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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 param- eters 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 parame- ters, which are difficult to measure such as natural mortality. In this study we show how to simulate 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.

RÉSUMÉ

Des études empiriques ont indiqué qu'il existait une corrélation importante entre les paramètres du cycle vital, tels que l'âge de la première reproduction, la mortalité naturelle, et le taux de croissance. Cela signifie qu'il est possible de déduire d'autres paramètres du cycle vital difficiles à mesurer, tels que la mortalité naturelle, à partir d'un fait facilement observable, comme la taille maximale. Dans cette étude, nous montrons comment simuler la dynamique des stocks à partir de la théorie du cycle vital. Le simulateur peut être utilisé pour estimer les points de référence et les taux de croissance de la population, obtenir des distributions a priori pour les évaluations de stock, valider les paramètres utilisés dans les évaluations, réaliser des analyses de sensibilité, élaborer des modèles de simulation pour l'évaluation de la stratégie de gestion et paramétrer les matrices de Leslie aux fins de leur utilisation dans les évaluations des risques écologiques.

RESUMEN

Los estudios empíricos han demostrado que existe una correlación significativa entre los parámetros del ciclo vital como la edad de primera reproducción, la mortalidad natural y la tasa de crecimiento. Esto significa que a partir de algo fácilmente observable como la talla máxima es posible deducir otros parámetros del ciclo vital que son difíciles de medir como la mortalidad natural. En este estudio se muestra cómo simular la dinámica del stock basándose en esta teoría sobre el ciclo vital. El simulador puede usarse para estimar puntos de referencia y tasas de crecimiento de la población, derivar distribuciones previas para las evaluaciones de stock, validar los parámetros utilizados en las evaluaciones, realizar análisis de sensibilidad, desarrollar modelos de simulación para la evaluación de estrategias de ordenación y parametrizar las matrices de Leslie para utilizarlas en las evaluaciones del riesgo ecológico.

KEYWORDS

Data-poor, FLR, life history relationships, reference points

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1. Introduction

Empirical studies have shown that there is significant correlation between life history parameters such as age at first reproduction, natural mortality and growth rate. This means that from something that is observable like maximum size it is possible to infer other parameters, which are difficult to observe directly such as natural mortality. In this study we show how to simulate stock dynamics based on life history theory (Gislason et al. 2008b). 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.

To illustrate potential usages 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 the stock recruitment relationship.

2. Material and Methods

Life history relationships were used to parameterise an age-structured equilibrium model, where SSB- per-recruit (S/R), yield-per-recruit (Y/R) and stock-recruitment analyses are combined. The stock recruitment relationship is reparameterised so that recruitment R is a function of S/R e.g., for a Beverton and Holt model.

$$S/R = (b + S)/a$$

This allows S/R to be derived from fishing mortality (F).

Growth was modelled following von Bertalanffy (1957) and natural mortality (M) at-age was derived from the life history relationship of Gislason et al. (2008a), based on the average length of an individual-at-age, maturity (Q) is then parameterised using the empirical relationship of Gislason et al. (2010).

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.

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).

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.

All modelling and analysis 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.

3. Results

Parameters such as the growth rate (K), age at first maturity and natural mortality-at-age can all be derived from $L\infty$; **Figure 1** shows how these parameters vary when $L\infty$ is a log normal random variable with a CV of 30%, K decreases whilst M 1 and a50 increase with $L\infty$.

Once the life history parameters are specified then it is possible to calculate the expected stock dynamics and reference points. **Figure 2** shows the equilibrium values of SSB and yield verses fishing mortality and recruitment and yield versus SSB for three values of $L\infty$. 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.

Next we evaluate 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 i.e.,

- Default -Based on the life history relationships with a value of $L\infty$ 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).
- 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.

Figure 4 shows equilibrium yield and **Figures 5** SSB as a function of fishing mortality. Points correspond to the MSY-based reference points. **Figure 6** shows pairwise scatter plots of harvest rate, yield, SSB and steepness. In **Figure 3** it is seen that changing M has the biggest effect, decreasing steepness reduces MSY and F_{MSY}. Changing growth to the Gascuel growth model increases stock productivity and the value of MSY reference points, since growth is more rapid at younger ages. A reduction in the age at maturity results in the stock being able to sustain a higher fishing mortality.

4. Discussion

The adoption of the Precautionary Approach requires a formal consideration of uncertainty. The ICCAT Commission therefore recommends 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 (Punt, 2007). 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 assessment working groups. This is important since often parameters such as natural mortality and stock recruitment parameters cannot 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 yellow fin 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 Cayre and Laloe (1986).

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 (McAllister et al., 1994).

5. 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. 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.

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 probability 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 evaluation 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 identify appropriate research to answer them.

Kobe 2 Strategy Matrices are important tools for communication of advice and uncertainty. The population simulator can be used 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 is 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 hypotheses across stocks and evaluate the benefits of alternative data collection and research programmes.

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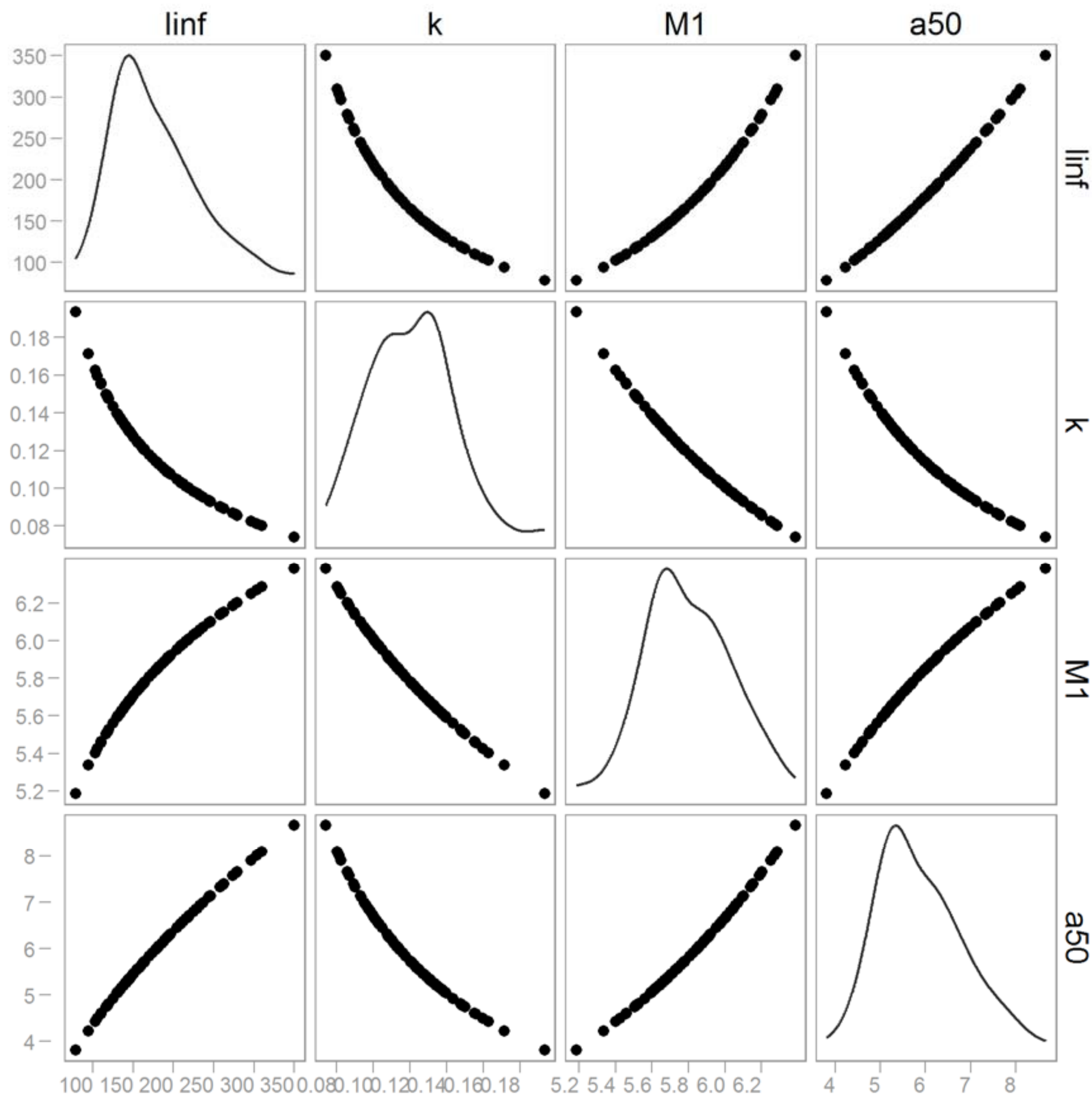

Figure 1. Pairwise scatter plots of life history parameters.

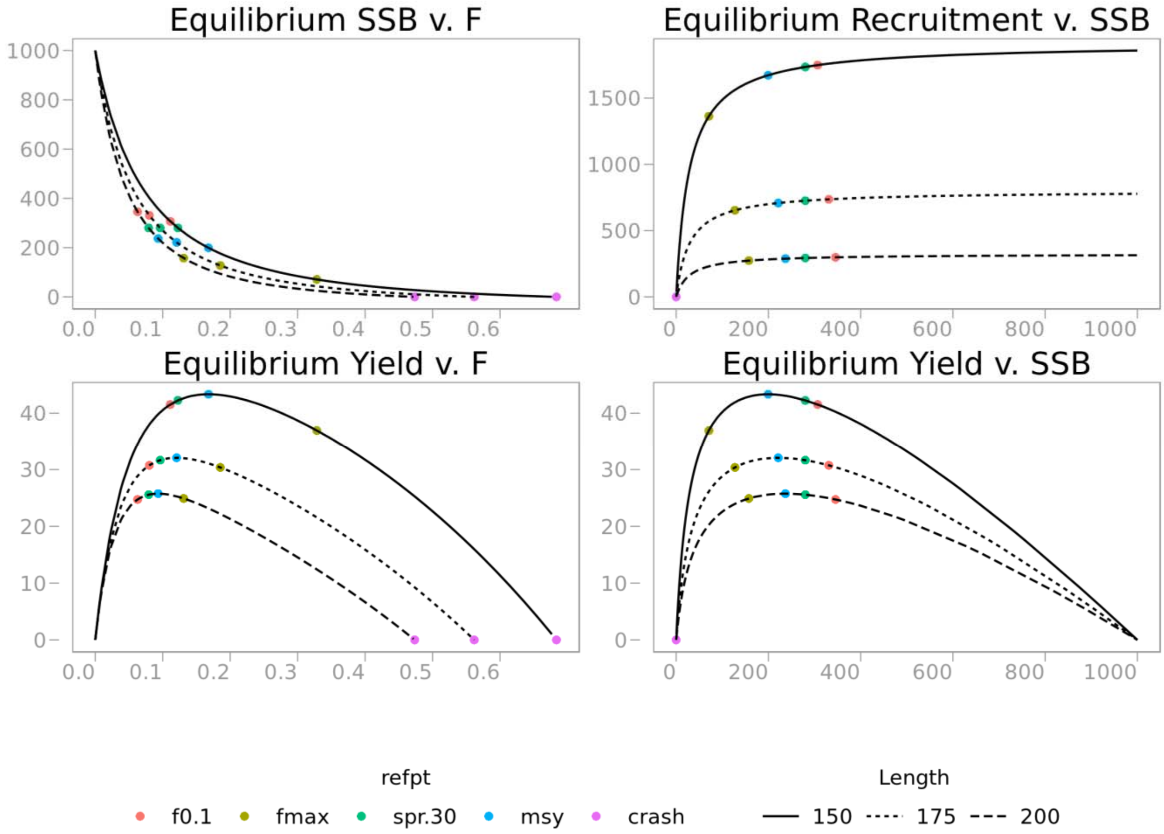

Figure 2. A comparison for three assumed values of L∞ (150, 175 and 200cm) of the equilibrium (i.e., expected) values of SSB and yield verses fishing mortality and recruitment and yield verses SSB; points correspond to MSY.

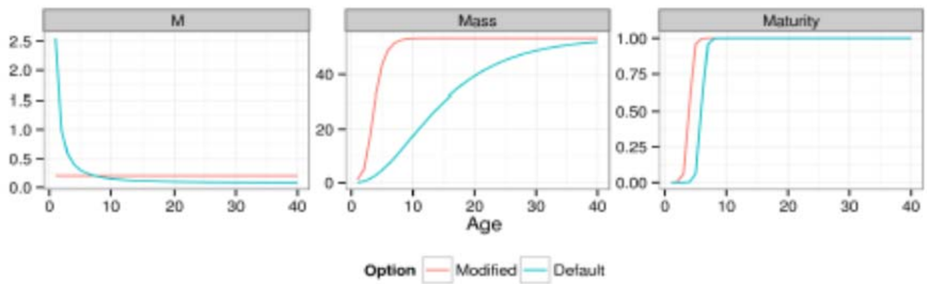

Figure 3. Natural mortality and proportion mature and mass-at-age from the five scenarios.

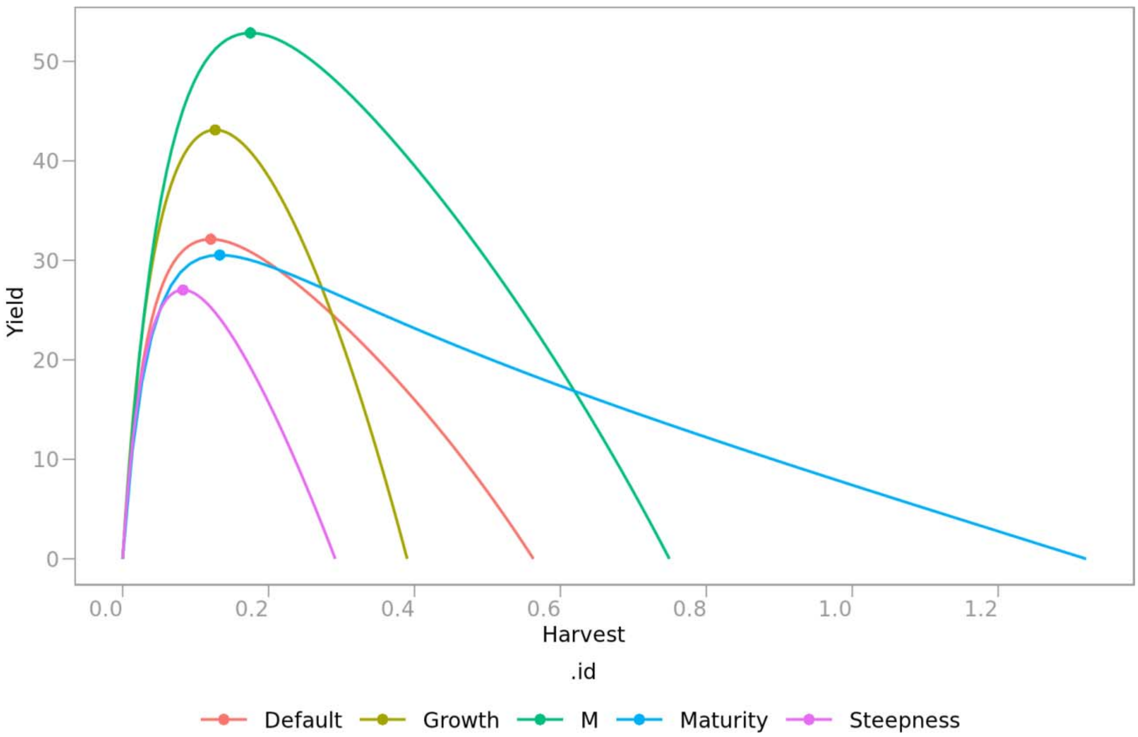

Figure 4: A comparison of the surplus production curves, i.e., equilibrium or expected values of SSB and yield by scenario; points correspond to MSY.

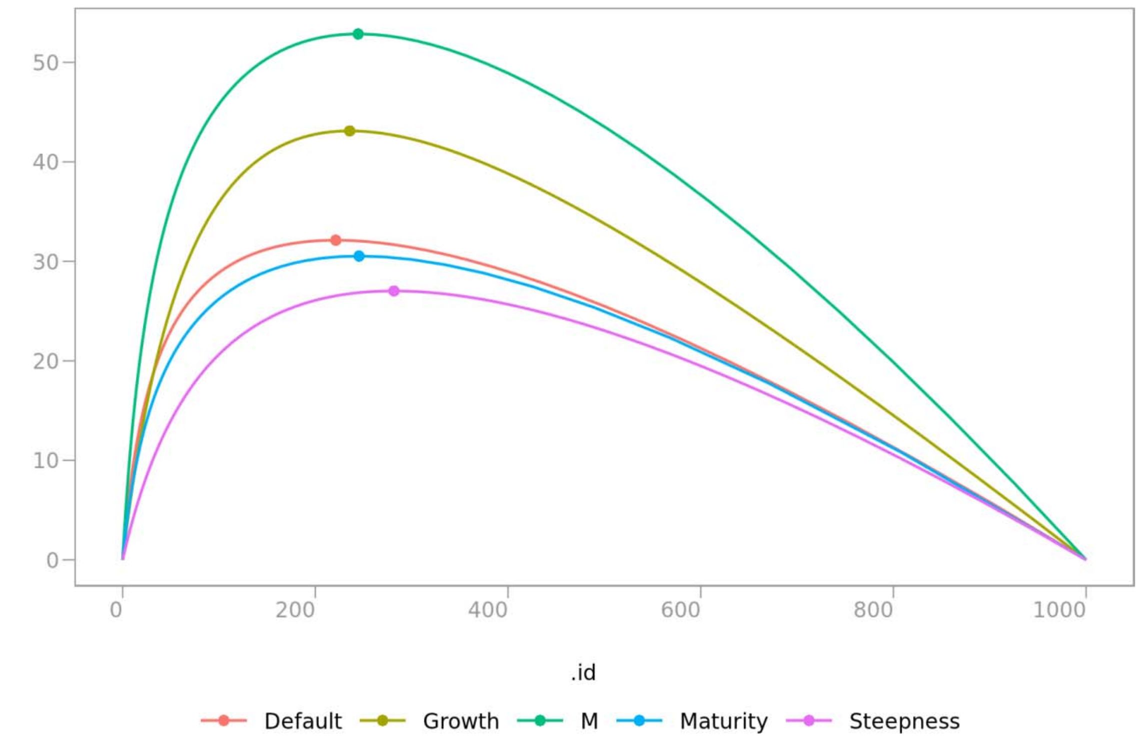

Figure 5: A comparison of the equilibrium or expected values of fishing mortality and yield by scenario; points correspond to MSY.

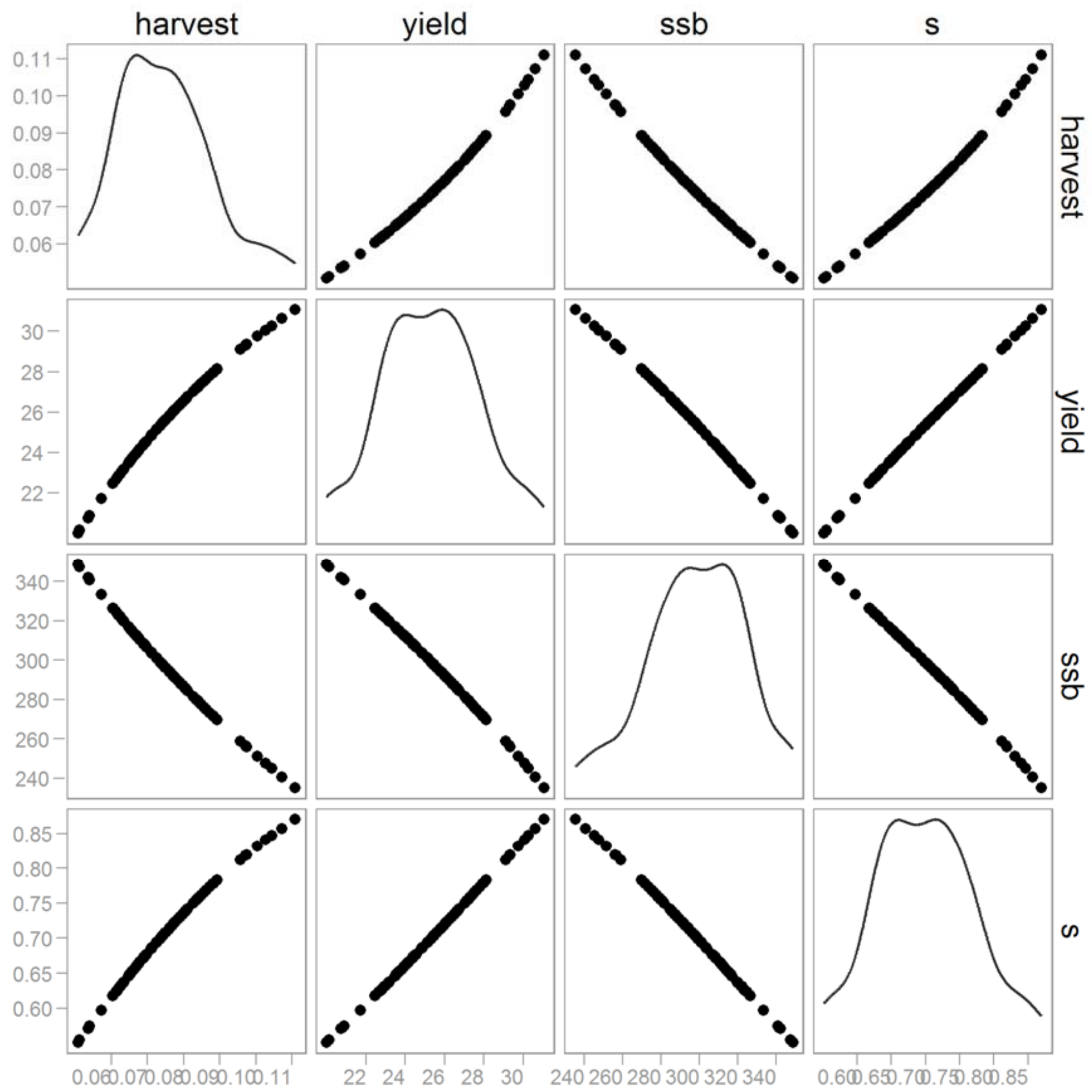

Figure 6. Pairwise scatter plots of harvest rate, yield, SSB and steepness.