

Everything Should be Made as Simple as Possible, but not Simpler; Life History Traits and Biological Reference Points.

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SUMMARY

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1. Introduction

The adoption of the Precautionary Approach (FAO, 1996) requires a formal consideration of uncertainty, including limits in our knowledge of the population dynamics assumed in stock assessment. 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. However, defining stocks as data rich or data poor based on availability of catch and effort data alone often hides the fact that many biological processes in commercially important stocks are not fully considered in stock assessments. Examples include natural mortality, stock structure, maternal and cohort effects that impact on egg production. 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. Biological knowledge therefore is important in allowing general rules, for example about choice of reference points, to be derived, and the robustness of the assumptions made in data-rich stock assessments to be evaluated.

Key questions for fisheries management are to identify the relative importance of the underlying biological assumptions made in stock assessment with respect to measures of interest and in achieving management objectives and how to prioritise research in order to reduce uncertainty. For example, does uncertainty about the stock recruitment relationship have a relatively bigger effect than uncertainty about natural mortality on the yield and sustainability of a stock?

Elasticity analysis can be used to measure the relative change in system characteristic to a change in a system parameter such as natural mortality or density dependence in recruitment. Elasticities have proved 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 [Grant and Benton \[2003\]](#) and to quantities of importance in management such as population viability [Heppell \[1998\]](#).

Elasticity analysis is different to a sensitivity analysis where outcomes conditional on assumptions are compared. For example what is the difference between estimates of MSY if it is assumed that M is 0.2 all ages compared to assuming that M declines with age as indicated by life history theory? Elasticity analysis evaluates the relative importance of the assumptions within the current model structure, i.e. does changing M change MSY more than change another parameter such as the steepness of the stock recruitment relationship.

A fuller consideration of uncertainty within fisheries advice frameworks requires either Bayesian approaches or Management Strategy Evaluation (MSE). Within MSE the impact of different managed measures are evaluated given a broad range of uncertainty. However performing an MSE is a costly process in 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 robust limit and target reference points? Elasticity analyses can easily be applied to answer these questions. It can also shift the current focus from both data poor and rich defined solely on fishery catch and effort towards a better understanding of biological processes.

In this study we demonstrate how elasticity analysis can be used for a generic study based on population dynamics based on life history theory. We do this by first simulating a stock based on life history relationships [Gislason et al. \[2008a\]](#) 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.

2. Material and Methods

Gislason et al. [2008a] summarised life history characteristics and the relationships between them for a range of stocks and species. Even when data are limited, 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 Roff [1984]. Additionally, size-spectrum theory and multispecies models suggest that natural mortality scales with body size Andersen and Beyer [2006], Pope et al. [2006] and Gislason et al. [2008b]. This means that from something that is easily observable like the maximum size it is possible to infer life history parameters that are not easily observable.

These relationships were used to parameterise an age-structured population model using model describing growth, maturation and natural mortality.

2.1 Life History Relationship

Parameterisation of the processes

Growth modelled by a Von Bertalanffy growth equation (with parameters k , L_∞ and t_0) for length converted to mass by the condition factor (a) and exponent (b)

Maturity Modelled by a logistic equation with 2 parameters, age at 50% mature and age at 95% mature.

Natural mortality Modelled by an exponentially declining curve, with 2 main parameters M1 (the asymptotic value of M) and M2 the rate of decline.

Stock Recruitment modelled by a Beverton and Holt with 3 parameters, steepness, virgin biomass and SPR0.

Selection pattern was represented by a double normal 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.

Growth was modelled by [Von Bertalanffy, 1957]

$$L_t = L_\infty - L_\infty \exp(-kt) \quad (1)$$

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

Mass-at-age can be derived from length using a scaling exponent (a) and the condition factor (b).

$$W_t = a \times L_t^b \quad (2)$$

Natural mortality (M) at-age can then be derived from the life history relationship Gislason et al. [2008a].

$$\log(M) = a - b \times \log(L_\infty) + c \times \log(L) + d \times \log(k) - \frac{e}{T} \quad (3)$$

where L is the average length of the fish (in cm) for which the M estimate applies.

While maturity (Q) can be derived as in Williams and Shetzer (2003) from the theoretical relationship between M , K , and age at maturity a_Q based on the dimensionless ratio of length at maturity to asymptotic length [Beverton, 1992].

$$a_Q = a \times L_\infty - b \quad (4)$$

2.2 Stock Recruitment Relationships

Stock recruitment relationships are needed to formulate management advice, e.g. when estimating reference points such as MSY and F_{crash} and making stock projections. Often stock recruitment relationships are reparamterised in terms of steepness and virgin biomass. Where steepness is the ratio of recruitment at 40% of virgin biomass to recruitment at virgin biomass. However, 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 Anonymous [2011].

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 proportion of the expected recruitment produced by 20% of virgin biomass relative to virgin recruitment (R_0). For the BevertonHolt stock-recruit formulation

$$R = \frac{0.8 \times R_0 \times h \times S}{0.2 \times S/R_{F=0} \times R_0(1-h) + (h-0.2)S} \quad (5)$$

2.3 Reference Points

To estimate reference points from an aged-based model requires a selection pattern as well as biological characteristics to be considered. The selectivity of the fishery can be represented by an appropriate functional form, for example by the double normal (see Hilborn et al. 2001) which allows the peak selectivity age and either a flat topped or dome shaped selection pattern to be used. This allows knowledge of factors such as gear selectivity, availability and post-capture mortality to be modelled.

F_{MSY} , the level of exploitation that would provide the maximum sustainable yield, and F_{Crash} the level of F that will drive the stock to extinction, both depend upon the selection pattern. Since not all ages are equally vulnerable to a fishery and if there is a refuge for older fish, a higher level of fishing effort will be sustainable.

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 Powell-Wetherall [Wetherall et al., 1987]. 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.

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

2.4 Elasticity

Elasticity is an important measure in economics of how changing a variable influences quantities of interest, e.g. if the price of an item changes how will this affect sales.

Mathematically the elasticity of y with respect to x is

$$E_{y,x} = \left| \frac{\partial \ln y}{\partial \ln x} \right| = \left| \frac{\partial y}{\partial x} \cdot \frac{x}{y} \right| \approx \left| \frac{\% \Delta y}{\% \Delta x} \right| \quad (6)$$

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.

3. Analysis

We conduct an analysis to evaluate the relative importance of 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. We compare estimates of stock status in absolute terms (e.g. SSB and biomass) and relative to reference points. We also compare target and limit reference points and F and SSB based reference points.

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.

4. Results

The growth, proportion mature, natural mortality and selectivity-at-age are shown in figure 1. While the expected or equilibrium dynamics, along with MSY, MSY proxies ($F_{0.1}$, F_{Max} , SPR30%) and limit (F_{crash}) reference points, are shown in figure 2. Based on these equilibrium dynamics a population was simulated that was fished at a constantly increasing fishing mortality, i.e. from 0 in year 1 to 75% of F_{Crash} (fishing mortality at equilibrium that would drive the stock to extinction) in year 51, figure 3.

The same trajectories are shown in Figure 4 in the form of a Kobe Phase plot; where the x-axis corresponds to *biomass* : B_{MSY} and the y-axis *harvest* : F_{MSY} . The red zone corresponds to a stock that is both over fished and where over fishing is occurring. Quadrants are defined for the stock and fishing mortality relative to B_{MSY} and F_{MSY} ; i.e. red when $B < B_{MSY}$ and $F > F_{MSY}$, green if $B > B_{MSY}$ and $F < F_{MSY}$, and yellow otherwise.

An example elasticity plot is presented in figure 5. This shows the the ratio of SSB/B_{MSY} (bottom panel) and the elasticities for M1 (the 'maximum' level of natural mortality) and the steepness of the stock recruitment relationship with respect to SSB/B_{MSY} (top panel). The vertical lines shows where the stock is in relation to the quadrants of figure 4 (i.e. left of the green line the stock is in the green quadrant, right of the red line it is in the red quadrant). This shows i) that the estimate of SSB relative to B_{MSY} is proportionally more dependent on steepness than the mean level of M. ii) that the sign of the dependency changes as the stock moves from the green quadrant, i.e. as it becomes overfished, so that if you over estimate steepness then for a stock that is within safe biological limits you will overestimate the stock status, while for a stock that is outside of safe biological limits if you overestimate steepness you will think stock status is worse than it actually is. iii) Overestimating natural mortality will always result in an underestimation of the stock relative to B_{MSY} , iv) the relative impact of steepness is more than that of mean level of M. What the example does not tell us is exactly what the changes are in the estimate of stock status for changes in these two parameters.

Next we use an elasticity analysis to compare the relative importance of the different processes (growth, Maturity, natural mortality, stock recruitment and selectivity) for assessing a stock relative to

MSY, $F_{0.1}$ (a proxy for MSY) and F_{Crash} a limit reference point. $F_{0.1}$ 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} .

In figure 6 [switch Figs 6 and 7 around in the Figs file] the analysis is conducted for SSB and in figure 7 for fishing mortality.

Examination of the plots for SSB show

SSB

Range The processes that have the largest overall effect with respect to SSB/B_{MSY} are the SRR and M, while growth has the least effect andersen2006 asymptotic maturity and selectivity have an intermediate effect. However, the actual impact depends on the current state of the stock, i.e. in which quadrant it is.

Important parameters the most important parameterisations are the shape (rate of decline) of natural mortality (M2) and the steepness of the SRR, next are the ages at 50% mature and the age of full selection. However, their relative importance depends upon where the stock is in relation to the green, yellow and red quadrants

Shape There are two main types of patterns, either the magnitude of the elasticity is similar to the value of SSB/B_{MSY} initially increasing at a high rate or else elasticities are similar in the red and green quadrant with a blip during the transition between them. For example steepness displays the former pattern and M2 the latter. This shape means that the relative importance of the parameters change depending on stock status. For a virgin stock the elasticities are smallest but generally greatest in the yellow quadrant when a stock is being overfished but is not yet overfished. Apart from the case of M and growth for $F_{0.1}$. M generally has less impact for overfished stocks than steepness.

Summary F_{Crash} is less robust (to changes in parameter values) since the greatest elasticities were seen in this case. In the red quadrant, i.e. for limit reference points, both MSY and $F_{0.1}$ appear to be more robust, while in the yellow quadrant $F_{0.1}$ is more robust and in the red MSY.

Fishing Mortality [Fishing Mortality]

Range Again M and SRR had the biggest effects, with the smallest effect seen for growth

Shape same as above

Difference between processes

Summary The biggest difference between SSB and F results is that elasticities are much less in the red zone for both MSY & $F_{0.1}$. However they increase for F_{Crash} . Suggesting that MSY & $F_{0.1}$ will be more robust limit reference points for F.

5. Discussion

Relative importance of processes

Robustness of reference points, Red v Green quadrant, also the points with the transition periods

Use of Gislason et al.'s mortality relationship more realistic than the common practice of using an M which does not vary with life history stage. Numerous studies on early life history mortality, highlight the Nash & Geffen (2012) paper place mortalities.

6. Conclusions

What we did Compared the relative importance of biological parameters when assessing stocks relative to target and limit reference points

What we found That in general target reference points such as MSY and $F_{0.1}$ are more robust as limit reference points than actual limit reference points such as F_{Crash} . The importance of processes and parameters depend upon stock status and current fishing mortality. This illustrates the importance of considering reference points not in isolation but as part of the design of HCRs. For example if you know that a parameter is highly uncertain then when choosing a target or limit reference point then you should choose a reference point that is robust to such uncertainty, i.e. if you don't know the shape of the M curve use a multiple (e.g. 1.5) of $F_{0.1}$ as a limit reference point instead of F_{Crash}

What we didn't The analysis is limited in that it assumes a given model structure, i.e. exponentially declining M , SSB is an appropriate measure of SRP and a Beverton and Holt SRR. There are two issues here a) we don't actually know the correct functional form of M and SRR and b) we don't know whether advice based on TEP is better than based on SSB .

Future work BBNs & MSE

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7. Figures