

## A note on variability in $R_0$ calculated from an individually based baleen whale energetic model.

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### Abstract

An individual based energetic model is used to derive possible relationships between the observed rates of increase of whale populations at low population sizes and observed levels of variability in fecundity.

### Introduction

At the MSYR workshop held in March 2013 in La Jolla (SC/65A/Rep05), I presented a model based on individual animals that uses a detailed energy budget to determine reproductive success and mortality in an environment where food has a patchy spatial distribution (de la Mare, 2013). The model will not be described further here.

The calculation of maximum sustainable yield rate (MSYR) from the rate of recovery of depleted whale populations needs to take into account the effects of environmental variability on both birth-rates and deathrates (Cooke, 2012). Counting calves on the breeding grounds provides information on the first source of variability, but direct observation of variability in death rates is not practical. However, birth-rates and death rates are both consequences of the amount of energy available to animals in the population. A reasonably comprehensive energetic model enables the calculation of plausible relationships between birth-rates, death rates and realised rates of population increase. The energetic model is used here to predict variability in the realised rate of increase ( $r_0$ ) in a generic depleted whale population given estimates of the variability and autocorrelation in birth-rates. The variability in the model's realised rates of increase is subject to the variability in death rates because the model links deathrates to birth-rates through the energetic requirements of the animals. The results are provided in the form used in the meta-analysis of (MSYR) according to the methods described in Punt (2012).

### The calculations

Variability in births and deaths in a population is modelled as a consequence of a variable food supply. The realised rates of increase depend both on the average amount of food available and the variability in the food supply. A wide range of variations in the food supply is modelled so as to produce a range of variations in birth-rates, deathrates and  $r_0$ . The results of the simulations are used in a linear model to predict the variability in  $r_0$  conditioned on given values of variability in birth-rate ( $\sigma_f$ ) and its autocorrelation ( $\rho_f$ ).

The procedure for the calculations starts with setting a number of scenarios for the prey population and running a single realisation of the population model for 1500 years to stabilise the composition of the population so that it is at carrying capacity (K) and adapted to each particular prey scenario. The population is then reduced to about 1% of K over a 50 year period with a constant harvest rate. This provides a starting point from which the population is allowed to recover with the numbers of animals alive in each year being used to calculate the rate of increase and the inter-annual variability in the rate of increase. The recovery trajectories are generated from the common starting point multiple times. The population is allowed to increase for 20 years before rates of increase and variability are calculated from the next ten years of population statistics. The 20 year period prior allows for the randomisation of the population statistics at the outset of the calculations. The calculation period is kept down to 10 years to ensure that the population statistics still reflect those of a population increasing well below K. The recovery period is repeated 200 times thus giving a total simulated time series of 2000 years.

For each 10 year replicate the rate of increase is estimated as:

$$\hat{r} = \log \left( \frac{N_y}{N_{y-1}} \right) \quad (1)$$

where  $N_y$  is the total abundance in year  $y$ .

Equation (1) has the effect of de-trending the numbers so that the coefficient of variation (CV) of the annualised rate of increase is standard deviation. The birth-rates (per mature female) and death rates (per total abundance) are analysed in a similar way. The summary statistics from the set of simulations are given in Table 1.

Unfortunately, the execution time for the model can be long and so it proved impractical in the time available after the workshop to condition the model to specific values of  $\sigma_f$  and  $\rho_f$ . Instead I attempted to condition the model statistically by running the model for a range of prey conditions that vary in abundance and variability. This produces a range of  $r_0/r_{max}$  values from around 0.1 to 1, along with variations in  $\sigma_f$  as shown in Fig. 1.

Fig 2 shows the relationship between  $CV(r_0)$  and  $1 - r_0/r_{max}$  with a fitted regression line through the origin. The regression line is:

$$CV(r_0) = -0.0441 \left( \frac{r_0}{r_{max}} - 1 \right) \quad (2)$$

The CV can be rescaled to  $r_{max}$  simply by dividing by the  $r_{max}$  value, which in these simulations is 0.118.

I then fitted linear regressions to predict values of  $r_0/r_{max}$ ,  $CV(r_0)$  and serial correlation in abundance using  $\sigma_f$  and  $\rho_f$  as independent variables. The regression for  $r_0/r_{max}$  used  $\log(r_0/r_{max})$  as the dependent variable and the regression line was forced to include the origin so that  $r_0/r_{max} = 1$  when there is no variability in fecundity. Figs 3 to 8 show the relationships between the mean values of  $r_0/r_{max}$ ,  $CV(r_0)$  and  $\rho(N)$  for the mean values of  $\sigma_f$  and  $\rho_f$ . The relationships from the full 200 replicates of each prey scenario are shown in figs 9 to 14. The results using these a linear model fitted to these results on the MSYR Working Group's selected stocks are given in Table 2.

The results show that in this particular set of trials that values for the mean variability in fecundity were lower than some of the values included in the table of selected stocks. This has had the consequence that the conditional mean values of  $r_0/r_{max}$  are quite low in those cases where  $\sigma_f$  is substantial.

The results for  $r_0/r_{max}$  and  $CV(r_0)$  for the specified values of  $\sigma_f$  and  $\rho_f$  for the various stocks are shown in table 2. Table 3 is based on regressions in which the values where the mean values of  $r_0/r_{max}$  less than 0.4 are excluded. Table 4 is based on the regressions using the total set of 5800 values, except that values where  $r_0/r_{max} < 0$  are excluded. The results in the three tables are similar, so it is not simply the case that the more extreme values of  $r_0/r_{max}$  are driving the results.

The current simulations are generally inconsistent with relatively high values of  $r_0/r_{max}$  co-occurring with the observed high variability in fecundity. However, in the total set of results high levels of variability in  $\sigma_f$  are found in some trials in these simulations and these higher values attained in the simulations are consistent with the higher values assigned to the selected stocks. The variability in death rates is higher than that of the birth-rates and adjusting some parameters of the energetic model might allow for the two sources of variability to be partitioned differently. The results suggests that uncertainty in the variability in fecundity and its unobserved relationship with variability in deathrates may be more important for the meta-analyses than has been considered so far, particularly considering that only 5 of the 13 stocks have direct estimates of  $\sigma_f$  and  $\rho_f$ . In addition, the statistical uncertainties in the estimates of  $\sigma_f$  and  $\rho_f$  are not taken into account in the meta-analysis.

### The resultant yield curves

The model with the various prey scenarios is used to calculate the corresponding yield curves by running it forward from the unexploited state (after 1500 years) for a further 50 years to randomise the starting state, and then for a further 400 years at various constant exploitation rates. The average catch and abundance in the last 200 years are taken as estimates of the long-term equilibrium yield and abundance. These simulations are replicated 25 times with the yields thus averaged over 5000 simulation years. A Pella-Tomlinson model is fitted to the simulated yields to estimate MSYR and MSYL.

These computations are very time consuming and several model scenarios were still running when this note was drafted. The results from those cases which were completed are shown in Table 4. An example of a fitted yield curve is shown in Fig. 15.

### References

- Cooke, J. G. 2008. The influence of environmental variability on baleen whale sustainable yield curves. SC/59/RMP10.
- de la Mare, W. K. 2013. Implications of energy budgets in determining the characteristics of whale yield curves. Paper presented to the Fourth MSYR Workshop, La Jolla, March 2013.
- Punt, A. E. 2012, Summary of progress relating to developing a posterior distribution for the rate of increase for an unknown stock. IWC/64/Rep1, Appendix 2.

Table 1. Statistics from the 29 different prey abundance and variability scenarios

Scenario	Prey abund.	Prey CV	K	CV(K)	r0	CV(r0)	$\rho(N)$	$\sigma(\rho(N))$	$\sigma_f$	$\sigma(\sigma_f)$	$\rho_f$	$\sigma(\rho_f)$	$\sigma_d$	$\sigma(\sigma_d)$	$\rho_d$	$\sigma(\rho_d)$	$\rho_{bd}$	$\sigma(\rho_{bd})$
1	10000	0.	56665	0.003	0.0950	0.00582	-0.0492	0.3015	0.0325	0.0099	-0.3695	0.2694	0.0775	0.0189	-0.1112	0.2804	0.1136	0.3359
2	10000	0.5	48976	0.217	0.0968	0.0061	0.0072	0.2832	0.0328	0.0098	-0.3925	0.2543	0.0805	0.0204	-0.1007	0.2768	0.0806	0.3455
3	10000	0.7	42759	0.271	0.1014	0.0056	-0.0255	0.2982	0.0286	0.0086	-0.4139	0.2182	0.0718	0.0197	-0.0437	0.2866	0.1462	0.3284
4	10000	0.9	37827	0.333	0.1111	0.0056	0.0682	0.2743	0.0226	0.0083	-0.3076	0.2736	0.0803	0.0584	-0.0016	0.3115	0.0788	0.3626
5	5000	0.5	23023	0.198	0.0962	0.0091	-0.1171	0.2982	0.0482	0.0150	-0.4678	0.2313	0.1244	0.0348	-0.1043	0.2921	0.1062	0.3861
6	5000	0.7	19184	0.242	0.0838	0.0134	-0.0963	0.3012	0.0811	0.0266	-0.4234	0.2528	0.1926	0.0551	-0.0799	0.2693	0.1236	0.3555
7	5000	0.9	16825	0.313	0.0964	0.0134	-0.0274	0.3210	0.0651	0.0233	-0.4565	0.2528	0.1768	0.0563	-0.0301	0.2933	0.0316	0.3682
8	3000	0.5	10777	0.234	0.0791	0.0181	-0.0862	0.3070	0.0968	0.0321	-0.4652	0.2427	0.2377	0.0720	-0.0714	0.2941	0.1160	0.3763
9	3000	0.7	8233	0.324	0.0695	0.0194	0.0158	0.2943	0.1065	0.0335	-0.4085	0.2481	0.2673	0.0872	0.0244	0.2985	-0.0068	0.3438
10	3000	0.9	5957	0.429	0.0564	0.0268	0.0540	0.2933	0.1420	0.0521	-0.3197	0.2432	0.3386	0.1408	0.0791	0.3093	-0.0229	0.3588
11	2500	0.5	6897	0.285	0.0658	0.0191	0.0441	0.3007	0.1007	0.0321	-0.3687	0.2570	0.2441	0.0746	0.0577	0.3229	0.0285	0.3403
12	2500	0.7	4880	0.423	0.0601	0.0293	0.0873	0.2748	0.1316	0.0463	-0.3490	0.2847	0.3292	0.1273	0.0952	0.3222	-0.0658	0.3631
13	2500	0.9	5957	0.429	0.0637	0.0294	0.0754	0.2981	0.1254	0.0482	-0.3297	0.2739	0.3390	0.1463	0.0613	0.3361	-0.0324	0.3568
14	3000	0.5	42677	0.210	0.0659	0.0127	0.2371	0.2960	0.0728	0.0215	-0.4159	0.2212	0.1645	0.0507	0.0025	0.3230	0.0267	0.3418
15	3000	0.7	39118	0.291	0.0586	0.0174	0.0463	0.2938	0.0992	0.0345	-0.3524	0.2452	0.2212	0.0708	0.0163	0.3222	0.0189	0.3641
16	3000	0.9	26921	0.304	0.0545	0.0226	0.1089	0.3004	0.1100	0.0382	-0.2931	0.2650	0.2699	0.1172	0.0854	0.3169	0.0854	0.3486
17	2500	0.5	30225	0.250	0.0549	0.0173	0.0695	0.2687	0.0961	0.0307	-0.3517	0.2316	0.2054	0.0607	0.0381	0.2965	-0.0042	0.3413
18	2300	0.9	20749	0.457	0.0563	0.0287	0.1301	0.2723	0.1226	0.0541	-0.2853	0.2838	0.3151	0.1294	0.0936	0.2897	-0.1187	0.3658
19	2300	0.7	30538	0.325	0.0582	0.0193	0.1177	0.2858	0.0957	0.0297	-0.3225	0.2676	0.2224	0.0884	0.0894	0.3123	-0.0317	0.3579
20	2500	0.7	52260	0.256	0.0622	0.0115	0.0697	0.2771	0.0641	0.0193	-0.3399	0.2573	0.1538	0.0600	0.0801	0.3328	-0.0189	0.3227
21	2500	0.9	40879	0.359	0.0641	0.0172	0.1362	0.2922	0.0666	0.0305	-0.2831	0.3113	0.1994	0.1111	0.1659	0.3023	-0.1033	0.3847
22	2000	0.9	15975	0.343	0.0509	0.0324	0.1325	0.2679	0.1385	0.0613	-0.2745	0.2867	0.3252	0.1342	0.0852	0.3157	-0.0736	0.3485
23	1800	0.9	7551	0.552	0.0386	0.0368	0.1328	0.2684	0.1884	0.0741	-0.2980	0.2356	0.4018	0.1403	0.0857	0.2850	-0.0774	0.3394
24	1600	0.9	2087	0.328	0.0287	0.0455	0.1667	0.2672	0.2176	0.1107	-0.2688	0.2743	0.4427	0.1499	0.1045	0.3008	-0.1076	0.3094
25	1500	0.9	829	0.313	0.0171	0.0444	0.2025	0.2580	0.2144	0.0911	-0.2276	0.2762	0.4351	0.1560	0.1315	0.3212	-0.1291	0.3471
26	1800	0.9	2179	0.452	0.0085	0.0410	0.1942	0.2538	0.2117	0.0950	-0.2270	0.2394	0.4113	0.1411	0.1173	0.3188	-0.0927	0.3172
27	1800	0.0	136635	0.034	0.0439	0.0061	-0.0363	0.2488	0.0391	0.0114	-0.3950	0.2174	0.0620	0.0161	-0.1401	0.2725	0.1023	0.3712
28	2500	1.0	48077	0.336	0.0665	0.0158	0.0245	0.2930	0.0826	0.0299	-0.3899	0.2456	0.2096	0.0892	0.0362	0.3073	0.0092	0.3455
29	1800	0.5	57669	0.187	0.0357	0.0206	0.2068	0.2475	0.0938	0.0290	-0.1635	0.2811	0.2025	0.0690	0.1349	0.3004	-0.1623	0.3446

Table 2. Predicted from the regressions on the means with predicted  $\rho(r)$  truncated at 0.5

	Variation in fecundity and mortality					
	$\sigma_f$	$\rho_f$	$r_{max}$	$r_0/r_{max}$	$CV(r)$	$\rho(r)$
<b>Blue</b>						
Central North Atlantic	0.380	-0.181	0.114	0.0451	0.0794	0.299
Southern Hemisphere	0.380	-0.181	0.114	0.0451	0.0794	0.299
Eastern North Pacific	0.380	-0.181	0.114	0.0451	0.0794	0.299
<b>Fin</b>						
North Norway	0.765	0.636	0.114	0.0013	0.1626	>1 (0.50)
Eastern North Pacific	0.765	0.636	0.114	0.0013	0.1626	>1 (0.50)
<b>Humpback</b>						
Western Australia	0.135	0.320	0.103	0.288	0.0293	0.715 (0.50)
Eastern Australia	0.135	0.320	0.103	0.288	0.0293	0.715 (0.50)
Eastern North Pacific	0.135	0.320	0.103	0.288	0.0293	0.715 (0.50)
Hawaii	0.135	0.320	0.103	0.288	0.0293	0.715 (0.50)
<b>Bowhead</b>						
Bering-Chukchi-Beaufort	0.995	0.065	0.043	0.0002	0.2093	0.724 (0.50)
<b>Southern Right</b>						
SE Atlantic	0.042	0.170	0.076	0.6606	0.0093	0.541 (0.50)
SW Atlantic	0.308	-0.074	0.076	0.0789	0.0645	0.382
SE Indian	0.042	0.170	0.076	0.6606	0.0093	0.541(0.50)

Table 3. Predicted from the regressions on the means, omitting cases where  $r_0/r_{max} < 0.4$ , with predicted  $\rho(r)$  truncated at 0.5

	Variation in fecundity and mortality					
	$\sigma_f$	$\rho_f$	$r_{max}$	$r_0/r_{max}$	$CV(r)$	$\rho(r)$
<b>Blue</b>						
Central North Atlantic	0.380	-0.181	0.114	0.0990	0.0836	0.309
Southern Hemisphere	0.380	-0.181	0.114	0.0990	0.0836	0.309
Eastern North Pacific	0.380	-0.181	0.114	0.0990	0.0836	0.309
<b>Fin</b>						
North Norway	0.765	0.636	0.114	0.0091	0.1735	>1 (0.50)
Eastern North Pacific	0.765	0.636	0.114	0.0091	0.1735	>1 (0.50)
<b>Humpback</b>						
Western Australia	0.135	0.320	0.103	0.433	0.0317	0.772 (0.50)
Eastern Australia	0.135	0.320	0.103	0.433	0.0317	0.772 (0.50)
Eastern North Pacific	0.135	0.320	0.103	0.433	0.0317	0.772 (0.50)
Hawaii	0.135	0.320	0.103	0.433	0.0317	0.772 (0.50)
<b>Bowhead</b>						
Bering-Chukchi-Beaufort	0.995	0.065	0.043	0.0023	0.2218	0.738 (0.50)
<b>Southern Right</b>						
SE Atlantic	0.042	0.170	0.076	0.769	0.0102	0.588 (0.50)
SW Atlantic	0.308	-0.074	0.076	0.153	0.0682	0.403
SE Indian	0.042	0.170	0.076	0.769	0.0102	0.588(0.50)

Table 4. Predicted from the regressions on all values with predicted  $\rho(r)$  truncated at 0.5

	Variation in fecundity and mortality					
	$\sigma_f$	$\rho_f$	$r_{max}$	$r_a/r_{max}$	$CV(r)$	$\rho(r)$
<b>Blue</b>						
Central North Atlantic	0.380	-0.181	0.114	0.0749	0.0777	0.260
Southern Hemisphere	0.380	-0.181	0.114	0.0749	0.0777	0.260
Eastern North Pacific	0.380	-0.181	0.114	0.0749	0.0777	0.260
<b>Fin</b>						
North Norway	0.765	0.636	0.114	0.0046	0.1622	>1 (0.50)
Eastern North Pacific	0.765	0.636	0.114	0.0046	0.1622	>1 (0.50)
<b>Humpback</b>						
Western Australia	0.135	0.320	0.103	0.374	0.0298	0.375
Eastern Australia	0.135	0.320	0.103	0.374	0.0298	0.375
Eastern North Pacific	0.135	0.320	0.103	0.374	0.0298	0.375
Hawaii	0.135	0.320	0.103	0.374	0.0298	0.375
<b>Bowhead</b>						
Bering-Chukchi-Beaufort	0.995	0.065	0.043	0.001	0.2065	0.658 (0.50)
<b>Southern Right</b>						
SE Atlantic	0.042	0.170	0.076	0.728	0.0097	0.264
SW Atlantic	0.308	-0.074	0.076	0.121	0.0634	0.275
SE Indian	0.042	0.170	0.076	0.728	0.0097	0.264

Table 5. Yield curve parameters for the mature population. The blank entries correspond to cases where the simulations have yet to finish.

Model number	K	$r_0$	MSYR	MSYL	MSYR/ $r_0$
1					
2					
3					
4					
5					
6					
7	11275	0.118	0.0681	0.533	0.579
8	8160	0.117	0.0536	0.485	0.459
9	5692	0.089	0.0472	0.511	0.527
10	3491	0.068	0.0437	0.564	0.643
11	4799	0.092	0.0445	0.493	0.483
12	2928	0.073	0.0435	0.543	0.599
13	3956	0.090	0.0410	0.484	0.457
14					
15					
16	19921	0.076	0.0300	0.464	0.397
17	22514	0.065	0.0339	0.508	0.521
18	14103	0.066	0.0311	0.491	0.475
19	22106	0.065	0.0352	0.515	0.539
20					
21					
22	12884	0.065	0.0283	0.477	0.437
23	8376	0.057	0.0203	0.452	0.358
24					
25	1581	0.050	0.011	0.413	0.215
26	4818	0.012	0.0055	0.485	0.459
27					
28					
29					

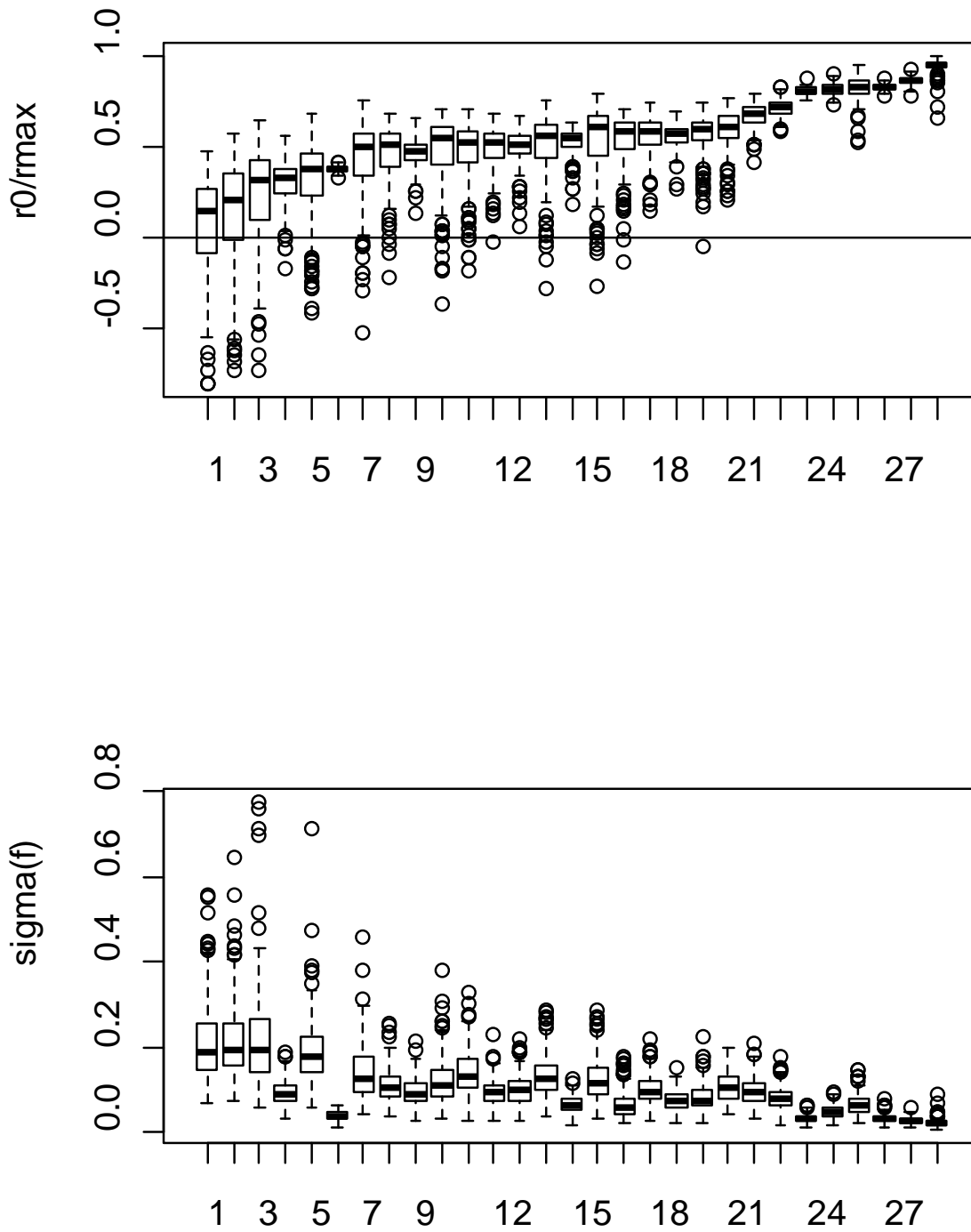


Fig 1. Rates of increase  $r_0/r_{\max}$  for the different models (sorted by mean values of  $r_0/r_{\max}$ ) (upper), and lower corresponding distributions of  $\sigma_f$ .



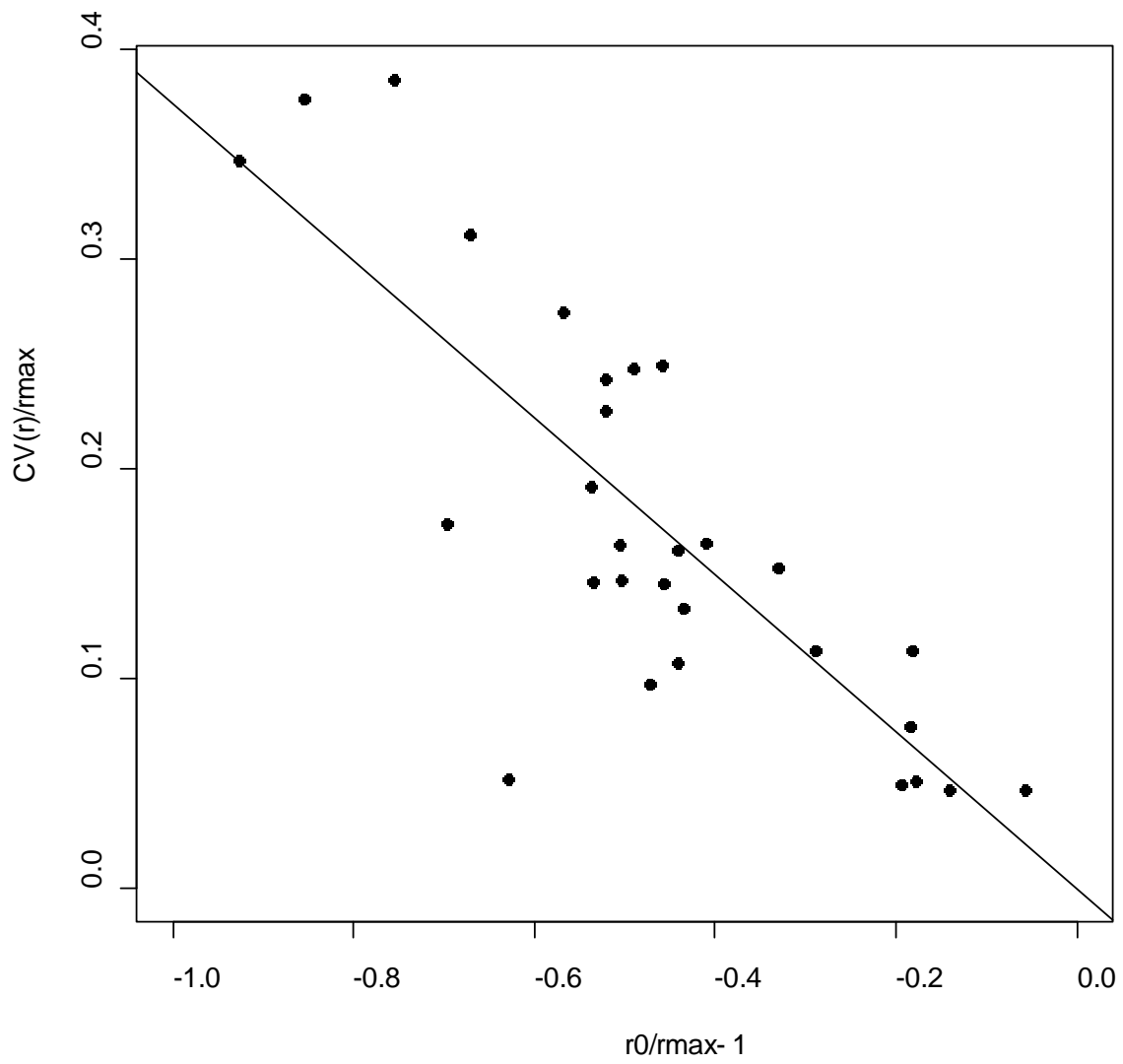


Fig 2. Relationship between  $CV(r_0)/r_{max}$  and  $r_0/r_{max}$ . The intercept is 0,0 and the slope is -0.0441. The value of  $r_{max}$  is 0.118.

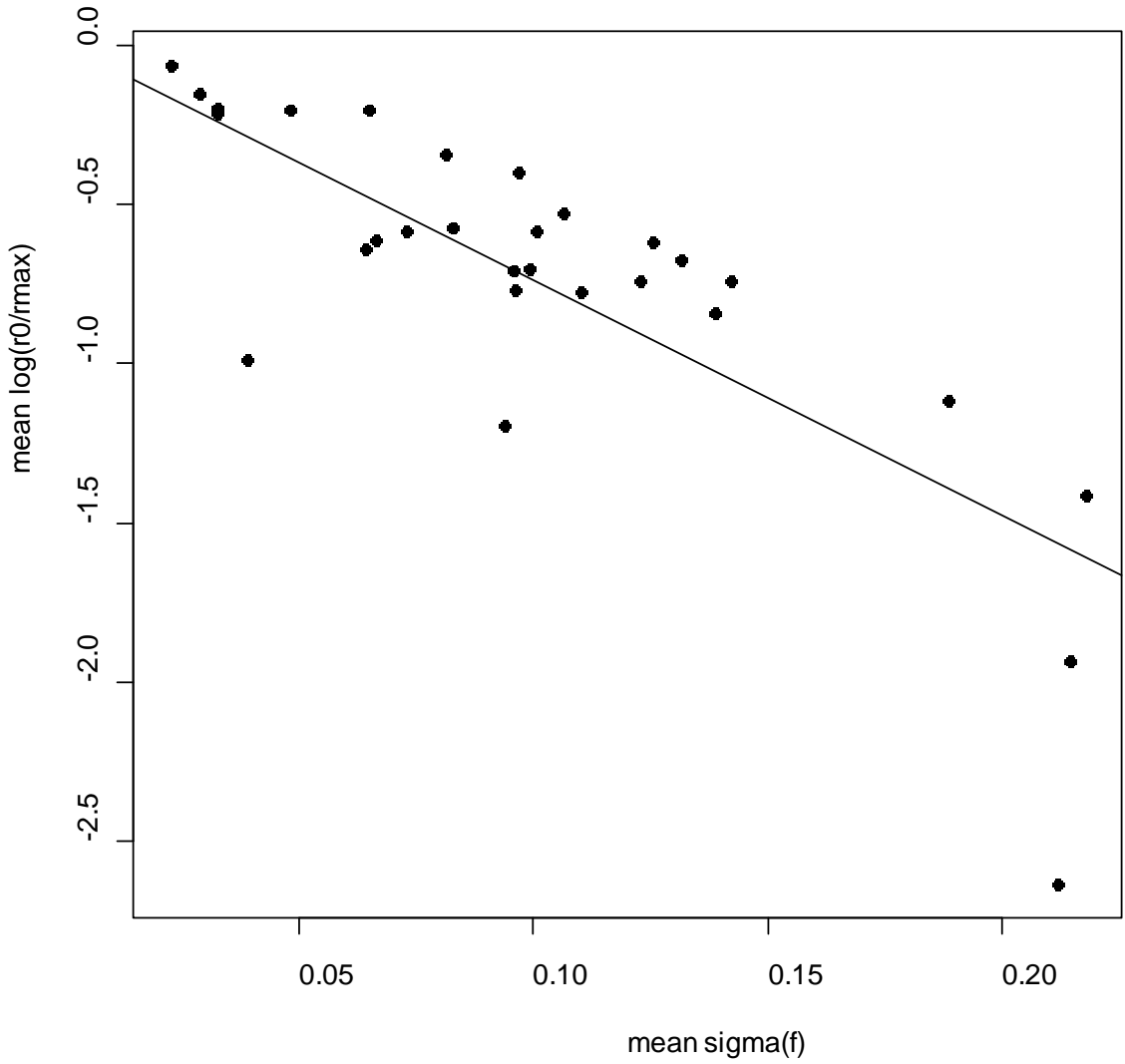


Fig 3. Regression relationship between  $\text{mean}(\sigma_f)$  and  $\log(r_0/r_{\max})$ .

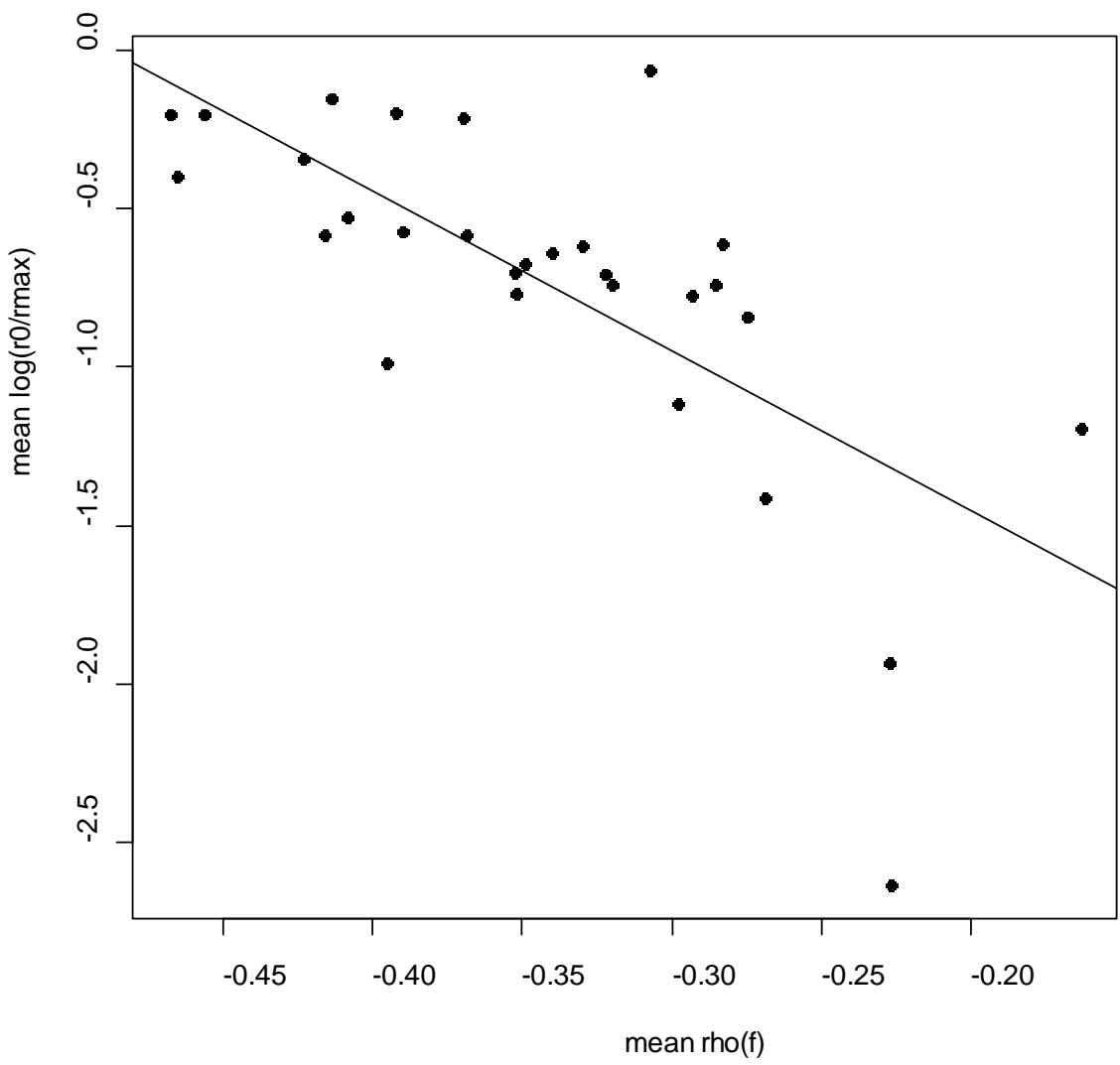


Fig 4. Regression relationship between mean correlation coefficient ( $\rho_f$ ) and  $\log(r_0/r_{\max})$ .

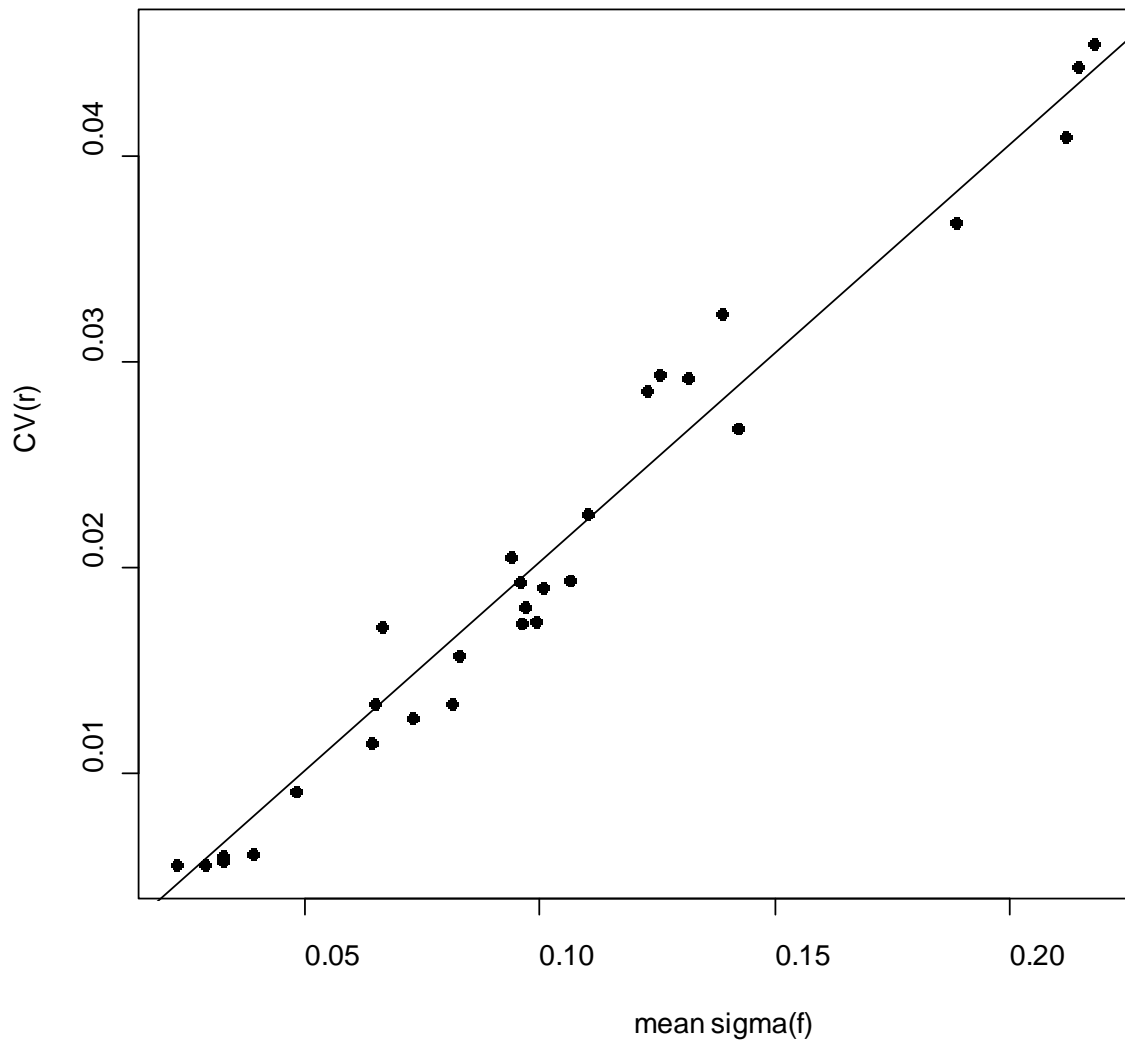


Fig 5. Regression relationship between  $\text{mean}(\sigma_f)$  and  $\text{CV}(r_0)$ .

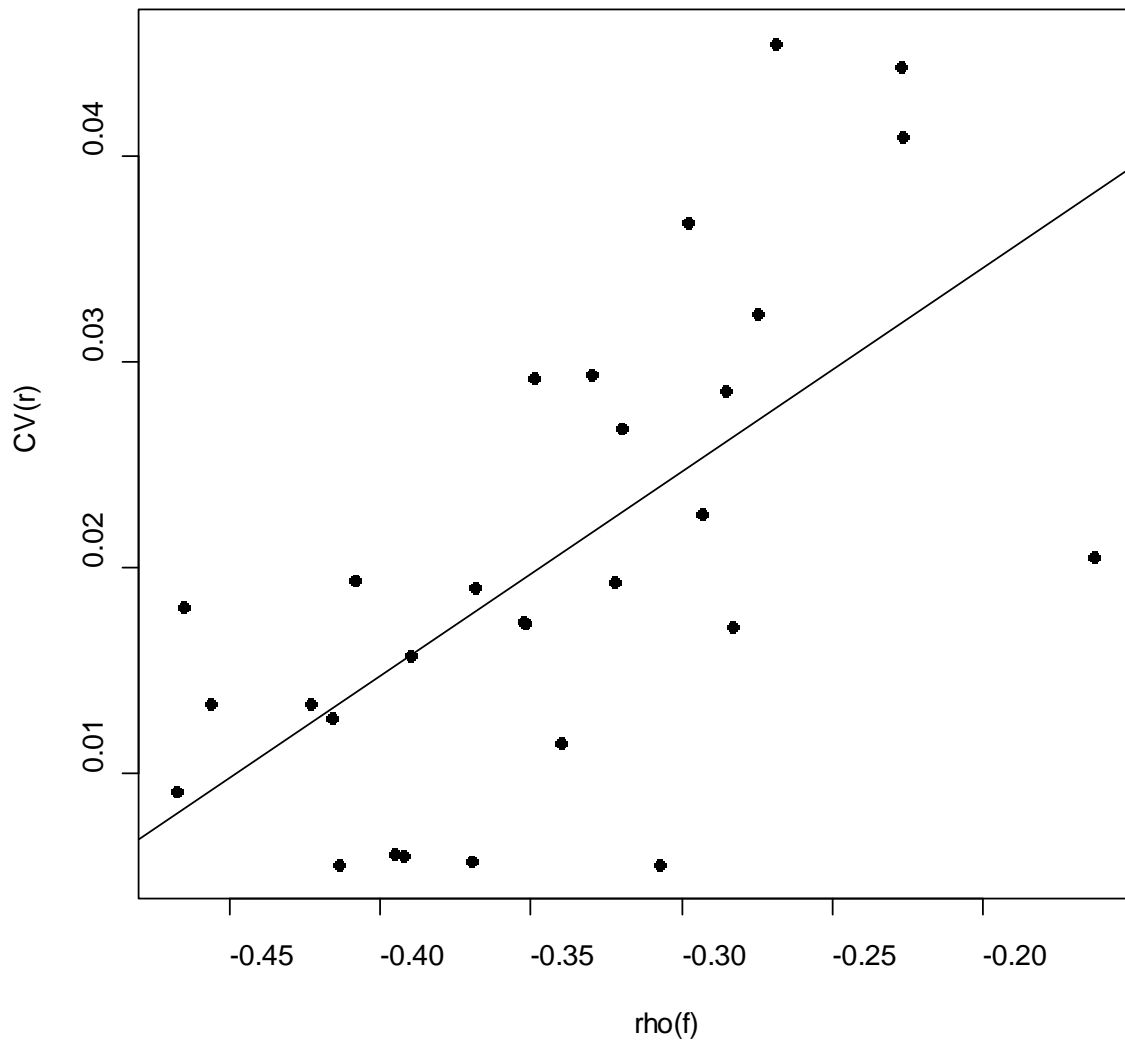


Fig 6. Regression relationship between  $\text{mean}(\rho_f)$  and  $CV(r_0)$ .

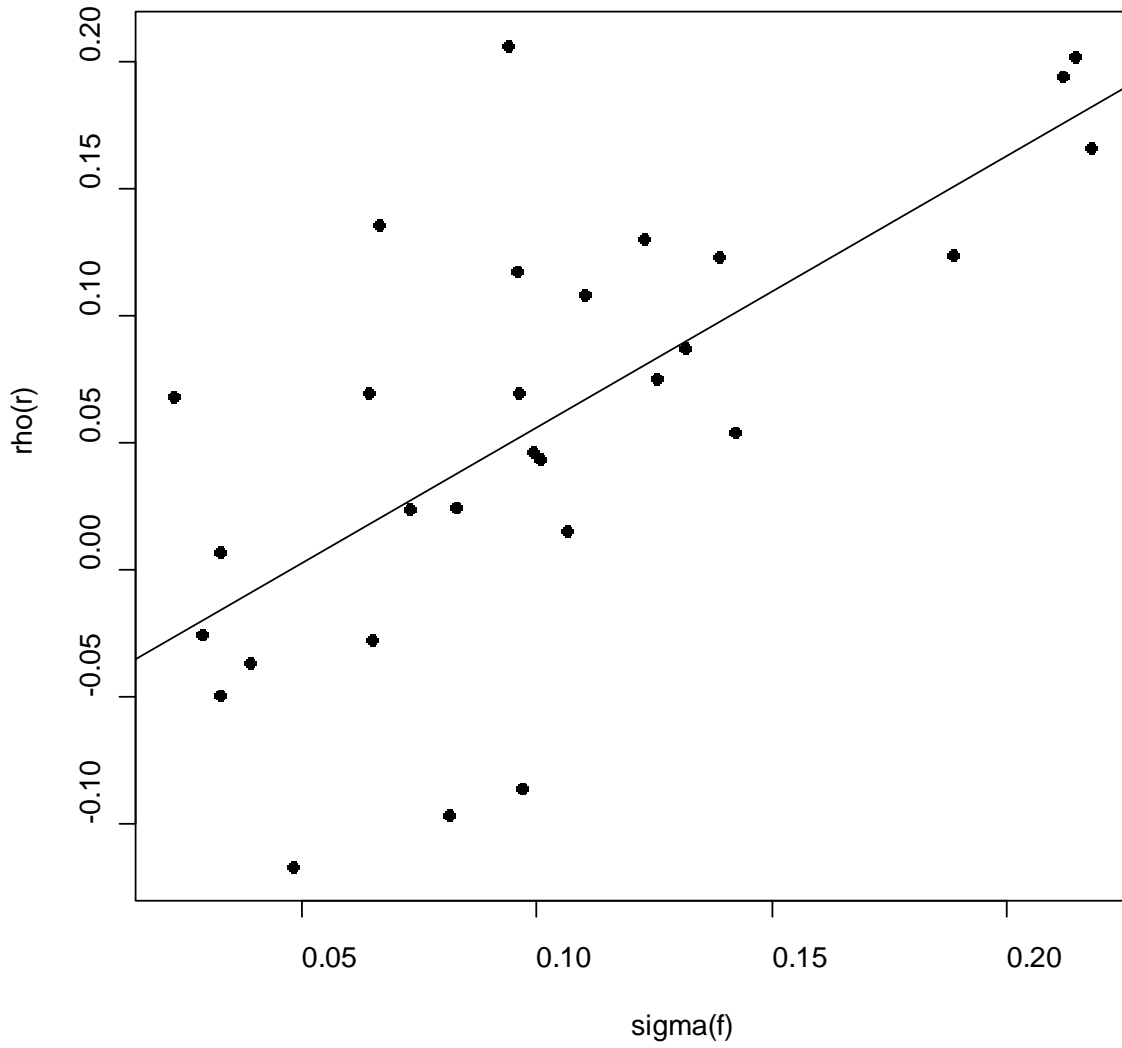


Fig 7. Regression relationship between mean( $\sigma_f$ ) and correlation coefficient  $\rho(r_0)$ .

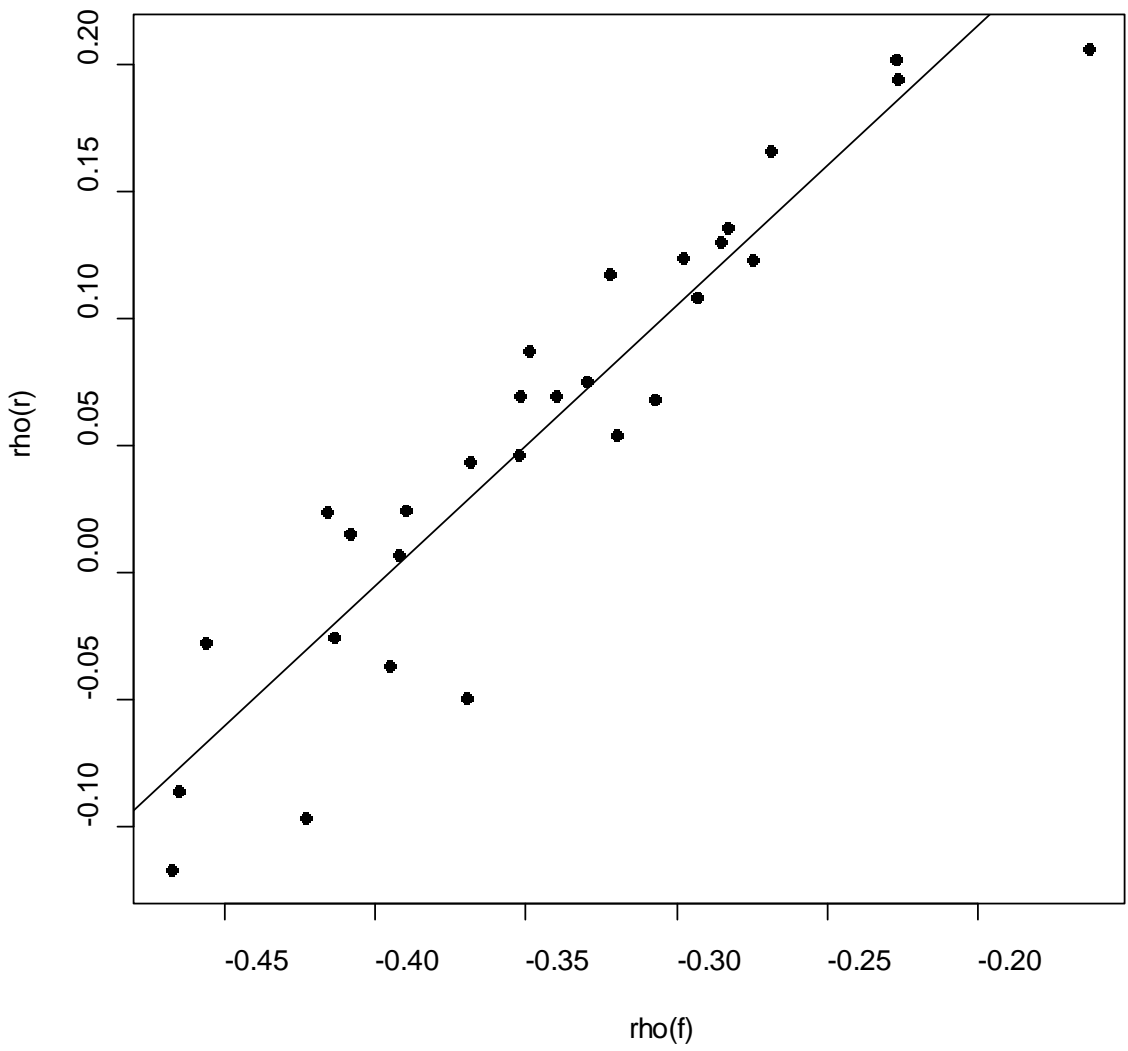


Fig 8. Regression relationship between correlation coefficient ( $\rho_f$ ) and correlation coefficient  $\rho(r_0)$ .

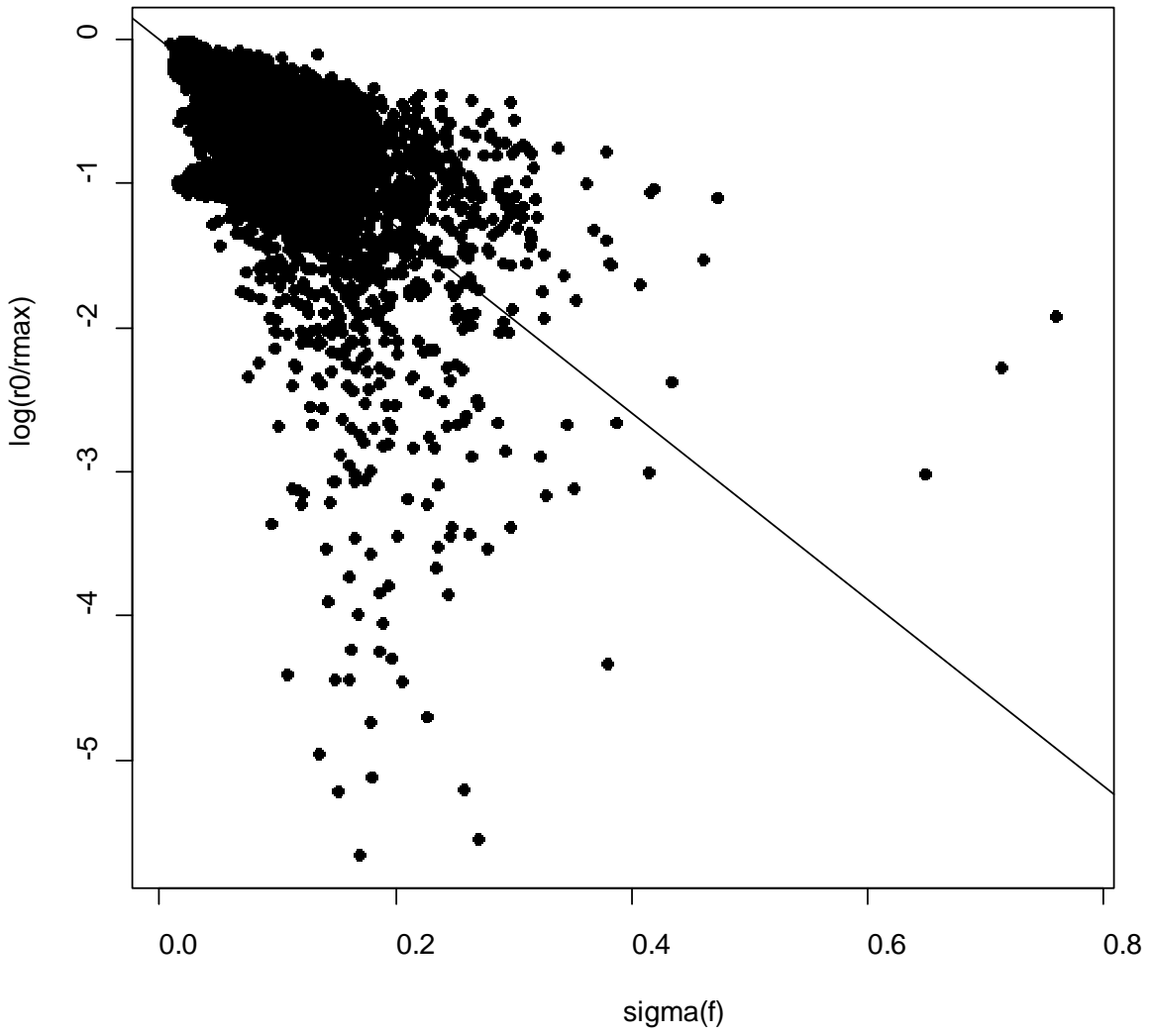


Fig 9. Regression relationship between  $\sigma_f$  and  $\log(r_0/r_{\max})$ .



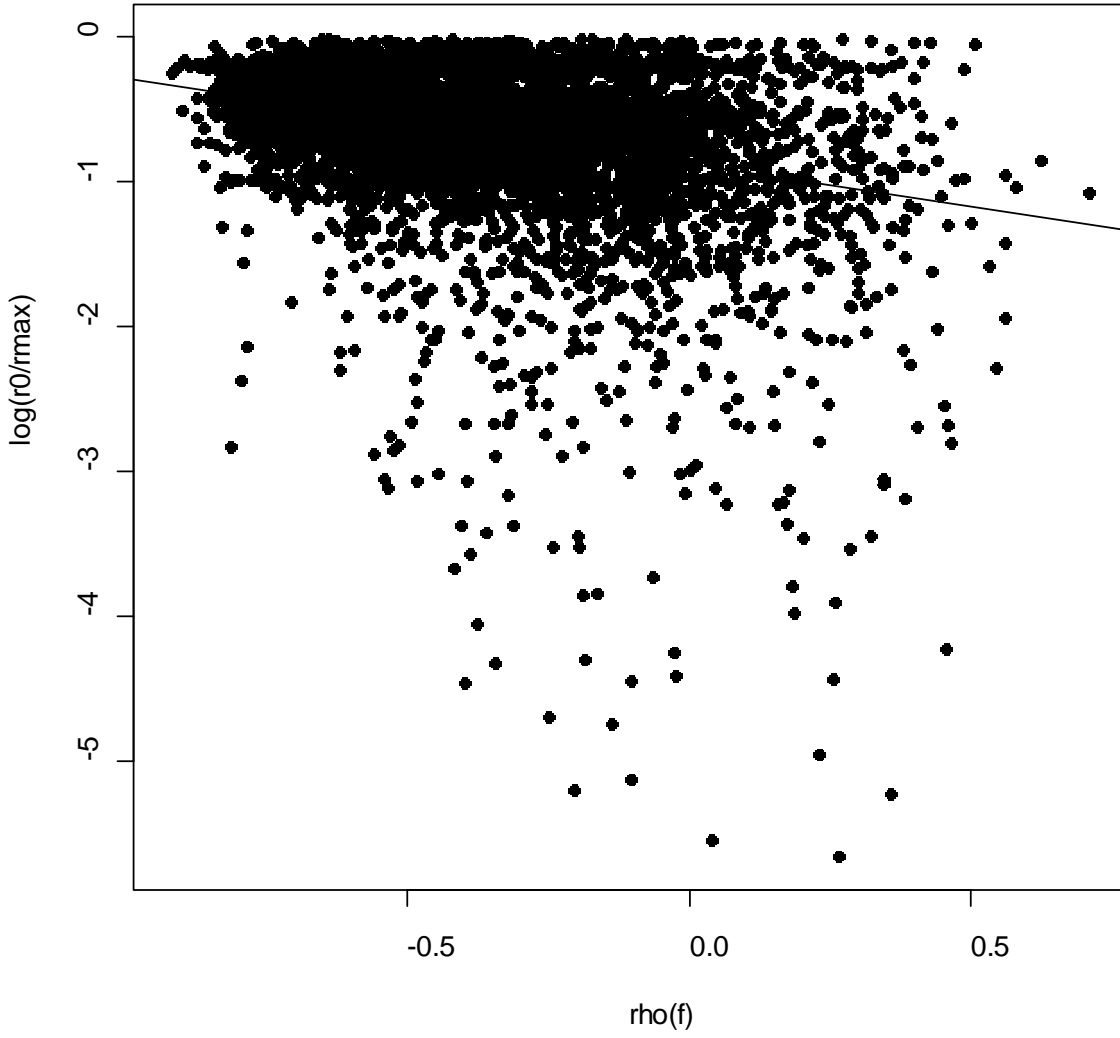


Fig 10. Regression relationship between correlation coefficient ( $\rho_f$ ) and  $\log(r_0/r_{\max})$ .

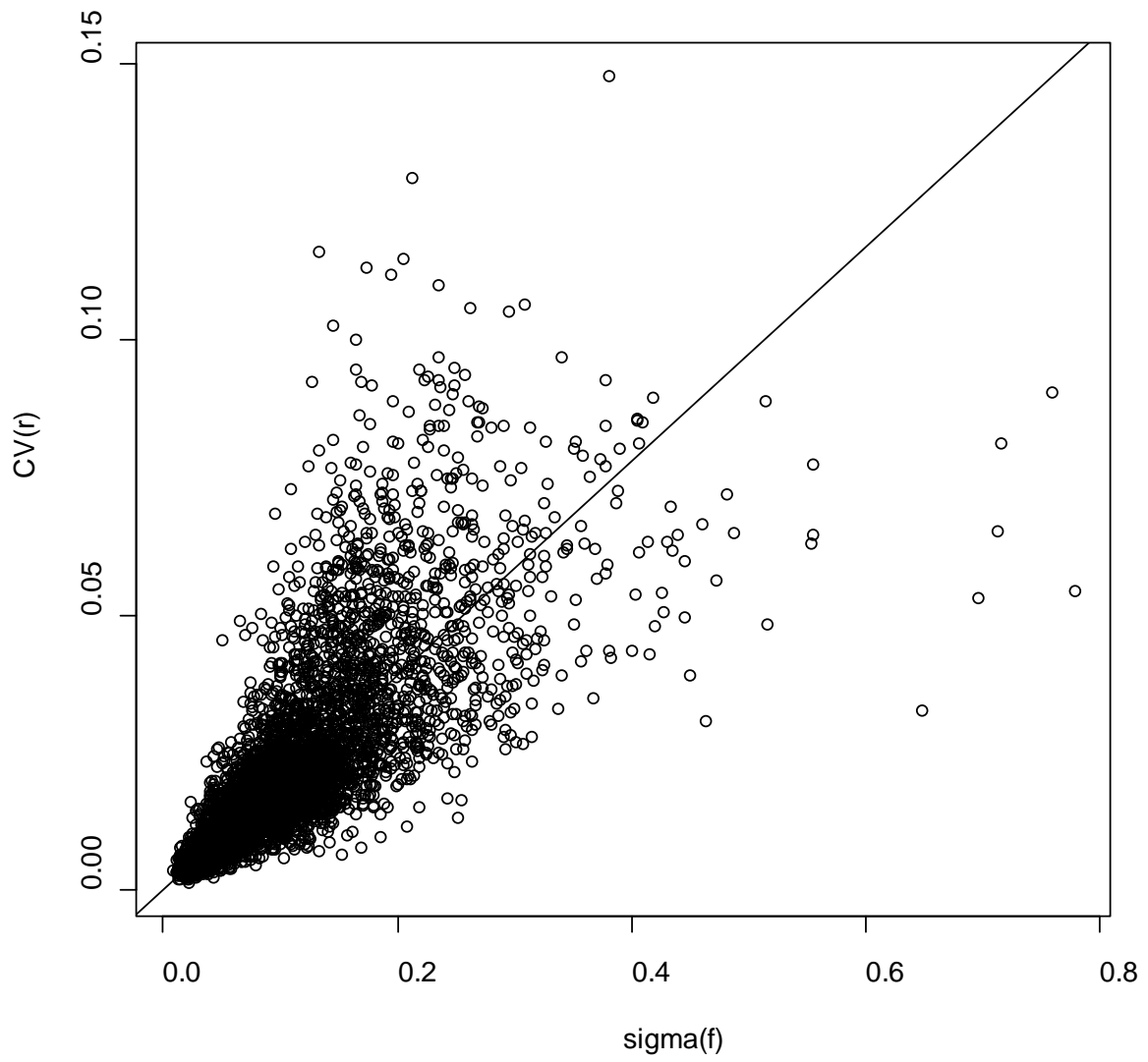


Fig 11. Regression relationship between  $\sigma_f$  and  $CV(r_0)$ .

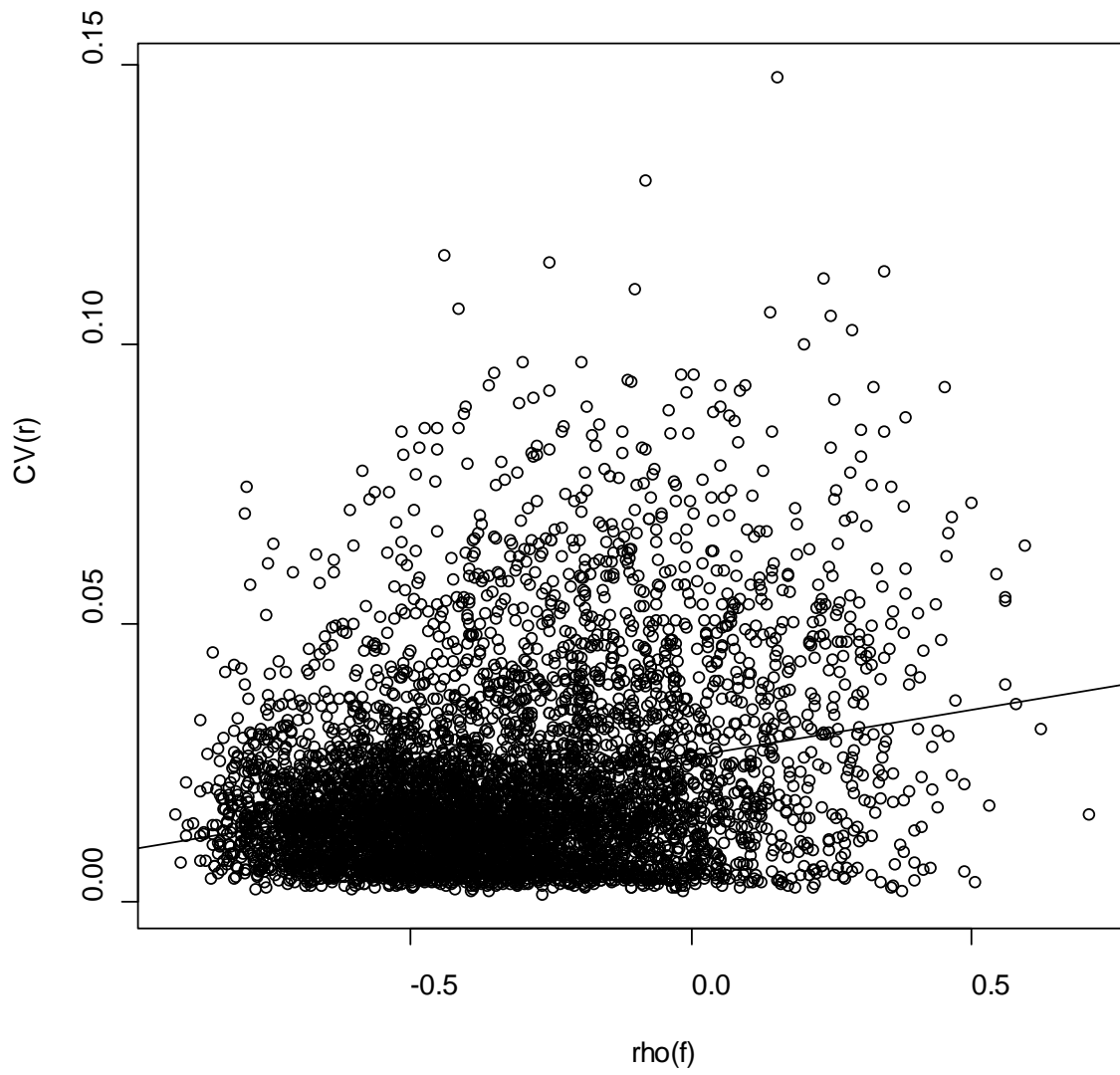


Fig 12. Regression relationship between  $\rho_f$  and  $CV(r_0)$ .

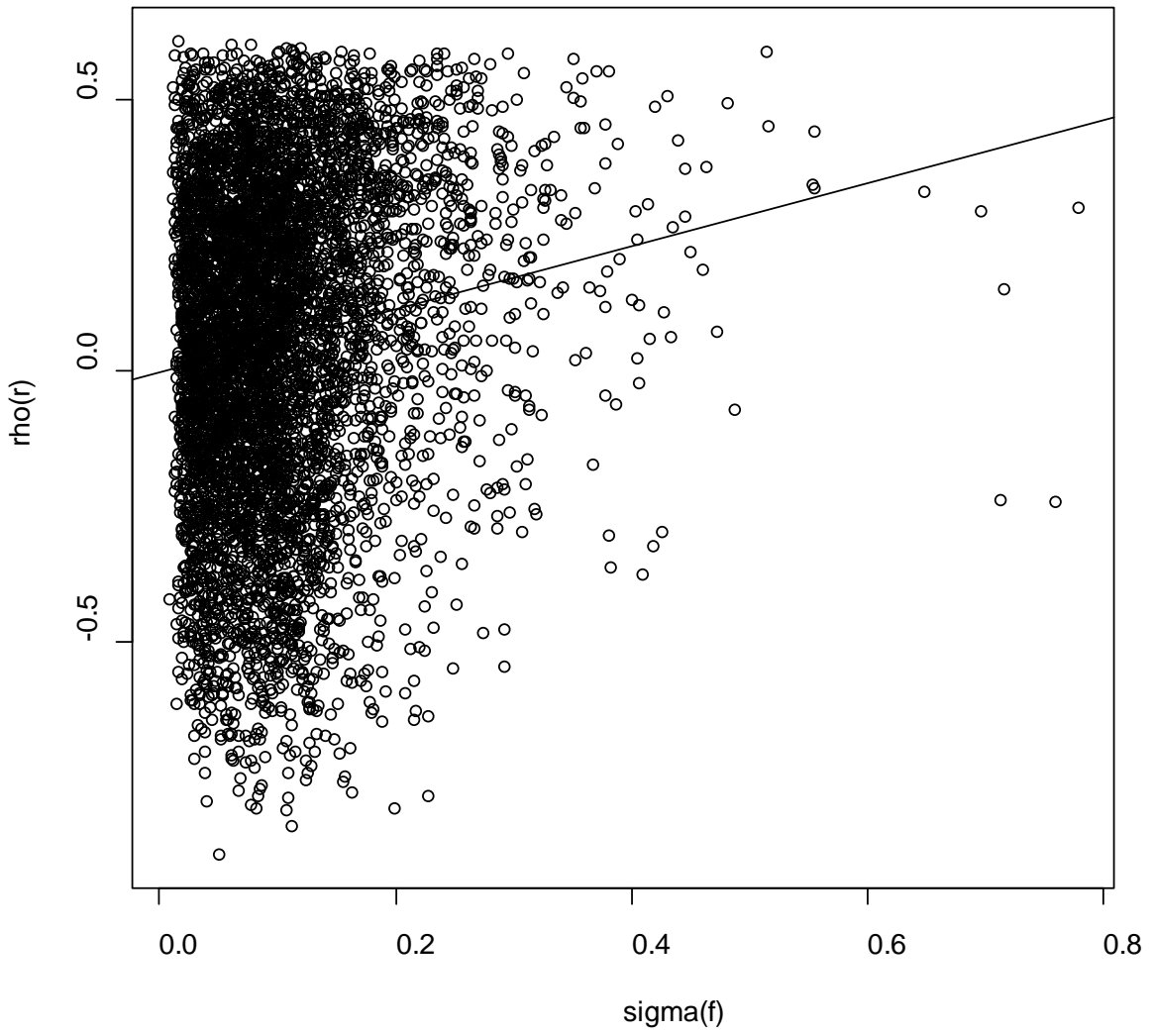


Fig 13. Regression relationship between  $\sigma_f$  and correlation coefficient  $\rho(r_0)$ .

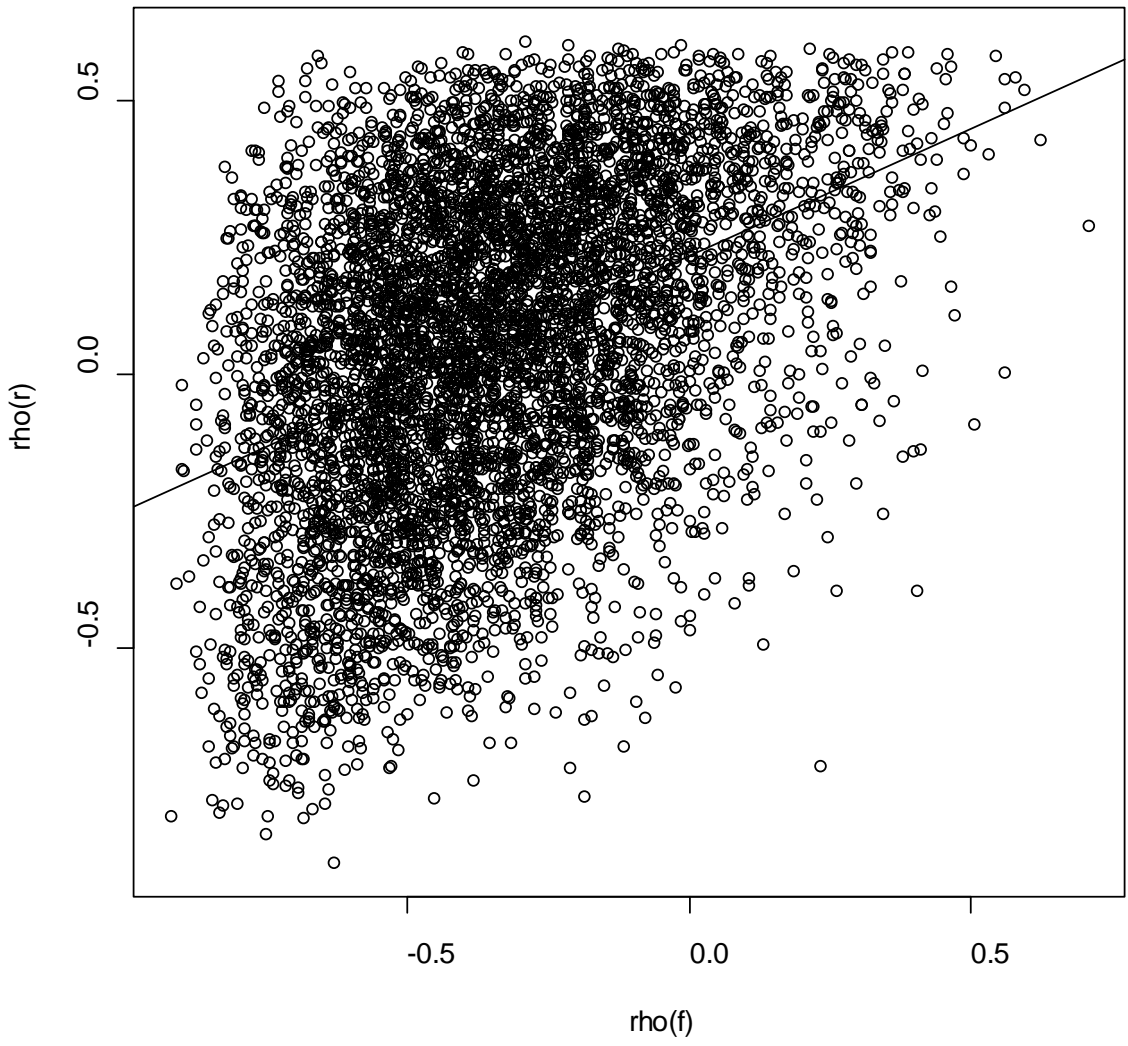


Fig 14. Regression relationship between correlation coefficient ( $\rho_f$ ) and correlation coefficient  $\rho(r_0)$ .

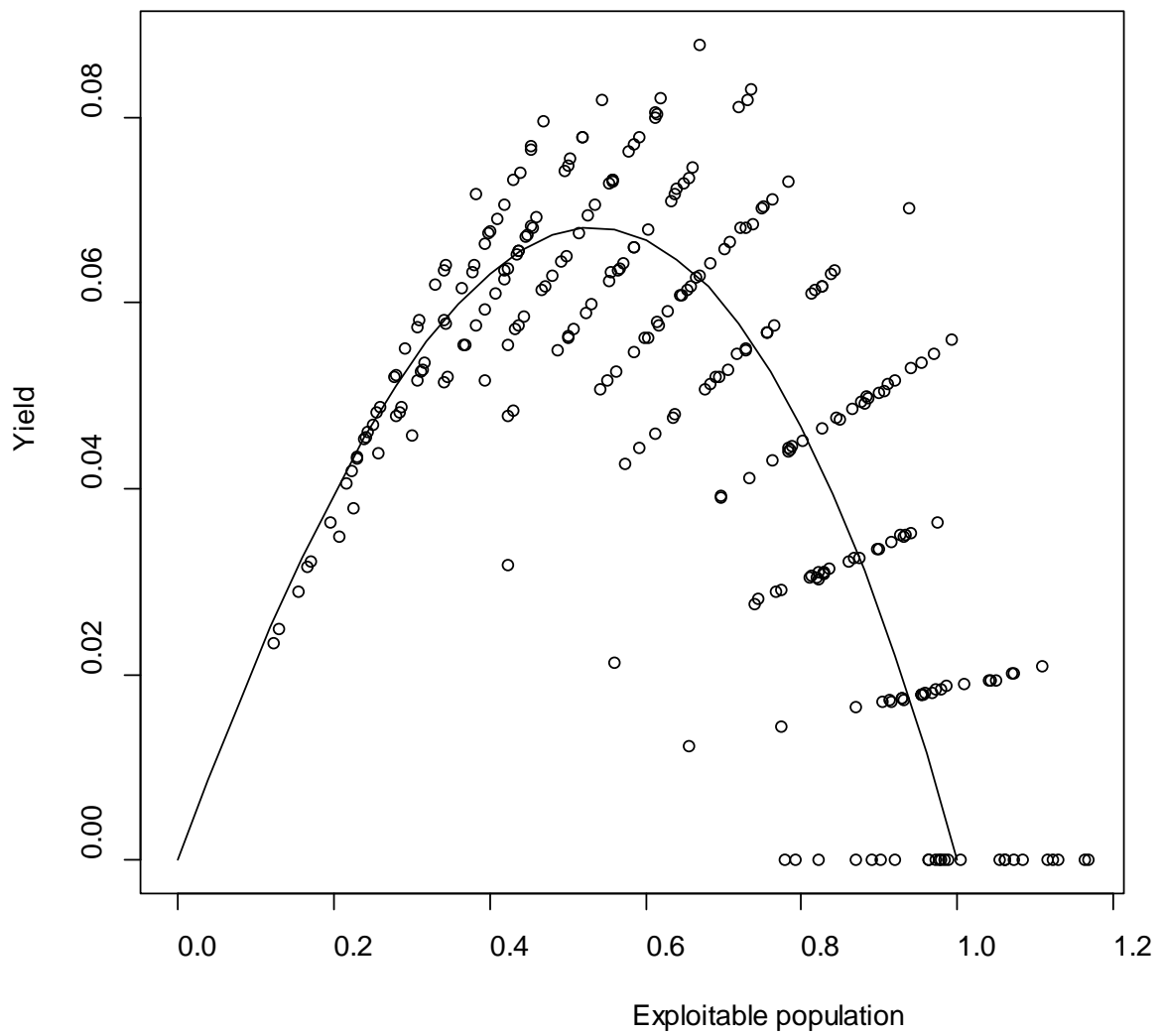


Fig. 15. Example of a fitted yield curve.