# GLMs relating penguin demographics to pelagic catches close to islands and to pelagic abundance 

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#### Abstract

Earlier GLM analyses of the impact of pelagic fishing in the vicinities of Robben and Dassen Islands on the dynamics of penguins breeding on those islands are extended to cover a wider set of data series, and to consider relationships involving sardine and anchovy separately as well as together. This in turn allows the estimation of the change in penguin population growth rate to be expected from suspending pelagic fishing in the vicinities of these islands. Interpretation of results is confounded by poor precision which is a consequence of the shortness of the time series. Likely the most that could be said with some confidence is that the results of the analyses do not support the hypothesis that suspending fishing around Robben and Dassen Islands would enhance penguin reproductive success there.


## Introduction

The work presented below extends the earlier GLM models developed first in Brandão and Butterworth (2007) to address the topic of this paper to a wider set of data series, and to consider relationships involving sardine and anchovy separately, rather than only in combination as earlier.

The results from these GLMs are then used to estimate the extent to which suspending fishing near Robben Island or Dassen Island would improve penguin population increase rates.

## Data

The penguin data used for these analyses are as agreed following discussions with Rob Crawford, who was assisted in their preparation by Newi Makhado.

Fledging success data are given in Table 1. There are two (non-comparable) data series for Robben Island, hence the addition of a third $\alpha$ parameter in GLMs (1) and (5) below to allow for an estimable multiplicative bias between these series.

Breeders per adult moulter (Table 2) are derived from the annual nest counts and moult counts. Data from after 2007 were ignored because the moult counts for those years seem unrealistically low (being well below breeder counts), probably as a result of some of the birds moulting elsewhere.

[^0]Table 3 gives the ratio of active nests to the total number of nests counted (active plus potential nests). Table 4 lists annual survival rates calculated from tagging data. Since the proportion of nests and the survival rates fall in the range [0,1], these two data sets are transformed using a logistic transformation in models (3), (4), (7) and (8) below.

The six series of estimates for pelagic catch in the vicinity of the islands, taken from Van der Westhuizen (2010), are given in Table 5. This six pelagic survey biomass series used are given in Table 6. The choice of pelagic biomass data are as agreed following discussions with Janet Coetzee.

## Models

General Linear Models are considered for fledging success $F_{y, i, s}$, breeders per adult moulter $G_{y, i}$, active nests as a proportion of total nests $P_{y, i}$, and adult survival $S_{y, i}$. The response variables are indexed by year $y$, island $i$ and data series $s$. The four equations are:

$$
\begin{align*}
& \ln \left(F_{y, i, s}\right)=\alpha_{s}+\beta_{y}+\lambda_{i} \frac{C_{y, i, p}}{\bar{C}_{i, p}}+\varepsilon_{y, i, s}  \tag{1}\\
& \ln \left(G_{y, i}\right)=\alpha_{i}+\beta_{y}+\lambda_{i} \frac{C_{y, i, p}}{\bar{C}_{i, p}}+\varepsilon_{y, i}  \tag{2}\\
& \ln \left(\frac{P_{y, i}}{1-P_{y, i}}\right)=\alpha_{i}+\beta_{y}+\lambda_{i} \frac{C_{y, i, p}}{\bar{C}_{i, p}}+\varepsilon_{y, i}  \tag{3}\\
& \ln \left(\frac{S_{y, i}}{1-S_{y, i}}\right)=\alpha_{i}+\beta_{y}+\lambda_{i} \frac{C_{y, i, p}}{\bar{C}_{i, p}}+\varepsilon_{y, i} \tag{4}
\end{align*}
$$

where
$\alpha_{s}, \alpha_{i}, \beta_{y}$ and $\lambda_{i}$ are estimable parameters,
$C_{y, i, p}$ is the catch taken in year $y$ around island $i$ of pelagic species $p$, where $p$ refers to either sardine, anchovy or the two combined, and
$\bar{C}_{i, p}$ is the average catch around island $i$ of pelagic species $p$, calculated over the years for which there is penguin data available for island $i$ for the model concerned.

An alternative form is considered where the year effect $\beta_{y}$ is replaced by the parameter $\gamma$ multiplied by the annual pelagic biomass $B_{y_{q}, p, q}$ where $q$ refers to either the November adult biomass or the May recruit biomass. If this relationship with biomass accounts for much of the year effect $\beta_{y}$ in equations (1)-(4), since this alternative form involves fewer estimable parameters it can potentially yield more precise estimates of the key $\lambda_{i}$ parameters.

$$
\begin{align*}
& \ln \left(F_{y, i, s}\right)=\alpha_{s}+\gamma B_{y_{q}, p, q}+\lambda_{i} \frac{C_{y, i, p}}{\bar{C}_{i, p}}+\varepsilon_{y, i, s}  \tag{5}\\
& \ln \left(G_{y, i}\right)=\alpha_{i}+\gamma B_{y_{q}, p, q}+\lambda_{i} \frac{C_{y, i, p}}{\bar{C}_{i, p}}+\varepsilon_{y, i}  \tag{6}\\
& \ln \left(\frac{P_{y, i}}{1-P_{y, i}}\right)=\alpha_{i}+\gamma B_{y_{q}, p, q}+\lambda_{i} \frac{C_{y, i, p}}{\bar{C}_{i, p}}+\varepsilon_{y, i}  \tag{7}\\
& \ln \left(\frac{S_{y, i}}{1-S_{y, i}}\right)=\alpha_{i}+\gamma B_{y_{q}, p, q}+\lambda_{i} \frac{C_{y, i, p}}{\bar{C}_{i, p}}+\varepsilon_{y, i} \tag{8}
\end{align*}
$$

Since November is closer to the following year's breeding season, $y_{q}=y-1$ when $q$ denotes the November adult biomass while $y_{q}=y$ when $q$ denotes the May recruit biomass.

The parameters of particular interest are the $\lambda_{i}$ and $\gamma$, which respectively relate commercial fishery catches and pelagic abundance to the penguin response variables.

## Results

The values of the estimated parameters $\gamma$ and $\lambda_{i}$ are given in Table 7, along with standard errors and significance levels. Note that no estimates are given for model (4) since there proved to be insufficient data for reliable estimation in this case.

Table 8 summarises the number of occurrences of parameter estimates with positive and negative signs.

## Analysis

The estimates of the GLM $\lambda_{i}$ parameters may be used to calculate estimates for the change in the penguin population growth rate to be expected from stopping fishing in the vicinity of the islands.

Assuming reproductive maturity occurs at age 4, the basic penguin population model is:

$$
\begin{equation*}
N_{y+1}=N_{y} S+H_{y-3} S^{3} N_{y-3} \tag{9}
\end{equation*}
$$

where $S$ is the adult annual survival rate and $H$ is a measure related to egg production and fledging success. In a steady situation, the population growth rate $\mu$ is thus related to $S$ and $H$ as follows:

$$
\begin{equation*}
\mu^{4}=\mu^{3} S+H S^{3} \tag{10}
\end{equation*}
$$

Differentiating implicitly and solving for $\Delta \mu$ (a change in the growth rate) gives:

$$
\begin{equation*}
\Delta \mu=\frac{\mu^{3}+3 S^{2} H}{4 \mu^{3}-3 \mu^{2} S} \cdot \Delta S+\frac{S^{3}}{4 \mu^{3}-3 \mu^{2} S} \cdot \Delta H \tag{11}
\end{equation*}
$$

The growth rates $\mu_{\text {ROB }}$ and $\mu_{\text {DAS }}$ were estimated from logarithmic regressions of the moult counts for Robben Island from 2004 to 2007 and for Dassen Island from 2003 to 2007, which are the years corresponding to the recent major declines at the two colonies. The average survival rate for the years 2004-2006 at Robben Island and 2003-2006 at Dassen Island from Table 4 were used as the adult survival rates $S_{\text {ROB }}$ and $S_{\mathrm{DAS}}$. Values for $H_{\mathrm{ROB}}$ and $H_{\mathrm{DAS}}$ were then calculated using equation (10). The results were as follows:

|  | $\mu$ | $S$ | $H$ |
| :--- | :---: | :---: | :---: |
| Robben | 0.712 | 0.604 | 0.178 |
| Dassen | 0.760 | 0.560 | 0.501 |

The parameters $\lambda_{i}$ corresponds to the effect on the dependent variable in question of increasing the catch around the island concerned from zero to its average value. Thus if such catches are suspended, the estimated change $\Delta H$ is given by $\exp \left(-\lambda_{i}\right)-1$ for the fledging success and breeders per adult moulter GLMs. The active/total nests ratio does not translate readily into such a relationship, but the $\lambda_{i}$ parameters of adult survival models of equations (4) and (8) relate similarly to $\Delta S$ after allowing through differentiation for the effect of the logistic transformation.

Table 9 and Figs 1-2 show estimates with approximate $95 \% \mathrm{Cls}^{2}$ of the change in penguin population growth occasioned by suspending fishing around colonies, as estimated from these various models. Note that the upper six plots in each figure correspond to results based on GLM analyses of reproduction-related data, while the final two plots relate to GLM 8 which considers survival.

## Discussion

In terms of the $\lambda_{i}$ parameters which estimate the impact of fishing close to islands on penguin demographic parameters, there are five cases (three positive and two negative) where the estimate is significant at the $5 \%$ level (see Table 7), but interpretation of such "significance" must be tempered by the multiplicity of the tests conducted and the incompleteness of their independence given use of partially common data. Similar problems would apply if performing non-parametric tests on the tallies of positive and negative estimates shown in Table 8. Nevertheless, the broad trends shown there are of interest and probably also not without meaning.

- When biomass is used rather than estimating a year factor separately for each year, relationships of reproduction and survival rates to pelagic biomass are nearly all positive.
- Estimates of the impact of additional fishing on penguin parameters related to reproduction are preponderantly positive rather than negative.

[^1]- Estimates of this impact on penguin survival rates are near equally split between positives and negative.

Fig. 2 probably provides the most easily interpretable summary of the estimated impacts on penguin growth rates of suspending pelagic fishing close to west coast colonies. For data series related to reproductive success the point estimates for changes in growth rate are in the main a few percent and negative, with the strongest effect related to the fledging success data for Dassen Island. The one notable positive effect is for Dassen Island when only sardine abundance is used to reflect common inter-year variability for the both islands.

Virtually the same comments could be made concerning the results for survival rate when the November spawner biomass surveys provide the co-variate to reflect that common inter-year variability. If the recruit survey results are used instead, all but one of the point estimates reflect positive impacts from suspending fishing, but the associated variances are much higher than for the other seven plots shown.

In summary, obtaining clear results from these analyses is frustrated by the short-ish time series available, which precludes precision estimation of the effects of interest. Likely the most that could be said with some confidence is that the results of the analyses do not support the hypothesis that suspending fishing around Robben and Dassen Islands would enhance penguin reproductive success there.

While further analyses of this type could be pursued (e.g. assuming different functional forms or error distributions for the models investigated), that would seem unlikely to yield results dissimilar to those above. However a case could still be made for some continued experimental closures to provide the contrast for more precise estimation of the effects of interest given further monitoring data.

## References

Brandão A, Butterworth DS. 2007. An initial analysis of the power of monitoring certain Indices to determine the effect of fishing on penguin reproductive success from an experiment where pelagic fishing is prohibited in the neighbourhood of Robben Island, but continues around Dassen Island. Document MCM EAFWG/OCT2007/STG/04.

Van der Westhuizen J. 2010. Estimating anchovy and sardine catches in the region of the penguin colonies. Document MCM/2010/SWG_PEL/Island Closure Task Team/04.

## Tables

Table 1: Fledging success data (GLM 1)

| Year | Island | Series | F |
| :---: | :---: | :---: | :---: |
| 1989 | Robben | Robben1 | 0.415 |
| 1990 | Robben | Robben1 | 0.319 |
| 1991 | Robben | Robben1 | 0.592 |
| 1992 | Robben | Robben1 | 0.590 |
| 1993 | Robben | Robben1 | 0.535 |
| 1994 | Robben | Robben1 | 0.446 |
| 1995 | Robben | Robben1 | 0.383 |
| 1996 | Robben | Robben1 | 0.654 |
| 1997 | Robben | Robben1 | 0.968 |
| 1998 | Robben | Robben1 | 0.748 |
| 1999 | Robben | Robben1 | 0.600 |
| 2001 | Robben | Robben2 | 0.756 |
| 2002 | Robben | Robben2 | 0.516 |
| 2003 | Robben | Robben2 | 0.449 |
| 2004 | Robben | Robben2 | 0.487 |
| 2005 | Robben | Robben2 | 0.811 |
| 2006 | Robben | Robben2 | 0.627 |
| 2007 | Robben | Robben2 | 1.142 |
| 2008 | Robben | Robben2 | 1.031 |
| 2009 | Robben | Robben2 | 0.937 |
| 1995 | Dassen | Dassen | 0.825 |
| 1996 | Dassen | Dassen | 1.022 |
| 1997 | Dassen | Dassen | 1.180 |
| 1998 | Dassen | Dassen | 1.343 |
| 1999 | Dassen | Dassen | 1.376 |
| 2009 | Dassen | Dassen | 1.060 |
|  |  |  |  |

Table 2: Breeders per adult moulter (GLM 2)

| Year | Island | p |
| :---: | :---: | :---: |
| 1989 | Robben | 0.478 |
| 1990 | Robben | 0.753 |
| 1991 | Robben | 0.796 |
| 1992 | Robben | 0.821 |
| 1993 | Robben | 0.665 |
| 1994 | Robben | 0.707 |
| 1995 | Robben | 0.575 |
| 1996 | Robben | 0.928 |
| 1997 | Robben | 0.914 |
| 1998 | Robben | 0.810 |
| 1999 | Robben | 0.926 |
| 2000 | Robben | 0.925 |
| 2001 | Robben | 0.998 |
| 2002 | Robben | 1.149 |
| 2003 | Robben | 0.825 |
| 2004 | Robben | 0.919 |
| 2005 | Robben | 1.150 |
| 2006 | Robben | 0.965 |
| 2007 | Robben | 1.839 |
| 1996 | Dassen | 1.536 |
| 1997 | Dassen | 1.336 |
| 1998 | Dassen | 1.348 |
| 1999 | Dassen | 1.408 |
| 2000 | Dassen | 1.354 |
| 2001 | Dassen | 1.636 |
| 2002 | Dassen | 1.760 |
| 2003 | Dassen | 1.604 |
| 2004 | Dassen | 2.993 |
| 2005 | Dassen | 2.610 |
| 2006 | Dassen | 2.335 |
| 2007 | Dassen | 3.050 |

Table 3: Active and potential nests (GLM 3)

| Year | Island | p |
| :---: | :--- | :--- |
| 2000 | Robben | 0.957 |
| 2001 | Robben | 0.951 |
| 2002 | Robben | 0.940 |
| 2003 | Robben | 0.973 |
| 2004 | Robben | 0.876 |
| 2005 | Robben | 0.789 |
| 2006 | Robben | 0.860 |
| 2007 | Robben | 0.824 |
| 2008 | Robben | 0.986 |
| 2009 | Robben | 0.826 |
| 1999 | Dassen | 0.953 |
| 2000 | Dassen | 0.915 |
| 2001 | Dassen | 0.850 |
| 2002 | Dassen | 0.804 |
| 2003 | Dassen | 0.658 |
| 2004 | Dassen | 0.543 |
| 2005 | Dassen | 0.489 |
| 2006 | Dassen | 0.403 |
| 2007 | Dassen | 0.432 |
| 2008 | Dassen | 0.613 |
| 2009 | Dassen | 0.482 |

Table 4: Adult survival (GLM 4)

| year | Island | Survival |
| :---: | :---: | :---: |
| 2002 | Robben | 0.765 |
| 2003 | Robben | 0.752 |
| 2004 | Robben | 0.644 |
| 2005 | Robben | 0.620 |
| 2006 | Robben | 0.548 |
| 2007 | Robben | 0.385 |
| 2002 | Dassen | 0.697 |
| 2003 | Dassen | 0.682 |
| 2004 | Dassen | 0.561 |
| 2005 | Dassen | 0.535 |
| 2006 | Dassen | 0.462 |
| 2007 | Dassen | 0.307 |

Table 5: Annual pelagic catch taken within 15 nautical miles of Robben Island and Dassen Island (in tonnes).

|  | Sardine | Robben <br> Achovy | Total | Sardine | Dassen Achovy | Total |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1987 | 1577 | 34686 | 36263 | 5706 | 51526 | 57232 |
| 1988 | 2953 | 44734 | 47687 | 10026 | 33909 | 43935 |
| 1989 | 2395 | 30736 | 33131 | 4090 | 24990 | 29080 |
| 1990 | 5262 | 5130 | 10392 | 9961 | 8686 | 18647 |
| 1991 | 2880 | 15993 | 18873 | 4657 | 10433 | 15090 |
| 1992 | 4166 | 32012 | 36178 | 6677 | 42180 | 48857 |
| 1993 | 3526 | 7767 | 11293 | 9205 | 14977 | 24182 |
| 1994 | 4861 | 21589 | 26450 | 5674 | 29424 | 35098 |
| 1995 | 2777 | 9498 | 12275 | 10616 | 20223 | 30839 |
| 1996 | 5981 | 4243 | 10224 | 23849 | 7530 | 31379 |
| 1997 | 9523 | 7945 | 17468 | 7041 | 3463 | 10504 |
| 1998 | 9678 | 3252 | 12930 | 19455 | 2927 | 22382 |
| 1999 | 9275 | 17000 | 26275 | 25922 | 36286 | 62208 |
| 2000 | 2264 | 12908 | 15172 | 6441 | 30003 | 36444 |
| 2001 | 4029 | 12023 | 16052 | 6465 | 51926 | 58391 |
| 2002 | 19829 | 17397 | 37226 | 21152 | 36436 | 57588 |
| 2003 | 24511 | 30581 | 55092 | 16583 | 31338 | 47921 |
| 2004 | 2388 | 17925 | 20313 | 2543 | 25800 | 28343 |
| 2005 | 385 | 11046 | 11431 | 1679 | 56067 | 57746 |
| 2006 | 2455 | 21442 | 23897 | 3685 | 40325 | 44010 |
| 2007 | 1977 | 35374 | 37351 | 3912 | 39741 | 43653 |
| 2008 | 808 | 48139 | 48947 | 1977 | 13338 | 15315 |
| 2009 | 1409 | 33100 | 34509 | 330 | 3359 | 3689 |

Table 6: Pelagic hydroacoustic survey estimates (in millions of tonnes). The November series comprises the aggregate adult biomass west of Cape Aguhlas. The May series comprises the total recruit biomass west of Cape Infanta.

|  | November spawner biomass |  | May recruit biomass |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Year | Sardine | Anchovy | Combined | Sardine | Anchovy | Combined |
| 1984 | 0.048009 | 1.461636 | 1.509645 |  |  |  |
| 1985 | 0.025457 | 1.014215 | 1.039672 | 0.038265 | 0.368623 | 0.406888 |
| 1986 | 0.238230 | 1.978652 | 2.216883 | 0.050073 | 0.621089 | 0.671162 |
| 1987 | 0.094165 | 1.866430 | 1.960595 | 0.098643 | 0.721578 | 0.820220 |
| 1988 | 0.128043 | 1.289624 | 1.417668 | 0.005223 | 0.563107 | 0.568329 |
| 1989 | 0.198328 | 0.517293 | 0.715622 | 0.066081 | 0.173349 | 0.239430 |
| 1990 | 0.248855 | 0.342812 | 0.591667 | 0.031208 | 0.170083 | 0.201291 |
| 1991 | 0.517180 | 1.254359 | 1.771539 | 0.026665 | 0.528177 | 0.554842 |
| 1992 | 0.247756 | 1.036580 | 1.284337 | 0.074822 | 0.458455 | 0.533278 |
| 1993 | 0.480822 | 0.439121 | 0.919942 | 0.114956 | 0.481108 | 0.596064 |
| 1994 | 0.389730 | 0.309981 | 0.699711 | 0.072462 | 0.145336 | 0.217797 |
| 1995 | 0.348832 | 0.468678 | 0.817510 | 0.205149 | 0.392016 | 0.597164 |
| 1996 | 0.257763 | 0.029748 | 0.287511 | 0.073612 | 0.074842 | 0.148453 |
| 1997 | 0.964835 | 0.377663 | 1.342498 | 0.396718 | 0.404620 | 0.801338 |
| 1998 | 1.082547 | 0.206586 | 1.289132 | 0.134907 | 0.453210 | 0.588116 |
| 1999 | 0.708029 | 0.741961 | 1.449990 | 0.235720 | 0.826090 | 1.061810 |
| 2000 | 0.726230 | 1.960122 | 2.686351 | 0.299473 | 2.553502 | 2.852975 |
| 2001 | 0.669617 | 2.301999 | 2.971617 | 0.573427 | 1.998427 | 2.571854 |
| 2002 | 1.184713 | 2.018570 | 3.203283 | 0.616331 | 1.560101 | 2.176432 |
| 2003 | 1.343118 | 1.181111 | 2.524229 | 0.600667 | 1.434900 | 2.035567 |
| 2004 | 0.292522 | 0.736973 | 1.029495 | 0.040419 | 1.071419 | 1.111838 |
| 2005 | 0.075604 | 0.670730 | 0.746334 | 0.011236 | 0.560518 | 0.571754 |
| 2006 | 0.177885 | 1.027009 | 1.204894 | 0.050394 | 0.275797 | 0.326191 |
| 2007 | 0.057666 | 0.889676 | 0.947342 | 0.034575 | 1.534523 | 1.569099 |
| 2008 | 0.211871 | 1.421593 | 1.633464 | 0.024461 | 1.491847 | 1.516308 |
| 2009 | 0.262853 | 2.098253 | 2.361106 | 0.063468 | 1.317059 | 1.380527 |
| 2010 |  |  |  | 0.499986 | 1.687118 | 2.187104 |

Table 7: Values of $\lambda_{i}$ in GLM A (top) and values of $\gamma$ and $\lambda_{i}$ in GLM B with adult biomass (middle) and recruit biomass (bottom). Estimates significant at the $5 \%$ level are in bold, and estimates significant at the $15 \%$ level are in italics.

| Estimate year effect directly |  | Sardine catch |  |  | Anchovy catch |  |  | Sardine and Anchovy catch |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Estimate | s.e. | t pr. | Estimate | s.e. | t pr. | Estimate | s.e. | t pr. |
| Fledging success | $\begin{aligned} & \lambda_{\text {Dassen }} \\ & \lambda_{\text {Robben }} \end{aligned}$ | $\begin{aligned} & 0.254 \\ & 0.221 \\ & \hline \end{aligned}$ | $\begin{array}{r} 0.25 \\ 0.277 \\ \hline \end{array}$ | 0.417 0.509 | $\begin{aligned} & 0.436 \\ & 1.142 \\ & \hline \end{aligned}$ | $\begin{aligned} & 0.145 \\ & 0.586 \\ & \hline \end{aligned}$ | 0.095 0.191 | $\begin{aligned} & 0.361 \\ & 0.335 \\ & \hline \end{aligned}$ | 0.181 0.505 | 0.184 0.575 |
| Breeders per adult moulter |  | $\begin{array}{r} -0.16 \\ -0.006 \\ \hline \end{array}$ | $\begin{gathered} 0.115 \\ 0.0743 \end{gathered}$ | 0.198 0.938 | $\begin{gathered} 0.076 \\ -0.051 \end{gathered}$ | $\begin{aligned} & 0.154 \\ & 0.152 \\ & \hline \end{aligned}$ | 0.633 0.745 | $\begin{gathered} -0.011 \\ 0.002 \end{gathered}$ | 0.223 0.147 | 0.962 0.992 |
| Active and potential nests |  | $\begin{aligned} & 1.662 \\ & 1.006 \end{aligned}$ | $\begin{aligned} & 0.962 \\ & 0.559 \end{aligned}$ | $\begin{aligned} & 0.128 \\ & 0.115 \end{aligned}$ | $\begin{array}{r} -0.436 \\ \mathbf{1 . 6 9 8} \end{array}$ | $\begin{aligned} & 0.519 \\ & 0.491 \end{aligned}$ | 0.428 $\mathbf{0 . 0 1 1}$ | $\begin{aligned} & 0.302 \\ & \mathbf{1 . 2 9 9} \end{aligned}$ | $\begin{aligned} & 0.499 \\ & \mathbf{0 . 4 5 2} \end{aligned}$ | $\begin{aligned} & 0.565 \\ & \mathbf{0 . 0 2 4} \end{aligned}$ |
| November adult biomass |  |  |  |  |  |  |  |  |  |  |
| Fledging success | $\begin{aligned} & \gamma \\ & \lambda_{\text {Dassen }} \\ & \lambda_{\text {Robben }} \end{aligned}$ | $\begin{gathered} -0.083 \\ 0.145 \\ -0.0735 \\ \hline \end{gathered}$ | $\begin{gathered} 0.202 \\ 0.213 \\ 0.0783 \\ \hline \end{gathered}$ | $\begin{aligned} & 0.685 \\ & 0.504 \\ & 0.359 \\ & \hline \end{aligned}$ | $\begin{gathered} -0.245 \\ -0.02 \\ 0.11 \\ \hline \end{gathered}$ | $\begin{aligned} & 0.124 \\ & 0.122 \\ & 0.119 \\ & \hline \end{aligned}$ | $\begin{gathered} 0.061 \\ 0.87 \\ 0.364 \\ \hline \end{gathered}$ | $\begin{gathered} -0.1843 \\ 0.075 \\ 0.066 \\ \hline \end{gathered}$ | $\begin{gathered} 0.0954 \\ 0.174 \\ 0.151 \\ \hline \end{gathered}$ | $\begin{gathered} 0.068 \\ 0.67 \\ 0.667 \\ \hline \end{gathered}$ |
| Breeders per adult moulter | $\begin{aligned} & \gamma \\ & \lambda_{\text {Dassen }} \\ & \lambda_{\text {Robben }} \end{aligned}$ | $\begin{aligned} & 0.025 \\ & -\mathbf{0 . 2 5 4} \\ & 0.0152 \end{aligned}$ | $\begin{aligned} & 0.147 \\ & \mathbf{0 . 1 1 3} \\ & 0.072 \\ & \hline \end{aligned}$ | $\begin{aligned} & 0.868 \\ & \mathbf{0 . 0 3 3} \\ & 0.834 \\ & \hline \end{aligned}$ | $\begin{gathered} 0.0215 \\ 0.259 \\ 0.065 \\ \hline \end{gathered}$ | $\begin{aligned} & 0.089 \\ & 0.161 \\ & 0.123 \\ & \hline \end{aligned}$ | 0.811 0.12 0.598 | $\begin{aligned} & 0.015 \\ & 0.143 \\ & 0.073 \end{aligned}$ | $\begin{gathered} 0.0748 \\ 0.251 \\ 0.15 \\ \hline \end{gathered}$ | $\begin{gathered} 0.843 \\ 0.573 \\ 0.63 \\ \hline \end{gathered}$ |
| Active and potential nests | $\begin{array}{\|l\|} \hline \gamma \\ \lambda_{\text {Dassen }} \\ \lambda_{\text {Robben }} \\ \hline \end{array}$ | $\begin{gathered} 0.267 \\ \mathbf{0 . 6 8} \\ 0.23 \\ \hline \end{gathered}$ | $\begin{gathered} 0.556 \\ \mathbf{0 . 3 1} \\ 0.237 \\ \hline \end{gathered}$ | 0.637 <br> $\mathbf{0 . 0 4 4}$ <br> 0.346 <br> 0.137 | $\begin{aligned} & 0.164 \\ & 0.345 \\ & 0.662 \end{aligned}$ | $\begin{gathered} 0.414 \\ 0.78 \\ 0.742 \\ \hline \end{gathered}$ | 0.698 0.664 0.386 | $\begin{aligned} & 0.189 \\ & 0.999 \\ & 0.923 \\ & \hline \end{aligned}$ | 0.269 <br> 0.719 <br> 0.7 | $\begin{aligned} & 0.492 \\ & 0.184 \\ & 0.205 \\ & \hline \end{aligned}$ |
| Adult survival | $\begin{array}{\|l\|} \hline \gamma \\ \lambda_{\text {Dassen }} \\ \lambda_{\text {Robben }} \\ \hline \end{array}$ | $\begin{aligned} & 0.441 \\ & 0.366 \\ & 0.287 \\ & \hline \end{aligned}$ | $\begin{aligned} & 0.262 \\ & 0.184 \\ & 0.156 \\ & \hline \end{aligned}$ | $\begin{aligned} & 0.137 \\ & 0.087 \\ & 0.108 \\ & \hline \end{aligned}$ | $\begin{gathered} \mathbf{0 . 7 4} \\ 0.268 \\ -0.792 \\ \hline \end{gathered}$ | $\begin{gathered} 0.197 \\ 0.7 \\ 0.438 \\ \hline \end{gathered}$ | 0.007 0.713 0.113 | $\begin{gathered} \mathbf{0 . 5} \\ 0.889 \\ -0.305 \\ \hline \end{gathered}$ | 0.129 0.75 0.389 | $\mathbf{0 . 0 0 6}$ <br> 0.274 <br> 0.459 |
| May recruit biomass |  |  |  |  |  |  |  |  |  |  |
| Fledging success | $\begin{aligned} & \gamma \\ & \lambda_{\text {Dassen }} \\ & \lambda_{\text {Robben }} \end{aligned}$ | $\begin{array}{r} 0.246 \\ 0.117 \\ -0.127 \\ \hline \end{array}$ | $\begin{aligned} & 0.516 \\ & 0.198 \\ & 0.102 \\ & \hline \end{aligned}$ | $\begin{gathered} 0.639 \\ 0.561 \\ 0.23 \\ \hline \end{gathered}$ | $\begin{aligned} & 0.132 \\ & 0.012 \\ & 0.066 \end{aligned}$ | $\begin{gathered} 0.167 \\ 0.13 \\ 0.128 \\ \hline \end{gathered}$ | 0.439 0.927 0.611 | $\begin{array}{r} 0.068 \\ 0.073 \\ -0.036 \\ \hline \end{array}$ | 0.137 0.189 0.163 | 0.627 0.704 0.827 |
| Breeders per adult moulter | $\begin{array}{\|l\|} \hline \gamma \\ \lambda_{\text {Dassen }} \\ \lambda_{\text {Robben }} \end{array}$ | $\begin{aligned} & -0.226 \\ & -\mathbf{0 . 2 2 9} \\ & 0.0541 \end{aligned}$ | $\begin{gathered} 0.296 \\ \mathbf{0 . 1 1 1} \\ 0.0799 \\ \hline \end{gathered}$ | $\begin{gathered} 0.451 \\ \mathbf{0 . 0 5} \\ 0.505 \\ \hline \end{gathered}$ | $\begin{gathered} 0.0696 \\ 0.234 \\ 0.061 \\ \hline \end{gathered}$ | $\begin{array}{r} 0.0775 \\ 0.155 \\ 0.115 \\ \hline \end{array}$ | 0.377 0.144 0.602 | $\begin{gathered} 0.0459 \\ 0.122 \\ 0.065 \end{gathered}$ | 0.0691 0.243 0.138 | 0.513 0.621 0.643 |
| Active and potential nests | $\begin{aligned} & \gamma \\ & \lambda_{\text {Dassen }} \\ & \lambda_{\text {Robben }} \end{aligned}$ | $\begin{gathered} 1.18 \\ 0.565 \\ 0.101 \\ \hline \end{gathered}$ | $\begin{gathered} 1.19 \\ 0.328 \\ 0.276 \\ \hline \end{gathered}$ | 0.336 <br> 0.105 <br> 0.72 | $\begin{aligned} & \mathbf{0 . 8 6 2} \\ & 0.551 \\ & 0.676 \\ & \hline \end{aligned}$ | $\begin{aligned} & \mathbf{0 . 3 4 9} \\ & 0.672 \\ & 0.634 \\ & \hline \end{aligned}$ | $\mathbf{0 . 0 2 5}$ 0.424 0.302 | $\begin{aligned} & 0.707 \\ & 1.014 \\ & 0.881 \\ & \hline \end{aligned}$ | 0.241 <br> 0.582 <br> 0.567 | $\mathbf{0 . 0 1}$ <br> 0.101 <br> 0.14 |
| Adult survival | $\begin{aligned} & \gamma \\ & \lambda_{\text {Dassen }} \\ & \lambda_{\text {Robben }} \end{aligned}$ | $\begin{gathered} 3.39 \\ -0.53 \\ -0.42 \\ \hline \end{gathered}$ | $\begin{gathered} 2.81 \\ 0.833 \\ 0.683 \\ \hline \end{gathered}$ | 0.267 0.545 0.558 | 0.38 -0.27 -0.867 | 0.44 1.17 0.784 | 0.417 0.821 0.305 | 0.385 0.56 -0.11 | 0.328 1.23 0.696 | 0.279 0.664 0.879 |

Table 8: Tallies of positive and negative estimated GLM parameters.
a) Reproduction GLMs

|  | Sardine | Anchovy | Combined | Overall |
| :--- | :---: | :---: | :---: | :---: |
| All $\gamma$ | $4: 2$ | $5: 1$ | $5: 1$ | $14: 4$ |
| All $\lambda_{i}$ | $12: 6$ | $15: 3$ | $16: 2$ | $43: 11$ |
| $\lambda_{i}$ significant at $15 \%$ | $4: 2$ | $4: 0$ | $3: 0$ | $11: 2$ |
| $\lambda_{i}$ significant at $5 \%$ | $1: 2$ | $1: 0$ | $1: 0$ | $3: 2$ |

b) Survival GLMs

|  | Sardine | Anchovy | Combined | Overall |
| :--- | :---: | :---: | :---: | :---: |
| All $\gamma$ | $2: 0$ | $2: 0$ | $2: 0$ | $6: 0$ |
| All $\lambda_{i}$ | $2: 2$ | $1: 3$ | $2: 2$ | $5: 7$ |
| $\lambda_{i}$ significant at $15 \%$ | $2: 0$ | $0: 1$ | $0: 0$ | $2: 1$ |
| $\lambda_{i}$ significant at $5 \%$ | $0: 0$ | $0: 0$ | $0: 0$ | $0: 0$ |

c) All GLMs

|  | Sardine | Anchovy | Combined | Overall |
| :--- | :---: | :---: | :---: | :---: |
| All $\gamma$ | $6: 2$ | $7: 1$ | $7: 1$ | $20: 4$ |
| All $\lambda_{i}$ | $14: 8$ | $16: 6$ | $18: 4$ | $48: 18$ |
| $\lambda_{i}$ significant at $15 \%$ | $6: 2$ | $4: 1$ | $3: 0$ | $13: 3$ |
| $\lambda_{i}$ significant at $5 \%$ | $1: 2$ | $1: 0$ | $1: 0$ | $3: 2$ |

Table 9: Point estimates and approximate $95 \%$ confidence intervals for the changes in penguin population growth attributable to stopping fishing, as estimated by various GLMs.

|  | Sardine |  |  |  | Anchovy |  |  | Sardine and Anchovy |  |  |
| :--- | :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Estimate year <br> effect directly | $\Delta \mu$ | $-95 \%$ | $+95 \%$ | $\Delta \mu$ | $-95 \%$ | $+95 \%$ | $\Delta \mu$ | $-95 \%$ | $+95 \%$ |  |
| Fledging | Dassen | $-5.0 \%$ | $-14.7 \%$ | $4.7 \%$ | $-7.9 \%$ | $-13.8 \%$ | $-2.0 \%$ | $-6.8 \%$ | $-14.0 \%$ | $0.5 \%$ |
| success | Robben | $-6.6 \%$ | $-26.4 \%$ | $13.2 \%$ | $-22.7 \%$ | $-59.0 \%$ | $13.7 \%$ | $-9.5 \%$ | $-42.0 \%$ | $23.0 \%$ |
| Breeders | Dassen | $3.9 \%$ | $-0.9 \%$ | $8.6 \%$ | $-1.6 \%$ | $-7.9 \%$ | $4.6 \%$ | $0.2 \%$ | $-8.5 \%$ | $9.0 \%$ |
| per moulter | Robben | $0.2 \%$ | $-5.7 \%$ | $6.1 \%$ | $1.7 \%$ | $-9.8 \%$ | $13.3 \%$ | $-0.1 \%$ | $-11.3 \%$ | $11.1 \%$ |


| November adult biomass |  | Sardine |  |  | Anchovy |  |  | Sardine and Anchovy |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\Delta \mu$ | -95\% | +95\% | $\Delta \mu$ | -95\% | +95\% | $\Delta \mu$ | -95\% | +95\% |
| Fledging | Dassen | -3.0\% | -11.4\% | 5.4\% | 0.5\% | -4.6\% | 5.5\% | -1.6\% | -8.6\% | 5.4\% |
| success | Robben | 2.5\% | -3.6\% | 8.7\% | -3.5\% | -12.7\% | 5.7\% | -2.1\% | -13.6\% | 9.4\% |
| Breeders | Dassen | 6.5\% | 1.8\% | 11.1\% | -5.1\% | -11.6\% | 1.4\% | -3.0\% | -12.7\% | 6.7\% |
| per moulter | Robben | -0.5\% | -6.2\% | 5.2\% | -2.1\% | -11.6\% | 7.4\% | -2.3\% | -13.8\% | 9.1\% |
| Adult survival | Dassen | -8.7\% | -18.1\% | 0.7\% | -6.7\% | -34.9\% | 21.4\% | -16.8\% | -46.3\% | 12.7\% |
|  | Robben | -6.3\% | -13.5\% | 0.8\% | 30.5\% | 13.0\% | 48.1\% | 9.0\% | -6.9\% | 25.0\% |


| May recruit biomass |  | Sardine |  |  | Anchovy |  |  | Sardine and Anchovy |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\Delta \mu$ | -95\% | +95\% | $\Delta \mu$ | -95\% | +95\% | $\Delta \mu$ | -95\% | +95\% |
| Fledging success | Dassen | -2.5\% | -10.3\% | 5.4\% | -0.3\% | -5.6\% | 5.1\% | -1.6\% | -9.1\% | 6.0\% |
|  | Robben | 4.5\% | -3.4\% | 12.5\% | -2.1\% | -12.0\% | 7.7\% | 1.2\% | -11.1\% | 13.6\% |
| Breeders per moulter | Dassen | 5.7\% | 1.1\% | 10.3\% | -4.7\% | -10.9\% | 1.6\% | -2.6\% | -12.0\% | 6.9\% |
|  | Robben | -1.8\% | -8.0\% | 4.5\% | -2.0\% | -10.9\% | 6.9\% | -2.1\% | -12.7\% | 8.5\% |
| Adult survival | Dassen | 19.9\% | -11.7\% | 51.6\% | 8.8\% | -29.7\% | 47.4\% | -12.2\% | -51.8\% | 27.3\% |
|  | Robben | 13.2\% | -11.3\% | 37.7\% | 34.9\% | 7.9\% | 61.8\% | 2.9\% | -21.9\% | 27.8\% |



Figure 1: Plots of growth rate change projected for suspending fishing, with $95 \%$ confidence intervals, corresponding to the horizontal blocks in Table 9. In each case the points are, from left to right, Dassen Island (sardine, anchovy, combined) then Robben Island (sardine, anchovy, combined).


Figure 2: A repeat of the plots in Fig. 1, but at a larger scale.


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[^1]:    ${ }^{2}$ Shortage of time precluded evaluating these in terms of the t-distributions involved. Instead what would be the reasonable approximation of use of +-2 standard errors was effected.

