A note on some implications of inter-specific competition when estimating MSYR by monitoring the recovery of depleted populations.

WILLIAM K. de la MARE

Australian Antarctic Division, Channel Highway, Kingston, Tasmania. Australia, 7050.
Contact email: bill.delamare@aad.gov.au

ABSTRACT

Some implications of estimating maximum sustainable yield rate (MSYR) from the recovery trajectories of competing populations are examined by simulation. Estimating MSYR from depleted populations makes strong assumptions about each population being isolated, stationary and recurrent. Possible competition undermines the assumption that populations are isolated. A model of intra-specific competition based on a multi-species version of the Pella-Tomlinson model is used to derive yield curves under various conditions. In this type of model the MSYR of interest to management is less than that applying to either species alone. Fitting a single species model to a recovery trajectory gives an estimate of the latter. The implications of these properties for the revision of the RMP are briefly discussed.

KEYWORDS: MSYR, SIMULATION, COMPETITION

INTRODUCTION

Estimating Maximum Sustainable Yield Rate (MSYR) by fitting a population model to a recovery trajectory is in essence a prediction about the future behaviour of a population, conditioned on current circumstances. If the future circumstances differ from the current ones then the prediction may not be reliable. Empirical predictions are only highly reliable for systems that are isolated, stationary (that is, have time invariant properties) and recurrent (Popper, 1963). These correspond to the assumptions of a single species population model. However, populations in natural systems do not generally satisfy any of these three conditions. One possible process that may lead to a failure of the single species assumption of isolation is the effects of inter-specific competition.

A modified form of the much abused multi-species logistic model or Lotka-Volterra (LV) competition model (Lotka, 1932) is used here to illustrate some potential pitfalls in estimating MSYR using the in-principle approach currently being applied by the Working Group on MSYR (IWC, 2009). The modification here is to depart from the logistic form of the model so that the single species yield curves are given by Pella-Tomlinson models. Of course this class of competition model is a gross and unreliable simplification of possible forms of inter-specific competition. However, the purpose here is to gain some insight into the possible effects of competition on the estimation of MSYR. Whether there is any general solution to these problems will require much deeper consideration. Inter-specific competition models involving more than two species can have more complex properties than the two-species modified LV model used here (Strobeck, 1973, Huisman and Weissing, 2001).

Cooke (2009a) presented the standard general theory of equilibria in the multi-species logistic model and demonstrated that MSYR depends on the pattern of exploitation. For a multi-species logistic model MSYR is 0.5r for each population alone if the others were eliminated (where r is a vector of maximum rates of increase for the set of competing populations). He also showed that the exploitation rate that maximised the yield for the joint set of populations was less than 0.5r and often substantially so. Cooke did not explore the implications of these observations on the estimation of MSYR from fitting a single species model to recovering populations, nor the sequential consequences of using those estimates for managing exploitation of populations that recover at different rates. The 2007 MSYR Workshop (IWC, 2009) did not take much account of the analysis apart from noting that it is important to be clear which MSYR is being referred to. The implications of Cooke's demonstration do not appear to have been given much consideration by the Scientific Committee. Cooke's rather mathematical demonstration may have contributed to the lack of appreciation of the potential issues.

Given that the empirical estimation of the effects of competition is of immense practical difficulty (Peters, 1992), a general solution that accounts for the effects of competition on estimates of MSYR may not be practically achievable. A cursory scan of the literature suggests that active research in this area is currently at low levels.

There is of course an even more gross simplification of the likely behaviour of real populations, and that is the single-species population model. The question is whether such a gross simplification can lead to robust estimates of parameters of interest, particularly if they are not constants as assumed in a single-species model.

The modified LV model for two competing populations P1 and P2 can be written in the form of difference equations as:

$$N_{1,t+1} = N_{1,t}\left(1 + r_1\left(1 - \left(\frac{N_{1,t}}{K_1}\right)^{z_1} - \frac{\alpha_{12} N_{2,t}}{r_1}\right) - H_{1,t}\right)$$

$$N_{2,t+1} = N_{2,t}\left(1 + r_2\left(1 - \left(\frac{N_{2,t}}{K_2}\right)^{z_2} - \frac{\alpha_{21} N_{1,t}}{r_2}\right) - H_{2,t}\right)$$

where $N_{.,t}$ is the abundance of populations (P1 or P2) in year t

$r_.$ is the maximum rate of a population's increase (when **both** populations are of negligible size)

$K_.$ is the carrying capacities of each population in the absence of the other

$\alpha_{..}$ are competition coefficients capturing the effect of one population on the other

$H_{.,t}$ are exploitation rates, that is, proportions of the population taken in year t

The two populations are set up with the parameters given in Table 1.

Table 1. Parameters used in the competition model

Parameter	Population 1	Population 2
K	5000	10000
r	0.08	0.04
z	2.39	2.39
α	$r_1/15000$	$r_2/20000$
Single species MSYL	3000	6000
Single species MSYR	0.0564	0.0282

The equations have an equilibrium solution when:

$$r_1\left(1 - \left(\frac{N_1}{K_1}\right)^{z_1} - \frac{\alpha_{12} N_2}{r_1}\right) - H_1 = r_2\left(1 - \left(\frac{N_2}{K_2}\right)^{z_2} - \frac{\alpha_{21} N_1}{r_2}\right) - H_2$$

The terms on either side of the equations are isoclines where the rate of increase of a population is zero. Since these are equilibrium solutions the t subscripts can be dropped. An equilibrium solution for the two equations occurs at population abundances where two isoclines intersect. The only solutions of interest in the illustrations in this paper are where the populations can coexist in stable equilibrium.

Fig. 1 gives some examples of the zero isoclines showing the equilibria for several exploitation rates. The isoclines 1 and 2 in Fig 1 both have $H_.$ set at zero. The unexploited equilibrium for the two populations occurs at $N_1 = 3344$ and $N_2 = 9263$, which will be referred to as K^*_1 and K^*_2 respectively. Isocline 3 has P1 exploited at a rate of 0.0267, which results in the isoclines intercepting at $N_1 = 0$ and $N_2 = K_2$. This means, in the absence of exploitation on P2, that an exploitation rate > 0.0267 on P1 will lead to its collapse despite the single species MSYR being more than twice that value. Isoclines 4 and 5 correspond to both populations being exploited simultaneously so that the resultant equilibrium occurs at $N_1 = 2007$ and $N_2 = 5558$, which are 60% of their respective K^* values.

In this class of model, the yield curves for either population depend on the abundance of the competing population. The equilibrium yields for either population are a 3 dimensional surface, and a yield curve is a section through that surface for a specified locus of abundances for the competing populations. Fig. 2 shows yield curves for P1 and P2 obtained under several conditions. The top curve is the single-species yield curve for both P1 and P2 (abundance is given as a fraction of their respective K values). These are the curves that apply for either species in the absence of the other. In this example, the maximum sustainable yield (MSY) has the

same numerical value for both populations because P1 has twice the MSY rate of P2, but half the carrying capacity (K). For these curves the MSYR values are equal to their single species values of 0.0564 and 0.0282 for P1 and P2 respectively.

The second curve down in Fig. 2 is the yield curve for P2 when P1 is held at its nominal MSYL of 60% of K^*_1. For this curve, not surprisingly MSY is less in the presence of the competitor, but MSYR is 0.0262, also less than its single species value. This curve and the second from the bottom are the two that are relevant if both species were to be managed to maintain their abundances relative to their joint equilibrium abundance (K^*). These MSYR values will be designated as MSYR*. The third curve from the top is for P2 where P1 is not exploited, and hence P1 increases in abundance above K^*_1. Obviously, MSY will be numerically smaller, but MSYR is also less at 0.0204. The second curve from the bottom is the yield curve for P1 with P2 maintained at 60% of K^*_2. For this curve the value of MSYR* is 0.0413. The lowest curve is for P1 exploited while P2 not unexploited; in this case the MSYR is 0.0197. For either population, both MSY and MSYR depend on the state of the competing population. In this model, the MSYR applying to either population in the absence of the other is greater than MSYRs attained when both populations exist.

To begin to explore the properties of fitting a single species model to recovery trajectories of competing populations, both competing populations are depleted to a few percent of their K^* values (3.5% of K^*_1 and 1.1% of K^*_2) and to approximately the same abundance. Without further exploitation the populations recover with the trajectories shown in Fig. 3. P1 overshoots K^*_1 because P2 recovers at a slower rate. P1 eventually declines towards K^*_1 as P2 becomes more abundant. The superabundance of P1 does not appear to have much effect on the recovery of P2. There are several instances where populations appear to recover above K, hence making them difficult to describe using single-species deterministic models (Cooke, 2009b). The effects of competition could be a contributing factor.

The method that fits a single species population model to the recovery trajectories is implemented here deterministically by fitting a Pella-Tomlinson single species model, with MSYL = 0.6K, to the recovery trajectories with 20 years of precise and unbiased absolute abundance data. Fig. 4 shows the "true" and fitted population trajectories. The estimates from the fitted single species models are given in Table 2. The recovery trajectories when both populations are substantially depleted are approximate estimates of r.. However, the single-species estimates of MSYR derived from r. are overestimates of MSYR*. There is some bias in the estimates of K^* because the downward trajectory of each population is affected by the changes in productivity arising from the changes in abundance of the competing population. These affects are absent in the fitted single-species model, so that estimates of K^* are biased down, although more substantially for P1.

Eventually these inconsistencies will lead to obvious departures between the recovering abundance and a single species model, particularly in the case of P1 when it begins to demonstrate recovery to above K_1.

Table 2. Estimated parameters of single species logistic models fitted to the recovery trajectories of the competing populations from a single deterministic trial.

Population	True K^*	Estimated K	True r	Estimated r	Estimated MSYR	Estimated MSYR/MSYR*
P1	3344	2809	0.080	0.0796	0.0561	1.36
P2	9263	9097	0.040	0.0392	0.0282	1.08

Fig. 5 shows the consequences of exploiting the two populations at the estimated MSYRs beginning in the year the populations each exceed 60% of their respective K^* levels. If the single-species model was accurate, P1 should stabilise at around this abundance level. However, P1 continues to increase until the recovery of P2 is further advanced, after which P1 begins to decline because the single-species estimate of MSYR is an overestimate of MSYR*, which is the rate required to stabilise P1 at 0.6K^*_1 (MSYR* = 0.0413) when P2 is at 0.6K^*_2. By the time P2 reaches 60% of K^*_2 the estimate of its single species MSYR will not stabilise the population despite being an over-estimate; P2 continues to increase because of the declining trend of P1. The trajectories continue to diverge.

If we consider a time horizon of about 100 years, the consequences of biased estimates of MSYR do not seem to have particularly serious consequences, and so it might be argued that the effects of competition on the

estimates have been relatively harmless in this case (and under the assumption that other improvements is management will occur in the interim).

However, the general revision of MSYRs as contemplated by the Scientific Committee would have the effect of applying the estimates in contexts other than those in which they were estimated. Suppose we were to apply those estimates to similar competing populations elsewhere, but neither of which have been substantially depleted. This scenario is shown in Fig. 6, where both populations were already at $0.6K^*$, but both now would decline because the single species MSYR estimates are overestimates of $MSYR^*$.

Whether either of these scenarios are serious problems for the RMP depends on the adaptive capacity of the management system to accommodate incorrect assumptions about MSYR.

DISCUSSION

Our prospect of reliably predicting MSYR even at the modest level of a distribution of MSYRs, assuming that such a thing exists, is inevitably low for natural systems because they are not isolated, stationary and recurrent. If the practical context available for estimating MSYR is from substantially depleted populations, this note indicates one class of mechanism that should make us wary about extrapolating those estimates to contexts where populations are not depleted. In the case of the simple competition model used here, MSYR is not necessarily a constant but changes over time with the changing abundance of the competing populations. Apart from inter-specific competition, competition of fisheries with marine mammals will affect apparent yield curves, as will the effects of climate change and ocean acidification that may lead to failures of the assumption that the systems are stationary.

The important question is whether the adaptive properties of the RMP are sufficient in the light of intractable uncertainties. When it is said that the RMP is "too conservative", the real issue is whether it has sufficient adaptive capacity to respond fully when yields are higher in the expected range. If the procedure is made "less conservative", the question is symmetric; would the revised procedure have sufficient adaptive capacity to respond fully when yields are at the lower end of the range. The primary problem is not the range of MSYRs; the problem is that adaptive capacity of the RMP is low and incomplete. However, this is a consequence of the rate of accumulation of information about population dynamics being limited because of imprecise abundance estimation, low acceptable risks of depletion and the objective of limiting fluctuations in catch limits to make them more predictable for the industry. The responsiveness of the procedure has to be low because of the constraints under which it operates. Making it "less conservative" may mean that it is not always conservative enough.

In principle, procedures used to modify the RMP are also part of the management system. The RMP development process demonstrated that the properties of methods depend on the context in which they are used and that they should be evaluated *in situ* rather than *ex situ* (de la Mare, 1986). Accordingly, if we are to use data, models and meta-analyses to modify the RMP we should also evaluate the consequences of using those methods to determine whether the whole management cycle retains robust management properties.

REFERENCES

Cooke, J. G. 2009a. A Note on the Definition of MSYR in a Multi-species Interaction Context. Report of the MSYR Workshop – Annex C. *J. Cetacean Res. Manage.* 11(Suppl):480.

Cooke, J. G. 2009b. A note on the interpretation of historical trends in baleen whale populations in the context of environmentally-induced variability in population dynamics, with implications for the estimation of MSY rates. SC/F09/MSYR 3.

de la Mare, W. K. 1986. Simulation studies on management procedures. *Rep. int. Whal. Commn* 36:429-50.

Huisman, J. and Weissing, F. J. 2001. Fundamental unpredictability in multispecies competition. *Am. Nat.*. 157: 488–94.

IWC, 2009. Report of the MSYR Workshop. *J. Cetacean Res. Manage.* 11(Suppl):467-80.

Lotka, A. J. 1932. The growth of mixed populations: two species competing for a common food supply. *J. Washington Acad. Sci.* 22:461-9.

Peters, R. H. 1991. *A critique for ecology*. Cambridge University Press, Cambridge, U.K. 366pp.

Popper, K. R. 1963. *Conjectures and refutations: the growth of scientific knowledge*. Routledge, London. p457.

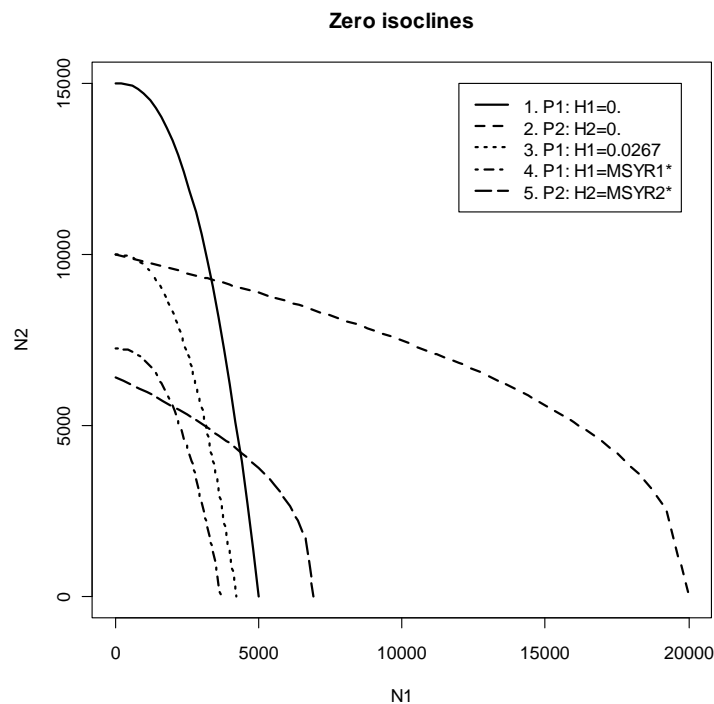Strobeck, C. 1973. N species competition. *Ecology* 54:650-4.

Zero isoclines

Fig. 1. Isoclines showing where the rate of change of population size is zero for the competing populations for some different rates (H) of exploitation.
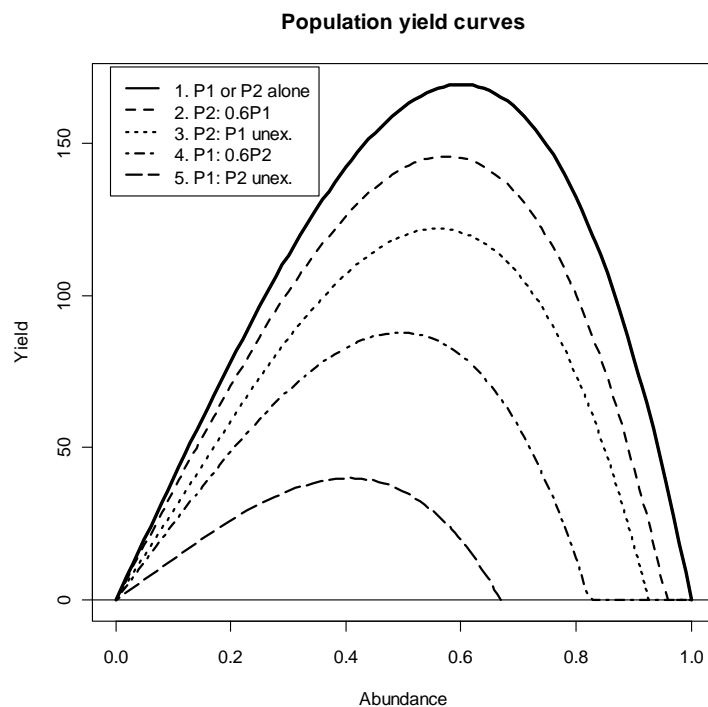
Population yield curves

Fig. 2. Yield curves for the two populations: curve 1; either P1 and P2 without the competition (the single species yield curves), curve 2; P2 with P1 maintained at 60% of its unexploited equilibrium abundance, curve 3; P2 without exploitation of P1; curve 4; P1 with P2 at 60% of its unexploited equilibrium, curve 5; P1 without exploitation of P2, bottom. Abundance is shown as a fraction of K_1 or K_2 as appropriate.
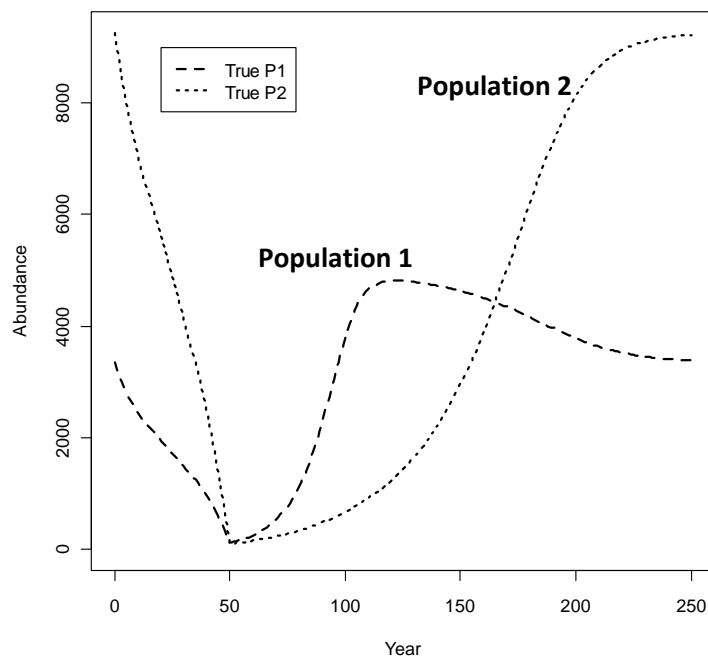
Fig. 3. Recovery of the two competing populations after simultaneous and substantial depletion and in the absence of further exploitation.
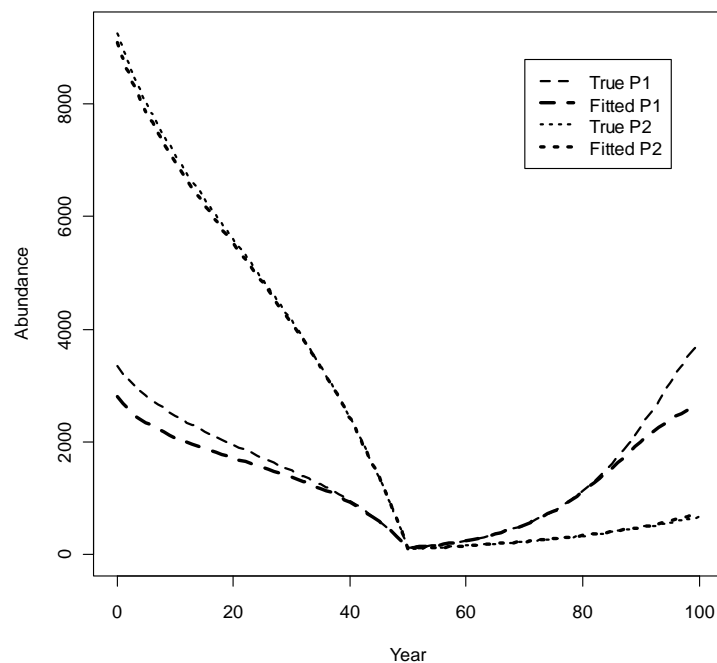

Fig. 4. "True" population trajectories generated from a model of two competing populations, both similarly depleted by simultaneous exploitation for 50 years. Also shown are two trajectories from fitting a single species model to the true abundance values from monitoring the recoveries over a 20 year period from year 56 to 76.
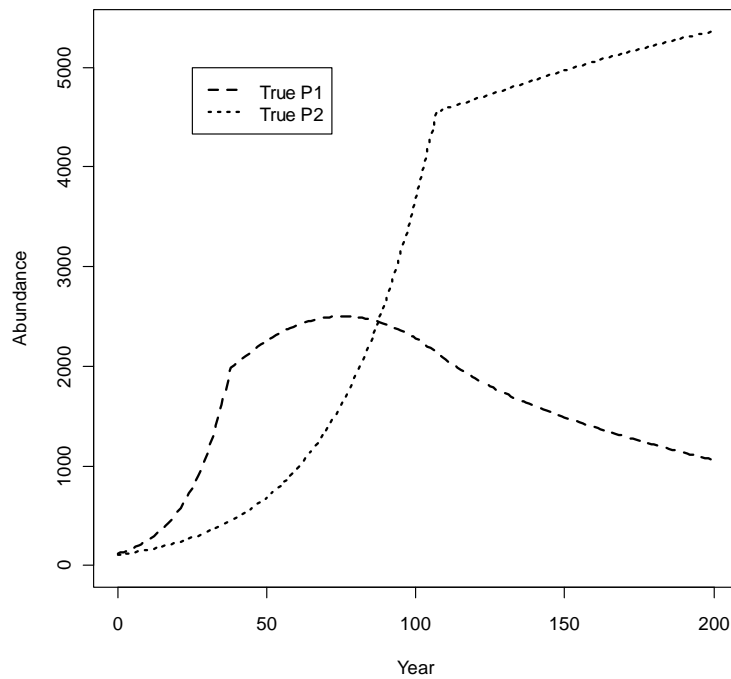
Fig. 5. Effects of applying an exploitation rate at the estimated values of MSYR to the two populations, starting when each was estimated to be recovered to more than 60% of their respective K^* values.
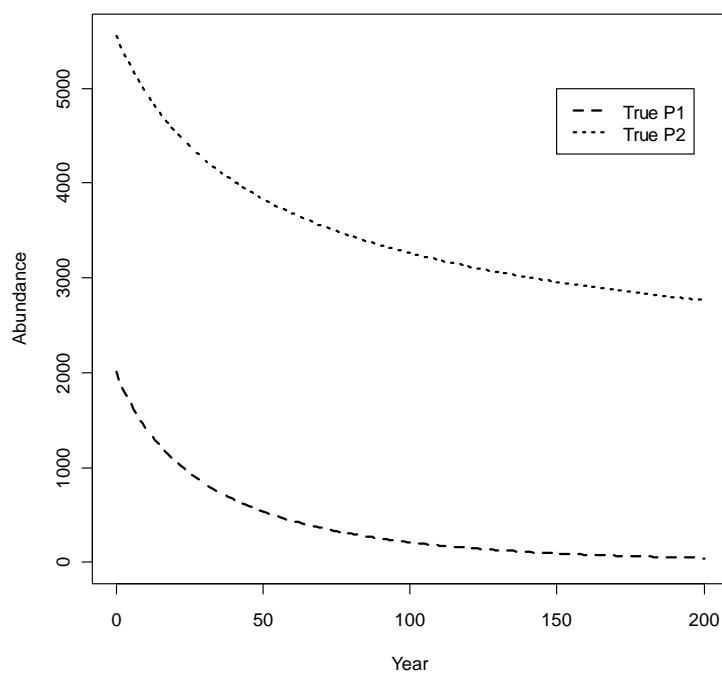

Fig. 6. Effect of applying the same MSYR estimates to other populations that were both at 60% of their unexploited equilibrium abundances previously.