

Use of state-space modelling to identify ecological covariates associated with trends in pinniped demography

Marjolaine Caillat, Sea Mammal Research Unit

Line Cordes, School of Ocean Sciences, Bangor University.

Paul Thompson, University of Aberdeen, School of Biological Sciences.

Jason Matthiopoulos, University of Glasgow, Institute of Biodiversity, Animal Health and Comparative Medicine,

Sophie Smout, Sea Mammal Research Unit

ABSTRACT

1 1. Identifying and understanding ecological drivers that influence wildlife populations is
2 challenging but critical for conservation. This typically requires integrating long-term data on
3 both the population and potential drivers within statistical models that are suitable for
4 analysing these complex relationships. State-space models offer one method for integrating
5 such data. Once implemented within a Bayesian framework, these analyses can control for
6 multifactorial influences on populations, allowing one to extract otherwise undetectable
7 correlations between the environment and the underlying, inferred demography.

8 2. In the Moray Firth, Scotland, harbour seals have been counted annually for 30 years (1988-
9 2018). A Bayesian state-space model, was used to explore whether patterns in vital rates were
10 correlated to changes in prey abundance, inter-specific competition (grey seal abundance),
11 environmental variables (NAO and SST) or level of biotoxins (saxitoxin and domoic acid) in the
12 Moray Firth waters.

13 3. The credible interval of the posterior distributions of three of these covariate coefficients
14 (sandeel proxy, NAO, and grey seal abundance) suggested that there was a relationship
15 between those covariates and vital rates. Both the sandeel proxy and NAO showed a positive
16 correlation with fecundity, whereas grey seal abundance had a negative impact on pup
17 survival.

18 4. This work demonstrates how an integrated state-space modelling approach can bring
19 together diverse data sets and point to important interactions with prey, and with other
20 predators in the system. This suggests that the wider-scale management of UK harbour seal
21 populations with their contrasting temporal trends needs to account for variation in the

marine ecosystem at appropriate spatial scales, in line with current policy concerning spatial planning in the marine environment.

KEY WORDS

Bayesian, environmental change, fecundity, harbour seal, inter-specific competition, population change, prey availability, survival.

INTRODUCTION:

To manage risks of extinction and substantial decline in wildlife populations, it is crucial to identify variables that regulate population demography. Estimating the vital demographic rates of a population (e.g. reproductive rate, survival rate) can help understand and anticipate its population dynamics, but these rates are rarely constant. Identifying the ecological drivers that influence them (e.g. food quality, predation) allows us to better understand a population's past trends, predict its future trajectories and its likely responses to conservation management. These tasks present three key challenges. First, there may be multiple causes of change interacting with each other, making them difficult to identify. Second, diverse long-term data sets maybe needed to identify the different ecological drivers. Third, developing a statistical model to analyse these multiple responses and drivers is complex and may require the integrated analysis of multiple types of data together with a sound understanding of the ecology of the system so the model structure is appropriate and prior assumptions consistent with evidence and expert opinion. (Clutton-Brock & Sheldon, 2010; NASEM, 2017). State-space models offer one method for integrating different sources of data to answer such multifactor questions. These models can include interactions between different drivers and can be fitted to observations to explore which drivers are regulating a population and through which demographic rate. Further, by implementing state-space models within Bayesian frameworks, it is possible to analyse relatively short time series by incorporating additional information, e.g. probable ranges of uncertain model parameters, in the form of the Bayesian prior distributions (Bled et al., 2017; Smout et al., 2010).

In state-space population models, the state of the population is changed from one time step to the next by demographic processes such as survival and birth. It is then possible to estimate demographic rates from a time series of population counts that consider uncertainties within

this observation process. Furthermore, the addition of data on potential drivers of population change (such as prey abundance or the presence of competitors) makes it possible to investigate whether these impact demographic processes. A fitted population model can then be used to predict (with a known level of credibility) how future demographic rates and population trajectories may respond to changes in intrinsic (e.g. density) or extrinsic (e.g. environmental change or human interventions) drivers (Newman, Buckland, Lindley, Thomas, & Fernández, 2006).

The harbour seal (*Phoca vitulina*) is one of the two seal species resident in the UK. Most of the UK population (79%) is found in Scotland, with a minimum of 25,150 individuals estimated in 2016 (SCOS, 2017). Since 1988, regular monitoring of the harbour seal population around Scotland has been carried out by the Sea Mammal Research Unit (SCOS, 2017). A sustained decline in harbour seal counts in some Scottish regions (up to 93% since 2000) has raised concerns about the possibility of a large-scale population decline (Lonergan et al., 2007). The substantial decrease of some Scottish populations cannot be explained as a result of direct human interventions such as culling (Matthiopoulos et al., 2013). Other possible explanations for the observed declines include: changes in the availability of prey (Soto, Trites, & Arias-Schreiber, 2004; Thompson, Van Parijs, & Kovacs, 2001; Trites & Donnelly, 2003), which could be driven by fishing or by environmental change (Arnotts & Ruxton, 2002; DeMaster, Fowler, Perry, & Richlen, 2001), interactions with predators/competitors (Bolt, Harvey, Mandleberg, & Foote, 2009; Brownlow, Onoufriou, Bishop, Davison, & Thompson et al., 2016), and the effect of algal blooms producing biotoxins (Hall & Frame, 2010; Jensen et al., 2015). Multiple stressors may interact to influence harbour seal population dynamics, with spatial variation in outcomes for different local populations. One important method for exploring such interactions is through demographic modelling, which can synthesize the impacts of multiple stressors at different stages of an animal's life cycle.

Over the last 30 years, the harbour seal population in the Moray Firth, NE Scotland (Figure 1) has been the subject of a long-term study by the University of Aberdeen (UoA), with much of this work carried out in collaboration with the Sea Mammal Research Unit (SMRU) at the University of St Andrews (e.g. Bailey, Hammond, & Thompson, 2014; Cordes, Duck, Mackey, Hall, & Thompson, 2011; Russell et al., 2015; Thompson et al., 1996). Underpinning this programme have been data from two decades of annual land-based surveys at haul-out sites

(Thompson, Mackey, Barton, Duck, & Butler, 2007), which were subsequently integrated into the Sea Mammal Research Unit's annual programme of aerial surveys. Since 2006, this work has been complemented by individual-based photo-identification studies of demography and phenology in Loch Fleet National Nature Reserve (Cordes & Thompson, 2013), now one of the major harbour seal breeding sites in the region (Cordes et al., 2011). Together these data provide an ideal case study to evaluate how state-space models can be used to explore the factors influencing population change in Scottish harbour seals. Initially, Matthiopoulos et al. (2013) developed a Bayesian state-space model to assess how reported levels of shooting (Thompson et al., 2007) had influenced recent population trends. Time-varying estimates of additional mortality from shooting were based upon reported numbers of seals shot. Critically, whilst Matthiopoulos et al. (2013) established that seal shooting had had a direct and strong impact on the survival rate of all age classes, the model suggested that the main driver of historical declines appeared to be a decreasing trend in juvenile survival with a backdrop of recovering fecundity. However, that study stopped short of explaining the observed patterns in terms of other plausible covariates

The analysis presented here includes new estimates of seasonal haul-out probabilities to inform the observation component of the model. It also includes additional covariates such as density of competitors, relative abundance of prey or climate trends that could directly or indirectly influence harbour seal population change, improving the inferential abilities of the process model and its predictive power.

METHODS:

Harbour seals aggregate at onshore "haul-out" sites either to rest, to give birth and nurse their pups (in the June-July pupping season) and to moult (in the August-September moulting season). There is evidence of strong fidelity to moulting and breeding sites (Bowen, Ellis, Iverson, & Boness, 2003; Cordes & Thompson, 2015; Härkönen & Harding, 2001), providing opportunities to observe and count individuals during these two important periods in annual cycle (Thompson, Tollit, Wood et al., 1997).

During the pupping period, each adult female gives birth to a maximum of one pup, after which they come ashore frequently to nurse their pup for 19 to 23 days (Cordes & Thompson,

2013). In Scotland, the pupping season occurs from the end of May to the end of July. During this period, adult males and juveniles only come ashore to rest. Juveniles (aged 1 year and older) and adults of both sexes continue to come ashore to rest during the moult, which extends from late July to late September, but the probability of hauling-out varies seasonally, dependent upon sex and age class (Cordes & Thompson, 2015; Härkönen, Harding & Lunneryd, 1999; Thompson & Rothery, 1987; Thompson, Tollit, Wood et al., 1997). Unless such variations in sightability are accounted for as part of the observation model, it is possible for the counts to yield spurious values, particularly if the peak dates of hauling out and observed effort drift in relation to each other.

Data:

Harbour seal data:

The model is based on survey data from the northern part of the Moray Firth (Figure 1), collected from haul-out sites associated with the Dornoch Firth, Loch Fleet, Brora and Helmsdale (Matthiopoulos et al., 2013; Thompson et al., 2007). Harbour seals typically forage within 50km of favoured haul-out sites, to which they return regularly (Cordes & Thompson, 2014; Jones et al., 2015; Sharples, Moss, Patterson, & Hammond, 2012; Thompson et al., 1996). During the period of the study, larger scale movements between haul-out regions appear to have occurred only infrequently (Jones et al., 2015). Based upon the spatial structure of haul-out sites (Thompson et al., 2007), and following the approach used in Matthiopoulos et al. (2013), the harbour seal population of the northern Moray Firth was considered to be a closed population for the period of this study.

Prior to 2006, annual land-based surveys were conducted by the UoA at the Dornoch and Loch Fleet sites (Table 1). During these surveys, animals were counted using a telescope within ± 2 h of low tide in good visibility (Thompson, Tollit, Wood et al., 1997). In most years, surveys were conducted several times a year ($n=3-10$) during both the pupping and moulting seasons. Exceptions were in 1991, when survey data were only available from the moult season, and 1997 when data were only available from the pupping season (Table 1). Additional land-based surveys were made by UoA at a site along the northern coast of the Moray Firth (Brora, Figure 1) in a few years (1995, 2000 & 2005) but only low numbers were counted on these occasions.

From 2006, the SMRU continued this time-series of surveys at all the sites in the northern Moray Firth using aerial survey techniques (Lonergan et al., 2007) during both the pupping (n=4-5) and moulting (n=1-4) seasons (see Table 1 for details). In 2006, both land-based and aerial surveys were conducted, and data from this year were used to compare results from the two survey methods. The shooting data for the period 1994-2004 were based upon reported numbers of seals shot and estimate provided by Thompson et al. (2007). Outside this period shooting numbers were treated as missing data and estimated during model-fitting (Matthiopoulos et al, 2013).

Two independent estimates of total population size in the northern part of the Moray Firth area were available. In 1993, an estimate was based on onshore counts, corrected using telemetry data to estimate the proportion of animals in the water (Thompson et al., 1997). In 2009, a mark-recapture estimate for Loch Fleet (Cordes & Thompson, 2015) was scaled up to the full region using aerial survey data.

Covariate data:

The current hypotheses proposed to account for harbour seal declines, can be summarised as 1) prey availability, 2) broader scale environmental variation, 3) inter-specific competition with grey seals, and 4) levels of biotoxins on demographic trends in harbour seals. We selected covariate data to reflect those.

Prey availability:

Studies of harbour seal diet (Tollit & Thompson, 1996, Wilson, 2014), condition (Thompson, Tollit, Corpe, Reid, & Ross, 1997), and fish biomass (Greenstreet, McMillan, & Armstrong, 1998), indicate that herring (*Clupea harengus*), Atlantic cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and sandeels (*Ammodytes marinus*) are likely to represent key prey stocks for this harbour seal population. Data for all species except sandeels were obtained from the International Council for the Exploitation of the Seas (ICES) (SuppInfo: Table S1_1). The normalized standing stock biomass (SSB) value of the year for the North Sea was used as an indicator of the local prey availability in the Moray Firth (ICES, 2012). There is no consistent

time-series survey of sandeels to estimate changes in local stocks. However, several studies have shown there is a correlation between regional variation in black-legged kittiwake (*Rissa tridactyla*) breeding success and sandeel availability (e.g. Frederiksen et al., 2005; Harris & Wanless, 1997). Therefore, data on kittiwake breeding success (number of fledged chicks/nest) at North Sutor (SuppInfo, Table S1_1), a local colony of kittiwakes in the Moray Firth, were used as a proxy for sandeel availability (see Figure 1 of Frederiksen et al., 2005).

Environmental data:

The ecology of many marine species has been shown to vary in relation to the North Atlantic Oscillation (NAO) (Stenseth et al., 2002). This proxy of large-scale environmental variation can reflect changes in low trophic levels (Reid, Planque, & Edwards, 1998) and in key prey species such as sandeel (Arnotts, & Ruxton, 2002). The NAO is also related to behavioural and demographic parameters in many marine top predators (Ferguson, Stirling, & McLoughlin, 2005; Lusseau, et al., 2004; Sandvik, Erikstad, & Sæther, 2012). Similarly, there is widespread variation in marine top predator biology in relation to variation in sea surface temperature (SST) (Burthe et al., 2012, Thackeray et al., 2016).

In this model the potential influence of larger scale environmental change on harbour seal population dynamics using both these proxies was explored. For the NAO, the Hurrell Station-based NAO winter Index (Hurrell et al., 2015) was downloaded from the National Centre for Atmospheric Research website (<https://ncar.ucar.edu/>) (SuppInfo: Table S1.2). Daily SST data were obtained from the National Oceanic and Atmospheric Administration (NOAA), and then used to produce an average value for the Moray Firth: a) from March in year (t-1) to May of the breeding year (t), and b) from April to September of the breeding year (SuppInfo: Table S1.2). The use of these two SST time series was based on the hypothesis that SST might impact population dynamics either through its effect on the fecundity rate (which could operate through an influence on prey availability in the year prior to breeding), or on juvenile survival (which is likely to be important in the months following the breeding season (see Harding, Fujiwara, Axberg & Härkönen, 2005)).

Biotoxin data:

Saxitoxin (STX) and domoic acid (DA) biotoxins are regularly detected in the Scottish waters during harmful algal blooms (HABs) (Jensen et al., 2015). The presence of STX in the water column, particularly if ingested secondarily through prey, can result in rapid mortality in marine mammals (Jensen et al., 2015; Van Dolah, Doucette, Gulland, Rowles, & Bossart, 2003). DA can also have both acute and chronic effects. It has caused mass mortalities among pinnipeds in other parts of the world (Hall & Frame, 2010) and can potentially impact reproductive success by causing abortions in exposed females (Hall & Frame, 2010). Biotoxin concentrations from mussels in the Dornoch Firth were used as covariates in this study (see SuppInfo: Table S1.3). To model the potential impact of DA on the pupping in year (t), an average from August in the year ($t-1$) to Jun in year (t) was used. To model the potential impact of DA on survival from year ($t-1$) to year (t), a normalized annual average from Jun year ($t-1$) to May year (t) was used. Given that STX has an immediate impact on marine mammals, the normalized average concentration between May to July in year (t) was used as a covariate for survival rate only.

Grey seal data:

In the Moray Firth, grey seals and harbour seal are sympatric, sharing the same haul-out sites in summer (Thompson et al., 1996), when there is also partial overlap in foraging grounds (Jones et al., 2015). Counts of grey seals hauling out in the area during the time of the harbour seal moult started in 2006. Counts varied between surveys, so where multiple counts were available, the average number of grey seals observed in a given year was used in the model (SuppInfo: Table S1.4). Prior to 2006, few local count data were collected for grey seals, but population estimates are available at broader spatial scales for the North Sea population in those years (Thomas, 2012). For the model to run with the grey seals covariate it was necessary to estimate the number of grey seals in the Moray Firth prior to 2006. This was done for each year t using a binomial distribution with parameters n as the North Sea abundance estimates in year t (Thomas, 2012) and p being an estimate of the ratio of the number of haul-out greys seal to the North Sea abundance estimates. A beta prior distribution was used to estimate p with its mean and variance being respectively the average and variance of the ratio observed between 2006 and 2014.

The extent of each of these time series varied slightly for different covariates (Table 1).

Model description:

Demographic model:

We used a stage-structured model that assumes that first reproduction occurs at age 5, and comprises one pup, three juvenile stages and one adult stage for each sex, a total of ten state variables (Matthiopoulos et al. 2013). These are specified to a time just following the pupping season, such that the deterministic version of the model is

$$N_{t+1} = R_t N_t \quad \text{Eq.1}$$

where $N_t = (n_{1,t} \dots n_{10,t})^T$ is the vector of population classes (the first five classes are males and the remaining are females) in year t . Survival and birth are assumed to be stochastic, binomial processes. R_t is the deterministic transition matrix (see Appendices: Matrix A.1). Binomial demographic stochasticity is assumed for both fecundity and survival.

The fecundity rate b_t (defined here as the probability that a mature female produces a pup in year t) (Eq.2) is modelled using a logistic function including time (t), total population size (N_t) and covariate (X_t) effects. Priors for the β coefficients were adjusted to reproduce the values for survival and the fecundity rates in 2009 (year 22), the year in which these values were estimated independently using mark-recapture methodology (Cordes & Thompson, 2015).

$$b_t = \frac{\exp(\beta_0 + \beta_T t + \beta_N N_t + \beta_X X_t)}{1 + \exp(\beta_0 + \beta_T t + \beta_N N_t + \beta_X X_t)} \quad \text{Eq.2}$$

The survival rate $s_{k,t}$ of age class k (pups, juveniles, adults) in year t , was modelled using the same form of logistic function (Eq.3), with additional mortality included in years in which shooting was known to occur.

$$s_{k,t} = \frac{\exp(\sigma_{0k} + \sigma_{Tk} t + \sigma_{Nk} N_t + \sigma_{Xk} X_t)}{1 + \exp(\sigma_{0k} + \sigma_{Tk} t + \sigma_{Nk} N_t + \sigma_{Xk} X_t)} (1 - \mu_t m) \quad \text{Eq.3}$$

The shooting parameter u takes values between 0 and 1 and represents the relative strength of shooting effort in different years. Maximum shooting mortality across all years is denoted by m .

Mark recapture studies suggest that the survival of immature seals is lower than that of adults (Hastings, Small & Pendleton, 2012), but it is difficult from existing data sets to estimate how survival may change with age before recruitment into the adult population. We therefore assumed a linear rate of change in survival in immature animals, and the coefficients in Eq. 3 were adjusted to reproduce this trend in $s_{k,t}$ (Table2).

The population model with removals due to shooting, and with only temporal variation in vital rates (and no additional covariates) is considered to be the “Baseline model”. This then allowed for the exploration the effect of covariates by adding them as terms in the linear predictor of the logistic function and estimating the associated parameters. SuppInfo S2 and S3 contain more detail on parameters and prior distributions.

Additional haul-out site at Brora/Helmsdale:

Exchange of animals between additional nearby haul-out sites (at Brora and Helmsdale) and haul-out sites in the original core study area (Loch Fleet and the Dornoch Firth) was explicitly included in the model. Between 1988 and 2005, annual count data were only available from the core study area in the Dornoch Firth and Loch Fleet. However, after 2006, seals present at nearby haul-out sites along the northern Moray Firth coast (between Brora and Helmsdale) were also systematically counted. GLMs based on data from 2006 onwards were used to estimate temporal trends in the ratio of counts at these two additional sites and the two main areas, and these were then used to ‘correct’ the pre-2006 population data to include individuals from the entire area (see SuppInfo S2-2).

Haul-out parameters and sensitivity analysis:

Only those seals hauled out on shore are counted during surveys. To estimate the total population size, it is necessary to estimate what proportion of the total population are hauled-out. This proportion is equivalent to an individual’s probability of hauling out. Different

methods have been used to estimate this. For instance, Thompson et al. (1997) used telemetry data whereas Cordes & Thompson (2015) used mark-recapture data. Haul-out probability is known to vary with sex, age and season (e.g. between the pupping and moulting periods) (Huber, Jeffries, Brown, Delong, & Vanblaricom, 2001; Lonergan, Duck, Moss, Morris, & Thompson, 2013; Thompson, Tollit, Wood et al., 1997). Other variables such as weather conditions, tide and anthropogenic disturbances can change this haul-out probability on a daily basis (Cunningham et al., 2009).

Given that haul-out probability is difficult to measure accurately as a result of numerous sources of variability, we adapted the approach used in Matthiopoulos et al (2013) to model them. A baseline value (μ_{kHO}) was selected for a given sex, age and season based on literature review (Table 3). The prior for the baseline value was assumed to be an independent beta distribution for each sex and age class. The beta distribution had a mean of μ_{kHO} and variance of σ_{kHO} . The variance simulates the daily stochasticity (e.g. due to unmodelled weather conditions). The impact of different baseline haul-out probabilities and daily variabilities on the estimated demographic rates of this model (see SuppInfo section S2.3) was then tested. The conclusion was that the estimation of vital rates and trends in these rates was robust to changes in haul-out probability (see SuppInfo, Figure S2.1). Consequently, for all the simulations with different covariates the mean haul-out probabilities presented in Table 3 with a daily variability $\sigma_{kHO} = 0.5$ were used for all the models.

Covariate coefficients:

For both the fecundity and survival functions, each environmental covariate was added to the baseline model separately. Depending on the covariate, it might be added to the survival function using a coefficient independent of age and sex category, or separate coefficients might be estimated for different age and sex classes. For example, any correlation with grey seal numbers was expected to vary for different age classes of harbour seals. However, data on the exact number of juveniles in aerial surveys were unavailable. Therefore, a model including a relationship between the number of grey seals and pup survival rate, and a model including a relationship between the number of grey seals and a common coefficient for adult/juvenile survival rate, were tested. In all cases, posteriors for the covariate coefficients

were obtained by fitting the integrated model to the data. If the coefficient was different from zero (i.e. if the 95% Bayesian credible interval (CRI) for a parameter did not include zero), then this was taken as evidence that the covariate has an effect on survival or fecundity. A prior sensitivity analysis of the covariate coefficient was conducted for numerous models tested to ensure that the model's posterior distributions were affected by both the covariate data and the prior distributions. All the models tested with their covariate coefficient posterior CRI are summarized in the appendices TableA.1.

Initial population structure and independent estimates:

The population's initial age and sex structure was unknown. It was assumed that a stable-state distribution had been achieved prior to the collection of the earliest data. The number of adult females present in the first year was given a uniform distribution ranging from 200 to 1000 individuals.

Model inference:

The software Openbugs was used to fit the model using MCMC (code in SupplInfo section 4). Two MCMC chains (starting from different points in the parameter space) were run for a minimum of 5×10^4 iterations, thinning every 10 iterations to conserve memory. Mixing was assessed by visual observation of the two chains for all the parameters of the model. Convergence was confirmed when the Brooks-Gelman_Rubin diagnostic tool in Openbugs was below 1.2 (Brooks & Gelman, 1998; King, Morgan, & Gimenez 2010). Once convergence was detected, the model was run for another 1×10^4 iterations, which were treated as the sample from the joint posterior distribution.

Model goodness of fit:

Unfortunately, information-criteria of model fit/predictive accuracy such as DIC could not be calculated in OpenBugs because inference was used to impute 'missing' data in some years. The goodness of fit (GOF) of the candidate models was estimated by measuring and comparing both the regression coefficients (R^2) and the weighted mean square (Eq.4) (Gelman, Carlin, Stern, & Rubin, 2004)

$$\frac{1}{n} \sum_{i=1}^n \frac{(y_i - E(y_i|\theta))^2}{var(y_i|\theta)} \quad \text{Eq.4}$$

for both the pup data during the breeding season and the non-pup data during both the breeding and moult seasons.

Validation and predictions

To validate the model, the observed survey data for 2014 (which were not used to fit the model) were compared with predictions of harbour seal counts for 2014. To explore the potential consequences of the ecological effects suggested by the model, once potential 'drivers' were identified that appeared to be important for the Moray Firth population, the predicted growth rate of the population for the next 10 years was projected for different plausible future values of these drivers.

RESULTS:

Baseline model goodness of fit and demographic rate trends:

The baseline model appeared to provide a good fit to the data, and the R^2 coefficients between observed and fitted data were $R^2=98.9\%$ and $R^2=97.4\%$ for the non-pup and pup counts, respectively (Figure A.1 and A.2 in the Appendices). The prediction of the total non-pup population size was very close, and within the confidence interval of the two independent abundance estimates (Figure 2.A) in 1993 and 2009. However, there was a difference in goodness of fit of the non-pup data between the breeding and the moulting data, with a weighted mean square of 0.26 and 1.33, respectively (Table 4), and the model tended to underestimate the number of non-pup seals in the moulting season.

Fecundity rate appeared to be the more variable demographic parameter in the baseline model, with a general increase during the early phase of the time series, and a steady decrease since 2010 (Figure 2.B). Survival of all age classes appeared to be more constant (Figure 2.C to E). Survival rates of pups and first year juveniles decreased by 6% and 13%, respectively, between 1988 and 2003. After 2003, the survival rate was more constant, and a small increase could be observed since 2010. The survival rate of the adults was higher than other age groups. Male survival was initially very close to the female survival rate but showed

a stronger decrease during the intense period of shooting and stayed lower afterward. For the adults, a 'dip' in survival was observed in 2009, with a smaller drop in juvenile survival also apparent that year.

Covariate sensitivity analysis:

Of the nine covariates included in the estimation of breeding or survival rates only three, (the proxy of sandeel abundance, winter NAO index, and grey seal abundance), appeared to have a correlation with one of the demographic rates (Appendices Table A.1).

Both the sandeel proxy and the NAO index had a positive correlation ($\beta_X > 0$) with fecundity rate (Figure 3, Table A.1). The credible intervals (CRI) of the posterior distributions were [0.067 – 0.19] and [0.025-0.13] for the sandeel proxy and the NAO index respectively. Across the range of the sandeel proxy and the NAO index, fecundity rate increased from 76% (CRI=75%-79%) to 83% (CRI=81-86) and 76% (CRI=71-80) to 84% (CRI=80-87), respectively (Figure 3). When either of these two covariates was added to the fecundity function, the estimates of numbers of pups improved, compared to the baseline model (Table 4) with a weighted mean error decreasing from 1.24 to 1.19 with the presence of sandeel proxy data, and 1.10 with the presence of the NAO index. However, the GOF for the adult counts did not improve. Except for the trend in fecundity rate (Figure 4.A and B), all other demographic trends did not change significantly (Figure A.4 and A.5) when either the NAO or the sandeel proxy were added to the model.

The number of grey seals appeared to have a negative correlation (Table A.1) with pup survival rate ($\sigma_{pX} < 0$, CRI: [-0.013 – 0.001]) (Figure A.6). First year survival rate declined to nearly 40% when the population of grey seals increased by 50% between 2005 and 2008 (Figure 5). The other demographic parameters showed similar trends to those observed with the baseline model (Figure 6). For the years after 2013 the model predicts a decline for all the demographic rates except fecundity (Figure 6). A future increase of grey seals at Moray Firth haul-out sites from 350 to 1000 individuals is predicted to generate a 60% decrease in pup survival rate (Figure 7). The addition of the grey seal abundance covariate to the pup survival function produced an estimate of pup counts that was closest to the observed count (the weighted mean squared decreased from 1.24 to 0.92; Table 4).

Prediction for 2014:

The observed 2014 data for pups and non-pups during the breeding or moult seasons all fall within the credible interval of the baseline model prediction (Table5). The number of non-pups during the breeding season is close to the lower limit of the prediction credible interval. The model including grey seal abundance has the best fit to the pup data. For this model the average prediction for 2014 is even closer to the observed data (Table 6). The results suggest the utility of this modelling approach for short-term prediction of population size, which may support sustainable management in areas where regular annual surveys are not always possible.

Prediction with different scenarios of grey seal population growth

Given observed variation in grey seal population within the northern Moray Firth, the model suggests that the harbour seal population is currently declining (growth rate <1). If the grey seal population continues to grow over the next 10 years, harbour seals are expected to decline (Figure 8) from 643 (CRI=590-702) individuals in 2012 to 503 (CRI=479-528) in 2022.

DISCUSSION:

The dynamics of natural populations are probably controlled by multiple drivers, that may vary in importance across time and space. Interactions between different factors and indirect effects may cause particular difficulties in identifying key individual drivers (Sharples, Moss, Patterson, & Hammond, 2012, Jones et al, 2015). By combining information from different sources to create a baseline state-space model, and including covariates that might influence demographic rates, it was possible to identify and assess the significance of potential drivers. This analysis suggests that sandeel availability, some aspects of environmental variation that is reflected by the winter NAO index, and the local abundance of grey seals are plausible drivers shaping recent changes in the dynamics of the Moray Firth harbour seal population.

In the baseline model, the prior distributions for the parameters of both fecundity and survival functions were given the same variance. However, these demographic rates did not show similar variability over time. While trends in survival were stable, varying only due to strong short-term action such as culling, temporal trends in fecundity were more variable.

Environmental conditions seem to impact fecundity more than survival (Table A.1). Detectable impacts of environmental variation or prey availability on survival rate are only likely where unfavourable conditions persist for several consecutive years. This is consistent with life history theory that suggests long-lived capital breeders 'prioritize' survival over breeding (Gaillard, Festa-Bianchet, & Yoccoz, 1998; Reed, Harris, & Wanless, 2015; Stenson, Buren, & Koen-Alonso, 2016). The availability and quality of food is known to impact body condition and may therefore impact fecundity rate (Thompson, Tollit, Corpe, & al., 1997; Trites & Donnelly, 2003). Among the four prey species added as candidate covariates, only the proxy for sandeel abundance was positively correlated with the fecundity rate. It is possible that there might be an alternative explanation for the relationship between kittiwake and seal breeding success, but given the known importance of sandeels as forage fish at the base of the food web in the North Sea ecosystem, a trophic explanation does seem most plausible (Dickey-Collas et al., 2013). Sandeels are a major component of the diet of both harbour (Brown & Pierce, 1998; Sharples, Arrizabalaga, & Hammond, 2009; Tollit et al., 1997; Wilson, 2014) and grey seals (Beck, Iverson, Bowen, & Blanchard, 2007; Hammond, Hall, & Prime 1994; Prime & Hammond, 1990; Ridoux, Spitz, Vincent, & Walton, 2007) making changes in the availability of this key prey species a likely driver of population dynamic changes. The lack of correlation with the other indices of important prey species data could be a consequence of lower geographical resolution between these data sets and the seal data rather than a real absence of correlation.

The significant relationship with the winter NAO index may well also be influencing the seals' demography through a change in prey availability. The NAO index is a general reflection of ecosystem state rather than a local index, but it has been shown to be related to variation in the biomass or quality of various fish species that contribute to harbour seal diets (Arnotts, & Ruxton, 2002; Dippner, 1997; Meng, Oremus, & Gaines, 2016; Stige, Ottersen, Brander, Chan, & Stenseth, 2006). Because harbour seals are generalists, adapting their feeding behaviour and diet to their local habitat (Reder, Lydersen, Arnold, & Kovacs, 2003; Sharples, Moss, Patterson, & Hammond, 2012), they may show a response to years that reflect low availability of multiple prey species. These years, in turn, may be better characterized by the NAO index than by the stock size of individual prey. Climate indices, such as the NAO, might also reflect changes in the availability of prey or foraging behaviour (e.g. Lea et al., 2009) as a result of a

relationship between these indices and oceanographic and weather systems (Dickson et al., 2000; Pirazzoli, Tomasin, & Ullmann, 2010).

The third important covariate was the local abundance of grey seals, which was negatively correlated with pup survival. Available data on the diet of grey and harbour seals in this area suggest that there is a high degree of overlap in diet, highlighting the potential for direct competition (Thompson et al., 1996; Wilson, 2014). In addition, there is potential for interference competition between these species, as suggested for other marine mammals (Spitz, Rousseau & Ridoux, 2006) or the two species may be responding in different directions to a change in environmental conditions, as reported over evolutionary timescales in other marine top predator communities (Younger, van den Hoff, Wienecke, Hindell, & Miller, 2016). Incidents of grey seals killing marine mammals have also been reported in recent years, including attacks on harbour seals (Brownlow et al., 2016; Leopold & al., 2015; van Neer, Jensen, & Siebert, 2015). The data did not allow to determine which of these factors might explain the correlation observed between grey seals and pup survival. It was only possible to observe that the estimated number of pups throughout the time series and the prediction for 2014 are more accurate when grey seal data are included in the model. Future research may provide information on the sex and age-classes typically targeted by grey seals, which could be used to explore this question by including stronger priors on age-dependent coefficients connecting vital rates to grey seal abundance.

Regarding the other covariates, no correlation was found between survival rates and toxin concentration in the marine environment, although recent analysis of urine and faeces of harbour seals around Scotland have shown that these populations are exposed to both toxins (Jensen et al., 2015). The lack of correlation could be due to the use of proxy data, data that are too far from the focal population, concentrations of environmental toxins that were insufficient to impact the vital rates or our particular method of model selection, which required single effects to be very strong to be retained.

The model outputs can also be used to provide an indication of the relative importance of these three different drivers on recent trends in the Moray Firth population. In general, the environmental drivers appear to have a lower impact on demographic rates than the interaction with grey seals (Figures 3 and 7). Grey seal competition or predation may have a direct impact on the younger age classes of the population, reducing recruitment into the

adult population. Further work on overlap in foraging areas and spatial variation in harbour seal demography in areas of contrasting grey seal abundance is now required to explore the nature and extent of this interaction both in the Moray Firth and contrasting populations.

This exploration of the potential drivers of variation in demographic parameters represents the main development of the original model presented by Matthiopoulos et al. (2013). The modification of this model, which included the addition of data from sites in the northern part of the Moray Firth, allowed the creation of a baseline model that provided predictions that were closer to the independent estimates of population size, and which had a better goodness of fit. However, goodness of fit differs between seasons, with a better fit of the breeding season data whereas numbers of non-pups were underestimated by the model during the moult. This may reflect deviation from one of the model's key assumptions, where the northern Moray Firth is considered a closed population. This discrepancy between the observed and the predicted data could be a result of seasonal variation in levels of site fidelity, with more animals coming from other populations during the harbour seal's moult than during the breeding season. There is certainly some evidence of longer-range movements (e.g. Jones, Sparling, McConnell, Morris, & Smout, 2017) in and out of the Moray Firth. Further analysis of an extended telemetry dataset is now required to quantify these movements and assess the extent to which they may occur during critical survey periods. If further evidence emerges that they may be important, the framework used here could be extended to account for this.

Conservation implications

This model was developed using a uniquely detailed data set from just one region of Scotland, collected up to the end of 2013. The model was originally developed by Matthiopoulos et al., (2013) to address the significance of one particular conservation threat; recognised but uncertain levels of shooting to protect salmon fisheries (Thompson et al. 2007). Matthiopoulos et al. (2013) highlighted how this approach could identify the proximate drivers underlying changes in abundance, and suggested that adult mortality from shooting was less likely to be causing declines than other factors affecting fecundity and juvenile survival. The current extensions to this model framework allowed the exploration of potential drivers that might influence these changes in vital rates, although our suite of candidate drivers was constrained by the availability of suitable environmental and ecological

covariates. Whilst this required to rely heavily on proxy data for key potential drivers, it does provide a framework for more focussed work to test relationships between these co-variables and vital rates more directly (Matthiopoulos et al. 2014). For example, the time-series of individual-based re-sighting data from this population (see Cordes & Thompson 2013, 2014) could now be used to determine if these same co-variables directly affect fecundity, or provide independent evidence of constant adult survival.

Counts of Moray Firth harbour seals have exhibited slight declines over recent decades, but some harbour seal populations in UK waters have increased dramatically while others have declined significantly (Thompson et al. This Volume). The reasons for these contrasting trends remain unclear, but our modelling work indicates that temporal variation in key vital rates is best explained by broad-scale ecological and environmental covariates that are unlikely to be amenable to direct conservation interventions. Instead, our results point to a more complex interaction between different top predator populations and their prey stocks, highlighting the need for ecosystem based management rather than a single species approach. Of particular interest is the potential interaction between harbour seal demography and the local abundance of grey seals, raising the possibility that the great conservation success that led to the recovery of the UK grey seal population (Thomas et al. This Volume) may now be influencing declines in some harbour seal populations. Evidence of an interaction between these two species has also emerged through changes in the Baltic seal community over much longer time-scales (Harkonen, Harding, Goodman, & Johannesson, 2005). Work is now required to better understand the ecological conditions each of these species favours, and how these compare with other marine top predators, such as harbour porpoise, which often occur in these same communities. Studies are being undertaken to collect photographic re-sighting data that can underpin independent estimates of harbour seal vital rates in other regions of Scotland. Further development of this modelling framework could be particularly important for understanding the proximate and ultimate drivers underlying these contrasting population trends. One of the key requirements to achieve this will be modifying the model structure to account for sparser data availability in other regions. This study also highlights the importance of long-term local biotic and abiotic data to identify potential drivers. The availability and quality of such data constrained the scope of this analysis, highlighting that

additional data collection at appropriate spatial scales should improve our ability to test emerging hypotheses about the key drivers influencing different demographic parameters.

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784 TABLES:

785 Table 1: Number (No) of count surveys per season and per year of grey and harbour seals and, time
786 series (dark grey when data were present, light grey when no data) for all the covariate data
787 used in this project. Surveys for the grey seals were conducted only during the harbour seal
788 moult. In survey types, G&A means ground and Aerial surveys.
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		1 2010	1 2011	1 2012	2 2013	3 2014	4 2015	1 2016	1 2017	2 2018	3 2019	1 2020	1 2021	2 2022	3 2023	4 2024	1 2025	2 2026	3 2027	4 2028	1 2029	2 2030	3 2031	4 2032	1 2033	2 2034	3 2035
	Survey Type	Ground																		6 2036	Aerial						
Harbour Seal	Winter Breeding surveys	4	5	12	4	7	7	4	5	4	5	8	12	9	9	11	5	21	4	14	4	4	4	4	4	4	4
	Post-Moult surveys	2	5	1	2	11	10	8	11	11	9	9	10	10	10	10	2	2	2	10	5	1	2	1	1	1	1
Grey Seal	No. of surveys																	5	4	5	4	5	4	4	4	4	4
Calypso count estimate							3														3						
Herring	Annual average																										
Cod	Annual average																										
Seal	Annual average																										
Sandwich	Annual Average																										
SST	Annual Average																										
NDA	Annual Average																										
Seabirdn	Annual Average																										
B.A	Annual average																										

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793 Table 2: Summary of the baseline demographic rates used in the model with their references.

Demographic Rate	Range	Reference
Fecundity (b_0)	0.83-0.91	Cordes and Thompson (2014)
Adult female survival (s_{f0})	0.94-1.0	Cordes and Thompson (2014)
Adult Male survival (s_{m0})	(0.85-0.95)	Cordes and Thompson (2014)
Juvenile survival (s_{j10})	0.68-0.88	Matthiopoulos et al (2013)

Juvenile survival (s_{j20})	0.77-0.97	
Juvenile survival (s_{j30})	0.85-0.91	
Pup survival (s_{p0})	0.6-0.8	Thompson et al (2007), Härkönen, & Heide-Jørgensen (1990)

Table 3: Baseline haul-out probabilities. The breeding probabilities are from Huber et al. (2001). The haul-out probabilities during the moult season are from Huber et al (2001) except for the adult males and the pups. The adult males data come from Lonergan et al. (2013). However, there are no data of the number of pups hauling-out at the moult season as it is difficult to discern them from juveniles. Consequently, the haul-out probability for this age class come from independent discussion with several experts.

		Pupping	Moulting
Females	Adult	0.75	0.50
	Juvenile	0.50	0.50
	Pup	0.85	0.10
Males	Adult	0.50	0.61
	Juvenile	0.50	0.50
	Pup	0.85	0.10

Table 4: Goodness of fit: Weighted mean square for the different models per category of observed data.

Weighted mean square error				
$\frac{1}{n} \sum_{i=1}^n \frac{(y_i - E(y_i \theta))^2}{var(y_i \theta)}$				
Model	Adult			Pup
	Moult	Breeding	Total	
Baseline	1.33	0.26	0.57	1.24
SE	1.31	0.27	0.57	1.19

GS	1.41	0.25	0.60	0.92
NAO	1.36	0.26	0.59	1.10
GS_SE	1.41	0.26	0.60	0.91

Table 5: Prediction for 2014 counts from the baseline model and observed count collected during the annual aerial surveys in 2014. In 2014, four aerial surveys were conducted during the breeding season and one during the moult season. The observed min and max correspond to the minimum and maximum number of seals counted during those surveys. The first survey has a very low number of pups due to being early in the breeding season. The numbers in parentheses correspond to the observed data with this first survey removed.

	Predicted			Observed		
	Lower 95% CI	mean	Higher 95% CI	Min	mean	Max
Non pups Breeding	251	410	533	218(218)	260(260)	286
Non Pups Moul	219	294	377		268	
Pups	97	121	146	47(109)	98 (115)	121

Table 6: Prediction for 2014 counts from the model with the grey seal covariate and observed count collected during the annual aerial surveys in 2014. In 2014, four aerial surveys were conducted during the breeding season and one during the moult season. The observed min and max correspond to the minimum and maximum number of seals counted among those surveys. The first survey has a very low number of pup due to be early in the breeding season. The numbers in parenthesis correspond to the observed data when this first survey was removed.

	Predicted			Observed		
	Lower 95% CI	mean	Higher 95% CI	Min	mean	Max
Non pups Breeding	202	357	481	218(218)	260(260)	286
Non Pups Moul	175	253	341		268	
Pups	95	119	145	47(109)	98 (115)	121

FIGURE LEGENDS

Figure1: Map of the Moray Firth study area showing the location of the haul-out sites in the northern Moray Firth. The dashed line separates the northern to the southern Moray Firth.

Figure 2: Demographic rates for the baseline model. For each graph the solid line is the median value of the demographic rate estimate, the dashed lines are the lower and upper 95% credible interval values. The shaded area highlights the prediction after 2013. A: Population size: Abundance estimation of the population including all age classes (grey) and the population without the pups (black). The 2 dots are the 2 independents estimate with their confidence intervals. B: Fecundity rate estimate. C & D Survival rates of the female pups and juveniles respectively. E: Male and Female adult survival rates.

Figure 3: Median fecundity rate (solid line) estimate versus NAO index (a) and Sandeel proxy (b) predicted by the state-space model. The dashed lines are the 95% credible interval of the estimate.

Figure 4: Trends of the fecundity rate with A) the sandeel proxy covariate (grey bars) and B) the NAO covariate (Light grey dot-dashed line) added to the baseline model. For both graphs the solid black line is the median value of the fecundity rate estimates, the dashed black lines are the 95% credible interval values and the grey area is the prediction after 2013. The solid grey line is the median of the fecundity rate estimate under the baseline model.

Figure 5: Median pup survival rate (black) and the credible interval (black dashed lines) with the grey seal covariate in the model (bars) in comparison to the baseline pup survival rate (grey line). The graph under the grey zone are the prediction after 2013.

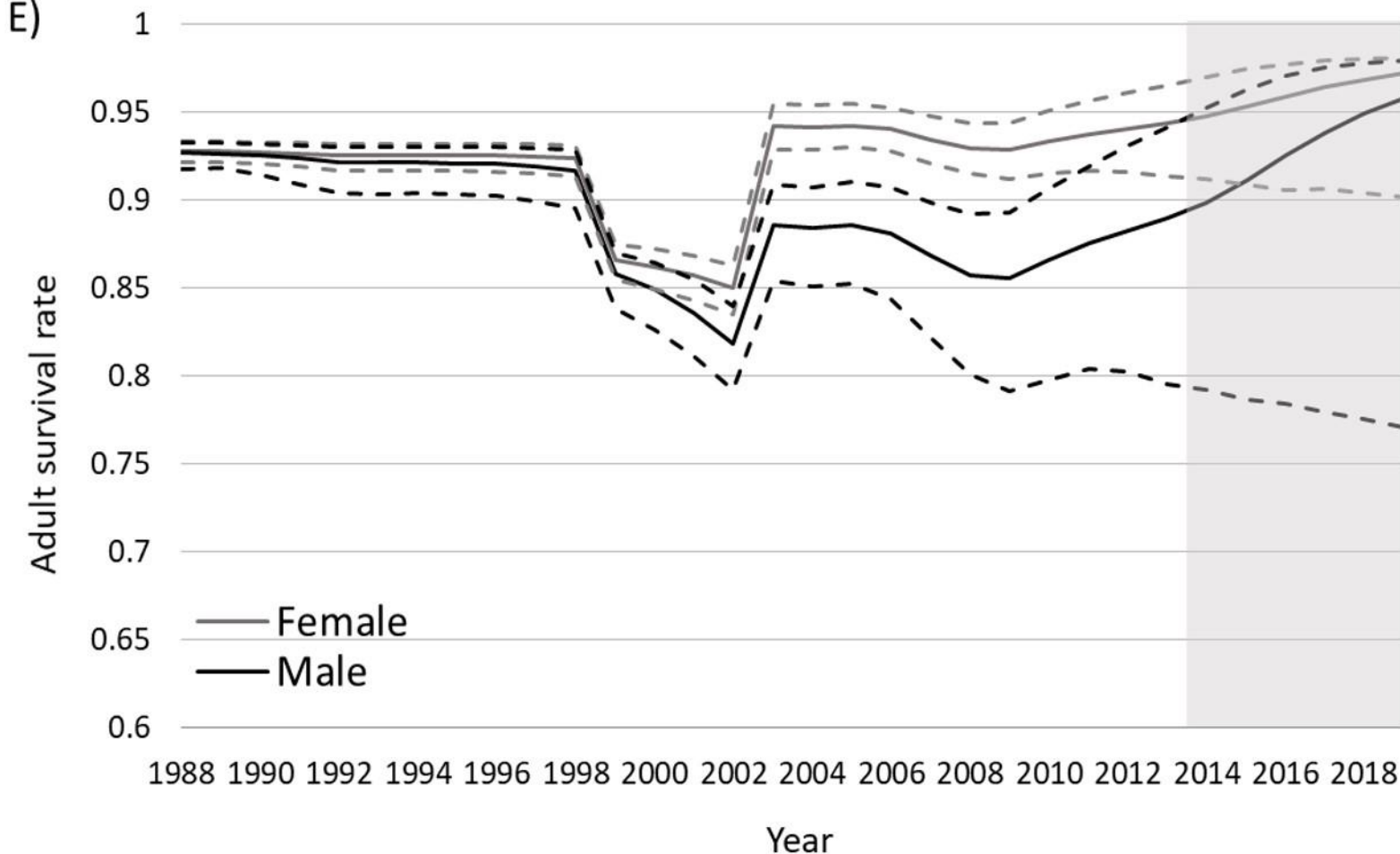
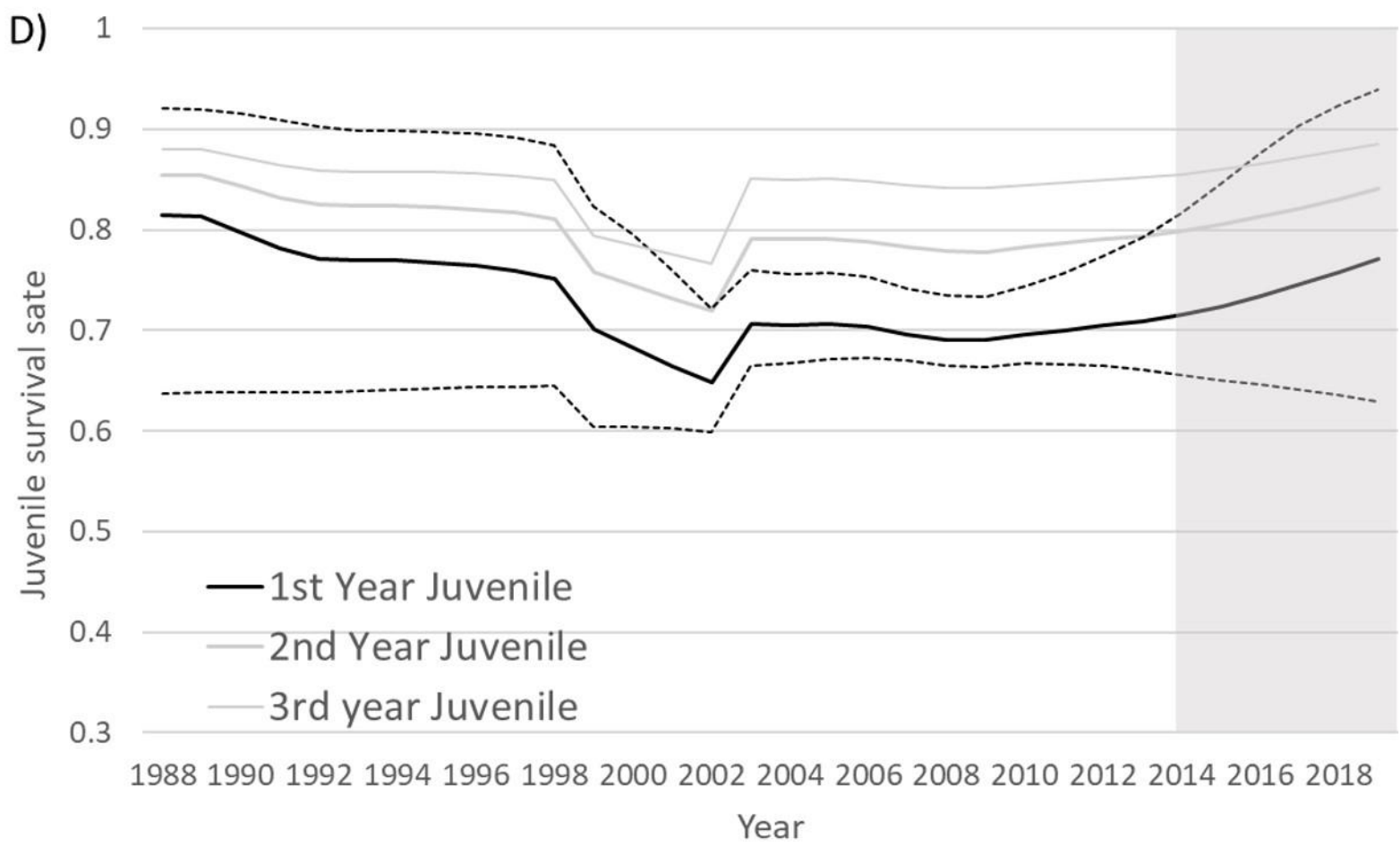
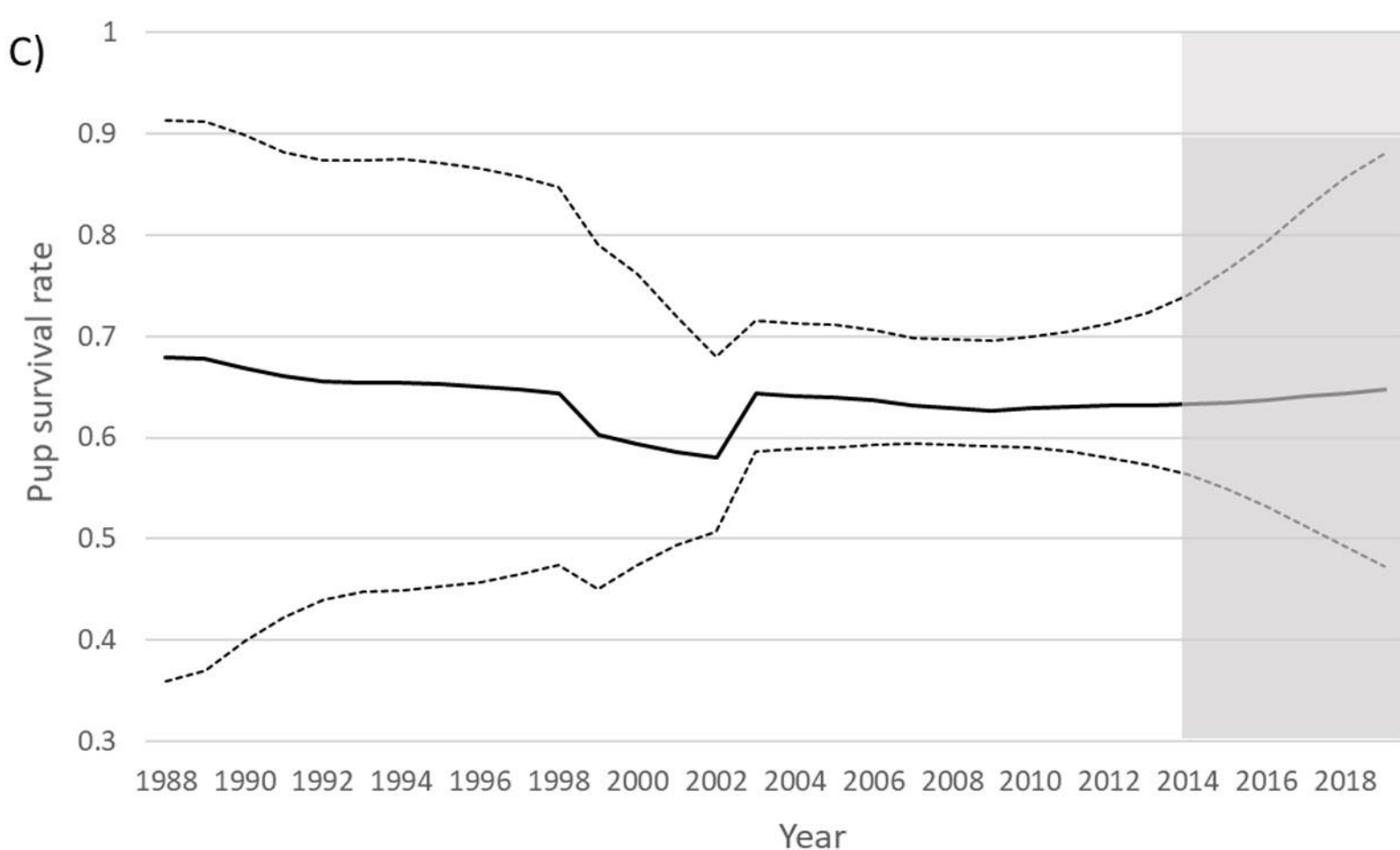
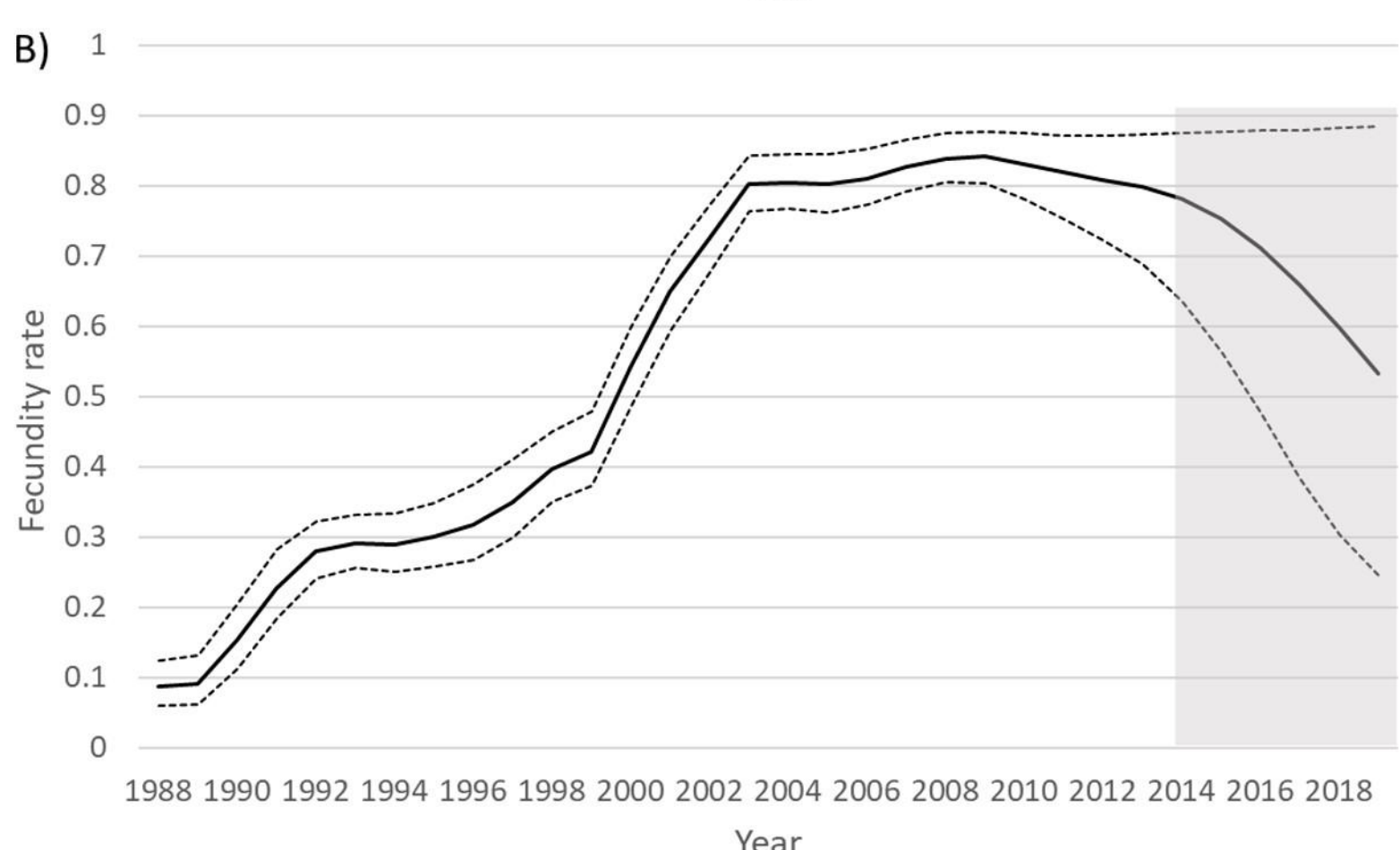
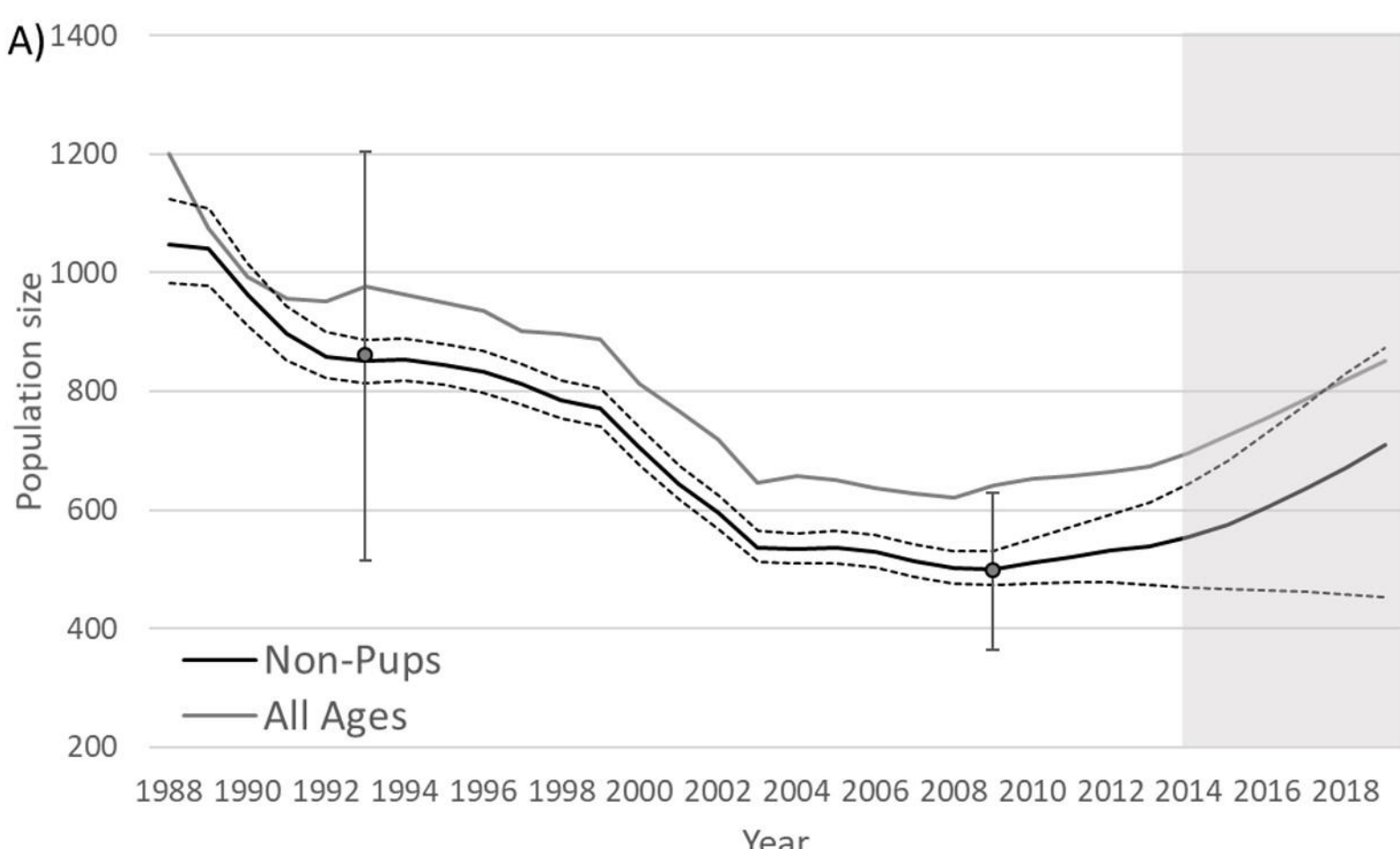
Figure 6: Demographic rates of the grey seal model. In the population size and fecundity rate graphs, the solid lines are the median values whereas the dashed lines are the CRI. The grey shaded area is the prediction after 2013.

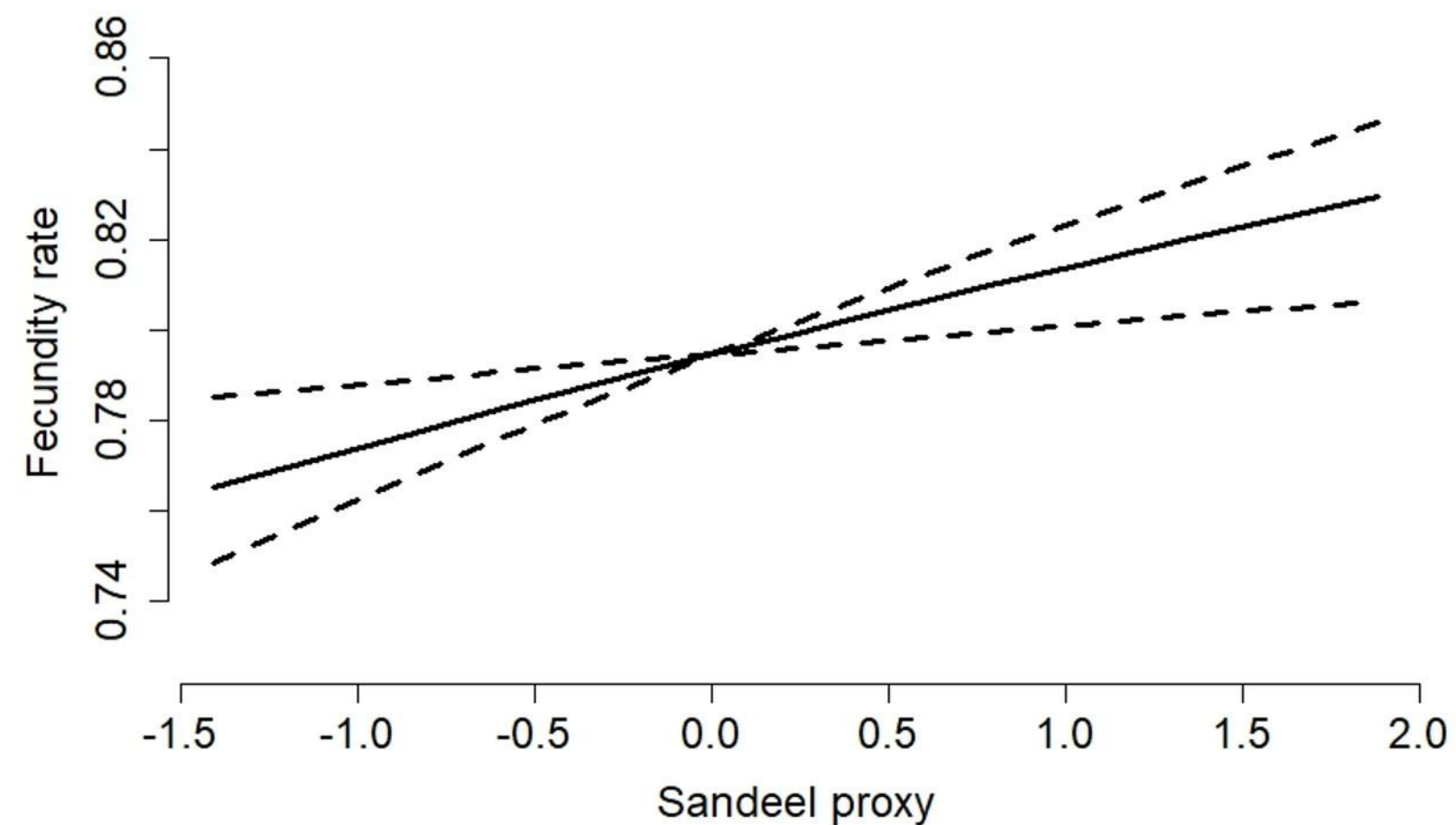
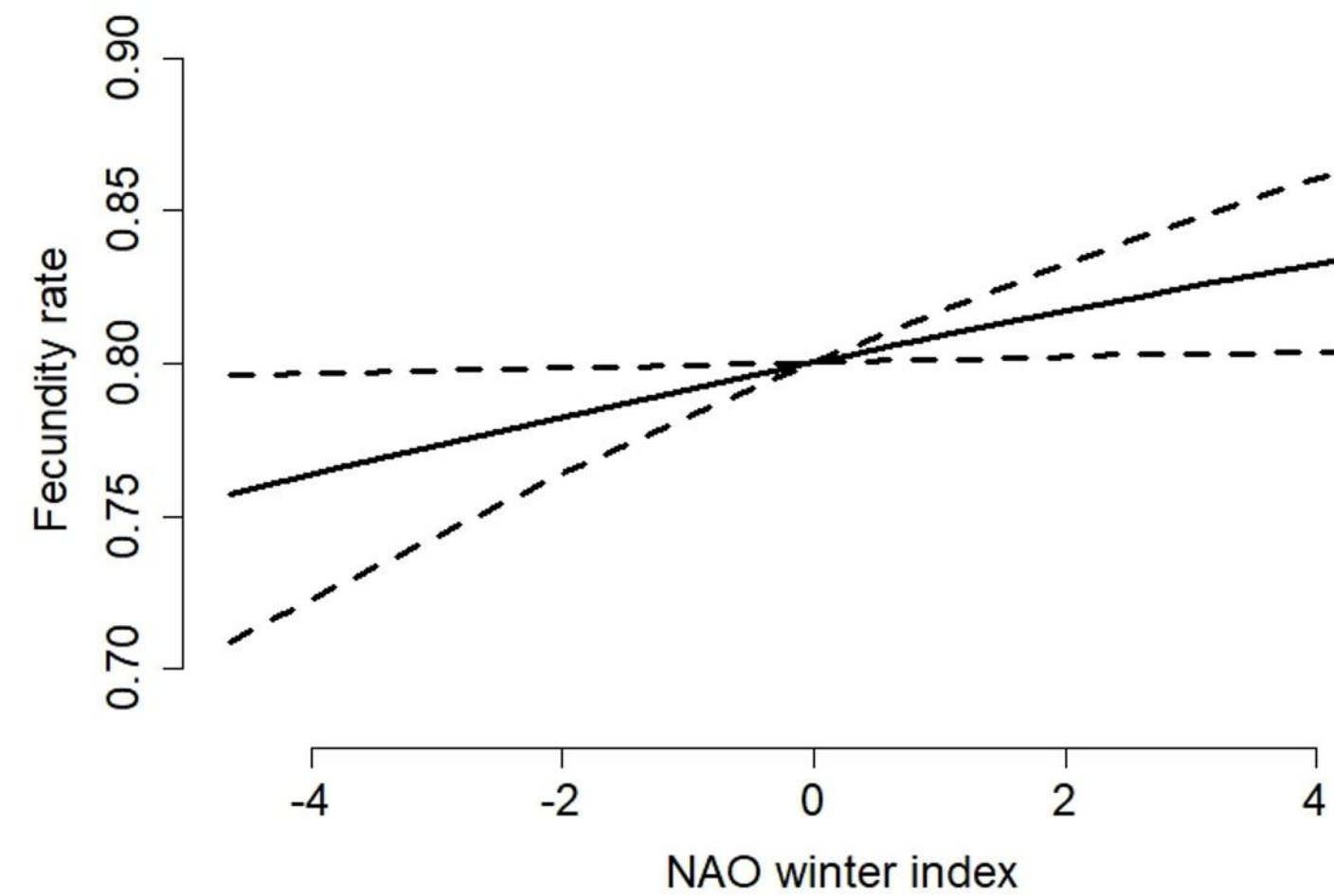
Figure 7: Mean prediction (solid line), and its credible interval (dashed line), of the pup survival rate given the number of hauled out grey seals.

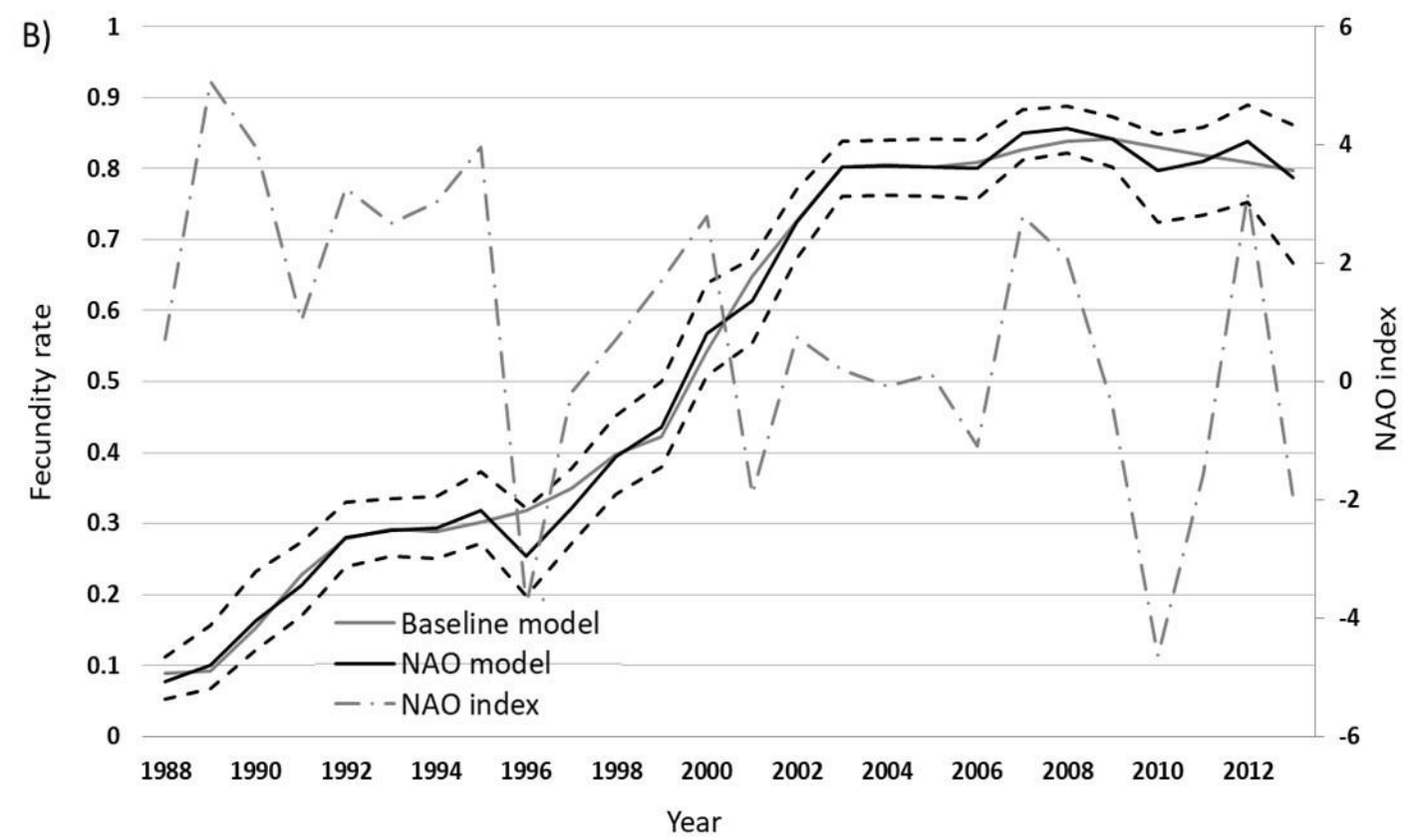
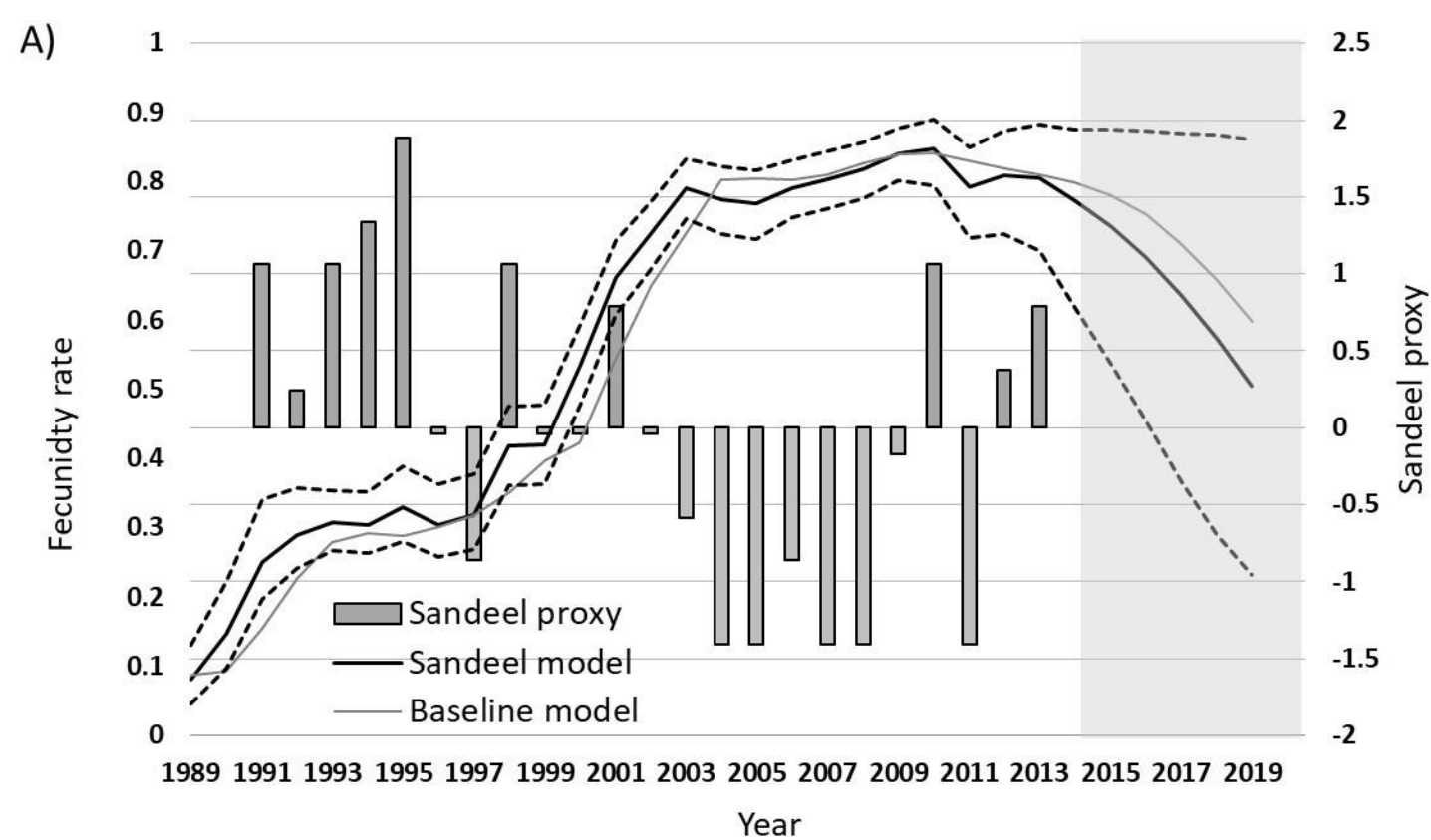
Figure 8: Growth rate prediction after 10 years with an increasing grey seal population.

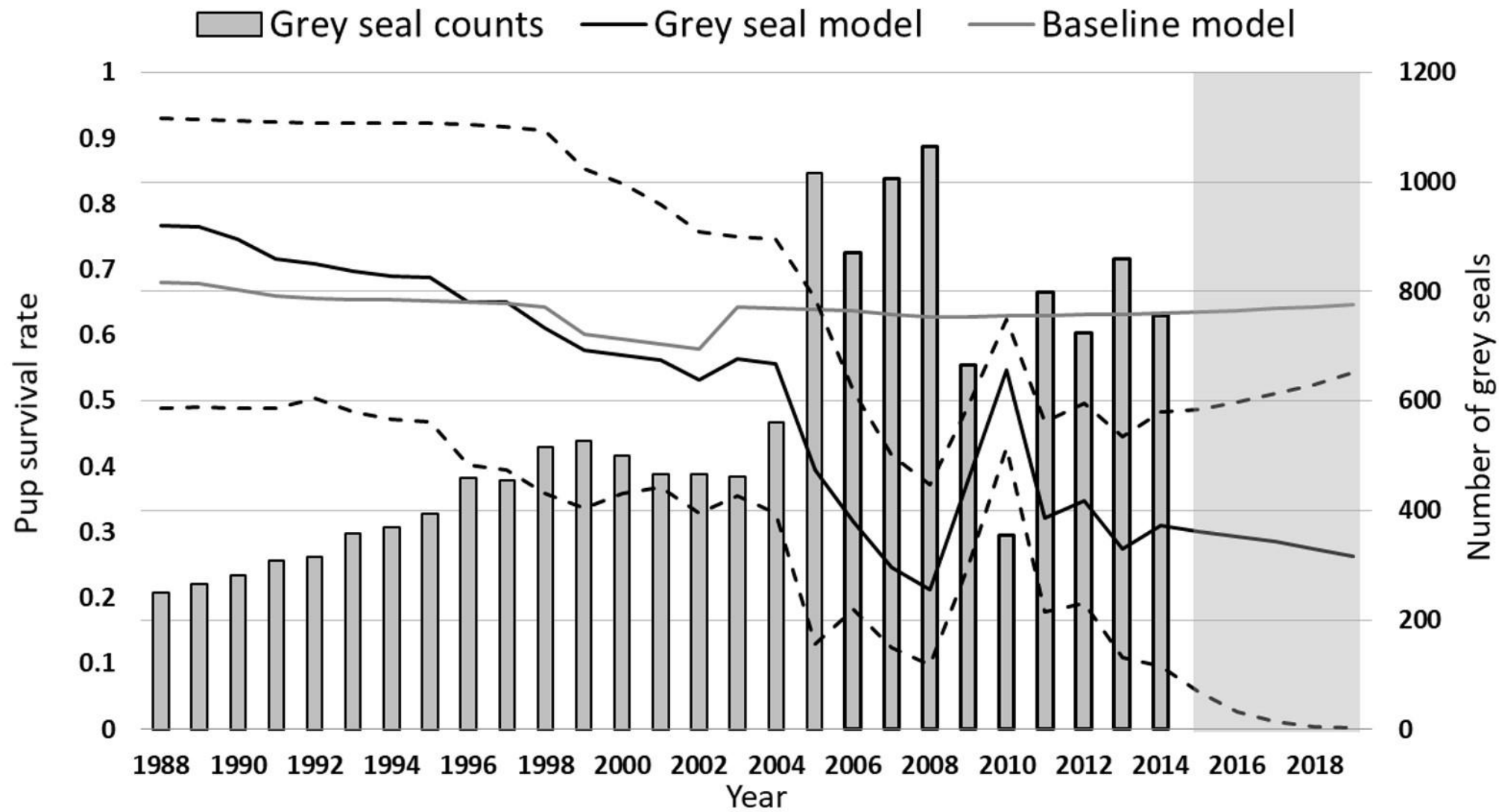
APPENDICES (see end of document)

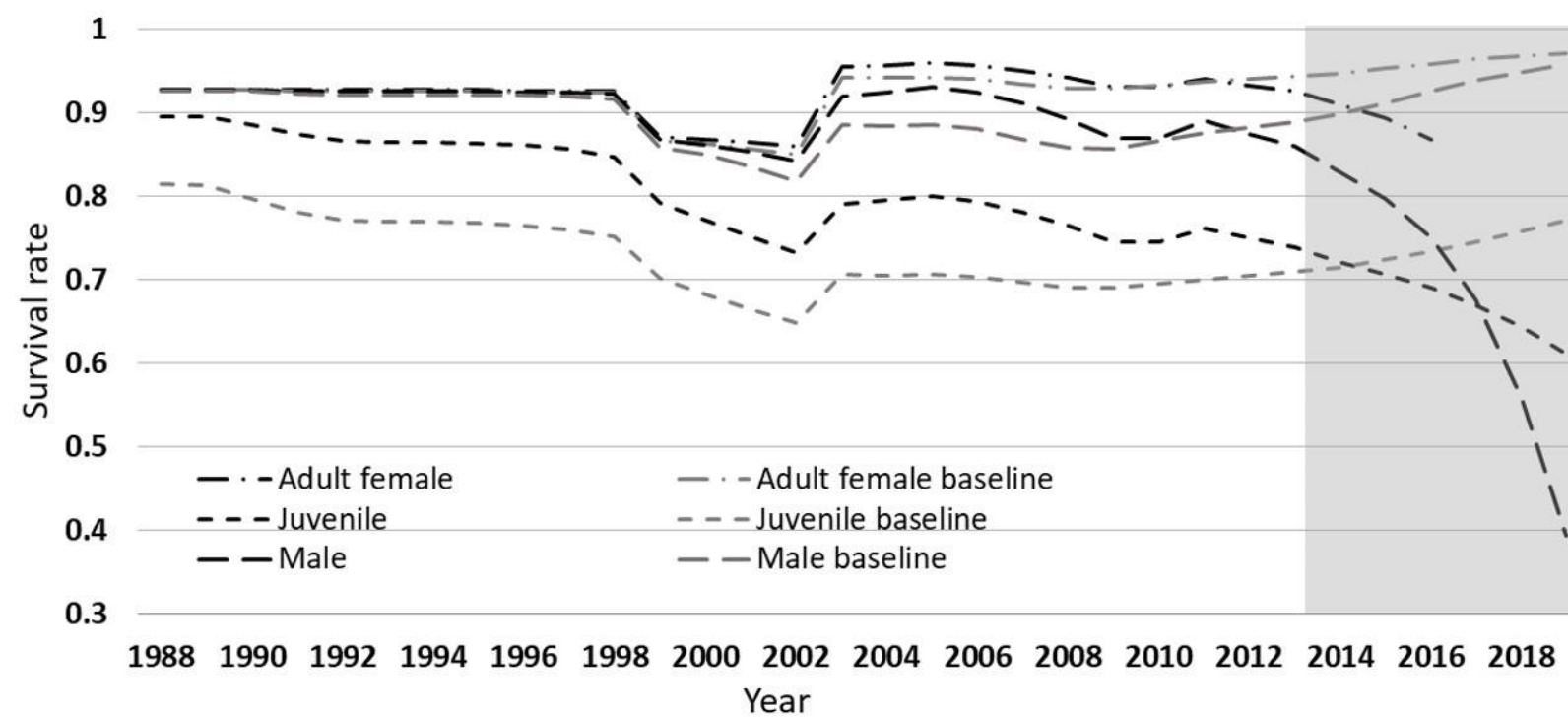
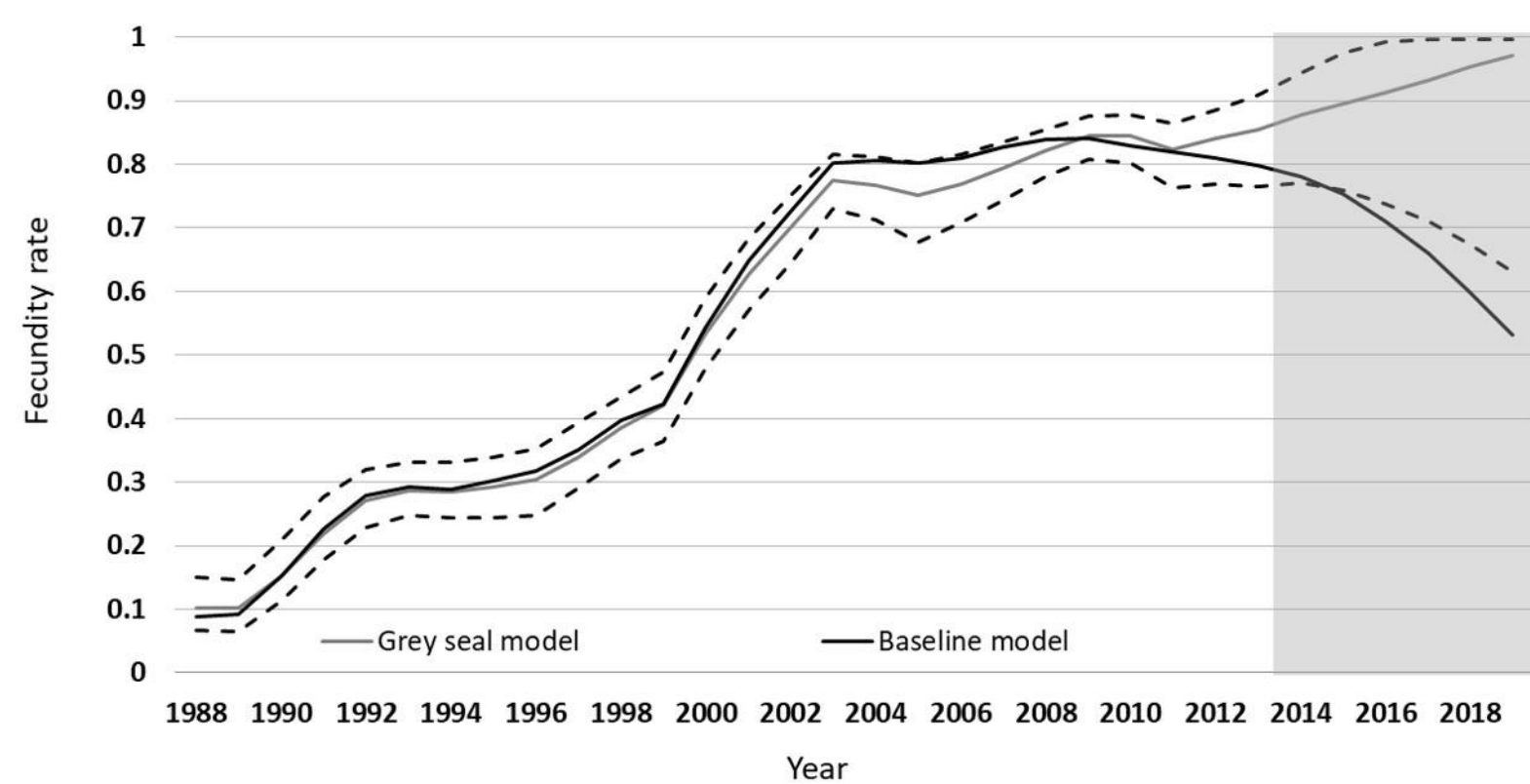
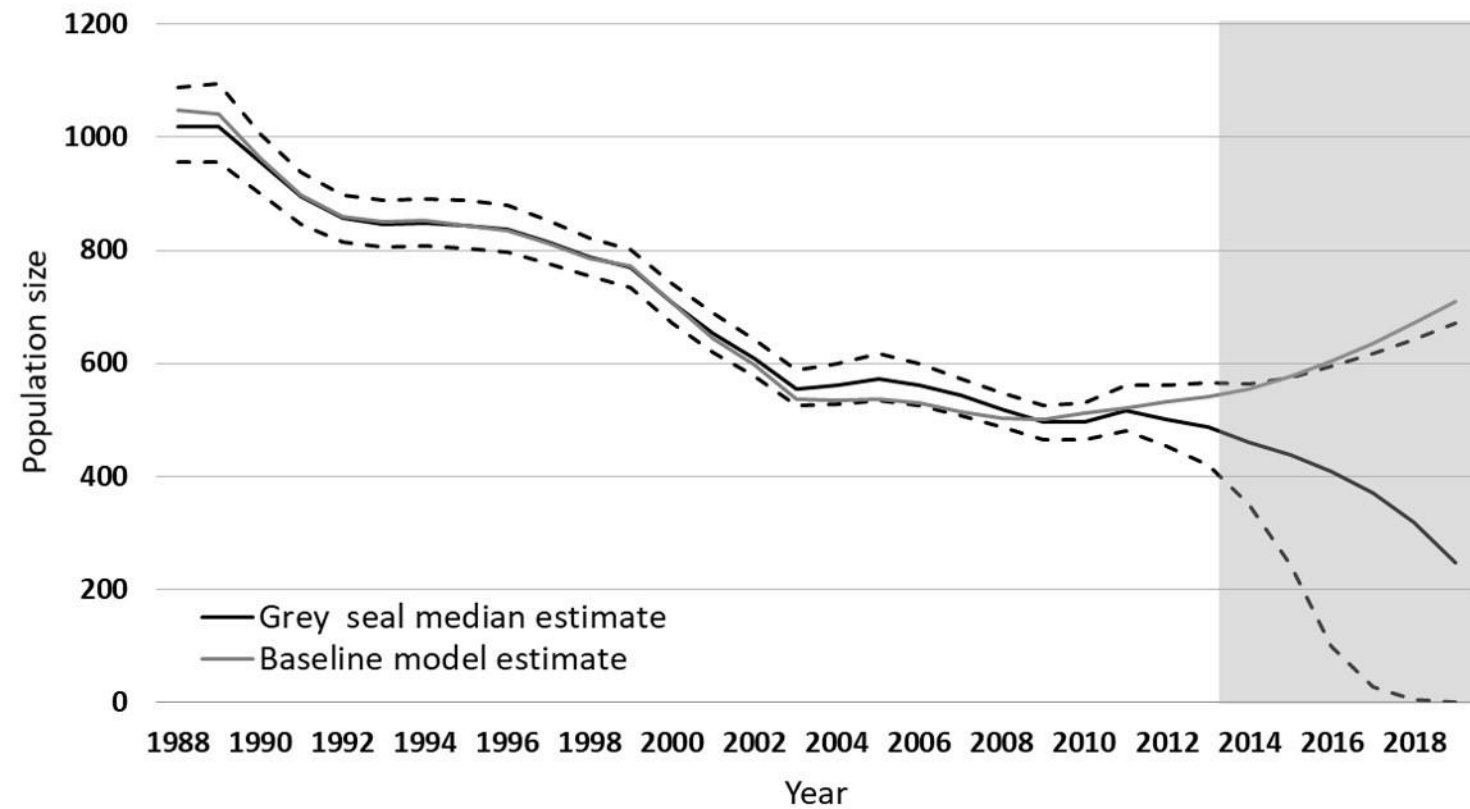


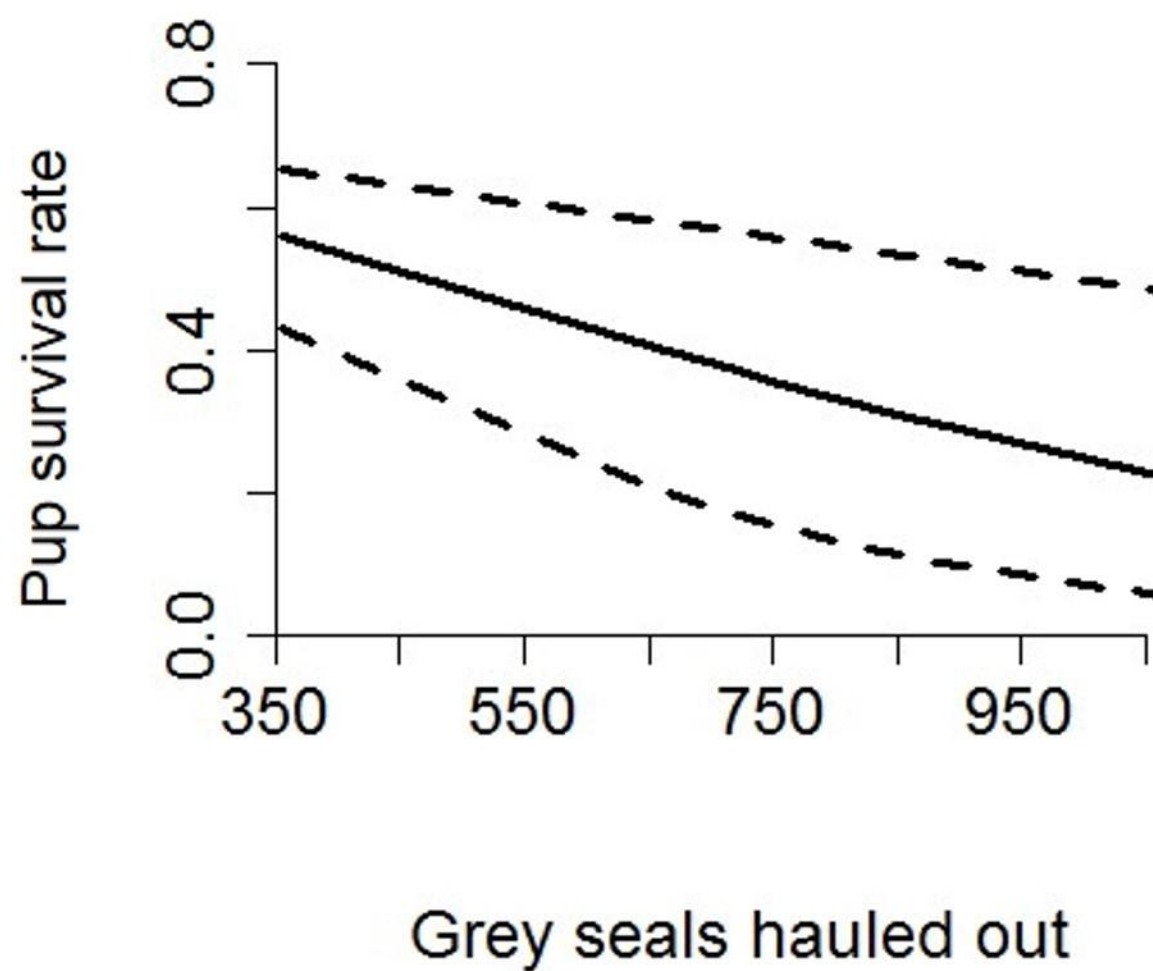


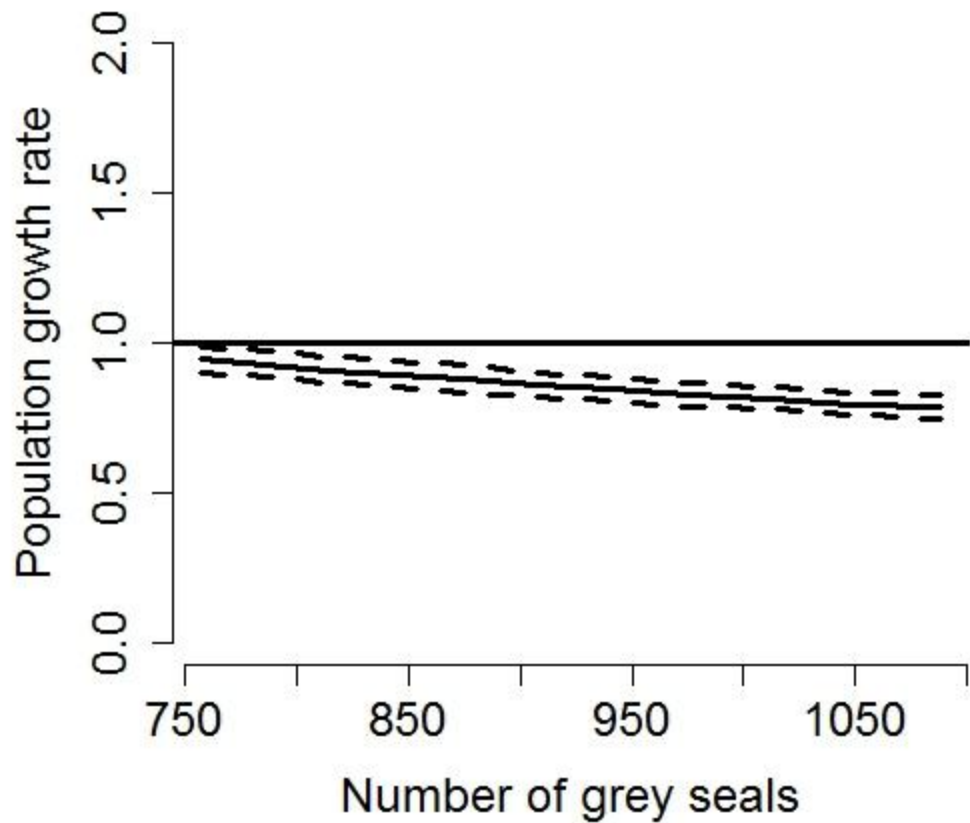












APPENDICES for CAILLAT et al..

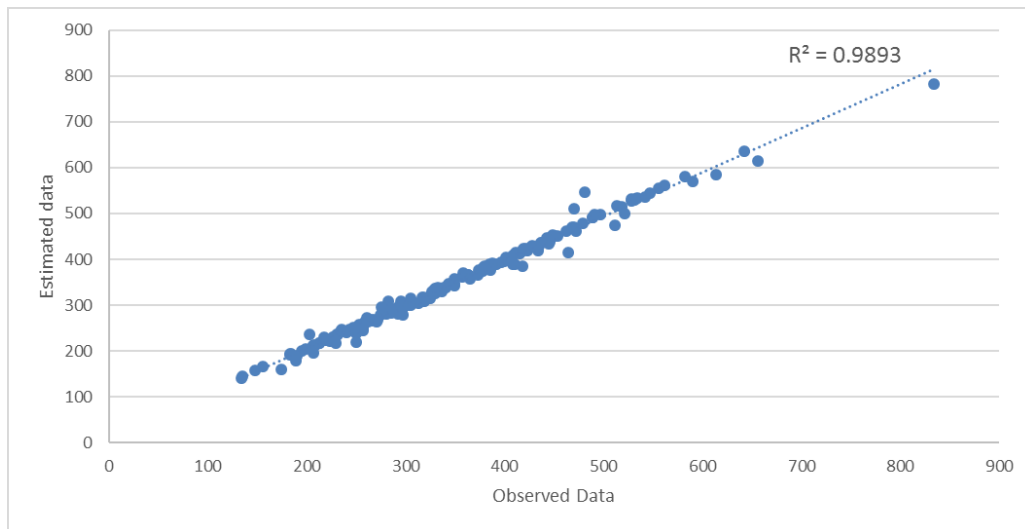


Figure A.1: Baseline Model results: Observed versus estimated data of non pup counts, with the associated regression coefficient R^2

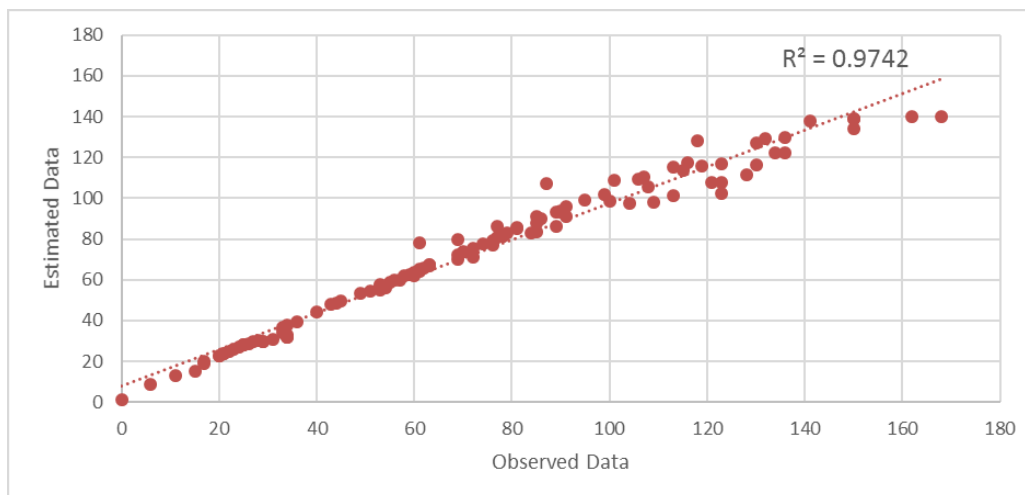
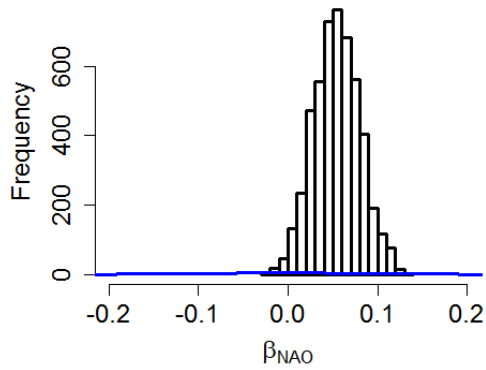


Figure A.2: Baseline Model results: Observed versus estimated data for pup counts, with the associated regression coefficient R^2

Prior and posterior distributions of the NAO covariate



Prior and posterior distributions of the Sandeel covariate

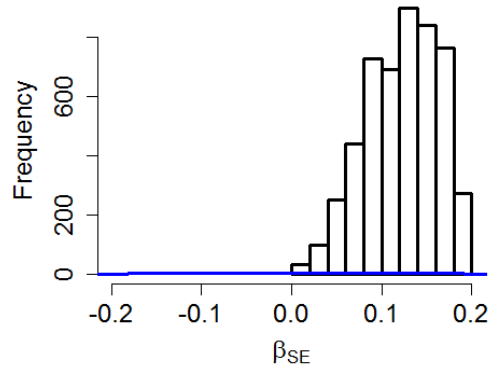


Figure A.3: Prior (line) and posterior distributions (bars) for the covariate coefficients of the NAO index (β_{NAO}) and the Sandell proxy (β_{SE}).

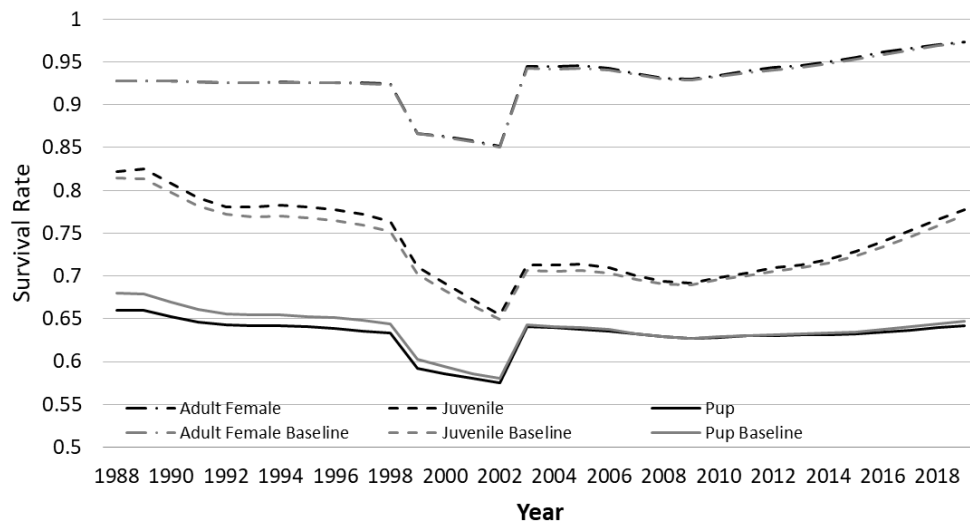


Figure A.4: Survival rates when the sandeel proxy covariate is included in the model.

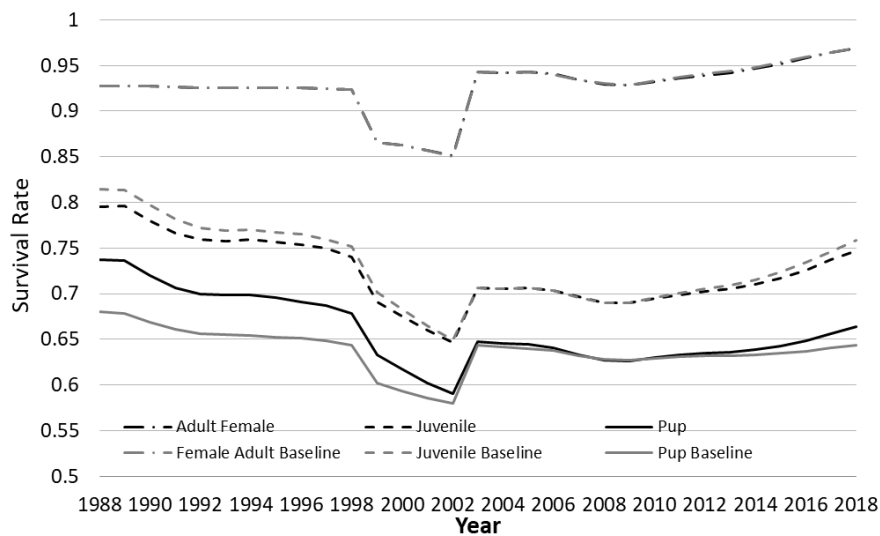


Figure A.5: Survival rates when the NAO Index covariate is included in the model.

Prior and posterior distributions of the Grey Seal covariat

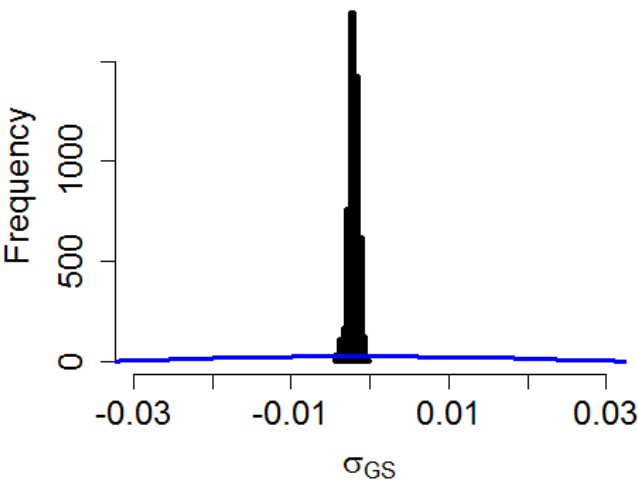


Figure A.6: Prior distribution (line) and posterior distribution (bars) of the Grey Seals covariate

Table A.1: Models tested to identify a possible correlation between covariates and demographic trends. “Where in Model” column describes in which demographic rate logit function the covariate was added with Fecundity rate=Fecundity, pup survival = pup surv, non-pup survival= Non pup surv, adult survival = adult surv, non adult (pups + juveniles) survival = non adult surv. The “Covariate prior value” shows the range of the prior values used in the model. The posterior values are the Bayesian credible intervals for the covariate parameters. Bold values are parameters whose posterior differs significantly from zero. * when the posterior distribution was bounded by the limit of the prior distribution, models were run again with a wider prior.

	Covariates	Were in Model	Covariates prior value	Posterior CI	
Prey	Herring	Fecundity	<i>(-0.03,0.03)</i>	-0.010	0.025
		Non pups	<i>(-0.03,0.03)</i>	-0.025	0.024
		Pup surv	<i>(-0.03,0.03)</i>	-0.025	0.023
	Cod	Fecundity	<i>(-0.03,0.03)</i>	-0.018	0.026
		Pup surv	<i>(-0.03,0.03)</i>	-0.024	0.025
		Non Pup surv	<i>(-0.03,0.03)</i>	-0.022	0.026
	Sprat	Fecundity	<i>(-0.03,0.03)</i>	-0.012	0.025
		Pup surv	<i>(-0.03,0.03)</i>	-0.025	0.024
		Non pup surv	<i>(-0.03,0.03)</i>	-0.025	0.023
	Sandeels	Fecundity	<i>(-0.03,0.03)</i>	-0.020	0.027
		Fecundity	<i>(-0.1,0.1)*</i>	0.004	0.094
		Fecundity	0.2	0.067	0.19
		Pup surv	<i>(-0.03,0.03)</i>	-0.023	0.024
		Non Pup surv	<i>(-0.03,0.03)</i>	-0.023	0.026
Grey seals	Grey seals	Fecundity	<i>(-0.03,0.03)</i>	Not converging	Not converging
		Pup surv	<i>(-0.03,0.03)</i>	-0.0029	-0.001
		Non Pup surv	<i>(-0.03,0.03)</i>	Not converging	Not converging
		Fecundity	<i>(-0.1,0.1)</i>	-0.003	0.002
		Pup surv	<i>(-0.1,0.1)</i>	-0.013	-0.0014
		Non Pup surv	0.1	Not converging	Not converging
		Juv surv	0.1	-0.0065	-0.0014
		Non adult surv	0.2	-0.0010	-0.0019
Environment	SST	Fecundity	0.03	-0.026	0.022
		Pup surv	0.03	-0.026	0.024
		Non adult surv	0.03	-0.023	0.026
	NAO	Fecundity	0.03*	-0.0097	0.027
		Fecundity	0.1*	-0.0035	0.090
		Fecundity	0.2	0.025	0.13
		Non pup surv	0.03	-0.021	0.025
Toxine	D.A	Pup surv	0.03	-0.024	0.024
		Fecundity	0.03	-0.022	0.022
		Non pup surv	0.03	-0.024	0.025
	Saxitoxin	Fecundity	0.03	-0.027	0.019
		Non pup surv	0.03	-0.024	0.024
		Pup surv	0.03	-0.024	0.024