



Rapid recovery of Dutch gray seal colonies fueled by immigration

SOPHIE M. J. M. BRASSEUR¹ and TAMARA D. VAN POLANEN PETEL, IMARES, Department of Ecology, PO Box 167, 1790 AD Den Burg, The Netherlands; TIM GERRODETTE, Southwest Fisheries Science Center, NOAA National Marine Fisheries Service, 8901 La Jolla Shores Drive, La Jolla, California 92037, U.S.A.; ERIK H.W.G. MEESTERS, IMARES, Department of Ecology, PO Box 167, 1790 AD Den Burg, The Netherlands; PETER J. H. REIJNDERS and GEERT AARTS, IMARES, Department of Ecology, PO Box 167, 1790 AD Den Burg, The Netherlands and Department of Aquatic Ecology and Water Quality Management, Wageningen University, Droevendaalse steeg 3a, 6708 PB Wageningen, The Netherlands.

ABSTRACT

Gray seals were first observed breeding in the Dutch Wadden Sea in 1985, after centuries of absence. The breeding colony there is now the largest on the European continent. We describe the changes in gray seal numbers and their geographical expansion, and estimate how these processes were influenced by immigration from other colonies. Counts of hauled out animals were carried out between 1985 and 2013, monitoring three different periods of the seals' annual cycle. Using priors determined for the UK population, a Bayesian demographic model was fitted to pup numbers to estimate the population parameters driving the growth. This included immigration of subadults into the breeding population, which contributed to an average growth rate in the pup counts of 19%/yr, much higher than expected in a closed population. This immigration may account for approximately 35% of the total annual growth. In addition, at least 200 gray seals from the UK visit the area temporarily. Recovery of the population in the Netherlands occurred more than 50 yr after gray seals were protected in the UK. These time scales should be taken into account when studying long living marine mammals, *e.g.*, in impact and conservation studies.

Key words: gray seal, *Halichoerus grypus*, population development, Bayesian demographic model, North Sea, Dutch Wadden Sea, aerial survey, molt, pups, migration.

Local extinction has occurred in many mammalian species, often as a result of a changing environment or human activities (Hoffmann *et al.* 2011, Schipper *et al.* 2008). However, in some cases recovery may occur through immigration from populations nearby, if conditions are favorable. Gray seals (*Halichoerus grypus* Fabricius, 1791) in the Netherlands are such a case. After centuries of virtual absence, they have recolonized Dutch waters and shown rapid population growth in recent decades.

¹Corresponding author (e-mail: sophie.brasseur@wur.nl).

The Wadden Sea, enclosed by a row of islands, forms the border between the eastern part of the southern North Sea and the Netherlands, Germany, and Denmark. Subfossil remains, some of which date back to 10,000 B.C. (Joensen *et al.* 1976, Reijnders 1978, van Bree *et al.* 1992), show that gray seals were present in all Wadden Sea regions prior to the 6th century. As gray seal pups remain ashore during the nursing and the postweaning period, they are an easy target for hunters (Hewer 1974). It is likely that in the late Middle Ages intensified hunting pressure in the area, related to human settlement, was the cause for the virtual disappearance of gray seals (Reijnders *et al.* 1995). Hunting also affected gray seals in other areas around the North Sea, but small populations persisted in the relatively remote areas of the United Kingdom (UK). Hunting restrictions introduced in the UK in 1914 under the Gray Seals Protection Act (Lambert 2002) allowed the species there to recover and subsequently colonize the Wadden Sea and adjacent areas once again (Reijnders *et al.* 1995). The numbers in continental Europe have grown and the species is now afforded protection under several conventions and treaties in Europe (Härkönen *et al.* 2007, Brasseur *et al.* 2011).

Recovery of gray seal stocks has been reported in much of its range including in the western Atlantic, in Canada, and the coast of the U.S.A. (Bowen *et al.* 2003, Wood *et al.* 2011), in the Baltic Sea (Harding and Härkönen 1999) and in the eastern Atlantic (Duck and Thompson 2007, Härkönen *et al.* 2007, Abt and Engler 2009). Reijnders *et al.* (1995) described the initial colonization of gray seals in Dutch waters. Gray seals were sporadically reported from the mid-1950s onwards (van Haaf-ten 1975), but it was not until 1980 that the first colony was established on a relatively high sandbar between the islands of Vlieland and Terschelling. The first pup born at this Dutch colony was only observed in 1985 (Reijnders *et al.* 1995), although prior to this pups were occasionally found along the Dutch coast. These early pups mainly originated from the east coast of the UK as deduced from tagged animals (Bonner 1972). Currently, the colony in the Dutch Wadden Sea is the largest on the European continent (Härkönen *et al.* 2007, Brasseur *et al.* 2013).

Since gray seals were virtually absent from Dutch waters prior to the 1980s, the establishment of a breeding population must have been initiated by immigrants from most likely the nearest large colonies located along the North Sea coasts of the UK (Hewer 1974). For example, pup production in the UK grew between 1980 and 2010 from 1,617 (SCOS 2006) to 10,107 (SCOS 2013). As the colonies in the UK grew, the influx of animals into Dutch waters possibly increased as well. Some of these started to breed in the Netherlands, while others may have visited the Dutch waters only on a temporary basis. If so, more animals would be present in Dutch waters than could be expected based on the yearly pup production, especially outside the breeding season.

Understanding population demography and how it is shaped by local reproduction, mortality, and immigration, based on counts alone is challenging, because pinnipeds spend a large proportion of time in the water, out of sight. In many areas, the number of seal pups born was used to infer the total number of animals in the area (Bowen *et al.* 2007, Duck and Thompson 2007). However, the maximum number of pups counted during a survey is always an underestimate of the total annual pup production. At the time of a survey, some pups are yet to be born, while others are not counted, as they may have already left the colony, or died (Boveng *et al.* 1998). Moreover, changes in population demography (Härkönen and Harding 2001) and exchanges with other populations nearby (this study) might affect the number of animals present in a way which is not deducible from pup counts alone.

The main objective of this study is to describe the changes in the number of gray seals and their geographical expansion in the Dutch Wadden Sea. In particular, we seek to understand if and how these changes have been influenced by temporary or permanent immigration.

MATERIALS AND METHODS

Data Collection

From 1985 to 2013, surveys were carried out during three periods in the gray seals' annual cycle: the molting season (March–April), the summer season, which is their most intensive foraging period (June–September, Beck *et al.* 2003), and the pupping season (November–February). Prior to 2001, hauled out gray seals were counted from marine conservation vessels during the pupping and molting seasons. In the period 1997–2001, the animals spread to different haul-out sites during the molting season and the boat surveys covered only part of the seals' distribution. Therefore, from December 2001 onwards, aerial surveys dedicated to gray seal counts replaced the boat surveys. As the range of gray seals grew, aerial surveys expanded to the western Wadden Sea in 2002 and to the entire Dutch Wadden Sea in 2007. Since 1959, annual harbor seal, *Phoca vitulina*, aerial surveys in the summer months provided for fortuitous data on gray seal occurrence in summer.

Aerial surveys were conducted from a fixed wing, single engine aircraft, flying at approximately 500 ft (~150 m) at 160–200 km/h. Surveys were conducted between 2 h before and 2 h after low tide and were aimed at low tides between 1000 and 1600 local time (Reijnders *et al.* 2003). Surveys were performed on good weather days, with rainfall <8.5 mm daily precipitation (measured over the period 0800 UTC preceding day to 0800 UTC present day), and winds generally below 25 kn (up to 6 Beaufort). In the early years, seal numbers were scored directly during the flight and additional comments were recorded on tape. From 1997 to 1999, areas with seals were photographed using an analog camera with slide film. From 2000 onwards, a digital camera, and a GPS unit was used to record the location of the photographs taken. At least two experienced observers counted animals from the projected pictures.

For this study, only data from 1985 onwards were used. For the pup counts, data from November, December, and January were included. Pup counts after extremely high tides (>2.0 m relative to Amsterdam Ordnance Datum [NAP] at Vlieland) were excluded from the analysis, because such tides may wash many pups away, and others were rescued and taken to rehabilitation centers, causing an underestimate in the counts. As at the beginning of the breeding season, consecutive counts prior to the first birth were zero, only the last zero count before the first non-zero count was used. Counts from March, April, and May were considered molting counts. Molting data from the years 1997–2000 were excluded from the analysis as they were incomplete. In 2013 molting counts were impeded by the weather (Brasseur *et al.* 2013), and therefore were not included in the study. All counts carried out from June through September were included as summer counts.

Comparison of Population Growth Rates

To describe the changes in gray seal numbers in the Netherlands, the growth rates observed in the counts during the different seasons were determined. These reflect the

speed at which the recolonization took place, allowing for comparison with other areas, but also the ability to examine differences between seasons. The latter could help for example, to recognize the underlying processes for the growth in numbers during the different seasons.

A generalized linear model (McCullagh and Nelder 1989) was used to estimate initial population size and population growth rate for each of the three time series of seasonal counts. We used a quasi-Poisson error distribution and log link function. All data from the pupping and summer time series were used to estimate population growth rates in these periods. For the molting season, only the annual maximum count was used. For each seasonal time series (pupping, molting, and summer), the expected count (C) was modeled as:

$$C_t = e^{\beta_0 + \beta_1 t} \quad (1)$$

where t was the number of years after 1985, β_1 the exponential population growth rate, and e^{β_0} the initial population size. Season was included in the model as a factor, and interaction between season and year was included to investigate whether there were differences in growth rates among the three time series. Parameter estimates and confidence limits were calculated using bootstrapping (Davison and Hinkley 1997, Canty and Ripley 2010). Models were fitted using the “glm” function in R3.0.2 (R Development Core Team 2013).

Breeding Population Demographic Model

Next, a Bayesian demographic model was fitted to the pup counts to estimate total numbers of animals involved in breeding, *i.e.*, the breeding population size and the demographic parameters that shape the observed changes in the breeding population (Matthiopoulos *et al.* 2014). This allowed us to estimate for example, the immigration of UK born juveniles into the Dutch breeding population.

The Bayesian demographic model fitted to pup data consisted of two components. The first component modeled the probability of a pup being present as a function of the timing of birth, mortality, and postweaning departure of pups. Departure was defined as the moment the pup was no longer identifiable as such (due to postweaning molt) or when the pup had left the breeding colony. The second component was a demographic model dictating the height of the curve, which was a function of the total reproductive output of the mature population. The shape of the curve defining the pup presence probability was defined as:

$$\gamma(t) = p_b(t) - p_d(t) - m(t) \quad (2)$$

where t was the number of days after 1 November, $p_b(t)$ was the birth probability, $p_d(t)$ was the departure probability and $m(t)$ was the mortality. On Sable Island, Canada (Bowen *et al.* 2003, 2007) and in the UK (Duck and Thompson 2007, Lonergan *et al.* 2011), independent data on mortality and the developmental stages of pups were collected. Such ground-based data were not available for this study. Boveng *et al.* (1998) and Reijnders *et al.* (1997) estimated mortality in Antarctic fur seals, *Arctocephalus gazella*, and harbor seals, *Phoca vitulina*, respectively, by recording the decline in pup counts after the peak in pup numbers. However, in gray seals the duration of lactation is relatively short (17–20 d; Boness and James 1979, Pomeroy *et al.* 1999), and next to mortality, the decline in pup numbers was largely driven by a departure of pups after a variable postweaning molting period (9–31 d, Hall 1998, Noren *et al.* 2008) or storms flushing the animals off the breeding grounds. It was

not possible to discern between departure of pups and mortality based on the survey data, and therefore in this part of the model, $m(t)$ could not be estimated as a separate parameter.

The cumulative distribution function for the birth of pups $p_b(t)$ was described using a logistic probability density function. Field observations suggested a forward shift in the pupping date, which was captured by allowing the mean birth date to vary as a linear function of year:

$$p_b(t) = \text{logit}^{-1}[\beta_1(t_i - \mu_{\text{birth}} - \beta_2 Y)] \quad (3)$$

where $\text{logit}^{-1}() = \frac{\exp()}{1+\exp()}$; μ_{birth} was the mean birth date when $Y = 0$, $\beta_2 Y$ describes the annual linear change in birth date, and β_1 was the slope of the logistic function and is a measure of the between-individual variability in birth date. Similarly, the pup departure probability was described as:

$$p_d(t) = \text{logit}^{-1}[\beta_1(t_i - \mu_{\text{birth}} - \mu_{\text{duration}} - \beta_2 Y)] \quad (4)$$

where μ_{duration} was the mean pup presence duration.

The demographic part of the model (Fig. 1) was defined by the vital processes of immigration, survival, and fecundity (Caswell 2001). Initial population size was defined in the model by a parameter estimating the number of mature individuals, $N_{6+,}$ in 1985. To capture the subsequent immigration, the model included a parameter α_{pup} , which estimated the influx of 1 yr old seals as a proportion of the number of pups born on the UK east coast the preceding year (Fig. 1). Thus, the number of 1 yr old seals in Dutch waters was modeled as:

$$N_{1,t} = \phi_{\text{pup}} N_{0,t-1} + \alpha_{\text{pup}} N_{0,t-1}^{\text{UK}} \quad (5)$$

where ϕ_{pup} was the survival of pups and $N_{x,t}$ was the number of seals of age x at time t . The numbers of pups born along the UK east coast N_0^{UK} were obtained from SCOS

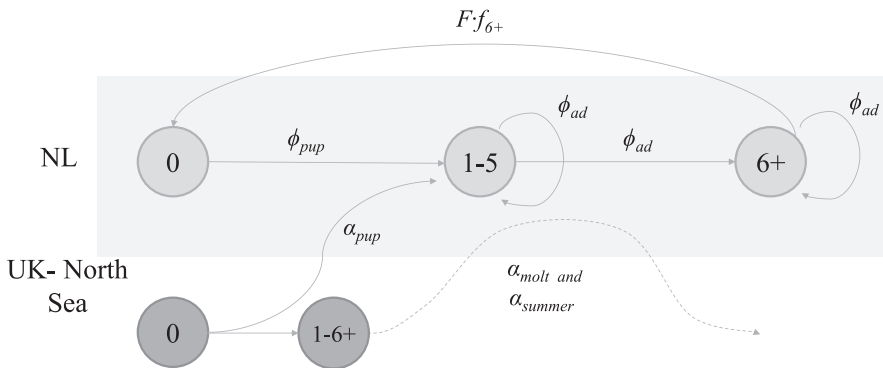


Figure 1. Population demographic changes influenced by survival of pups (ϕ_{pup}) and adults (ϕ_{adult}), adult fecundity (the product of female fecundity [$f_{6+,}$] and the proportion of females [F]), and immigration, which is a function of the number of pups born on the UK east coasts (α_{pup}). Temporary import from the UK observed during molting season and summer were expressed as α_{molt} and α_{summer} . The number in each circle represents the age-class. Reproduction in a particular age class occurs prior to survival into the following age class.

(2010, table 3 of SCOS-BP 10/1) for 1985–2004 and from SCOS (2013, table 2 of SCOS-BP 13/01) for 2005–2012. The expected number of pups during a survey was the product of the total annual pup production (N_0) and the pup presence probability (γ). The actual pup counts during the i 'th survey (P_i) were assumed to follow a Poisson distribution:

$$P_i \sim \text{Poisson}(N_{0,i}\gamma_i) \quad (6)$$

Survival was estimated separately for pups (ϕ_{pup}) and (sub)adults (ϕ_{adult}). Estimates of survival and fecundity (f_{6+}) were not available for the Dutch population, so informative priors from the UK (SCOS 2012) were used (table 1 of SCOS-BP 12/02). The gray seals occur in adjacent waters and these parameters were likely to be similar. For juvenile survival, a new, less informative prior was suggested in SCOS (2012). Although this change in prior was not accepted for the UK, we felt the less informative prior would be appropriate for the Dutch situation because extensive rescue efforts for pups in the Netherlands may affect pup survival. The ratio between the number of females and males (F) was defined as beta-distribution with an upper limit of 2:1, corresponding to a mean female-male ratio of 0.55 (Table 1). This parameter was fixed and not estimated by the model. No useful prior information was available for the parameters μ_{duration} , μ_{birth} , $\beta_2 Y$, β_1 , α 's, and $N_{6+, t=0}$, and hence these were defined as uniform distributions with boundaries as specified in Table 1.

Table 1. Priors used in the population model.

Parameter	Name	Distribution	Mean	SD	Reference
Informative priors					
ϕ_{adult}	Adult survival	0.8 + 0.2 Beta (1.6, 1.2)	0.91	0.05	SCOS-BP 12/02
ϕ_{pup}	Pup survival	Beta (2.87, 1.78)	0.62	0.20	SCOS-BP 12/02
f_{6+}	Fecundity 6+	0.6 + 0.4 Beta (2, 1.5)	0.83	0.09	SCOS-BP 12/02
v	Summer haul-out fraction	Normal (0.25, 0.4)	0.25	0.40	This study
F	Female fraction	[1+ Beta (2, 8)]/[2+ Beta (2, 8)]	0.55	0.06	This study ^a
Vague priors					
μ_{duration}	Pup duration ^b	Uniform (26, 57)			
μ_{birth}	Mean birth date	Uniform (10, 80)			
β_1	Variability in pup duration	Uniform (30, 80)			
β_2	Annual shift in birth date	Uniform (-2, 2)			
$N_{6+, t=0}$	Initial number of individuals	Uniform (1, 100)			
α_{pup}	Relative import fraction	Uniform (0.0001, 0.02)			
α_{summer}	Relative import summer	Uniform (0.00001, 1)			
α_{molt}	Relative import molt	Uniform (0.00001, 1)			

^aSimilar to female:male ratio = 1 + gamma (2, 0.1) as suggested in SCOS-BP 12/02, but with upper limit of 2:1.

^bLower value (26) based on Noren *et al.* 2008. Upper value, lactation duration (Pomeroy *et al.* 1999) of 17 d plus the maximum fasting duration of 40 d (Bennett *et al.* 2010).

The Relative Contribution of Seasonal Influx of Gray Seals in Dutch Waters

Studies from the UK suggest that female gray seals show high site fidelity during the breeding season (Pomeroy *et al.* 2005), and hence it seemed safe to assume that the pup counts depended only on the local breeding population. However, molting and summer counts may be affected by adults and subadults using Dutch waters temporarily. Such possible temporary immigration was estimated by comparing the estimated size of the breeding population with the size of the population present during the summer and molting counts.

The size of the summer population was estimated based on tagging data, which could be used to correct for the proportion of animals at sea. In 2006–2008, 12 subadult and adult gray seals (seven females ranging in total length from 132 to 212 cm and five males ranging from 140 to 196 cm) were equipped with GSM-relayed data loggers (GPS-Phone Tags, SMRU). The tags were glued to the hair on the back of the head of the animals (Fedak *et al.* 1983). The loggers contained sensors to measure geographic position (Fastloc), depth (pressure sensor) and whether the unit was dry or wet (conductivity sensor). When the data logger was dry for at least 10 min, the seal was recorded as being hauled out. Haul-out events were summarized into 2 h blocks, in which the percentage of time hauled out was recorded. Haul-out summary data from 2 h before and after low tide between 1000 and 1600 UTC were used to estimate the percentage of time individuals spent hauled out. The total population size could then be estimated by dividing the seal count by the mean haul-out fraction (Ries *et al.* 1998, Matthiopoulos *et al.* 2004, Hayward *et al.* 2005, Lonergan *et al.* 2011).

An intercept-only generalized mixed model (GLMM) was fitted to the 2 h haul-out fractions from these months. The intercept was treated as a mixed effect term, where the random component was allowed to vary by individual (Pinheiro and Bates 2000). The fixed effect estimate and corresponding uncertainty were used to estimate haul-out fractions at a population level. Models were fitted using the “glmmPQL” function of the “MASS” package in R (R Development Core Team 2013).

The contribution of temporary immigrants to the summer population was estimated with the demographic model by including a parameter α_{summer} ; the proportion of UK gray seals in addition to the Dutch seals from the local breeding population. The proportion of summer immigrants, as a fraction of the UK east coast gray seal population, was assumed to be the same each year. Thus, the summer counts S were modeled as:

$$S \sim \text{Poisson} \left[v \left(N_{0-6+} + \alpha_{\text{summer}} N_{0-6+}^{\text{UK}} \right) \right] \quad (7)$$

where v was the haul-out fraction during the summer months. The logit^{-1} of v had a prior distribution of Gaussian (η , σ), and η and σ were, respectively, the mean and corresponding standard error estimate of the intercept (reflecting haul-out probabilities) estimated from the tagging data with the GLMM described above. The temporary visitors in summer were assumed to be a fraction (α_{summer}) of the estimated total number of gray seals residing along the UK east coast prior to breeding N_{0-6+}^{UK} (Appendix SCOS-BP 13/02, p. 109 in SCOS 2013). There was no UK estimate available for 2013. Instead, this was obtained by projecting the 2012 estimate (*i.e.*, 20,300) using the mean UK east coast population growth from 2003 to 2012 (*i.e.*, 1.027). This resulted in an estimate of 20,858 individuals for 2013.

Similarly, the contribution of temporary immigrants to the molting population was estimated by including a parameter α_{molt} as the proportion of nonpup UK gray seals in addition to the Dutch seals from the local breeding population. Due to frequent foraging trips, pups of the year were assumed to have the same haul-out fraction ν during the molting season. The fraction of nonpup seals hauled out during the molting season is not known, because the molt causes tags to fall off. A minimum estimate of population size during the molting season was based on assuming that all adults and subadults were hauled out, so the molting counts M were modeled as:

$$M \sim \text{Poisson}(\nu N_0 + N_{1-6+} + \alpha_{\text{molt}} N_{1-6+}^{\text{UK}}) \quad (8)$$

Conservatively one could say that if the number observed during the molting season was similar to, or higher than the maximum number estimated based on the pup counts, it was likely that animals from elsewhere were in the area. The prior distributions of α_{summer} and α_{molt} were assumed to follow uniform distributions (Table 1).

Model Fitting

The Bayesian demographic model was fitted using WinBUGS14.² Parameters of the model were estimated from all the data, with the following restrictions: (1) Summer and molting data were used to estimate α_{summer} and α_{molt} , but the other demographic parameters were based on pupping data only. (2) The summer haul-out fraction ν and the fraction of females in the population F were not updated by the likelihood function. These restrictions were implemented with the WinBUGS function “cut” (Spiegelhalter *et al.* 2003). With the sparse demographic data, it was not possible to update the summer haul-out fraction (derived from tagging data) or estimate the fraction of females in the population, so we chose to treat them as non-stochastic values, although with uncertainty specified by the prior. The model was fitted using three MCMC chains, each containing 10,000 steps, with thinning of 10. The first 100 samples were excluded (*i.e.*, burn in period), resulting in 900 posterior samples of each chain. Convergence was assessed by examining the history of each chain, comparing posterior distributions starting with different initial values, and comparing different chains. The three chains were combined for inference. The R-code used in the data analysis described above can be found in Appendix S1.

RESULTS

Expansion of Gray Seals Throughout the Wadden Sea

The first pups born in the Netherlands were observed in 1985 between the Islands of Vlieland and Terschelling (no. 1, Fig. 2; Reijnders *et al.* 1995). By 2013, gray seals had expanded their range from the one central area, to the west and later to the eastern Wadden Sea and south into the Delta area bordering Belgium. Despite such an expansion in range in the Dutch Wadden Sea, the area first colonized remained by far the most important breeding site with more than 90% of pups being born there. Most animals were also seen in this area throughout the year.

²Available at <http://www2.mrc-bsu.cam.ac.uk/bugs/winbugs/contents.shtml>.

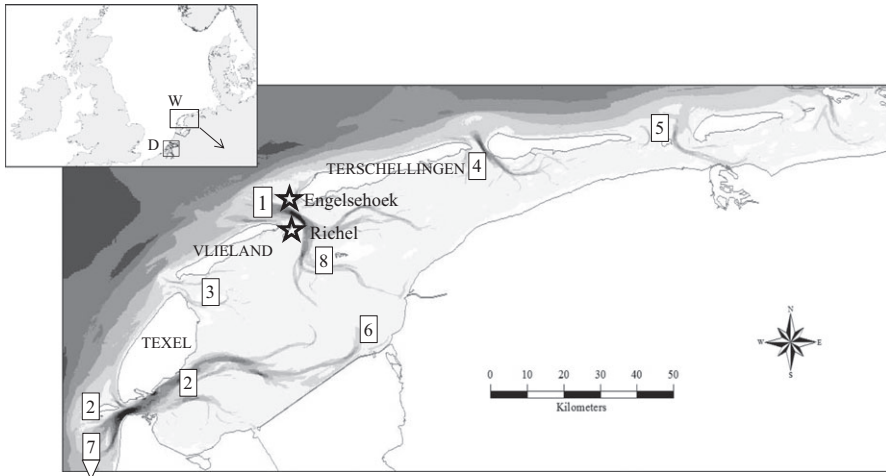


Figure 2. Expansion of the distribution of gray seals in the Dutch Wadden Sea (W, in inlay) from 1985 to 2013. Black stars represent the location of the first and most important haul-out sites for gray seals in the Dutch Wadden Sea. 1. First area colonized by gray seals in 1980; pupping started in 1985; 2. first gray seal observed in 1988; first group >5 in 1997; 3. first gray seal observed in 1988; first group >5 in 2000; 4. first gray seal observed in 1989; first group >5 in 1998; 5. first gray seal observed in 1998; first group >5 in 2001; 6. first gray seal observed in 1997; first group >5 in 1998; 7. first gray seal group >5 in the Dutch delta area (D, in inlay) 2003 (Strucker 2006); 8. first gray seal observed in 2009; first group >5 in 2009.

Population Growth Rates

During the past 30 yr, gray seal numbers counted in the Dutch Wadden Sea have grown exponentially from a few seals in the early 1980s to a maximum of 3,062 individuals counted during the molt in the spring of 2012. During the pupping season (winter) of 2013/2014, 412 pups were counted and in the summer a maximum of 1,169 seals (of all age classes) were counted in 2013. The estimated growth rates based on pup counts was 19% (CL 15, 23), on molting counts 15% (CL 14, 17), and on summer counts 15% (CL 14, 16). These rates were not significantly different ($F = 1.9349$, $df = 2$, $P = 0.1466$). The initial numbers of animals estimated for each time series were 2.3 pups, 65.2 molting seals, and 17.9 seals hauled out during summer.

Breeding Population Demography

Figure 3 shows the pup counts compared to the model estimates. In general, the estimated number of pups fits well with the survey results. Between 1985 and 2013, the mean date of birth shifted forward an estimated 1.27 d/yr (β_1 in Fig. 4, Table 2). In the winter of 1985–1986, when the first seals were assumed to have given birth in the area, the mean date of birth was estimated to be 7 January and pup numbers were estimated to peak on 21 January. In contrast, in 2013 the estimated mean birth date was 2 December, and the estimated peak in pup numbers was 16 December, which implies a forward shift of 36 d in 28 yr. In 2013, pupping began in November and the last pups were born by mid-January. Pups remain (recognizable) onshore for an estimated 28.2 d (μ_{duration} , Fig. 4, Table 2). Assuming a suckling duration of 17 d

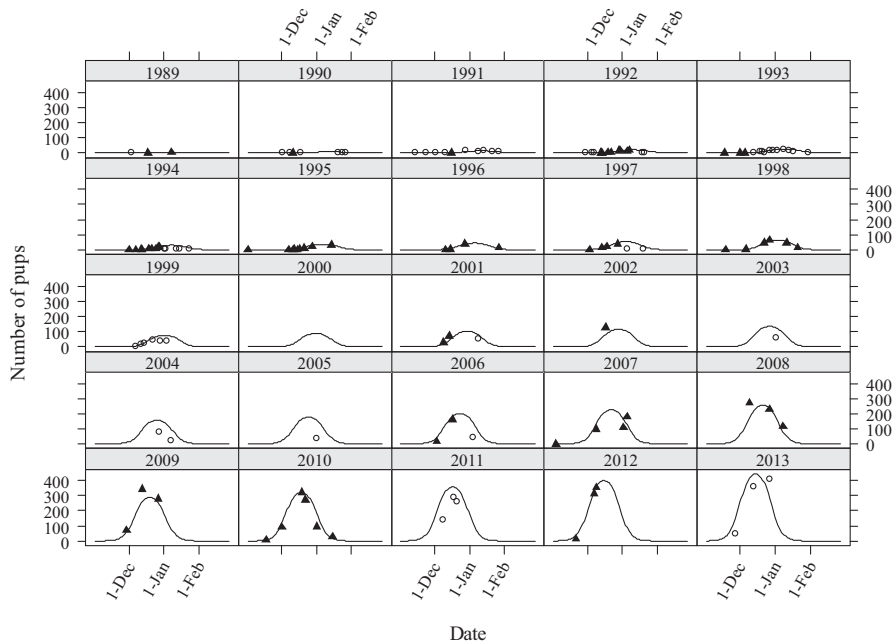


Figure 3. Observed (\blacktriangle , \circ) and estimated (line) number of pups by month and year. Triangles (\blacktriangle) represent the observed pups used to estimate model parameters, open circles (\circ) represent the number of pups observed after an extreme tide event (>2 m NAP). These data were excluded when fitting the population model.

(Pomeroy *et al.* 1999), this would imply an average postweaning period of at least 11 d. The estimate of pup production has increased from 0 in 1979 to 488 in 2013 (Fig. 3). The demographic model estimates that in recent years the ratio between pup production and total population size is about 0.16.

Adult survival was estimated to be 0.95 (Table 2), which is considerably higher than the prior (Fig. 4). In contrast, the estimated pup survival was 0.59 (Table 2), slightly lower than the mean of the prior distribution. To explain the rapid population growth, the model could also have increased pup survival. Figure 5 shows that large changes in pup survival leads to only small changes in adult survival.

The estimated fecundity f was 0.79 (Table 2), which coincides with the (relatively wide) prior distribution (Table 2, Fig. 4). The parameter α_{pup} describing the influx of 1 yr old individuals from the UK, was estimated at 0.0133 (Table 2.), which corresponds to ~ 134 animals in 2013. The estimated fecundity was negatively correlated with ϕ_{adult} and α_{pup} (Pearson correlation = -0.28 and 0.36 , respectively). This implies that increases in one can be compensated by increases in the other, and may explain the inability of the model to accurately estimate this parameter f .

Comparison of the Summer, Molting and Breeding Population Size

The parameter α_{molt} is estimated to be 0.0122 (Table 2), suggesting that at least 255 animals temporarily visited the Wadden Sea during the molting season in 2013

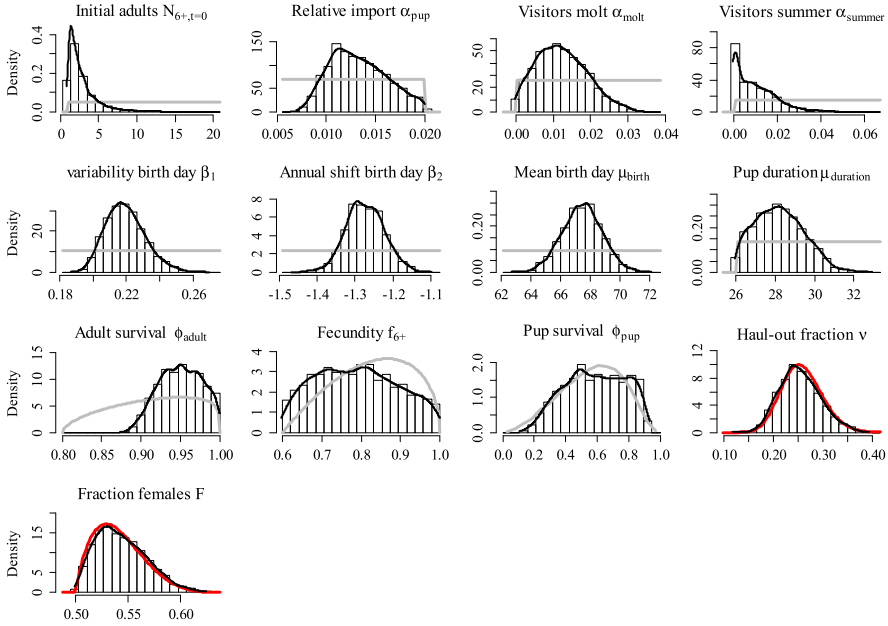


Figure 4. Prior (gray lines) and posterior (histograms, black lines) of the demographic parameters for the model fitted to pup data only. Red lines indicate the fixed fraction for haul-out and females.

(Fig. 6). The parameter α_{summer} is estimated to be 0.0093 (Table 2), which suggests that in the summer of 2013 at least 195 UK “visitors” were present in the Dutch Wadden Sea.

DISCUSSION

Gray seal population dispersion and growth in the Wadden Sea

It is evident that the number of gray seals in the Wadden Sea has grown exponentially between 1985 and 2013. Starting in the 1980’s with a few vagrant seals, the counts during the pupping season of 2013 yielded 412 pups, and our model estimates 488 to be born in total. This would represent a breeding population of 3,088 animals. The first gray seals formed a small haul-out colony in the area between the islands of Vlieland and Terschelling (Reijnders *et al.* 1995). As the population grew, gray seals gradually expanded their range to haul-out sites throughout the entire Dutch Wadden Sea, though by far the largest groups are still observed where the first colony formed. Smaller, but growing colonies, are also seen to the east along the German Wadden Sea coasts (Czeck and Paul 2008, Abt and Engler 2009), south in the Dutch Delta (Strucker *et al.* 2010), and even further south in northern France (Dupuis 2011).

The average growth rate in pup numbers observed in the Dutch Wadden Sea was estimated at 19% (CL 15%–23%) which is much higher than observed elsewhere or can be explained assuming natural growth in a closed population. For example,

Table 2. Posteriors.

Parameter	Name	Mean	SD	2.50%	Median	97.50%
ϕ_{adult}	Adult survival	0.95	0.027	0.899	0.951	0.996
ϕ_{pup}	Pup survival	0.586	0.188	0.239	0.588	0.888
f_{6+}	Fecundity 6+	0.79	0.104	0.616	0.788	0.982
v	Summer haul out fraction	0.253	0.041	0.182	0.251	0.341
F	Female-Male ratio	0.544	0.024	0.507	0.541	0.597
μ_{duration}	Pup duration	28.2	1.237	26.17	28.14	30.68
μ_{birth}	Mean birth date	67.45	1.346	64.74	67.47	70.04
β_1	Variability in pup duration	-1.274	0.05	-1.369	-1.276	-1.173
β_2	Annual shift birth date	0.219	0.012	0.199	0.219	0.245
$N_{6+, t=0}$	Initial number of adults	2.858	2.152	1.044	2.157	9.026
α_{pup}	Relative import pup	0.013	0.003	0.009	0.013	0.019
α_{summer}	Relative import summer	0.009	0.01	0	0.007	0.033
α_{molt}	Relative import molt	0.012	0.007	8.0E-04	0.012	0.027

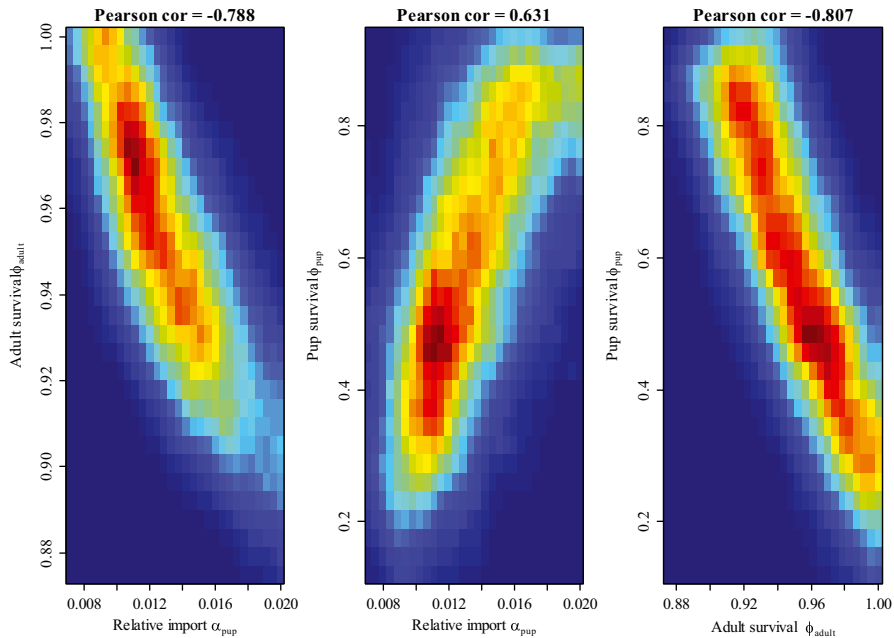


Figure 5. Correlations of the MCMC samples between adult survival, and the relative import of young animals from the UK (left), pup survival, and the relative import of young animals from the UK (middle) and between pup survival and adult survival (right).

during 25 yr the observed annual rate of increase in pup production on Sable Island in Canada averaged 12.8% (Bowen *et al.* 2003). For a shorter period (*i.e.*, 5 yr) similar growth was seen in the colony of Donna Nook in the UK (Duck and Thompson 2007). The growth rates in this paper also contrast with the statement derived from other demographic analyses, which show that maximum annual rates of increase in

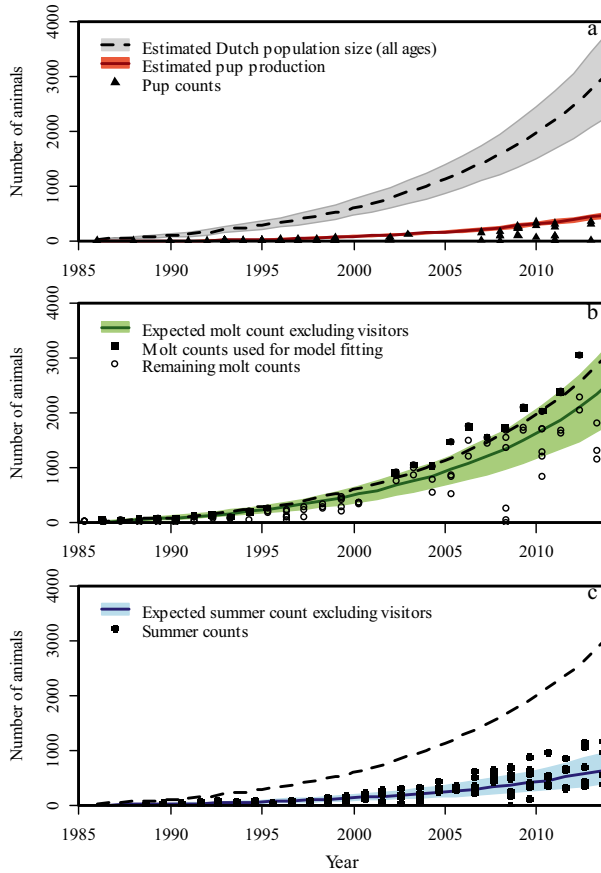


Figure 6. (a) Modeled population estimates based on the model fitted to pup data only, and hence excluding temporary visitors; (b) estimated and observed molting counts; (c) estimated and observed summer counts. For comparison, the dashed line of the estimated Dutch population size is repeated in every graph. Shaded areas indicated 95% confidence intervals.

closed populations of gray seals do not exceed 11% (Harwood 1978, Harding and Härkönen 1999). Initially, when the colonies had just settled in the Dutch Wadden Sea, the unstable population structure of the new colony could have explained an apparent higher growth rate. However, here we show persisting high growth rates over more than 30 yr, during breeding but also in the molting and summer counts, possibly indicating seals continuously immigrating into the area.

Sources of Immigration

While this study shows that local reproduction is at least responsible for part of the increase in observed numbers, the influx of animals from other areas was actually the driver for the initial recolonization and continues to play a prominent role in the growth. The immigrating animals most likely come from the eastern North Sea coast of the UK, where the population is relatively large with growing numbers (SCOS

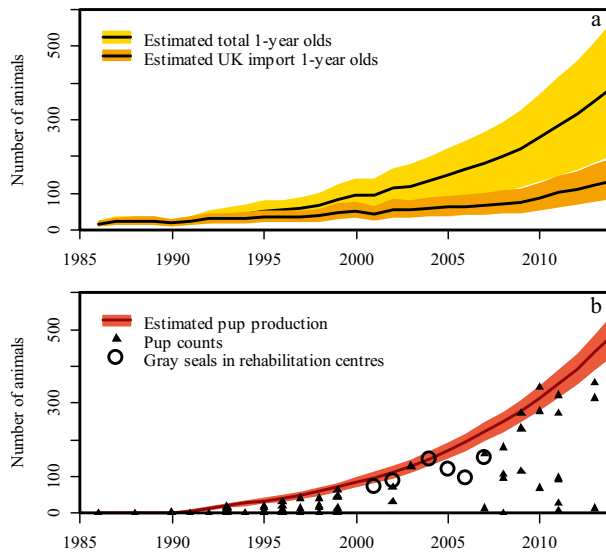


Figure 7. (a) Estimate of the total number of 1-yr-old gray seals in the Dutch Wadden Sea, compared to the estimated import of young animals from the UK; (b) Estimated pup production compared to counts and for some years, number of gray seals in rescue center. Data on rescue was obtained from Ecomare⁴ and diverse public media (Anonymous 2000–2012). For the data on the rescued seals only the years are presented where data covering the breeding season was available (1 December–15 May the next year). In other years it was not clear when seals were collected or the data were incomplete. The data from Ecomare shows that only 6 out of 271 gray seals rescued in this period were older than a few months.

2010), and distances are small enough for the animals to traverse. Young gray seals are known to swim relatively large distances (McConnell *et al.* 1999) and have been recorded on several occasions to cross the channel between the UK and the Netherlands (Coulson 1964, Bonner 1972, Hewer 1974, Reijnders *et al.* 1995). Even very young pups may cross the channel. White coated pups bearing color marks applied at the Farne Islands³ have been found alive on the Dutch coast. In addition, weaned gray seal pups marked at the Isle of May, in Scotland were reported in the Netherlands (Hall *et al.* 2001). Our population model suggests that on average 1.3% of the pups born on the east coast of the UK immigrate into the Dutch breeding population each year. This amounts to slightly less than 35% of the annual growth of the breeding population in most recent years (Fig. 7).⁴

Adult animals would also easily cover the distance from the eastern UK coasts to the Wadden Sea, though the idea of adult animals moving between areas could appear to contradict other studies showing that gray seals tend to show high site fidelity. However, those studies only measured site fidelity within one phase in the seals' annual cycle and not between seasons (Wilmer *et al.* 2000, Harrison *et al.* 2006). Site fidelity is observed during breeding (Twiss *et al.* 1994; Pomeroy *et al.*

³Personal communication from David Steel, Head Warden, National Trust, The Farne Islands, Northumberland, U.K., October 2013.

⁴Personal communication from Ecomare, Ruijslaan 92, Texel 1796 AZ, The Netherlands, June 2014.

2000a, b, 2005) and during summer, after the molt (Karlsson *et al.* 2005), but few studies have been conducted throughout the year. Animals could move around, still showing site fidelity at given moments. Tagging data collected just after the molt in the Wadden Sea show that large-scale trips occur. For example in 2005 four of the six satellite-tracked seals (two males ~1.80 m and two females ~1.70 m) tagged just after the molt, swam from the Dutch Wadden Sea to the UK during the summer. Two even traveled as far as the Orkney Islands, almost 1,000 km (Brasseur *et al.* 2010). The present study shows that both during the molting counts and the summer counts more animals seem to be present than would be expected based on the size of the breeding population. Further studies (*e.g.*, photo id and/or genetic studies) are needed to understand fully the mechanism of exchange between the various colonies within the North Sea.

Using the count results during the molting and summer, we estimate that a number of animals must come to the area outside the breeding season as “visitors.” These estimates are most probably underestimates. The demographic model fitted to the pup counts estimates that if all adults and a proportion of the young of the year were ashore during the molting season in 2012 the total local population should count 2,769 individuals. However, quite a lot more (3,062) were seen during a molting count on 3 April 2012, indicating that there should be animals from elsewhere. The model estimates that in addition to the local animals, on average 1.2% of nonpup UK gray seals from the North Sea coasts are in the area (Table 2.). This corresponds to 200–250 individuals annually in the past 10 yr (2004–2013). However, the assumption that all molting animals are present ashore is quite unlikely. An unknown proportion may be at sea at the time of the survey, so even more “visitors” may be present in the Dutch part of the North Sea during this period. Moreover, we could not take into account that like the UK seals, some of the seals of the Dutch breeding population could have chosen to molt outside the Wadden Sea. Consequently, an even higher proportion of gray seals seen during the molting season might actually be seals breeding in the UK, or other areas. With the current data, it is not possible to estimate the extent of this exchange more accurately.

The demographic model suggests that also in summer more seals use the Wadden Sea than would be expected based on the size of the breeding population (0.9%; Table 2, 150–200 animals/yr). This estimate relies on the estimated haul-out fraction (*i.e.*, 0.25) derived from the telemetry data. Despite the relatively small number of animals used to determine the correction factors, the correction factor seems to be realistic as they were similar to other studies (*i.e.*, 0.31 in August alone, Lonergan *et al.* 2011). The relatively low haul-out fraction also coincides with the observations by Beck *et al.* (2003) that shows that a large proportion of seals are feeding in this period.

Limitations

To estimate the breeding population, the total pup production was modeled based on the pup counts. There are a few apparent abnormalities in the fit of the estimated number of pups to the original pup counts. In most years, when storms resulted in extreme high tides during the pupping season, this lead to lower numbers of observed pups (*e.g.*, in 1992, 1994, 1997, 2005, and 2006). We decided therefore to omit pup counts after these surges. However, in some years (*e.g.*, 1993, 1999, and 2001) high tide did not affect the pup numbers and the difference between the observed and expected number of pups is relatively small. In 1999 a storm occurred on 4 December

(~222 NAP). As this was several weeks prior to the mean birth date this may not have affected many individuals. Larger model residuals also occurred during the first surveys in 2002, 2004, and 2008, which seems to suggest that the forward shift of the pup presence curve was larger in those years. Finally, in some years (*e.g.*, 2008 and 2009) the observed number of pups was higher than predicted by the model. This could be due to relative larger fecundity or sudden increase in the influx of mature females.

Compared to ground surveys carried out in other areas (*i.e.*, the UK and Canada; Pomeroy *et al.* 1999, Bowen *et al.* 2007), aerial surveys in the Netherlands give a shorter period in which pups are recognized as pups (μ_{duration}); estimated here at 28.2 d. It might be that from the air any remnants of white hair on the molting pup are easily missed, and therefore pups are easily confused with older animals, or with harbor seals using the same haul-out sites. In addition, pups might actually disappear earlier than in other countries because they are easily washed off the breeding site.

Another source of error in our pup counts lays in the fact that in some years a large proportion of pups were picked up by seal rehabilitation centers, in some years affecting 50%–98% of the total number of pups born (Fig. 7). It is unknown if and how the rescuing of pups by seal centers has affected the counts and consequently the estimation of pup production. News clippings suggested that most pups were collected after the peak in pups, or after the first winter storm. As we omitted the data collected after the storms, and even in the years these occurred, we carried out a number of surveys before the peak in pups, we expect that the numbers in the rescue centers would not affect our estimates too much. More detailed data on these rescue practices are not available.

Our results of the population model (Fig. 4) show a relatively high adult survival (ϕ_{adult} ; 0.95), and a pup survival (ϕ_{pup} ; 0.59) that was slightly lower than the prior (see also Table 1, 2). To explain the rapid population growth, the model could have increased pup survival. However, Figure 5 (right panel) shows that a large change in pup survival would lead to only a small change in adult survival. This might explain the slightly increased adult survival, rather than pup survival. Adult and pup survival are correlated with the relative import from the UK (α_{pup}). As expected, a higher estimate for ϕ_{adult} would lead to a lower estimate for immigration. Because of this correlation, one could hypothesize that due to the extreme rescue efforts, instead of immigration, ϕ_{adult} could be extremely high. Interestingly, the contrary holds for the relation between α_{pup} and ϕ_{pup} (Fig. 5). Moreover for all likely values of adult and pup survival, α_{pup} exceeds 0.008, demonstrating that at least some relative import occurs.

Shift in Timing of Breeding

The timing of the peak in pup numbers in the Netherlands, which currently occurs in early December, could suggest that individuals descended from the UK colony. Throughout the gray seals' range in Europe, there is a geographical cline in peak pupping: beginning in August–September in southwest Britain, between September and November in Scotland, and November to mid-December in eastern England (SCOS 2010). In the Baltic, the gray seals' pupping season is from late February to early April (Hook and Johnels 1972). In the Dutch Wadden Sea, the original peak was on 21 January (with a mean birth date 7 January), later than the east coast of the UK. However since then, a shift forward of 1.27 d/yr was observed in the Wadden Sea, with the maximum number of pups observed on the 16

December in 2013, five weeks earlier than in 1985. The shift could suggest a growing synchronicity with the colonies on the UK coasts. However, this shift could also be a result of the population maturing (Härkönen *et al.* 2002), or could result from the similar phenomenon observed in the harbor seals in the Wadden Sea area (Reijnders *et al.* 2010). It was suggested there, that an improvement in environmental conditions sustained a long-term high annual growth rate, and a progressing earlier birth date.

Why Did Gray Seal Recolonize the Wadden Sea?

There could be a number of reasons why gray seals have recolonized the area after being absent for so many years. As gray seal numbers increased in the UK, a growing number of seals would have moved to the southeastern North Sea in a search for new feeding grounds and reached the Wadden Sea. The growth of the seal numbers coincides well with the growth rates observed in the different colonies along the English east coasts where the recent average change in pup production lies between 3.5% and 15.8% (SCOS 2010). Possibly, similar processes throughout the larger area of the southern North Sea drive the increase in gray seals in our study area. Likewise, other marine top predators in the region, such as the harbor seal and the harbor porpoise, *Phocoena phocoena*, have also shown a large increase in numbers over the same period (Camphuysen 2004, Reijnders *et al.* 2009). This indicates a favorable environment to sustain larger numbers of different marine mammal species. Despite the regular loss of pups due to bad weather during the pupping season, the continuous and relatively high growth rates in gray seal numbers in the Netherlands, but also in the colonies in the southern UK, suggests that the population is not close to its carrying capacity. Presently resources, such as food and haul-out sites are apparently not limiting the population. Although adults may come to the area outside of the pupping season, high site fidelity during pupping season would make it unlikely for them to stay. Therefore, immigrants into the breeding population were presumed to have arrived as pups and subadults.

This case, where immigrants continuously arrive into the population, seems clearly different from the southern elephant seal (*Mirounga leonina*) colony on Peninsula Valdez (Ferrari *et al.* 2013). There apparently, immigration from other areas occurred only for a short time and the population developed further in relative isolation, probably within one century.

Additionally, favorable conditions in the Wadden Sea area could have enhanced the seals to move into the area. Many sand bars in the Wadden Sea are protected either by law or by the fact that they are not easily accessible from land. The question is whether this might change in the future as increasing development of human activities in the southern North Sea, such as offshore wind farming, sand mining, tourism, fisheries, and aquaculture, could negatively affect the carrying capacity of the area for these apex predators, and influence the exchange of gray seals between colonies.

Finally, though this is, to our knowledge, not supported by any existing study in gray seals, the growing number of seals hauled out could have been an incentive for new seals to haul out as well, creating (perceived) safety in numbers. Increased density may have a positive effect on individual fitness, known as the Allee effect (Drago *et al.* 2011). This could explain the persisting concentration of seals in the area initially colonized. Possibly the presence of growing numbers of harbor seals could also instigate the colonization of new areas.

Conclusion

This study shows that large mammals, after hundreds of years of virtual extinction, may ultimately recolonize an area and undergo rapid exponential population growth. What are needed are favorable environmental conditions, large source meta populations, and the mobility of individuals.

In this specific case, growth of the population in the UK and subsequent recovery in the Netherlands, occurred more than 50 yr after gray seals were protected in the UK. In current impact assessments and conservation plans for long-lived marine mammals, these time scales are rarely taken into account. Changes in the human use of the southern North Sea (*e.g.*, the recent development of wind farms) could influence the population development, but remain unobserved during the relatively short duration of most monitoring and impact assessment studies.

ACKNOWLEDGMENTS

The surveys were conducted in the framework of the yearly monitoring commissioned by the Ministry of Economic Affairs. We specifically thank Aad Droog, who has been flying since the 1960s, for most of our surveys and the crew of the M/V *Pboca*: Jan van Dijk, Dirk Kuiper, and later Bram Fey, collecting data in the early years and the crew of the other patrol vessels of the Wadden-Unit (the M/V *Harder*, the M/V *Krukkel*, and the M/V *Stormvogel*) who cooperated with us in finding all new gray seal haul-out sites. We also thank Elze Dijkman and Jenny Cremer for their help with surveys, the GIS database, and the creation of maps. Steve Geelhoed, for his critical reading of previous versions. We much appreciate the willingness of the personnel of Ecomare on Texel and David Steel on the Farne Islands, for exchanging data on pups washed up along the Dutch coasts.

LITERATURE CITED

- Abt, K., and J. Engler. 2009. Rapid increase of the grey seal (*Halichoerus grypus*) breeding stock at Helgoland. *Helgoland Marine Research* 63:177–180.
- Anonymous. 2000–2010. Robbenbulletin. Available at <http://www.zeehondencreche.nl>.
- Beck, C. A., W. D. Bowen and S. J. Iverson. 2003. Sex differences in the seasonal patterns of energy storage and expenditure in a phocid seal. *Journal of Animal Ecology* 72:280–291.
- Bennett, K. A., B. J. McConnell, S. F. Moss, J. R. Speakman, P. P. Pomeroy and M. A. Fedak. 2010. Effects of age and body mass on development of diving capabilities of gray seal pups: Costs and benefits of the postweaning fast. *Physiological and Biochemical Zoology* 83:911–923.
- Boness, D. J., and H. James. 1979. Reproductive behaviour of the grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. *Journal of Zoology* 188:477–500.
- Bonner, W. N. 1972. The grey seal and commons seal in European waters. *Oceanography and Marine Biology: Annual Review* 10:461–507.
- Boveng, P. L., L. M. Hiruki, M. K. Schwarz and J. L. Bengtson. 1998. Population growth of Antarctic fur seals: Limitation by a top predator, the leopard seal? *Ecology* 79:2863–2877.
- Bowen, W. D., J. McMillan and R. Mohn. 2003. Sustained exponential population growth of grey seals at Sable Island, Nova Scotia. *ICES Journal of Marine Science* 60:1265–1274.
- Bowen, W. D., J. I. McMillan and W. Blanchard. 2007. Reduced population growth of gray seals at Sable Island: Evidence from pup production and age of primiparity. *Marine Mammal Science* 23:48–64.

- Brasseur, S., T. van Polanen Petel, G. Aarts, E. Meesters, E. Dijkman and P. Reijnders. 2010. Grey seals (*Halichoerus grypus*) in the Dutch North Sea: Population ecology and effects of wind farms. IMARES Report number C137/10. Available at <http://edepot.wur.nl/260049>.
- Brasseur, S. M. J. M., P. J. H. Reijnders, T. Borchardt, et al. 2011. Trilateral Seal Expert Group (TSEG). Aerial surveys of grey seals in the Wadden Sea in 2010–2011: Continued growth, through birth and immigration. Common Wadden Sea Secretariat (CWSS). Available at <http://www.waddensea-secretariat.org/monitoring-tmap/topics/marine-mammals>.
- Brasseur, S. M. J. M., B. Diederichs, R. Czeck, et al. 2013. Trilateral Seal Expert Group (TSEG). Aerial surveys of grey seals in the Wadden Sea in 2012–2013: Mixed messages. Common Wadden Sea Secretariat (CWSS). Available at <http://www.waddensea-secretariat.org/monitoring-tmap/topics/marine-mammals>.
- Bree, P. van, L. Vedder and L. 't Hart. 1992. De grijze zeehond in Nederland—terug van weggeweest [The return of the gray seal in the Netherlands]. *Zoogdier* 3(4):11–15.
- Camphuysen, C. J. 2004. The return of the harbour porpoise (*Phocoena phocoena*) in Dutch coastal waters. *Lutra* 47:113–122.
- Canty, A., and B. Ripley. 2010. Boot: Bootstrap R (S-Plus) functions. R package version 1.2-42.
- Caswell, H. 2001. Matrix population models. Construction, analysis, and interpretation. Sinauer Associates, Inc. Publishers, Sunderland, MA.
- Coulson, J. C. 1964. The breeding biology of the grey seal, *Halichoerus grypus* (Fab), on the Farne Islands, Northumberland. *Journal of Animal Ecology* 33:485–512.
- Czeck, R., and M. Paul. 2008. Grey seals—a homecoming species in the Wadden Sea. *Marine Biodiversity* 38:143–146.
- Davison, A. C., and D. V. Hinkley. 1997. Bootstrap methods and their applications. Cambridge University Press, Cambridge, U.K.
- Drago, M., L. Cardona, N. García, S. Ameghino and A. Aguilar. 2011. Influence of colony size on pup fitness and survival in South American sea lions. *Marine Mammal Science* 27:167–181.
- Duck, C., and D. Thompson. 2007. The status of grey seals in Britain. Pages 69–78 in T. Haug, M. Hammil and D. Ólafsdóttir, eds. Grey seals in the North Atlantic and the Baltic. NAMMCO Scientific Publications Volume 6. Polar Environmental Centre, Tromsø, Norway.
- Dupuis, L. 2011. Bilan 2010 Étude et protection des phoques. Picardie Nature. Available at http://www.picardie-nature.org/IMG/pdf/Bilan_2010_Etude_et_protection_des_phoques.pdf.
- Fedak, M. A., S. S. Anderson and M. G. Curry. 1983. Attachment of a radio tag to the fur of seals. *Journal of Zoology* 200:298–300.
- Ferrari, M. A., C. Campagna, R. Condit and M. N. Lewis. 2013. The founding of a southern elephant seal colony. *Marine Mammal Science* 29:407–423.
- Haafden, J. L. van. 1975. Zeehonden langs de Nederlandse kust [Seals along the Dutch coast]. *Wetenschappelijke mededelingen K.N.N.V.* 101:1–36.
- Hall, A. J. 1998. Blood chemistry and hematology of gray seal (*Halichoerus grypus*) pups from birth to postweaning. *Journal of Zoo and Wildlife Medicine* 29:401–407.
- Hall, A. J., B. J. McConnell and R. J. Barker. 2001. Factors affecting first-year survival in grey seals and their implications for life history strategy. *Journal of Animal Ecology* 70:138–149.
- Harding, K. C., and T. J. Härkönen. 1999. Development in the Baltic grey seal (*Halichoerus grypus*) and ringed seal (*Phoca hispida*) populations during the 20th century. *Ambio* 28:619–627.
- Härkönen, T., and K. C. Harding. 2001. Spatial structure of harbour seal populations and the implications thereof. *Canadian Journal of Zoology* 79:2115–2127.

- Härkönen, T., K. C. Harding and M. P. Heide-Jørgensen. 2002. Rates of increase in age-structured populations: A lesson from the European harbour seals. *Canadian Journal of Zoology* 80:1498–1510.
- Härkönen, T., S. M. J. M. Brasseur, J. Teilmann, C. Vincent, R. Dietz, K. Abt and P. J. H. Reijnders. 2007. Status of grey seals along mainland Europe from the southwestern Baltic to France. Pages 57–68 *in* T. Haug, M. Hammil and D. Ólafsdóttir, eds. *Grey seals in the North Atlantic and the Baltic*. NAMMCO Scientific Publications Volume 6. Polar Environmental Centre, Tromsø, Norway.
- Harrison, P. J., S. T. Buckland, L. E. N. Thomas, R. O. B. Harris, P. P. Pomeroy and J. Harwood. 2006. Incorporating movement into models of grey seal population dynamics. *Journal of Animal Ecology* 75:634–645.
- Harwood, J. 1978. The effect of management policies on the stability and resilience of British grey seal populations. *Journal of Applied Ecology* 1978:413–421.
- Hayward, J. L., S. M. Henson, C. J. Logan, C. R. Parris, M. W. Meyer and B. Dennis. 2005. Predicting numbers of hauled-out harbour seals: A mathematical model. *Journal of Applied Ecology* 42:108–117.
- Hewer, H. R. 1974. *British seals. The new naturalist*. Collins, London, U.K.
- Hoffmann, M., J. L. Belant, J. S. Chanson, *et al.* 2011. The changing fates of the world's mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366:2598–2610.
- Hook, O., and A. G. Johnels. 1972. The breeding and distribution of the grey seal (*Halichoerus grypus* Fab.) in the Baltic Sea, with observations on other seals of the area. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 182:37–58.
- Joensen, A. H., N. O. Søndergaard and E. B. Hansen. 1976. Occurrence of seals and seal hunting in Denmark. *Danish Review of Game Biology* 10:1–20.
- Karlsson, O., L. Hiby, T. Lundberg, M. Jussi, I. Jussi and B. Helander. 2005. Photo-identification, site fidelity, and movement of female gray seals (*Halichoerus grypus*) between haul-outs in the Baltic Sea. *Ambio* 34:628–634.
- Lambert, R. A. 2002. The grey seal in Britain: A twentieth century history of a nature conservation success. *Environment and History* 8:449–474.
- Lonergan, M., C. D. Duck, D. Thompson, S. Moss and B. McConnell. 2011. British grey seal (*Halichoerus grypus*) abundance in 2008: An assessment based on aerial counts and satellite telemetry. *ICES Journal of Marine Science* 68:2201–2209.
- Matthiopoulos, J., B. McConnell, C. Duck and M. Fedak. 2004. Using satellite telemetry and aerial counts to estimate space use by grey seals around the British Isles. *Journal of Applied Ecology* 41:476–491.
- Matthiopoulos, J., L. Cordes, B. Mackey, *et al.* 2014. State-space modelling reveals proximate causes of harbour seal population declines. *Oecologia* 174:151–162.
- McConnell, B. J., M. A. Fedak, P. Lovell and P. S. Hammond. 1999. Movements and foraging areas of grey seals in the North Sea. *Journal of Applied Ecology* 36:573–590.
- McCullagh, P., and J. A. Nelder. 1989. *Generalized linear models*. Chapman and Hall, London, U.K.
- Noren, S. R., D. J. Boness, S. J. Iverson, J. McMillan and W. D. Bowen. 2008. Body condition at weaning affects the duration of the postweaning fast in gray seal pups (*Halichoerus grypus*). *Physiological and Biochemical Zoology* 81:269–277.
- Pinheiro, J. C., and D. M. Bates. 2000. *Mixed-effects models in S and S-PLUS*. Springer-Verlag, New York, NY.
- Pomeroy, P. P., M. A. Fedak, P. Rothery and S. Anderson. 1999. Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *Journal of Animal Ecology* 68:235–253.
- Pomeroy, P. P., S. D. Twiss and C. D. Duck. 2000a. Expansion of a grey seal (*Halichoerus grypus*) breeding colony: Changes in pupping site use at the Isle of May, Scotland. *Journal of Zoology* 250:1–12.

- Pomeroy, P. P., S. D. Twiss and P. Redman. 2000*b*. Philopatry, site fidelity and local kin associations within grey seal breeding colonies. *Ethology* 106:899–919.
- Pomeroy, P. P., P. R. Redman, S. J. S. Ruddell, C. D. Duck and S. D. Twiss. 2005. Breeding site choice fails to explain interannual associations of female grey seals. *Behavioral Ecology and Sociobiology* 57:546–556.
- R. Development Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reijnders, P. J. H. 1978. De grijze zeehond in de Waddenzegebied [The gray seal in the Wadden Sea area]. *Waddenbulletin* 13:500–502.
- Reijnders, P. J. H., J. van Dijk and D. Kuiper. 1995. Recolonization of the Dutch Wadden Sea by the grey seal *Halichoerus grypus*. *Biological Conservation* 71:231–235.
- Reijnders, P. J. H., E. H. Ries, S. Tougaard, *et al.* 1997. Population development of harbour seals *Phoca vitulina* in the Wadden Sea after the 1988 virus epizootic. *Journal of Sea Research* 38:161–168.
- Reijnders, P., K. Abt, S. Brasseur, S. Tougaard, U. Siebert and E. Vareschi. 2003. Sense and sensibility in evaluating aerial counts of harbour seals in the Wadden Sea. *Wadden Sea Newsletter* 28:9–12.
- Reijnders, P. J. H., S. M. J. M. Brasseur, T. Borchardt, *et al.* 2009. Marine mammals. Quality Status Report 2009 Thematic Report No. 20. Common Wadden Sea Secretariat Trilateral Monitoring and Assessment Group, Wilhelmshaven, Germany.
- Reijnders, P. J. H., S. M. J. M. Brasseur and E. H. W. G. Meesters. 2010. Earlier pupping in harbour seals, *Phoca vitulina*. *Biology letters* 6:854–857.
- Ries, E. H., L. R. Hiby and P. J. H. Reijnders. 1998. Maximum likelihood population size estimation of harbour seals in the Dutch Wadden Sea based on a mark-recapture experiment. *Journal of Applied Ecology* 35:332–339.
- Schipper, J., J. S. Chanson, F. Chiozza, *et al.* 2008. The Status of the world's land and marine mammals: Diversity, threat, and knowledge. *Science* 322:225–230.
- SCOS. 2006. Scientific advice on matters related to the management of seal populations: 2006 Reports of the UK Special Committee on Seals. Available at <http://smub.st-andrews.ac.uk>.
- SCOS. 2010. Scientific advice on matters related to the management of seal populations: 2010 Reports of the UK Special Committee on Seals. Available at <http://smub.st-andrews.ac.uk>.
- SCOS. 2012. Scientific advice on matters related to the management of seal populations: 2012 Reports of the UK Special Committee on Seals. Available at <http://smub.st-andrews.ac.uk>.
- SCOS. 2013. Scientific advice on matters related to the management of seal populations: 2013 Reports of the UK Special Committee on Seals. Available at <http://smub.st-andrews.ac.uk>.
- Spiegelhalter, D. J., A. Thomas, N. G. Best and D. Lunn. 2003. WinBUGS Version 2.0 Users Manual. MRC Biostatistics Unit, Cambridge, U.K. Available at <http://mathstat.helsinki.fi/openbugs/>.
- Strucker, R. C. W., F. A. Arts, S. Lilipaly, C. M. Berrevoets and P. L. Meininger. 2006. Watervogels en zeezoogdieren in de Zoute Delta 2004/2005 [Water birds and marine mammals in the Zoute Delta 2004/2005]. RIKZ, Rijksinstituut voor Kust en Zee Middelburg, The Netherlands.
- Strucker, R. C. W., F. A. Arts and S. Lilipaly. 2010. Watervogels en zeezoogdieren in de Zoute Delta 2008/2009. RWS Waterdienst BM, Middelburg, The Netherlands.
- Twiss, S., P. P. Pomeroy and S. S. Anderson. 1994. Dispersion and site fidelity of breeding male grey seals (*Halichoerus grypus*) on North Rona, Scotland. *Journal of Zoology London* 233:683–693.
- Wilmer, J. W., A. J. Overall, P. P. Pomeroy, D. Twiss and W. Amos. 2000. Patterns of paternal relatedness in British grey seal colonies. *Molecular Ecology* 9:283–292.

Wood, S. A., T. R. Frasier, B. A. Mcleod, *et al.* 2011. The genetics of recolonization: An analysis of the stock structure of grey seals (*Halichoerus grypus*) in the Northwest Atlantic. *Canadian Journal of Zoology* 89:490–497.

Received: 18 May 2012

Accepted: 3 July 2014

SUPPORTING INFORMATION

The following supporting information is available for this article online at <http://onlinelibrary.wiley.com/doi/10.1111/mms.12160/supinfo>.

Appendix S1. R-code (Seal_Population_Analysis.R) of the Dutch gray seal population demography data analysis.