

Stock–environment recruitment models for Norwegian spring spawning herring (*Clupea harengus*)

Øyvind Fiksen and Aril Slotte

Abstract: Different stock–environment recruitment models for Norwegian spring spawning herring (*Clupea harengus*) are fitted to a time series of spawning stock, recruitment, and temperature data extending back to 1907. In addition to the traditional temperature index from the Barents Sea (the average annual temperature in the Kola transect), we also developed a new index based on the temperature in the larval drift trajectories during early larval life. The models show highly significant effects of both spawning stock and temperature. The inclusion of the temperature term in the stock–recruitment models removes the autocorrelation from the residuals and improves their explanatory ability by 6–9%. We explore the interdependence between recruitment success and subsequent spawning stock biomass and conclude that this is not likely to generate the stock–recruitment relationship. Our analysis suggests that the collapse of the Norwegian spring spawning herring stock in the period 1950–1970 was not caused by reduced recruitment, but by the drop in spawning stock biomass induced by the increased fisheries in this period.

Résumé : Divers modèles de stock–recrutement reliés à l’environnement appliqués à des harengs norvégiens à reproduction printanière (*Clupea harengus*) sont ajustés ici à des séries temporelles de données remontant à 1907 sur les stocks des géniteurs, le recrutement et la température. En plus du coefficient traditionnel de température dans la mer de Barents (la température annuelle moyenne sur le transect de Kola), nous avons créé un nouvel indice basé sur la température le long des trajectoires de dérive des larves au cours du début de leur vie. L’insertion du terme de température dans les modèles de stock–recrutement enlève l’autocorrélation des résiduels et améliore le potentiel explicatif des modèles de 6–9 %. Un examen de l’interdépendance entre le succès du recrutement et la biomasse subséquente du stock des géniteurs nous amène à conclure que ce n’est vraisemblablement pas ce qui génère la relation stock–recrutement. Notre analyse laisse croire que l’effondrement du stock norvégien de harengs à reproduction printanière dans la période 1950–1970 n’est pas dû à une réduction du recrutement, mais à une diminution de la masse du stock des géniteurs à cause de l’accroissement des activités de pêche à cette époque.

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Introduction

Relating environmental variability and spawning stock biomass (SSB) to fluctuations in recruitment (R) is an intensive area of research and discussion in fisheries science (e.g., Myers and Barrowman 1996; Gilbert 1997; Myers 1997). Establishing stock–recruitment models is difficult for several reasons. First, the biomass of spawners has turned out to be a weak indicator of egg production in some populations (Marshall et al. 1999). Second, there is often a lack of data at extreme population levels and long, high-quality time series of stock abundance and recruitment success are only rarely available. Third, the inherent variability of recruitment from other sources such as predation, competition, and the

physical environment often hide the signal from the spawning stock size (Walters and Korman 1999). Finally, stock–recruitment analysis is difficult because of the lack of independence between the spawning stock and recruitment. Since all recruits eventually become part of the spawning stock, a spurious SSB– R relationship may be generated if there is periodicity in recruitment success (Sparholt 1996; Myers and Barrowman 1996).

Recently, Toresen and Østvedt (2000) compiled an extensive time series on the abundance and age structure of Norwegian spring spawning herring (NSS herring, *Clupea harengus*) back to 1907. During the period 1950–1970 the SSB of NSS herring was decimated from about 16 million to only a few thousand tonnes (Fig. 1). This dramatic event has been related to a very high fishing pressure, particularly on the juvenile stages (Dragesund et al. 1980), and to climatic changes (Cushing and Dickson 1976; Toresen and Østvedt 2000). The climatic changes can be tracked by two comparably long time series of sea temperature at the spawning grounds along the Norwegian coast (Aure and Østensen 1993) and at the nursery grounds in the Barents Sea (Bochkov 1982).

It is these historic data on fluctuations in temperature, SSB, and recruitment of NSS herring that form the basis of the present paper. Our main objective is to differentiate

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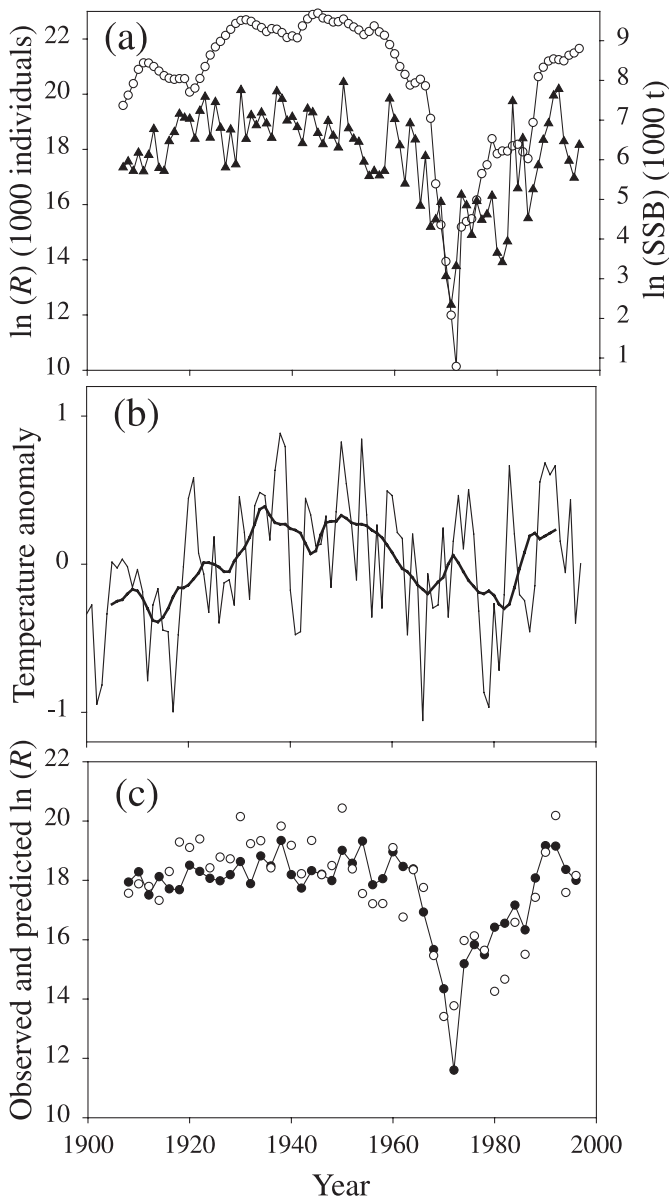
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Fig 1. (a) The data on spawning stock biomass (\ln SSB, in $t \times 10^3$, \circ) and recruitment (0-group, \ln (individuals $\times 10^{-3}$), \blacktriangle). (b) The annual mean temperature in the Kola transect (thin line) and its 10-year running mean (thick line). (c) Predicted (\bullet) and observed (\circ) values from fitting a Ricker model with temperature using every second year to estimate the parameters and the remaining years to test the predictions.



between the respective influences of SSB and climate in the recruitment process of NSS herring, in particular with regard to the collapse and recovery of the stock. We search for the appropriate stock–recruitment model, including the effect of sea temperature, and explore the susceptibility of the model to the interdependence of SSB and recruitment success.

Materials and methods

The stock and temperature data

Toresen and Østvedt (2000) describe the stock structure of NSS herring back to 1907 using virtual population analysis

(VPA) and we applied these data for this study (Fig. 1). In NSS herring, the VPA seems to produce estimates of recruitment that agree reasonably well with both larval indices as well as acoustic and abundance estimates of the 0-group from the Barents Sea and Norwegian fjords (ICES 2000). The larval index is most variable compared to the VPA estimate, whereas the two 0-group indices correlate quite well.

We have analyzed two different indices of the sea temperature that are likely to affect larval herring. The first of these is the annual mean temperature in the 0- to 200-m Kola transect at $33^{\circ}00'E$ in the Barents Sea (Fig. 1), which has proven to be a reasonably good statistic of the climatic fluctuations in the area (Ottersen et al. 2000). A record back to the year 1900 of regular measurements in this section is available (Bochkov 1982; Toresen and Østvedt 2000). However, the Barents Sea temperatures may deviate from the ambient temperatures experienced by the larvae drifting in the Norwegian Coastal Current. Thus, we have included sea temperatures that have been measured at several fixed locations along the Norwegian coast since 1936 (Aure and Østensen 1993). These measures have high resolution (up to several per week) and correspond well with the drift route of the herring larvae (Slotte and Fiksen 2000). NSS herring spawn along the Norwegian coast from the southern tip of Norway to Lofoten, northern Norway (Slotte 1999). After hatching, the larvae drift northwards in the Norwegian Coastal Current. Some of the larvae end up in coastal waters and fjords, but the majority end up in the Barents Sea (Holst and Slotte 1998), where they stay until 2–3 years of age before joining the adult population in the Norwegian Sea (Dragesund et al. 1980).

Based on the data from the coastal stations, we have developed an index that should correspond closely to the temperature experienced by the larvae (Fiksen and Slotte 2000). We interpolated the data in time and space, such that for each day, a temperature is accessible for each 25th kilometre along the Norwegian coast from south to north. We assumed that the temperature at a depth of 10 m is the most relevant to herring larvae. The interpolation was linear between each measured point, and done for Julian day 91–140 (i.e., starting 1 April) for all 65 years from 1936 to 2000. In addition, we assumed a normal distribution of egg deposition along the coast and a major northward shift after 1950 (Dragesund et al. 1980). By assuming the larvae drift with the average current speed ($12.5 \text{ km}\cdot\text{day}^{-1}$), we obtained a measure of the integrated temperature that fish larvae were exposed to during their first seven weeks. In some years the coastal temperature data were scarce or missing. When the missing data were at Lista or Ingøy (at the southern and northern boundaries), these data were extrapolated from the nearest station using the long-term monthly average difference (from Aure and Østensen 1993) between the two locations. This was necessary for 1936–1941 and 1954–1957 at Lista (the most southern station), and for 1945–1968 and 1977–1978 at Ingøy (the most northern station, at the entrance to the Barents Sea). If data from the other intermediate stations were missing, data were interpolated between adjacent stations to the north and south, balanced by the distance between them. This was done for the station Bud (western Norway) during 1936–1946, 1955–1971, and 1994–1995, and for Eggum (Lofoten, northern Norway) in 1972.

A comparison of the two temperature indices reveals that they are positively correlated ($r = 0.67$, $p < 0.0001$, $N = 61$), but variable enough to warrant separate examinations for their abilities to predict recruitment success.

Data analysis

The models used for the analysis were the Ricker model

$$(1) \quad R = SSB \exp(a - bSSB + cT + w)$$

and the Beverton–Holt model

$$(2) \quad R = \left(\frac{aSSB}{b + SSB} \right) \exp(cT + w)$$

where w is the unexplained variance (residuals), a , b , and c are parameters, T is the temperature index (as deviations from the mean), R is recruitment (numbers at age 0 from the VPA), and SSB is in $t \times 10^3$. General discussions of these methods can be found in Hilborn and Walters (1992), among others. The stock–recruitment models were fitted with and without the environmental terms.

The residuals w were checked for autocorrelation $r(k)$ at lag k (in years) using the formulation suggested by Hilborn and Walters (1992, p. 281)

$$(3) \quad r(k) = \left[\frac{\Omega - 1}{\Omega - 1 - k} \right] \frac{\sum_{y=1}^{\Omega-k} \hat{w}_y \hat{w}_{y+k}}{\sum_{y=1}^{\Omega} \hat{w}_y^2}$$

Here, \hat{w} is the residual from any particular year, y , and Ω is the total number of years included. In addition, the Durbin–Watson statistic (D–W) was calculated to check for significant first order serial correlation, and all residuals were tested for normality.

Results

We fitted the models with no term for temperature (Table 1). Clearly, both models explain the data quite well (56% for the Ricker and 57% for the Beverton–Holt model). However, D–W revealed a significant first-order serial correlation for both models ($r(1) = 0.29$, $r(2) = 0.16$, $r(3) = 0.0$), suggesting that there is an additional factor influencing the recruitment success. The residuals from the Ricker model were checked for additional effects from sea temperature on recruitment success (Fig. 2). These plots indicate that both the average Barents Sea temperature and the coastal sea temperature explain some (13% versus 15%, respectively) of the residual variance. If the Barents Sea time series is limited to the years 1936–1996 (as the coastal index), then they become very similar (15%).

The logged recruitment index ($\ln R$) is correlated with the Barents Sea temperature ($r = 0.36$, $p < 0.01$; or $r = 0.47$, $p < 0.01$ for the period 1936–1996), the coastal temperature index ($r = 0.52$, $p < 0.01$), and SSB ($r = 0.57$, $p < 0.01$). Including the sea temperature in the stock–recruitment model increased the r^2 values by 6–9% and revealed highly significant environmental terms (Table 1). Both indices of sea temperature improved the models equally well for the period 1936–1996, whereas recruitment success seems to have been

less associated with the Barents Sea temperature index during 1907–1936. More importantly, including sea temperature in the stock–recruitment model removed the serial correlation in the residuals (Table 1). This is explained by the effect temperature has on the recruitment success and the strong correlation between temperature in adjacent years y and $y + 1$. The first-order autocorrelation coefficients are 0.44 for the Barents Sea temperature and 0.37 for our coastal temperature index, whereas no autocorrelation is evident at higher lags.

To facilitate transparency and repeatability, we use the temperature from the Kola transect for our remaining analyses. The original stock–recruitment data, the corresponding data corrected for the temperature effect, and the values predicted by the model including both stock and environment are presented (Fig. 3). Clearly, correcting for temperature tends to draw the points closer to the fitted line, particularly for high SSB and recruitment success (the upper right corner of Fig. 3).

The long time series allows us to split the data in two groups, so that one group can be used for estimating parameters and the other group for testing the predictions. We removed every second year and fitted an environmental stock–recruitment curve to the remaining data. This model explains the independent data quite well and suggests that the model is a robust representation of the recruitment process in NSS herring (Fig. 1c). Reversing the model gave similar results.

The model can also be applied to study the cause of the collapse of the stock in the late 1960s. The smoothed temperature fluctuations (Fig. 1b) indicate that the climate switched from a warm to a colder period as the herring stock was reduced (Toresen and Østvedt 2000). If this climatic change contributed to the stock collapse by reducing recruitment, this should be evident as a systematic negative deviation from the long-term stock–recruitment relationship in the period when the stock was reduced. Similarly, for the recovery period, a positive deviation from the stock–recruitment curve would be expected. However, no such trends in the residuals are evident (Fig. 4), either for the model with or the model without the temperature term. In addition, the drop in recruitment and SSB in the 1960s is not lagged, thus there is no sign that the climate affected the collapse, at least not through recruitment.

Discussion

Our analysis shows that there is a strong relationship between SSB and recruitment in NSS herring. The inclusion of sea temperature in the stock–recruitment model increased the explanatory ability and removed the autocorrelation from the residual variability. The model is based on a time series that is probably among the most extensive in the history of fisheries science, and appears to be a robust representation of the recruitment dynamics in this stock. The NSS herring underwent a dramatic reduction in spawning stock size, from about 16 million tonnes at its peak level in 1945 to 2000 tonnes at the lowest in 1972 (Toresen and Østvedt 2000). This event revealed a clear effect of spawning stock size on recruitment, an effect that probably would not be clear if the stock had remained at historic levels. Zheng (1996) found significant relationships between spawning biomass and year

Table 1. The stock–recruitment models with and without a term for sea temperature (from 1907 or 1936 to 1996).

Model	Temperature index	a	b	c	$R^2_{adj.}$	N	D–W
Beverton–Holt	None	1.88×10^8 $p = 0.0009$	5139 $p = 0.034$	0	0.57	89	1.43 (1.68)
	Barents Sea (1907–1996)	2.71×10^6 $p = 0.36$	3129 $p = 0.0195$	1.015 $p = 0.0002$	0.63	89	1.71 (1.70)
	Barents Sea (1936–1996)	6.3×10^6 $p = 0.47$	2280 $p = 0.037$	1.30 $p = 0.0002$	0.66	60	2.0 (1.65)
	Coastal (1936–1996)	1.11×10^8 $p = 0.0002$	2189 $p = 0.038$	1.050 $p = 0.0002$	0.66	60	1.94 (1.65)
	Ricker	None	10.36 $p < 0.0001$	8.95×10^{-5} $p = 0.0004$	0	0.56	89
Ricker	Barents Sea (1907–1996)	10.52 $p < 0.0001$	-1.2×10^{-4} $p < 0.0001$	1.030 $p = 0.0002$	0.62	89	1.71 (1.70)
	Barents Sea (1936–1996)	565 $p < 0.0001$	-1.26×10^{-4} $p < 0.0001$	1.22 $p = 0.0005$	0.65	60	1.89 (1.65)
	Coastal (1936–1996)	10.50 $p < 0.0001$	-1.2×10^{-4} $p < 0.0001$	0.960 $p = 0.0006$	0.64	60	1.80 (1.65)

Note: The Ricker model was fitted using $\ln(R) = a - bSSB + \ln(SSB) + cT$, and the Beverton–Holt model with $\ln(R) = \ln(aSSB/(b + SSB)) + cT$ (Hilborn and Walters 1992). D–W, Durbin–Watson statistic with the corresponding significance threshold (at $p = 0.05$) in parentheses (Hamilton 1992); N , number of years available for each analysis; $R^2_{adj.}$, R^2 adjusted.

class strength in only about half of 19 different herring stocks. It appears as if a very large reduction in spawning biomass is required to expose the downside of the stock–recruitment curve in herring. We think the extreme fluctuations in spawning biomass of NSS herring have generated a quite reliable stock–recruitment model.

The study by Fossum (1996) indicated that the match between first feeding of the larvae and the abundance of prey affected the survival of the early herring larvae, in particular, the 1993 year class experienced a favourable prey situation. Some of the remaining unexplained variance in our model may be due to variations in prey availability, but the available data on prey abundance and overlap with first feeding larvae is too scarce to be included in the stock–recruitment models.

The NSS herring matures at age 3–5 (Toresen and Østvedt 2000), so the variability of recruitment also depends on the conditions for the juveniles in the Barents Sea. Among the factors influencing the juvenile survival are the predation pressure from cod, temperature, and the prey availability in the adolescent period (Hamre and Hatlebakk 1998). Still, there is a reasonably good correlation between the abundance of 0-group and the age-3 group in the VPA data ($r = 0.49$, $p < 0.01$), and a full treatment of the survival to age 3 is beyond the scope of this paper.

The models revealed significant terms for density dependence in the recruitment success. The mechanism behind this is not clear, but could be related to a limiting number of suitable spawning areas. Although the Norwegian coast is long, NSS herring deposit their eggs quite patchily, and at specific depths, bottom substrata, and current conditions (Runnstrøm 1941). Sometimes thick layers of eggs (up to 1 m thick) have been observed (Runnstrøm 1941), and several authors have pointed out that this will increase the mortality of the eggs (Runnstrøm 1941; Hourston and Rosental 1981; Zheng 1996). It is therefore not unlikely that a large spawning stock size and a massive egg deposition could cause increased egg mortality rates at the preferred spawning grounds.

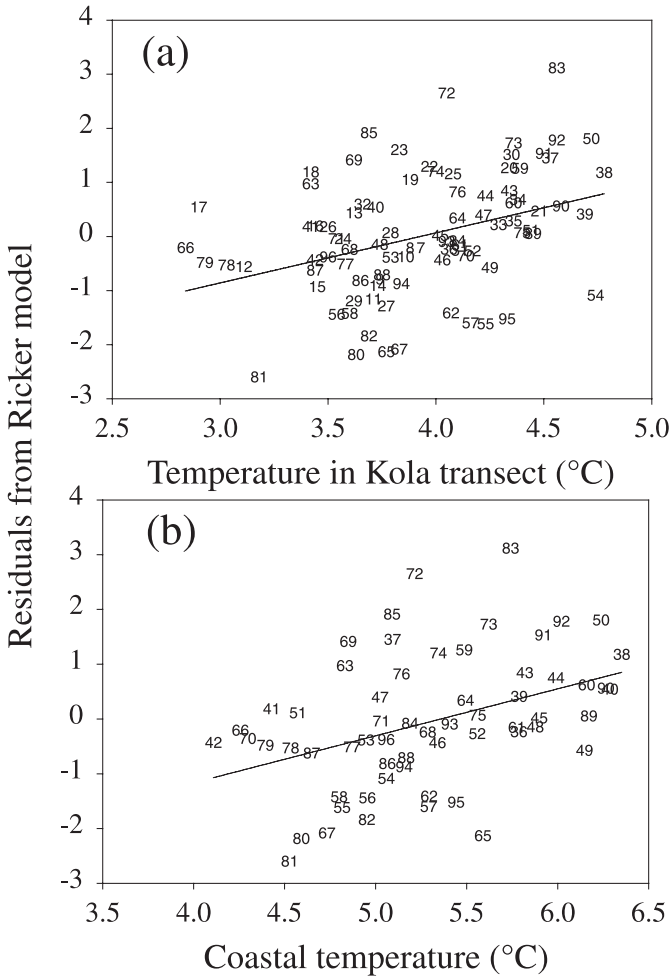
Several authors (Ottersen and Sundby 1995; Ottersen and Loeng 2000; Toresen and Østvedt 2000) have noted the importance of sea temperature and climate for the recruitment of fish in the Barents Sea. Ottersen and Loeng (2000) found that the abundance of 0-group individuals of cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), and herring were positively correlated with their length. They also found that the average 0-group individual was longer in warm years compared with cold years. This suggests that the improved recruitment success with temperature is related to enhanced growth during the early stages. The positive effect on growth from increased temperature given sufficient food is well known from models and rearing experiments of herring larvae (Fiksen and Folkvord 1999).

It has been a general consensus that the intense herring fisheries following the invention of the power block in the early 1960s induced the collapse of the stock (Dragesund et al. 1980). However, the long-term drop in temperature that coincided with the stock decline has raised some questions on how severe the decline of the stock would have been if the climate were favourable during this period (Toresen and Østvedt 2000). The present results suggest that the climate (temperature) in fact played a minor role in the collapse. We found no trend in the residuals from the stock–recruitment model, and conclude that there was no recruitment-driven reduction in the stock biomass for NSS herring. This interpretation is also supported from the simultaneous drop in the SSB and the recruitment, i.e., there is no temporal lag in the reduction of the SSB with recruitment.

Potential effects from the dependence of SSB on recruitment success

To what extent is the predicted stock–recruitment relationship of NSS herring a result of the dependence of SSB on preceding recruitment success? According to Myers and Barrowman (1996), the erroneous explanatory effect of SSB on recruitment is given by r^{2m} , where r is autocorrelation in the time series of recruitment and m is age at maturity. For

Fig. 2. The unexplained variances from the Ricker model without temperature in Table 1 versus (a) the average annual temperature in the Kola transect and (b) our temperature index. The fitted lines are given by (a) $w = -3.66 + 0.93T$ ($r^2 = 0.13$, $p < 0.001$, $n = 89$) for the Kola index and (b) $w = -4.6 + 0.86T$ ($r^2 = 0.15$, $p = 0.0012$, $n = 60$) for the coastal temperature index.



NSS herring, we estimated the first-order autocorrelation in recruitment (before correcting for the influence of temperature) to 0.272, and since age at maturity is four years, the “false” explanatory element from SSB should be negligible. However, there are examples where this effect causes difficulties, such as in Baltic cod where a spurious SSB– R relationship is evident (Sparholt 1996). The problem is detected from strong autocorrelation in the residuals of the fitted curve, but since there is no significant autocorrelation in our data (after correction for temperature), we do not expect this “chicken or egg” effect to be strong in NSS herring.

To illustrate how recruitment-driven fluctuations in SSB might generate a stock–recruitment curve in NSS herring, we have performed some simulations with a simple age-structured population model. Let $N_{a,y}$ be the number of individuals of age a in year y , and

$$N_{a,y} = N_{a-1,y-1} \exp(-\mu), \quad \text{SSB}_y = \sum_{a=m}^{15} N_{a,y}, \quad R_y = N_{0,y}$$

Fig. 3. This figure shows the observed values of $\ln(\text{SSB})$ (spawning stock biomass) versus $\ln(R)$ (recruitment) at each SSB after correcting for the effect of temperature ($\ln R - cT$, where c is from Table 1) in the Barents Sea (●), the predicted recruitment from the Ricker model including the temperature (+), and the fitted Ricker model with no environmental term (line).

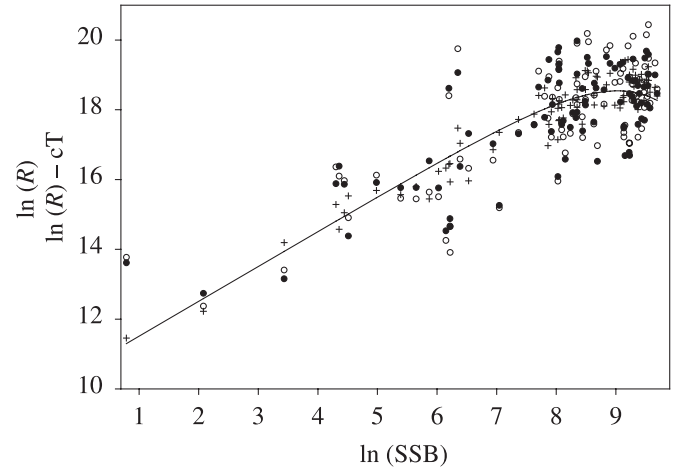
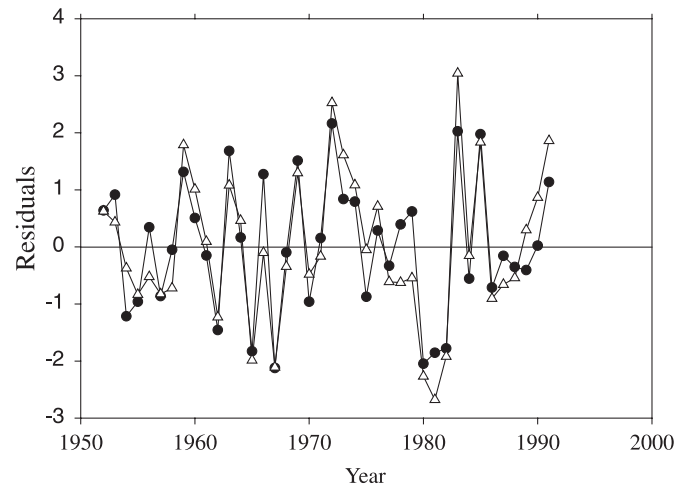
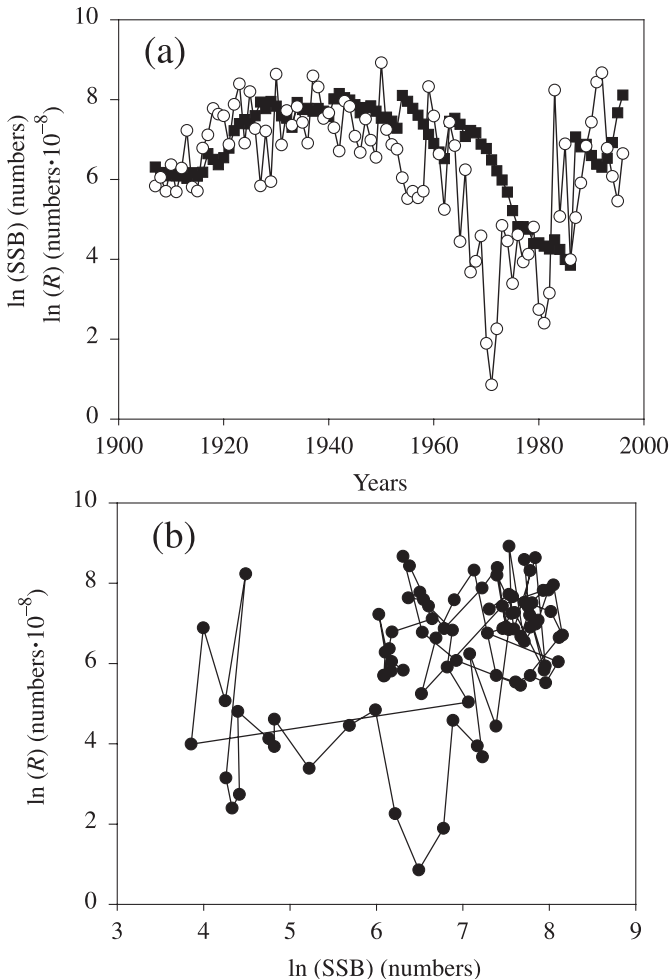


Fig. 4. The residuals of the Ricker model with (●) and without (△) the Barents Sea temperature term for the period of the collapse and recovery of the stock. The spawning stock biomass (SSB) reached its minimum in 1971, and there are no systematic trends in the residuals that can explain the collapse or the recovery.



where m is the age at maturation (4 years), μ is the annual mortality rate (0.3), and the maximum age is 15. Note that recruitment in year y varies independently of SSB, and that we assume SSB to be proportional to mature population abundance $N_{a>m}$ (i.e., no growth after maturity). We then feed this model with the recruitment time series of NSS herring back to 1907, and obtain a corresponding time series of SSB (Fig. 5a) and a (spurious) stock–recruitment relationship (Fig. 5b). Fitting Beverton–Holt or Ricker curves to the modelled SSB– R data in Fig. 5b did not yield significant values for the parameters a or b , whereas the linear regression $\ln(R) = a + b\ln(\text{SSB})$ (i.e., the Cushing model) gave b significantly different from zero ($r^2 = 0.22$, $p < 0.0001$). These regressions all reveal strongly autocorrelated residuals ($D-W = 0.85$), and the statistical analysis is therefore invali-

Fig. 5. Predicted spawning stock biomass (SSB) from a simple age-structured model where R is independent of SSB. (a) The observed time series of R_y (recruitment in year y) in NSS herring (○) and the modelled SSB _{y} (■). (b) The combinations of (SSB _{y} , R_y) emerging from the simulations.



dated. We consider it quite unlikely that recruitment-driven variations in SSB could generate our stock–recruitment relationship without significant autocorrelation in the residuals. If we double the mortality rate ($\mu = 0.6$) from 1965 to 1973 to mimic the high fishing pressure during this period, the artificial Cushing SSB– R relationship improves ($r^2 = 0.42$, $D-W = 1.15$), but is still far from the critical Durbin–Watson value of 1.68 ($N = 89$, $p = 0.05$; Hamilton 1992). In addition, we performed a number of similar simulations with stochastic (lognormally distributed deviates) and autocorrelated time series of recruitment, and found it quite impossible to generate significant stock–recruitment relationships even with autocorrelation coefficients >0.9 ($m = 4$ years). This is in agreement with the equation from Myers and Barrowman (1996), but a more thorough treatment of the issue is warranted.

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