Age-structure-dependent recruitment: a meta-analysis applied to Northeast Atlantic fish stocks

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Exploitation alters the age structure of fish stocks. Several stock-specific studies have suggested that changes in the age structure might have consequences for subsequent recruitment, but the evidence is not universal. To investigate how common such effects are among 39 Northeast Atlantic fish stocks, relationships were tested between age structure (spawner mean age, age diversity, and proportion of recruit spawners) and recruitment (number of recruits, sensitivity to environment, and recruitment variability). Significant correlations in the expected direction were observed for a few stocks, but not for the majority; significant correlations in the opposite direction were also found. Meta-analyses combining the stock-level tests revealed that none of the effects were significant overall. However, effects were significant for some species (cod, haddock, and plaice) and indices. The low variability in the age structure might explain the absence of significant effects for individual stocks. Other reasons could be the absence of a biological basis (reproductive characteristics not dependent on age) or the stronger influence of environmental variability than of age structure on recruitment.

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Introduction

The consequences of exposing fish stocks to high fishing mortalities are manifold. The most obvious one, on which current management practices are based, is the depletion of the spawning-stock biomass (SSB), which increases the risk of recruitment failure and stock collapse. Other potential effects of fishing on stock dynamics have been somewhat neglected, for instance the consequences of changes in the age structure of the spawners caused by heavy exploitation. Exploitation typically causes a loss of older individuals, resulting in a decrease in the average age and in the number of age classes in the spawning stock (Berkeley et al., 2004b; Ottersen et al., 2006). Over the years, indications that the age composition of the SSB might influence recruitment have been provided by correlative studies for an increasing number of stocks (Lambert, 1990; Marteinsdottir and Thorarinsson, 1998; Cardinale and Arrhenius, 2000; Vallin and Nissling, 2000; O'Brien et al., 2003; Ottersen et al., 2006). Investigating the relationship between maternal age, spawning time, and early survivorship in North Sea haddock (Melanogrammus aeglefinus), Wright and Gibb (2005) found substantially lower survival for the eggs spawned by individuals reproducing for the first time, suggesting that recruitment success could be related to the proportion of recruit spawners in the SSB. However, studying four Northwest Atlantic cod (Gadus morhua) and American plaice (Hippoglossoides platessoides) stocks, Morgan et al. (2007) found that such effects on recruitment were not always observed. They pointed out the need for further research to establish whether age structure commonly affects recruitment among fish stocks.

The idea of age-structure-dependent recruitment stems from the existence of age-related differences in the reproductive characteristics of spawners. For several species, both field observations and experimental studies provide evidence that reproduction by larger and older (and consequently more experienced) females is more successful than reproduction by their smaller and younger congeners. For cod (Kjesbu et al., 1996; Trippel et al., 1997; Marteinsdottir and Thorarinsson, 1998), haddock (Hislop, 1988), plaice (Pleuronectes platessa; Rijnsdorp, 1991), and winter flounder (Pseudopleuronectes americanus; Buckley et al., 1991), relative fecundity (number of eggs produced per unit of weight) is lower for young females than for older ones. In cod, young females (second-time spawners) are also more likely than older ones to skip spawning when environmental conditions are unfavourable (Jørgensen et al., 2006). Size and age also affect egg quality. Eggs produced by young female cod are smaller and have lower fertilization and hatching rates than eggs produced by older females (Solemdal et al., 1995; Kjesbu et al., 1996; Trippel et al., 1997; Vallin and Nissling, 2000). In addition, larvae hatching from larger eggs are more successful in developing a swimbladder and have a higher specific growth rate (Trippel et al., 1997; Marteinsdottir and Steinarsson, 1998; Nissling et al., 1998), which increases their probability of survival. In black rockfish (Sebastes melanops), eggs spawned by old females have more energy reserves and the larvae are larger, have a faster growth rate, and a better survival during a period of starvation (Berkeley et al., 2004a). Collectively, all of these studies suggest that the age structure

affects both the number and the quality of the eggs produced by a stock for a given level of SSB.

Temporal and spatial aspects of spawning activity could also be related to age. For cod, experiments have demonstrated that older females tend to have a longer spawning period than younger fish (Kjesbu *et al.*, 1996), whereas field observations indicate age-dependent timing, duration, and location of spawning (Hutchings and Myers, 1993; Begg and Marteinsdottir, 2002). The latter is true also for haddock (Wright and Gibb, 2005). In herring, different age classes spawn at different times, with older ones maturing and spawning first (Lambert, 1987). In female North Sea plaice, spawning starts earlier in older fish, but the ending of spawning does not differ between age groups (Rijnsdorp, 1989). If age significantly affects the timing of repro- duction, a decrease in age diversity and mean age in a stock would result in shifts in the onset and peak of spawning, as well as in a shortening of the spawning season (Wright and Trippel, 2009). Similarly, the spatial extent of spawning might change. In turn, this might decrease the likelihood that larvae could utilize the period (and areas) of peak zooplankton abundance and, there- fore, reduce the probability of successful recruitment (Wright and Gibb, 2005).

All of these considerations combined suggest that the age struc- ture might affect both the reproductive potential of a stock and the probability of survival of the offspring until recruitment. Therefore, one might expect reduced recruitment when the age structure of the spawning stock is shifted to the younger age classes and the SSB is composed of fewer age classes (Effect 1). Releasing more robust offspring and spreading the spawning season over a longer period makes the reproductive success of a stock less dependent on the environmental conditions encoun- tered (Hutchings and Myers, 1993; Brander, 2005). For that reason, a decrease in age diversity and mean age might increase the sensitivity of recruitment to environmental conditions (Effect 2; Ottersen *et al.*, 2006). As a corollary, higher recruitment variability might be expected (Effect 3).

This analysis is aimed at resolving the issue of whether age-structure-dependent recruitment is a common feature among species, by drawing information from 39 Northeast Atlantic fish stocks assessed regularly by ICES and by testing these three hypotheses about the potential effects of a shift of the age structure towards younger age classes: (i) reduced recruit- ment, (ii) increased effects of the environment on recruitment, and (iii) enhanced recruitment variability. The primary methods used are similar to those used in previous studies. A meta-analysis is then applied to investigate whether the effects are significant among (subsets of) all stocks, by combining the results of the stock-level tests.

Material and methods
Fish stocks

The essential information—matrices of stock abundances in numbers-at-age, weight-at-age, and the proportion of individuals mature-at-age—were drawn from the reports of ICES stock assessment working groups for 2008. Only stocks with ≥ 25 years of data were included, resulting in 39 stocks belonging to ten species and distributed over 12 fishing areas (Figure 1).

The recruiting age class is classically defined as the youngest age class caught by the fishery, in this study varying between ages 0 and 4, depending on the stock. All recruitment time-series were hence
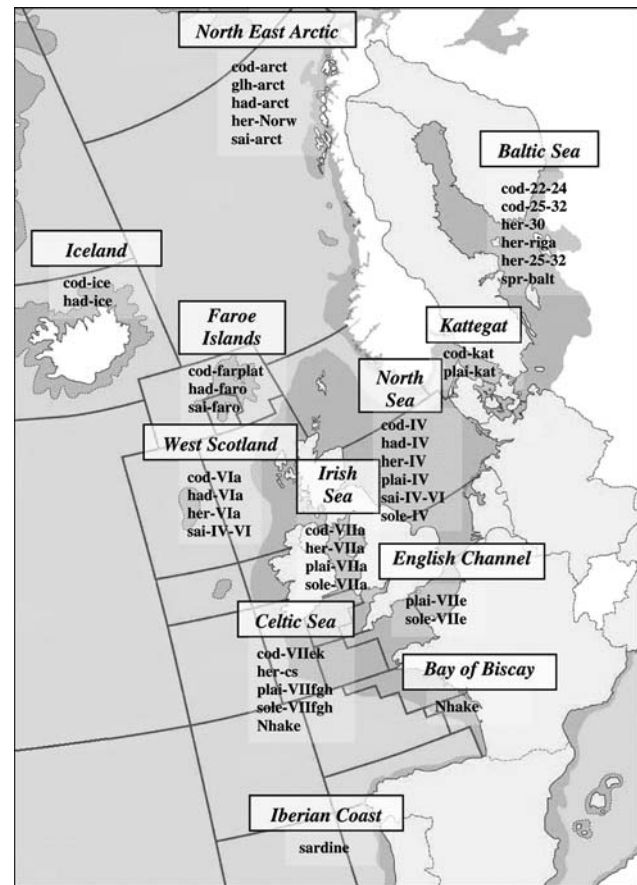

Figure 1. Map of the Northeast Atlantic with the ICES fishing areas and the 39 fish stocks investigated. Abbreviations for species names: had, haddock; glh, Greenland halibut; her, herring; spr, sprat; sai, saithe; plai, plaice. Other abbreviations: arct, Arctic; Norw, Norway; ice, Iceland; riga, Gulf of Riga; balt, Baltic; farplat, Faroe Plateau; faro, Faroes; kat, Kattegat; cs, Celtic Sea.

lagged by the number of years corresponding to the age-at-recruitment, so that the dates in the series correspond to the year of birth of the year class. Because of uncertainties in the most recent estimates, the final 2 years of the series were removed.

The SSB-at-age by year was calculated as:

$$\text{SSB}_{a,y} = N_{a,y} W_{a,y} \text{Mat}_{a,y}, \qquad (1)$$

where $N_{a,y}$, $W_{a,y}$, and $\text{Mat}_{a,y}$ are the stock numbers, weight, and proportion of individuals mature at-age a in year y, respectively.

The indices used to describe the age structure of the spawning stock were copied from previous studies (Marteinsdottir and Thorarinsson, 1998; Ottersen *et al.*, 2006; Morgan *et al.*, 2007). The meanAge was calculated as the mean of the ages weighted by the proportion of the SSB in each age class

$$\text{meanAge}_y = \sum_{a=a\min_y}^{a\max_y} p_{a,y} a, \qquad (2)$$

where $a\min_y$ and $a\max_y$ are the ages of the youngest and the oldest age groups in year y, and $p_{a,y}$ is the proportion of the SSB

represented by age group *a*:

$$p_{a,y} = \frac{\text{SSB}_{a,y}}{\sum_{a=a\,\min_y}^{a\,\max_y} \text{SSB}_{a,y}}. \qquad (3)$$

The Shannon diversity index, *H*, describes both the number of age classes and the diversity of their distribution in the SSB:

$$H_y = -\sum_{a=a\,\min_y}^{a\,\max_y} p_{a,y} \ln p_{a,y}. \qquad (4)$$

The proportion of SSB represented by recruit spawners, Pfirst$_y$, was calculated as (Morgan *et al.*, 2007):

$$\text{Pfirst}_y = \frac{\sum_{a=a\,\min_y}^{a\,\max_y} (\text{Mat}_{a,y} - \text{Mat}_{a-1,y-1})/\text{Mat}_{a,y}\text{SSB}_{a,y}}{\sum_{a=a\,\min_y}^{a\,\max_y} \text{SSB}_{a,y}}. \qquad (5)$$

Variability in age structure

Variations in the age structure of the spawning stock could have multiple causes (Morgan *et al.*, 2007): changes in age at maturation and sex ratio, truncation of the age structure caused by size-selective fishing, and/or natural variations in stock demography caused by recruitment variability. The importance of these factors might vary among stocks, resulting in different patterns of age-structure variability. To investigate the existence of such patterns, the temporal variability of meanAge, *H*, and Pfirst for each stock was described by two measures: the coefficient of variation (*CV*), representing the overall variability in these indices, and the proportion of variance explained by a moving average smoother (*T*), indicating whether the variability occurs as a temporal trend. Principal component analysis and hierarchical clustering were then applied on the *CV*s and the *T*s of the three age-structure indices.

Effects on recruitment

(1) To investigate whether the number of recruits produced by a stock is influenced by the age structure of the SSB, the relationship between recruitment and the three indices was investigated first. Because variations in SSB might explain a part of the variability in recruitment (Myers and Barrowman, 1996), recruitment time-series were transformed to account for these effects. To do so, three stock–recruitment models—Ricker, Beverton and Holt, and Cushing—were fitted to the data for each stock and the residuals from the model with the best fit, resR, were used to describe the variations in recruitment not explained by the variation in SSB. The effect of age structure on the number of recruits produced was then investigated by calculating the correlations between resR and meanAge, *H*, and Pfirst in each stock.

A second test was conducted by investigating whether incorporating an age-structure index as a covariate in a stock–recruitment model improved the proportion of variance in recruitment explained by the model (Marteinsdottir and Thorarinsson, 1998). For each stock, the Ricker and the Beverton and Holt models were fitted both without and with the index as a covariate:

The Ricker model with covariate *X*

$$R = \alpha(1 - \delta X)\text{SSB}e^{-\beta(1-\rho X)\text{SSB}}, \qquad (6)$$

The Beverton and Holt model with covariate *X*

$$R = \frac{\alpha(1 - \delta X)\text{SSB}}{\beta(1 - \rho X) + \text{SSB}}, \qquad (7)$$

where *R* is the recruitment, α and β the parameters of the stock–recruitment model, *X* one of the three age-structure indices, and δ and ρ are the coefficients for the effect of *X* related to α and β, respectively. The stock–recruitment models were fitted by maximizing the log-likelihood using the flme routine from the FLCore package (Kell *et al.*, 2007) implemented with R (R Development Core Team, 2008). For each stock and each model, an analysis of variance was done to test whether including the age-structure index as a covariate significantly improved the fit.

(2) To test the hypothesis that changes in the age structure modify the sensitivity of recruitment to the environment, the correlation between temperature and recruitment was investigated. Temperature was chosen, because it might affect recruitment processes directly or it may be used as a proxy for other environmental variations. Besides, significant temperature–recruitment correlations have been found for several Northeast Atlantic fish stocks (Planque and Frédou, 1999; Brunel and Boucher, 2007). Annual values of sea surface temperature (SST) were calculated for each stock by averaging monthly values (provided by the ICOADS dataset: http://icoads.noaa.gov) over the ICES fishing area(s) occupied.

For each stock, the sensitivity of recruitment to temperature was described by the correlation between resR and SST. A 15-year moving window was used (Ottersen *et al.*, 2006). For each position of the window, the correlation between resR and SST was calculated [hereafter referred to as $r_{15}(\text{resR}-\text{SST})$]. Moving the window throughout the time-series generated a time-series of $r_{15}(\text{resR}-\text{SST})$, representing temporal changes in the sensitivity of recruitment to temperature. The correlations between this series and each age-structure index were calculated for each stock.

(3) Changes in recruitment variability were investigated by calculating the variance of resR in a 15-year moving window. As above, the correlation between these time-series of recruitment variability and meanAge, *H*, and Pfirst was calculated to test for a link between age structure and recruitment variability.

Statistical tests

Biological and environmental time-series are often autocorrelated. Because these autocorrelations violate the assumption of serial independence required for hypothesis testing, significance tests of correlation coefficients could be biased owing to overestimation of the degrees of freedom (Pyper and Peterman, 1998). For that reason, the number of degrees of freedom used to test the significance of a correlation between two variables was corrected using the modified Chelton method (Pyper and Peterman, 1998):

$$\frac{1}{N_2} = \frac{1}{N} + \frac{2}{N}\rho_1(1)\rho_2(1), \qquad (8)$$

where *N* and N_2 are the initial and corrected numbers of degrees of

freedom, respectively, and $\rho_1(1)$ and $\rho_2(1)$ are the 1-year lag autocorrelations in the two variables considered.

To test the three hypotheses among stocks of the same species and among all stocks, the stock-level correlation coefficients were combined using a random-effects meta-analysis (Hedges and Olkin, 1985). Weighted mean correlation coefficients and their associated confidence intervals and p-values were computed from the stock-level correlations and their respective numbers of degrees of freedom using the method described in Worm and Myers (2003). In a fixed-effects analysis, the effects (correlations) for each stock are assumed to have the same value. The random-effects meta-analysis allows for variation in the effects (assuming a normal distribution) among stocks. This method was chosen to allow for variability among stocks in the way age structure might affect their recruitment, which seems a more realistic assumption than assuming an identical response.

To test the effect of including age structure as a covariate in the stock–recruitment models among stocks, the p-values of the analyses of variance done at the stock level were combined using a weighted Z-method. This method was chosen because of its higher power and precision than Fisher's combined probabilities test, which usually is applied in such a meta-analytical approach (Whitlock, 2005). The weighted Z-method involves computing

the Z_w statistic:

$$Z_w = \frac{\sum_{st=1}^{S} N_{2,st} Z_{st}}{\sqrt{\sum_{st=1}^{S} N_{2,st}^2}}, \qquad (9)$$

where S is the number of independent tests done for a given relationship (here equal to the number of stocks), Z_{st} the quantile of the standard normal distribution corresponding to the p-value of the individual test of the relationship for stock st, and $N_{2,st}$ refers to the weights for the independent test for stock st, equal to the numbers of degrees of freedom, as suggested by Whitlock (2005). The corresponding p-value, assuming a standard normal distribution for Z_w, was used to test the significance of the relationship among stocks.

Results

Variability in age structure

The first principal component (PC1) of the PCA on the CVs and Ts of the age-structure indices described well the overall variability (CV) of the age structure, whereas the PC2 was representative of the presence of a temporal trend (T; Figure 2). A partitioning of the stocks into five groups was done, based on a hierarchical clustering using the Ward criterion (maximization
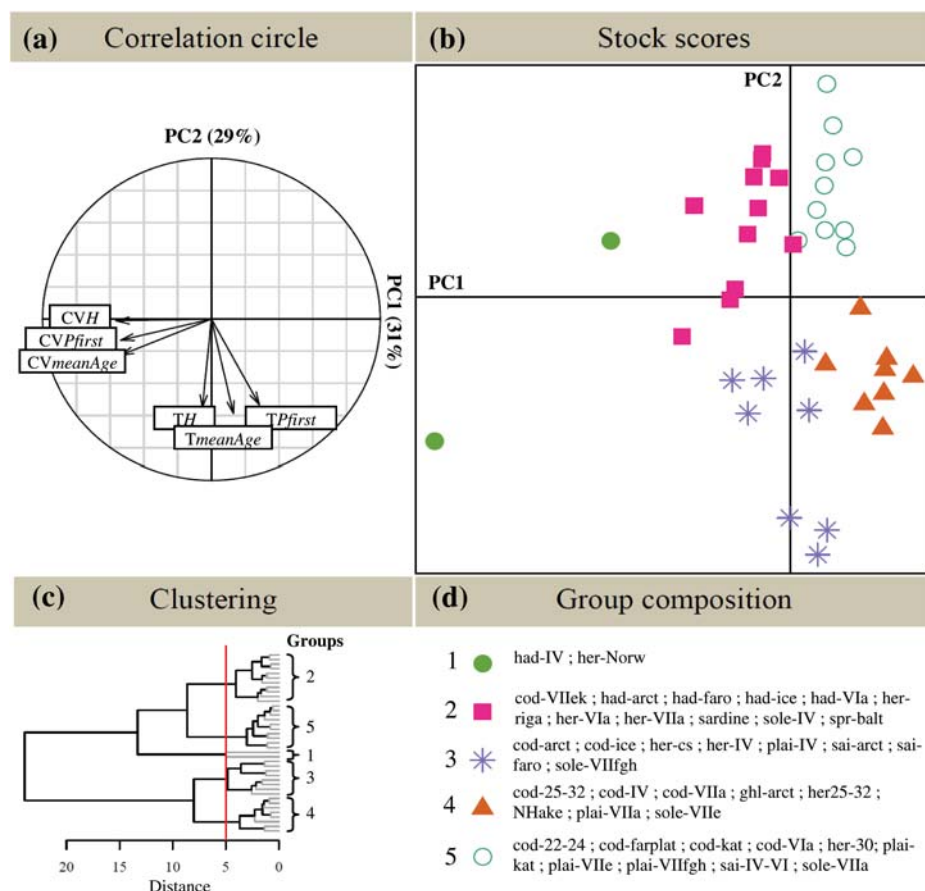

Figure 2. Typology of the variability in the age structure of the spawning stock for the 39 stocks: (a) PCA on the descriptors of age-structure variability (coefficient of variation, CV, and proportion of variability explained by the trend, T, in the three indices: meanAge, H, and Pfirst); (b) scores of the stocks on the two first principal components (labelled by group); and (c) hierarchical clustering of the stocks and delimitation of the five groups of stocks with similar type of age-structure variations; (d) composition of the groups identified.

of the intergroup variance). Group 1 was composed of two stocks characterized by high age-structure variability, stocks in groups 2 and 3 by moderate age-structure variability, and stocks in group 4 and 5 by low age-structure variability. In addition, stocks in groups 3 and 4 were characterized by a long-term trend.

Effects on recruitment

The expected sign of the correlations between resR and age-structure indices was positive for meanAge and *H*, and negative for Pfirst. There was no indication that the correlation was consistently positive or negative for any of the three indices (Figure 3a). At the stock level, correlations were significant for a very small number of stocks only (ghl-arct and had-IV for meanAge and Pfirst, plai-IV for Pfirst, and cod-ice, cod-VIIa, ghl-arct, and sai-faro for *H*) and for each index, the number of positive and negative correlations was balanced. The weighted average correlation, calculated over all 39 stocks, was close to zero for all three indices. Average correlations calculated for groups of stocks by species were also not significant, except for the average correlation with *H* for cod, which was positive and significant ($\bar{r} = 0.17$, $p = 0.003$).

For almost half of the stocks, the stock–recruitment models without an age-structure index as a covariate (both Ricker and Beverton and Holt) had an R^2 equal or close to zero (results not

given; R^2 was defined by $R^2 = 1 - (SS_{res}/SS_{tot})$, with SS_{tot} and SS_{res} being the total and residual sum of squares, respectively; by convention, we set $R^2 = 0$ for cases where $SS_{res} > SS_{tot}$, because R^2 would be negative). R^2 was >0.2 only for nine and seven stocks for the Ricker and the Beverton and Holt models, respectively. The only case for which both models explained $>60\%$ of recruitment variability was cod-kat. Including age structure as a covariate in the models improved the fit in $\sim25\%$ of the cases, but this improvement was significant only for a small number of stocks (Table 1). Not surprisingly, the meta-analytical tests concluded that, overall, the fit of the models was not improved by including age-structure indices ($p > 0.4$ for all tests done with the weighted *Z*-method).

The second hypothesis, that a decrease in meanAge or *H* results in an increased sensitivity of recruitment to temperature, would correspond, for the stocks for which $r_{15}(resR-SST)$ is on average positive (or negative), to a negative (or positive, respectively) correlation between meanAge or *H* and $r_{15}(resR-SST)$. For Pfirst, the opposite reasoning applies. To test a relationship of the same sign among all stocks, whatever the sign of the average $r_{15}(resR-SST)$, the opposite of the correlation between age-structure indices and $r_{15}(resR-SST)$ was taken for the stocks for which $r_{15}(resR-SST)$ was on average negative. Hence, in Figure 3b, negative correlations are expected for meanAge and *H*, and positive correlations for Pfirst.
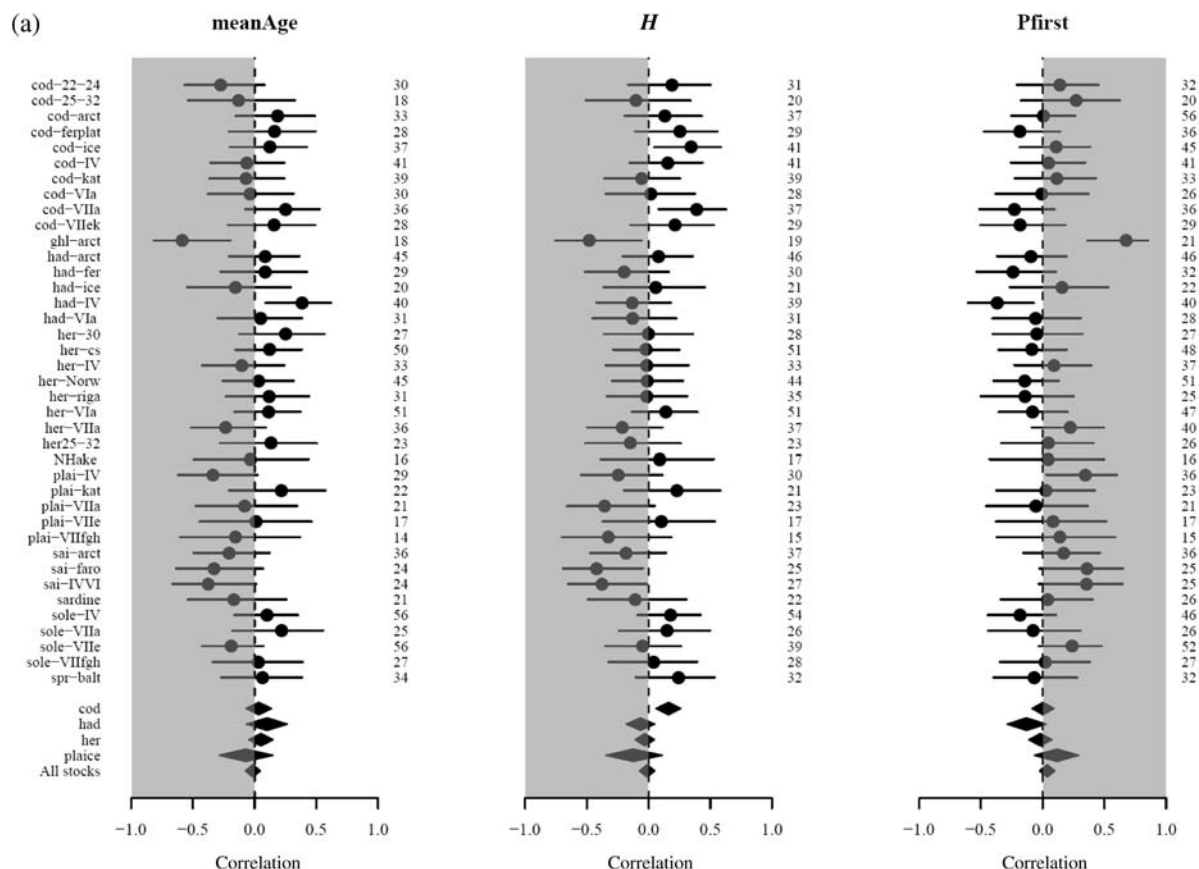

Figure 3. Meta-analysis of the effect of age structure on recruitment characteristics in terms of the correlation between each of the three age-structure indices (meanAge, *H*, and Pfirst) and (a) number of recruits, (b) sensitivity of the recruitment–temperature relationship, and (c) recruitment variability (dots and bars: value and 95% CI for each stock; diamonds: weighted mean value and 95% CI among stocks by species or among all stocks; weights given in the columns; grey areas: signs of the correlation that do not conform to expectations).
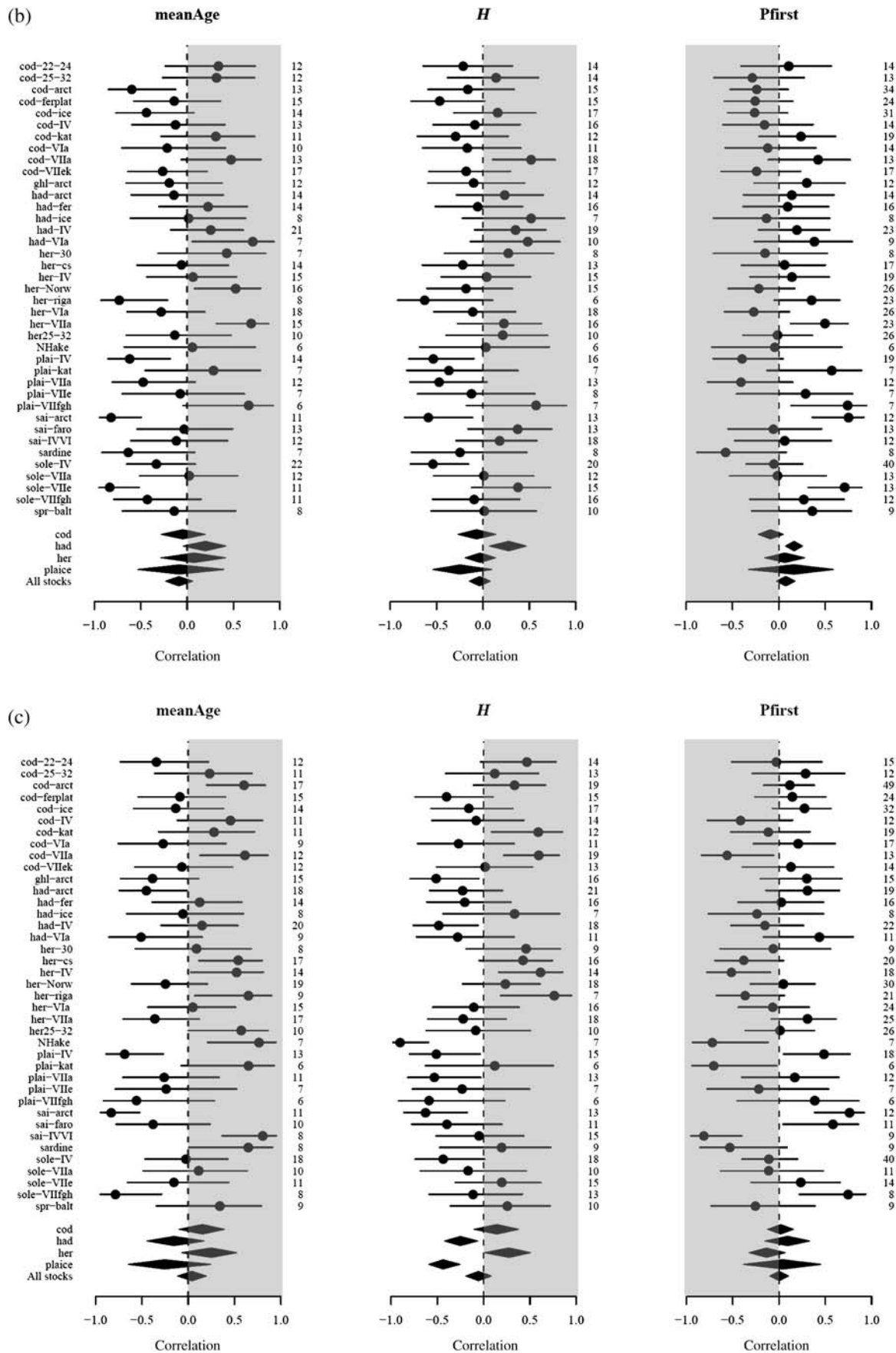
Figure 3. Continued.

Table 1. Stocks for which the Ricker or the Beverton and Holt stock–recruitment models were significantly improved when different age-structure indices were added as a covariate.

	Ricker			Beverton and Holt		
	meanAge	H	Pfirst	meanAge	H	Pfirst
$p < 0.01$	–	cod-VIIa	ghl-arct	cod-ice	cod-VIIa	ghl-arct
			plai-IV	ghl-arct	ghl-arct	sai-faro
			sai-faro	plai-kat	NHake	
					plai-kat	
					sole-VIIfgh	
$p < 0.05$	her-VIa	cod-VIIek	cod-25-32	cod-VIIa	–	NHake
	her25-32			NHake		sai-IVVI

Correlations between age-structure indices and r_{15}(resR–SST) generally had a large confidence interval (Figure 3b), because of the limited degrees of freedom (7 years of data were lost at the beginning and at the end of the time-series because of the 15-year moving window). Correlations with meanAge, H, and Pfirst were significant for eight, four, and four stocks, respectively. For each index, the number of positive and negative correlations was more or less balanced. For meanAge, the weighted average correlation among the 39 stocks was negative, as expected, but not significant. Weighted average correlations for individual species were also not significant. For H, they were close to zero among all stocks and among both cod and herring stocks. Only the correlation among plaice stocks was clearly negative, as expected, but not significant. Contrary to expectations, the correlation among haddock stocks was positive and significant ($\bar{r} = 0.28$, $p = 0.013$). For Pfirst, the weighted average correlation was positive, as expected, among all stocks and among plaice, herring and haddock stocks, though significant only for haddock ($\bar{r} = 0.17$, $p < 0.001$). The correlation was negative among cod stocks, but not significant.

Recruitment variability was expected to increase when meanAge or H decreases and when Pfirst increases (Effect 3). Compared with the other two effects, the number of stocks with significant correlations between variability and age-structure indices was relatively high (12, 8, and 7 for meanAge, H, and Pfirst, respectively; Figure 3c), but significant correlations were as often negative as positive, except for meanAge (only 4 negative out of 12 significant correlations).

For meanAge, the weighted average correlation among all stocks was almost zero. The correlation was positive for cod and herring, and negative for haddock and plaice, but significant for none of the species. The weighted average correlation among all stocks was also zero for H, but the correlation for herring was significant and positive ($\bar{r} = 0.28$, $p = 0.05$) and for haddock and plaice significant and negative ($\bar{r} = -0.25$, $p = 0.015$ and $\bar{r} = -0.44$, $p < 0.001$, respectively). For Pfirst, all correlations had values close to zero and none was significant.

Discussion

The concept that changes in the age composition of the spawning stock caused by heavy exploitation could have detrimental effects on recruitment is becoming increasingly popular (Berkeley *et al.*, 2004b; Birkeland and Dayton, 2005; Morgan *et al.*, 2007; Ottersen, 2008; Venturelli *et al.*, 2009; Wright and Trippel, 2009). This concept has already been accepted by management authorities, such as the European Commission, which considers that one of the criteria for a "Good Environmental Status" in marine ecosystems is that "Populations of all commercially exploited fish are exhibiting an age and size distribution indicative of a healthy stock" (CEC, 2007). Evidence of different types of effect of the age structure of the spawning stocks on recruitment has been provided so far by a limited number of stock-specific studies. However, the results from applying these statistical methods systematically to all regularly assessed stocks in the ICES Area clearly indicate that significant effects are observed only in a minority of stocks, that the sign of the correlations is often in contradiction with the expectations, and that the conclusions drawn from a few individual studies should not be proclaimed a rule. It might well be that for some species there is no biological basis for such effects. Age-dependent reproductive characteristics, such as relative fecundity, egg size or timing, and duration of spawning, has been reported only for a limited number of species (see the "Introduction" section) and might not apply universally to fish species.

Studies on the effects of age structure on recruitment mostly relate to the number of recruits produced. Year-class strength has been related to the number of modes in the age distribution of the spawning stock for Norwegian spring-spawning herring (Lambert, 1990), to age diversity in Icelandic cod (Marteinsdottir and Thorarinsson, 1998), Georges Bank cod (O'Brien *et al.*, 2003), and Chesapeake Bay striped bass (*Morone saxatilis*; Secor, 2000), and to the biomass of older spawners in Baltic Sea cod (Cardinale and Arrhenius, 2000; Vallin and Nissling, 2000). The results of this meta-analysis provide very little evidence of a general correlation between year-class strength of the 39 Northeast Atlantic stocks investigated and any of the three indices of age structure, except cod, for which a significant positive correlation between age diversity and recruitment was observed across stocks. The reproductive biology of this species has been studied intensively, and age-dependent relative fecundity, as well as maternal influence on size and viability of the eggs, have been firmly established (see the "Introduction" section). However, this was not evidenced in the results here, because the correlations with meanAge and Pfirst were not significant. The significant correlation with age diversity suggests that the effect on the timing and duration of the spawning season might be a critical factor. Age-dependent spawning activity has been observed, older cod spawning later, but for a longer period than younger individuals (Hutchings and Myers, 1993).

As an alternative to the two methods used to investigate possible effects of age structure on the stock recruitment model (by removing the effect of SSB using the residuals and introducing

age structure as a covariate), the approach of Cardinale and Arrhenius (2000) was also tested. They investigated whether an index of the reproductive potential of Baltic cod incorporating information on age structure explained recruitment variability better than SSB. The results of fitting the three different stock–recruitment models for all 39 stocks using repeat spawner biomass and comparing these with the fit of the same model using SSB are not shown because they were qualitatively similar to the results presented here: a significant effect for some stocks (Baltic cod being one), but not for the majority; a meta-analytical test concluding that overall these effects were not significant.

The absence of a general relationship between recruitment and age structure does not exclude the possible existence of a causal link, because for many stocks a large part of variability in recruitment is caused by environmental variability (Garrod and Colebrook, 1978; Shepherd et al., 1984; Cushing, 1996). The effect of age structure might be only a second order effect that could hardly be detected if the first order effects are not taken into account. For stocks where a strong relationship between recruitment and environment could be taken into account, the probability of observing a significant effect of age structure increased (Cardinale and Arrhenius, 2000; O'Brien et al., 2003).

Additionally, the accuracy of the data used might not be sufficient to reflect adequately the true variations in the age structure of the spawning stock. For instance, because of the lack of data, constant maturity ogives have been used for entire time-series (or parts of these) for many stocks, which, for changes in maturation schedules, could result in a wrong perception of the variations in the age structure of the spawning stock. Besides, this study is based on recruitment estimates calculated by virtual population analysis models, which could be affected by various sources of error (Ulltang, 1977). These uncertainties in the data used could blur any underlying relationship between age structure and recruitment.

Brander (2005) demonstrated that the link between recruitment and environmental variability [as represented by the North Atlantic Oscillation (NAO) index] for six cod stocks was stronger when their biomasses were relatively small. However, whether this was an effect of relaxation of density-dependent regulation at low stock size or of changes in age structure along with changes in stock size remained an open question. Northeast Arctic cod appears to be the only stock for which indications have been found that changes in age structure might modify the strength of the link between recruitment and the environment (Ottersen et al., 2006). Although based on a different set of temperature data, the negative correlation between meanAge and r_{15}(resR–SST) for Northeast Arctic cod (Figure 3b) confirmed their results. The results suggested that similar effects also apply for other stocks (plai-IV, sai-arct, and sole-IV and -VIIe). However, the meta-analysis was inconclusive and, contrary to expectations, indicated for haddock a significant increase in the effect of temperature when age diversity increases. To some extent, the absence of a general relationship might be explained by the choice of only one environmental factor. Temperature is undoubtedly an important factor for recruitment in many stocks, but other factors, such as salinity or wind intensity, should not be discounted.

A way to circumvent this problem could be to use climate indices as proxies of the overall environmental conditions, instead of a single environmental variable (Stenseth et al., 2003).

This approach was tested by redoing the analysis using the winter NAO (Hurrell, 1995) instead of SST. Again, a significant effect of age structure on the correlation between recruitment and the NAO was found for some stocks (cod-arct and cod-ice, her-Norw, plai-IV for meanAge), but the opposite effects were also observed, and the relationships were not significant overall (results not shown).

The third effect investigated was the link between age structure and recruitment variability. The underlying hypothesis was that a truncated age structure would result in a contracted spawning season, both in time and space, thereby increasing the probability of a mismatch between the presence of the feeding larvae and the production of their planktonic food. James et al. (2003) tested this hypothesis with a model of larval survival of haddock using a realistic description of the dynamics of their planktonic prey and the interactions with the environment. Their main conclusion was that decreasing the length of the hatching period in the model resulted in more-variable recruitment, because of an increased frequency of recruitment failures. In a comparative analysis, Fogarty et al. (2001) found that haddock stocks consistently exhibited a higher recruitment variability than cod stocks, and they speculated that this was related to the shorter spawning season of haddock. Empirical evidence also suggests that cod stocks characterized by a shorter spawning period tend to have higher recruitment variability (Mertz and Myers, 1994). Although differences in spawning duration might explain differences in recruitment variability among species or between different populations of the same species, this relationship has not been investigated within a population in the context. The current meta-analysis suggests that recruitment variability increases when age diversity decreases for haddock and plaice, as expected. However, the opposite relationship seems true for herring, which is surprising, because Lambert (1987) provided strong evidence that the timing and duration of the spawning season is related to age diversity in this species.

One might expect that the correlations found somehow depend on the level of variation in the age structure. Significant effects are more probably obtained for stocks exhibiting greater variations in age structure. This may be checked by comparing the distributions of significant correlations conforming to expectations (Figure 3) among the five groups of stocks identified by PCA (Table 2), because these reflected different levels of variability and different levels of temporal trends. Group 3 (medium variability, strong trend) contained most of the stocks exhibiting such correlations, but they were also frequently observed in groups 1 (high variability, no trend) and 4 (low variability, but trend), relative to the number of stocks in those groups. In contrast, they were scarce in groups 5 (low variability, no trend) and 2 (medium variability, no trend). This classification suggests indeed that for significant effects to be observed, age structure must exhibit moderate to high variability and/or a temporal trend. However, these two characteristics do not provide a sufficient condition: the stock with the highest variability and one of the most important trends, her-Norw, did not yield any significant correlation in the expected direction.

Independent of whether recruitment effects of variations in age structure have been identified, there are other reasons why more attention should be given to the age structure of the spawning stock in assessment and management advice (Berkeley et al., 2004b; Birkeland and Dayton, 2005). For instance, using total egg production as a measure of the stock's reproductive potential

Table 2. Partition of the significant correlations of the expected sign between the three indices of age structure and the three effects on recruitment (from Figure 3) among the five groups identified by PCA on age-structure variability (Figure 2): Effect 1, number of recruits; 2, sensitivity of the recruitment–temperature relationship; 3, recruitment variability.

Group		1	2	3	4	5
Group size		2	11	8	8	10
Variability		H	M	M	L	L
Trend		−	−	+	+	−
Effect 1	meanAge	1				
	H		1	2		
	Pfirst	1		1		
Effect 2	meanAge		1	3	1	
	H			1	2	
	Pfirst		1	1	1	1
Effect 3	meanAge		1	3		
	H	1		2	3	
	Pfirst			3		
Total		3	4	16	7	1

instead of SSB would be a way to take account of the age-related differences in relative fecundity (Marshall *et al.*, 1998), and more accurate reference points might be derived (Murawski *et al.*, 2001). Importantly, paying more attention to age-related information on maturation in routine sampling programmes might overcome some of the deficiencies of the current datasets for evaluating potential effects of age structure on recruitment.

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