

Analyses of the Results from the Island Closure Feasibility Study for the Dassen/Robben and St Croix/Bird Island Pairs

W. M. L. Robinson, D. S. Butterworth and L. B. Furman

Marine Assessment and Resource Management Group, University of Cape Town

Abstract

The results from the Island Closure Feasibility Study are analysed using the GLMs as set out at the 2010 international stock assessment workshop. Estimates of residual variance for a random year effects GLM for the various penguin response variables are considered to be sufficiently precise to enable power analyses to be conducted to contribute to the evaluation of whether to transition to a full experimental closures programme, so that the feasibility study may be considered successfully concluded. For the Dassen and Robben Islands about 80% of the estimates of the fishing effect parameter λ are positive, with this same proportion maintained for those (about one sixth) of these estimates which are significant at the 5% level. Thus the preponderance of the evidence from these analyses is that the impact of fishing around these islands has been positive. The rather fewer instances available to analyse for the Eastern Cape colonies suggest a weakly positive effect at Bird Island, but a somewhat stronger negative effect at St Croix. The power analyses suggest that in cases for Dassen and Robben Islands where further data collection might render currently non-significant λ estimates significant at the 5% level within the next two decades, the likely period required for such further collection would typically be in the vicinity of five years. The advantage provided by continuing the closure programme itself seems however to be slight, as the natural variation over time in normal catches would be sufficient to provide the contrast to achieve such results with only typically two years' extension to those five years. For the two Eastern Cape islands, it seems that results which are statistically significant at the 5% level seem unlikely to be achieved in the foreseeable future – a result which may be a consequence of the relatively low levels of sardine catches typically taken close to those islands.

Historical background

Commencing in 2006 concerns were raised about rapid decreases in penguin numbers at colonies on the South African west and south coasts. A number of these colonies had been increasing through the 1990's, a period when abundances of two of their main sources of food, anchovy and sardine, had also been increasing. However after a boom around the turn of the century, sardine (though not anchovy) abundance dropped rapidly as a results of successive poor recruitments, and questions arose as to whether this was related to the penguin declines. Suggestions were made to close the neighbourhoods of at least some penguin breeding colonies to pelagic fishing to assist the penguin populations to recover. However it was unclear from existing data whether or not such actions would be likely to show much success, and debates arose around the impacts of different mechanisms possibly at work on the penguins: less fishing would mean higher fish abundance near colonies, but fishing also breaks up their shoals which are a defence mechanism against predation employed by small pelagic fish, conceivably rendering them easier for predators to catch.

In response, DAFF agreed in principle to conduct a programme of experimental closures to pelagic fishing of areas around penguin breeding colonies to determine whether or not such closures were advantageous to penguins. The initial component of the programme was a feasibility study to determine whether such an experiment could deliver a definitive result within a reasonable period (considered to be less than one to two decades). As illustrated in an initial analysis by Brandão and Butterworth (2007), the power analysis required to address this question required information on the variance in any relationship between measures of penguin reproductive success and fish abundance (which would be impacted by catches), and the primary purpose of this feasibility study was to estimate this variance to enable such power analyses to be conducted.

For reasons elaborated below, the feasibility study centred on two pairs of nearby breeding colonies: Dassen and Robben Islands off the west coast, and St Croix and Bird Islands off the south coast. To promote contrast for enhanced estimation capability, closures were planned to alternate for each pair, and commenced at Dassen Island in 2008 and a year later at St Croix Island.

The approach and intended method for analysing the results was discussed in some detail during the year end annual international stock assessment review meeting in 2010, where details of the design of this study were finalised and agreed (Parma *et al.*, 2010). DAFF subsequently agreed that this feasibility study would continue to 2014, with results to be reviewed at that time unless definitive conclusions had already emerged earlier.

Methods

A fundamental problem in interpreting the results from monitoring of measures (likely) related to penguin reproductive success is that two effects are confounded: if a measure shows improvement one year, is that, for example, because the forage fish biomass was larger that year as a result of good recruitment, or because fish catches were lower and so had less impact on what was available for penguins to eat? Although data on annual catches near islands are available, information on fish abundance comes from surveys covering a wide area, those abundance estimates have a relatively high variance, and this variance would be even higher if survey strata were sub-divided in an attempt to better measure fish abundance close to island colonies. One can either attempt to use such high variance information, or assume (as seems plausible) that nearby colonies experience rather similar (i.e. highly positively correlated) fish densities in any given year. However, either approach still requires the use of statistical estimation procedures to try to distinguish the otherwise confounded effects of naturally varying fish biomasses and the fish catches near each colony.

Basically two methods are applied in this document. First GLMs are used as a means to attempt to distinguish and thereby also to estimate the magnitude of the effect of fish catches around islands on the reproductive success of penguins breeding at those islands. Then a power analysis is conducted to ascertain how many years an experiment would need to continue to obtain a result for the magnitude of that effect which is significantly different from zero at the 5% level. The basis underlying the formulation of the specific GLM analysis method applied is detailed in Appendix A.

The GLMs

The basic GLM conducted for a penguin response variable F , for year y and island i , takes the form:

$$\ln(F_{y,i}) = \alpha_y + \beta_i + \lambda_i \frac{C_{y,i,p}}{\bar{C}_{i,p}} + \varepsilon_{y,i} \quad (1)$$

where

α_y is a year effect reflecting prevailing environmental conditions (assumed to be the same each year, random variation excepted, for both islands in a pair),

β_i is an island effect,

λ_i is a fishing effect,

$C_{y,i,p}$ is the catch taken in year y in the neighbourhood of island i of pelagic species p ,

$\bar{C}_{i,p}$ is the average catch taken over the years considered, and

$\varepsilon_{y,i}$ is an error term.

However, the large number of estimable α_y parameter values for this approach can result in few degrees of freedom remaining, so that in a variant of this approach α_y is treated as a random instead of as a fixed effect.

For the approach that makes use of abundances estimates from the DAFF acoustic surveys of pelagic fish abundance, the α_y term in equation (1) is replaced by one reflecting linear proportionality dependence on that abundance estimate, i.e.:

$$\ln(F_{y,i}) = \mu B y + \beta_i + \lambda_i \frac{C_{y,i,p}}{\bar{C}_{i,p}} + \varepsilon_{y,i} \quad (2)$$

where B indicates the survey biomass for the pertinent area surveyed¹ of the same species as considered for the catch (C), and is taken to be either the estimate from the spawner biomass survey of the preceding November (which measures the fish on which the penguins would feed before commencing breeding, and hence may relate to their pre-breeding condition), or the May recruitment survey for that same year (which relates to fish present during the penguin breeding season). This approach has the advantage of increasing the number of degrees of freedom available for the estimation, but this is at the expense of introducing further error into the relationship as a result of the differences between the survey estimates and the appropriate true underlying biomass values.

The Power Analysis

The power analysis methodology follows the basic approach that was first set out in Brandão and Butterworth (2007), and is described in detail in Appendix B. That Appendix also explains what effect sizes are considered and what future scenarios for open and closed areas around islands are investigated. Note that better power will be provided by longer series and lower residual variances.

Obviously power is not evaluated for cases where the estimate of the fishing effect λ is already significantly different from zero at the 5% level. Where this is not so, the probability of obtaining such a result with n additional years of data is calculated, with this n value being reported when this probability reaches 80% and when it reaches 95%, though calculations extend only to a maximum of 20 years into the future (consistent with the maximum period for which an experiment might be considered realistic).

Response Variables

Coetzee (2014) provides details of the penguin response variable series, which have different lengths, that have been agreed for consideration for both the Dassen/ Robben and St Croix/Bird pairs of islands, though these are available for fewer variables for the latter pair (see Table 1).

For each response variable, nine pelagic catch series have been considered for Robben and Dassen Islands, *viz.* sardine, anchovy, and the combined total taken within either a 10, 20 or 30 nm distance around the island concerned (see Coetzee, 2014, for an explanation of how this restriction is implemented for analysis purposes in terms of the 10x10 nm fishing blocks into which the whole region is divided for fishery reporting procedures). However for St Croix and Bird Islands, such catch series are considered for sardine only (i.e. three catch series in total for the same three distances as above) as catches of anchovy in those areas have been negligible.

¹ West or east of Cape Agulhas according as Western Cape or Eastern Cape colonies are under consideration.

Results and Discussion

Estimation of residual variances

A primary purpose of the feasibility study has been to determine whether variance of the residuals for equation (1) could be determined with sufficient precision to allow meaningful power analyses to be carried out. (This would then be to allow determination of whether it would be worthwhile to embark on some full-scale closure experiment.)

Table 1 shows a sample of the results obtained for the random year effects variant of equation (1), showing both the estimates of the standard deviations of these residuals σ_ϵ and the associated upper 95% confidence limit. The values of these estimates do differ amongst the response variables for the examples shown, but importantly the upper confidence limits are not too much bigger than the estimates themselves.

Estimation of fishing effects

Table 2 lists estimates of the fishing effect λ from applications of the GLM equations (1) or (2), with the associated standard errors for each island for the various combinations of estimation models, response variables, survey biomass results and catch series detailed above; these results are also plotted in Figures 1-8 for the fixed and random effects year factor implementations of equation (1). Values significantly different from zero at the 15% and 5% level are indicated in Table 2, where this has been determined on the basis of t -statistics, except for the random year effects model for which z -statistics were used under the assumption of distribution normality.

A potential problem arises in cases where there is a high correlation between the biomass and the catch series used, which confounds the ability of the estimator to distinguish the effects of biomass and of catch on the response variable, rendering unstable results with high variance likely. Robinson (2013) carefully reviewed the correlation coefficients r between the biomass and catch time-series used in each model which he considered (which include the great majority of those analysed here). That investigation revealed that the average correlation was $r \sim 0.3$, which is reasonably small. (Compare the plots of survey biomass against catches for the full time-series in Robinson's figures 2.4-2.6.) Severe distortion of parameter estimation tends to occur only when $|r| > 0.7$ (Dormann *et al.* 2013), and this threshold was breached in only a very few cases. In these cases, the variance-inflation factor (VIF, whose square root is the factor by which the standard error for the parameter in question is increased because of collinearity between predictor variables) was calculated. Results never exceeded 10, which is often used as a threshold for indicating severe collinearity, although even higher VIFs are often considered acceptable (O'Brien 2007). Nevertheless, given these concerns, cases in Table 2 for which $|r|$ exceeds 0.7 have been indicated.

The broad pattern of the Table 2 results for the fishing effect parameters for Dassen and Robben Islands, taking both direction and significance levels into account, is of strongly positive values for active nest proportion and for foraging trip duration (though there only for Dassen Island), a mixture though favouring positive values for chick growth, and a direction that varies depending on the prey species for fledging success. For Bird and St Croix Islands, effects are generally weakly positive for the former, but somewhat more strongly negative for the latter.

As a further aid in assimilating these results, Table 3 presents tallies of the positive and negative estimates of λ obtained, where this is done separately for the Western Cape and for the Eastern Cape penguin colonies considered. These tallies also include values for estimates significant at the 15% and 5% levels, as well as showing the impact of omitting cases where $|r|$ exceeds 0.7 from the tallies.

For the Western Cape colonies 318 of the total of 414 estimates of the fishing effect parameter λ , i.e. about 80%, are positive. For estimates that are significant at the 5% level, this proportion is about the same, though a much greater fraction (about one third) of the estimates for the random year factor effects models are significant at this level compared to only about 10% for the other three model variants. The proportion positive remains about the same if some 20% of cases for which $|r|$ exceeds 0.7 are excluded from these tallies.

For the Eastern Cape colonies there are almost equal proportions of positive and negative estimates of λ , though the positive proportion increases to about 60% when cases with $|r| > 0.7$ are omitted.

Power Analyses

Results for the power analysis for Dassen and for Robben Island to indicate the time required to achieve a 95% probability of a result significant at the 5% level for the estimate of the fishing effect parameter λ are shown in Table 4, with those for St Croix and Bird Islands in Table 5. For a lower probability of 80%, the shorter periods then needed are reported in Tables 6 and 7 respectively.

For the Western Cape colonies, these results are of little “interest” for chick condition, active nest proportion and foraging trip duration, as attainment of estimates significant at the 5% level is generally forecast to require over 20 years further data collection except in the few cases where such significance has already been achieved. In contrast, for the active nest proportion, fledging success and foraging path length response variables, in cases where such significance is achievable for catch series within 10 nm of the islands, a further period of typically six years data collection is required, shrinking to four if an 80% rather than a 95% probability of achieving this is the basis used for determination. If the alternating closures are not put in place, and instead catches continue as normal, typically two further years are required to obtain estimates that are significantly different from zero at the 5% level. (These “typical” summary numbers reflect averages taken across the pertinent cases.)

In contrast, little chance is indicated of achieving statistically significant results at the 5% level within the next 20 years for the Eastern Cape colonies. This may seem surprising given that a number of the current estimates for St Croix Island in Table 2 reflect statistical significance at the 15% level. The reason for this result may relate to the relatively small values of the fishing effect parameter λ that are estimated for the Eastern Cape colonies. About 50% of these have magnitudes below the “biologically meaningful” default effect size of 0.1 (see Appendix B), compared with only some 20% for the same response variables for the Western Cape colonies (see Table 2). It must be remembered though that values for λ are scaled to past average catches, and that past annual sardine catches near to the Eastern Cape islands have been typically somewhat smaller than for the Western Cape islands (see Figure 9). Hence, in terms of tonnage, cessation of fishing around the former colonies has a lesser impact than cessation around the latter.

Conclusions

The fact that the upper confidence limits for the estimates of residual variance are not too much bigger than the estimates themselves suggests that estimates with adequate precision have been obtained, and the feasibility study can be concluded (with a decision then to be made on whether to move on to full scale closure experiments).

For the Dassen and Robben Islands about 80% of the estimates of the fishing effect parameter λ are positive, with this same proportion maintained for those of these estimates which are significant at the 5% level. Thus the preponderance of the evidence from this analysis is that the impact of fishing around these islands is positive. The rather fewer instances available to analyse for the Eastern Cape colonies suggest a weakly positive effect at Bird Island, but a somewhat stronger negative effect at St

Croix. While these results may seem surprising to some, it must be remembered that a number of mechanisms with effects in different directions may well be at work, that their net result may differ in different locations, and that this net effect can only be determined by empirical analyses such as those developed here (see Appendix B).

The power analyses suggest that in cases for Dassen and Robben Islands where further data collection might render currently non-significant λ estimates significant at the 5% level within the next two decades, the likely period required for such further collection would typically be in the vicinity of five years. The advantage provided by continuing the closure programme itself seems however to be slight, as the natural variation over time in normal catches would be sufficient to provide the contrast to achieve such results with only typically two years' extension to those five years. For the two Eastern Cape islands, it seems that results which are statistically significant at the 5% level are unlikely to be achieved in the foreseeable future – a result which may be a consequence of the relatively low levels of sardine catches typically taken close to those islands.

Further work

As advised by Coetzee (2014), amended and slightly extended data for penguin foraging path length and duration response variables at various of the islands have only very recently become available. It is intended to analyse these data using the same methods as above to ascertain whether they result in any qualitative changes to the conclusions evident above from the existing analyses for those variables.

The power analyses conducted for this document used a fixed year effects GLM model to estimate parameters from the pseudo-data generated for projections into the future. If the Panel so request, it might be possible in the time before the December workshop to repeat these analyses using instead the random year effects model as the estimator in this process.

References

- Brandão A and 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. Unpublished report, Marine and Coastal Management, South Africa. Report No. EAFWG/OCT2007/STG/04.
- Butterworth DS. 1989. The Benguela Ecology Programme: successful and appropriate? *S. Afr. J. Sci.* 85: 633-643.
- Clark CW. 1976. *Mathematical bioeconomics*. New York: John Wiley & Sons. 352 pp.
- Coetzee JC. 2014. The current set of available data for evaluation of the Island Closure Feasibility study. Document MARAM/IWC/DEC14/Peng/C1: 1-15.
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carr_e G, Marquez JRG, Gruber B, Lafourcade B, Leitao PJ, Munkemuller T, McClean C, Osborne PE, Reineking B, Schroder B, Skidmore AK, Zurell D and Lautenbach S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36: 27-46.
- O'Brien RM. 2007. A caution regarding rules of thumb for variance inflation factors. *Quality & Quantity*, 41: 673-690.

Parma A, Punt AR and Stefansson G. 2010 International Review Panel report of the 2010 International Fisheries Stock Assessment Workshop, 29 November – 3 December. Document MARAM/IWS/DEC10/REP/1: 1-14.

Robinson WML. 2013. Modelling the impact of the South African small pelagic fishery on African penguin dynamics. PhD thesis, University of Cape Town. xiv + 207 pp.

Table 1: Residual standard error σ_ε and upper 95% confidence limits $\sigma_{\varepsilon,+95}$ (estimated using a likelihood profile approach) for each penguin response series available for assessing the power of the island closure experiment are listed for the random year effects model. Note that these estimates are unbiased through use of REML. The number of past data points n and the number of model parameters estimated p are indicated for the model. Results are given for the case of total catch within 30 nmi for the Western Cape and sardine catch within 30 nmi for the Eastern Cape.

(a) Dassen and Robben islands

Penguin response	n	p	σ_ε	$\sigma_{\varepsilon,+95}$
Chick condition	11	5	0.215	0.335
Active nest proportion	27	5	0.405	0.533
Fledging success	32	6	0.084	0.109
Chick growth	14	5	0.051	0.075
Foraging path length	11	5	0.042	0.066
Foraging trip duration	11	5	0.171	0.266

(b) St Croix and Bird islands

Penguin response	n	p	σ_ε	$\sigma_{\varepsilon,+95}$
Foraging path length	11	5	0.086	0.134
Foraging trip duration	11	5	0.099	0.154

Table 2: Fishing effect parameters λ with associated standard errors for (i) fixed year effects, (ii) random year effects, (iii) year effects given by spawner biomass, and (iv) year effects given by recruit biomass. Values significantly different from zero at the 15% and 5% levels are indicated by one and two asterisks respectively. Statistical significance is based on a normal approximation for the random effects model and a two-sided t -test for the other models. Cases where the correlation between the catch and the (recruit or spawning) biomass exceeds $r = 0.7$ are indicated by a †. Results are left blank in cases where there are no degrees of freedom.

(a) Dassen Island

Penguin response	Fish	Area	λ				s.e.			
			(i)	(ii)	(iii)	(iv)	(i)	(ii)	(iii)	(iv)
Chick condition	Sardine	10 nmi	0.10	-0.03	-0.02	-0.01	0.25	0.18	0.20	0.22
		20 nmi	0.29	0.09	0.01	0.05	0.33	0.24	0.26	0.28
		30 nmi	0.42	0.20	0.04	0.07	0.30	0.19	0.23	0.25
	Anchovy	10 nmi	-1.00 *	-0.08	0.10	0.04	0.40	0.23	0.29	0.24
		20 nmi	-0.37	-0.06	0.09	0.07	0.27	0.26	0.30	0.28
		30 nmi	-0.98	0.11	0.14	0.10	1.02	0.31	0.34	0.34
	Total	10 nmi	-1.11	-0.06	0.14	0.01	0.65	0.24	0.32	0.25
		20 nmi	-0.35	0.03	0.13	0.07	0.35	0.31	0.36	0.33
		30 nmi	-0.19	0.18	0.19	0.18	1.23	0.40	0.43	0.44
Active nest proportion	Sardine	10 nmi	0.96 *	0.54**	0.29	0.33	0.58	0.27	0.31	0.32
		20 nmi	1.32	0.78**	0.66 **	0.72**	1.00	0.27	0.31	0.31
		30 nmi	0.81	0.85**	0.79 **	0.92**	1.13	0.29	0.34	0.37
	Anchovy	10 nmi	0.14	0.15	0.06	0.29	0.37	0.35	0.60	0.51
		20 nmi	0.04	0.18	0.79	0.77	0.42	0.41	0.75	0.65
		30 nmi	0.46	0.53	0.96	0.73	0.88	0.79	1.12	0.98
	Total	10 nmi	0.25	0.31	0.31	0.48	0.36	0.35	0.60	0.51
		20 nmi	0.50	0.87**	1.44 **	1.33**	0.47	0.43	0.65	0.56
		30 nmi	1.04	1.68**	2.07 **	1.75**	0.90	0.67	0.81	0.74
Fledging success	Sardine	10 nmi	0.30**	0.07	0.10 †	0.09	0.09	0.11	0.14	0.13
		20 nmi	0.23	0.09	0.13 †	0.12	0.17	0.12	0.16	0.14
		30 nmi	0.48	0.04	0.19 †	0.16	0.45	0.15	0.20	0.17
	Anchovy	10 nmi	0.17 *	0.14**	-0.03	-0.03	0.09	0.08	0.12	0.14
		20 nmi	0.15	0.12 *	-0.01	-0.01	0.10	0.10	0.14	0.16
		30 nmi	0.37**	0.17 *	0.02	-0.02	0.14	0.11	0.14	0.17
	Total	10 nmi	0.24 *	0.22**	0.04	0.01	0.12	0.10	0.15	0.17
		20 nmi	0.24	0.20 *	0.09	0.08	0.15	0.13	0.18	0.20
		30 nmi	0.51 *	0.21 *	0.17	0.14	0.25	0.19	0.24	0.27
Chick growth	Sardine	10 nmi	-	0.11**	0.08	0.12**	-	0.06	0.06	0.05
		20 nmi	-	0.15**	0.11 †	0.16**	-	0.06	0.08	0.05
		30 nmi	-	0.20**	0.23**†	0.19**	-	0.06	0.10	0.06
	Anchovy	10 nmi	-	-0.03	-0.01	-0.03	-	0.07	0.07	0.07
		20 nmi	-	-0.18**	-0.11	-0.12	-	0.07	0.10	0.09
		30 nmi	-	-0.17**	-0.15 *	-0.14 *	-	0.06	0.08	0.07
	Total	10 nmi	-	0.03	0.03	0.02	-	0.10	0.11	0.10
		20 nmi	-	0.02	0.07	0.02	-	0.16	0.17	0.18
		30 nmi	-	-0.22 *	-0.12	-0.15	-	0.20	0.22	0.22
Foraging path length	Sardine	10 nmi	0.01	0.02	-0.10	0.26 †	0.05	0.05	0.11	0.22
		20 nmi	0.18	0.15 *	-0.13	0.19 †	0.21	0.14	0.13	0.25
		30 nmi	0.29	0.24**	-0.13	0.22 †	0.15	0.12	0.13	0.26
	Anchovy	10 nmi	0.14	0.13	0.20	0.24	0.17	0.16	0.44	0.43
		20 nmi	-0.29	-0.21	0.75	0.74	0.20	0.20	0.49	0.50
		30 nmi	0.14	0.26	0.44	0.42	0.64	0.42	0.52	0.58
	Total	10 nmi	0.11	0.11 *	0.11	0.25	0.08	0.08	0.38	0.39
		20 nmi	0.07	0.12	0.47	0.65	0.19	0.18	0.47	0.49
		30 nmi	0.47	0.44 *	0.28	0.48	0.53	0.35	0.44	0.49
Foraging trip duration	Sardine	10 nmi	-0.12	0.15**	0.08	0.16 †	0.21	0.09	0.10	0.15
		20 nmi	0.70	0.18**	0.10	0.19 †	0.86	0.11	0.13	0.16
		30 nmi	0.13	0.18 *	0.10	0.19 †	0.99	0.11	0.13	0.17
	Anchovy	10 nmi	0.33	0.53**	0.56 **	0.57**	0.36	0.20	0.21	0.21
		20 nmi	-0.69	0.65**	0.65 *	0.67 *	0.36	0.29	0.31	0.32
		30 nmi	0.38	0.13	0.18	0.21	1.25	0.34	0.37	0.41
	Total	10 nmi	0.37	0.53**	0.52 **	0.54**	0.24	0.16	0.19	0.18
		20 nmi	0.47	0.65**	0.64 *	0.70**	0.47	0.23	0.27	0.26
		30 nmi	1.12	0.38 *	0.33	0.44	1.48	0.26	0.30	0.32

Table 2: Continued.

(b) Robben Island

Penguin response	Fish	Area	λ				s.e.			
			(i)	(ii)	(iii)	(iv)	(i)	(ii)	(iii)	(iv)
Chick condition	Sardine	10 nmi	-0.11	0.16	0.17 †	0.18	0.33	0.17	0.26	0.20
		20 nmi	0.10	0.20	0.20 †	0.28	0.46	0.27	0.40	0.34
		30 nmi	0.47	0.34 *	0.38 †	0.36	0.57	0.22	0.29	0.24
	Anchovy	10 nmi	0.56	-0.10	-0.21 †	-0.17	0.30	0.18	0.24	0.19
		20 nmi	-0.06	-0.09	-0.11 †	-0.16	0.23	0.22	0.29	0.27
		30 nmi	-0.65	0.15	0.19	0.13	0.90	0.26	0.31	0.31
	Total	10 nmi	0.63	-0.11	-0.23 †	-0.14	0.48	0.18	0.25	0.19
		20 nmi	-0.05	-0.08	-0.13 †	-0.12	0.28	0.24	0.32	0.28
		30 nmi	0.07	0.27	0.31	0.26	0.97	0.31	0.36	0.36
Active nest proportion	Sardine	10 nmi	0.71 *	0.41**	0.16	0.17	0.35	0.17	0.19	0.20
		20 nmi	0.81	0.44**	0.25	0.28 †	0.55	0.18	0.22	0.25
		30 nmi	0.66	0.57**	0.38	0.49 †	0.83	0.24	0.29	0.33
	Anchovy	10 nmi	1.04**	0.98**	0.69	0.73 *	0.31	0.29	0.50	0.42
		20 nmi	1.45**	1.39**	1.10 *	0.94 *	0.33	0.32	0.60	0.52
		30 nmi	1.49**	1.31**	0.75	0.64	0.62	0.56	0.80	0.70
	Total	10 nmi	1.07**	1.02**	0.73 *	0.84**	0.28	0.27	0.48	0.40
		20 nmi	1.40**	1.40**	1.26**	1.13**	0.35	0.34	0.54	0.47
		30 nmi	1.91**	1.98**	1.39 *	1.20 *	0.74	0.59	0.74	0.67
Fledging success	Sardine	10 nmi	0.59**	-0.14**	-0.14**	-0.15**	0.15	0.04	0.05	0.05
		20 nmi	0.27	-0.17**	-0.18**	-0.22**	0.20	0.06	0.07	0.08
		30 nmi	0.30	-0.16**	-0.15 *	-0.18*†	0.33	0.07	0.09	0.09
	Anchovy	10 nmi	-0.11	-0.08 *	-0.03	-0.07	0.09	0.07	0.09	0.10
		20 nmi	0.03	0.01	0.03	-0.02	0.12	0.09	0.11	0.13
		30 nmi	0.37 *	0.14 *	0.08	0.07	0.19	0.13	0.13	0.15
	Total	10 nmi	-0.12	-0.13**	-0.09	-0.14	0.10	0.08	0.09	0.10
		20 nmi	0.04	-0.10	-0.08	-0.19	0.14	0.11	0.13	0.14
		30 nmi	0.36	-0.07	-0.04	-0.18	0.26	0.16	0.17	0.19
Chick growth	Sardine	10 nmi	-	0.17**	0.07 †	0.18 *	-	0.09	0.14	0.08
		20 nmi	-	0.26**	0.06 †	0.27 *	-	0.15	0.31	0.14
		30 nmi	-	0.22**	0.32 †	0.23**	-	0.10	0.26	0.09
	Anchovy	10 nmi	-	0.04	0.06 †	0.06 †	-	0.14	0.16	0.16
		20 nmi	-	0.06	0.04	0.10 †	-	0.09	0.17	0.17
		30 nmi	-	-0.04	0.00	0.05 †	-	0.12	0.16	0.16
	Total	10 nmi	-	0.01	-0.01	0.04 †	-	0.14	0.16	0.16
		20 nmi	-	0.06	0.02	0.08 †	-	0.16	0.19	0.20
		30 nmi	-	0.01	0.06	0.13 †	-	0.18	0.23	0.24
Foraging path length	Sardine	10 nmi	-0.12	-0.11 *	-0.26 †	0.39 †	0.08	0.07	0.17	0.41
		20 nmi	0.08	0.05	-0.20 †	0.22 †	0.21	0.14	0.15	0.26
		30 nmi	0.21	0.15 *	-0.23 †	0.26 †	0.16	0.13	0.16	0.29
	Anchovy	10 nmi	-0.13	-0.12 *	0.07	0.04	0.11	0.10	0.29	0.30
		20 nmi	-0.22	-0.17**	0.19	0.21	0.10	0.10	0.27	0.26
		30 nmi	0.13	0.24	0.38	0.37	0.60	0.40	0.49	0.58
	Total	10 nmi	-0.14	-0.13**	-0.00	0.11	0.07	0.07	0.33	0.36
		20 nmi	-0.13	-0.09	0.16	0.32	0.15	0.15	0.39	0.43
		30 nmi	0.32	0.30	0.35	0.58	0.57	0.38	0.49	0.56
Foraging trip duration	Sardine	10 nmi	-0.41	0.03	-0.09 †	0.03 †	0.34	0.14	0.17	0.26
		20 nmi	0.60	0.10	0.00 †	0.12 †	0.88	0.12	0.15	0.16
		30 nmi	0.01	0.10	-0.01 †	0.13 †	1.11	0.13	0.16	0.18
	Anchovy	10 nmi	0.06	0.08	0.08	0.07	0.24	0.13	0.14	0.15
		20 nmi	-0.53 *	0.15	0.14	0.16	0.18	0.15	0.17	0.17
		30 nmi	0.69	0.40 *	0.34	0.39	1.18	0.33	0.35	0.41
	Total	10 nmi	0.09	0.12	0.10	0.11	0.20	0.14	0.16	0.16
		20 nmi	0.33	0.23 *	0.22	0.29	0.39	0.19	0.22	0.23
		30 nmi	1.22	0.43 *	0.37	0.50	1.60	0.29	0.33	0.36

Table 2: Continued.

(c) Bird Island

Penguin response	Fish	Area	λ				s.e.			
			(i)	(ii)	(iii)	(iv)	(i)	(ii)	(iii)	(iv)
Foraging path length	Sardine	10 nmi	0.03	0.04	0.04	0.04	0.14	0.07	0.06	0.08
		20 nmi	0.21	0.08	0.06	0.08	0.19	0.09	0.08	0.10
		30 nmi	0.09	0.07	0.07	0.10	0.16	0.10	0.09	0.13
Foraging trip duration	Sardine	10 nmi	-0.05	0.02	0.02	-0.01	0.16	0.06	0.07	0.06
		20 nmi	0.24	0.04	0.04	0.03	0.20	0.07	0.08	0.07
		30 nmi	0.04	0.04	0.05	0.04	0.17	0.08	0.09	0.08

(d) St Croix Island

Penguin response	Fish	Area	λ				s.e.			
			(i)	(ii)	(iii)	(iv)	(i)	(ii)	(iii)	(iv)
Foraging path length	Sardine	10 nmi	-0.02	-0.06*	-0.01†	-0.08	0.07	0.05	0.06	0.05
		20 nmi	-0.09	-0.13*	-0.04†	-0.16	0.12	0.09	0.11	0.10
		30 nmi	-0.22	-0.26	0.04	-0.28	0.44	0.34	0.36	0.48
Foraging trip duration	Sardine	10 nmi	-0.02	-0.03	-0.01†	-0.04	0.08	0.04	0.06	0.04
		20 nmi	-0.16	-0.09*	-0.11†	-0.08	0.13	0.07	0.10	0.07
		30 nmi	-0.51	-0.39*	-0.33	-0.26	0.45	0.28	0.34	0.29

Table 3: Tallies of positive and negative values of λ , those significantly different from zero at the 15% level, and those significantly different from zero at the 5% level. "Both no †" tallies omit instances where the catch-biomass correlation exceeds $r = 0.7$.

(a) Western Cape

		Fixed year effects			Random year effects			Spawner Biomass			Recruit Biomass		
		all	15%	5%	all	15%	5%	all	15%	5%	all	15%	5%
Chick condition	Dassen	3:6	0:1	0:0	5:4	0:0	0:0	8:1	0:0	0:0	8:1	0:0	0:0
	Robben	5:4	0:0	0:0	5:4	1:0	0:0	5:4	0:0	0:0	5:4	0:0	0:0
Active nest proportion	Dassen	9:0	1:0	0:0	9:0	5:0	5:0	9:0	4:0	4:0	9:0	4:0	4:0
	Robben	9:0	7:0	6:0	9:0	9:0	9:0	9:0	4:0	1:0	9:0	5:0	2:0
Fledging success	Dassen	9:0	5:0	2:0	9:0	6:0	2:0	7:2	0:0	0:0	6:3	0:0	0:0
	Robben	7:2	2:0	1:0	2:7	1:5	0:4	2:7	0:3	0:2	1:8	0:3	0:2
Chick growth	Dassen				5:4	3:3	3:2	5:4	1:1	1:0	5:4	3:1	3:0
	Robben				8:1	3:0	3:0	8:1	0:0	0:0	9:0	3:0	1:0
Foraging path length	Dassen	8:1	0:0	0:0	8:1	4:0	1:0	6:3	0:0	0:0	9:0	0:0	0:0
	Robben	4:5	0:0	0:0	4:5	1:4	0:2	5:4	0:0	0:0	9:0	0:0	0:0
Foraging trip duration	Dassen	7:2	0:0	0:0	9:0	8:0	6:0	9:0	4:0	2:0	9:0	4:0	3:0
	Robben	7:2	0:1	0:0	9:0	3:0	0:0	7:2	0:0	0:0	9:0	0:0	0:0
Total	Dassen	36:9	6:1	2:0	45:9	26:3	17:2	44:10	9:1	7:0	46:8	11:1	10:0
	Robben	32:13	9:1	7:0	37:17	18:9	12:6	36:18	4:3	1:2	42:12	8:3	3:2
	Both Both no †	68:22	15:2	9:0	82:26	44:12	29:8	80:28	13:4	8:2	88:20	19:4	13:2
		67:19	12:4	7:2	68:19	19:3	13:2						

(b) Eastern Cape

		Fixed year effects			Random year effects			Spawner Biomass			Recruit Biomass		
		all	15%	5%	all	15%	5%	all	15%	5%	all	15%	5%
Foraging path length	Bird	3:0	0:0	0:0	3:0	0:0	0:0	3:0	0:0	0:0	3:0	0:0	0:0
	St Croix	0:3	0:0	0:0	0:3	0:2	0:0	1:2	0:0	0:0	0:3	0:0	0:0
Foraging trip duration	Bird	2:1	0:0	0:0	3:0	0:0	0:0	3:0	0:0	0:0	2:1	0:0	0:0
	St Croix	0:3	0:0	0:0	0:3	0:2	0:0	0:3	0:0	0:0	0:3	0:0	0:0
Total	Bird	5:1	0:0	0:0	6:0	0:0	0:0	6:0	0:0	0:0	5:1	0:0	0:0
	St Croix	0:6	0:0	0:0	0:6	0:4	0:0	1:5	0:0	0:0	0:6	0:0	0:0
	Both Both no †	5:7	0:0	0:0	6:6	0:4	0:0	7:5	0:0	0:0	5:7	0:0	0:0
		7:1	0:0	0:0	5:7	0:0	0:0						

Table 4: The number of additional years' data required to detect a fishing effect significant at the 5% level with **95%** probability is given for each of Dassen and Robben islands, where the true values of λ are assumed to be the random effects model-estimates. However, if a model-estimated λ value is small (i.e. $|\lambda| < 0.1$) then $\lambda = \pm 0.1$ is assumed instead for the effect size, where the sign is chosen according to the sign of the model-estimate for λ . A value of 0 indicates that the existing estimate of λ is already significant at the 5% level. C/O indicates future alternating periods of three years of the area being closed and three of it being open to fishing; O indicates the area is always open in the future.

Response	Fish	Area	Dassen		Robben		
			C/O	O	C/O	O	
Chick condition	Sardine	10 nmi	> 20	> 20	> 20	> 20	
		20 nmi	-	> 20	-	> 20	
		30 nmi	-	> 20	-	15	
	Anchovy	10 nmi	> 20	> 20	> 20	> 20	
		20 nmi	-	> 20	-	> 20	
		30 nmi	-	> 20	-	> 20	
	Total	10 nmi	> 20	> 20	> 20	> 20	
		20 nmi	-	> 20	-	> 20	
		30 nmi	-	> 20	-	> 20	
	Active nest proportion	Sardine	10 nmi	0	0	0	0
			20 nmi	-	0	-	0
			30 nmi	-	0	-	0
Anchovy		10 nmi	> 20	> 20	0	0	
		20 nmi	-	> 20	-	0	
		30 nmi	-	> 20	-	0	
Total		10 nmi	> 20	> 20	0	0	
		20 nmi	-	0	-	0	
		30 nmi	-	0	-	0	
Fledging success		Sardine	10 nmi	> 20	> 20	0	0
			20 nmi	-	> 20	-	0
			30 nmi	-	> 20	-	0
	Anchovy	10 nmi	0	0	12	16	
		20 nmi	-	17	-	> 20	
		30 nmi	-	5	-	18	
	Total	10 nmi	0	0	0	0	
		20 nmi	-	9	-	> 20	
		30 nmi	-	> 20	-	> 20	
	Chick growth	Sardine	10 nmi	0	0	0	0
			20 nmi	-	0	-	0
			30 nmi	-	0	-	0
Anchovy		10 nmi	1	> 20	1	> 20	
		20 nmi	-	0	-	12	
		30 nmi	-	0	-	> 20	
Total		10 nmi	1	> 20	1	> 20	
		20 nmi	-	> 20	-	> 20	
		30 nmi	-	> 20	-	> 20	
Foraging path length		Sardine	10 nmi	13	13	9	8
			20 nmi	-	5	-	12
			30 nmi	-	0	-	5
	Anchovy	10 nmi	10	17	7	6	
		20 nmi	-	9	-	0	
		30 nmi	-	16	-	15	
	Total	10 nmi	6	8	0	0	
		20 nmi	-	> 20	-	13	
		30 nmi	-	4	-	6	
	Foraging trip duration	Sardine	10 nmi	0	0	> 20	> 20
			20 nmi	-	0	-	> 20
			30 nmi	-	20	-	> 20
Anchovy		10 nmi	0	0	> 20	> 20	
		20 nmi	-	0	-	> 20	
		30 nmi	-	> 20	-	19	
Total		10 nmi	0	0	> 20	> 20	
		20 nmi	-	0	-	> 20	
		30 nmi	-	> 20	-	20	

Table 5: The number of additional years' data required to detect a fishing effect significant at the 5% level with **95%** probability is given for each of Bird and St Croix islands, where the true values of λ are assumed to be the random effects model-estimates. However, if a model-estimated λ value is small (i.e. $|\lambda| < 0.1$) then $\lambda = \pm 0.1$ is assumed instead for the effect size, where the sign is chosen according to the sign of the model-estimate for λ . A value of 0 indicates that the existing estimate of λ is already significant at the 5% level. C/O indicates future alternating periods of three years of the area being closed and three of it being open to fishing; O indicates the area is always open in the future.

Response	Fish	Area	Bird		StCroix	
			C/O	O	C/O	O
Foraging path length	Sardine	10 nmi	> 20	> 20	> 20	> 20
		20 nmi	-	> 20	-	> 20
		30 nmi	-	> 20	-	> 20
Foraging trip duration	Sardine	10 nmi	> 20	> 20	> 20	> 20
		20 nmi	-	> 20	-	> 20
		30 nmi	-	> 20	-	> 20

Table 6: The number of additional years' data required to detect a fishing effect significant at the 5% level with **80%** probability is given for each of Dassen and Robben islands, where the true values of λ are assumed to be the random effects model-estimates. However, if a model-estimated λ value is small (i.e. $|\lambda| < 0.1$) then $\lambda = \pm 0.1$ is assumed instead for the effect size, where the sign is chosen according to the sign of the model-estimate for λ . A value of 0 indicates that the existing estimate of λ is already significant at the 5% level. C/O indicates future alternating periods of three years of the area being closed and three of it being open to fishing; O indicates the area is always open in the future.

Response	Fish	Area	Dassen		Robben		
			C/O	O	C/O	O	
Chick condition	Sardine	10 nmi	> 20	> 20	> 20	> 20	
		20 nmi	-	> 20	-	> 20	
		30 nmi	-	12	-	10	
	Anchovy	10 nmi	> 20	> 20	> 20	> 20	
		20 nmi	-	> 20	-	> 20	
		30 nmi	-	> 20	-	> 20	
	Total	10 nmi	> 20	> 20	> 20	> 20	
		20 nmi	-	> 20	-	> 20	
		30 nmi	-	> 20	-	> 20	
	Active nest proportion	Sardine	10 nmi	0	0	0	0
			20 nmi	-	0	-	0
			30 nmi	-	0	-	0
Anchovy		10 nmi	> 20	> 20	0	0	
		20 nmi	-	> 20	-	0	
		30 nmi	-	> 20	-	0	
Total		10 nmi	> 20	> 20	0	0	
		20 nmi	-	0	-	0	
		30 nmi	-	0	-	0	
Fledging success		Sardine	10 nmi	> 20	> 20	0	0
			20 nmi	-	> 20	-	0
			30 nmi	-	> 20	-	0
	Anchovy	10 nmi	0	0	7	11	
		20 nmi	-	11	-	> 20	
		30 nmi	-	1	-	11	
	Total	10 nmi	0	0	0	0	
		20 nmi	-	6	-	> 20	
		30 nmi	-	14	-	> 20	
	Chick growth	Sardine	10 nmi	0	0	0	0
			20 nmi	-	0	-	0
			30 nmi	-	0	-	0
Anchovy		10 nmi	1	1	1	1	
		20 nmi	-	0	-	9	
		30 nmi	-	0	-	> 20	
Total		10 nmi	1	1	1	1	
		20 nmi	-	> 20	-	> 20	
		30 nmi	-	20	-	> 20	
Foraging path length		Sardine	10 nmi	11	9	3	6
			20 nmi	-	4	-	7
			30 nmi	-	0	-	3
	Anchovy	10 nmi	7	11	5	5	
		20 nmi	-	6	-	0	
		30 nmi	-	11	-	9	
	Total	10 nmi	4	6	0	0	
		20 nmi	-	20	-	9	
		30 nmi	-	3	-	4	
	Foraging trip duration	Sardine	10 nmi	0	0	> 20	> 20
			20 nmi	-	0	-	18
			30 nmi	-	13	-	> 20
Anchovy		10 nmi	0	0	> 20	> 20	
		20 nmi	-	0	-	> 20	
		30 nmi	-	> 20	-	11	
Total		10 nmi	0	0	> 20	> 20	
		20 nmi	-	0	-	> 20	
		30 nmi	-	> 20	-	12	

Table 7: The number of additional years' data required to detect a fishing effect significant at the 5% level with **80%** probability is given for each of Bird and St Croix islands, where the true values of λ are assumed to be the random effects model-estimates. However, if a model-estimated λ value is small (i.e. $|\lambda| < 0.1$) then $\lambda = \pm 0.1$ is assumed instead for the effect size, where the sign is chosen according to the sign of the model-estimate for λ . A value of 0 indicates that the existing estimate of λ is already significant at the 5% level. C/O indicates future alternating periods of three years of the area being closed and three of it being open to fishing; O indicates the area is always open in the future.

Response	Fish	Area	Bird		StCroix	
			C/O	O	C/O	O
Foraging path length	Sardine	10 nmi	> 20	> 20	> 20	> 20
		20 nmi	-	> 20	-	19
		30 nmi	-	> 20	-	> 20
Foraging trip duration	Sardine	10 nmi	> 20	> 20	> 20	> 20
		20 nmi	-	> 20	-	> 20
		30 nmi	-	> 20	-	17

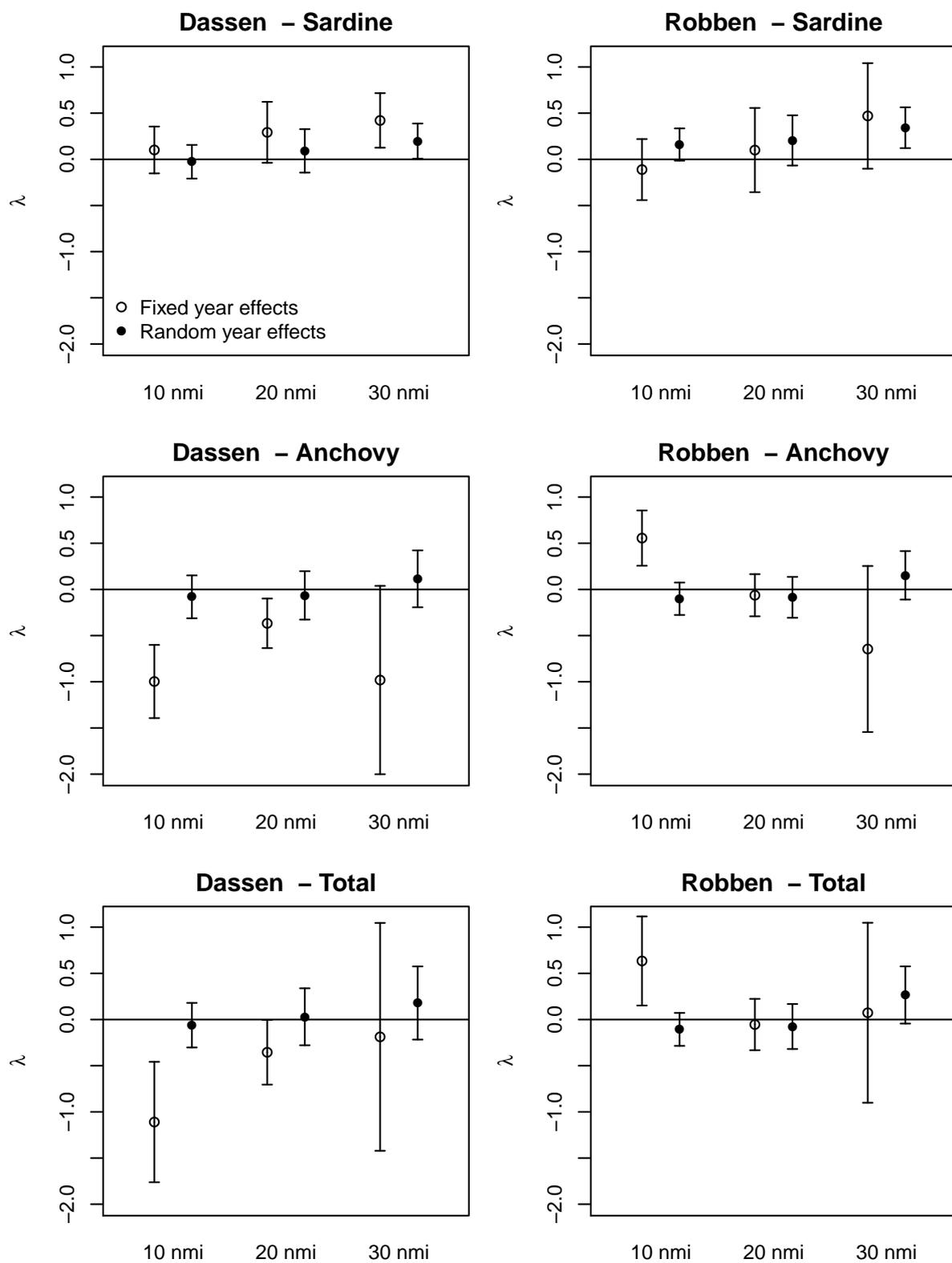


Figure 1: Dassen and Robben Islands fishing effect parameter estimates: for the **chick condition** response variable. Bars indicate one standard error.

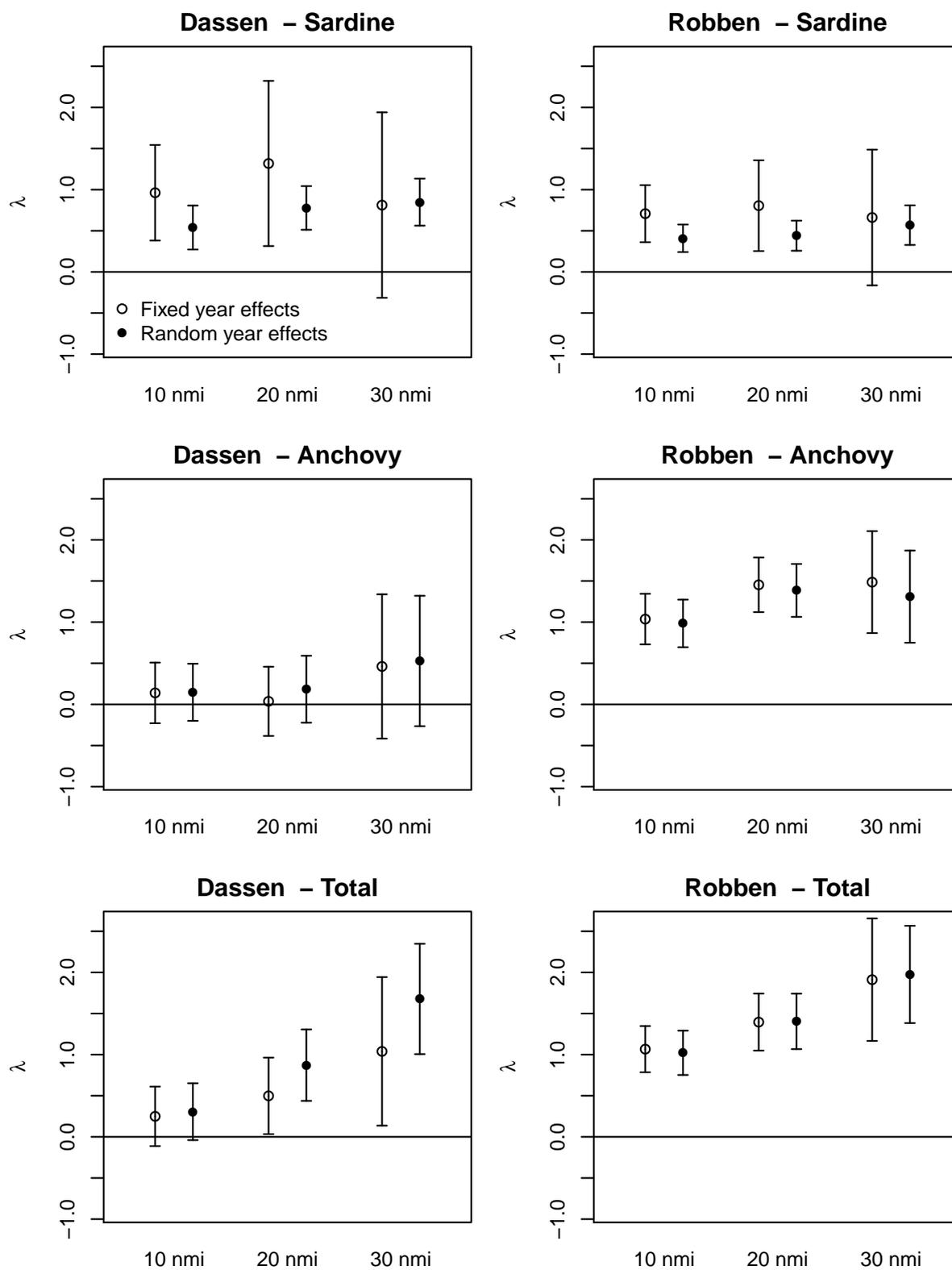


Figure 2: Dassen and Robben Islands fishing effect parameter estimates: for the **active nest proportion** response variable. Bars indicate one standard error.

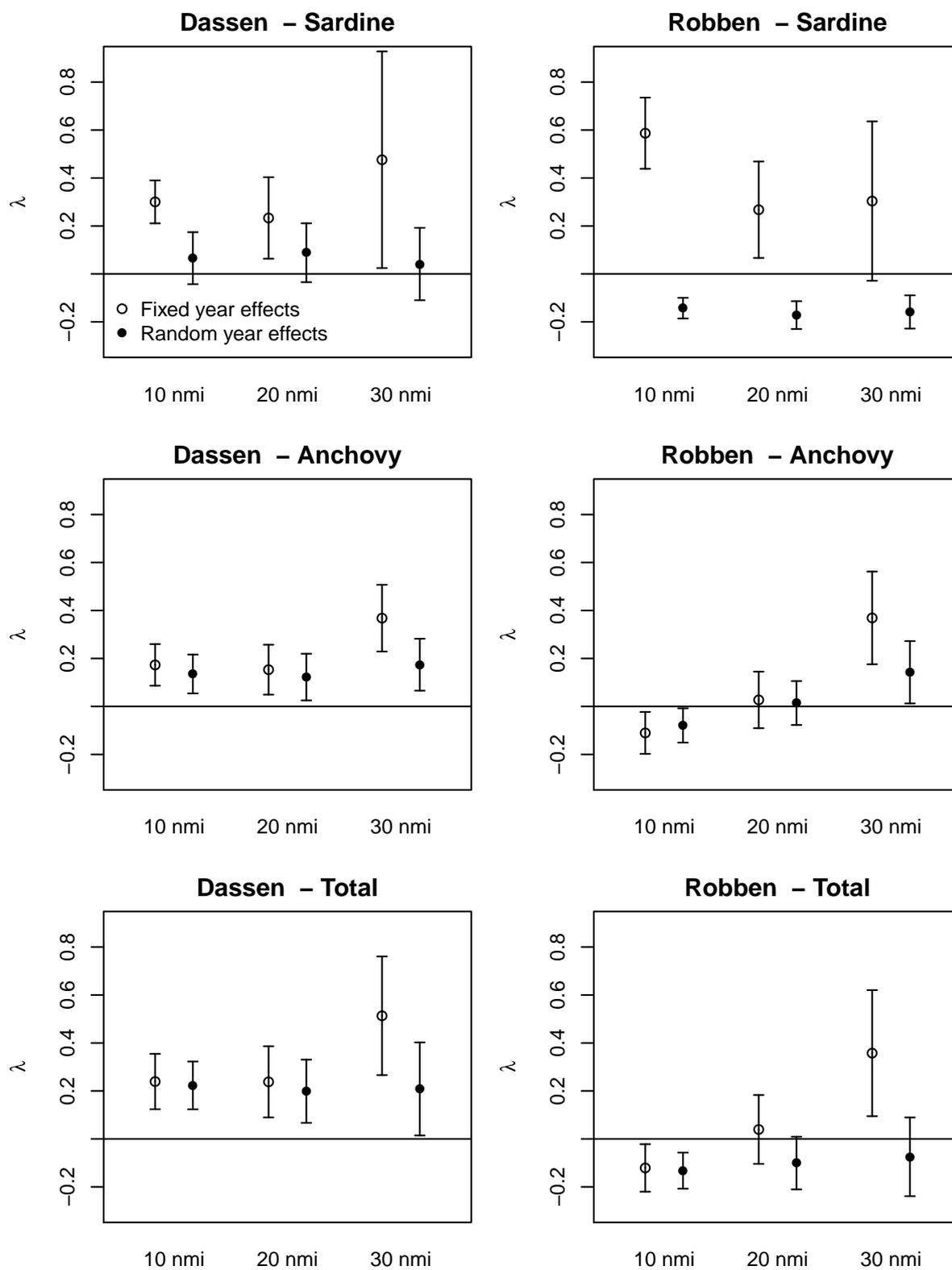


Figure 3: Dassen and Robben Islands fishing effect parameter estimates: for the **fledging success** response variable. Bars indicate one standard error.

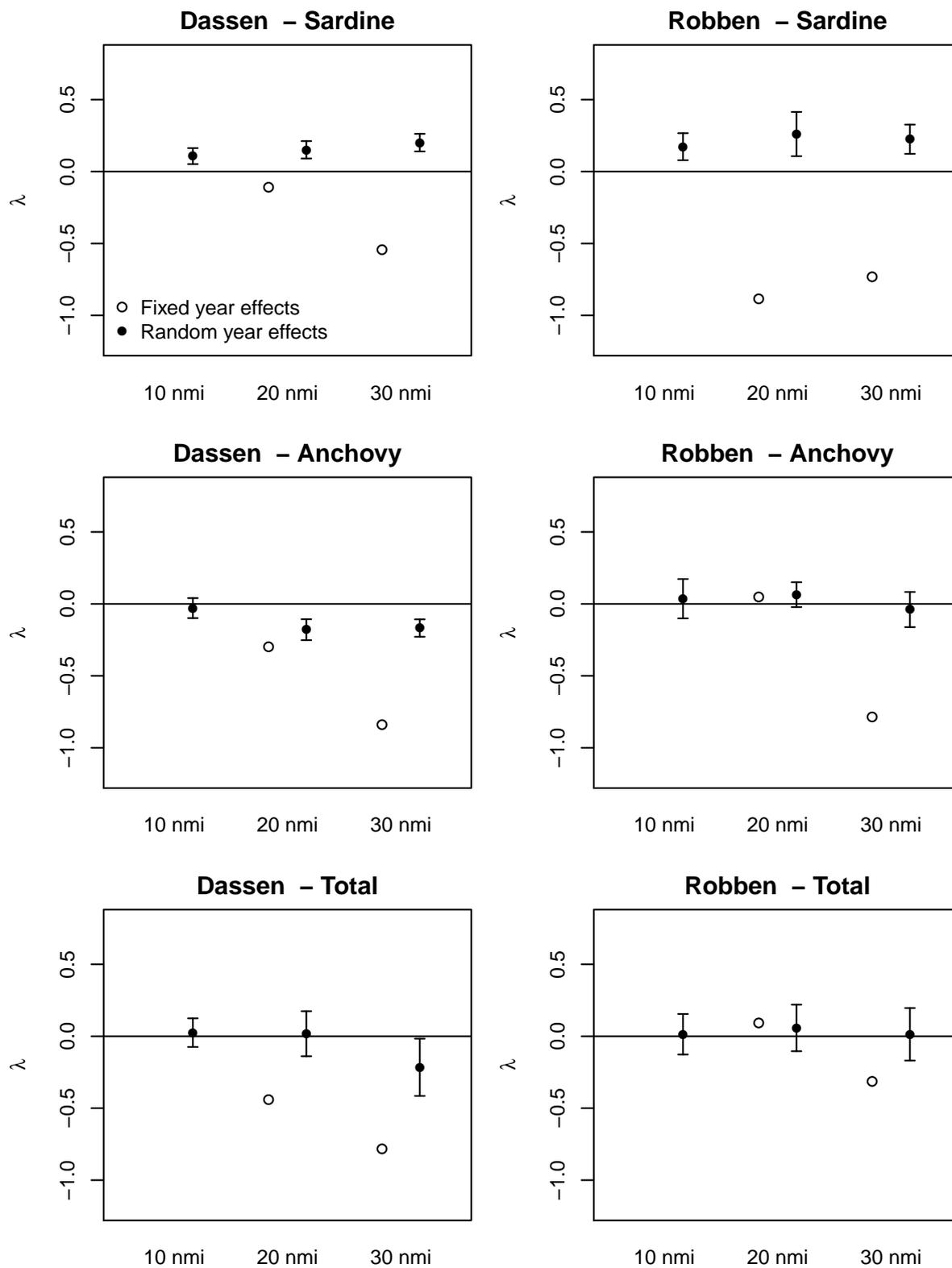


Figure 4: Dassen and Robben Islands fishing effect parameter estimates: for the **chick growth rate** response variable. Bars indicate one standard error.

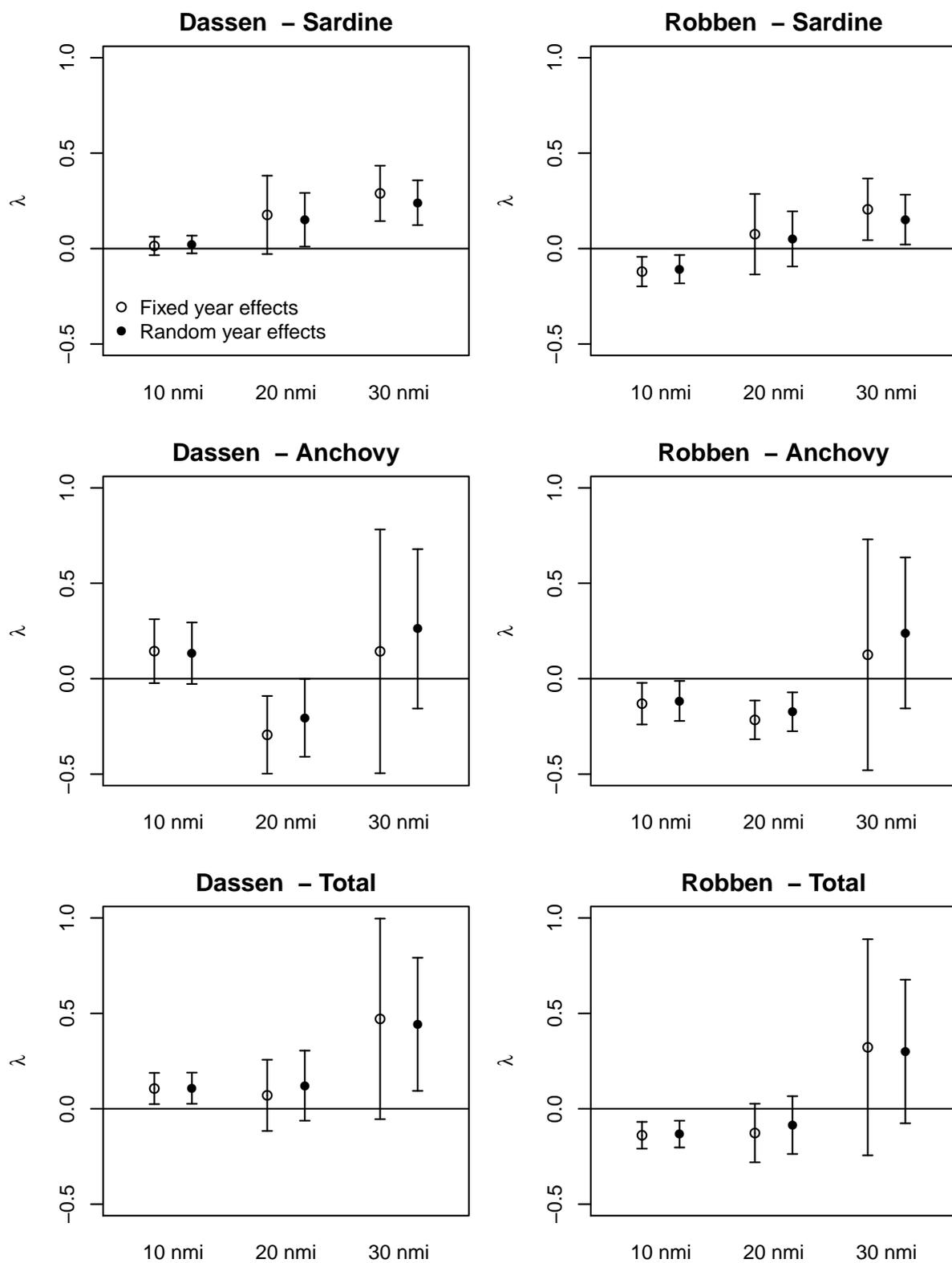


Figure 5: Dassen and Robben Islands fishing effect parameter estimates: for the **foraging path length** response variable. Bars indicate one standard error.

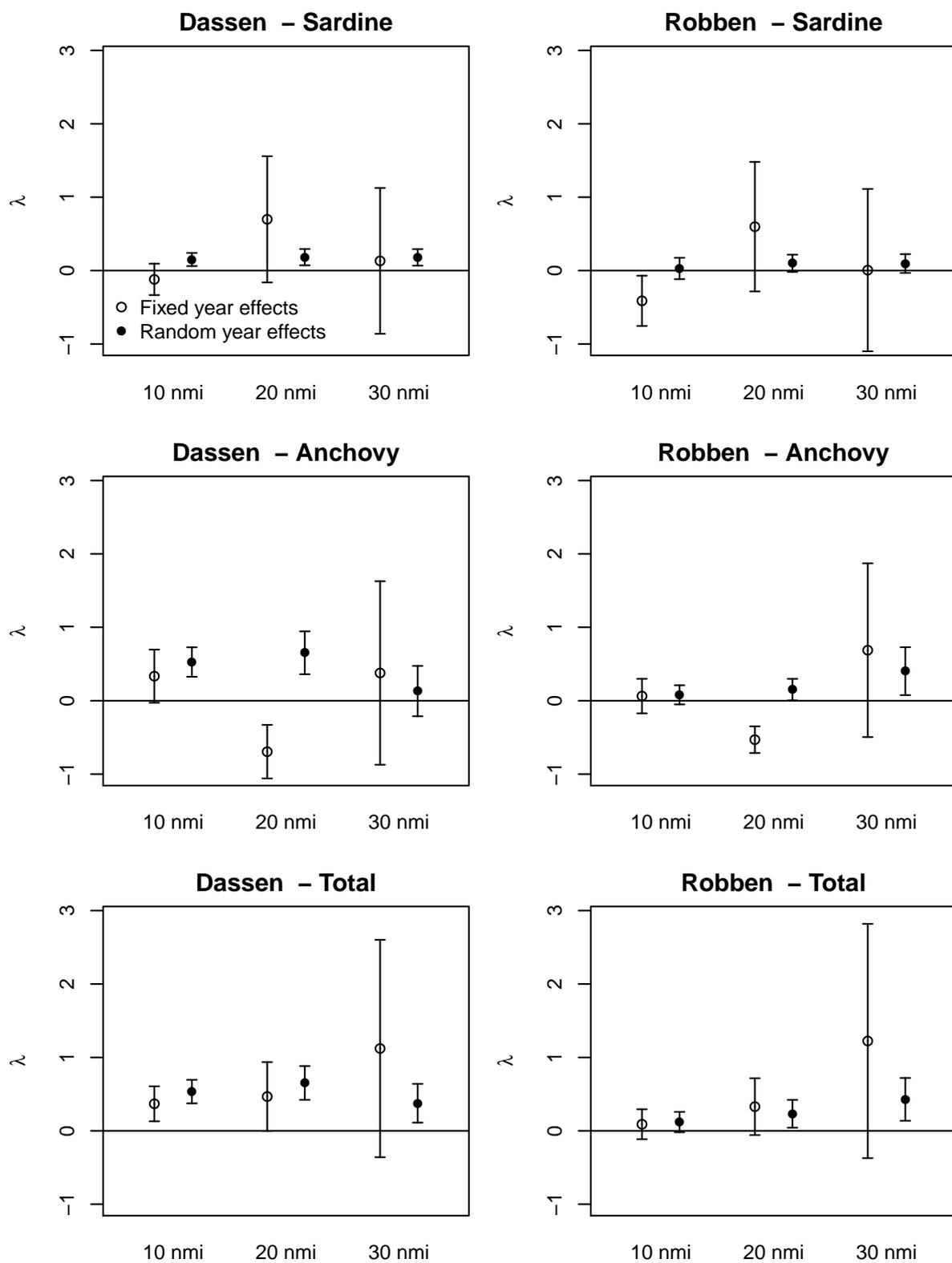


Figure 6: Dassen and Robben Islands fishing effect parameter estimates: for the **foraging trip duration** response variable. Bars indicate one standard error.

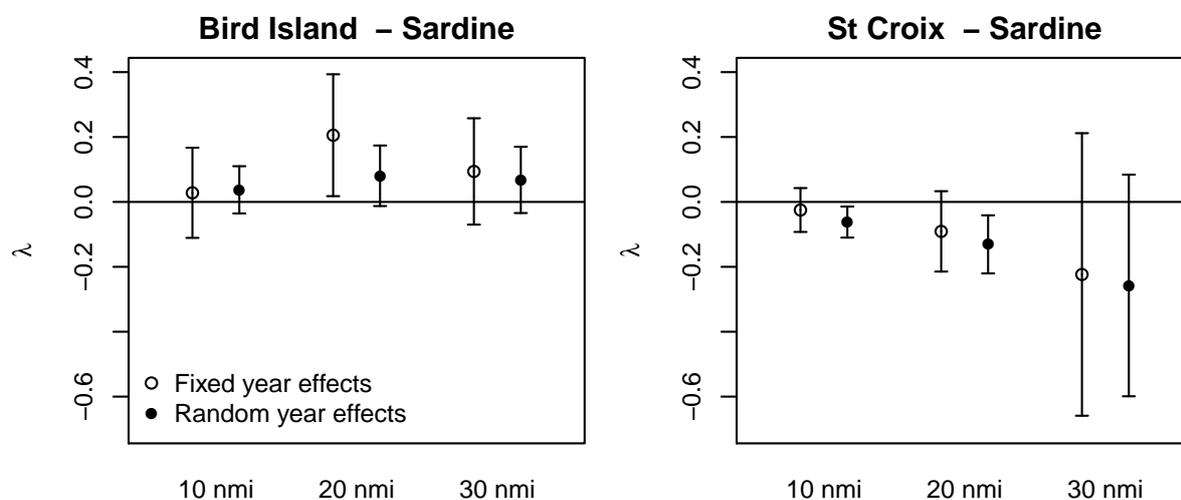


Figure 7: Bird and St Croix Islands fishing effect parameter estimates: for the **foraging path length** response variable. Bars indicate one standard error.

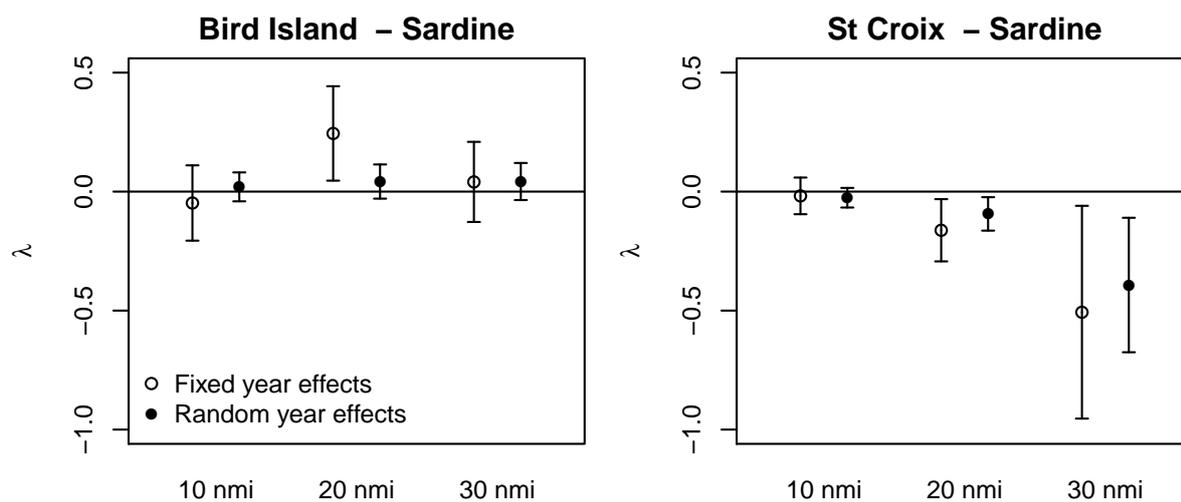


Figure 8: Bird and St Croix Islands fishing effect parameter estimates: for the **foraging trip duration** response variable. Bars indicate one standard error.

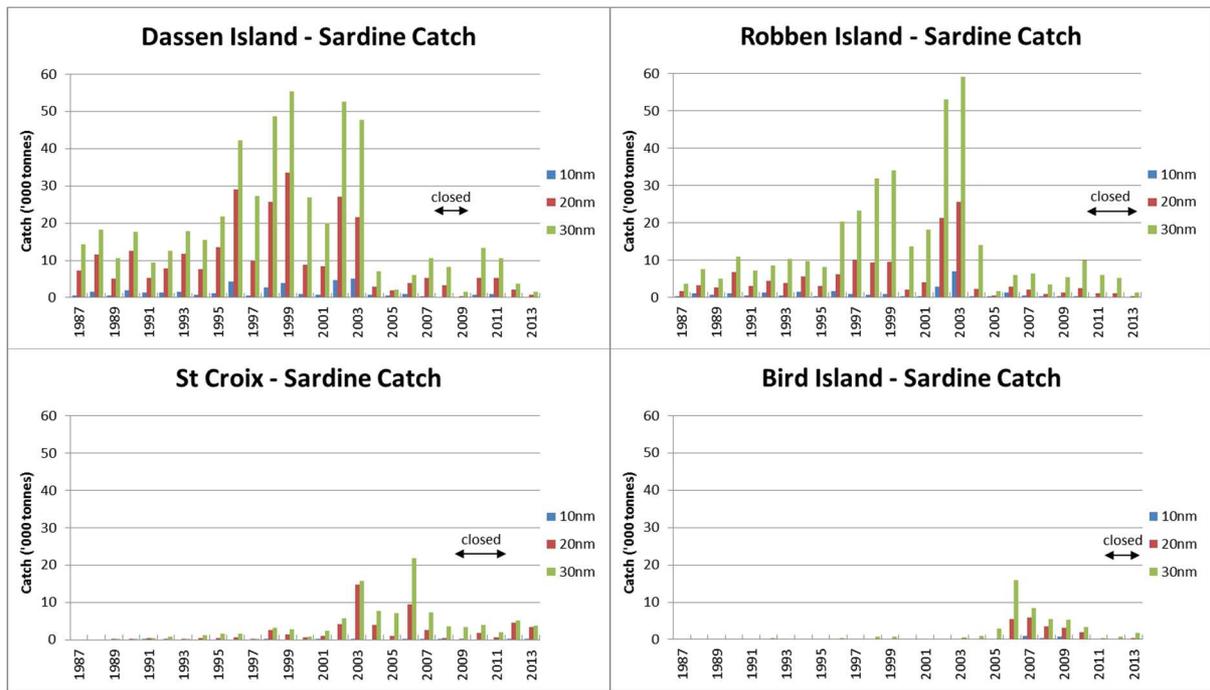


Figure 9: The time series of catches of sardine within 10, 20 and 30 nm of Dassen, Robben, St Croix and Bird Islands. Periods where the regions within 10 nm were closed to pelagic fishing are also indicated.

APPENDIX A

The Basis Underlying the GLM Analysis Method Applied

At the simplest level, an index R related to breeding success will be a monotonically increasing function of initial resource biomass in the region of interest B , e.g. under linear proportionality:

$$R = \gamma B \quad (\text{A.1})$$

where γ reflects what is often termed ‘‘catchability’’. More generally though, B will be reduced during the season (or period under consideration) by the catch made (C), while γ will be impacted by the effect of fishing on the schools, e.g. the mechanism put forward by Clark (1976) which suggests that γ will be an increasing function of C^2 . Thus:

$$B \rightarrow f(C, B) \quad (\text{A.2})$$

where $\frac{\partial f}{\partial C} < 0$. For example, under Pope’s approximation the average biomass during the season would be:

$$f(C, B) = 0.5(1 - e^{-M})B - 0.5e^{-M/2}C \quad (\text{A.3})$$

and under the Clark mechanism:

$$\gamma \rightarrow g(C, B)$$

where for example

$$g(C, B) = \tilde{g}(C/B\omega) \quad (\text{A.5})$$

where ω measures the extent to which the effect of the catches is absolute ($\omega = 0$) or relative ($\omega = 1$). In either event $\frac{\partial g}{\partial C} > 0$.

Writing $R = g(C, B)f(C, B)$ and taking logarithms gives:

$$\ln R = \ln g(C, B) + \ln f(C, B) = g^*(C, B) + f^*(C, B) \quad (\text{A.6})$$

where $\frac{\partial g^*}{\partial C} > 0$ and $\frac{\partial f^*}{\partial C} < 0$.

Linearising (first order Taylor series expansion) about some typical biomass \tilde{B} and $C = 0$ gives:

$$\begin{aligned} \ln R &= g_0^* + \left. \frac{\partial g^*}{\partial C} \right|_{\tilde{B}, 0} C + \left. \frac{\partial g^*}{\partial B} \right|_{\tilde{B}, 0} (B - \tilde{B}) + f_0^* + \left. \frac{\partial f^*}{\partial C} \right|_{\tilde{B}, 0} C + \left. \frac{\partial f^*}{\partial B} \right|_{\tilde{B}, 0} (B - \tilde{B}) \\ &= g_0^* + c_1 C + d_1 (B - \tilde{B}) + c_2 C + d_2 (B - \tilde{B}) \end{aligned} \quad (\text{A.7})$$

where c_1 , d_1 , c_2 and d_2 are constants with $c_1 > 0$ and $c_2 < 0$. Re-arranging:

$$\begin{aligned} \ln R &= (g_0^* - d_1 \tilde{B} - d_2 \tilde{B}) + (d_1 + d_2)B + (c_1 + c_2)C \\ &= \beta + \mu B + \lambda C \end{aligned} \quad (\text{A.8})$$

² While the Clark model, which produces this effect through γ being a decreasing function of school size, and mean school size being reduced through fishing disturbing schools, has been used for illustration here, it is not the only mechanism that might be at work to produce a trend in this same direction. For example, the purse-seine catching operations are not 100% efficient, and will see some injured fish left in the water which are potentially more easily taken by predators. A well-known example of this effect is discarding of fish/fish parts by trawlers leading to increasing populations of some species of scavenging seabirds.

with $= c_1 + c_2$. Thus for year y and colony i , and where C^* is now normalised by the average catch at the island:

$$\ln R_{y,i} = \beta_i + \mu B_y + \lambda_i C_{y,i}^* \quad (\text{A.9a})$$

or

$$\ln R_{y,i} = \beta_i + \alpha_y + \lambda_i C_{y,i}^* \quad (\text{A.9b})$$

i.e. exactly of the form assumed by Robinson (2013).

Importantly $\lambda_i = c_{1,i} + c_{2,i}$ where $c_{1,i} > 0$ and $c_{2,i} < 0$ so that the sign of λ_i can be positive or negative, depending on which of the effects of the catch is dominant in a particular case: availability of the fish to the predators (c_1) or the average abundance present given catching (c_2).

This is a specific example of a more general principle that was first fully realized in fisheries science perhaps some three decades ago (see comments in Butterworth, 1989, pg 635), and is the underlying reason why detailed studies of particular biological mechanisms unfortunately can frequently be of little assistance in a population modelling context. Many and complex mechanisms are generally at work, and not all in the same direction in response to changes in fishing intensity. Though some can be measured and hence possibly effectively modelled, others cannot, and may well be in the opposite directions to those which can. Thus the associated issues (such as here the impact of fishing around islands on penguin reproductive success) cannot be resolved by micro-studies and related modelling, but rather only by empirical measurements of net combined effects.

It is for this reason the island closure programme and the method to analyse the results were proposed and agreed in their present empirical form. The net impact of effects such as those discussed above can be reliably determined only by empirical analyses.

APPENDIX B

Power Analysis Methodology

This Appendix indicates how the general linear model (GLM) analyses of the main text which estimate the fishing effect parameters λ_i are extended to estimate the power of an Island Closure Experiment. Statistical power reflects the probability that an experiment will detect an effect if it exists.

Methods

Fixed year effects model

The GLM for a reproductive success parameter F is:

$$\ln(F_{y,i,s}) = \alpha_y + \gamma_s + \lambda_i \frac{C_{y,i,p}}{\bar{C}_{i,p}} + \varepsilon_{y,i,s} \quad (\text{B.1})$$

for year y , island i , and data series s , where

α_y is a year effect reflecting prevailing environmental conditions,

γ_s is a series effect (subsuming an island effect),

λ_i is a fishing effect,

$C_{y,i,p}$ is the catch taken in year y in the neighbourhood of island i of pelagic species p ,

$\bar{C}_{i,p}$ is the average catch taken over the years considered, and (excluding years for which fishing was prohibited), and

$\varepsilon_{y,i,s}$ is an error term.

Following Brandão and Butterworth (2007), future penguin response data are generated as follows:

$$\ln(F_{y,i,s}) = \hat{\alpha}_y + \hat{\gamma}_s + \hat{\lambda}_i \frac{\hat{C}_{y,i,p}}{\hat{C}_{i,p}} + \hat{\varepsilon}_{y,i,s} \quad (\text{B.2})$$

where

$\hat{\alpha}_y$ are generated by sampling with replacement from estimates for α_y ,

$\hat{\gamma}_s$ are the best estimates of γ_s ,

$\hat{\lambda}_i$ are the best estimates of λ_i ,

$\hat{C}_{y,i,p}$ are generated by sampling with replacement from the time-series of observed catches for series s for years in which the island concerned is “open” to fishing, and zero otherwise, and

$\hat{\varepsilon}_{y,i,s}$ are generated from $N(0, \sigma_\varepsilon^2)$, where σ_ε^2 is the variance of the residuals when the model is fit to the historic data.

The future data are appended to the historic time-series.

The GLM is fit to obtain estimates for λ_i and the associated t -probability using a fixed year effects model.

The process is repeated a large number of times (for results in this paper 950 times).

Experimental power is calculated as the number of λ_i estimates which are statistically significant (at the 5% level) divided by the number of simulations performed.

Random year effects

Calculating power based entirely on a fixed year effects model does however give rise to some difficulties, the chief on which is that for the data sets available such models often have relative few degrees of freedom so that ML estimates of residual variance σ_ε^2 may be substantially negatively biased. Accordingly the power analyses have made use of results from some random effects models – specifically the GLM model parameter estimates which are more precise because of the greater associated number of degrees of freedom, and the estimate for the residual variance which is unbiased because of the use of REML – for the generation of future response data. The GLM fitted to these future data remains a fixed year effects model, but in future work a mixed model for which the year factor is treated as a random effect could also be applied.

Effect size

Effectively the approach outlined above is taking the effect size for the power analysis to be equal to the current best estimate of the fishing effect parameter λ_i under the random year effects model. This does however raise the problem that if that estimate is very small (perhaps so small as not to be meaningfully different from zero biologically), it is of no real interest to ascertain the exact value of the rather large number of years which would be needed to collect sufficient data to determine that the value had been distinguished from zero at the 5% significance level.

Instead therefore, for cases where the point estimate of λ_i is small, it has been replaced by a fixed value, of the same sign as the point estimate of λ_i , but of a magnitude which is (arguably) biologically meaningful. The actual fixed value chosen is 0.1. The justification for this choice comes from the following consideration of penguin population dynamics.

If penguin reproductive maturity is assumed to occur at age 4, the basic equation used by Robinson (2013) for the mature female component of the population (numbering N in year y) may be written:

$$N_{y+1} = N_y S + H_{y-3} S^3 N_{y-3} \quad (\text{B.3})$$

where S is the mature female annual survival proportion and H is a measure related to the product of egg production and fledging success. In a situation where the population is changing at a steady rate:

$$\eta = N_{y+1}/N_y \quad (\text{B.4})$$

then

$$\eta^4 = \eta^3 S + H S^3 \quad (\text{B.5})$$

which if H changes by ΔH leads to a corresponding change in penguin growth rate $\Delta \eta$ given by:

$$\Delta \eta = \frac{S^3}{4\eta^3 - 3\eta^2 S} \Delta H \quad (\text{B.6})$$

Now results in Robinson (2013) suggest that for $S=0.88$, the Robben island penguin population abundance was approximately steady, so that substituting $\eta=1$ in equation (B.5) yields $H = 0.176$, and hence from equation (B.6):

$$\Delta \eta / \eta = 0.088 \Delta H / H \quad (\text{B.7})$$

Now from differentiating equation (B.1), the relative change in the penguin response variable F arising from a suspension of fishing (C changes from \bar{C} to 0) will be given by:

$$\Delta F/F = -\lambda \quad (\text{B.8})$$

so that if one assumes as a first approximation that a relative change in F results in the same relative change in H (i.e. $\Delta H/H = \Delta F/F$), it then follows that:

$$\Delta \eta/\eta = -0.088 \lambda \sim -0.1\lambda \quad (\text{B.9})$$

If then 1% is to be regarded as a meaningful change in the penguin population growth rate (to be achieved, conceivably, by a suspension of fishing in the neighbourhood of the colony concerned), it follows that the corresponding value for the magnitude of λ is about 0.1, which is why this value was chosen for what is in effect a default minimum effect size above.

Future closure sequences

At the International Panel Review meeting in 2010 when the feasibility study was discussed (Parma *et al.*, 2010), the schedule of alternating closures, each of three years' duration, which was agreed was for Robben and then Dassen Island commencing in 2011. For St Croix, a three year closure period was to be completed by a further closure in 2011, which then was to be followed by three years of closure around Bird Island.

This schedule was implemented, with closures extending for 10 nm around the islands (taken to correspond to a single grid block – see Coetzee, 2014). Thus closures are assumed to impact only the catch within this area, which is reduced to zero. However for models fitted to catches over greater distances from the islands, such as 20 and 30 nm, it is assumed that closures have no impact, as any catch that would have been made within the 10 nm distance from the island seems most likely simply to be displaced to the area between 10 and 20 nm from the island.

Thus the results reported in the main text contrast future alternating closure approaches [denoted C/O for closed/open] with those with no closures at all (and hence typical catches continuing every year) [denoted O] only for models related to catches within a 10 nm distance from islands. Models for catches within greater distances are treated only as “no closures” scenarios [O].