

Elasticity Analysis

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Submitted to Proceedings of the National Academy of Sciences of the United States of America

When exploiting populations, reference points for exploitation rate or biomass are often set as targets or limits. Determining these reference points can be difficult, especially when there is little understanding of a populations dynamics. A lack of understanding is often confused with a lack of data on exploitation or trends over time of a population. Here we show that elasticity analysis can be used to investigate and prioritise which elements of uncertainty in life history dynamics are relevant when determining reference points for exploited populations. The analysis allows several important questions to be addressed. What is the relative impact of the different biological processes and parameters on the estimates of population 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 population is depleted or within safe biological limits? Does the exploitation rate impact on the suitability of reference points? We suggest that answering these questions with the aid of elasticity analysis will help in choosing robust target and limit reference points and prioritising research effort.

Elasticity | fisheries management

Abbreviations: MSY, maximum sustainable yield; SRP, spawning reproduction potential

The adoption of the Precautionary Approach to fisheries management REF requires a formal consideration of uncertainty. An important principle of the approach is that the level of precaution should increase as uncertainty increases, i.e. 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 population structure of commercially important fish populations. 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 and transferable to all populations. 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 population. 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 population 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 REF. 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. 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 REF and to quantities of importance in management such as population viability REF. Previously, elasticity analysis has focused on terrestrial ecology [XXX] with limited application to marine populations [REFS]. 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.

Reserved for Publication Footnotes

It can also shift the current focus from defining populations 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 population based on life history theory. As such the study is not modelled on one species of fish. First we simulate a population based on life history relationships [REF] and then by projecting the population from an unfished to an over-exploited state. We then calculate elasticities to allow us to evaluate the relative importance of the different system or biological parameters when assessing the population relative to system characteristics defined by biological reference points. This allows us to address two important questions: 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 [?]. Additionally, size-spectrum theory and multispecies models suggest that natural mortality scales with body size [?], [?] [?]. 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.

[?] summarised life history characteristics and the relationships between them for a range of stocks and species. These 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.

SSB and F relative to their reference point values corresponding to F_{MSY} , $F_{0.1}$ and F_{crash} reference points were used as indices of stock status and exploitation. 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. In the case of F equal to F_{crash} , SSB is 0 by definition, therefore an SSB corresponding to 75% of F_{crash} was used.

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_{∞}).

The calculation of reference points and fishing mortality also depend upon the selection pattern, since not all ages are equally vulnerable to a fishery. For example, 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 than a consideration of the interactions between biology and selectivity will be important.

Life History Relationships. The Russell equation [?] summarises the key processes influencing the dynamics of exploited populations i.e.

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

where 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: the gains through immigration (I) and losses through emigration (E). These modify 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.

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

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

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 :

$$SRP = \sum n \times Q \times F \quad [5]$$

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 [?].

Proportion mature is modelled by the logistic equation with three 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 [?]:

$$a_{50} = 0.72 \log L_{\infty}^{0.93} \quad [8]$$

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 Beverton and Holt 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 [?]. Steepness and virgin biomass were set to 0.9 and 1000 t respectively.

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

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

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 is represented by a double normal (see [?]) with three parameters that describe the age at maximum selection ($a1$), the rate at which the left-hand 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 [?].

$$f(x) = \begin{cases} 2^{-[(x-a1)/s_L]^2} & \text{if } x < a1 \\ 2^{-[(x-a1)/s_R]^2} & \text{otherwise} \end{cases} \quad [11]$$

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 can occur in different seasons of the year. The stock mass and lengths-at-age are calculated at spawning time (the start of year), catch mass-at-age is calculated in mid year and natural mortality is a function of the lengths-at-age mid year.

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.

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:

$$E_{SSB_{MSY}, L_\infty} = \left| \frac{\partial \ln relSSB_{MSY}}{\partial \ln L_\infty} \right| \quad [13]$$

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.

Elasticities could have been calculated that are 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.

Management 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 actually relative i.e. advice is based on whether stock or fishing mortality is increasing or decreasing. Kell et al REF 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 types 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} . 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 ???. The relationship between equilibrium values of SSB, yield, recruitment and F are shown in Figure 1; 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 2) 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 3 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 5 and 6.

From figure 3 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 4 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.

Discussion

Since the example is not based on a specific stock the discussion of the results will concentrate on general aspects. There is a need for a conceptual change from categorising stocks as data or information rich or poor based solely on stock assessment needs. An understanding of the biological uncertainties and how to provide robust advice is equally if not more important. Elasticity analysis can help in identifying where a better understanding is required.

To do this the collection of information needed to support the science that underpins advice needs to be prioritised based on management objectives. For example, the definition of data rich often means data sufficient to conduct virtual population analysis (VPA). Rather, researchers should ask do we have sufficient knowledge about stock structure and the variability in productivity to ensure that the assumptions of VPA are met and that the advice based on the analysis is robust.

Fisheries science focuses on favoured factors, such as catch and time trends in abundance, and pretends that other processes, such as natural mortality and spatial structure are unimportant to the sustainable exploitation of the populations.

The approach described here will allow researchers to rationally prioritise what uncertainty in the assumptions about biological processes impact on the setting of management objectives. 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 [REF]. Relationships between body size and life history parameters have been described for many taxonomic groups [REF]. 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 provide robust advice on the uncertainty about those processes. This approach will provide

insight into what characteristics from population considered data rich can reliably be transferred to data poor populations. Currently the length and reproductive traits of populations are being used to link data rich and data poor populations. However, it has not yet been tested if this is appropriate.

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 relatively 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 parameterised and case studies to be compared. This provides a readily available tool to researchers to pin point where uncertainty is most relevant to the sustainable exploitation of their particular population. Considering life history relationships ensures consistency in advice, allows the transfer of knowledge about biological processes from one stock to another. It 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 especially when considering exploitation at MSY.

The elasticities of SSB varied with the level of depletion and F . However, the F elasticities did not vary. There was little difference between F_{MSY} and $F_{0.1}$, but for F_{crash} bigger differences were seen. In our generic simulated study, these questions were relatively easy to answer so when applied to existing populations, elasticity analysis will help in the choice of robust target and limit reference points to be incorporated into harvest control rules.

This study has shown that the uncertainty in some processes are more relevant to the setting of reference points in certain situations. For the simulated population, 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 $SSB_{F_{0.1}}$ but less so relative to $SSB_{F_{crash}}$. 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. Steepness has less of an effect compared to the analysis for SSB. MSY has the lowest elasticities and so is the more robust reference point for fishing mortality. Not all of these outcomes are intuitive without the analysis. This illustrates that 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 cannot 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 . The use of only the direction may provide enough guidance for the determination of robust reference points. Although we considered growth, maturity, natural mortality and recruitment as separate processes, these processes are linked. The steepness of the stock recruitment relationship depends on spawning reproductive potential (SRP), which depends on viable egg production [REF] and subsequent recruitment. Recruitment is also linked with the assumptions about gonadal growth and the processes involved in the first year of life. A single independent estimate of M is often used for the earliest life history stage i.e. eggs to the end of the first year of life [REF] and [REF]. Various mortality processes serially affect life history stages through the first year of life, e.g. in relation to settlement, overwintering and juvenile stages [REF], [REF] and [REF]. However, there is very little information on many of the commercially important species that will allow an estimate of stock recruitment parameters such as steepness (e.g. [REF]). The growth trajectories of individuals may not follow a von Bertalanffy growth curve due to M causing differen-

tial mortality within a cohort. 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 [REF] and the influence on the assessment process [REF] and sub-stock structure or metapopulations are known to exist for quite a few stocks e.g. cod in the Western [REF] and Eastern Atlantic (North Sea) [REF] and bluefin tuna in the Mediterranean (ref ?). Elasticity analysis can be extended to consider such problems e.g. [REF] and [REF] and help identify key processes. This study offers a simple, effective approach to not only prioritise what uncertainty impacts the determination of reference points for exploited populations but also provides insight in how to rationally transfer understanding between data rich and data poor populations. It is very clear that the overall objective is not just to reduce all uncertainty for informations sake, but to provide information for the sustainable exploitation of populations through the setting of robust reference points. It also highlights that uncertainty in various processes may not matter to sustainable exploitation, whereas increasing effort to reducing uncertainty in other processes may be of great value. The study also highlights that the ranking of relevant processes may change based on the exploitation status of the population.

ACKNOWLEDGMENTS. Finlay Scott was funded by the UK government projects MF12-5 and MF12-1.

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Fig. 1. Equilibrium (i.e. expected) values of SSB and yield verses fishing mortality and recruitment and yield verses SSB; points correspond to MSY and MSY proxies ($F_{0.1}$, F_{Max} , SPR30%) and limit (F_{crash}) reference points.

Fig. 2. Simulated trajectories of recruitment, SSB and yield for a increasing F.

Fig. 3. Plots of elasticities of SSB relative to the MSY, $F_{0.1}$ and F_{crash} reference points.

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

notes

'fi' and 'ff' will sort

references bibtex bibliography is up to date, it is just that in the PNAS format they do not use a bib file but include the refere directly; need to look at IFAs and redo tex file

figs This is a PNAS eps issue; need to look at IFAs and redo tex file

maternal & repeat spawners There is stuff on maternal effects and repeat spawners at the end of the first section of Materials and Methods, and also in the Recruitment bit. However, as this is not actually included in the elasticity analysis move this to the Discussion.

Eqn 2 Equation 2 (the second Russell equation) is defined and then we say we don't use it. Maybe we should remove it and move the point about including immigration/emigration to the Discussion.

M&M The last paragraph of Material and Methods essentially repeats what has already been said. I suggest that we delete it and maybe move the point about relative advice to the Introduction or Discussion.

results is still thin. Specifically, there is almost no analysis of Figures 5 and 6 which are arguably the juiciest plots in the paper. My proposal was actually to remove figures 5 and 6. So first do we agree or do we want 3,4,5and6?

[favoured factors Rather than "fix" this sentence rethread the paper so that the issue is discussed as appropriately in the intro, m-m, results and discussion

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

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