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CSD 4:

Report

Harbour seal decline: population modelling

Sea Mammal Research Unit
Report to
Scottish Government

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Editorial Trail			
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Contents

1 Executive summary

A baseline model was developed to estimate harbour seal (*Phoca vitulina*) demographic rates, such as fecundity and survival for different age classes. Count data and two independent estimates of population size based on capture-recapture photo-ID studies, were used to fit the model along with historical records of shooting of seals in the area. Modifications made to an earlier model (Matthiopoulos *et al.*, 2013) resulted in a more realistic and robust version. The estimated demographic trends are very similar to the original model but with a considerably better fit to the independent estimates. Using simulations based on the fitted model, the sensitivity of the population growth rate to different scenarios of fecundity, survival or seal management was investigated. The results of fitting the baseline model suggest that of the demographic trends, the fecundity rate appears to be the most variable in time and the parameter most sensitive to environmental changes. The most important age class in the population are the adult females (Harwood & Prime, 1978). If the adult female annual survival rate decreases by 5% per annum then the population will decline.

Next, the possible effects of other covariates that could potentially have an impact on these rates were investigated, including prey covariates: herring (*Clupea harengus*), Atlantic cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and sandeels (*Ammodytes marinus)*; environmental covariates: sea surface temperature (SST), North Atlantic oscillation (NAO) winter index; interaction covariates: counts of grey seals in northern Moray Firth; and biotoxin data: mussel concentration of saxitoxin and domoic acid. Over all the models two covariates were significantly different to zero, indicating a correlation between (a) grey seal (*Halichoerus grypus*) abundance and harbour seal pup survival, and (b) sandeel abundance and fecundity. With the grey seal abundance covariate included in the model the trend in the pup survival rate is very different to the one in the baseline model, with a decreasing pup survival rate linked to an increase in the grey seal population size.

Finally, to explore the potential to fit such models at sites where fewer data are available, the baseline model was modified such that only one part of the data was used to fit the model. Results were then compared with those obtained using the full data set. For the model run with only moult data either the fecundity rate was fixed using the value estimated by Cordes (2011) or an informative prior to the fecundity rate was set. The model overestimated the abundance but abundance trends were similar to estimates based on the full dataset. With a minimum of one breeding survey per year the results were much better. This time the non-pups were slightly overestimated but the fecundity and the pup survival trends were very close to the credible interval of the baseline model.

In conclusion, if the objective is to understand what parameters drive harbour seal vital rates (fecundity and survival), and to predict the status of the population, it is very important, as a minimum to collect both regular harbour seal moult counts and pup counts and to collect covariate data on potential drivers at a local level.

2 Introduction

The goal of this work was to evaluate and test different hypotheses about the causes of the harbour seal population decline based on the analysis of data from a single well-studied location, the northern Moray Firth.

First, a baseline model was developed to estimate harbour seal demographic rates such as fecundity and survival for different age classes. Count data, and two independent estimates of population size based on telemetry and capture-recapture photo-ID studies, were used to fit the model along with historical records of shooting of seals in the area. Using simulations based on the fitted model, the sensitivity of the population growth rate to different scenarios of fecundity, survival or seal management was investigated. Next, the possible effects of other covariates which could potentially have an impact on these rates were investigated: the model was fitted again to the seal count data and independent estimates, but also to covariate data including prey abundance, climate indices, and the local population size of grey seals. Finally, to explore the potential to fit such models at sites where fewer data are available, the baseline model was modified such as only one part of the data was used to fit the model. Results were then compared with those obtained using the full data set.

3 Baseline model

3.1 Methods

An age-structured, discrete time, population model was fitted to harbour seal count data collected during surveys of animals hauled-out during the breeding and moulting seasons in Loch Fleet. Two estimates of total population size based on photo-ID capture-recapture studies were also included as data points when fitting the model (these are referred to as ‘independent estimates’). A Bayesian hidden process method was used to estimate age and sex-specific survival rates and female fecundity. The original model presented in Matthiopoulos *et al*., (2013) was developed further:

- Data up to 2012 were used (Table 1).
- The original two-peak seasonal model of haul out probability was changed to a step-function model that includes two different estimates of haul out probability, one for breeding and one for moult and specific to each age class and sex. A daily variability representing the ‘noise’ around each average haul out probability was added to the constant baseline probabilities. This daily variability can be due to; individual variation (breeding or not breeding, stage of moulting, body condition and food requirements), anthropogenic disturbances prior or during the survey, and environmental conditions (tide, weather conditions, food availability).
- The model now allows that some animals counted at moult (a small proportion) might be pups born in the same year.
- The time-dependence in survival and fecundity has been simplified, reducing the number of parameters in the model. Vital rates are now linear functions of time with a density-dependent term.
- The division of the population between the main haul outs in Loch Fleet and other haul outs that are only included in the aerial surveys (e.g. at Brora) is explicitly modelled.

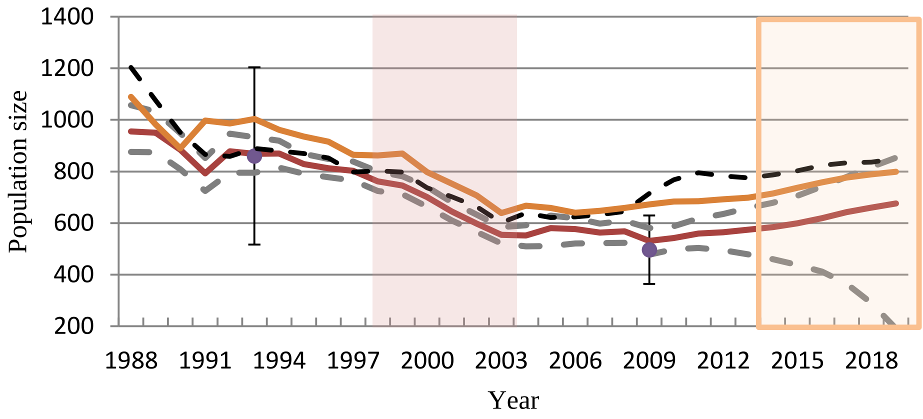
4 Results

These modifications make the model more realistic and robust. The estimated demographic trends are very similar to the original model with a considerably better fit to the independent estimates (Figure 1).

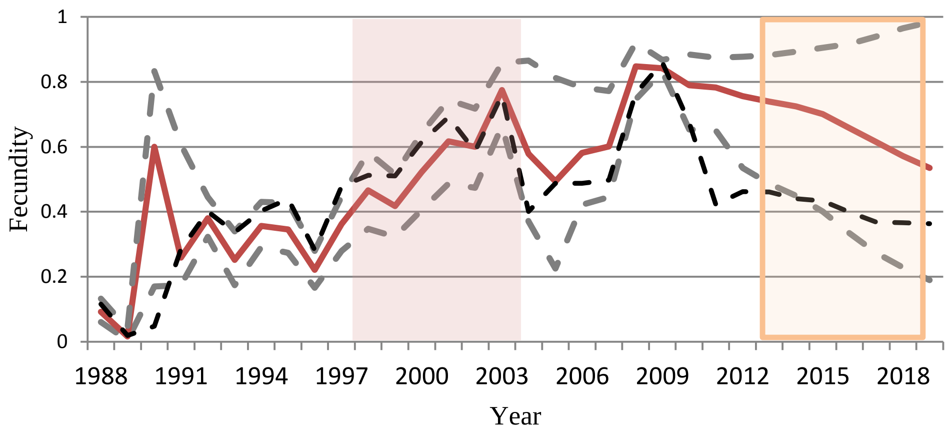
Table 1. Length of time series for all the data (counts and covariates) used in this project.

		1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
	Survey types	**Ground**																		**Ground and aerial**	**Aerial**					
Harbour Seals	No of Breeding Surveys	2	6	2	0	2	8	4	5	5	5	5	5	5	5	5	5	2	4	10	4	5	4	5	4	4
	No of Moult Surveys	1	1	1	2	2	10	0	2	2	0	3	2	5	3	2	2	2	2	2	2	2	1	1	1	1
Grey Seals	No of surveys																			5	4	5	4	5	4	4
	Independent estimate						1																1			
	Herring																									
	Cod																									
	Sprat																									
	Sandeels																									
	SST																									
	NOA																									
	Saxitoxin																									
	D.A																									

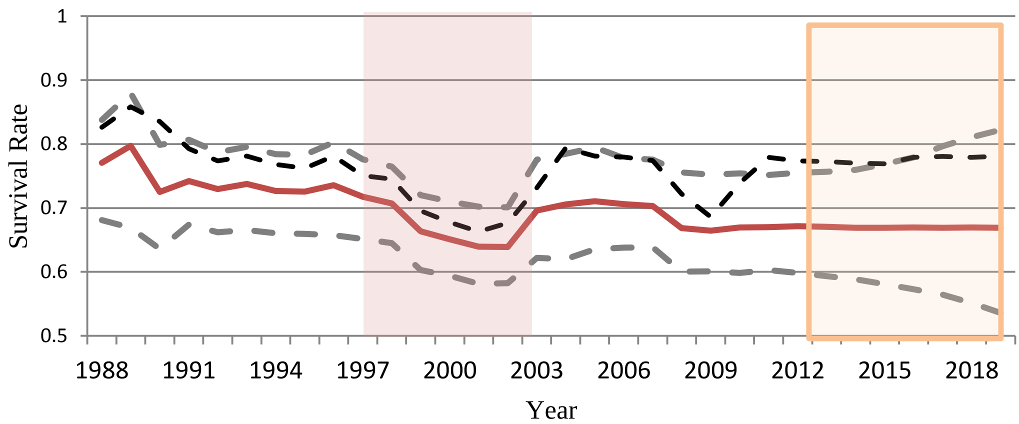
a) Population size



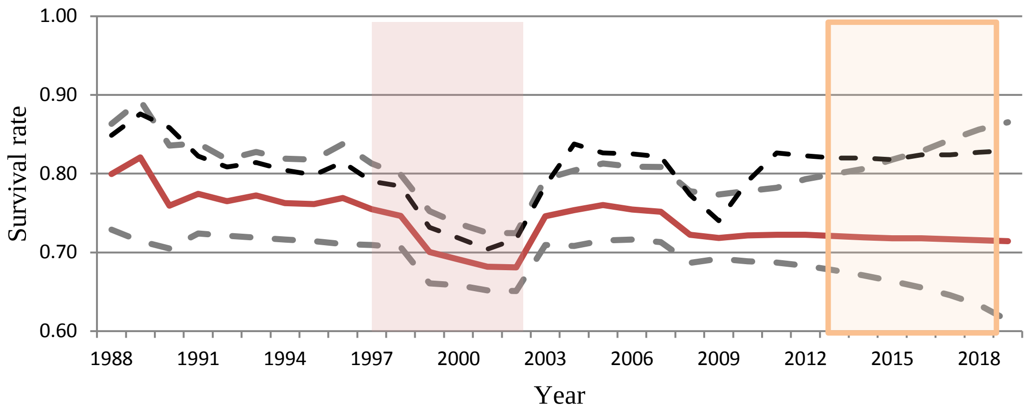
b) Fecundity



c) Pup survival



d) Juvenile survival



e) Adult survival (Females)

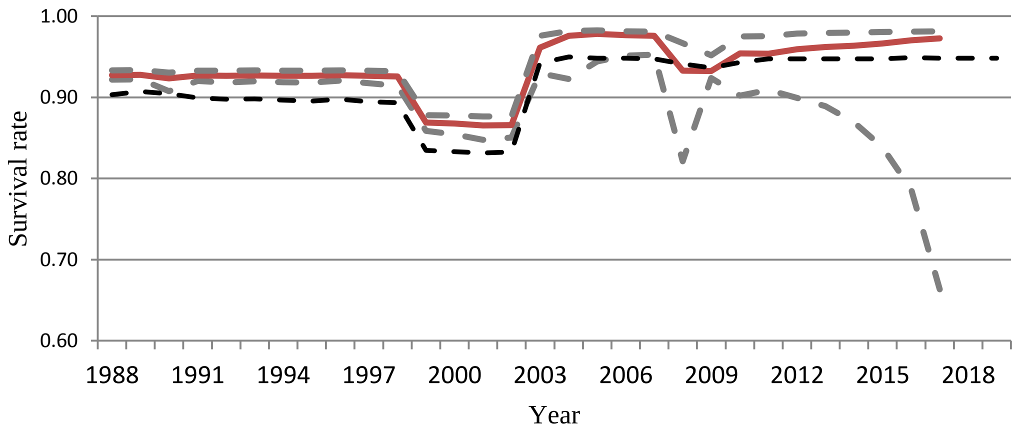


Figure 1. Demographic trends (a) population size, (b) fecundity rate, (c) pup survival, (d) juvenile survival, (e) adult female survival of the baseline model (median red) with 95% confidence intervals (grey dashed lines) compared with the results (black dashed line) of Matthiopoulos *et al.*, (2013). The red area illustrates a period of intense shooting whereas the orange area indicates years where the model predicts forward in time. In Figure 1(a) the two points are the independent estimates of the population size excluding pups.

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Based on this model the observed number of counts in 2013 was compared with the model prediction for 2013 (Table 2). This comparison showed that the observed number of counts in 2013 fall within the 95% confidence interval of the 2013 predictions. In 2013, four breeding surveys were carried out. The count of pups for the first survey was very low (15) in comparison with the counts for the remaining breeding surveys (average of 116). This was probably because the first survey was very early in the breeding season and consequently only few pups had been born. When this first survey was included in the comparison with the model prediction, the observed data were close to the lower limit of the confidence interval. However, once removed the observed data were closer to the average of the predictions (number in parenthesis in Table 2).

Table 2. Predicted and observed counts of harbour seals in the Northern Moray Firth sites in 2013. The non-pups count includes one year and older animals. The observed counts contain the minimum and maximum number of counts over the four surveys and the average number of counts for the four surveys. The numbers in the parenthesis do not include the first breeding survey of the year.

	Predicted			**Observed**		
	Lower 95% CI	Mean	Higher 95% CI	Min	Mean	Max
Non pups	255	331	422	225 (228)	261 (273)	306 (306)
pups	78	112	71	15 (99)	90 (116)	130 (130)

4.1 Model

4.1.1 Methods

The model was adapted with the objective of quantifying the possible contribution of specific environmental mechanisms (for example inter-species competition, prey availability, climate variation, biotoxin exposure) to shaping observed dynamics.

The effects of four categories of direct or indirect covariates were explored and were added to the baseline model:

- Prey covariates: herring (*Clupea harengus*), Atlantic cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and sandeels (*Ammodytes marinus*).
- Environmental covariates: sea surface temperature and North Atlantic oscillation winter index
- Interaction covariates: counts of grey seals in northern Moray Firth
- Biotoxin data: concentration of saxitoxin (STX) and domoic acid (DA) in mussels

The extent of the time series coverage of the different covariates are also summarised in Table 1.

The prey species tested covered the range of different types and nutritional qualities present in the diet of harbour seals (Wilson, 2014). Atlantic cod are a gadoid species which is considered to be a fish of low nutritional value (Fritz & Hinckley, 2005; Wilson, 2014). Herring, sprat and sandeels are all classified as highly nutritional fishes (Wilson, 2014). The data for all species, except sandeels, were collected from the International Council for the Exploitation of the Seas (ICES) website (http://www.ices.dk/ accessed July 2015) and the standing stock biomass (SSB) value of the year for the North Sea was used as an indicator of the fish abundance in the Moray Firth area (ICES, 2012). Sandeels are an important part of harbour seal diet, but it was not possible to find reliable data about the sandeel stock in the Moray Firth. However, as several studies have shown a correlation between black-legged kittiwake (*Rissa tridactyla*) breeding success and sandeel availability (Frederiksen *et al*., 2005; Harris & Wanless, 1997), this parameter was used as a proxy for sandeel abundance.

The sea surface temperature (SST) and the North Atlantic oscillation (NAO) winter index were collected respectively from the National Oceanic and Atmospheric Administration (NOAA) and University Corporation for Atmospheric Research (UCAR), Climate Data Guide websites (http://www.ospo.noaa.gov/Products/ocean/sst/contour/ and https://climatedataguide.ucar.edu/climate-data/ respectively, accessed July 2015). Two types of SST data were tested; both are an average of the SST for the Moray Firth but over different periods of time. The first period of time was from March, year t-1, to May of the breeding year and the second between May to September of the breeding year. The decision to test the two SST time series was based on the hypothesis that the SST has either a long term impact on population dynamics (through affecting the fecundity rate) or a short term impact (affecting pup and juvenile survival).

The interaction covariate tested the relationship between harbour seals and the population of grey seals present in the same area. The count of grey seals hauling out on the study sites started in 2006. Counts varied between surveys, so where counts were available, the average number of grey seals observed in a given year was used in the model. Prior to this date no local data were available. So the ratio (estimated using a linear model estimated from the count data and abundance estimate for the North Sea, from 2006 to 2013) between the count of grey seals in the northern Moray Firth and the estimate of the total population size of grey seals in the North Sea was used multiplied by the estimate of the North Sea population before 2006 (Thomas, 2012).

The last set of covariates tested focussed on the impact of biotoxins produced during harmful algal blooms (HABs). The STX and DA biotoxins were selected as they are regularly detected in the Scottish waters. The presence of STX in the water column and particularly if ingested in the prey can result in very rapid mortality. DA can have both acute and chronic effects and has caused mass mortalities among other pinnipeds worldwide (Hall & Frame, 2010). DA can also potentially have an impact on the reproductive success as exposed females can abort their pups (Hall & Frame, 2010).

Each covariate was tested individually in the baseline model by including it in the linear predictor for the fecundity function or the survival function, with an associated multiplier which was estimated during model fitting. If this coefficient was significantly different to zero then this is evidence that the covariate has an effect on survival or fecundity ('significantly different' means that the 95% Bayesian credible interval around the estimate does not span zero). In addition, for some models, a prior sensitivity analysis was conducted.

4.1.2 Results

More than 35 models were tested. Table 3 presents a summary of the models, with the median and credible interval for the covariate coefficients.

In almost all the models two covariates were significantly different from zero, indicating a correlation between (a) grey seal abundance and harbour seal pup survival and (b) sandeel abundance and fecundity.

The sandeel covariate was positively correlated with the fecundity rate (Figure 2). However the impact on the breeding rate was small. An increase in the normalised black-legged kittiwake breeding success from -1.5 to 2 generated an increase of 5% in the harbour seal fecundity rate (Figure 3). All the demographic trends showed only a very small difference compared to the baseline trends.

The second covariate showing an impact on the demographic trends was the grey seal covariate. When added to the survival function of the pups, the posterior distribution was negative (Figure 4).

With this covariate included in the model the trend in the pup survival rate was very different to the one in the baseline model with a decreasing pup survival rate linked to an increase in the grey seal population (Figure 5, pup survival). To compensate, this decreases the juvenile survival which is higher than the one predicted by the baseline model. The abundance estimate of the non-pups is closer to the 2009 independent estimates than with the baseline model. The most important difference between the two models can be observed at the end of the time series. Indeed from 2008 the abundance trends start to differ between the two models, with an increase in the population with the baseline model and a decrease in the population with the model including the grey seal data. The prediction after 2012 was totally the opposite. This difference was due to a succession of consecutive years with fewer pups, generating lower juveniles and adults combined with a continuous prediction of a high number of grey seals by the model. Figure 6 shows that if there are more than 800 grey seals hauling out for 10 years, the harbour seal population declines. Since 2006, grey seal counts were approximately 800 or more in 60% of the years. The demographic trends when the grey seal covariate was added to the baseline model for pup survival are shown in Figure 7.

Table 3. Models tested to identify a possible correlation between covariates and demographic trends. The column headed 'Hypothesis' explains briefly how the covariates may influence fecundity or survival. The 'In model' column describes which demographic rate is influenced by the covariate (i.e. has the covariate as a term in the linear predictor). The "Covariate prior value" shows the prior values used when sensitivity analyses were conducted. The posterior values are the Bayesian credible intervals and medians for the covariate parameters. Highlighted in grey are the parameters whose posterior differs significantly from zero.

	Hypothesis	**Covariates**	**In model**	**Covariate prior value**	**Posterior values**		
Prey	Lack of food impacts fecundity and/or pregnancy success and pup survival	Herring	Fecundity	*cov=0.03*	-0.02669	-0.009804	0.01897
			Pup surv	*cov=0.03*	-0.08213	-0.002418	0.08156
		Cod	Fecundity	*cov=0.03*	-0.02073	0.007702	0.02644
			Pup surv	*cov=0.07*	-0.02386	0.001169	0.02495
			Pup surv	*cov=0.03*	-0.02386	0.001169	0.02495
		Sprat	Fecundity	*cov=0.03*	-0.02192	0.005099	0.0258
			Fecundity	*cov=0.07*	-0.07239	0.02342	0.08761
			Pup surv	*cov=0.03*			
		Sandeels	Fecundity	*cov=0.03*	-0.02171	0.006605	0.02619
			Fecundity	*cov=0.1*	0.000669	0.07019	0.09556
			Pup surv	*cov=0.1*	-0.07675	0.01131	0.08473
			Pup surv	*cov=0.03*	-0.02385	0.001368	0.02478
			Fecundity + Pup surv	*none*	-0.01916	0.009601	0.02684
Predator	Inter-specific competition for food – results in increased pup mortality	Grey Seals	Pup surv from 1988	*cov=0.05*	-0.04348	-0.007327	-0.0023
			Pup surv from 1988	*cov=0.03*	-0.00503	-0.002569	-0.00112
Environment	SST and NAO may have a direct impact on plankton production and on the food web	SST	Fecundity	*Mch-May*	-0.04432	-0.0152	0.03144
			Fecundity		-0.09153	-0.04076	0.05875
			Pup surv	*Mch-Sept*	-0.04008	0.000427	0.0404
		NAO (winter index)	Fecundity	*cov=0.03*	-0.03386	0.01198	0.04355
			Pup surv	*cov=0.05*	-0.04044	2.72E-05	0.04064
			Pup surv	cov=0.1	-0.08308	-0.004108	0.0794
			Breeding	cov=0.1	-0.07997	0.02144	0.08965
			Non pup surv	cov=0.1	-0.08452	-0.006132	0.08088
	Causes neurological effects - disorientated animals and impacts on fecundity	DA	Fecundity	cov=0.1	-0.08782	-0.00624	0.08357
			Non-pup surv	cov=0.1	-0.08781	-0.02022	0.07694
			Pup surv	cov=0.1	-0.08308	-0.004108	0.0794

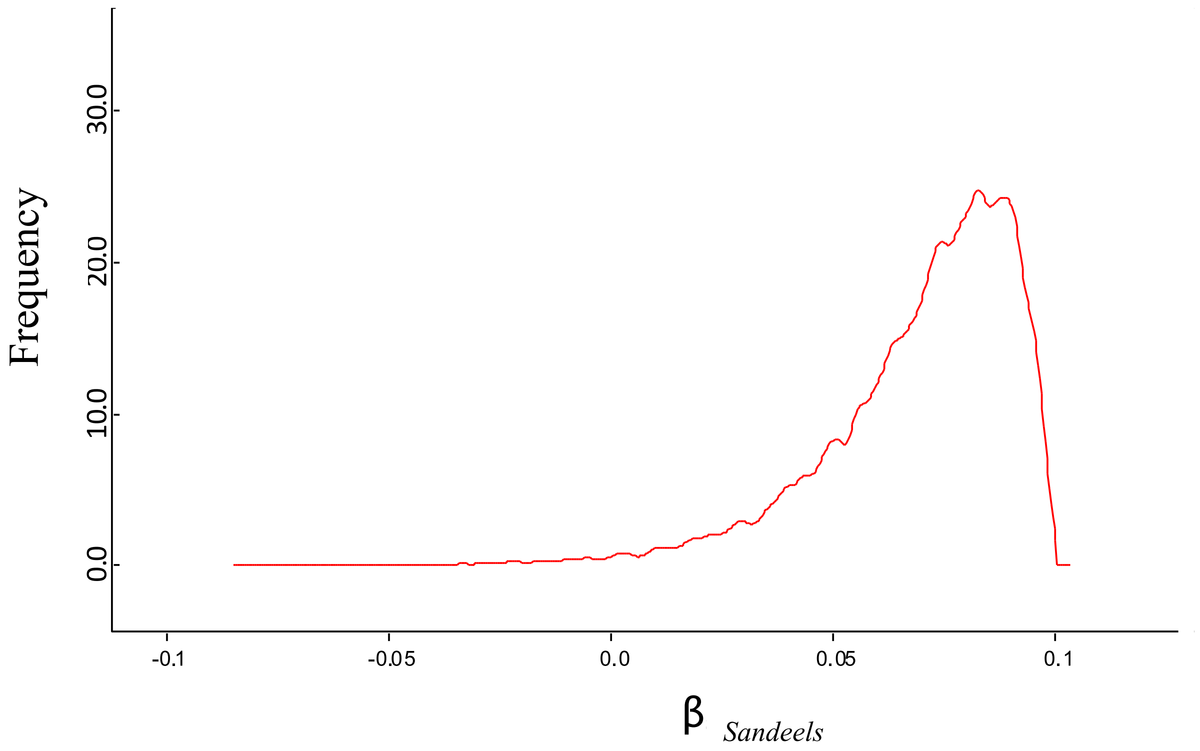


Figure 2. Posterior distribution of the sandeel coefficient ($\beta_{sandeels}$) in the logistic equation for fecundity.

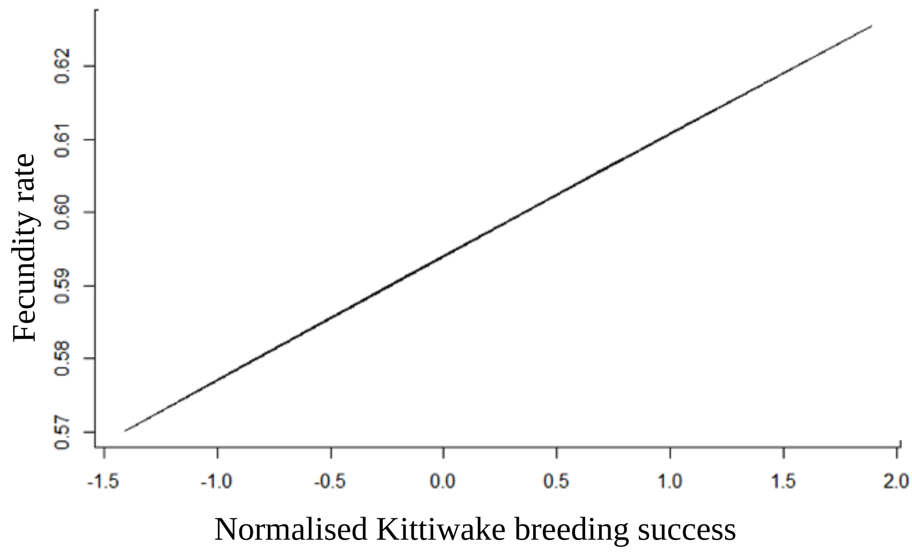


Figure 3. Correlation between the fecundity rate and the normalised breeding success rates for black-legged kittiwakes.

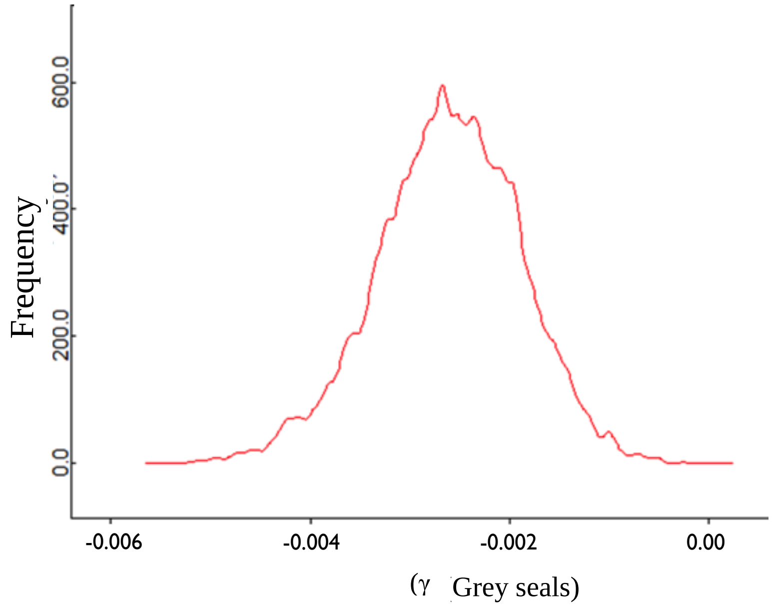


Figure 4. Posterior distribution of the grey seal coefficient (γ grey seals) in the logistic equation for fecundity.

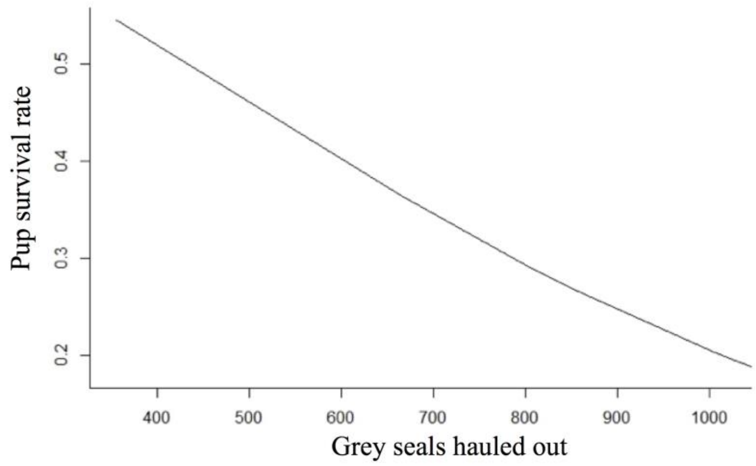


Figure 5. Correlation between the harbour seal pup survival rate and the number of grey seals on the haul-out sites.

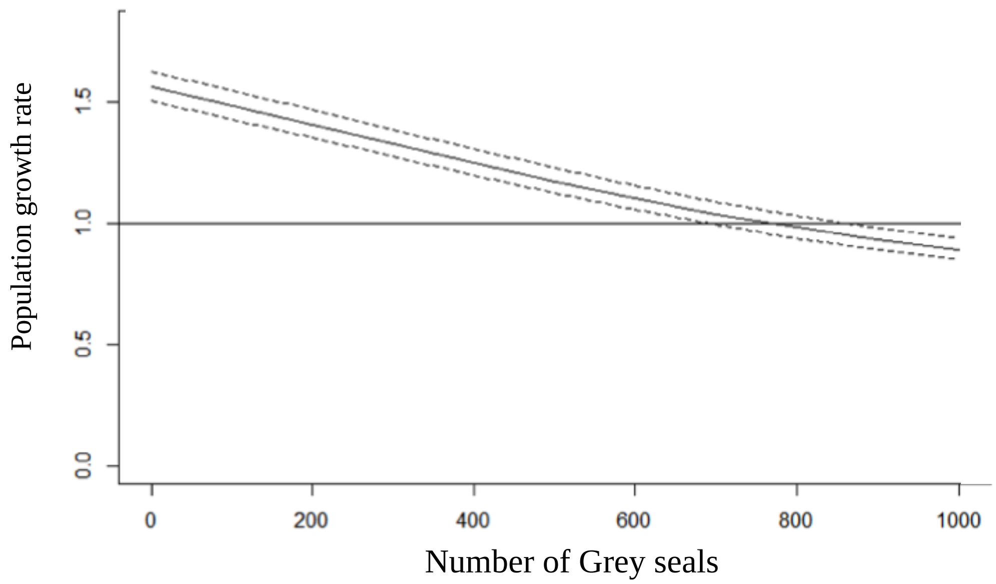
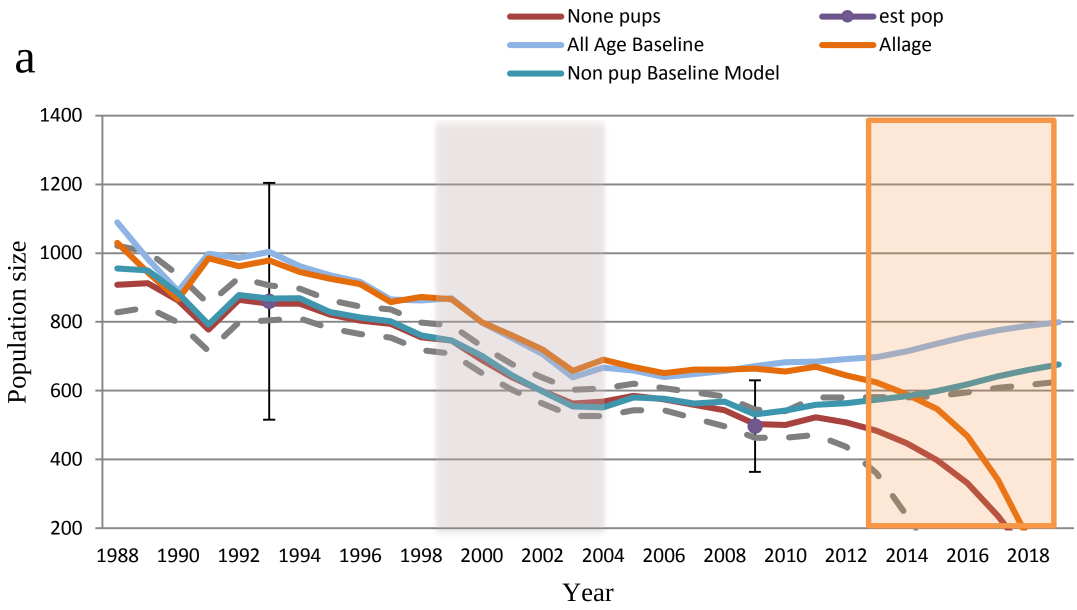
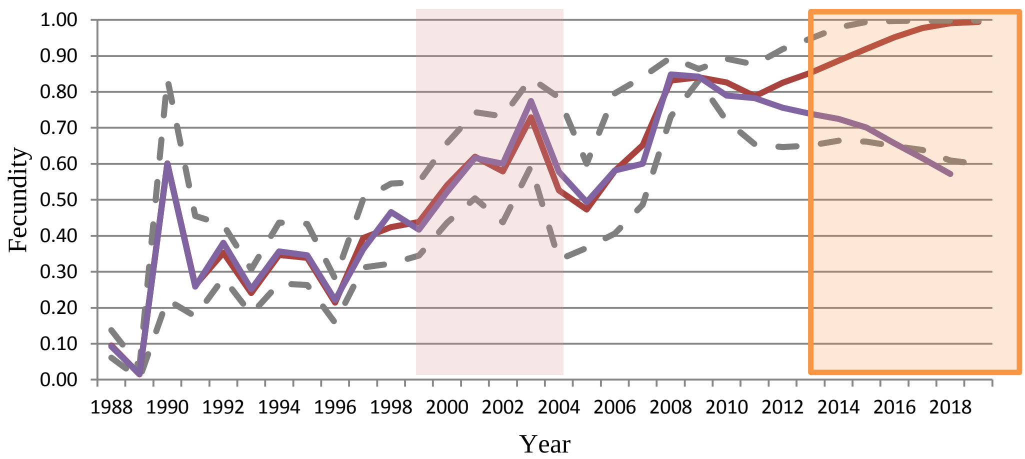


Figure 6. The Moray Firth harbour seal population growth rate over 10 years as a function of the size of the local grey seal population.

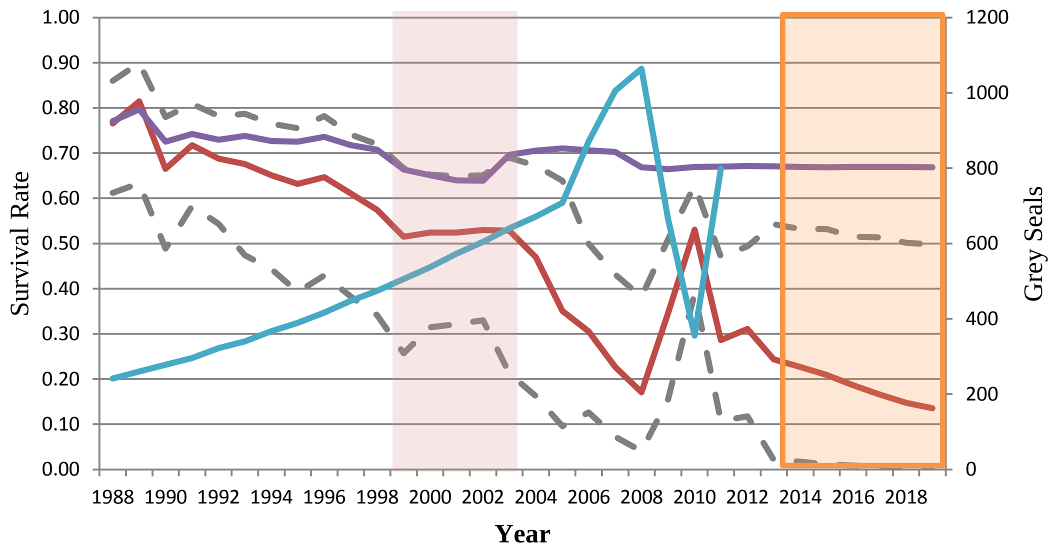
a


None pups
est pop
All Age Baseline
Allage
Non pup Baseline Model
1400
1200
1000
800
600
400
200
Population size
1988 1990 1992 1994 1996 1998 2000 2002 2004 2006 2008 2010 2012 2014 2016 2018
Year

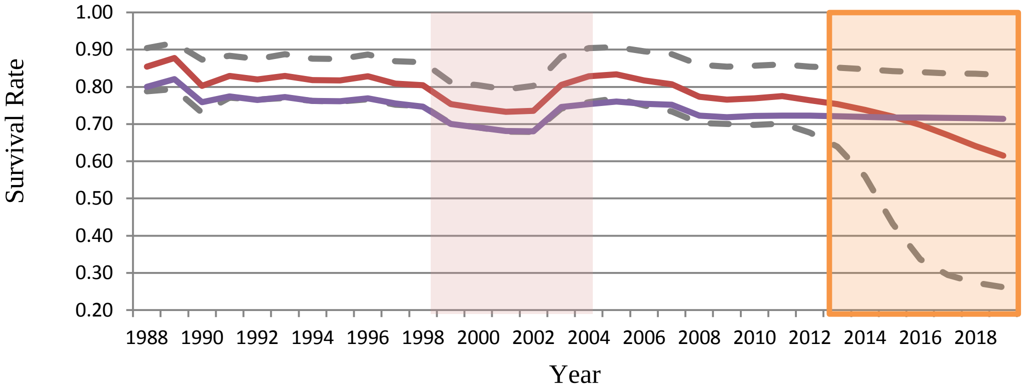
b


1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Fecundity
1988 1990 1992 1994 1996 1998 2000 2002 2004 2006 2008 2010 2012 2014 2016 2018
Year

c


1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Survival Rate
1200
1000
800
600
400
200
0
Grey Seals
1988 1990 1992 1994 1996 1998 2000 2002 2004 2006 2008 2010 2012 2014 2016 2018
Year

d



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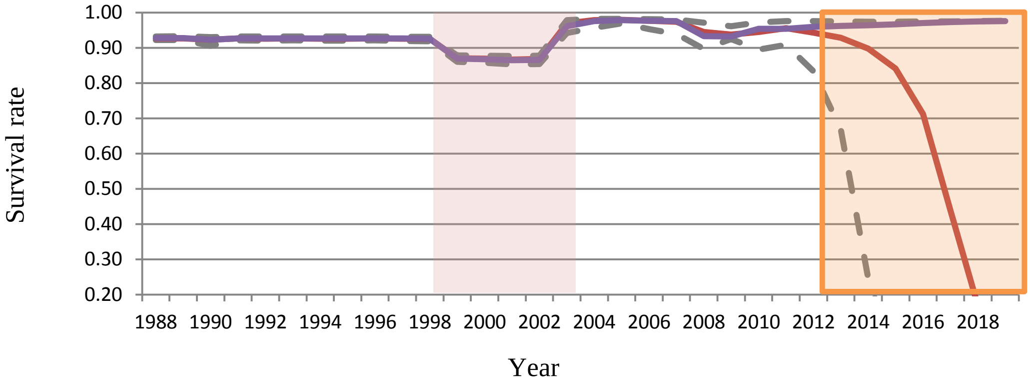
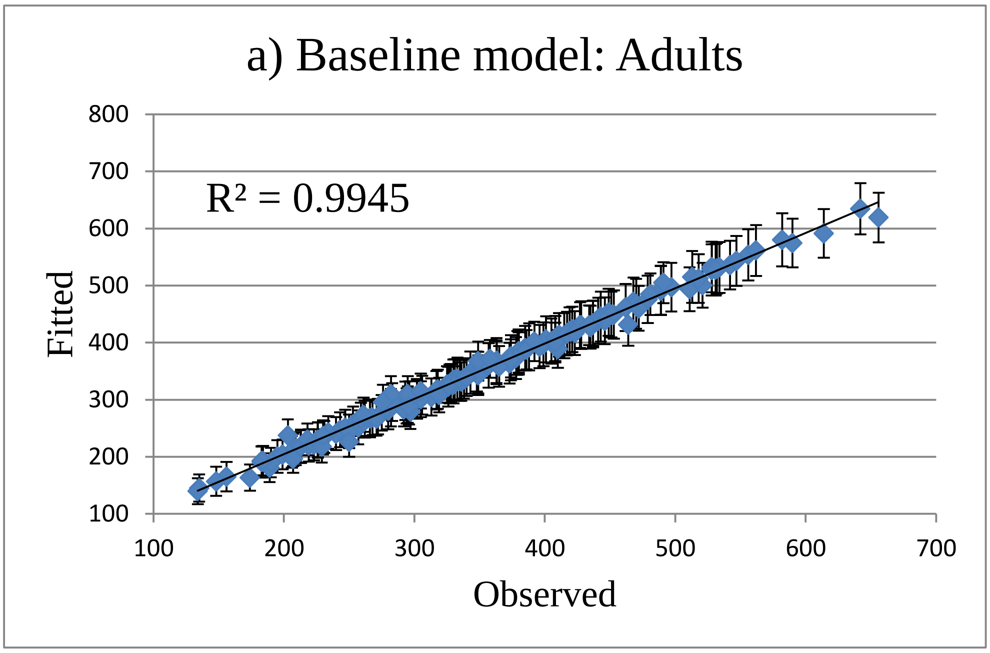
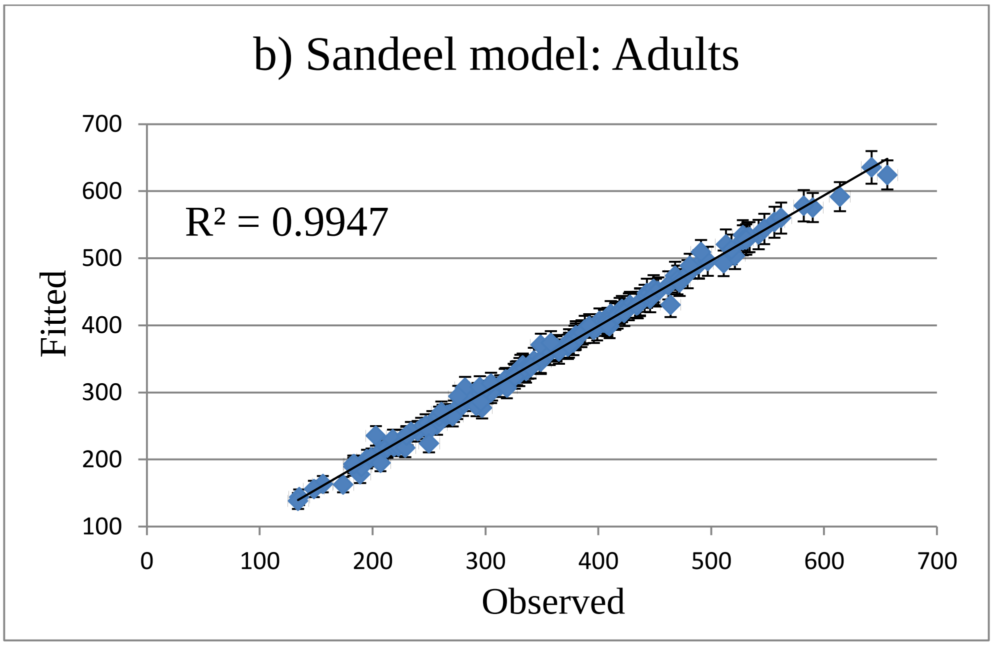
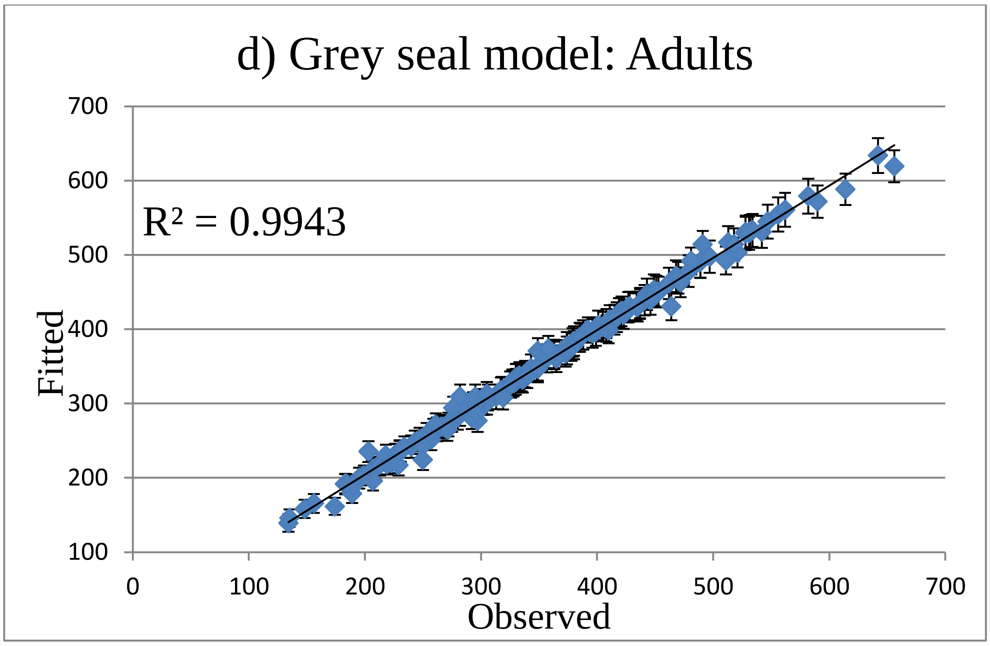


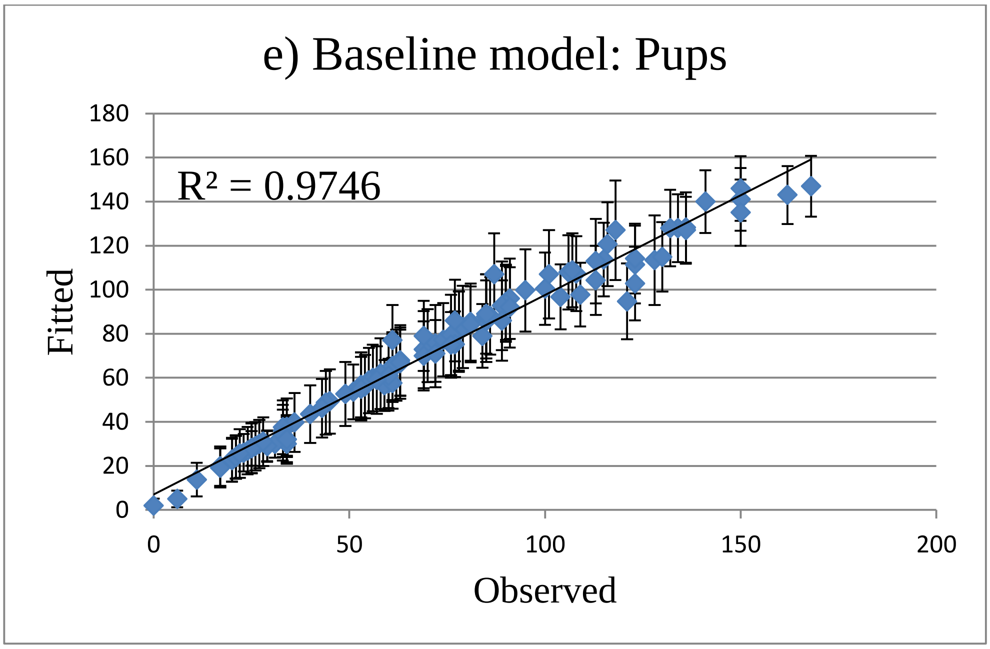
Figure 7. Demographic trends (red and grey curves 95% CIs): (a) population size (b) fecundity (c) pup survival (d) juvenile survival (e) adult female survival when the grey seal covariate is added to the baseline model for pup survival (purple lines). The red area illustrates the period of intense shooting whereas the orange area shows model predictions. In the pup survival plot, the blue line is the average number of grey seals counted at local haul-out sites.

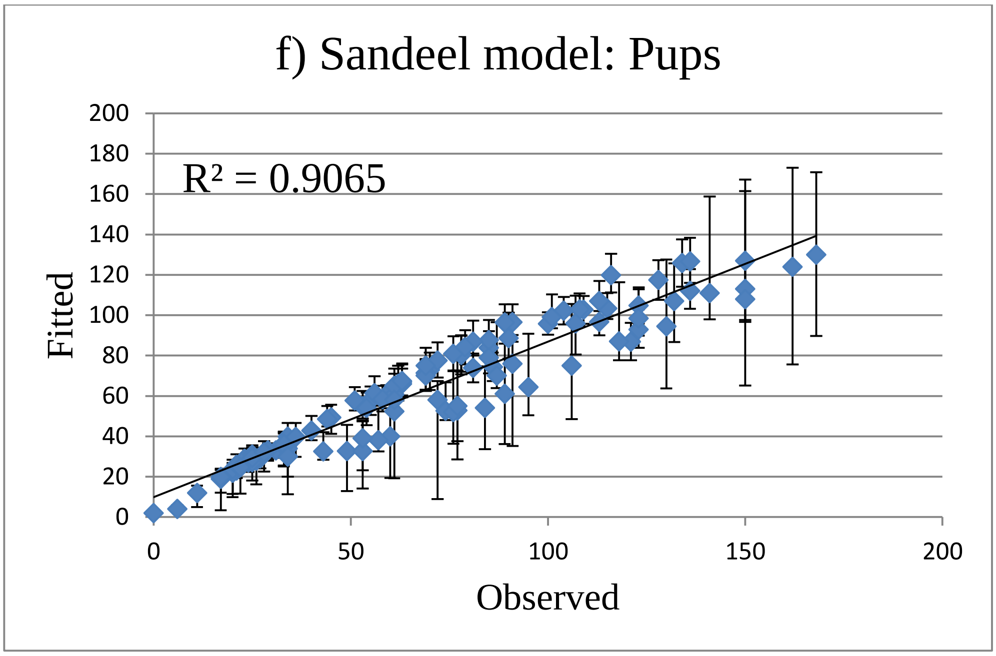
To determine which model best fitted the data the value of R^2 was calculated. For all models R^2 was greater than 90% with a better fit to the adult data (Figure 8). Adding the grey seal covariate slightly improved the R^2 for the pup data whereas adding the sandeel covariate improved R^2 for the adult data (Figure 8).


a) Baseline model: Adults
R² = 0.9945
Fitted
Observed
800
700
600
500
400
300
200
100
100
200
300
400
500
600
700


b) Sandeel model: Adults
R² = 0.9947
Fitted
Observed
700
600
500
400
300
200
100
0
100
200
300
400
500
600
700


d) Grey seal model: Adults
R² = 0.9943
Fitted
Observed
700
600
500
400
300
200
100
0
100
200
300
400
500
600
700


e) Baseline model: Pups
R² = 0.9746
Fitted
Observed
180
160
140
120
100
80
60
40
20
0
0
50
100
150
200



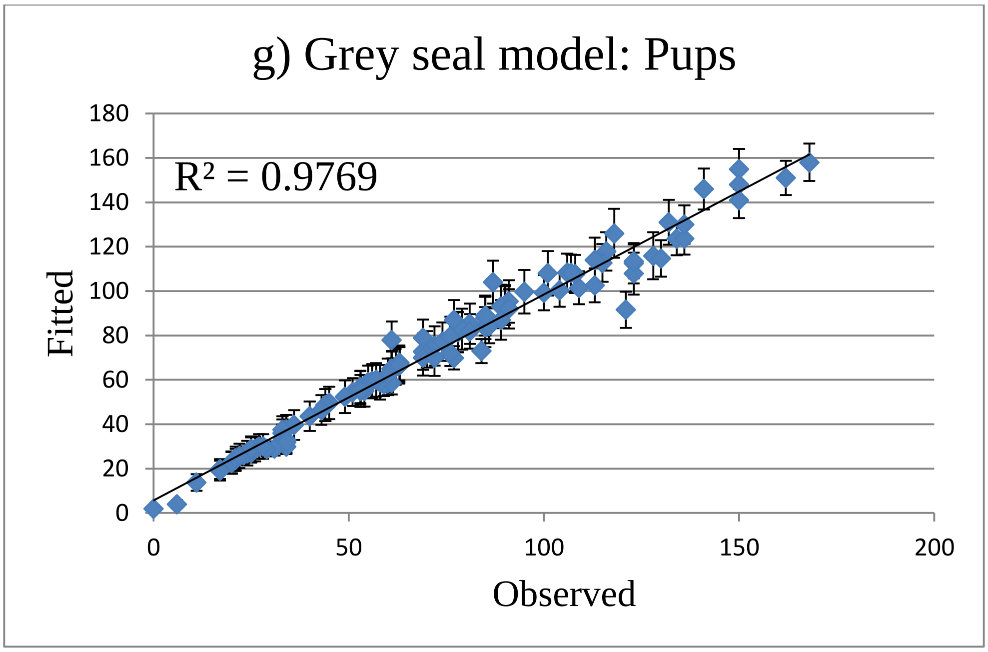


Figure 8. Observed versus fitted data with the R^2 value for (a and e) the baseline model; (b and f) the model with the sandeel covariate and (c and g) the model with the grey seal covariate for both the adult and pup predictions.

5 Obtain population projections for the future given particular environmental scenarios

The posterior parameters were extracted from the 2012 baseline model and demographic trend predictions for the next 10 years, with different scenarios, were carried out. As shown in the studies including the covariates, environmental or biological parameters will have an impact on the demographic rates and consequently on the abundance trend. The potential impact of environmental change was simulated by varying the demographic trends one at a time; the growth rate of the population over the 10 years of predictions was then calculated. Four scenarios were investigated:

- Change in the fecundity rate.
- Change in the survival rate in different age classes.
- Direct mortality of individuals in different age classes.
- Impact of the local grey seal population size.

The results of fitting the baseline model suggest that of the demographic trends, the fecundity rate appears to be the most variable in time and it is suggested that this parameter is most sensitive to environmental change. To simulate the impact of a decreasing fecundity rate in the population the survival rates were allowed to vary according to the prediction of the baseline model. For each simulation the fecundity rate was decreased from 5% to 50% of the predicted value in 2012 (by steps of 5%). After each simulation the net population growth rate over 10 years with these specific parameters was calculated (Figure 9).

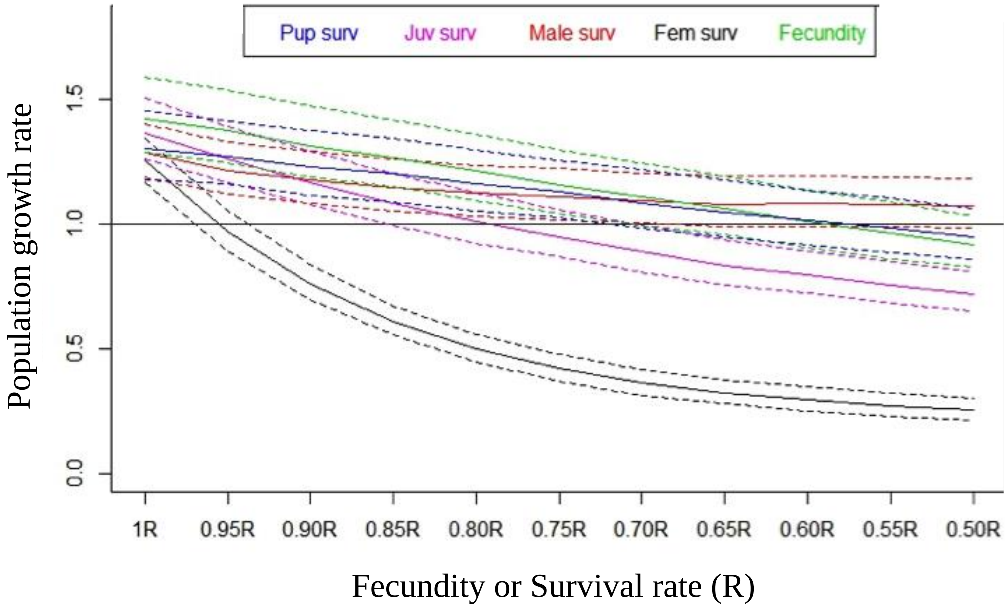


Figure 9. Population growth rate over 10 years under different scenarios of changes in fecundity and survival rates.

The same simulation was carried out with a stochastic fecundity rate but the survival rate of the pups, juveniles, adult males and adult females were fixed with values ranging from 50% to 95% of the estimated survival rates in 2012.

Finally to simulate the impact of additional mortality (e.g. due to boat collision) on the different age classes, between 1 to 50 individuals of a specific age class were removed every year, and the impact of such additional mortality on the growth rate of the population over 10 years was recorded. Also a mortality rate varying from 0.5% to 20% was simulated.

This work showed that the most important age class in the population are the adult females, a conclusion highly consistent with earlier studies (Harwood & Prime, 1978.) If the adult female survival rate decreases by 5% then the population will decline (Figure 9). By contrast, the other demographic parameters would need to decrease between 20% (juvenile) and more than 50% (adult males) for the population to decline (Figure 9). The male age category has the lowest impact on the population growth rate, even with a drop of 50% in the adult male survival rate, after 10 years the population will still be growing but at a slower rate (1% per annum).

Consistent with the demographic rates above, any additional adult female mortality will have a substantial impact on the total population size. If an additional 12 females in the northern Moray Firth population die every year over a 10 year period the population will decline (Figure 10). More generally if there is a factor generating a decrease of 3% in the survival rate for all age classes, the population will decline in 10 years (Figure 11).

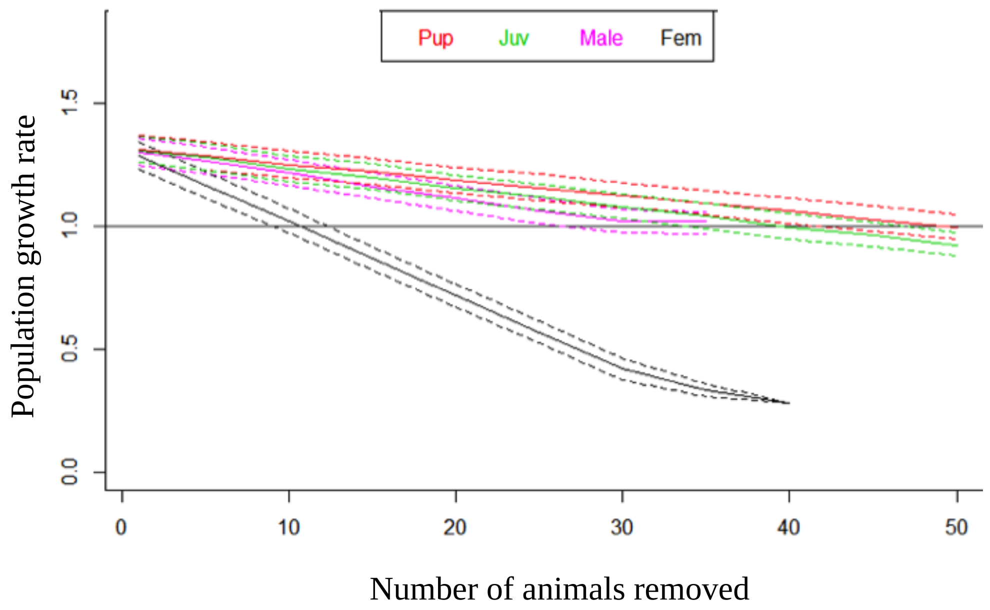


Figure 10. Population growth rate over 10 years, with additional mortality affecting an increasing number of animals in different age classes.

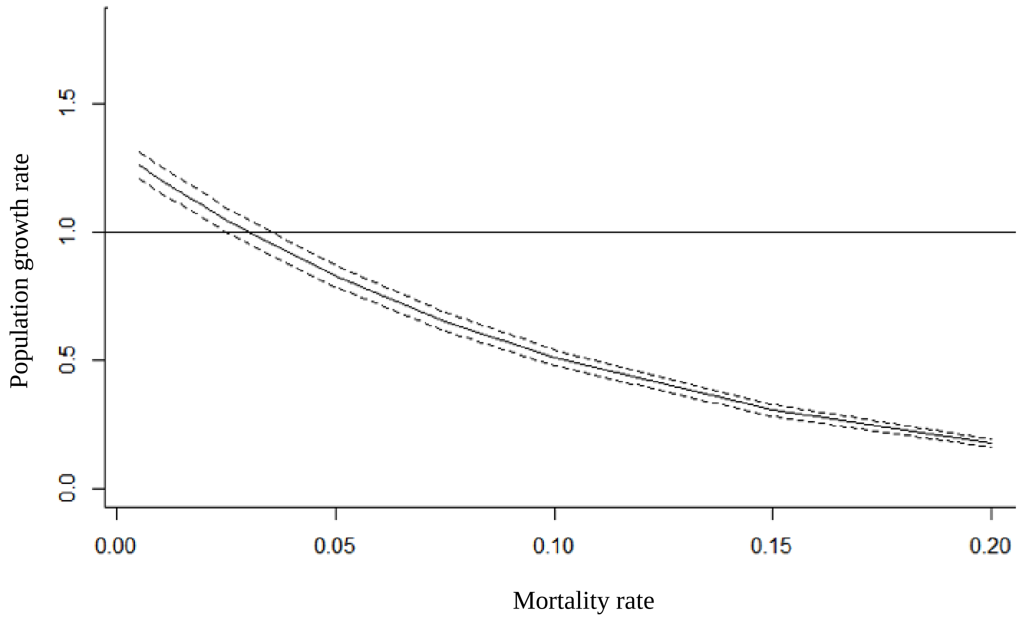


Figure 11. Relationship between population growth rate over 10 years and an increasing mortality rate (from 5% to 20%).

The interaction with grey seals seems to have an impact on the population growth rate. If the number of grey seals hauling out during the harbour seal surveys remains above an average of 800 individuals for 10 years, then the harbour seal population is predicted to decrease.

6 Evaluate the sensitivity of model results to the availability of survey data

It is important to note that the count data used in this study are exceptional due to the long time series and the number of repeated surveys per year (Table 1). All the other time-series count data at Scottish sites are collected during the moult, with very few or no breeding season counts. Thus different scenarios of 'reduced' data were investigated (extracted from the original data set) to determine the minimum quantity of data necessary to obtain a result close to the model with the full dataset.

Two approaches to simulate these datasets were evaluated:

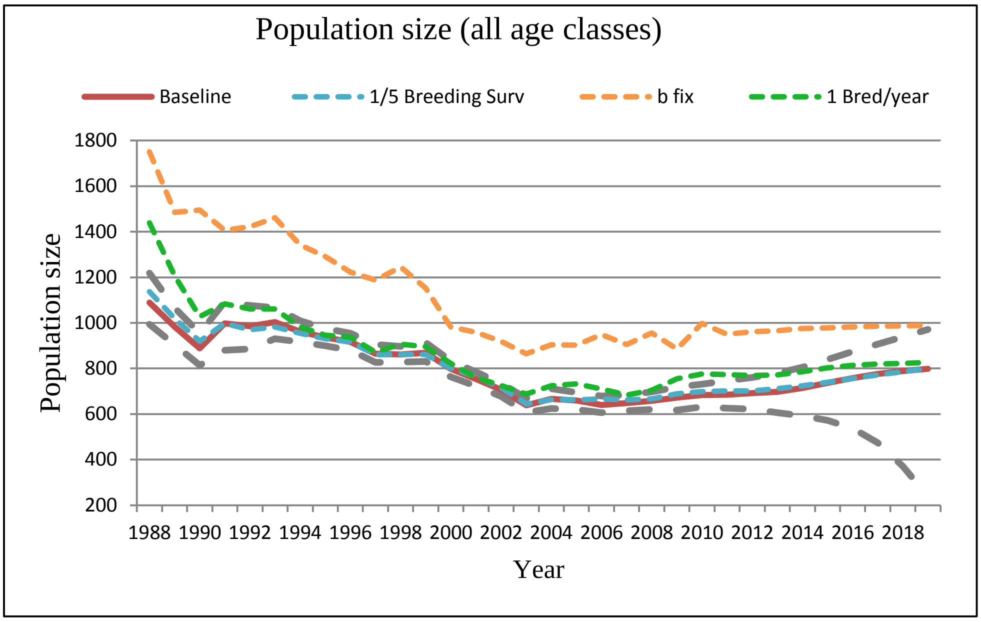
- Only the moult data.
- The amount of breeding surveys was decreased to determine if it is possible to identify a minimum frequency of breeding surveys required for reliable results. The different scenarios of breeding survey pattern tested are presented in Table 4.

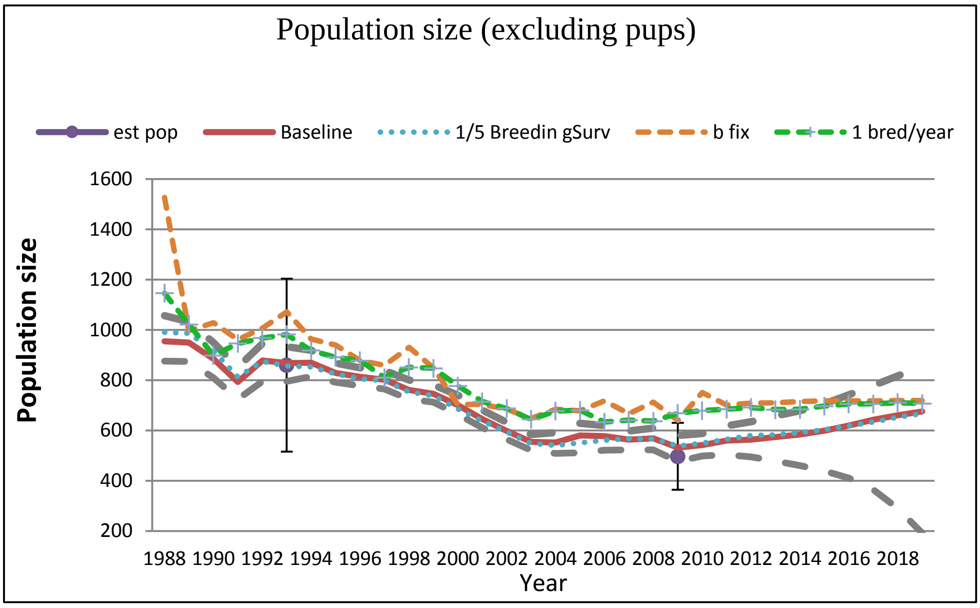
Table 4. Summary of the model tested with different types of dataset.

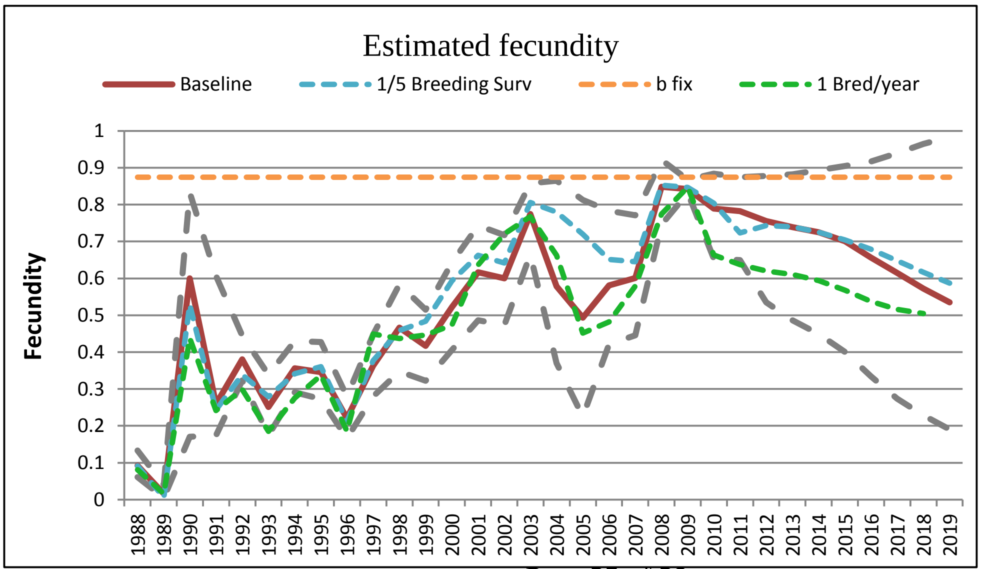
Data used	Breeding survey pattern	Summary of results
Moult data only	Fecundity fixed at a constant value	Over-estimation of population size; pup and juvenile survival very variable, falling outside credible intervals of the baseline model
	Fecundity variable	
Full dataset	Remove 1/5 breeding surveys	Trends within credible interval of baseline model
	Retain one breeding survey per year	Trends close to or within credible interval of baseline model, minor over-estimation

For the model run with only moult data either the fecundity rate using the value estimated by Cordes (2011) was fixed or an informative prior for the fecundity rate was set. The model over-estimated the abundance but the abundance trends were similar to estimates based on the full dataset (Figure 12). It is the abundance of pups that is greatly overestimated (non-pup population size is just over the credible interval of the baseline model (Figure 12a)). The model did not contain any pupping data to influence the fecundity prior parameters. Consequently the fecundity rate was based on the prior, which was relatively high.

With a minimum of one breeding survey per year the results were much better. This time it was the non-pups that were slightly over-estimated but the fecundity and the pup survival trends were within or very close to the credible interval of the baseline model.


Population size (all age classes)
Baseline
1/5 Breeding Surv
b fix
1 Bred/year
Population size
1800
1600
1400
1200
1000
800
600
400
200
1988 1990 1992 1994 1996 1998 2000 2002 2004 2006 2008 2010 2012 2014 2016 2018
Year


Population size (excluding pups)
est pop
Baseline
1/5 Breedin gSurv
b fix
1 bred/year
Population size
1600
1400
1200
1000
800
600
400
200
1988 1990 1992 1994 1996 1998 2000 2002 2004 2006 2008 2010 2012 2014 2016 2018
Year


Estimated fecundity
Baseline
1/5 Breeding Surv
b fix
1 Bred/year
Fecundity
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
1988 1989 1990 1991 1992 1993 1994 1995 1996 1997 1998 1999 2000 2001 2002 2003 2004 2005 2006 2007 2008 2009 2010 2011 2012 2013 2014 2015 2016 2017 2018 2019

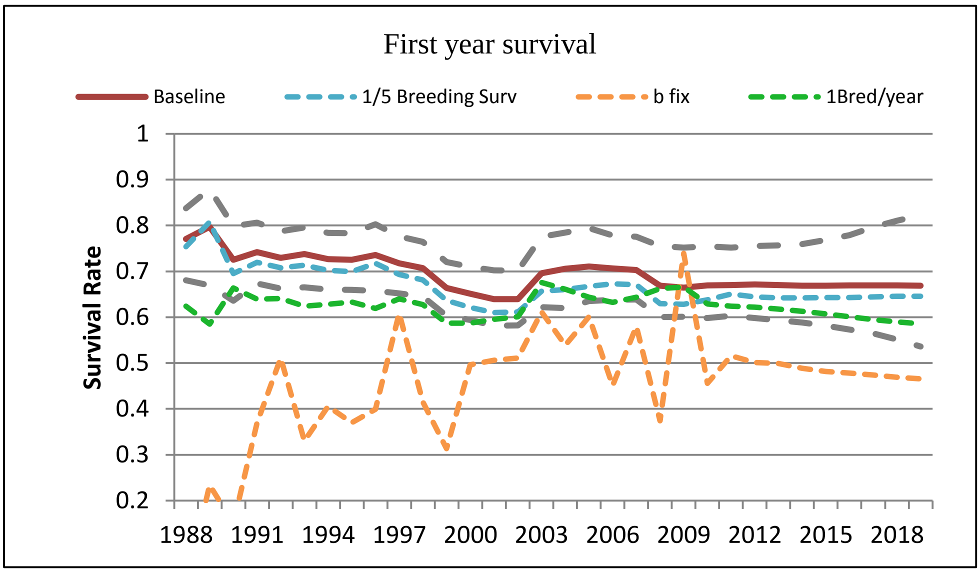


Figure 12. Demographic trends under different scenarios. The trends for the baseline model and its credible intervals are the red and dashed grey curves respectively. The trends for the model with one breeding survey out of five removed are the blue dotted lines. The trends for the model using moult only data with a fixed fecundity rate are the orange dashed lines and the trends for the model with only one breeding survey per year are the dashed green lines.

7 Conclusions

This work illustrates the utility of the state-space model to predict what may happen to the Moray Firth harbour seal population trajectory under the influence of external drivers such as additional mortality.

There is confidence in the quality of the baseline model which is robust to changes in haul out probability. The haul out probability can vary from site to site (Huber *et al*., 2001; Lonergan *et al*., 2013) and at numerous sites the magnitude of the haul out probability is not known. Using this revised model, demographic trends will be detected even if there is uncertainty around the haul out probabilities.

The predictions of the effect of different vital rates (keeping demographic parameters constant for 10 years) simplified reality, but helped to identify which age classes are critical for the survival of the population. Adult females play a crucial role. For example, from the additional mortality predictions if 5% of the current adult females in the northern Moray Firth (an additional 12) are killed every year, then this population will probably decline.

The covariate study showed that at least two covariates, sandeels and local grey seal abundance, seem to have an impact on the population. Wilson (2014) confirmed that the diet of harbour seals in the Moray Firth remains predominantly sandeels so they are a very important (and high-energy) food source for this population. Because of the importance of this prey species for both seal species in the region (Wilson, 2014) the result showing a positive correlation between sandeels and fecundity rate should be investigated further. Data on the abundance and distribution of sandeels in the Moray Firth would also help in understanding the relationship between this prey species and seals in Scotland more generally.

The result with the annual summary grey seal covariate is also interesting. Most of the grey seal abundance data used were not from direct counts (from 1988 to 2006 an approximation was used). Consequently for most of the time series the increase in grey seals was a smooth time trend which is unrealistic, given that the data after 2006 suggests the number of grey seals can vary substantially between years. The strong correlation observed should perhaps lead to further investigation especially in the light of recent evidence that adult grey seals can cause additional direct mortality in grey seal pups, suggesting the possibility of grey seal induced mortality also for harbour seals.

These two covariates are the only ones for which there was local data for a long period of time. This observation raises the possibility that given better geographical resolution for the prey covariates other interactions would have been detected.

No correlation was found between the demographic trends and biotoxin levels in mussels on the east coast of Scotland. Biotoxins in mussels are regularly monitored as part of the Shellfish Monitoring Regulations and therefore provided surrogate covariate data for the time series study. However, biotoxin concentrations in mussels may not be representative, due to the quantity and variation in contaminated prey consumed by harbour seals. It is possible that investigating the role of biotoxins using data from seals directly as seen from recent studies (Hall and Frame, 2010) may allow for the detection of effects at population level.

Nonetheless with two significant covariates, this work illustrates how the modelling approach has the potential not only to estimate demographic rates, but also to understand what processes may be driving the demographic trends. Such understanding will assist in the prediction of future population trajectories under different environmental scenarios.

The final part of this study highlights the importance of having a sufficiently large dataset at the appropriate spatial scale to detect and understand population demographic changes. A comprehensive data set exists for the Moray Firth area. However, for the other harbour seal haul-out sites around Scotland, most surveys conducted have been during the moult only. With moult survey data only it is possible to estimate population trends and potentially infer changes in survival rates. However, because of the difficulty in estimating fecundity rates, it may not be possible to explain why the population is declining or increasing, so that it becomes more difficult to predict the consequences of environmental variability and regime shifts. This prompted the investigation into how the model will behave in the absences of breeding season counts. The conclusion was that with at least one breeding survey per year the estimates of the demographic rate will be close to reality.

In conclusion: if the objective is to understand what parameters drive the vital rates (fecundity and survival) and to predict demographic trends in the harbour seal population it is very important to collect:

- Regular harbour seals counts including pup counts.
- Local covariate data.

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