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A Generic Population Simulator Based on Life History Theory.

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SUMMARY

Empirical studies have shown that there is significant correlation between the life history parameters such as age at first reproduction, natural mortality, and growth rate. This means that from something that is easily observable like maximum size it is possible to infer other life history parameters, which are difficult to measure such as natural mortality. In this study we show how to simulated stock dynamics based on life history theory. The simulator can be used to estimate reference points and population growth rates, derive priors for stock assessments, validate parameters used in assessments, conduct sensitivity analysis, develop simulation models for Management Strategy Evaluation and parameterise leslie matrices for use in Ecological Risk Assessments.

KEYWORDS: data-poor, FLR, life history relationships, reference points

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1. Introduction

The adoption of the Precautionary Approach [Garcia, 1996] requires a formal consideration of uncertainty, for example, in the quality of the available data and knowledge of the stocks and fisheries. An important principle is that the level of precaution should increase with uncertainty about stock status, so that the level of risk is approximately constant across stocks.

A stock may be classified as data-poor when fishery data are lacking, implying a high level of uncertainty.However, even when data are limited empirical studies of teleosts have shown that there is significant correlation between life history parameters such as age at first reproduction, natural mortality, and growth rate [Roff, 1984], while size-spectrum theory and multispecies models suggest that natural mortality scales with body size [Andersen and Beyer, 2006, Pope et al., 2006, Gislason et al., 2008b]. Therefore, the biologically plausible parameter space is restricted, and from a quantity that is easily observable, like maximum size, it is possible to infer other life history parameters, such as natural mortality.

In this study we show how to simulate stock dynamics based on life history theory using the life history relationships described in [Gislason et al., 2008b]. The simulator can be used to conduct sensitivity and other types of analyses and to build simulation models for use in Managemement Strategy Evaluation (MSE). As the simulator is well suited to cases where data and knowledge are limited , such as bycaught species, this will allow MSE to be extended to data-poor stocks. The simulator can also be used to develop and test general rules, for example about reference points (e.g. [Williams and Shertzer, 2003, Fromentin and Fonteneau, 2001]).

Within theoretical ecology, population dynamics have been classified as high or low risk using life history traits. For example, stocks or species with low productivity and a long life span will be expected to respond differently to fishing and management interventions when compared to those with a short life span and high productivity. The simulator is able to estimate stock productivity using only basic life history information and can therefore be used to conduct ecological risk assessments [Arrizabalaga et al., 2011, Cortés et al., 2010].

To illustrate the utility of the life history simulator we first show how it can be used to model stocks with limited information. i.e. where the main sources of uncertainty are lack of data and of studies of the stock's dynamics. We then show how it can also be used for data rich stocks, where uncertainty exists about key processes, e.g. on natural mortality or thestock recruitment relationship. We do this by conducting a sensitivity analysis, i.e. varying one parameter at a time and evaluating how other quantities change, and then by treating a key parameter as a random variable.

2. Material and Methods

We use life history relationships to parameterise an age-structured equilibrium model, where SSB-per-recruit, yield-per-recruit and stock-recruitment analyses are combined.

SSB-per-recruit (S/R) is given by:

$$S/R = \sum_{a=r}^{n-1} e^{\sum\limits_{i=r}^{a-1} -F_i - M_i} W_a Q_a + e^{\sum\limits_{i=r}^{n-1} -F_n - M_n} \frac{W_n Q_n}{1 - e_{-F_n - M_n}} \tag{1}$$

based on fishing mortality (F), natural mortality (M), proportion mature (Q) and mass (W) -at-age. Where a is age and n the oldest age, and r is the age at recruitment. The second term is the plus-group (i.e. the summation of all ages from the last age to infinity).

Similarly, yield-per-recruit (Y/R) is given by:

$$Y/R = \sum_{a=r}^{n-1} e^{\sum_{i=r}^{a-1} -F_i - M_i} W_a \frac{F_a}{F_a + M_a} \left(1 - e^{-F_i - M_i}\right) + e^{\sum_{i=r}^{n-1} -F_n - M_n} W_n \frac{F_n}{F_n + M_n} \tag{2}$$

The stock recruitment relationship is reparameterised so that recruitment R is a function of S/R e.g. for a Beverton and Holt model

$$S/R = (b + S)/a \tag{3}$$

and for Ricker's formulation

$$S/R = \frac{e^{bS}}{S} \tag{4}$$

S can then be derived from F by combining equation 3 or 4 with equation 1.

2.1 Life History Relationships

There are various models to describe growth, maturation and natural mortality and the relationships between them. Here we model growth following [Von Bertalanffy, 1957]

$$L_t = L_\infty - L_\infty exp(-kt) \tag{5}$$

where L_∞ is the asymptotic length attainable, K is 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).

$$W_t = a \times W_t^b \tag{6}$$

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

$$log(M) = a - b \times log(L_\infty) + c \times log(L) + d \times log(k) - \frac{e}{T} \tag{7}$$

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

Maturity (Q) is then parameterised using age at maturity a_Q, by using the emprical realtionship from [Gislason et al., 2010]

$$a_Q = a \times L_\infty - b \tag{8}$$

2.2 Seasonality

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, lengths-at-age, mass-at-age and size-based maturity are all calculated at spawning time. Fishing is assumed to happen mid year so the catch length-at-age, mass-at-age and size-based selectivity is calculated at mid year. Natural mortality is a function of the lengths-at-age in mid year.

2.3 Stock Recruitment Relationships

Stock recruitment relationships are needed to estimate reference points such as MSY and making stock projections. Often stock recruitment relationships are reparameterised in terms of steepness and virgin biomass, where steepness is the ratio of recruitment at 20% 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 would allow the estimation of steepness [Anonymous, 2011].

Here, we use a Beverton and Holt stock recruitment relationship reformulated in terms of steepness, h, virgin biomass, v and $S/R_{F=0}$:

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

2.4 Reference Points

Estimating reference points from an age-based model requires a fishing selection pattern as well as biological characteristics to be considered. The selectivity of the fishery can be represented by an appropriate functional form. Here we use a double normal (see [Hilborn et al., 2000]), which allows the age of peak selectivity, and either a flat topped or dome shaped selection pattern, to be specified. 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. Not all ages are equally vulnerable to a fishery, and if, for example, there is a refuge for older fish, a higher level of fishing effort will be sustainable.

3. Analysis

First we show how the maximum length or L_∞ can be used to derive other parameters such as K, the age at first maturity and natural mortality, and how these parameters and the MSY-based reference points vary with L_∞. We then show how to treat L_∞ as a random variable and how the other life history parameters vary accordingly. Finally, we show how the processes derived from the life history relationships can be varied in order to conduct sensitivity analyses, i.e. to evalute the consequence for the expected stock dynamics and MSY based reference points for changes in assumptions about growth, natural mortality, maturity and the stock recruitment relationship. We do this for five scenarios corresponding to:

Default Based on the life history relationships with a value of L_∞ equal to 175 and S equal to 0.9

Growth Growth model changed from von Bertalanffy to the Gascuel growth model [Gascuel et al., 1992].

$$L_a = 37.8 + 8.93t + (137.0 - 8.93 * t) * (1 - exp(-0.808 * data))^{7.49} \tag{10}$$

Natural Mortality In the default life history model it is assumed that M varies by age, while in this scenario M is set as 0.1 at all ages

Maturity Fish mature at a younger age

Stock Recruitment Steepness of the stock recruitment relationship is 0.75, i.e. recruitment is reduced at low values of S and MSY

The value of virgin biomass is 1000 t for all scenarios. Selectivity is not a function of the life history. Therefore, for illustration we assumed that the fishery was targeted on spawners, i.e. age at full selection was equal to the age at 50% mature.

All modelling and analoysis was carried out using the FLR software system [Kell et al., 2007], which can be used to build simulation models representing alternative hypotheses about stock and fishery dynamics. This allows a higher level of complexity and knowledge than used by stock assessment models and to explicitly include a greater range of uncertainty. Examples of the R code developed are given in the appendix.

4. Results

Figure 1 shows the relationships between L_∞, the K parameter of the von Bertalanffy growth equation, the mean level of M ($M2$) and the age at which 50% of individuals are mature (a_{50}). To investigate the sensitivity of these life history parameters to L_∞, L_∞ was modelled as a lognormal random variable with a CV of 30%. K decreases whilst $M1$ and a_{50} increase as L_∞ increases.

Once all parameters are specified then it is possible to calculate the expected stock dynamics and reference points. In figure 2 we show the equilibrium values of SSB and yield verses fishing mortality and recruitment and yield versus SSB for three values of L_∞.

Next we show how parameters can be varied for (i) growth, (ii) natural mortality, (iii) maturity and (iv) the steepness of the stock recruitment relationship. The default values of growth, natural mortality and maturity (blue) are compared with the different scenarios (red) in figure 3.

The expected values of yield verses fishing mortality are shown in figure 4 and expected yield versus SSB (i.e. the surplus production curve) in figure 5; points correspond to the MSY-based reference points.

If yield as a function of fishing mortality is compared to the default (red) then it is seen that decreasing steepness reduces MSY and F_{MSY}, i.e. productivity. Changing growth to the Gascuel relationship increases the stock productivity and the value of MSY reference points, since growth is more rapid at younger ages. M has the biggest effect of all parameters tested, and productivity is also increased. Changing selectivity or a reduction in the age at maturity have similar effects in that the stock can sustain a higher fishing mortality and F_{MSY} increases. However, MSY increases for an increase in selectivity and decreases for a reduction in age at maturity.

As well as conducting sensitivity analysis by varying a single parameter, it is also possible to make any parameter a random variable. This allows probability distributions to be generated for any derived quantity, e.g. MSY. To illustrate this, we model steepness as a lognormally distributed random variable with an expected value of 0.7 and a CV of 10%. The results are shown in Figure 6

5. Discussion

The adoption of the Precautionary Approach requires a formal consideration of uncertainty. The ICCAT Commission therefore recommended [REC-xxx] that the scientific advice provided by the SCRS includes a statement describing the uncertainty associated with stock estimates and projections, and a characterisation of the robustness of modeling approaches used and assumptions made. Traditionally stock assessments mainly consider only uncertainty in observations and process such as recruitment). However uncertainty about the actual dynamics (i.e. model uncertainty) has generally a larger impact on achieving management objectives Therefore when providing management advice it is important to consider all appropriate sources of uncertainty and to evaluate the robustness of management advice to the different sources, particularly so when providing advice based on probabilistic statements on management outcomes.

The approach based on life histories can be used both for data poor stocks and to conduct sensitivity analyses to evaluate the impact of the underlying biological assumptions for data rich stocks. It will allow the processes to be modelled for a range of species and stocks under a variety of assumptions, i.e. so that stock specific analyses can be performed, but also so that life history knowledge can be used to validate the assumptions made by assessmemt working groups. This is important since often parameters such as natural mortality and stock recruitment parameters can not be estimated from the available data and have to be assumed. The assumptions employed by different authors and groups can be widely different, even for the same species. For example, for yellowfin tuna, the value of K employed ranges from 0.28 to 0.86, while for skipjack it does so from 0.38 in the equatorial area to 2.08 in the tropical area

This approach can also be used to derive priors for important parameters, such as the intrinsic rate of growth, for use with bayesian biomass dynamic models

6. Conclusions

Life History relationships were shown to be useful for parameterising biological process models. They can be useful for data poor stocks and rich stocks. In the former they will allow hypotheses and parameters for processes such as growth, maturity and natural mortality to be generated. In the former they will be valuable for generating consistent hypotheses across stocks. Since in data rich stocks often assumptions between stocks and within species are inconsistent; for example in some stocks M is assumed constant at age and in other to vary with age. Use of life history theory could be used to generate consistent hypotheses for sensitivity testing and conducting projections when providing management advice in the form of Kobe II Strategy Matrices (K2SM).

Use of the simulator can be used for a variety of purposes e.g. toestimate reference points and population growth rates, derive priors for stock assessments, validate parameters used in assessments, conduct sensitivity analysis, develop simulation models for Management Strategy Evaluation and parameterise leslie matrices for use in Ecological Risk Assessments.

Priors can be developed using the parameters derived from the life history relationships and associated estimates of uncertainty using Monte Carlo simulation. This will allow probablity distributions for parameters required in stock assessment, for example population growth, as used in biomass dynamic stock assessments. Using the life history simulator will allow these to be generated in a consistent and transparent way across stocks.

Management Strategy Evaluation is an important method for evlaution the performance of scientific advice frameworks. The life history simulator will be useful for setting up simulation models (i.e. Operating Models) as part of an MSE framework to evaluate generic questions and identifty apropriate research to answer them.

Kobe 2 Strategy Matrices are important tools for communication of advice and uncertainty. The population simulator can be used to to conduct sensitivity analyses to evaluate the robustness of advice based on the K2SM. For example to evaluate whether stock assessment advice based on MSY-based reference points are more sensitive to uncertainty in one process than another; e.g. by comparing their relative sensitivity to assumptions about such as steepness or natural mortality.

Future work should concentrate on collating life history data on species, populations and stocks of interest to ICCAT, for example tunas, sharks and bycatch species and developing consistent hypotheses for biological processes. These can then be used to evaluate the uncertainty in and robustness of advice provide by the SCRS and to provide consistent hypothese across stocks and evaluate the benefits of alternative data collection and research programmes.

7. References

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8. Figures

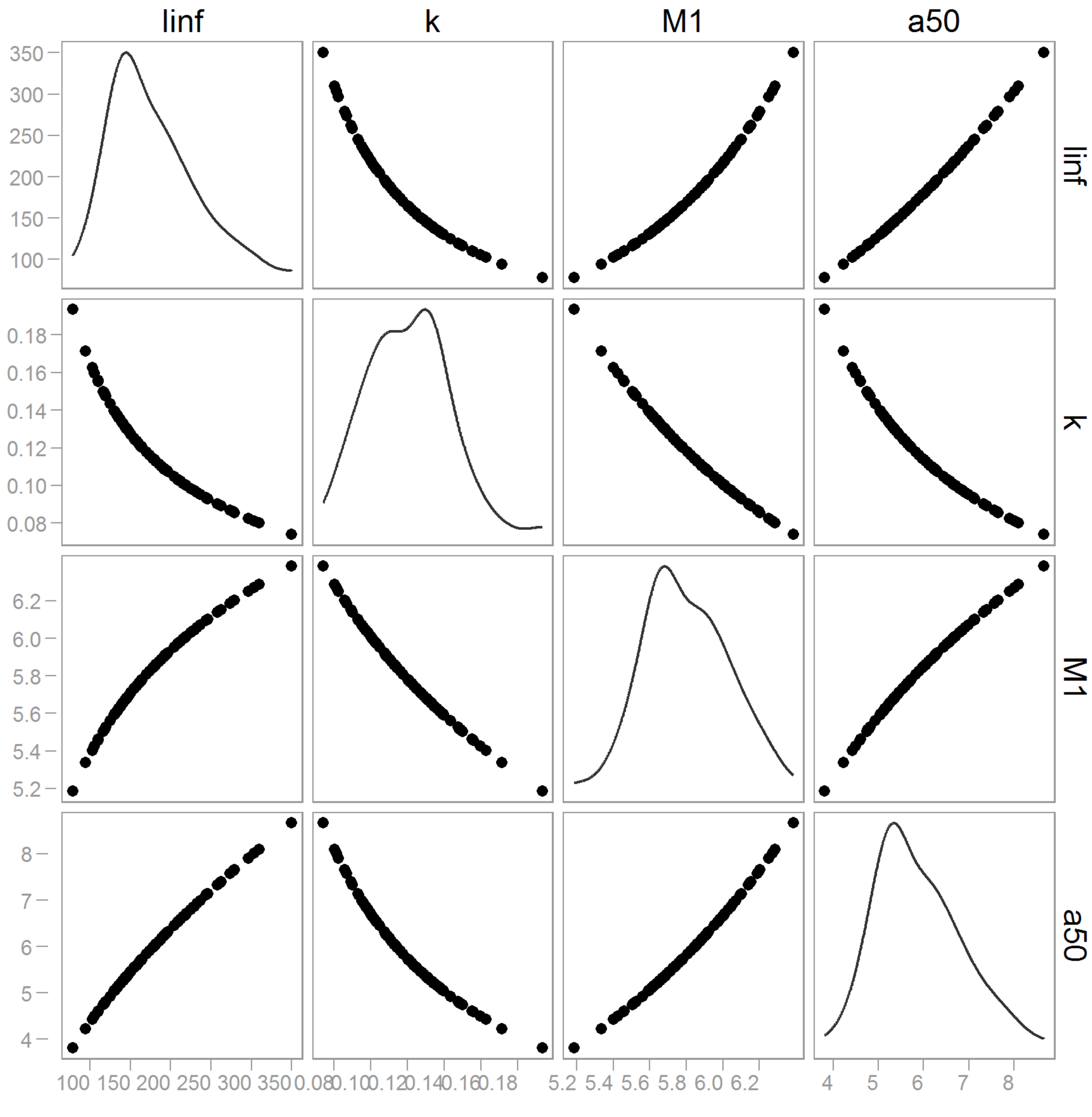

Figure 1: Pairwise scatter plots of life history parameters.

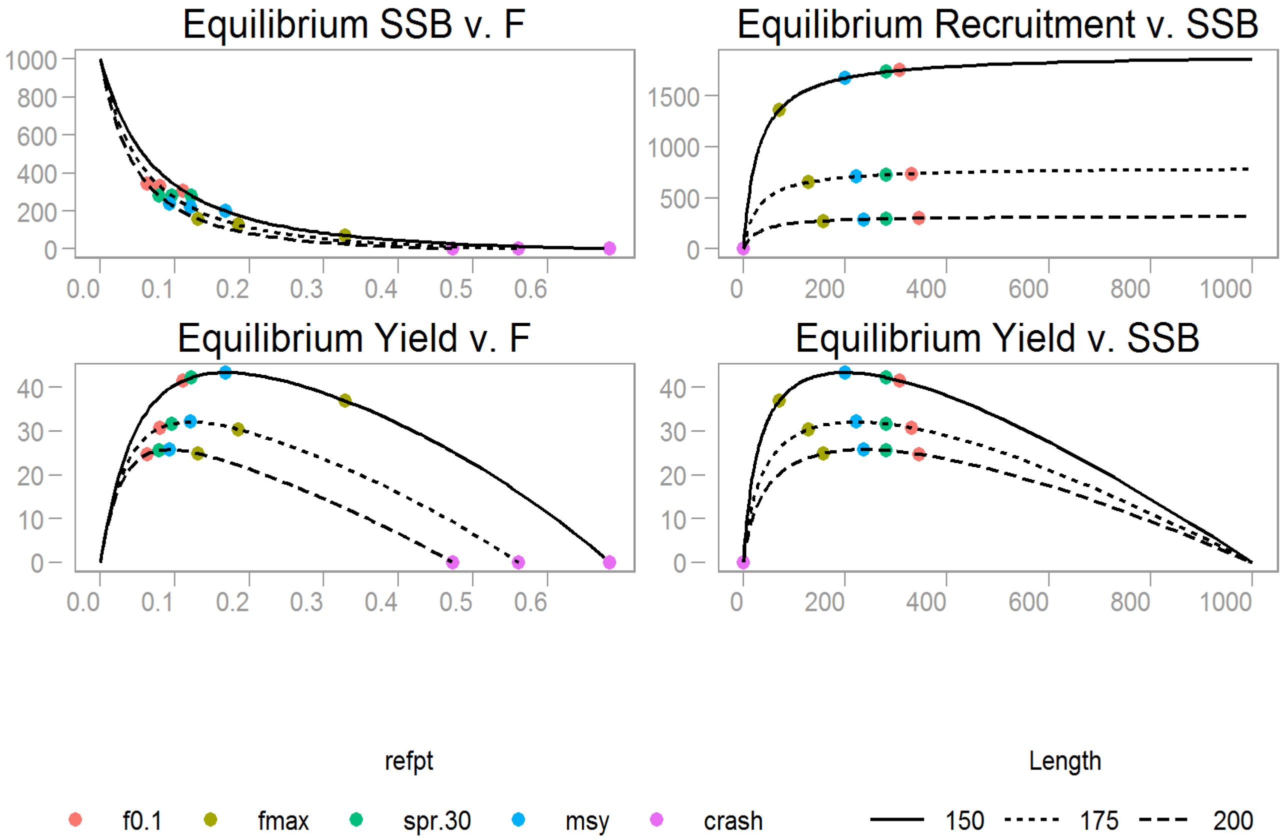

Figure 2: A comparison for three assumed values of L_∞ (150, 175 and 200cm) of the equilibrium (i.e. expected) values of SSB and yield verses fishing mortality and recruitment and yield verses SSB; points correspond to MSY.

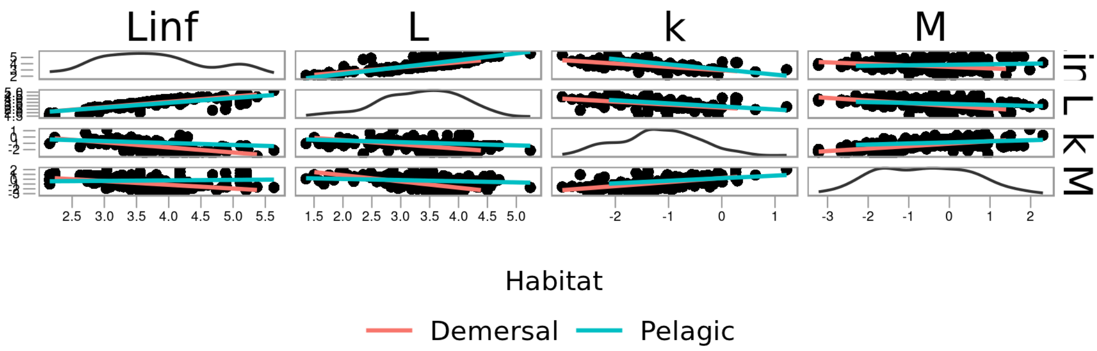

Figure 3: Natural mortality and proportion mature and mass-at-age from the five scenarios.

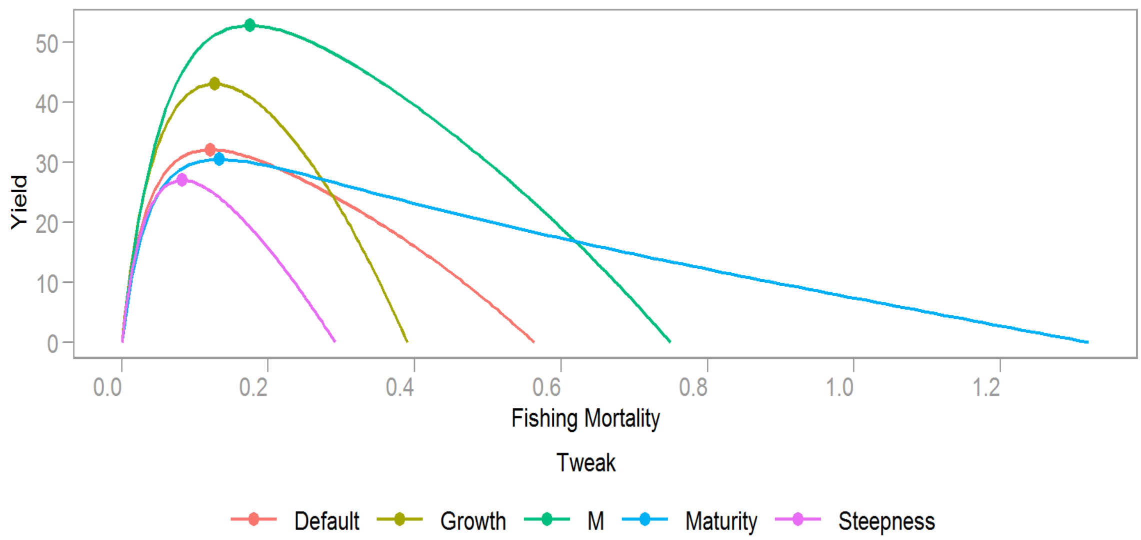

Figure 4: A comparison of the surplus production curves, i.e. equilibrium or expected values of SSB and yield by scenario; points correspond to MSY.

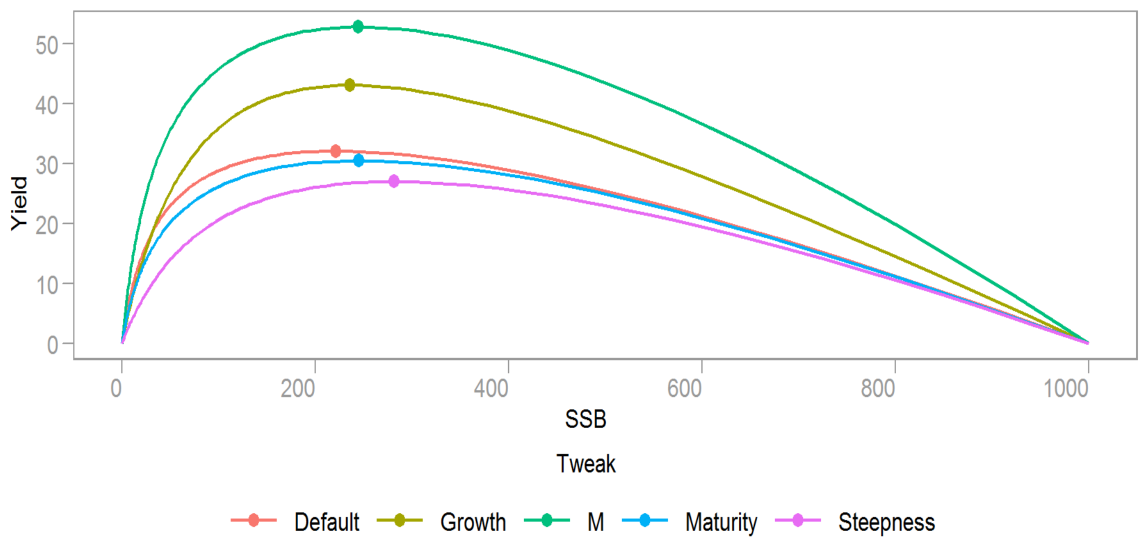

Figure 5: A comparison of the equilibrium or expected values of fishing mortality and yield by scenario; points correspond to MSY.

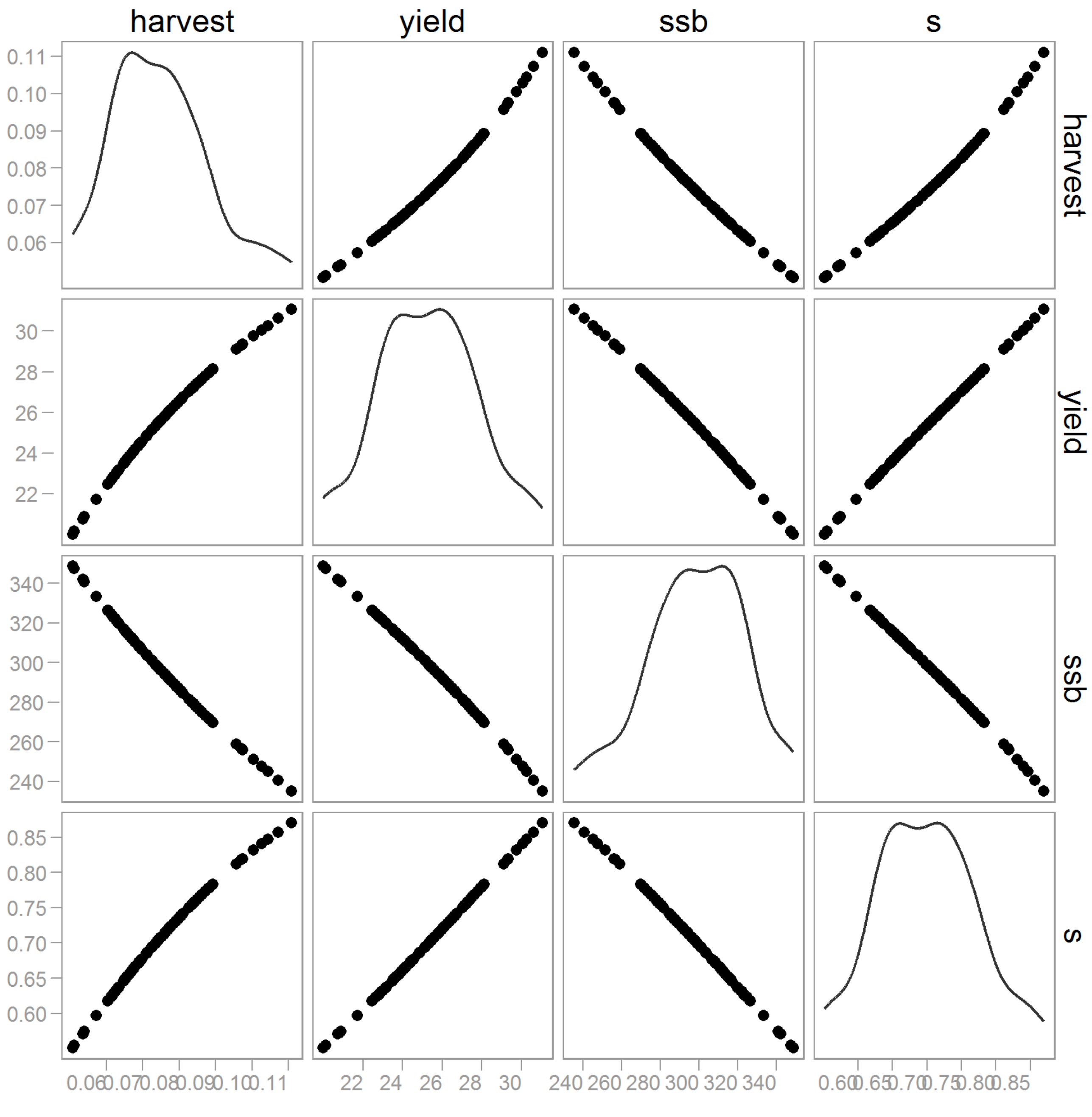

Figure 6: MSY based reference points as a function of steepness.

9. Code

params must contain as a minimum linf, since most other parameters are derived from this. If other parameters are provided they will over ride the Gislason relationships. However some parameters are arbitary (t0, the condition and allometric scaling factors (a&b), the age at 95% mature (ato95) and the selectivity pattern (sl, sr, the age at full selection is assumed to be the same as age at 50% mature) and the SRR (s&v). These are provided as extra arguments, although if supplied as part of par will be over ridden. This gives the greatest flexibility, since gislasim creates all the parameters needed to run lh()

```
library(FLAdvice)

params=gislasim(FLPar(linf=100))

eql100=lh(params)

plot(eql100)
```