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Fluctuations and declines in fish populations in the context of species at risk

Fluctuation et déclin des populations de poisson dans le contexte des espèces en péril

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ABSTRACT

Fish populations fluctuate naturally but severe declines and collapses resulting from overfishing or other causes that are outside the normal range of variation can be cause for concern. In a species at risk context, it would be useful to be able to recognize when a decline is outside the bounds of natural fluctuation expected given the life history characteristics of the population. In this study decline criteria used by the Committee on the Status of Endangered Wildlife in Canada are reviewed. A population with the life-history characteristics of a circa 1960s northern cod is simulated to describe what might be considered natural fluctuations. Simulations include examining fluctuations in an unfished population, a population fished at F_{msy} and 2x F_{msy}, a population fished down to MSY and a population fished down to a very low level. Different population metrics and measures of decline are compared. Steepness in the stock-recruit function, age at first maturity and body growth rate are varied to determine the effect of these life history characteristics on natural population fluctuations. The effect of random and autocorrelated error around a Beverton-Holt stock-recruitment curve is examined. Some tentative conclusions are drawn regarding fluctuations and declines in a species at risk context for a population similar to that being modeled. While a 90% decline in spawner biomass over 15 years is probably cause for considerable concern irrespective of the initial size of the population, declines of 70 to 80% can more commonly occur under a variety of conditions, not all of which would be indicative of extinction risk. An alternative approach based on extent of decline is briefly considered.

RÉSUMÉ

Les populations de poisson fluctuent naturellement, mais un déclin sévère et l’effondrement résultant de surpêche ou d’autres causes, qui dépassent l’échelle de fluctuation normale peuvent être une source de préoccupation. Dans le contexte d’une espèce en péril, il serait utile de pouvoir reconnaître aisément une baisse qui va au-delà des limites de fluctuation naturelle prévues, compte tenu des caractéristiques biologiques de la population. Dans le cadre de cette étude, nous avons examiné les critères de déclin utilisés par le Comité sur la situation des espèces en péril au Canada. Une population ayant les caractéristiques biologiques de la morue du Nord autour des années 1960 a été simulée afin de déterminer ce que l’on pourrait considérer comme des fluctuations naturelles. Les simulations comprennent l’examen des fluctuations d’une population non exploitée, d’une population exploitée à F_{MSY} et à deux fois F_{MSY}, une population exploitée jusqu’au seuil de rendement équilibré maximal (MSY) et une population exploitée jusqu’à un très faible niveau. L’étude montre ensuite les résultats de la comparaison des données et des mesures de déclin des différentes populations. On a varié la raideur de la pente de la fonction stock-recrues, l’âge à la maturité et le taux de croissance corporelle en vue de déterminer les effets de ces caractéristiques biologiques sur les fluctuations naturelles de la population. L’effet de l’erreur aléatoire et autocorrélée autour d’une courbe stock-recrutement de Beverton-Holt est examiné. On tire des conclusions provisoires à propos des fluctuations et du déclin dans le contexte d’une espèce en péril, pour une population semblable à celle du modèle. Bien qu’une baisse de 90 % de la biomasse génitrice sur 15 ans puisse être une cause de grande préoccupation, quelle qu’ait été la taille initiale de la population, une diminution de 70 à 80 % peut survenir plus souvent dans diverses conditions, sans être nécessairement indicatrice d’un risque d’extinction. Une solution de rechange basée sur l’ampleur du déclin est brièvement examinée.

INTRODUCTION

Fish populations fluctuate naturally but severe declines and collapses resulting from overfishing or other factors that are outside the normal range of variation can be cause for concern. In a species at risk context, it would be useful to be able to recognize when a decline is outside the bounds of natural fluctuation expected given the life history characteristics of the population.

COSEWIC decline criteria
The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) uses quantitative decline criteria based on the IUCN Red List criteria (IUCN 2001) to guide the status assessment of species (COSEWIC 2003). These criteria do not take into account differences in life history characteristics among populations, except in terms of the calculation of generation time (and maturation processes if mature population is used instead of total population, see IUCN criteria below). Under the COSEWIC decline criteria a population is considered to be "Endangered" when one of the following apply: (1) ≥70% population size reduction that is observed, estimated, inferred, or suspected in the past 10 years or 3 generations, whichever is longer, where the causes of the reduction are clearly reversible and understood and ceased, based on (and specifying) any combination of (a) direct observation, (b) an index of abundance appropriate for the taxon, (c) a decline in area of occupancy, extent of occurrence and/or quality of habitat, (d) actual or potential levels of exploitation, and (e) the effects of introduced taxa, hybridisation, pathogens, pollutants, competitors or parasites; (2) ≥50% population size reduction that is observed, estimated, inferred or suspected over the last 10 years or 3 generations, whichever is longer, where the reduction or its causes may not have ceased or may not be understood or may not be reversible, based on (and specifying) any combination of a-e above; (3) population size reduction that is projected or suspected to be met within in the next 10 years or 3 generations, whichever is longer (up to a maximum of 100 years), based on (and specifying) any combination of b-e above; (4) population size reduction that is observed, estimated, inferred, projected or suspected over any 10 year or 3 generation period, whichever is longer (up to a maximum of 100 years), where the time period includes both the past and the future, and where the reduction or its causes may not have ceased or may not be understood or may not be reversible, based on (and specifying) any of a-e above. The declines associated with a "Threatened" classification under (1) and (2) are ≥50% and ≥30% respectively. While overfishing is the predominant cause of severe decline in many fish populations, the interplay between fishing and other factors in the collapses of populations is not always clear so that at least some cases may fall under (2) in which a decline of ≥50% would lead to an "endangered" classification under these criteria.

IUCN decline criteria

The IUCN Red List Categories and Criteria Version 3.1 (2001) prepared by the IUCN Species Survival Commission (http://www.redlist.org/info/categories_criteria2001.html) notes that the criteria do not take into account the life histories of every species. Hence, in certain individual cases, the risk of extinction may be under- or over-estimated. For functional reasons, primarily owing to differences between life forms, population size is normally measured as numbers of mature individuals only under the IUCN criteria. The IUCN criteria note that a reduction should not be interpreted as part of a fluctuation unless there is good evidence for this, and that a downward phase of a fluctuation will not normally count as a reduction. Recognizing the distinction between a fluctuation and a decline is important. Under the IUCN criteria, a continuing decline is a recent, current or projected future decline (which may be smooth, irregular or sporadic) which is liable to continue unless remedial measures are taken. Fluctuations will not normally count as continuing declines, but IUCN considers that an observed decline should not be considered as a fluctuation unless there is evidence for this. The IUCN criteria take note of the fact that extreme fluctuations can occur in some taxa where population size varies widely, rapidly and frequently, typically with a variation greater than one order of magnitude (i.e. a tenfold increase or decrease). The IUCN criteria consider 3 scenarios with respect to declines: (i) a population size reduction over the last 10 years or three generations, whichever is the longer, where the causes of the reduction are clearly reversible AND understood AND ceased; (ii) a population size reduction projected or suspected to be met within the next 10 years or three generations, whichever is the longer; (iii) population size reduction over any 10 year or three generation period, whichever is longer where the time period must include both the past and the future, and where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible. Under scenario (i) “critically endangered” is associated with a ≥90% decline, “endangered” with a ≥70% decline and “vulnerable” with a ≥50% decline. Under both scenarios (ii) and (iii) the respective declines are ≥80%, ≥50% and ≥30% for the three risk categories.

CITES decline criteria

CITES applies decline criteria in its efforts to ensure that international trade in specimens of wild animals and plants does not threaten their survival. Under Resolution Conf. 9.24 (Rev. CoP12) (http://www.cites.org/eng/res/09/09-24.shtml), Annex 1, Biological criteria for Appendix I, a species is considered to be threatened with extinction if, amongst other criteria, the wild population is small, and is characterized by an observed, inferred or projected decline in the number of individuals, or there has been decline in the number of individuals in the wild, which has been either observed as ongoing or as having occurred in the past (with a potential to resume). CITES defines a decline as a reduction in the number of individuals, or a decrease of the area of distribution, the causes of which are either not known or not adequately controlled. It need not necessarily still be continuing. Natural fluctuations will not normally count as part of a decline under CITES, but an observed decline should not be considered part of a natural fluctuation unless there is evidence for this. A decline that is the result of a harvesting program that reduces the population to a planned level, not detrimental to the survival of the species, is not identified as a 'decline' under CITES. For some species in trade where data exist to make an estimate, a decrease of 50% or more in total within 5 years or two generations, whichever is the longer, has been found to be an appropriate guideline (not a threshold) of what constitutes a decline. CITES considers these decline rates as examples, since they believe it is impossible to give numerical values that are applicable to all taxa. CITES considers that there will be many cases where these numerical guidelines do not apply and they are engaged in ongoing review of decline and other criteria.

FAO Consultations on decline criteria

FAO hosted a Meeting of the FAO *ad hoc* Expert Group on Listing Criteria for Marine Species Under CITES in Cape Town in 1998 (http://www.cites.org/eng/com/SC/41/E41-19-1.pdf). This led to two technical consultations on the suitability of the CITES criteria listing commercially exploited aquatic species; the first in Rome in 2000 (http://www.fao.org/docrep/meeting/x4894e.htm) and the second in Windhoek, Namibia in 2001 (http://www.fao.org/docrep/meeting/003/Y1455E.htm). In the first consultation it was noted that the decline criteria present both conceptual and practical problems for applications to harvested marine species. The conceptual concern was that the decline criterion may cause many false alarms. Many marine species may have experienced declines sufficiently large to prompt listing although the population remains so large that there is negligible risk of biological extinction. The Consultation considered that listing such species could cause unnecessary social and economic disruption and would weaken the moral force of CITES' listing of those species which are truly at risk of extinction. The Consultation suggested that two practical concerns will often make implementation of the decline criterion difficult and controversial for exploited marine species (i) inconclusive scientific evidence about causes of a decline would invite debate about whether a decline is a "natural" fluctuation; (ii) species' survivorship schedules and the potential fecundity of spawners must be considered to interpret what a decline of any percentage means for a species' viability.

In the second FAO Consultation it was concluded that the most important property of a species or population, in relation to the risk of extinction, is its resilience, which is best reflected by the productivity of the species – more productive species being more resilient. Of the various CITES criteria, the decline criterion was considered to be the one most likely to be applied to exploited fish populations. The Consultation distinguished between the overall long-term historical extent of decline and recent rate of decline, drawing on a NMFS/Interagency Working Group report (see below). They considered that the time-frame for assessing the historical extent of decline should be as along as possible, not the standard three generations. The reference base-line against which the historical extent of decline should be measured is typically derived from the carrying capacity at some point in the history. In analysis of 111 spawner biomass – recruit data sets, the Consultation used the average of the four largest spawner biomass values and the average of the four corresponding recruitments as baselines. They found that in 70% of the stocks the spawner biomass had dropped below 30% of the baseline. They found that spawning biomass must drop to a least 15% of the base line for nearly all stocks before recruitment drops noticeably and consistently to very low values (four year averages below 20% of the recruitment baseline). There was only one stock for which the rule appeared to definitely not hold (a gadoid stock). The Consultation concluded that listing under Appendix I should occur if historical extent of decline is 90-95% in high productivity species and 80-85% in medium productivity species.

The Consultation suggested that the cumulative annual rate of decline that would drive the population down to the historical extent of decline reference levels (upper limit of the ranges, i.e. 20% of the baseline for low productivity populations, 15% for medium productivity populations and 10% for high productivity populations) in the near future (10 years) would be a criterion for Appendix II listing (species that are not necessarily now threatened with extinction but that may become so unless trade is closely controlled). The Consultation felt that in general the historical extent of decline should be at least 50% of the baseline before considering a species for listing using the annual rate of decline approach. The Consultation considered uncertainty in the estimated extent of decline and rate of decline and suggested the use of a 5% buffer zone on the extent of decline reference level. For a species above the extent of decline reference level, the risk of falling below extent of decline reference level could also be used. De-listing from Appendix II could occur when this risk became negligible. The Consultation suggested that under the Precautionary Approach, the transfer of a population from Appendix I to Appendix II should only occur once the population had reached a higher level than the extent of decline level that had led to the listing under Appendix I.

Under “modifying factors” the Consultation noted that various factors may increase or decrease the risk of extinction in species and may necessitate appropriate modification of the historical extent of decline and annual rate of decline reference levels. These factors need to be considered on a case-by-case basis and may include life history (e.g. growth rate, age at first maturity).

NMFS/Interagency Working Group

An NMFS/Interagency Working Group reported on an evaluation of CITES criteria and guidelines in 2002 (Mace *et al*. 2002). Note that this work fed into the second FAO consultation reviewed above. The WG concluded that the historical extent of decline should be the ultimate criterion for triggering concern about the long-term viability of a species. The timeframe for evaluating historical extent of decline should be as long as possible, regardless of the mean generation time of the species, to enable a meaningful baseline to be chosen. Declines of 5-30% of historical or potential levels should trigger concern regarding long-term viability of the species, depending on the productivity (5% for high productivity species and

30% for low productivity species. The baseline may relate to some point in history, or may be modified to take into account changes in the environment that have affected current carrying capacity. The WG recommended that recent (5-10 year average) rates of decline should be considered in combination with historical extents of decline. They suggested that threshold recent rates of decline should be defined as the cumulative annual rate of decline that would drive a population down from its current level to the threshold extent of decline in the near future (e.g. 10 years). Appendix I of the report provides a useful examination of the relationship between threshold extent of decline, resilience and productivity, and provides the justification for the 5-30% range of historical extent of decline thresholds.

Other studies

Musick (1999) provided a discussion of criteria used to define extinction risk in marine fish based on discussions within the American Fisheries Association and elsewhere. He suggests that the IUCN decline criteria (earlier version of IUCN criteria than those reviewed above) for critically endangered (80%), endangered (50%) and vulnerable (20%), while effective at flagging rapid population change in the short term, grossly overestimate the extinction risk of many if not most marine fish. He noted that a 50% reduction from total (all ages) virgin biomass is thought to lead to MSY in many fisheries and that many management plans call for spawning biomass targets of 20-30% virgin biomass of mature individuals (i.e. 70-80% decline). He noted that interannual natural fluctuations of fish towards the "*r*-selected" end of the spectrum may approach two orders of magnitude, making it difficult to distinguish anthropogenic effects from natural fluctuations. He suggested that the IUCN decline criteria are appropriate primarily for strongly *K*-selected species. He presented a productivity/resilience categorization based on *r* (intrinsic rate of natural increase), *K* (von Bertalanffy growth parameter), *Fec* (fecundity at first maturity), *Tmat* (age at first maturity) and *Tmax* (oldest age). From these characteristics, four productivity/resilience categories were derived: high, medium, low and very low. The decline thresholds measured in numbers or biomass of mature individuals he assigned were 0.99, 0.95, 0.85 and 0.70 respectively.

In a series of papers with a common theme, Hutchings (2000, 2001a, 2001b, 2003) and Hutchings and Reynolds (2004) looked at declines, collapses and recoveries in marine fish populations. Hutchings (2000) found very little evidence of recovery from prolonged declines in contrast to the perception that marine fish are highly resilient to large population reductions. Note "resilience" is generally defined as the "ability to rebound after perturbation" (Holling 1973). As examples, he found that many gadoids and flatfish had experienced little, if any, recovery 15 years after 45-99% reductions in reproductive biomass. Mace (2004) has outlined three major problems with Hutchings (2000) conclusion: (i) no allowance made for the extent of depletion at the start of the 15 year period over which he computed maximum decline; (ii) no regard to whether fishing mortality had in fact been sufficiently reduced to rebuild the population; (iii) no updating of the data base used in the analysis since the early 1990s.

Hutchings' (2000) finding that the magnitude of the decline negatively influenced population recovery may be partly spurious. He measured decline as

$$\text{Decline} = 1 - \frac{N_{15}}{N_0},$$

and recovery as

$$\text{Recovery} = \frac{N_{t+15}}{N_0}.$$

Thus, if N_0 is large then Decline will be large and Recovery will be small. Using these measures, the larger the decline, the longer the population will take to recover. The purported relationship between Recovery and Decline is illustrated for the base population (northern cod *circa* 1960s) described below, modeled with an underlying Beverton-Holt stock recruit mode with $\sigma = 0.8$ (random lognormal variation). This population was subject to episodes of fishing and no fishing by means of the following code:

```
if year <= 30 then f=0.01*year;
else f=0;
if year > 60 then f=0.01*(year-60);
if year > 80 then f=0;
```

to generate declines and recoveries. Examples of the resulting 100 year timeseries are illustrated in Fig. 1. This was repeated 100 times (i.e. 100 repeats of 100 years) and all 15 year declines >0 and associated 5 year recoveries were plotted (Fig. 2). The negative linear relationship between decline and recovery was highly significant (p <0.0001).

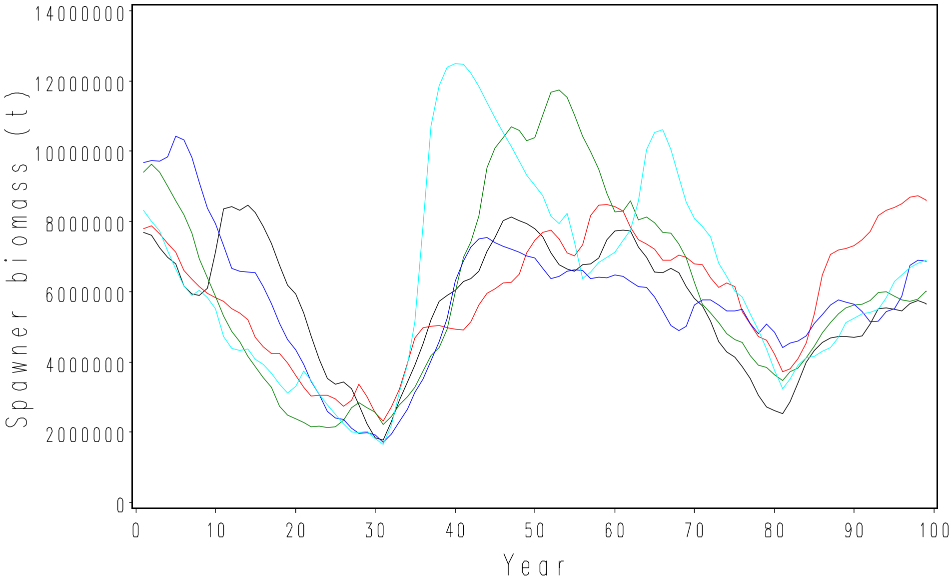


Fig. 1. Five example timeseries of spawner biomass for the modeled cod population subject to bouts of fishing and moratorium.

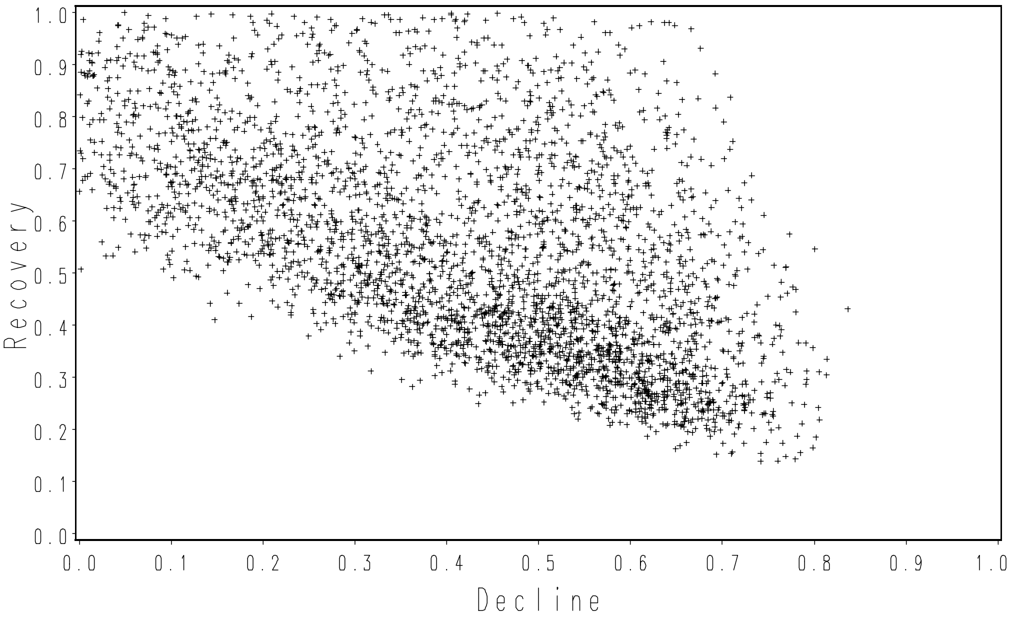


Fig. 2. Relationship between decline and recovery 5 years later demonstrating the spurious negative relationship.

This purported relationship between degree of decline and subsequent recovery is the basis for Hutchings' (2000) argument that it would be inconsistent with a precautionary approach and conservation of marine biodiversity to suggest that marine fishes should be exempt from the existing quantitative criteria used to assign extinction risk. Species that continue in a collapsed state can be argued to have a higher probability of extinction. In addition there are the negative aspects of lack of recovery in terms of ecosystem functioning and societal benefits. In reality, it should be noted that although a number of commercially exploited fish stocks have collapsed to very low levels as a consequence of severe overfishing, there have been no actual biological extinctions of these species in Canadian waters, suggesting that persistence facilitated by some means, such as natural refugia from fishing activity, may be at play in marine habitats.

Hutchings (2001a) expanded on issues raised in Hutchings (2000). The emphasis is on the comparison of marine fish with anadramous fish species. He is dismissive of the observation that part of the decline in fished populations may be managed reduction from B_0 down to B_{msy}, and therefore not indicative of increased risk of extinction. He argues that this point moot because for most stocks the time series do not include estimates of B_0 and therefore it is largely an unknown. In practice, MSY, B_{msy}, F_{msy} and B_0 are generally estimated by fitting a model, rather than from direct observations over the limited number of years for which data are available. These models are typically age-aggregated production models (e.g. Schaefer) and age-disaggregated models involving estimation of a spawning stock – recruit function. Estimates of B_0 from these models may have large variance and bias in some instances, whereas in other cases may provide reasonable estimates of the initial size of the population before exploitation against which current population size can be compared. $\%B_0$ has long been considered as a potential biological reference point, e.g. 20% B_0 (Beddington and Cooke 1983). New Zealand orange roughy is estimated to have a B_{msy} about 30% of B_0, so that a decline of 70% in this population would not be an appropriate trigger for highlighting concern about risk of extinction if the decline occurred during the initial fishing-down phase of exploitation (Mace *et al.* 2002).

Hutchings (2001a) appropriately challenges the notion that marine fish are more resilient than other taxa (e.g. Musick 1999, Powles *et al.* 2000). Although fish have high fecundity this does not necessarily translate into higher maximum reproductive rates (Dulvy *et al*. 2003). The high fecundity in fish is primarily a risk-spreading - bet-hedging strategy aimed at maximizing geometric mean *r* (intrinsic rate of natural increase) in a highly varying and unpredictable environment (e.g. Armstrong and Shelton 1990, Shelton 1992). Maximum reproductive rates (e.g. recruits per spawner) and the intrinsic rate of natural increase *r* for a range of marine fish species are not that different from various other animals. Clearly life-history strategy plays a major role in resilience, persistence, population recovery rate and extinction probability under different conditions such as heavy exploitation, habitat destruction *etc*., however there does not appear to be an *a priori* reason for treating marine fish any differently from other animals. In contrast, Powles *et al*. (2000) have suggested that marine species have characteristics which should make them more resilient to extinction risk, including something they call “opportunistic” life history characteristics (high fecundity, planktonic larvae, highly mobile adults, low age at maturity) and other characteristics such as high abundance and wide distribution. Similarly, Musick (1999) included fecundity along with other population characteristics (*r*, von Bertalanffy *K*, age at first maturity and terminal age) as factors to be used in determining into which of 4 productivity/resilience categories a population falls, and the associated decline thresholds consistent with a classification of “vulnerable”. Note that “steepness” in the stock-recruit relationship (Mace and Doonan 1988) combines some of these life history characteristics into a single measure related to resilience in the examination of overfishing thresholds. Results from these analyses could be considered in the species at risk context.

The role of ongoing fishing mortality on post-collapse stocks, either from small directed fisheries for social reasons, bycatch or illegal fishing, needs to be given more emphasis as a possible explanation for the apparent lack of resilience (lack of recovery) in some stocks, particularly Atlantic groundfish. It is touched on in Hutchings (2000) and given slightly more attention in Hutchings (2001a). It may, however, be the major cause for lack of recovery of northern cod, southern Grand Bank cod, Grand Bank American Plaice, northern Gulf cod and southern Gulf cod stocks. Analyses in support of this view are presented in Shelton and Morgan (2005) for southern Grand Bank cod and Grand Bank American plaice and in Shelton *et al*. (2006) for northwest Atlantic cod stocks in general.

Hutchings (2001b) attempts to address purported criticism of previous studies: that the effects of fishing on recovery were not accounted for; that the spawner biomass benchmark (N_0) was too “stringent”; and that there was no attempt to account for the large amount of variability in marine fish and the effect this may have on resilience. He correctly notes that even after stock declines of >90%, fishing mortality may continue to be >0 as a consequence of small quotas, discarding, bycatch and illegal fishing. However, he found no association between the magnitude of post-collapse fishing mortality and stock recovery 5, 10 and 15 years after collapse, even for those stocks where fishing mortality declined following collapse. He did however find a weak (non-significant) difference in average recovery after 5 years between stocks with decreased fishing mortality (greater recovery) compared to those stocks where fishing mortality remained the same or increased. He concluded that although stock recovery almost certainly depends on a reduction in fishing mortality, recovery appears to be independent of the magnitude of this reduction. He considers that a possible weakness in the analysis of the effect of post-moratorium fishing mortality in his study may be that the post-moratorium reductions in fishing mortality may have been to a level that was still in excess of what the population can sustain, which he explains as $F > r$ in his notation.

This idea is worth pursing further. In general, under common assumptions in fish production models and population models incorporating a compensatory stock-recruit function, if a level of F (fully recruited instantaneous rate of fishing mortality) drives a population down, and F is then reduced to a lower level, the population will increase to an equilibrium size consistent with the new level of F (all else being equal). If the reduction in F is small, the population increase will also be small. If a particular level of F is unsustainable, the population will decrease until it reaches an equilibrium level where this level of F becomes sustainable (as a consequence of compensatory population processes). If the level of F is above a threshold (F_{crash}, in ICES 1997 F_{T} in Mace 1994) the population will collapse to zero. For stock recovery to be independent of the magnitude of the reduction in F, there would either have to be some kind of depensatory stock-recruit process going on (see for example Myers *et al*. 1995, Lierman and Hilborn 1997, Shelton and Healey 1999) or changes in other processes related to stock productivity, such as increased natural mortality rate, or decreased body growth rate (some of these processes have been inferred in the lack of recovery of Atlantic cod stocks, see Rice *et al*. 2003, Shelton *et al*. 2006). For stocks at low population size, it is likely that there is a large variance associated with the estimate of both F and N, so that it may take a number of years of reduced fishing before a positive population response becomes clear in the data. For three collapsed Atlantic cod stocks on which fisheries re-opened prematurely in the late 1990s after brief moratoria, there may have been some small increases in population size over the moratoria (during which fishing mortality was reduced but not eliminated), but these increases were rapidly nullified when small but unsustainable fisheries reopened after only a few years (Rice *et al*. 2003, Shelton *et al*. 2006). Thus there was only limited empirical testing of the ability of these populations to recover under reduced fishing mortality. Note that it is extremely difficult to monitor fishing mortality associated with small

TACs <10,000 tons using systems designed for monitoring and controlling TACs of the order of hundreds of thousands of tons.

In considering the purported criticism that a benchmark of N_0 (the population size at the start of the maximum 15 year decline) is too stringent, Hutchings (2001b) argued that because the stocks had been fished for a period of time, N_0 in his calculations (population size at the start of the largest 15 year decline) would likely be much less than the virgin population size. In fact he found that N_0 was 81.4% of $N_{\max}$ (highest population size in the timeseries) for the 90 stocks examined. It therefore appears that the commencement of the biggest 15 year decline is generally associated with relatively large population size. Since Hutchings measure is a point to point estimate of the biggest 15 year decline, peak to trough would be expected to account for most of the declines. The start and end of the decline would be offset from the peak and trough depending on where the greatest 15 year decline would be obtained, but it would be expected to be in close proximity, i.e. consistent with the 81% of $N_{\max}$ that he found. In addition to consideration of the effect of fishing on post-collapse recovery and the defense of his metrics of decline and recovery based on N_0, Hutchings (2001b) also addressed the issue of whether greater variability in marine fish implies greater reliance and more rapid recovery following collapse, an argument put forward in Musick (1999) and Powles *et al.* (2000). He compared the ratio $N_{\min}/N_{\max}$ for fish and found that, with the exception of clupeids, the variation in marine fish is not greater than that found in birds and mammals. For marine fish, he found a negative correlation between this ratio and recovery 5 years post collapse (defining recovery as N_{t+5}/N_0) – a similar result to that obtained when he compared his measures of collapse against recovery.

Hutchings (2003) re-examined the possible relationship between rate of population decline and the effect of fishing mortality on the probability of recovery. He confirmed his finding that rate of decline is highly informative regarding recovery and that this also holds for populations in which fishing mortality decreased after the population declined. He concluded that, although recovery is greater for populations in which fishing mortality decreased after the decline, the magnitude of the recovery is independent of the magnitude of the reduction in fishing mortality, even when corrected for population specific estimates of the intrinsic rate of natural increase, r. Hutchings and Reynolds (2004) is the most recent of the 5 papers with the common theme of decline-collapse-recovery-extinction risk, consolidating much of the work from the previous papers.

Powles *et al*. (2000) stressed that “conservative” life-history characteristics such as late maturation, low fecundity, low mobility as young or adults, combined with high vulnerability to trawling from an early age, will increase the vulnerability of a population to extinction. Conversely, “opportunistic” life-history characteristics that would make species resilient to extinction risk include high fecundity, planktonic larvae, highly mobile adults and low age at maturation. They noted that declines and increases of up to 10-fold are relatively common in exploited fish stocks, and that while often associated with harvesting, also occur naturally. In drawing an analogy with the assessment of stock status, they suggested that consideration of a wide range of biological indicators and of data on all aspects of species status is necessary to assess extinction risk. They suggested that exiting CITES and IUCN criteria could be modified in a number of ways, including comparing rates of decline with natural fluctuations in abundance, and rather than comparing these to fixed thresholds for all species, using different rates of decline for different groups of species (as in Musick 1999). They consider "endangerment" in the context of the precautionary approach which triggers pre-agreed conservation action when stocks or species reach stated biological reference points. They conclude that the precautionary approach could be a powerful tool for preventing species from becoming endangered. However, it should be noted that the precautionary approach has yet to be implemented with respect to management of Canadian fisheries and current fisheries management practices may not be effective in a species at risk context.

Punt (2000) carried out a demographic analysis of extinction of marine renewable resources using a simple deterministic population dynamics model. He found that F_{crash} is greatest for highly productive species and that $F_{\text{crash}} / F_{\text{msy}}$ is a decreasing function of the productivity of the population, contradicting the results of Mace (1994; see Mace *et al*. 2002 which points out an inconsistency between the text and tables in Punt's study). He found that depensation has little impact on F_{msy} but can substantially reduce the ratio $F_{\text{crash}} / F_{\text{msy}}$. In addition he carried out a stochastic analysis of three generations/10 years declines in population size of 20%, 50% and 80% (earlier IUCN thresholds for vulnerable, endangered and critically endangered respectively) to evaluate the "power" of these criteria to assess extinction risk. The simulations involved projecting a population from its pre-exploitation level under a range of constant fishing mortality rates for 500 years. Under the earlier IUCN criteria, vulnerable was considered to be roughly consistent with a 10% probability of extinction within 100 years, endangered => 20% and critically endangered => 50% probability. He used the operational definition of extinction of 1/1000 of the initial size, and suggested that this reflected a level at which "critical" depensation might occur. He considered a range of life-history characteristics expressed in 6 species. This covered a range in steepness from 0.37 to 0.9, MSYR (ratio of MSY to B_{msy}) from 0.03 to 5.97 and σ (characterizing the variation in births) of 0.1 to 1. Results were evaluated for generations 1-3 and 7-9 (i.e. commencement of fishing and later on) for F_{msy}, F_{50R} (fishing mortality corresponding to an equilibrium SSB that is half the SSB corresponding to maximum recruitment) and 1.5 F_{crash} strategies. Based on the results, he concluded that there are substantial probabilities of incorrectly identifying species being harvested at F_{msy} as being threatened during the fishing down phase and also of not identifying species actually at risk of extinction if fishing mortality is not reduced, when applying the IUCN decline criteria.

Dulvy *et al*. (2003) also examined extinction vulnerability in marine populations, but used an empirical approach. They compiled a list of 133 local, regional and global extinctions of marine populations. Exploitation was the major cause, followed closely by habitat loss. They suggested that marine species should not be considered less vulnerable on the basis of their biological attributes such as high fecundity or large-scale dispersal characteristics. They found evidence to suggest that fish populations do not fluctuate more than those of mammals, birds or butterflies and that fish exhibit extinction vulnerability similar to these other species. They suggested that for high valued species or non-target species caught in multispecies fisheries, economic extinction did not necessarily occur before biological extinction. They argued that the perceived high potential for recovery, high variability and low extinction vulnerability invoked for marine fish needs to be considered in the context of depensation effects, ecosystem shifts and the spatial dynamics and connectivity of subpopulations before the nature of responses to severe depletions can be fully understood.

Depensation

A number of the decline criteria studies refer to the importance of depensatory processes in relation to the risk of population extinction. As pointed out by Butterworth (2000) and a number of preceding authors, the existence of some threshold population level below which a species will go extinct, even in the absence of human intervention, requires that it's population dynamics exhibit depensation. Depensation is said to occur when reproductive rate (e.g. recruits per spawner) decreases with decreasing population size over some range of population size (i.e. contrary to the expected standard compensatory process in which reproductive success increases continually with decreasing population size). Depensation can cause a second, lower, population equilibrium to exist. This equilibrium point, however, is unstable; any variation in recruitment or spawning stock biomass will cause the population to either grow towards an upper, stable equilibrium level (determined by compensatory processes and mortality rate) or to collapse to zero. Existence of depensation could therefore imply quite rapid extinction but would not necessarily explain prolonged lack of recovery (although reduced reproductive rate above the unstable equilibrium, while greater than that required for replacement, might still be lower than in a population without depensation, and this would slow recovery) . A more complicated form of depensation, typified by the "predator-pit" phenomenon, in which a reproductive rate increases again at even lower population size, results in a stable lower equilibrium which would be consistent with prolonged lack of recovery (see Walters 1986, p83). Depensation is very difficult to detect in most stock-recruit data sets (Shelton and Healey 1999). Liermann and Hilborn (1997), using a Bayesian approach of hierarchical modeling, found that for all taxa they examined, the most likely values for the depensation parameter fell close to or within the range of no depensation. However, because the distributions were very broad, they suggested that analysis of stock recruitment data should incorporate spawner–recruit curves that include the possibility of depensation. Depensation is clearly of considerable concern in terms of risk of species extinction. It is likely to occur at quite low population sizes where Allee effects, such as difficulty in finding a mate, occur – although clearly mating behavior of species such as cod, which appears to be dependent on the formation of aggregations of spawners, needs to be taken into consideration – cod may still number in the hundreds of thousands, but if effective spawning aggregations are no longer forming or spawning behavior is severely disrupted, depensation may be effected. Predator-pit processes, for which there may be some evidence in northern cod in the context of harp seal predation (Shelton and Healey 1999), would be difficult to predict given its dependence on predator abundance and the relative abundance and "suitability" of alternative prey. In any event, clearly keeping a population above some very low level, and the ability to rapidly reduce fishing mortality to near-zero as population size decreases (resulting in "shallower" depensation), would be very important considerations in the context of depensation and species at risk. In addition to biological processes, it is quite possible that the behaviors of some fishing fleets could precipitate an anthropogenic form of the "predator pit" phenomenon. Valued populations that are driven to low levels but which continue to be fished as bycatch in other ongoing fisheries could be prevented from recovering (see for example Shelton and Morgan 2005; Shelton *et al.* 2006).

Brief summary of literature

While it is not possible to provide a comprehensive synthesis of decline criteria in the context of species at risk without a more thorough evaluation of the published literature, a number of tentative points can be made:

(i) marine fish have reproductive rates and intrinsic rates of population increase that are not dissimilar to those of a number of other species;

(ii) with the exception of clupeiods, the variation in marine fish population size falls within the range of a number of other species;

(iii) the historical extent of decline from the unexploited state is important in determining extinction risk – the level of B_{msy} may result in some existing decline criteria being triggered during a fishing-down phase associated with initial exploitation, which would be inconsistent with a high risk of extinction;

(iv) recent rates of decline need to be viewed in the context of the overall historic extent of decline – a recent 80% decline in a population being supposedly managed at B_{msy} would pose much greater concern than a similar decline from the unfished state;

(v) populations fluctuate naturally and these fluctuations need to be distinguished from declines that are outside the range of normal fluctuations;

(vi) life-history characteristics are important considerations in determining the potential risk of extinction in the context of population declines – these should be evaluated on a case by case basis;

(vii) lack of recovery following a large decline is a serious concern, not only in terms of risk of extinction but also in ecological and societal terms;

(viii) the ability of populations to recover from large declines is not well understood and the reality that F can seldom be reduced completely to zero is a complicating factor – even a small amount of removals from a small population can result in a high F and slow or prevent recovery;

(ix) extinction risk is strongly linked to depensation – an as yet poorly understood phenomenon which is hard to detect and even harder to predict – keeping populations above some historic extent of decline threshold and the ability to rapidly reduce F on a declining population are key to minimizing the risk of entering the depensation zone.

This study

In this study a population with the life-history characteristics of a *circa* 1960s northern cod is simulated to describe what might be considered natural fluctuations. Simulations include examining fluctuations in an unfished population, a population fished at F_{msy} and 2x F_{msy}, a population fished down to MSY and a population fished down to a very low level. Different population metrics and measures of decline are compared. Steepness, age at first maturity and body growth rate are varied to determine the effect on natural fluctuations. Some tentative conclusions are drawn regarding fluctuations and declines in a species at risk context.

Methods

Base population model

The population characteristics of northern cod circa 1960s as given in a recent stock assessment (Lilly *et al*. 2003) was used for a base population. The characteristics are listed in Table 1.

Table 1. Characteristics of the base population model.

Process	Parameter	Value
Natural mortality	M	0.2
Growth	Linf	153.534
	Lo	7.940
	K	0.0540
Length weight	a	6.15744E-06
	b	3.088
Maturation	u	-15.596
	v	2.485
Stock-recruit	alpha	4
	K	300000
	Steepness	0.838
Population-fishery		
SSBo		5916474.6
r		0.265
Bo		6908451.1
Fmsy		0.23
SSBmsy		1520168.6
Bmsy		2338731.2
SSBmsy/SSBo		0.257
Bmsy/Bo		0.339
No 1+		5123667.1
Maximum age		25
Partial recruitment		Average 1962-66

Growth in length was modeled using the von Bertalanffy equation, $L_t = L_\infty - (L_\infty - L_0)\ e^{-kt}$, and weight was modeled as function of length by $W = aL^b$. The predicted values based on Table 1 are plotted in Fig. 3.

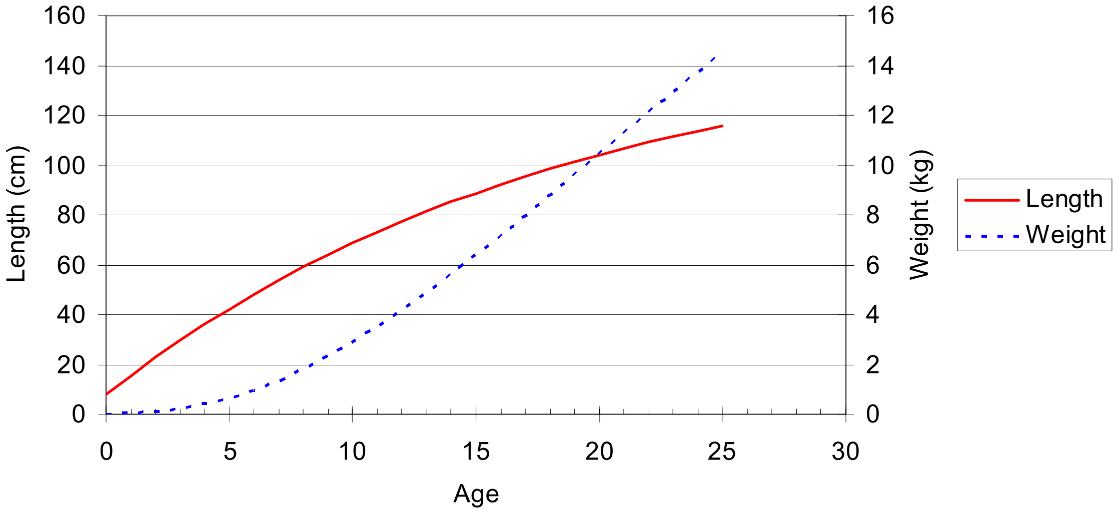


Fig. 3. Predicted values of length and weight at age for base population model.

The proportion mature at age a, P_a was modeled by $P_a = 1/(1+e^{(-(u+v*age))})$ for the base population. The plot of proportion mature against age is given in Fig. 4.

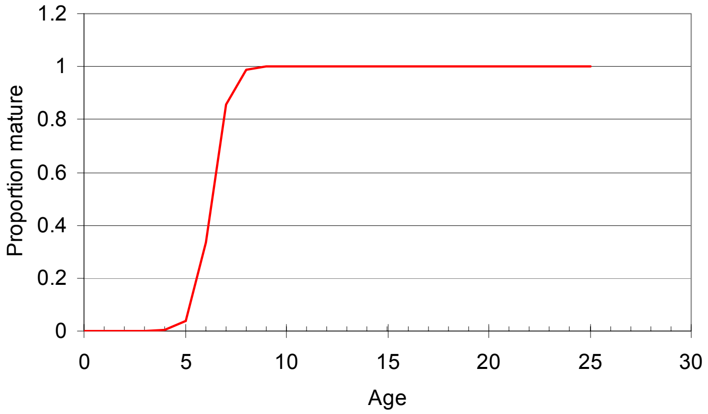


Fig. 4. Proportion mature at age for the base population.

Recruitment (R) was modeled as a function of spawner stock (S) size by applying a Beverton-Holt model where

$$R = \frac{\alpha S}{(1+\frac{S}{K})}.$$

Parameters were chosen to give a steepness of 0.84 (ratio of *R* at 20%B_0 to *R* at $B_{0;}$ Mace and Doonan 1988) to be consistent with the mean steepness for 21 *Gadus morhua* stocks (Myers *et al.* 1999), and to be approximately consistent with the estimate of *r* for northern cod of 0.26 (Myers *et al.* 1997). Note, this estimate of *r* is from the revised Table 1 – Table 1 in the published paper has a computational error.

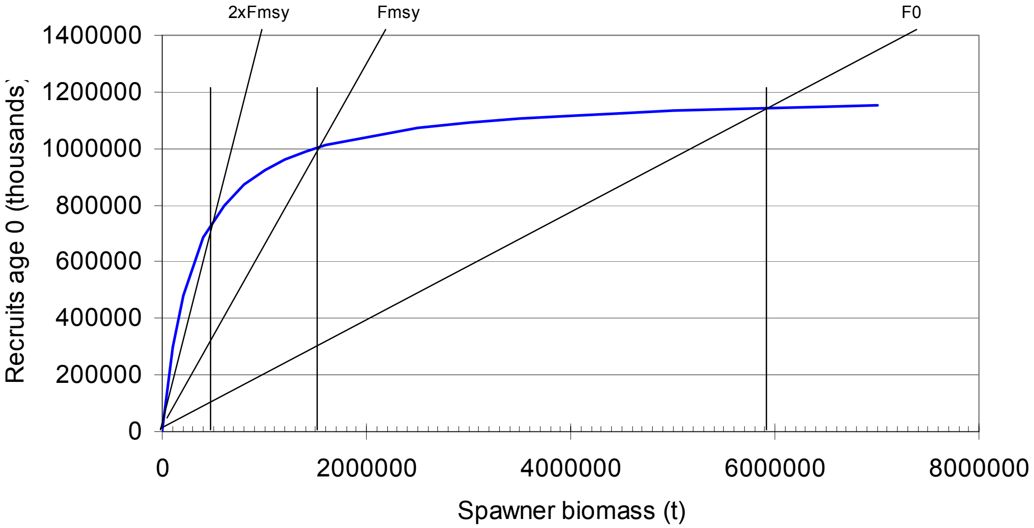


Fig. 5. Beverton-Holt stock-recruit model and replacement lines for F=0, F_{msy} and 2+F_{msy}. See Table 1 for parameters.

In combination, the parameters used to describe the base model (Table 1) result in an unexploited 1+ biomass of about 7 million tons, and an unexploited spawner biomass of about 6 million tons. MSY is achieved at an SSB which is about 26% of SSB_0. F_{msy} is 0.23.

The population model applied in the simulation was:

$$N_{a+1,y+1} = N_{a,y} e^{-(M+F_{a,y})},$$

where $N_{a,y}$ is the number alive at age *a* (*a* = 0 to 25 in the base model) and the beginning of year *y*, *M* is the annual instantaneous rate of natural mortality and $F_{a,y}$ is the fishing mortality on age *a* in year *y*, obtained from

$$F_{a,y} = K_a F_y,$$

where K_a is the partial recruitment value at age *a* and F_y is the fully recruited fishing mortality in year *y*. The partial recruitment vector was computed from the rescaled fishing mortality at age estimated for northern cod for the period 1962-66 and is plotted in Fig. 6.

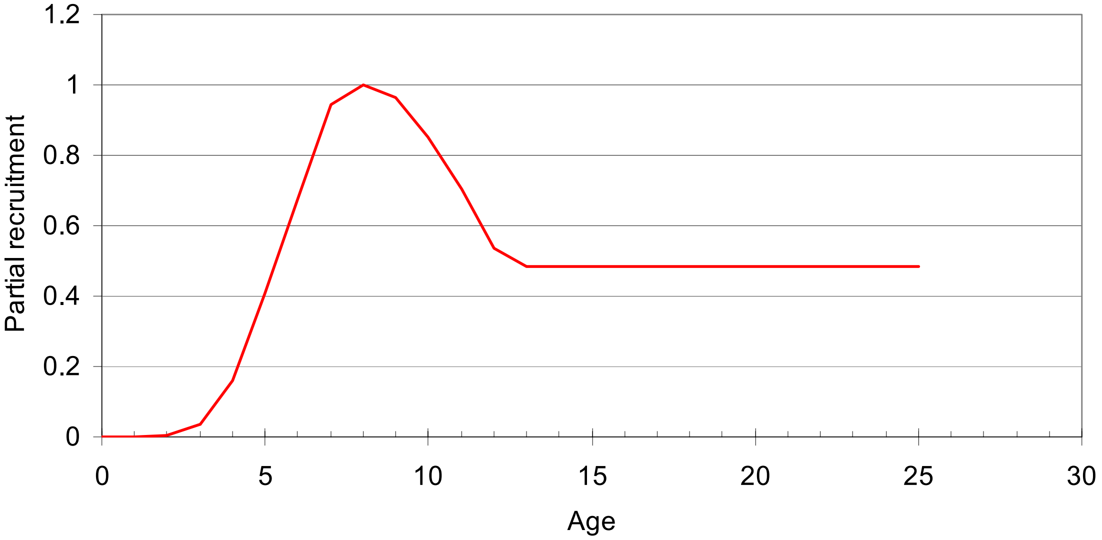


Fig. 6. Partial recruitment vector for the base model derived from fishing mortality at age estimated for northern cod over the period 1962-66 on ages 1-13, extended out to age 25. The PR vector is rescaled to have a value of 1 at the fully selected age.

Spawning stock biomass at the beginning of year *y* was calculated as:

$$SSB_y = \sum_a N_{a,y} W_{a,y} P_{a,y} \,.$$

Recruitment was generated by a Beverton-Holt model with lognormal error. Pattern in the time-series of residuals was modeled by applying a first order autoregressive process (Needle *et al*. 2003):

$$x_i = \phi x_{i-1} + a_i \,,$$

where x_i is the *i* th residual and $a_i \sim N(0,\sigma^2)$.

Recruitment at the beginning of year *i* is then generated by

$$R_i = \exp(\log(\alpha S_i /(1+\frac{S_i}{K})) + x_i) \,.$$

Note that σ is usually thought of in terms of the standard error of the residuals around a stock-recruit model fitted under the assumption of random lognormal error and not from an autoregressive process, denoted here as σ_{AR}. The relationship between these two quantities is

$$\sigma_{AR} = \sqrt{((\sigma^2)/(1\text{-}\phi^2))} \,.$$

In each simulation run the initial population was the equilibrium population with stable age distribution consistent with the value of *F* and with no noise around the stock-recruit function. The model was then run for 30 years under recruitment noise (either simple random or first order autoregressive) before beginning to capture a 100 year time series of population size. From each 100 year series 70 different 15 year declines were measured, leaving 15 more years of data for calculating recovery in future studies. It was found that 100 repeats of the 70 x 15 year declines gave reasonably smooth cumulative frequency distributions of the probability of a decline (see below) greater than or equal to any value on the scale 0 to 1 (after discarding 15 year spans for which there were no declines).

Alternative decline models

Alterative methods for computing decline were considered briefly in Smedbol *et al*. (2003) in the context of Canadian Atlantic cod stocks. Hutchings (2000) computed the largest 15 year decline (here termed point-to-point ratio decline and denoted RD_{15}) from historic population size estimates for a number of marine fish populations by applying the equation

$$RD_{15} = 1 - (N_{15} / N_0),$$

where N_0 is the population size (Hutchings used mature biomass) at the start of the 15 year decline period and N_{15} is the population size at the end of the period. He computed recovery (here termed ratio recovery and denoted RR_t) as

$$RR_t = N_{t+15} / N_0,$$

Where N_{t+15} is the population size *t* years after the 15 year decline. A ratio measure of decline and recovery may be appropriate where changes are reasonably monotonic and measurement error is low but for most situations a model estimate of decline rate may be preferable. The simplest approach is to fit an exponential decline model to the data of the form

$$N_t = \alpha \exp^{\beta t},$$

where N_t is the abundance at time t and β is the instantaneous rate of change. In this model normally distributed error is assumed. An alternative exponential decline model would be

$$\ln(N_t) = \alpha + \beta t,$$

where β is again the instantaneous rate of change, but error is assumed to be normally distributed on the log scale (i.e. lognormal before logarithmic transformation). Because these models make different assumptions about error, they can give different estimates of β. Log-normally distributed error is preferred in many biological cases involving process error and measurement error. The modeled decline (*MD*) for both exponential decline model with either normal or lognormal error is computed by

$$MD = 1 - \exp(\beta \Delta t),$$

where Δt is the duration over which the cumulative decline is estimated, typically 15 years in this study.

Simulation experiments

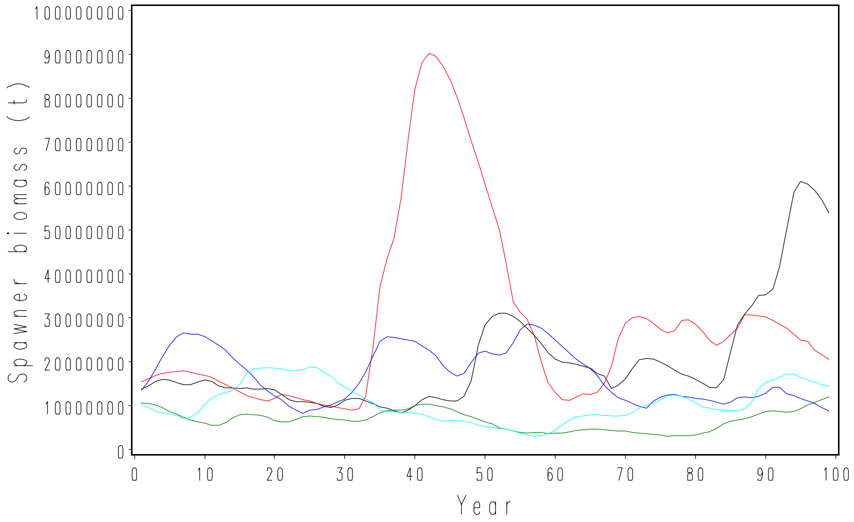
Simulation experiments were carried out with the base model under a range of settings in an attempt to investigate the nature of the fluctuations for the base model under no fishing and under a range of fishing mortality scenarios. The results are reported on the separate sheets that follow. Five sample runs 100 years in length are plotted, together with the cumulative probability (decreasing) of a decline greater than or equal to a value 0 to 1 based on 100 repeats of 70 declines of 15 years duration.

Experiment 1:

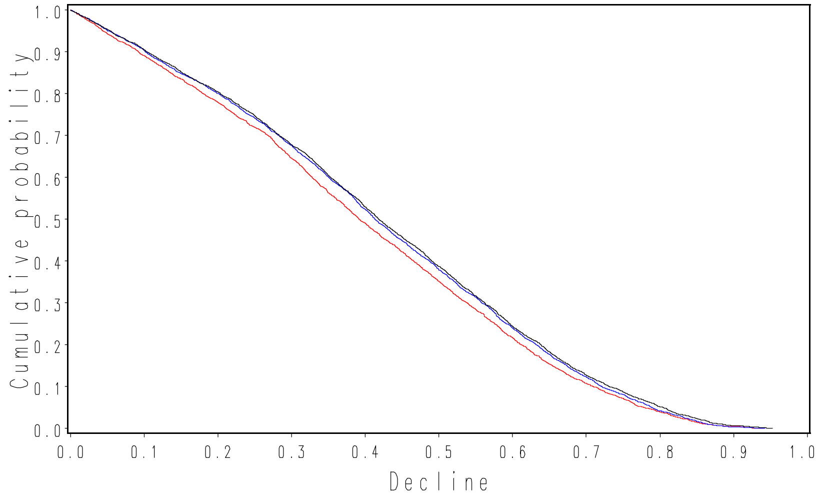
Purpose: Comparison of three models of 15 year decline, point to point (red), exponential (blue) with normal error and exponential with lognormal error (black).

Settings: $F = 0$, $\sigma = 1$, $\phi = 0.6$, units = spawner biomass, lifespan = 25 years

Sample 100 year timeseries from 5 runs:



Cumulative probability of decline:



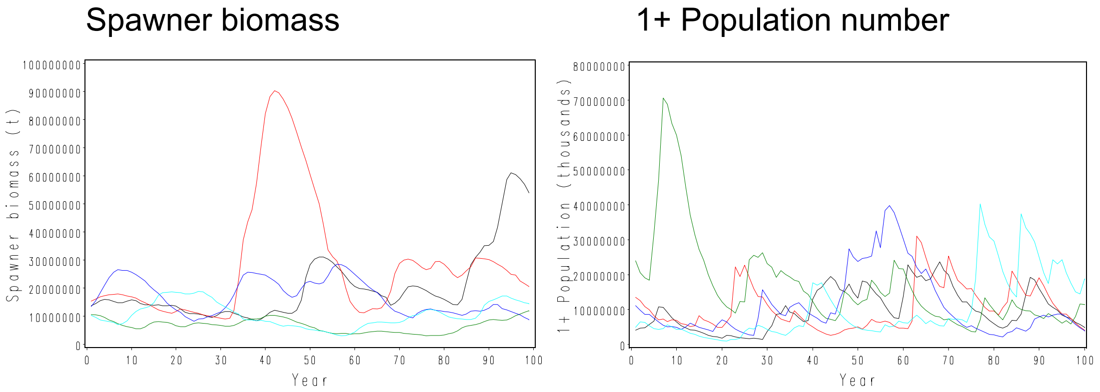
Conclusions: Cumulative probability of decline is similar for all three measures (red=point to point ratio decline, blue=exponential decline model with normal error, black=exponential decline model with lognormal error). The point-to-point ratio estimate tends to slightly underestimate probability of declines in the 0.2 to 0.7 range relative to the other two measures. The exponential decline model with lognormal error is used subsequent runs.

Experiment 2:

Purpose: Comparison of two different units of population size – spawner biomass and 1+ population numbers in the absence of a fishery

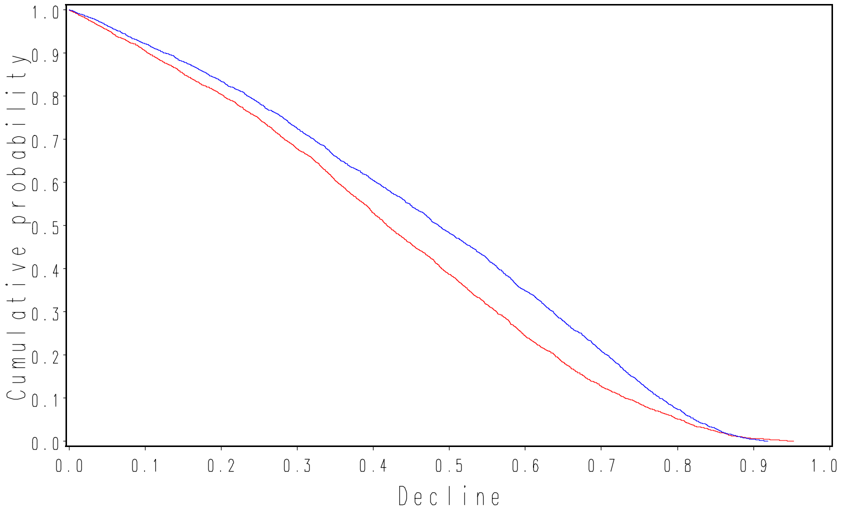
Settings: $F = 0$, $\sigma = 1$, $\phi = 0.6$, units = 1+ numbers and spawner biomass, lifespan = 25 years, decline model= exponential lognormal

Sample 100 year timeseries from 5 runs:


Spawner biomass

1+ Population number

Cumulative probability of decline: (SSB plotted in red and 1+ numbers in blue)



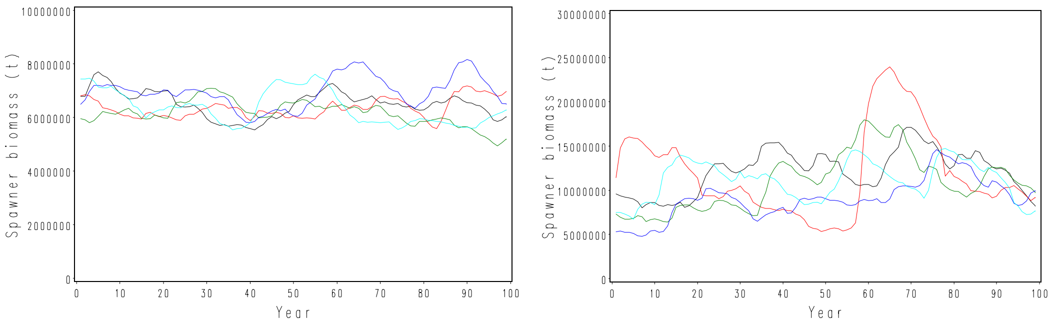
Conclusions: Higher probabilities of larger declines when 1+ population numbers are measured compared with spawning stock biomass. The difference becomes quite small at F_{msy} and 2x F_{msy}. For a trend of increasing F leading to severe long-term population decline, the pattern is reversed with a substantially higher probability of larger declines in the spawner biomass measure compared with the 1+ population measure. The spawner biomass is used in subsequent runs.

Experiment 3:

Purpose: Comparison of fluctuations under two different values of σ

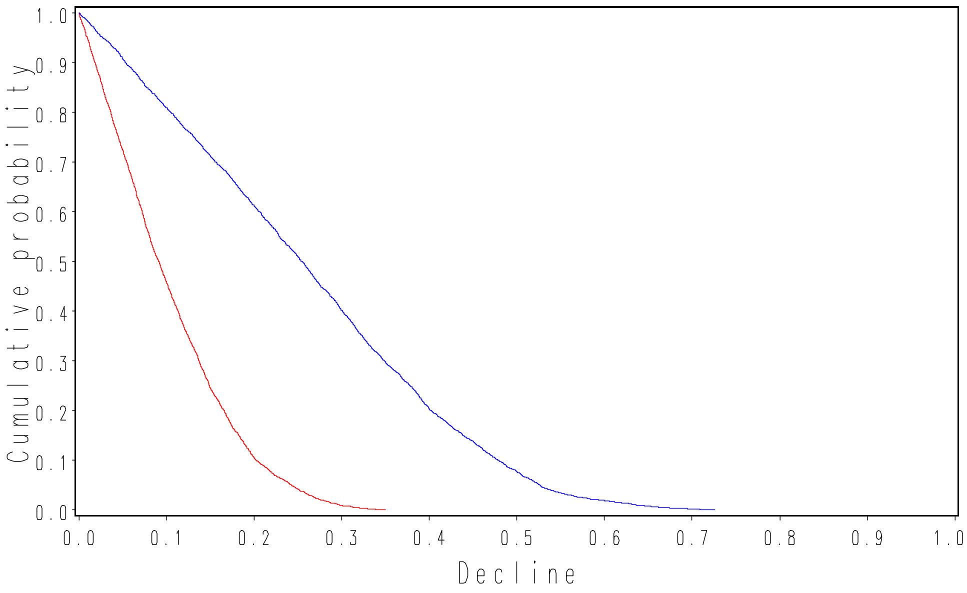
Settings*:* *F* = 0, $\sigma = 0.4 \text{ and } 1.0$, $\phi = 0$, units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

Sample 100 year timeseries from 5 runs:



$\sigma = 0.4$ $\sigma = 1.0$

Cumulative probability of decline: ($\sigma = 0.4$ in red and $\sigma = 1.0$ in blue)



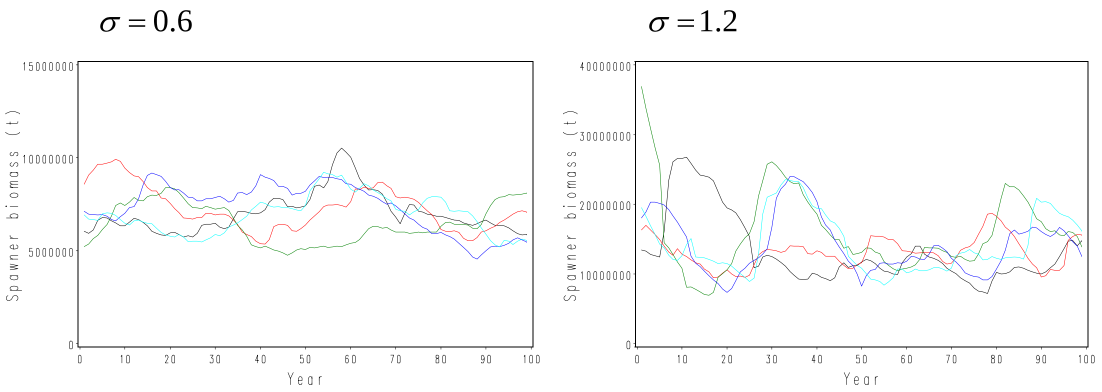
Conclusions: The higher value of σ leads to a substantially higher probability declines in the 0.1 to 0.7 range. Note that at in runs with the larger σ, the population fluctuates at a higher level (caused by high recruitments accumulating across the 25 year age span). Even at the higher level of σ there is very low probability of a decline over 15 years of greater than 0.7.

Experiment 4:

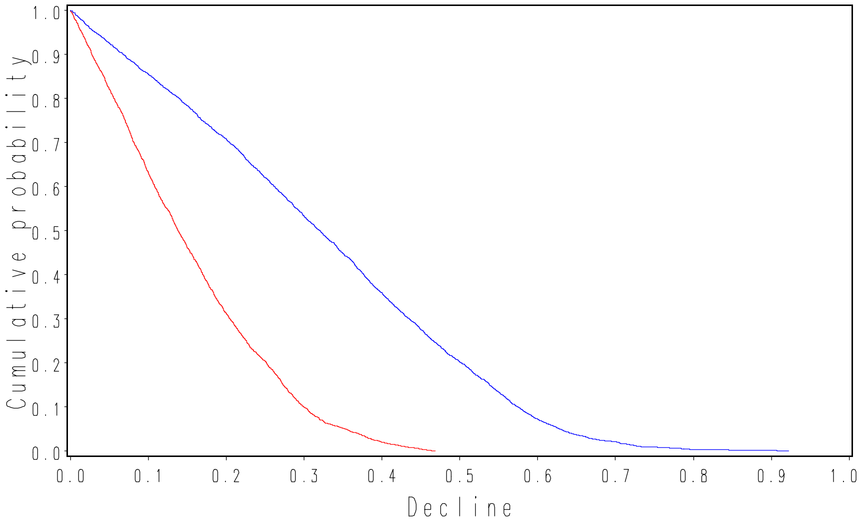
Purpose: Comparison of fluctuations under two different values of σ

Settings: F = 0, $\sigma = 0.6$ and 1.2, $\phi = 0$, units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

Sample 100 year timeseries from 5 runs:



Cumulative probability of decline: ($\sigma = 0.6$ in red and $\sigma = 1.2$ in blue)



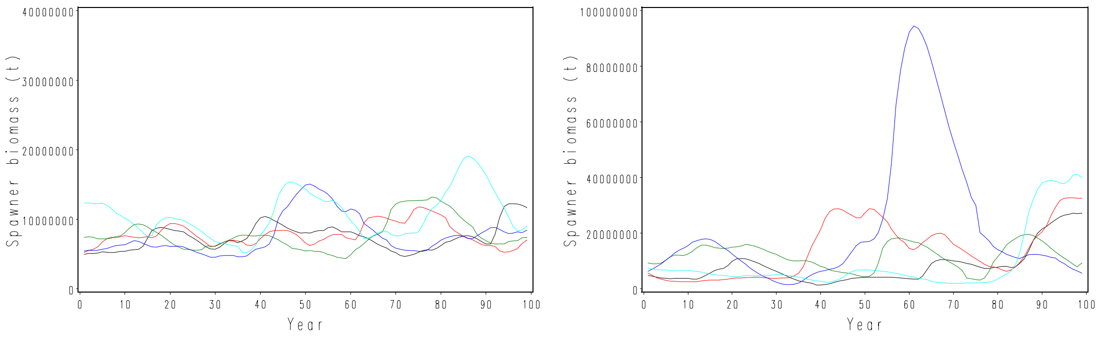
Conclusions: The higher value of σ leads to a higher probability of larger declines. However, even at a level of $\sigma = 1.2$ there is only a very small probability of a decline over 15 years of greater than 0.8. Values of σ for Beverton-Holt models with log-normal error fitted to Atlantic cods from the northwest Atlantic given in Myers *et al.* (1995) ranged from 0.34 to 1.93 with a mean of 0.74. The value estimated for northern cod was 0.75. The increase in probability of larger decline with increase in σ held for populations fished at F_{msy} and fished down to collapse with an increasing trend in F

Experiment 5:

Purpose: Comparison of fluctuations under two different values of ϕ

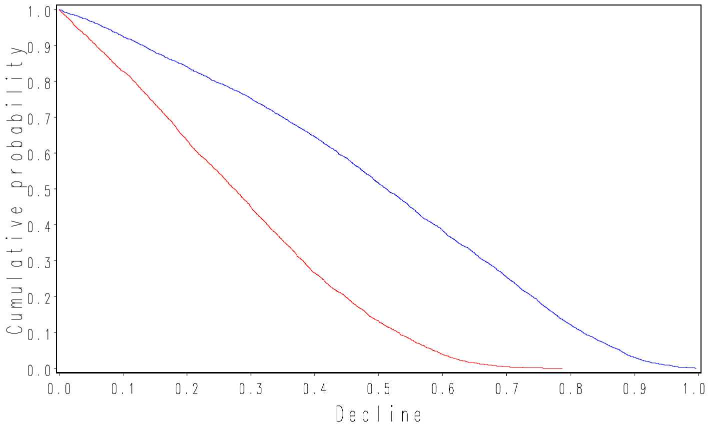
Settings*:* *F* = 0, $\sigma = 0.8$, $\phi = 0.4 \text{ and } 0.8$, units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

Sample 100 year timeseries from 5 runs:



$\phi = 0.4$ $\phi = 0.8$

Cumulative probability of decline: ($\phi = 0.4$ in red and $\phi = 0.8$ in blue)



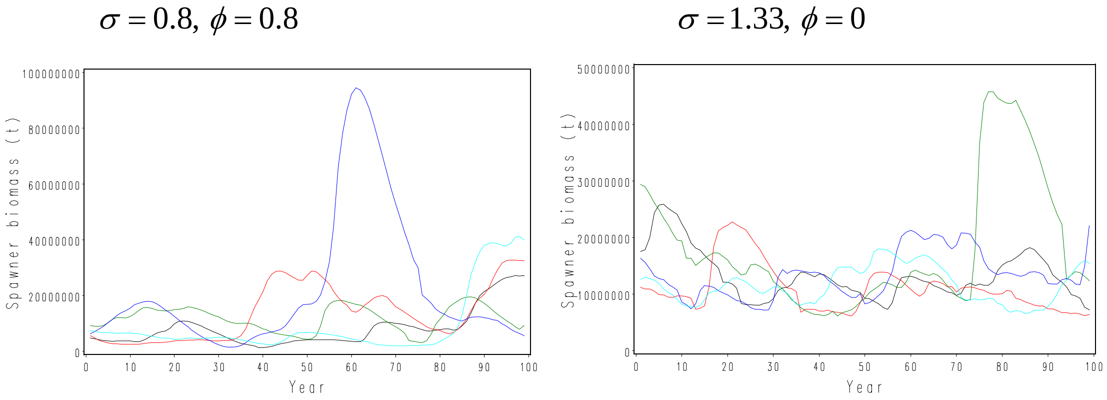
Conclusions: The higher value of ϕ leads to a substantially higher probability of larger declines. Under the higher level of autoregression, there is a 0.12 probability of a decline of 0.8 or greater over 15 years and a 0.03 probability of a decline of 0.9 or greater. The increase in the probability of larger declines with increasing ϕ holds under different *F* scenarios. Given the paucity of information on the degree of autoregression in real stock-recruit data sets, it is difficult to put this into context, but 0.8 is probably a high value. Note that the residuals for the run with $\sigma = 0.8$ and $\phi = 0.8$ would give a combined $\sigma_{AR} = 1.33$. The next experiment examines this further.

Experiment 6:

Purpose: Comparison of fluctuations under overall $\sigma = 1.33$, with and without autoregression.

Settings*:* *F* = 0, $\sigma = 0.8$ and $\phi = 0.8$ compared with $\sigma = 1.33$ and $\phi = 0$, units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

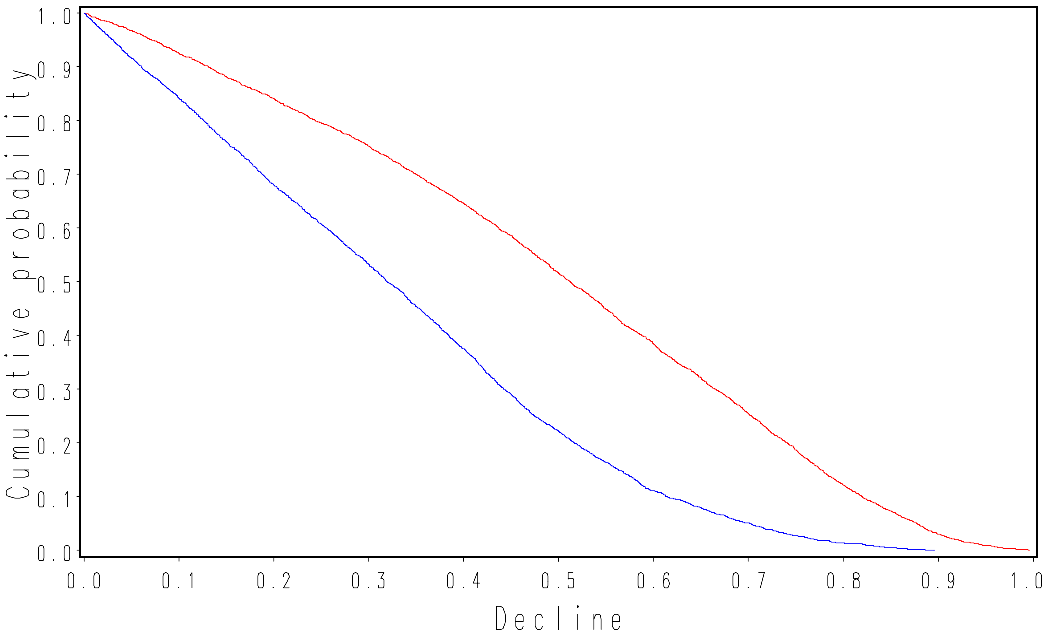
Sample 100 year timeseries from 5 runs:



$\sigma = 0.8,\ \phi = 0.8$

$\sigma = 1.33,\ \phi = 0$

Cumulative probability of decline: ($\sigma = 0.8,\ \phi = 0.8$ in red and $\sigma = 1.33,\ \phi = 0$ in blue)



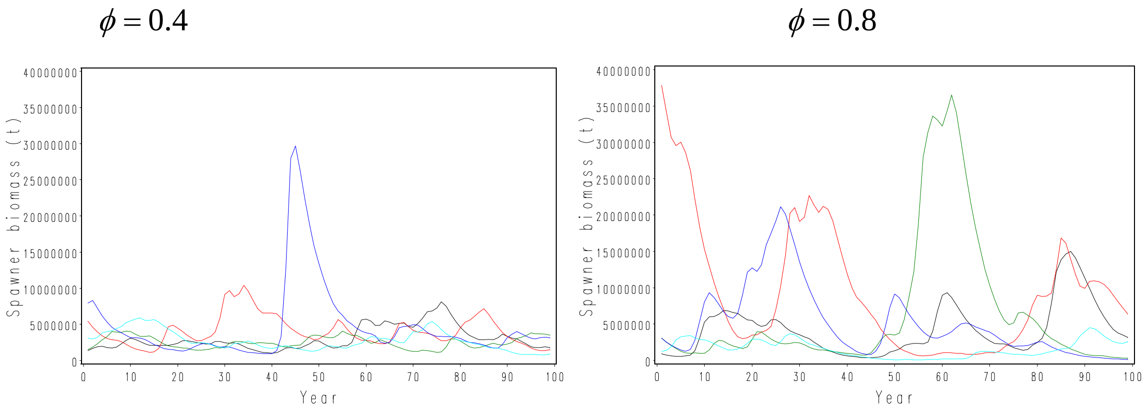
Conclusions: Clearly the autoregressive component in the recruitment variability results in a higher probability of larger declines than recruitment variability with the same overall σ but with $\phi = 0$.

Experiment 7:

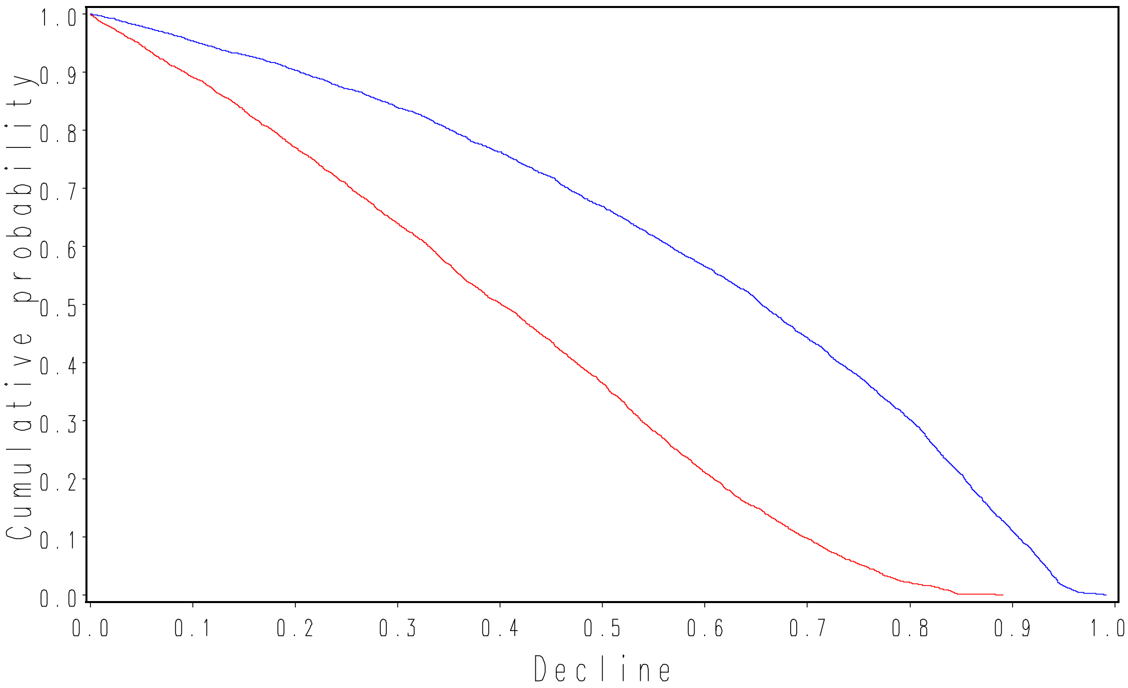
Purpose: Comparison of fluctuations under F_{msy}, with two levels of autoregression.

Settings: F = 0.23, $\sigma = 1$, $\phi = 0.4$ and $\phi = 0.8$, units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

Sample 100 year timeseries from 5 runs:



Cumulative probability of decline: ($\phi = 0.4$ in red and $\phi = 0.8$ in blue)



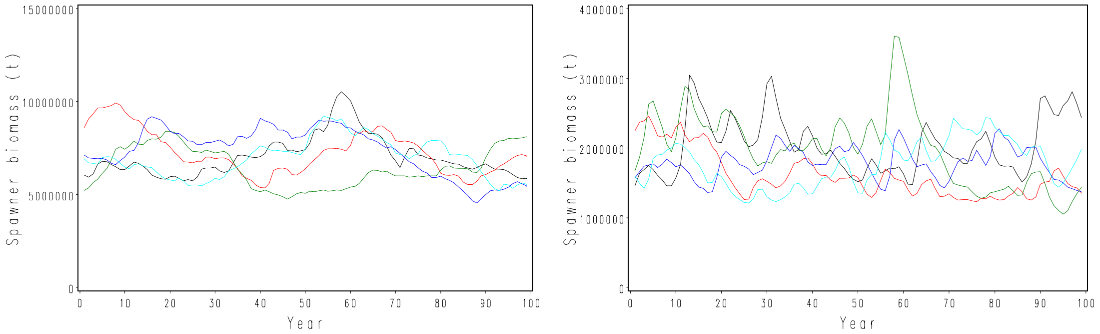
Conclusions: There is a substantial increase in the probability of larger declines with a high level of autoregression at F_{msy}.

Experiment 8:

Purpose: Comparison of fluctuations at *F*=0 and F=F_{msy}

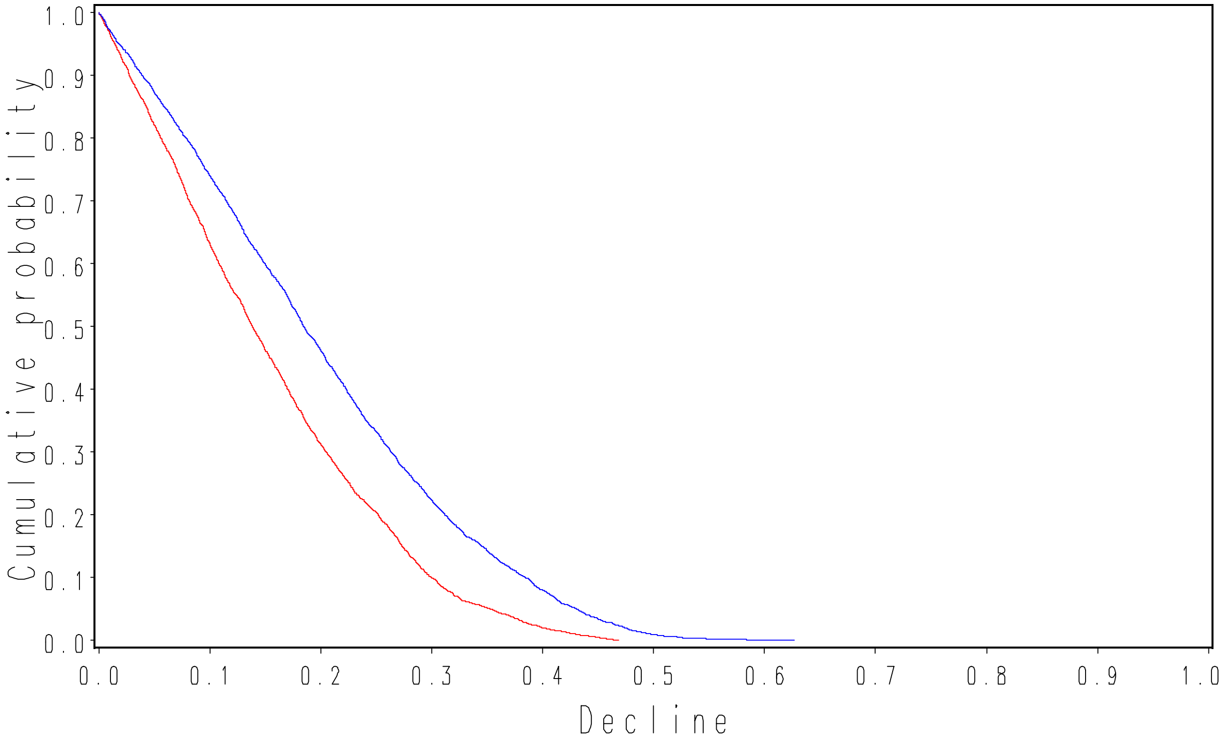
Settings*:* *F* = 0 and 0.23, $\sigma = 0.6$, $\phi = 0$, units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

Sample 100 year timeseries from 5 runs:



$F = 0$ $F = 0.23$

Cumulative probability of decline: ($F = 0$ in red and $F = 0.23$ in blue)



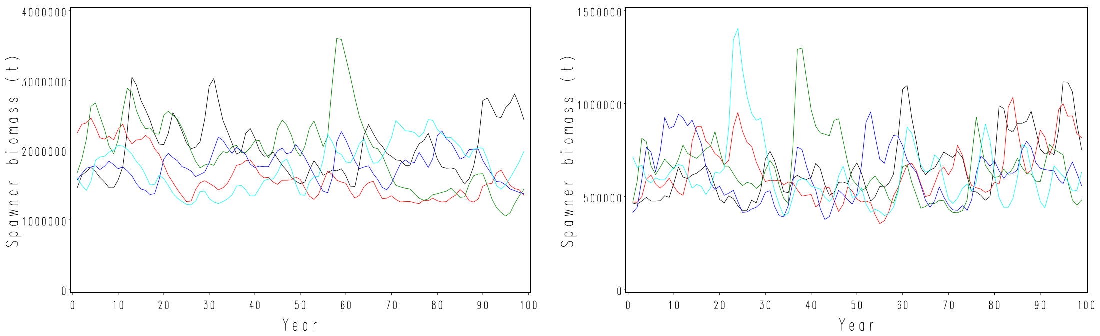
Conclusions: There is a somewhat higher probability of bigger declines when fishing at F_{msy} compared to fluctuations that occur in the unfished state.

Experiment 9:

Purpose: Comparison of fluctuations at and F=F_{msy} and at F=2x F_{msy}

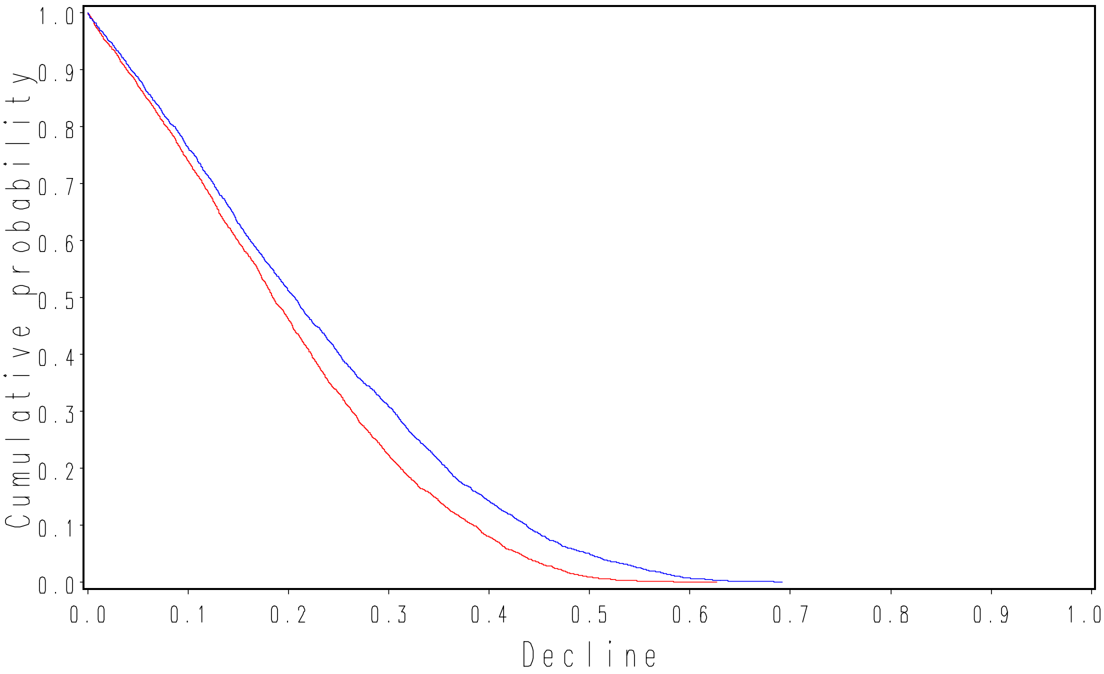
Settings*:* F = 0.23 and 0.46, $\sigma = 0.6$, $\phi = 0$, units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

Sample 100 year timeseries from 5 runs:



$F = 0.23$ $F = 0.46$

Cumulative probability of decline: ($F = 0.23$ in red and $F = 0.46$ in blue)



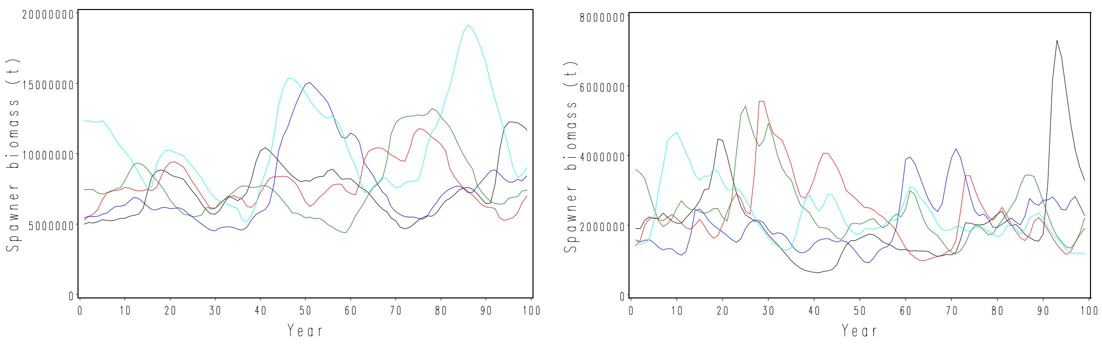
Conclusions: There is a somewhat higher probability of bigger declines when fishing at 2xF_{msy} compared to fluctuations that occur at F_{msy}.

Experiment 10:

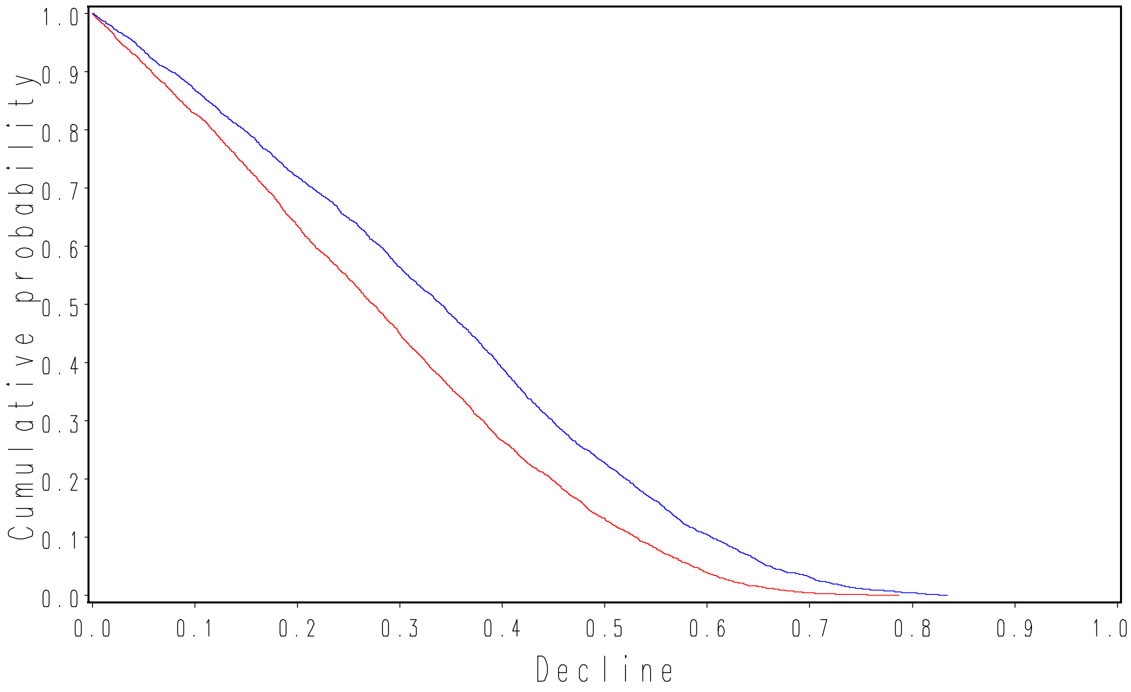
Purpose: Comparison of fluctuations at and F=0 and at F=F_{msy} when an autoregressive component is included in the recruitment variability

Settings*:* F = 0and 0.23, $\sigma = 0.8$, $\phi = 0.4$, units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

Sample 100 year timeseries from 5 runs:


$F = 0$ $F = 0.23$

Cumulative probability of decline: ($F = 0$ in red and $F = 0.23$ in blue)



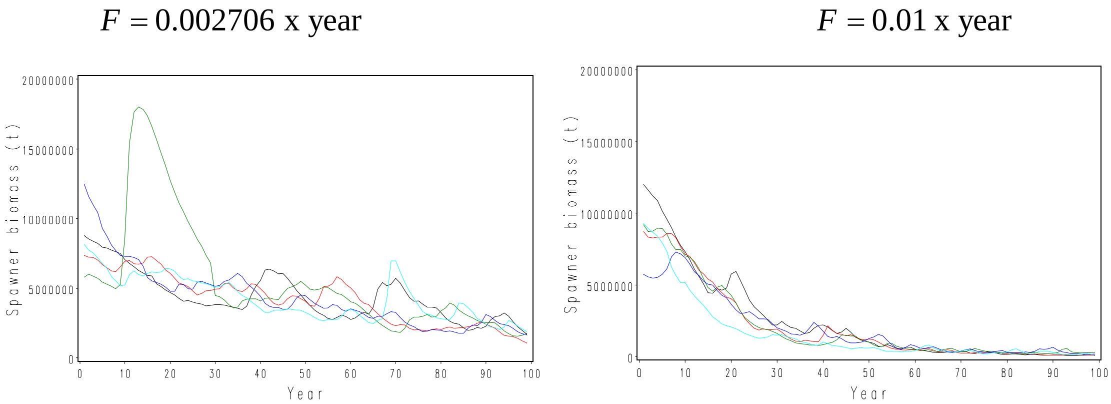
Conclusions: There is a somewhat higher probability of bigger declines when fishing at F_{msy} compared to fluctuations that occur at F=0.

Experiment 11:

Purpose: Comparison of fluctuations fishing down to B_{msy} and collapse

Settings: F = 0.002706*year and 0.01*year, $\sigma = 0.8$, $\phi = 0$, units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

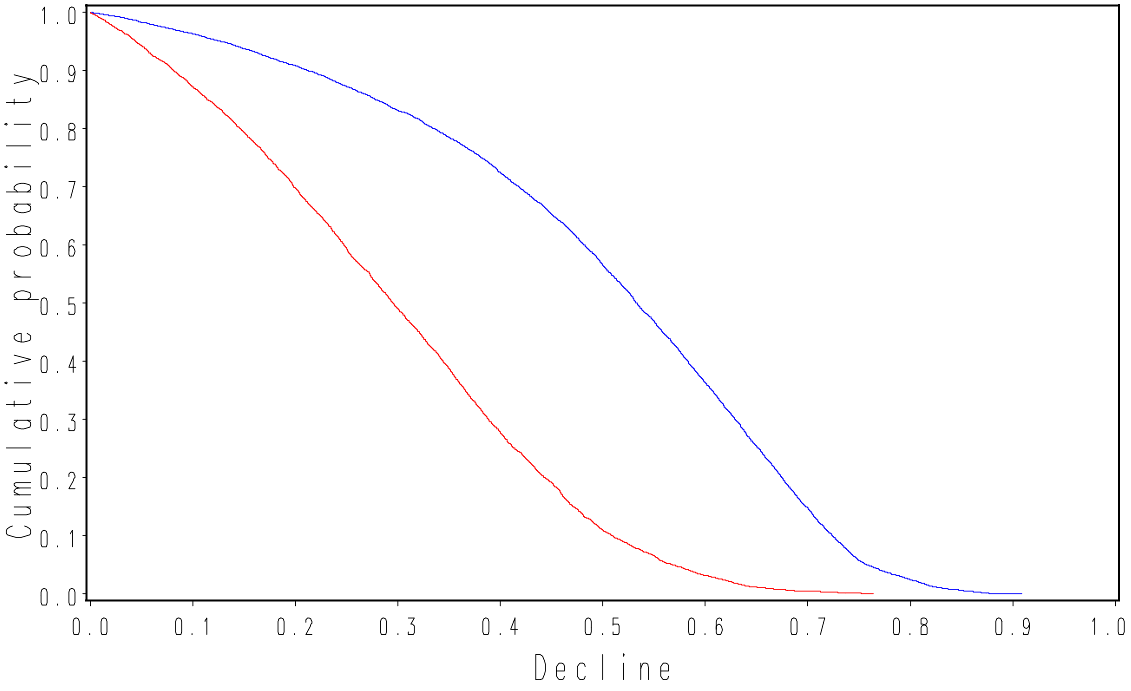
Sample 100 year timeseries from 5 runs:



$F = 0.002706$ x year

$F = 0.01$ x year

Cumulative probability of decline: ($F = 0.002706$ x year in red and $F = 0.01$ x year in blue)



Conclusions: Substantially greater probability of larger declines under the fishing down to collapse secenario compared to fishing down to B_{msy}.

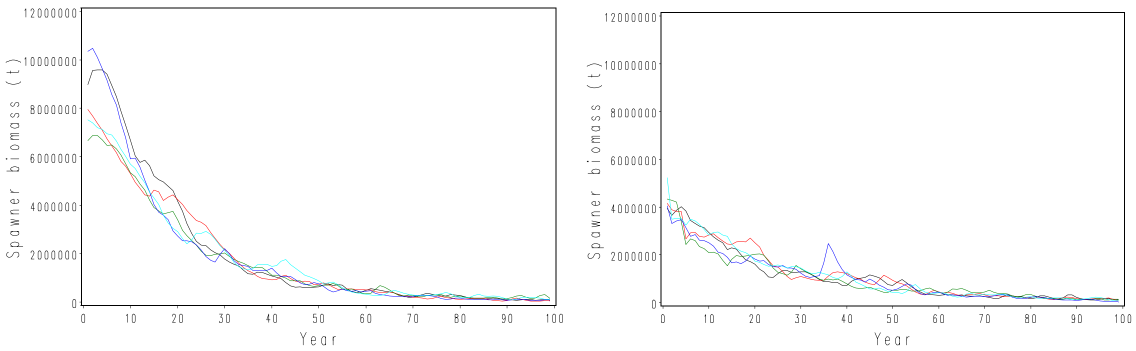
Experiment 12:

Purpose: Comparison of fluctuations fishing down to collapse when units are spawner biomass out to age 25 and spawner biomass out to age 13

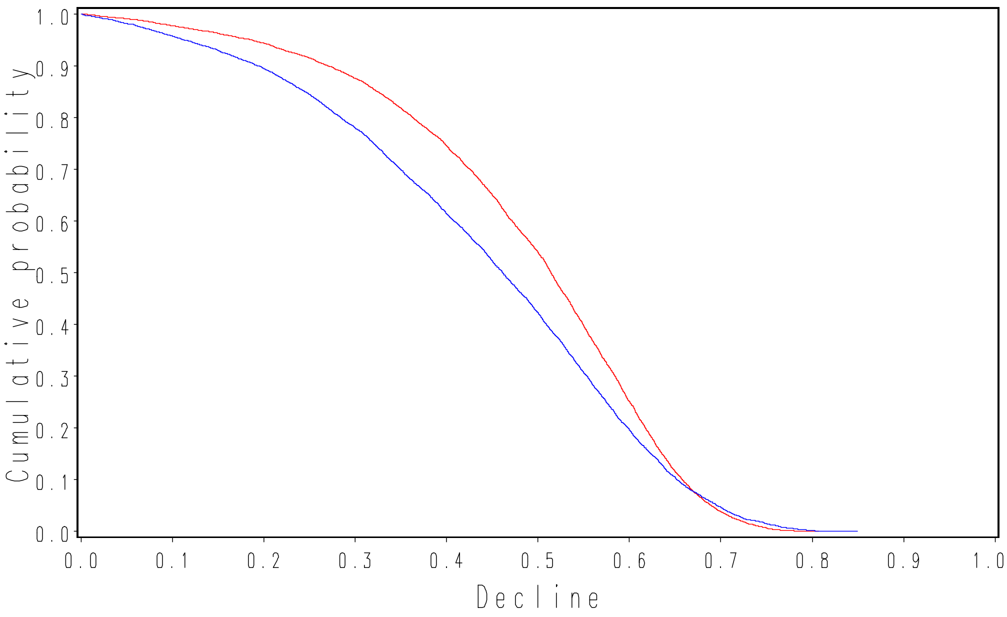
Settings*:* *F* = 0.01*year, $\sigma = 0.6$, $\phi = 0$, units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

Sample 100 year timeseries from 5 runs:

SSB to 25 years SSB to 13 years



Cumulative probability of decline: (SSB to 25 years in red and SSB to 13 years in blue)



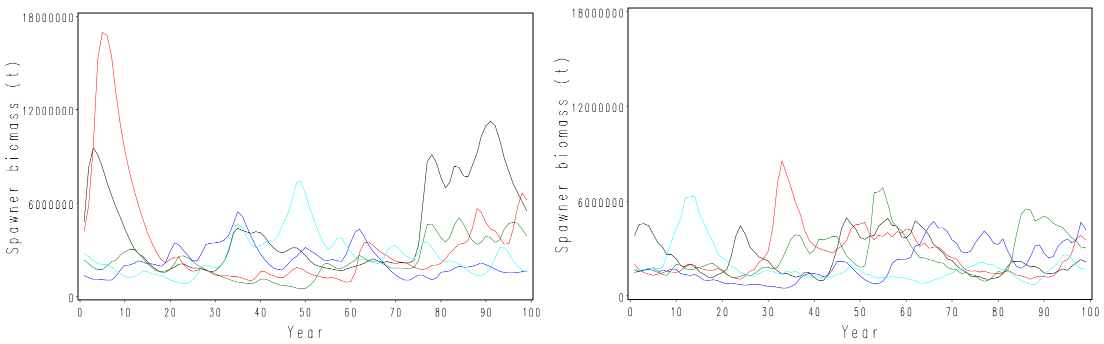
Conclusions: For the same trend in fishing mortality there is a greater probability of a larger decline in the SSB measured to age 25 compared to SSB truncated to age 13 over the range of declines of 0.1 to 0.6.

Experiment 13:

Purpose: Comparison of fluctuations under F_{msy} with and without variation in *M*.

Settings: F = 0.23, $\sigma = 0.8$, $\phi = 0.6$, *M*=0.2 and $M \,\square\, U[0.1, 0.3]$, units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

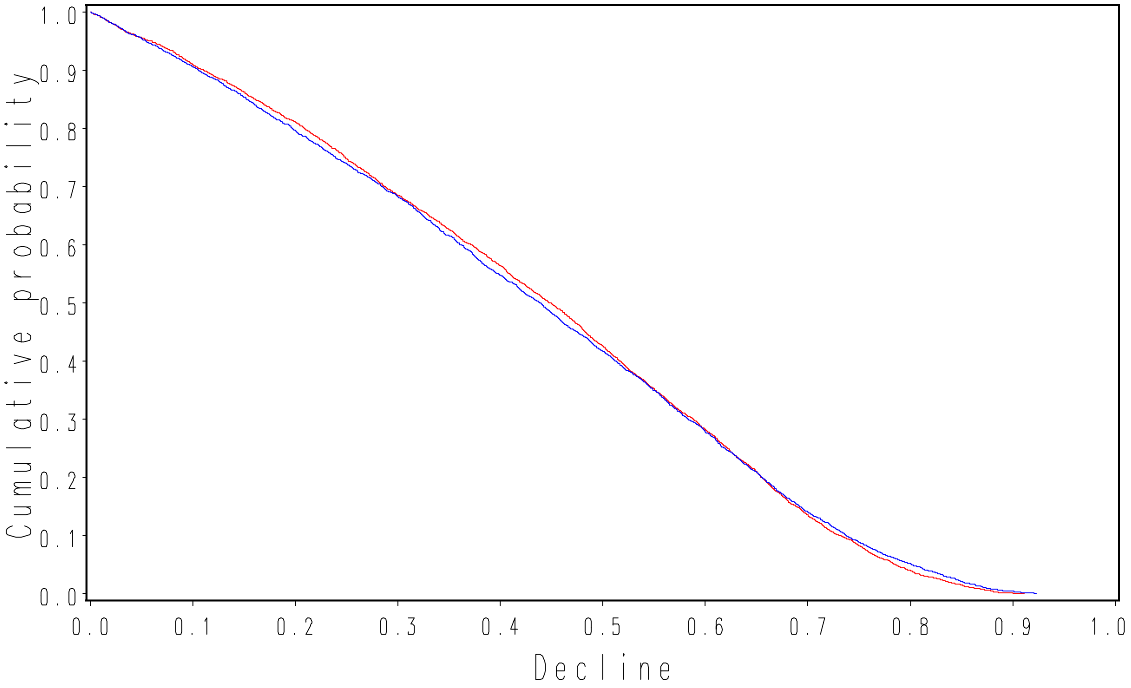
Sample 100 year timeseries from 5 runs:



$M = 0.2$

$M \,\square\, U[0.1, 0.3]$

Cumulative probability of decline: ($M = 0.2$ in red and $M \,\square\, U[0.1, 0.3]$ in blue)



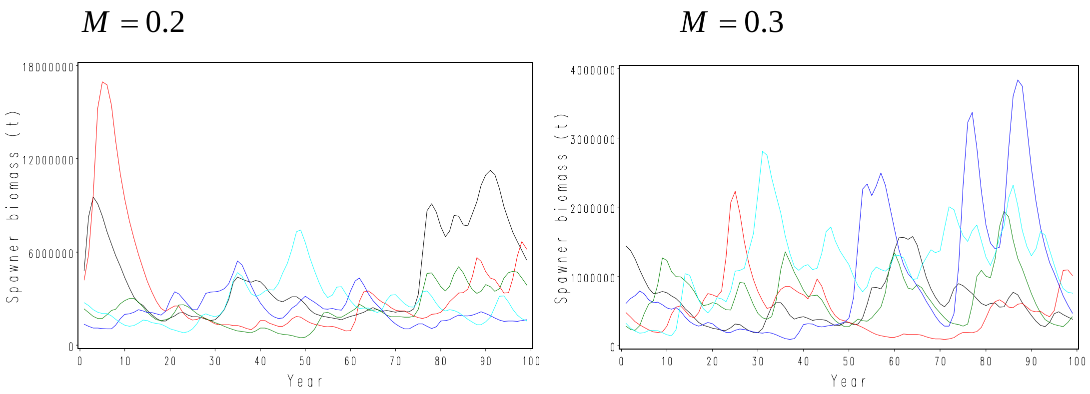
Conclusions: Including variation in *M* has very little effect on the cumulative probability of decline.

Experiment 14:

Purpose: Comparison of fluctuations under *F* = 0.23 with and without an increase in *M* from 0.2 to 0.3.

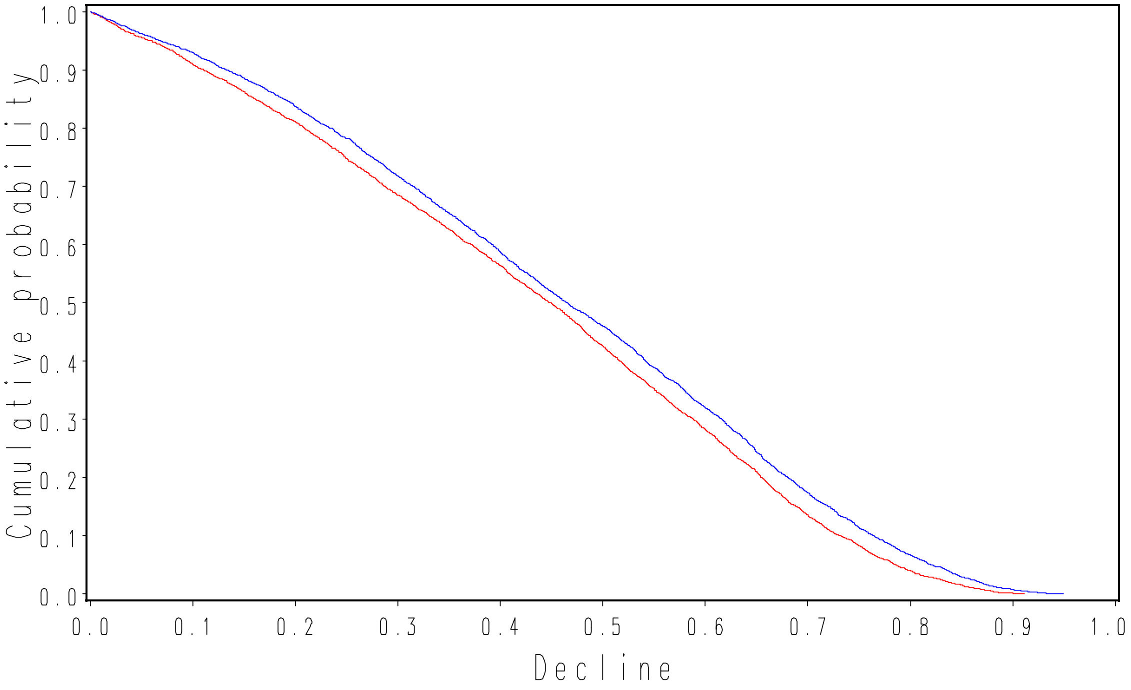
Settings*:* *F*=0.23, $\sigma = 0.8$, $\phi = 0.6$, *M*=0.2 and $M = 0.3$, units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

Sample 100 year timeseries from 5 runs:



$M = 0.2$ $M = 0.3$

Cumulative probability of decline: ($M = 0.2$ in red and $M = 0.3$ in blue)



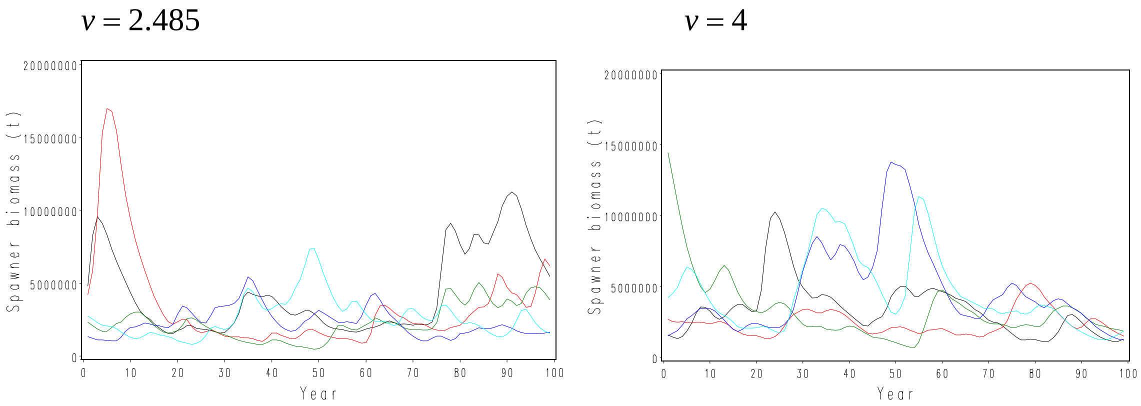
Conclusions: An increase in *M* from 0.2 to 0.3 gives a slight increase in the probability of declines greater than 0.1 Note that under *M* = 0.3, *F*=0.23 is no longer F_{msy}.

Experiment 15:

Purpose: Comparison of fluctuations under *F* = 0.23 before and after a change to earlier maturation. Note that F_{msy} changes with changes in population parameters.

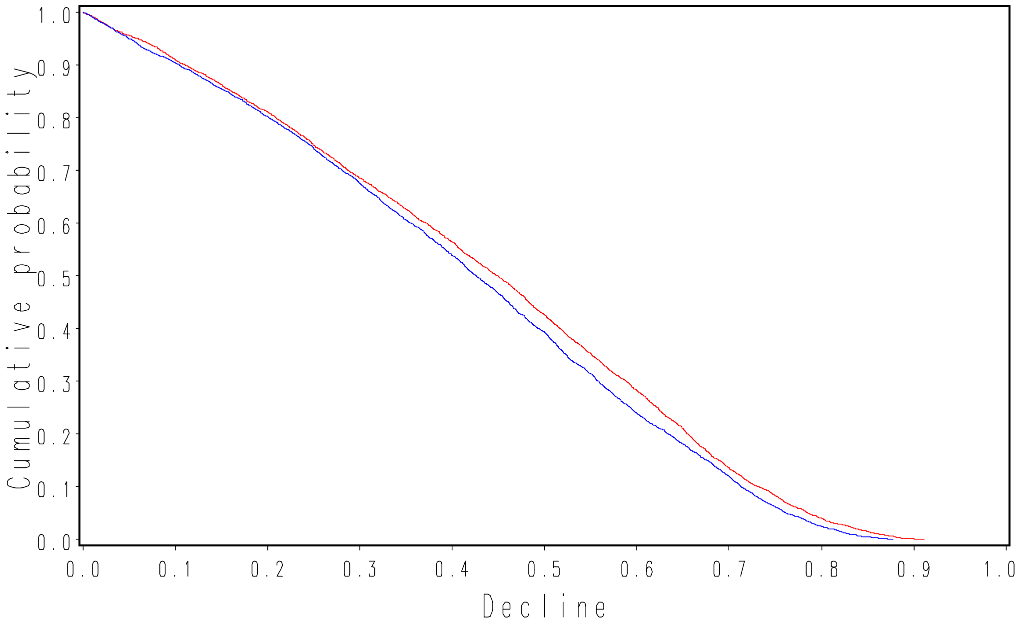
Settings*:* *F*= 0.23, $\sigma = 0.8$, $\phi = 0.6$, *M*=0.2, maturation parameter $v = 2.485$ and $v = 4$ (early maturation), units = spawner biomass, lifespan = 25 years, decline model = exponential lognormal

Sample 100 year timeseries from 5 runs:



$v = 2.485$ $v = 4$

Cumulative probability of decline: ($v = 2.485$ in red and $v = 4$ in blue)



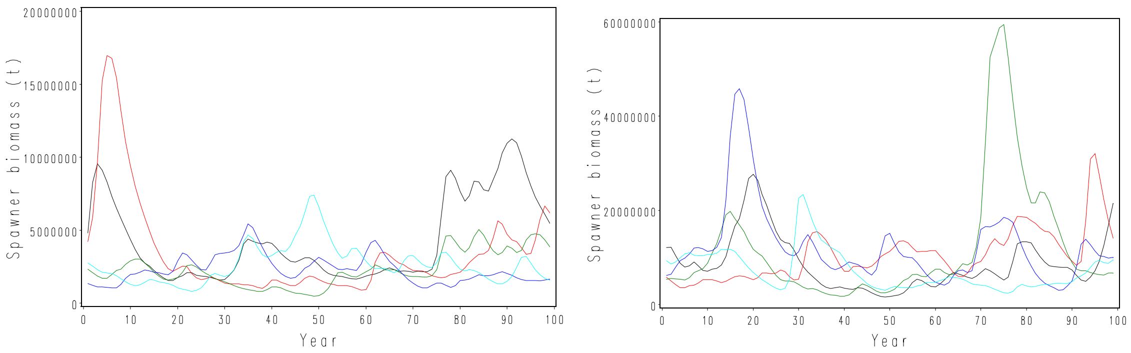
Conclusions: Earlier maturation (for the run with $v = 4$, the population matures approximately 2 years earlier with 60% mature at age 4, compared to the base model maturation curve in Fig. 2) resulted in a slight decrease in the probability of decline over the range 0.3 to 0.9.

Experiment 16:

Purpose: Comparison of fluctuations under *F*=0.23 before and after an increase in body growth rate.

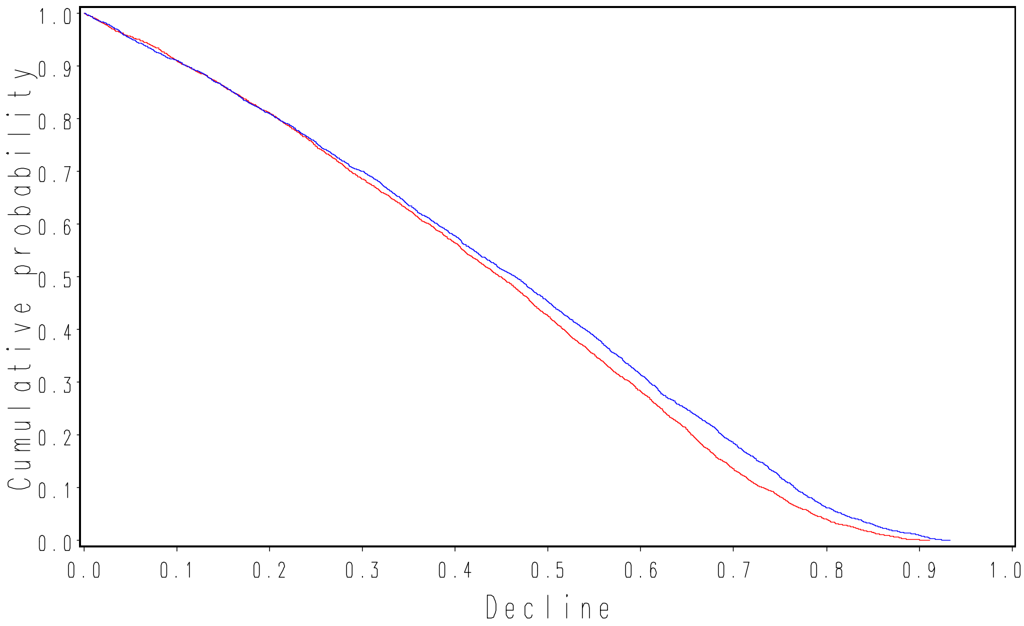
Settings*:* *F* = 0.23, $\sigma = 0.8$, $\phi = 0.6$, *M* = 0.2, growth parameter $K = 0.054$ and $K = 0.108$, units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

Sample 100 year timeseries from 5 runs:



$K = 0.054$ $K = 0.108$

Cumulative probability of decline: ($K = 0.054$ in red and $K = 0.108$ in blue)



Conclusions: Higher growth rate (doubling of the *K* parameter in the growth equation) resulted in a slight increase in the probabilities of declines greater than about 0.4.

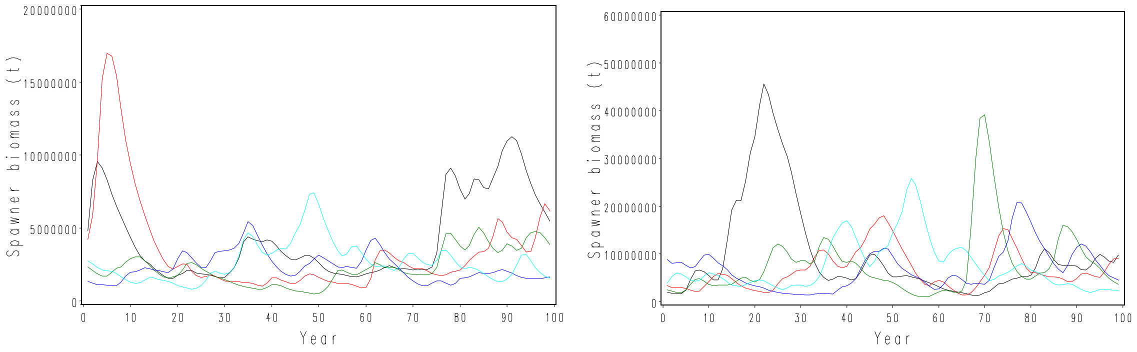
Experiment 17:

Purpose: Comparison of fluctuations under *F*=0.23 before and after an increase in body growth rate, maturation rate and natural mortality rate.

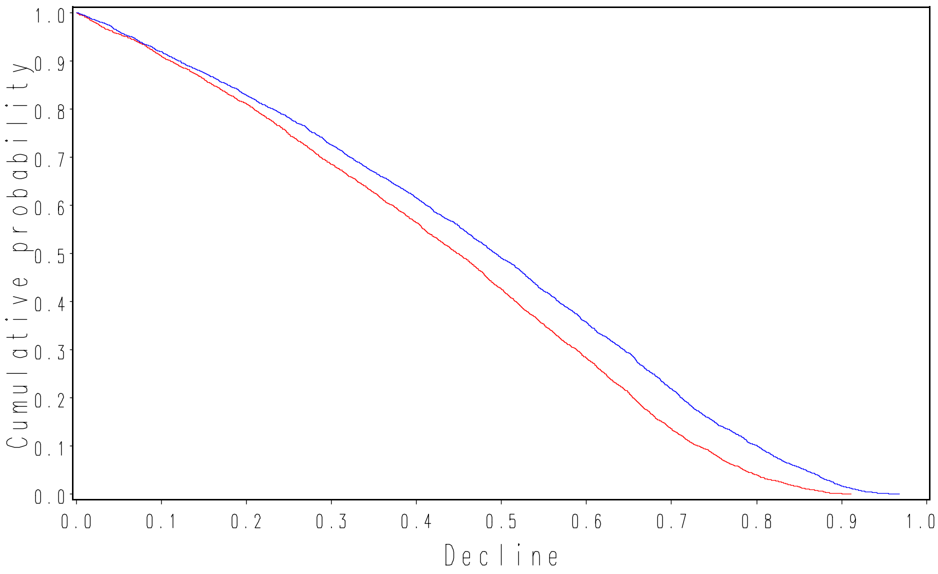
Settings*:* *F* = 0.23, $\sigma = 0.8$, $\phi = 0.6$, *M* = 0.2, $K = 0.054$ and $v = 2.485$ compared to *M* = 0.3, $K = 0.108$ and $v = 4$, units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

Sample 100 year timeseries from 5 runs:

M=0.2, $K = 0.054$, $v = 2.485$ *M*=0.3, $K = 0.108$, $v = 4$,



Cumulative probability of decline: ($K = 0.054$ in red and $K = 0.108$ in blue)



Conclusions: The population with the earlier maturation, higher growth rate and higher natural mortality shows an increased probability of declines of 0.2 and greater compared to the base population. The difference is greatest in the 0.6 to 0.8 decline range.

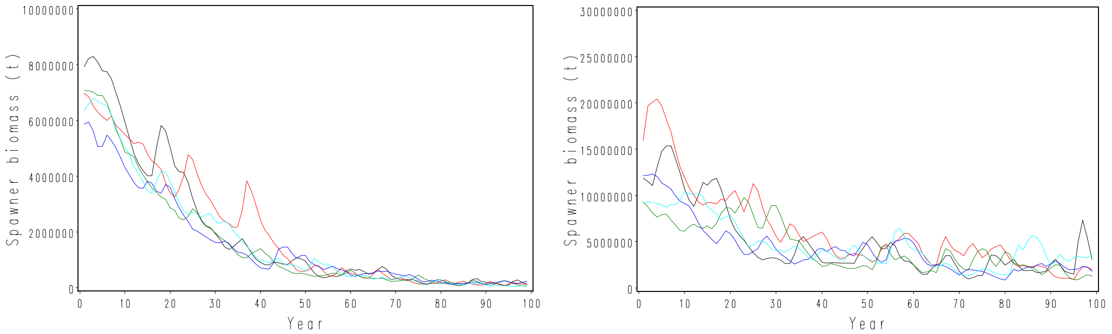
Experiment 18:

Purpose: Comparison of fluctuations under a fishing down to collapse scenario before and after an increase in body growth rate, maturation rate and natural mortality rate.

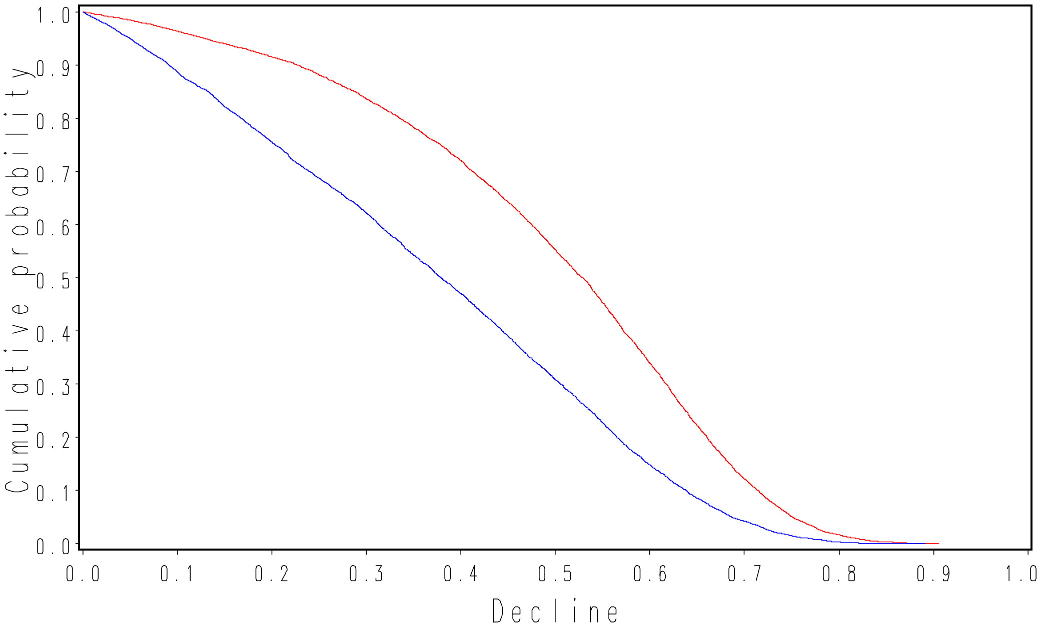
Settings*:* F = 0.01xYear, $\sigma = 0.8$, $\phi = 0$, M = 0.2, $K = 0.054$ and $v = 2.485$ compared to M = 0.3, $K = 0.108$ and $v = 4$, units = spawner biomass, lifespan = 25 years, decline model = exponential lognormal

Sample 100 year timeseries from 5 runs:

M=0.2, $K = 0.054$, $v = 2.485$ M=0.3, $K = 0.108$, $v = 4$,



Cumulative probability of decline: ($K = 0.054$ in red and $K = 0.108$ in blue)



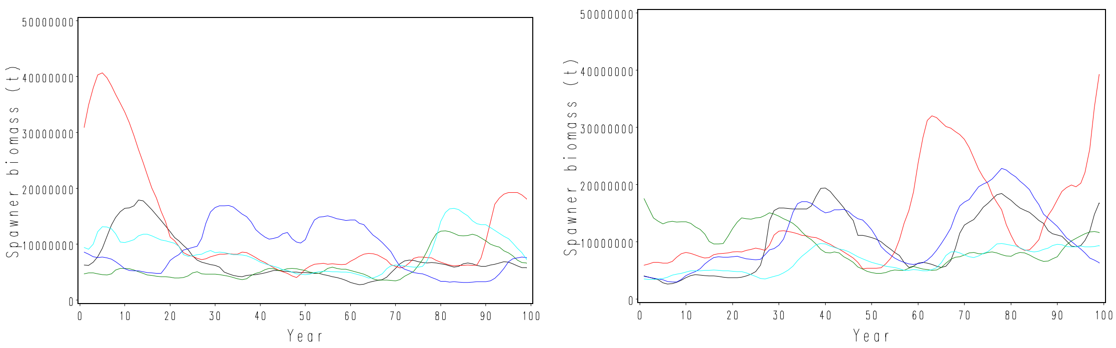
Conclusions: The population with the earlier maturation, higher growth rate and higher natural mortality shows a decreased probability of larger declines under the severe fishing down scenario.

Experiment 19:

Purpose: Comparison of fluctuations for different levels of steepness in the absence of fishing.

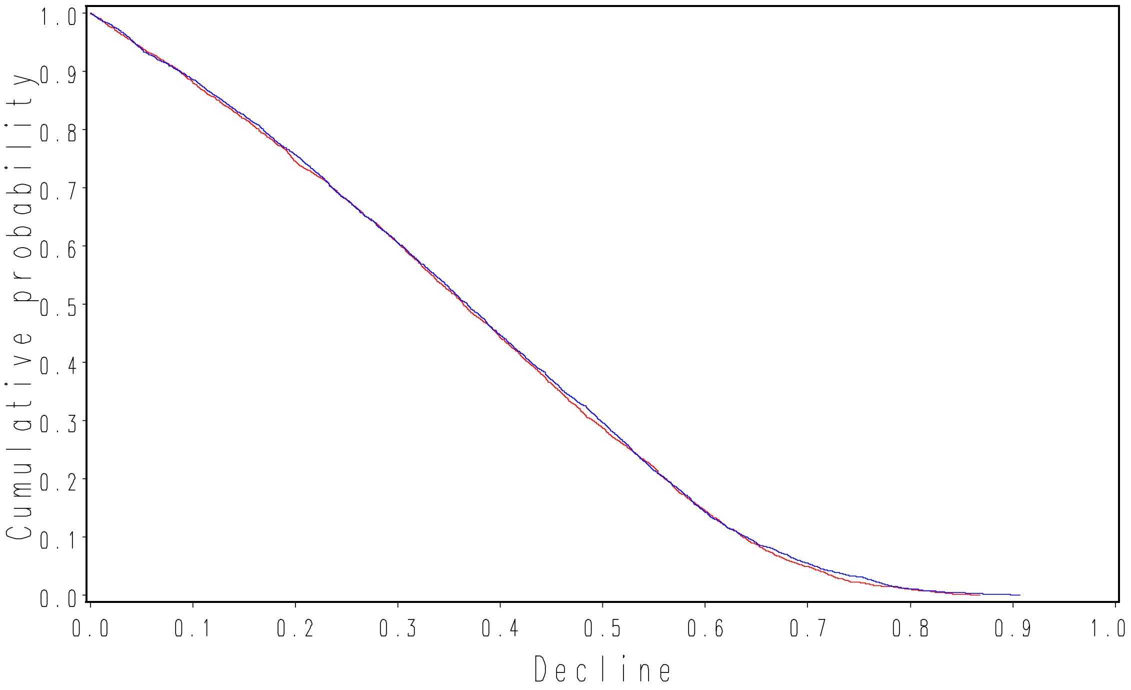
Settings: *F* = 0, $\sigma = 0.8$, $\phi = 0.6$, *M* = 0.2, steepness = 0.838 compared to 0.564, units = spawner biomass, lifespan = 25 years, decline model = exponential lognormal

Sample 100 year timeseries from 5 runs:


steepness = 0.838

steepness = 0.564

Cumulative probability of decline: (steepness = 0.838 in red and steepness = 0.564 in blue)



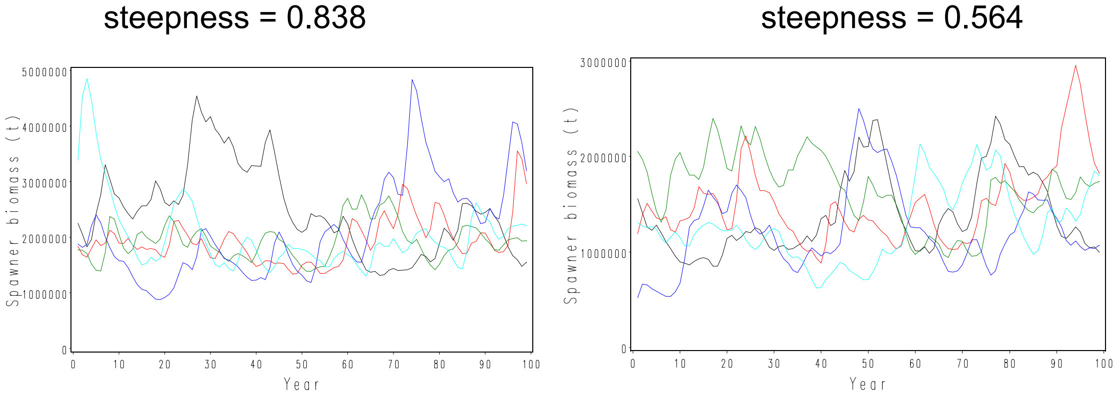
Conclusions: The change in steepness had no discernable influence on the probability of decline in the unfished populations.

Experiment 20:

Purpose: Comparison of fluctuations for different levels of steepness at *F*= 0.23.

Settings*:* *F* = 0.23, $\sigma = 0.8$, $\phi = 0$, *M*=0.2, steepness = 0.838 compared to 0.564, units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

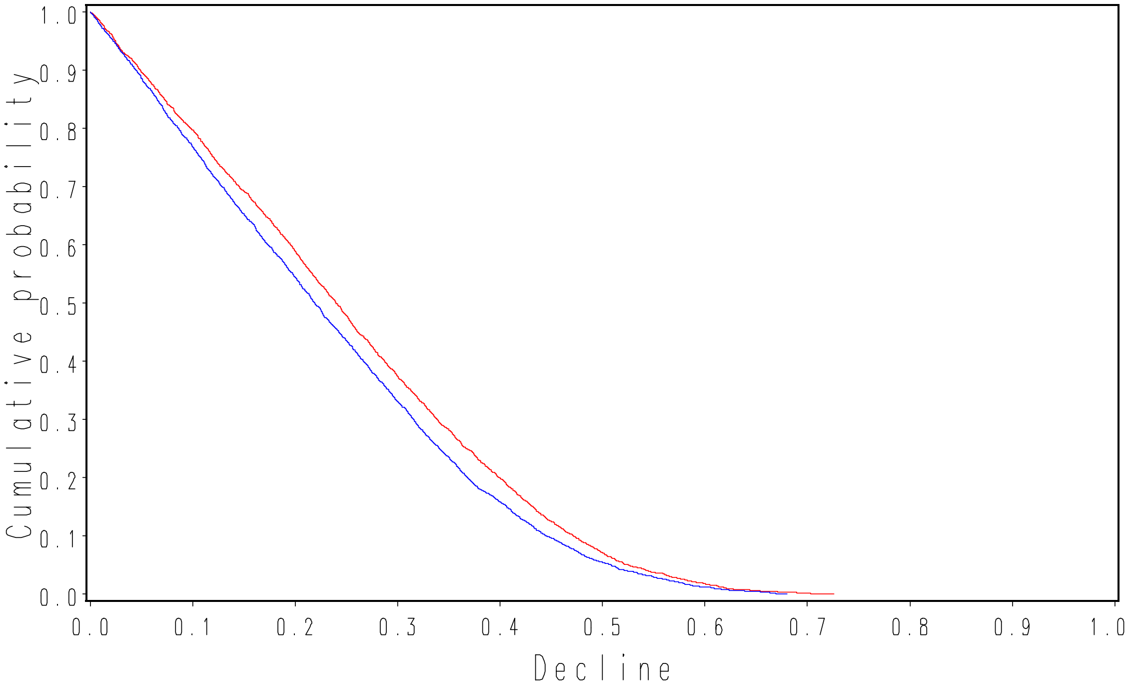
Sample 100 year timeseries from 5 runs:



steepness = 0.838

steepness = 0.564

Cumulative probability of decline: (steepness = 0.838 in red and steepness = 0.564 in blue)



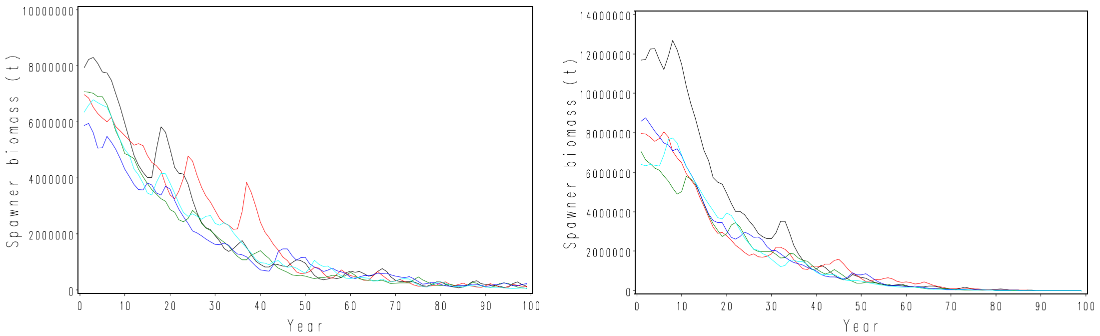
Conclusions: There is only a slight difference in the probability of decline between the two runs, with the higher steepness giving a slightly higher probability.

Experiment 21:

Purpose: Comparison of fluctuations for different levels of steepness on a stock that is being fished down.

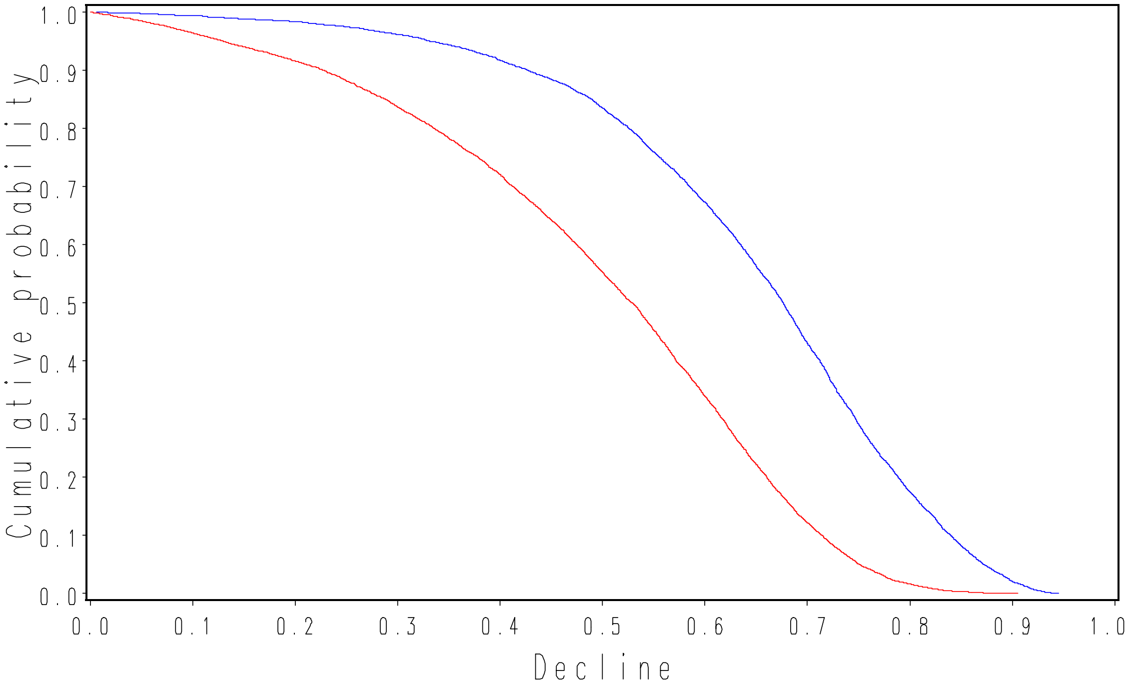
Settings*:* *F* = 0.01xYear, $\sigma = 0.8$, $\phi = 0$, *M*=0.2, steepness = 0.838 compared to 0.564 units = spawner biomass, lifespan = 25 years, decline model= exponential lognormal

Sample 100 year timeseries from 5 runs:


steepness = 0.838

steepness = 0.564

Cumulative probability of decline: (steepness = 0.838 in red and steepness = 0.564 in blue)



Conclusions: The population with a lower steepness had a much higher probability of large declines when being fished down to collapse.

Discussion and conclusions

Models and measures
Fluctuations under a range of measures of population size, models of decline and life history characteristics were examined. The three decline models, point to point, exponential decline with normal error and exponential decline with lognormal error, gave very similar results. The units of population size can make some difference in determining decline. Spawner biomass and 1+ population numbers give different probabilities of decline for the same population, but the effect depends of the level and pattern of F. For a trend of increasing F leading to severe long-term population decline, there is a substantially higher probability of larger declines in the spawner biomass measure compared with the 1+ population measure. Under the same pattern of F, quantifying the spawner biomass out to age 25 shifts the probability curve to the right (higher probability of large declines) compared to quantifying spawner biomass to age 13 for the same population. Thus assessments based on truncated age compositions relative to the true population could be misleading regarding decline rates.

Recruitment variation
Increasing the amount of variability in recruitment substantially increased the probability of larger declines under no fishing and under all F scenarios examined. A similar result is obtained when increasing the degree of autocorrelation in the recruitment residuals. The effect of increasing ϕ is greater than simply the increase to the overall σ.

Effect of fishing
Increasing fishing mortality increases the probability of larger declines. Fishing down from F=0 to F_{msy} results in an increased probability of large declines compared to fishing at F_{msy}. Fishing down to collapse causes a substantial increase in the probability of large declines compared with fishing at 2x F_{msy}.

Life-history characteristics
Random variation in natural mortality had very little effect on the probability of decline under F=0.23 (F_{msy} for the base model, but not F_{msy} under altered life history characteristics) while a shift in M from 0.2 to 0.3 resulted in a small increase in the probability of larger declines. Earlier maturation resulted in a slight decrease in the probability of larger decline whereas faster body growth rate resulted in a slight increase in the probability of larger declines. The combined effect of a shift to higher natural mortality, earlier maturation and faster body growth resulted in increased probability of decline under F=0.23 over the range of 0.2 to 0.9 compared with the base model, but the effect was not very large. Under a severe fishing down scenario, the population with higher natural mortality, earlier maturation and faster body growth had a reduced probability of larger declines. The effect of changing steepness in the stock-recruit model had almost no effect under F=0 and only a slight effect under F=0.23 (lower steepness shifted the probability curve to the left slightly). However, with an incremental increase in F

resulting in the population being fished down to collapse, there was a major shift in the probability curve to higher declines with decreased steepness. Thus the implications of life history strategy have to be interpreted in the context of the fishing mortality regime being imposed.

Overall
Declines over 15 years of greater than 0.9 tended to be generated only under conditions of high variance and high autoregression in the recruitment residuals, and in severe fishing down to collapse scenarios. Lower steepness increased the probability of declines greater than 0.9 under a fishing down to collapse scenario. In comparison, 15 year declines of 0.7 to 0.8 were more commonly encountered in the simulation results even in unfished populations with higher levels of ϕ and σ. Fairly substantial changes in life-history characteristics in terms of higher natural mortality, faster growth and earlier maturation had a smaller than expected effect on the probability of decline under F=0.23 fishing scenario (F_{msy} for the base population). However, under a fishing down to collapse scenario the population with the higher natural mortality, faster growth and earlier maturation had a substantially reduced probability of large declines.

Tentative conclusion
For a fish population similar to the modeled cod population, a 90% decline in spawner biomass over 15 years is probably cause for considerable concern irrespective of the initial size of the population, whereas declines of 70 to 80% can more commonly occur under a variety of conditions, not all of which would be indicative of extinction risk.

If extinction risk is related mainly to depensatory processes in the stock-recruit relationship, then historic extent of decline criteria may be more important than 3 x generation time/15 year (recent) rate of decline criteria in terms of indicating extinction risk. In combination, recent rate of decline evaluated in the context of historic extent of decline could be very useful in determining risk status. However, recent rate of decline on its own must be carefully interpreted in the context of natural levels of recruitment variability including autoregression, fishing mortality regime and population life history characteristics, on a case by case basis. As is the case for IUCN, COSEWIC has the flexibility to take these considerations into account and does so on a routine basis to arrive at sensible determinations of risk status.

Historic extent of decline criteria share the same conceptual basis as the Precautionary Approach and can potentially run into the same difficulty in terms of demarcating serious harm/extinction threat in a non-arbitrary manner. Details regarding life-history characteristics have not factored as significantly in the precautionary approach debate thus far, beyond consideration of the shape of the stock-recruit curve and the amount of variability around the curve. However considerations regarding possible “regime shifts”, changes in stock productivity and the existence of depensatory processes are major issues.

Clearly, consistency between species at risk criteria and precautionary approach criteria would be useful. The difference is largely in terms of the degree of perceived harm. Efforts should be made to harmonize these two approaches to facilitate responsible fisheries management practices on depleted populations. However, it is of concern that it is proving difficult to manage fishing mortality at levels that will promote recovery in Atlantic Canadian groundfish stocks under either SARA or the UN Fish Stocks Agreement/ Precautionary Approach, and that commercially exploited fish populations continue to be vulnerable to biological extinction caused by overfishing and lack of recovery.

References

Armstrong, M. J. and Shelton, P.A. 1990. Clupeoid life-history styles in variable environments. Environ. Biol. Fish. 28:77-85.

Beddington, J.R. and J.G. Cooke. 1983. The potential yield of fish stocks. Food and Agriculture Organi-zation (FAO) of the United Nations. Fisheries Technical Paper No. 242. 50p.

COSEWIC. 2003. COSEWIC's Assessment Process and Criteria, 19p. http://www.cosewic.gc.ca/pdf/English/Assessment_process_e.pdf

Dulvy, N.K., Sadovy, Y., and Reynolds, J.D. 2003. Extinction vulnerability in marine populations. Fish and Fisheries 4:25-64.

Holling, C.S. 1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Systematic. 4:1-23.

Hutchings, J.A. 2000. Collapse and recovery of marine fishes. Nature 406:882-885.

Hutchings, J.A. 2001a. Conservation biology of marine fishes: perceptions and caveats regarding assignment of extinction risk. Can. J. Fish. Aquat. Sci. 58:108-121.

Hutchings, J.A. 2001b. Influence of population decline, fishing, and spawner variability on the recovery of marine fishes. J. Fish. Biol. 59:306-322.

Hutchings, J.A. 2003. Interactions among collapse, recovery and extinction risk in marine and anadrmous fishes. Chapter 3. World Summit on Salmon. Vancouver, June 10-13, 2003. http://www.sfu.ca/cstudies/science/summit/pdf/03-%20hutchings.pdf

Hutchings, J.A. and Reynolds, J.D. 2004. Marine fish population collapses: consequences for recovery and extinction risk. BioScience 54:297-309.

ICES 1997. Report of the study group on the precautionary approach to fisheries management. ICES CM 1997/Assess:7, 41 p.

IUCN. 2001. IUCN Red List Categories: Version 3.1. IUCN Commission. IUCN, Gland, Switzerland and Cambridge, UK.

Liermann, M., and Hilborn, R. 1997. Depensation in fish stocks: a hierarchic Bayesian meta-analysis. Can. J. Fish. Aquat. Sci. 54:1976–1984.

Lilly, G.R., Shelton, P.A., Brattey, J., Cadigan, N.G., Healey, B.P., Murphy, E.F., Stansbury, D.E., and Chen, N. 2003. An assessment of the cod stock in NAFO Divisions 2J+3 in February 2003. CSAS Res. Doc. 2003/023, 157p.

Mace, P.M., and Doonan, I.J. 1988. A generalized bioeconomic simulation model for fish population dynamics. N.Z. Fish. Assess. Res. Doc. 88/4.

Mace, P.M. 1994. Relationships between common biological reference points used as thresholds and targets of fisheries management strategies. Can. J. Fish. and Aquat. Sci. 51: 110-122.

Mace, P.M. *et al*. 2002. NMFS / Interagency Working Group Evaluation of CITES Criteria and Guidelines. NOAA Technical Memorandum NMFS-F/SPO-58, 70p.

Mace, P.M. 2004. In defence of fisheries scientists, single species models and other scapegoats: confronting the real problems. Mar. Ecol. Prog. Ser. 274:269-303.

Musick, J.A. 1999. Criteria to define extinction risk in marine fishes. Fisheries 24:6-14.

Musick, J.A., Berkeley, S.A., Cailliet, G.M., Camhi, M., Hunstman, G., Nammack, M. and Warren, M.L. 2000. Protection of marine fish stocks at risk of extinction. Fisheries 25:6-8.

Myers, R.A., Barrowman, N.J., Hutchings, J.A., and Rosenberg, A.A. 1995. Population dynamics of exploited fish stocks at low population levels. Science (Washington, D.C.), 269: 1106–1108.

Myers, R.A., Bridson, J., and Barrowman, N.J. 1995. Summary of worldwide spawner and recruitment data. Can. Tech. Rep. Fish. Aquat. Sci. 2024.

Needle, C.L., O’Brien, C.M., Darby, C.D., and Smith, M.T. 2003. Incorporating time-series structure in medium-term projections. Sci. Mar. 67 (Suppl. 1):201-209.

Powles, H., Bradford, M.J., Bradford, R.G., Doubleday, W.G., Innes, S., Levings, C.D. 2000. Assessing and protecting endangered marine species. ICES J. Mar. Sci. 57:669-676.

Punt, A.E. 2000. Extinction of marine renewable resources: a demographic analysis. Popul. Ecol. 42:19-27.

Rice, J.C., Shelton, P.A., Rivard, D., Chouinard, G.A., and Fréchet, A. 2003. Recovering Canadian Atlantic cod stocks: the shape of things to come? ICES CM 2003/U:06.

Shelton, P.A. 1992. The shape of recruitment distributions. Can. J. Fish. Aquat. Sci. 49: 1754–1761.

Shelton, P.A. and Healey, B.P. 1999. Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock? Can. J. Fish. Aquat. Sci. 56:1521-1524.

Shelton, P.A., and Morgan, M.J. 2005. Is By-catch mortality preventing the rebuilding of Cod (*Gadus morhua*) and American Plaice (*Hippoglossoides platessoides*) stocks on the Grand Bank? e-Journal of Northwest Atlantic Fishery Science, V 36, art. 1 http://journal.nafo.int/36/shelton/1-shelton.html

Shelton, P.A., Sinclair, A.F., Chouinard, G.A., Mohn, R., and Duplisea, D.E. 2006. Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 63:235-238.

Smedbol, R.K., Shelton, P.A., Swain, D.P., Fréchet, A., and Chouinard, G.A. 2002. Review of population structure, distribution and abundance of cod (*Gadus morhua*) in Atlantic Canada in a species-at-risk context. CSAS Res. Doc. 2002/082, 134p.

Walters, C.J. 1986. Adaptive management of renewable resources. Macmillan Publishing Co., New York.