

How to Eliminate the Unnecessary So That The Necessary May Speak. Biological Reference Points.

Laurence T. Kell^{1,*}, Finlay Scott², Paul De Bruyn³, Richard D.M. Nash⁴

1 ICCAT Secretariat, C/Corazón de María, 8. 28002 Madrid, Spain.

3 The Fisheries Laboratory, Lowestoft, NR33 0HT, Suffolk, England

2 AZTI Tecnalia. Herrera kaia portualdea z/g, 20110 Pasaia, Gipuzkoa, Spain

4 Institute of Marine Research, PO Box 1870 Nordnes, 5817 Bergen, Norway

*** E-mail: Corresponding Laurie.Kell@iccat.int**

Abstract

elasticity analysis uncertainty life history

The analysis allowed several important questions to be addressed, i.e. what is the relative impact of the different biological processes and parameters on the estimates of stock status and exploitation? Does the impact depend on the reference point and quantity (e.g. SSB or F) chosen or on the status of the stock. I.e. does knowledge of particular parameters and processes depend on whether the stock is depleted or within safe biological limits? Answering these questions will help in choosing robust target and limit reference points to be made.

Author Summary

Introduction

The adoption of the Precautionary Approach to fisheries management [1] requires a formal consideration of uncertainty. An important principle of the approach is that the level of precaution should increase as uncertainty increases, e.g. from data rich to poor situations. The definition of data rich and poor is often made on the availability of catch and effort data. However this obscures the fact that considerable uncertainty often exists about the biological processes such as natural mortality, recruitment processes and stock structure of commercially important fish stocks. Conversely even when data are limited, empirical studies have shown that life history parameters, such as age at first reproduction, natural mortality, and growth rate are strongly correlated. Therefore biological knowledge is important both for evaluating the robustness of advice obtained from data-rich stock assessments and in allowing general rules, for example about choice of reference points (indicators of the status of a stock e.g. biomass too low or fishing pressure too high etc), to be derived for all stocks.

Fisheries management is concerned with trying to set, and then achieve, realistic management objectives. This is carried out through defining management measures of interest, for example spawning stock biomass (SSB) and fishing mortality (F), and then setting values of a range of reference points for these measures. These reference points can be used as targets, for example B_{MSY} , or limits, for example, F_{crash} . However, achieving these management objectives is made difficult by, amongst other things, the impact of biological and ecological uncertainty on the dynamics of the stock.

A key question for fisheries management is therefore how can research be prioritised so that the impact of biological uncertainty on achieving management objectives can be reduced? In other words how can we provide advice that is robust to uncertainty. Answering this question requires the estimation of the relative importance of the underlying biological assumptions made about the stock with respect to the management measures of interest. For example, does uncertainty about the stock recruitment relationship have a relatively bigger effect on yield and sustainability than uncertainty about natural mortality?

Sensitivity and elasticity analyses can be used to evaluate the effect of changes in system parameter values on system outputs. They are commonly used in financial and economic management, but have

also have been applied to biology and conservation [2]. Such analyses can be used within fisheries management to identify the stock assumptions that have the greatest impact on management measures and therefore where the impact of uncertainty may have the greatest effect on achieving management objectives. Sensitivities measure absolute changes, for example, by how much does the estimate of MSY change as the estimate of age at first maturity change. While elasticities measure the relative change and can be used to compare between a range of different sources of uncertainty. For example, does the length of first maturity have a larger proportional impact on estimates of MSY than the steepness of the stock recruitment relationship? Elasticity analysis has proven to be a useful tool in a number of areas of population and conservation biology, for example relating changes in vital rates to changes in the population life history [3] and to quantities of importance in management such as population viability [4]. Previously, elasticity analysis has focused on terrestrial ecology [5–7] with limited application to marine populations [8, 9]. The applicability of this approach to resource management has therefore been demonstrated and here we use it to evaluate the relative importance of the biological assumptions made in fishery stock assessment. that are too seldom questioned.

A fuller consideration of uncertainty within fisheries advice frameworks can be performed using Bayesian approaches or Management Strategy Evaluation (MSE). MSE is commonly used to evaluate the impact of different management measures, given a broad range of uncertainty. However, performing an MSE is a costly process in terms of human resources and can take several years. Therefore, tools such as elasticity analysis, which is comparatively less demanding to carry out, are important to help identify and focus research and management efforts. For example, is it more important to reduce uncertainty about the stock recruitment relationship or natural mortality or to develop harvest control rules that are robust to such uncertainty? Elasticity analyses can be used to answer such questions and prioritise research effort. It can also shift the current focus from defining stocks either as data poor or rich defined solely on fishery catch and effort towards a better understanding of biological processes.

Here we demonstrate the use of elasticity analysis for prioritising research effort with a study of the population dynamics of a fish stock based on life history theory. As such the study is not modelled on one specific species of fish. We do this by first simulating a stock based on life history relationships [10] and then by projecting the stock from an unfished to an over-exploited state. We do this in order to compute elasticities to allow us to evaluate the relative importance of the different system or biological parameters when assessing the stock relative to system characteristics defined by biological reference points. This allows us to address two important questions i.e. what is the relative importance of the different biological processes in providing advice and how robust is advice based on the common biological reference points.

Materials and Methods

Empirical studies have shown that in teleosts there is significant correlation between the life history parameters such as age at first reproduction, natural mortality, and growth rate [11]. Additionally, size-spectrum theory and multispecies models suggest that natural mortality scales with body size [12], [13] [10]. This means that from something that is easily observable, like the maximum size, it is possible to infer the life history parameters of species for which data are not easily observable or available.

[10] summarised life history characteristics and the relationships between them for a range of stocks and species. These relationships were used to parameterise an age-structured population model using relationships that describe growth, maturation and natural mortality. This population was then projected at a constant fishing mortality until equilibrium was reached for a wide range of fishing mortalities.

The analysis allows us to evaluate where more biological knowledge is needed and to identify robust reference points for use in management. Following this analysis sensitivity analysis could be conducted to help quantify the costs and benefits and MSE to develop robust management advice.

SSB and fishing mortality (F) relative to the corresponding quantity estimated from each of the

F_{MSY} , $F_{0.1}$ and F_{Crash} reference points were used as indices of stock status and exploitation. In the case of a fishing mortality equal to F_{Crash} , SSB is 0, by definition, therefore an SSB corresponding to 75% of F_{Crash} was used. F_{MSY} corresponds to the level of exploitation that provides the maximum sustainable yield, $F_{0.1}$ is a proxy for F_{MSY} and is the fishing mortality that corresponds to a point on the yield per recruit curve where the slope is 10% of that at the origin) and F_{Crash} the level of F that will drive the stock to extinction.

The elasticities of these indices in each year relative to the parameters in model were then used to evaluate the relative importance of the various processes (i.e. growth, maturation, stock recruitment, natural mortality and selectivity of the fishery) and the parameterisation of those process (e.g. K the rate of growth and L_∞) with respect to stock status.

The calculation of reference points and fishing mortality also depend upon the selection pattern, since not all ages are equally vulnerable to a fishery. If there is a refuge for older fish, a higher level of fishing effort will be sustainable. Also, if the fecundity of older fish is greater than the fecundity of younger fish of the same mass-at-age, e.g. due to maternal effects or repeat spawners being more fecund then a consideration of the interactions between biology and selectivity will be important.

[Uh oh just realised we have a problem with F for fishing mortality and fecundity - maybe best to switch the F for fecundity to EP i.e. egg production or have it as Fec]

0.1 Life History Relationships

The Russell equation [14] summarises the key processes influencing the dynamics of exploited populations i.e.

$$f(B_2) = B_1 + (G + R) - (F + M) \quad (1)$$

where a biomass B_2 is a function of the biomass in the previous year (B_1), gains due to growth (G) and recruitment (R) and losses due to fishing (F) and natural mortality (M). Two other factors have been recognised since Russel originally formulated this equation i.e. the gains through immigration (I) and losses through emigration (E) thus modifying the original equation to:

$$f(B_2) = B_1 + (G + R + I) - (F + M + H) \quad (2)$$

The knowledge about these processes affects our ability to provide robust scientific advice. In this paper we concentrate on G,R,F and M as we assume a single heterogeneous population with out emmigration (H) or immigration (I); However our approach could be extended to include H and I.

In order to provide a generic framework for modelling stock dynamics, life history relationships were used to parameterise appropriate functional forms for the various processes This allows processes to be modelled for a range of species and stocks under a variety of assumptions and for the impact of the various parameters to be evaluated.

Growth was modelled by the Von Bertalanffy growth equation [15]

$$L_t = L_\infty(1 - \exp(-k(t - t_0))) \quad (3)$$

where K is the rate at which the rate of growth in length declines as length approaches the asymptotic length L_∞ and t_0 is the time at which an individual is of zero length.

Length is converted to mass using the condition factor, a and allometric growth coefficient, b .

$$W = a \times L_t^b \quad (4)$$

Recruitment is split into Stock Reproductive Potential (SRP) and the stock recruitment relationship (SRR).

SRP is the sum of the products of the numbers of females, n , proportion mature-at-age, Q and their mean fecundity-at-age, F , i.e.

$$SRP = \sum n \times Q \times F \quad (5)$$

where their mean fecundity-at-age is equal to

$$O = a \times L^{b'} \quad (6)$$

if a and b are the same as in equation 3 then SRP is equivalent to female spawning stock biomass (SSB). However, generally the fecundity to length relationship differs from the weight to length relationship due to variations caused by fish condition and age effects altering the relationship between weight and eggs produced [16].

Proportion mature is modelled by the logistic equation with 3 parameters: age at 50% (a_{50}) and 95% (a_{95}) mature and the asymptotic value m_{∞} . The latter allows SRP to not be equivalent to stock mass-at-age.

$$f(x) = \begin{cases} 0 & \text{if } (a_{50} - x)/a_{95} > 5 \\ a_{\infty} & \text{if } (a_{50} - x)/a_{95} < -5 \\ \frac{m_{\infty}}{1.0 + 19.0^{((a_{50} - x)/a_{95})}} & \text{otherwise} \end{cases} \quad (7)$$

Here the value of a_{50} comes from the empirical relationship between L_{∞} and age at maturity [10]:

$$a_{50} = 0.72 \log L_{\infty}^{0.93} \quad (8)$$

We use a Beverton and Holt stock recruitment relationship reformulated in terms of steepness (h), virgin biomass (v) and $S/R_{F=0}$, where steepness is the ratio of recruitment at 20% of virgin biomass to virgin recruitment (R_0).

For the BevertonHolt stock-recruit formulation:

$$R = \frac{0.8 \times R_0 \times h \times S}{0.2 \times S/R_{F=0} \times R_0(1 - h) + (h - 0.2)S} \quad (9)$$

Steepness is difficult to estimate from stock assessment data sets and there is often insufficient range in biomass levels that is required for its estimation [17]. Steepness and virgin biomass were set to 0.9 and 1000 t respectively.

Natural mortality at size is derived from the life history relationship [18].

$$M = \exp(M1 + M2 \log(L) + 1.51 \log(L_{\infty}) + 0.97 \log(k) + a[5]/T), \quad (10)$$

where $M1$ (which determines the average natural mortality) = -2.11, $M2$ (which determines the rate at which natural mortality declines with length) = -1.70 and L is the average length of the fish (in cm) for which the M estimate applies. Here we use the length at mid-year to calculate the natural mortality at age.

Selection pattern of the fishery can be represented by a double normal (see [19]) with three parameters that describe the age at maximum selection (a_1), the rate at which the lefthand limb increases (sl) and the righthand limb decreases (sr) which allows flat topped or domed shaped selection patterns to be chosen.

Even in data poor situations where catch-at-age for the entire catch time series is not available, some data will normally exist for some years or gears or for similar stocks and species. In cases where some length frequency data are available the shape of selection pattern, i.e. age at recruitment to the fishery, can be estimated using a method like that of [20]. This allows a double normal curve to be parameterised, i.e. age at maximum selectivity and whether the selection pattern is flat topped or dome shaped.

$$f(x) = \begin{cases} 2^{-[(x-a_1)/s_L]^2} & \text{if } x < a_1 \\ 2^{-[(x-a_1)/s_R]^2} & \text{otherwise} \end{cases} \quad (11)$$

0.2 Seasonality

The model is a discrete population model where the number of individuals in a year-class in a year is a function of the number of individuals in the previous year. However, processes like growth, maturation, natural mortality and fishing occur in different seasons of the year. Therefore to take account of this the age for which the expected values of mass, maturity and natural mortality-at-age can vary. For the stock mass and lengths-at-age are calculated at spawning time, catch mass-at-age is calculated in mid year and natural mortality is a function of the lengths-at-age mid year.

0.3 Stock projections

Using the relationships described above we generate a fully specified age-structured stock based on a value of $L_\infty=100$ cm. The stock is projected forward through time at different levels of constant fishing pressure ranging from no fishing ($F=0$) to over exploited ($F = F_{crash}$). The management measures of interest are the equilibrium SSB, yield and biomass relative to their reference point values corresponding to F_{MSY} , $F_{0.1}$ (a proxy for F_{MSY}) and F_{crash} , a limit reference point, e.g. SSB/SSB_{MSY} , $SSB/SSB_{F0.1}$ etc.

$F_{0.1}$ is the fishing mortality on the yield per recruit curve where the slope is 10% of that at the origin, a conservative proxy for F_{MSY} . F_{crash} is the fishing mortality that will drive the stock to extinction since it is equivalent to a R/S greater than the slope at the origin of the stock recruitment relationship, i.e. recruitment can not replace removals for a fishing mortality equal to F_{crash} .

0.4 Elasticity

As mentioned above, elasticity analysis can be used to measure the proportional change of a system characteristic to a change in a system parameter. The general equation for calculating the elasticity of system characteristic y with respect to system parameter x is:

$$E_{y,x} = \left| \frac{\partial \ln y}{\partial \ln x} \right| \quad (12)$$

The absolute value operator is used for simplicity although the elasticity can also be defined without the absolute value operator when the direction of change is important, e.g. to evaluate if a reduction in natural mortality increases or decreases MSY reference points.

Here we calculate the elasticities of the management measures described above with respect to the life history and selectivity parameters grouped into the categories: growth (K, t_0, a, b, L_∞), maturity

($a50$, $ato95$ and $asym$), natural mortality ($M1$ and $M2$), the stock recruitment relationship (h and vb) and the selectivity ($a1$, sl and sr). For example, the elasticity of SSB relative to SSB_{MSY} with respect to L_∞ is calculated as:

$$E_{SSB_{MSY}, L_\infty} = \left| \frac{\partial \ln SSB_{MSY}}{\partial \ln L_\infty} \right| \quad (13)$$

Elasticities are calculated for every level of F used in the projections and therefore show how the current state of the stock and exploitation rate affect the relative importance of the different life history parameters, i.e. where the most important source of uncertainty is.

Using life history theory means that elasticities could have been calculated conditional on L_∞ alone since parameters such as K , age at first maturity and natural mortality at age are functions of L_∞ . However, in this study these values were set before the elasticities are calculated, i.e. the elasticities with respect to L_∞ do not reflect the impact of L_∞ on these life history relationships, only on the impact of the stock dynamics through the von Bertalanffy growth and other equations.

Advice requires estimates of stock status relative to reference points. Even though many aged based assessment methods are assumed to provide absolute estimates of stock status a small change in M can result in a large change in the estimates of abundance and fishing mortality. Since M is never known exactly then advice is in fact relative. I.e. advice is based on whether stock or fishing mortality is increasing or decreasing. Kell et al showed that relative advice i.e. stock or fishing mortality relative to a reference point is more robust than an absolute estimate. Therefore in our elasticity analysis we used relative values, i.e. SSB relative to B_{MSY} and F relative to F_{MSY} , we also compared type of reference points, i.e. target reference points such as those based on MSY and reference points designed to be limits such as F_{Crash} . This the robust of different reference points to be evaluated, e.g. are reference points based on fishing mortality more robust than those based on biomass, are some reference points more robust when used as targets and others more robust when used as limits.

Results

The assumed growth, natural mortality, proportion mature and selectivity-at-age for the simulated stock are shown in Figure 1. The equilibrium values of SSB and Yield for a range of fishing mortalities and recruitment and yield for a range of $SSBs$ are shown in Figure 2; the corresponding values for the MSY , $F_{0.1}$ and F_{Crash} reference points are also shown.

The equilibrium dynamics over the range of fishing mortalities from 0 to 75% of F_{Crash} are presented as a phase plot (Figure 3) where the x-axis corresponds to *biomass* relative to B_{MSY} and the y-axis to *harvest* relative to F_{MSY} . Quadrants are defined for stock and fishing mortality relative to B_{MSY} and F_{MSY} ; i.e. red when $B < B_{MSY}$ and $F > F_{MSY}$, green if $B \geq B_{MSY}$ and $F \leq F_{MSY}$ and yellow otherwise. The red quadrant therefore refers to an overfished stock subject to overfishing and green to a stock which is neither overfished or subject to overfishing.

Elasticities with respect to each parameter are plotted for SSB in Figure 4 and for F in Figure ??, the yellow vertical line indicates the boundary between the red and green quadrants and the horizontal line where the value of the elasticity is 0, i.e. where varying a parameter has no effect on the measure of interest. The elasticities are then plotted by process in Figures 6 and 7.

The plots allow several important questions to be addressed, i.e. what is the relative impact of the different biological processes and parameters on the estimates of stock status and exploitation? Does the impact depend on the reference point and quantity (e.g. SSB or F) chosen or on the status of the stock. I.e. does knowledge of particular parameters and processes depend on whether the stock is depleted or within safe biological limits? Answering these questions will help in choosing robust target and limit reference points to be made.

From figure 4 MSY and $F_{0.1}$ it can be seen that elasticities increase in magnitude as F increases (and SSB decreases). Overall the elasticities are similar, in that the most important process is natural mortality, followed by steepness, L_∞ , age of recruitment to the fishery and then age at 50% mature. The main difference between MSY and $F_{0.1}$ is that steepness has a bigger impact on the latter reference point. For F_{crash} the shape of the elasticities are similar but their signs change; for example $M1$ is initially positive but as F increases becomes negative. This means that the magnitude of the elasticities is smallest at around B_{MSY} and F_{MSY} . The magnitudes of the elasticities for F_{crash} are in general less than for B_{MSY} and F_{MSY} .

Figure 5 presents the results for F , the main difference with the SSB elasticities is that they do not vary with F or SSB and on average have smaller magnitudes. Again natural mortality has the biggest effect for MSY and $F_{0.1}$; followed by L_∞ for MSY and L_∞ and steepness for $F_{0.1}$. For F the allometric scaling coefficient (b) becomes important. For F_{crash} natural mortality has less of an impact and steepness becomes more important as does age at recruitment to the fishery.

Since the example is not based on a specific stock the discussion of the results will concentrate on general aspects.

Discussion

Stock assessment mainly considers uncertainty in observations and processes such as recruitment variability when uncertainty about the dynamics (i.e. model uncertainty) has a larger impact on achieving management objectives [21]. Relationships between body size and life history parameters have been described for many taxonomic groups [22]. This means that biological parameters are often strongly correlated and so life history theory can be used to evaluate the assumptions made in stock assessments, infer parameters for data poor stocks and allow general rules and principles to be derived. A main aim of this study is to use life histories relationships and elasticity analysis to evaluate the relative importance of different biological processes and the robust of advice to uncertainty about those processes.

The approach is important both for data rich and poor stocks since uncertainty about key biological processes such as growth, spawning reproductive potential, natural mortality and stock structure exists in data rich assessments (Kell et al, submitted, Kell et al), although is often ignored. There is also a need to change from considering stocks as being mainly data rich/poor to being information rich/poor so that the collection of information needed to support scientific analysis can be prioritised. For example the definition of data rich means often means data sufficient to conduct virtual population analysis (VPA), rather than do we have sufficient knowledge about stock structure, natural mortality, growth, catches and the stationarity of processes to ensure that the assumptions of VPA are met and that advice based on the analysis is robust.

The evaluation of the value of biological information can be done through a variety of approaches, e.g. developing priors for use in Bayesian estimation or conducting sensitivity analyses as part of an MSE. However, both approaches are relative complex and time consuming so that they are unlikely to be routinely applied to many stocks. Applications also tend to be case specific and so difficult to compare. In contrast elasticity analysis is relatively simple to apply and using life histories relationships allows models to be readily parametrised and case studies to be compared.

Considering life history relationships ensure consistency in advice, allow the transfer of knowledge about biological processes from one stock to another. Will also assist in designing research to provide a better understanding of biological processes and how to develop robust advice frameworks. For example why is natural mortality of cod in the Irish Sea and bluefin tuna in the West Atlantic assumed to be 0.2 and 0.14 respectively at all ages but for North Sea cod and East Atlantic and Mediterranean bluefin assumed to vary with age? What are the consequences of these assumptions and are they relatively more important than the assumptions about spawning reproductive potential. To be consistent with life history theory M should vary with age and comparative studies could help in estimating appropriate

functional relationships.

The analysis allowed several important questions to be addressed, i.e. what is the relative impact of the different biological processes and parameters on the estimates of stock status and exploitation? Does the impact depend on the reference point and quantity (e.g. SSB or F) chosen or on the status of the stock. I.e. does knowledge of particular parameters and processes depend on whether the stock is depleted or within safe biological limits? Answering these questions will help in choosing robust target and limit reference points to be made.

The elasticities of SSB varied with the level of depletion and F . However, for F elasticities did not vary. There was little difference between F_{MSY} and $F_{0.1}$, but for F_{crash} bigger differences were seen. This means that elasticity analysis may help identify appropriate reference points for use as limits and targets within harvest control rules.

For both SSB and F the natural mortality parameters $M1$ and $M2$ had the biggest proportional effect. The next most important parameter for SSB was $a1$ the selectivity parameter for age at full selection. The steepness of the stock recruitment relationship is important when considering SSB relative to SSB_{MSY} and $SSB_{F0.1}$ but less so relative to SSB_{Fcrash} . The other processes (growth and maturity) have similar impacts to each other; the most important parameters are K , age at 50% mature and age at recruitment to the fishery. The natural mortality parameters ($M1$ and $M2$) are again the most important process more important than for example the stock recruitment relationship. Steepness have less of an affect compared to the analysis for SSB. MSY has the lowest elasticities and so is the more robust reference point for fishing mortality.

Elasticity analysis is a potentially important method for determining robustness of scientific advice. Since if a particular reference point is dependent upon a parameter or process which is highly uncertain then it may be better to find a reference point that is less dependent on that parameter or process. Especially if reducing uncertainty on that parameter is costly or difficult. For example if a reference point depends upon a parameter such as M or steepness that can not be observed directly it may be better to use a reference point that is less sensitivity to knowledge about these processes, i.e. use a reference point where uncertainty can more readily be reduced through data collection, e.g. growth and maturity.

Typically, elasticity analysis is only concerned with the magnitude of the elasticity. However, the sign or direction of the elasticity can be important when the uncertainty, or noise, driving the parameter has an autocorrelation structure i.e. can not be represented by white noise. For example, it has been shown that there can be important cohort effects and autocorrelation in growth processes (REF 3 stocks paper). This may result in several continuous years of high or low values for K .

Although we considered the processes of growth, maturity, natural mortality and recruitment as separate processes these processes are linked. Since the steepness of the stock recruitment relationship depends on spawning reproductive potential (SRP). Which depends on viable egg production [23] and subsequent recruitment which is linked with the assumptions about gonadal growth and the processes involved in the first year of life. Although a single M is often used for the earliest life history stage i.e. eggs to the end of the first year of life [24] and [25]. Various mortality processes serially affect life history stages through the first year of life, e.g. in relation to settlement, overwintering and juvenile stages [26], [27] and [28]. However there are very little information on many of the commercially important species that will allow an estimate of stock recruitment parameters such as steepness (e.g. [29]). The growth trajectories of individuals may not follow a von Bertalanffy growth curve due to M causing differential mortality within a cohort. While length-weight relationships and condition can affect the maturity ogives and schedules and these can vary due to changes in ecosystem productivity and density-dependent effects. Other factors that need to be considered include sub-stock structure and their associated dynamics. Examples include herring [30] and the influence on the assessment process [31] and sub-stock structure or metapopulations are known to exist for quite a few stocks e.g. cod in the Western [32] and Eastern Atlantic (North Sea) [33] and bluefin in the Mediterranean (ref ?).

Elasticity analysis can be extended to consider such problems e.g. [34] and [35] and help identify key

processes.

1 Conclusions

Main message • Reprise Intro

- Prioritising uncertainty and assumptions in biological processes for management objectives.
- conceptual change] from thinking from just about data poor/rich to understanding poor/rich
- Transfer of knowledge] about boil processes data rich to data poor test robustness (life history characteristics) something that ICES/EU is struggling with now.

Further exploration of issues b

- Uncertainty in biological processes targets & ref points
- Explore ref points robust to changes in priorities
- Impact of exploitation on priorities and rankings (above FMSY and below FMSY)
- Impact of correlation between biological processes
- Discuss our results of priorities/ranking of processes
- Use of sign or direction of elasticity, rather than magnitude
- Methods and approaches we used:
- Use of sensitivity and elasticity, & why better than Bayesian or MSE, but why not replace it. Simplify may be better and cheaper.

Briefly comment on our assumptions c

- Relevance of this study
- Briefly talk about M, growth, recruitment, sex dimorphism, substock structure] (already written)
- What can this study offer the world and how is it relevant

Acknowledgments

References

1. Garcia S (1996) The precautionary approach to fisheries and its implications for fishery research, technology and management: an updated review. FAO Fisheries Technical Paper : 1–76.
2. de Kroon H, Plaisier A, van Groenendael J, Caswell H (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* 67: 1427–1431.
3. Grant A, Benton T (2003) Density-dependent populations require density-dependent elasticity analysis: an illustration using the LPA model of tribolium RID c-6493-2009. *Journal of Animal Ecology* 72: 94–105.
4. Heppell S (1998) Application of life-history theory and population model analysis to turtle conservation. *Copeia* : 367–375.
5. Benton TG, Grant A (1999) Elasticity analysis as an important tool in evolutionary and population ecology. *Trends in Ecology and Evolution* 14: 467 - 471.
6. Hunter C, Moller H, Fletcher D (2000) Parameter uncertainty and elasticity analyses of a population model: setting research priorities for shearwaters. *Ecological Modelling* 134: 299 - 324.
7. Pichancourt JB, Burel F, Auger P (2006) A hierarchical matrix model to assess the impact of habitat fragmentation on population dynamics: an elasticity analysis. *Comptes Rendus Biologies* 329: 31 - 39.
8. Rogers-Bennett L, Leaf RT (2006) Elasticity analyses of size-based red and white abalone matrix models: Management and conservation. *Ecological Applications* 16: 213-224.
9. Heppell S (2007) Elasticity analysis of green sturgeon life history. *Environmental Biology of Fishes* 79: 357-368.
10. Gislason H, Pope J, Rice J, Daan N (2008) Coexistence in north sea fish communities: implications for growth and natural mortality. *ICES Journal of Marine Science: Journal du Conseil* 65: 514–530.
11. Roff D (1984) The evolution of life history parameters in teleosts. *Canadian Journal of Fisheries and Aquatic Sciences* 41: 989–1000.
12. Andersen K, Beyer J (2006) Asymptotic size determines species abundance in the marine size spectrum. *The American Naturalist* 168: 54–61.
13. Pope J, Rice J, Daan N, Jennings S, Gislason H (2006) Modelling an exploited marine fish community with 15 parameters—results from a simple size-based model. *ICES Journal of Marine Science: Journal du Conseil* 63: 1029–1044.
14. Russell E (1931) Some theoretical considerations on the overfishing problem. *Journal du conseil* 6: 3.
15. Von Bertalanffy L (1957) Quantitative laws in metabolism and growth. *Quarterly Review of Biology* : 217–231.
16. Pérez-Rodríguez A, Morgan M, Rideout R, Dominguez-Petit R, Saborido-Rey F, et al. (2012) Study of the relationship between total egg production, female spawning stock biomass, and recruitment of flemish cap cod (*gadus morhua*).
17. Anonymous (2011) Report of the 2011 issf stock assessment workshop. ISSF Technical Report 2011-02.

18. Gislason H, Daan N, Rice J, Pope J (2010) Does natural mortality depend on individual size. *Fish and Fisheries* 11: 149–158.
19. Hilborn R, Maunders M, Parma A, Ernst B, Paynes J, et al. (2000) Documentation for a general age-structured Bayesian stock assessment model: code named Coleraine. FRI/UW 00/01. Fisheries Research Institute, University of Washington.
20. Wetherall J, Polovina J, Ralston S (1987) Estimating growth and mortality in steady-state fish stocks from length-frequency data. In: *ICLARM Conf. Proc.* pp. 53–74.
21. Punt A (2008) Refocusing stock assessment in support of policy evaluation. *Fisheries for Global Welfare and Environment* : 139–152.
22. Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters R, et al. (1978) Relationships between body size and some life history parameters. *Oecologia* 37: 257–272.
23. Trippel E (1999) Estimation of stock reproductive potential: history and challenges for canadian atlantic gadoid stock assessments. *Journal of Northwest Atlantic Fishery Science* 25: 61–82.
24. Houde E (1989) Subtleties and episodes in the early life of fishes. *Journal of Fish Biology* 35: 29–38.
25. Houde E (2002) Mortality. *Fishery science: the unique contributions of early life stages* Blackwell Science, Oxford : 64–87.
26. Nadsh R, Geffen A Mortality through the early life-history of fish: What can we learn from european plaice (*pleuronectes platessa l.*)? .
27. McGurk M (1986) Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. *Marine Ecology Progress Series* 34: 227–242.
28. Pepin P (1991) Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 503–518.
29. Mangel M, Brodziak J, DiNardo G (2010) Reproductive ecology and scientific inference of steepness: a fundamental metric of population dynamics and strategic fisheries management. *Fish and Fisheries* 11: 89–104.
30. Dickey-Collas M, Nash R, Brunel T, Van Damme C, Marshall C, et al. (2010) Lessons learned from stock collapse and recovery of north sea herring: a review. *ICES Journal of Marine Science: Journal du Conseil* 67: 1875.
31. Kell L, Dickey-Collas M, Hintzen N, Nash R, Pilling G, et al. (2009) Lumpers or splitters? evaluating recovery and management plans for metapopulations of herring. *ICES Journal of Marine Science: Journal du Conseil* 66: 1776–1783.
32. Frank K, Brickman D (2001) Contemporary management issues confronting fisheries science. *Journal of Sea Research* 45: 173–187.
33. Heath M, Kunzlik P, Gallego A, Holmes S, Wright P (2008) A model of meta-population dynamics for north sea and west of scotland cod—the dynamic consequences of natal fidelity. *Fisheries Research* 93: 92–116.
34. Root K (1998) Evaluating the effects of habitat quality, connectivity, and catastrophes on a threatened species. *Ecological Applications* 8: 854–865.

35. Henle K, Sarre S, Wiegand K (2004) The role of density regulation in extinction processes and population viability analysis. *Biodiversity and Conservation* 13: 9–52.

Figure Legends

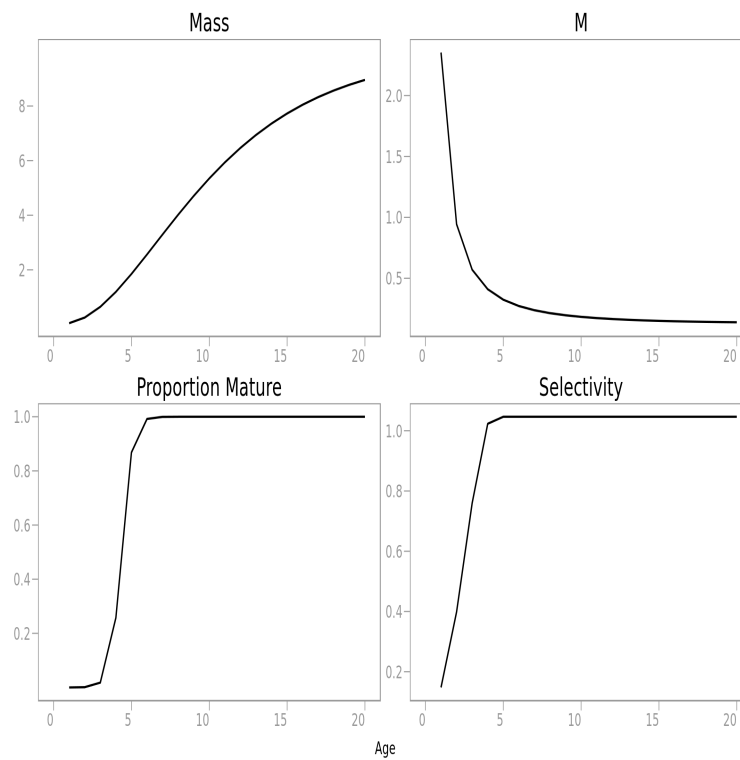


Figure 1. Mass, natural mortality, proportion mature and selection pattern-at-age.

Tables

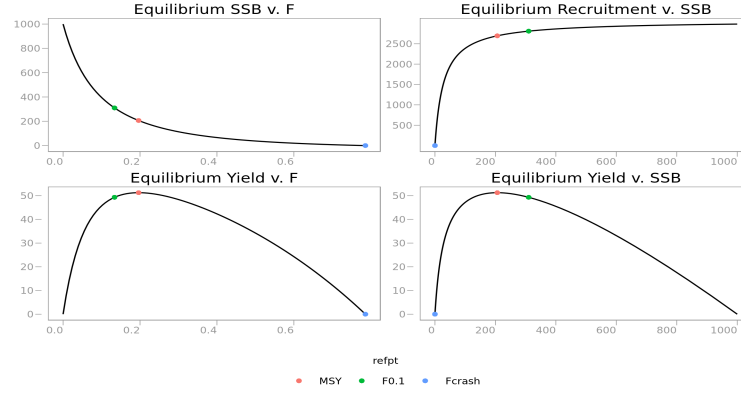


Figure 2. Equilibrium (i.e. expected) values of SSB and yield versus fishing mortality and recruitment and yield versus SSB; points correspond to MSY and MSY proxies ($F_{0.1}$, F_{Max} , SPR30%) and limit (F_{crash}) reference points.

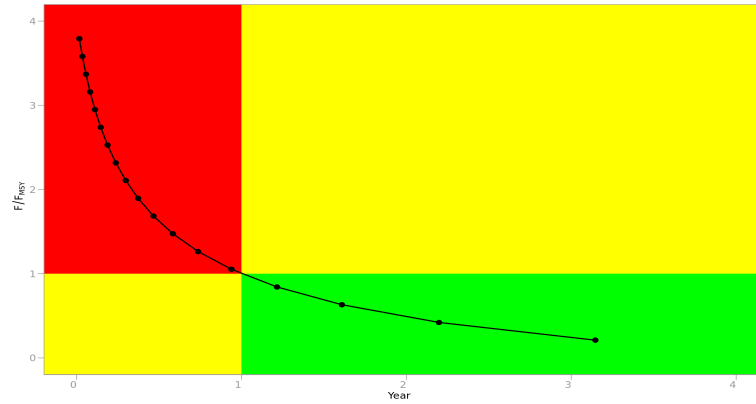


Figure 3. Simulated trajectories of recruitment, SSB and yield for a increasing F.

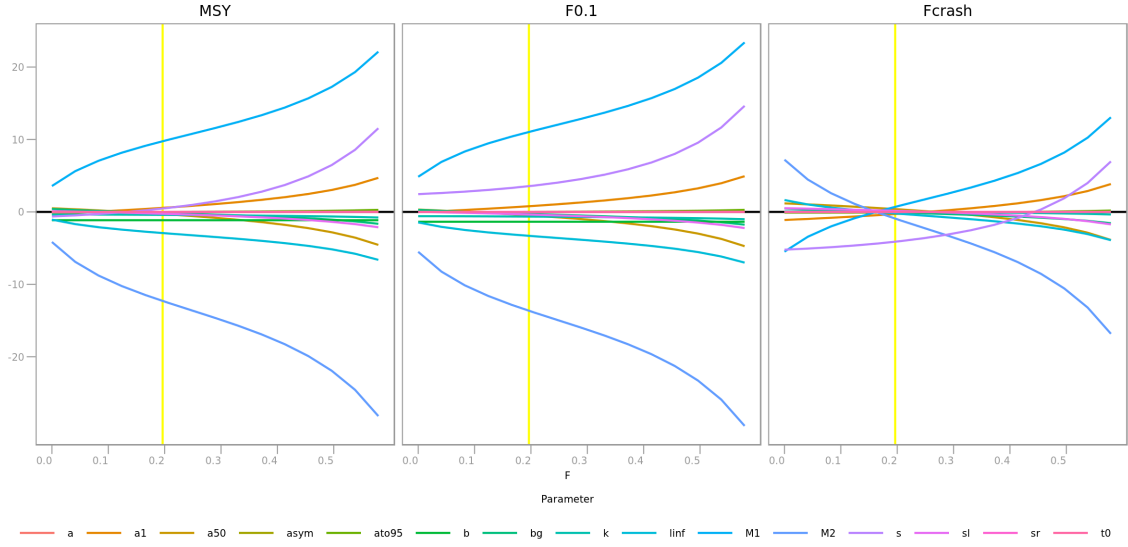


Figure 4. Plots of elasticities of SSB relative to the MSY, $F_{0.1}$ and F_{crash} reference points.

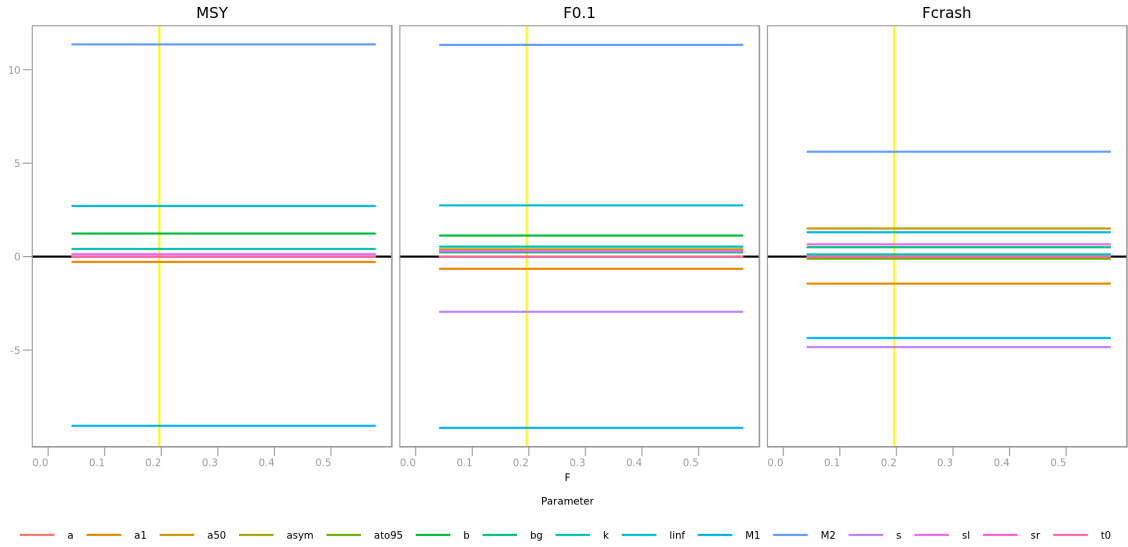


Figure 5. Plots of elasticities of F relative to the MSY, $F_{0.1}$ and F_{crash} reference points.

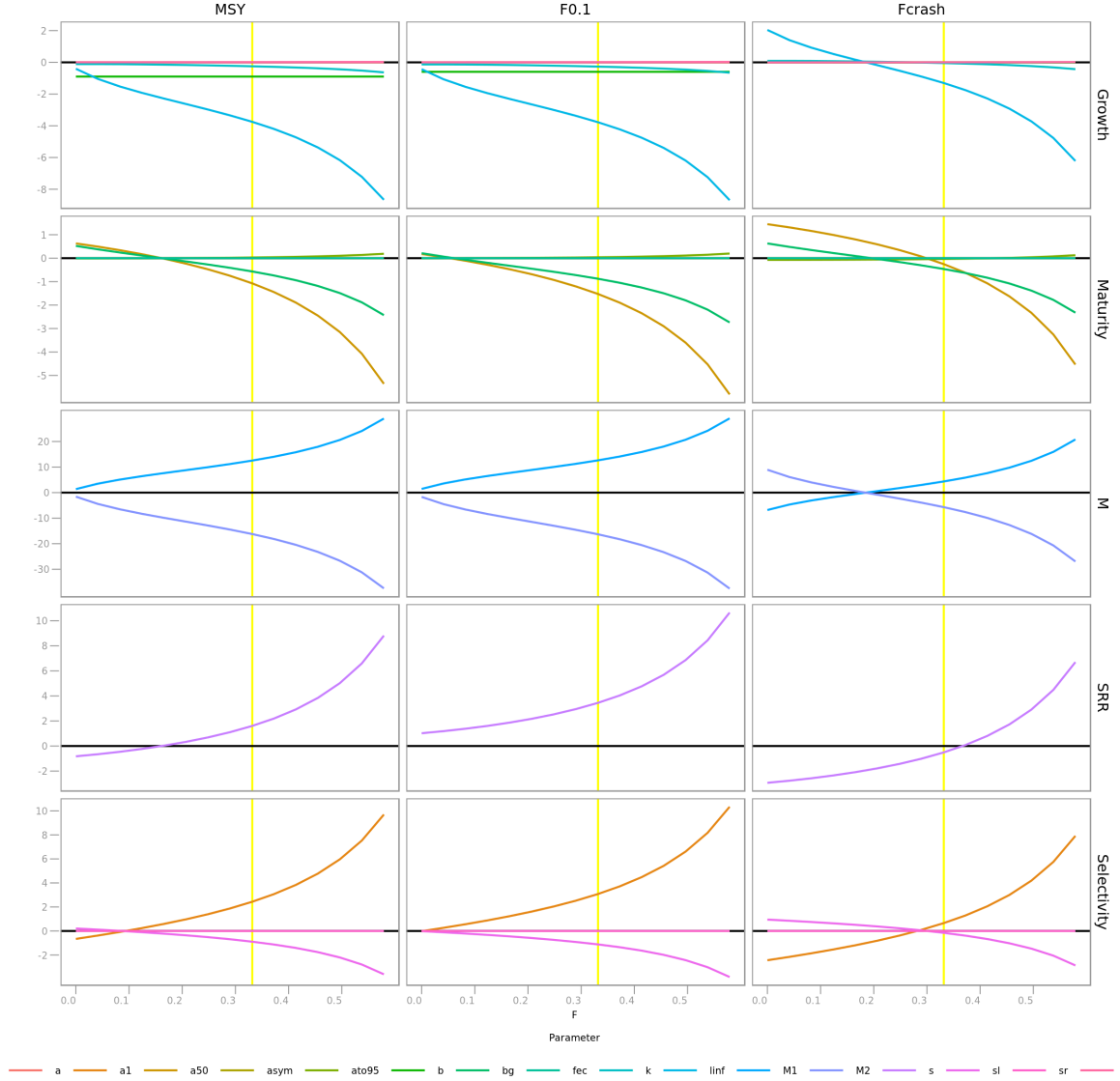


Figure 6. Plots of elasticities of SSB relative to the MSY, $F_{0.1}$ and F_{crash} reference points.

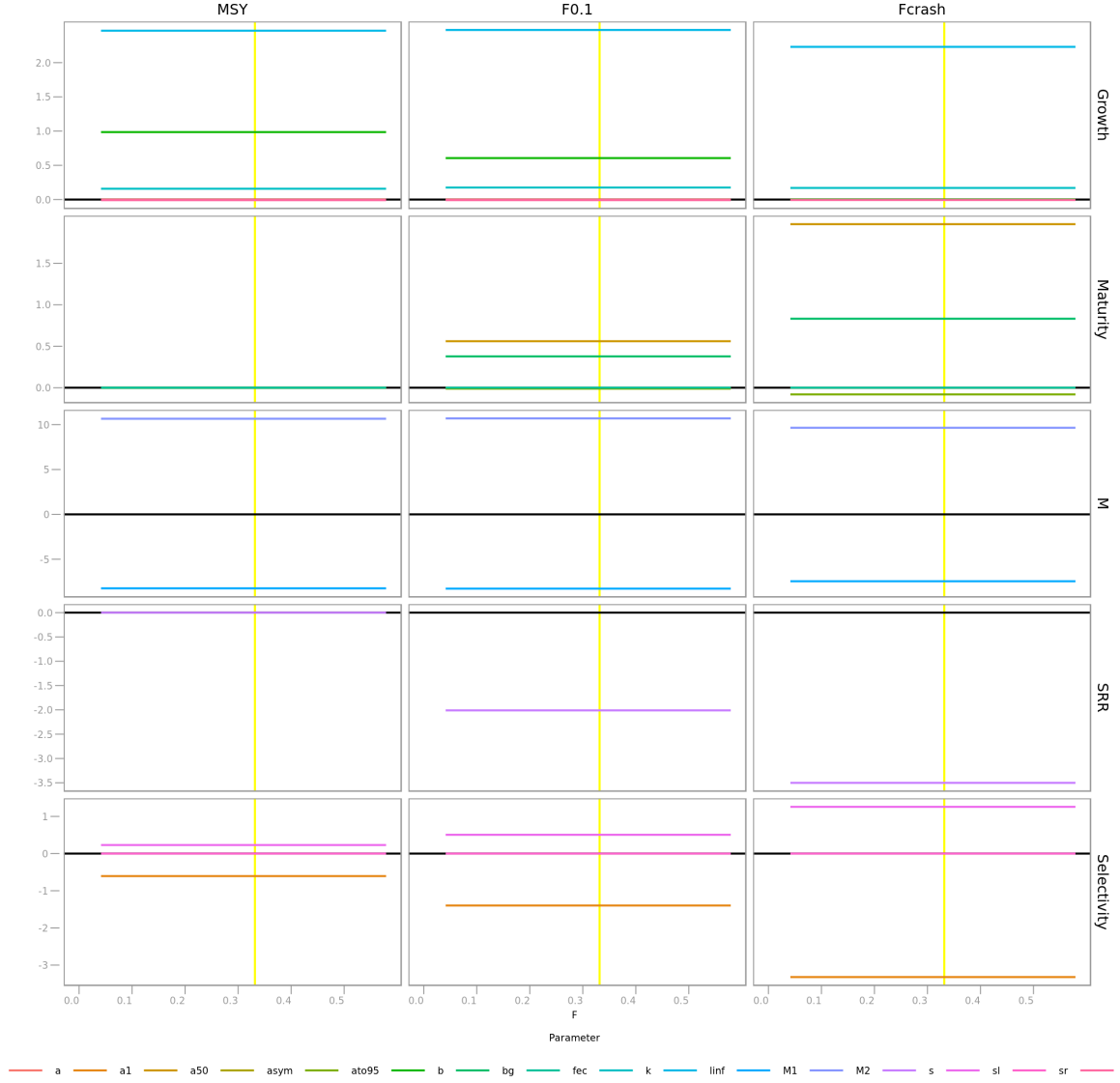


Figure 7. Plots of elasticities of F relative to the MSY , $F_{0.1}$ and F_{crash} reference points.