

Fine-scale population dynamics in a marine fish species inferred from dynamic state-space models

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Summary

1. Identifying the spatial scale of population structuring is critical for the conservation of natural populations and for drawing accurate ecological inferences. However, population studies often use spatially aggregated data to draw inferences about population trends and drivers, potentially masking ecologically relevant population sub-structure and dynamics.

2. The goals of this study were to investigate how population dynamics models with and without spatial structure affect inferences on population trends and the identification of intrinsic drivers of population dynamics (e.g. density dependence).

3. Specifically, we developed dynamic, age-structured, state-space models to test different hypotheses regarding the spatial structure of a population complex of coastal Atlantic cod (*Gadus morhua*). Data were from a 93-year survey of juvenile (age 0 and 1) cod sampled along > 200 km of the Norwegian Skagerrak coast. We compared two models: one which assumes all sampled cod belong to one larger population, and a second which assumes that each fjord contains a unique population with locally determined dynamics. Using the best supported model, we then reconstructed the historical spatial and temporal dynamics of Skagerrak coastal cod.

4. Cross-validation showed that the spatially structured model with local dynamics had better predictive ability. Furthermore, posterior predictive checks showed that a model which assumes one homogeneous population failed to capture the spatial correlation pattern present in the survey data. The spatially structured model indicated that population trends differed markedly among fjords, as did estimates of population parameters including density-dependent survival. Recent biomass was estimated to be at a near-record low all along the coast, but the finer scale model indicated that the decline occurred at different times in different regions. Warm temperatures were associated with poor recruitment, but local changes in habitat and fishing pressure may have played a role in driving local dynamics.

5. More generally, we demonstrated how state-space models can be used to test evidence for population spatial structure based on survey time-series data. Our study shows the importance of considering spatially structured dynamics, as the inferences from such an approach can lead to a different ecological understanding of the drivers of population declines, and fundamentally different management actions to restore populations.

Key-words: age-structured model, Bayesian modelling, *Gadus morhua*, Norway, observation error, population dynamics, Skagerrak, spatial structure, state-space models, time series

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Introduction

The concept of scale is central to ecological research and understanding (Levin 1992). A mismatch between study scale and the scale of relevant ecological processes can lead to failure to identify the mechanisms driving a system (Allen & Hoekstra 1992). This is particularly true in population ecology, where processes such as density-dependent survival may go undetected if the study scale or resolution is large relative to the scale of population spatial structuring (Ray & Hastings 1996; Williams & Liebhold 2000). If multiple independent or semi-independent population subunits are considered as one, spatial differences in abundance are averaged out, and local population processes are obscured (Einum & Nislow 2005; Thorson *et al.* 2015). Thus, studies of populations which may be structured in space (for instance, have low exchange rates among subareas and exhibit heterogeneous population densities) require an explicit consideration of scale.

In an applied context, mischaracterization of the scale of population spatial structuring can have important consequences. In recent years, population spatial structure has been documented in a number of fish stocks, often at finer spatial scales than those at which assessment or management occurs (Reiss *et al.* 2009; Berger *et al.* 2012; Holmes *et al.* 2014). Failure to appropriately account for spatial structure can lead to the overexploitation of weaker population units and the erosion of stock diversity (Hutchinson 2008; Ying *et al.* 2011). Appropriate consideration of population spatial structure is important for assessing the conservation status of threatened or overexploited species (e.g. Ward *et al.* 2010), as well as for developing effective recovery plans. It is, therefore, critical to identify the appropriate spatial scale at which to study, monitor and assess populations.

To track population abundance through time, survey counts are often aggregated spatially into an index of abundance, which is then used for studies of population dynamics or for management. In this approach, population processes such as density dependence and productivity are implicitly assumed to be homogeneous across the study area, and any heterogeneity or asynchrony among survey counts distributed in space is attributed to observation error, that is, noise associated with the sampling process. In reality, variation among locations may also be due to true differences in abundance trends, for instance, due to differences in external influences on the population(s) or local intrinsic dynamics. Distinguishing the 'true' differences from observation errors is a challenge, and yet necessary for drawing appropriate ecological inferences (Freckleton *et al.* 2006; Thorson *et al.* 2015).

State-space models provide a flexible framework for fitting complex models of ecological processes to data which are associated with observation error, for example, field survey data. The data are treated as noisy observations of

an underlying dynamical/stochastic process or system. One set of equations describes the underlying process(es) (in this case the stochastic population dynamics), while a second set of equations describes the relationship between the 'true' state of the population and the data, essentially modelling the error associated with the sampling process (Clark & Bjørnstad 2004). Within this framework, spatial population structuring can be specified explicitly by choosing the number of populations (i.e. processes) to model, describing how these may be linked (e.g. through migration or correlated process errors), and specifying which data are observations of which processes.

In this study, we developed a set of state-space models for a fish stock with evidence of spatial population structure: Atlantic cod (*Gadus morhua*) on the Skagerrak coast of Norway. We considered multiple hypotheses for the biological processes underlying the observed spatial and temporal patterns in survey data, and through posterior predictive checks, tested the ability of models incorporating these hypotheses to explain the observed patterns in the data. Furthermore, we investigated how the alternative models influenced the identification of intrinsic drivers of population dynamics (e.g. density dependence), and inferences on population trends. We then used this model framework to reconstruct the historical spatial and temporal dynamics of these cod populations going back nearly 100 years.

Materials and methods

STUDY SYSTEM

Skagerrak coastal cod reside in nearshore waters along the southern coast of Norway and Sweden. They are highly fecund batch spawners, spawning primarily from February to April (Gjøsæter 1990; Espeland *et al.* 2007). After pelagic egg and larval phases, juveniles settle in nearshore demersal habitats during May and June. Coastal cod display a 'fast' life-history relative to most cod stocks: over 50% are mature by age 3, and few individuals survive past age 5, giving a generation length of c. 4 years (4.28 years in Knutsen *et al.* 2011). While older fish (age 2+) are often found in deeper waters (Hjort & Dahl 1900), habitat overlap between age-0 and age-1 cod results in strong competitive and cannibalistic interactions between cohorts (Gjøsæter 1990; Bjørnstad *et al.* 1999).

The question of population spatial structure in Skagerrak coastal cod dates back to the pioneering fisheries scientist Johan Hjort, who supposed that mixing of eggs and larvae must be sufficient to result in one homogeneous population along the coast (Hjort & Dahl 1900). Subsequent work has identified patterns and mechanisms supporting finer scale structuring. Some genetic differentiation occurs on the scale of individual fjords (c. 30 km), although the signals are relatively weak, as is common with marine species where eggs and larvae can be mixed in ocean currents (Waples 1998; Jorde *et al.* 2007; Knutsen *et al.* 2011). Data on juveniles collected along the coast (see below) have shown elevated correlation in recruitment within regions, but nearby regions appear to be no more correlated than the most distant regions (Fromentin *et al.* 2000; Rogers *et al.* 2014). Tagging

studies of age-1+ cod indicate that most individuals are sedentary, not dispersing more than a few kilometres on average (Rogers *et al.* 2014), and eggs can be retained within fjords by inward-flowing currents (Ciannelli *et al.* 2010), thus suggesting mechanisms through which local populations may be maintained.

Skagerrak coastal cod have been harvested by commercial and recreational fishers for centuries. Already by the mid-1800s there was concern that fish were disappearing from the nearshore fjord habitats due to increasing fishing pressure (Hjort & Dahl 1900; Dannevig 1907). By the early 1900s some fjord populations showed typical signs of intense exploitation; that is, a marked truncation of the age and size structure (Lund *et al.* 2011). Fishing pressure continues to be high, with recreational hook and line gear and fixed gears such as gillnets and traps responsible for much of the fishing mortality (Fernández-Chacón *et al.* 2017). The cod fisheries on the Norwegian Skagerrak coast are largely unregulated apart from recent restrictions on size (40 cm minimum since 2010, roughly corresponding to 2-year-old fish) and the recent (2006) implementation of three small (<1 km²) marine reserves where only hook and line gear is allowed (Moland *et al.* 2013). A fourth reserve (1.5 km²) was established in 2012.

TIME-SERIES DATA

Every autumn since 1919, juvenile cod were sampled at a set of fixed locations along the Norwegian Skagerrak coast. The survey initially included 66 sampling stations between the southern tip of Norway and Kragerø, but was later expanded (in 1936, 1953 and 1962) north to Oslofjord and east to the Swedish border (Fig. 1). At each sampling station, a beach seine was hauled, covering an area up to 700 m². Captured in the hauls were age-0 cod hatched that spring as well as age-1 cod. Numbers and individual

lengths of cod were recorded, and ages were determined based on a mixture analysis applied to length-frequency distributions for each year and region (details in Rogers *et al.* 2011). Only stations with at least 40 years of observations ($n = 108$) and survey years through 2011 were included in this analysis.

PROCESS MODELS

We considered two alternative hypotheses regarding the spatial structuring of Skagerrak coastal cod: (1) One panmictic population ('coast-wide model'); and (2) Fjord-specific populations with locally determined dynamics and spatially correlated recruitment variation, representing for instance shared climatic effects on recruitment ('spatially structured model'). In case 1, all individuals are modelled as belonging to one population, thus only one set of process equations is used to describe the dynamics of Skagerrak coastal cod. In case 2, the population dynamics within each fjord (f) are modelled according to their own age-structured dynamics, resulting in a separate set of process equations for each fjord. These fjord-specific process models are linked through b_y , a random year effect describing interannual variation in recruitment common to all populations. Note that while we refer to spatial units in this study as 'fjords', some of the areas are bays or inshore areas protected by islands, and not proper fjords.

The population dynamics equations for the spatially structured model are as follows:

$$N_{0,f,y} = \text{SSB}_{f,y} e^{2y - \gamma_f N_{0,f,y-1} + b_y + \varepsilon_{0f,y}} \quad \text{eqn 1a}$$

$$N_{1,f,y} = N_{0,f,y-1} e^{-\sigma_f + \varepsilon_{1f,y}} \quad \text{eqn 1b}$$

$$N_{a,f,y} = N_{a-1,f,y-1} e^{-Z}, \quad \text{for } 2 \leq a \leq 5 \quad \text{eqn 1c}$$

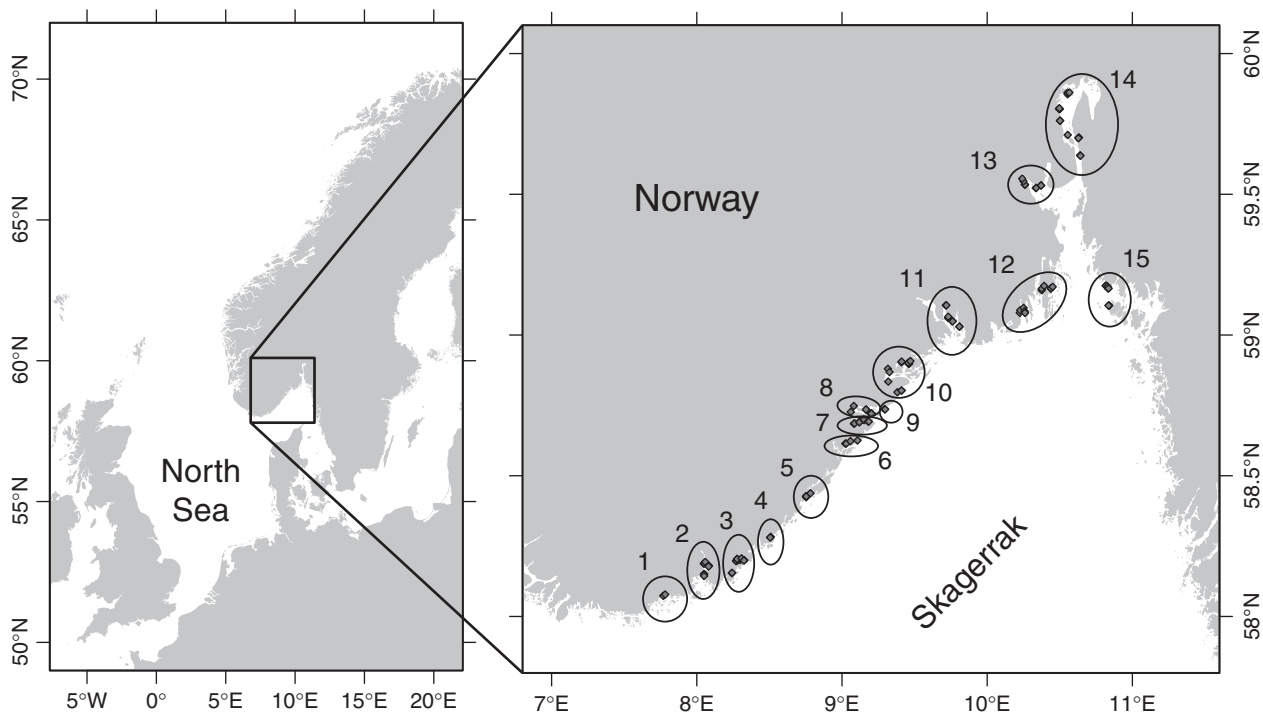


Fig. 1. The Skagerrak coast of southern Norway. Sampling stations (diamonds) are grouped into fjords as follows: 1. Torvefjord, 2. Topdalsfjord, 3. Høvåg, 4. Buåfjord, 5. Flødevigen, 6. Lyngor, 7. Sandnesfjord, 8. Søndeledfjord, 9. Risør Skerries, 10. Kragerø, 11. Langesund, 12. Tjøme – Sandefjord, 13. Holmestrand, 14. Inner Oslofjord, 15. Hvaler.

$$\text{SSB}_{f,y} = \sum_{a=2}^5 N_{a,f,y} W_a M_a \quad \text{eqn 1d}$$

$$b_y \sim N(0, \sigma_b^2), \varepsilon_{0f,y} \sim N(0, \sigma_{0f}^2), \varepsilon_{1f,y} \sim N(0, \sigma_{1f}^2), \quad \text{eqn 1e}$$

where $N_{a,f,y}$ is the number of individuals in age class a in fjord f in year y . Recruitment within each fjord (N_0) is a function of the spawning stock biomass (SSB) in that fjord, a constant productivity rate (α_f), a reduction in survival due to intercohort competition and/or cannibalism (γ_f), a random year effect (b_y) describing interannual variation in recruitment common to all populations, and a normally distributed error term, which describes population-specific stochasticity in recruitment. The age-0 process errors ($b_y + \varepsilon_{0f,y}$) are thus correlated across all populations, with a correlation between fjords i and j equal to:

$$\sigma_b^2 / \left(\sqrt{\sigma_{0i}^2 + \sigma_b^2} \sqrt{\sigma_{0j}^2 + \sigma_b^2} \right)$$

Survival to age 1 depends on the mortality rate c and a stochastic error term. The adult mortality rate (Z) is assumed to be constant at $Z = 0.916$, corresponding to an annual survival rate of 40%. Estimating Z within the model is not possible without time-series data on adults, as adult mortality becomes confounded with α_f ; therefore, this estimate is based on mark-recapture studies and life-table analysis (see Julliard *et al.* 2001; Knutsen *et al.* 2011) and incorporates both natural and fishing mortality. Spawning stock biomass (in kg) depends on the abundance, mass (W_a) and maturation probability (M_a) of individuals in each age class. Maturation probabilities (M_a) and body mass-at-age (W_a), were estimated based on an analysis of gillnet survey data from 2001 to 2006 (see Table S1, Supporting Information; Olsen *et al.* 2004, 2008; Knutsen *et al.* 2011), and given fixed values for this study. While cod age 10 and older have been reported in the coastal Skagerrak, individuals older than age 5 make up <1% of the cod captured in the gillnet surveys and are probably uncommon in these populations. Life-history studies from the 1900s and 2000s suggest that the basic life-history parameters have not changed in the last century (Lund *et al.* 2011).

The dynamics for the coast-wide single-population model are similar, but all individuals are modelled as belonging to a single population (no fjord subscript), and necessarily the shared random year effect (b_y) is excluded, meaning the year effect goes into the age-0 error term.

OBSERVATION MODEL

When fitting models to data, observation error in the data can obscure the underlying population processes. In state-space models, the sampling (observation) process is modelled explicitly. For Skagerrak coastal cod, which are sampled at many survey stations along the coast, the catch at any one station (s) is a function of the total abundance of cod in the sampled population ($N_{a,f,y}$ or $N_{a,y}$ depending on whether the spatially structured or coastwide model is used) and the proportion that is vulnerable to the sampling gear at that station ($q_{f,s}$). Our observations were station-specific catches of age-0 (I^0) and age-1 (I^1) cod. Because catches at individual stations were sometimes zero, often low (<10) and occasionally very high (maximum age-0 catch = 934), catches were modelled according to a Poisson log-normal error distribution (Knape, Jonzén & Sköld 2011):

$$z_{s,f,y}^0 = N_{0,f,y} q_{f,s} e^{\eta_{0,s,f,y} - \frac{\tau_0^2}{2}}, \eta_{0,s,f,y} \sim N(0, \tau_0^2) \quad \text{eqn 2a}$$

$$I_{s,f,y}^0 \sim \text{Poisson}\left(z_{s,f,y}^0\right) \quad \text{eqn 2b}$$

$$z_{s,f,y}^1 = N_{1,f,y} q_{f,s} e^{\eta_{1,s,f,y} - \frac{\tau_1^2}{2}}, \eta_{1,s,f,y} \sim N(0, \tau_1^2) \quad \text{eqn 2c}$$

$$I_{s,f,y}^1 \sim \text{Poisson}\left(z_{s,f,y}^1\right) \quad \text{eqn 2d}$$

Observation errors were assumed to be independent among years, stations and age classes. The log-normal bias correction $\tau^2/2$ adjusts the expected value of the Poisson distribution (z) to be equal to the mean rather than median population size times catchability ($q_{f,s}$).

Because our goal was to draw inferences on the dynamics of cod, and not to determine the absolute abundance of cod (which is not possible without additional data), $q_{f,s}$ effectively becomes a scalar – scaling up the survey catches to total population abundance. For identifiability, $q_{f,1}$ (the catchability at the first station in each fjord) was set to a constant ($q_{f,1} = 0.01$), and all other catchabilities within that fjord were defined relative to this constant ($q_{f,s} = q_{f,1} \times q_{f,s}$). The estimated abundances are thus only relative to a fjord-specific constant, and should not be compared in an absolute sense across fjords or populations. The relative catchability of age-0 vs. age-1 fish is not estimable from the data, as it is confounded with the mortality rate from age 0 to 1 (c_f), so we set catchability to be identical for age-0 and age-1 cod, for simplicity. However, it is likely that a relatively smaller proportion of the age-1 cod are vulnerable to the beach-seine gear than the age-0 cod, and thus c_f is an overestimate of the mortality rate.

PARAMETER ESTIMATION

Models were fit within a Bayesian framework with vague priors (Table S2). Samples from the posterior distribution were obtained by Markov chain Monte Carlo (MCMC) sampling implemented in JAGS 4.2.0, using the 'rjags' package (Plummer 2016) from within the program R (R Core Team 2016). We ran three chains, each with a burn-in length of 100 000 and a monitoring period of 200 000. A thinning rate of 1/200 resulted in a total of 3000 posterior samples. Convergence was assessed using visual inspection of trace plots and Gelman–Rubin R statistics (Gelman & Rubin 1992). A simulation study was used to confirm the ability of this method to estimate population parameters and relative abundances (Appendix S1, Fig. S1).

MODEL SELECTION AND VALIDATION

Common model comparison tools such as DIC do not perform well for hierarchical models, and the Poisson log-normal model in particular (Millar 2009; Hooten & Hobbs 2015). We used k -fold cross-validation for model selection, whereby predictive ability was assessed by fitting the model to only a subset of data and comparing left out data points to model predictions (Hooten & Hobbs 2015). This was repeated $k = 10$ times with $1/k$ of the data excluded for each fold. Data were randomly assigned to a fold by sampling event; that is, age-0 and age-1 counts for a station in a year were left out simultaneously. Rather than comparing each left out data point to a discrete point estimate such as the mean of the posterior predictive distribution, we instead incorporate our uncertainty

regarding the predictions and use the log predictive density as a scoring function (Hooten & Hobbs 2015). A model with higher log predictive density across data points and k -folds has better predictive ability. A cross-validation score was calculated as follows: the predictive density of each left out data point was estimated based on MCMC samples, and then summed (on a log scale) over data points and across folds (Hooten & Hobbs 2015). Predictive density was calculated using the `dpoilog()` function in R (Grøtan & Engen 2008). The CV scores for each model were multiplied by -1 so that smaller values indicate better predictive ability, consistent with other model selection metrics.

We used posterior predictive checks (Gelman, Meng & Stern 1996; Chambert, Rotella & Higgs 2014) for further model validation. Posterior predictive checks are a way to assess whether a given model is appropriate for the data. Posterior predictive checks take the fitted model and use it to simulate replicated data to generate posterior predictive distributions. These distributions are then compared to the observed data, where an observation that fits poorly with the predictive distribution indicates that the model also is poor. Posterior predictive checks can focus on any feature of the observed data. In our case, we were particularly interested in reproducing the spatial patterns in the age-0 count data (spatial decorrelation scale), as an indicator of whether the model was capturing the spatial dynamics of the population(s). Graphical assessment (as recommended by Gelman, Meng & Stern 1996) was used to compare the spatial patterns observed in the true data to the spatial patterns in replicated datasets simulated under the different models.

Spatial patterns in the true data and model-simulated data were characterized by fitting a three-parameter correlation-by-distance model, which describes how the pairwise correlations among survey time series vary with distance between stations (Rogers *et al.* 2014). The correlation-by-distance model was

$$\rho(d) = \rho_r + \rho_0 e^{-\frac{d}{v}} \quad \text{eqn 3}$$

where $\rho(d)$ is the modelled correlation among survey time series at distance d , ρ_r is the asymptotic correlation, or background regional correlation in recruitment, and $\rho_r + \rho_0$ is the estimated correlation at zero distance. The parameter v describes the rate at which correlations decrease with distance. This model was used for validation only, and was not incorporated directly into the population model in eqn (1a). Correlation-by-distance relationships were estimated for the spatially structured and coast-wide models by fitting eqn (3) to sets of age-0 count data simulated under those models ($I_{\text{new},n}^0$, n from 1 to 3000 MCMC samples). Specifically, the pairwise Pearson's correlations among time series of simulated age-0 count data (log-transformed) were used to fit the correlation-by-distance models. The correlation-by-distance relationships ($n = 3000$) generated by each of the two models were then compared to the correlation-by-distance relationship estimated from the observed data by graphically comparing the fitted relationships. A graphical concordance between the correlation-by-distance relationship of the true data with the relationship in the model-simulated data indicate that the model captures the spatial structure in the data.

ENVIRONMENTAL DATA

Seasonal thermal conditions were characterized by averaging daily temperature measurements taken at 1-m depth in the bay

near Flødevigen (Fig. 1) since 1924. Sea surface temperatures (SSTs) measured at Flødevigen are highly correlated with records from elsewhere in the Skagerrak, and we reconstructed SSTs for 1919–1923 based on regressions with historical temperatures from nearby Torungen Lighthouse (see Rogers *et al.* 2011). Mean May–June temperatures were used to characterize the environment corresponding to the sensitive late larval and early settlement stages. Data with which to assess fjord-scale deviations from the regional temperature trend were not available.

Results

Posterior predictions for abundances (N) indicated large changes in the relative abundance of Skagerrak coastal cod over the last century (Fig. 2). In the coast-wide model, where dynamics were assumed to be homogeneous throughout the survey area, highest abundances occurred at the beginning of the time series in the 1920s, followed by a dramatic decline up until 1940. Abundance peaked again in the late 1950s, and was variable but declining until present (Fig. 2). Current SSB was estimated to be at a record low.

In contrast, the spatially structured model estimated substantial regional differences in abundance trends (Figs 2 and S2). These differences are illustrated by the SSB estimates in Fig. 2, which show regions with significant population declines beginning in the 1960s (region 11), strong declines beginning in the 1970s through present (region 5), increasing abundance during the 1960s followed by strong declines in the 1990s and 2000s (region 8), and finally, highly variable abundance throughout the time period (region 9). While local population trends differed, the spatially structured model did estimate strong correlations in recruitment of age-0 cod along the coast. The standard deviation (σ_b) for the random effect b_y gives the shared component of the age-0 process error, which constituted the majority of the process error variance for age-0 cod in most regions (Fig. 3). Oslofjord (region 14) deviated the most from the shared pattern, as indicated by the high estimate for $\sigma_{0,14}$, whereas regions 4, 6 and 9 displayed recruitment dynamics similar to the overall pattern given by b_y . A post-hoc analysis found a significant negative correlation ($r = -0.358$, $P < 0.001$) between SST measured at Flødevigen in May and June (the period of late larval development and early settlement) and the shared component of recruitment variation (b_y).

Estimates of parameters for the population dynamics were found to differ among fjords in the spatially structured model (Fig. 3). In particular, the productivity parameter (α_f) and the age-0 to age-1 survival rate (c_f) displayed a latitudinal gradient, indicating higher productivity and lower survival (e^{-c}) from age 0 to 1 in the south relative to north. Regions 12 and 15 were exceptions to this pattern, having high productivity and lower survival despite being in the north. Estimated age-0 survival rates (e^{-c}) ranged from c. 5% to 24%, but these are likely under-estimates due to being unaccounted for differences

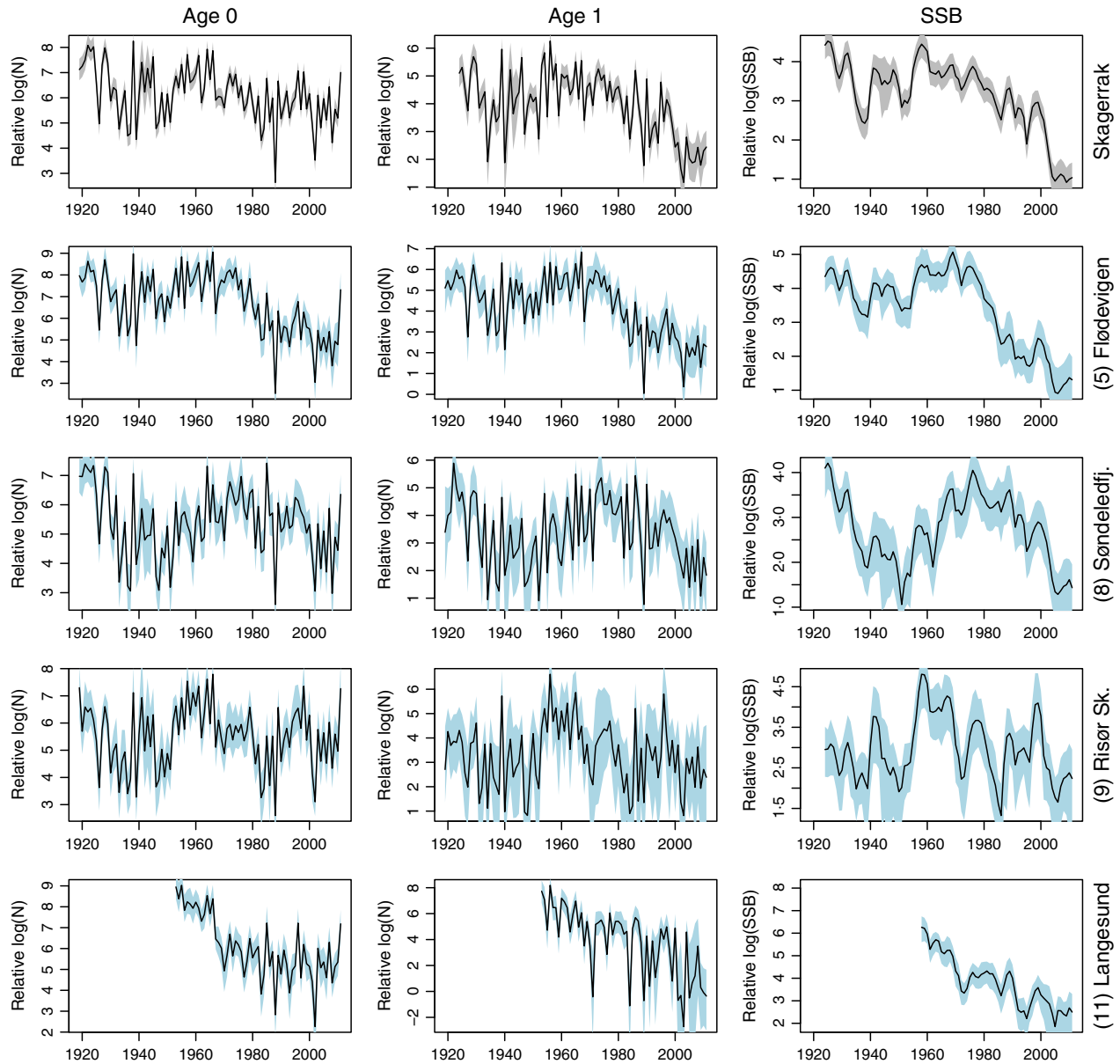


Fig. 2. Posterior means (solid black lines) of relative abundances of age-0 and age-1 cod and spawning stock biomass. Shaded areas show 90% credible intervals. The top panels give results from the coast-wide model, while the lower panels show results for 4 of the 15 regions estimated using the spatially structured model. The absolute numbers are arbitrary but the relative magnitude of changes can be compared across regions. (Fig. S2 has results for all fjords/regions.)

in catchability between age-0 and age-1 cod, as mentioned previously.

We found evidence that the strong year-to-year variation in age-0 abundance was driven in part by intercohort density dependence (γ_f). The 95% credible intervals (CIs) for γ_f were clearly different from zero for most regions in the spatially structured model, although because the prior for γ_f was constrained to be positive, this is not a true test of significance. In the coast-wide model, support for density dependence was less clear, with a 95% CI approaching zero (Fig. 3). Density dependence was estimated to be strongest in regions 12 and 15, with estimated reductions in survival of 21% and 19%, respectively, given average

abundance of the previous cohort. Density dependence estimates are given as per-capita parameters multiplied by the average model-estimated abundances because estimated absolute abundance levels (and thus per-capita rates) cannot be compared among fjords (see Materials and methods).

Observation errors were large ($\tau > 1$) for both the coast-wide model and the spatially structured model, reflecting the high degree of noise associated with sampling at small, fixed locations on the coast. Errors were higher for age 1 than for age 0, and higher for the coast-wide model than for the spatially structured model, which partitioned some of the variation in observations among

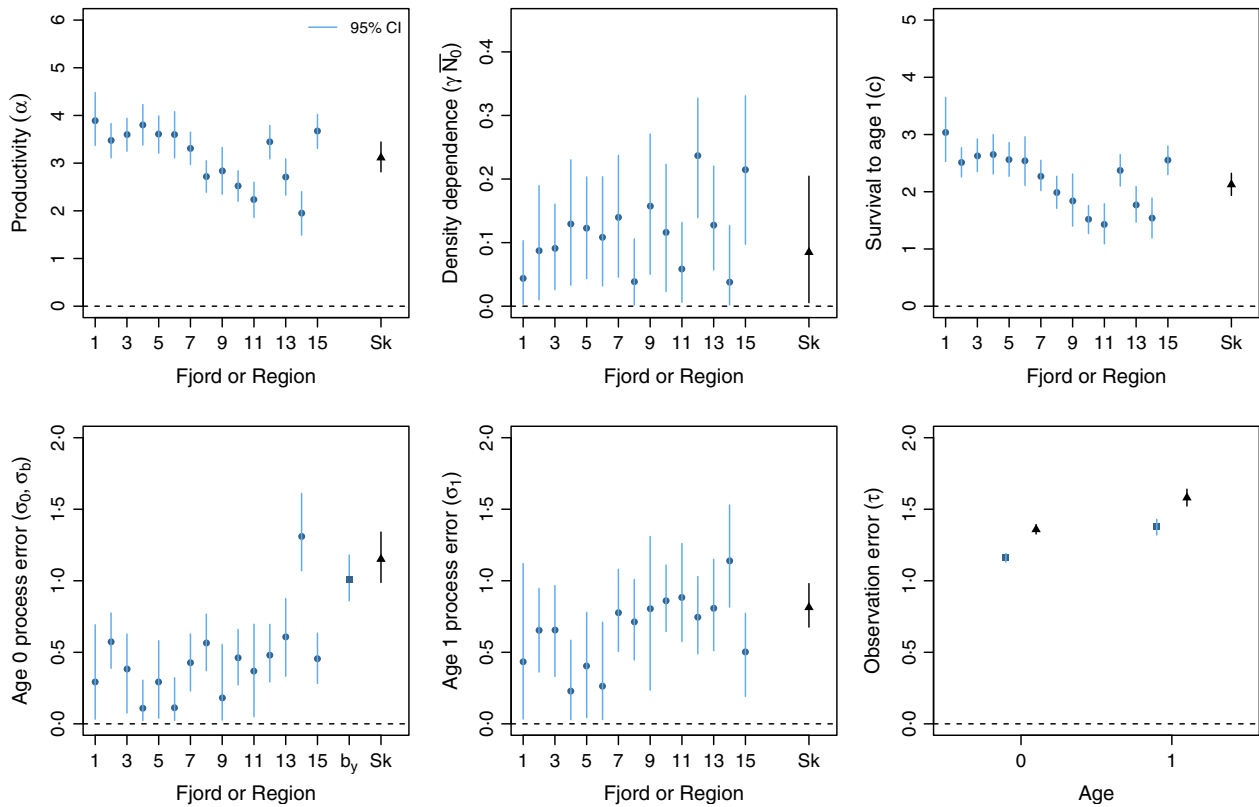


Fig. 3. Posterior means and 95% credible intervals of key parameters for the spatially structured model (blue circles and squares) and the coast-wide Skagerrak model ('Sk'; black triangles). Squares indicate shared parameters within the spatially structured model (i.e. σ_b , τ_0 , τ_1), and the variance of the shared random year effect is labelled ' b_y '. To compare among regions, the density-dependent term (γ) was multiplied by the mean age-0 abundance through time ($\frac{1}{93} \sum_{y=1}^{93} N_{0,f,y}$) and CIs were calculated using MCMC samples from the posterior distributions for γ_f and $N_{0,f,y}$.

regions into differences in the population processes rather than observation error. Observation errors were estimated with high certainty, reflecting the fact that we had multiple concurrent observations of each process (2–13 stations per fjord).

Cross-validation scores indicated support for the spatially structured model over the coast-wide model (CV scores of 30 377 and 31 163 respectively). Posterior predictive checks further showed that the coast-wide model failed to capture the spatial correlation pattern in the data (Fig. 4a), indicating that this model failed to capture an important aspect of the spatial dynamics of Skagerrak coastal cod. The spatially structured model, which assumed separate populations in each region connected only through recruitment, did capture the majority of the spatial correlation pattern in the data (Fig. 4b), including the high correlations among nearby stations, and the levelling-off of correlations among stations separated by c. 50 km or more. However, correlations at zero distance (y-intercept) were slightly underestimated by the spatially structured model.

Discussion

In marine fish and other organisms with heterogeneous population densities, identifying the intrinsic and extrinsic

drivers of population dynamics may depend on correctly characterizing population spatial structure (Ray & Hastings 1996; Thorson *et al.* 2015). We used a state-space modelling approach to compare alternative models of the population structuring of Skagerrak coastal cod, finding strong support for spatially structured population dynamics. The spatially structured model had better predictive ability, better captured the spatial correlation pattern in recruitment and indicated differing biomass trends among the fjords. Furthermore, density-dependent parameters were estimated to be different from zero for most of the fjords in the spatially structured model, whereas the coast-wide model estimate was ambiguous. Our findings highlight how the choice of spatial scale can have important consequences for understanding population processes, especially in spatially structured systems.

For Skagerrak coastal cod, current biomass is estimated to be at a near-record low all along the coast, but the finer scaled model indicates that the decline occurred at different times in different regions. For instance, the 1960s saw a strong decline in cod abundance in the Langesund region (11), likely due to pollution (e.g. dioxins and mercury) from a local industry and declines in eel-grass nursery habitat (Tveite 1984). Levels of pollutants in the sediments and cod livers remain high (Green *et al.* 2013) and cod in this region have never recovered.

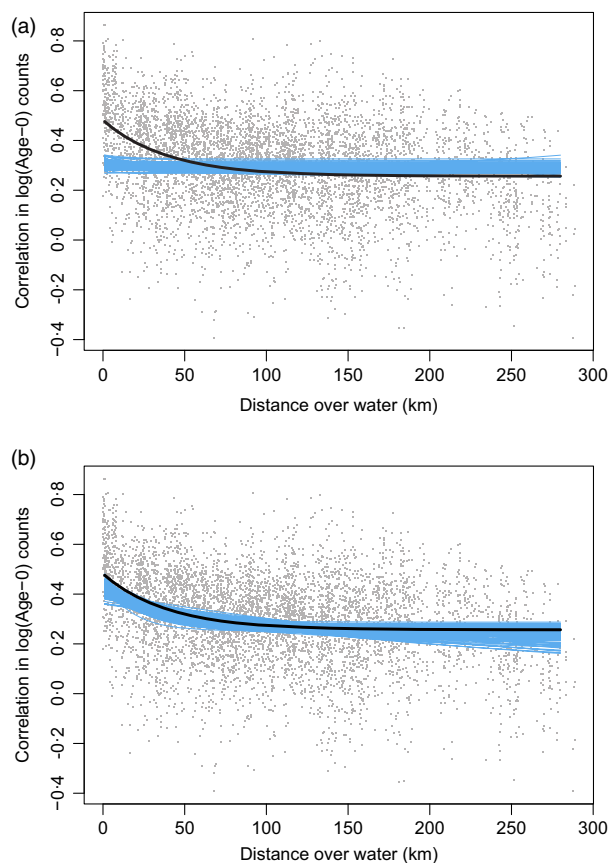


Fig. 4. Posterior predictive checks comparing the spatial decorrelation pattern in observed survey time series with those simulated under (a) the coast-wide model and (b) the spatially structured model. Dots show pairwise correlations among the original station-specific time series of age-0 cod (I^0), the thick black lines show the correlation-by-distance model fit for the original data, and the thin blue lines show the correlation-by-distance model fits ($n = 3000$) for each simulated set of data under the two different models.

Regions farther south had increasing cod abundance during the 1960s, followed by declines in the 1970s, 1980s or 1990s. Such differences in timing could reflect spatio-temporal differences in fishing mortality. Coastal cod are directly targeted by both commercial and recreational fisheries using a variety of gear, and are captured as by-catch in fisheries targeting other taxa (e.g. shrimp). Recreational fishing is currently the dominant source of fishing mortality (Kleiven *et al.* 2016; Fernández-Chacón *et al.* 2017), and its intensity could be related to the growth of tourism and holiday houses along the coast (Julliard *et al.* 2001). Unfortunately, without a monitoring programme for recreational fishing in Norway we lack quantitative data on how pressures have changed through time or across space. Historically, commercial fishing may have been more important, but the number of registered fishing vessels and fishers on the Norwegian Skagerrak coast have been steadily declining since the 1940s (Statistics Norway 2017). Data on commercial landings are not available at a spatial or temporal scale relevant to this

study. Without fine-scale data, we are unable to assess the relative importance of changes in recreational or commercial fishing to the spatial-temporal dynamics of Skagerrak coastal cod. Instead, variation in mortality due to harvest or other pressures is incorporated into the age-0 and age-1 process errors.

The spatially structured model included an overall shared and potentially climate-associated component of recruitment variation (b_y), but individual regions departed from this common pattern, perhaps due to overriding local influences. Climate conditions were generally considered to be good for cod in this region during the 1960s (the gadoid outburst in the North Sea linked to climate-associated increases in *Calanus* copepods; Beaugrand *et al.* 2003), but have become increasingly poor in the last two decades as summer water temperatures have warmed (Olsen *et al.* 2011; Rogers *et al.* 2011; Freitas *et al.* 2015). A comparison of the estimated shared recruitment deviates (b_y) with SSTs measured in late spring showed a significant negative relationship, indicating that warm springs were associated with lower age-0 abundance, on average. Thus, extrinsic climate trends are likely driving some of the temporal variation in cod abundance. Further disentangling extrinsic drivers of spatio-temporal variation in cod dynamics, such as climate, industrial pollution, fishing or habitat change, is an area for future research. Our results suggest that such research should consider both local and regional drivers, as both appear to have contributed to the dynamics of coastal cod.

It is not only extrinsic factors that drive variation among cod stocks but intrinsic dynamics also appear to play a role. The strength of density dependence, modelled here as an intercohort effect, differed among regions. Furthermore, in the spatially structured model, density dependence depended on local population densities rather than coast-wide densities, providing an additional mechanism for local differences in population fluctuations. In a similar vein, evidence for density-dependent growth was stronger when considering local rather than regional densities (Rogers *et al.* 2011), better reflecting the scale at which ecological processes occur. In the spatially structured model, recruitment was assumed to depend on local spawning biomass, not the coast-wide biomass, and is thus another intrinsic mechanism for fjord-level differences in dynamics. Fjords also demonstrated clear differences in estimates of population productivity α and survival c . The correlated spatial trends in these two parameters reflect the way the model partitioned spatial variability in the ratio of age-0 to age-1 catches (i.e. regions in the south had a higher age-0 : age-1 ratio than other regions). This spatial variability could reflect biological differences among populations (e.g. Olsen *et al.* 2008) or subtle spatial or temporal differences in the catchability of age-0 or age-1 cod. For instance, although the survey occurs over a contracted period of c. 3 weeks, northern stations were typically surveyed last and older cod could begin to exhibit a

seasonal shift in habitat use, changing their susceptibility to the survey gear (Freitas *et al.* 2016).

Inferences drawn from the competing assumptions about population spatial structure presented herein point to fundamentally different management actions to rebuild populations. If local abundance depends on the local biomass of spawners, local efforts such as a reduction in fishing pressure or habitat remediation may be necessary to restore the stock. However, if local abundance depends on the overall number of spawners along the coast in addition to some stochastic settlement processes, local management efforts such as a no-take marine reserve would have a relatively small effect on abundance and would need to be implemented as part of a coordinated coast-wide management plan (Gaines *et al.* 2010). An overall climate-driven decrease in survival will require broad actions to increase the resilience of the cod populations, including maintaining population age and spatial structure (Hilborn *et al.* 2003) and an overall reduction in fishing mortality (Brander 2010).

The models presented here attempt to describe the spatial structure and dynamics of Skagerrak coastal cod. However, as all models, they are simplified representations of what is a highly complex and dynamic system. While it appears inappropriate to describe the dynamics as resulting from sampling one panmictic population, there are many possible alternative models, of which we present only one. The spatially structured model underestimates the correlation among time series of age-0 counts sampled in close proximity (Fig. 4), suggesting that there is some fine-scale spatial structure that our model fails to capture. This could reflect, for instance, gradients in environmental conditions or fine-scale movement patterns within fjords. Individual fjords are likely not completely independent with regard to movement of individuals. While adults are largely sedentary (Rogers *et al.* 2014), they may make migrations during spawning, mixing with adults from nearby fjords and despite a tendency for eggs to be retained within fjords, both eggs and larvae may disperse from spawning aggregations in along-shore currents. Furthermore, an influx of larval cod from the North Sea has been documented in some years (Knutsen *et al.* 2004). As more genetic data on larvae and juveniles become available as well as surveys of spawning adults, our population model can be adjusted to reflect additional ecological knowledge.

This model builds on that of Bjørnstad *et al.* (1999), but differs in some fundamental ways. First, the Bjørnstad model divided the Skagerrak into two regions (N and S) and summed the survey counts by region, thus not considering local dynamics. Second, only four age classes were modelled, all individuals were assumed to reach maturity at age 2, and fecundity of 2- and 3-year-olds was set to be equal, relatively strong assumptions that do not accurately represent the life history of Skagerrak cod (Olsen *et al.* 2008; Knutsen *et al.* 2011). Finally, we modelled the intercohort density-dependent interaction to occur before

6 months of age (age 0) rather than between ages 0 and 1, which better captures the tendency of strong cohorts to be followed by weaker ones already at age 0. We did not model intracohort density dependence, although previous studies have found it to be significant (Bjørnstad *et al.* 1999; Fromentin *et al.* 2001) because preliminary model runs indicated it only accounted for a small proportion of the variation in survival to age 1 and was difficult to separate from the intercohort density-dependent term.

The state-space modelling approach presented here allows data to be used at their original level of collection and can be used to test hypotheses about drivers of population dynamics and the scale at which ecological processes occur. Previous state-space modelling approaches for identifying population structure and regional trends from time-series data have focused on population growth rates or abundance trends, and not incorporated age-structured dynamics. For instance, Ward *et al.* (2010) used multivariate state-space models to identify population sub-structuring in sea lions based on population growth rates. Fay & Punt (2013) used a linear state-space model to estimate trends in sea lion pup production, comparing models with regional trends to models with spatially correlated rookery-specific deviations from an overall trend. Our study extends previous work on identifying spatial structure from time-series data by modelling age-structured dynamics. Age-structured interactions can have a significant effect on population dynamics, especially in the case of strong intercohort density-dependent survival as documented here, and are likely to play out at local scales, thus contributing to local variation in dynamics.

This work contributes to a growing body of literature showing that by incorporating local dynamics and considering population dynamics at appropriate spatial scales, one can better estimate population parameters, detect local differences in population trends and design more effective plans for conservation or management.

Authors' contributions

L.A.R. conceived the project idea; L.A.R., G.O.S. and N.C.S. designed modelling methodology; E.M.O. and H.K. collected the data; L.A.R. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.td8nb> (Rogers *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Simulation study results.

Fig. S2. Posterior predictive distributions for relative abundances of age-0 and age-1 cod and spawning stock biomass.

Table S1. Age-specific maturation probabilities and body masses.

Table S2. Prior distributions for model parameters.

Appendix S1. Simulation study description.