Fisheries and Oceans Canada / Pêches et Océans Canada
NOAA FISHERIES
NATIONAL MARINE FISHERIES SERVICE

CERT

Comité d'évaluation des
ressources transfrontalières

Document de référence 2013/06
Ne pas citer sans
autorisation des auteurs

TRAC

Transboundary Resources
Assessment Committee

Reference Document 2013/06
Not to be cited without
permission of the authors

A Population Model for Eastern Georges Bank Atlantic Cod Incorporating Estimated Time Trends in Natural Mortality

D.P. Swain

Fisheries and Oceans Canada
Gulf Fisheries Centre, 343 Avenue de l'Université
Moncton, New Brunswick E1C 9B6
Canada

Ce document est disponible sur l'Internet à :
This document is available on the Internet at :
http://www.mar.dfo-mpo.gc.ca/science/TRAC/trac.html

Canada

TABLE OF CONTENTS

ABSTRACT

The assessment of the eastern Georges Bank (EGB) stock of Atlantic cod (*Gadus morhua*) has suffered from a strong retrospective pattern, indicating a non-stationarity in the population dynamics of this stock or in the observation process (i.e., the bottom-trawl surveys used to monitor this stock). This retrospective problem was temporarily solved by “splitting” the survey time series between 1993 and 1994, allowing estimated catchability to all three surveys (a winter DFO survey and spring and fall National Marine Fisheries Service (NMFS) surveys) to increase greatly between 1993 and 1994 (despite no changes in these surveys in this period). However, even with this split, the retrospective problem has returned in recent years. An alternate solution to this problem, allowing *M* (the instantaneous rate of natural mortality) to vary over time, is examined here. A virtual population analysis (VPA) was conducted using the EGB cod data, allowing *M* to vary independently for two (ages 1-5 and 6+ years) or three (1-2, 3-5 and 6+) age groups. These *M*-trends were modelled as random walks. Estimated *M* increased sharply for the 6+ age group beginning around 1990, rising from values near 0.25 prior to 1990 to 1.8 in 2011. Estimated *M* decreased slightly for younger age groups (e.g., from 0.35 in the 1980s to 0.1 in recent years for the 1-5 age group). Retrospective patterns were negligible (unless survey time series were split between 1993 and 1994). Allowing *M* to vary over time provides a solution to the retrospective problem for this stock. The large increases in *M* indicated by these models might be considered implausible for a large-bodied demersal fish. However, it is accepted that *M* has increased to unusually high levels for adults of large-bodied demersal fishes in the southern Gulf of St. Lawrence and for cod on the eastern Scotian Shelf. It is thought that increased predation by grey seals is an important cause of the elevated *M* of cod in the southern Gulf of St. Lawrence. Tracking of seals tagged with satellite transmitters indicates that adult male grey seals from the Sable Island herd forage on Georges Bank and in neighbouring waters in winter and early spring. Adult males grey seals are known to forage heavily on overwintering cod in the southern Gulf of St. Lawrence. It is plausible that increased predation by grey seals contributes to elevated natural mortality of older EGB cod.

RÉSUMÉ

L'évaluation du stock de morue franche (*Gadus morhua*) de l'est du banc de Georges a subi une forte tendance rétrospective, ce qui indique une absence de stationnarité dans la dynamique des populations de ce stock ou dans le processus d'observation (c.-à-d. les relevés au chalut de fond utilisés pour le surveiller). Ce profil rétrospectif a été résolu temporairement en « fractionnant » la série chronologique du relevé entre 1993 et 1994, ce qui a permis à la capturabilité estimée pour les trois relevés (le relevé d'hiver de Pêches et Océans Canada [MPO] et les relevés de printemps et d'automne du National Marine Fisheries Service [NMFS]) d'augmenter considérablement entre 1993 et 1994 (même si aucun changement n'a été apporté à ces relevés pendant cette période). Cependant, même avec cette division, le profil rétrospectif est revenu au cours des dernières années. Une solution de rechange à ce problème, qui permet à M (le taux instantané de mortalité naturelle) de varier au fil du temps, est examinée dans le présent document. Une analyse de population virtuelle (APV) a été réalisée à l'aide des données sur la morue de l'est du banc de Georges, permettant ainsi à M de varier de façon indépendante pour deux ou trois groupes d'âge (âges 1 à 5 et 6+ ou âges 1 à 2, 3 à 5 et 6+). Ces tendances de M ont été modélisées selon la méthode de marche aléatoire. La valeur estimée de M a fortement augmenté pour le groupe d'âge 6+ à partir de 1990, passant de valeurs proches de 0,25 avant 1990 à 1,8 en 2011. La valeur estimée de M a légèrement diminué pour les groupes d'âge les plus jeunes (p. ex. de 0,35 dans les années 1980 à 0,1 ces dernières années pour le groupe d'âge 1 à 5). Les tendances rétrospectives ont été négligeables (à moins que la série chronologique des relevés n'ait été divisée entre 1993 et 1994). Le fait de permettre à M de varier au fil du temps fournit une solution au profil rétrospectif pour ce stock. L'augmentation importante de M indiquée par ces modèles pourrait être considérée comme improbable pour un poisson de fond de grande taille. Toutefois, il est convenu que M a augmenté pour atteindre des niveaux anormalement élevés pour les adultes des poissons de fond de grande taille dans le sud du golfe du Saint-Laurent et pour la morue de l'est du plateau néo-écossais. Il semblerait que l'augmentation de la prédation par les phoques gris est une cause importante de la valeur élevée de M pour la morue dans le sud du golfe du Saint-Laurent. Le suivi des phoques marqués avec des émetteurs satellites indique que les phoques gris mâles adultes du troupeau de l'île de Sable sont en quête de nourriture sur le banc de Georges et dans les eaux avoisinantes en hiver et au début du printemps. Les phoques gris mâles adultes sont connus pour se nourrir abondamment de morues qui passent l'hiver dans le sud du golfe du Saint-Laurent. Il est probable que l'augmentation de la prédation par les phoques gris contribue à la mortalité naturelle élevée des morues de l'est du banc de Georges les plus âgées.

INTRODUCTION

Natural mortality has risen to exceptionally high levels for large individuals of many groundfish stocks in the southern Gulf of St. Lawrence and on the eastern Scotian Shelf (Sinclair 2001, Chouinard et al. 2005, Swain et al. 2009a, Swain et al. 2012a,b, Swain and Mohn 2012, Morin et al. 2013, Swain et al. 2013). In contrast, estimated natural mortality of small individuals has shown little long-term trend or has declined (e.g., Benoît and Swain 2008; Swain et al. 2009a, Swain et al. 2013). Increased survival and abundance of small fish in the southern Gulf ecosystem have been attributed to a release from predation following the collapse in biomass of large demersal fish, possibly combined with reduced incidental mortality in fisheries due to sharp declines in fishing effort (Benoît and Swain 2008; Swain et al. 2013). Causes of increased natural mortaility of older/larger fish have been examined in most detail for Atlantic cod. Swain et al. (2011) examined a suite of hypotheses for causes of elevated natural mortality of cod in the southern Gulf, and concluded that the weight of evidence most strongly supported the hypothesis that predation by grey seals is a major cause of the elevated natural mortality of cod (see also Swain 2011). A similar conclusion has been reached for most other southern Gulf groundfish with elevated natural mortality (e.g., Benoît et al. 2011a,b).

In order to address retrospective patterns and other data and model fit issues, recent assessments of eastern Georges Bank (EGB) cod have ‘split’ survey time series between 1993 and 1994, either assuming a constant *M* (instantaneous rate of natural mortality) of 0.2, or assuming that *M* increased from 0.2 to 0.5 in 1994 (O’Brien and Worcester 2009). However strong retrospective patterns were evident in the most recent assessment of this resource (Wang and O’Brien 2012), suggesting that population dynamics processes (e.g., *M*) may be continuing to change. This document describes the results of fitting a population model to the data for EGB cod allowing for time trends in *M*, estimated using random walks.

METHODS

A virtual population analyses (VPA) implemented in AD Model Builder (Fournier et al. 2011) was fit to the data. Data inputs were fishery catch at ages 1 to 10+ yr from 1978 to 2011, and survey catch rates at age (at the scale of trawlable abundance) for the DFO survey (ages 1-8, 1986-2012), the NMFS spring survey (ages 1-8, 1978-2012), and the NMFS fall survey (ages 1-5, 1978-2011). Due to a change in gear in 1982, catchability at age was estimated separately between 1978-1981 and 1982-2012 for the National Marine Fisheries Service (NMFS) spring survey. *F* (the instantaneous rate of fishing mortality) of the oldest age group (the plus group) was assumed to equal that of the previous age in the same year. Plus group calculations followed the FRATIO method described by Gavaris (1999). *M* was modelled as a random walk:

$$M_{j,1978} = M\text{init}_j \quad (1)$$

$$M_{j,y} = M_{j,y-1} e^{M\text{dev}_{j,y}} \text{ if } y>1978 \quad (2)$$

where *y* indexes year and *j* indexes age group. Age groups were either 1-5 and 6+ (Models 1 and 3, see below), or 1-2, 3-5 and 6+ (Model 2). $M\text{init}_j$ and $M\text{dev}_{j,y}$ are parameters estimated by the model. *M*dev was assumed to be normally distributed with a mean of 0 and standard deviation *Msd* (set at 0.1). The value of *Msd* affects the degree to which the random walk is constrained. Prior values were supplied for $M\text{init}_j$: 0.25 and 0.15 for ages 1-5 and 6+ respectively, or 0.4, 0.25 and 0.15 for ages 1-2, 3-5 and 6+. 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:

$$\mathrm{f}_1 = \sum_{i,y,k} (\log(I_{i,y,k} \ / \ (q_{i,k} N_{i,y,k})))^2$$

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, and $q_{i,k}$ is catchability at age i for index k. Based on Wang and O'Brien (2012), survey timing was assumed to be month 2 for the DFO survey, month 3.36 for the NMFS spring survey and 9.48 for the NMFS fall survey.

(2) a penalty for departures of $M\mathrm{init}_j$ from its prior value:

$$\mathrm{f}_2 = 0.5 \cdot \sum_j (((M\mathrm{init}_j - M\mathrm{prior}_j) / std)^2 + \log(std)) \tag{3}$$

where *std* was set at 0.05 (or 0.075 for ages 1-2 in Model 2).

(3) a penalty for departures of $M\mathrm{dev}_{j,y}$ from 0

$$\mathrm{f}_3 = 0.5 \cdot (\sum_{j,y} M\mathrm{dev}_{j,y}^2) / Msd^2$$

Survey catch rates of zero were treated as missing values.

Three models were fit: 1) *M* age groups 1-5 and 6+, survey indices not split between 1993 and 1994; 2) *M* age groups 1-2, 3-5 and 6+, survey indices not split between 1993 and 1994; and 3) *M* age groups 1-5 and 6+, survey indices split between 1993 and 1994.

A simulation test was conducted to examine the ability of these models to estimate time trends in *M* given data with characteristics similar to the EGB cod data. Simulated populations were generated as follows. Abundance at the youngest age in all years and at all ages in the earliest year were set equal to estimated abundance from Model 1. The population was then projected forward using given patterns in *M* and *F*, based on the estimated trends in *M* and *F*max from Model 1 and average partial recruitment to the fishery in 3 periods (1978-1988, 1989-1994 and 1995-2011, again based on the *F* estimates from Model 1). Survey indices were generated by fishing the population with given age-dependent catchability profiles. Survey indices were then perturbed by applying random lognormal error based on the average CVs at age given by Wang and O'Brien (2012). The population model was then used to estimate *M* and other population parameters using the perturbed indices and the catch-at-age used to generate the population. This procedure was repeated 200 times.

RESULTS

MODEL 1

Residual patterns were acceptable (Fig. 1). Any tendencies for positive or negative residuals to "block" together differed between surveys, suggesting that they reflected observation error.

Estimated catchability was highest for the DFO survey, intermediate for the NMFS spring survey (both gears) and very low for the fall survey (Fig. 2). Except for the fall survey, there was no indication of a dome in catchability to the surveys. Average *F* at age was estimated to be considerably higher in the 1978-1993 period than in more recent periods (Fig. 3). F was highest for the oldest ages in all periods.

Based on Model 1, spawning stock biomass (SSB) declined from an average of about 59,000 t in the late 1970s and early 1980s to an average of 20,000 t since 1994 (Fig. 4). The estimates of SSB for 2011 and 2012 are the lowest in the time series (11,500 – 12,000 t). Estimated abundance of age-1 recruits declined sharply in the late 1980s and early 1990s, from an average of about 17 million in 1978-1988 to less than 3.3 million on average in 1994-2011. The 2003 and 2010 year-classes were estimated to be stronger than other recent year-classes. Estimated *M* of ages 1-5 averaged about 0.34 in the late 1970s and early 1980s, declining to about 0.1 since 2000. Estimated *M* of ages 6+ averaged 0.25 near the start of the time series but increased sharply in the early 1990s to a level near 1 (63% mortality annually). The model indicated a second sharp increase, beginning in about 2005, to levels above 1.5. Estimated *F* on ages 4-9 increased sharply in the early 1990s, peaking at 0.82 in 1993, and then declined sharply to a low level since 1995. *F*4-9 has been at the lowest level on record in recent years, averaging 0.084 since 2005, about a quarter of the level at the start of the time series.

Retrospective patterns in SSB and *F*4-9 were negligible for Model 1 (Fig. 5). Retrospective patterns were also negligible for estimates of *M*, except for a pattern in estimates of M6+ around 2005, associated with the second sharp increase in estimated *M*.

MODEL 2

Model 2 was like Model 1, except trends in *M* were estimated separately for three age groups: 1-2, 3-5, and 6+. Estimated *M* was greater for ages 1-2 than for 3-5, but estimated *M* for both age groups showed a slight decline between 1978 and 2000 (Fig. 6). Estimated *M* of ages 6+ showed the same increasing trend as in Model 1. Estimates of *F*4-9 and catchabilities to the surveys were also very similar between the two models. Estimated SSB also showed similar trends in the two models, though estimated SSB in the late 1970s and early 1980s was slightly lower for Model 2, reflecting the lower value of M for ages 3-5 estimated by Model 2.

MODEL 3

Model 3 was like Model 1, except that survey indices were “split” between 1993 and 1994 in Model 3. In Model 3, estimated.catchabilities were much higher for older ages in the period since 1994 compared to the earlier period: 2 to 4 times greater for ages 4-8 in the DFO survey, 1.5 to 2.5 times greater for ages 3-8 in the NMFS spring survey, and 2 to 5 times higher for ages 2-5 in the fall survey (Fig. 7). Model 3 estimates of SSB were substantially lower than those from Model 1 in the 1994-2012 period (Fig. 8), reflecting the increase in catchability estimated by Model 3 for this period. In Model 3, estimated *M* of ages 6+ began to increase in the early 1990s, though not as sharply as in Model 1. Nonetheless, estimated M 6+ in Model 3 reached values of 1 or more by 2006. For ages 1-5, M estimated by Model 3 initially declined slightly but increased slightly in recent years. Estimates of *F* for ages 4-9 in Model 3 were substantially greater than those in Model 1 beginning in the early 1990s.

Unlike Model 1, Model 3 showed strong retrospective patterns in *F* and *M* (Fig. 9).

SIMULATION TEST

Survey catchability curves estimated by Model 1 were similar to the true values in the simulated data, except there was a tendency to overestimate catchability at older ages (Fig. 10). Nonetheless, model estimates of *M*, *F* and SSB closely matched the true values (Fig. 11). The largest discrepancies were for *M* of ages 1-5, which was underestimated in the late 1970s and early 1980s and slightly overestimated between 2000 and 2005. The values of 6+ M were also underestimated for 2010 and 2011.

DISCUSSION

VPA models incorporating random walks in *M* are a solution to the retrospective problem in assessment models of EGB cod. These models do not require a "split" in the survey time series. In fact, when random walks in M are incorporated in models, models without a "split" in the survey time series provide a more reliable fit to the EGB cod data than models with a split, at least in terms of retrospective patterns. VPA models which estimate time trends in *M* could be implemented in ADAPT (Gavaris 1999) by estimating 6+ *M* in blocks of about 5 years beginning in about 1991. Examples of this approach are given in Chouinard et al. 2005 and Swain et al. 2009b.

When a split in the surveys is allowed in 1994, catchability increases sharply for all surveys even though there were no changes in the surveys. This would imply a substantial change in the distribution of cod between 1993 and 1994, consistent across all seasons (winter, spring and fall), resulting in a large increase in availability of cod to the surveys. Is there evidence for such important changes in cod distribution?

Even when a split in the surveys is employed, estimated *M* of ages 6+ increases to levels near 1 in recent years. When no split is employed, estimated 6+ *M* increases to a level near 1 from the mid 1990s to the mid 2000s and then increases further to levels above 1.5 in recent years. Such high levels of *M* might be considered implausible for a large-bodied demersal fish. Yet, estimated *M* has increased to unusually high levels for adults of large-bodied demersal fishes throughout the marine fish community in the southern Gulf of St. Lawrence (e.g., Benoît and Swain 2011). For example, *M* of adult white hake in the southern Gulf is estimated to now be about 2. Similarly, M of eastern Scotian Shelf cod 5 years and older increased to about 1 in the early 1990s (e.g., Swain and Mohn 2012).

Possible causes of elevated M have been examined in detail for cod in the southern Gulf of St. Lawrence (Swain et al. 2011). Hypotheses examined included unreported catch (i.e., some of the increased mortality is unknown fishing mortality, not natural mortality), emigration (i.e., older fish are leaving the ecosystem, not dying), or increased natural mortality due to disease, contaminants, poor fish condition, life-history change (early maturation, early senescence), heavy parasite loads, or increased predation mortality. There was no support for most of these hypotheses. Unreported catch may have been an important component of the increased mortality attributed to natural causes in the late 1980s and early 1990s, but this source of mortality was deemed negligible since the late 1990s due to the very low levels of fishing effort since then. Early maturation in combination with poor fish condition may have contributed to increases in natural mortality in the early to mid 1980s but neither factor was supported as an important cause of elevated natural mortality in the 2000s. The weight of evidence most strongly supported the hypothesis that predation by grey seals is a major cause of the elevated natural mortality of cod.

Increases in *M* of cod and other large-bodied demersal fishes in the southern Gulf have been coincident with dramatic increases in the abundance of grey seals. This has occurred at a time when the biomass of these fishes is severely depleted, suggesting the hypothesis that increases in M may be partly due to a "predator pit" or predation-driven Allee effect (Gascoigne and Lipcius 2004). In the Gulf of St. Lawrence, satellite tagging data indicates that grey seals, in particular adult males, forage in the vicinity of overwintering aggregations of southern Gulf cod (Harvey et al. 2012). Diet samples taken from these seals contain a high proportion of cod (e.g., 64% - 75% of the energy in intestine and stomach contents, respectively; M.O. Hammill, unpublished data). Based on the otoliths found in digestive tracts of seals, a high proportion of the cod in the winter diets are the larger cod with elevated M in the southern Gulf population (e.g., DFO 2011). Due to wide spatial, seasonal and individual variation in the diet of grey seals and spatial and seasonal gaps in the diet samples, it is not yet possible to reliably estimate the percent contribution of predation by grey seals to the elevated natural mortality of southern Gulf cod. Nonetheless, based on the energy requirements of seals and estimates of their spatiotemporal overlap with southern Gulf cod, Benoît et al (2011a) concluded that it was plausible that predation by grey seals could account for a high proportion of the natural mortality of cod, even if their contribution to the average seal diet was modest (15%).

Based on satellite tagging, a high proportion of adult male grey seals from the Sable Island herd forage on Georges Bank and neighbouring waters in winter and early spring (February-April; Breed et al. 2006). In diet studies in the southern Gulf, consumption of large demersal fish is greatest in the adult males. This suggests that predation by grey seals should be considered as a possible factor contributing to elevated *M* of EGB cod.

If predation is an important component of the elevated M of EGB cod, it seems suprising that *M* is elevated only for cod 6 years and older. In the southern Gulf and on the eastern Scotian Shelf, *M* is elevated for cod 5 years and older. These age groups include cod the size of EGB cod aged 3 years and older. However, in the southern Gulf, increases in *M* are much greater for older cod in the 5+ group than for younger cod in this group (e.g., Swain et al. 2009b). One possibility is that this reflects differences in cod abundance and grey seal prey preferences between cod size groups.

ACKNOWLEDGEMENTS

I thank Bob Mohn for introducing me to VPA models with random walks in M and for help in implementing these models in ADMB, Mike Hammill for permission to cite unpublished results, Yanjun Wang for providing the EGB cod data and information on these data, and Hugues Benoît for discussion.

REFERENCES

Benoît, H.P., and Swain, D.P. 2011. Changes in size-dependent mortality in the southern Gulf of St. Lawrence marine fish community. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/039. iv + 22 p.

Benoît, H.P., and D. P. Swain. 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.

Benoît H.P., Swain, D.P., and Hammill, M.O. 2011b. A risk analysis of the potential effects of selective and non-selective reductions in grey seal abundance on the population status of two species at risk of extirpation, white hake and winter skate in the southern Gulf of St. Lawrence. DFO Can Sci Advis Sec Res Doc 2011/033.

Benoît, H.P., Swain, D.P., Bowen, W.D., Breed, G. ., Hammill, M.O., and Harvey, V. 2011a. Evaluating the potential for grey seal predation to explain elevated natural mortality in three fish species in the southern Gulf of St. Lawrence. Mar. Ecol. Progr. Ser. 442: 149-167.

Breed, G.A., Bowen, W.D., McMillan, J.I., and Leonard, M.L. 2006. Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. Proc. R. Soc. B Biol. Sci. 273: 2319−2326

Chouinard, G.A., Swain, D.P., Hammill, M.O., and Poirier, G.A. 2005. 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.

DFO. 2011. Impacts of Grey Seals on Fish Populations in Eastern Canada. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2010/071.

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen, A., and Sibert, J. 2011. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods & Software. doi: 10.1080/10556788.2011.597854

Gascoigne, J.C., and Lipcius, R.N. 2004. Allee effects driven by predation. J. Appl. Ecol. 41: 801-810.

Gavaris, S. 1999. ADAPT (ADAPTive framework). User's Guide. Vers. 2.1.

Harvey, V., Hammill, M.O., Swain, D.P., Breed. G.A., Lydersen, C., and Kovacs, K.M. 2012. Winter foraging by a top predator, the grey seal *Halichoerus grypus*, in relation to the distribution of prey. Mar. Ecol. Progr. Ser. 462: 273-286.

Morin, R., Swain, D.P., and LeBlanc, S.G. 2013. A biomass Limit Reference Point for the NAFO 4T American plaice (*Hippoglossoides platessoides*) fishery. DFO Can. Sci. Advis. Sec. Res. Doc. 2012/108. ii + 37 p.

O'Brien, L., and Worcester, T. (Editors). 2009. Transboundary Resources Assessment Committee Eastern Georges Bank cod benchmark assessment. TRAC Proceedings 2009/02: 47p.

Sinclair, A.F. 2001. Natural mortality of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. ICES J. Mar. Sci. 58: 1-10.

Swain, D.P. 2011. Life-history evolution and elevated natural mortality in a population of Atlantic cod (*Gadus morhua*). Evolutionary Applications 4: 18-29.

Swain, D.P., and R.K. Mohn. 2012. Forage fish and the factors governing recovery of Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf. Can. J. Fish. Aquat. Sci. 69: 997-1001.

Swain, D.P., Hurlbut, T.R. and Benoît, H.P. 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. iii + 74 p.

Swain, D.P., Savoie, L. and 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. ii + 50 p.

Swain, D.P., Benoît, H.P., Hammill, M.O., McClelland, G., and Aubry, É. 2011. Alternative hypotheses for causes of the elevated natural mortality of cod in the southern Gulf of St. Lawrence: the weight of evidence. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/036. iv + 33 p.

Swain, D. P., I. D. Jonsen, J. E. Simon, and Davies, T.D. 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.

Swain, D.P., Jonsen, I.D., Simon, J.E., and Myers, R.A. 2009a. Assessing threats to species at risk using stage-structured state-space models: mortality trends in skate populations. Ecological Applications 19: 1347-1364.

Swain, D.P., 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. vi + 129 p.

Wang, Y., and O'Brien, L. 2012. Assessment of Eastern Georges Bank Atlantic Cod for 2012. TRAC Ref. Doc. 2012/02.

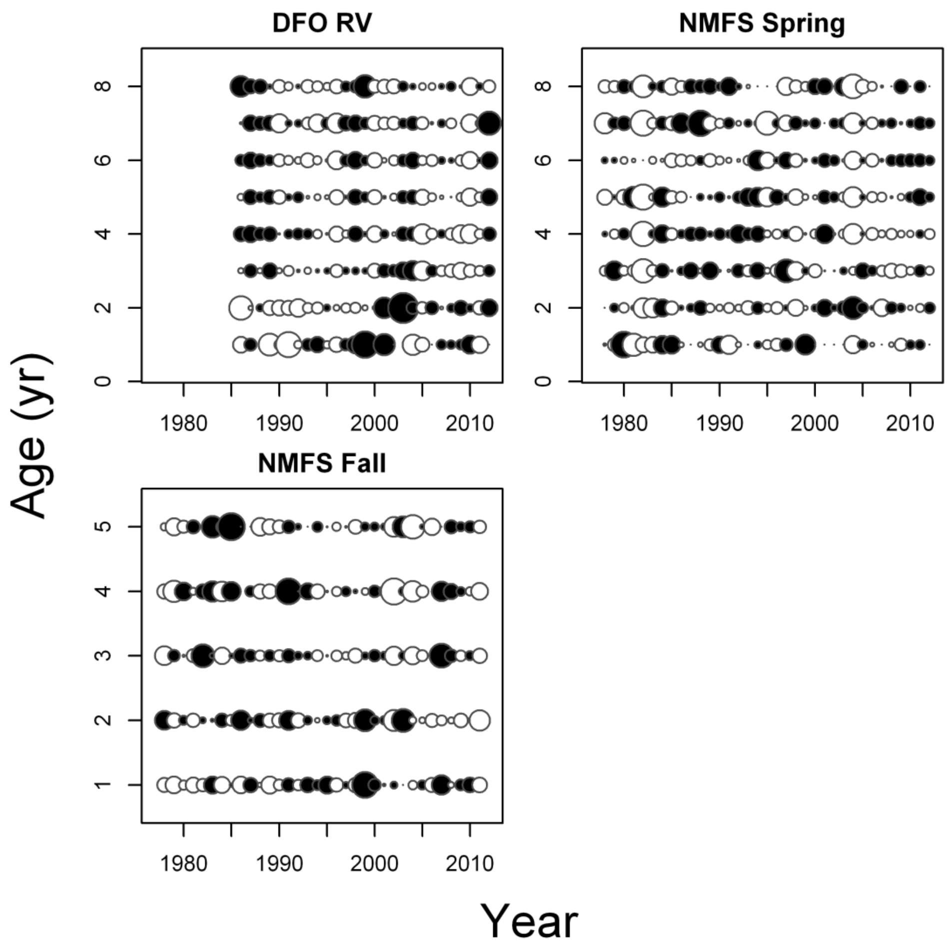

Figure 1. Residuals from the observed survey indices for Model 1. Black circles are negative residuals (i.e. observed index < predicted index). Residuals are on the log scale.

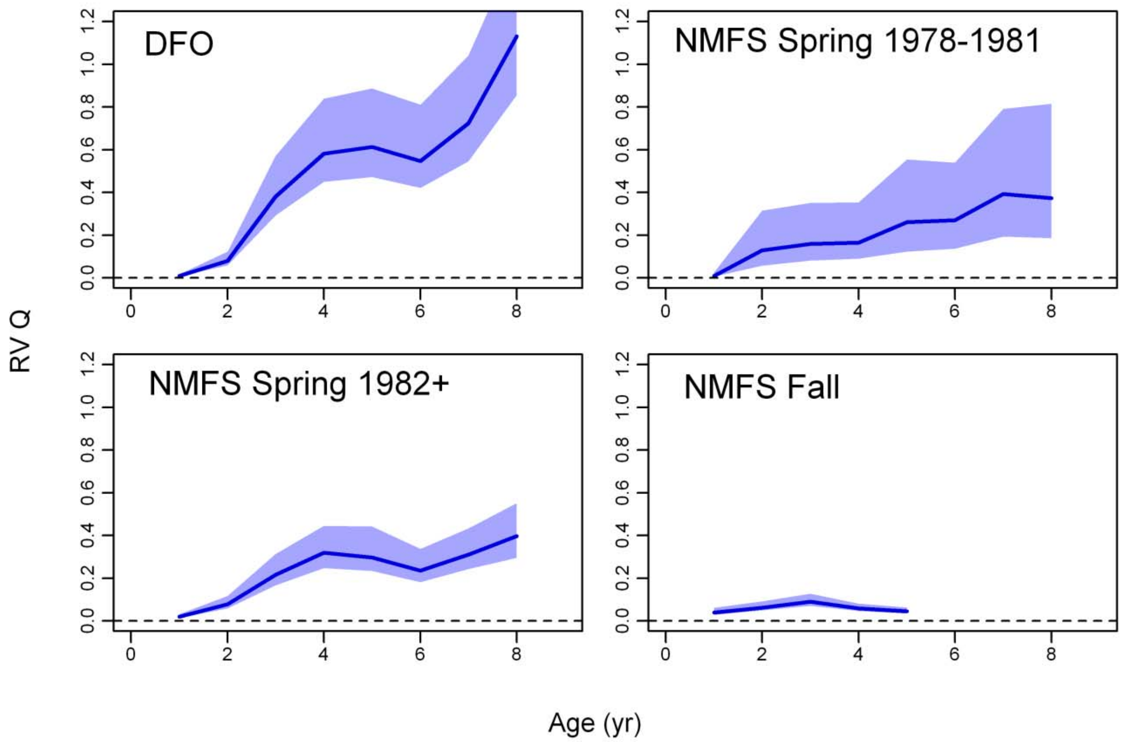

Figure 2. Estimated catchability at age to each of the RV surveys based on Model 1. Shading indicates 95% confidence intervals based on MCMC sampling.

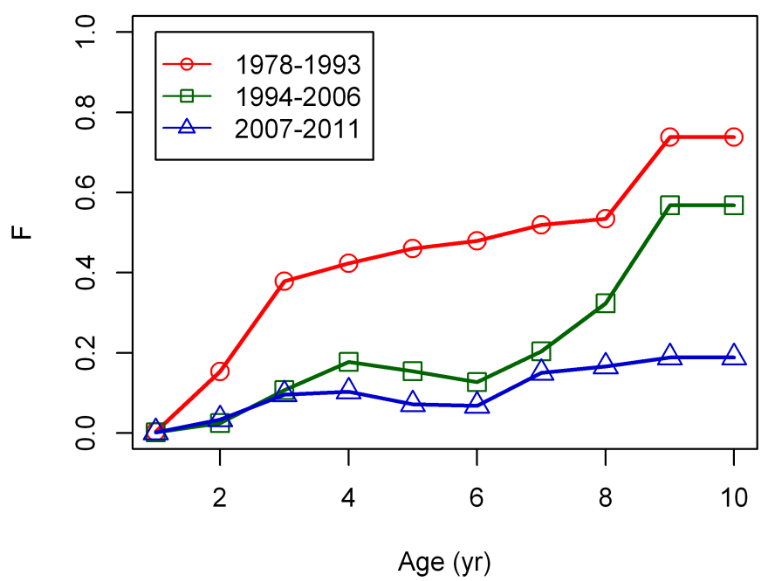

Figure 3. Average fishing mortality at age in 3 time periods, based on Model 1.

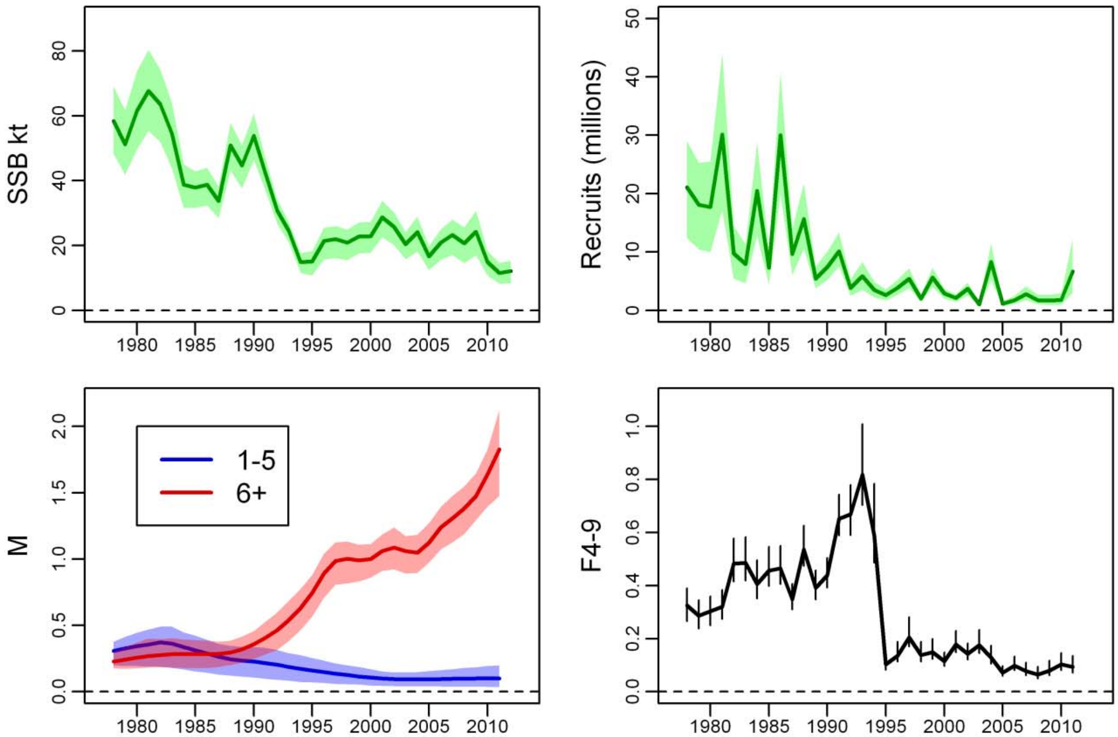

Figure 4. Model 1 estimates of spawning stock biomass (SSB), abundance of age-1 recruits, and the instantaneous rates of natural mortality (M) on ages 1-5 and 6+ years and fishing mortality on ages 4 to 9 years (F4-9). F4-9 is a weighted average, with weighting based on abundance at age. Shaded bands and vertical lines indicate 95% confidence intervals based on MCMC sampling.

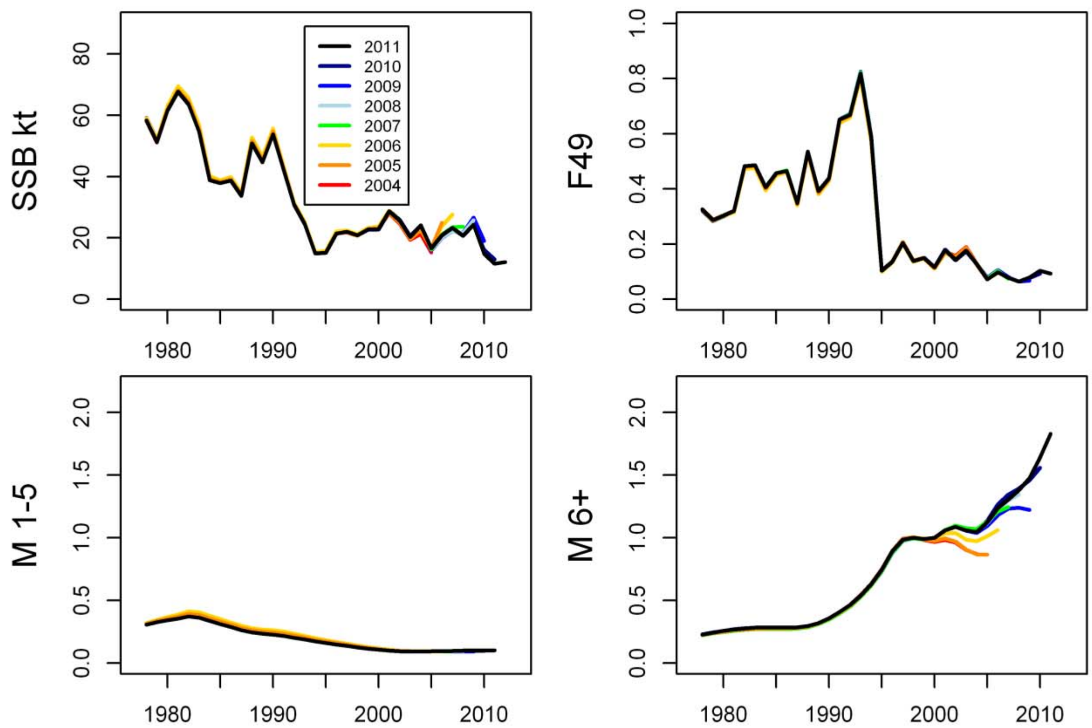

Figure 5. Retrospective patterns for Model 1.

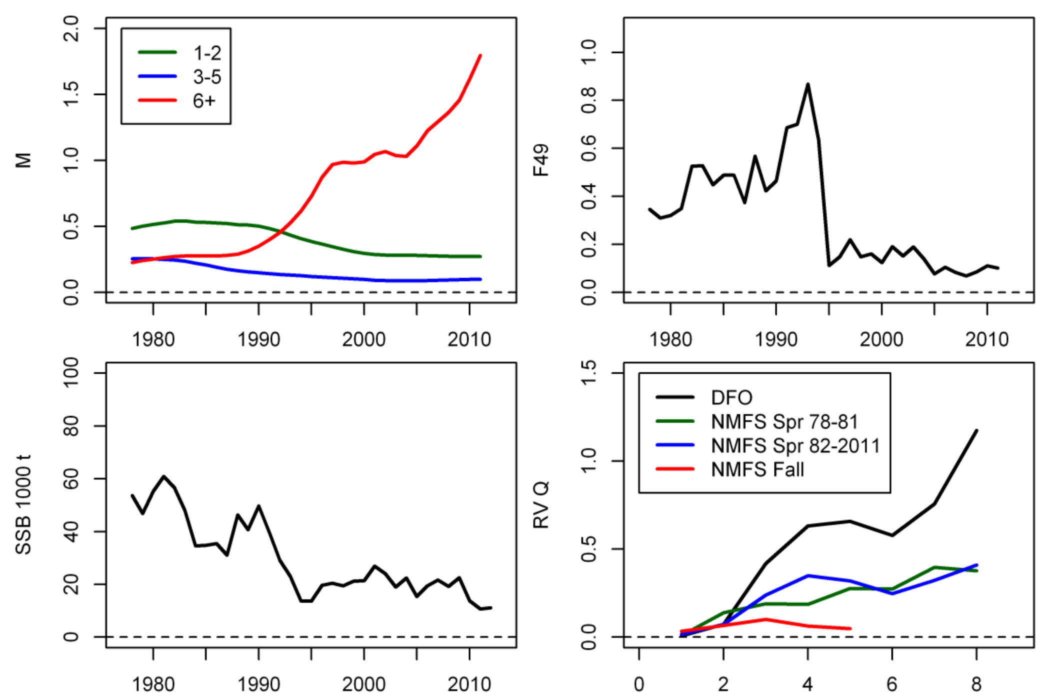

Figure 6. Estimates from Model 2.

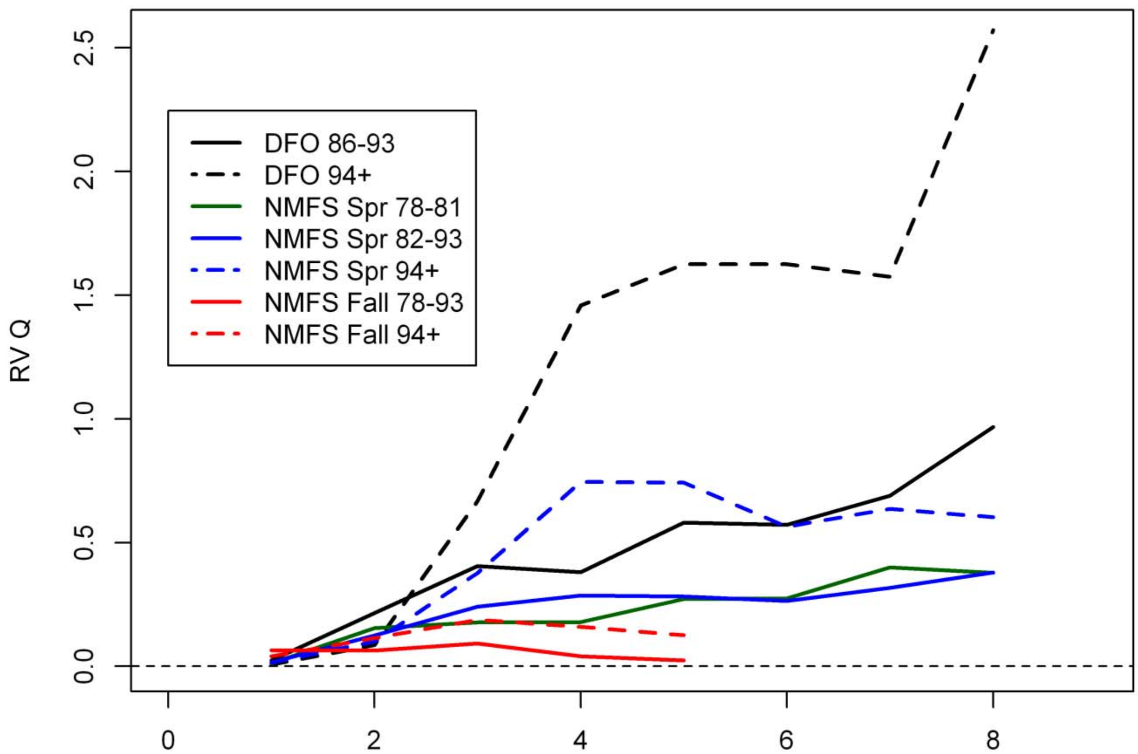

Figure 7. Estimates of survey catchabilities based on Model 3.

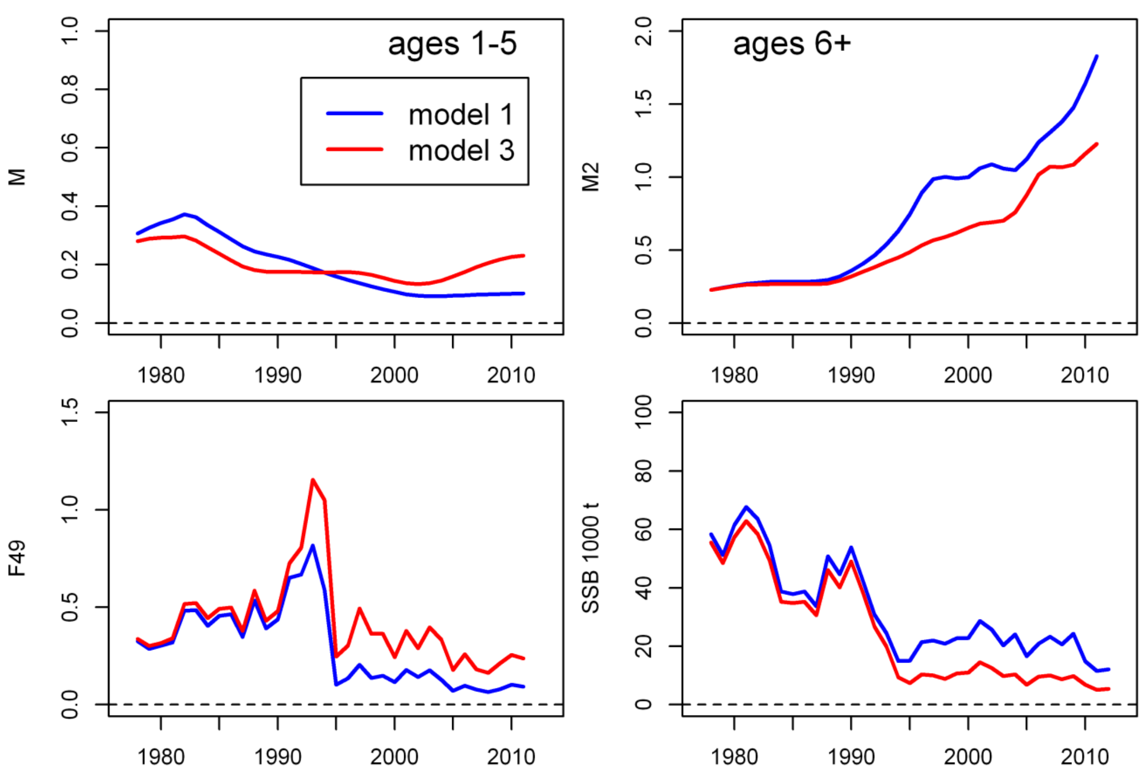

Figure 8. Comparison of estimates between Model 1 and Model 3.

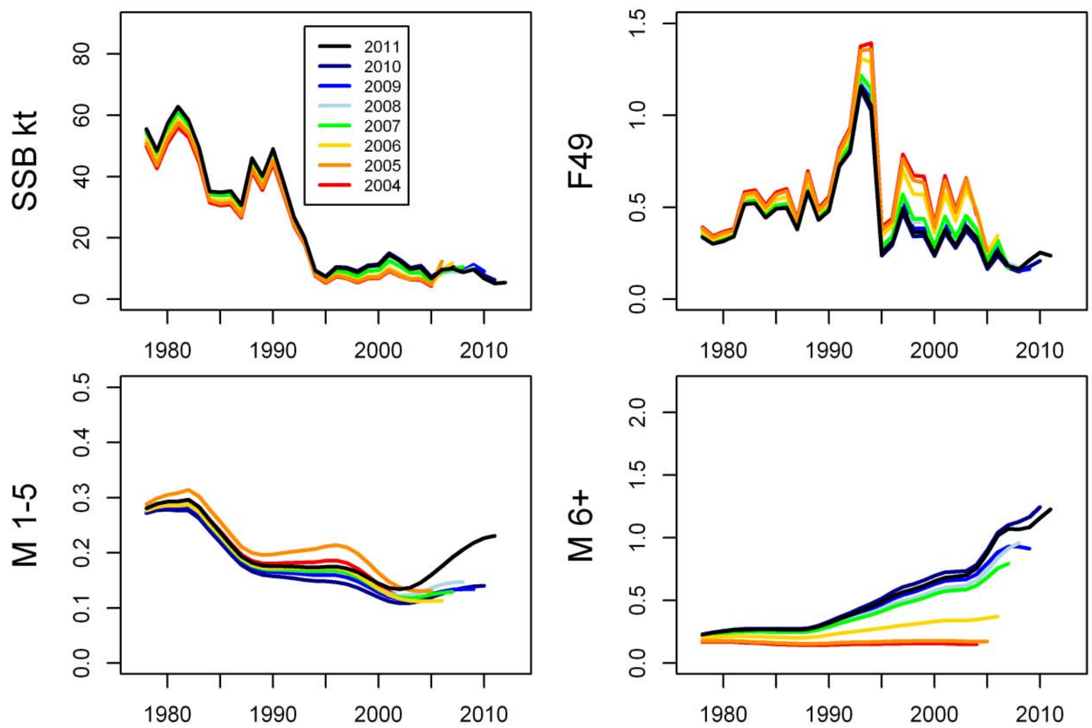

Figure 9. Retrospective patterns in Model 3.

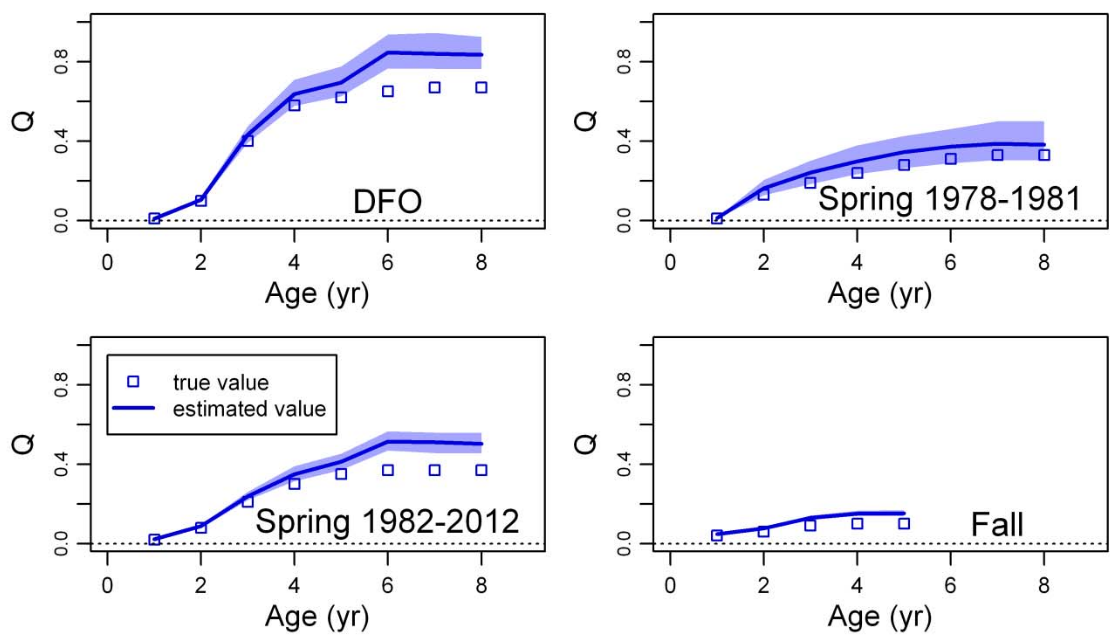

Figure 10. Simulation test of Model 1: estimated survey catchabilities (line and shading) compared to the true values in the simulated data (squares). Line gives the median estimate and shading covers the 2.5th to 97.5th percentiles of estimates from 200 simulations.

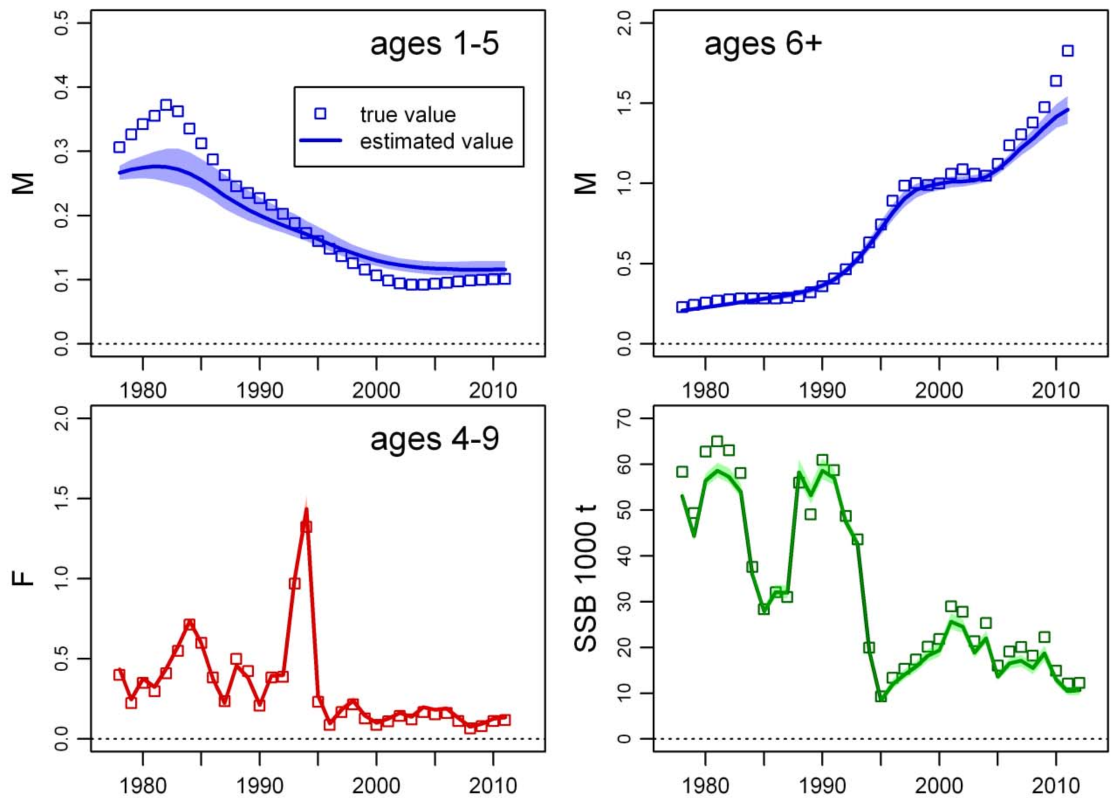

Figure 11. Simulation test of Model 1: estimated values of M, F and SSB (line and shading) compared to the true values in the simulated data (squares). Line gives the median estimate and shading covers the 2.5th to 97.5th percentiles of estimates from 200 simulations.