 0.005	+	
Model 2							743
Plankton	1.64	0.102	(+)	−0.453	0.651	(+)	
Model 3							721
Temperature	−2.18	0.030	−	−3.30	0.001	+	
Plankton	2.55	0.011	+	1.33	0.185	(−)	
Model 4							677
Temperature	−1.84	0.066	(−)	−3.09	0.002	+	
Plankton	2.43	0.015	+				
Condition	−2.62	0.009	−	1.86	0.063	(−)	
Model 5							671
Temperature	−2.01	0.045	−	−3.10	0.002	+	
Plankton	2.85	0.005	+				
Condition	2.24	0.026	+	1.68	0.006	−	
Condition * Plankton	−2.74	0.006	−				
Model 6							661
Temperature	0.627	0.531	(+)	−3.91	< 0.0005	+	
Plankton	2.93	0.004	+				
Condition	2.01	0.045	+	−3.53	< 0.0005	+	
Condition * Temp.	−0.784	0.433	(−)	3.75	< 0.0005	−	
Condition * Plankton	−2.82	0.005	−				

DISCUSSION

This study provides improved understanding why a significant fraction of adult Norwegian spring-spawning herring does not spawn strictly annually, but instead may skip the second reproductive season (Engelhard & Heino submitted). First, it describes considerable interannual variability 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. Third, relationships between condition, environmental variables, and survival of adult herring are revealed.

The results corroborate well with life-history theory predicting that adult individuals are expected to skip reproduction, if the loss in fecundity in the current year is balanced by the likelihood of increased fecundity in the future, discounted by the survival probability up to that point (Roff 2002). Investment in reproductive activity implies costs and risks, such as a reduction in growth and survival chances, and thereby 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 negatively related with the extent to which spawning is skipped the year after (Figure 4a-c). Thus, strong support is provided for the hypothesis (Engelhard & Heino submitted) that young adult herring, due to their small size, after first reproduction often need an extra year to re-gain the energy stores required for reproduction, in contrast to older adult herring which are advantaged by larger sizes (compare with Figure 3). Correspondingly, negative relationships between condition and the likelihood of skipped reproduction have also been found for several other species (fish: Rijnsdorp 1990, Oganesyan 1993, Burton et al. 1997, Rideout et al. 2000; reptiles: Broderick et al. 2003).

It may not be surprising that first-time spawning herring are more likely to skip the following 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 & 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 & Bergstad 1999; Axelsen et al. 2000). Under the given conditions, skipping of a reproductive season is likely to be an optimal life-history strategy leading to improved lifetime reproductive success.

The negative relationship between condition and survival was opposite to the expected (Figure 4c). This may be due to errors in relative stock numbers that confound the survival estimates. 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 environmental conditions in the early life stages will result in high survival but reduced growth and condition due to reduced per capita food intake, as a density-dependent effect (Barros & Toresen 1998). Second, strong year-classes, characterised by reduced growth and low condition indices (Toresen 1990; Holst 1996) are likely to suffer relatively low predation and exploitation mortality. Third, a positive trend in condition over the study period (in particular from 1935–1960; Figure 3c) coincided with an increase in fishing mortality; the latter was due to rapid expansion of the fishing fleet, improved technology for catching herring, and a general decline in spawning stock (e.g. Toresen & Jakobsson 2002).

Alternatively, if skipped reproduction is not restricted to the second spawning season but also occurs in older spawners, then the negative relationship between condition and survival might even be the result of skipped reproduction *per se*. In strict sense, survival estimates presented here indicate annual changes in fish numbers present in the spawning area. In a year of low body condition, all adult herring might have a tendency to skip reproduction and thus be under-represented in the spawning area: if the same fish return to spawn the year after, this will lead to a negative relationship between condition and survival 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 fish due to skipping from absence due to mortality (Engelhard & Heino submitted).

The interpretation of the environmental influences on skipped reproduction and survival revealed here is moreover complicated. The positive relationship of zooplankton biomass in the Norwegian Sea with survival is as expected; plankton biomass was not, however, related with skipped reproduction (Table 2). It should be noticed, though, that the zooplankton index is not based on direct measurements, and its performance during the study period is not known. Remarkably, temperature in the Kola section of the Barents sea was negatively related with survival and positively related with frequency of skipped reproduction (Table 2), even though higher temperatures are generally favourable for plankton abundance (e.g. positive correlation of temperature with plankton biomass, $P < 0.0005$). However, warm temperatures may also have negative effects for herring, such as increased energy expenditure and possible changes in predation mortality. Further, interaction effects of condition with temperature and zooplankton biomass on survival and skipped reproduction complicated interpretation of results. Nevertheless, interannual variability in the Norwegian Sea environment, combined with variations in the size and condition of spawning herring (Figures 3, 5) may well help explain the dynamics in frequency of skipped reproduction in this stock over the period examined (Figure 2). For example, the decrease in frequency of skipped reproduction in herring from the 1930s–1950s may have resulted from a gradual increase in herring condition (Holst 1996), combined with particularly warm temperatures in the beginning of the time-series (Figure 5).

Interestingly, the negative link between size and condition of first-time spawners and their likelihood of skipping reproduction may imply a dampening effect on the substantial population fluctuations that characterise Norwegian spring-spawning herring. High biomass levels are generally related with slow growth and low condition indices (e.g. Toresen 1990;

Holst 1996; Engelhard & Heino 2004), and therefore likely with more frequent skipping of reproductive seasons. 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 & Heino 2004); infrequent skipping of reproduction may have 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 fish (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 stock dynamics and reproductive potential illustrate the need for careful and critical re-evaluation of a common presumption in fisheries science—that adult fish spawn strictly annually.

ACKNOWLEDGEMENTS

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