

Evaluating the performance of the CLA when population structure is not correctly identified

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ABSTRACT

Identifying the appropriate ‘Unit to Conserve’ (UTC) is critical to the success of any management scheme. While the need to define the UTC appropriate to the IWC’s Catch Limit Algorithm (CLA) has long been recognized by the Scientific Committee, little progress has been made on this issue. The CLA was rigorously tested prior to its adoption. However, most of those original performance trials focused on single-stock scenarios, and none of them considered the possibility of two populations with ongoing dispersal among them. In this study, we used the TOSSM package to examine the performance of the CLA under a variety of population structure scenarios. Ours is the first study to investigate the levels of connectivity (i.e., dispersal rate) for which populations require separate management in order to meet the conservation goals of the CLA. All of our trials consisted of two populations that were managed as a single stock for 100 years. Both historic and modern harvests were spatially biased so that population 1 was the primary target of harvest. Parameters varied across trials were the relative carrying capacities (K) of the populations, the dispersal rate among them, maximum sustainable yield rate ($MSYR_{1+}$), and the precision in simulated abundance estimates. All of these parameters had strong effects on population persistence under the CLA. Trials with a low $MSYR_{1+}$ (1%) generally ended with the abundance of population 1 below $0.54K$, regardless of the dispersal rate or relative carrying capacities of the two populations. The same was true of trials in which the carrying capacity of population 1 represented only 20% or less of the total landscape carrying capacity, even when dispersal between populations was high ($5X10^{-3}$ /year) and $MSYR_{1+}$ was 4%. These results highlight the value of spatially diffuse harvest patterns that avoid potential overharvest of unrecognized stocks. The results also underline the need for powerful genetic methods as a tool in management, as populations connected even by dispersal rates as high as $5X10^{-3}$ are shown here to be vulnerable to overharvest if not managed separately.

INTRODUCTION

The success of any management scheme hinges on accurate identification of the management units the scheme is intended to conserve. The level of connectivity at which ‘Units to Conserve’ (UTCs) should be defined will depend on the management objectives those units are intended to meet (Palsbøll *et al.*, 2007; Taylor, 2005; Taylor *et al.*, submitted; Waples and Gaggiotti, 2006). For instance, in the United States, the two major pieces of legislation aimed at conserving marine mammals are the Endangered Species Act (ESA), and the Marine Mammal Protection Act (MMPA). The goal of the ESA is to prevent the extinction of species, while the goal of the MMPA is to maintain populations as ‘functioning elements of their ecosystems.’ Because of the differing goals of these two conservation acts, the levels of connectivity between their respective UTCs also differ. In order to achieve the goal of the ESA, it is necessary to identify and separately manage units that are following independent evolutionary trajectories (Waples, 1991). Consequently, units

managed separately under the ESA typically experience gene flow at the rate of one disperser or fewer per generation (Gardenfors *et al.*, 2001; Taylor *et al.*, submitted). Units with this level of connectivity are typically referred to as ‘Evolutionarily Significant Units,’ or ESUs (Moritz, 1994; Waples, 1991). The more ambitious conservation goal of the MMPA, on the other hand, requires separate management if two units are demographically independent (Angliss and Wade, 1997). Specifically, simulations have shown that separate management is necessary even for populations exchanging dispersers at rates in excess of 1% per year if the goals of the MMPA are to be met (Taylor, 1997). Units at this level are referred to as ‘Demographically Independent Populations,’ or DIPs (Taylor, 1997; Waples and Gaggiotti, 2006).

The Revised Management Procedure (RMP) is the management scheme that the International Whaling Commission has agreed to use to manage commercial whaling, should the moratorium on commercial whaling be lifted (IWC, 1994). At the heart of the RMP is a Catch Limit Algorithm (CLA) recommended by the Scientific Committee in 1991 (IWC 1992a) and subsequently adopted by the Commission. Prior to its recommendation by the Scientific Committee, the CLA was subjected to extensive performance testing to ensure that it balanced the three competing management objectives of maximizing catch, minimizing variability in catch, and adequately conserving populations (IWC, 1991; 1992; 2007). Most of the performance testing of the CLA focused on trials in which there is a single population. However, some testing examined performance when two populations are erroneously managed as one stock (‘stock’ is the name given to management units in the RMP framework) and when one stock is managed as two (Smith *et al.*, In press). These trials have confirmed that the CLA is vulnerable to errors in stock definition (IWC, 1991; 1992). However, because all of these two-population trials assumed zero dispersal between populations, they do not provide insight into the level of connectivity necessary to warrant separate management under the CLA. The RMP includes options (variants) such as catch cascading and catch capping to account for stock structure uncertainty, and evaluations of the consequences of stock definition errors have been conducted as part of selecting among these variants for individual stocks based on case-specific *Implementation Simulation Trials* (e.g., IWC, 2004; 2007). However, the case-specific nature of *Implementation Simulation Trials* limits their utility for drawing general conclusions regarding the circumstances under which management as separate stocks is necessary to adequately protect populations.

In this paper, we examine the performance of the CLA under a variety of population structure scenarios. In all of our simulations, two populations are erroneously managed as a single stock. We measure the performance of the CLA as a function of the relative sizes of the two populations and the dispersal rate between them. By determining the range of population structure scenarios under which separate management is necessary in order to adequately protect populations, our results will provide guidance to researchers attempting define stocks for individual species being managed under the RMP, as well as to those seeking to develop new approaches to defining stocks for use under the RMP.

METHODS

We used the TOSSM package (Martien *et al.*, 2008) to evaluate performance of the CLA in the face of unrecognized population structure. To do this, we conducted a series of simulations in which two populations are combined into a single management unit (MU). A single catch limit is calculated by the CLA for the MU, and is therefore based on the combined abundance of both populations. The entire catch limit is removed each year and, if possible, is taken entirely from

population 1. If there are not enough individuals in population 1 to meet the catch limit, the balance of the catch limit is taken from population 2.

All simulations were initialized with both populations at carrying capacity (K). The combined carrying capacity of the two populations (K_{TOT}) was set to 7,500 in all simulations. In the first year of each simulation, population 1 was depleted to $0.3K$ and population 2 to $0.99K$. The two populations then underwent 100 years of simulated management, with both populations combined into a single MU. During this management period, abundance in the MU was estimated and the catch limit re-calculated every 5 years. We performed 100 replicates of each simulation.

Preliminary analyses showed that our results were strongly dependent on the coefficient of variation (CV) of the abundance estimate for the MU. In the TOSSM package, CV is modeled according to the formula

$$CV = 0.1\sqrt{x/N}$$

where N = estimated abundance of the MU and x = the abundance at which $CV = 0.1$.

Taylor *et al.* (2007) found that CVs for stocks of large whales in US territorial waters ranged from 0.08 (western North Pacific humpback whales) to 0.73 (CA/OR/WA minke whales), with an average of 0.29. We chose values of x such that when both populations in the MU were at carrying capacity, the CV was 0.30, 0.17, or 0.04 (Fig. 1). The highest of these values represents a typical level of precision, while the middle value represents a realistic high precision case. The lowest CV value we examined is unlikely to apply to any large whale species, but allowed us to fully characterize the behavior of the CLA. We did not examine higher values of CV. Doing so would have resulted in adequate protection under virtually all population structure scenarios and would therefore not have contributed to our objective of identifying the population structure scenarios under which the CLA failed to adequately protect populations if population structure went undetected.

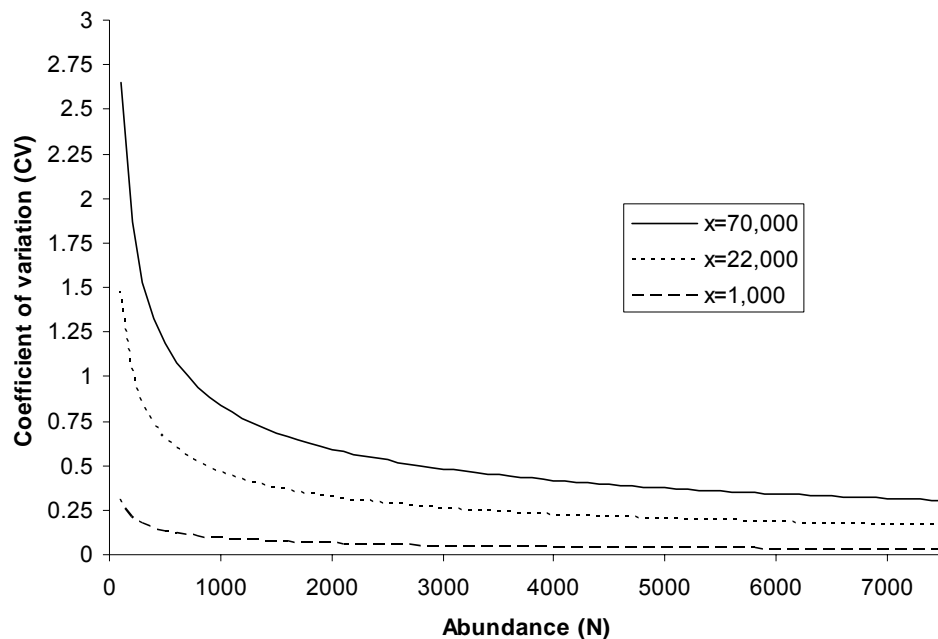


Fig. 1. Relationship between abundance and CV for the three values used for the CV tuning parameter (x). The values chosen for x result in CVs at $N=7,500$ of 0.3 ($x=70,000$), 0.17 ($x=22,000$), and 0.04 ($x=1,000$).

TOSSM simulations must be initialized with a dataset generated by the R package ‘rmetasim’ (Strand, 2002). An array of datasets with various parameterizations were generated in ‘rmetasim’ for this study. The ‘R’ code used to generate these datasets was the same as that used to generate the TOSSM datasets (Martien, 2006). The three parameters varied in these datasets were: 1) the maximum sustainable yield rate ($MSYR_{1+}$), 2) the carrying capacities of the two populations (always summing to 7,500), and, 3) the dispersal rate between the two populations. A full description of all population parameters used when generating these datasets is included in the Appendix.

Two main sets of trials were performed. The first set of trials was performed to determine the effect of dispersal rate on population sustainability at two values for $MSYR_{1+}$. In these trials, the carrying capacity of each population was set at $K=3,750$ (half of the total for the landscape). These trials were conducted using the highest CV scenario ($x=70,000$; Fig. 1). Four dispersal rates ($5X10^{-6}$, $5X10^{-5}$, $5X10^{-4}$, and $5X10^{-3}$) were examined. Simulations using these four dispersal rates were performed for $MSYR_{1+}=4\%$ and $MSYR_{1+}=1\%$.

The second set of trials explored the effect of the CV of the abundance estimates on population sustainability across five different levels of relative population carrying capacity. In these trials, the parameters held constant were dispersal rate ($5X10^{-3}$) and $MSYR_{1+}$ (4%). For each of the three CV curves shown in Fig. 1, the relative carrying capacities of the two populations were varied so that population 1 comprised 10, 20, 30, 40, or 50% of the total landscape carrying capacity.

Only the time-trajectory of the size of population 1 was recorded, because this is the population most heavily impacted by harvest. Population 1 is the population that is depleted to $0.3K$ prior to the first application of the CLA. Catches during the management period of the trials also comes primarily from population 1 due to a spatial bias in harvest within the TOSSM package. This spatial bias is intended to simulate a situation in which whalers attempt to minimize effort by concentrating their effort close to home port, which assumed to be at the lefthand side of the study area. The extent of spatial bias in removals is controlled by the ‘harvest.interval’ argument to the TOSSM package. Harvest always occurred initially in the leftmost interval of the 10 harvest intervals spanning the landscape, and proceeded successively to the right upon depletion of the animals in each interval. Whales are always removed from population 1 first because populations are numbered left to right.

We ran two single-stock simulations and compared the results with those from previous analyses to confirm that the CLA as implemented in the TOSSM package was working properly. These trials each consisted of a single population with a carrying capacity of 7,500 that was initially depleted to $0.3K$. $MSYR_{1+}$ was set at 1% in one trial and 4% in the other. Thus, these trials correspond to the R1 and R4 base-case trials used during the development of the CLA (IWC, 1991), except that $MSYR$ refers to the 1+ rather than mature component of the population. These single-stock trials were run for 500 years, with median abundance (across 100 replicates) recorded at years 100 and 500.

RESULTS

Population 1 always recovered to greater than $0.54K$ (Fig. 2) after 100 years of CLA management when the initial carrying capacities of the two populations were equal to half of the total landscape K and $MSYR_{1+}$ was set at 4%. However, this was not the case when $MSYR_{1+}$ was instead set at 1%. In these trials population 1 did not generally recover. The exception to this was when the dispersal rate, d , equaled $5X10^{-3}$. This trial resulted in marginal conservation performance (Fig. 2), with population 1 recovering to above the $0.54K$ threshold in 87% of replicates. The abundance

trajectories for the three lowest dispersal rates ($d = 5 \times 10^{-6}$ to 5×10^{-4}) were fairly consistent (Fig. 2); only when the dispersal rate reached 5×10^{-3} was a large effect of dispersal rate seen on population 1 recovery.

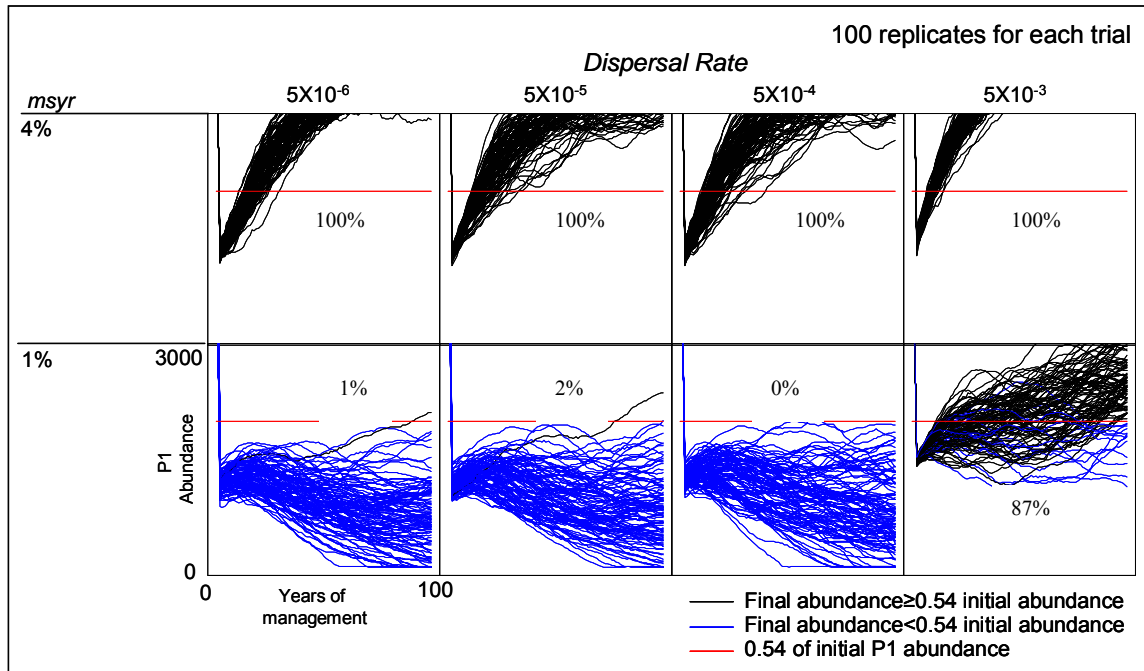


Fig. 2. Time-trajectories of total (1+) population size for population 1 (P1) as a function of $MSYR_{1+}$ (1% and 4%) and dispersal rate (ranging from 5×10^{-6} to 5×10^{-3}). The carrying capacity for each population was 3,750, and the CV at carrying capacity was 0.3 (see Fig. 1 for relationship between the CV and abundance). The percentage of replicates whose final abundance was greater than 0.54K is shown on each panel. $MSYL$ was 0.518K and 0.547K for the 1% $MSYR_{1+}$ and 4% $MSYR_{1+}$ simulations, respectively.

The CVs for the abundance estimates strongly affect the population trajectories, as do the relative sizes of the carrying capacities of the two populations. Population 1 was sustained only when carrying capacities were equal for the lowest CV (Fig. 3). Population 1 generally failed to recover to greater than 0.54K when the carrying capacity of population 1 was lower than that of population 2. The extent of recovery was larger when the CV of the abundance estimates was higher. Population 1 recovered to above 0.54K in all trials using the highest CV curve, except when it constituted 10% of the total landscape K initially. The impact of higher CVs on population recovery rates is not unexpected; the CLA sets the catch limit as the 40.2th percentile of a posterior distribution for the catch limit; greater uncertainty in abundance estimates thus results in a wider posterior distribution for the catch limit and hence a lower catch limit overall. Note that these results are based on the most optimistic assumptions regarding $MSYR_{1+}$ (4%) and dispersal rate (5×10^{-3}).

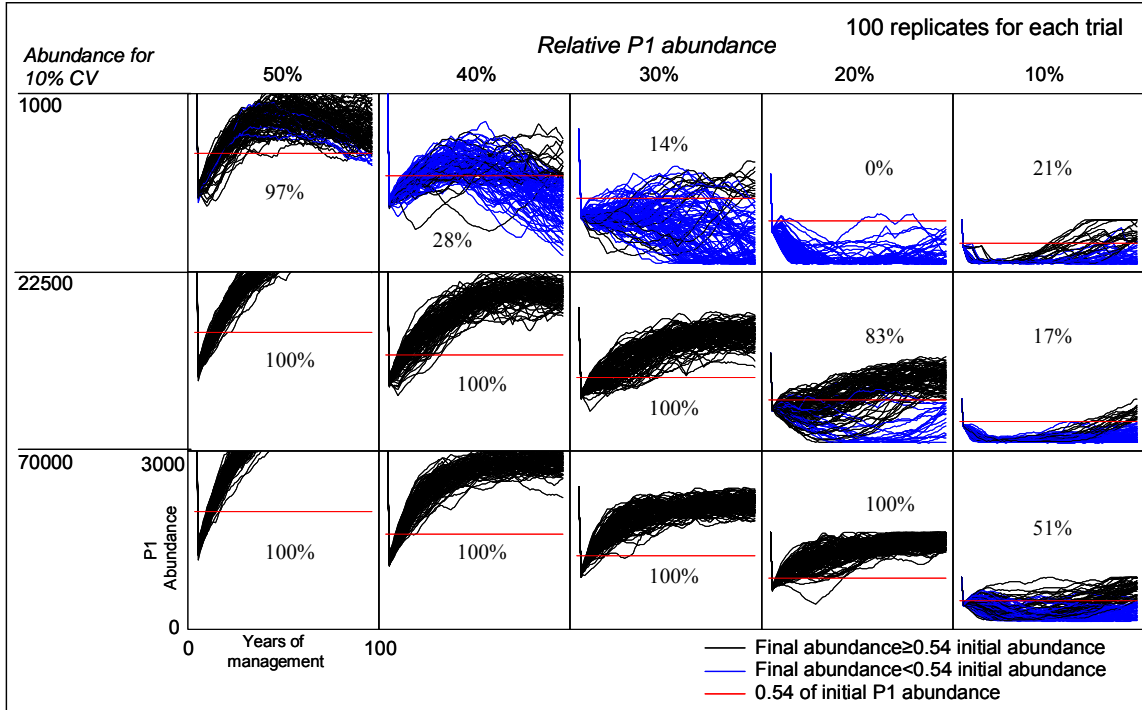


Fig. 3. Time-trajectories of total (1+) population size for population 1 (P1) as a function of the fraction which P1 constitutes of the entire landscape carrying capacity and the CV curve (see Fig. 1). Dispersal level and MSYR were held constant at 5×10^{-3} and 4% respectively. The percentage of replicates whose final abundance was greater than 0.54K is shown on each panel. MSYL for these simulations is 0.547

The results of our single-stock trials were not inconsistent with those published by Butterworth and Punt (1994) (Table 1)¹, indicating that the CLA is correctly implemented in the TOSSM package. Comparisons between our results and the graphical summaries of Aldin *et al.* (2006) also provides support for the CLA working correctly within TOSSM.

Table 1. Median of abundance at years 100 and 500 for single stock trials. The 5th and 95th percentiles are shown in parentheses. ‘B&P 1994’ refers to results published in Butterworth and Punt, 1994.

MSYR	TOSSM package		B&P 1994	
	Year 100	Year 500	Year 100	Year 500*
1%	0.702 (0.564-0.803)	0.885 (0.627-1.00)	0.624 (0.559-0.663)	0.85
4%	0.966 (0.932-1.00)	0.971 (0.912-1.01)	0.943 (0.843-0.981)	0.85

* Butterworth and Punt (1994) only report median abundance for year 500 in graphical form. Thus, the values reported here are approximate.

DISCUSSION

It will be necessary to separately manage populations between which annual dispersal rates are relatively high, at least from an evolutionary perspective, to protect and sustain populations of large whales. Failure to manage populations separately resulted in poor conservation performance of the CLA for many of the parameter combinations we examined even with dispersal as high as 0.5% per year, the highest value we examined. These results indicate that the unit-to-convert of relevance to

¹ The results of Butterworth and Punt (1994) were based on MSYR defined in terms of the mature rather than 1+ population component.

the RMP is much more similar to the ‘Demographically Independent Populations’ (DIPs) of the MMPA than to the ‘Evolutionarily Significant Units’ (ESUs) of the ESA. This is not surprising, given that the management objective of the RMP (i.e., maintaining sustainable fisheries) is focused on an ecological scale rather than an evolutionary one (Waples and Gaggiotti, 2006).

Defining stocks that adequately protect populations managed under the RMP is likely to be difficult, especially if catches are not spread out spatially (e.g., using techniques such as catch cascading). In recent decades, genetic data have emerged as the most powerful tool available for defining units to conserve (Taylor *et al.*, submitted) and hence for identifying hypotheses for consideration when developing *Implementation Simulation Trials* (ISTs) for RMP testing. However, dispersal rates on the order of 5×10^{-3} result in very low levels of genetic differentiation. Most existing analytical methods are unable to detect such low levels of differentiation (Chen *et al.*, 2007; Latch *et al.*, 2006; Martien and Gregovich, 2008; Morin *et al.*, 2008; Taylor *et al.*, submitted; Waples and Gaggiotti, 2006). Accurately identifying stocks of large whales is made more difficult by the large abundance and long generation times of most species, both of which tend to reduce genetic differentiation for a given dispersal rate (Morin *et al.*, 2008).

The impact of errors in stock definition on the performance of the CLA increases as the CV of abundance estimates decreases (Fig. 3). This interaction reflects the fact that an error in stock definition is, in essence, an error in estimating the geographic range, and therefore abundance, of the unit that is being impacted by removals. The CV is the only input to the CLA that reflects uncertainty associated with the estimates of the abundance of the stock, although the CLA imposes a minimum CV for all abundance estimates, partially to reflect the fact that abundance estimates can contain sources of error not captured by sampling error alone. A high CV implies greater uncertainty regarding the number of animals available for harvest, and can therefore partially compensate for abundance estimation errors due to mis-identification of stocks.

The TOSSM package differs slightly from the model typically used in *ISTs* with respect to the way that CV is calculated. In the TOSSM package, the CV is inversely proportional to the total abundance. In contrast, *ISTs* (and the trials which were used to test the CLA) generate abundance estimates using CVs that include a constant term and a term that depends on the inverse of total abundance (e.g. IWC 2004, 2007). The generation process includes both log-normal and Poisson components. Moreover, *ISTs* account for uncertainty caused by errors when estimating the sampling CV from a survey and often the impacts of temporal variation in migration of stocks. The TOSSM package is therefore less amenable to the type of case-specific, highly realistic simulations for which the models used in *ISTs* are designed. However, the differences between the TOSSM package and the *IST* models do not affect the conclusions of this study.

Our results show that extra caution is necessary to ensure that stocks have been correctly defined in cases where CVs of abundance estimates are low. Similarly, species with low MSYR warrant special attention with respect to defining stocks. It remains to be seen whether existing analytical methods are capable of identifying population structure at the level required for proper stock definition. Preliminary results of performance tests suggest that the Monmonier algorithm (Monmonier, 1973) and the clustering method proposed by Waples and Gaggiotti (2006) may be up to the task (Martien and Gregovich, 2008). However, further testing is required to determine the sampling regimes that will be necessary in order for these methods to detect dispersal rates higher than 5×10^{-4} . In case studies for which power analysis indicates that available analytical methods would be unable to detect relevant levels of population structure, managers should employ methods to ensure spatially diffuse harvest patterns so as to reduce the risk of over-exploiting unrecognized populations.

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Appendix: TOSSM dataset generation

The TOSSM datasets used in this paper were generated following the methodology and parameter values described by Martien (2006). Rmetasim implements density dependence by linearly interpolating between matrices describing life history rates at zero population density (*ZPD*) and at carrying capacity (*K*). All 4% MSYR datasets were generated using the life history matrices developed by Martien (2006; Table App.1) from empirical data for Eastern Pacific grey whales (Reilly 1984, Perryman 2002). The *ZPD* and *K* matrices developed by Martien (2006) have growth rates of $\lambda = 1.072$ and 1.0003 , respectively, and result in an $MSYR_{1+}$ of 3.9%.

Table. App.1. Life history matrices for used to generate 4% MSYR datasets. Matrices describe life history parameters at a) zero population density and b) carrying capacity. Stage class abbreviations are juve1 = juvenile1, juve2 = juvenile2, fert = fertile female, lact = lactating female, and male = adult male.

a)	juve1	juve2	fert	lact	male	b)	juve1	juve2	fert	lact	male
juve1	0.730	0	0.889	0	0	juve1	0.768	0	0.278	0	0
juve2	0.210	0	0	0	0	juve2	0.157	0.720	0	0	0
fert	0	0.47	0	0.946	0	fert	0	0.102	0.648	0.946	0
lact	0	0	0.946	0	0	lact	0	0	0.300	0	0
male	0	0.47	0	0	0.954	male	0	0.102	0	0	0.954

Generating datasets with an MSYR of 1% required developing a new *ZPD* matrix with a growth rate of $\lambda = 1.02$. We interpolated between the elements of the two matrices developed by Martien (2006; Table 1) to produce a matrix with the desired growth rate (Table App.2). When combined with the *K* matrix developed by Martien (2006), this matrix results in an $MSYR_{1+}$ of 1.0%.

Table. App.2. Life history matrices for used to generate 1% MSYR datasets. Matrices describe life history parameters at a) zero population density and b) carrying capacity. Note that the carrying capacity matrix is identical to the one used to produce 4% MSYR datasets (Table App.1b). Stage class abbreviations are juve1 = juvenile1, juve2 = juvenile2, fert = fertile female, lact = lactating female, and male = adult male.

a)	juve1	juve2	Fert	lact	male	b)	juve1	juve2	fert	lact	male
juve1	0.760	0	0.404	1.0	0	juve1	0.768	0	0.278	0	0
juve2	0.168	0.570	0	0	0	juve2	0.157	0.720	0	0	0
fert	0	0.179	0.513	0.946	0	fert	0	0.102	0.648	0.946	0
lact	0	0	0.434	0	0	lact	0	0	0.300	0	0
male	0	0.179	0	0	0.954	male	0	0.102	0	0	0.954