



Original Article

Maternal age effects on Atlantic cod recruitment and implications for future population trajectories

Andrew Olaf Shelton^{1*}, Jeffrey A. Hutchings^{2,3}, Robin S. Waples⁴, David M. Keith², H. Resit Akçakaya⁵, and Nicholas K. Dulvy⁶

¹Conservation Biology Division, Northwest Fisheries Science Center, NMFS, NOAA, 2725 Montlake Blvd. E, Seattle, WA 98112, USA

²Department of Biology, Dalhousie University, Halifax, NS, Canada

³Department of Biosciences, Centre for Ecological and Evolutionary Synthesis, University of Oslo, Oslo, Norway

⁴Northwest Fisheries Science Center, NMFS, NOAA, 2725 Montlake Blvd. E, Seattle, WA 98112, USA

⁵Department of Ecology and Evolution, Stony Brook University, New York, NY, USA

⁶Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada V5A 1S6

*Corresponding author: e-mail: ole.shelton@noaa.gov.

Shelton, A. O., Hutchings, J. A., Waples, R. S., Keith, D. M., Akçakaya, H. R., and Dulvy, N. K. Maternal age effects on Atlantic cod recruitment and implications for future population trajectories. – ICES Journal of Marine Science, 72: 1769–1778.

Received 22 October 2014; revised 9 March 2015; accepted 16 March 2015; advance access publication 4 April 2015.

Exploited fish populations frequently exhibit truncated age-structure. To address a basic question in fisheries science and conservation biology—how does age truncation affect population dynamics and productivity?—we explored the effect of age-structure on recruitment dynamics of ten stocks of Atlantic cod (*Gadus morhua*). Based on six alternative stock–recruitment relationships, we compared models that included and excluded maternal age-structure effects on recruitment. In all ten stocks, a recruitment model that included a maternal age-dependent effect was preferred over the standard Ricker model and in seven of the ten stocks, the preferred statistical model included a positive effect of either maternal age or mass on recruitment. Simulations comparing standard and maternal age dependent recruitment two decades into the future suggest that the inclusion of maternal age in recruitment models has little effect on projected biomasses. However, this similarity in biomass trajectory masked an increased sensitivity of populations with maternal age-dependent recruitment to stock age-structure. In particular, simulations with maternal age-dependent recruitment responded strongly to changes in fishing mortality on the oldest age classes, while simulations using standard recruitment models did not. Populations with maternal age-dependent recruitment can exhibit increased biomass catch even if fishing mortality on older individuals was reduced. Overall, simulations suggested that the influence of maternal age on population dynamics are more nuanced than suggested by previous research and indicate that careful consideration of the effects of age-structure on populations may lead to substantially different fisheries management reference points—particularly with respect to age-specific fishing mortality—than classical models. While these results suggest a link between maternal age and population productivity, future research requires the incorporation of biologically reasonable and empirically defensible mechanisms to clarify the effect of age on population dynamics.

Keywords: age-structure, age truncation, maternal effects, recruitment, Ricker, productivity.

Introduction

Fisheries exploitation nearly always changes the age and size structure of harvested populations. In general, when a population is initially exploited, the largest, oldest individuals are removed first. After a period of persistent fishing, the age- and size-selectivity of most fishing gear will tend to produce a truncated age and size distribution (Hutchings and Myers, 1994; Levin *et al.*, 2006;

Hixon *et al.*, 2014). The collapse of Newfoundland's northern Atlantic cod (*Gadus morhua*) stock provides an illustrative example. The contribution of eggs by cod 10 years and older to the population has declined from an annual average of 30% in the 1960s (reaching a high of 46% in 1962) to 17% in the 1970s and 12% in the 1980s (Hutchings and Myers, 1994). Their low incidence in fishery and survey catches (Brattey *et al.*, 2009) suggests that cod

10 years and older have contributed a negligible proportion of eggs to the Newfoundland population since 1992.

In recent years, many studies have asserted that age truncation plays an important role in the dynamical properties of fish populations. Simulation and time-series analyses have suggested that changes in age-structure can affect the variability, productivity, stability, and yield of fish populations (Bjørnstad and Nisbet, 2004; O'Farrell and Botsford, 2006; Rouyer et al., 2012; Wikström et al., 2012; Botsford et al., 2014). However, there is considerable disagreement about the mechanism by which age truncation causes changes to fish dynamics (Ottersen et al., 2006; Anderson et al., 2008; Shelton and Mangel, 2011; Botsford et al., 2014). Several proposed mechanisms can yield very similar patterns in time-series. Furthermore, meta-analytic studies examining the pattern of recruitment as a function of maternal age have reached varied conclusions about the prevalence and magnitude of changes to age-structure (Morgan et al., 2007; Venturelli et al., 2009; Brunel, 2010; Rouyer et al., 2012). The results of these studies appear to depend on the statistical methods used to estimate age truncation effects. Together, these results suggest that there is a need to move towards more biologically motivated, mechanistic, and empirically testable models for age truncation effects.

We suggest that the best way to resolve such disputes is to more strongly link statistical methods investigating the consequences of age truncation with empirical studies of reproductive biology. To date, empirical studies have shown that the quality of eggs can increase with maternal age (Vallin and Nissling, 2000; Murawski, 2001; Scott et al., 2006; Sogard et al., 2008), as can the fecundity per unit of maternal biomass (Scott et al., 1999; Dick, 2009).

Here, we explore the effect of age-structure on recruitment dynamics of ten stocks of Atlantic cod in the wild by determining the relative importance of maternal age and mass for explaining the observed recruitment dynamics. We estimate parameters for six stock–recruitment relationships (SRRs) using the maternal-effect recruitment models proposed by Shelton et al. (2012). We compare classical SRRs that omit age-structure with those that include age-structure. For each stock, we ask two initial questions. First, does inclusion of age-structure improve the estimated SRR? Second, what is the magnitude and direction of any age-structure effect on the observed recruitment? For a subset of the populations, we use simulation methods to explore the population dynamical consequences of including age-dependent recruitment. We then ask two subsequent questions. Third, do estimated age-structure effects on recruitment produce substantially different population projections from those that do not incorporate age-structure? Fourth, do populations with maternal age-dependent recruitment

differ substantively from populations without age-dependent recruitment to feasible management actions?

Methods

Estimating the effect of maternal age on SRRs

We collected stock and recruitment data from ten stock assessments for Atlantic cod stocks spanning the North Atlantic (see Table 1 for sources). In general, we used stock assessments conducted between 2009 and 2012. We required estimates of spawning biomass-at-age, weight-at-age, and number of recruits. When the stock assessments provided output from multiple, alternative models, we used the biomass and recruitment estimates used for management determinations. In the following, we use the terms “stock” and “population” interchangeably.

We first estimated SRRs separately for each stock, using the method outlined by Shelton et al. (2012) to incorporate age information into the Ricker SRR (Ricker, 1954; Quinn and Deriso, 1999). Specifically, the formulation allows for offspring from different-aged mothers to have distinct mortality rates. Parameters are estimated from time-series of biomass at age and recruitment. Because all of the cod stock assessments in our study use a plus-group in their assessments—the Icelandic cod assessment, for example, uses a 14+ group to account for all individuals 14 years old and older—we lack information about the distribution of ages in the plus group. Therefore, we treat all individuals in the plus group as if they were the minimum age in the plus group (e.g. for Icelandic cod all biomass age 14 and older is treated as if it is 14 years old). Because we expect the largest effects of any age-dependent reproductive parameter to be evident at young ages, we feel that this is an empirically justified approach. Additionally, without more detailed information about the age-structure, it is not clear what other options are available.

For the ten stocks, we considered three alternative models outlined below.

The classic Ricker SRR assumes that the per unit biomass fecundity and egg quality is equivalent among mothers of different ages. Recruitment of age τ individuals spawned in year t , $R_{t+\tau}$, can be written as a deterministic function of two parameters (α , a parameter combining the per-unit-biomass fecundity and density-independent survivorship of young fish, and β the parameter controlling density-dependent mortality), and two variables (the spawning biomass of age i fish in year t , S_{it} , and the biomass contributing to recruitment density-dependence, S_{Dt}). Then

$$R_{t+\tau} = \sum_{i=j}^{\omega} \alpha S_{it} e^{-\beta S_{Dt}}, \quad (1)$$

Table 1. Summary of Atlantic Cod, *G. morhua*, stocks, and abbreviations.

Cod population abbreviation	Location	Management	Length of time-series (years)	Age of recruitment	Reference
CS	Celtic Sea	ICES	36	1	ICES (2008a)
GB	George's Bank	NAFO	33	1	NEFSC (2013)
NS	North Sea	ICES	46	1	ICES (2012a)
Vla	West of Scotland	ICES	30	1	ICES (2008b)
BA2532	Baltic Sea	ICES	42	2	ICES (2012b)
FAPL	Faroe Plateau	ICES	47	2	ICES (2012c)
3NO	Canada	NAFO	49	3	Power et al. (2010)
4TVn	Canada	NAFO	36	3	Swain et al. (2009)
ICE	Iceland	ICES	52	3	ICES (2012c)
NEAR	Northeast Artic	ICES	61	3	ICES (2012d)

where j is the age at first reproduction and ω the maximum age. We refer to this model as the “base model”. Shelton *et al.* (2012) show how to generalize Equation (1) to allow biomass from different age classes to vary in their density-independent mortality rate. If we consider the density-independent mortality rate to change linearly with age, the recruitment function becomes

$$R_{t+\tau} = \sum_{i=j}^{\omega} \gamma S_{it} e^{-\beta S_{Dt} - gi}, \quad (2)$$

so gi represents the effect of maternal age on density-independent mortality. We refer to this as the “age model” hereafter. Note that we replace α from Equation (1) with the parameter γ to emphasize that they have distinct biological interpretations and are not directly comparable.

Because prerecruit mortality rates need not be explicit functions of age, we also consider models where mortality rates for each aged fish are a function of the average weight-at-age, w_i . Then, the recruitment model becomes

$$R_{t+\tau} = \sum_{i=j}^{\omega} \gamma S_{it} e^{-\beta S_{Dt} - hw_i}, \quad (3)$$

with h representing a parameter controlling the effect of maternal mass on recruitment. We refer to this as the “mass model” hereafter. For simplicity, we assume the biomass contributing to density-dependence is the sum of the age-specific spawning biomass, $S_D = \sum_i S_i$. We know that there is considerable variability around these deterministic relationships (Quinn and Deriso, 1999), so we consider two forms for stochastic annual variation around the three deterministic functions. After logarithmic transformation, the age model [Equation (2)] is

$$\log(R_{t+\tau}) = \log(\gamma) - \beta S_{Dt} + \log\left(\sum_{i=j}^{\omega} S_{it} e^{-gi}\right) + \varepsilon_t, \quad (4)$$

with ε_t representing the stochastic annual variation in recruitment. We consider independent errors, $\varepsilon_t \sim N(0, \sigma^2)$ and lag-1 autocorrelated errors, $\varepsilon_t \sim N(\rho\varepsilon_{t-1}, \sigma^2)$, where ρ is the autocorrelation parameter. For stationary time-series, $-1 < \rho < 1$. In total, we considered six alternative models. We acknowledge that this is a small subset of possible models for including age-structure effects in recruitment (see Shelton *et al.*, 2012). However, adding age-dependent effects, the density-independent term in Equation (4) corresponds to current biological knowledge; much of the value of older fish is thought to arise from allowing α in the classic Ricker [Equation (1)] to change with age (Scott *et al.*, 1999; Dick, 2009; Shelton *et al.*, 2012).

All models were estimated using Bayesian Markov chain Monte Carlo techniques (MCMC). Details are presented in Shelton *et al.* (2012). Model selection was performed using posterior predictive loss which balances model fit and model complexity (Clark and Bjørnstad, 2004; Shelton *et al.*, 2012; Hooten and Hobbs, 2015). Smaller numbers of posterior predictive loss indicate a better match between model and data.

After identifying the statistically preferred recruitment model for each stock, we compared the explanatory value of increased maternal age or mass across stocks. However, the highly variable life history among cod stocks, in adult mortality, growth, and

age-at-recruitment, complicates efforts to compare stocks unless the estimated effect of age or mass on cod recruitment is converted to a common scale for all populations. To resolve this, we calculated the ratio for equivalent biomass of age i and age $i-1$ fish—or for mass models, the value of fish 1 kg heavier—using the preferred model structure. We refer to this ratio as the “productivity ratio”, λ . Then for at the age model $\lambda_a = e^{-g}$, and for the mass model, $\lambda_w = e^{-h}$. These ratios have a straightforward interpretation. For example, $\lambda_a = 1.2$ would indicate that an age 4 fish produces 20% more recruits on average than a 3-year-old fish.

Consequences of age truncation on population dynamics and fisheries

The previous section provides a way to estimate the value of increasing maternal age on recruitment. An important subsequent question is whether the estimated differences have consequences for the conservation and management of cod populations. However, rather than derive rules for changes to fisheries reference points under different simulation scenarios or life-histories (O’Farrell and Botsford, 2006; Spencer *et al.*, 2014), we address a specific, management-relevant question: Do different recruitment models generate substantially different near-term population dynamics? In short, is the inclusion of age-structure effects likely to change how we think about the management of the age-structure of cod populations?

We perform two sets of simulations on three of the cod populations with the longest fishery time-series (FAPL, Faroe Plateau; ICE, Iceland; and NEAR, Northeast Arctic). We focus on these three populations because of the quality of their data and in all three of these populations, the age model was the preferred model (see the Results section). Additionally, attempts to perform simulations using parameters obtained from several of the other stock assessments yielded population extinctions or unrealistically fast growing populations. This problem is not unique to our work but a general challenge in some of the stock assessments from which our parameter estimates were derived (e.g. NEFSC, 2013). We used a standard age-structured discrete-time model for the number of fish at age i in year t ,

$$N_{i,t} = N_{i-1,t-1} e^{-M_i - F_i}, \quad (5)$$

where M_i and F_i are the natural and fishing mortality-at-age, respectively. The number of individuals at the age of recruitment, $R = N_j$, is determined by Equations (1), (2), or (3). The spawning biomass of age a individuals is a function of maturity-at-age (mat_a) and weight-at-age (w_a), $B_{i,t} = N_{i,t} mat_i w_i$. Note that in the simulations, maturity-at-age and weight-at-age are considered constant across time (see Supplementary material).

For the first simulation, we projected all three populations with the estimated base model and the preferred estimated age model over the next 20 years (see Supplementary material for simulation parameters). We initiated each population at the biomass provided in the stock assessment. Each simulation was identical except for the estimated recruitment function. Values for natural mortality, weight-at-age, maturity-at-age, and fishing mortality were considered constant over the simulation and derived from the stock assessment (see Supplementary material). We performed 2000 independent simulations for the base and age model. Each simulation used an independent draw from the appropriate posterior distribution of the recruitment parameters so that simulations integrate across the uncertainty in estimated recruitment parameters.

Comparing the base and age models allows us to ask: under current management, do the base and age models provide different predictions for future population trajectories?

Second, we simulated populations under two scenarios with decreased fishing pressure to explore the potential consequences of implementing increased protection of particular age groups. We first simulated reduced fishing mortality on old fish, as advocated by a number of authors (Hixon *et al.*, 2014). Specifically, we performed the same simulations as above, but instead of using current fishing mortality, we reduced fishing mortality by 50% for the five oldest age classes (see Supplementary material). To contrast with the protection of the oldest age classes, we also simulated decreased fishing mortality all age classes; we reduced fishing mortality by 10% across for ages (see Supplementary material). For both simulation scenarios, we used draws from the posterior estimates of recruitment parameters to properly account for uncertainty in the estimated SRRs.

In addition to comparing the base and age models in each simulation, we compared outputs between current and reduced mortality simulations to describe value of both old and young age classes for spawning biomass and fisheries catch. We calculated the proportional change in biomass and the change in expected catch at the end of the 20-year simulation between the base model simulations and the age model simulations. The comparisons provide insight into how alternative fishing scenarios and assumptions about recruitment change inform the responsiveness of the population to potential changes in fisheries management.

Results

Recruitment estimation

Our model selection reveals the importance of either maternal age or maternal mass in all ten cod stocks, with the maternal age model preferred in six stocks and the maternal mass model preferred for the remaining four (Table 2). In some cases, however, the difference between the maternal age or weight model and the base Ricker model was very slight, indicating nearly equivalent fits for multiple models (e.g. GB and 4TVn; Table 2). The preferred model for eight of ten stocks incorporated an AR(1) error structure.

For seven of ten stocks, the median estimate of the maternal age (λ_a) or maternal mass recruitment production ratio (λ_w) was larger than 1, indicating that populations with older, larger fish produce more recruits (Figure 1a and b). The productivity ratio ranged from 0.80 to 1.43 (λ_a ; across stock median: 1.23) for the six stocks using the age model, indicating that, across stocks, fish a year older produced 23% more recruits than those a year younger. For the mass model, the productivity ratio ranged from 0.71 to 1.27 (λ_w ; across stock median = 0.995). However, these median values

obscure the fact that the three stocks (GB, 3NO, BA2532) were estimated to have small, young fish produce more recruits than their larger elders. Furthermore, the uncertainty in the age effect was large for most of the stocks such that the 95% credible intervals overlapped 1.0 (i.e. no effect of age) for all stocks except Icelandic cod (ICE; Figure 1a). Thus, although model selection suggests that including an effect of maternal age or mass provides a better match to the data, usually uncertainty about this effect is substantial.

We also found a negative trend between the maternal recruit production ratio (λ_a or λ_w) and the autocorrelation parameter, ρ (Figure 2). As ρ has an interpretation as the strength of correlated environmental noise on recruitment, this result suggests that recruitment in some cod populations is dominated by unmeasured environmental forces that obscure any maternal age effects. The two populations with an inverse maternal mass effect such that younger fish apparently produce more offspring than fish a year older ($\lambda_w < 1$) are from the Baltic Sea (BA2532) and the Grand Banks, Canada (3NO). Pronounced environmental effects upon recruitment have been documented for each [Baltic Sea (Köster *et al.*, 2005), Grand Banks (Brander, 2005)]. One stock, George's Bank cod (GB), stands out as an outlier in the relationship between maternal effects on recruitment (λ) and autocorrelation (ρ). It has a low median value of age-specific recruit production ($\lambda_a = 0.80$) and minimal autocorrelation (ρ is ~ 0), but it has large uncertainty bounds on all parameters and we view the model estimates for this stock especially uncertain.

Consequences of age truncation on population projections

We performed simulations to explore the future consequences of fishing on the three populations with strong estimated maternal age effects on recruitment (FAPL, ICE, and NEAR; Figure 1a). Under current fishing mortality, our simulations suggest that biomass over the next 20 years is expected to be very similar between the base and maternal age models (Figure 3a–c). For all three populations, the age model predicts slightly lower biomass at the end of 20 years and the age model has lower variability in projected biomass than the standard model always (substantially lower for Icelandic cod). Overall, the qualitative time-series of biomass is broadly similar between the base and age models and under current fishing mortality (Figure 3a–c) as well as when fishing pressure is reduced on the five oldest age classes (Figure 3d–f).

The effect of maternal age only becomes apparent when we compared the base model in the two fishing mortality simulations and the age model in fishing mortality simulations (Figure 4). We calculated the median proportional change in biomass between current and two reduced fishing scenarios. All scenarios with decreased fishing mortality resulted in increased SSB for both the base and

Table 2. Posterior predictive loss of six alternative stock–recruitment models.

Model	Error	Cod population									
		CS	GB	NS	Vla	BA2532	FAPL	3NO	4TVn	ICE	NEAR
Base	Indep.	41.2	24.4	42.2	23.8	23.3	35.3	150.4	24.5	13.4	41.4
	AR(1)	40.9	25.4	43.2	22.8	10.6	27.1	67.7	12.5	13.4	31.6
Age	Indep.	40.8	21.9	–	–	22.1	32.8	110.8	21.2	10.0	40.5
	AR(1)	41.1	21.9	–	–	10.7	25.8	62.0	12.5	9.6	31.1
Mass	Indep.	41.2	–	41.3	23.5	16.0	33.8	118.2	16.7	11.07	41.6
	AR(1)	41.0	–	42.1	22.0	9.7	26.6	59.4	12.9	11.21	31.7

Overall preferred models are in bold. The dashes “–” denote models that did not converge to a stationary distribution and were not considered further. Smaller numbers indicate better match between the model estimate and observed data. See Table 1 for explanation of the Atlantic cod population codes.

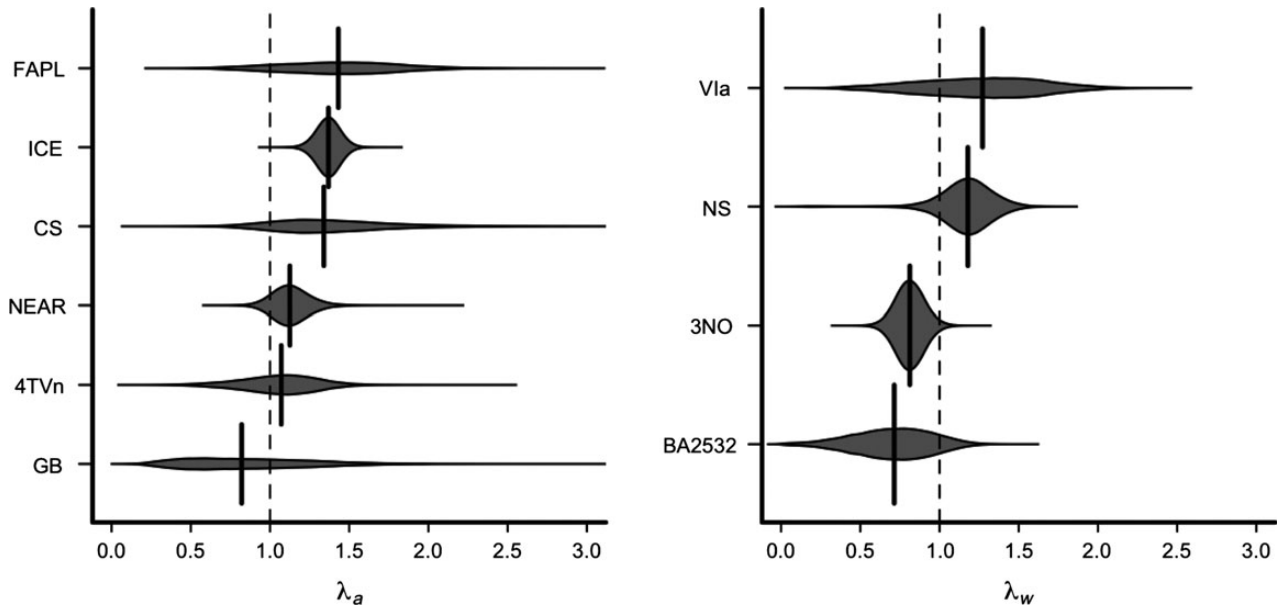


Figure 1. Posterior estimates of the maternal age (λ_a) or maternal mass (λ_w) productivity ratio, which shows the proportional increase in Atlantic cod recruitment expected from increasing age by 1 year (λ_a , left panel) or increasing mass by 1 kg (λ_w , right panel). For each stock, we plot results from the preferred model (see Table 1 for explanation of the Atlantic cod population codes). Vertical lines show the posterior median for each stock and shaded bean plots show the posterior distribution of λ for each stock. The dashed vertical line shows $\lambda = 1$ (no change in productivity ratio with age or mass).

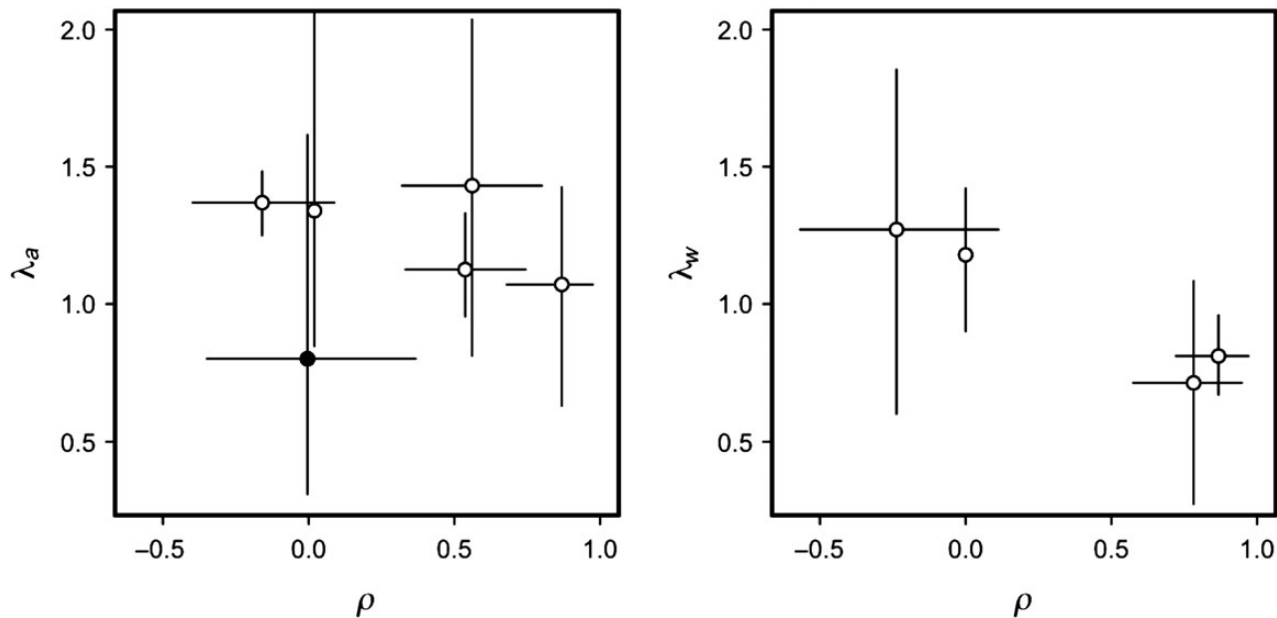


Figure 2. Estimated maternal age effect vs. the autocorrelation parameter ρ for Atlantic cod. Left panel shows the populations where a maternal age term is preferred; right panel shows where a maternal mass term is preferred. Median estimates ($\pm 90\%$) credible intervals are shown. Points without error bars on the x-axis are for populations that did not include an autocorrelation parameter (i.e. $\rho = 0$; points at $\rho = 0$ have been jittered slightly to prevent overlap). Note the general negative relationship in both panels. The filled circle indicates the GB population.

age models in all three populations (Figure 4a and c). For simulations with reduced fishing mortality on old fish, the maternal age model predicts much larger increases in biomass in response to reduced fishing mortality (median increase in biomass for the age

model: 23–73% for the three populations; median increase in the base model: 8–25%; Figure 4a). Simulations with reduced fishing mortality across all ages showed responses of biomass to reduced fishing (Figure 4c), but the differences between the base and age

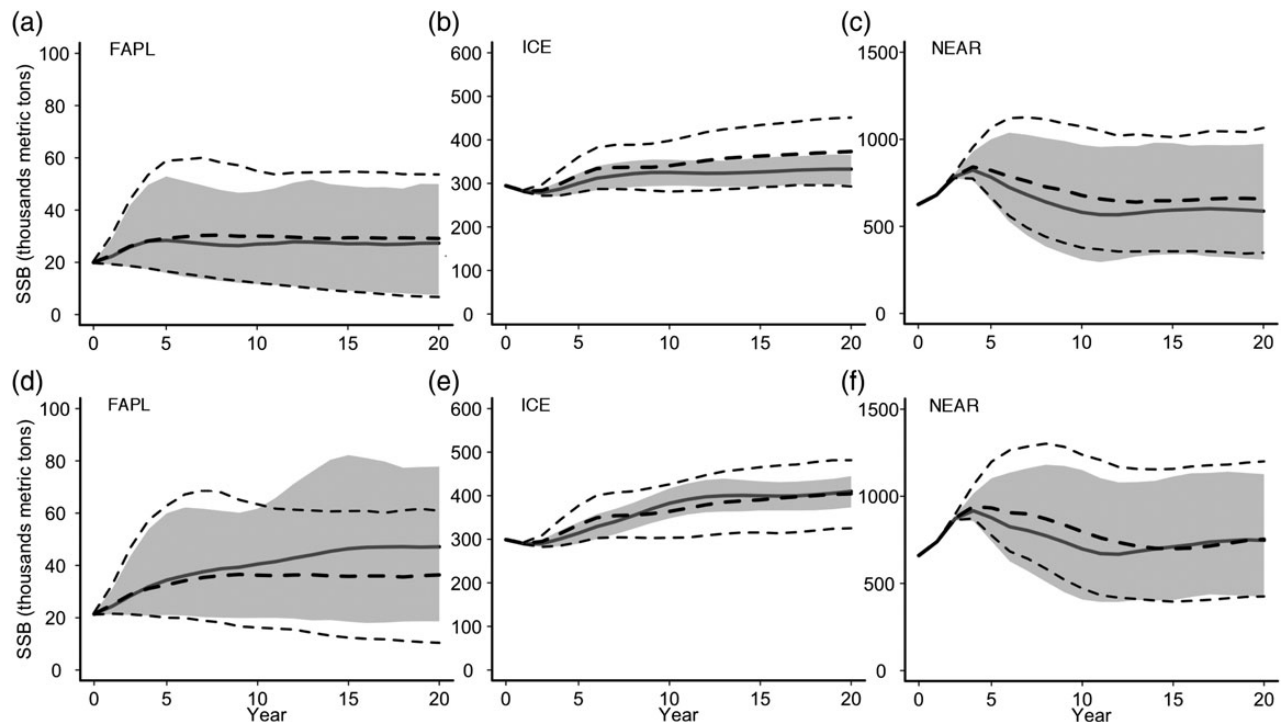


Figure 3. Results of simulations of Atlantic cod populations for three populations (Faroe Plateau—a and d; Iceland—b and e; NE Arctic c and f). All panels show the projected spawning-stock biomass for each population using the base Ricker recruitment model (dashed lines) and the preferred age model (solid line and shaded area). The median and 90% CI are shown for all simulations. For each population, the top row shows the projected abundance time-series under the average fishing mortality-at-age calculated from the past decade. The bottom row shows the projected population with fishing mortality reduced by 50% in the oldest 5 age classes (see Supplementary Table S1 for age-specific mortality rates used in the simulation).

models were relatively small. For all three populations, the difference in standing the base and age model was greater in simulations with reduced mortality on old fish (compare Figure 4a and c).

For catch, the base model only showed small proportional changes in catch between current and reduced mortality scenarios (-0.03 to 0.08 ; Figure 4b). In contrast, the age model predicts increased catch in all three populations, despite lower fishing mortality rates on older age classes (Figure 4b). The increase in recruitment from the increased abundance of old fish produces more catch from younger fish in the age model. This change in catch more than compensates for decreased catch of old fish. Reducing fishing mortality on young fish also leads to increases in catch after 20 years in both the base and age models (Figure 4d); total biomass caught were simulated to increase by 8.5–24% under the base model and 12–33% in the age model (Figure 4d). When fishing mortality was reduced across all ages, the results followed a similar pattern with increases in catch for all models. As in the biomass comparisons, the difference between the base and age models for each stock was much smaller under decreased fishing mortality across all age classes (compare Figure 4b and d).

Taken together, the simulation scenarios indicate that maternal age effects make populations more sensitive to changes in age-specific fishing mortality, such that populations with age-dependent recruitment mostly show a stronger response to reductions in fishing mortality. Our simulations show that differences between the base and age model were largest under scenarios with reduced fishing mortality on the oldest age classes (Figure 4a and b), but differences also occur at a reduced level if fishing mortality is reduced

across all ages. Despite this difference in sensitivity, simulations show that predicted biomass is very similar between the base and age models.

Discussion

Recent reviews of the effect of age-structure on fish population dynamics have argued for greater consideration of the maternal effects on fish population dynamics (Venturelli et al., 2009; Hixon et al., 2014) and asserted that the population dynamic consequences of protecting large old female fish will be substantial. These authors echo a much older call for greater incorporation of fish reproductive biology in fisheries (Beverton and Holt, 1957; Rothschild and Fogarty, 1989). Our findings broadly support the importance of considering maternal age in fisheries management. We show that the preferred statistical model includes a positive effect of maternal age or maternal mass on recruitment for seven of ten stocks of Atlantic cod. The three remaining stocks are estimated to have reduced recruitment productivity with increasing maternal age or maternal mass. However, two of these populations were estimated to have very large autocorrelated errors, suggesting that the presence of a strong environmental signal (or, potentially, temporal variability in measurement error) in recruitment success might obscure any recruitment signature of maternal age in some populations. The third population (GB) had exceptionally large uncertainty bounds for all SRRs examined (see also NEFSC, 2013). As with any analysis of SRRs, there is always the possibility that other, unmeasured variables that affect recruitment are co-varying with age-structure and/or total biomass and the effect of this unmeasured variable is

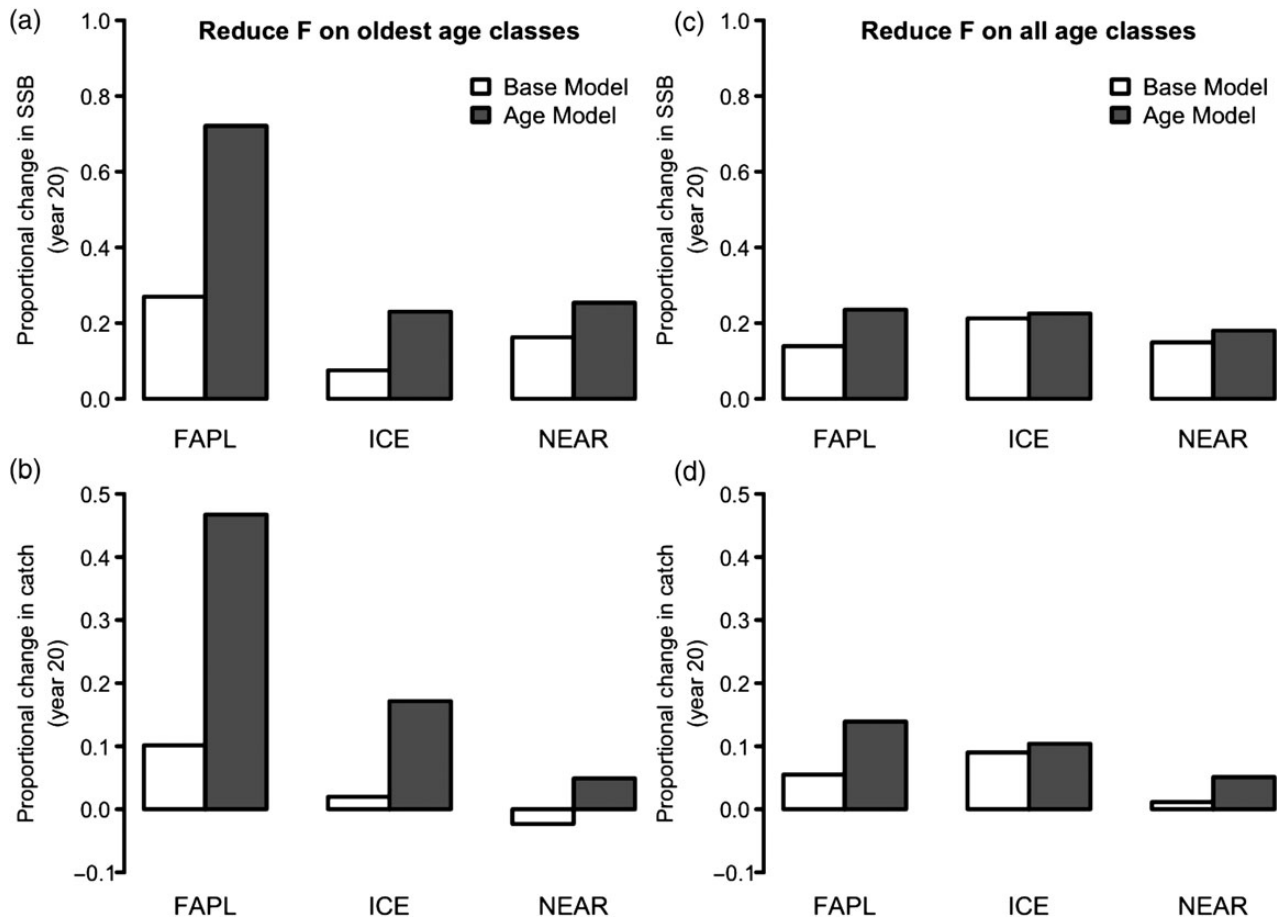


Figure 4. Assessing the value of old fish for population processes. The proportional change in spawning-stock biomass when age-specific fishing mortality is reduced on the oldest cod (a) or all ages (c; see Supplementary Table S1). Positive values indicate that limiting fishing increases biomass. (b and d) The proportional change in the annual biomass catch in year 20 under the two fishing mortality scenarios. The standard Ricker model shows relatively minor proportional changes in response to changes in fishing mortality on old fish (c; range: -0.03 to 0.08), while the age model predicts positive changes in catch in response to reduced fishing mortality (range: 0.04 – 0.48). Differences between the models are much reduced when fishing mortality is reduced across all age (d).

contributing to the estimated effect of age-structure. We suspect such effects may be contributing to the very large estimated maternal age effect for some populations (e.g. FAPL; Figure 1), but without additional information, we cannot directly assess any such effects.

Despite the detection of a positive effect of increasing maternal age on recruitment (Figure 1a), our simulations show that incorporating maternal age effects may not have a large effect on spawning biomass in the near term (Figure 3a–c). In response to a feasible reduction in fishing mortality on the oldest age classes—as has been advocated by several authors (Berkeley *et al.*, 2004; Hixon *et al.*, 2014)—the age model produced higher biomass and catch after 20 years in all three populations. However, these differences between the base and age models were not substantial, particularly in the light of the uncertainty (Figure 3). The small differences between the base and maternal age model simulations can be understood by recognizing that the base model implicitly averages any maternal age-dependence in the deterministic component of recruitment. Furthermore, the base model attributes more recruitment variability to stochastic forces than the maternal age model. Again, these simulations are intended to reflect near-term dynamics, not the asymptotic variance and spectral characteristics of

populations captured by other approaches (Bjørnstad and Nisbet, 2004; Worden *et al.*, 2010; Botsford *et al.*, 2014).

The population response to reduced fishing on old cod suggests that populations with maternal age-dependent recruitment will be more sensitive to changes in age-specific fishing mortality. This observation further suggests that models that ignore maternal age-dependent recruitment will underestimate the effectiveness of changes in age-specific fishing mortality as a management tool. Indeed, reducing fishing mortality by half on old cod led to large proportional increases in spawning biomass and catch after 20 years (Figure 4a and b). This result also is pertinent for the converse scenario where fishing mortality is increased on older fish: populations with age-dependent recruitment will show greater declines in biomass and catch as fishing mortality is increased. Simulations that lowered fishing mortality across all ages also showed increased biomass and catch in all three populations, but that the base and age models were more similar than when fishing mortality was reduced on older fish (Figure 4c and d). Overall, our results suggest that using models that directly incorporate maternal age-dependent recruitment result populations that strongly respond to changes in fishing mortality on older fish. It must be

emphasized to recognize that reducing mortality on old fish is not the only path for increasing biomass or catch. When recruitment depends on maternal age, reducing fishing mortality across the all ages results in larger numbers of older cod and leads to increased stock productivity and, ultimately, increased biomass and catch (Figure 4c and d). This is an important reminder that while maternal age is an important aspect of fish biology, reducing mortality of old fish is far from the only available method for helping to recover stocks from low biomass or maintaining sustainable fisheries. Depending on the circumstances, modifying age-specific fishing mortality rates may not be easy to implement in real fisheries.

Our results suggest that examining of biomass trends alone will likely obscure and underestimate the consequences of maternal age-dependent recruitment for populations. While we only explored a few simulation scenarios in three populations with relatively large estimated age-effects, our simulations motivate a wide range of future simulation work on the repercussions of age-structured recruitment for many aspects of fish population dynamics.

Many previous investigations of the consequences of age truncation for fish dynamics rely on univariate analysis of fish abundance metrics like biomass in response to changes in age-structure [e.g. the variability of larval fish abundance (Anderson *et al.*, 2008) or frequency spectra of total biomass (Rouyer *et al.*, 2012)]. These analyses have difficulty linking observed changes to any measurable biological rate or process. Generally, wavelet analyses of univariate biomass time-series (Hidalgo *et al.*, 2011; Rouyer *et al.*, 2012) are correlative and have a looser link to biological mechanisms than age-structure simulations based on explicit, process based consideration of age-structure effects (Wikström *et al.*, 2012; Spencer *et al.*, 2014). We advocate a more explicit link to measurable processes, such as that considered here, to provide a check on whether estimated recruitment parameters are biologically reasonable. Given that cod are a very well-studied species from a reproductive biology perspective (Marshall *et al.* 1998; Vallin and Nissling, 2000; Ottersen *et al.* 2006, 2014), we hope incorporating increase biological realism will be relatively easy to incorporate into SRRs.

Our work shows that the mechanistic details of how one incorporates the effects of maternal age matter. Small differences in methodological assumptions can yield strong differences in inference. For example, assuming a constant SRR while adult mortality is allowed to vary temporally (Worden *et al.*, 2010; Rouyer *et al.*, 2012) might provide substantially different answers than approaches that link age to recruitment (Shelton *et al.*, 2012). The available experimental data certainly support changes in fecundity and offspring quality with maternal age and/or size (reviewed in Hixon *et al.*, 2014). Furthermore, how age effects on recruitment are modelled can influence their estimated strength and importance. Previous investigators of age-dependent recruitment have assumed the recruitment curve can be approximated as a linear relationship (Venturelli *et al.*, 2009), or have incorporated the diversity of age classes (Marteinsdottir and Thorarinsson, 1998) or average maternal age (Brunel, 2010) as regression predictors. In particular, Venturelli *et al.* (2009) and Brunel (2010) come to starkly different conclusions about the importance of maternal age, despite using very similar data. While each approach might be appropriate in some cases, we prefer the model form presented here because the estimates have direct biological interpretations that are directly comparable to measurable rates (see also Shelton *et al.*, 2012). Nearly all analyses of age truncation have used the mean age as the descriptor of the age-structure of populations (Venturelli *et al.*, 2009; Brunel, 2010; Rouyer *et al.*, 2012) despite it being a poor

descriptor of age composition. Furthermore, mean age—a property of the population—is difficult to link to individual-level traits like maternal age. Improved understanding of recruitment dynamics require the gulf between empirical reproductive work and statistical curve fitting to be narrowed. We expect that the short-term detailed field observations and laboratory-based experimental results will be used to challenge the estimated population-scale maternal age effects presented in this paper and we view this as a very good thing.

Our analysis has implications for the use of meta-analyses in analysing SRRs. While meta-analytic approaches have advanced our understanding of shared recruitment processes across species and stocks, the variety of maternal age responses and environment interactions demonstrated in this paper suggest that some of the assumptions of classical meta-analytical approaches are potentially being violated. These results suggest that the cod stocks examined may not represent exchangeable samples from a single shared process. Therefore, combining information across stocks in a meta-analysis may yield biased or invalid conclusions about shared drivers of populations. Our analysis suggests a more careful consideration of how and what processes are shared in meta-analytic approaches is warranted (see also Thorson *et al.*, in press).

There are a variety of ways the methodology presented here could be improved. As with many analyses of SRR (Myers *et al.*, 1995, 1999), we use stock assessment output, not raw data, to estimate the SRR. While this is a convenient approach, the recruitment estimates are model output and therefore both recruitment and spawning biomass estimates depend strongly upon the stock assessment model assumptions. This may bias estimates of recruitment processes (Thorson *et al.*, in press). Additionally, we consider two forms for SRR that include age-dependent effects and two forms of stochastic recruitment. However, we do not incorporate ocean temperature or other environmental covariates directly in the estimation of recruitment (Jacobson and MacCall, 1995; Olsen *et al.*, 2011). Incorporating well-motivated environmental covariates is an important next step for these types of analyses. The fact that a substantial stochastic component remains in the SRRs investigated here suggests that there may be scope for additional covariates to be included. However, the measurement noise remains an important limiting factor impeding understanding of SRR relationships. The among-population variation in age-effects indicates a need for research into why certain populations of the same species might be more or less responsive to environmental signals and why certain stocks show apparently strong age-dependent recruitment.

Supplementary data

Supplementary material is available at the ICES/JMS online version of the manuscript.

Acknowledgements

We thank four anonymous reviewers for helpful comments. M. Mangel and W. Satterthwaite provided comments on earlier versions of the manuscript. This is a contribution from the “Red Flags and Species Endangerment” working group, sponsored by the National Center for Ecological Analysis and Synthesis (NCEAS), Santa Barbara, CA, USA. We thank working group members, S.H.M. Butchart, B. Collen, E.E. Holmes, D.A. Keinath, M.K. Schwartz, and M. Nammack, for helpful discussion and comments.

References

- Anderson, C., Hsieh, C., Sandin, S., Hewitt, R., Hollowed, A., Beddington, J., May, R., *et al.* 2008. Why fishing magnifies fluctuations in fish abundance. *Nature*, 452: 835–839.
- Berkeley, S. A., Hixon, M. A., Larson, R. J., and Love, M. S. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, 29: 23–32.
- Beverton, R. J. H., and Holt, S. J. 1957. *On the Dynamics of Exploited Fish Populations*. Chapman & Hall, London.
- Bjørnstad, O. N., and Nisbet, R. M. 2004. Trends and cohort resonant effects in age-structured populations. *Journal of Animal Ecology*, 73: 1157–1167.
- Botsford, L. W., Holland, M. D., Field, J. C., and Hastings, A. 2014. Cohort resonance: a significant component of fluctuations in recruitment, egg production, and catch of fished populations. *ICES Journal of Marine Science*, 71: 2158–2170.
- Brander, K. M. 2005. Cod recruitment is strongly affected by climate when stock biomass is low. *ICES Journal of Marine Science*, 62: 339–343.
- Bratley, J., Cadigan, N. G., Dwyer, K., Healey, B. P., Morgan, M. J., Murphy, E. F., Maddock Parsons, D., *et al.* 2009. Assessment of the cod (*Gadus morhua*) stock in NAFO Divisions 2J+3KL in 2009. Canadian Science Advisory Secretariat, Department of Fisheries and Oceans, Research Document 2009/061.
- Brunel, T. 2010. Age-structure-dependent recruitment: a meta-analysis applied to Northeast Atlantic fish stocks. *ICES Journal of Marine Science*, 67: 1921–1930.
- Clark, J., and Bjørnstad, O. 2004. Population time series: process variability, observation errors, missing values, lags, and hidden states. *Ecology*, 85: 3140–3150.
- Dick, E. J. 2009. Modeling the reproductive potential of rockfishes (*Sebastes* spp.). University of California Santa Cruz, February 1. 256 pp.
- Hidalgo, M., Rouyer, T., Molinero, J. C., Massutí, E., Moranta, J., Guijarro, B., and Stenseth, N. C. 2011. Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. *Marine Ecology Progress Series*, 426: 1–12.
- Hixon, M. A., Johnson, D. W., and Sogard, S. M. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES Journal of Marine Science*, 71: 2175–2185.
- Hooten, M. B., and Hobbs, N. T. 2015. A guide to Bayesian model selection for ecologists. *Ecological Monographs*, 85: 3–28.
- Hutchings, J. A., and Myers, R. A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Canadian Journal of Fisheries and Aquatic Sciences*, 51: 2126–2146.
- ICES. 2008a. Report of the Working Group on the Assessment of Southern Shelf Demersal Stocks (WGSSDS). ICES CM 2008/ACOM: 12. Copenhagen, Denmark. 552 pp.
- ICES. 2008b. Report of the Working Group on the Assessment of Northern Shelf Demersal Stock (WGNSSD). ICES CM 2008/ACOM: 8. Copenhagen, Denmark. 757 pp.
- ICES. 2012a. Report of the Working Group on the Assessment of Demersal Stocks in the North Sea and Skagerrak (WGNSSK). ICES CM 2012/ACOM: 13. Copenhagen, Denmark. 1346 pp.
- ICES. 2012b. Report of the Baltic Fisheries Assessment Working Group 2012 (WGBFAS). ICES CM 2012/ACOM: 05. Copenhagen, Denmark. 835 pp.
- ICES. 2012c. Report of the North-Western Working Group (NWWG). ICES CM 2012/ACOM: 07. Copenhagen, Denmark. 1375 pp.
- ICES. 2012d. Report of the Arctic Fisheries Working Group 2012 (AFWG). ICES CM 2012/ACOM: 05. Copenhagen, Denmark. 633 pp.
- Jacobson, L. D., and MacCall, A. D. 1995. Stock-recruitment models for Pacific sardine (*Sardinops sagax*). *Canadian Journal of Fisheries and Aquatic Sciences*, 52: 566–577.
- Köster, F. W., Möllmann, C., Hinrichsen, H-H., Wieland, K., Tomkiewicz, J., Kraus, G., Voss, R., *et al.* 2005. Baltic cod recruitment—the impact of climate variability on key processes. *ICES Journal of Marine Science*, 62: 1408–1425.
- Levin, P. S., Holmes, E. E., Piner, K. R., and Harvey, C. J. 2006. Shifts in a Pacific ocean fish assemblage: the potential influence of exploitation. *Conservation Biology*, 20: 1181–1190.
- Marshall, C. T., Kjesbu, O. S., Yaragina, N. A., Solemdal, P., and Ulltang, Ø. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 1766–1783.
- Marteinsdottir, G., and Thorarinnsson, K. 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua*) by including age diversity of spawners. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 1372–1377.
- Morgan, M., Shelton, P., and Bratley, J. 2007. Age composition of the spawning stock does not always influence recruitment. *Journal of Northwest Atlantic Fishery Science*, 38: 1–12.
- Murawski, S. 2001. Impacts of demographic variation in spawning characteristics on reference points for fishery management. *ICES Journal of Marine Science*, 58: 1002–1014.
- Myers, R., Barrowman, N., Hutchings, J., and Rosenberg, A. 1995. Population dynamics of exploited fish stocks at low population levels. *Science*, 269: 1106–1108.
- Myers, R., Bowen, K., and Barrowman, N. 1999. Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 2404–2419.
- NEFSC. 2013. 55th Northeast Regional Stock Assessment Workshop (55th SAW) Assessment Summary Report. US Department of Commerce, Northeast Fisheries Science Center Reference Document. 13-01.
- O'Farrell, M. R., and Botsford, L. W. 2006. The fisheries management implications of maternal-age-dependent larval survival. *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 2249–2258.
- Olsen, E. M., Ottersen, G., Llope, M., Chan, K-S., Beaugrand, G., and Stenseth, N. C. 2011. Spawning stock and recruitment in North Sea cod shaped by food and climate. *Proceedings of the Royal Society B*, 278: 504–510.
- Ottersen, G., Bogstad, B., Yaragina, N. A., Stige, L. C., Vikebø, F. B., and Dalpadado, P. 2014. A review of early life history dynamics of Barents Sea cod (*Gadus morhua*). *ICES Journal of Marine Science*, 71: 2064–2087.
- Ottersen, G., Hjermmann, D. Ø., and Stenseth, N. C. 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fisheries Oceanography*, 15: 230–243.
- Power, D., Morgan, J., Murphy, E. F., Bratley, J., and Healey, B. 2010. An Assessment of the Cod Stock in NAFO Divisions 3NO. SCR Document No. 10/42. St. John's, Newfoundland, Canada. 52 pp.
- Quinn, T. J., II, and Deriso, R. B. 1999. *Quantitative Fish Dynamics*. Oxford University Press, New York.
- Ricker, W. E. 1954. Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, 11: 559–623.
- Rothschild, B., and Fogarty, M. 1989. Spawning-stock biomass: a source of error in recruitment/stock relationships and management advice. *ICES Journal of Marine Science*, 45: 131–135.
- Rouyer, T., Sadykov, A., Ohlberger, J., and Stenseth, N. C. 2012. Does increasing mortality change the response of fish populations to environmental fluctuations? *Ecology Letters*, 15: 658–665.
- Scott, B., Marteinsdottir, G., Begg, G., Wright, P., and Kjesbu, O. 2006. Effects of population size/age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*). *Ecological Modelling*, 191: 383–415.

- Scott, B., Marteinsdottir, G., and Wright, P. 1999. Potential effects of maternal factors on spawning stock-recruitment relationships under varying fishing pressure. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 1882–1890.
- Shelton, A. O., and Mangel, M. 2011. Fluctuations of fish populations and the magnifying effects of fishing. *Proceedings of the National Academy of Sciences of the United States of America*, 108: 7075–7080.
- Shelton, A. O., Munch, S. B., Keith, D., and Mangel, M. 2012. Maternal age, fecundity, egg quality, and recruitment: linking stock structure to recruitment using an age-structured Ricker model. *Canadian Journal of Fisheries and Aquatic Sciences*, 69: 1631–1641.
- Sogard, S., Berkeley, S., and Fisher, R. 2008. Maternal effects in rockfishes *Sebastes* spp.: a comparison among species. *Marine Ecology Progress Series*, 360: 227–236.
- Spencer, P. D., Kraak, S., and Trippel, E. A. 2014. The influence of maternal effects in larval survival on fishery harvest reference points for two life-history patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, 71: 151–161.
- Swain, D. P., Savoie, L., Hurlbut, T., Surette, T., and Daigle, D. 2009. Assessment of the southern Gulf of St. Lawrence cod stock, February 2009. DFO Canadian Science Advisory. Secretariat Research Document 2009/037, vi + 129 pp.
- Thorson, J. T., Cope, J. M., Kleisner, K. M., Samhouri, J. F., Shelton, A. O., and Ward, E. J. (in press). Giants' shoulders 15 years later: lessons, challenges and guidelines in fisheries meta-analysis. *Fish and Fisheries*, doi: 10.1111/faf.12061.
- Vallin, L., and Nissling, A. 2000. Maternal effects on egg size and egg buoyancy of Baltic cod, *Gadus morhua*: implications for stock structure effects on recruitment. *Fisheries Research*, 49: 21–37.
- Venturelli, P., Shuter, B., and Murphy, C. 2009. Evidence for harvest-induced maternal influences on the reproductive rates of fish populations. *Proceedings of the Royal Society B: Biological Sciences*, 276: 919–924.
- Wikström, A., Ripa, J., and Jonzén, N. 2012. The role of harvesting in age-structured populations: disentangling dynamic and age truncation effects. *Theoretical Population Biology*, 82: 348–354.
- Worden, L., Botsford, L. W., Hastings, A., and Holland, M. D. 2010. Frequency responses of age-structured populations: Pacific salmon as an example. *Theoretical Population Biology*, 78: 239–249.

Handling editor: Howard Browman