Variable natural mortality rate of juvenile Norwegian spring-spawning herring (*Clupea harengus* L.) in the Barents Sea

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Understanding the patterns of mortality rate in the juvenile stages of exploited fish populations is essential for improving current stock assessment procedures. Most of the research on "the recruitment problem" has focused on the larval stages, but recent work indicates that a large part of the variability in year-class strength may be associated to variable mortality rates during the juvenile stages. The data on abundance of juvenile Norwegian spring-spawning herring in the Barents Sea collected by the Bergen Institute of Marine Research between 1983 and 1993 was analysed to test this hypothesis. The results give strong support to the hypothesis. Survival from the start of the 0-group stage to age 3 years may have varied from 0 to 30% for the cohorts investigated. Mortality rate is shown to be strongly age-dependent, and between 75% and 99% of the total juvenile mortality occurs during the first year of life.

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Introduction

The large year-to-year variations in recruitment have long been recognized as the central question of fisheries science and a major source of uncertainty in fisheries management (Hilborn and Walters, 1992). Most research on this topic has focused on Hjort's (1914) hypothesis that year-class strength was determined by variations in mortality of the early larval stages due to starvation (Wooster and Bailey, 1989).

Recently, it has been suggested that (i) variable mortality rates during the juvenile phase may account for a large part of the observed variability in recruitment (Sissenwine, 1984, 1986; Smith, 1985; Daan, 1987; Sparholt, 1990; Fogarty *et al.*, 1991) and (ii) this mortality rate should decrease strongly with size (or age) during the early life stages, to stabilize at approximately constant levels as the fish approach adulthood (Vetter, 1988; Beyer, 1989; Caddy, 1991).

Sissenwine (1984) and Beyer (1989), particularly, have noted that even though it is likely that mortality rates in the juvenile phase are lower than during the larval stages, they apply for a much longer period. The mortality corresponding to the juvenile period has thus the potential to represent an important part of the total pre-recruit mortality. The multispecies modelling carried out for the North Sea (e.g. Daan, 1987; Sparholt, 1990) and for the Barents Sea (Tjelmeland and Bogstad, 1993), indicate that predation-induced mortality rate is likely to show a large year-to-year variability, and that it tends to be higher the smaller (and younger) the prey.

The Norwegian spring-spawning herring stock has one of the largest recruitment variabilities in the north-east Atlantic (Dragesund, 1970; Serebryakov, 1991), and it is often dominated by a couple of strong year-classes. Exceptional year-classes seem to occur only in years when a large part of the juveniles are distributed in the Barents Sea area (Dragesund, 1970; Seliverstova, 1990a, b). The fish whose nursery is located in this area have a long juvenile period (approx. 3 years), meaning that recruitment will be quite sensitive to changes in mortality rate at this stage.

The Institute of Marine Research in Bergen (IMR) has run regular acoustic surveys of the juvenile herring

in the Barents Sea from 1959, to the collapse of the stock in 1969, and again since 1983. The data series from the latter survey series include abundance estimates for different ages of each herring cohort that entered the Barents Sea in this period.

From these data, it was possible to conclude that some cohorts, with a high estimated abundance at the early juvenile stages, failed to produce a significant recruitment, while other cohorts, with much lower estimated abundance at the same stages, did result in high recruitment levels (ICES, 1994). It was argued (Hamre, 1988, 1994) that this apparent discrepancy in fate of different cohorts could be evidence of a wide variability in juvenile mortality rates, probably associated to large changes in the stock of north-east Arctic cod, the largest predator stock in the area. In this work, we use a statistical modelling approach to investigate whether the acoustic herring abundance estimates data provide enough evidence to support the contention of a large inter-cohort variability in juvenile mortality rate, and of a decrease of mortality rate with age in this life-stage. For use in stock assessment work and for later investigations, we also present estimates of the actual survival levels experienced by the different cohorts in the data set, and investigate the precision of these estimates.

Materials and methods

The data

The work presented in this paper is based on an analysis of the series of acoustic abundance estimates of pre-recruit herring in the Barents Sea nursery area collected by IMR between 1983 and 1994. These estimates cover the juvenile period of the herring year-classes 1983 to 1993, with the exception of the year-classes 1986 and 1987, which recruited in such low numbers to the 0-group stage that they were considered to be about entirely absent from in the Barents Sea (ICES, 1994).

The age of the individuals corresponding to each abundance estimate was calculated by computing the time interval (in years) between the assumed hatching date and the date assigned to the estimate. Based on the hatching curves derived for this stock (Fossum, 1993), it was assumed that all fish in one cohort hatched simultaneously on 1 April. The date assigned to each estimate was simply the mid-point of the start and end dates for that survey.

The survey procedure used in the acoustic surveys in the Barents Sea during the period investigated did not include a regular procedure for the estimation of the precision of the abundance estimates. It is thus, not yet possible to evaluate objectively the precision of the individual estimates. However, the highly standardized

survey procedures, and the long survey experience of the team running the surveys, ensure that the quality of the estimates is relatively constant. Nevertheless, problems, mostly related to rough sea conditions, too little time allocated for the survey, or fish distribution (e.g. being distributed inside an area forbidden to the Norwegian research vessels, or being too high in the water column), arise in some surveys. Among the 50 acoustic abundance estimates used in this study, 16 corresponded to surveys for which the reports indicated some kind of difficulty (Fig. 1). In most of these cases, the nature of the difficulties reported and the echo-integrator maps indicate either incomplete coverage of the herring distributions (no 0-line found), or that a part of the stock was out of the echo-sounder range. It is thus likely that the corresponding acoustic estimates significantly underestimated true herring abundance.

These estimates, although less reliable than the remaining ones, still convey important information about the survival of the different cohorts, and were included in the analysis. To reduce their influence on the results, they were assigned an arbitrary relative "external weight", ω_{e_i}, of 0.5. The "external weight", ω_{e_i}, assigned to the other estimates was 1.

Modelling procedure

In this study, two sets of hypothesis tests were performed.

The first set may be described as testing the null hypothesis that all Norwegian spring-spawning herring cohorts entering the Barents Sea as 0-group herring between 1983 and 1993 experienced the same mortality rate patterns.

The second set corresponds to testing the null hypothesis that the mortality rate pattern of a cohort during the whole pre-recruit phase can be described by a constant mortality rate (this will be called the age-independent mortality rate hypothesis).

For the age-independent mortality rate hypothesis, the instantaneous mortality rate suffered by cohort c at age t, $M_c(t)$,

$$M_c(t) = -\frac{1}{N_c(t)}\frac{dN_c(t)}{dt} \qquad (1)$$

where $N_c(t)$ is the number of cohort c at time t, is simply

$$M_c(t) = M_c \qquad (2)$$

where M_c is independent of age.

For the alternative, age-dependent mortality rate hypothesis, and to keep consistency with the most
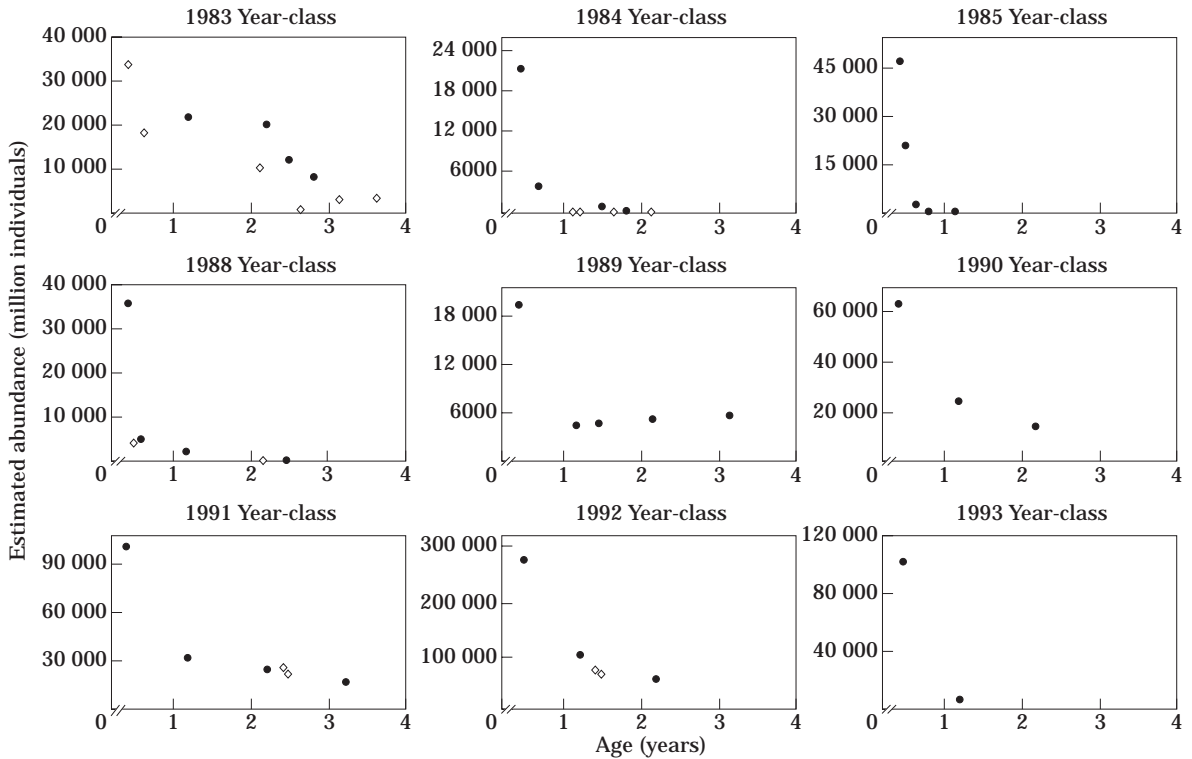
Figure 1. Acoustic estimates of abundance and corresponding ages used as the basis for modelling mortality of juvenile Norwegian spring-spawning herring. Estimates of sufficient quality (●); estimates of lower quality (◇).

generalized view of mortality in the young stages of fish (Vetter, 1988; Beyer, 1989; Caddy, 1991), we need a model providing a pattern of a very high mortality rate in the youngest stages, declining rapidly as the fish grow older, to achieve a relatively stable level as the fish approach the age of recruitment to the adult stock. In order to keep some consistency with earlier work, we chose a generalization of the inverse or power functions used by Beyer (1989), Sparholt (1990) and Caddy (1991),

$$M_c(t) = M_{c_R} + (M_{c_{t_0}} - M_{c_R}) \left(\frac{t}{t_0} \right)^{-a}, \tag{3}$$

where M_{c_R} is the mortality rate suffered by cohort c after recruitment age, $M_{c_{t_0}}$ is the mortality rate experienced by the same cohort at the initial age t_0, and α is a ''shape parameter'', defining how fast the change is from the high mortality rate typical of the young stages, to the relatively stable and lower mortality rate of the adults.

These two alternative models, integrated from the initial age t_0 to age t_1, give the corresponding expressions for the abundance-at-age,

$$N_c(t_1) = N_c(t_0) e^{-M_c(t_1 - t_0)} \tag{4}$$

for the age-independent mortality rate hypothesis, and

$$N_c(t_1) = \tag{5}$$

$$\begin{cases} N_c(t_0) e^{-\left(M_{c_R}(t_1 - t_0) + (M_{c_{t_0}} - M_{c_R}) t_0 \left(\frac{(t_1/t_0)^{(1-\alpha)} - 1}{1-\alpha} \right) \right)} & \text{if } \alpha \neq 1 \\ N_c(t_0) e^{-\left(M_{c_R}(t_1 - t_0) + (M_{c_{t_0}} - M_{c_R}) t_0 \ln\left(\frac{t_1}{t_0} \right) \right)} & \text{if } \alpha = 1 \end{cases}$$

for the alternative hypothesis of a mortality rate declining with age, as in (3).

Fitting Model (5) to the data requires the estimation of three parameters ($N_c(t_0)$, M_{c_R} and $M_{c_{t_0}}$) separately for each cohort, plus one more (α) common to all cohorts. Since the data available include some cohorts with only 2 or 3 data points, this cannot be achieved. We thus simplify Model (5) by introducing some constraints that correspond to assuming that the mortality experienced by each cohort after recruitment age will be at least approximately the same for all cohorts, i.e. $M_{y_R} = M_R$ (y=83, . . . 93). Model (5) is thus reduced to

$$N_c(t_1) = \tag{6}$$

$$\begin{cases} N_c(t_0) e^{-\left(M_R(t_1 - t_0) + (M_{c_{t_0}} - M_R) t_0 \left(\frac{(t_1/t_0)^{(1-\alpha)} - 1}{1-\alpha} \right) \right)} & \text{if } \alpha \neq 1 \\ N_c(t_0) e^{-\left(M_R(t_1 - t_0) + (M_{c_{t_0}} - M_R) t_0 \ln\left(\frac{t_1}{t_0} \right) \right)} & \text{if } \alpha = 1 \end{cases}$$

Earlier studies on the Barents Sea herring (Hamre, 1994) suggest that the 1983, 1989, 1990, 1991 and possibly also the 1992 cohorts should be expected to have experienced a relatively high juvenile survival rate, while the 1984, 1985, 1988 and 1993 cohorts are expected to have experienced a low survival rate during this period. This corresponds to considering that two levels of juvenile survival could be distinguished. Consideration of the predator levels in the area (ICES, 1994), however, suggests that the 1992 cohort should have experienced a relatively lower juvenile survival rate than the three previous year-classes, corresponding thus to the inclusion of a third level of juvenile survival rate. We thus test the following specific hypotheses:

(a) the null hypothesis, or the single-level mortality rate hypothesis, corresponding to the introduction in Model (6) of the constraints

$$M_{83_{t_0}} = M_{84_{t_0}} = M_{85_{t_0}} = M_{86_{t_0}} = M_{88_{t_0}} = M_{89_{t_0}} = M_{90_{t_0}} = M_{91_{t_0}} = M_{92_{t_0}} = M_{93_{t_0}};$$

(b) the 2-level mortality rate hypothesis, corresponding to the constraints

$$M_{83_{t_0}} = M_{89_{t_0}} = M_{90_{t_0}} = M_{91_{t_0}} = M_{92_{t_0}} \neq M_{84_{t_0}} = M_{85_{t_0}} = M_{88_{t_0}} = M_{93_{t_0}};$$

(c) the 3-level mortality rate hypothesis, with the constraints

$$M_{83_{t_0}} = M_{89_{t_0}} = M_{90_{t_0}} = M_{91_{t_0}} \neq M_{92_{t_0}} \neq M_{84_{t_0}} = M_{85_{t_0}} = M_{88_{t_0}} = M_{93_{t_0}}.$$

These hypotheses were tested by comparing the fit of the corresponding models to that of the full model, i.e. Model (6) with no constraints on the $M_{c_{t_0}}$ values.

The relationship between natural mortality rate and age was investigated next. For this, we tested the age-independent mortality rate hypothesis against the alternative age-dependent mortality rate hypothesis i.e. tested whether it was indeed required to consider a natural mortality rate varying with age, or if a model considering a mortality rate independent of age could represent our data adequately.

The simplest model describing the variation of juvenile survival among cohorts – corresponding to hypotheses (a), (b) or (c) above – which was not rejected was taken as the start point. So, the age-dependent mortality rate hypothesis was represented by Model (6), with the constraints corresponding to the results of the earlier tests. The age-independent mortality rate hypothesis was represented by Model (4), with the corresponding constraints applying to the M_c parameters.

Since neither of the models is nested in the other, they were compared to an even more general model. This model is Model (5), again with the same constraints on equality of mortality parameters among cohorts, but this time applying to the $M_{c_{t_0}}$ and M_{c_R} parameters. Thus, if hypothesis (b) was considered the ''best'' hypothesis, the full model would be Model (5) with the constraints

$$M_{83_{t_0}} = M_{89_{t_0}} = M_{90_{t_0}} = M_{91_{t_0}} = M_{92_{t_0}} \neq M_{84_{t_0}} = M_{85_{t_0}} = M_{88_{t_0}} = M_{93_{t_0}}$$

and

$$M_{83_R} = M_{89_R} = M_{90_R} = M_{91_R} = M_{92_R} \neq M_{84_R} = M_{85_R} = M_{88_R} = M_{93_R}.$$

The procedure of testing the different hypotheses was the same in all cases: Each candidate model was fitted to the data, and its goodness-of-fit was compared with that of the full model, using F-ratio tests in an extra-sums-of-squares analysis (Bates and Watts, 1988). If the model did not give a significantly worse fit than the full model, it was retained for the second step of the evaluation. In the second step, the residual plots were examined, to detect possible lack of fit due to inadequacy of the model specification (Bates and Watts, 1988) which would not have been detected by the first test. Models that were shown to have lack of fit were rejected at this step, even if they had non-significant F-ratios. The final model selected was the simplest model of those, which passed both tests.

For the error structure, a multiplicative error model (McCullagh and Nelder, 1989) was used,

$$N_c(t) = E[N_c(t)]e^\varepsilon \tag{7}$$

where $N_c(t)$ are the observed values, $E[N_c(t)]$ represent the values expected from the model, and ε is a random variable, with null expectation

$$E[\varepsilon] = 0 \tag{8}$$

and standard error $SE(\varepsilon)$ inversely proportional to

$\ln(E[N_c(t)])$:

$$SE(\varepsilon) = \frac{1}{\ln(E[N_c(t)])}\,\sigma, \tag{9}$$

where σ represents a common measure of the unscaled overall standard deviation of the distribution of residuals.

The model was fitted by minimizing the weighted sum-of-squares of the residuals $\Sigma_i \omega_i \cdot e_i^2$, where

$$e_i = \ln(N_i(t) + 1) - \ln(E[N_i(t)] + 1) \tag{10}$$

(1 is added to the expected values to avoid problems with taking the logarithm of zero in the minimization
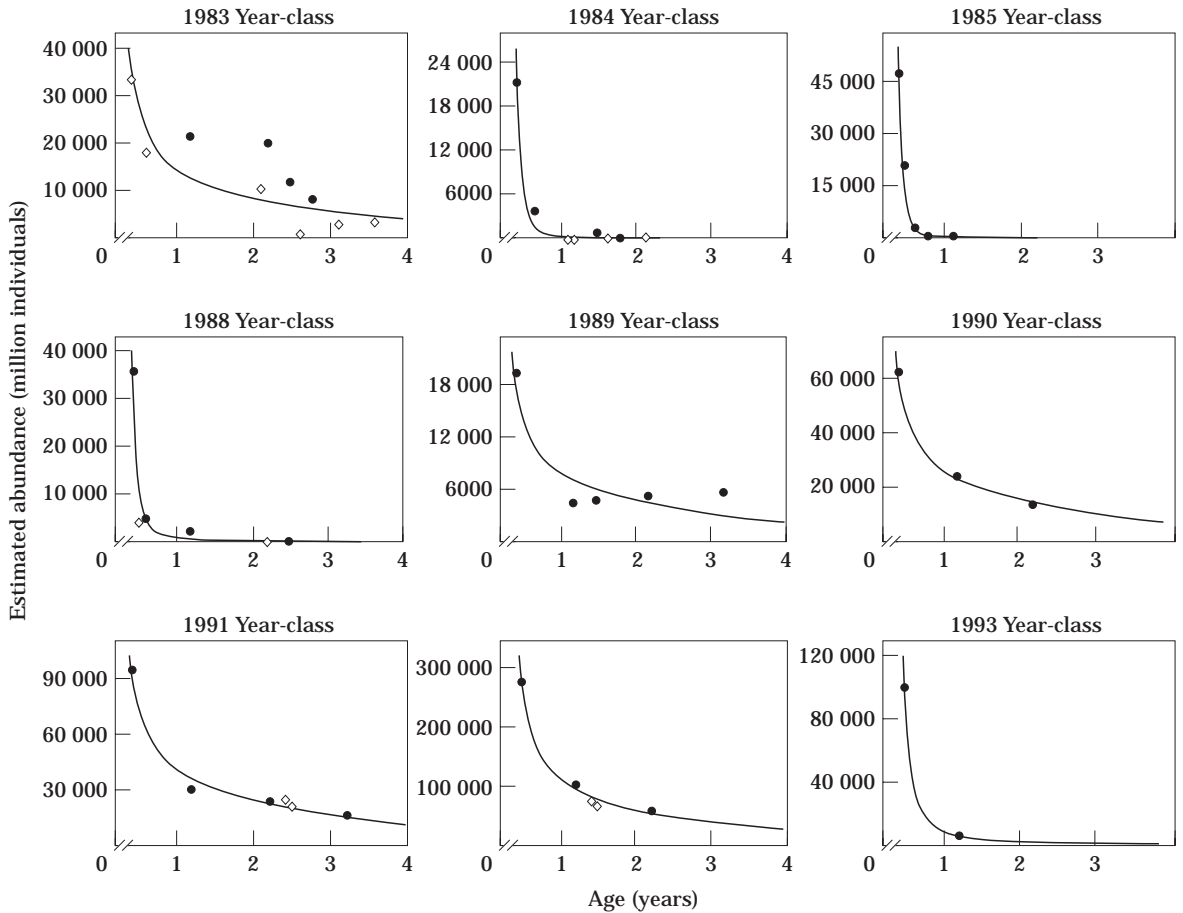
Figure 2. Abundance-at-age predicted from the full model and corresponding acoustic estimates, for the juvenile stage of cohorts 1983–1993 in the Barents Sea. Estimates of sufficient quality (●); estimates of lower quality (◇).

process), and the weights are calculated as

$$\omega_i = \omega_{e_i} \ln^2(E[N_i(t)] + 1) \qquad (11)$$

Where ω_{e_i} is the external weight assigned to the ith observation.

A non-linear regression procedure, in this case a direct-search routine, the Nelder-Mead Simplex method (Mittertreiner and Schnute, 1985; Nash and Walker-Smith, 1987), was used for fitting the models.

The use of a non-linear model with a non-additive error term whose distribution is not completely specified prevents us from using the tabulated F-distributions to determine the significance level of the observed F-ratios. To overcome this problem, the significance of the observed F-ratios was computed using a bootstrap procedure (Efron, 1982) modified to ensure that the significance levels were computed under the null hypothesis (Hall and Wilson, 1991) – Appendix A.

The confidence regions around the predicted survival curves were also computed using a bootstrap procedure (Appendix B).

Results

The abundance-at-age values estimated for the different cohorts by fitting the full model (Model 6) are compared to the acoustic estimates in Figure 2. With the exception of the year-classes 1983, which has a large number of low-quality estimates, and 1989, for which the observed values show an increasing trend after age 1 year, the model succeeds in reproducing the main trends in the data, and shows no evident lack of fit.

The survival-to-age

$$S_c(t) = \frac{N_c(t)}{N_c(t_0)}$$

curves of the different cohorts estimated under the full model (Fig. 3) have a markedly clustered appearance. The curves for the 1983, 1989, 1990 and 1991 year-classes are clearly very similar, with a high survival, while those for the 1984, 1985, 1988 and 1993 are also relatively similar, with a lower survival. The estimated survival curve for the 1992 cohort lies somewhere
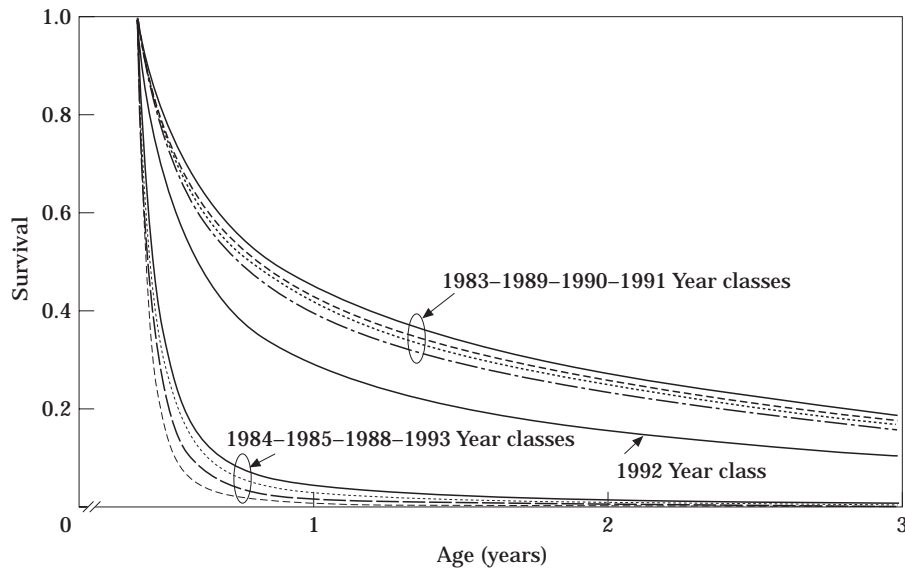
Figure 3. Survival curves for the different cohorts, estimated under the full model.

Table 1. Extra-sum-of-squares analysis comparing the fit of different alternative models for the similarity in survival patterns among the cohorts studied. d.f. – degrees-of-freedom; ESS – extra sum of squares; MES – mean extra square; SS – sum-of-squares; MS – mean square.

Model	Parameters	d.f.	ESS	MES	F-ratio	p-value
Single survival level	12	8	1539.06	192.38	6.949	<0.001
Two survival levels	13	7	81.37	11.63	0.420	0.757
Three survival levels	14	6	67.87	11.31	0.409	0.787
			SS	MS		
Full model	20	30	830.50	27.68		

All values presented in table (except the last row, which represents the fit of the full model) refer to the extra sum-of-squares relatively to the full model.

between these two extremes, but is closer to the high-survival group.

The extra-sum-of-squares analysis (Table 1) confirms this qualitative appreciation, but indicates also that the available data do not allow us to clearly distinguish between the survival curves estimated for the 1992 cohort and for the "high survival" cohorts.

The analysis thus leads to rejecting the null hypothesis that all cohorts in the data-set experienced approximately the same level of survival. However, only two levels of survival can be distinguished with the data available.

Since only two levels of survival could be distinguished, the null hypothesis of an age-independent natural mortality rate was tested under the two-level model. The extra sum-of-squares analysis (Table 2) leads to rejection of the null hypothesis of an age-independent mortality rate.

The confidence regions for the estimated survival curves are presented in Figure 4(a)–(c). When estimating separate survival curves for each cohort the intervals have a very large degree of overlap. The survival curves estimated under the assumption of only two different survival levels are much better determined, and are well separated, even if the confidence intervals are still relatively wide. In both cases, the confidence regions are widest at the intermediate ages, where the degree of curvature is highest.

Most herring leave the Barents Sea nursery areas at spring in their third year of life (Dragesund *et al.*, 1980). Survival during the juvenile period may therefore be approximated by survival up to age 3. Table 3 presents these estimated survivals, for the full model (nine different survival curves) and for the reduced model (only two different survival curves). Survival for the whole juvenile period is estimated to range between 16% and 19% for

Table 2. Extra-sum-of-squares analysis comparing the fit of the age-independent and the age-dependent mortality rate models. d.f. – degrees-of-freedom; ESS – extra sum of squares; MES – mean extra square; SS – sum-of-squares; MS – mean square.

Model	Parameters	d.f.	ESS	MES	F-ratio	p-value
Age-independent	11	3	543.56	181.19	7.155	<0.001
Age-dependent	13	1	0.19	0.19	0.008	0.858
			SS	MS		
Full model	14	36	911.68	25.32		

All values presented in table (except the last row, which represents the fit of the full model) refer to the extra sum-of-squares relative to the full model.

Table 3. Survival from age 0.4 up to age 3 for different groups of survival curves estimated. The confidence intervals were computed using a bootstrap technique.

Mortality model	Survival level	Survival up to age 3 (%)	
		Point estimate	95% confidence interval
Two survival levels	High	15.8	9.4–26.8
	Low	0.3	0.0–0.6
Full model (nine survival levels)	83	15.8	3.2–77.6
	84	0.2	0.0–1.2
	85	0.1	0.0–0.4
	88	0.4	0.0–3.5
	89	17.6	5.7–50.5
	90	17.0	9.7–28.5
	91	18.8	13.0–32.7
	92	10.4	5.2–20.1
	93	0.7	0.1–1.5

the 1983, 1989, 1990 and 1991 cohorts, while for the 1984, 1985, 1988 and 1993 cohorts it is close to 0%, and close to 10% for the 1992 cohort. With the exception of the 1992 cohort, these values are again quite well approximated by the two-level model.

Figure 5 shows that most of the mortality suffered during the juvenile period is concentrated on the first few months of this period. For the ''high-survival'' cohorts, approximately 75% of the overall juvenile mortality occurs during the first year of life, with about 55% during the first three months of the juvenile period. For the ''low-survival'' cohorts these percentages are even higher. About 99% of the total juvenile mortality occurs during the first year of life, with 96% in the first three months.

There seems to be no association between the estimated juvenile survivals and the initial herring densities. High and low juvenile survivals are associated with both high and low 0-group abundance estimates (Fig. 6), and they also show a clear time-pattern (Fig. 7), with several consecutive years of low or high survival.

Discussion

The results obtained in this study show that there is a high level of inter-cohort variability in survival of juvenile Norwegian spring-spawning herring, and that mortality rates during this life-stage are strongly dependent on age.

There are substantial differences in overall juvenile survival among the cohorts investigated. The survival experienced by the cohorts in the ''low-survival'' group was so low that they were practically extinct by the end of the juvenile period. Given this large difference, and because only two levels of survival could be distinguished among cohorts, the dynamics of the juvenile herring in the period investigated can be described as an ''all or nothing'' situation. Approximately half of the cohorts studied produced practically no recruits, even though some of them were estimated to be quite abundant at the start of the juvenile period, and can thus be classified as ''failures''. On the contrary, a significant proportion of the individuals in the other half managed
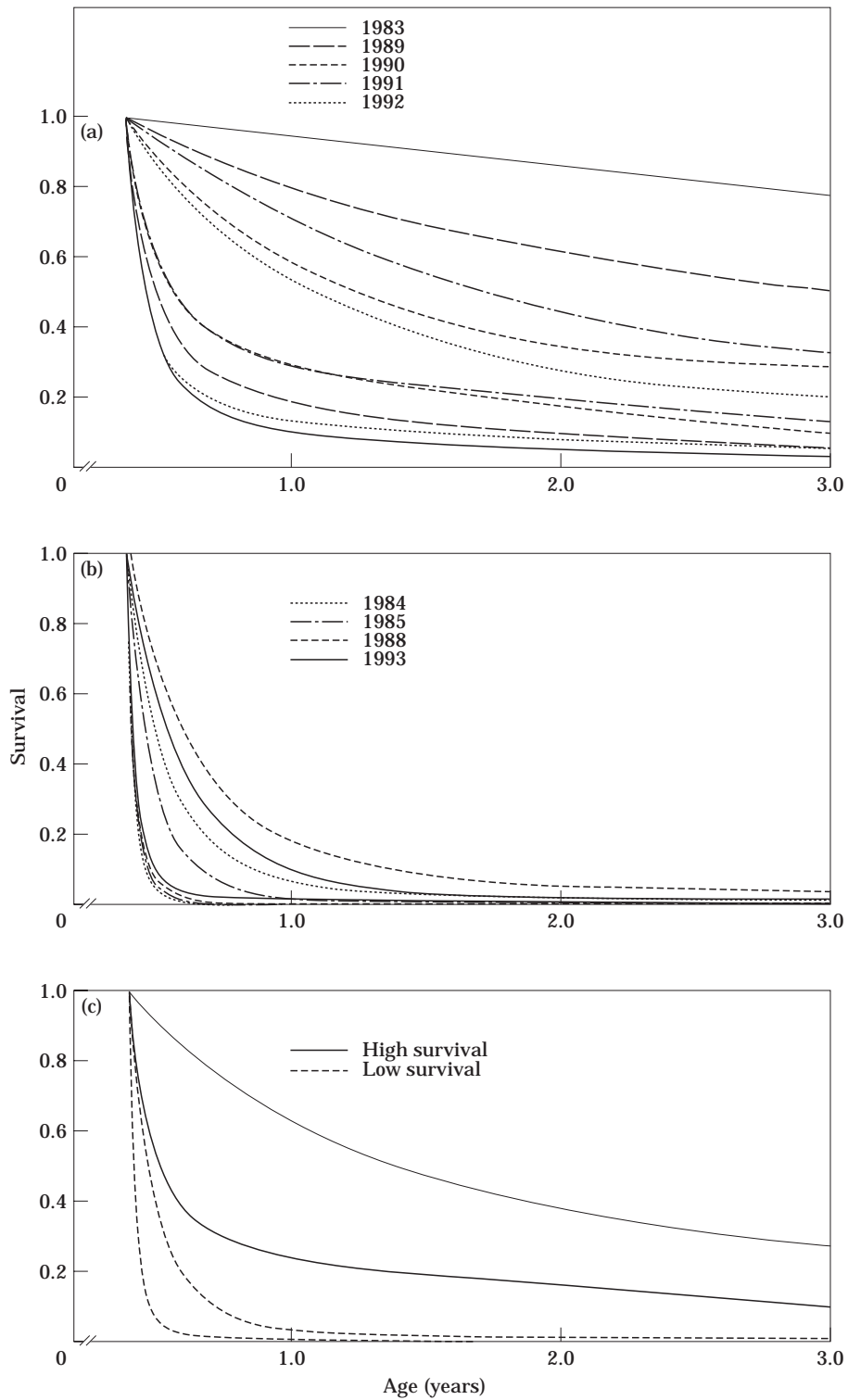
Figure 4. Confidence regions for survival-at-age during the juvenile stage of herring in the Barents Sea. (a) Full model, high-survival cohorts. (b) Full model, low-survival cohorts. (c) Reduced model, high- and low-survival cohorts.
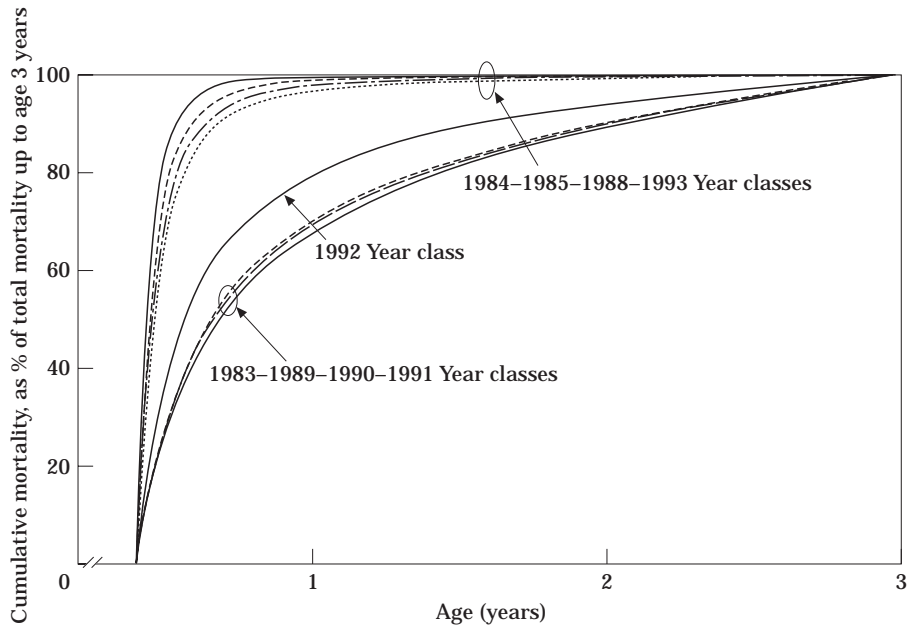
Figure 5. Cumulative mortality estimated to have been suffered by the low-survival and the high-survival cohorts through the juvenile period, as a percentage of the total mortality suffered during that period.
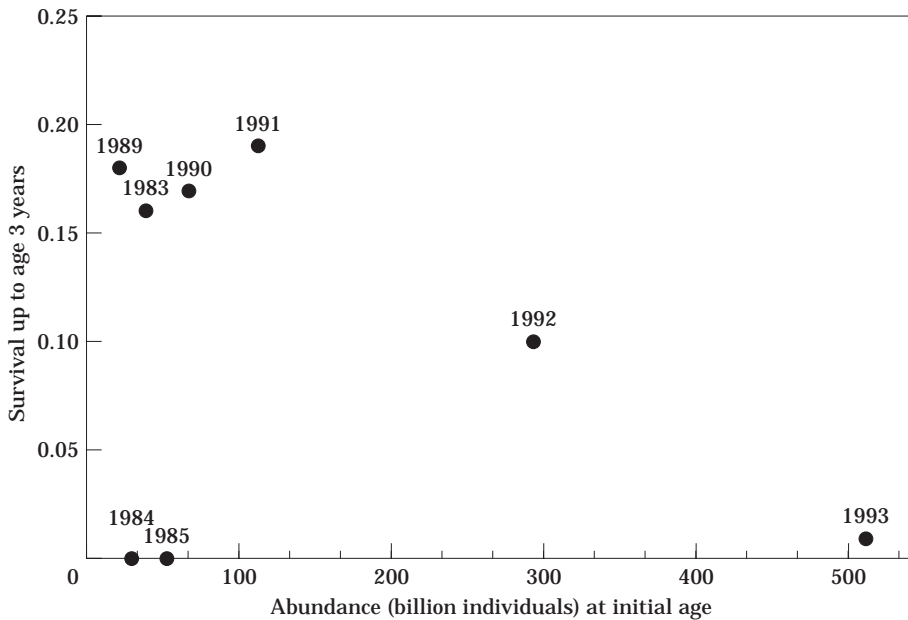

Figure 6. Survival during whole juvenile period (age 0.4 up to 3 years) vs. Abundance at the start of the juvenile stage.

to survive through the juvenile period, and these cohorts can thus be classified as ''successful''. This can be considered as evidence that year-class strength of this stock may be strongly influenced by variations in mortality rates at the juvenile stage. The age effect in mortality rates was estimated to be very strong. This implies that most of the juvenile mortality occurs during the first year of life, and that older herring (2-group and late 1-group) are much less susceptible to these variations in mortality rates.

The only other study we know of that has tried to directly investigate the variability of mortality in the juvenile stages of fish is the comprehensive work of Myers and Cadigan (1993a,b). In their study, these
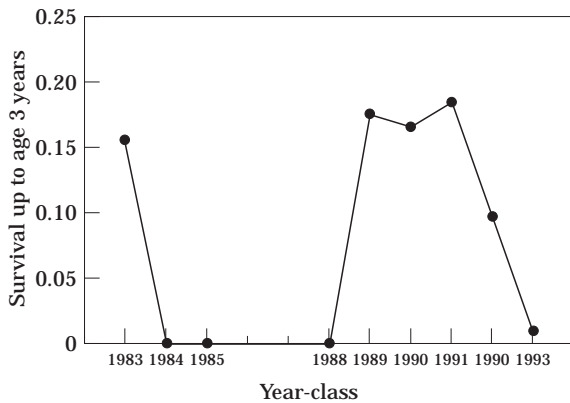
Figure 7. Survival of different year-classes during whole juvenile period (age 0.4 up to 3 years).

authors concluded that, for the stocks they investigated, the largest part of the variability in juvenile mortality was associated with density-dependent processes. The survival rates estimated in this study show no such pattern. The data used in this analysis, however, correspond to a period of very low spawning stock sizes. It is therefore possible that the 0-group densities observed during this period are below the level at which the density-dependent mechanisms become more important.

Although the general results of this study are in good agreement with what was expected from general ecological considerations, the relative lack of fit of the model to the acoustic abundance data for the 1983 and 1989 cohorts, apparent from Figure 2, may raise some concerns.

Acoustic estimates of abundance of pelagic schooling fish are subject to a number of sources of error, and it is thought that errors of $\pm 35\%$ or more are common in these estimations (Simmonds *et al.*, 1992). As long as these errors are not systematic, they will not bias our results. There are however several indications that some systematic errors may have affected the acoustic abundance estimates of the 1983 and 1989 year-classes in particular. Due to lack of ship time and bad weather, the first two estimates of the 1983 year-class did not cover the whole distribution area of the juvenile herring, and it is thought that the true stock abundance may have been double that which was indicated by these estimates. The last two measurements of the abundance of this year-class were done as the cohort was migrating out of the Barents Sea, and they probably also appreciably underestimate the true cohort abundance, as it is likely that some of the fish already had left the Barents Sea at the time of the surveys.

It is thus quite plausible that the abundance-at-age curve estimated for this cohort is a strong underestimation of the abundance of this year-class. This interpretation is supported by the fact that all "good" acoustic abundance estimates of this year-class are above the fitted curve, and by the results of the VPA performed on this cohort by the ICES Atlanto-Scandian Herring and Capelin Working Group (ICES, 1996), which estimated the abundance of this cohort at age 3 to be about two to three times the abundance predicted by the fitted abundance-at-age curve. The survival-at-age curve estimated for this cohort, however, will not have been affected in the same way as the absolute abundance estimates. The relative errors affecting the estimates at the early ages are not likely to be widely different from the relative errors affecting the estimates at the end of the series, and it is thus reasonable to assume that the estimated survival curve will not be strongly biased. In fact, if all abundance estimates were in error by exactly the same relative factor, the survival curve would be correct, even though the abundances were grossly underestimated. Besides, the constraints used in the model imply that, even in the case of the full model, only the M_{83_0} parameter of the survival curve depends exclusively on the data from the 1983 cohort, while both the α and M_R parameters are estimated from the whole data-set. This effect is even reinforced in the reduced model, under which all survival parameters are estimated from data for several cohorts, meaning that there is an added robustness in the estimation of survival curves against errors affecting primarily a small number of cohorts.

As for the 1989 cohort, one observes that the estimates of abundance-at-age increase regularly after age 1, indicating a systematic error in the estimation of the abundance of this cohort. This cohort was very abundant in the fjords of Finnmark, as 0-group fish (ICES, 1994), and its size-at-age at the older ages of the juvenile stage was much higher than the average for Barents Sea herring (I. Røttingen, I.M.R., pers. comm.). This indicates that there was probably a significant emigration of young herring from the Finnmark fjords into the Barents Sea after age 1. It is thus likely that the abundance of the Barents Sea component of this cohort will have been overestimated. In this case, however, only the estimates in the latter ages were affected, and it is thus probable that this effect will also have led to overestimating the survival of this cohort. Although it is difficult to quantify the contribution of immigration, it is known that in years when there are large numbers of 0-group herring in Barents Sea, the abundance of the fjord component of juvenile Norwegian spring-spawning herring is in general much lower than that of the Barents Sea component (Dragesund *et al.*, 1980). This means that it must be considered unlikely that immigration would increase the overall abundance of juvenile herring very significantly. It seems, therefore, reasonable to accept that the errors arising from this effect will not have been large enough to change the classification of this cohort from a "low-survival" to a "high-survival"

cohort, and that they, therefore, will not have affected significantly the main conclusions of this study. The precision of the mortality parameters estimated for the 1993 year-class is obviously difficult to evaluate, as only two data points are available. Yet, the observed changes in abundance are too large for it to be likely that they would have occurred by chance, so it seems safe to conclude that this cohort experienced a low survival.

In a management perspective, the main application of studies on the survival of juveniles lies in improving the forecasts of recruitment. The results obtained here suggest that it might be possible to predict whether a given cohort will have a low or high juvenile survival, and set tighter bounds on expected recruitment levels, based solely on the estimated survival during the first 3 to 6–7 months of the juvenile period. Given the long juvenile period of this stock and the large influence recruitment has in total stock abundance, such capability can be very useful for stock assessment purposes. More studies on the reliability of such inferences would be needed, but provided this relationship held on a longer time-series, it could provide a simple yet powerful means to reduce the uncertainty about the forecasts of recruitment to the adult stock for 3 to 4 years ahead.

Acknowledgements

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Appendix A

In a hypothesis testing situation, the critical values for the test statistic must be computed under the null hypothesis. The resampling procedure used in the hypothesis-testing part of this work was thus designed to ensure that the resampling procedure effectively reflects the null hypothesis, even when this is false (Hall and Wilson, 1991).

Our null hypothesis states that the reduced model describes the data as well as the full model. The procedure used for computing the significance level of the observed F-statistics was as described below:

(1) Fit the full model. Compute the expected abundances under it, $E_f[N_{ci}(t)]$.

(2) Compute the residuals $e_{ci_f} = \ln(N_{ci}(t) + 1) - \ln(E_f[N_{ci}(t)] + 1)$.

(3) Compute the Residual-sum-of-squares

$$RSS_f = \sum_{i=1}^{n} e_{ci}^2.$$

Calculate the corresponding mean square error,

$$MSE_f = \frac{RSS_f}{n - p}.$$

(4) Fit the reduced model. Compute the expected abundances under it, $E_r[N_{ci}(t)]$.

(5) Compute the residuals, $e_{ci_r} = \ln(N_{ci}(t) + 1) - \ln(E_r[N_{ci}] + 1)$.

(6) Compute the Residual-sum-of-squares,

$$RSS_r = \sum_{i=1}^{n} e_{ci_r}^2.$$

(7) Compute the Extra Residual-Sum-of-Squares $ERSS_r = RSS_r - RSS_f$ and the corresponding Extra Mean Square,

$$EMS_r = \frac{ERSS_r}{p - q}.$$

(8) Compute the F-ratio statistic for this fitting,

$$F_o = \frac{EMS_r}{MSE_f}.$$

(9) Create 999 vectors of bootstrapped residuals e^*_{ci}, by repeatedly drawing n residuals,* with replacement, from the full model residuals.

(10) Combine the 999 residual vectors with the expected values under the reduced model§, to create 999 new ''observed'' data vectors,

$$N^*_{ci}(t) = E_r[N_{ci}(t)] e^{\frac{e^*_{ci}}{w_{ci} \ln(E_r[N_{ci}(t)] + 1))}}$$

(11) Repeat steps 1 to 8 for each of the 999 bootstrapped data sets.

(12) Compute the significance level of the observed F-ratio, as

$$P = \frac{\#(F_j : F_j > F_0)}{1000}.$$

Appendix B – Summary of the procedure used for computing the confidence regions for the estimated survival-at-age

(1) Fit the model to the data and compute the expected abundances under it, $E[N_{ci}(t)]$.

(2) Compute the residuals $e_{ci} = \ln(N_{ci}(t) + 1) - \ln(E[N_{ci}(t)] + 1)$.

(3) Compute the Residual-sum-of-squares

$$RSS = \sum_{i=1}^{n} e_{ci}^2$$

and the corresponding mean square error

$$MSE = \frac{RSS}{n - p}.$$

(4) Create 999 vectors of bootstrapped residuals e^*_{ci}, by repeatedly drawing n residuals,* with replacement, from the observed residuals.

(5) Combine the 999 bootstrap samples of residual vectors with the expected values,§ to create 999 new "observed" vectors,

$$N^*_{ci}(t) = E[N_{ci}(t)] e^{\frac{e^*_{ci}}{w_{ci} \ln(E[N_{ci}(t)] + 1)}}.$$

(6) Fit the model to each of the 999 bootstrapped data vectors.

(7) For each age, compute the 2.5% and the 97.5% quantiles of the estimated survival-at-age

$$S_{.025} = S_j : \frac{\#(S \le S_j)}{\#S} = 0.025$$

$$S_{.975} = S_j : \frac{\#(S \le S_j)}{\#S} = 0.975.$$

The 95% confidence region for survival at each age t is then the region between the smoothed curves joining the lower and upper limits of these 500 confidence intervals.

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*Before the residuals are resampled, they are centred by cohort (Leger *et al.*, 1992), inflated by a factor, $\sqrt{n/n-p}$ (Freedman and Peters, 1984), and rescaled by a factor $\omega_{ei} \ln(E[N_{ci}(t)] + 1)$, to achieve homoscedasticity (Carrol and Rupert, 1986). Sampling is stratified by cohort and uses a balanced resampling technique (Gleason, 1988).

§Heteroscedasticity of residuals is reinstated before they are used, by reversing the transformation used before.