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Density- and size-dependent mortality in fish early life stages

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Abstract

The importance of survival and growth variations early in life for population dynamics depends on the degrees of compensatory density dependence and size dependence in survival at later life stages. Quantifying density- and size-dependent mortality at different juvenile stages is therefore important to understand and potentially predict the recruitment to the population. We applied a statistical state-space modelling approach to analyse time series of abundance and mean body size of larval and juvenile fish. The focus was to identify the importance of abundance and body size for growth and survival through successive larval and juvenile age intervals, and to quantify how the dynamics propagate through the early life to influence recruitment. We thus identified both relevant ages and mechanisms (i.e. density dependence and size dependence in survival and growth) linking recruitment variability to early life dynamics. The analysis was conducted on six economically and ecologically important fish populations from cold temperate and sub-arctic marine ecosystems. Our results underscore the importance of size for survival early in life. The comparative analysis suggests that size-dependent mortality and density-dependent growth frequently occur at a transition from pelagic to demersal habitats, which may be linked to competition for suitable habitat. The generality of this hypothesis warrants testing in future research.

KEYWORDS
Bayesian state-space analysis, comparative analysis, growth–survival relationships, population regulation, predation, recruitment dynamics

1 | INTRODUCTION

Understanding how processes early in life influence year-class strength has been a central topic of fisheries research for more than a century. This is because year-to-year variations in year-class strength at the age when the fish enter into the fisheries ("recruitment") is a main driver of changes in population size of many harvested marine fishes and a key determinant of the new harvestable biomass (Hjort, 1914; Houde, 2008). Quantifying associations between changes in abundance and body size distribution through early life is an important step to explain, and potentially predict, fish recruitment. Specifically, such quantification may reveal interconnections between growth, survival and population regulation, and, thereby the relevance of growth and survival variations at different early life stages for recruitment.

Changes in abundance and mean body size during the early life stages of marine fish are often correlated because of associations between the mean mortality rate, which influences abundance, and growth and size-dependent mortality, which influence mean body size (Figure 1). Several ecological processes link the changes in abundance and mean body size. For example, predation may simultaneously influence abundance and size distribution by causing size-dependent mortality, while competition may do so by causing density-dependent growth and mortality (Bailey & Houde, 1989; Cushing, 1995).

For a population to persist over many generations, compensatory density dependence has to operate for at least some point of the life cycle, so that the population growth rate tends to increase when abundance is low and decrease when abundance is high; such regulation can occur by long-term mean "input" rates (birth and immigration) scaling negatively with abundance and/or by "loss" rates (mortality and emigration) scaling positively with abundance (Hassel, 1975; Hixon, Pacala, & Sandin, 2002; Rose, Cowan, Winemiller, Myers, & Hilborn, 2001). For example, intra-specific competition for limited resources such as food or habitat can potentially lead to increased mortality or reduced fecundity when abundance is high. Other mechanisms for density-dependent mortality include numerical or behavioural responses of predators, parasites and diseases (Bailey & Houde, 1989; Hixon et al., 2002). The compensatory density dependence is commonly assumed to take place early in life for most marine fishes and is typically embedded in the relationship between the biomass of spawners and the number of recruits in fisheries models (e.g. Ricker, 1954, Beverton & Holt, 1957). This assumption appears to be valid for many populations (Lorenzen & Camp, 2018; Zimmermann, Ricard, & Heino, 2018), although density dependence may also occur later in life for some populations (Andersen, Jacobsen, Jansen, & Beyer, 2017). When in the pre-recruitment period the density dependence occurs, warrants further investigation. Quantifying at which life stage density dependence occurs is important, for example, to assess population consequences of environmental influences on abundances of fish eggs and larvae, as such environmental effects tend to be dampened if

the subsequent juvenile stages show strong compensatory density dependence (van Gemert & Andersen, 2018; Ohlberger, Rogers, & Stenseth, 2014).

Competition can affect survival directly, for example through starvation mortality, or indirectly, by leading to reduced growth and development—which has survival consequences if mortality depends on size or stage. In particular, there is strong evidence for compensatory density dependence in growth during the early juvenile stage, which contributes to regulation of recruitment when combined with increased mortality at small body size (Houde, 2008). Competition can also hypothetically lead to increased mean body size at high abundance. Specifically, if competition causes mortality that disproportionally affects small individuals, mean body size may
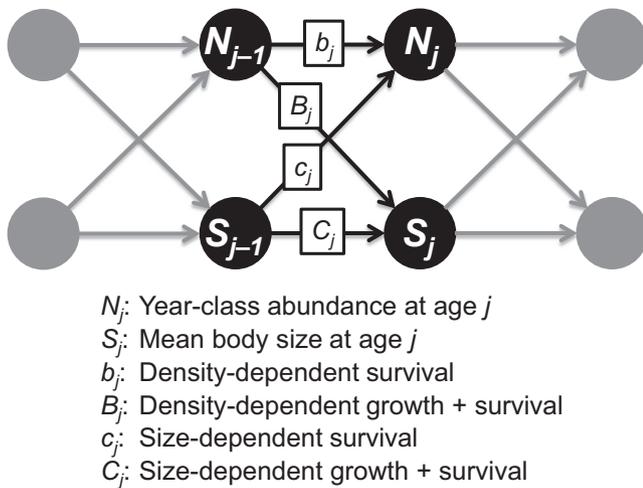
N_j: Year-class abundance at age j
S_j: Mean body size at age j
b_j: Density-dependent survival
B_j: Density-dependent growth + survival
c_j: Size-dependent survival
C_j: Size-dependent growth + survival

FIGURE 1 Schematic outline of main processes that link abundance and mean size of a year-class at subsequent ages or stages (e.g. j = 0, 1, 2 and 3 years of age)

increase and this effect may counteract the growth rate effect of competition.

In general, mortality rates of larval and juvenile marine fishes have been found to decline with body size (Bailey & Houde, 1989; Sogard, 1997), although for single stages, size–mortality relationships may be absent or even positive (e.g. Pepin, 2015). A key mechanism behind the general pattern is likely to be size-dependent predation mortality, as small individuals are typically exposed to more potential predators than large individuals and escape ability typically increases with body size (Bailey & Houde, 1989). Fast growth through the vulnerable size ranges of early life stages may then lead to high survival (the 'stage duration hypothesis', Houde, 1987). Furthermore, mortality rates may decline with body size because tolerance to starvation and physical extremes may be higher for larger individuals (Miller, Crowder, Rice, & Marschall, 1988; Sogard, 1997). In such cases, fast growth prior to a period with adverse environmental conditions, for example the first winter of life for many high-latitude species, may be important for survival through that period (Sogard, 1997).

Long-term monitoring surveys of eggs, larvae and juveniles exist for a number of commercial fish populations. The time series data have often been collected to get an early indication of year-class strength to inform fisheries management (e.g. Dragesund, Hylen, Olsen, & Nakken, 2008, Bailey, Zhang, Chan, Porter, & Dougherty, 2012, McClatchie et al., 2014, Megrey, Hollowed, Hare, Maclin, & Stabeno, 1996). Analyses of such time series have shown that reasonable predictions of recruitment can sometimes be obtained as early as the egg stage (Helle et al., 2000; Mukhina, Marshall, & Yaragina, 2003), although processes at later ages also come into play (Bogstad, Yaragina, & Nash, 2016; Stige, Hunsicker, Bailey, Yaragina, & Hunt, 2013). Moreover, it has been shown that not only abundance but also body size distribution of early life stages provides information on future year-class strength (Bailey, 2000; Campana, 1996; Ottersen & Loeng, 2000; Stige et al., 2015). Such data can provide valuable insights into the mechanisms

that determine year-class strength, such as effects of density dependence and the connections between growth and survival. However, measurement errors and incomplete time series complicate interpretations, as illustrated by the finding that abundance indices of older pre-recruit life stages sometimes provide less accurate predictions of recruitment than indices of younger life stages (Stige et al., 2013).

We applied a statistical state-space analysis approach on six commercially and ecologically important fish populations from cold temperate and sub-arctic marine ecosystems. For each population, we quantified how deviations in the abundance and mean body size of a year-class during early life propagated through subsequent pre-recruit age intervals. We thus identified both relevant ages and mechanisms (i.e. density and size dependence in survival and growth) linking recruitment variability to early life dynamics. The state-space approach is well suited to account for common limitations in long-term time series data such as measurement errors and incomplete data coverage, and provides one coherent analysis that links processes occurring through multiple age intervals. Our results identified processes and ages that are important in influencing year-class strength, and which warrant increased attention in terms of monitoring and analysis to better understand and ultimately predict recruitment variations. Specifically, the results underscored the importance of large body size early in life for strong recruitment, but also showed differences in the survival value of large body size and in density dependence across life stages and species that we hypothesize are explained by variations in the habitat and life histories of the populations.

2 | CASE STUDIES

To obtain an in-depth understanding of the intertwined processes of growth and survival at early life stages, we selected a number of case studies based on populations for which we had access to long-term fishery-independent time series of abundance and mean body size for several pre-recruitment age groups (Table 1). These populations included three economically and ecologically important, and therefore well-monitored, species in the sub-arctic Barents Sea (BS). The three fishes were the gadoids Atlantic cod (*Gadus morhua*, Gadidae) and haddock (*Melanogrammus aeglefinus*, Gadidae), and the forage fish capelin (*Mallotus villosus*, Osmeridae). To generate hypotheses of general patterns that may be valid beyond the BS, we also included three comparable, well-monitored gadoid populations from other sub-arctic and cold temperate ecosystems, one population of haddock and two of walleye pollock (*Gadus chalcogrammus*, Gadidae). All species are highly fecund with large interannual variability in the number of offspring that survive to recruitment.

The BS cod (also referred to as Northeast Arctic cod) is currently the world's largest population of Atlantic cod. The BS cod spawns along the north and west coasts of Norway, from where eggs, larvae and pelagic juveniles drift with the currents into the BS, which is the

TABLE 1 Summary of data series analysed

Population	Years[a]	Age classes analysed	Size metric
Barents Sea cod	1959–2015	Larvae (~3 mo.), age-0 (~5 mo.), age-1 (~10 mo.), age-2, age-3	Length
Barents Sea haddock	1959–2015	Larvae (~3 mo.), age-0 (~5 mo.), age-1 (~10 mo.), age-2, age-3	Length
Scotian Shelf and Bay of Fundy haddock	1970–2013	Age-0 (only size), age-1, age-2, age-3, age-4	Weight
Barents Sea capelin	1959–2015	Larvae (~3 mo.), age-0 (~5 mo.), age-1 (~18 mo.), age-2	Length
Eastern Bering Sea pollock	1982–2016	Age-1, age-2, age-3, age-4	Weight
Gulf of Alaska pollock	1979–2017	Larvae (~2 mo.), age-0 (~6 mo.), age-1 (12 mo.), age-2, age-3	Mixed[b]

[a]Total year range. There were frequently gaps in several of the time series.
[b]Length for larvae and age-0, weight for ages 1–3. To facilitate interpretation of results, log lengths were multiplied with 3 (equivalent to cubic transformation of lengths) to be on a comparable scale as log weights.

nursery area and the feeding area of adults (reviewed by Ottersen et al., 2014). At an age of around 6 months, the juveniles move from pelagic to more demersal habitats, and at around 3 years, they enter into the fishery.

The BS haddock (also referred to as Northeast Arctic haddock) spawns along the west coast of Norway and the western shelf break of the BS to the north of Norway at around 300 to 600 m depth (Olsen et al., 2010). The pelagic eggs, larvae and juveniles drift with the currents into the BS, where the juveniles largely switch to a demersal life style in their first fall.

The BS capelin is a small pelagic fish that plays a key role in the ecosystem as the main predator on mesozooplankton, and prey of cod and haddock as well as several other fish species, sea birds and marine mammals (Yaragina & Dolgov, 2009). The BS capelin is also fished commercially, with the main fisheries in recent decades targeting spawners (mostly 3- and 4-year-olds). Eggs are spawned on the sea floor along the southern coasts of the BS where they develop and hatch into larvae. The larvae are pelagic and drift northwards and eastwards into the nursery areas in the central BS, which, together with the northern BS, are feeding areas of adults (Gjøsæter, 1998).

Haddock on the southern Scotian Shelf and in the Bay of Fundy (SSBF) are demersal and occupy waters from around 50 to 250 m depth (DFO, 2006). The haddock from this population spawn in bottom waters on offshore banks, principally Brown's Bank between Nova Scotia and Georges Bank (DFO, 2003; Shackell, Frank, Petrie, Brickman, & Shore, 1999). Eggs are positively buoyant and rise to pelagic waters (10 to 50 m) (Cargnelli, Griesbach, Berrien, Morse, & Johnson, 1999). Eggs and larvae are either retained on Brown's Bank (due to a clockwise gyre circulation) or advected, often inshore, for example, into the Bay of Fundy (Campana, Smith, & Hurley, 1989). Larvae metamorphose at about 30 to 42 days and descend to bottom water habitats (Cargnelli et al., 1999). While seasonal migrations occur, there is little exchange with other haddock populations (DFO, 2006).

Walleye pollock is an ecologically and commercially important species in the Eastern Bering Sea (EBS) ecosystem. They provide forage for other commercially important fishes and species of conservation concern and support the largest commercial fishery in the United States (around 1.2 million tons and >US$1 billion annually, Hiatt et al., 2011, Ianelli, Honkalehto, Barbeaux, Fissel, & Kotwicki, 2016). Pollock are pelagic spawners, and they spawn along the outer continental shelf in the early spring. In general, they are semi-demersal and become increasingly demersal with age, although age-2 pollock are thought to school higher in the water column than age-1 (Duffy-Anderson et al., 2003). In most years, pollock recruit to the fishery at age 4. The EBS pollock population is most likely composed of multiple spawning aggregations varying in timing. The earlier spawning aggregations (March) occur in the Bogoslof Island and Unimak Pass regions, near the Aleutian Islands. Later spawning aggregations (March–May) occur along the Alaska Peninsula and Pribilof Islands region (Bacheler, Ciannelli, Bailey, & Duffy-Anderson, 2010; Hinckley, 1987).

Walleye pollock in the Gulf of Alaska (GOA), while not as abundant as in the Bering Sea, do play a nodal role in the ecosystem as both predator and prey (Gaichas & Francis, 2008), and support a US$40M fishing industry (Dorn et al., 2016). In March and April, GOA pollock gather to spawn primarily in the Shelikof Strait region between Kodiak Island and the Alaska Peninsula. As in the EBS, pollock occupy midwater habitat across the shelf as age-0 juveniles (Brodeur & Wilson, 1996), moving to deeper water with age.

3 | METHODS

3.1 | Correlation analysis

For each fish population, we first conducted a simple correlation analysis between year-class strength and mean body size at the earliest age with available data, and year-class strength and mean body size around the age of recruitment to the fisheries. Pearson's correlations were computed for log-transformed time series, consistent with the scale used in subsequent analyses. These correlations

served as motivation for developing statistical state-space models that showed in detail the links between abundance and body size across multiple age intervals leading up to recruitment.

3.2 | State-space statistical models of age-resolved dynamics

All populations were analysed using a state-space modelling framework for analysing time series of abundance and mean body size at different ages. The focus was to identify the roles of abundance and body size for growth and survival from one age to the next. Year-to-year changes in abundance and mean body size of a year-class were described by a multivariate discrete Gompertz model, which has the advantage that it can be written in a linear form and is also a good first-order approximation of more complex dynamics (Ives, Dennis, Cottingham, & Carpenter, 2003). The Gompertz model differs from the commonly used Ricker model for fish recruitment (Ricker, 1954) in that the density-dependent mortality rate is assumed to scale with log-abundance rather than with abundance. The support in the data for using a Gompertz model was assessed for all populations and ages (see "Estimating model parameters"). The model structure was based on Figure 1 and is described by the following equations:

$$\ln\left(N_{i,j}\right) = a_j + b_j \cdot \ln\left(N_{i,j-1}\right) + c_j \cdot \ln\left(S_{i,j-1}\right) + \varepsilon_{i,j} \quad (1)$$

$$\ln\left(S_{i,j}\right) = A_j + B_j \cdot \ln\left(N_{i,j-1}\right) + C_j \cdot \ln\left(S_{i,j-1}\right) + \zeta_{i,j} \quad (2)$$

Here, $N_{i,j}$ is the abundance of a year-class born in year i at an age j. $S_{i,j}$ is average body size (measured as length or weight dependent on population; see the section "Observation data"). Predictor effects in Equation 1, describing changes in log-abundance, have a straightforward interpretation in terms of effects on instantaneous mortality rate (e.g. Ives et al., 2003). This can be seen by writing Equation 1 on arithmetic scale:

$$N_{i,j} = \exp\left(r_{i,j}\right) \cdot N_{i,j-1}, \quad \text{where} \quad (3)$$

$$r_{i,j} = a_j + \left(b_j - 1\right) \cdot \ln\left(N_{i,j-1}\right) + c_j \cdot \ln\left(S_{i,j-1}\right) + \varepsilon_{i,j} \quad (4)$$

Here, $r_{i,j}$ is the instantaneous rate of change in abundance, that is, immigration − (mortality + emigration) rates for a given year and age interval. If immigration and emigration can be ignored, Equation 4 captures linear and additive effects of log-abundance and log-size on the instantaneous mortality rate. Correspondingly, Equation 2 can be written on arithmetic scale as follows:

$$S_{i,j} = \exp\left(g_{i,j}\right) \cdot S_{i,j-1}, \quad \text{where} \quad (5)$$

$$g_{i,j} = A_j + B_j \cdot \ln\left(N_{i,j-1}\right) + \left(C_j - 1\right) \cdot \ln\left(S_{i,j-1}\right) + \zeta_{i,j} \quad (6)$$

Here, $g_{i,j}$ is the instantaneous rate of change in mean body size, which reflects growth and size-dependent survival. The age-specific intercept (a_j) in Equations 1 and 4 reflects the level of density-independent mortality and, if relative indices are used, scaling. Note that for convenience, we refer to effects of abundance as

density dependence, assuming that year-class abundance is a relevant measure of crowding. In a supplementary analysis, we considered, however, an alternative model that explicitly included inter-cohort density dependence (Ricard, Zimmermann, & Heino, 2016), by adding effects of year-class $i − 1$ to Equations 1 and 6. Coefficient b_j quantifies density dependence in mortality (with no density dependence at $b = 1$, complete compensation at $b = 0$ and overcompensation at $b < 0$). Coefficient c_j quantifies the effect of mean body size on survival. The coefficient B_j in Equations 2 and 6 quantifies the effect of abundance on the instantaneous rate of change in mean body size. Coefficient C_j quantifies compensation in body size with age (with no compensation of anomalies in body size at $C = 1$, complete compensation at $C = 0$ and overcompensation at $C < 0$). ε and ζ are normally distributed (potentially correlated) process errors with means zero. The process errors capture effects of environmental conditions not explicitly modelled. The equations for the youngest age analysed only include the intercept and process noise terms.

A possible drawback of this model formulation is that with some parameter values, year-class abundance may be predicted to increase with age. In our empirical analysis, this feature mainly affects the interpretation of the results, meaning that posterior distributions may include biologically unrealistic parameter values (as is often the case in statistical analyses). This model formulation simplified, however, the inclusion of relative abundance indices with unknown scaling to true abundance, as we did not have to estimate the scaling factors (which would have been strongly correlated with the levels of density-independent mortality).

The model was fit in a state-space framework, whereby N and S were considered unobserved state variables that were linked to the observations through an observation model. This way, uncertainties about biological processes and observation noise were explicitly accounted for, to provide unbiased parameter estimates and appropriate confidence bands (Clark & Bjørnstad, 2004). The approach also accommodated missing values in the time series. Specifically, the observed abundance $\acute{N}_{i,j}$ and body size $\acute{S}_{i,j}$ were linked to $N_{i,j}$ and $S_{i,j}$ according to Equations 7 and 8:

$$\ln\left(\acute{N}_{i,j}\right) = \ln\left(N_{i,j}\right) + e_{i,j} \quad (7)$$

$$\ln\left(\acute{S}_{i,j}\right) = \ln\left(S_{i,j}\right) + z_{i,j} \quad (8)$$

Here, e and z are independent and normally distributed observation errors with means zero and standard deviations $\sigma_{\acute{N}j}$ and $\sigma_{\acute{S}j}$.

3.3 | Estimating model parameters

All parameters of the model were estimated jointly by using a Bayesian Markov Chain Monte Carlo (MCMC) approach. For this purpose, we used the program JAGS (Just Another Gibbs Sampler) and the rjags and R2jags packages of R (Plummer, 2016). The likelihood function was created based on the model and the data, and

in combination with the prior distributions of the parameters, the posterior distributions were estimated.

We modelled correlated process errors by drawing $\varepsilon_{i,j}$ (Equation 1) from a normal distribution with standard deviation σ_{Nj} and by drawing $\zeta_{i,j}$ (Equation 2) from a normal distribution with standard deviation σ_{Sj} and adding $\rho_j \cdot \varepsilon_{i,j}/\sigma_{Nj}$. We thus estimated three variance parameters, σ_{Nj}, σ_{Sj} and ρ_j, for each age j. The variance of $\varepsilon_{i,j}$ is σ_{Nj}^2, the variance of $\zeta_{i,j}$ is $\sigma_{Sj}^2 + \rho_j^2$ and the covariance between $\varepsilon_{i,j}$ and $\zeta_{i,j}$ is $\rho_j \cdot \sigma_{Nj}$.

As recommended by Ives et al. (2003), we used best guesses of observation error variances when possible. To obtain convergence when we had no information on the magnitude of observation errors, the observation error variance was generally assumed to be the same for all years and identical to the corresponding process error variance (i.e. $\sigma_{\acute{N}j}^2 = \sigma_{Nj}^2$, $\sigma_{\acute{S}j}^2 = \sigma_{Sj}^2 + \rho_j^2$). In a sensitivity analysis, we multiplied the observation error standard deviations by either 0.5 or 1.5 and assessed effects on posterior parameter distributions. As part of the sensitivity analysis, standard deviations of observation errors that were assumed known were multiplied with 1.5 (but not with 0.5) to assess the influence of possible unknown error sources. For some of the most data-rich populations (BS cod and BS capelin), unknown observation error variances were estimated from the data (independent of process error variances).

Prior distributions for parameters in the process model were uniform and broad to let the data drive the inferences. We chose the following uniform prior distributions of model parameters. Intercepts a_j, A_j: (−20, 20), density dependence in survival b_j: (−1, 1), density dependence in size changes B_j: (−1, 1), size dependence in survival c_j: (−20, 20), size dependence in size changes C_j: (−1, 1), variance parameters σ_{Nj}, σ_{Sj}, $\sigma_{\acute{N}j}$, $\sigma_{\acute{S}j}$: (0, 10), ρ_j: (−10, 10). A wider prior distribution for size effects on abundance (c_j) than abundance effects on size (B_j) was used because of much larger ln-scale variance in abundance than size. Prior distributions for the values of the unobserved state variables at the first time step $i = 1$ ($N_{1,j}$, $S_{1,j}$) were uniform and bounded by the observed ranges of the variables.

We used three independent chains with 300,000 iterations, where the first 30% of the iterations were used as "burn-in" iterations to ensure that the chains had converged. In addition, we thinned the chains to reduce autocorrelation in the posterior samples and to produce a reasonable amount of output, in this case resulting in 1,000 samples from each chain, in total 3,000.

We used the Gelman and Rubin $\hat{R}$ convergence diagnostics (Gelman & Rubin, 1992) and visual inspection of the chains to ensure convergence. The $\hat{R}$ compares within-chain and between-chain variance and should be close to 1 at convergence (Gelman & Rubin, 1992). If the multivariate $\hat{R}$ or the upper 95% confidence limit for $\hat{R}$ for one or more model parameters was larger than 1.03 or there were other signs of poor convergence, we first increased the number of iterations from 300,000 to 1,000,000, and if that did not solve the issue, we simplified the model formulation as described in the description of the model development for each population in Appendix S2 (Supporting Methods).

We checked for violations of key model assumptions by inspecting (a) time series plots of state variables for abundance and body size (posterior medians and 95% credibility intervals) and observations, (b) pairwise plots of log-abundance and log-size at time t versus log-abundance and log-size at time $t + 1$, which should show approximately linear relationships if the Gompertz model formulation is appropriate and (c) quantile–quantile normal probability plots of "residuals", calculated as deviations between log-scale observations and posterior medians of state variables, which would reveal possible outliers and strong departures from normality. We used the Grubbs test (Grubbs, 1969) to assess whether outlier residuals were more extreme than expected by chance and refitted the model without the statistically significant outliers to assess their possible influence on results.

To identify correlated parameters that should be interpreted jointly, we computed correlations between posterior distributions for all parameter pairs and plotted those larger than 0.4 in absolute value.

3.4 | Hypothetical example

To illustrate the analysis approach, we analysed synthetically generated data. The synthetic data were randomly generated based on the generic model presented in Figure 1 and analysed as the real data. Computer code and results are shown in the online Appendix S1.

3.5 | Observation data

The data needed for the proposed analyses are time series of abundance and mean length or weight at different ages or stages prior to recruitment, preferably including uncertainty estimates. Whether to prefer length or weight data if both are available is not obvious. Both length and weight could potentially be important for dynamics. Weight may be the best indicator of condition, and length an indicator of role as predator or prey in the food web. Measurement issues can also influence which size measure to prefer. For example, as weight is more seasonally variable than length, weight is potentially more sensitive to year-to-year differences in sampling time. Weight may also to a larger degree than length be susceptible to fluctuations at timescales from hours to weeks, which may be of little relevance for interannual dynamics. The analysis framework can accommodate relative abundance indices, that is, with unknown scaling to true abundance, and the time series can include missing values. More than one index of an age-class can also be used, if available. For this analysis, we assembled time series of abundance and size (weight and/or length, dependent on data availability), for age classes ranging from the earliest age measured (larvae, age-0 or age-1) through to the age at which recruitment to the fishery occurs (age 2 to 4; summarized in Table 1, with more detailed information about year coverage, data sources and uncertainty estimates provided in the online Appendix S2, Tables S1–S5; the time series are shown in Appendix S3, Figures S1–S6, and provided in Appendix S4. Data). Changes in survey coverage or methodology could potentially bias parameter estimates if coinciding with trends in size or abundance. We took into account

that the survey coverage for BS cod and BS haddock at ages 1–3 changed in 1993 by adding an extra parameter to the observation equations for abundance (Equation S1, Appendix S2). All data series were centred to have a mean of zero prior to analysis.

4 | RESULTS

4.1 | Correlation analysis

The correlation analysis focused on the relationship between abundance and mean size around the age of recruitment to the fisheries and the youngest age with data for each population. This analysis showed that for BS cod as well as for BS haddock, age-3 abundance was similarly strongly correlated with abundance and annual mean length of the larvae three years previously (Figure 2). For SSBF haddock and EBS pollock, age-4 abundance was significantly correlated with abundance but not mean weight at age 1 three years previously. For SSBF haddock, weight but not abundance at age 0 was

FIGURE 2 Correlation analysis for associations between abundance (*N*) and mean body size (*S*) at the youngest and oldest age analysed for each population (subscripts denote age). The number below each arrow is Pearson's correlation coefficient for the association represented by the arrow. Negative correlations are shown by red arrows, positive by blue, with arrow width proportional to correlation strength. Dotted-lined arrows are not statistically significant at *p* < 0.05

available, showing a positive association of age-0 weight with age-4 abundance (r = 0.59, p = 0.01) but not with age-4 weight (r = 0.29, p = 0.28) four years later. For BS capelin and GOA pollock, abundance at age 2 (for capelin) or 3 (for pollock) was neither correlated with abundance nor mean length as larvae.

None of the six populations showed significant correlations between body size at the youngest age analysed and body size at the oldest age analysed. For two of the populations, BS cod and BS capelin, there were statistically significant negative correlations between larval abundance and mean body size of the year-class at the oldest age analysed. For BS haddock, the statistical power of these correlation tests is low due to small sample size (N = 12 years). Hence, we also analysed the age-0 data for this population, finding that mean length at age 3 was negatively correlated with age-0 abundance (r = −0.42, N = 33, p = 0.02) as well as length (r = −0.44, N = 33, p = 0.01) three years previously.

The age-resolved state-space analysis explored the links between variability in abundance and body size early in life in more detail.
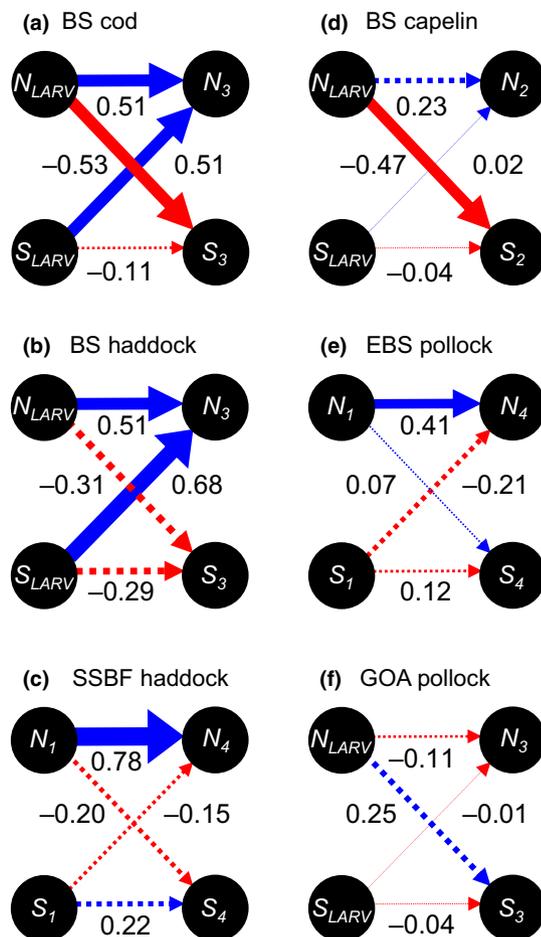
4.2 | Model diagnostics and sensitivity analyses for age-resolved dynamics

Model diagnostics and sensitivity analyses suggested that the main results of the state-space statistical analysis of age-resolved dynamics were robust to the key model assumptions. Nonetheless, it should be noted that while results appeared qualitatively robust, the assumptions made regarding magnitudes of observation errors do influence some of the parameter estimates (see Appendix S3: Supporting Results for details).

4.3 | Across-population comparison

All populations with sufficient data showed low (close to 0) estimates for effects of size as larvae or age-0 juveniles on size at subsequent ages (2nd column in Figure 3, representing C_j coefficients in Equation 2. Low estimates for effects of size on size mean little consistency across ages in size deviations: mean body size of larvae and age-0 juveniles are poor predictors of mean body size at later ages—as also shown by correlation analysis.

Three populations, BS cod, BS haddock and SSBF haddock, showed positive associations between age-0 size and age-1 abundance (1st column in Figure 3, representing c_j coefficients in Equation 1. Note that while age-0 size was not necessarily a good predictor of size later in life for these populations, it did predict abundance.

For four of the populations, BS cod, BS haddock, BS capelin and GOA pollock, there was statistical evidence for negative effects of abundance on size for at least one age interval (4th column in Figure 3, representing B_j coefficients in Equation 2. There did not seem to be a pattern of age intervals with negative effects of abundance on size, the expected consequence of compensatory density dependence in growth (4th column), also showing weak associations in abundance—the expected consequence of compensatory density
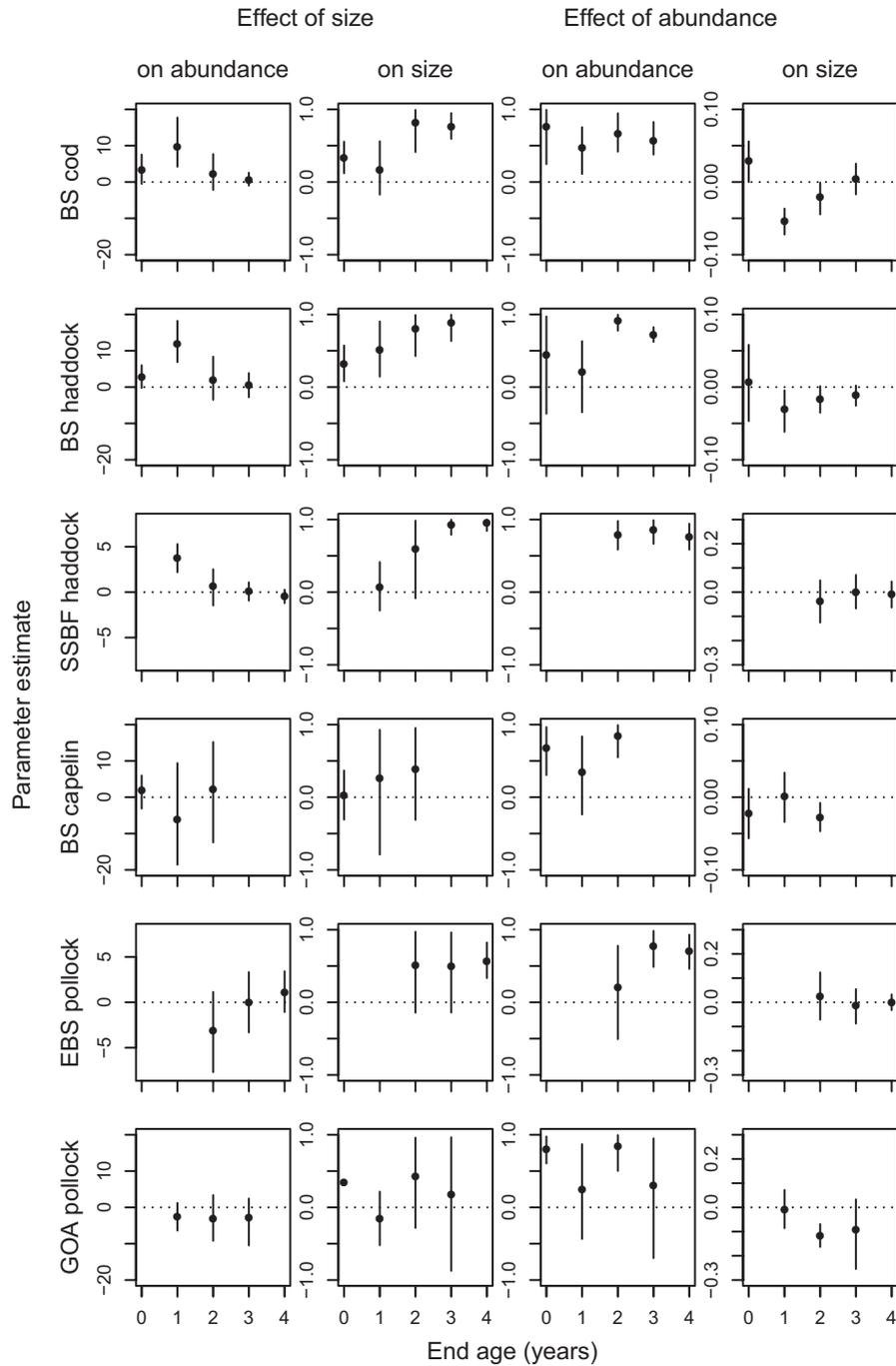
FIGURE 3 Parameter estimates for state-space statistical model results for the six populations analysed. Points and error bars represent posterior means and 95% credibility intervals of parameters. The four columns represent, respectively, parameters c_j, C_j, b_j and B_j in Equations 1 and 2 with the x-axis representing the subscript j

dependence in survival (3rd column, representing b_j coefficients in Equation 1.

4.4 | Barents Sea cod age-resolved results

State-space analysis of the processes that link the larvae to recruitment at age 3 for BS cod suggested that the positive association between larval length and recruitment identified in the correlation analysis was mainly a result of a positive association between age-0

length and age-1 abundance (Figure 4a, Table S6). The negative association between larval abundance and age-3 length was explainable through a negative association between age-0 abundance and age-1 length. Age-to-age associations in abundance were similarly strong for all age intervals from larvae to age-3 while age-to-age associations in length were weakest at the earliest age intervals, with, in particular, age-0 length being a poor predictor of age-1 length. Note that parameters for effects of abundance and length were correlated with each other, which leads to higher variance of
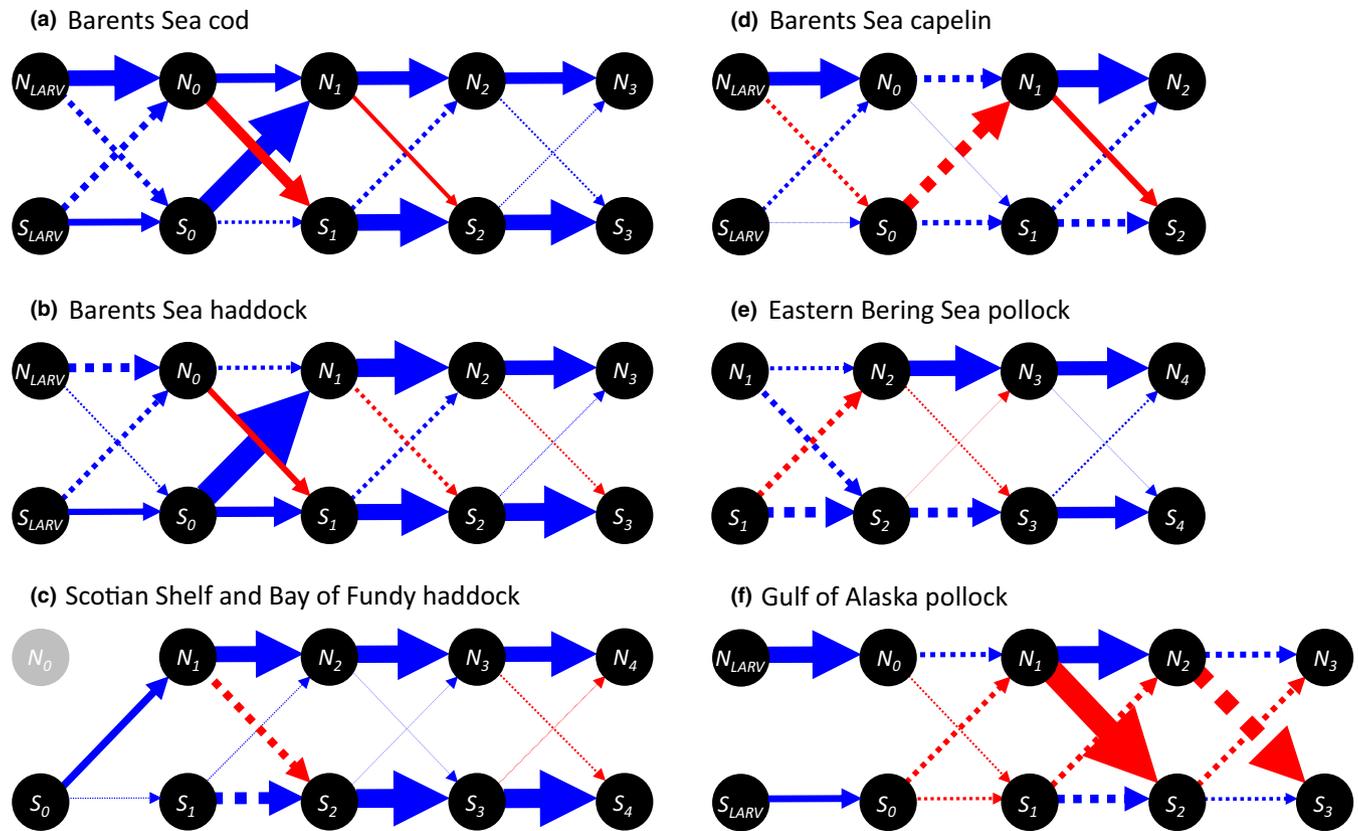
FIGURE 4 Schematic presentation of state-space statistical model results for the six populations analysed. The results show associations between abundance (N) and mean body size (S) at subsequent ages early in life (subscripts denote age). Negative estimates are shown by red arrows, positive by blue, with arrow widths proportional to parameter estimates. Dotted-lined arrows: 95% credibility intervals include zero

each parameter when interpreted alone (Figure S7 in Appendix S3: Supporting Results).

4.5 | Barents Sea haddock age-resolved results

Similar to BS cod, we found that the positive association between larval length and recruitment in BS haddock was mainly a result of a positive association between age-0 length and age-1 abundance (Figure 4b, Table S7). Results also showed negative associations between abundance and changes in mean length from age 0 onwards, but these associations were weaker than for BS cod. The uncertainty in these and other parameters was inflated because of correlation between parameters (Figure S8 in Appendix S3). Interestingly, the negative association between mean lengths of a year-class at ages 0 and 3 (while not statistically significant for larvae, Figure 2) seemed to be due to positive associations between length and changes in abundance at early ages combined with negative associations between abundance and changes in length at later ages.

4.6 | Scotian Shelf and Bay of Fundy haddock age-resolved results

The age-resolved analysis for SSBF haddock showed that the positive association between age-0 weight and age-4 abundance

identified in the correlation analysis was caused by a positive association between age-0 weight and age-1 abundance (Figure 4c, Table S8). However, without data on age-0 abundance, it was not possible to assess whether this association might be confounded by a possible positive association between weight and abundance at age 0. We found no evidence for abundance effects on weight or weight effects on abundance between ages 1 and 4. Lack of associations between weights at ages 0 and 1 with weight at age 4 was caused by weak age-to-age associations in weight before age 2.

4.7 | Barents Sea capelin age-resolved results

Consistent with the correlation analysis, we found no evidence for effects of length on subsequent abundance for BS capelin (Figure 4d, Table S9). The negative association between larval abundance and length at age 2 shown by the correlation analysis seemed to be explained by a negative association between age-1 abundance and age-2 length. Note, however, that parameters for effects of abundance and length at age 0 on abundance and length at age 1 were correlated with each other, which leads to higher variance of each parameter when interpreted alone (Figure S10 in Appendix S3). Age-to-age associations in abundance were weakest from age 0 to age 1. Age-to-age associations in length were particularly weak from larvae to age 0 and uncertain for later ages.

4.8 | Eastern Bering Sea pollock age-resolved results

Consistent with the correlation analysis, we found no evidence for effects of weight on subsequent abundance or abundance on weight for EBS pollock (Figure 4e, Table S10). Age-to-age associations in abundance were weakest from age 1 to age 2. Age-to-age associations in weight were uncertain for early age intervals because of correlated parameters for weight and abundance effects (Figure S11 in Appendix S3).

4.9 | Gulf of Alaska pollock age-resolved results

While the correlation analysis for GOA pollock revealed no significant links between larval abundance and length with age-3 abundance and weight, the age-resolved analysis revealed a negative association between age-1 abundance and age-2 weight (Figure 4f, Table S11). One consequence of this negative association (combined with the positive association between abundances at ages 1 and 2) is that a negative correlation between abundance and size is established at age 2 ($r = -0.73$). As a result, model coefficients for the transition from age 2 to age 3 are uncertain, because it is difficult to separate effects of abundance from effects of size (Figure S12 in Appendix S3). If we parsimoniously assume no effects of age-2 size on age-3 abundance (c_3) or of age-2 abundance on age-3 size (B_3), the coefficients for the age-to-age associations in abundance (b_3) and size (C_3) are both between 0.5 and 1 (Figure S12). This means that the weak correlations between larval and age-3 abundances and lengths found by the correlation analysis were mainly explainable by weak links between age-0 and age-1 abundances and lengths.

We found no evidence for size effects on abundance; this conclusion did not change if the sparse age-0 data were omitted from the model, and associations between larval abundance and length and age-1 abundance were assessed directly (shown as the "baseline model" for GOA pollock in Figure S15 in Appendix S3). While the effects of larval abundance on age-0 length and of larval length on age-0 abundance were not modelled, the available data did not suggest strong correlations (larval abundance—age-0 length: $r = -0.21$, $N = 9$, $p = 0.58$; larval length—age-0 abundance: $r = 0.03$, $N = 9$, $p = 0.94$).

Note that parameter estimates for effects on age-0 abundance and length should be interpreted with caution as they unrealistically assumed no process errors and known observation errors (see the description of the model development for GOA pollock in Appendix S2). Based on simple correlation analysis, the associations were significant at $\alpha = 0.10$ rather than 0.05 (larval—age-0 abundances: $r = 0.66$, $N = 9$, $p = 0.05$; larval—age-0 lengths: $r = 0.60$, $N = 9$, $p = 0.09$).

4.10 | Inter-cohort density dependence

Models that included inter-cohort density dependence (Figure S15 in Appendix S3: Supporting Results) suggested that age-2 length in BS haddock was more strongly and negatively associated with the abundance of age-2 fish the year before than with the abundance

of its own year-class (i.e. age-1 the year before). The same was the case for BS capelin. There was no indication of negative effects of abundance of the older fish on survival; on the other hand, some estimates were positive. These results should be treated with some caution due to slow convergence and several strongly correlated parameters for inter- and intra-cohort density dependence (not shown).

5 | DISCUSSION

Monitoring surveys of fish eggs, larvae and juveniles are routinely conducted for a range of commercially important species to get early indications of year-class strength and to understand better the "black-box" recruitment process (e.g. Dragesund et al., 2008). Here, we demonstrate how we can gain new insights into early life dynamics prior to recruitment to the fishery by linking abundance and size information at several pre-recruitment ages in one coherent analysis. Specifically, by moving beyond abundance correlations, we identify relevant stages and mechanisms that shape recruitment variability. Key findings for the six populations analysed are a possible link between life history and when size matters for survival, a possible link between size-dependent mortality and density-dependent growth, and a possible "decoupling" between density dependence in growth and density dependence in survival.

5.1 | When does size influence abundance?

Our results suggest size-dependent survival for three of the six populations. Specifically, for BS cod, BS haddock and SSBF haddock, large mean body size as larvae and/or juveniles is associated with high survival during the first winter (i.e. as expressed as high age-1 abundance) and with strong recruitment three to four years later. The associations between mean body size and changes in abundance are most parsimoniously explained in terms of survival, as we consider systematic associations between body size and migration in and out of the survey areas or with catchability less likely. For SSBF haddock, some caution is needed, as we lack abundance data from the first year of life, and it is possible that the size-abundance relationship is already established at the onset of the first winter. These associations are consistent with earlier studies correlating larval and juvenile size of BS cod and BS haddock to recruitment (e.g. Ottersen & Loeng, 2000, Stige et al., 2015) and with findings that large size of temperate juvenile fishes is frequently associated with enhanced winter survival (Sogard, 1997). One implication of these findings is that in order to understand and potentially predict recruitment in these populations, it is important to investigate how environmental factors influence size and abundance during the first growing season, in contrast to later ages when size appears to be relatively unimportant for survival.

For BS capelin, EBS pollock and GOA pollock, we found no associations between body size and survival. Note that for EBS pollock, we lacked data prior to the first winter. However, year-class strength

of EBS pollock has previously been associated with total energetic reserves acquired by juvenile fish before the first winter, as measured by the product of energy density and body size; thus, body size alone may not be sufficient for high survival (Heintz, Siddon, Farley, & Napp, 2013). One possible explanation for the lack of association for GOA pollock is a long-term increase in predation rates by a growing predator population (arrowtooth flounder), which has had a major impact on juvenile survival (Bailey et al., 2012), and may have masked any patterns of size-dependent survival. Hence, lack of detected association in our study does not necessarily imply lack of a biologically significant relationship, as it was not feasible in our study to control for effects of environmental changes on survival that potentially dominated over the effects of intra-population factors. The non-significant effect of size on age-0 and age-1 abundance in BS capelin is, however, consistent with an age-resolved analysis that did account for effects of environmental covariates (Stige et al., 2010).

One possible explanation for survival benefits of large size is that large individuals are more tolerant of starvation or physical extremes than smaller conspecifics (Miller et al., 1988; Sogard, 1997). Large body size often means high energy reserves, which can increase survival through a period with adverse environmental conditions. The finding that size appears to be particularly important for survival during the first winter of life supports this explanation: The first winter of life may be energetically demanding for high-latitude fishes due to lower food availability than in summer, limited light available for visual feeding, unfavourable temperature conditions and, for many species, needs for behavioural adaptations as the juveniles move from pelagic to more demersal habitats. We note that low recruitment in BS cod and BS haddock is associated with low temperatures during the first winter of life (Bogstad, Dingsør, Ingvaldsen, & Gjøsæter, 2013), indicating that environmental conditions in this period of life are important for survival. However, predation regimes may also change around this period of life, especially for species that move from pelagic to demersal habitats. For example, at this time, BS cod and BS haddock become more exposed to predation from demersal fish, including from the older, demersal stages of cod, which are known to significantly affect recruitment of both BS cod and haddock (e.g. Yaragina, Bogstad, & Kovalev, 2009, Stige et al., 2010). Such increased predation may be size selective, as large individuals are likely to have fewer predators and be better at escaping the predators than smaller conspecifics (Bailey & Houde, 1989; Houde, 1987). Stomach content data suggest that large body size at the end of the first growing season may potentially reduce predation risk: cod of 10–14 cm is the most abundant prey length group of cannibalistic BS cod (Yaragina et al., 2009), while annual mean lengths of age-1 BS cod in our data vary from 10 to 18 cm (and of age-1 BS haddock from 14 to 17 cm). It is therefore possible that in years with high mean body size of age-0 cod and haddock, the juveniles grow more rapidly out of the size range most susceptible to predation from older cod, leading to increased survival.

We note that all the populations with evidence of size-dependent survival change from pelagic to more demersal habitats as juveniles, prior to their first winter (Bergstad, Jørgensen, & Dragesund,

1987; Cargnelli et al., 1999). In comparison, walleye pollock in the EBS and GOA appear to have a more gradual transition from pelagic to demersal habitats, with age-0 fish being pelagic, age-4 and older fish being demersal, and age-1 and age-2 fish being found in both habitats (Duffy-Anderson et al., 2003). Capelin are pelagic as larvae, juveniles as well as adults (Gjøsæter, 1998). The transition from pelagic to demersal habitat is associated with habitat-linked shifts in density-dependent mortality, diet and predators (Juanes, 2007). As a hypothesis for further research, we propose that our findings may reflect a general pattern, namely that large body size at a transition from pelagic to demersal habitats may often give increased survival due to either size-dependent predation by demersal fish or increased energy reserves.

5.2 | When does abundance influence size?

Our results suggest compensatory density dependence in growth for four of the six populations. Specifically, for BS cod, BS haddock, BS capelin and GOA pollock, we found that high abundance is associated with low mean body size at a later age, mainly at age 1 for BS cod and BS haddock and age 2 for BS capelin and GOA pollock. No such associations were found for SSBF haddock or EBS pollock, but we note that we lacked data to analyse possible effects on size at age 1 for both these populations. These associations can be interpreted as compensatory density dependence in growth, that is, that at high abundance, mean growth is reduced, and/or as a combination of density-dependent mortality and size-dependent mortality, that is, that increased mortality at high abundance disproportionally affects large individuals. We consider that compensatory density dependence in growth is the most parsimonious explanation, as a pattern of size-selective mortality disproportionally affecting large individuals would be contrary to what is expected under crowding.

The timing of the apparent density-dependent growth of BS cod and BS haddock coincides with the size-dependent survival during the first winter of life and is consistent with competition for suitable space for feeding as well as shelter from predation when pelagic juveniles settle to the sea floor (Juanes, 2007). As we found no indication of size-dependent survival after age 1, we do not expect that reduced size at age 1 at high abundance influences survival to ages 2 and 3 (i.e. recruitment), although it could influence, for example, reproductive potential later in life. Unfortunately, we lack data to assess whether SSBF haddock also show density-dependent growth when they change from pelagic to demersal habitat. Density-dependent growth during pelagic stages of BS capelin is likely a result of exploitative competition, as the capelin have a strong top–down effect on the biomass of their zooplankton prey, which in turn have a positive bottom-up effect on capelin size at age (Gjøsæter, Dalpadado, & Hassel, 2002; Stige, Kvile, Bogstad, & Langangen, 2018). The timing of strong intra-specific competition at age 2 in capelin is consistent with the average total biomass doubling from age 1 to age 2 before declining in ages 3 and 4 (according to 1972–2015 survey data). Interestingly, density-dependent growth to age 2 in BS capelin impacts population dynamics by fast growth leading to earlier (size-dependent)

maturation and higher mortality after age 2 (as most of the capelin are thought to die shortly after spawning, Gjøsæter, 1998). Results suggested density-dependent growth of GOA pollock from age 1 to age 2, while EBS pollock showed no density dependence in growth. We hypothesize that this difference may be related to winters being longer and colder in the EBS relative to the GOA. Hence, growth of EBS pollock may more often be temperature limited rather than food limited (Laurel, Spencer, Iseri, & Copeman, 2016), and thereby less likely to show density dependence.

It should be added that the negative associations between abundance and changes in body size do not necessarily reflect causal effects of crowding, but could be caused by extrinsic factors correlated with abundance. For example, the negative associations between abundance and changes in body size in BS cod and BS haddock can alternatively be explained by high temperatures causing both high survival of eggs, larvae and early juveniles and strong currents transporting the juveniles farther eastwards than normal in the Barents Sea, where ambient temperatures are low and individual growth slow (Ottersen, Helle, & Bogstad, 2002). The resulting contrast between temperatures experienced at different ages would also explain the negative correlation found between BS haddock size at ages 0 and 3. Analyses of spatially resolved data would be needed to assess this hypothesis.

5.3 | When is mortality density-dependent?

Our study provides estimates of the strength of compensatory density dependence in survival, a key factor for understanding population dynamics and how fishing and other factors influence fish populations (Rose et al., 2001). To our surprise, the ages with strongest indications of compensatory density dependence in growth were not the ages with strongest indications of compensatory density dependence in survival. A possible interpretation is that there may not be a direct correspondence between density dependence in growth and density dependence in survival. For example, for both BS capelin and GOA pollock it appears that density dependence in survival occurs at a younger age than density dependence in growth. This pattern could be caused by low energy storage capacity of small fish (Miller et al., 1988), which may make young life stages particularly susceptible to starvation mortality under crowding, whereas older life stages may to a larger extent be able to grow poorly while still surviving periods of starvation. This result must be interpreted with caution, as our method may provide rather rough estimates of density-dependent survival. The pattern is, however, consistent with density dependence early in life typically being reported to affect abundance (i.e. recruitment), whereas density dependence after the recruitment age mostly being reported to occur through growth rather than survival (Andersen et al., 2017; Zimmermann et al., 2018).

5.4 | Inter-cohort density dependence

Our main models only considered within-cohort density dependence. When also considering the possible density effects of the preceding year-class, results suggested that growth of BS capelin and BS haddock was more strongly regulated by the older fish than by the year-class itself. We speculate that this result might reflect asymmetric competition, for example because the older fish displace the younger fish to sub-optimal habitats (which is consistent with the age-1 and age-2 groups of capelin dividing the Barents Sea by forming migratory waves that move in opposite directions, Fauchald, Mauritzen, & Gjøsæter, 2006). We note that also the main models suggested density dependence in growth at these age intervals, but that the additional results provide more detailed insights into which density (which age) the growth depends on. The positive estimates for density effects of the preceding year-class on abundance are likely caused by auto-correlated effects of factors not explicitly modelled, such as predation effects on survival. Similarly, Ricard et al. (2016) found positive lag-1 autocorrelation in recruitment residuals for a large number of Atlantic fish stocks. Ricard et al. (2016) found, however, negative autocorrelation in a number of stocks at time lags from three to five years, suggesting cannibalism or inter-cohort competition. Accounting for such interactions in the state-space analysis of age-resolved dynamics would require careful consideration of which ages are potential competitors or predators on other ages, for example, based on diet data. Our consideration of only the one-year-older age-class most likely addressed the competitors, while potentially missing cannibalism by older fish.

5.5 | Methodological limitations and prospects for future studies

While the state-space analysis approach here applied has potential to reveal new insights, the method has limitations. In particular, the estimation of density dependence may be strongly sensitive to observation error assumptions, thus necessitating sensitivity analyses unless the magnitudes of observation errors are known (Auger-Méthé et al., 2016; Ives et al., 2003). As shown by the sensitivity analysis we conducted (Figure S14 in Appendix S3), uncertain magnitudes of measurement errors contribute to uncertainty in the parameter estimates in our study, although our main findings appear robust. Further, factors not explicitly modelled could bias parameter estimates if correlated with abundance or body size. Such variables include climate factors, abundances of prey, predators and competitors from other year-classes or species, and unaccounted-for changes in survey coverage or mesh size. Adding such variables in the analysis would lead to more unbiased parameter estimates, but with more variables in the model, the credibility intervals for the parameters may increase, and model development would be more complicated and computation time might be restrictive. Alternatively, resulting patterns revealed by the state-space approach can be interpreted with respect to other possible factors (e.g. prey, predators, competitors) before underlying mechanisms are theorized. We chose not to add environmental covariates, but note that, as in all statistical modelling, the results are in principle correlative and need to be interpreted accordingly. Strong trends in the data, due to, for example, overfishing or regime shifts, would also complicate analysis

and interpretation of results, both for statistical reasons (the effective degrees of freedom would be low) and because the population dynamics may have changed (become non-stationary). Variability at timescales of around 1–10 years generally dominated over the long-term trends in our data (Figures S1–S6 in Appendix S3), but we note that the negative association between age-0 abundance and age-1 length in BS cod was likely driven by a long-term increase in age-0 abundance and a decrease in age-1 length since the 1980s.

Despite these limitations, using a state-space analysis approach has advantages compared with simple correlation analysis, by utilizing information from several ages or life stages in a coherent analysis framework. For example, while the correlation analysis identified positive relationships between larval or juvenile size and recruitment in three populations, the age-resolved state-space analysis showed at which age these relationships were established. Hence, our results shed light on the possible mechanisms that link early life stages to recruitment. Further, correlation results might be inconsistent, for example showing strong association between abundance at ages 1 and 3 but not between ages 2 and 3, hence implicitly pointing to uncertainties in the data. Results from a state-space analysis are easier to interpret as such inconsistencies are avoided while uncertainties in the data are explicitly accounted for.

6 | CONCLUSIONS

Our study provides a novel perspective to study recruitment dynamics by focusing in-depth on the intertwined processes of growth and survival at early ages. The approach paves a way for a better, more meaningful understanding of recruitment processes compared with directly linking recruitment to the biomass of spawners, as is often done in recruitment models. We encourage others to apply the method presented in our study to other populations where data are available. Our results underscore the importance of size for survival early in life and suggest that size-dependent mortality and density-dependent growth frequently occur at a transition from pelagic to demersal habitats. Overall, these findings can be used to develop mechanistically based hypotheses of large-scale patterns in early life dynamics, guide future research by identifying stages and processes that are particularly important for recruitment and improve recruitment predictions.

DATA AVAILABILITY STATEMENT

Appendix S4 contains tables with all time-series analysed in this study. See Appendix S2 for a full description of data sources and original citations.

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