

3. EARLIER PUPPING IN HARBOUR SEALS, *PHOCA VITULINA*

Published as: Peter J.H. Reijnders, Sophie M. J. M. Brasseur, Erik Meesters (2010) Earlier pupping in harbour seals, *Phoca vitulina*. Biol. Lett. (2010) 6, 854–857

SUMMARY

The annual reproductive cycle of most seal species is characterized by a tight synchrony of births. Typically, timing of birth shows little inter-annual variation. Here, however we show that harbour seals *Phoca vitulina* from the Wadden Sea (southeast North Sea) have shortened their yearly cycle, moving parturition to earlier dates since the early 1970s. Between 1974 and 2009, the birth date of harbour seals shifted on average by -0.71 d yr^{-1} , three and a half weeks (25 days) earlier, in the Dutch part of the Wadden Sea. Pup counts available for other parts of the Wadden Sea were analysed, showing a similar shift. To elucidate potential mechanism(s) for this shift in pupping phenology, possible changes in population demography, changes in maternal life-history traits and variations in environmental conditions were examined. It was deduced that the most likely mechanism was a shortening of embryonic diapause. We hypothesize that this could have been facilitated by an improved forage base, e.g. increase of small fishes, attributable to overfishing of large predator fishes and size-selective fisheries.

Keywords: pupping phenology; seals; forage base; fisheries impact.

INTRODUCTION

Harbour seals are seasonal breeders. The female reproductive cycle after parturition consists of lactation followed by oestrus and mating. Placental gestation starts after an obligate period of delayed implantation (Reijnders 1986, Boyd 1991b).

The annual reproductive cycle of most seal species is characterized by a tight synchrony of births, ensuring that pups are born at the optimal time of year (Boyd 1991b). Typically, timing of birth in most seal species shows little inter-annual variation (Atkinson 1997). Here, we report that harbour seals *Phoca vitulina* from the Wadden Sea (southeast North Sea) have shortened their yearly cycle, resulting in a birth peak 25 days earlier than in the 1970s. We investigated in which phase of the reproductive cycle these changes might have occurred, and possible underlying mechanisms generating the observed changes.

MATERIAL AND METHODS

The harbour seal population in the Wadden Sea (southeast North Sea), regarded as a discrete population, is monitored through a series of annual aerial surveys (Reijnders *et al.* 1997a). From 1974 to 2009, the total number of seals and number of pups are counted throughout the whelping period. Data for harbour seals in the Dutch Wadden Sea were used to investigate the timing of pupping. Given the distribution of births over the whelping period (Reijnders *et al.* 1997a), the date where the maximum number of pups is counted each year was chosen as a proxy for the peak timing of birth.

We fitted a model to the pup count data using generalized additive models (Wood 2006a). Data collected in years 1988, 1989, 2002 and 2003 were excluded as two virus outbreaks in 1988 and 2002 caused increased variation in the counts. The following model was found to best describe the data:

$$E[PUPS_i] = f(\text{year}_i, \text{julian_day}_i)$$

where $PUPS_i$ negative binomial, f is a smooth function combining year and julian_day and i indicates the observation.

The fitted model (M1) was used to generate predictions for the number of pups that would have been counted daily in the pupping seasons between 1974 and 2009 and to estimate the date of the maximum pup count each year. To limit the influence of estimated smoothing parameters of M1, we first generated a bootstrap sampling distribution (20 bootstraps) of the parameters to approximate the true function (Wood 2006a). Each bootstrap was then used to simulate 50 replicate parameter sets from the posterior distribution of the estimated parameters producing 1000 simulations. The median Julian day at which the maximum number of pups occurred and confidence limits were calculated from the simulations. Note that for these predictions, the years around the virus epizootics were included.

All computations were calculated within the R environment (R Development Core Team 2009) v. 2.10.0, 2009, using package mgcv (Wood 2006a).



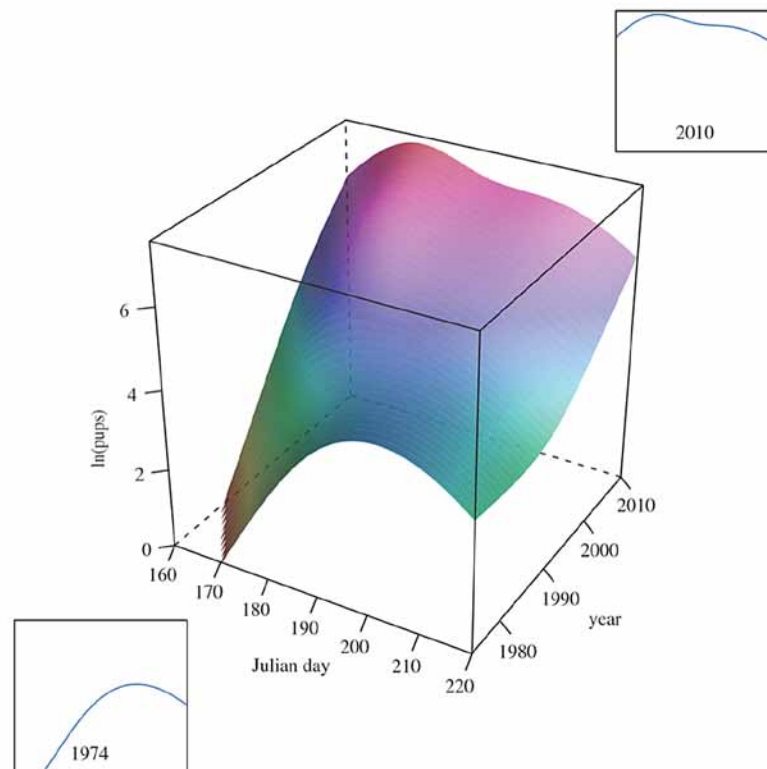


FIGURE 1. ESTIMATED PUP COUNT (LOGARITHMICALLY TRANSFORMED) VERSUS JULIAN DAY AND YEAR. VISUALIZATION OF THE GENERALIZED ADDITIVE MODEL (GAM), WHICH USED A TWO-DIMENSIONAL SMOOTHER COMBINING JULIAN DAY AND YEAR TO ESTIMATE PUP COUNT. THE MODEL EXPLAINED 94.6% OF THE TOTAL DEVIANCE. NOTE HOW THE YEARLY PEAK MOVES FROM RIGHT TO LEFT OVER THE YEARS, WHILE PUP NUMBERS INCREASE SIMULTANEOUSLY. INSETS: TWO-DIMENSIONAL PANELS FOR FIRST AND LAST YEAR OF TIME SERIES.

RESULTS

The model outcome is shown in figure 1. The observed annual pup counts enabled the estimation of the most likely date at which the number of pups reached its maximum value. The median Julian day at which maximum number of pups occurred, and the 95% confidence interval, are given in figure 2. (For count dates and variance associated with model fit, see supplement) Between 1974 and 2009, the pupping time of harbour seals in the Dutch part of the Wadden Sea shifted by -0.71 d yr^{-1} (95% confidence limits (CL): 0.57, 0.83), which equates to a mean pupping date three and a half weeks earlier (25 days, CL 20, 29 days) by 2009. This shift was continual but not constant over the period studied (figure 2), and strongest between 1986 and 1990 (see also supplement figure 1, lower panel). The persistent shift since 1974 indicates that the changed phenology in pupping may have started prior to survey start. However, there are no pup counts to investigate that. Pup counts available for other parts of the Wadden Sea (Schleswig Holstein and Niedersachsen) for the same period were analysed and similar shifts (-0.68 d yr^{-1} , CL 0.56, 0.82, respectively, -0.59 d yr^{-1} , CL 0.35, 1.0) were found (supplement figure 2 & 3).

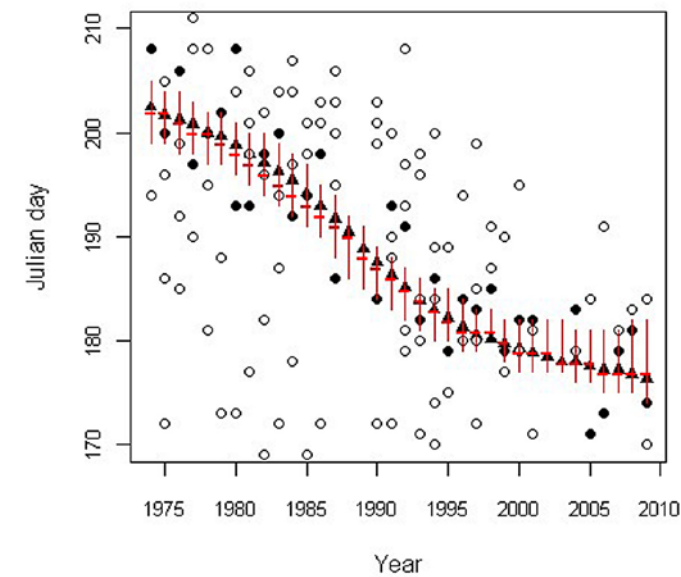


FIGURE 2. DATES ON WHICH MAXIMUM NUMBER OF PUPS IS ESTIMATED TO HAVE OCCURRED. ESTIMATES WERE OBTAINED BY USING A COMBINATION OF BOOTSTRAPPING AND SAMPLING FROM THE POSTERIOR DISTRIBUTION OF THE GAM COEFFICIENTS TO GET 1000 SIMULATIONS. FROM EACH SIMULATION, THE YEARLY DATE WITH MAXIMUM NUMBER OF PUPS WAS CALCULATED, USING A PRE-CONSTRUCTED PREDICTION DATASET, PROVIDING 1000 DATES FOR EACH YEAR. HORIZONTAL DASHES SHOW MEDIAN DATE, BARS: 95% CL BASED ON THE 2.5 AND 97.5 QUANTILES; OPEN CIRCLES, DAY NUMBERS WHEN COUNTS WERE CARRIED OUT; BLACK SQUARES, WHEN MAXIMUM WAS COUNTED.

DISCUSSION

Here, we report on a continual shift in birth date of harbour seals in the Dutch Wadden Sea over decades. Given the similar results found for harbour seals in other parts of the Wadden Sea, we conclude that the factor causing this shift has acted on the entire harbour seal population.

A possible mechanism for this shift in pupping could be a shortening of one or several stages in the reproductive cycle, including lactation, delayed implantation and placental gestation. Most pinnipeds have highly synchronized annual reproduction, however, variation in the mean date of parturition may occur. Photoperiod at the time of implantation is an important factor in the timing of reproduction in seals (Temte 1994). However, there has been no change in day length in the Wadden Sea over the period of study (KNMI Database).

Body condition at the time of implantation may cause changes in the timing of births (Boyd 1984). For instance, reduced prey availability may lead to later birth and implantation, and increase the time from conception to birth (Bowen *et al.* 2003, Jemison & Kelly 2001). Finally, changes in age structure may also influence pupping phenology, as older females tend to give birth earlier than younger females (Boyd 1996, Reiter *et al.* 1981).

As a possible explanation for the shift, we examined changes in population age-structure. The two virus epizootics (1988 and 2002), killing about 50 per cent of the population, are considered to have temporarily (5–6 years) affected age structure (Härkönen *et al.* 1999). Given the episodic character of these events compared with the smoothness of the trend (figure 2), it appears unlikely that changes in age struc-

ture would explain our observations. Except for the epizootics, the relative growth rate remained constant, supporting our conclusion that the change in pupping time is not driven by internal age-structure.

We then investigated changes in maternal nutritional condition and related life-history traits as possible explanatory factors, starting with placental gestation. Birth mass is positively correlated with maternal mass in seals, but the duration of active gestation is only marginally influenced by maternal condition (Boyd 1991b, Mellish *et al.* 1999). Apparently heavier mothers produce heavier pups, but in the same time span as lighter mothers. It seems unlikely that a shortened placental gestation would cause the observed shift, as the duration of placental gestation hardly varies among species (Boyd 1991b). Consequently, only a shortening of either lactation period and/or period of delayed implantation could explain our observations. Duration of lactation in harbour seals was not affected during the years of reduced prey availability Bowen *et al.* (2003) and furthermore, in grey seals (*Halichoerus grypus*) lactation duration was unrelated to postpartum maternal mass (Kovacs & Lavigne 1986). Maternal mass apparently influences weaning mass but not the duration of lactation.

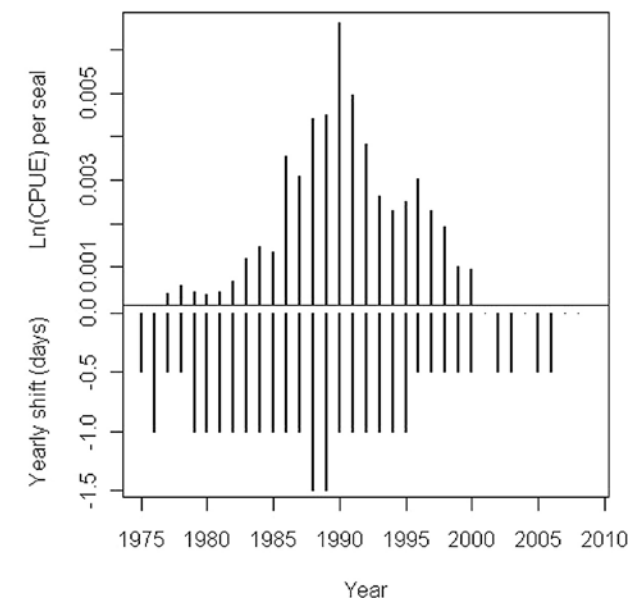
Implantation date in harp seals (*Pagophilus groenlandicus*) was, however, affected by maternal condition (Stewart *et al.* 1989). We therefore suggest earlier timing of implantation as the most likely mechanism explaining the observed shift. Possibly, nutritional condition of the mother after lactation and during embryonic diapause is of importance. Females undergo rapid weight loss during lactation and mating, and may need to acquire a fatness threshold prior to implantation (Stewart *et al.* 1989). However, during the early part of embryonic diapause, animals haul-out frequently for moulting and time for feeding is limited. In other words, the better the food acquisition during and after lactation, the earlier they regain the mass needed for implantation. Improved prey availability, may therefore accelerate the replenishment of used fat reserves, and thus facilitate a shortening of embryonic diapause. Harbour seals consume a variety of small, generally demersal (bottom dwelling) fish species, and forage in both the Wadden Sea and North Sea (Brasseur *et al.* 2004). Long-term trawl surveys (1977–2001) in the North Sea revealed that abundance of small fishes including demersal species have increased steadily and significantly from 1977 till 1987 (Daan *et al.* 2005). Intense fishing of larger fishes in the North Sea has caused both a shift to smaller species and a decrease of large predator fishes, and hence predation on small fishes has decreased (Jennings *et al.* 2002). In parallel, total biomass in Dutch estuarine and coastal fishes increased from 1970 to mid-1980s (Tulp *et al.* 2008). It is therefore plausible that over the last three to four decades, as a result of fisheries, the prey available to seals has increased in our study area. This is supported by the increase of avian predators specializing on similar small prey (e.g. red throated divers *Gavia stellata*) in our study area since 1972 (Camphuysen 2009). There is a strong correlation (Spearman's rho 20.79) between the shift in pupping and increase in small fishes (less than or equal to 20 cm) in the southeast North Sea (see also supplement figure 1). We hypothesize that the observed shift in pupping phenology has been facilitated by an improved forage base as a result of overfishing predator fishes and size-selective fisheries. That improved the condition of females in the pre-implantation period and triggered a shortening of embryonic diapause. It is interesting to see whether this shift might be reversed when this exponentially growing population (Reijnders *et al.* 2009) approaches carrying capacity of the area.

SUPPLEMENT

We first examined whether a seasonal shift in food availability could be related to the observed earlier pupping time. Many studies have examined biological changes in relation to climatic change by analysing systematic trends across diverse taxa and regions (Parmesan & Yohe 2003, Root *et al.* 2003). Of interest and related to our study are data on phenological changes in relation to changes in temperature. Data on mammals were so scarce, however, that no estimated means of phenological shifts could be examined (Parmesan & Yohe 2003, Root *et al.* 2003). As a proxy for a temporal shift in food availability we used data on peak spring/summer abundance of brown shrimp (*Crangon crangon*) in the Wadden Sea, collected by the Royal NIOZ. Brown or common shrimp represents an abundant and well documented species in the region, and due to its high abundance forms a key component of the trophic web. It is an extensive food source for several predators including fish, crustaceans and shorebirds (del Norte-Campos & Temming 1994, Pihl 1985, Walter & Becker 1997). We tested the months at which shrimp abundance peaked, versus year. Regression analysis showed that the regression coefficient was far from significant ($F_{1,31} = 0.142$, $p = 0.71$). We concluded that it was therefore unlikely that the earlier pupping could be attributed to a seasonal shift in food availability.

Fish community changes

We used data on changes in abundance of small fish (from the Demersal Young Fish Survey) to examine the relative abundance of small fish in the south eastern North Sea (Fig.7c in Daan *et al.* (2005)). These are the main foraging grounds for harbour seals from the Wadden Sea (Brasseur *et al.* 2004). Intense fishing has caused both a



SUPPLEMENT FIGURE 1. UPPER PANEL: THE RATIO BETWEEN NUMBER OF SMALL FISH ($\ln(\text{CPUE})$) FROM (DAAN ET AL. 2005) AND TOTAL NUMBER OF HARBOUR SEALS (MAXIMUM NUMBER COUNTED) FOR EACH YEAR AS A MEASURE OF SMALL FISH AVAILABILITY TO SEALS; LOWER PANEL: THE YEARLY SHIFT IN PUPPING TIME AS ESTIMATED BY LINEAR REGRESSION BETWEEN THE PREVIOUS AND THE NEXT YEAR. BECAUSE THE PREDICTIONS ONLY INCLUDE WHOLE DAYS, THESE VALUES CAN ONLY BE MULTIPLES OF 0.5.

shift to smaller species and a decrease of large predator fish, and hence predation on small fish has decreased (Jennings *et al.* 2002, Greenstreet & Rogers 2006). As stated in the paper by Daan *et al.* (2005) on changes in the North Sea fish community, there has been a marked change in abundance of different size classes of fish. The smallest class (≤ 20 cm) increased significantly ($p < 0.01$), whereas the intermediate class (20.1-33.1 cm) as well as the large classes (33.1- >148.4 cm) declined significantly ($p < 0.05$ respectively $p < 0.01$).

Seal counts

Data on number of seals counted in the Dutch part of the Wadden Sea, used to calculate abundance of fish per seal for each year in the study period (supplement figure 1, upper panel) are our own survey data (Reijnders *et al.* 2009).

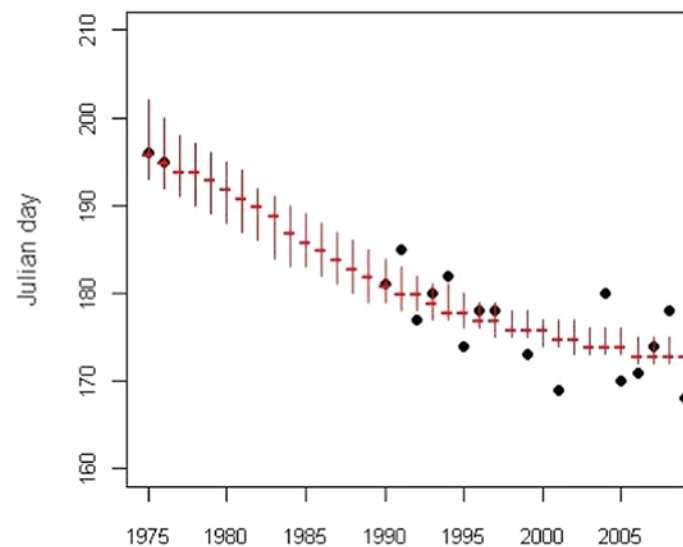
Statistical methods

The data consisted of yearly counts of the number of seals, including pups, in the Dutch Wadden Sea (Reijnders *et al.* 2009). The pup counts are carried out during June and July. The counted number of pups each year showed a clear pattern throughout the whelping period (Reijnders 1978b, Reijnders *et al.* 2009). Preliminary analyses using only the Julian day when maximum number of pups was counted (*i.e.* one data point per year), indicated a strong linear trend that included an annual decrease of 0.876 days (s.e. 0.065, $n = 36$, $F_{1,34} = 181$, $p = 3.557e^{-15}$). However, residual plots indicated a non-linear trend. Analysis using a Generalized Additive Model (GAM) (Hastie & Tibshirani 1986, Wood 2006a) indicated that the model may as well be described by a smooth function. An analysis of deviance com-

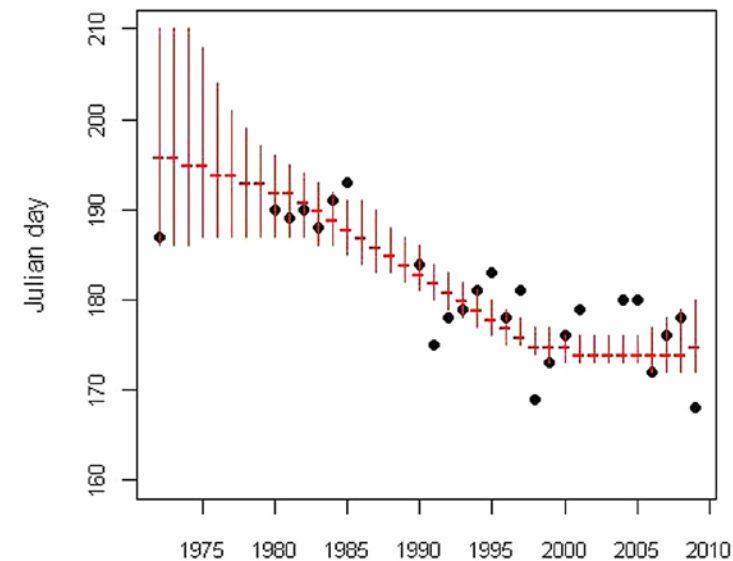
parison between a linear model and a non-linear model indicated an approximate probability of 0.095 that the GAM is better. We therefore decided to try a different approach using all counts from each year. The zeros in these counts did not delineate the moment pupping started or ended. This added unnecessary variation to the model. We therefore excluded these zero values, ending up with 162 data points. Furthermore, we found that 1989 and 2002 had large residual variation and because these years followed (respectively included) the two virus epizootics we decided to exclude 1988 to 1989 and 2002 to 2003 from further analyses. The best model in terms of AIC was:

$$E[PUPS_i] = f(\text{year}_i, \text{julian_day}_i)$$

Where $PUPS_i \sim \text{negativebinomial}$, f is a smoothing function combining the two predictors and i indicates the observation. Two types of smooth functions are possible, isotropic smooths and tensor product smooths. The tensor product smooths used here are invariant to linear rescaling of covariates and can be computationally more efficient (Wood 2006b). To reduce numerical computing complexity, we initially set the upper limit of the degrees of freedom for each smoother to 4. Furthermore, to prevent over-fitting without compromising model fit the smoothers were penalized further by setting the parameter gamma to 1.4 (Kim & Gu 2004). A negative binomial distribution was used to reduce the over-dispersion that was apparent (dispersion factor around 8.6) when using a Poisson distribution. We also investigated whether the model would improve by including a temporal correlation structure. A variogram indicated a slightly higher correlation between data points within a



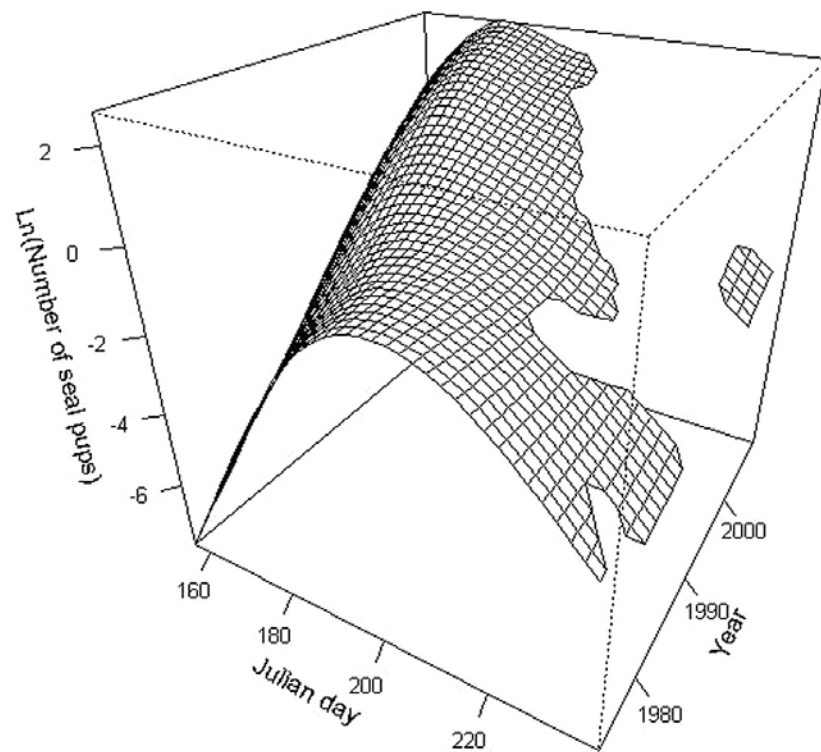
SUPPLEMENT FIGURE 2. THE ESTIMATED DATES THAT MAXIMUM NUMBER OF PUPS OCCURRED THROUGH TIME FOR THE AREA OF SCHLESWIG HOLSTEIN. ESTIMATES WERE OBTAINED BY USING A COMBINATION OF BOOTSTRAPPING AND SAMPLING FROM THE POSTERIOR DISTRIBUTION OF THE GAM COEFFICIENTS TO GET 1000 SIMULATIONS. FROM EACH SIMULATION YEARLY DATE WITH MAXIMUM NUMBER OF PUPS WAS CALCULATED, USING A PRE-CONSTRUCTED PREDICTION DATA SET, RENDERING 1000 DATES FOR EACH YEAR. HORIZONTAL DASHES SHOW MEDIAN DATE, BARS: 95% CONFIDENCE LIMITS BASED ON THE 2.5 AND 97.5 QUANTILES, AND BLACK DOTS: DAY NUMBERS AT WHICH THE MAXIMUM WAS COUNTED.



SUPPLEMENT FIGURE 3. THE ESTIMATED DATES THAT MAXIMUM NUMBER OF PUPS OCCURRED THROUGH TIME FOR THE AREA OF NIEDERSACHSEN. ESTIMATES WERE OBTAINED BY USING A COMBINATION OF BOOTSTRAPPING AND SAMPLING FROM THE POSTERIOR DISTRIBUTION OF THE GAM COEFFICIENTS TO GET 1000 SIMULATIONS. FROM EACH SIMULATION YEARLY DATE WITH MAXIMUM NUMBER OF PUPS WAS CALCULATED, USING A PRE-CONSTRUCTED PREDICTION DATA SET, RENDERING 1000 DATES FOR EACH YEAR. HORIZONTAL DASHES SHOW MEDIAN DATE, BARS: 95% CONFIDENCE LIMITS BASED ON THE 2.5 AND 97.5 QUANTILES, AND BLACK DOTS: DAY NUMBERS AT WHICH THE MAXIMUM WAS COUNTED.

period of 4 years, but a mixed model with a spherical correlation structure did not improve the AIC and the range of the variogram was close to zero. The final model explained 94.6% of the deviance and included a two dimensional smoother with approximately 14 effective degrees of freedom. The theta parameter of the negative binomial distribution was estimated at 12.77. Supplement figure 4 is a visualisation of the estimated model. Parts where data were lacking were not included in the plot. The fitted model (M1) was then used to generate predictions for the relevant period in each year to enable estimation of date at which the maximum number of pups would have been counted. To reduce estimated smoothing parameter influence of M1, we first generated a bootstrap sampling distribution (20 bootstraps) to approximate the true function (Wood 2006a). Each bootstrap was then used to simulate 50 replicate parameter sets from the posterior distribution of the estimated parameters producing 1000 simulations. These were subsequently used to estimate the median Julian day at which the maximum number of pups occurred, within the relevant part of the data range of that year, as well as the 95% confidence interval (Figure 2). Note that for these predictions, the years around the virus epizootic were included.

All computations were calculated within the R environment (version 2.10.0, 2009) using package mgcv (see (Wood 2006a) in main text). Three Dimensional visualisation was calculated using package lattice (Sarkar 2009).



SUPPLEMENT FIGURE 4. ESTIMATED NUMBER OF SEAL PUPS VERSUS JULIAN DAY AND YEAR. AS THE YEARLY PEAK SHIFTED TO EARLIER DATES, GRADUALLY LESS PUP DATA WERE OBTAINED IN JULY AS COMPARED TO THE BEGINNING OF THE MONITORING. BECAUSE GENERALIZED ADDITIVE MODELS ARE KNOWN TO BE RELATIVELY PRONE TO ERRORS OUTSIDE THE DATA RANGE, THESE AREAS WERE EXCLUDED FROM THE PLOT.



HARBOUR SEAL WITH TRACKER DURING THE BREEDING SEASON IN THE DOLLARD AREA (PHOTO KLAAS KREUIJER).