Hale Whales

Target Reproduction Numbers and Sensitivity Analysis for Resident Killer Whales

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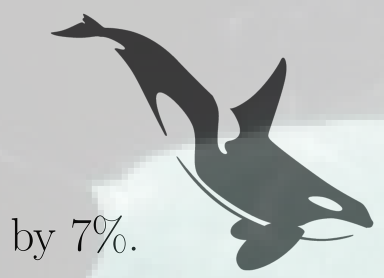
Project Abstract

We used existing population projection matrix models of female Resident Killer Whales (*Orcinus orca*) [1,4], and the target reproduction number framework developed in [3], together with senstivity analysis from [2], to identify key parameter values to aid in population recovery strategies. We found that reproductive adult survival and adult transition had the greatest impact on the net reproductive value of the population.

Motivating Example *(not actual values)*

Suppose for a population of killer whales to survive in the long term, the total growth rate needs to increase the population by 2% per year. This is a *threshold parameter*, or the target reproduction number for the entire population. Suppose we have two conservation strategies that could achieve this and their associated anual costs:



- Strategy 1: Increase average fecundity by 5%. Cost: $25,000.
- Strategy 2: Decrease reproductive adult mortality by 7%. Cost: $18,000.

The most *effective* strategy achieves the best results for the least effort (cost), and by studying target reproduction numbers, we are looking to optimize this relationship. In this example, we would choose the second strategy.

Matrix Population Modelling:

A model for the dynamics of a *stage-structured population*, a *discrete-time matrix model* is given by

$$\mathbf{n}_{t+1} = P\ \mathbf{n}_t.$$

where n_t and n_{t+1} are a vectors of stages at times t and $t+1$, respectively, and P is a *population projection matrix*.

Killer Whale Model - Brault and Caswell (1993)

- Assumed four life stages: yearlings (stage 1), juveniles (stage 2), reproductive adults (stage 3), and post reproductive adults (stage 4).
- Population projection matrix model for *female* Resident Killer Whales based on yearly time-intervals.

$$P = \begin{pmatrix} 0 & F_2 & F_3 & 0 \\ T_1 & P_2 & 0 & 0 \\ 0 & T_2 & P_3 & 0 \\ 0 & 0 & T_3 & P_4 \end{pmatrix}. \qquad \text{(Equation 1.)}$$

Here, P_i is the probability of surviving and remaining in the same stage (i), T_i describes the probability of surviving and transitioning to the next stage ($i+1$), and the fertility F_i is the number of female offspring at $t+1$, per adult female at time t.

Killer Whale Model (Continued)

For each stage i, the basic parameters that could be estimated for the population were: stage-specific survival probability σ_i, transition probability to the next stage γ_i, and mean reproductive output of adult females $\bar{m}$. Parameter estimates came from published data from 1973 through 1987.

Table 1: [1] Each element of Equation 1 can be written in terms of the basic, estimated parameters: σ_i, γ_i and $\bar{m}$.

Matrix Element	Formula
P_2	$(1-\gamma_2)\sigma_2$
P_3	$(1-\gamma_3)\sigma_3$
P_4	σ_4
T_1	$\sigma_1^{1/2}$
T_2	$\gamma_2\sigma_2$
T_3	$\gamma_3\sigma_3$
F_2	$\sigma_1^{1/2}T_2\bar{m}/2$
F_3	$\sigma_1^{1/2}(1+P_3)\bar{m}/2$

Table 2: [1] Estimated parameters for the entire Resident Killer Whale population from 1973-1987 .

Parameter	Estimated Value
σ_1	0.9554
σ_2	0.9847
σ_3	0.9986
σ_4	0.9804
γ_2	0.0747
γ_3	0.0453
$\bar{m}$	0.1186

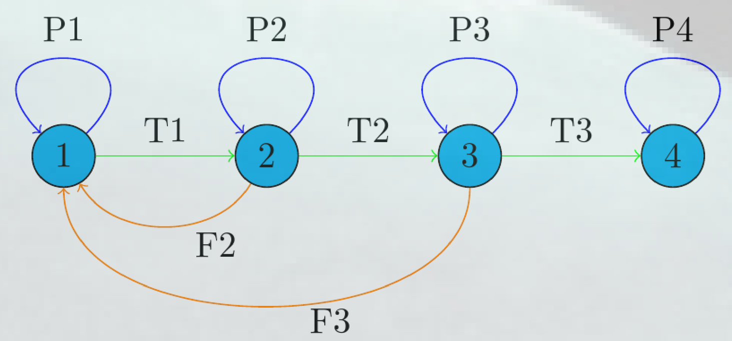


Figure 1: Life-cycle graph corresponding to Equation 1.

Target Reproduction Numbers

Conservation strategies focus on particular parameters that are important for the population.

In a given matrix model, we can determine which parameters are important by examining target reproduction numbers. These quantify the amount of effort corresponding to each conservation strategy.

Definition 1. [3] Let A, B, C be nonnegative $n \times n$ matrices such that $A = B + C$ is irreducible, $C \neq 0$, and $\rho(B) < 1$. Then the *target reproduction number* $\mathcal{T}_C > 0$ is defined as

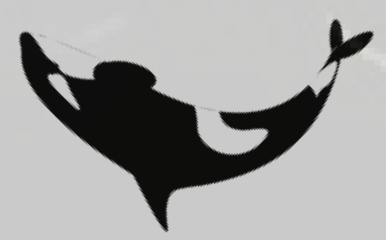
$$\mathcal{T}_C = \rho(C(I-B)^{-1}),$$

where I is the $n \times n$ identity matrix, and ρ is the spectral radius.

Here, C is the target matrix which contains all targeted entries of the population projection matrix A, and B is the residual matrix left over from decomposition.

Commonly used target reproduction numbers:

- *Population growth rate* $\lambda = \mathcal{T}_P = \rho(P) \approx 1.0257$ [1]
- *Net reproductive value* $R_0 = \mathcal{T}_m = \rho(F(I-T)^{-1})$



Sensitivity Analysis

It can also be helpful to examine how $\mathcal{T}_C$ responds to perturbations in parameters.

Definition 2. [2] The *sensitivity* s_i of $\mathcal{T}_C(\theta_1, \theta_2, \ldots, \theta_n)$ to changes in the parameter θ_i is given by

$$s_i = \frac{\partial \mathcal{T}_C}{\partial \theta_i}.$$

Results

Mean values are used as estimates rather than as statistically significant values.

Table 3: Target reproduction numbers for the model [1]. Targeted matrices consisted of all entries in Equation 1 containing the parameter of interest.

Target Reproduction Number	Expression	Value
$\mathcal{T}_{\sigma_1}$	$\sqrt{\frac{\gamma_2\sigma_1\sigma_2 m}{(1-\sigma_2(1-\gamma_2))(1-\sigma_3(1-\gamma_3))}}$	1.42
$\mathcal{T}_{\sigma_2}$	$\frac{\sigma_2(1+\gamma_2(\sigma_1 m-1)-\sigma_3(1-\gamma_3)(1-\gamma_2))}{1-(1-\gamma_3)\sigma_3}$	1.09
$\mathcal{T}_{\sigma_3}$	$\frac{\sigma_3(1-\gamma_3)(1-\sigma_2(1-\gamma_2))}{1-\gamma_2\sigma_1\sigma_2 m-\sigma_2(1-\gamma_2)}$	1.05
$\mathcal{T}_m = R_0$	$m\ \sigma_1 \left(\frac{\sigma_2\gamma_2}{1-\sigma_2(1-\gamma_2)}\right)\left(\frac{1}{1-\sigma_3(1-\gamma_3)}\right)$	2.01

Table 4: Sensitivities of R_0 to perturbations in model parameters.

Parameter	Sensitivity	Value
$\bar{m}$	$\frac{R_0}{\bar{m}}$	16.96
σ_1	$\frac{R_0}{\sigma_1}$	2.11
σ_2	$\frac{R_0}{\sigma_2(1-\sigma_2(1-\gamma_2))}$	22.99
σ_3	$\frac{R_0(1-\gamma_3)}{(1-\sigma_3(1-\gamma_3))}$	**41.17**
γ_2	$\frac{R_0(1-\sigma_2)}{\gamma_2(1-\sigma_2(1-\gamma_2))}$	4.64
γ_3	$\frac{R_0(-\sigma_3)}{(1-\sigma_3(1-\gamma_3))}$	**-43.07**

Net Reproductive Value

- R_0 is the average number of offspring per female over her lifetime
- $R_0 > 1$ indicates that the population size is increasing
- Perturbations in σ_3 (reproductive adult survival) have largest positive impact on R_0
- Perturbations in γ_3 (reproductive adult transition) have largest negative impact on R_0

More Recent Data Set - Vélez-Espino *et al.* (2014)

- Newer model, with net reproductive value $R_0 = 1.41$, (data from 1987-2011) suggests that it is more accurate to split the reproductive feale adult life-stage into two separate stages.
- Perturbations in the main reproductive adult survival and transition probabilities show similar trends to the earlier model having the largest positive and negative impact on R_0, respectively.
- Juvenile survival perturbations also had a significant positive impact on R_0, unlike the Brault and Caswell model.
- **Future work** will compare target reproduction numbers from these data with those from the original model [1].

References

[1] Brault S, Caswell H (1993) Pod-specific demography of killer whales (*Orcinus orca*). Ecology 74:1444-1454

[2] Caswell H (2001) Matrix Population Models: Construction, Analysis, and Interpretation, 2nd edn. Sinauer Associates, Sunderland

[3] Lewis MA, Shuai Z, van den Driessche P (2019) A general theory for target reproduction numbers with applications to ecology and epidemiology. J Math Biol 78: 2317-2339.

[4] Vélez-Espino LA, Ford JKB, Araujo HA, Ellis G, Parken CK, Balcomb KC (2014) Comparative demography and viability of northeastern pacific resident killer whale populations at risk. Canadian Technical Report of Fisheries and Aquatic Sciences 3084: 1–66.

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