

Stochastic stock-recruitment driven dynamics.

A discussion document from FRS FL project SF0274

WILLIAM S.C. GURNEY*^{1,2}

¹*Department of Statistics and Modelling Science, University of Strathclyde, GLASGOW
G1 1XH, Scotland*

²*F.R.S. Marine Laboratory, ABERDEEN, Scotland.*

*Corresponding author

1. Executive Summary

This paper addresses the estimation and implications of the relationship between spawning stock and recruitment in salmon populations. Although such relationships are without exception highly stochastic they are often characterised by a smooth curve which formally represents the mean recruitment outcome at each spawner abundance. We discuss the estimation of mean stock recruitment curves and consider the identification of site to site variations from typical datasets. We then discuss the implications of the estimation issues for identification of the deterministic dynamics of a given stock.

We next consider stochastic stock-recruitment relations and investigate their influence in driving generation to generation and year to year stock fluctuations. We develop a computationally efficient stochastic sub-catchment population model, which we use to consider the relation between year to year correlation in population fluctuations and the temporal pattern of return to spawn. Finally we investigate the effects of conservation limit driven management policies on the stability, persistence and yield of an exploited salmon population. We conclude that:

- The shape of the mean stock-recruitment relation at low stock levels plays a critical role in determining the degree to which demographic and environmental variability influence population persistence.
- This low-stock shape is systematically poorly defined by empirical data, implying that mechanistic descriptions of the underlying mechanisms form the only plausible route to reducing uncertainty and consequent policy risks.
- The serial correlation of population fluctuations driven by recruitment and survival variability is critically related to the age range of returning spawners. If all individuals return at the same age the population divides into a group of unconnected ‘lineages’ and there is no correlation between spawning populations in sequential years. This has clear implications for management actions predicated on observations the previous year.
- Generational correlations can be positive, negative or insignificant according to the shape of the stock-recruitment relation and the position of the mean population with respect to the S-R maximum. Populations with mean stocks well below the S-R maximum tend to be vulnerable and it may be possible to identify such vulnerability from the ACF of an observed time-series.
- Short-term correlation in spawning stock fluctuations is frequently weak, in which case conservation limit driven management policies will produce seriously deleterious effects even when applied to a statistically uniform and well characterised population.
- Where spawners return uniformly over three years, CL driven exploitation systematically underexploits good years and overexploits bad ones, thereby inducing short period population fluctuations of considerably greater intensity than those implied by natural variability in recruitment and survival.
- Where spawners return predominantly at a single age, ‘pseudo-lineages’ are regularly driven to extinction and only rekindled by leakage from their cousins. As a result both the mean spawning stock and the long-run average catch are far below those which would be obtained by constant effort exploitation.

2. Modified Ricker stock-recruitment

Stock-recruitment relations are very often fitted using the standard Ricker form

$$R_t = R_{max} \left[\frac{S_t}{S_{max}} \right] \exp \left[1 - \frac{S_t}{S_{max}} \right] \quad (1)$$

where R_{max} is the maximum possible population output of recruits and S_{max} is the number of reproductively active adults (spawning stock) who produce this output. In this investigation we use a modified form of this relation, which allows the curve to have a sigmoidal (or knee'd) form, namely

$$R_t = R_{max} \left[\frac{S_t}{S_{max}} \right]^k \exp \left[k \left(1 - \frac{S_t}{S_{max}} \right) \right] \quad (2)$$

where R_{max} and S_{max} retain their original interpretation and k is the sigmoidality parameter. When $k \leq 1$ the slope of the stock-recruitment curve decreases monotonically as S_t rises from zero, with the slope at zero being infinite for all $k < 1$ and finite for $k = 1$. When $k > 1$ the slope at the origin is zero and initially increases with S_t (see Fig. 1b).

If the species concerned is semelparous, the proportion of recruits who survive to spawn is P and all individuals who spawn do so after g years then the population dynamics are described by

$$S_{t+g} = PR_{max} \left[\frac{S_t}{S_{max}} \right]^k \exp \left[k \left(1 - \frac{S_t}{S_{max}} \right) \right] \quad (3)$$

Equilibrium in this system clearly requires each spawner to produce exactly one spawning adult in the next generation, that is the net reproduction per individual spawner (r) must be unity, i.e.

$$r_t \equiv \left[\frac{PR_{max}}{S_{max}} \right] \left[\frac{S_t}{S_{max}} \right]^{k-1} \exp \left[k \left(1 - \frac{S_t}{S_{max}} \right) \right] = 1. \quad (4)$$

If all a cohort's members do not spawn simultaneously, the population's transient dynamics are no longer described by equation (3), but the requirement for equilibrium is still equation (4).

Examination of Fig. 1a lets us identify the number and stability of stationary solutions to equation (3). If $k < 1$ then there is always exactly one solution with $S^* > 0$ which is guaranteed to be an attractor. If $k = 1$, then there is a single attracting stationary solution provided that $r(0)$ is greater than 1, that is

$$\frac{PR_{max}e^1}{S_{max}} > 1 \quad \Leftrightarrow \quad P > P_c^R \equiv \frac{S_{max}e^{-1}}{R_{max}}, \quad (5)$$

and no non-zero stationary solution otherwise. If $k > 1$ then there are two non-zero solutions or none. If the maximum value of r is smaller than unity then there is a single attracting solution at the origin ($S^* = 0$). If it is larger than unity, this solution is joined by two more, the lower one being a repeller and the upper an attractor. Thus, for $k > 1$ the system has one non-zero attracting solution, with a basin of attraction bounded below by the second interior steady state. A few lines of elementary algebra suffice to show that the requirement for the existence of such a solution is

$$P > P_c^M \equiv \frac{S_{max}e^{-1}}{R_{max}} \cdot \left[\frac{k}{k-1} \right]^{k-1}. \quad (6)$$

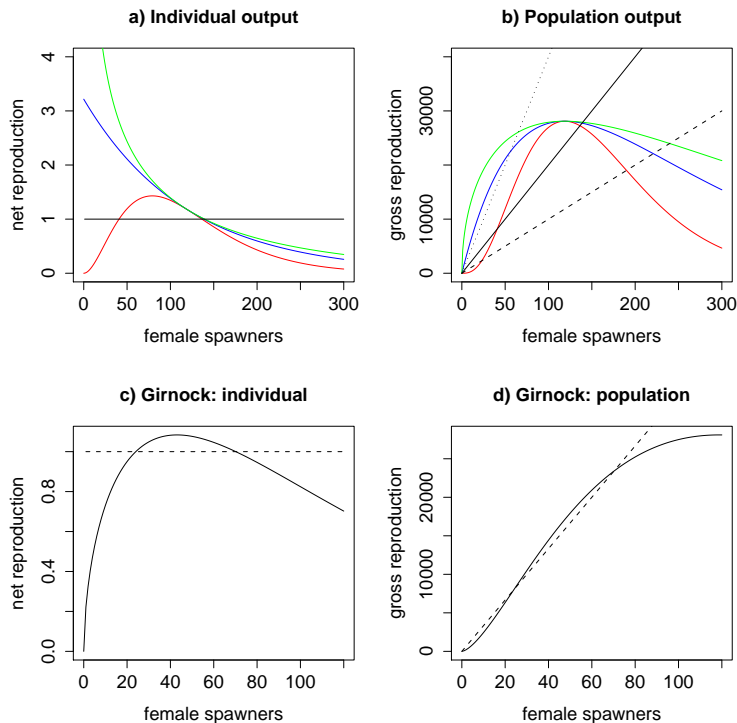


Figure 1: The modified Ricker stock recruitment curve. a) and b) illustrate the behaviour of this relation for $k = 0.5$ (green), $k = 1$ (blue) and $k = 3$ (red). a) shows the implied net individual reproductive output (equation 4) if the survival to spawn $P = 0.005$ compared to the equilibrium requirement (black line), b) shows the gross population reproductive output (equation 2) compared to that needed for equilibrium when $P = 0.005$ (solid line), $P = 0.01$ (dashed line) and $P = 0.0025$ (dotted). c) and d) show net individual and gross population reproduction for the Girnock (spawner-fry) best fits ($R_{max} = 28095$, $S_{max} = 118.7$, $k = 1.569$) compared to the equilibrium requirement if $P = 0.003$, implying a steady state population of about 70 females.

3. Fitting the MR curve to data.

To investigate the shape of observed stock-recruitment curves we have fitted the modified Ricker (and some alternative forms) to a number of datasets. In each case we determined the best fit to the data using the Nelder-Meade non-linear optimisation algorithm implemented in the R routine ‘optim’. The best fit curves implied by this process, together with the observations are shown in Fig. 2.

Examination of the standardised residuals yielded by the fitting process (see Appendix A) suggests that their standard deviation at any given spawner number is proportional to the fitted mean. To determine confidence limits for the fitted curves we generated a thousand (statistically equivalent) simulated data sets with points at the same spawner numbers as the observed dataset. Output at those spawner numbers was drawn from a normal distribution with mean equal to the best fit and standard deviation equal to the product of that mean with the overall standard deviation of the standardised residuals. We fitted each simulated dataset in the same way as the observations and then scanned the envelope of predicted curves to find the 2.5% and 97.5% percentiles for each input

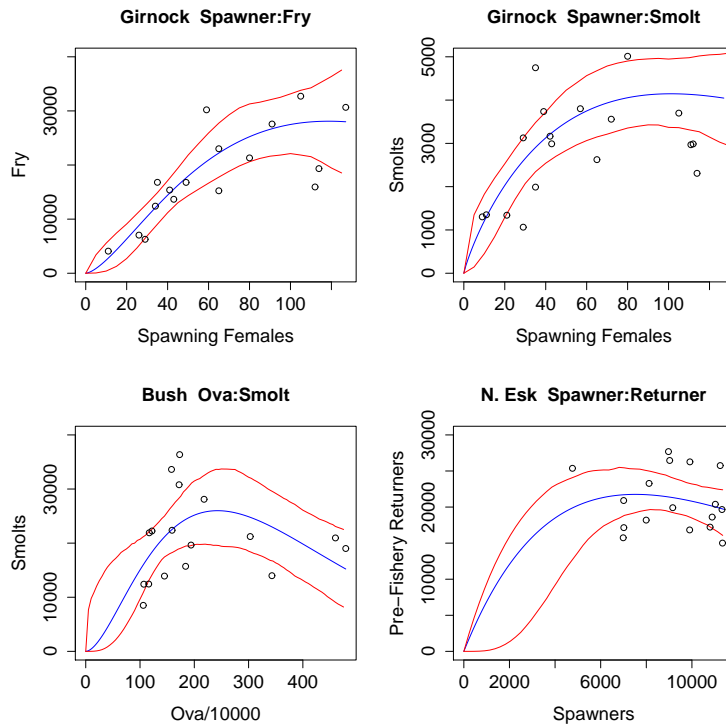


Figure 2: Modified Ricker SR curves fitted to data from the Girnock Burn and the rivers Bush and N. Esk. In all cases the points show observations, the blue line shows the best fit and the red lines show 95% confidence limits. a) shows a fit to the fry abundance in the Girnock determined from electrofishing data for the years 1968-78, 1981-89 and 1999. Best fit parameters are $R_{max} = 28096$, $S_{max} = 118.7$, $k = 1.569$. b) shows a fit to Girnock smolt trap data for the years 1966-76, 1981-89, 1992-99. Best fit parameters are $R_{max} = 4145.9$, $S_{max} = 101.17$, $k = 0.87247$. c) shows data on ova input and smolt output for the river Bush for 1973-89 (<http://ram.biology.dal.ca/ftp/pub/sr/ASALBUS2.dat>). Best fit parameters against $ova \times 10^{-5}$ are $R_{max} = 25997$, $S_{max} = 242.9$, $k = 1.828$. d) shows data on spawners and pre-fishery adult returners from the N. Esk, which were fitted with the constraint $k \geq 1$. Best fit parameters are $R_{max} = 21759$, $S_{max} = 7522$, $k = 1.000$.

value. The resulting confidence limits are shown in Fig. 2. The full parameter distributions and samples of the simulated data are shown in Appendix A.

We note from Appendix A.3 that the R^2 for the Bush fit given here is 0.227 which contrasts rather unfavourably with the value of 0.422 claimed by Crozier and Kennedy when fitting the same data with a standard Ricker curve. We have refit this data with a standard (two parameter) Ricker curve and find $R^2 = 0.183$. Perhaps not coincidentally $\sqrt{0.183} = 0.427$ which is very close to Crozier and Kennedy's result if they erroneously identified R as R^2 .

We also note that the fit to the N. Esk data (which might arguably be more appropriately fitted by a horizontal straight line – see Appendix A.8) was constrained to have the sigmoidality parameter $k \geq 1$, in contrast to the other three fits in which the constraint was $k > 0$. Alternative fits to this data with weaker constraints showed that the best fit value of k was always close to the constraint value, leading to best fit lines which are essentially horizontal down to very low values of spawner numbers.

4. Steady states, noise and persistence

To aid understanding of the way steady states vary with model parameters, we restate equation (3) as a requirement that any equilibrium state S^* must be a solution of

$$\frac{1}{P}S^* = R_{max} \left[\frac{S^*}{S_{max}} \right]^k \exp \left[k \left(1 - \frac{S^*}{S_{max}} \right) \right] \quad (7)$$

The R.H.S. of this relation is just the stock recruitment curve, while the L.H.S is a straight line through the origin with slope $1/P$. An equilibrium occurs wherever these two are equal, that is where the ‘replacement line’ intersects the stock recruitment curve.

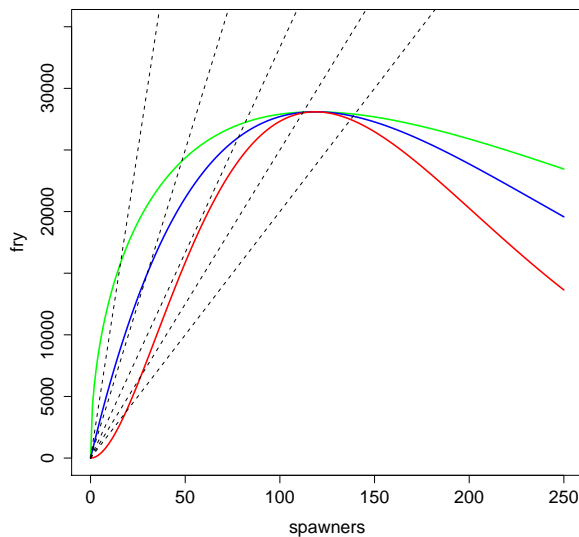


Figure 3: Stock-Recruitment Curves and Steady States. The three solid curves show possible stock-recruitment curve shapes given by equation (2) with $k=0.5$ (green), 1 (blue) and 2 (red). The dotted lines show the renewal condition for five values of P ranging from 0.005 (extreme right) to 0.001 (extreme left).

We illustrate this for three characteristic stock recruitment curve shapes in Fig. 3. When the survival to spawn (P) is ‘large’ then all three curve shapes predict an attracting steady state. However, as P decreases the behaviour of the three curve types diverges. Only for the (rather implausible) case of $k < 1$ does the steady state exist regardless of the value of P . When $k = 1$ (that is for the standard Ricker) the interior ($S^* > 0$) steady state exists only so long as the slope of the replacement line ($1/P$) is less than that of the stock-recruitment relation at the origin. The requirement that this should be so is that $P > P_c^R$ given by inequality (5). When this inequality is reversed the population experiences ‘deterministic extinction’.

When $k > 1$ the behaviour is even more complex. Here there are two positive steady states, the upper one being the attractor and the lower being a threshold below which the population crashes to zero. When P is large the threshold steady state is close to the origin and will have no practical effect. However as P decreases (the slope of the

replacement line increases) the upper and lower steady states converge and eventually meet when $P = P_c^M$ (equation 6). For $P < P_c^M$ the only steady state is the origin, so the population crashes (deterministically) to extinction.

The foregoing discussion shows that sigmoidality of the stock-recruitment relation (the value of k) has considerable influence on the survival to spawn at which the population experiences deterministic extinction. However, its importance is greatly increased when we take recruitment and survival variability into account. In Fig. 4 we show a series of

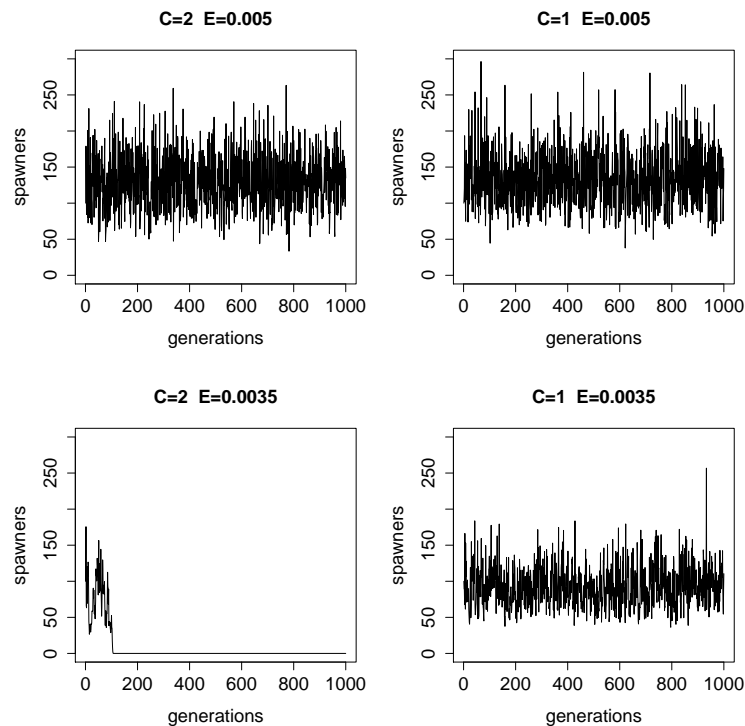


Figure 4: Stochastic Simulations with recruitment negative binomially distributed ($\theta = 15 \Rightarrow c.v. \approx 0.25$) around the mean shown in Fig. 3 for $k = 2$ (left-hand frames) and $k = 1$ (right-hand frames) and P normally distributed around 0.005 (upper frames) or 0.0035 (lower frames) with $CV=0.1$. The mean time to extinction for the case in the lower left frame is 50.9 generations.

simulations in which we assume that for any given value of spawning stock the recruitment is negatively binomially distributed around the mean recruitment appropriate to that stock (see Fig. 3) with a shape factor $\theta = 15$, which approximates to a c.v. of around 25% for spawning stocks from 10-100 females. To add an additional element of realism we also assume that the survival to spawn P is normally distributed around its designated mean value with a c.v. of 10%.

In the upper frames of the figure we show simulations with mean survival to spawn well above the critical value for $k = 2$ ($P_c^M = 0.0031$). In this case the lower (threshold) and upper steady states for $k = 2$ are about 20 and 100 females respectively and the behaviour of the model with $k = 2$ is remarkable similar to that with $k = 1$. However, with a mean survival to spawn of 0.0035 (which is still comfortably above the critical level for deterministic extinction when $k = 2$), the lower and upper steady states are

around 30 and 70 respectively and the stochastic population trajectory goes quite rapidly to extinction – the mean time to extinction for these parameters being 50.9 generations. By contrast the model with $k = 1$ (and hence critical survival to spawn $P_c^R = 0.0015$) shows continued statistically stable variability around the expected mean population.

These simulations show that the details of the low-stock shape of the stock recruitment relation can have a very significant effect on the possibility of both stochastic and deterministic extinction. This leads to a rather serious difficulty in setting conservation limits. Few populations will explore the very low stock region of the S-R curve very frequently. Indeed, if the curve is S-shaped, any stock which does so is bound for almost certain extinction in the absence of remedial measures.

Hence, to add to the general chronic lack of stock recruitment data, we can add a further impediment, that even good (long-term) data for spatially restricted regions such as the Girnock are unlikely to define the low-stock behaviour well. Shorter term datasets for spatially extended regions are likely to yield no useful information at all on this critical region of the stock recruitment curve.

Prudent discussion of whether a stock is or is not endangered must take appropriate account of the uncertainty in the low-stock shape of the S-R curve, and acknowledge the possibility that it may be curved in such a way as to enhance the noise sensitivity of the population and hence its probability of becoming extinct. The only practical way to meet this requirement is to develop sufficient understanding of the mechanisms which determine the stock-recruitment relationship, so that a fit to the high-stock region of the curve can be confidently extrapolated to the low-stock region. To fail to do so, for example by simply assuming that the S-R curve is a standard Ricker curve through a highly dispersed set of data is likely to yield very poor management advice.

5. Population fluctuations in a single deme

The strategic population model defined by equation (3) assumes that offspring of individuals who reproduce in year y themselves reproduce in year $y + g$. The implication of this assumption is that the population divides into g unconnected ‘lineages’ whose fluctuations are completely uncorrelated (see Fig. 5). To develop a better understanding of the fluctuations in real populations we need to represent the fact that even individuals who return after a fixed number of sea winters may have spent different lengths of time in the river and thus have spent different amounts of time since they were ova.

To facilitate development of a year-by-year (as opposed to generation by generation) model we first define total age a as the age of a returner *since it was spawned*. We now use S_y to represent the number of spawners in year y and $R_y(S_y)$ to denote the number of individuals recruited to the population as a result of the spawning activity in that year. If the proportion of these recruits who survive to spawn (at any age) is P_y and the proportion of those survivors who spawn at total age a is $Q_y(a)$ then the total spawning population in year Y is given by

$$S_Y = \sum_{y=Y-1}^{Y-a_m} Q_y(Y-y)P_yR(S_y) \quad (8)$$

where a_m is the maximum age at which any individual ever returns to spawn.

In the deterministic variant of this model the stock recruitment function R_y is a deterministic function \widehat{R} , the spawning survival P_y is a constant \widehat{P} and the return fraction Q_y is a deterministic function \widehat{Q} . In this case the steady state S^* is a solution of

$$S^* = \sum_{y=Y-1}^{Y-a_m} \widehat{Q}(Y-y) \widehat{P} \widehat{R}(S^*) = \widehat{P} \widehat{R}(S^*) \sum_{y=Y-1}^{Y-a_m} \widehat{Q}(Y-y) = \widehat{P} \widehat{R}(S^*), \quad (9)$$

thus demonstrating that the equilibrium requirement is equation (4).

A plausible stochastic variant of the model continues to regard the return fraction $Q(a)$ as a deterministic function, but regards the stock recruitment and survival to spawn as random variables. Following our earlier practice, we define the survival to spawn P as a normally distributed random variable with mean \widehat{P} , and the stock recruitment as a negative binomially distributed random variable with (constant) shape factor θ and mean related to the spawning stock by equation (2). This model is extremely simple to simulate (R code to do so is given in Appendix B.1).

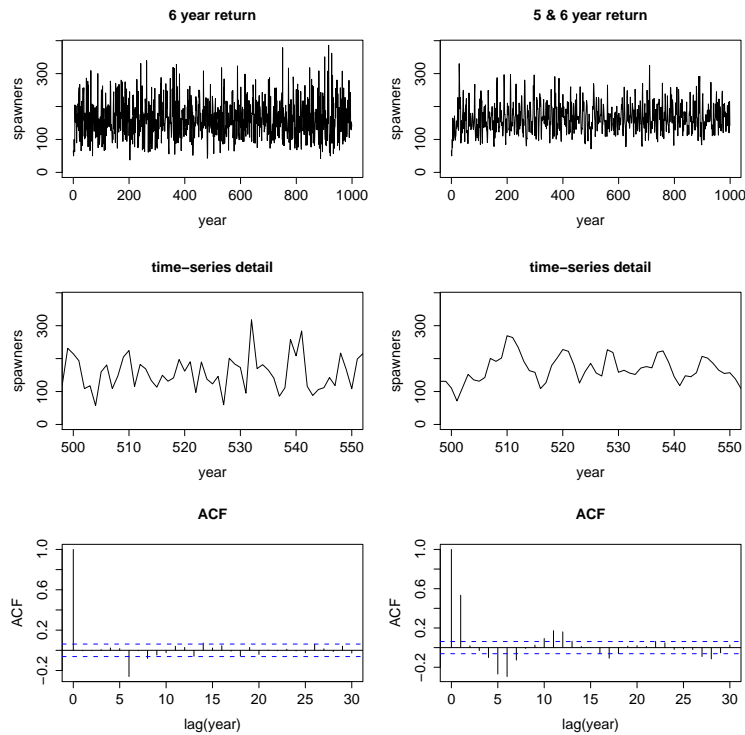


Figure 5: Year by year stochastic simulations of the single deme model. Left hand frames show a 1000 year simulated time series (top), a 50 year time-series segment (middle), and the autocorrelation function (bottom) for a run with all spawners returning at total age $a = 6$ – corresponding to a two sea-winter fish which spends three years in the river. The right hand frames show an identical simulation except that the returning spawners arrive in equal numbers at ages 5 and 6. Common model parameters are: $R_{max} = 3 \times 10^4$, $S_{max} = 120$, $k = 1$, $\theta = 10$, $\widehat{P} = 0.006$, $CV_P = 0.1$.

Fig. 5 shows results of two simulations. Both depict a population of individuals who return after two sea-winters to spawn with a mean output given by a standard Ricker

stock recruitment relation with $S_{max} = 120$. The parameters are chosen so as to put the deterministic steady state ($S^* = 168.5$) well above the maximum of the S-R curve. One simulation assumes that all individuals smolt after 3 years in the river (that is at $a = 6$) while the other assumes that 50% of returners spawn at $a = 5$ while the remainder spawn at $a = 6$.

Both simulations show statistically stationary fluctuations around means (162 for the 6 year return, 165.4 for the 5 and 6 year returns) which are close to the deterministic stationary state. As we might expect the amplitude of the fluctuations is smaller in the case where returns are spread over two years (six year returns $\Rightarrow CV_S = 35\%$, five and six year returns $\Rightarrow CV_S = 25\%$). Again as we might expect, the ACF's show that if the returners from a given years spawning all arrive in a single year, the population in effect consists of a group of independent (and thus uncorrelated) sub-units, whereas if returners are spread over more than one year, there is significant year to year correlation in fluctuations.

A final point of interest from the ACF's shown in Fig. 5 is that the correlation between generations is negative. We hypothesise that this occurs because the mean spawner population in these simulations is well above the maximum of the S-R curve. In this case a larger than average spawner population will produce a smaller than average recruitment and vice-versa. This suggests that if the mean spawner population is below the maximum of the stock-recruitment curve we should expect a positive generational correlation.

This hypothesis is confirmed by the simulations shown in Fig. 6, which also demonstrate that if the mean is close to the maximum of the S-R curve, the generational correlation disappears. This experiment also demonstrates that the number of year-classes which show positive year to year correlation is determined by the width of the return probability distribution $Q(a)$.

6. Managing a single deme - conservation limits

In this section we use the single deme model developed above to explore the implications of conservation limits in salmon management. We base our investigation on the Girnock spawner-smolt data which we fit with a broken-stick stock recruitment curve (see Appendix A.6). We postulate that the spawning population in year y is the difference between the numbers returning to the coastal region and the catch in year y which we denote by C_y . We examine two models. In the first model variant, post return exploitation is supposed to remove a constant fraction of the returners (which we call the river exploitation fraction and denote by ρ). In the second, the number of individuals removed after return to the coastal region is equal to the difference between a conservation limit and the previous year's spawning stock, or to the current spawning stock, whichever is smaller.

We explore the effects of these models of exploitation on two systems. In one, the returning spawners from a given hatch class arrive with equal probability at ages 5, 6 and 7, thus ensuring that the population fluctuations have strong serial correlation. In the other we assume that 80% of the returners are aged 6, with the remaining 20% divided equally between ages 5 and 7. This implies population fluctuations with weak serial correlation.

The results of our simulations are shown in Fig. 7. We have set the combination of river exploitation (50%) and the sea-survival (4%) so as to give a deterministic steady

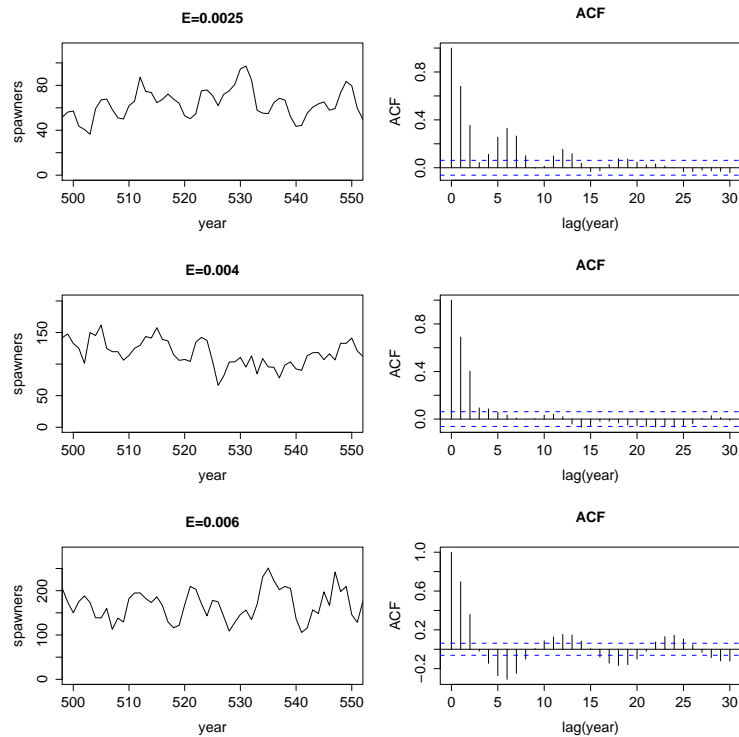


Figure 6: The effect of changing mean on the ACF of population fluctuations. This figure shows a series of simulations with $R_{max} = 3 \times 10^4$, $S_{max} = 120$, $k = 1$, $\theta = 10$, $CV_P = 0.1$ and spawner return occurring with equal probability at $a = 5, 6$ and 7 . The top frames show a run with $\hat{P} = 0.0025$ implying $\hat{S} = 64.4$. The middle frames show a run with $\hat{P} = 0.004$ implying $\hat{S} = 118.8$. The bottom frames show a run with $\hat{P} = 0.006$ implying $\hat{S} = 166.9$.

state of 80 females. Constant effort river-exploitation gives a long-term mean population of around 79 females and an almost exactly equal long-term mean yearly catch in both the strong and weak serial correlation cases.

To apply the conservation limit policy we set the CL at 50 individuals, although we note that this experiment is quite favourable to this policy. Appendix A.6 shows the confidence limits on S_{max} to be such that we should expect to get its value wrong by as much as 20% even if we have correctly identified the functional form of the S-R relation. If we have misidentified the shape of the S-R relation then our likely error will be much larger.

Despite strong structural similarities between the strong and weak serial correlation cases, the results of applying CL determined exploitation are much more severe in the weak serial correlation case. In both cases we see that the tendency of the CL policy to allow high exploitation after a strong returning year class and close down exploitation after a weak one, produces periods of high-frequency population oscillations, which are (not unexpectedly) less persistent in the case where the unmanaged population time-series would show strong serial correlation. In the weak correlation case the induced fluctuations are severe enough to repeatedly drive single pseudo lineages to extinction, requiring that they be (slowly) replenished by leakage from their cousins spawning in nearby sequences of years.

Examination of the catch time series also shown in Fig. 7 exposes the full inefficiency

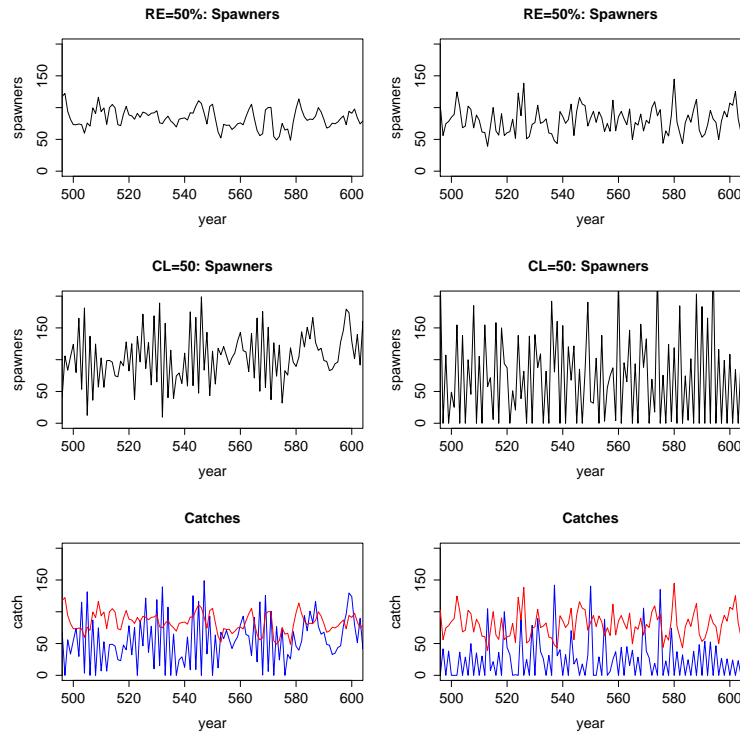


Figure 7: The effects of conservation limited exploitation. This figure shows a series of simulations driven by a broken-stick stock recruitment curve with $R_{max} = 4 \times 10^3$, $S_{max} = 50$, $\theta = 10$, mean sea-survival $\hat{P} = 0.04$ and $CV_P = 0.1$. In the left-hand column spawner return occurs with equal probability at $a = 5, 6$ and 7 . In the right-hand column 80% of return is at $a = 6$ with 10% in each of the preceding and succeeding years. The top frames show a run with river exploitation $\rho = 0.5$. The middle frames show runs with a conservation limit of 50 females and catch in year y equal to the difference between spawners in year $y - 1$ and the CL. The bottom frames show catches under constant effort (red) and CL driven (blue) management.

of the CL driven management policy. In the strong serial correlation case the mean catch is considerably more variable than the constant effort catch and its long-run average is rather smaller, despite a small increase in the long-run average population. In the weak correlation case, the CL driven policy actually manages to reduce the long-run mean spawning stock to below 70 females, and reduce the long-run average catch to 21 fish per year (compared to nearly 80 under the constant effort policy). The reason for this reduction is the policy's tendency to produce near extinction of certain pseudo-lineages which in turn imply multiple years in which the fishery is completely shut (an outcome likely to imply disproportionate financial damage to the industry !).

Appendix

A. Data fits

A.1. Modified Ricker: Girnock Spawner → Fry

Figure 8: Girnock Spawner-Fry Fits. a) Best fit with data. b) Standardised residuals c) Best fit with 95% conf. lims d) Data with implied mean (solid), one s.d. (dashed) and two s.d. (dotted).

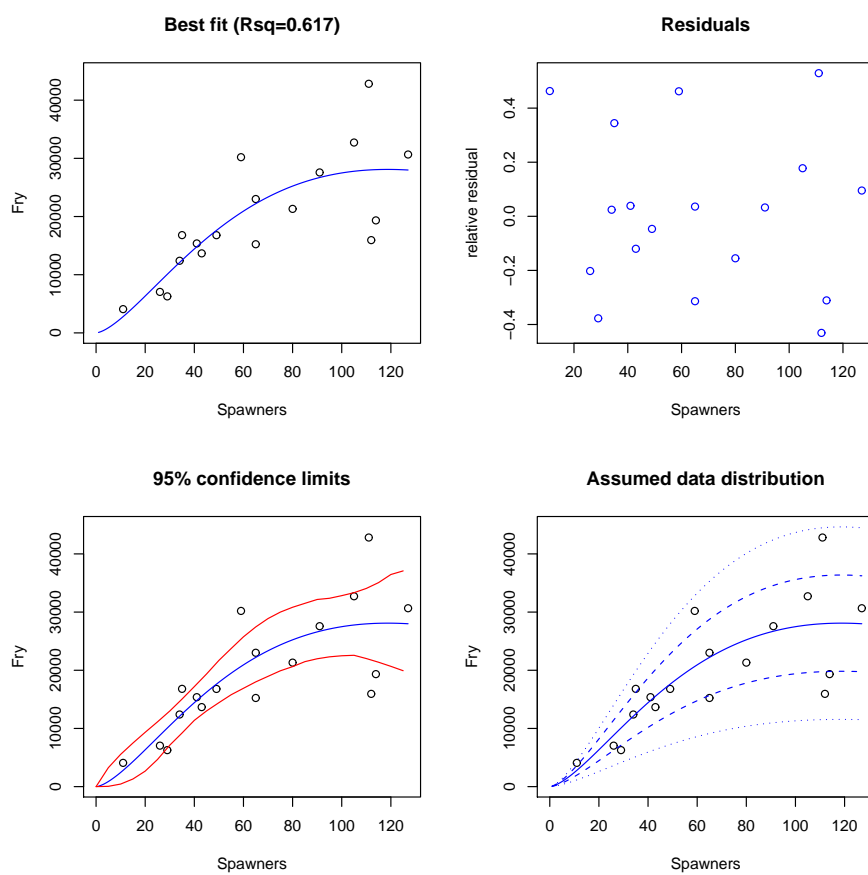


Figure 9: *Girnock Spawner-Fry Parameters. Top – histograms. Bottom – scattergrams.*

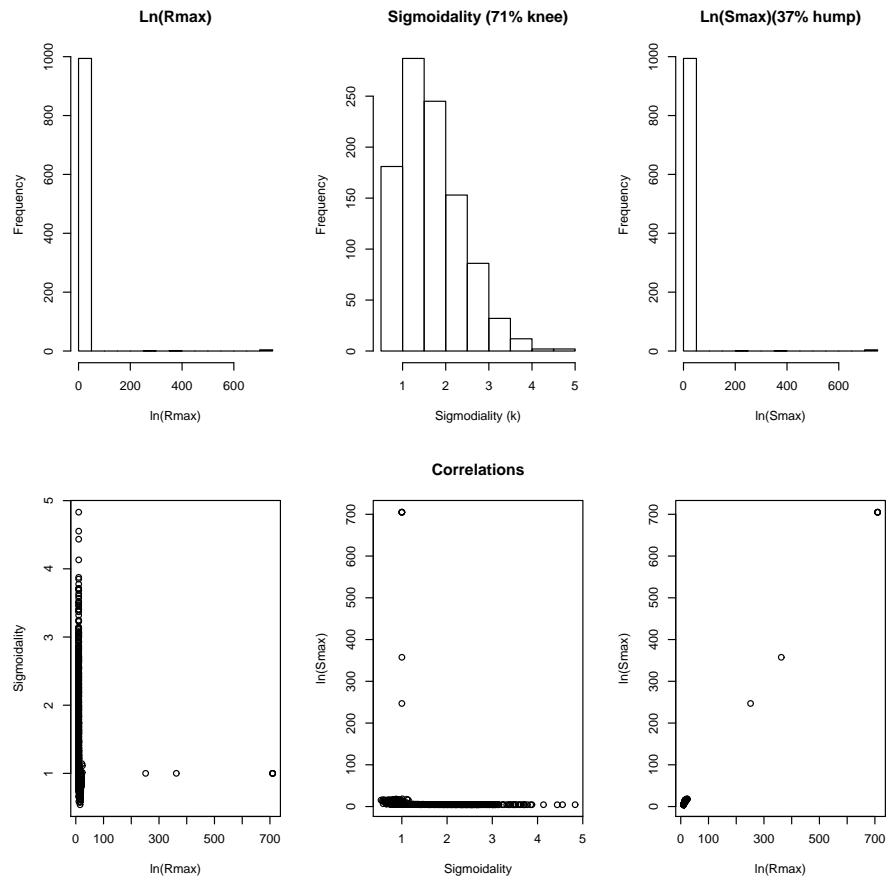
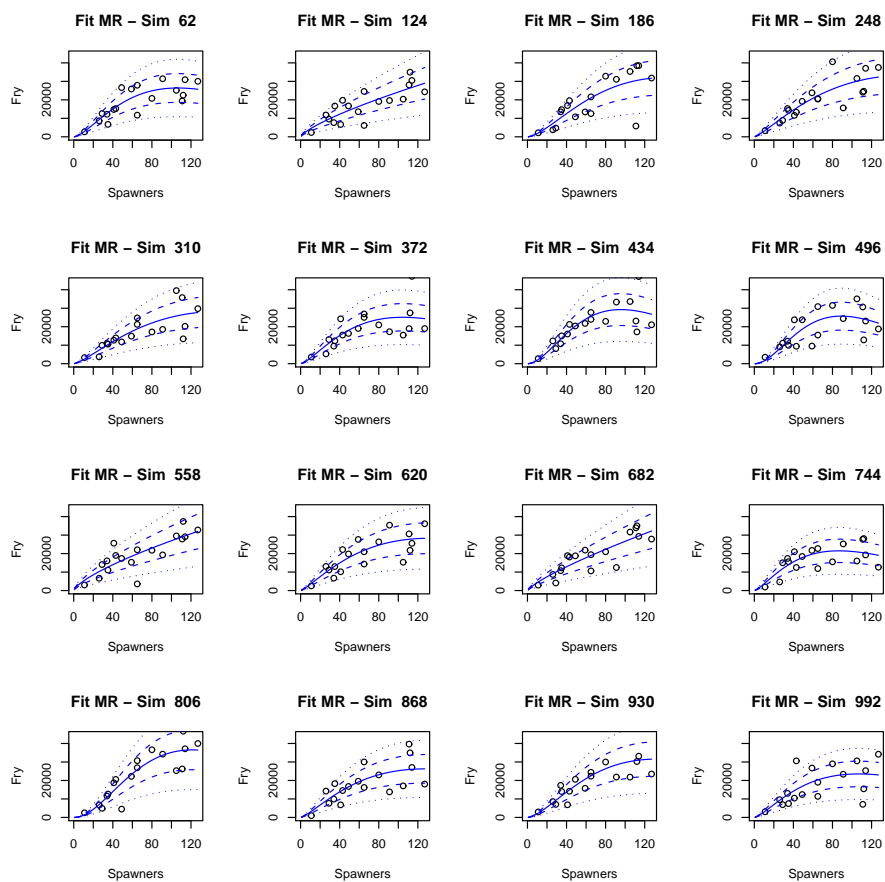


Figure 10: *Girnock Spawner-Fry Simulations*

A.2. Modified Ricker: Girnock Spawner → Smolt

Figure 11: Girnock Spawner-Smolt Fits. a) Best fit with data. b) Standardised residuals c) Best fit with 95% confidence limits d) Data with implied mean (solid), one s.d. (dashed) and two s.d. (dotted).

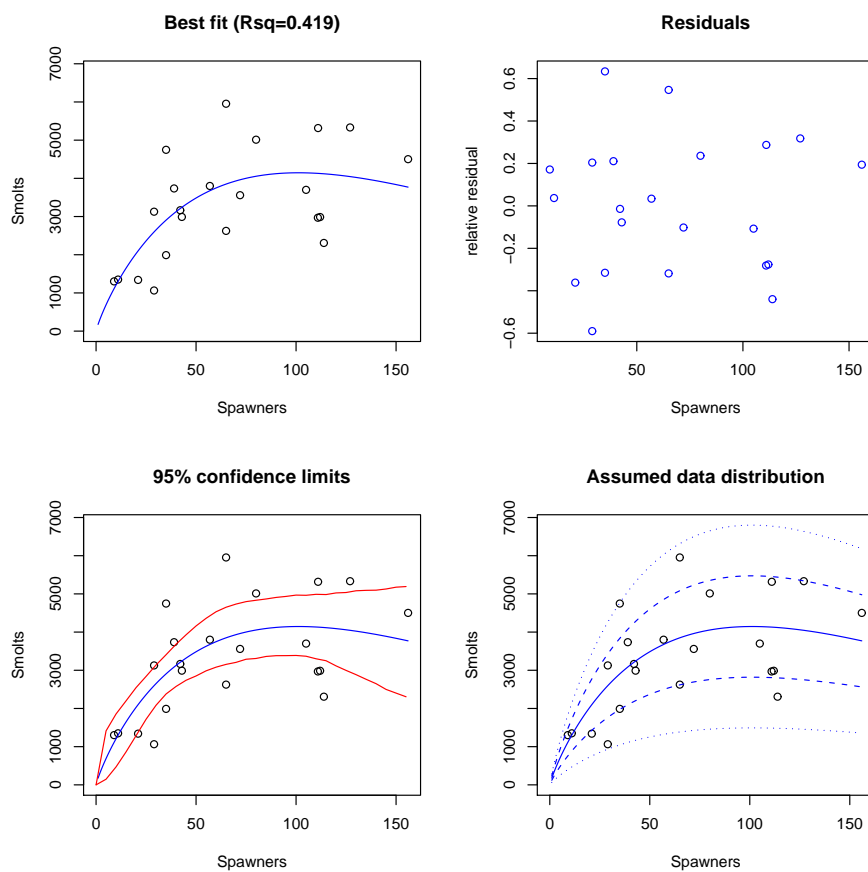


Figure 12: *Girnock Spawner-Smolt Parameters. Top – histograms. Bottom – scattergrams.*

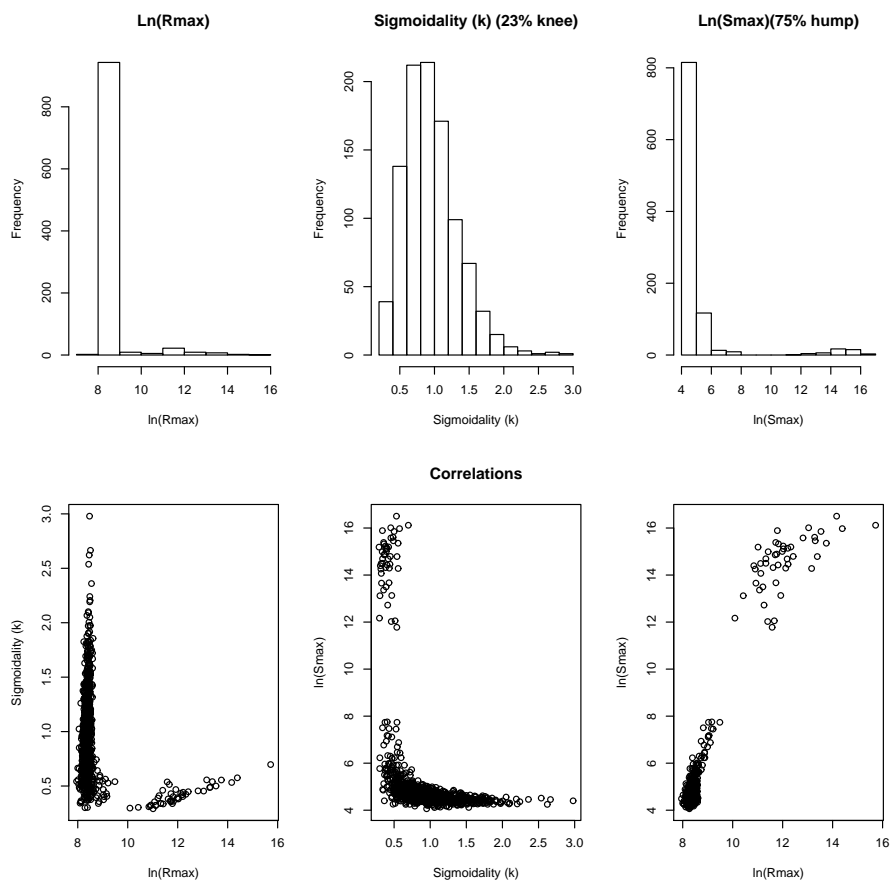
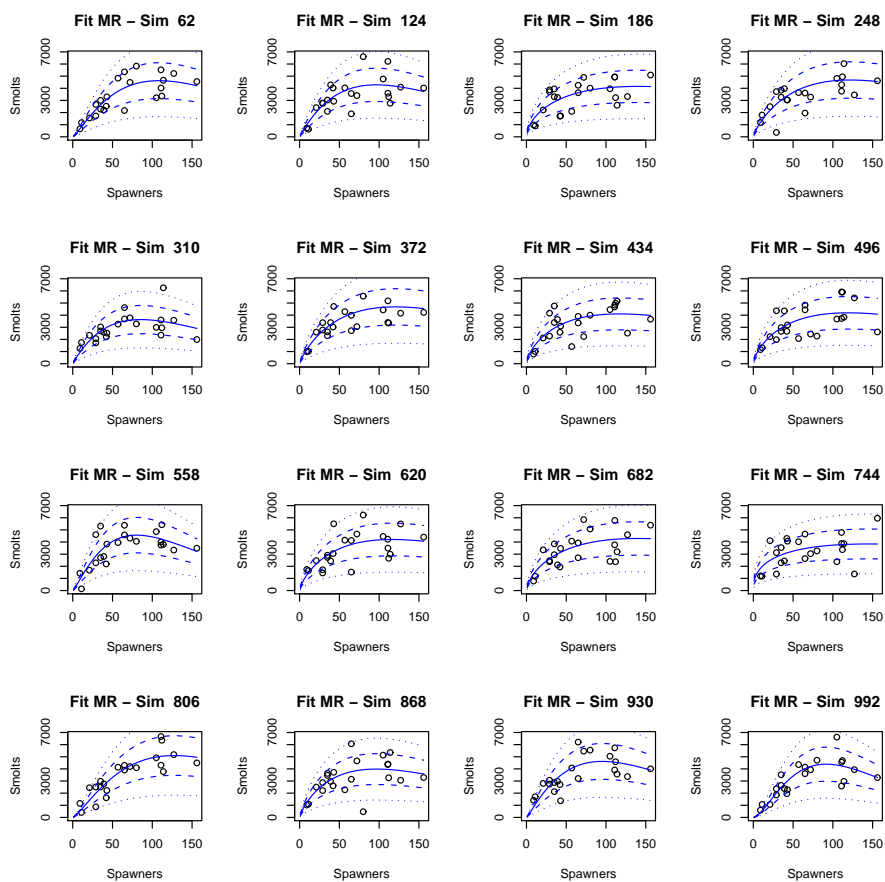


Figure 13: *Girnock Spawner-Smolt Simulations*

A.3. Modified Ricker: Bush Ova \rightarrow Smolt

Figure 14: Bush Ova-Smolt Fits. a) Best fit with data. b) Standardised residuals c) Best fit with 95% confidence limits d) Data with implied mean (solid), one s.d (dashed) and two s.d. (dotted).

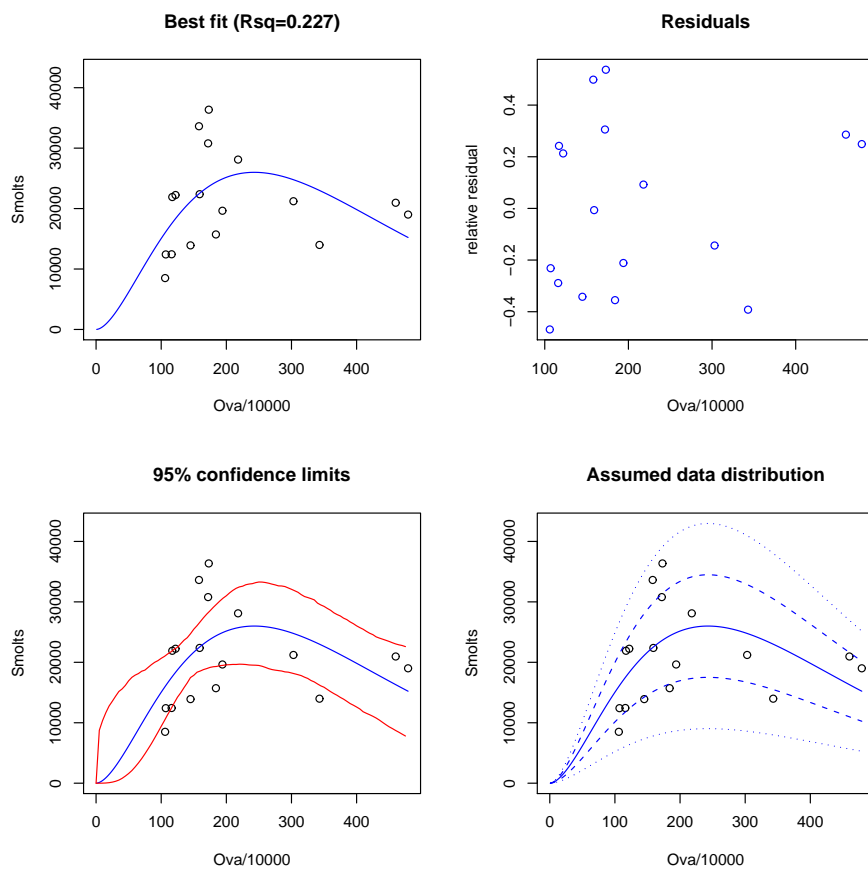


Figure 15: *Bush Ova-Smolt Parameters. Top – histograms. Bottom – scattergrams.*

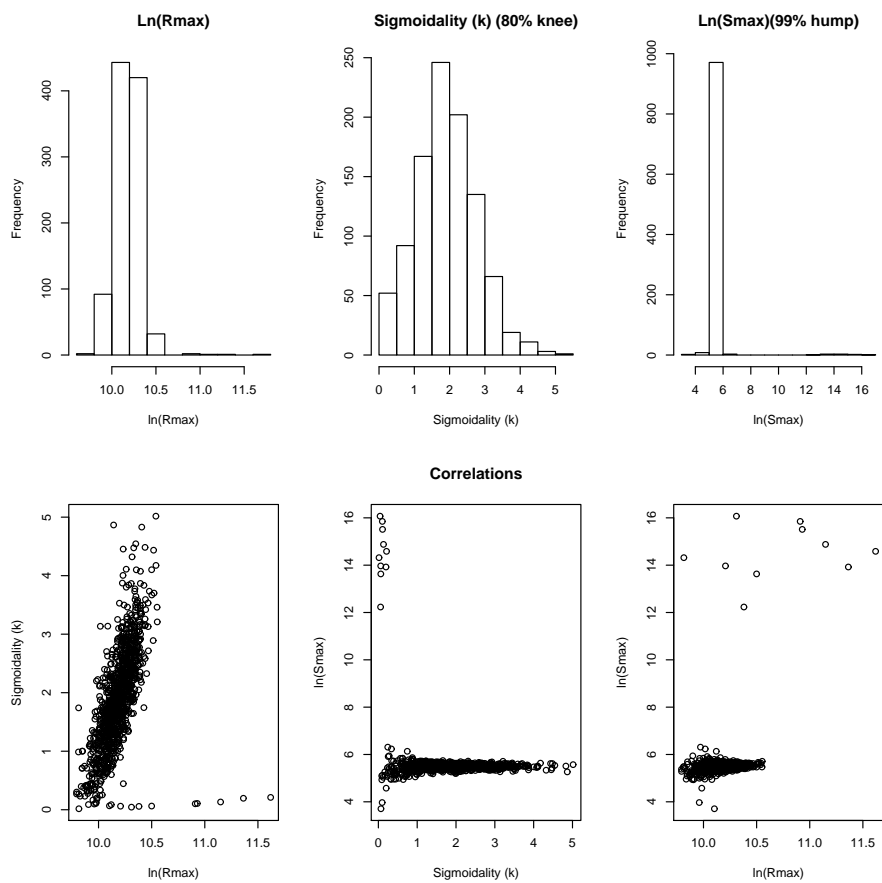
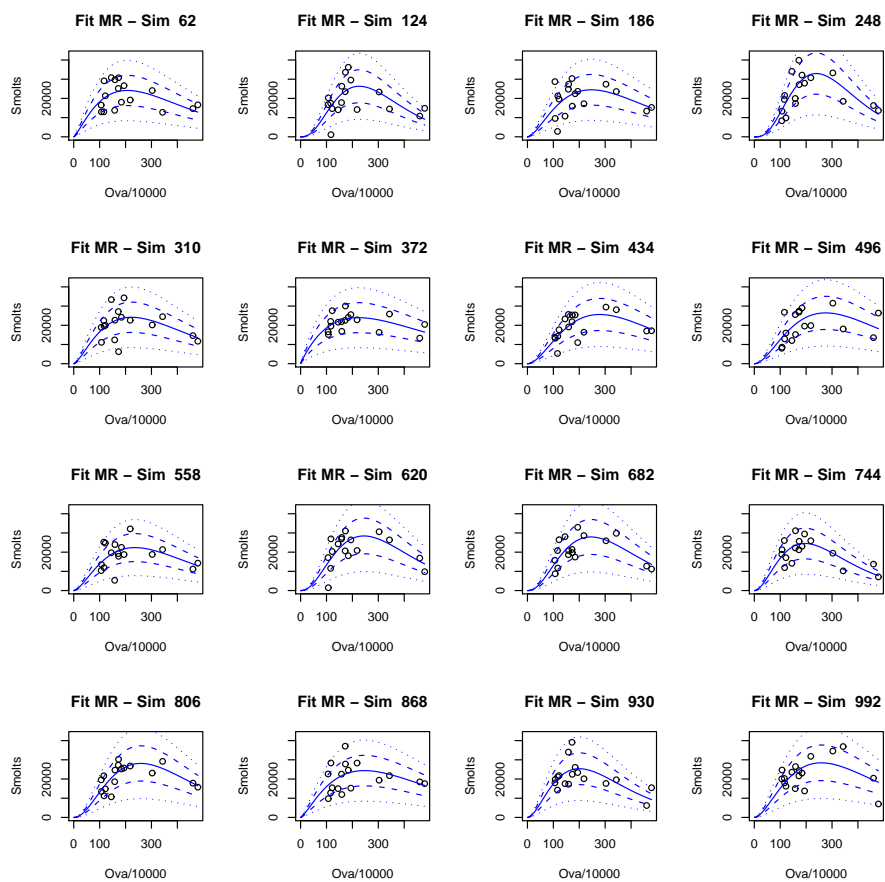


Figure 16: *Bush Ova-Smolt Simulations*

A.4. Modified Ricker: N. Esk Spawner → Pre-fisheries Returner

Figure 17: N. Esk Adult-Adult Fits. a) Best fit with data. b) Standardised residuals c) Best fit with 95% confidence limits d) Data with implied mean (solid), one s.d (dashed) and two s.d. (dotted).

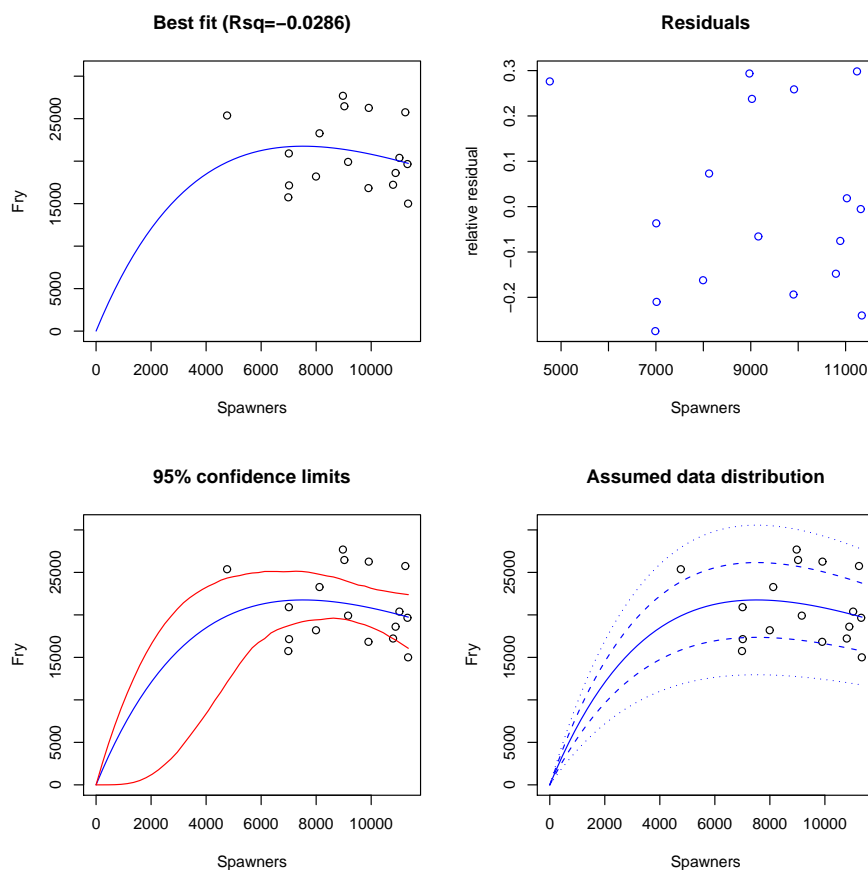


Figure 18: *N. Esk Adult-Adult Parameters. Top – histograms. Bottom – scattergrams.*

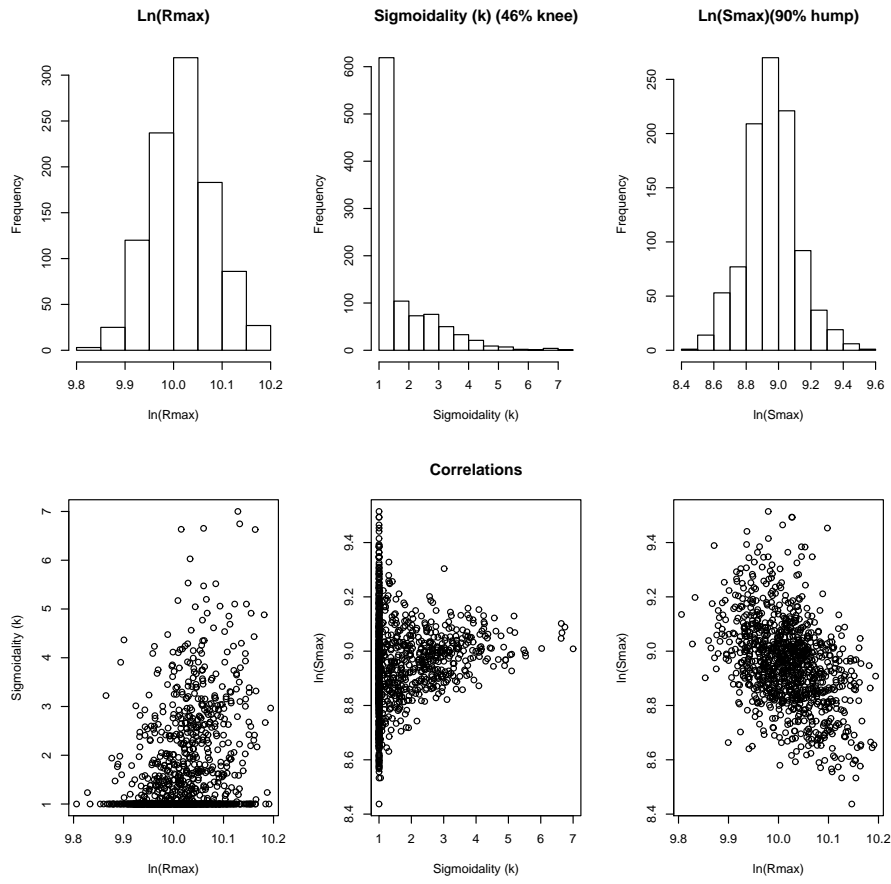
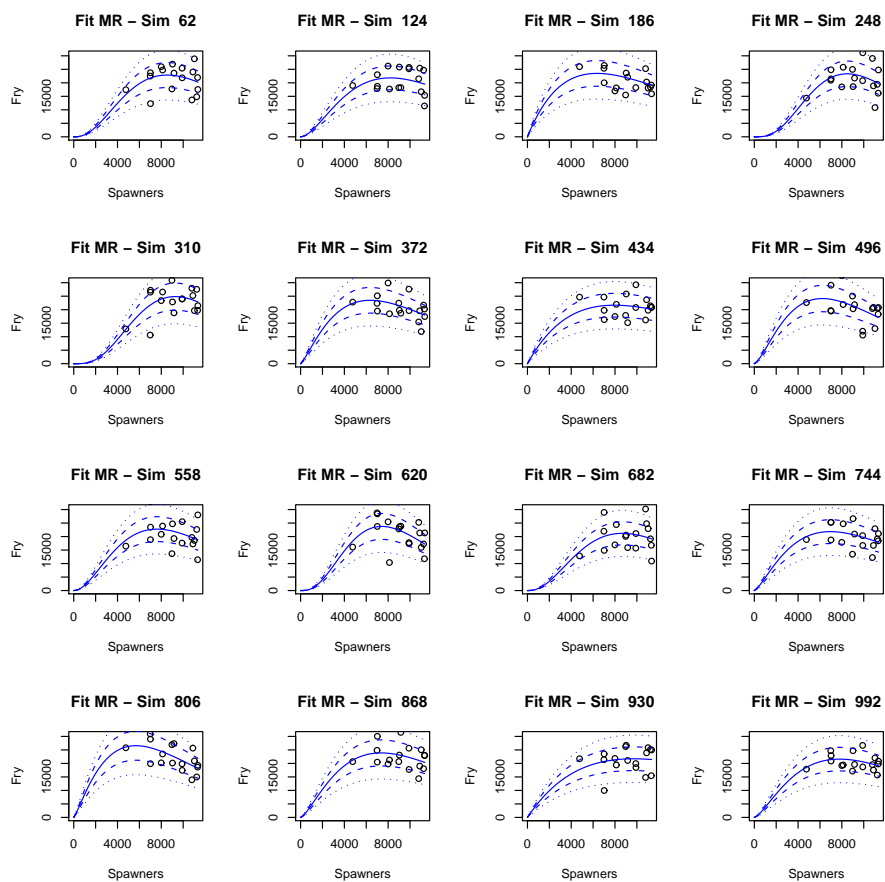


Figure 19: *N. Esk* Adult-Adult Simulations

A.5. Broken Stick: Girnock Spawner → Fry

Figure 20: Girnock Spawner-Fry Fits. a) Best fit with data. b) Standardised residuals c) Best fit with 95% confidence limits d) Data with implied mean (solid), one s.d (dashed) and two s.d. (dotted).

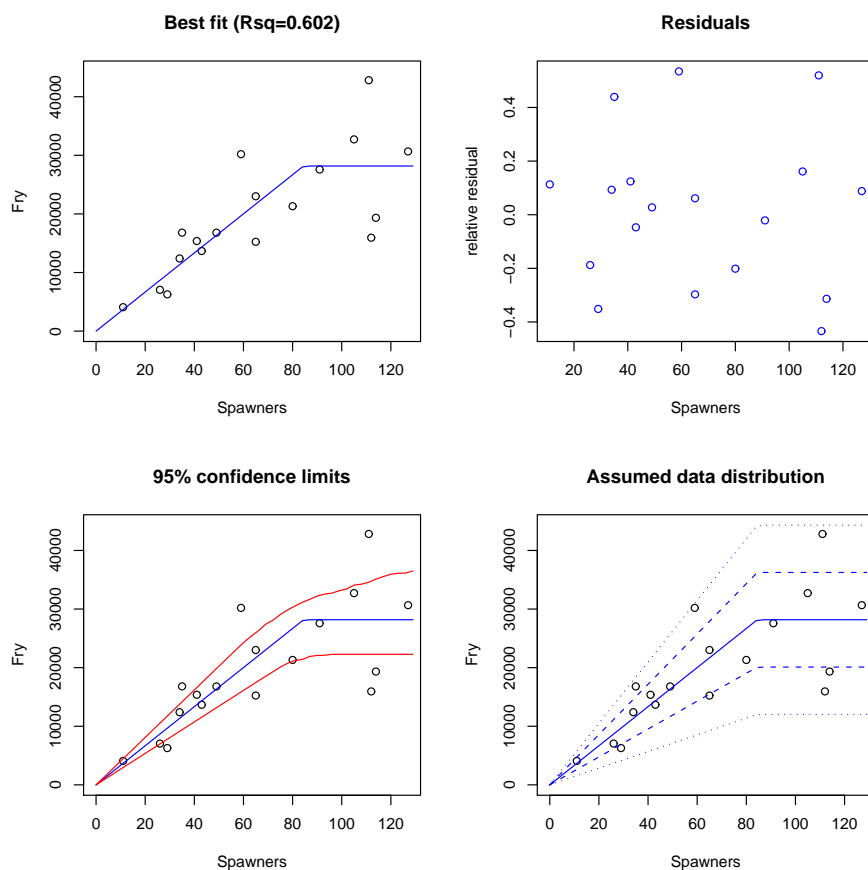


Figure 21: *Girnock Spawner-Fry Parameters*. Top – histograms. Bottom – scattergrams.

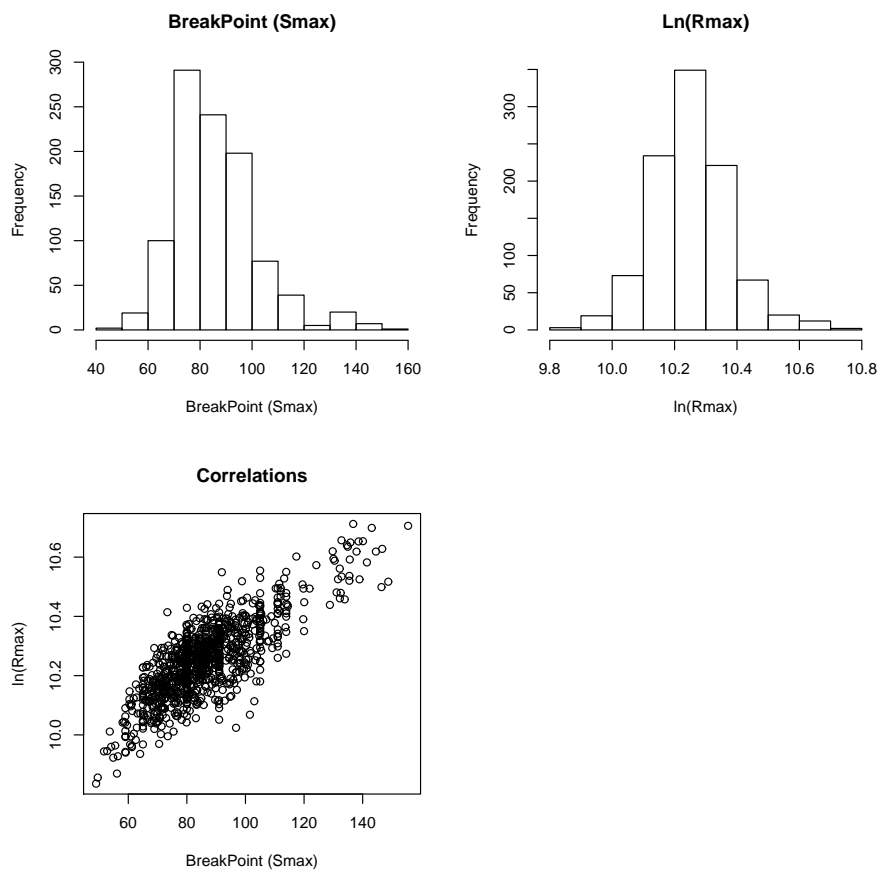
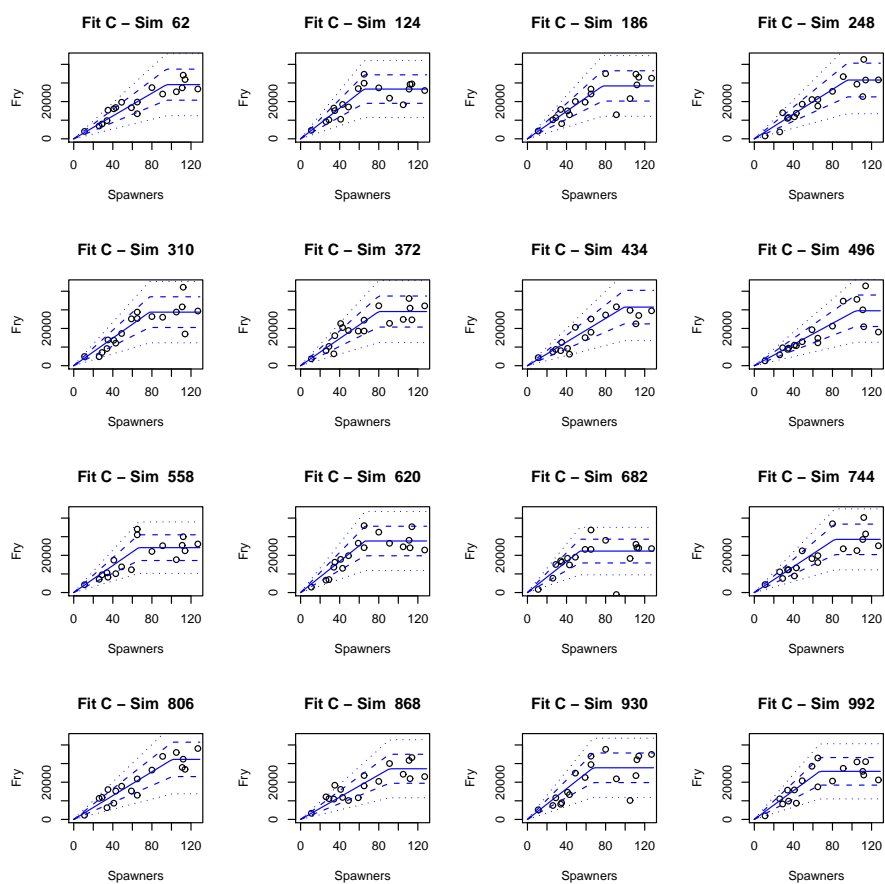


Figure 22: *Girnock Spawner-Fry Simulations*

A.6. Broken Stick: Girnock Spawner → Smolt

Figure 23: Girnock Spawner-Smolt Fits. a) Best fit with data. b) Standardised residuals c) Best fit with 95% confidence limits d) Data with implied mean (solid), one s.d. (dashed) and two s.d. (dotted).

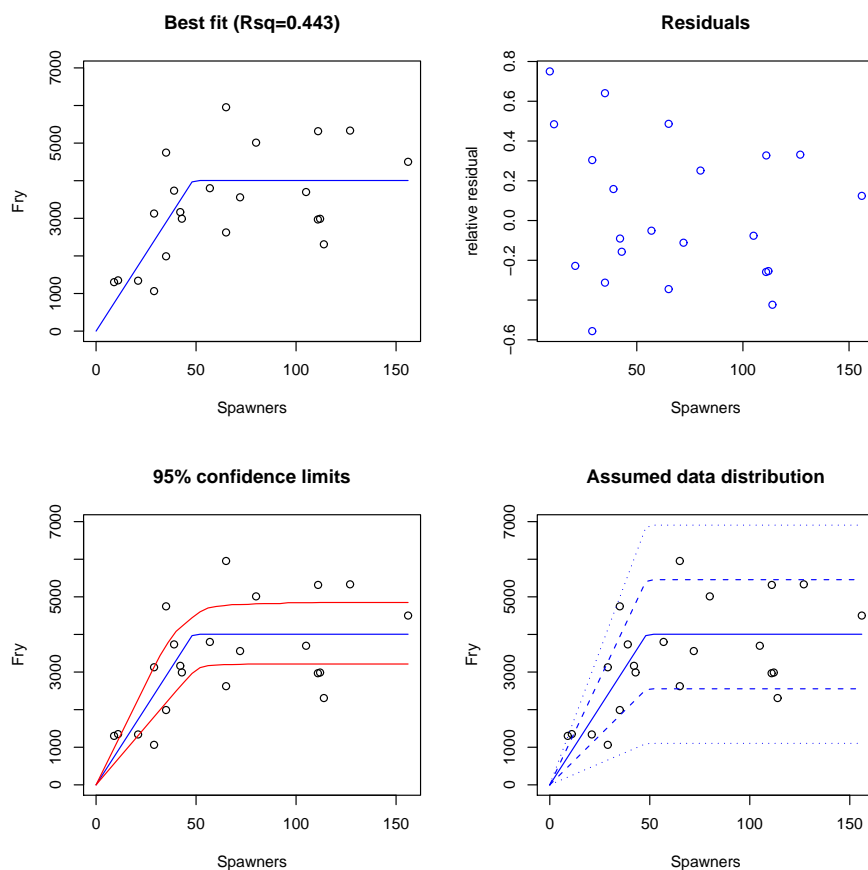


Figure 24: *Girnock Spawner-Smolt Parameters. Top – histograms. Bottom – scattergrams.*

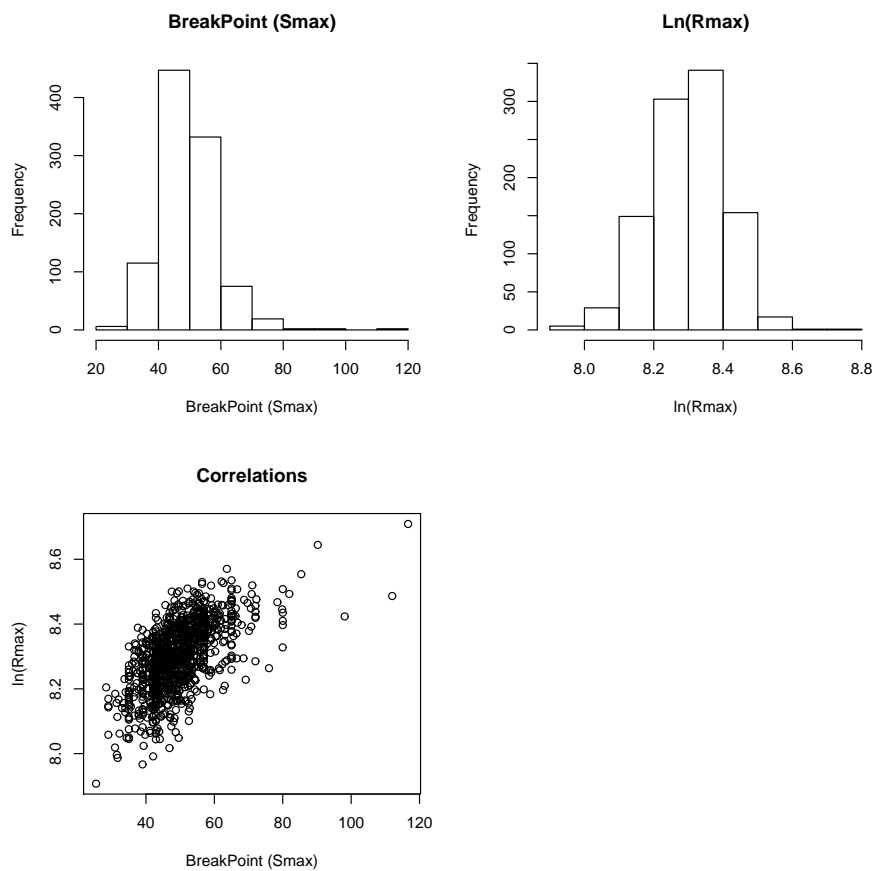
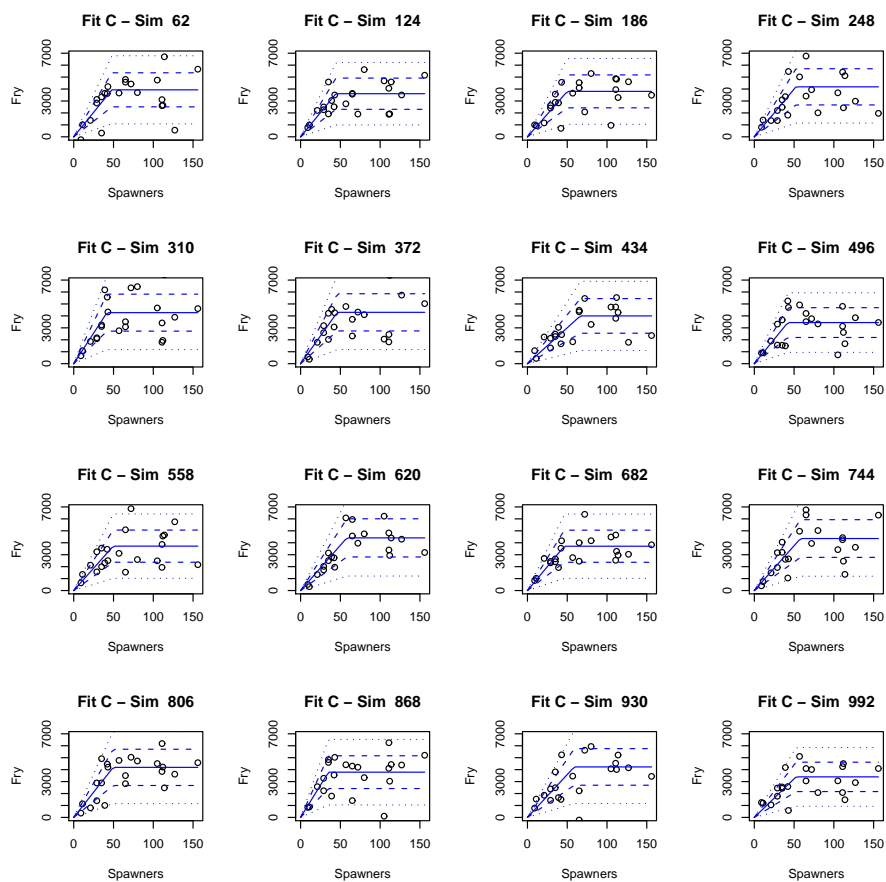


Figure 25: *GirnockSpawner-Smolt Simulations*

A.7. Straight line: Bush Ova → Smolt

Figure 26: Bush Ova-Smolt Fits. a) Best fit with data. b) Standardised residuals c) Best fit with 95% confidence limits d) Data with implied mean (solid), one s.d (dashed) and two s.d. (dotted).

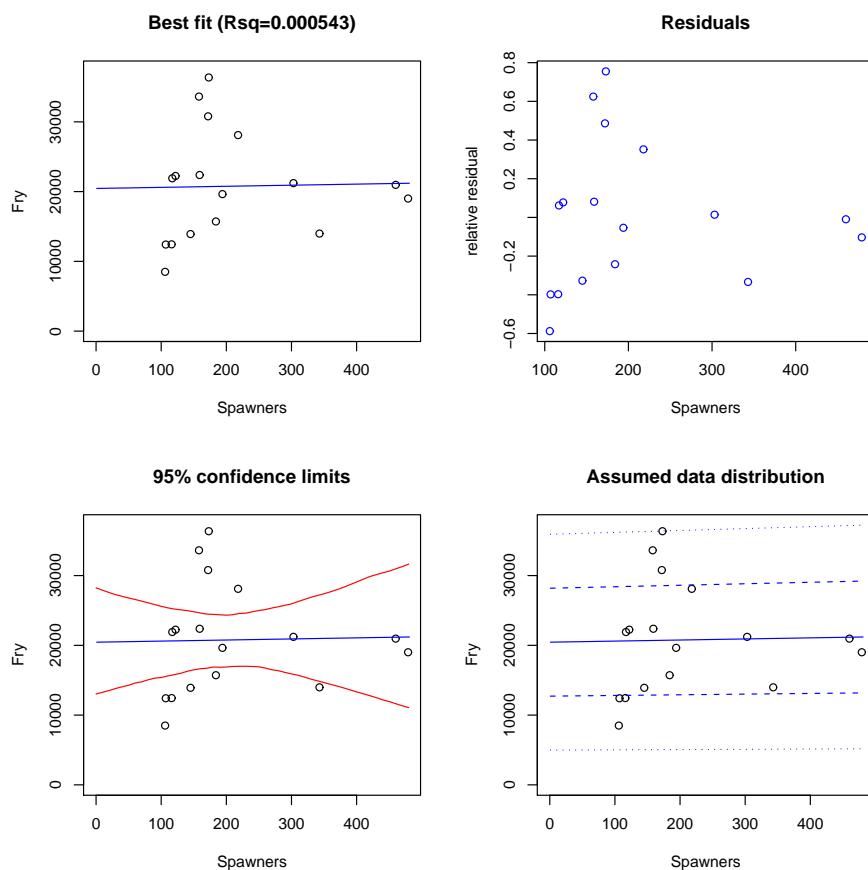


Figure 27: *Bush Ova-Smolt Parameters*. Top – histograms. Bottom – scattergrams.

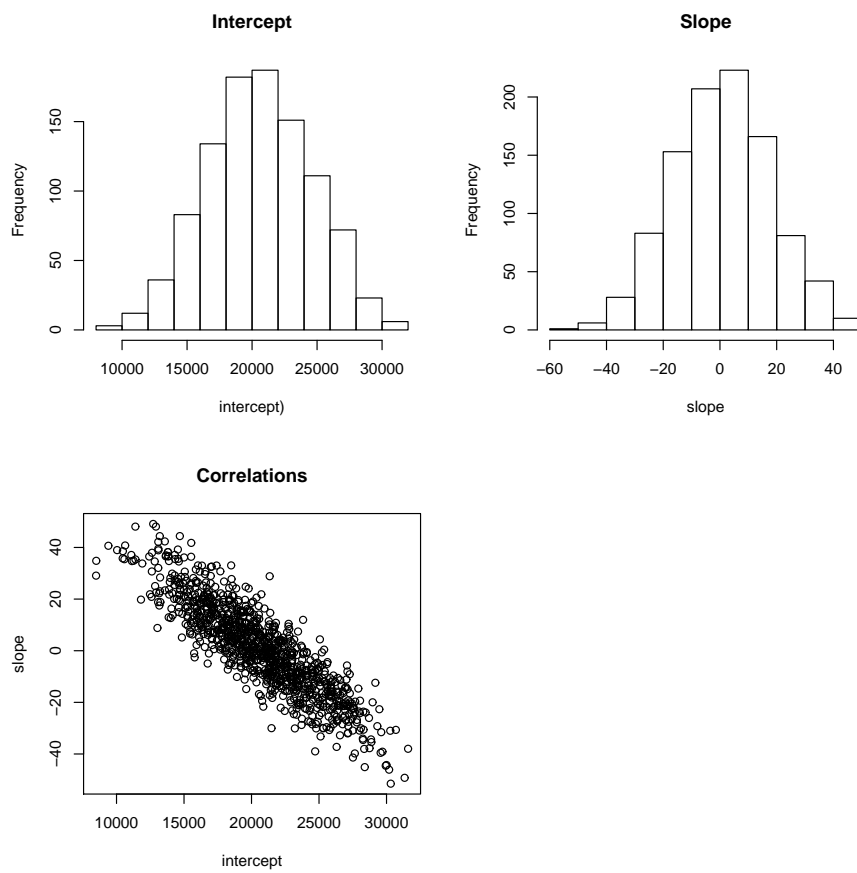
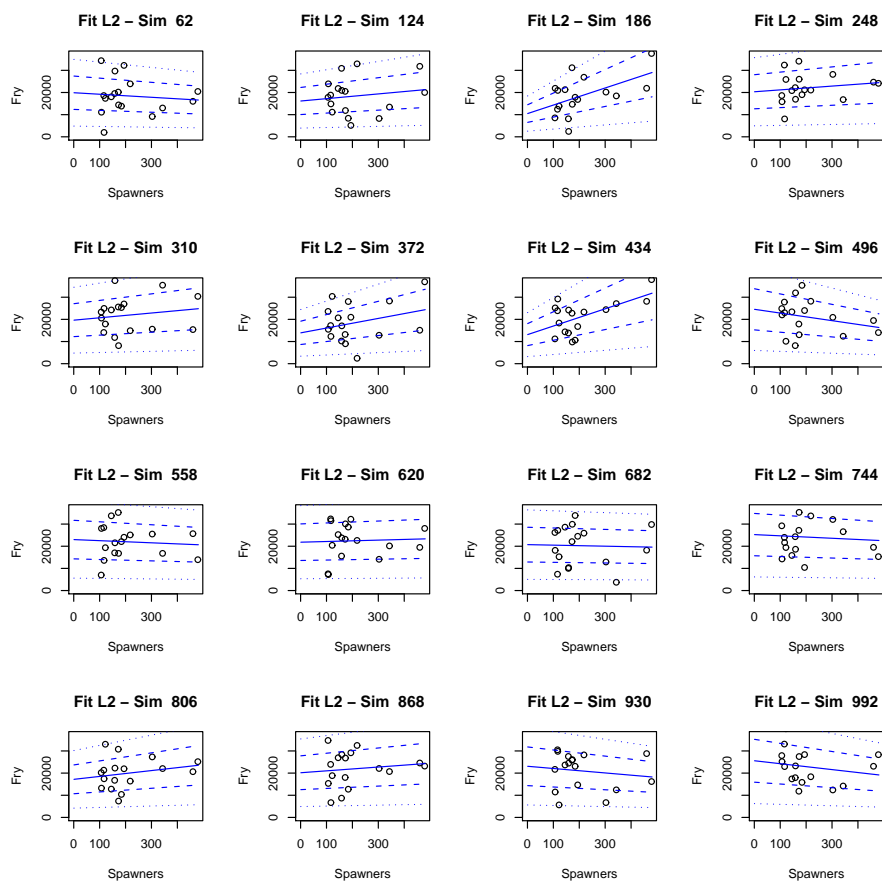


Figure 28: *Bush Ova-Smolt Simulations*

A.8. Straight line: N Esk Spawner \rightarrow Returner

Figure 29: NEsk Spawner-Returner Fits. a) Best fit with data. b) Standardised residuals c) Best fit with 95% confidence limits d) Data with implied mean (solid), one s.d. (dashed) and two s.d. (dotted).

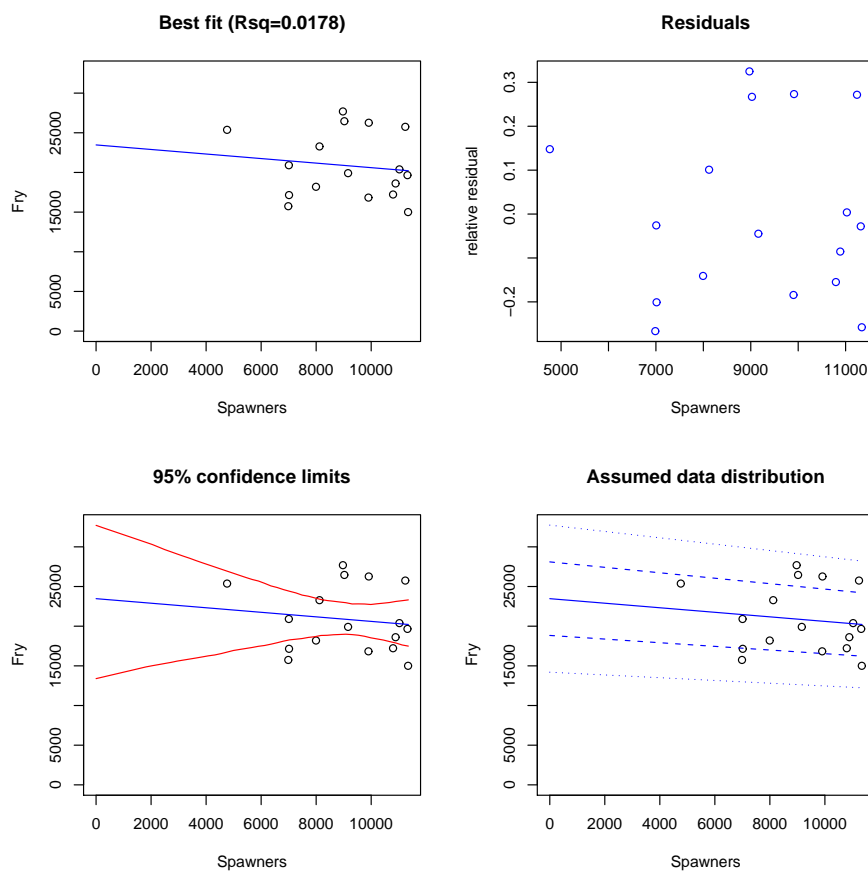


Figure 30: *NEsk Spawner-Returner Parameters. Top – histograms. Bottom – scattergrams.*

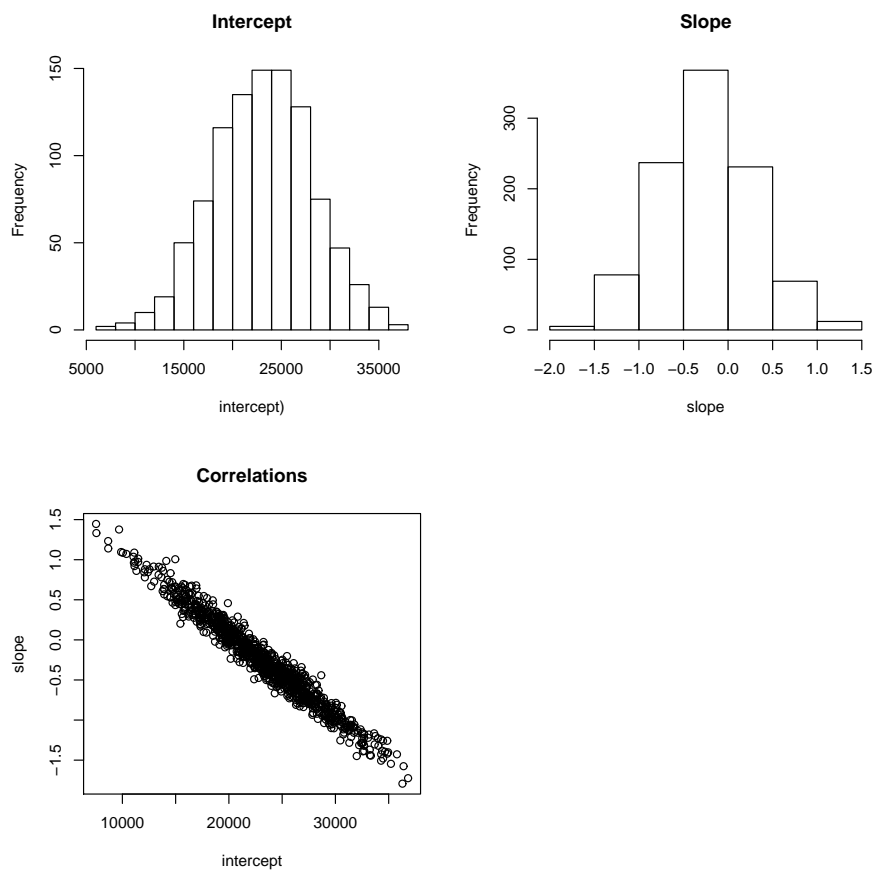
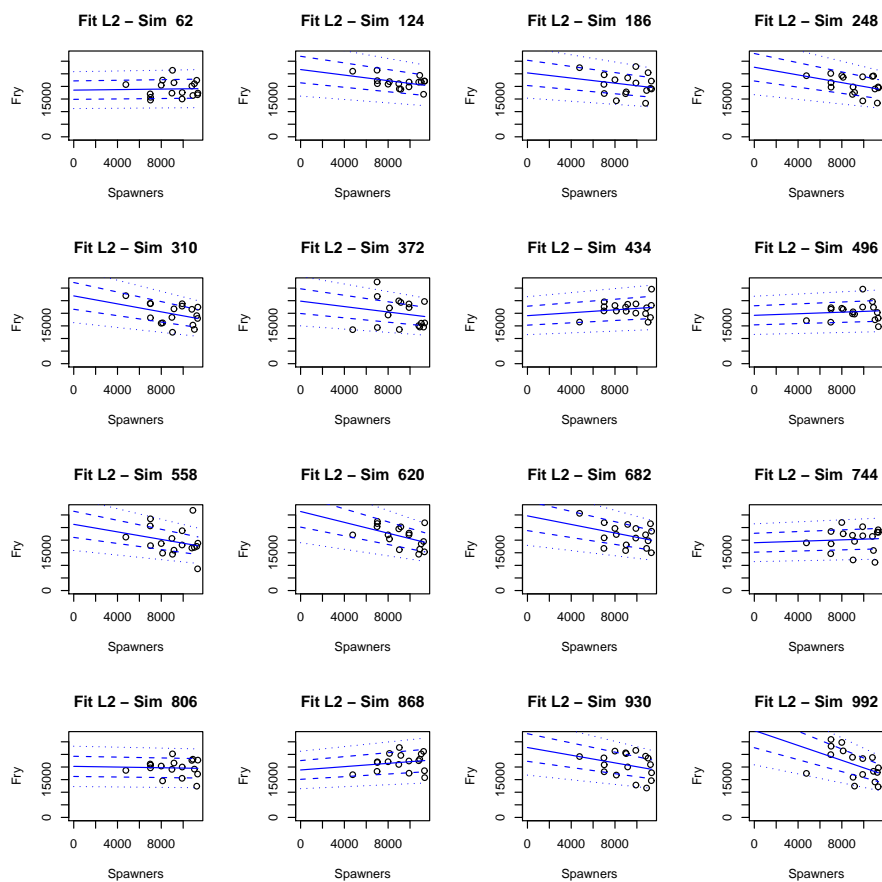


Figure 31: *NEsk Spawner-Returner Simulations*

B. R code

B.1. The generation by generation single deme model

```

%*****
%               R-code to simulate the single deme model
%*****

nextS<-function(S,Rmax=30000,Smax=120,k=1,
                Theta=10,meanP=0.006,cvP=0.1)
{ meanR<-Rmax*(S/Smax)^k*exp(k-k*S/Smax);
  Rnext<-rnbinom(1,size=Theta,mu=meanR);
  P<-meanP*(1+rnorm(1,mean=0,sd=cvP))
  Snext<-P*Rnext;
  return(Snext);
}

make.sequence<-function(max.year=1000,
                        init.S=c(65,50,70,100,75),
                        prop.ret=c(0,0,0,0,1,1,0),
                        Rmax=30000,Smax=120,k=1,Theta=10,
                        meanP=0.006,cvP=0.1)
{ prop.ret<-prop.ret/sum(prop.ret);
  sl<-length(prop.ret);
  seq<-vector(mode='double',length=max.year+sl);
  seq[1:length(init.S)]<-init.S;

  for (y in 1:max.year)
    { new<-prop.ret*nextS(seq[y],Rmax,Smax,k,Theta,meanP,cvP);
      seq[(y+1):(y+sl)]<-seq[(y+1):(y+sl)]+new;
    }
  o<-data.frame(year=0:(max.year-1),spawners=seq[1:max.year]);
  return(o);
}

```

B.2. The year by year single deme model

```
nextSC<-function(S,Rmax=4000,Smax=50,Theta=10,meanP=0.02,cvP=0.1)
{ meanF<-ifelse(S>Smax,Rmax,Rmax*S/Smax);
  Rnext<-rnbino(1,size=Theta,mu=meanF);
  P<-meanP*(1+rnorm(1,mean=0,sd=cvP))
  Snext<-P*Rnext;
  return(Snext);
}
```

```
make.sequenceC<-function (max.year=1000,
                          init.S=c(65,50,70,100,75,63,80),
                          prop.ret=c(0,0,0,0,1,1,0),
                          Rmax=4000, Smax=50, sCL=NA, Rho=0.5,
                          Theta=10, meanP=0.04, cvP=0.1)
{ prop.ret<-prop.ret/sum(prop.ret);
  if(!is.na(Rer)){init.S<-init.S/Rer;}
  sl<-length(prop.ret);
  seq<-vector(mode='double',length=max.year+sl);
  cat<-seq;
  seq[1:length(init.S)]<-init.S;

  for (y in 2:max.year)
    { if (is.na(sCL)) {cat[y]<-seq[y]*Rho;}
      else          { allowed<-max(0,seq[y-1]-sCL);
                    cat[y]<-min(seq[y],allowed)
                  }
      seq[y]<-seq[y]-cat[y];
      new<-prop.ret*nextSC(seq[y],Rmax,Smax,Theta,meanP,cvP);
      seq[(y+1):(y+sl)]<-seq[(y+1):(y+sl)]+new;
    }
  o<-data.frame(year=0:(max.year-1),
                spawners=seq[1:max.year],
                catch=cat[1:max.year]);
  return(o);
}
```