The relationship between $MSYR_{mat}$ and $MSYR_{1+}$ based on energetics modelling.

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ABSTRACT

An individual based energetics model is used to examine the relationship between the MSY (maximum sustainable yield) rates applicable to the population aged one year and above compared with that from the mature component of the population. The results are compared with those from the standard baleen whale model. The energetics based model indicates that MSY rates of 1% to 7% for the mature population translates into a range for MSY rates for the population aged one and above of 1% to 6%. The relationships between the one plus and mature MSY rates are quite different from those derived from the standard baleen model.

KEYWORDS: MSY RATE, RMP, ENERGETICS, INDIVIDUAL BASED MODELS, BALEEN II,

SIMULATION

Testing and tuning of the Revised Management Procedure (RMP) is based on simulations using predominantly deterministic population models. The most important feature of those models is captured in the maximum sustainable yield rate (MSYR). Recently the Scientific Committee adopted a new range and metric for MSYR in the RMP by refining the range of MSYR to 1% to 4% (IWC; 2013). The substantive change is that this range is now applied as if the population of animals aged one year and above were exploited. Previously the range applied to the mature population. It has usually been assumed that commercial whaling is likely to exploit larger and hence mature animals. Consequently in RMP trials it is necessary to convert the new range of MSYRs inferred for populations aged one and above (designated $MSYR_{1+}$) to MSYRs of mature populations ($MSYR_{mat}$).

Tuning of the RMP has been undertaken using $MSYR_{mat}$ = 1%. The consequence of the change to $MSYR_{1+}$ assumed, for example, that $MSYR_{1+}$ = 1% leads to $MSYR_{mat}$ calculated to be greater than 1%. Conventional population modelling using BALEEN II (which uses a Pella-Tomlinson model stock recruitment relationship) (de la Mare and Cooke, 1992) shows that the relationship between $MSYR_{1+}$ and $MSYR_{mat}$ depends on assumptions on the component of the population deemed to drive density dependence (de la Mare and Cooke 1994) and the rate of natural mortality (M) (Butterworth and Punt, 1992). For M ~ 0.05, the value typically used in the RMP models, $MSYR_{1+}$ was multiplied by 1.5 to convert it to $MSYR_{mat}$.

However, the conventional Pella-Tomlinson model used in the RMP has density dependence only on recruitment. Natural mortality rates were assumed both density-independent and independent of age except for calves. Calf mortality is set using an implicit balance equation, and is assumed to be density independent. Even without density dependence in mortality, age dependence in mortality leads to the average natural mortality being related to exploitation rate (de la Mare, 1985) and this is not accounted for in the conventional formulation.

The analyses that led to the revision of the range of MSYR relied on inferring MSY rate from the rate of increase of depleted populations (IWC; 2013). These analyses took into account evidence the rate of increase was influenced by random environmental fluctuations (Cook; 2011). Density dependence in mortality was also shown to be potentially important, but there was little in the way of direct evidence to calculate the likely magnitude of any such density dependence. De la Mare (2013a) developed an individual based energetics model (IBEM) to determine the likely size of such effects by using a process-based model in which whale population rate of increase is dependent on prey abundance and variability. This model leads to density dependence in both birthrates and in calf and age-dependent natural mortality and also includes the effects due to harvest induced changes in age structure on reproduction and mortality. This model thus allows for the relationship between MSYR1+ and $MSYR_{mat}$ to be calculated taking into account that density dependence will be occur in both recruitment and mortality.

De la Mare (2013b) presented results from 29 realisations of the IBEM covering ranges of $MSYR_{1+}$ from less than 1% to greater than 7%. The energetics of the species and its relationships to population demography are the same in all 29 models. Thus the differences in the model realisations derive only from the characteristics of the prey populations; the different yield curves do not derive from changes in the functional relationships between population energetics and food. The same 29 models will be used here to calculate $MSYR_{1+}$ and $MSYR_{mat}$ from yield curves derived from exploiting the corresponding population segments at a range of fixed harvest rates. The yield curves are estimated by fitting a Pella-Tomlinson yield curve to the model outputs from 25 replicates of 200 years of exploitation (in the lowest yield realisation the year span was increased to 4000 years to reduce inter-replicate variability). The fitted curve is used purely as a descriptive model to calculate MSYR and MSYL. Figure 1 shows an example of the 1+ and mature yield curves fitted to outputs from model 3.

Table 1 shows the properties of the yield curves from all 29 model realisations including the ratio of MSY_{mat} to $MSYR_{1+}$. In all cases this ratio is substantially less than the standard value of 1.5 and becomes closer to 1 for the lower the value of $MSYR_{1+}$. Fig 2 shows a quadratic regression passing through the origin to give the following expression for converting $MSYR_{1+}$ (y_{mat}) to $MSYR_{mat}$ (y_{1+}):

$$y_{mat} = y_{1+}\left(0.932 + 3.809 y_{1+}\right)$$

Thus at $MSYR_{1+}$ = 0.01, $MSYR_{mat}$ = 0.0097 (effectively 0.01), that is a multiplier of 1.0. The value $MSYR_{1+}$ = 0.0603 produces $MSYR_{mat}$ = 0.0701, which is a multiplier of 1.16. Over the range of MSYR1+ consistent with $MSYR_{mat}$ = 1% to 7% the multiplier is considerably less than the value 1.5 used heretofore.

Table 2 shows ratios of MSY_{mat} to $MSYR_{1+}$ calculated using BALEEN II (de la Mare and Cooke, 1992) with density dependence on the 1+ population with $MSYL_{mat}$ fixed at 0.5 and age at 50% maturity = 5. Figure 3 shows the relationships between $MSYR_{mat}$ and $MSYR_{1+}$ at various values of M. The general shape of these curves is quadratic passing through the origin. The curve from the IBEM is also quadratic, and thus to that extent the IBEM results are consistent with the properties of the BALEEN II model.

Figure 3 shows the BALEEN II calculations as the ratio of $MSYR_{mat}$ to $MSYR_{1+}$ in relation to $MSYR_{1+}$ at various values of natural mortality (M). The results from BALEEN II are not quantitatively consistent with those from the IBEM. The figure also shows that, while the value of 1.5 is roughly in the middle of the set of curves, there is not a single value of multiplier to be used in converting from $MSYR_{1+}$ to $MSYR_{mat}$ even for BALEEN II.

Why the results of the IBEM and BALEEN II models are substantially different can be understood by examining the effects of density dependence on the main demographic parameters that emerge from the IBEM and comparing these with the assumptions of BALEEN II. Table 3 gives the values of demographic parameters for the 29 different model realisations comparing the parameters from an unexploited population with those from a population exploited at a rate equal to $MSYR_{mat}$. Fig 5 shows the birthrates at carrying capacity (K) and the population level attained in equilibrium when exploited at $MSYR_{mat}$ ($MSYL_{mat}$) for a range of $MSYR_{1+}$ values. Unsurprisingly, there is a strong positive correlation between birthrate and $MSYR_{1+}$ and the magnitude of the effects of density dependence become greater with increasing MSYR as shown in Fig 6.

Fig 7 shows the relationship of mature natural mortality to MSYR at both K and $MSYL_{mat}$. There is a negative correlation between $MSYR_{mat}$ and $MSYR_{1+}$. In the BALEEN II model there is no fixed relationship between natural mortality and $MSYR_{1+}$ because MSYR depends on two parameters (natural mortality and birthrate) and so natural mortality can be fixed and MSYR can be set as required by means of the birthrate parameter. In the IBEM model birthrates and natural mortality rates are not independent because both are affected by food supply. The IBEM clearly has mature mortality as density dependent. This is in contrast to the BALEEN II model where natural mortality is assumed to be density independent. The natural mortality rates over the suite of 29 different models are consistent with the levels assumed in the RMP simulations.

Fig 8 shows the relative change in calf mortality between K and $MSYL_{mat}$. Interestingly, with the IBEM model calf natural mortality <u>increases</u> with exploitation and the relative change in calf mortality is positively correlated with MSYR Again this is inconsistent with the assumptions of BALEEN II where calf natural mortality is assumed to be density independent. It might be supposed a priori that calf mortality would decrease as per capita food increases. However, in the IBEM calf mortality depends on birth mass and the mothers' milk production, which in turn depends on energy ingested by mothers between births. In the IBEM older females have, on average, greater fat mass and hence produce calves with higher birth mass and produce more milk. Consequently, the increase in calf mortality arises because higher MSYR exploitation leads to a greater reduction in the average age of the mature female population and an increase in birthrates. Both these effects act together to reduce the average birth mass of calves, which then results in an increase in calf mortality. However, Fig 9 shows that there is a still a net increase in recruitment to the 1+ population because the increase in birthrates more than compensates for the increase in calf mortality, although the relative increase in 1+ recruitment is obviously less than the relative increase in birthrate.

Figs 10 and 11 show that both juvenile and adult mortality decrease with MSYR and are highly density dependent.

CONCLUSION

An energetics based model leads to values for the ratio of $MSYR_{mat}$ to $MSYR_{1+}$ that are substantially below the value of 1.5 used heretofore. The model indicates that the range of $MSYR_{mat}$ of 1% to 7% translates into a range for $MSYR_{1+}$ of 1% to 6%. The ratios are quite different from those derived from BALEEN II, which assumes that the only density dependent effect is in recruitment. The IBEM model leads to density dependent changes across a range of demographic parameters, which is the likely reason that the BALEEN II and IBEM models produce such different results. Given the implausible assumptions about density dependence in BALEEN II it should not be used to infer the ratio of $MSYR_{mat}$ to $MSYR_{1+}$.

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

Model	Prey abund.	Prey CV	1+					Mature					MSYRmat / MSYR1+
			K	r0	MSYR	MSYL	MSYR/r0	K	r0	MSYR	MSYL	MSYR/r0	
1	10000	0.	50060	0.1023	0.0768	0.630	0.7503	41980	0.1319	0.0930	0.600	0.7051	1.211
2	10000	0.5	40264	0.104	0.0727	0.596	0.6984	34915	0.1341	0.0864	0.565	0.6444	1.188
3	10000	0.7	35721	0.103	0.0704	0.587	0.6832	30748	0.1398	0.0847	0.546	0.6055	1.203
4	10000	0.9	31362	0.1137	0.0754	0.575	0.6629	26576	0.1579	0.0907	0.531	0.5745	1.202
5	5000	0.5	19359	0.0939	0.0649	0.591	0.6910	15978	0.1236	0.0780	0.558	0.6314	1.202
6	5000	0.7	16202	0.0833	0.0538	0.566	0.6463	13744	0.1109	0.0644	0.534	0.5806	1.197
7	5000	0.9	13883	0.0924	0.0560	0.546	0.6058	11273	0.1176	0.0681	0.533	0.5789	1.216
8	3000	0.5	9381	0.0847	0.0489	0.532	0.5773	7642	0.1009	0.0547	0.517	0.5420	1.119
9	3000	0.7	6375	0.0770	0.0428	0.523	0.5562	5691	0.0896	0.0472	0.511	0.5270	1.103
10	3000	0.9	4134	0.0719	0.0386	0.515	0.5368	3491	0.0680	0.0437	0.564	0.6424	1.132
11	2500	0.5	5272	0.0768	0.0410	0.513	0.5335	4799	0.0923	0.0445	0.493	0.4825	1.085
12	2500	0.7	3212	0.0715	0.0415	0.534	0.5800	2887	0.0703	0.0436	0.553	0.6212	1.051
13	2500	0.9	4413	0.0813	0.0376	0.486	0.4619	3956	0.0899	0.0410	0.484	0.4619	1.090
14	3000	0.5	40938	0.0728	0.0392	0.515	0.5385	31424	0.0777	0.0399	0.504	0.5134	1.018
15	3000	0.7	34756	0.0659	0.0373	0.528	0.5667	26820	0.0663	0.0382	0.532	0.5764	1.024
16	3000	0.9	24650	0.0656	0.0287	0.477	0.4380	20415	0.0761	0.0296	0.461	0.3888	1.031
17	2500	0.5	30002	0.0636	0.0336	0.512	0.5290	22513	0.0651	0.0339	0.508	0.5208	1.009
18	2300	0.9	20632	0.0675	0.0313	0.487	0.4641	14571	0.0662	0.0306	0.486	0.4618	0.978
19	2300	0.7	30789	0.0679	0.0334	0.497	0.4918	22103	0.0653	0.0352	0.515	0.5384	1.054
20	2500	0.7	47346	0.0765	0.0400	0.509	0.5227	35505	0.0696	0.0433	0.554	0.6219	1.083
21	2500	0.9	38411	0.0903	0.0387	0.474	0.4282	28789	0.0724	0.0404	0.524	0.5576	1.044
22	2000	0.9	17608	0.0671	0.0311	0.487	0.4638	15863	0.0708	0.0331	0.488	0.4676	1.064
23	1800	0.9	12108	0.0902	0.0239	0.426	0.2650	8379	0.0568	0.0203	0.452	0.3579	0.849
24	1600	0.9	4841	0.0449	0.0211	0.489	0.4698	4508	0.0441	0.0228	0.506	0.5163	1.081
25	1500	0.9	1675	0.0243	0.0104	0.474	0.4266	1467	0.0189	0.0103	0.517	0.5411	0.990
26	1800	0.9	7604	0.0102	0.0057	0.526	0.5638	6540	0.0093	0.0061	0.571	0.6557	1.070
27	1800	0.0	121706	0.0490	0.0298	0.547	0.6078	108177	0.0536	0.0318	0.540	0.5929	1.067
28	2500	1.0	44763	0.0742	0.0386	0.508	0.5200	36636	0.0926	0.0449	0.494	0.4847	1.163
29	1800	0.5	62674	0.0446	0.0216	0.494	0.4833	56255	0.0489	0.0228	0.487	0.4657	1.056
Mean				0.0744	0.0486	0.522	0.0544		0.0821	0.0456	0.522	0.547	1.089

Table 2. $MSYR_{mat}$ to $MSYR_{1+}$ ratios from Baleen II MSYL fixed for matures at 0.5K (density dependence on 1+ population)

M	$MSYR_{1+}$	$MSYL_{1+}$	$MSYR_{mat}$	$MSYL_{mat}$	$MSYR_{mat}$/ $MSYR_{1+}$
0.02	0.01	0.528	0.0117	0.500	1.169
0.02	0.02	0.559	0.0246	0.499	1.230
0.02	0.03	0.591	0.0389	0.498	1.297
0.02	0.04	0.625	0.0542	0.496	1.355
0.04	0.01	0.528	0.0128	0.500	1.282
0.04	0.02	0.558	0.0269	0.499	1.345
0.04	0.03	0.590	0.0422	0.497	1.407
0.04	0.04	0.623	0.0590	0.495	1.475
0.06	0.01	0.528	0.0140	0.500	1.397
0.06	0.02	0.557	0.0292	0.499	1.460
0.06	0.03	0.589	0.0458	0.497	1.527
0.06	0.04	0.622	0.0638	0.494	1.595
0.08	0.01	0.528	0.0151	0.499	1.514
0.08	0.02	0.557	0.0316	0.498	1.580
0.08	0.03	0.588	0.0494	0.496	1.647
0.08	0.04	0.621	0.0688	0.493	1.720
0.10	0.01	0.527	0.0163	0.499	1.632
0.10	0.02	0.556	0.0340	0.498	1.700
0.10	0.03	0.587	0.0531	0.496	1.770
0.10	0.04	0.619	0.0738	0.493	1.845

Table 3. Natural mortality and birth rates for various population segments at K and when exploited at $MSYR_{mat}$

Model	Prey abund	Prey CV	MSYR1+	Population at K					Population exploited at $MSYR_{mat}$				
				Birthrate	M_{calf}	$M_{juvenile}$	M_{1+}	M_{mature}	Birthrate	M_{calf}	$M_{juvenile}$	M_{1+}	M_{mature}
1	10000	0.	0.0768	0.320	0.157	0.206	0.101	0.069	0.445	0.237	0.040	0.031	0.028
2	10000	0.5	0.0727	0.351	0.171	0.184	0.103	0.077	0.428	0.244	0.060	0.041	0.036
3	10000	0.7	0.0704	0.345	0.165	0.171	0.097	0.073	0.437	0.234	0.058	0.041	0.035
4	10000	0.9	0.0754	0.368	0.165	0.170	0.097	0.073	0.500	0.244	0.067	0.048	0.040
5	5000	0.5	0.0649	0.335	0.154	0.176	0.101	0.076	0.425	0.223	0.062	0.043	0.036
6	5000	0.7	0.0538	0.301	0.150	0.149	0.086	0.066	0.372	0.205	0.070	0.047	0.039
7	5000	0.9	0.0560	0.330	0.151	0.153	0.088	0.067	0.400	0.215	0.080	0.053	0.044
8	3000	0.5	0.0489	0.321	0.155	0.166	0.095	0.072	0.381	0.202	0.102	0.062	0.048
9	3000	0.7	0.0428	0.304	0.143	0.154	0.089	0.068	0.373	0.196	0.109	0.067	0.052
10	3000	0.9	0.0386	0.300	0.157	0.156	0.090	0.069	0.369	0.195	0.118	0.072	0.056
11	2500	0.5	0.0410	0.308	0.149	0.164	0.093	0.070	0.369	0.202	0.127	0.072	0.054
12	2500	0.7	0.0415	0.320	0.147	0.165	0.094	0.068	0.416	0.190	0.128	0.079	0.057
13	2500	0.9	0.0376	0.295	0.153	0.151	0.087	0.066	0.371	0.195	0.126	0.076	0.058
14	3000	0.5	0.0392	0.298	0.147	0.151	0.087	0.065	0.336	0.187	0.114	0.066	0.050
15	3000	0.7	0.0373	0.294	0.151	0.153	0.085	0.066	0.327	0.193	0.120	0.069	0.055
16	3000	0.9	0.0287	0.284	0.144	0.138	0.081	0.063	0.321	0.180	0.126	0.075	0.058
17	2500	0.5	0.0336	0.281	0.149	0.155	0.086	0.066	0.310	0.187	0.125	0.068	0.053
18	2300	0.9	0.0313	0.300	0.150	0.163	0.093	0.071	0.338	0.187	0.141	0.080	0.061
19	2300	0.7	0.0334	0.289	0.152	0.151	0.085	0.067	0.331	0.191	0.129	0.073	0.057
20	2500	0.7	0.0400	0.308	0.152	0.155	0.088	0.068	0.334	0.196	0.110	0.064	0.051
21	2500	0.9	0.0387	0.324	0.151	0.153	0.089	0.067	0.361	0.194	0.122	0.073	0.057
22	2000	0.9	0.0311	0.290	0.170	0.207	0.106	0.082	0.342	0.204	0.151	0.081	0.064
23	1800	0.9	0.0239	0.273	0.162	0.192	0.100	0.079	0.320	0.181	0.159	0.087	0.068
24	1600	0.9	0.0211	0.262	0.170	0.242	0.121	0.094	0.253	0.174	0.132	0.074	0.060
25	1500	0.9	0.0104	0.257	0.168	0.237	0.119	0.094	0.282	0.169	0.174	0.089	0.072
26	1800	0.9	0.0057	0.248	0.160	0.225	0.113	0.088	0.252	0.185	0.172	0.089	0.072
27	1800	0.0	0.0298	0.269	0.162	0.193	0.094	0.072	0.324	0.200	0.178	0.078	0.055
28	2500	1.0	0.0386	0.309	0.142	0.134	0.080	0.060	0.339	0.185	0.095	0.061	0.048
29	1800	0.5	0.0216	0.272	0.165	0.198	0.100	0.077	0.312	0.191	0.181	0.084	0.064

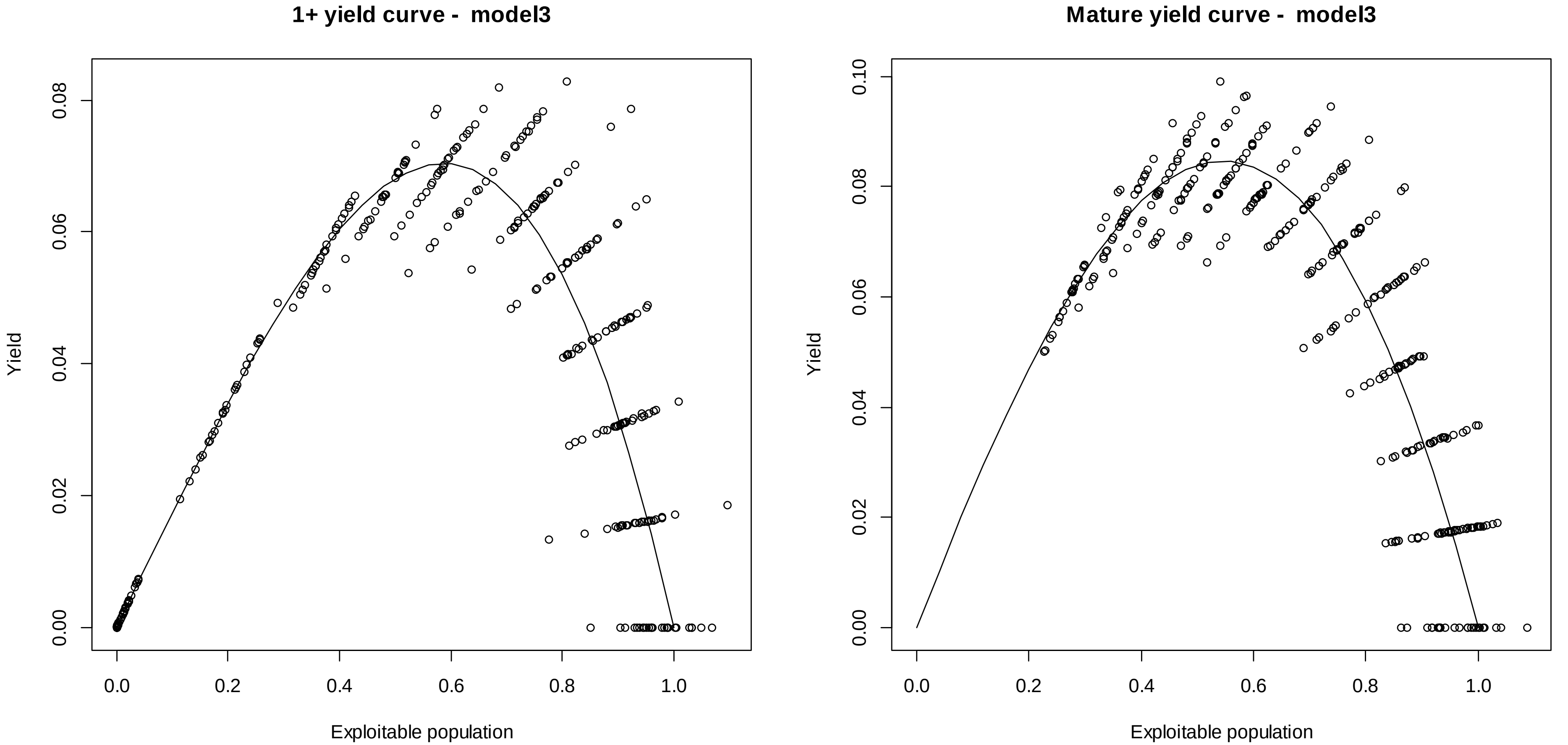

Fig 1. Examples of simulated yield curves for 1+ (left) and matures (right) from the same population model.

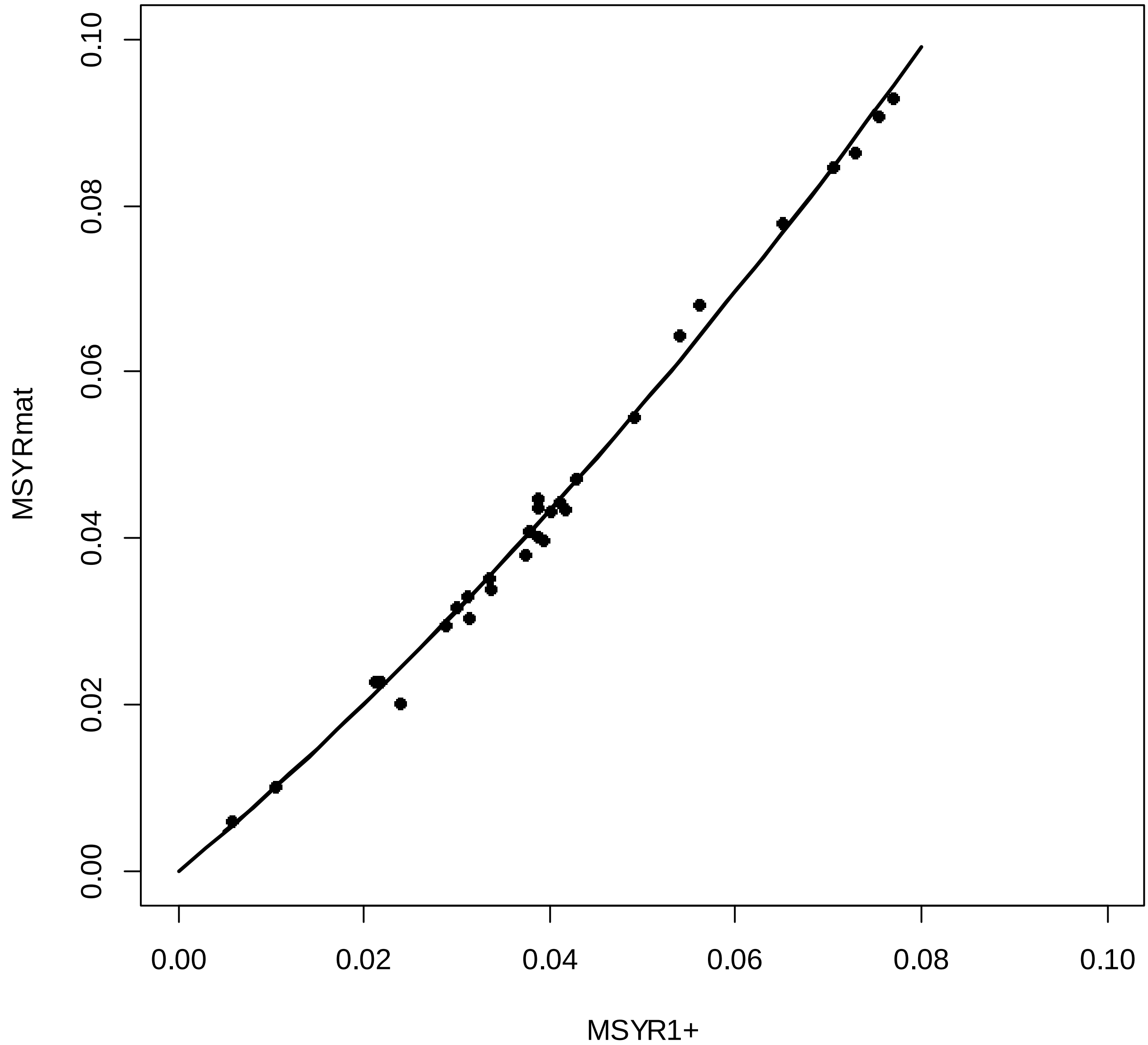

Fig 2. Relationship between $MSYR_{mat}$ and $MSYR_{1+}$. Curve is a quadratic regression passing through the origin.

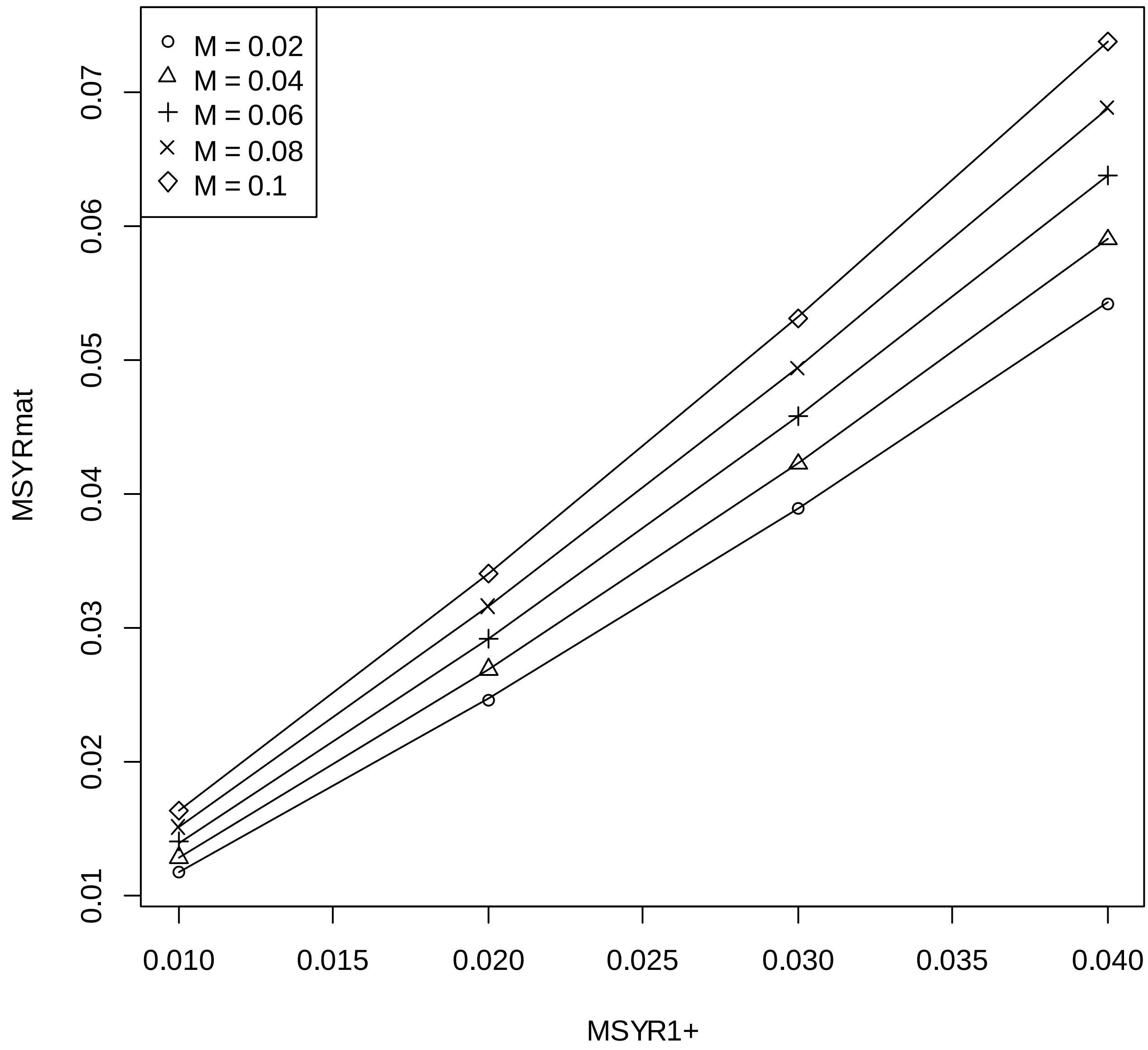

Fig 3. $MSYR_{1+}$ vs $MSYR_{mat}$ for a range of values of M using the BALEEN II model with density dependence on the total population. The curves are quadratic regressions passing through the origin

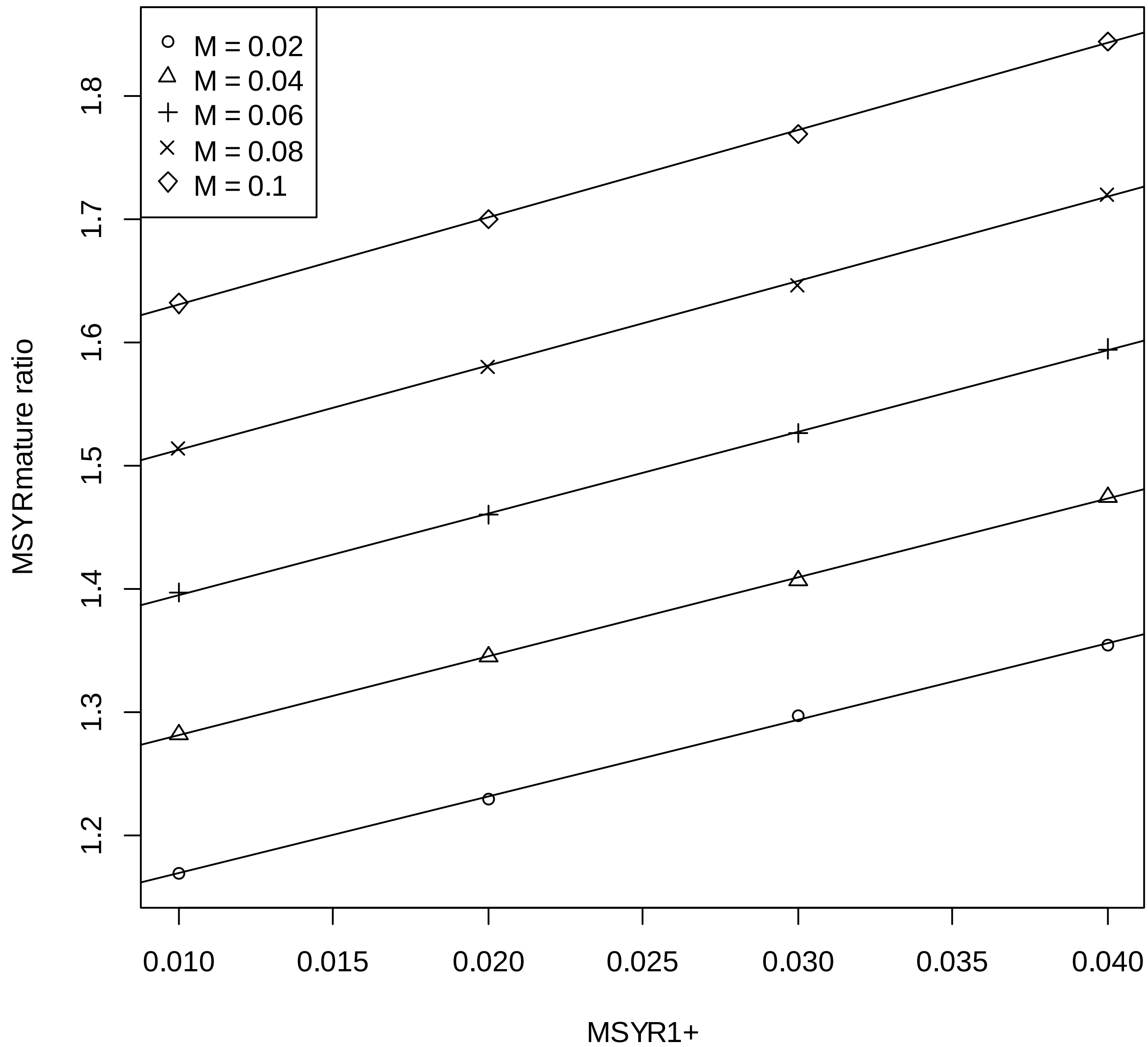

Fig 4. Ratio of $MSYR_{mat}$ to $MSYR_{1+}$ for a range of values of M using the BALEEN II model with density dependence on the total population. The curves are linear regressions.

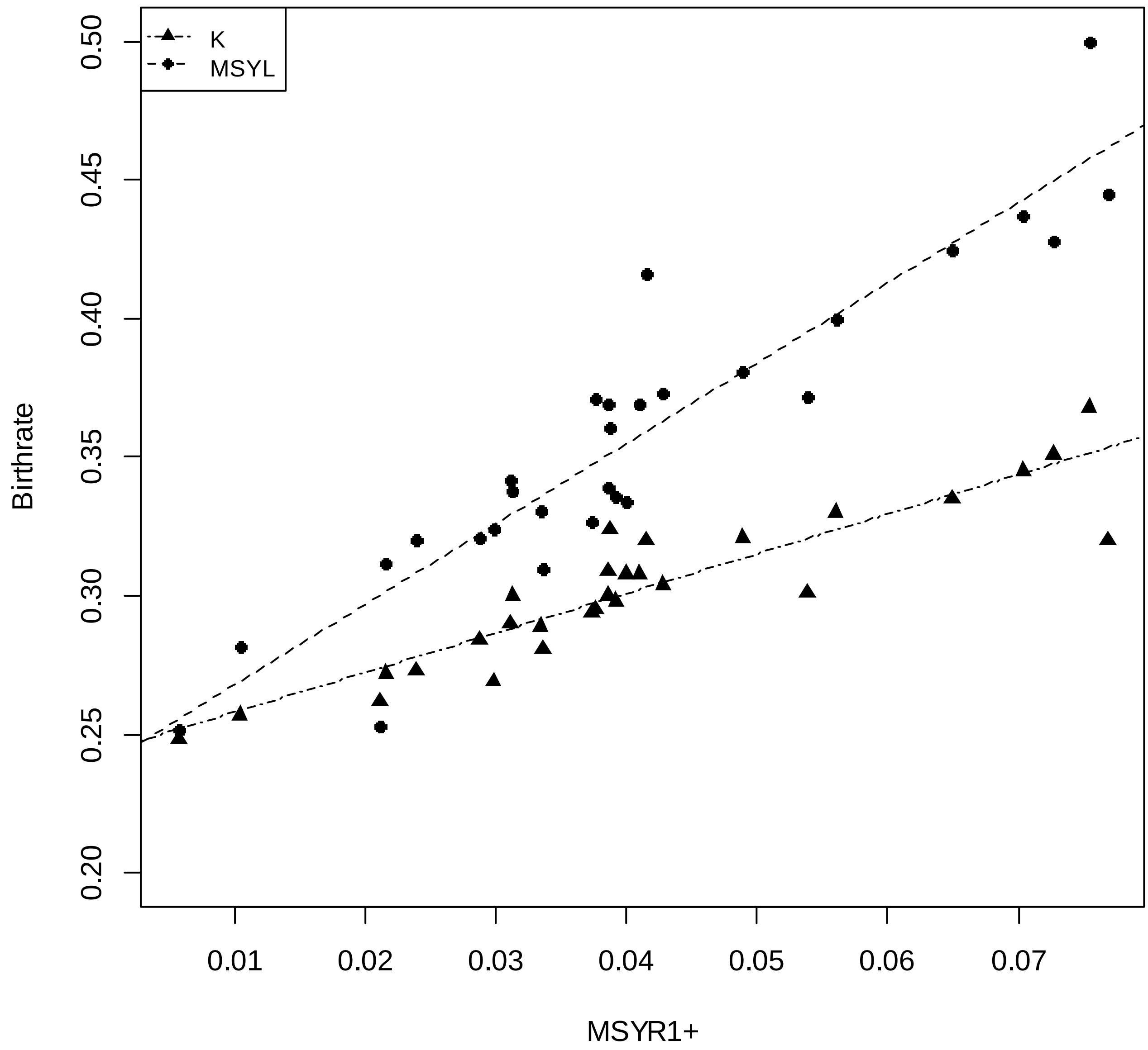

Fig 5. Birthrates at K and at $MSYL_{mat}$ from the 29 realisations of the IBEM model

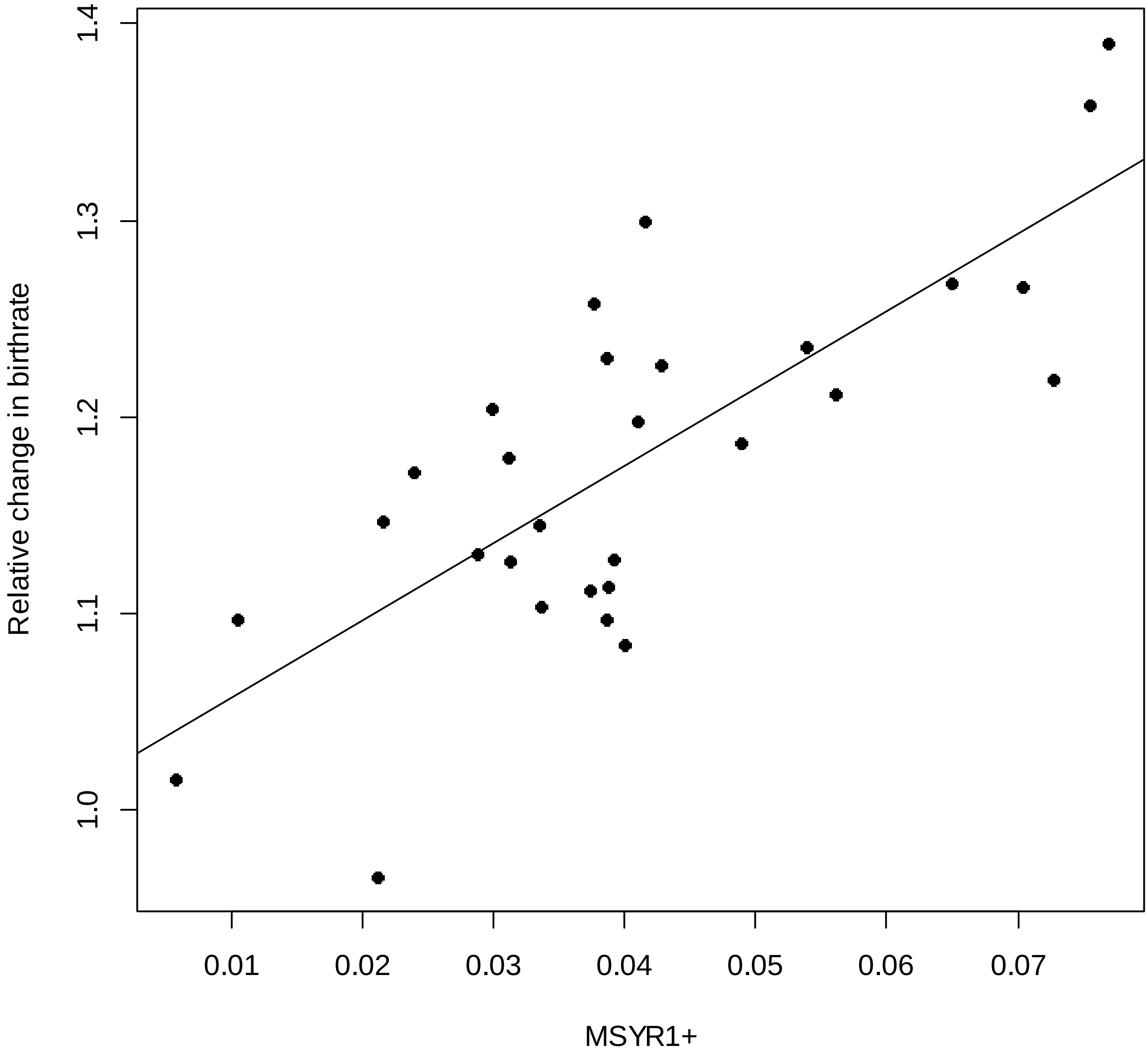

Fig 6. Relative increase in birthrates between K and at $MSYL_{mat}$ from the 29 realisations of the IBEM model

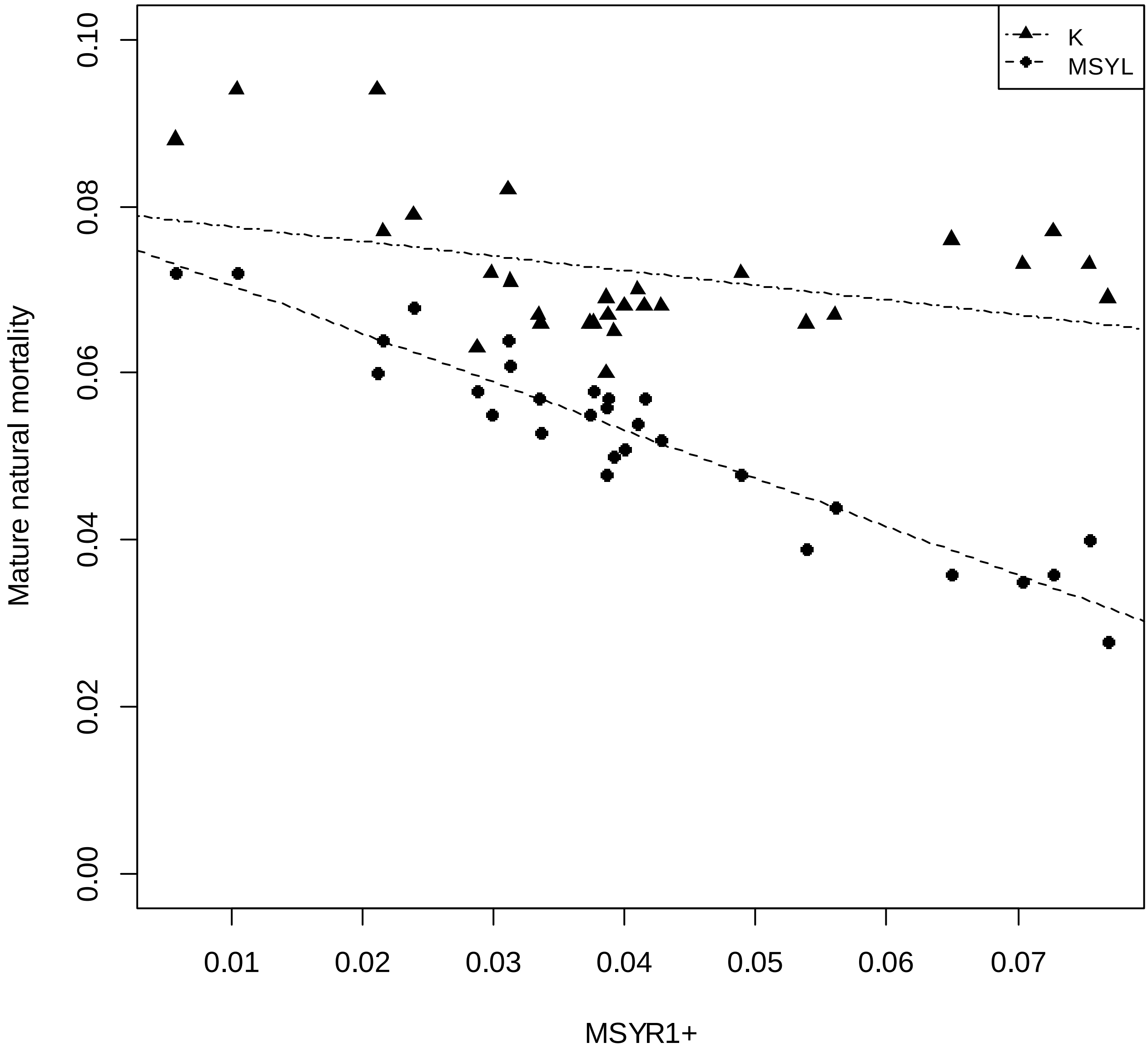

Fig 7. Natural mortality rates of matures at K and at $MSYL_{mat}$ from the 29 realisations of the IBEM model

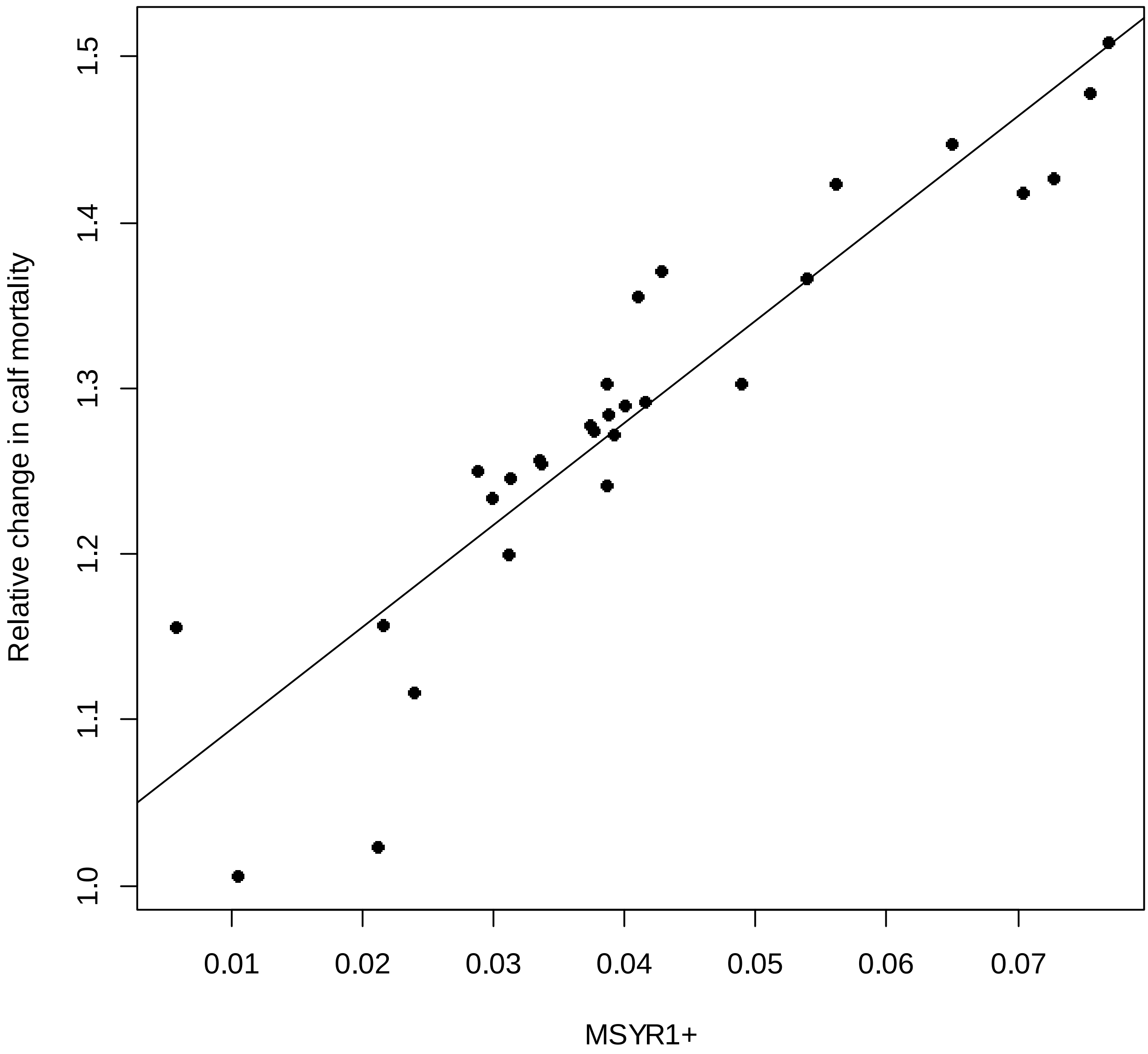

Fig 8. Relative increase in calf mortality between K and at $MSYL_{mat}$ from the 29 realisations of the IBEM model

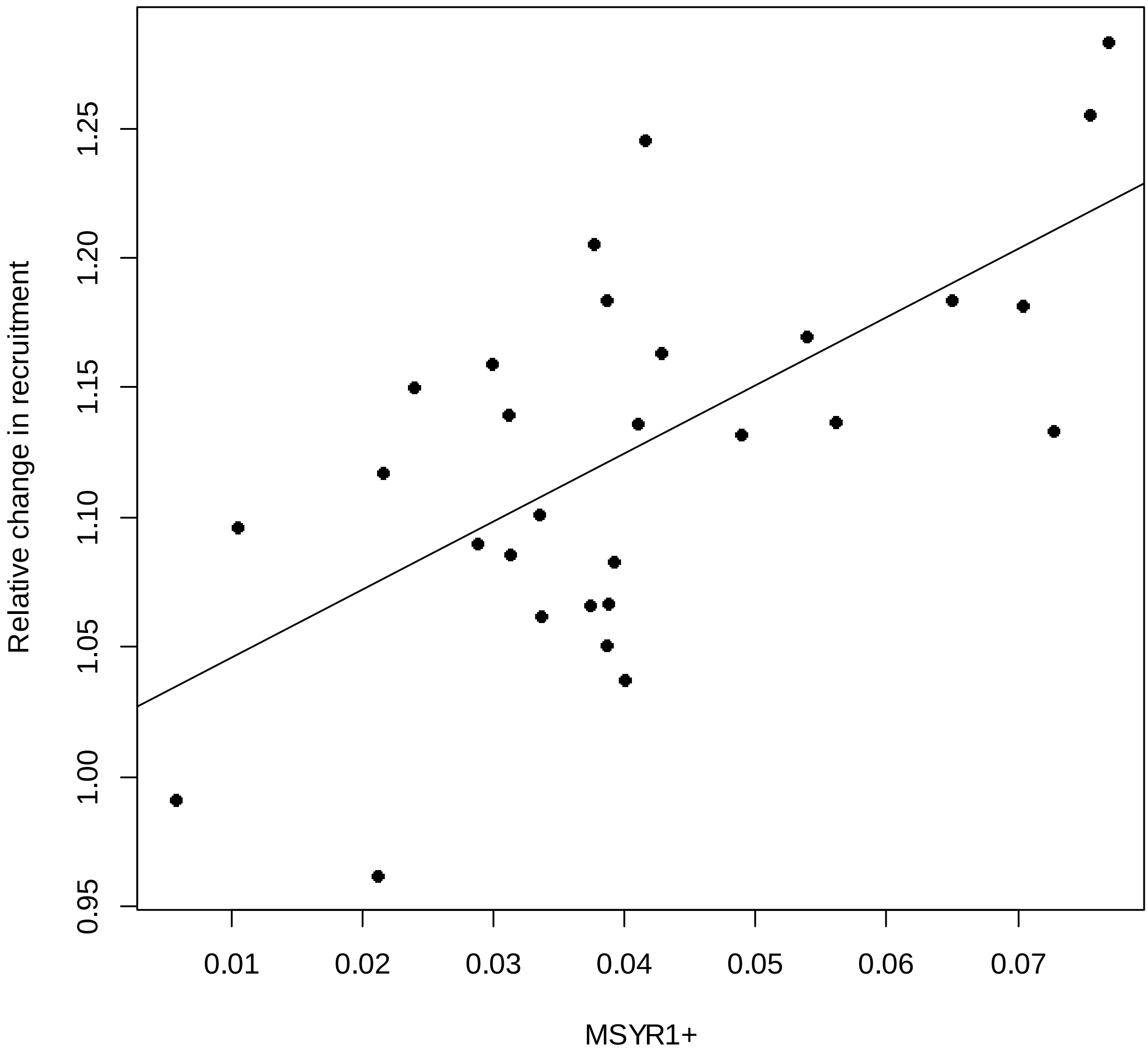

Fig 9. Relative increase in recruitment to the 1+ population between K and at $MSYL_{mat}$ from the 29 realisations of the IBEM model

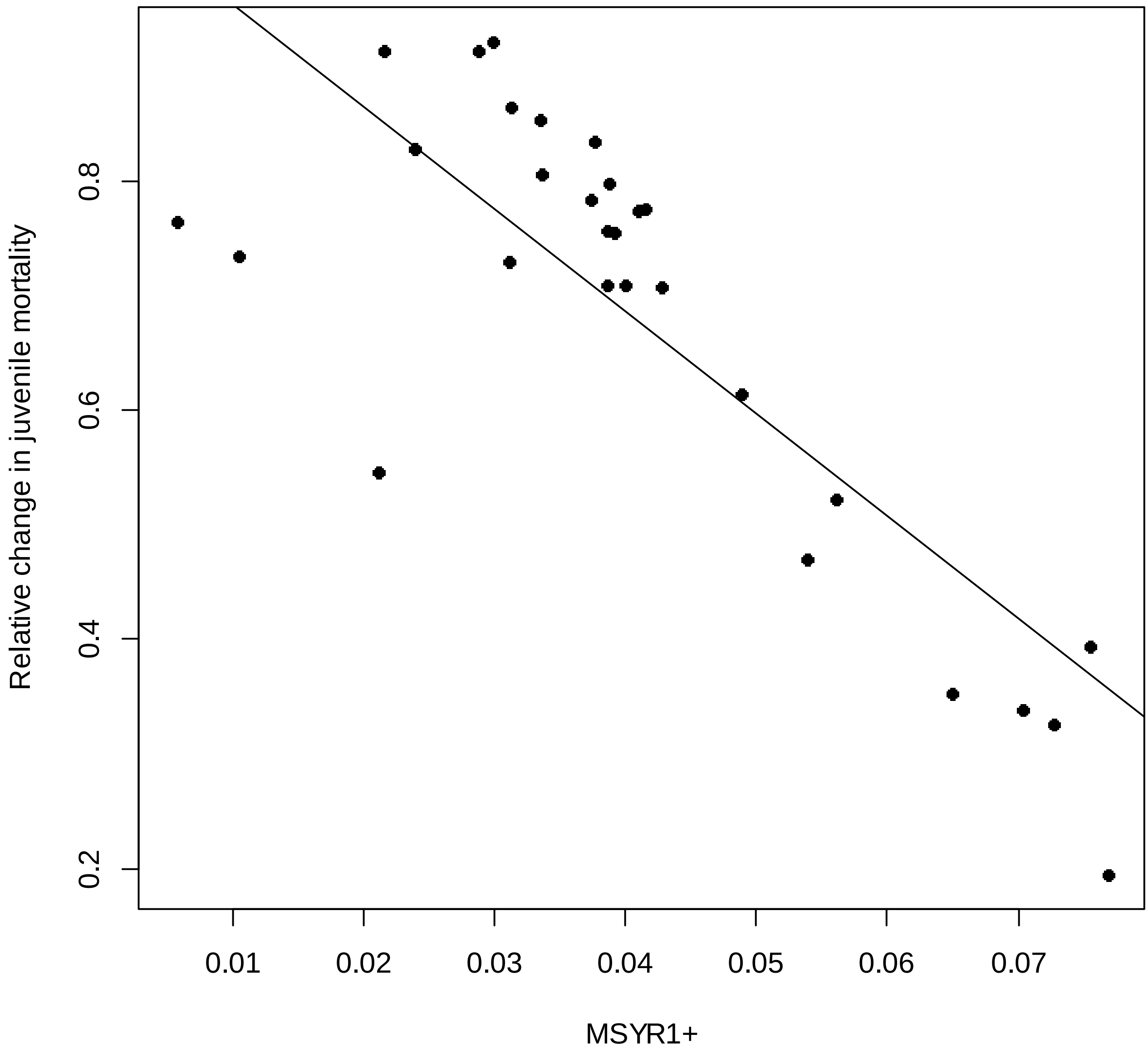

Fig 10. Relative decline in juvenile mortality rates between K and at $MSYL_{mat}$ from the 29 realisations of the IBEM model

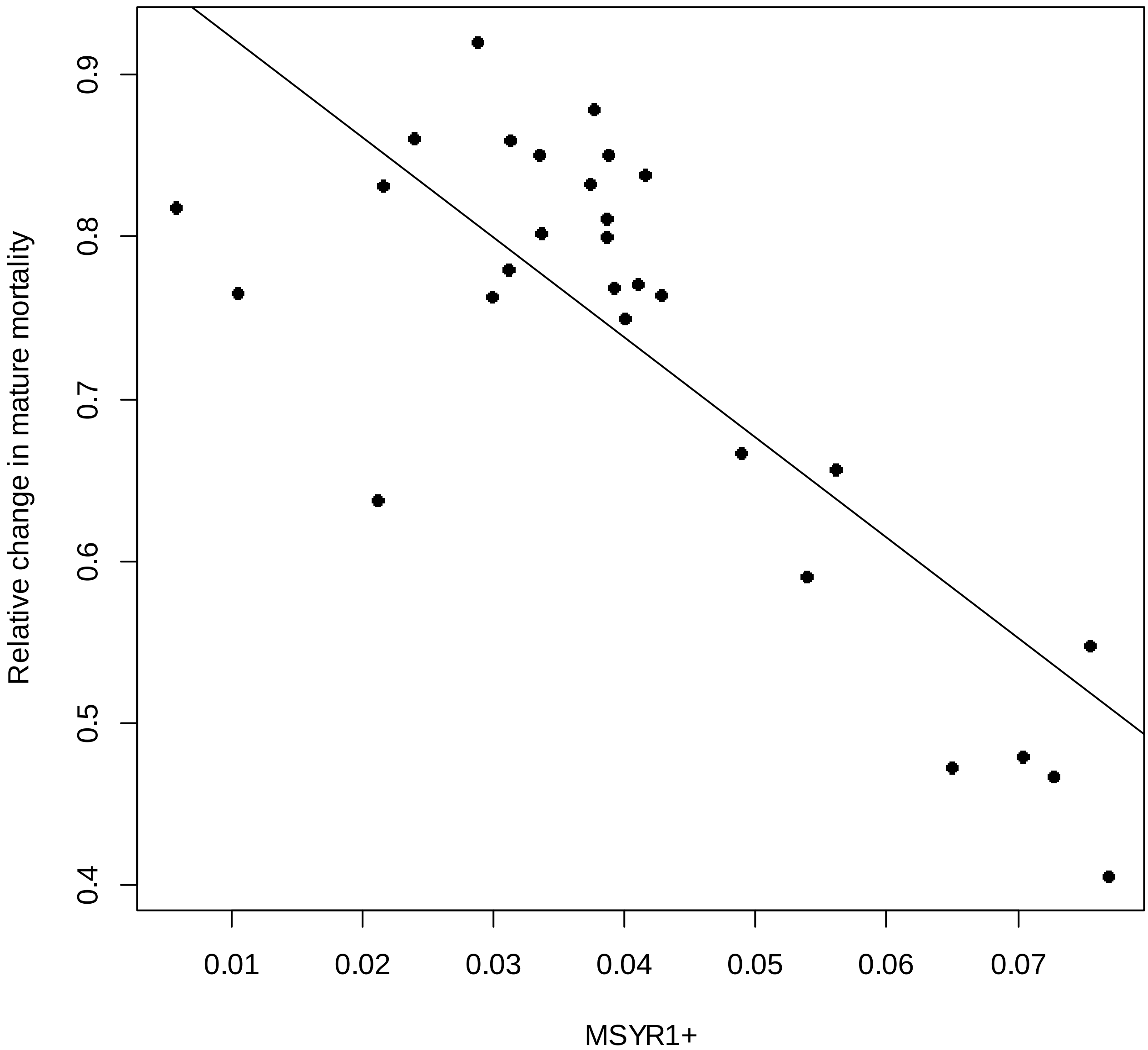

Fig 10. Relative decline in mature mortality rates between K and at $MSYL_{mat}$ from the 29 realisations of the IBEM model