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Predicting density-dependent somatic growth in Norwegian spring-spawning herring

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Density-dependent growth, which might influence the effects of fisheries on a population, is often ignored when management strategies are evaluated, mainly due to a lack of appropriate models readily available to be implemented. To improve on this, we investigated if somatic growth in Norwegian spring-spawning herring (*Clupea harengus*) depends on cohort density using a formulation of the von Bertalanffy growth function on cohorts from 1921 to 2014 and found a significant negative correlation between estimated asymptotic length and density. This clearly indicates density-dependent effects on growth, and we propose a model that can be used to predict the size-at-age of Norwegian spring-spawning herring as a function of herring density (the abundance of two successive cohorts) in short-term predictions of catch advice, and in Management strategy evaluations, including estimation of their reference points such as F_{MSY}.

Keywords: cohort effects, density dependence, herring, length-at-age, von Bertalanffy growth function.

Introduction

Density-dependent effects on vital rates such as somatic growth and reproduction have been documented in fish populations, although density-independent environmental factors such as temperature and food availability also play an important role (Lorenzen and Enberg, 2002); Brunel and Dickey-Collas, 2010; Cormon *et al.*, 2016; Zimmermann *et al.*, 2018; Landa *et al.*, 2019, Claireaux *et al.*, 2022). It has been shown that temporal variability in growth caused by density-independent environmental variability is an important contributor to population fluctuations for some species (Stawitz and Essington, 2019), which might cause bias if not accounted for (Stawitz *et al.*, 2019; Correra *et al.*, 2021). If variability in growth is density-dependent, caused by competition for limiting resources such as food, it can also influence the relationship between exploitation, stock biomass, and yield (Lorenzen, 2016), and knowledge about such effects is therefore important for management. Density-dependent effects on reproduction are often included in management strategy evaluations (MSE) through stock-recruitment relationships (e.g. ICES, 2018). Density-dependent effects on somatic growth are, however, largely ignored despite their potential importance for management (Lorenzen, 2016; van Gemert and Andersen, 2018; Ahrens *et al.*, 2020; Sparholt *et al.*, 2020).

Ignoring density-dependent growth can influence short-term predictions of catch advice since assumptions of weight-at-age both in catch and stock for the advisory year must be made (Jaworski, 2011). Presently, average weight-at-age for a period preceding the advisory year are typically used in the predictions, and this does not allow for the implementation of cohort specific growth, which might be influenced by density-dependent effects. Variable stock density can lead to wrong predictions of weight-at-age, which in the worst case may lead to a catch advice that is unsustainable. The scientific advice on annual catches [e.g. from the International Council for the Exploration of the Seas (ICES)] are often based on a fishing mortality, which produces the maximum sustainable yield (F_{MSY}) in the long term, while still being precautionary. In the estimation of F_{MSY}, long-term stochastic simulations of stock development under different fishing pressures are conducted, but in the absence of scientific evidence or appropriate mechanistic models for including density-dependent growth, individual somatic growth is frequently assumed independent of stock size and time invariant (Sparholt *et al.*, 2020). Accounting for density-dependent growth would improve management both in the short and in the long term provided predictions of growth are sufficiently reliable.

Norwegian spring-spawning herring (NSSH, *Clupea harengus*) is a highly important stock in the northeast Atlantic both ecologically and economically (Holst *et al.*, 2004). It is widely distributed in the Norwegian Sea (adults) and the Barents Sea (juveniles) with only limited spatial overlap between adults and juveniles (Dragesund *et al.*, 1980). It is therefore likely that competition between adults and juveniles is weaker than competition among individuals of a cohort, and it has therefore been proposed to use cohort size as a measure of density when studying density-dependent effects on growth (Toresen, 1990). There is, however, a considerable spatial overlap between successive cohorts (Dragesund *et al.*, 1980), potentially influencing the level of competition experienced by individuals within a cohort. Because of the wide and variable distribution of both juveniles and adults, confounding effects of environmental factors such as temperature and feeding conditions on

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growth should also be considered (Toresen, 1990; Ottersen and Loeng, 2000; Husebø *et al.*, 2009).

The reference points (including F_{MSY}) used in the management of NSSH were estimated in 2018 and following this, an MSE was conducted. It was noted that "in the data there is evidence that individual weight-at-age decreases with density, hence ignoring this effect will artificially create too high SSB at higher stock sizes and too low SSB at low stock sizes" (ICES, 2018). However, although Engelhard and Heino (2004) found significant differences in length-at-age between periods of low and high stock sizes of NSSH (1935–2000), ICES (2018) concluded that density-dependent effects on growth were not documented well enough in published literature to be implemented in the simulations. Instead, a fixed weight-at-age was assumed. If this assumption is wrong and growth is negatively related to stock size as indicated in Engelhard and Heino (2004), F_{MSY} might be underestimated (Lorenzen, 2016; Horbowy and Luzenczyk, 2016; van Gemert and Andersen, 2018; Sparholt *et al.*, 2020), and, consequently, the fishing pressure applied in the management strategy, too low.

NSSH is a data-rich stock. The time series of stock sizes extend back to 1907 (Toresen and Østvedt, 2000) and individual length/weight-at-age data are available back to 1935. The time series include a wide range of stocks and cohort sizes from high in the 1940's to a collapsed state in the 1970's, followed by a recovery (Toresen and Østvedt, 2000; Gullestad *et al.*, 2018). This long time series and wide range of stock densities make NSSH well-suited for studies of density-dependent growth. A recent reconstruction of the time series of NSSH stock size (ICES, 2018) has, however, revealed large discrepancies in estimated stock size compared to previously constructed time series (Toresen and Østvedt, 2000; ICES, 2007), and our present study will use the revised stock size time-series estimated with the contemporary state-of-the-art assessment method (ICES, 2018).

The aims of this study are first to investigate if cohort somatic growth in NSSH is dependent on herring density measured as the abundance of the cohort and successive cohorts. Second, we aim to formulate a model where length growth depends on density. The proposed model can be implemented in future short-term predictions of catch advice and in MSE and estimations of reference points for NSSH. The growth model will be based on the von Bertalanffy growth function (VBGF; von Bertalanffy, 1957), which is the most used function for modelling fish growth (van Poorten and Walters, 2016). The reason for using length and not weight in the model is to avoid complications caused by annual and inter-annual variability in condition factor (dos Santos Schmidt *et al.*, 2020). Predicted length-at-age can later be converted to weight-at-age using appropriate length–weight relationships. We will also explore alternative models where other factors expected to influence growth such as temperature are included.

Material and methods

Herring biological data

Data based on samples of NSSH individuals from both commercial catches and scientific cruises in the period 1935–2019 were extracted from the Institute of Marine Research (IMR) database (https://doi.org/10.21335/NMDC-496562593). The extracted dataset includes data on cohorts produced in the years 1921–2014. Relevant information about the sampled individuals includes geographical position, time of capture, age (determined based on scales or otoliths), length, and weight. Juvenile NSSH reside in the Barents Sea, while adults migrate to the Norwegian Sea. However, adults of the much smaller population of White Sea herring (*Clupea pallasii marisalbi*) reside in the eastern Barents Sea (Lajus *et al.*, 2007) and might occur in samples from that area. Juveniles sampled in the Barents Sea will be dominated by the much more numerous NSSH, but to avoid including adult White Sea herring in the analysis, adult herring sampled in the Barents Sea were not used. We used the following criteria for including sampled individuals in the analyses: a) juveniles (i.e. ages 1–3); all length-measured individuals in the dataset were used. b) adults (i.e. ages 4+); (1) season of the year between January 1 and April 30 (before the feeding period), (2) samples west of 23oE to avoid mixing with White Sea herring in the Barents Sea, (3) length measured.. In addition, if the number of individuals in a given age group and year was <10, then these were excluded as the precision of mean length and mean age then are considered too low. A total of 394690 individual herring, fitting the chosen criteria, were included in the analyses. The individuals had been sampled along the Norwegian coast, in the Norwegian Sea and in the Barents Sea (Figure 1). In addition to the main nursery areas in the Barents Sea, there are also Fjord nurseries along the Norwegian coast, but the largest year classes originate from the Barents Sea (Holst and Slotte, 1998), and size-at-age of juveniles has been shown to increase southwards (Husebø *et al.*, 2007). It should be noted that the material used in the present study includes herring at ages 1–3 from both the Barents Sea and Fjord nurseries, yet with interannual variability in proportions sampled north and south of 69°N following year class abundance, being more frequent in the north for large year classes (Supplementary Figure S1). It is interpreted that this variability in general follows the overall structure and distribution of the stock at early ages, resulting in representative samples for the purpose of this study.

Time series of NSSH abundance

There are several published time-series of NSSH abundance spanning various time periods from 1907 (Toresen and Østvedt, 2000; Tjelmeland and Lindstrøm, 2005; ICES, 2007; ICES, 2018; Toresen *et al.*, 2019), and discrepancies between time series have been described by ICES (2018). In this study, we used the time series published in ICES (2018). This time-series was constructed using the contemporary state-of-the-art assessment model (XSAM) adopted as the stock assessment model for NSSH by ICES (ICES, 2022). The model is based on a state-space model and structural time-series models for fish stock assessment and is described by Aanes (2016). The model framework builds on well-known statistical models but offers the possibility to utilize prior knowledge about sampling errors entering the observation model. For NSSH, the model uses catch-at-age data and survey indices from 1988 and onwards. In the period before 1988, the only data source is catch-at-age. From the time series, we selected two indicators of density: abundance of the explored cohort at age 3, $N_{(3)}$, and the sum of the abundance of the explored cohort at age 3 and the abundance of its preceding cohort at age 4, $N_{(3)} + N_{(4)}$. We chose not to include more than two cohorts in the indicator of abundance since there is considerable spatial segregation between different age groups of NSSH (Dragesund et al., 1980; Eliassen *et al.*, 2021). Numbers at age from the XSAM time-series are found in Supplementary Table S3.

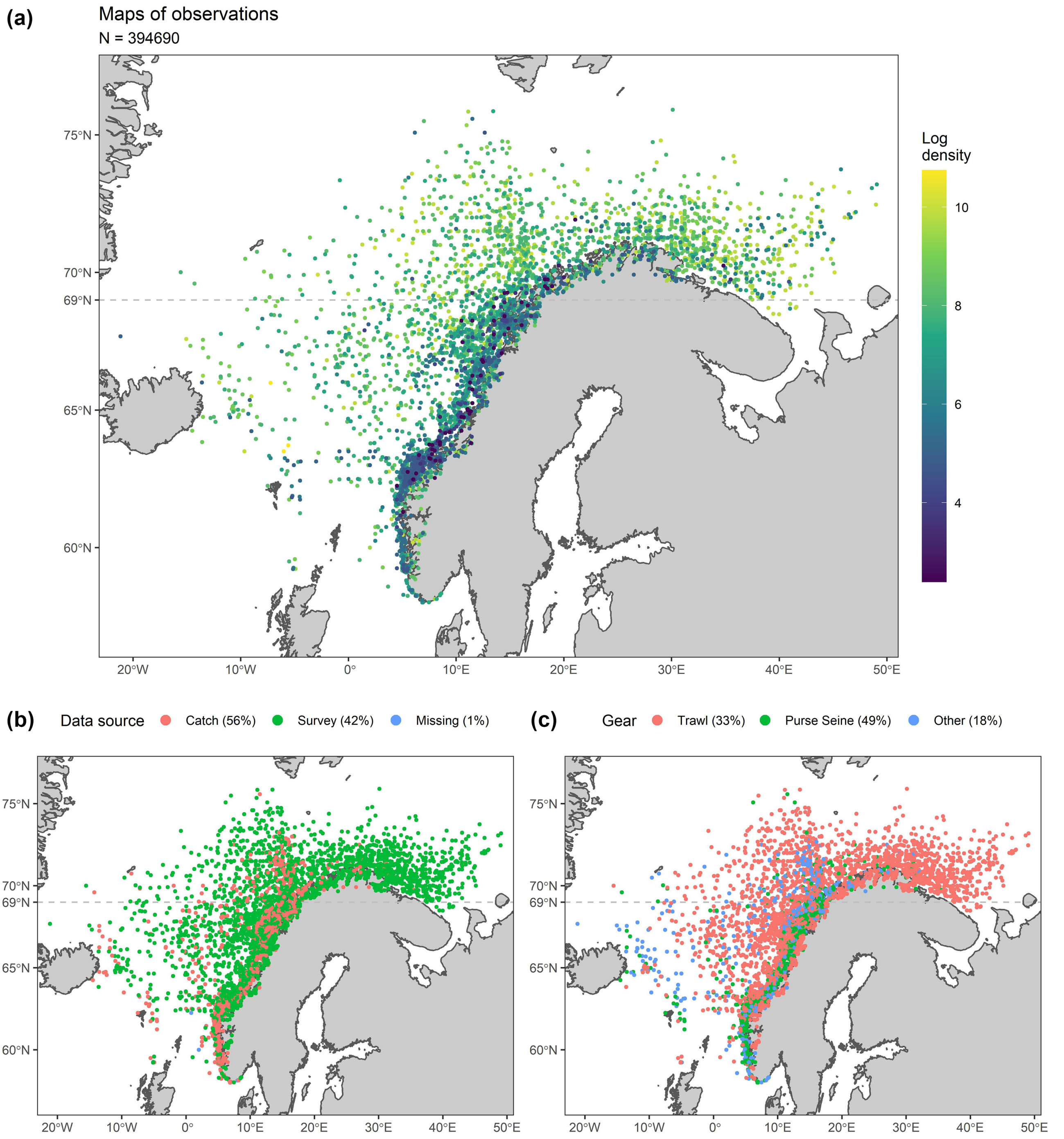

Figure 1. Maps showing where the 394690 observations are located with the colours showing (a) log cohort size-at-age 3 (log $N_{(3)}$) of the cohort associated with the individual observation, (b) how the observation was sampled (from catch, survey, or unknown), and (c) which type of gear the individual fish was caught by. Note that points are overlapping and in dense areas the order in which the points are plotted may influence the overall impression. They are ordered so that the smaller cohorts are plotted on top. Note that there are very few individuals from small cohorts caught in the Barents Sea.

Temperature time-series

We used temperature data from the Kola section in the Barents Sea (Karsakov, 2009; Karsakov *et al.*, 2019) for which data exist for the whole period we are analysing. Based on the raw temperature data in the upper 200 m, we calculate the average temperature for each sampled individual during the summer months (June–August) for ages 0–3. For individuals sampled younger than 3 years old, we only average over the years they were alive (see Equation (S1) in supplementary material for further details).

Data analyses of cohort specific growth

The von Bertalanffy growth function (VBGF; von Bertalanffy, 1957) is given by

$$L(a) = \ell_\infty \left(1 - e^{-K(a - t_0)}\right),$$

where $L(a)$ is the expected length of a fish at age a, and conventionally ℓ_∞ is the asymptotic length, K is the growth rate, and t_0 is the age at length zero. We adopt the VBGF to describe cohort-specific growth for the cohorts 1921–2014. We first estimated one von Bertalanffy growth curve for each cohort separately. Due to limited data for some cohorts, we were not able to estimate all three VBGF parameters for each cohort. We therefore estimated K and t_0 for all cohorts together and kept them fixed when estimates of ℓ_∞ per cohort were made. For parameter estimation, a weighted maximum likelihood was used, where the likelihood contribution from each age group is equal. This is to avoid too much weight on young fish when observations of older ages are scarce. The weighted likelihood was implemented using the template model builder (TMB, Kristensen et. al, 2016) package for the statistical software R (R Core Team, 2020, version 4.0.3) assuming independent Gaussian residuals. According to Lorenzen (2016), variability in food availability such as caused by density-dependent effects should conceptually be reflected in the asymptotic size, ℓ_∞, and not the growth rate, K, of the VBGF. Therefore, we explored how much of the variability in cohort specific ℓ_∞ could be explained by variability in density by linear regression of cohort specific ℓ_∞ against herring density. A Pearson correlation t–test is performed.

Prediction model

The following non-linear model for predicted length-at-age, $L(a)$, is a parametrization of the VBGF, where the asymptotic length, ℓ_∞, depends linearly on fish density. Let Y_i be the length of individual fish i, of age a_i, and $L(a_i, N_i)$ be its expected length. N_i refers to the density experienced by the i^{th} fish. Further, let n be the total number of individual fish in our sample and N_{median} the median fish density. Then the model can be formulated as

$$\begin{aligned} Y_i &= L(a_i, N_i) + Z_i, \qquad i = 1, 2, \ldots, n, \\ L(a, N) &= \ell_\infty(N)(1 - e^{-K(a-t_0)}), \\ \ell_\infty(N) &= \ell_0^\infty + \ell_1^\infty(\log N - \log N_{median}), \end{aligned} \tag{1}$$

where the residuals, $\{Z_i\}_{i=1,\ldots,n}$, are independent normally distributed with age-dependent variance, $\sigma_{a_i}^2$. The expected length $L(a, N)$ follows a VBGF with parameters ℓ_0^∞, ℓ_1^∞, K, and t_0, where the former two describe the asymptotic length dynamics. In particular, ℓ_0^∞ is the asymptotic length of a fish growing up at median herring density; N_{median}. We assume a linear relationship between asymptotic length and herring density, and ℓ_1^∞ is the parameter describing this. We will explore the density, N, being either $N_{(3)}$ or $N_{(3)} + N_{(4)}$.

The parameters of model (1), ℓ_0^∞, ℓ_1^∞, K, t_0, $\sigma_1, \sigma_2, \ldots, \sigma_{A-1}$, and σ_A, where A is the maximum age, are estimated using maximum likelihood, assuming independence between each individual fish. Model selection, which mainly involves choosing which age groups should have the same variance, is based on Akaike's information criterium (AIC). In terms of parameter restrictions, we require $\sigma_a > 0$ for all a. The maximum-likelihood estimation is implemented using TMB, which uses automatic differentiation to calculate the gradient for the optimization.

Exploratory models

Alternative models were explored. In (1), ℓ_∞ is a function of N (either $N_{(3)}$ or $N_{(3)} + N_{(4)}$), but for the exploratory models, we let the growth rate K depend on a covariate in the same manner. A total of seven modelling scenarios were considered, including those described above. For the other scenarios, we have a model where ℓ_∞ depended on herring density and K on sample location (latitude), and a model where ℓ_∞ depended on herring density and K on temperature. We also included two scenarios where ℓ_∞ depended on herring density and t_0 was fixed to 0. In addition, possible effects of variable fishing gear used in the sampling were explored. The results from these explorations and more details on the models can be found in the Supplementary material.

Results

Cohort size as estimated by the stock assessment model (XSAM) has fluctuated considerably (Figure 2A). In the early part of the time series, before 1950, cohort size was mostly large to average with some inter-annual variability. In the 1960s, the stock collapsed and during the 1970s only very small cohorts were produced. In the late part of the time series cohort size has again fluctuated between large, average, and small cohorts, but never as small as during the collapse period. Based on the empirical analysis, growth for each cohort, as estimated by ℓ_∞, has also fluctuated (Figures 2B and 3), and we found a significant ($p < 0.05$) negative correlation between estimated asymptotic length (ℓ_∞) and both $\log(N_{(3)})$ and $\log(N_{(3)} + N_{(4)})$ (Figure 4). The estimated correlations with standard errors are −0.66 (0.07) and −0.69 (0.07), respectively. Cohorts produced during the collapse period in the 1970s had high ℓ_∞ (Figure 2) compared to cohorts before and after the collapse which had variable but generally lower ℓ_∞.

Growth curves predicted by the VBGF model (Equation 1), where asymptotic length (ℓ_∞) was dependent on herring density, clearly showed that the model predicted increased asymptotic length (ℓ_∞) at lower densities, as expected (Figure 5). Based on AIC, the best model was the one with $N_{(3)} + N_{(4)}$ as indicator of density (Table 1), with 1 *SD* parameter per age group and this is the model we continue with. The model parameter estimates from the AIC-selected model are found in Table 2, and the model estimated relationship between asymptotic length (ℓ_∞) and logarithmic density (assuming a linear relationship) for this model is shown in Figure 6. Modelled asymptotic length (ℓ_∞) varies between 34.5 cm for high densities and 42 cm for the lowest densities. Asymptotic length (ℓ_∞) at median density (ℓ_0^∞) is 36.48 cm. In the model, the other VBGF parameter estimates are $t_0 = -0.114$ and $K = 0.349$. Figure 5 also shows the observed average length-at-age for the cohorts included in the analyses. There is considerable variability in observed average length-at-age, but it appears that the model predicts length-at-age relatively well. There is, however, a tendency of the model to predict higher than observed length-at-age for some ages. A more in-depth residual analysis can be found in the supplementary material (Figures S2 and S3). When relating the cohort specific temperature index to the model residuals (Figure 7), we did not find any clear patterns which suggests there is no strong temperature influence.

Among the exploratory scenarios (S4–S7), the lowest AIC was found when ℓ_∞ was dependent on $N_{(3)} + N_{(4)}$ and K on location (latitude). Having ℓ_∞ depending on $N_{(3)} + N_{(4)}$ and K on temperature also produced a better AIC than the selected model. Fixing t_0, however, gave a higher AIC. The details

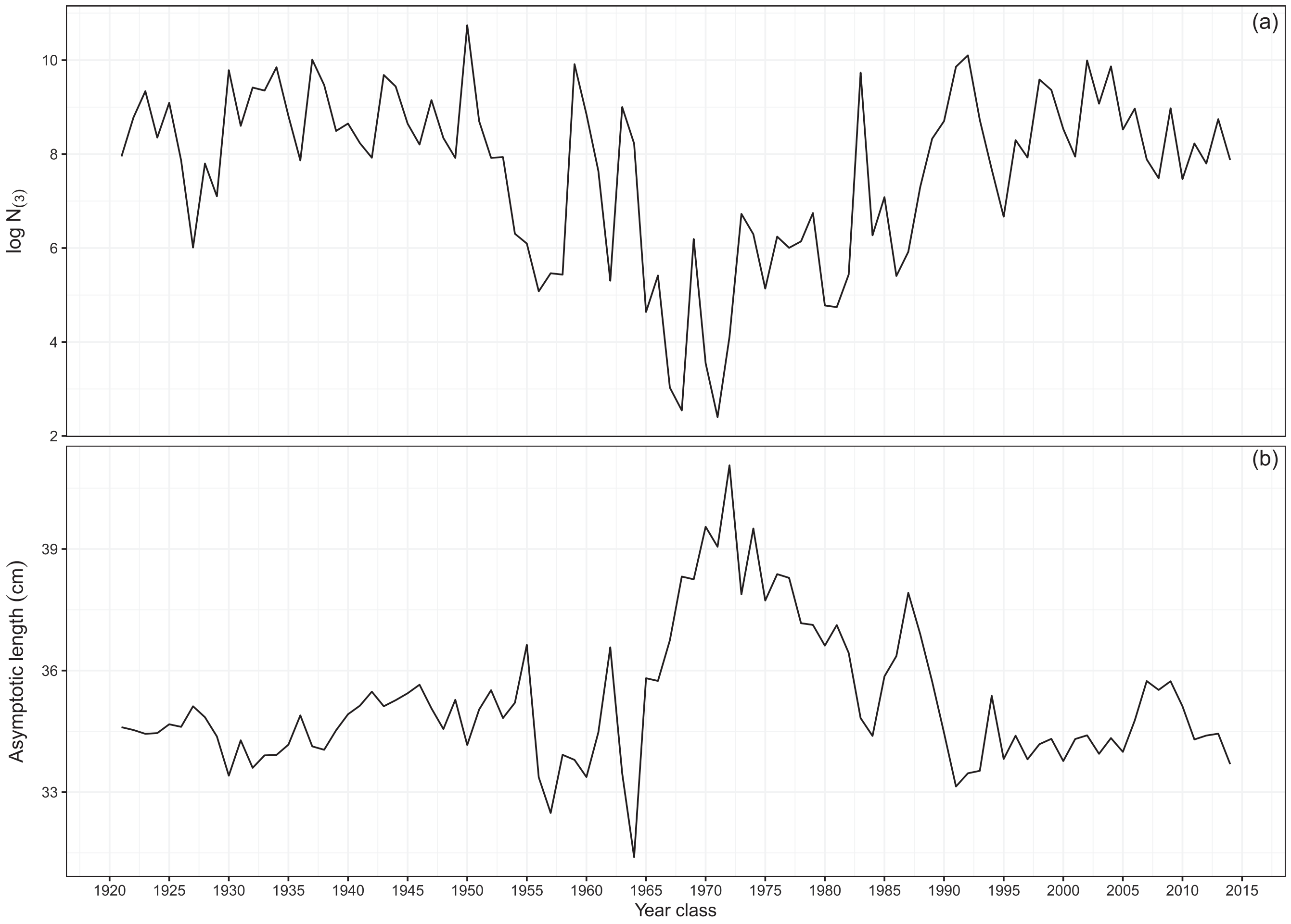

Figure 2. Time series of (a) logarithmic cohort size-at-age 3 and (b) asymptotic length (ℓ_∞) from VBGF estimated from historical data for each year class.

from the different model fits can be found in Supplementary Table S1.

Discussion

We investigated the effect of population density (represented by the abundance of a cohort and of two successive cohorts) on somatic growth of NSSH for cohorts produced from 1921 to 2014 with the aim of formulating a model to predict size-at-age as a function of herring density in management-related processes. In the data, we found a significant negative relationship between estimated asymptotic length in the VBGF (von Bertalanffy, 1957) and herring density. Individuals experiencing high densities had a lower length-at-age and grew towards a lower asymptotic length than individuals experiencing low densities. Particularly, during the collapse period in the 1970s, high levels of asymptotic length ranging up to 40 cm for some cohorts, were found. This is an expected result if higher density leads to increased competition for food. Two indicators of density were tested and the best predictive model (based on AIC) was the one where density was represented by the size of two successive cohorts indicating that growth is influenced by competition not only among individuals within a cohort but also among individuals of successive cohorts. Fish density, however, does not explain all the variability in the data, and other factors will be discussed below.

Support for density-dependent growth has been equivocal in the literature and so also for NSSH. Huse *et al.*, (2012) summarized the results from the INFERNO project, which studied interactions between major fish populations in the Norwegian Sea. They concluded that although growth is influenced by many factors, density-dependent growth caused by both intraspecific and interspecific competition did occur. For NSSH, the effects of interspecific competition with the other species (mackerel and blue whiting) were found to be smaller than the intraspecific competition. Husebø *et al.*, (2007) found that part of the variability in growth of juvenile NSSH in fjord nursery areas could be explained by density-dependent effects. Brunel and Dickey-Collas (2010), however, found contrasting support for density-dependent growth in weight among 15 herring populations in the northeast Atlantic, and no significant relationship between asymptotic weight and population density in NSSH. They did, however, use weight-at-age data from ICES stock assessment reports and those data are poorly documented and difficult to reproduce. Zimmerman *et al.*, (2018) investigated density dependence in 70 populations in the northeast Atlantic and found that although density dependence in recruitment was generally stronger than density dependence in somatic growth, the latter was not uncommon. In several of the populations they investigated, density dependence in growth was comparable to or stronger than density dependence in recruitment, but no significant effect on growth

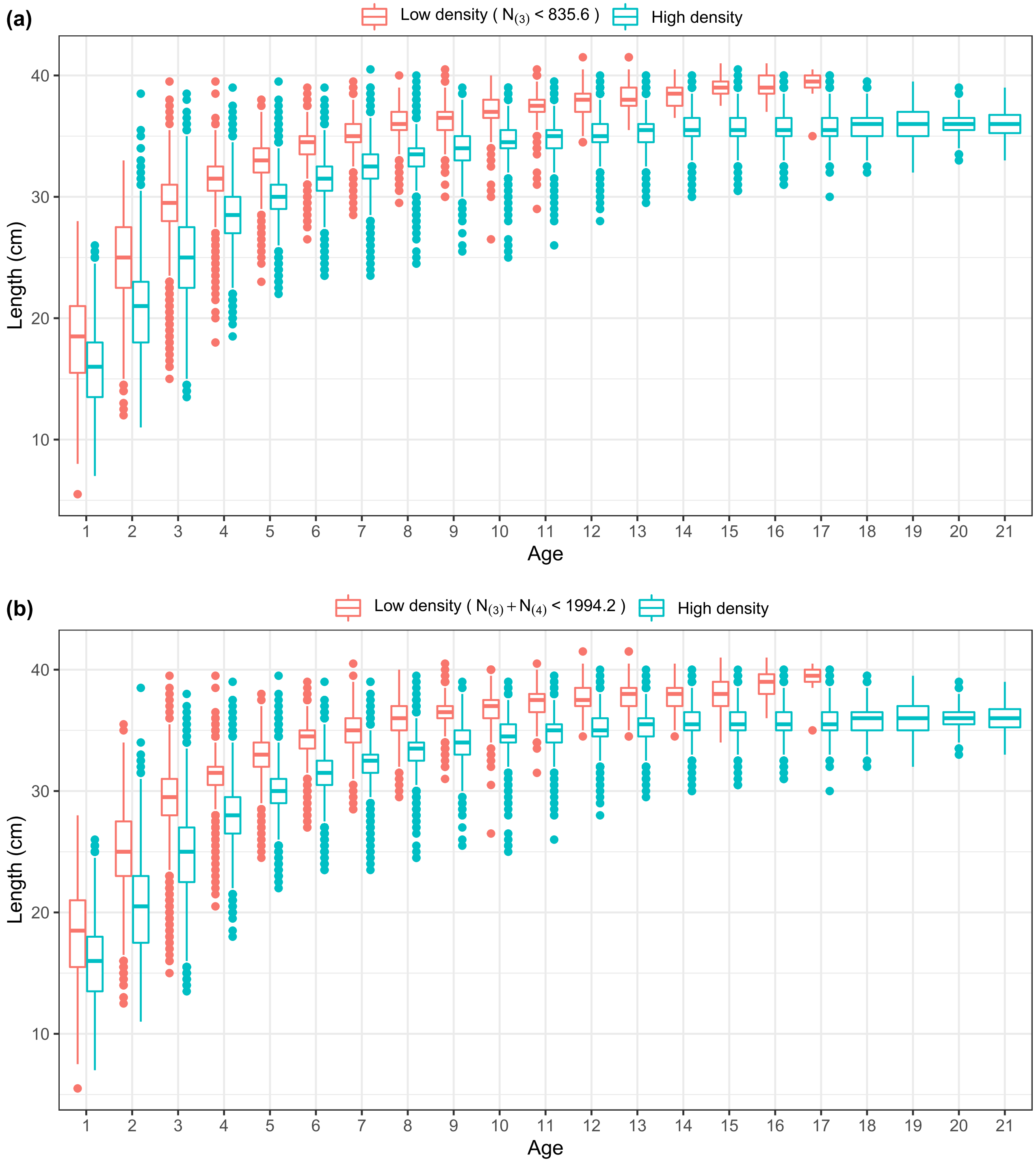

Figure 3. Boxplots of length-at-age for cohorts with different densities. In (a) low density is defined as $N_{(3)} < 835.6$ and in (b) as $N_{(3)} + N_{(4)} < 1994.2$ million individuals. High density is defined as not low. These thresholds are based on the lower quartiles of the respective density measures in year classes from 1921 to 2014.

was found for NSSH. Lorenzen and Enberg (2002) found significant density-dependent growth at the adult stage in 9 out of 16 analysed populations (both freshwater and marine) and concluded that the among-population relationship they found between asymptotic length and population density could be indicative of density-dependent growth when population specific data are not available. In a recent review, Lorenzen (2016) concluded that a lack of focus on growth plasticity has in some cases led to sub-optimal management of fish stocks, and that key drivers should be investigated on a stock specific basis and not be based on global averages.

NSSH is a population that due to its large span in population/cohort size is well suited to study effects of variable density on vital rates such as growth, but it is important to carefully consider how the functional relationship between density and growth is formulated and which indicator for density to use (Lorenzen, 2016). NSSH is a highly migratory stock where the young individuals (1–3 year old’s) have very little

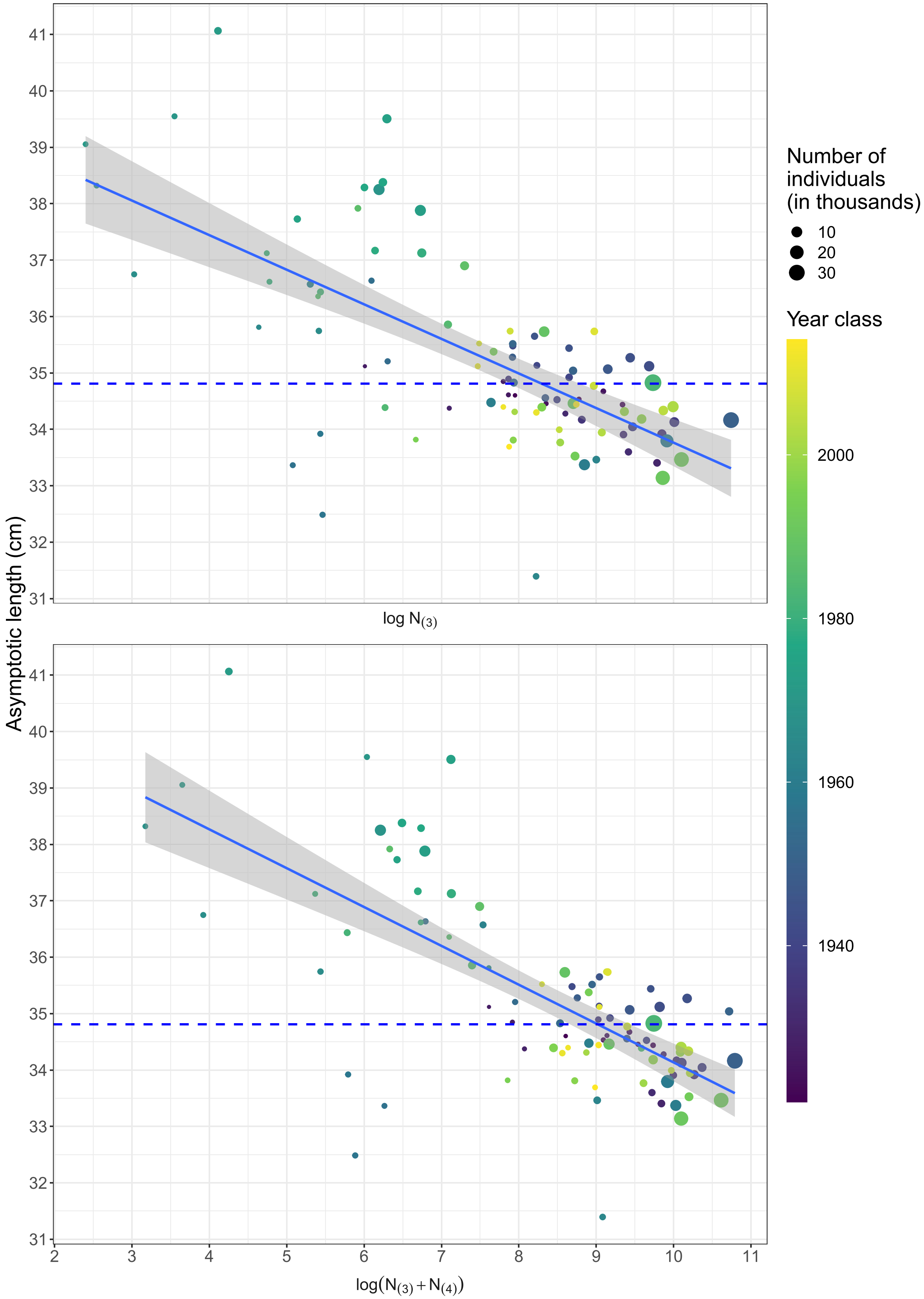

Figure 4. Estimated ℓ_∞ from VBGF against logarithm of the two density measures for each year class. The blue line results from a linear regression of the points (with 95% confidence bands). The blue dashed line shows ℓ_∞ when estimated for all cohorts together.

overlap with the adult part of the population (Dragesund *et al.*, 1980). Even after maturity the old and young fraction of the population might be spatially segregated during the feeding period (Eliassen *et al.*, 2021). In such cases, numerical abundance of a cohort is probably the best predictor for density-dependent growth (Lorenzen, 2016), and we followed this approach by using indicators of density related to the abundance of a cohort and to the abundance of two successive cohorts. Furthermore, we based our analysis on estimates of cohort abundance from the contemporary state-of-the-art assessment model and on individual length-at-age data from the huge amount of NSSH data sampled by IMR since 1935, and not the partly undocumented average values of weight-at-age published in ICES assessment reports, which has been commonly used (e.g. Brunel and Dickey-Collas, 2010;

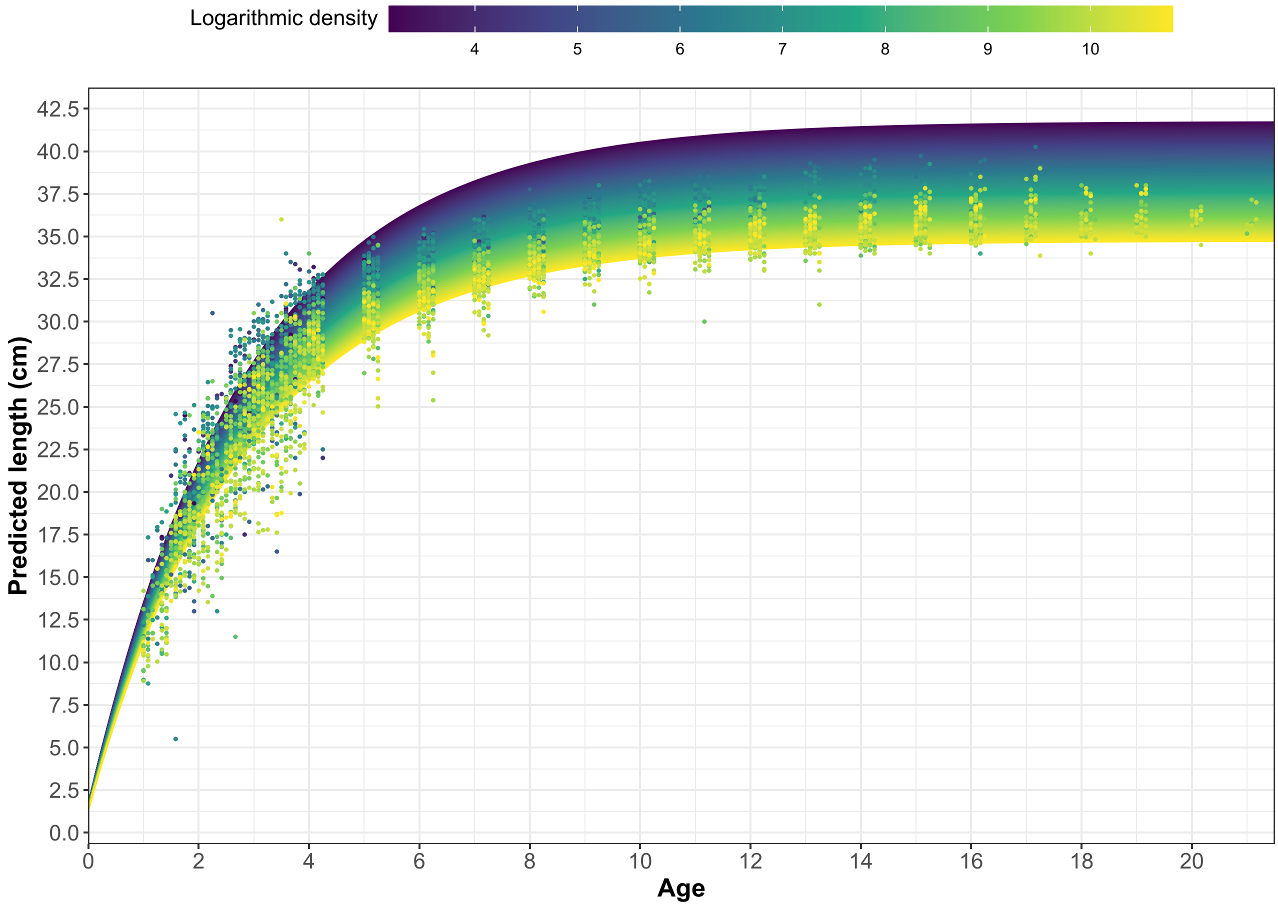

Figure 5. Model-predicted mean growth curve by age coloured by different logarithmic densities based on $N_{(3)}+N_{(4)}$. The points are the mean observed fish length of all ages (by year and month) for the different observed densities.

Table 1. Difference in AIC (relative to the AIC-selected model) and von Bertalanffy parameter estimates for the models using either $N_{(3)}$ or $N_{(3)}$ + $N_{(4)}$ as measure of density.

N	$N_{(3)}$	$N_{(3)} + N_{(4)}$
ΔAIC	23 882	0
ℓ_0^∞	36.661	36.479
ℓ_1^∞	− 0.751	− 0.915
k	0.356	0.349
t_0	− 0.089	− 0.114

Table 2. Parameter estimates for the main model. The *p*-values are based on a Gaussian approximation.

Parameter	Estimate	Standard Error	Z-score	*p*-value	
ℓ_0^∞	36.479	0.007	5133.6	0.000	***
ℓ_1^∞	−0.915	0.003	− 363.3	0.000	***
k	0.349	0.000	775.5	0.000	***
t_0	−0.114	0.003	− 34.9	0.000	***
σ_1	2.735	0.010	271.8	0.000	***
σ_2	3.224	0.012	276.4	0.000	***
σ_3	3.120	0.010	303.5	0.000	***
σ_4	2.167	0.009	253.4	0.000	***
σ_5	1.604	0.005	299.6	0.000	***
σ_6	1.338	0.005	286.5	0.000	***
σ_7	1.372	0.005	262.2	0.000	***
σ_8	1.191	0.005	235.5	0.000	***
σ_9	1.141	0.005	212.0	0.000	***
σ_{10}	1.198	0.006	192.9	0.000	***
σ_{11}	1.200	0.007	166.9	0.000	***
σ_{12}	1.245	0.008	156.4	0.000	***
σ_{13}	1.341	0.010	131.2	0.000	***
σ_{14}	1.395	0.015	94.1	0.000	***
σ_{15}	1.396	0.018	79.5	0.000	***
σ_{16}	1.437	0.021	67.3	0.000	***
σ_{17}	1.358	0.026	52.5	0.000	***
σ_{18}	1.242	0.030	41.7	0.000	***
σ_{19}	1.420	0.044	32.5	0.000	***
σ_{20}	1.172	0.055	21.2	0.000	***
σ_{21}	1.251	0.111	11.2	0.000	***

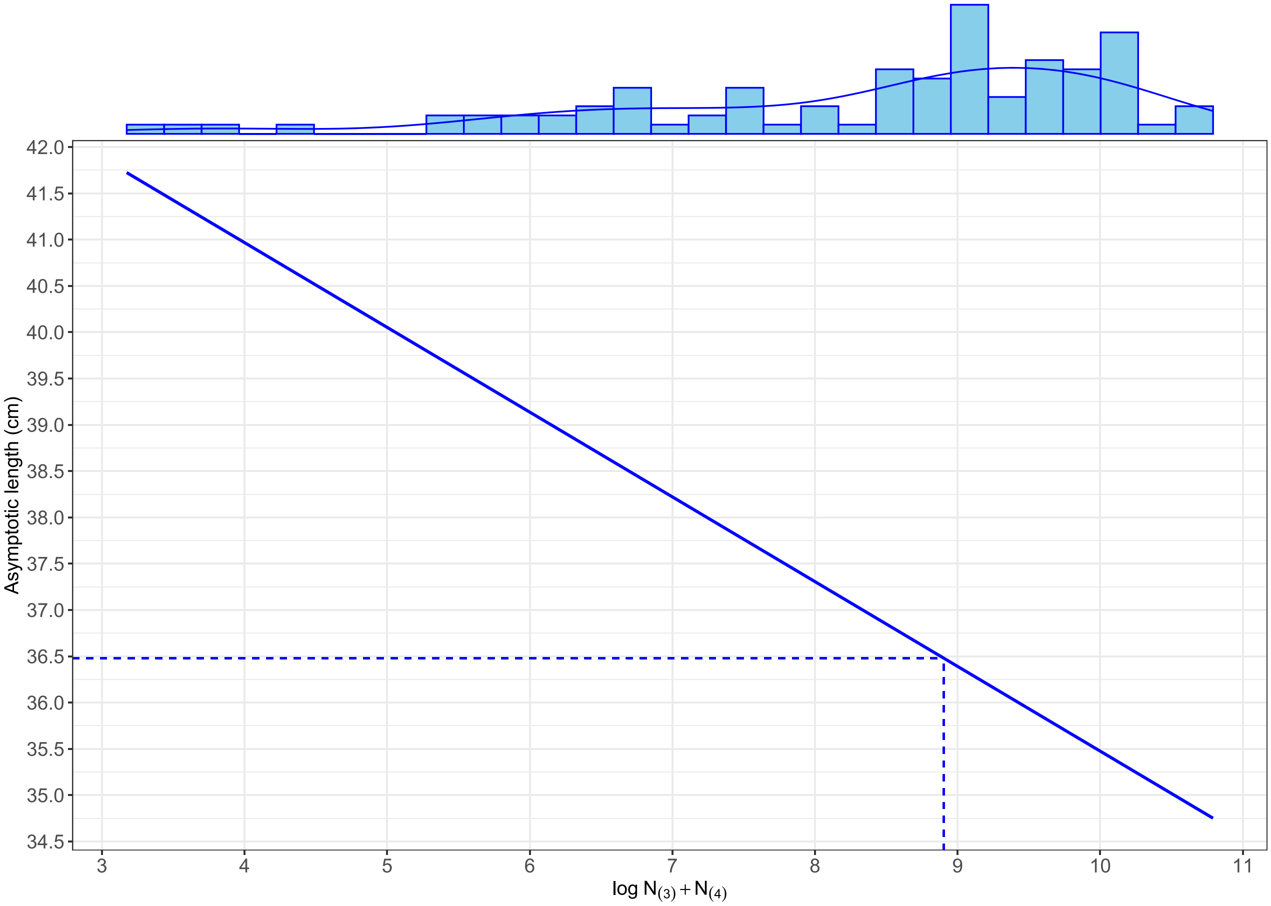

Figure 6. Model-estimated relationship between asymptotic length (ℓ_∞) and logarithmic density of the selected model using $N_{(3)} + N_{(4)}$. The parameter ℓ_0^∞ is the value of ℓ_∞ at the density level $N_{(3)} + N_{(4)} = 7355.9$ million individuals (log 7355.9 = 8.90). At the top is a histogram of the observed density levels with a kernel density estimate for the distribution.

Zimmermann *et al.*, 2018) because of its availability. The data we used were filtered to exclude irrelevant data and still close to 400000 sampled individuals were included in the analyses. The representation of functional relationship between density and growth in our study was made by comparing the cohort specific asymptotic length in the VBGF, ℓ_∞, to density experienced by a cohort. This choice was founded by the underlying concepts of the VBGF. Conceptually, density-dependent growth caused by competition for limited food resources should be manifested in ℓ_∞ and not in the growth parameter of the VBGF. The growth parameter (K) should be influenced by factors such as temperature affecting the basal metabolism (Brunel and Dickey-Collas, 2010; Lorenzen, 2016).

From the above, we conclude that there is support in the data that cohort density is a major factor affecting growth in NSSH, and that this should be accounted for when modelling NSSH growth. The drivers behind the variability in cohort density has been extensively studied for NSSH (Garcia *et al.*, 2020). It has been shown that past fishery has had a significant effect on cohort density (Fiksen and Slotte, 2002), but variability in environmental factors such as temperature (Toresen and Østvedt, 2000), larval drift pattern (Skagseth *et al.*, 2015; Tiedemann *et al.*, 2021), and large-scale climate cycles (Tiedemann *et al.*, 2020) has also been shown to be important drivers of recruitment success and hence cohort density. Particularly in recent years when the stock has been managed with a relatively low fishing mortality (ICES, 2022), it can be hypothesized that the environmental variability has been the strongest driver of cohort density.

The effect of density dependence should be manifested in the asymptotic length parameter in the VBGF (ℓ_∞), and we have formulated a model where ℓ_∞ depends on the abundance of two successive cohorts. The model, which is a parametrization of the VBGF, predicts growth curves with higher ℓ_∞ at lower densities and seems to perform relatively well on average. Residual analyses indicated no major age effect. The residual distribution, however, shows signs of heavy left-tail behaviour. We suspect this is due to the influence of North Sea herring and local herring populations along the Norwegian coast being occasionally partly mixed with NSS herring. These other populations are characterized by different life history strategies with slower somatic growth and lower asymptotic length (Silva *et al.*, 2013; Berg *et al.*, 2017; Schmidt *et al.*, 2021), and have also been shown to be genetically different from NSS herring (Pampoulie *et al.*, 2015; Han *et al.*, 2020). However, it is difficult to split them perfectly out from NSS herring on an individual level in the historic material. Still, this was further explored using an additional filtration, described in the supplementary material. The removal of individuals potentially not being NSS herring had little effect on the prediction but resulted in large improvements of the

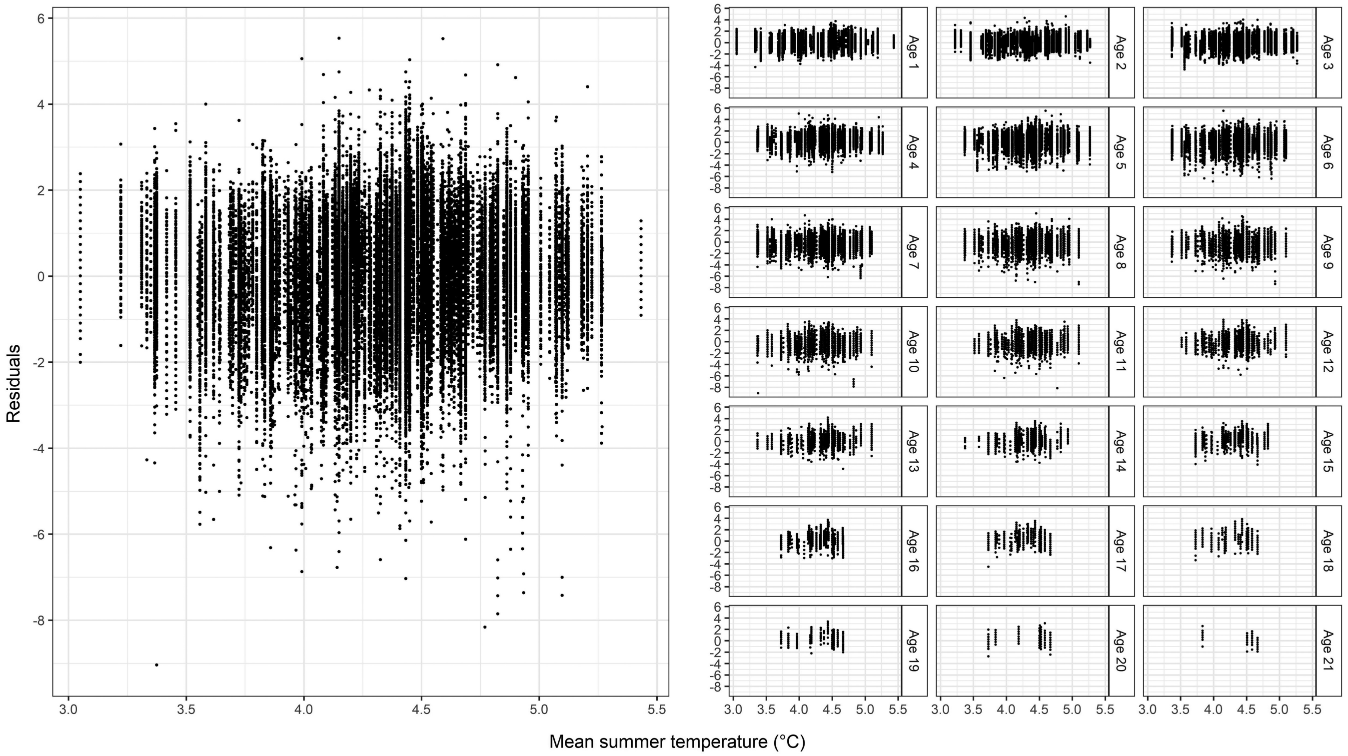

Figure 7. Model residuals against mean Kola temperature averaged over 0–200 m depth for June–August in the years the individual fish were 0–3 years old. For an individual that died before reaching age 3, the average is taken for the years it was alive.

residual left tail supporting our suspicion. However, since the effect of this filtering on the prediction was negligible, and the risk of removing NSSH samples from the data was potentially high, we did not apply this additional filtering in the final model.

Since population density is not the only factor potentially influencing growth, we explored alternative models. Comparing population density to somatic growth assumes that the carrying capacity of the ecosystem is constant over time. If, however, this is not the case, which is the more likely scenario, using fish density alone might not be a good proxy for the strength of density-dependent and density-independent data on food availability should be included (Brunel and Dickey-Collas, 2010). There are, however, limited data on food availability and it would only be possible to incorporate this for the last few years of the investigated time period. Therefore, food availability is not included here, and we had to assume that variability in fish density is a good indication of the variability in strength of the density dependence (Brunel and Dickey-Collas, 2010). This assumption finds support in Lorenzen (2016), who concluded that density-dependent effects have often been shown to be the dominant effect when both environmental and density-dependent effects are studied simultaneously.

Size-selective sampling may cause bias in estimates of growth parameters particularly when samples are mainly from fishery-dependent sampling which is often selective (Schueller *et al.*, 2014). The data used come from both fishery-dependent and fishery-independent sampling and should, consequently, be expected to contain all size classes of NSSH. There might, however, be bias related to variable selectivity of the different gear used in the sampling. The effects on selectivity of different sampling gear in the time series were investigated by looking at patterns in model residuals when splitting by gear type and we observed no major effects indicating no major bias due to sampling gear (Supplementary Figures S8 and S9). Estimates of VBGF parameters may be biased from Lee's phenomenon (Lee 1912) whereby the survivors tend to be slower growers due to size selective mortality, and hence estimated size at older ages are dominated by slow growing fish. This may be particularly problematic if fishing mortality is highly variable (Brunel and Dickey-Collas, 2010) and could cause spurious variability in estimated parameters, particularly if high fishing mortality occurs at large cohort sizes. Fishing mortality is, however, negatively correlated to cohort size in our study, and it is therefore unlikely that variable F has caused spurious correlation between growth parameters and cohort size.

Ambient temperature will influence growth (Toresen, 1990; Ottersen and Loeng, 2000), and temperature time-series exists, which covers the range of years as the NSSH data. We used data (average in the upper 200 m of the water column) from the Kola hydrographic section in the Barents Sea (Karsakov, 2009; Karsakov *et al.*, 2019), which extends back to 1900. The juvenile NSSH reside mainly in the Barents Sea, and the temperature index we have constructed is therefore most relevant for the first 3 years of life. However, because of the lack of other appropriate data covering the long time series and because of the highly migratory and spatially variable distribution of the adult stock, it is in our view not possible to construct an index of mean temperature experienced throughout its life span for each cohort in the time series without introducing considerable noise (but see Brunel and Dickey-Collas, 2010). We acknowledge the limitations in our approach but assume that the temperature in the nursery areas during the first three years of life is nevertheless a relevant index when modelling growth of NSSH with the VBGF. There were no clear patterns in model residuals against temperature indicating limited effects of temperature in the main model. From the exploratory model runs, a model with $N_{(3)} + N_{(4)}$ on ℓ_∞ and temperature on K provided a lower AIC. This indicates that inclusion of temperature as a covariate on K would improve the predictive abilities of the model. Temperature is, however, a potential confounder between cohort size and somatic growth and including temperature is therefore not unproblematic. Among the models investigated, the best model with respect to AIC used $N_{(3)} + N_{(4)}$ on ℓ_∞ and latitude of sample location on K.

AIC comparisons should, however, not be the only criterion considered since we were aiming for a model with highest possible predicting capabilities and consequently had to compromise between realism and simplicity (Lorenzen, 2016; van Poorten and Walters, 2016). Although some of the exploratory models performed marginally better than the main model, we did not find strong arguments to reject the main model (effect of herring density on asymptotic length) as our selected model. Our main objective was to formulate a model that can be used in a management context to predict growth in simulations that only have herring density as a factor possibly affecting growth, and we suggest that the simple model where asymptotic length depend on herring density could be used for this purpose. Although time-variable density-independent growth may be an important contributor to population fluctuations for some species (Stawitz and Essington, 2019), it may have minor effects on abundance in an MSE framework because the relationship between growth and a specific environmental factor needs to be strong for it to be an important source of variation (Punt *et al.*, 2013). It was, however, important to investigate the realism of our model by comparing the chosen model to models including other factors such as temperature.

To avoid complications caused by variability in condition factor, our model is based on fish length and not weight, which is used to estimate stock biomass. Appropriate length/weight relationships that can be used to convert from predicted length-at-age to weight-at-age for long-term simulations of stock biomass are presented in the supplementary material (Table S2, Figure S10). Given a length L in cm, the expected weight in grams can be calculated by $e^{-5.394} L^{3.165}$ according to the fitted length–weight model.

We conclude that cohort density affects growth in NSSH and that our selected model performs relatively well and can be used to predict size-at-age of Norwegian spring-spawning herring as function of herring density (the abundance of two successive year-classes) in short-term predictions of catch advice and in MSE including estimation of reference points (F_{MSY}). Our model has therefore filled a knowledge gap, but the impacts on the estimation of reference points remains to be seen. Variability in other biological parameters such as recruitment (ICES, 2018) and natural mortality are important. Although recruitment is often identified as the driver with the strongest impact on the estimation of reference points as in the most recent work on NSSH (ICES, 2018), density-dependent growth might dampen the effects of recruitment variability (Stawitz and Essington, 2019). Variable natural mortality is also a potential cause of population fluctuations in pelagic fish by magnifying fluctuations caused by other mechanisms such as recruitment (Johnsen *et al.*, 2015; Jacobsen and Essington, 2018). Natural mortality is, however, difficult to estimate and in the absence of reliable data on natural mortality as is the case for NSSH, the benefits of assuming temporal variability in natural mortality are uncertain (Johnsen *et al.*, 2015).

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Supplementary material

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Author contribution

EK Stenevik initiated the work and all authors contributed to conceiving the ideas. ÅH and AS organized the data. SH carried out the analyses. EKS and SH wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

All code in this project is available at https://github.com/holleland/NSSHdensGrowth. The biological data are available at https://doi.org/10.21335/NMDC-496562593. The XSAM time-series on stock numbers at age is available in Supplementary table S3. Requests to access temperature data from the Kola section must be made to the Polar Branch of the VNIRO, Russian Federation.

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