Elasticity and Life History Relationships

Laurence T. Kell *, Finlay Scott †, Paul De Bruyn ‡, Richard D.M. Nash § and Mark Dickey-Collas ¶

*ICCAT Secretariat, C/Corazón de María, 8. 28002 Madrid, Spain.,†The Fisheries Laboratory, Lowestoft, NR33 0HT, Suffolk, England.,‡AZTI Tecnalia. Herrera kaia portualdea z/g, 20110 Pasaia, Gipuzkoa, Spain,§Institute of Marine Research, PO Box 1870 Nordnes, 5817 Bergen, Norway, and ¶Wageningen IMARES, P.O. Box 68, 1970 AB IJmuiden, The Netherlands ICES, H. C. Andersens Boulevard 44-46, DK-1553 Copenhagen V, Denmark.

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

When exploiting populations, references 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 allowes 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.

term | term | term

Elasticity | fisheries management | life history

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

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 so that risk remains constant. So that yields are greater in data rich than poor situations. Where the definition of data rich and poor is often made on the availablity of fisheries data. This can obscure the fact that considerable uncertainty also often exists about biological processes such as natural mortality, recruitment and population structure for commercially important fish populations. For example natural mortality is unknown for many stocks and is commonly assumed to be constant. However, even when data are limited, empirical studies have shown that life history parameters, such natural mortality and as age at first reproduction are strongly correlated with and growth rate and size [2].

Biological knowledge can therefore be important both for evaluating the robustness of advice obtained from data-rich stock assessments and in allowing general rules, to be derived and transferable to all populations. For example about choice of indicators of stock status, i.e. reference points to indicate whether biomass is too low or fishing pressure too high, for use in fisheries management.

Fisheries management is concerned with setting and then trying to achieve, realistic management objectives. This requires defining limit and target reference points, e.g. for spawning stock biomass (SSB) and fishing mortality (F) and agreeing associated management measures.

However, achieving agreed 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 be reduced? In other words, how can we provide advice that is robust to uncertainty? Answering this question requires the evaluation of the relative importance of the underlying biological assumptions made with respect to the management measures of interest. For example, does uncertainty about recruitment have a relatively bigger effect on longterm yield and sustainability than uncertainty about natural mortality?

Senstivity and elasticity analyses can be used to evaluate the effect of changes in system parameters on system outputs. 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?

Se[illegible]vity analysis is often used in stock assessment to see how much the perception of the stock changes when an option of a stock assessment program is change[illegible]However, elasticity analysis has seldom been used althoug[illegible]mmonly used in financial and economic managment and despite being applied in conservation biology [3[illegible] the latter case it is has been used to relate changes in v[illegible]rates to changes in the population life history [4] and to quantities of importance in management such as population viability [5]. Previously, elasticity anaysis has focused on terrestrial ecology [6, 7, 8] with limited application to marine populations [9, 10]. 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.

Consideration of uncertainty within fisheries advice frameworks has been conducted using Bayesian approaches or Management Strategy Evaluation (MSE) and is regarded as state-of-the-art. 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, can take several years and requires a high level of expertise. Therefore, tools such as elasticity analysis, which is comparatively less demanding to carry out, will be important to help identify and focus and prioritise research and management efforts. For example, to answer such

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questions as is it more important to reduce uncertainty the biology or to develop better management measures such as reference points that are robust to such uncertainty?

Elasticity analyses 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. Ourstudy is not a case study that considers a single species, instead we simulate a population based on life history relationships in order to develop a framework that can be used to derive general rules and applied to a range of case studies.

Our elasticity analysis evaluates the relative importance of the biological processes and assumptions for assessing a stock relative to biological reference points. We do this by projecting a population from an unfished to an over-exploited state and then evaluate the elasticity of stock status and fishing mortality relative to a range of reference points. The elasticities allow us to evaluate the relative importance of the different biological parameters when assessing the population relative to system characteristics defined by the reference points. We use relative estimates since these have been shown to be more robust that absolute estimates [11] and are used ny the tuna Regional Fisheries Management Organisations (tRFMOs) when providing advice. 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?

Results

The assumed growth, natural mortality, proportion mature and selectivity-at-age for the simulated stock are shown in Figure 1. The relationship between the equilibrium values of SSB, yield, recruitment and F are 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 a range of fishing mortalities from 0 to 75% of F_{crash} are presented as a phase plot in figure 3, where the x-axis corresponds to *biomass* relative to B_{MSY} and the y-axis to *harvest* relative to F_{MSY}. The 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.

The results of the elasticity analysis, i.e. SSB and fishing mortality relative to each of the three reference points with respect to the biologicalparameters are plotted in figures 4 and 5. The 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 plots allow us to idntify the relative importance of the different biological processesand and how robust is advice based on the three reference points? Figure 4 shows that elasticites of are similar for MSY and $F_{0.1}$, i.e. increasing in magnitude as fishing mortality increases (and SSB declines). Natural mortality is the parameter with the biggest effect, followed by steepness and L_∞. Trends and relative importance by parameter are similar for F_{Crash}. However the magnitudes of the elasticities are not, changing sign as fishing mortality increases. This means that F_{Crash} is robust to chanegs in M when the target levels of B_{MSY} is reached and robust to the assummed value of steepness at high fishing mortalities and for a depleted stock.

Inspection by process shows that for growth the key parameter is L_∞, for Maturity it is age at first maturity, for M both the average level and how fast declines as fish grow are equally important and for selectivity the age at recruitment to the fishery is more important than whether selectivity declines at older ages.

Figure 5 repeats the analysis for fishing mortality; in this case elasticity is not a function of the level of fishing mortality or SSB. M is again the most important parameter, followed by steepness and L_∞ and parameters have the same relative importance by process.

Discussion

There is a need for a conceptual change from catagorisng stocks as data or information rich or poor based on the requirements of stock assessment models. An understanding of biology and how to provide robust advice given is equally if not more important. Elasticity analysis can help in identifying where a better understanding is required and the benifits of obtaining it.

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 aged based assessments such as virtual population analysis (VPA). Rather, researchers should ask do we have sufficient knowledge, e.g. 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 often 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 [22]. Relationships between body size and life history parameters have been described for many taxonomic groups [23]. 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 by conducting MSE. However, such approaches can be 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. While sensitivity analyses are often conducted when assessing a stock and in some fora alternative assessment models when making projections to set catch quotas. The choice of scenarios is often made on an ad-hoc basis, elasticity analysis can be conducted to identify scenarios which potentially have the biggest impact and there provide a basis for discussing and agree which scenarios to run.

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 $_{F0.1}$, 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 $SSB_{F0.1}$ 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. Steepness has less of an affect compared to the analysis for SSB. MSY has the lowest elasticites 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 points 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.

Although we concentrated on assessing stock status relative to reference points any system output could have been evaluated with respect to any system parameter.

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 direction of the elasticity in such cases 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 [24] 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 [25] and [26]. Various mortality processes serially affect life history stages through the first year of life, e.g. in relation to settlement, overwintering and juvenile stages [27], [28] and [29]. 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. [30]). The growth trajectories of individuals may not follow a von Bertalanffy growth curve due to M causing differential 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 [31] and the influence on the assessment process [32] and sub-stock structure or metapopulations are known to exist for quite a few stocks e.g. cod in the Western [33] and Eastern Atlantic (North Sea) [34] and bluefin tuna in the Mediterranean [35]. Elasticity analysis can be extended to consider such problems e.g. [36] and [37] 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 releavnt processes may change based on the exploitation status of the population.

Materials and Methods

Elasticity. Elasticity analysis is 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:

$$E_{y,x} = \left| \frac{\partial \ln y}{\partial \ln x} \right| \quad [1]$$

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 selectivty 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:

$$E_{SSB_{MSY},L_\infty} = \left| \frac{\partial \ln relSSB_{MSY}}{\partial \ln L_\infty} \right| \quad [2]$$

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 conditional on L_∞ alone since paramters such as K, age at first maturity and natural mortality at age can be derived from L_∞ based on life history relationships. 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.

Mangement advice requires estimates of stock status and fishing mortality relative to target and limit reference points. Although often 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. Relative advice i.e. stock or fishing mortality relative to a reference point has been shown to be more robust than absolute estimate [11] and therefore management advice is often based on relative values.

The analysis allows use to pose questions such as are fishing mortality reference points based more robust than biomass reference points?, are target reference points more robust than limits? is a particular reference points more robust when used as targets than a limit? and what are the most importance biological assumptions in each case?

The elasticities in each year, (i.e. for the different levels of SSB and F) were then used to evaluate the relative importance of the parameterisation (e.g. K the rate of growth and L_∞) of the various processes (i.e. growth, maturation, stock recruitment, natural mortality and selectivity of the fishery).

Life History Relationships.

Empirical studies have shown that in teleosts there are significant correlations between the life history parameters such as age at first reproduction, natural mortality, and growth rate [2]. Additionally, size-spectrum theory and multispecies models suggest that natural mortality scales with body size [13], [14] [12]. This means that from something that is observable, like the largest sized individuals in a population, it is possible to infer life history parameters for are not easily observed or are unavailable.

Life history characteristics and relationships between a range of stocks and species [12] 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 Russell equation [15] summarises the key processes influencing the dynamics of exploited populations i.e.

$$f(B_2) = B_1 + (G + R) - (F + M) \quad [3]$$

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 i.e.

$$f(B_2) = B_1 + (G + R + I) - (F + M + H) \quad [4]$$

Knowledge about these processes determines 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 dymanics, life history relationships were used to parameterise appropriate functional forms for the different 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 [16]

$$L_t = L_\infty(1 - exp(-k(t - t_0)) \quad [5]$$

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.

$$W = a \cdot L_t^b \quad [6]$$

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, G:

$$SRP = \sum_{i=1}^{m} n_i Q_i O_i \quad [7]$$

where m is the maximum age and mean fecundity-at-age is equal to

$$O = a \cdot L^{b'} \quad [8]$$

If a and b are the same as in equation 3 then SRP is equivalent to female spawning stock biomss (SSB). However, generally the fecundity to length relationship differs from the weight to length relationship due to variations caused by condition and age effects altering the relationship between weight and the number of eggs produced [17].

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.

$$f(x) = \begin{cases} 0 & \text{if } (a_{50} - x)/a_{95} > 5 \\ a_\infty & \text{if } (a_{50} - x)/a_{95} < -5 \\ \frac{m_\infty}{1.0 + 19.0^{(a_{50} - x)/95)}} & \text{otherwise} \end{cases} \quad [9]$$

The value of $a50$ comes from the empirical relationship between L_∞ and age at maturity [12]:

$$a50 = 0.72 log L_\infty^{0.93} \quad [10]$$

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:

$$R = \frac{0.8 \cdot R_0 \cdot h \cdot S}{0.2 \cdot S/R_{F=0} \cdot R_0(1-h) + (h-0.2)S} \quad [11]$$

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 [18]. Steepness and virgin biomass were set to 0.9 and 1000 t respectively.

Natural mortality at size is derived from the life history relationship [19].

$$log(M) = M1 + M2log(L) + 1.51log(L_\infty) + 0.97log(k) \quad [12]$$

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.

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_∞=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 ($F = F_{crash}$).

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. reference points designed as targets such as those based on MSY and those designed as limits such as F_{crash}.

B_{MSY} and F_{MSY} correspond to the stock level and 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. F_{crash} the level of F that will drive the stock to extinction.

The management measures of interest are the equilibrum 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.

SSB and F relative 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 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 fecudity of younger fish of the same mass-at-age, e.g. due to maternal effects or repeat spawners being more fecund then a condideration of the interactions between biology and selectivity will be important.

Selection pattern of the fishery is represented by a double normal (see [20]) with three parameters that describe the age at maximum selection ($a1$), 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 situtations 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 [21].

$$f(x) = \begin{cases} 2^{-[(x-a_1)/s_L]^2} & \text{if } x < a_1 \\ 2^{-[(x-a_1)/s_R]^2} & \text{otherwise} \end{cases} \quad [13]$$

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

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

Figure 2 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.

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

For figures with multiple panels, the first sentence of the legend should be a brief overview of the entire figure. 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.