

# Ecosystem modelling provides clues to understanding ecological tipping points

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## Supplement. Additional model descriptions, analyses and results

Steady state analysis of deterministic spatial multi-species operating model (SMOM)

Consider the non-spatial non-seasonal and deterministic SMOM equations as summarised in Tables S1 and S5.

The prey equation describing the abundance of a prey species in year  $y$ , when assuming zero harvest, is given by:

$$B_{y+1}^{\text{prey}} = B_y^{\text{prey}} + r B_y^{\text{prey}} \left( 1 - \frac{B_y^{\text{prey}}}{K} \right) - \frac{1}{\omega_j} \sum_j \frac{\lambda^j B_y^{\text{prey}} N_y^j}{B_j + B_y^{\text{prey}}} \quad (\text{S1})$$

with variables as defined in Table S2 but ignoring the area  $a$  subscripts and superscripts. This simplifies to the following at equilibrium:

$$r \left( 1 - \frac{B_y^{\text{prey}}}{K} \right) = \frac{1}{\omega_j} \sum_j \frac{\lambda^j N_y^j}{B_j + B_y^{\text{prey}}} \quad (\text{S2})$$

The predator equation describing the abundance of a single predator species (and hence dropping the superscript  $j$ ), in year  $y$ ,  $N_y$ , when assuming zero harvest is as follows:

$$N_{y+1} = N_y S + N_{y-T+1} q f(B_{y-T+1}^{\text{prey}}) P S_{\text{juv}}^* (1 - N_y / K^*) S^{T-1} \quad (\text{S3})$$

At equilibrium  $N_{y+1} = N_y = N_{y-T+1}$  and hence it follows:

$$1 - S = q f(B_{y-T+1}^{\text{prey}}) P S_{\text{juv}}^* (1 - N_y / K^*) S^{T-1} \quad (\text{S4})$$

Rearranging this equation to solve for the equilibrium breeding success factor gives:

$$f(B_{y-T+1}^{\text{prey}}) = \frac{1-S}{qPS_{\text{juv}}^* S^{T-1} (1 - N_y/K^*)} \quad (\text{S5})$$

This is equivalent to the original formulation for  $f(B_y^{\text{prey}})$  expressed in terms of prey depletion level  $B_y^{\text{prey}}/K_{\text{prey}}$  :

$$f(B_{y-T+1}^{\text{prey}}) = \frac{\alpha B_y^{\text{prey}}/K_{\text{prey}}}{\alpha - 1 + B_y^{\text{prey}}/K_{\text{prey}}} \quad (\text{S6})$$

where  $\alpha$  is computed from the relation  $\alpha = \frac{4h}{5h-1}$  (with  $h$  given as per Table S3) and the functional forms for the 3 predators are shown in Fig. S4.

Hence, by equating Eqs. (S5) & (S6), the predator equilibrium depletion level  $N_y/K^*$  can be solved as a function of the prey depletion level:

$$\frac{N_y}{K^*} = 1 - \frac{1-S}{qPS_{\text{juv}}^* S^{T-1} \frac{\alpha B_y^{\text{prey}}/K_{\text{prey}}}{\alpha - 1 + B_y^{\text{prey}}/K_{\text{prey}}}} \quad (\text{S7})$$

i.e.

$$\frac{N_y}{K^*} = 1 - \frac{(1-S)(\alpha - 1 + B_y^{\text{prey}}/K_{\text{prey}})}{qPS_{\text{juv}}^* S^{T-1} \alpha B_y^{\text{prey}}/K_{\text{prey}}} \quad (\text{S8})$$

For each predator modelled, the parameters  $q, P, S_{\text{juv}}^*, S, T, \alpha$  are known (or estimated), and hence predator depletion levels can be computed for a range of prey depletion levels, as shown in Fig. S1.

The predator–prey relative depletion plots (Fig. S1) are useful to assess the equilibrium population level (relative to the carrying capacity) of each predator as a function of prey depletion level. Hence, as expected, the plots show that predator populations will stabilize at successively lower levels if the prey population on which they depend stabilizes at lower levels. The solutions differ for the different species groups because they depend on both the breeding success parameter settings (Fig. S4) and the demographic parameters for each group. Hence, seals are predicted to be able to maintain high population levels unless prey is substantially depleted, whereas the penguin and fish group equilibrium population levels depend more directly on the prey depletion level.

Interestingly, penguins are unable to sustain themselves once prey drops below around 25% of the prey carrying capacity level (Fig. S1A), i.e. there are no equilibrium solutions possible for penguins at lower prey depletion levels as the populations are predicted to decline rather than stabilize. This is an equilibrium analysis only, and hence this result assumes that the prey population remains fixed at a very low level with the predicted consequence that the penguins would go extinct. However, in the dynamic model simulations as described in the main text, prey abundance is more variable and the net effect can be explored of periodic but non-persistent decreases in prey abundance.

The equilibrium analyses also assume that predator demographic parameters remain fixed (at the Table S3 values) despite predator and prey populations dropping to low levels. Eq. (S3) has a term to account for density-dependent changes in juvenile survival, and there is not much room to increase the adult or juvenile survival parameters (because they are bounded by 1), so that the only scope for growth is to be found in the parameter  $P$ , which describes the maximum number of chicks produced. Hence, for example, if this parameter value is doubled, the predator population could theoretically maintain itself down to prey depletion levels of about 13% (from Eq. S8), but it seems unlikely that reproductive outputs could be maintained at a high level when prey becomes limiting. So can penguin populations exist at low prey levels? That depends on whether the assumed sensitivity of penguins to declines in their prey (Fig. S4) is valid (and there is some empirical evidence that it is) and also whether the penguins are able to switch to alternative prey (and the Antarctic ecosystem is an extreme example in the sense that there are few alternative prey available). The analyses presented here thus highlight that unless alternative prey are available, penguins cannot sustain themselves at very low prey abundance levels, and the simulations focus instead on more temporary prey shortages. Moreover, the analyses assume that no alternative prey are available as computations that take into account multiple alternative prey species are more complex (see e.g. May 1977) and the subject of future work instead.

The fish example is not discussed in detail here as it is similar in many respects to the penguin example, except that there is more scope for density-dependent changes in population parameters.

Table S1. Summary of key model equations from Plagányi & Butterworth (2012), including discrete prey equation and the delay difference equation applied to the 3 predator groups (penguins, seals, fish) for each of the summer and winter seasons. The steepness parameter  $h$  largely controls the shape of the relationship between predator breeding success and prey availability. See Table S2 for a list of symbols and Plagányi & Butterworth (2012) for a full description of the model

Description	Equation
Krill	$B_{t+1}^a = B_t^a + r_t^a B_t^a \left(1 - \frac{B_t^a}{K_a}\right) - \frac{1}{\omega_j} \sum_j \frac{\lambda^j B_t^a N_{y,seas}^{j,a}}{B_j^a + B_t^a} - F_t^a B_t^a$
Predators (penguins, seals, fish)	
summer (s1)	$N_{y+1}^{j,a} = N_y^{j,a} \sqrt{S_{s1}^j S_{s2}^j} + N_{y-T+1}^{j,a} q^j f(B_{y-T+1}^a) P^j S_{juv}^{*,j} \left(1 - N_y^{j,a} / K^{*,j,a}\right) \left(S_{s1}^j S_{s2}^j\right)^{\frac{T-1}{2}}$
winter (s2)	$N_{y,s2}^{j,a} = N_y^{j,a} \sqrt{S_{s1}^j} + N_{y-T+1}^{j,a} q^j f(B_{y-T+1}^a) P^j S_{juv}^{*,j} \left(1 - N_y^{j,a} / K^{*,j,a}\right) \left(S_{s1}^j\right)^{\frac{T-1}{2}} \left(S_{s2}^j\right)^{\frac{T-2}{2}}$
Breeding success as a function of krill biomass	$f(B_y^a) = \frac{\alpha^a B_y^a / K_a}{\alpha^a - 1 + B_y^a / K_a}$
Steepness of predator-prey interaction relationship	$h = \frac{\alpha^a}{5\alpha^a - 4}$
Predator fishing mortality	$F_t^{j,a} = \frac{\lambda^j B_t^a N_{y,seas}^{j,a}}{\omega_j (B_j^a + B_t^a)} \bigg/ B_t^a$

Table S2. List of the model parameters, with descriptions, which appear in Table S1

Parameter / Variable	Description
$B_y^a$	Biomass of krill in small scale management unit (SSMU) $a$ in year $y$ and at time step $t$ (with 2 time steps per year $y$ ) but the seasonal subscript has been omitted to simplify the notation
$r_t^a$	Intrinsic growth rate ( $\text{yr}^{-1}$ ) of krill in SSMU $a$ at time $t$ (seasonal dependence not indicated by a subscript to avoid cluttering the notation throughout)
$K_a$	Average carrying capacity of krill in SSMU $a$
$\lambda^j$	Maximum per capita consumption rate ( $\text{yr}^{-1}$ ) of krill by predator species $j$
$N_y^{j,a}$	Number of predator species $j$ in SSMU $a$ in year $y$
$B_j^a$	Krill biomass when the consumption and hence also birth rate of species $j$ in SSMU $a$ drops to half of its maximum level
$\omega_j$	Proportion of mature females in the mature population of predator species $j$
$F_y^a$	Fishing proportion (catch = $F_y^a B_y^a$ ) on krill in SSMU $a$ in year $y$
$S_{\text{seas}}^j$	Post-first-year annual survival rate of predator species $j$ in season seas where s1 = summer and s2 = winter
$T$	Age at first maturity, taken for simplicity to be one less than the age at first reproduction (i.e. assuming a one year gestation period)
$q^j$	Fraction of chicks/pups that are female for predator species $j$
$P^j$	Maximum proportion of fledged chicks or pups surviving to the end of their first year of life per pair of predator $j$ per year
$f(B_y^a)$	Breeding success factor (multiplier for $P$ ) which is a non-linear function of the biomass of krill in SSMU $a$ in year $y$
$S_{\text{juv}}^{*,j}$	Maximum first year (juvenile) survival rate (post-fledging or post-weaning) of predator species $j$ , with realized annual juvenile survival rate computed as $S_{\text{juv}}^{*,j} \left(1 - N_y^{j,a} / K^{*,j,a}\right)$
$K^{*,j,a}$	Carrying capacity-related term for predator species $j$ in SSMU $a$
$\alpha^a, \beta^a$	Parameters for the (predator-dependent) breeding success function for SSMU $a$ , with $\beta = (\alpha - 1)K_a$
$h$	“Steepness” parameter for the breeding success function

Table S3. Summary of input parameters  $P^j$  and  $T$ , together with survival parameters  $S^j$  and  $S_{\text{juv}}^j$  used in model simulations for each predator group. The interaction curve steepness  $h$  parameters are the average estimates that Plagányi & Butterworth (2012) obtained by fitting to historic trend information. See Table S2 for description of parameters

	$S^j$	$S_{\text{juv}}^j$	$h$	$P^j$	$T$
Penguins	0.89	0.94	0.26	0.91	3
Fish	0.71	0.65	0.40	3.00	3
Seals	0.94	0.91	0.79	0.88	4
Whales	0.975	0.86	0.98	0.50	5

Table S4. List of the model variables and parameters for the penguin–sardine model. All rate-related parameters have units  $\text{yr}^{-1}$

Parameter	Description	Value
$r^{\text{sard}}$	Intrinsic growth rate ( $\text{yr}^{-1}$ ) of sardine	estimated
$K_{\text{sard}}$	Average carrying capacity of sardine (maximum value of observed series)	1 343 118 t
$F^{\text{sard}}$	Average fishing proportion ( $\text{yr}^{-1}$ )	0.3 with pulse simulated using 0.9 in years 2003–04
$T$	Age at first maturity for penguins	4
$q^{\text{peng}}$	Fraction of chicks that are female	0.5
$P^{\text{peng}}$	Maximum proportion of fledged chicks surviving to the end of their first year of life per pair of penguins per year	1.8
$K^{*,\text{peng}}$	Carrying capacity-related term for penguins (maximum observed value)	40000
$S^{\text{peng}}$	Post-first-year annual survival rate of penguins	estimated
$S_{\text{juv}}^{*,\text{peng}}$	Maximum first year (juvenile) survival rate (post-fledging) of penguins (realized rate is less)	0.98
$h^{\text{peng}}$	“Steepness” parameter for the breeding success function for penguins	0.26

Table S5. Simplified non-spatial non-seasonal spatial multi-species operating model (SMOM) equations. See Tables S2 & S4 for description of variables not defined here

Description	Equation
Krill	$B_{y+1}^{\text{sard}} = B_y^{\text{sard}} + r^{\text{sard}} B_y^{\text{sard}} \left( 1 - \frac{B_y^{\text{sard}}}{K_{\text{sard}}} \right) - F^{\text{sard}} B_y^{\text{sard}}$
Predator (penguin)	$N_{y+1}^{\text{peng}} = N_y^{\text{peng}} S^{\text{peng}} + N_{y-T+1}^{\text{peng}} q^{\text{peng}} f(B_{y-T+1}^{\text{sard}}) P^{\text{peng}} S_{juv}^{*,\text{peng}} \left( 1 - \frac{N_y^{\text{peng}}}{K^{*,\text{peng}}} \right) (S^{\text{peng}})^{T-1}$
Breeding success as a function of sardine biomass	$f(B_y^{\text{sard}}) = \frac{\alpha B_y^{\text{sard}} / K_{\text{sard}}}{\alpha - 1 + B_y^{\text{sard}} / K_{\text{sard}}}$
Steepness of predator-prey interaction relationship	$h = \frac{\alpha}{5\alpha - 4}$
Negative of the log likelihood	$-\ln L = \sum_{sp} \left[ \sum_y \ln \sigma_y^{sp} + \left( \ln(I_y^{sp}) - \ln(\hat{I}_y^{sp}) \right)^2 / 2(\sigma_y^{sp})^2 \right]$ <p>where <math>I_y^{sp}</math> is the abundance index for year <math>y</math> and species <math>sp</math> and <math>\hat{I}_y^{sp} = q^{sp} B_y^{sp}</math>, with the catchability coefficient <math>q^{sp}</math> estimated by its maximum likelihood value: <math>\ln \hat{q}^{sp} = \frac{1}{n_{sp}} \sum_y (\ln I_y^{sp} - \ln \hat{B}_y^{sp})</math> where <math>n_{sp}</math> is the number of data points for species <math>sp</math>.</p>
Standard deviation of the residuals for the logarithm of abundance series for species $sp$	$\hat{\sigma}^{sp} = \sqrt{\frac{1}{n_{sp}} \sum_y (\ln I_y^{sp} - \ln \hat{I}_y^{sp})^2}$

Table S6. Comparison of negative log-likelihood and Akaike's information criterion (AIC) model scores for the 3 case studies (predator–prey pairs) and for each of the 3 alternative scenarios: (Scenario I) a smooth continuous relationship between predator performance and prey abundance; (Scenario II) a threshold response whereby predator breeding success decreases abruptly below a critical prey threshold level, with the extent of decrease either (a) fixed or (b) estimated as shown; and (Scenario III) a threshold response whereby adult predator survival rate decreases abruptly below a critical prey threshold level, with the extent of decrease either (a) fixed or (b) estimated as shown. The lowest AIC scores are shown in **bold**. COTS: crown-of-thorns starfish; BR: breeding threshold

<b>A) Penguin-sardine model</b>										
Model	I) No threshold		IIa) Breeding threshold fixed		IIb) Breeding threshold est.		IIIa) Survival threshold fixed		IIIb) Survival threshold est.	
<i>Estimated parameters</i>	Value	SD	Value	SD	Value	SD	Value	SD	Value	SD
r <sub>prey</sub> (intrinsic growth rate (yr <sup>-1</sup> ) of prey)	0.745	0.225	0.745	0.225	0.519	0.058	0.692		0.589	0.064
S <sub>pred</sub> (predator annual adult survival rate)	0.911	0.032	0.911	0.033	0.970	0.023	0.980		0.970	0.020
Surv <sub>decr_prop</sub> (survival decrease proportion)	-		-		-		fixed 0.5		0.818	0.025
BR <sub>decr_prop</sub> (breeding decrease proportion)	-		fixed 0.1		0.000	0.0003	-		-	
<i>Likelihoods</i>										
No. parameters estimated	2		2		3		2		3	
-lnL(total)	-19.209		-19.2089		-20.5825		0.862		-30.535	
AIC	-34.418		-34.4178		-35.165		5.72339		<b>-55.0694</b>	
-lnL(predator)	-12.665		-12.665		-13.9975		7.808		-23.273	
-lnL(preay)	-6.544		-6.544		-6.58503		-6.946		-7.262	
<b>B) COTS-coral Model</b>										
<i>Estimated parameters</i>	Value	SD	Value	SD	Value	SD	Value	SD	Value	SD
Initial number of 2+ COTS	0.505	0.119	0.496	*	0.504	*	1.000	0.001	0.969	0.961
Stock-recruitment residual for year 1994	4.307	0.378	4.838	*	4.741	*	5.052	0.512	4.040	0.446
Immigration for year 1996	4.292	0.352	4.338	*	4.244	*	3.372	0.581	2.705	0.589
Natural mortality (M)	2.560	0.146	2.547	*	2.540	*	1.708	0.282	1.461	0.961
Effect of COTS on fast-growing coral	0.129	0.041	0.129	*	0.127	*	0.267	0.177	0.172	0.124
Effect of fast-growing coral on COTS	0.258	0.167	0.272	*	0.276	*	0.066	0.199#	0.489	0.317
Effect of COTS on slow-growing coral	0.268	0.106	0.232	*	0.241	*	0.363	0.131	0.340	0.269
Surv <sub>decr_prop</sub>	-		-		-		-		0.094	0.146#
BR <sub>decr_prop</sub>	-		-		0.122	*	-		-	
<i>Likelihoods</i>										
No. parameters estimated	7		7		8		7		8	
-lnL(total)	-19.704		-15.831		-20.943		-24.793		-28.215	
AIC	-25.408		-17.662		-25.886		-35.5858		-40.43	
-lnL(COTS)	8.374		7.526		7.239		3.560		2.417	
-lnL(fast-growing coral)	-14.039		-11.679		-14.091		-14.176		-15.316	
-lnL(slow-growing coral)	-14.039		-11.679		-14.091		-14.176		-15.316	
<b>C) Abalone - urchin model</b>										
<i>Estimated parameters</i>	Value	SD	Value	SD	Value	SD	Value	SD	Value	SD
Starting lobster biomass (MT)	314	381	265	*	494	0.520	242	*	494	0.520
Lobster-abalone interaction parameter 1	0.007	9.807	0.004	*	0.008	1.070	0.007	*	0.899	1.380
Lobster-abalone interaction parameter 2	5.768	8.457	5.770	*	6.000	10.700	5.768	*	0.658	1.030
Lobster-urchin interaction parameter 1	0.0019	0.006	0.002	*	0.004	0.0004	0.003	*	0.004	0.0004
Lobster-urchin interaction parameter 2	0.0002	0.0004	0.000	*	0.0002	0.00003	0.000	*	0.0001	0.00004
Lobster spawning biomass carrying capacity	1510.6	1935	1550.000	*	1970.0	11.5	1575.0	*	759.0	0.59000
Surv <sub>decr_prop</sub>	-		-		-		-		0.327	0.089
BR <sub>decr_prop</sub>	-		-		1.000	0.001	-		-	
<i>Likelihoods</i>										
No. parameters estimated	6		6		7		6		7	
-lnL(total)	-156.716		-151.439		-158.498		-151.511		-168.660	
AIC	-301.432		-290.878		-302.996		-291.022		<b>-323.32</b>	
-lnL(abalone)	-144.927		-143.193		-145.240		-142.820		-157.576	
-lnL(interactions)	-11.789		-8.246		-13.258		-8.691		-11.084	

\* Hessian non positive definite

# not well-estimated

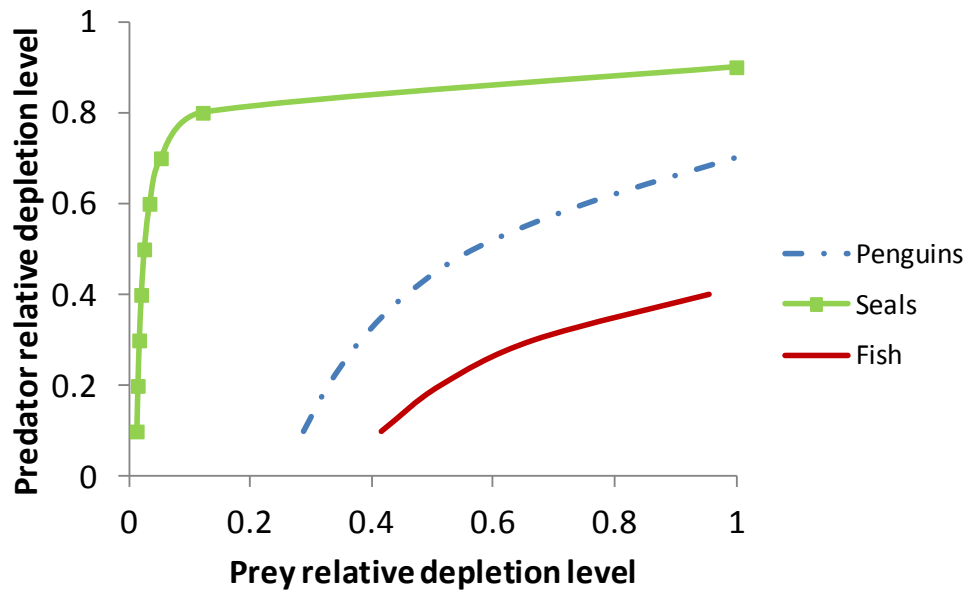


Fig. S1. Equilibrium solutions showing predator relative depletion as a function of prey relative depletion, for predator groups penguins, seals and fish, all preying on krill

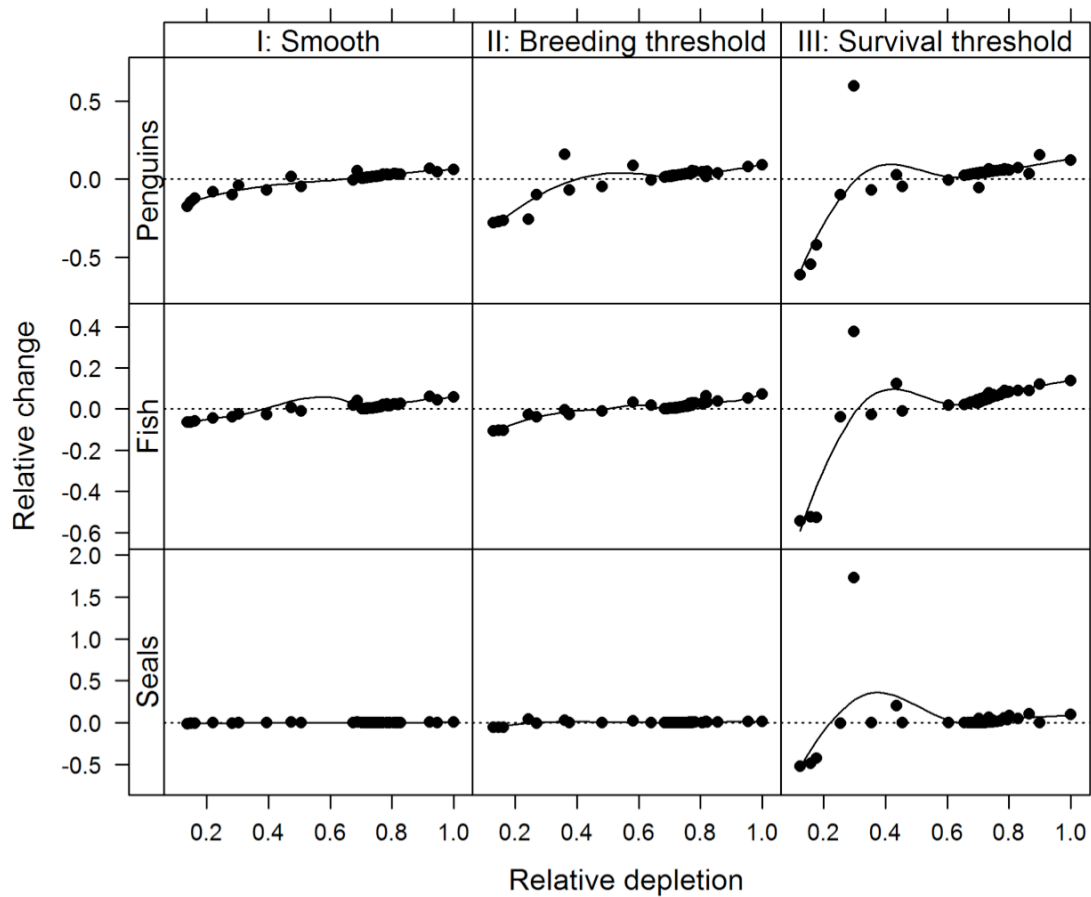


Fig. S2. Model-derived predator relative rates of change plotted against the relative depletion of krill, for penguins (top row), fish (middle) and seals (bottom row) under the assumption of Scenario I, a smooth continuous relationship between predator performance and prey abundance; Scenario II, a threshold response whereby predator breeding success decreases abruptly below a critical prey threshold level; and Scenario III, a threshold response whereby adult predator survival rate decreases abruptly below a critical prey threshold level. Relative depletion was calculated as the current (prey) abundance relative to the maximum observed value (used as a proxy for pristine abundance). Each curve is a local least-squares regression (loess) smooth with degree 2



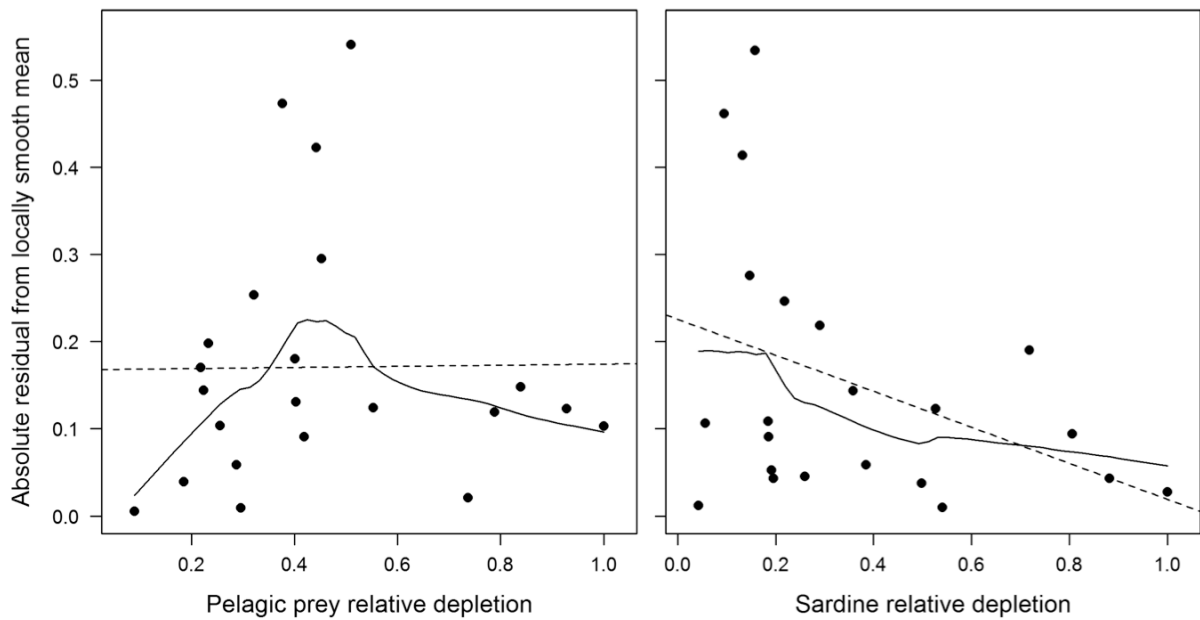


Fig. S3. Plots of absolute loess residuals versus depletion using the empirical data (and smooth curve) shown in Fig. 4,GH in the main text for the relationship between penguins and their combined prey (left panel) and penguins and sardine (right panel). The slope estimates are provided in Table 1 in the main text

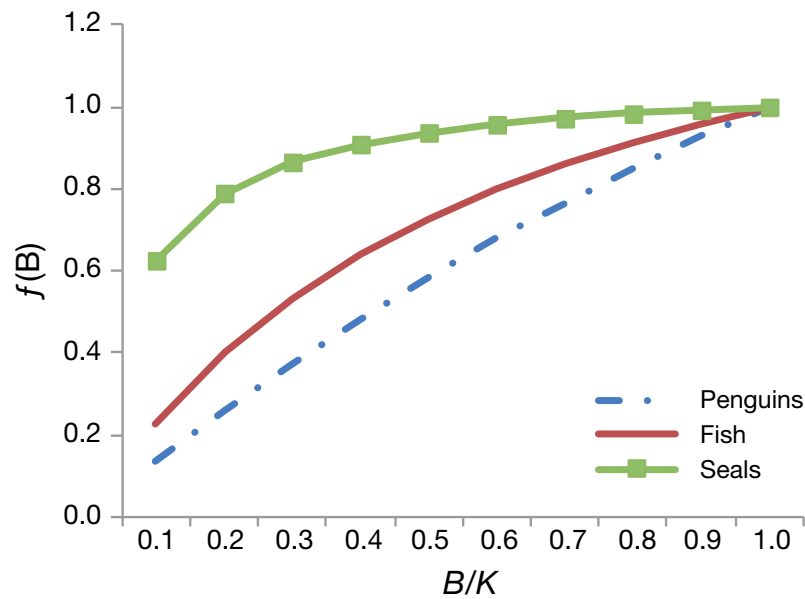


Fig. S4. Breeding success factor  $f(B)$  as a function of prey depletion ( $B/K$ ) level shown for the penguin, fish and seal groups, based on the steepness parameter  $h$  shown in Table S3

#### LITERATURE CITED

Plagányi ÉE, Butterworth DS (2012) The Scotia Sea krill fishery and its possible impacts on dependent predators: modeling localized depletion of prey. *Ecol Appl* 22:748–761