

Extreme increases in natural mortality prevent recovery of collapsed fish populations in a Northwest Atlantic ecosystem

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SUPPLEMENT 1. ADDITIONAL INFORMATION ON DATA INPUTS

Annual research vessel (RV) survey

A stratified-random bottom-trawl survey has been conducted by the Canadian Department of Fisheries and Oceans (DFO) in the southern Gulf of St. Lawrence (sGSL) each September since 1971 (Fig. S1). The trawl used to conduct the survey changed in 1985 and the survey vessel changed in 1985, 1992 and 2004/2005. Both the old and new vessels were used in 2004 and 2005, though fishing in 2004 was primarily by the new vessel. Relative fishing efficiencies between these vessels and gears were estimated for each species based on paired fishing experiments conducted during or shortly before the survey in 1985 ($N = 60$ sets of paired tows), 1992 ($N = 66$) and 2004/2005 ($N = 101$, with an additional 173 paired tows conducted on the neighbouring Scotian Shelf in July). The gear change in 1985, from the Yankee 36 to the Western IIA trawl, was a relatively minor change and no length-dependent differences in catchability were detected in the 1985 experiment, though statistical power was low except for cod and plaice. A significant length-independent change in catchability was detected for plaice (a 43% increase), winter flounder (a 130% increase) and eelpouts (a 120% increase) in the 1985 experiment. For years in which only the vessel changed, significant catchability changes were detected for cod (a depth-dependent change, e.g. a 37% increase at 40 m and a 33% decrease at 200 m), thorny skate (a 34% decrease) and eelpouts (a length-dependent decrease, e.g. a 57% decline at 25 cm and a 22% decline at 57 cm) in 1992, and for plaice (15% decline) and hake (32% decline) in 2004/2005. An uncalibrated vessel, the sister ship to the vessel used in 1992–2002 (and for comparative fishing in 2004 and 2005), conducted the survey in 2003. Catchability to this vessel was assumed to be the same as that to its sister ship. Catches by earlier vessels were adjusted to be equivalent to those by the current vessel when the comparative fishing indicated a change in fishing efficiency (Benoît & Swain 2003b, Benoît 2006a).

An important change in protocol occurred in the survey in 1985, with fishing conducted during daylight hours only (07:00–19:00 h) prior to 1985 and 24 h per day since then. In order to adjust catch rates for this change in protocol, Benoît & Swain (2003a) estimated diel differences in catchability to the survey using 2 approaches. First, they compared catches in paired day and night survey tows conducted at the same locations in 1988 (67 pairs) and in 1998–2000 (68 pairs). Second, they examined diel differences in the 1985–2001 survey data controlling statistically for annual and spatial variation in catch rates. The estimated species-

specific diel effects were remarkably similar between approaches and between time periods and vessels, and were comparable to results from studies in other areas. In most species, catchability was greater at night, with this diel effect stronger at shorter fish lengths. Among the species examined here, no diel effect was detected for Atlantic cod, plaice or winter flounder. Smooth skate and Greenland cod were about twice as catchable at night compared to day regardless of length. Diel differences in catchability of white hake were length dependent, with catchability 3–4 times higher at night at a length of 20 cm, about equal between day and night at 30 cm and 2 times higher in the day at 50 cm. The remaining species were more catchable at night at all lengths, with the ratio of night/day catchability varying between 2 and 15 at small lengths and between 1 and 8 at large lengths, depending on species. When diel differences in catchability occurred, night catches were adjusted to be equivalent to day catches in order to maintain a consistent time series, as described by Benoît & Swain (2003b) and Benoît (2006a).

Sampling intensity in this survey has been relatively high since 1985, when the average number of successful tows conducted annually increased from 70 to 180 tows per year. The survey covers nearly the entire sGSL, extending from inshore areas with depths less than 20 m to depths of 350 m or more along the slope of the Laurentian Channel. This area includes virtually all of the habitat occupied by the sGSL stocks of species such as Atlantic cod, American plaice and thorny skate in September, but the distribution of some species such as winter flounder and winter skate extends into the narrow inshore area not covered by the survey. The survey area includes relatively little untrawlable bottom that would limit the availability of fish to the survey. The survey is conducted during the feeding season of sGSL demersal fish, a time of year when these fish are dispersed and not undertaking directed migrations. Because of these features, abundance indices for widely distributed sGSL fishes, such as Atlantic cod and American plaice, exhibit relatively few ‘year effects’ (i.e. large fluctuations related to sampling error rather than changes in abundance) and relatively high precision. Coefficients of variation for the survey abundance indices at age average 21.4% for cod (ages 2–11 yr), 12.9% for plaice (ages 4–15 yr) and 31.6% for hake (ages 2–7 yr). Ageing of otoliths collected on the surveys is conducted by 1 or 2 technicians who calibrate regularly to reference collections in order to maintain consistency over time. The survey tracks cohorts exceptionally well (Fig. S2), indicating that the age composition data from the survey are highly informative, a prerequisite for successful estimation of natural mortality (Lee et al. 2011). Correlations along cohorts exceed 0.75 for most ages 1 yr apart for cod, plaice and hake, and remain significant for ages up 8 yr apart for cod, 9 yr apart for plaice and 3 yr apart for hake.

Additional abundance indices

A number of additional time series of relative abundance at age are available from ‘sentinel’ programs conducted by DFO in collaboration with the fishing industry. These programs used commercial vessels, gears and crews fishing using standardized protocols. Programs included a ‘mobile’ (bottom-trawl) survey conducted each August since 2003 using the same stratified-random design as the September RV survey and a longline program conducted in summer and autumn since 1995 (Chouinard et al. 2005a, Swain et al. 2009b, Savoie & Surette 2010). In the longline program, about 40 fixed sites were each fished several times per year between July and October and standardized catch rates were obtained using a multiplicative model with terms for year, month and site (Swain et al. 2009b).

Relative fishing mortality of skates

Relative fishing mortality of thorny, smooth and winter skate for 1991–2011 was estimated by Benoît (2013) using trawlable abundance estimates from the annual survey and annual estimates of losses to fisheries based on landings and on discard reports provided by fishery observers. Lack of data from fishery observers prevented directly estimating discard mortalities and species-specific landings of the skates prior to 1991. For winter skate, Benoît (2006b) used the average estimated bycatch rates (kilogram winter skate per kilogram target species i) for 1991–1993, adjusted by the relative abundance of winter skate and target species i in the survey and multiplied by the landings of species i , to calculate annual winter skate bycatch for 1971–1990. For thorny and smooth skate a different approach was used. The sGSL cod and flatfish (mainly American plaice) mobile gear fisheries were an important source of thorny and smooth skate catch throughout the 1990s and 2000s, particularly during the early 1990s (Benoît 2013). These fisheries were the predominant sources of demersal fishing effort in the sGSL in the 1971–1990 period and are likely to have generated most of the thorny and smooth skate catches in the sGSL prior to 1991. Consequently, we regressed annual relative fishing mortality of each of the 2 skates against those of cod and plaice for 1991–2011, and used these regressions to predict skate fishing mortalities for 1971–1990 based on the estimates of relative fishing mortalities for cod and plaice over the same period.

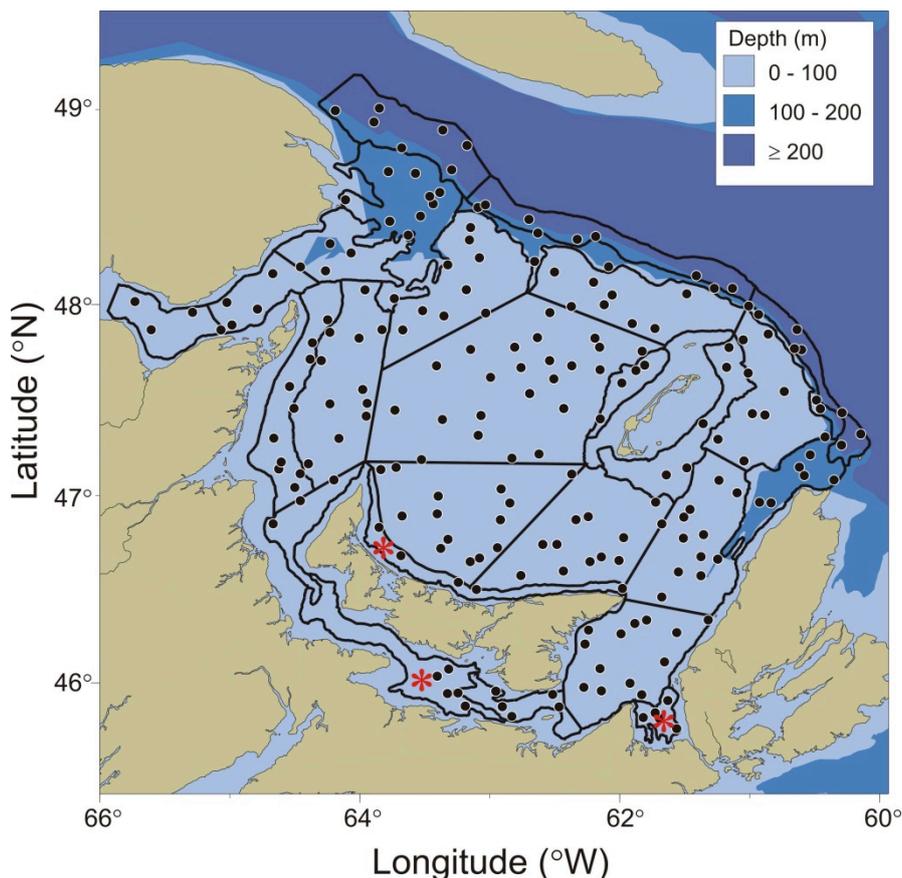


Fig. S1. Stratification used in the research vessel (RV) and sentinel bottom-trawl surveys of the southern Gulf of St. Lawrence. Circles show the locations of fishing stations in the 1996 RV survey. Red asterisks indicate 3 strata added in 1984 and omitted from analyses of the RV data to maintain a consistent survey area

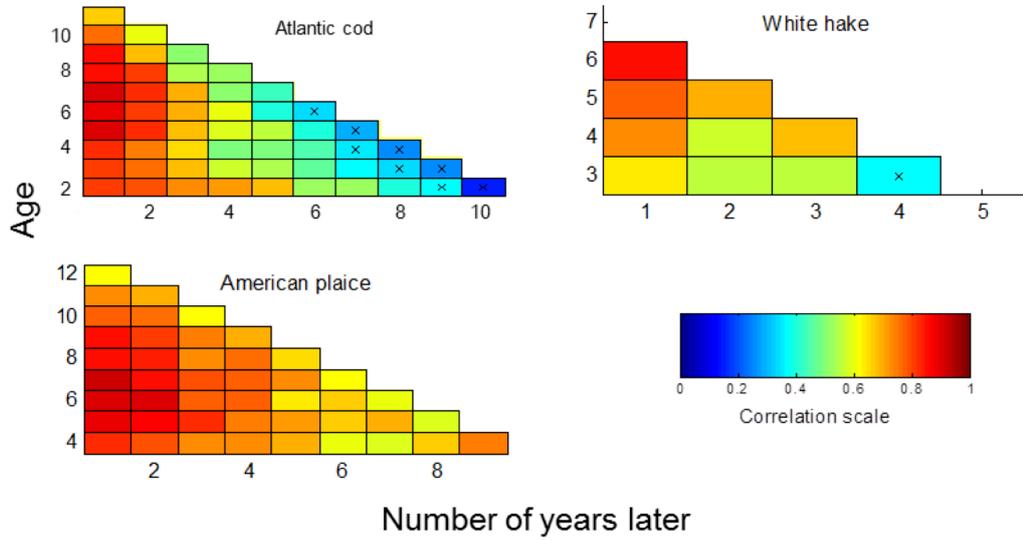


Fig. S2. Cohort tracking by the RV survey for Atlantic cod, American plaice and white hake. Colour indicates the correlation between the survey catch rate at age a in year t and the catch rate at age $a + n$ in year $t + n$. Non-significant correlations ($p > 0.05$) are denoted by ‘x’

SUPPLEMENT 2. AGE-STRUCTURED POPULATION MODELS

Modeling methods

Models used for Atlantic cod, American plaice and white hake were similar to those used in the most recent assessments of these stocks (Morin et al. 2012, Swain et al. 2012a,b). These models are virtual population analyses implemented in AD Model Builder (Fournier et al. 2011), and are based on the following relationships:

$$C_{i,y} = \frac{F_{i,y}}{F_{i,y} + M_{i,y}} N_{i,y} (1 - e^{-(F_{i,y} + M_{i,y})}) \quad (S1)$$

$$N_{i+1,y+1} = N_{i,y} e^{-(F_{i,y} + M_{i,y})} \quad (S2)$$

where C is fishery catch in numbers of fish, N is population abundance, F and M are the instantaneous rates of fishing and natural mortality, respectively, i indexes age and y indexes year. Using these relationships, the models work backwards in time along cohorts (i.e. the fish born in the same year). F of the oldest age group was assumed to equal that of the previous age in the same year. Models included a plus group (e.g. 12+, fish aged 12 yr and older); plus group calculations followed the FRATIO method described by Gavaris (1999). Data inputs were fishery catch at age and survey indices of relative abundance at age. For the RV and sentinel bottom-trawl surveys, indices were at the scale of trawlable abundance, the standardized number of fish caught per tow multiplied by A_S/A_{tow} , where A_S is the survey area and A_{tow} is the area swept by a standard tow (based on nominal wingspread and the standard distance towed,

3.24 km). For each index, selectivity was modelled as a logistic function of age. Parameters estimated by the models were survivors at age in the terminal (most recent) year, 2 selectivity parameters and fully recruited catchability for each of the abundance indices, standard deviations at age of observation error in the indices and parameters used to calculate $M_{j,y}$, the instantaneous rate of natural mortality in year y for age group j . Age groups were 2–4, 5–8 and 9+ yr for cod, 4–9, 10–14 and 15+ yr for plaice, and 2–3, 4–5 and 6+ yr for hake. M was modelled as a random walk:

$$M_{j,y1} = Minit_j \quad (S3)$$

$$M_{j,y} = M_{j,y-1} e^{Mdev_{j,y}} \text{ if } y > y1 \quad (S4)$$

where $Minit_j$ is M in year $y1$, the first calibrated year (i.e. the first year in the model with abundance indices: 1971 for cod, 1976 for plaice and 1978 for hake). For cod, $M_{j,y}$ in 1950 to 1970 was assumed to equal $M_{j,1971}$. $Minit_j$ and $Mdev_{j,y}$ are parameters estimated by the model. $Mdev$ was assumed to be normally distributed with a mean of 0 and standard deviation sd (set at 0.05 in all cases). Priors were supplied for $Minit_j$. These priors were normally distributed with means of 0.65, 0.15 and 0.15 for cod aged 2–4, 5–8 and 9+ yr, respectively; 0.6, 0.3 and 0.2 for plaice aged 4–9, 10–14 and 15+ yr, respectively; and 0.55, 0.3 and 0.2 for hake aged 2–3, 4–5 and 6+ yr, respectively. These values were selected based on estimates of M of sGSL cod in the 1950s and 1960s (Dickie 1963, Beverton 1965, Paloheimo & Kohler 1968) and empirical relationships between M and length and growth characteristics of marine fishes (Gislason et al. 2010). The sensitivity of the results to the values chosen for the standard deviation of process error (i.e. the M deviations) and the means and standard deviations of the priors for initial M is examined below.

Parameters were estimated by minimizing an objective function with the following components:

1) A component for the discrepancy between observed and predicted values of the abundance indices:

$$f_1 = 0.5 \cdot \sum_{i,y,k} (\log(I_{i,y,k} / (q_{i,k} N_{i,y,k})) / s_{i,k})^2 + \sum_{i,y,k} \log(s_{i,k}) \quad (S5)$$

where $I_{i,j,k}$ is abundance index k at age i in year y , $N_{i,j,k}$ is estimated population abundance of age i in year y adjusted to the time of year when index k was obtained, $q_{i,k}$ is catchability at age i for index k , and $s_{i,k}$ is the standard deviation of observation error for index k at age i .

2) A penalty for departures of $Minit_j$ from its prior value:

$$f_2 = 0.5 \cdot \sum_j (((Minit_j - Mprior_j) / std)^2 + \log(std)) \quad (S6)$$

where $Mprior_j$ is the mean of the prior for age group j and std was set at 0.10 for the 2–4 yr age group of cod and 0.05 in all other cases.

3) A penalty for departures of $Mdev_{j,y}$ from 0:

$$f_3 = 0.5 \cdot (\sum_{j,y} Mdev_{j,y}^2) / sd^2 \quad (S7)$$

Abundance indices from the RV survey were used for all 3 stocks. In addition, indices from the sentinel bottom-trawl survey were used for cod and plaice, and indices from the sentinel longline program were used for cod. Zeros in the abundance indices at age were replaced by

one-fifth the minimum non-zero value at age (1 case for plaice, 6 cases for hake). Zero values in the fishery catch of hake at ages 7–10 yr were replaced by a small value (10 fish). Confidence intervals for estimated quantities were based on Markov chain Monte Carlo sampling, with every 20th of 100000 samples saved. The 2.5th and 97.5th percentiles of the saved samples were used as confidence intervals.

Models used here differed from those used in recent assessments in the following ways:

1) The assessment models estimated M for 2 age groups (e.g. 2–4 and 5+ yr for cod) whereas 3 age groups were used here (e.g. 2–4, 5–8 and 9+ yr for cod).

2) The assessment model for cod used assumed values for M in 1971–1976, whereas the model used here estimated M for these years with a prior for M in 1971.

3) The assessment models did not estimate the standard deviation of observation error, and thus Eq. (S5) reduced to the sum of squared residuals in terms of model fitting.

4) The assessment models freely estimated catchability at each age for the abundance indices whereas the models used here calculated catchability at age as the product of fully recruited catchability and selectivity at age, modelled as a logistic function of age.

5) The assessment models used larger values for sd , the standard deviation of process error in M . The value of sd determines the smoothness of the estimated trends in M . The estimated trends will be strongly influenced by noise in the data if sd is too large and will fail to track the true trends if sd is too small.

Model fit

Model fit was evaluated by comparing model estimates of population abundance at age to the abundance indices at age. The estimates of M and F at age were used to adjust estimated population abundance at the beginning of the year (January 1) to mid-September (to match the timing of the RV survey and the midpoint of the longline program). Survey indices were scaled to absolute abundance based on the estimates of catchability at age. The scaled indices from the sentinel trawl survey (conducted in August) were adjusted to mid-September using the estimates of M and F at age. Based on these comparisons, models generally fit the observed abundance indices well (Fig. S3). For hake 4 yr and older, there was a tendency to overestimate relative abundance in the late 1970s and early 1980s.

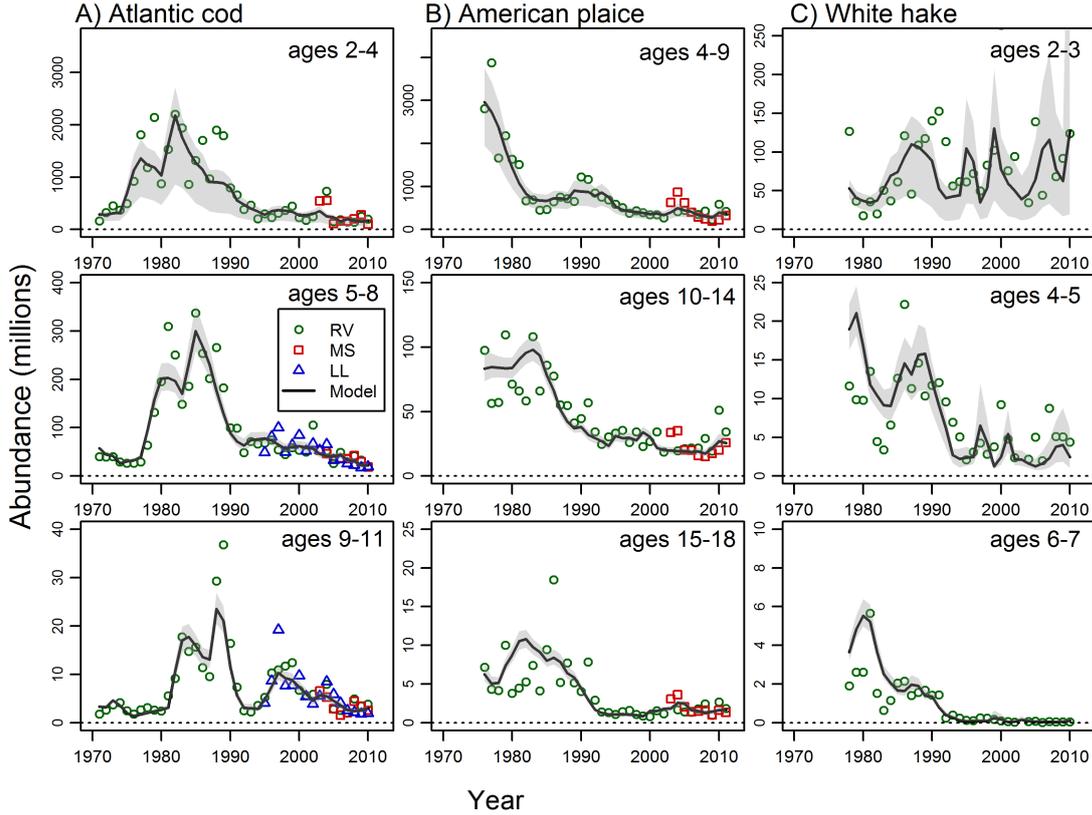


Fig. S3. Comparison of model estimates of population abundance (line, grey shading = 95% confidence interval) and catchability-corrected abundance indices from the September research vessel (RV) survey (green circles), the August sentinel survey (MS, red squares) and the longline index (LL, blue triangles) in the southern Gulf of St. Lawrence for Atlantic cod (A), American plaice (B) and white hake (C). Comparisons are restricted to the ages used in model calibration (i.e. in Eq. S5)

Simulation tests

Simulation studies were used to examine the ability of these models to estimate time trends in M given data with characteristics similar to our data (i.e. a sharp drop in fishing effort to very low levels and substantial variation in cohort strength). Pseudo-data were generated based on the population model for each species, following the approach used by Deroba et al. (2014) for model self-tests. Model estimates of $N_{i,y}$, population abundance at age i in year y , were adjusted to the time of year when the surveys were conducted using the model estimates of $M_{i,y}$ and $F_{i,y}$. Indices $I_{i,y,k}$ for survey k were then generated using the adjusted $N_{i,y}$ and the estimated catchabilities $q_{i,k}$. Log-normal noise was added to these indices based on the standard deviations of the residuals at age for each index. Simulated catch-at-age data were generated for each year by drawing random samples from a multinomial distribution with a sample size of 200 and expected proportions at each age equal to those in the predicted catch data for that year (based on Eq. S1). The simulated catch at age was then scaled to the predicted total catch numbers for that year. This procedure was repeated to produce 300 sets of simulated data. Examples of the pseudo-data generated for cod are shown in Fig. S4.

The main features of time trends in M were well estimated by the models in these simulations, except in the case of juvenile hake (Fig. S5). For age groups that were well recruited to the

fishery and well represented in the populations (age groups 5–8 and 9+ yr for cod, 10–14 yr for plaice and 4–5 yr for hake), the median estimate of the trends in M closely matched the true values, with little bias in most years. Older ages of plaice (15+ yr) and hake (6+ yr) had declined to very low abundance in the 1990s and 2000s and were not well represented in survey catches in these periods (Fig. S6). Thus, the information available to estimate M trends was limited for these age groups in these periods, and details of their trends in M were not well estimated in the 1990s and 2000s. Nonetheless, the models did detect that M underwent a substantial increase between 1980 and 2010 for these age groups, leading to correct conclusions about the general trends in M . For the youngest age groups, estimated M matched true M relatively well for plaice, but changes in M for juvenile cod and hake were underestimated by the models. This may reflect limited information to estimate changes in M of juvenile cod and hake, which have very low partial recruitment to the fishery compared to the youngest age group of plaice. In conclusion, these simulations indicate that, given data with the characteristics of the data in this study, the models used here are able to detect the general trends in M of older commercial-sized fish (5+ yr cod, 10+ yr plaice and 4+ yr hake), correctly identifying that M had increased substantially for these fish between the early 1980s and the 2000s. Changes in M were also well identified for younger plaice but were substantially underestimated for juvenile hake. Additional simulation tests of models similar to those used here are given by Chouinard et al. (2005b) and Swain (2011).

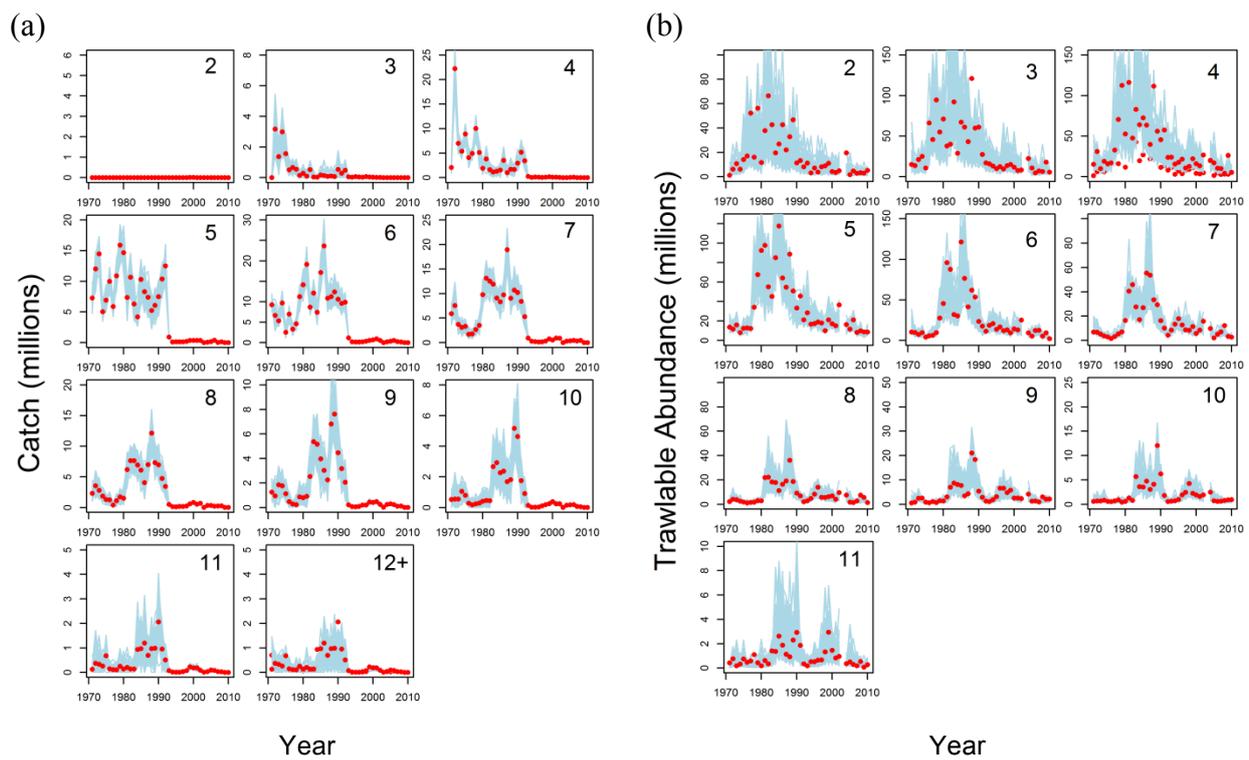


Fig. S4. Observed (red circles) and simulated (light blue lines) data in the cod simulation for (a) fishery catch at ages 2–12+ yr and (b) RV abundance indices for ages 2 to 11 yr

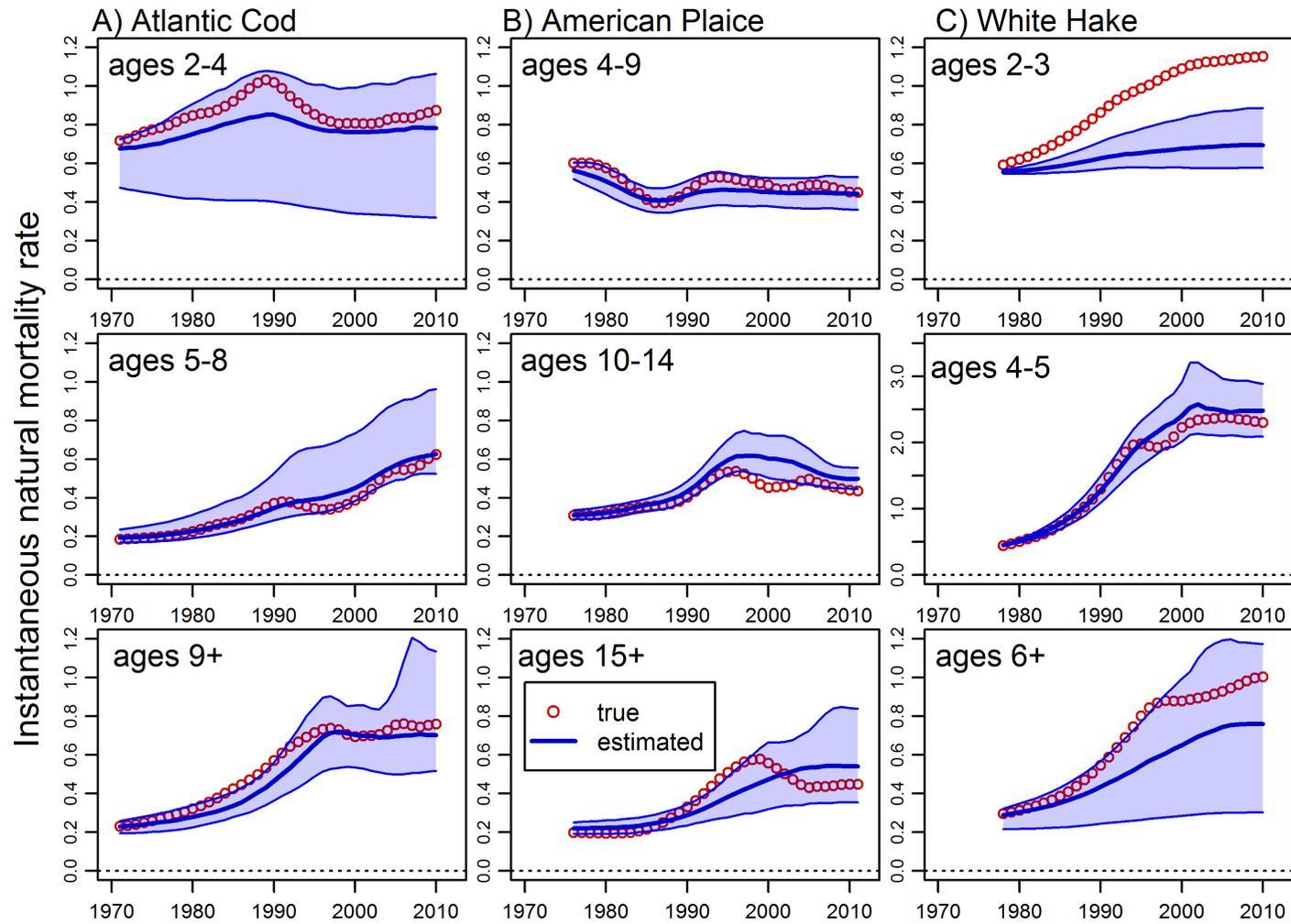


Fig. S5. Simulation tests of the ability of population models to recover true values (red circles) of the instantaneous rates of natural mortality for 3 age (years) groups. Lines indicate the median estimates of these rates based on 300 sets of simulated data, and shading extends from the 2.5th to the 97.5th percentiles of these estimates

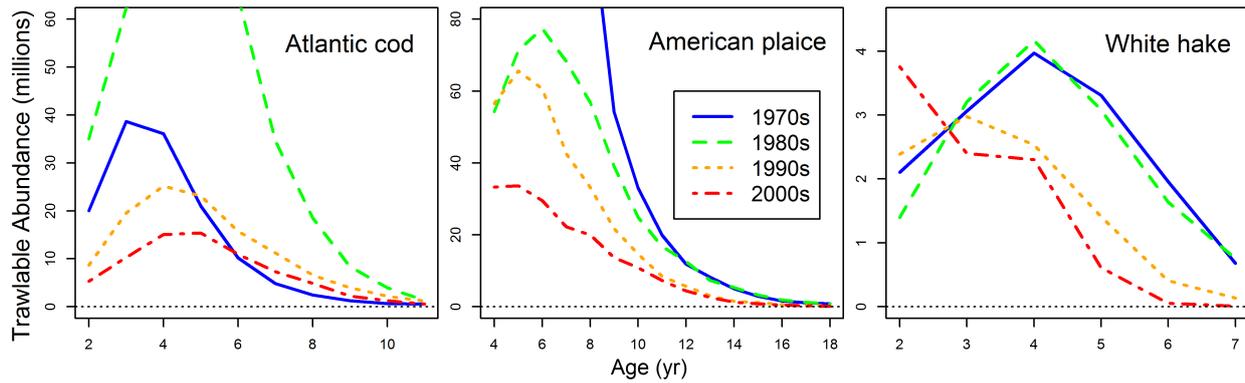


Fig. S6. Mean catch rates of Atlantic cod, American plaice and white hake in the September RV survey of the southern Gulf of St. Lawrence by age and decade

Sensitivity analyses

Analyses were conducted to examine the sensitivity of results to the values chosen for sd , the standard deviation of process error in M , and for the prior distribution for initial M . Three values for sd were examined: 0.01, 0.05 (the value used in the final models) and 0.1. For cod, trends in estimated M were similar between $sd = 0.05$ and 0.1, except that trends were smoother with narrower fluctuations using $sd = 0.05$, particularly at the younger ages (Fig. S7). With sd reduced to 0.01, little change in M was estimated for ages 2–4 and 5–8 yr, and the change in M of 9+ yr cod was reduced, primarily due to an increase in the estimated initial value for M . The fit of the model to the RV data was considerably worse using a value of 0.01 for sd than using values of 0.05 or 0.1 (Fig. S8). The sum of squared residuals was 35% higher with sd set at 0.01 compared to 0.05. Likewise, residual patterns (i.e. ‘blocking’ of negative and positive residuals) were substantially more severe with sd at 0.01 instead of 0.05. In contrast, differences were relatively minor between values of 0.05 and 0.1 for sd . Trends in estimated M , residual patterns and the sum of squared residuals (8% lower with sd set at 0.1 compared to 0.05) were all similar between the 2 values. Finally, using sd of 0.05 or 0.1 resulted in estimates of M in the early 1970s that are consistent with independent estimates of 0.1–0.2 for commercial-sized cod in the 1950s and 1960s (e.g. Dickie 1963, Paloheimo & Kohler 1968), whereas sd of 0.01 resulted in values higher than these estimates. Results were similar for plaice and hake. Estimated time trends in M were similar for $sd = 0.05$ and 0.1, but smoother with $sd = 0.05$. An exception was juvenile hake, which showed a substantially greater increase in M with $sd = 0.1$. Fit to the survey data was much poorer with $sd = 0.01$, with extreme residual patterns and large increases in the sum of squared residuals. The sum of squared residuals with $sd = 0.01$ was over 1.5 times the value with $sd = 0.05$ for plaice and over 3 times this value for hake. In conclusion, setting sd at 0.05 appeared to be a good compromise between the risk of an undue influence of noise in the RV data on estimated M trends at high values of sd and the risk of a poor fit to the RV data due to a failure to track true variation in M at low values of sd .

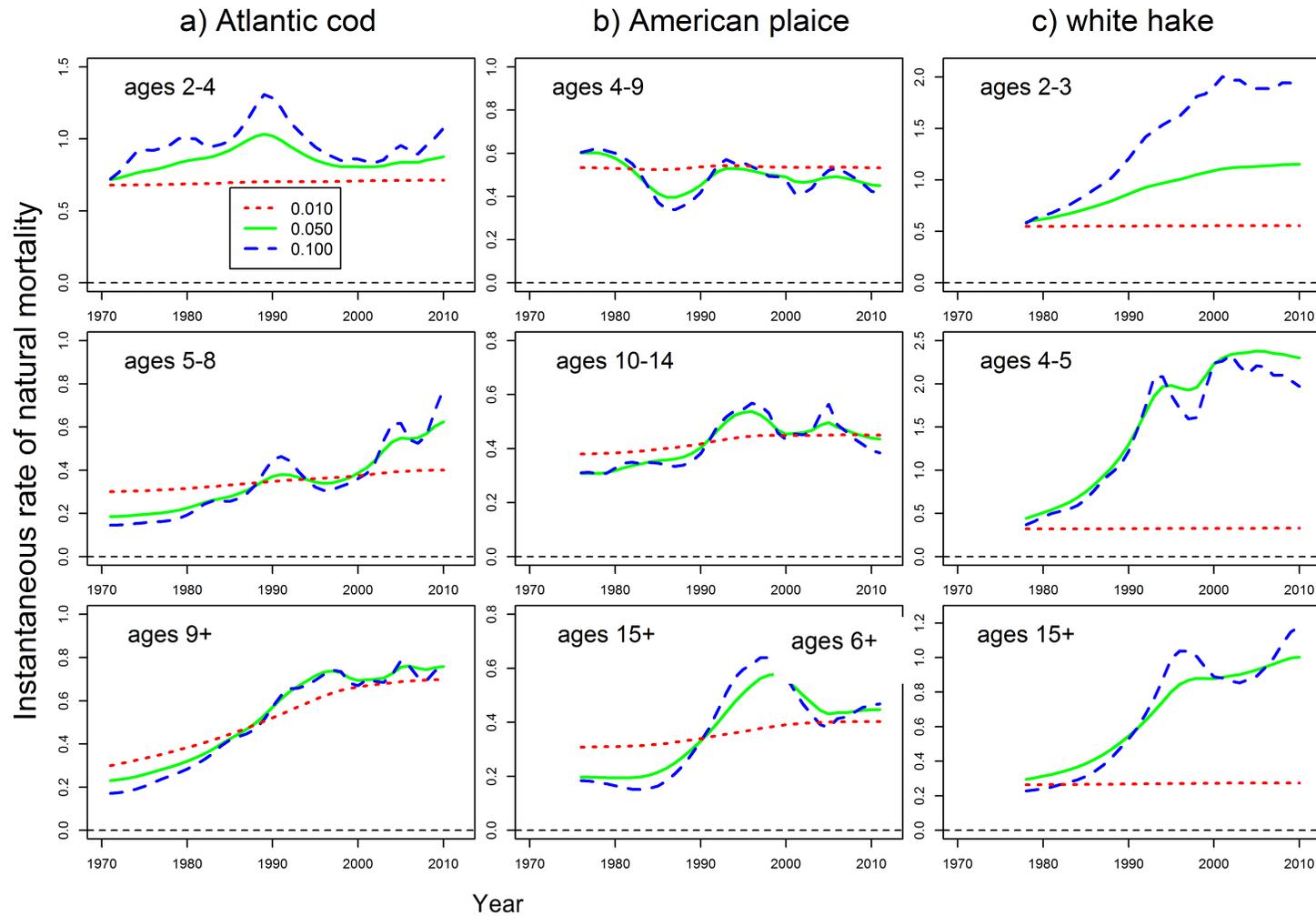


Fig. S7. Estimates of the instantaneous rates of natural mortality M of 3 age groups of (a) Atlantic cod, (b) American plaice and (c) white hake, assuming that the standard deviation of process error in M is 0.01, 0.05 or 0.10

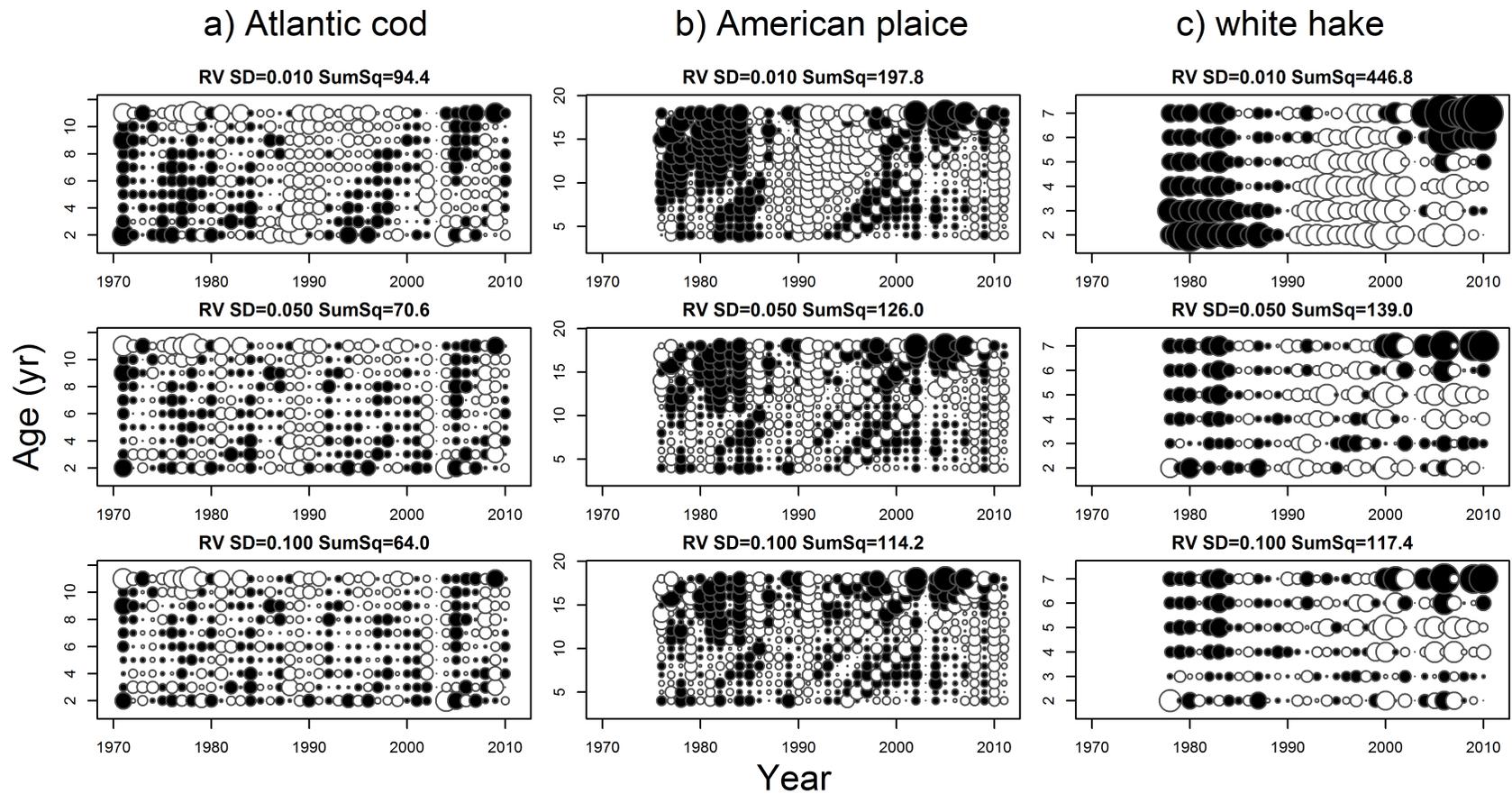


Fig. S8. Fit of models to the abundance indices from the RV survey for (a) Atlantic cod, (b) American plaice and (c) white hake, assuming that the standard deviation (SD) of process error in M is 0.01, 0.05 or 0.10. Circle area is proportional to the residual (observed index – predicted index). Black circles indicate negative residuals. SumSq is the sum of squared residuals

The effect of the prior distribution for initial M on results differed between age groups and species. The prior means for initial M in the cod model were 0.65, 0.15 and 0.15 for ages 2–4, 5–8 and 9+ yr, respectively. This resulted in the M estimates shown in grey in Fig. S9. In all cases, the estimate for initial M (0.72, 0.19 and 0.23, respectively) was slightly higher than the prior mean. Changing the prior mean for the 2–4 yr age group had a large effect on the estimates of M for that age group, but no effect on the estimates for the other age groups (Fig. S9a,b). When the standard deviation (std) of the prior distribution for age 2–4 yr M was 0.05, decreasing or increasing the prior mean resulted in lower or higher estimates respectively but roughly the same trend over time in age 2–4 M . When the prior mean was decreased to 0.4 and std was increased to 0.3 for the 2–4 yr age group, the estimated initial M moved to a much higher level for this age group (0.94), but the time trend in estimated M remained the same (Fig. S9c). When the prior for initial M of ages 5–8 or 9+ yr is increased to a higher level, the estimates for initial M move from this higher prior towards the original estimate. When std is set at 0.05, the estimates remain above the original values (Fig. S9d,e,g,h). When std is set at 0.30, the estimate for initial M returns to (5–8 yr) or close to (9+ yr) its original value (Fig. S9f,i). Again changes to one age group have only negligible effects on estimates for other age groups. When the prior mean remains unchanged but std is increased, there is a large effect on the level but not the time trend of estimated M for ages 2–4 yr and no effect or a negligible effect on both the level and trend for ages 5–8 and 9+ yr (Fig. S10). In conclusion, the level but not the time trend in estimated M of cod aged 2–4 yr is determined by the prior distribution for initial M . For older (5+ yr) cod, neither the level nor the time trend in estimated M was determined by the prior distribution for initial M .

For plaice, the mean of the prior for initial M affected the level but not the temporal pattern in estimated M of the youngest age group, though even the level converged on that in the final model when std was sufficiently high (Fig. S11). For the older age groups, the prior mean had at most a minor effect on M estimates, and estimates converged on those from the final model with std of 0.1 or more. With prior means held constant at those values in the final model, the value of std had no effect on M estimates of plaice (Fig. S12). Thus, the estimates of M obtained from the final plaice model do not appear to be determined by the priors used for initial M . It appears that different priors, if sufficiently uninformative (i.e. with std sufficiently high), would result in the same M estimates as the priors used in the final model.

For hake, the estimated level of M was affected by both the mean and the std of the prior distribution for initial M (Figs. S13, S14). This effect was greatest for ages 2–3 yr, substantial for ages 4–5 yr and slight for ages 6+ yr. However, the estimated change in M over time was not affected by the prior. Thus, conclusions about changes in hake M over time do not appear to be affected by the priors for initial M .

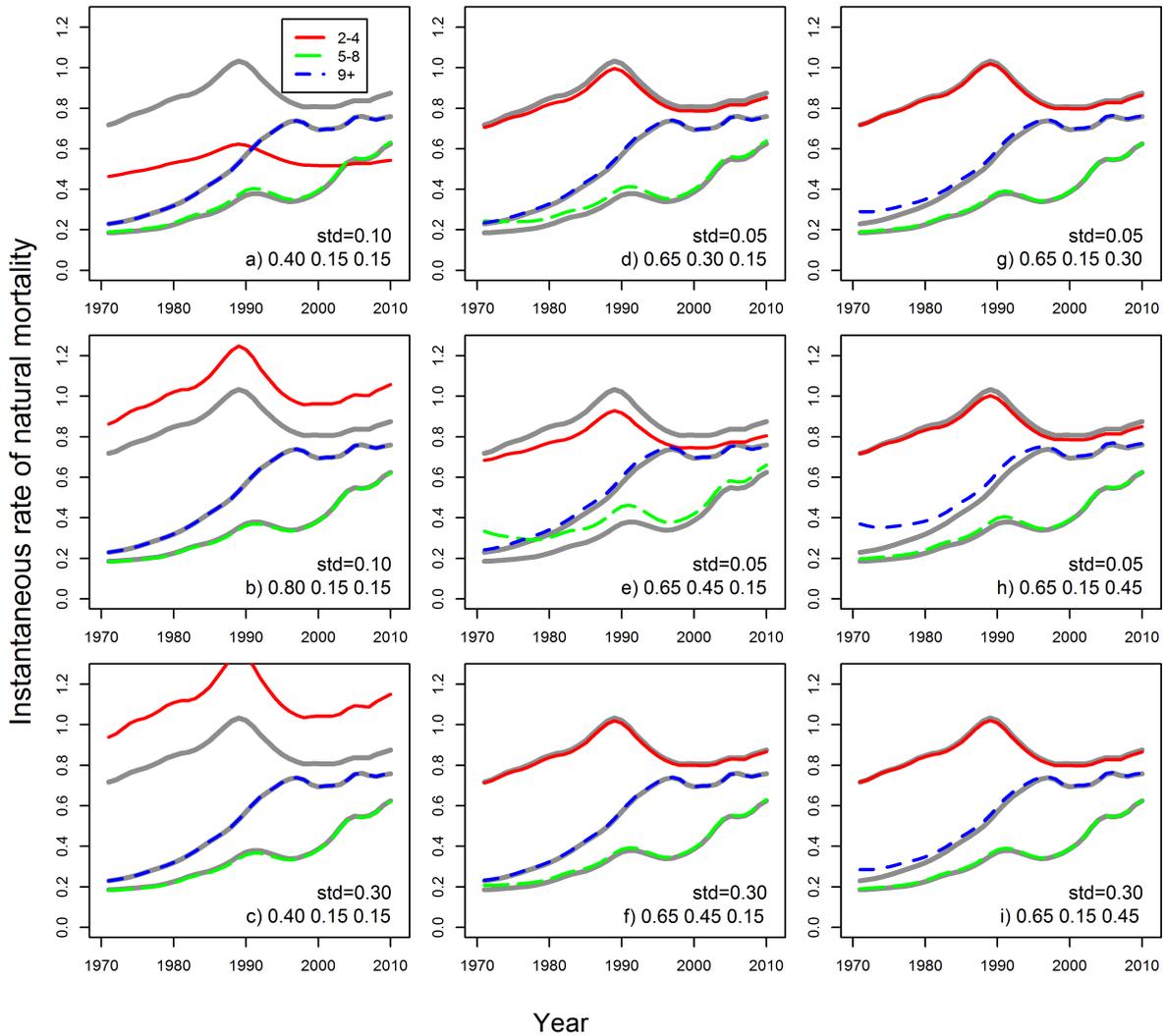


Fig. S9. Effect of the prior mean for initial M on estimated M of cod aged 2–4 (red solid lines), 5–8 (green dashed lines) and 9+ yr (blue dashed lines). Grey lines show the estimates from the final model using prior means of 0.65, 0.15 and 0.15 and standard deviations (std) of 0.1, 0.05 and 0.05 for ages 2–4, 5–8 and 9+ yr, respectively. The prior means for the coloured lines are given in each panel in the order of increasing age. For the age group with a change in prior mean, std is also indicated in each panel

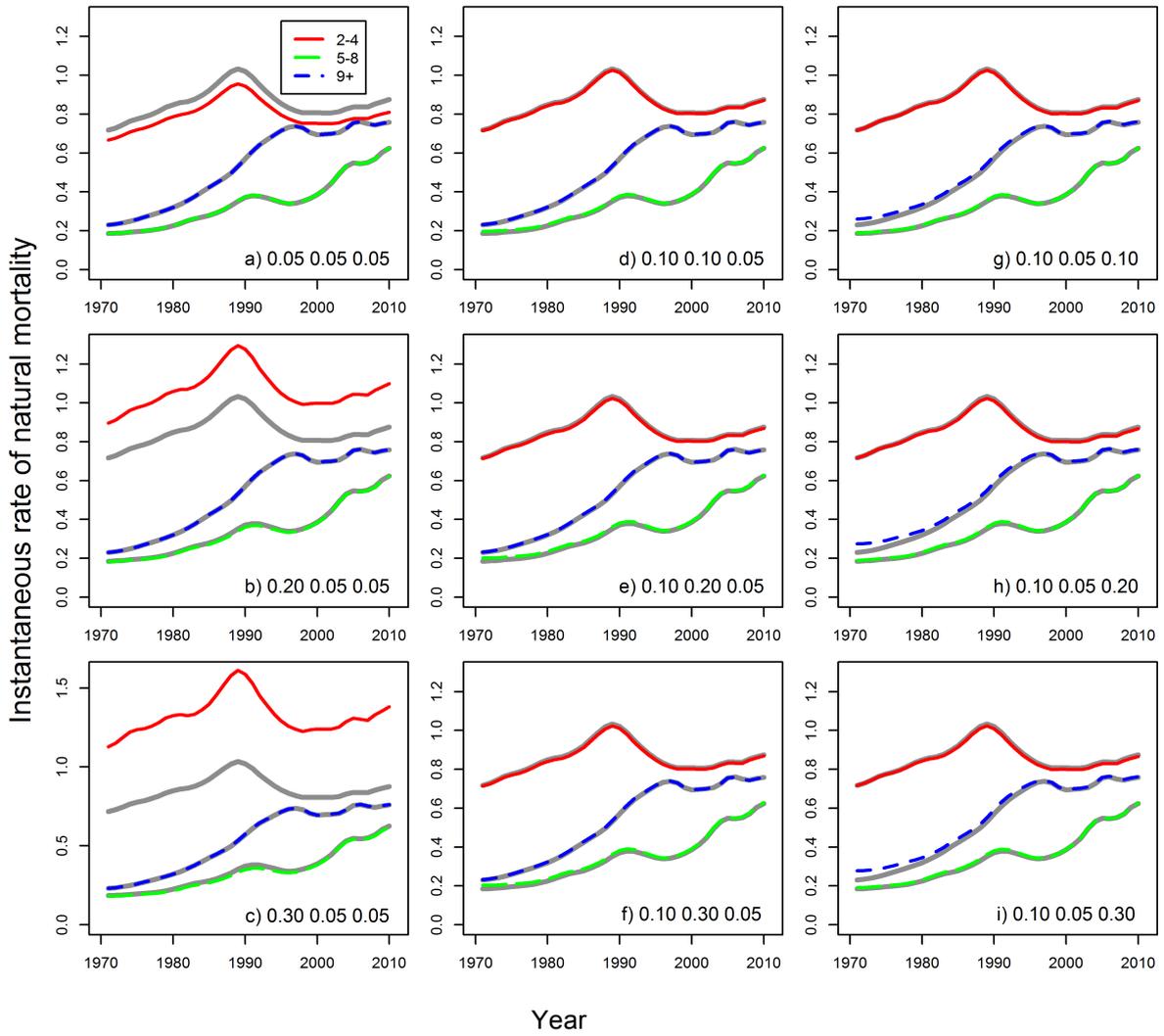


Fig. S10. Effect of the standard deviation (*std*) of the prior distribution for initial *M* on estimates of *M* for cod aged 2–4 (red), 5–8 (green) and 9+ yr (blue). Numbers indicate *std* in order of increasing age. Grey lines indicate estimates using *std* of 0.1, 0.05 and 0.05, the values used in the final model

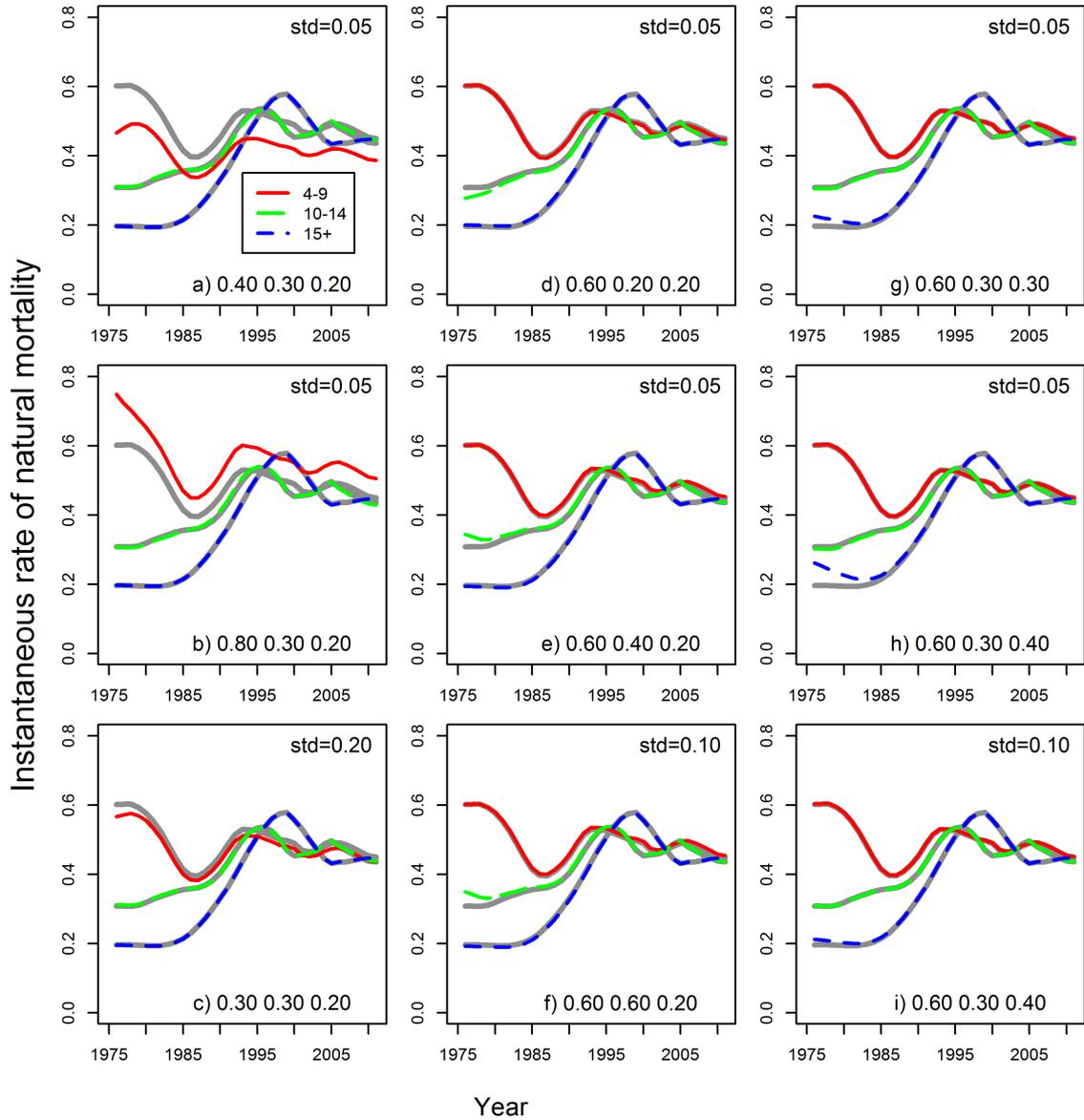


Fig. S11. Effect of the prior mean for initial M on estimated M of plaice aged 4–9 (red lines), 10–14 (green dashed lines) and 15+ yr (blue dashed lines). Grey lines show the estimates from the final model using prior means of 0.6, 0.3 and 0.2 for ages 2–4, 5–8 and 9+ yr, respectively, and a standard deviation (std) of 0.05 for all ages. The prior means for the coloured lines are given in each panel in the order of increasing age. For the age group with a change in prior mean, std is also indicated in each panel

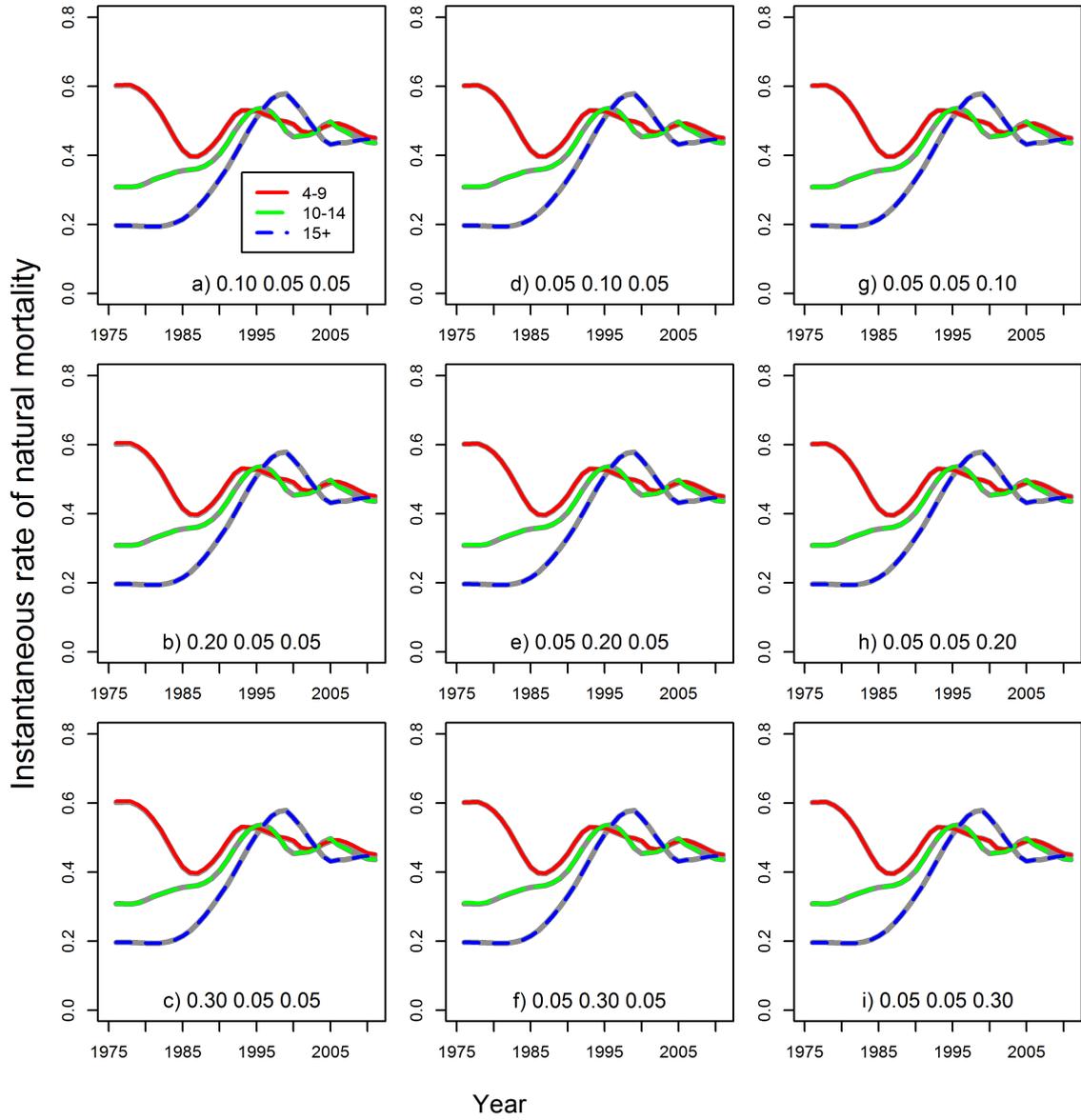


Fig. S12. Effect of the standard deviation (*std*) of the prior distribution for initial *M* on estimates of *M* for plaice aged 4–9 (red), 10–14 (green) and 15+ yr (blue). Numbers indicate *std* in order of increasing age. Grey lines indicate estimates using *std* of 0.05, the value used in the final model

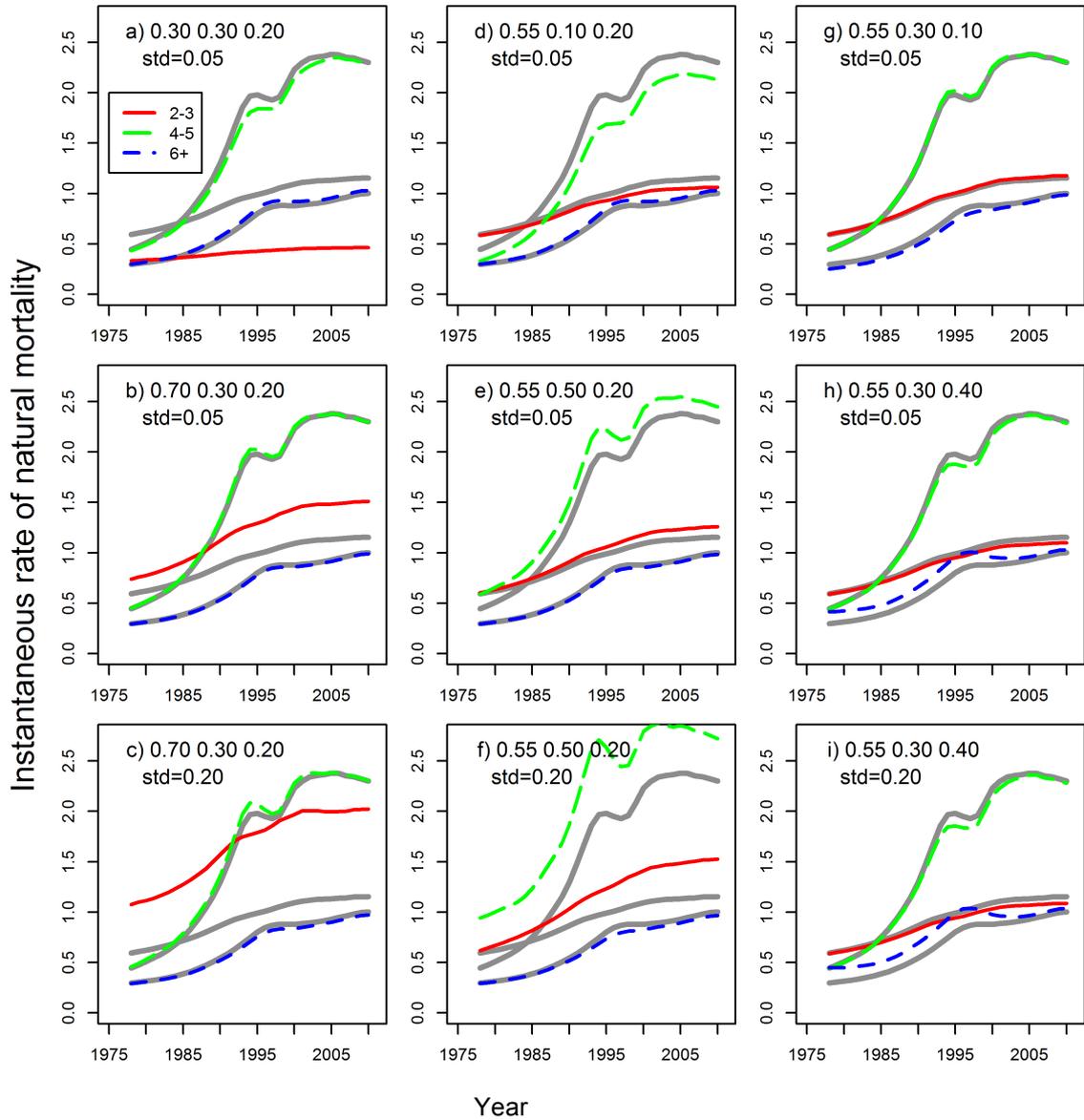


Fig. S13. Effect of the prior mean for initial M on estimated M of white hake aged 2–3 (red lines), 4–5 (green dashed lines) and 6+ yr (blue dashed lines). Grey lines show the estimates from the final model using prior means of 0.55, 0.3 and 0.2 for ages 2-3, 4-5 and 6+ yr, respectively, and a standard deviation (std) of 0.05 for all ages. The prior means for the coloured lines are given in each panel in the order of increasing age. For the age group with a change in prior mean, std is also indicated in each panel

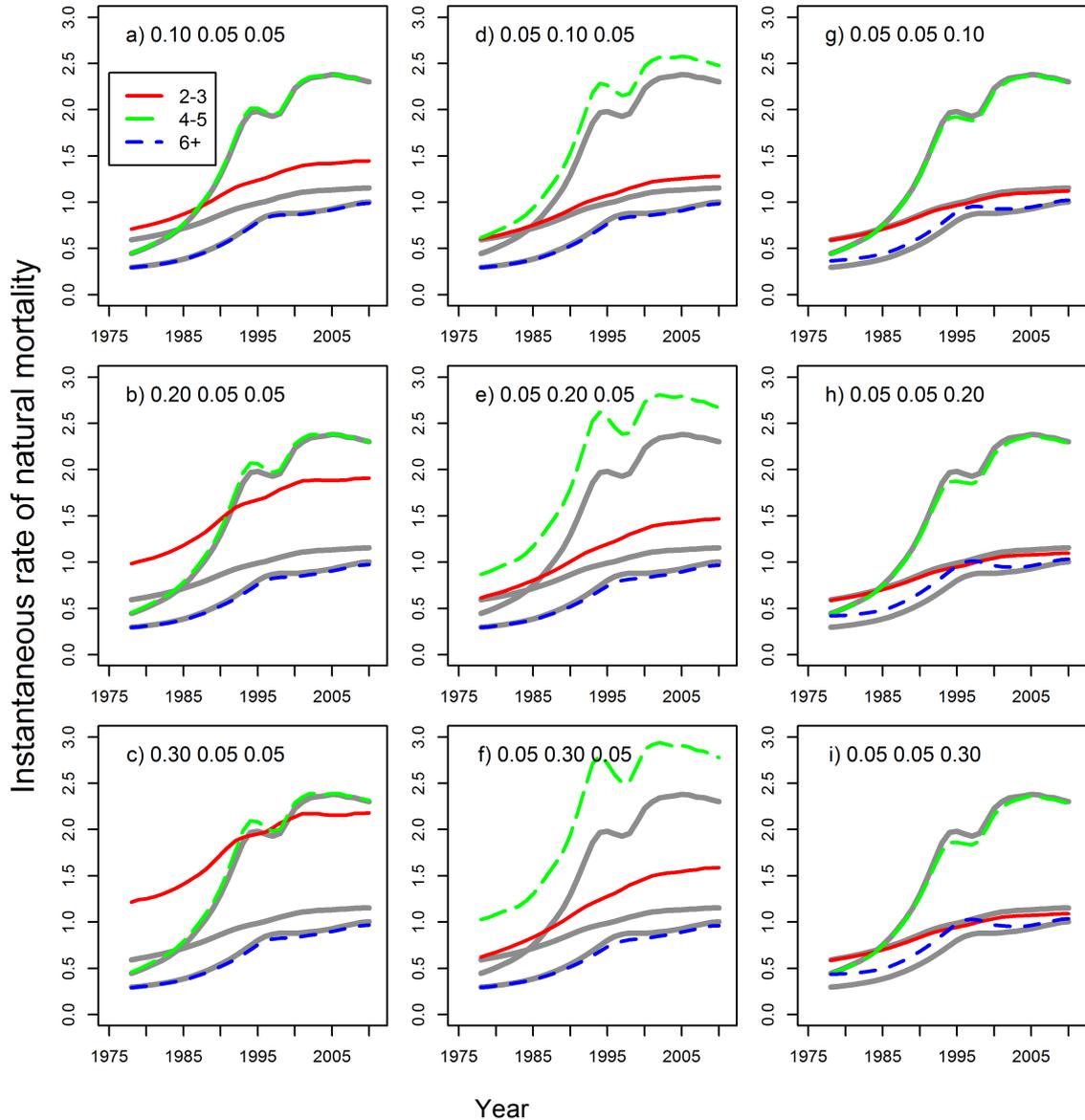


Fig. S14. Effect of the standard deviation (*std*) of the prior distribution for initial M on estimates of M for white hake aged 2–3 (red), 4–5 (green) and 6+ yr (blue). Numbers indicate *std* in order of increasing age. Grey lines indicate estimates using *std* of 0.05, the value used in the final model

SUPPLEMENT 3. TIME-VARYING NATURAL MORTALITY OR TIME-VARYING CATCHABILITY?

Some studies have concluded that estimating M is problematic due to correlation between estimates of M and parameters such as catchability and selectivity (Schnute & Richards 1995, Fu & Quinn 2000), and Lee et al. (2011) found that unrealistic estimates of M can result from high correlations between M and parameters such as those determining selectivity. In our models, correlations were low between M parameters and parameters related to catchability and selectivity. For example, in the cod model, the average and maximum absolute values of the correlation with M parameters were 0.032–0.037 (average) and 0.31–0.42 (maximum) for

catchability parameters and 0.014–0.039 and 0.09–0.46 for selectivity parameters. The simulation tests described above confirmed that our models can correctly identify the general time trend in M for ages well recruited to the fishery.

In our models, we have modelled the non-stationarity in our data as time-varying natural mortality rather than time-varying catchability and/or selectivity. The rationale for this approach is that selectivity and catchability to the survey should vary little over time because the surveys use standardized protocols and, to the extent possible, the same gear and vessel each year. Furthermore, whenever there has been a change in protocol, gear or vessel (1985, 1992 and 2004), catch rates have been standardized as necessary to account for the change (see Materials and Methods). In addition, for species such as cod and plaice, the survey covers virtually all the habitat utilized by these populations in September (e.g. Swain & Morin 1996, Swain 1999, Swain et al. 2012c), so substantial changes in availability to the survey are implausible. Nonetheless, it is possible that changes in fishing efficiency in the survey in 1985, 1992 and 2004 were poorly estimated or were not detected due to low statistical power. Thus, we investigate here whether the non-stationarity that we model as changes in M might instead reflect changes in selectivity and/or catchability. In these revised models, M is assumed to be constant over time and across ages, the typical assumption in stock assessment models. For cod, M was set at 0.2, the value typically assumed for cod. For the southern Gulf cod stock, tagging studies and other analyses indicated that M was indeed near this value in the 1950s and 1960s for commercial-sized cod, and model estimates were also near this value in the early 1970s for cod aged 5 yr and older. For plaice, we used a value of either 0.2 or 0.25, the average of the model estimates for M of plaice aged 10–14 and 15+ yr in 1976. For hake, we used a value of either 0.2 or 0.375, the average of the model estimates for M of hake aged 4–5 and 6+ yr in 1978. Results were similar and conclusions the same using either value of M for plaice and hake, and results are shown here just for the models using M of 0.25 (plaice) or 0.375 (hake). Selectivity at age (S_a) and fully recruited catchability (q) were allowed to change whenever there was a change in the survey (1985, 1992 and 2004). For each stock, the revised model will be referred to as Model 2, and the original model with time-varying M will be referred to as Model 1. The abundance indices used for Model 2 were the standardized indices used for Model 1 (see Materials and Methods for details).

In Model 2, large changes in estimated catchability at age ($Q_a = S_a \times q$) to the RV survey occurred between time periods (Fig. S15). The greatest change in the survey occurred in 1985, when there were changes in protocol (day only versus 24-h fishing), gear and vessel. However, the estimated change in catchability at age in 1985 was modest compared to the changes in 1992 and 2004. For cod, Q_a in 1971–1984 was similar to Q_a in Model 1, with q estimated to be 1.05 in 1971–1984 and 0.89 in Model 1. In contrast, q was estimated to be 1.64 in 1985–1991, 7.50 in 1992–2002 and 7.30 in 2004–2010 in Model 2. This large change in 1992 is too large to be attributed to a change in vessel with no change in gear. Changes in fishing efficiency identified by the comparative fishing in 1992 were an order of magnitude lower. Finally, a q of 7 or more is not physically possible in this case. Survey indices were at the scale of ‘trawlable abundance’, with mean survey catches expanded from the area swept by a tow to the area of the survey. The swept area in this expansion equalled the distance towed times trawl wingspread. This may underestimate the area fished by a tow, due to herding of fish into the path of the trawl by the trawl doors, and consequently overestimate trawlable abundance. Thus, it is possible for q to be greater than 1 if herding is efficient and a high proportion of fish in the path of the trawl are caught. At the depths fished in the RV survey, doorspread is about 4 times wingspread. Thus, if all fish between the doors were herded into the path of the trawl and all fish in the path of the trawl were caught, it would be possible to have q near 4. Because neither herding nor fishing efficiency of the net are this effective, q would be expected to be considerably lower than 4. It would also be possible to obtain a q greater than 1, potentially much greater than 1, if (1) the

survey covered only a portion of the stock area, (2) fish density was higher in the area covered than in the area not covered, and (3) catches were expanded to the full stock area rather than just the survey area in the trawlable abundance calculation. This is not the case here. Thus, the very high q to the RV survey estimated by Model 2 for cod in the period since 1992 is not plausible.

Estimated q of plaice to the RV survey in 1992–2002 and 2004–2011, of hake to the RV survey in 1992–2002, and of cod and plaice to the mobile sentinel survey are all also impossibly high in Model 2 (Fig. S15). Likewise, the Model 2 estimates of the increase in RV q for plaice in 1992 and 2004 and for hake in 1992 and the decrease for hake in 2004 are implausibly large for just a vessel change. The selectivity curves estimated by Model 2 were also not plausible in many cases. For example, plaice do not appear to be fully recruited to the RV survey until age 8 yr or later (Morin et al. 2008), yet selectivity of the RV survey was estimated to be near 1 by age 4 or 5 yr in Model 2.

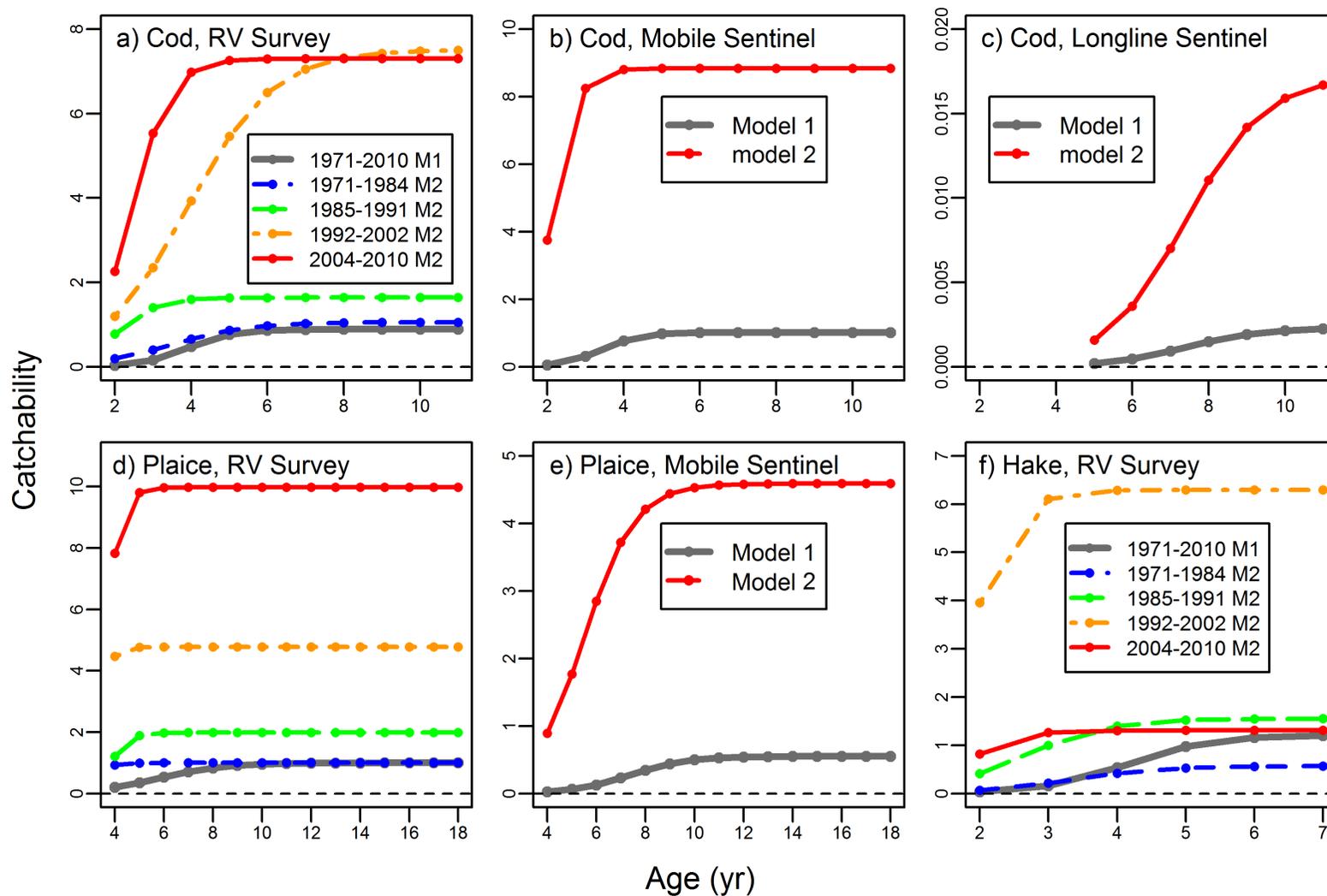


Fig. S15. Estimated catchability at age of Atlantic cod to the research vessel (RV), mobile sentinel and longline sentinel surveys of the southern Gulf of St. Lawrence (a–c), of American plaice to the RV and mobile sentinel surveys (d,e), and of white hake to the RV survey (f) for 2 models. In Model 1 (M1), catchability at age (Q_a) is assumed to be constant over time and the rate of natural mortality (M) is allowed to vary over time. In Model 2 (M2), M is assumed to be constant over time and Q_a is allowed to change in 1985, 1992 and 2004 for the RV survey

The estimated rates of fishing mortality (F) are shown for Models 1 and 2 in Fig. S16. In Model 1, F declined sharply for cod and hake in the mid-1990s, when fishing effort for these species dropped sharply (Benoît & Swain 2008). For plaice, F dropped sharply in the mid-1990s and then declined steadily to the present in Model 1, again reflecting the trend in fishing effort (Morin & LeBlanc 2012). In contrast, in Model 2 periods of high F occurred after the mid-1990s for all 3 species. F in these periods often exceeded the levels that prevailed in the 1980s. These high levels of F in Model 2 are not plausible given the sharp drop in fishing effort known to occur beginning in the mid-1990s.

Based on the Model 2 estimates of catchability and fishing mortality, this model is not plausible for cod, plaice and hake, and the non-stationarity in our data cannot be explained by the changes in catchability and selectivity allowed in this model. In Model 2, catchability at age was constrained to be monotonically increasing or ‘flat-topped’ because selectivity was modelled as a logistic function of age. Catchability at age to a commercial fishery can be dome-shaped rather than flat-topped. For example, this could occur in a bottom-trawl fishery if fish were spatially segregated by size or age and the fishery targeted the relatively abundant and well-recruited intermediate ages or sizes. This is not expected to occur in a research survey that fishes at random with respect to fish distribution. However, catchability at age to a research survey could be dome-shaped if older fish were less available to the survey because a higher proportion of older fish occurred outside of the survey area or if large, older fish can outswim the trawl. This is unlikely in our case. The survey covers virtually all of the habitat used by the southern Gulf populations of cod and plaice (e.g. Swain & Morin 1996, Swain et al. 2012c). Some hake occur in the small area inshore of the survey, but the proportion in shore would be higher for small rather than large hake (Herder et al. 2005). The survey towing speed (3.5 knots) and duration (30 min) were chosen to ensure a high catchability of large cod to the survey. Thus, it is very unlikely that catchability to the survey is dome-shaped for cod, plaice and hake. Nonetheless, we examined models (Model 3) in which a separate catchability was estimated for each age (thus permitting dome-shaped catchability) and catchability at age was allowed to change whenever there was a change in the survey (1985, 1992 and 2004).

Given the assumption that M is constant over time in Model 3, this model attempted to account for the increased rate of loss of older fish in the 1990s and 2000s by increasing catchability to very high values in these decades and changing the relationship between catchability and age from increasing or flat-topped in the 1970s and 1980s to strongly dome-shaped in the 1990s and 2000s (Fig. S17). The very high catchability estimates for the 1990s and 2000s reduced population size to very low values, increasing F to high values (as is shown in Fig. S16). The sharp decline in estimated catchability with age in the 1990s and 2000s also contributed to the high rate of loss of older fish in a cohort from the survey catches. However, for the reasons described above for Model 2, the very high catchabilities estimated by Model 3 for the 1992–2002 and/or 2004–2010 periods are not possible. Furthermore, as in Model 2, these high catchabilities result in high F during a period of sharply reduced fishing effort. Finally, the strongly domed survey catchabilities estimated by this model for recent periods are also not plausible because: (1) based on survey coverage and the geographic distributions of these stocks (see above), there is no indication of a decline in availability in recent years, (2) given the tow speed and duration in the RV survey, it is not plausible that these fish could outswim the trawl, particularly at the early age and small size when catchability begins to decline (i.e. cod – age 6 yr, mean length in the 2000s of 46.5 cm; plaice – age 11 yr, 30.5 cm; hake – age 5 yr, 51.5 cm), and (3) there are no evident changes in the survey or fish populations that could account for the extreme changes in both the level of catchability and its relation to age as estimated by the model. Thus, like Model 2, Model 3 is not plausible.

Model 4 allowed changes in selectivity and catchability as in Model 2 and random walks in M as in Model 1. Results from this model are summarized but not shown here. For cod, the

estimated time trends in M for age groups 5–8 and 9+ yr were the same as in Model 1, M was estimated to remain relatively constant for the 2–4 yr age group, and estimated catchabilities were at reasonable levels (<1), with only minor differences in the shape and level of the catchability at age curve between time periods. For plaice and hake, large changes in catchability between time periods persisted in this model, with catchability reaching implausible levels in recent periods. For plaice, estimated increases in M were only about 0.15 for the 2 older age groups, increasing to 0.25 if the standard deviation of process error was increased from 0.05 to 0.1. For hake, estimated increases in M were only about 0.3 for the 2 older age groups, increasing to 2.25 (ages 4–5 yr) or 0.5 (ages 6+ yr) if the standard deviation of process error was increased from 0.05 to 0.1. Again, the large increases in M estimated by Model 1 cannot be attributed to plausible changes in catchability or selectivity based on the results of Model 4. In the case of cod, the same large increases in M were estimated by Model 4. For plaice and hake, the changes in M estimated by Model 4 were not as great as in Model 1 in most cases, but this required increases in catchability that are not plausible.

In conclusion, it is not plausible that the large increases in natural mortality identified by Model 1 are instead due to unidentified changes in catchability and/or selectivity. The changes in catchability and selectivity that would be required to account for an important part of the non-stationarity in the data attributed to an increase in natural mortality are too great to be plausible. In contrast, the large increases in natural mortality identified by Model 1 are not implausible if there have been large changes in sGSL ecosystem that have reduced the viability of these populations.

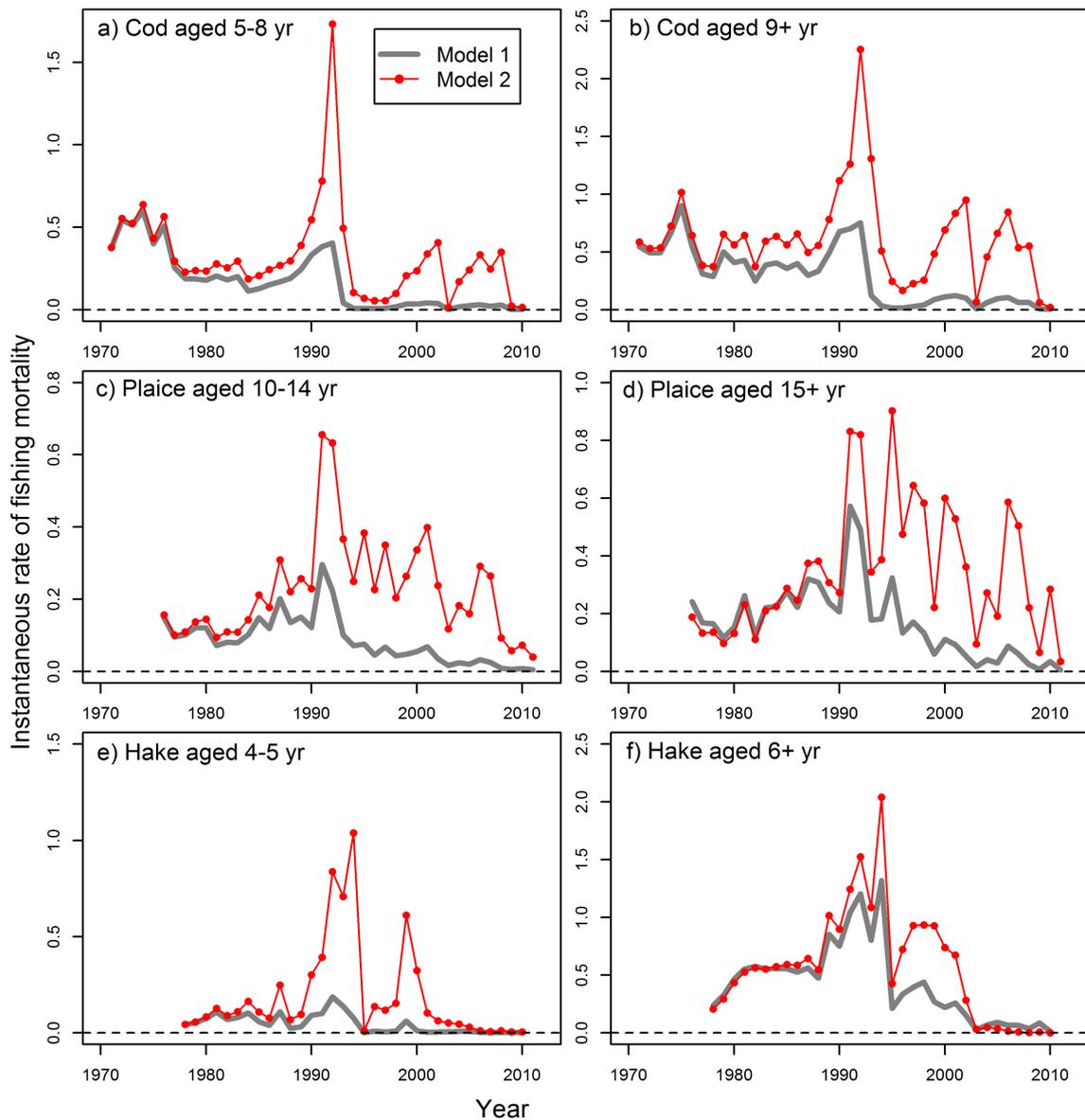


Fig. S16. Estimated fishing mortality of 2 age groups of Atlantic cod, American plaice and white hake based on 2 types of models. In Model 1 (M1), catchability at age (Q_a) is assumed to be constant over time and the rate of natural mortality (M) is allowed to vary over time. In Model 2 (M2), M is assumed to be constant over time and Q_a is allowed to change in 1985, 1992 and 2004 for the research vessel survey

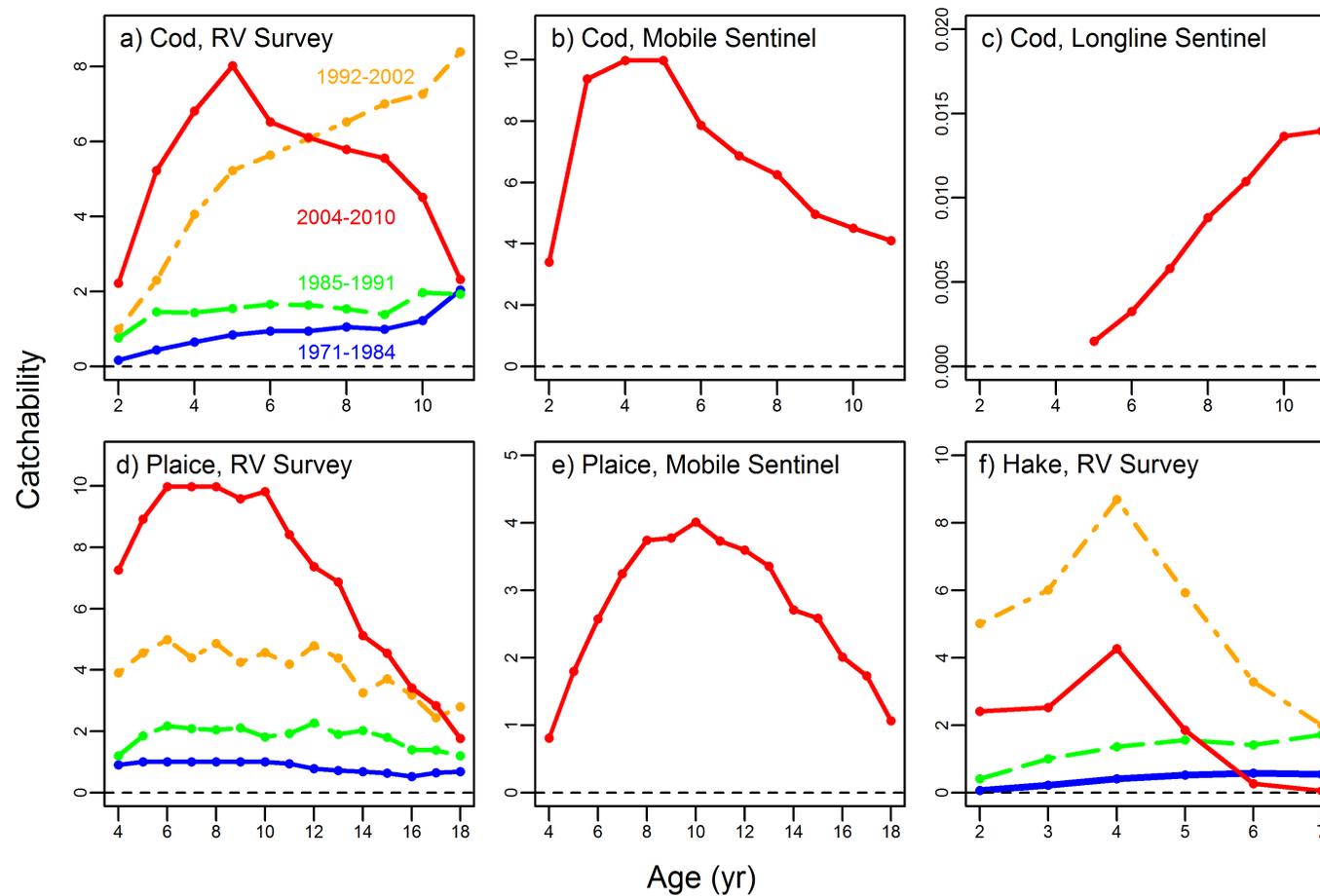


Fig. S17. Estimated catchability at age of Atlantic cod to the research vessel (RV), mobile sentinel and longline sentinel surveys of the southern Gulf of St. Lawrence (a–c), of American plaice to the RV and mobile sentinel surveys (d,e), and of white hake to the RV survey (f) for Model 3. In Model 3, M is assumed to be constant over time and catchability at age is allowed to change in 1985, 1992 and 2004

SUPPLEMENT 4. STAGE-STRUCTURED POPULATION MODELS FOR SKATES

Estimates of decadal variation in total mortality rates of length classes of thorny, winter and smooth skate in the southern Gulf of St. Lawrence were obtained by Swain et al. (2009a, 2013) using stage-structured state–space models. Thorny and smooth skate were divided into 2 juvenile stages and an adult stage based on length. A single juvenile stage was used for winter skate due to the early age and small size at maturity for this species in the sGSL. For thorny and smooth skate, transitions from year $t-1$ to year t were modeled as follows:

$$N_{1,t} = (N_{1,t-1}(1-\theta_1) + \frac{1}{2}(rN_{3,t-a}))e^{-Z_{1,t}}e^{\eta_{1,t}} \quad (\text{S8})$$

$$N_{2,t} = (N_{2,t-1}(1-\theta_2) + N_{1,t-1}\theta_1)e^{-Z_{2,t}}e^{\eta_{2,t}} \quad (\text{S9})$$

$$N_{3,t} = (N_{3,t-1} + N_{2,t-1}\theta_2)e^{-Z_{3,t}}e^{\eta_{3,t}} \quad (\text{S10})$$

where $N_{i,t}$ ($i = 1, 2, 3$) is abundance in year t for the i th life stage, θ_i is the transition probability to the next stage, a is the time between laying of egg cases and recruitment to juvenile stage 1 (1 or 2 yr depending on population), $Z_{i,t}$ is the stage-specific instantaneous rate of total mortality in year t , and r is the recruitment rate (i.e. annual fecundity per female discounted by egg case mortality and mortality between hatching and recruitment). A sex ratio of 1:1 was assumed to compute recruit production. The probability of transition directly from the first juvenile stage to the adult stage in one year was assumed to be zero based on plausible growth rates for these skates. $\eta_{1,t}$, $\eta_{2,t}$ and $\eta_{3,t}$ are independent normal random variables with mean 0 and variance σ_i^2 , representing process stochasticity in each of the 3 stages. The model for winter skate had the same form except that transition was directly from the first juvenile stage to the adult stage. These models assume that recruitment and transition between stages occur prior to mortality events.

Survey catch rates were related to $N_{i,t}$ with the following observation model:

$$y_{i,t} = q_i N_{i,t} e^{\varepsilon_{i,t}} \quad (\text{S11})$$

where q_i is the catchability coefficient of stage i that scales relative abundance to $N_{i,t}$ ($i = 1, 2, 3$) and $\varepsilon_{i,t}$ are independent normal random variables with mean 0 and variance τ_i^2 , representing observation error in the abundance index for stage i . There was no attempt to scale $N_{i,t}$ to true abundance. Instead, survey catch rates were adjusted for size selectivity using a research-trawl selectivity curve. Small and large individuals were adjusted to the same relative catchability, but not to 100% catchability

Models were fit using a Bayesian approach, placing informative priors on a number of parameters (e.g. transition probabilities and recruitment rates) based on life-history information.

Transition probabilities were assumed to be stationary. This is equivalent to assuming that there was no change in growth rate over the time series. Sensitivity of results to this assumption were investigated. Estimated changes in mortality could not be attributed instead to changes in growth rate within plausible limits. See Swain et al. (2009a, 2013) for further details.

SUPPLEMENT 5. GROWTH RATE AND SIZE COMPOSITION

Changes in the size composition of a population can reflect changes in growth rates as well as changes in mortality rates. We have argued that declines in the abundance of large individuals in the 1990s and 2000s despite relatively high or increasing abundance of small individuals mainly reflect increases in mortality of large individuals rather than decreases in growth rates. This is clearly the case for the 3 species examined with age-based models (Atlantic cod, American plaice and white hake). It also appears to be the case for the species examined using length-based analyses, for the following reasons.

First, the declines in growth rate that would be required to account for these changes in size composition are extreme. For example, the declines in abundance of large juveniles and/or adults of thorny and winter skates that are attributed to increased mortality in the stage-structured models could not instead be attributed to declines in growth rates within plausible limits (Swain et al. 2009a, 2013). To account for the observed changes in size composition of thorny skate without changes in mortality rates would require a decline in growth rate by an order of magnitude (Swain et al. 2013).

Second, conditions for growth of large demersal fish improved in the sGSL in the 1990s and 2000s, not the reverse. Abundance of these large fish declined to low levels in the 1990s and 2000s. In contrast, abundance of their prey (e.g. small forage fishes, invertebrates such as shrimp, echinoderms and some crabs) increased to high levels during this period (Benoît & Swain 2008, Dufour et al. 2010). Thus, density-dependent effects should favour rapid growth of large demersal fish in the 1990s and 2000s. Furthermore, while bottom waters were cold in the sGSL in the late 1980s and early to mid-1990s, they warmed to levels near the long-term average in the 2000s (Galbraith et al. 2011).

Finally, there are no indications from species with length-at-age data that growth rates have declined in the past 20–25 yr (Fig. S18). Size at age declined in these species in the late 1970s and early to mid-1980s but has changed little since then.

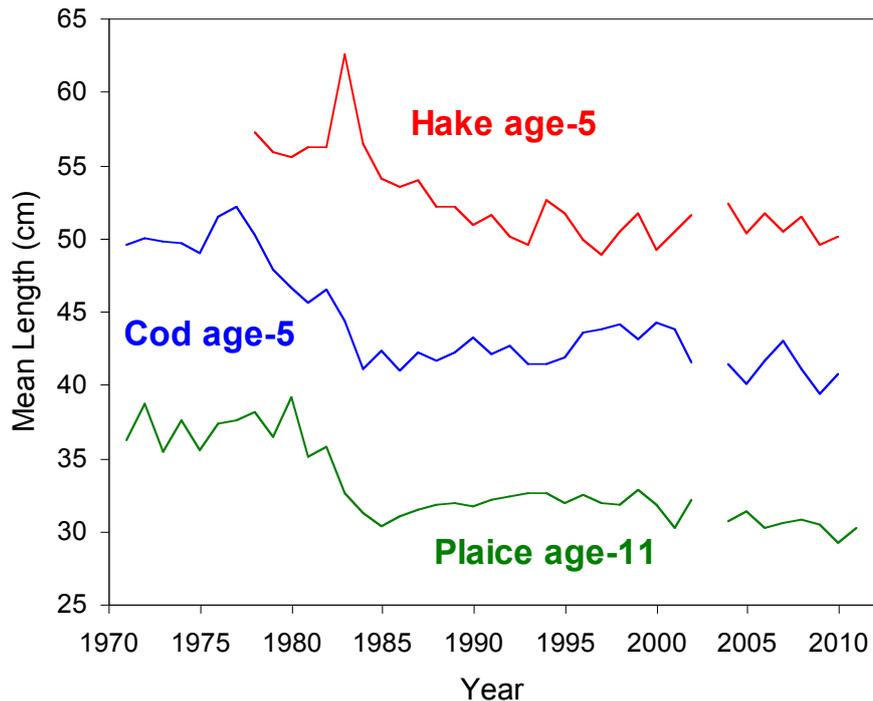


Fig. S18. Mean length (cm) for white hake aged 5 yr, Atlantic cod aged 5 yr and American plaice aged 11 yr, based on catches in the annual September research vessel survey of the southern Gulf of St. Lawrence

LITERATURE CITED

- Benoît HP (2006a) Standardizing the southern Gulf of St. Lawrence bottom-trawl survey time series: results of the 2004-2005 comparative fishing experiments and other recommendations for the analysis of the survey data. DFO Can Sci Adv Sec Res Doc 2006/008. Fisheries and Oceans Canada, Ottawa
- Benoît HP (2006b) Estimated discards of winter skate (*Leucoraja ocellata*) in the southern Gulf of St. Lawrence, 1971-2004. DFO Can Sci Adv Sec Res Doc 2006/002. Fisheries and Oceans Canada, Ottawa
- Benoît HP (2013) Two decades of annual landed and discarded catches of three southern Gulf of St. Lawrence skate species estimated under multiple sources of uncertainty. ICES J Mar Sci 70:554–563
- Benoît HP, Swain DP (2003a) Accounting for length and depth-dependent diel variation in catchability of fish and invertebrates in an annual bottom-trawl survey. ICES J Mar Sci 60:1298–1317
- Benoît HP, Swain DP (2003b) Standardizing the southern Gulf of St. Lawrence bottom-trawl survey time series: adjusting for changes in research vessel, gear and survey protocol. Can Tech Rep Fish Aquat Sci No 2505. Fisheries and Oceans Canada, Ottawa
- Benoît HP, Swain DP (2008) Impacts of environmental change and direct and indirect harvesting effects on the dynamics of a marine fish community. Can J Fish Aquat Sci 65:2088–2104
- Beverton RJH (1965) Catch effort of some ICNAF fisheries. Res Bull Int Comm Northwest Atl Fish 2:59–72
- Chouinard GA, Currie LG, Poirier GA, Swain DP, Benoit HP, Hurlbut T, Daigle D, Savoie L (2005a) Assessment of the southern Gulf of St. Lawrence cod stock, February 2005. DFO Can Sci Adv Sec Res Doc 2005/007. Fisheries and Oceans Canada, Ottawa
- Chouinard GA, Swain DP, Hammill MO, Poirier GA (2005b) Covariation between grey seal (*Halichoerus grypus*) abundance and natural mortality of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can J Fish Aquat Sci 62:1991–2000
- Deroba JJ, Butterworth DS, Methot RD Jr, De Oliveira JAA and others (2014) Simulation testing the robustness of stock assessment models to error: some results from the ICES strategic initiative on stock assessment methods. ICES J Mar Sci (in press) doi:10.1093/icesjms/fst237
- Dickie LM (1963) Estimation of mortality rates of Gulf of St. Lawrence cod from results of a tagging experiment. Spec Publ Int Comm Northwest Atl Fish 3:71–80

- Dufour R, Benoît HP, Castonguay M, Chassé J and others (2010) Ecosystem status and trends report: Estuary and Gulf of St. Lawrence ecozone. DFO Can. Sci Advis Sec Res Doc 2010/030. Fisheries and Oceans Canada, Ottawa
- Fournier DA, Skaug HJ, Ancheta J, Ianelli J and others (2011) AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optim Methods Softw* 27:233–249
- Fu C, Quinn TJ II (2000) Estimability of natural mortality and other population parameters in a length based model: *Pandalus borealis* in Kachemak Bay, Alaska. *Can J Fish Aquat Sci* 57:2420–2432
- Galbraith PS, Chassé J, Gilbert D, Larouche P and others (2011) Physical Oceanographic Conditions in the Gulf of St. Lawrence in 2010. DFO Can Sci Advis Sec Res Doc 2011/045. Fisheries and Oceans Canada, Ottawa
- Gavaris S (1999) ADAPT (ADAPTive framework). User's Guide. Version 2.1. Fisheries and Oceans Canada, Ottawa
- Gislason H, Daan N, Rice JC, Pope JG (2010) Size, growth, temperature and the natural mortality of marine fish. *Fish Fish* 11:149–158
- Herder EC, Methven DA, Hurlbut TR (2005) Long-term changes in size–depth distributions of *Urophycis tenuis* white hake in the southern Gulf of St Lawrence and Cabot Strait. *J Mar Biol Assoc UK* 85:1203–1210
- Lee HH, Maunder MN, Piner KR, Methot RD (2011) Estimating natural mortality within a fisheries stock assessment model: An evaluation using simulation analysis based on twelve stock assessments. *Fish Res* 109:89–94
- Morin R, LeBlanc SG (2012) Assessment of the southern Gulf of St. Lawrence (NAFO Division 4T) American plaice (*Hippoglossoides platessoides*). DFO Can Sci Advis Sec Res Doc 2012/099. Fisheries and Oceans Canada, Ottawa
- Morin R, LeBlanc SG, Chouinard G, Swain D (2008) Status of NAFO Division 4T American plaice, February 2008. DFO Can Sci Advis Sec Res Doc 2008/067. Fisheries and Oceans Canada, Ottawa
- Morin R, Swain DP, LeBlanc SG (2012) A biomass Limit Reference Point for the NAFO 4T American plaice (*Hippoglossoides platessoides*) fishery. DFO Can Sci Advis Sec Res Doc 2012/108. Fisheries and Oceans Canada, Ottawa
- Paloheimo JE, Kohler AC (1968) Analysis of the southern Gulf of St. Lawrence cod population. *J Fish Res Board Can* 25:555–578
- Savoie L, Surette T (2010) Results from the August 2008 sentinel bottom trawl survey of the southern Gulf of St. Lawrence. DFO Can Sci Advis Sec Res Doc 2010/033. Fisheries and Oceans Canada, Ottawa
- Schnute JT, Richards LJ (1995) The influence of error on population estimates from catch–age models. *Can J Fish Aquat Sci* 52:2063–2077
- Swain DP (1999) Changes in the distribution of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence — effects of environmental change or change in environmental preferences? *Fish Oceanogr* 8:1–17
- Swain DP (2011) Natural mortality and projected biomass of southern Gulf of St. Lawrence cod. DFO Can Sci Advis Sec Res Doc 2011/040. Fisheries and Oceans Canada, Ottawa
- Swain DP, Morin R (1996) Relationships between geographic distribution and abundance of American plaice (*Hippoglossoides platessoides*) in the southern Gulf of St. Lawrence. *Can J Fish Aquat Sci* 53:106–119
- Swain DP, Jonsen ID, Simon JE, Myers RA (2009a) Assessing threats to species-at-risk using stage-structured state-space models: mortality trends in skate populations. *Ecol Appl* 19:1347–1364
- Swain DP, Savoie L, Hurlbut T, Surette T, Daigle D (2009b) Assessment of the southern Gulf of St. Lawrence cod stock, February 2009. DFO Can Sci Advis Sec Res Doc 2009/037. Fisheries and Oceans Canada, Ottawa
- Swain DP, Hurlbut TR, Benoît HP (2012a) Pre-COSEWIC review of variation in the abundance, distribution and productivity of white hake (*Urophycis tenuis*) in the southern Gulf of St. Lawrence, 1971–2010. DFO Can Sci Advis Sec Res Doc 2012/066. Fisheries and Oceans Canada, Ottawa
- Swain DP, Savoie L, Aubry É (2012b) Recovery Potential Assessment for the Laurentian South designatable unit of Atlantic Cod (*Gadus morhua*): the southern Gulf of St. Lawrence cod stock (NAFO Div. 4T-4Vn(Nov–Apr)). DFO Can Sci Advis Sec Res Doc 2012/052. Fisheries and Oceans Canada, Ottawa
- Swain DP, Benoît HP, Chouinard GA, Hurlbut TR, Morin R, Savoie L, Surette T (2012c) Stock assessment of cod in the southern Gulf of St. Lawrence: science response to issues raised by members of the fishing industry, October 2008. *Can Manuscr Rep Fish Aquat Sci* 2992. Fisheries and Oceans Canada, Ottawa
- Swain DP, Jonsen ID, Simon JE, Davies TD (2013) Contrasting decadal trends in mortality between large and small individuals in skate populations in Atlantic Canada. *Can J Fish Aquat Sci* 70:74–89