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Monitoring long-term changes in UK grey seal pup production

DJF Russell[1*], CD Morris[1], CD Duck[1], D Thompson[1], Hiby L[2]

1. *Sea Mammal Research Unit, University of St Andrews, St Andrews, KY16 8LB, UK.*
2. *Conservation Research Ltd., 110 Hinton Way, Great Shelford, Cambridge, CB2 5AL, UK.*

*Corresponding author: djf.russell@gmail.com

Abstract

1. The population size of many species, particularly those in the aquatic environment, cannot be censused directly. Counts, during the breeding season, of one component of the population (e.g. breeding females) are often used as an index to allow investigation of trends. In species, such as grey seals (*Halichoerus grypus*), for which births are not tightly synchronous, single counts of pups represent an unknown proportion of the total number of pups born (pup production) and thus breeding females (each pup born represents a breeding female).
2. Grey seals pup at large colonies around the coast of the UK. Information on their populations is required under national and international legislation.
3. In the UK, pup production has been monitored at some colonies since 1956. Currently large colonies (c. 90% of UK pup production) are monitored either using ground (c. 10%; annually) or aerial surveys (c. 80%; annually until 2010, and thereafter biennially) .
4. Here, the model used to estimate pup production at aerially surveyed colonies from 1987 to 2010 is described; structured pup counts from multiple surveys are combined with knowledge of life-history parameters to model birth curves.
5. The resulting trends in pup production up to 2010 (aerially surveyed colonies) and 2016 (ground surveyed colonies) are examined.
6. In 2010, over 45,000 pups were estimated to be born in the UK. Pup production appeared to have reached an asymptote in the Inner Hebrides, Outer Hebrides and Orkney, whereas it is still increasing exponentially in the North Sea. Although density dependent processes acting at sea are likely to be responsible for these regional trends, we suggest that the substantial variation in trends within regions are likely caused by processes acting at the colony level. Some long-established colonies, including Special Areas of Conservation (SACs), are exhibiting decreasing trends.
7. SACs often serve as *defacto* monitoring sites and are the focus of management efforts. The observed temporal and spatial variability in patterns of colony growth rates highlight the potential risks of using such sites to develop wider management policies.

Keywords: coastal, monitoring, modelling, mammals, conspecific attraction hypothesis, density dependent survival, local population dynamics, metapopulations, natal dispersal, pinnipeds.

1. Introduction

Effective conservation and management of a species is dependent on knowledge of its abundance and trends therein. Few populations of wild vertebrates can be directly counted, and this is especially true for widely dispersed species such as marine vertebrates. However, some species congregate at various stages of their life cycle (e.g. migratory stopovers and breeding) when they are concentrated and highly visible, and therefore countable. This is the case for aquatic species which spend a proportion of their time on land, particularly those that breed colonially (i.e. seals and seabirds). Estimating trends in some ecologically relevant component of the population is dependent on quantifying the relationship between this component and counts of observable individuals.

For species which exhibit tightly synchronous breeding with extended periods of parental care on land (e.g. seabirds), single counts of breeding indicators (e.g. apparently occupied nests) can be used directly as indices of the size of a component of the population (e.g. Mitchell, Newton, Ratcliffe, & Dunn, 2004). However, in species with less tightly synchronous breeding or for which time ashore is short, single counts may not be representative index. At the time of any given survey some individuals may have finished breeding and left, while others may not have started. Number of births (production) can be calculated by counting each individual born through the season, either by marking positions (on ground or on photographs) if young are tied to one site (e.g. bird nests) or by marking individual animals (e.g. Piazza & Wright, 2018). However, the required survey effort is often impractical. A less intensive capture-mark-recapture approach (superpopulation approach; Crosbie & Manly, 1985) can be used to estimate production, but this still requires the identification of individuals over multiple surveys. When this is not possible, the highest count during the season (peak count) has been used as an index of total production (Link & Sauer, 1998). The reliability of such an index is dependent on capturing the true peak which is difficult to achieve if the timing of the breeding varies spatially or annually (Summers, 1978; Williams, Frederick, & Nichols, 2011), and on a constant relationship between the peak and total production. To estimate production for species, such as the grey seal (*Halichoerus grypus*), for which the large numbers and wide geographical spread of colonies necessitates the use of aerial surveys, across which individual animals cannot be tracked, an alternative method is required.

Grey seals pup in large aggregations (colonies) on both sides of the North Atlantic. Females give birth to a single pup which suckles for 15–21 days (Pomeroy, Fedak, Rothery, &

Anderson, 1999), and then undergoes a post-weaning fast before leaving the colony. When born, they have fluffy white coats (lanugo) and moult into an adult type pelage at a mean age of between 23 (UK; Radford, Summers, & Young, 1978; Wyile, 1988) and 27 days (Canada; Bowen, McMillan, & Mohn, 2003). The duration of the pupping season at many sites exceeds the maximum length of stay of any individual pup, so an unknown proportion of the total pup production at a colony is present during any one survey (Radford et al., 1978) and no survey will count all the pups. On the ground, pups can be classified into five stages, which can be related to pup age (Radford et al., 1978; Kovacs & Lavigne, 1986;). The first three stages comprise pups that have not started moulting their natal coat; these stages are defined using various characteristics including body shape. The fourth and fifth stages are assigned to moulting and moulted pups, respectively. On Sable Island, the largest colony in the north-west Atlantic, ground surveys at a sample of sites are used to estimate the proportion of pups in each of the five stages; these proportions are applied to a single aerial survey count of the colony allowing pup production to be estimated (Bowen, McMillan, & Blanchard, 2007). This method is not applicable to the UK grey seals; pupping occurs between September and December, and gets progressively later in a clockwise cline around the UK, starting in the south-west. The number of colonies that would need to be ground surveyed is unfeasible.

The UK holds approximately 40% of the world's grey seal population (SCOS, 2017) and the population is protected under both national (e.g. The UK Conservation of Seals Act 1970, Marine Scotland Act 2010) and international (e.g. EU Habitats Directive) legislation. The management actions defined under these different legislative procedures require appropriately detailed and up-to-date information on the population status of grey seals at several different spatial scales. For example, in Scotland, seals are managed in large regional Seal Management Units (SMUs; Figure 1) under the Marine Scotland Act. The EU Habitats Directive requires monitoring and assessment of abundance at key sites called Special Areas of Conservation (SACs). In Europe, SACs have been established for grey seals to support the maintenance of Favourable Conservation Status (FCS; Council of the European Communities, 1992). In the UK, these SACs were selected to include large breeding colonies while covering their geographic breeding range (Supplement 1). Abundance data are required to address specific questions of conservation and management concern: e.g. to assess any potential impact of human activities on the integrity of SACs; population size is combined with diet composition data to determine the magnitude of potential interactions and competition with commercial fisheries (Wilson & Hammond, This Issue); spatially structured population data are required to estimate the at-sea distribution of grey seals (Jones et al., 2015; Russell, Jones, & Morris, 2017) for use in marine spatial planning; grey seal population data are required in combination with harbour seal population data to investigate the potential role of grey seals in regional harbour seals declines (Thompson, Duck, Morris, & Russell, This Issue).

To inform these legislative requirements, the majority of colonies (hereafter regularly monitored colonies) have been surveyed annually between 1984 (or earlier depending on the colony) and 2010 (and at least biennially thereafter). These regularly monitored colonies are within four study regions: Inner Hebrides (which in terms of grey seal colonies is synonymous with the West Scotland SMU), Outer Hebrides (Western Isles SMU), Orkney (within the North Coast & Orkney SMU), and North Sea (Figure 1). The regularly monitored colonies in the North Sea fall into two geographically distinct groups and thus are considered as subregions here: central (combination of East Scotland and Northeast England SMUs) and south (Southeast England SMU). These regions can be viewed as sub-populations of a metapopulation; each region is comprised of smaller units, the individual colonies. Pup production in these regularly monitored colonies accounts for c. 90 % of UK grey seal pup production. Surveys at small, less frequently monitored colonies, or outwith these regions (e.g. within Moray Firth, Shetland, Wales, Southwest England, and Northern Ireland SMUs), are not considered here. Scouting surveys are conducted every few years to cover potential grey seal pupping sites within the study regions. Whether or not newly established colonies identified during such surveys are included as regularly monitored colonies thereafter is dependent on the colony size and location. As colonies have become established, the number of regularly monitored colonies has increased from 39 (1987) to 62 (2010; Supplement 1). The regional pup production estimates from these regularly monitored colonies are input into a Bayesian age-structured model to provide annual estimates of population size (Thomas et al., This Issue).

Regularly monitored colonies are aerially or ground surveyed. Scottish colonies have been surveyed using vertical aerial photography since 1963 (Hiby, Thompson, & Ward, 1988). Since 1987, at least four surveys have been attempted per season. Pups counted on the photographs were assigned to two classes: whitecoat (≥5% lanugo remaining; stages 1-4) and moulted (stage 5; <5% lanugo remaining). The multiple counts within a season are used to trace the rise and fall of the number of whitecoats and moulted pups on the colony. Specifically, the apportioned counts are modelled along with distributions relating to the age at which pups fully moult and leave the colony, to estimate a birth curve and thus total pup production. The aerial survey methodology was changed after 2010, and thus only results up to 2010 are presented here. Colonies on the east coast of England are ground surveyed; the earliest surveys being in 1956 (Farne Islands; Bonner & Hickling, 1974). Ground survey methods differ between the colonies, but at each colony have been consistent through time, thus all available pup production estimates (until 2016) are presented here. In this paper, the method used to estimate pup production from aerially and ground surveyed colonies is described; and the trends in pup production are examined for the four key study regions, and the encompassed SACs and larger individual colonies (i.e. max. annual production of > 150).

2. METHODS

2.1 Pup production at aerially surveyed colonies

2.1.1 Aerial surveys

Consistent survey methods, in terms of both the camera equipment and pup classification, were used between 1987 and 2010 (inclusive). Since 1987, four or more aerial surveys per colony were carried out each year where possible. Surveys were flown at a height of 365 m, using a medium format camera in a purpose built mount that compensated for drift and image motion. The camera was fitted with a critically pre-focussed 150 mm lens. The overlapping pictures were full colour vertical images on colour transparency film, with a spatial resolution of just under 5 cm on the ground (Hiby et al., 1988). The survey height and focal length combination produced images of seal pups approximately 0.4 mm long. The overlapping areas between frames were marked on the colour transparencies to avoid double counting. Each transparency was viewed on a microfiche reader at 22x magnification, and the numbers of whitecoat and moulted pups were recorded. In some years, poor weather conditions or camera malfunction resulted in fewer surveys being conducted for certain colonies. In 2008, survey altitude was reduced from 365 m to 335 m which resulted in slightly improved image quality, and this altitude was used thereafter. The last film survey was conducted in 2010.

Prior to 1987, pups were not classified into whitecoat and moulted categories, and flights (usually three) were designed to coincide with the time when the maximum number of pups was present at each colony. Peak counts were then converted to pup production estimates using a scaling factor derived from series of ground counts in Orkney and the Hebrides (Summers, 1978). Prior to 1986, black and white photographs were taken using a pair of Hasselblad 70 mm format cameras without image motion compensation. Images were printed and overlapping images were viewed using a stereoscopic viewer. Pups were marked on an acetate overlay on one of the stereo pairs.

2.1.2 Pup production model

The model developed to estimate pup production is, in essence, a state-space model; the underlying process (birth, moulting and leaving) is modelled along with an observation model relating this process to the observations (counts; Figure 2). In the underlying process, individuals are recruited into the whitecoat class at a rate determined by the underlying birth curve (assumed to be lognormal; see below). They leave this class once they have fully moulted. Thus, the duration pups are in this class equals the age at which pups have moulted (time-to-moult; TTM). In reality, some individuals may die and remain in this class until their carcasses disappear, though this is not modelled. Once moulted, individuals transition to the moulted class, where they remain until the age at which pups leave the colony (time-to-leave, TTL), thus the duration of this class is TTL-TTM, although (again) some individuals may die. On survey days, the number of individuals in each class (whitecoat and moulted) is related to the numbers counted using an observation model (Figure 2b). The observation model accounts for the fact that not all pups will be counted (PCount) and some may be misclassified (PCorrectMoult).

2.1.2.1 Distribution of births

Ground counts of marked pups suggest that the distribution of birth date is unimodal and skewed to the right, and can be represented by a lognormal distribution:

$$b(t) = \frac{1}{(t-\psi)\sqrt{2\pi\sigma^2}} \exp\left\{-\left(\ln(t-\psi)-\mu\right)^2 / 2\sigma^2\right\}$$

where $b(t)$ is the probability of a pup being born on day t and ψ is the first day on which any pups can be born. If ψ is much less than the mean birth date, $\psi + exp(\mu+\sigma^2/2)$, the distribution is almost symmetrical, whereas if ψ is close to the mean it is heavily skewed to the right. The expected number of births that have occurred by the date of a given flight is therefore B times the integral of $b(t)$ from ψ to that date, where B is the total pup production.

2.1.2.2 Life history parameters

Parametrised distributions were required for the two life-history parameters: TTM and TTL. The values used were based on observations of known-age pups on the Isle of May (Supplement 1) from 1985 to 1987 (Wyile, 1988). TTM was found to be normally distributed with a mean of 23 days (SD = 5) and did not differ significantly between years. TTL was also normally distributed, with a mean of 31.5 days (SD = 7 days). There was an indication that TTL decreased as the season progressed, though this was not quantified. Ages of moulting and leaving for individual pups were uncorrelated. The probability of a pup having moulted *M(a)* or left *G(a)* by age *a* are therefore treated as independent within the model.

2.1.2.3 Observation model parameters

There are two reasons why a pup would not be counted: (1) because is not visible on the photographs, and (2) because visible pups may be missed by the counter. Although live pups may be hidden (e.g. under overhanging cliff), most pups not visible are likely to be dead, and washed into the sea or too decomposed. Mortality and its effect on visibility of pups is not modelled (see Discussion); visible dead pups are counted and apportioned to the whitecoat class (>95% of dead pups are whitecoats; Quaggiotto *et al.*, 2018). A term PCount, the probability that a pup is counted, is used to account for both reasons. A value of 0.95 for PCount was based on a comparison between ground and aerial survey counts (conducted on the same day; Thompson & Wyile, 1985).

To some extent the classification of whitecoat and moulted pups, from the aerial photographs, is subjective; it may be affected by pup pelage, habitat, light conditions and the individual counter. It is also affected by the way a pup is lying; the underside of moulted pups is typically much lighter than their side or back, and thus they are more likely to be misclassified as whitecoat if lying on their back. Partially moulted pups can also be misclassified as moulted if their remaining lanugo is not visible from above. Close to concurrent ground and aerial surveys of seven colonies at Orkney in 1994 revealed that classifications from aerial surveys are biased towards whitecoats. From these comparisons, it was estimated that a mean of 0.55 (across colonies; SD = 0.07) moulted pups had been correctly classified as moulted from the aerial survey photographs, and the rest misclassified as whitecoats.

2.1.2.4 Model Fitting

The model was written in Fortran 77 and fitted within a Maximum Likelihood framework. The vector of counts for a particular colony in a particular year was assumed to have a multivariate normal density, defined by a vector of expectations and a covariance matrix (Supplement 2). So, if four flights were completed then the vector of expectations had eight elements (4 for whitecoats and moulted pups, respectively). Those expectations and the covariance matrix were defined as functions of the distributions for the set (TTM, TTL, PCorrectMoult) and free parameters (start date, mean and standard deviation of birth curve). The covariance matrix was adjusted to account for the variance of PCorrectMoult (see 2.1.2.3). This effectively reduced the relative weight of the separate whitecoat and moulted counts compared to the total count. Observed birth curves were more noisy than expected, given the number of pups born. Thus, for each colony and year, a variance scaling factor was estimated and applied to the covariance matrix to account for the likely violation of the assumption that the birth and development processes are independent for different pups. The negative log of the multivariate normal density was minimized iteratively with respect to the three parameters of the birth date distribution, and the variance scaling factor; the minimum log likelihood value for *B* was available as a function of the other parameters for each iteration of the optimization. More details of the pup production model are given in Supplement 2. Colony/year-specific Coefficients of Variation (CVs) could be calculated using the likelihood ratio method if there are three or more surveys. Here the range of CVs for the year which encompassed the highest number of regularly monitored colonies (2010) are presented.

2.2 Pup production at ground surveyed colonies

There are four large colonies on the east coast of England, all of which were ground surveyed: Farne Islands (since 1956), Donna Nook (since 1970), Blakeney Point (since 2002) and Horsey (since 2002). Ground surveys predated aerial surveys for two Scottish colonies in the North Sea, Isle of May (since 1979; SMRU) and Inchkeith (since 2003; Fife Seal Group), and one in Orkney, South Ronaldsay (Scottish Natural Heritage). Annual aerial surveys started at the Isle of May in 1991, and at Inchkeith in 2008. A single aerial survey was conducted at South Ronaldsay in 2008.

Survey methods differed between the colonies. On the Farne Islands, during surveys, which were conducted by the National Trust, all non-marked whitecoat pups were counted and marked with dye to avoid recounting. Provided that counts encompassed the entire pupping season and were sufficiently close together that no pups could be born and leave the colony in inter-survey interval, such methods provide a virtually error-free estimate of pup production. The pups at the more recently formed colonies of Donna Nook (surveyed by Lincolnshire Wildlife Trust), Blakeney Point (surveyed by National Trust) and Horsey (surveyed by Friends of Horsey Seals) were not marked. Instead, pup counts were conducted weekly (or more frequently at Blakeney Point) with the number deemed to have been born since the last count (i.e. estimated to be younger than the inter-survey interval) used to estimate cumulative pup production through the season. The total number of pups counted on each survey was used to refine this estimate, especially early in the season before many pups had left.

Ground surveys on the Isle of May were conducted in the same way as at the Farne Islands. When ground surveys began at Inchkeith, the peak count (65 in 2003) was used as the estimate of pup production (and thus was likely an underestimate). In later years, two counts were conducted three weeks apart and the number of whitecoats were summed across both surveys to estimate production. The reasoning being that, on average, whitecoats counted in one survey should have moulted by the next one. Dead whitecoats were added to estimates if they are deemed to have been born since the last survey. The timing of these surveys ensured pups born early in the season were not missed but it is likely that some pups were born after the second survey. For South Ronaldsay, pups were classified as whitecoat or moulted, and thus pup production was estimated within the pup production model used for aerial survey data (see above). There were no estimates of uncertainty available for ground surveyed colonies.

2.3 Trends in pup production

Trends in pup production over time were investigated using Generalised Linear Models (GLMs) and Generalised Additive Models (GAMs). Uncertainty surrounding estimates of pup production were not propagated into the trend analyses. These analyses were conducted for all colonies combined as well as by study region, SAC, and individual colonies for which >150 pups were born in any year. For aerially surveyed colonies, the trend models were only fitted to pup production estimates from 1987 onwards because these estimates were produced by the model described above, and thus represent a consistent time series; estimates of pup production prior to 1987 are shown in the figures for information. Only since 1984 were pup production estimates available from almost all established colonies included in this study, and thus regional estimates are shown from 1984 and analysed from 1987. All available estimates for ground-surveyed colonies were included in the trend analysis.

A minimum of three models were fitted to each colony/region with pup production modelled as a function of: (1) an intercept within a GLM, (2) year modelled within a GLM, and (3) year modelled within a GAM (fitted in mgcv; Wood, 2011). A negative binomial distribution was assumed and the GLMs were fitted using the function glm.nb in the MASS library (Venables & Ripley, 2002). If a limited number of data points prohibited the fitting of such models, models were instead fitted with Poisson errors (allowing over-dispersion by using a quasi-likelihood). The GAMs were constrained to a maximum of 5 knots to avoid overfitting. Model selection was conducted using AIC_C. The aim here was to describe the temporal trends in pup production. To facilitate this, for colonies/regions for which a GAM was selected but visual inspection of the results indicated that there were periods of exponential increase or decrease, these periods were fitted separately to estimate rates of change.

3. Results

3.1 Model fit

For most colonies, visual inspection showed a reasonable or good fit between the predicted and actual counts of both whitecoats and moulted pups (Figure 3). However, there was evidence of an underestimation of moulted pups in some colonies (e.g. Figure 3b). In 2010, the mean CV across all colonies was 0.125 (SD: 0.02, range: 0.036, 0.242). High CVs were associated with medium (CV > 0.15; estimated pup production of < 500 pups) to small colonies (CV > 0.20; < 150 pups; Figure 3d). However, although a high CV score is indicative of a poor fit, a low CV score may not always be indicative of a good fit (Figure 3; see Discussion). There are no estimates of uncertainty for the ground surveyed colonies (Farne Islands and all colonies in the south subregion).

3.2 Estimates of pup production and trends

Total pup production from regularly monitored colonies increased at a rate of 7.6% p.a. between 1987 and 1995 (95% CIs: 6.3, 8.9). It reached an apparent asymptote of around 40,000 pups in the early 2000s, although pup production continued to increase in the North Sea. Total pup production from regularly monitored colonies was estimated to be 41,600 in 2010. Trends were fitted to estimated production from regularly monitored colonies in the UK combined (Figure 4), and also separately for six subregions (Figure 5), six SACs (for which grey seals were a primary reason for designation; Figure 6), and 38 colonies (for which maximum pup production > 150; Supplement 3).

3.2.1 Inner Hebrides

Pup production at regularly monitored colonies in the Inner Hebrides was estimated to be 3,100 in 2010 (Figure 5a). Pup production increased until reaching an asymptote of between 3,000 and 3,500 pups in the early to mid-1990s. A quarter of pups in the Inner Hebrides were produced within the single SAC in this region (Treshnish Isles SAC; Figure 6a). Until the mid-1990s, the trend in pup production within the Treshnish Isles SAC mirrored the regional trend, after which pup production in the SAC showed indications of a decline.

3.2.2 Outer Hebrides

Pup production at regularly monitored colonies in the Outer Hebrides was estimated to be 11,850 in 2010. Approximately 80% of these pups were produced within the two SACs in this region: 9,200 on the Monach Islands and 550 on North Rona. Pup production in the Outer Hebrides increased at a rate of 6.5% p.a. (1987-1993; CIs: 4.7, 8.2) until the early 1990s, when the growth rate decreased as the pup production approached an asymptote of around 12,000 pups (Figure 5b). Not surprisingly, pup production on the Monach Islands showed a similar trend (Figure 6b) to that of the region; pup production increased at a rate of 7.4% p.a. (CIs: 6.3, 8.4) between the mid-1980s and mid-1990s before levelling off.

North Rona SAC, which used to be the biggest colony in the Western Isles (c. 2,000 pups in 1960s and 1970s; Figure 6c), exhibited declines since 1995 at a rate of 5.1% p.a. (1995-2010: CIs: 4.2, 6.0). Many of the other key historical colonies (Supplement 1) in this region underwent similar decreases in pup production (Supplement 3) within the survey period (e.g. Causamul: 8% p.a. (CIs: 6.8, 9.3); Haskeir: 3.3% p.a. (CIs: 2.4, 4.1)). More recently, Shillay in the Sound of Harris, and Gasker also declined (Gasker: 4% p.a. (2000-2010; CIs: 2.7, 5.3)), whereas newly-established colonies (e.g. Berneray, Mingulay and Pabbay) in the south of the region increased.

3.2.3 Orkney

Pup production at regularly monitored colonies in Orkney was estimated to be 18,550 in 2010. The Faray & Holm of Faray SAC accounted for c.15% of this production. Pup production in Orkney reached an asymptote of 18,000 to 19,000 pups in c.2000 (Figure 5c). Pup production within the Faray & Holm of Faray SAC increased at a rate of 9.4% p.a. (1987-1995; CIs: 7.5, 1.4) reaching a maximum of 4,100 pups in the late 1990s before decreasing at a rate of 2% p.a. since 2000 (CIs: 0.8, 3.2; Figure 6d).

Trends at individual colonies within Orkney were variable (Supplement 3). Many colonies showed a similar pattern to the Faray & Holm of Faray SAC, in terms of an increase to a maximum followed by a decrease (e.g. Holm of Huip (2010 production: 1,000), Calf of Eday (550), Copinsay (1,750), Little Green Holm (150), Little Linga (550), Muckle Green Holm (650), Rusk Holm (150)). Pup production at other colonies appeared to have reached an asymptote (e.g. Calf of Flotta (200)). The rate of increase at the biggest colony in Orkney, Linga Holm (c. 4,000 pups), appeared to have slowed after increasing at a rate of 14.3% p.a (1987-1999: CIs: 11.9, 16.8). Some colonies, mainly relatively new colonies in southern Orkney, were still growing (e.g. North Flotta (500)) but some showed signs of nearing an asymptote in recent years (Stroma (1,800), Stronsay Sty Taing (400), Sweyn Holm & Gasirsay (500), Switha (500), Swona (1,400)).

3.2.4 North Sea

Pup production at regularly monitored colonies in the North Sea was estimated to be 8,100 in 2010; 5,550 in the central subregion and 2,550 in the southern subregion. Approximately 80% of these pups were produced within SACs. The central subregion encompasses two SACs: Isle of May (2010 production: c. 2,050) and Berwickshire & North Northumberland coast (3,200) which is made up of Fast Castle (1,700) and the Farne Islands (1,500). The south subregion encompasses Donna Nook which is in the Humber Estuary SAC, for which grey seals are a qualifying feature (2010 pup production: 1,400).

The pup production in the North Sea has increased since 1987 at an average rate of 6.6% p.a. (1987-2010; CIs: 6.1, 7.0; Figure 5d). The patterns of growth differed between the two subregions of the North Sea. There was a close to exponential increase in pup production in the central North Sea, averaging 5% p.a. between 1987 and 2010. (CIs: 4.4, 5.5; Figure 5e). However, rates of increase at the three main colonies vary. Production at the Isle of May increased exponentially at 9.9% p.a. (CIs: 7.5, 12.3), since surveys began (1979), before reaching an asymptote of c.2,000 pups in the late 1990s (Figure 6e). Pup production in the Berwickshire & North Northumberland Coast SAC did not show any indication of reaching an asymptote (Figure 6f). Fast Castle continued to increase at a rate of 16.9% p.a. (CIs: 15.2, 18.7). Production at the Farne Islands increased from the beginning of the surveys in the 1950s until the mid-1970s, when production fell rapidly likely due to the culls (Summers, 1978) between 1967 and 1985 (pre-cull pup production between 1956-1965: 7.5% p.a.; CIs: 6.5, 8.5; Supplement 3). Production increased at a slower rate of 4.2% p.a. in recent years (2005 – 2014; 95% CIs: 3.2, 5.2).

Production in the southern subregion increased at a rate of 16.5% p.a. (1984-2016; CIs: 15.8, 17.1; Figure 5f) from c. 800 pups in 2002 (when monitoring at Blakeney Point began) to c. 5,900 in 2016. Production at Donna Nook (Humber Estuary SAC) increased from c.30 pups in 1984 to almost 2,000 in 2016. The colony increased most rapidly between 1995 and 2005; 13.0% p.a. (CIs: 11.6, 14.3), after which it showed signs of decreased growth rate. There was a very rapid increase in production at two relatively new colonies, Blakeney Point and Horsey; c. 50 pups were born in 2002 at each colony. Blakeney Point grew at 32.79% p.a. (2002 - 2016: CIs: 30.1, 35.3) with pup production estimated to be c. 2,400 in 2016. However, pup production in the last three years (2014-2016) was stable indicating that this rapid growth may have ceased. Discounting the last three years resulted in an estimated growth rate of 33% p.a. (95% CIs: 30.8, 35.3). Horsey increased exponentially at 27.1% p.a. (1991-2016; CIs: 25.8, 28.4) with pup production estimated to be c. 1,500 in 2016.

4. Discussion

4.1 Review of pup production estimates

The accuracy of pup production estimates will vary with method – both across different ground survey protocols, and compared to aerially surveyed colonies. For ground surveyed colonies, the highest accuracy will result from marking all individual pups as at the Farne Islands. Such methods can cause substantial disturbance (Fogden, 1971) and are not used at the other ground surveyed colonies. Estimation of production at the other main ground surveyed colonies will be much less accurate as it relies on age-classification of pups. However, methods have been consistent through time within colonies, and despite being conducted by various counters, the resulting pup production estimates show clear trends. Thus, although the production estimates of these ground surveyed colonies should be treated with caution, the broad trends are likely to be robust. Uncertainty estimates (CVs) are only available for aerially surveyed colonies. CVs are calculated assuming an adequate model and thus if there is directional bias in the estimation of pup production, then the values can be misleading (Figure 3).

The reliability of estimates of pup production from aerial surveys is dependent on the reliability of the parameterised model, both in terms of the process (moulting and leaving) and relating that process to the observations. There are two distributions used within the process model: TTM and TTL. The TTM (the age at which <5% lanugo remains) used in the model (Wyile, 1988) is supported by other studies on the Isle of May (2010: 23.14 days (n=23); Bennett unpublished data) and North Rona (Radford et al., 1978). TTL, in the model, represents the age at which pups choose to leave the breeding colony. The mean TTL used in the model (31.5 days) was derived from direct observation with an adjustment to account for study pups which had not left by the end of the study period. It was likely to be an underestimate of TTL, as defined in the model, because it included individuals which left the breeding beach before moulting. Most pups that leave before completing moult presumably haul out elsewhere (and thus are potentially available to be counted) or die. Examination of model fits also suggests that a mean TTL of 31.5 days may be too low; cases of poor model fit (e.g. Figure 3) were often due to a higher number of moulted pups (but not whitecoats) counted than predicted by the model. For small colonies this could be the result of the presence of groups of moulted pups, which were born elsewhere (see below). TTL may vary with habitat and weather conditions, but could also potentially vary with colony density. Moulted pups often congregate on areas of relatively low density or move to the periphery of the colony, presumably with the aim of minimising aggressive interactions. If areas of relatively low density become less available as the colony density increases, moulted pups may be less likely to stay. However, visual inspection of photographs suggest that even in dense colonies, such areas are still available. Furthermore, visual examination of model fits at different points in colony trajectories shows no evidence of a pattern in TTL. Studies have rarely focused on estimating TTL directly, but examination of the duration of the constituent parts (lactation and post-weaning fast; PWF), which are independent of each other (Noren, Boness, Iverson, McMillan, & Bowen, 2008), suggests that both at the Isle of May and elsewhere, mean TTL is much higher than 31.5 days. Mean lactation duration is reasonably consistent at 17-19 days across studies both in the UK (Pomeroy et al., 1999; Bennett unpublished data) and at Sable Island (Noren et al., 2008). However, PWF duration is more plastic and appears to be dependent on both habitat (Jenssen, Åsmul, Ekker, & Vongraven, 2010) and pup condition (Noren et al., 2008). Noren et al., (2008) found a mean PWF duration of 21 days and TTL of 40 days (SE=1.1, n=30) on Sable Island. However, TTM is higher in Canada than in the UK (Bowen et al., 2003), which may result in a higher TTL. Within the pup production model, increasing TTL to the highest reported mean TTL (40 days) resulted in reduction in estimated pup production; the extent of this reduction varied with the specific colony and year combination considered but could be substantial (e.g. 15% decrease for Isle of May in 2008; Russell, Duck, Morris, & Thompson, 2015).

There are two parameters involved in relating the pup production process to the aerial survey counts: PCorrectMoult and PCount. Pup production estimates are not very sensitive to changes in PCorrectMoult; a 10% increase would result in a c.1% increase in estimated pup production (SCOS, 1998). Increasing the value of PCorrectMoult used in the model decreases the number of pups counted as whitecoats that, in the model, are reassigned to the moulted class. The result is a higher ratio of whitecoats to moulted pups, and thus a higher estimated pup production. In contrast to PCorrectMoult, pup production estimates are very sensitive to the value of PCount because the parameter is essentially a scalar; e.g. setting PCount to 0.90 (rather than 0.95) would result in a 5.6% increase in estimated pup production. Although there is a variance term included for PCorrectMoult (derived from variation across multiple colonies), no variation around PCount is modelled. In reality one or both of these parameters could be influenced by survey height, habitat, environmental conditions, individual counter, and mortality. Comparing trends across regions and colonies suggests there was no impact, on these parameters, of the 9% reduction in survey height, and resultant increase in picture quality, from 2008. The majority of photographs were counted by the same individual. Counts from a subset of photographs were compared between counters during training to ensure consistency. However, it is likely that there would be some variation in both parameters within and between counters, and this is not accounted for in the model. The assigned value of PCount (0.95), based on a comparison between ground and aerial survey counts, may be an overestimate as it does not account for pups which were born but not ground surveyed (either missed or not visible – e.g. washed into the sea). PCount is also likely to be influenced by mortality. Almost all mortality occurs in the whitecoat class (>95%; Quaggiotto *et al.*, 2018), and its impact on pup production estimates depends on whether, on average, a carcass is visible for (1) a shorter, (2) the same, or (3) a longer duration than the pup would have remained in the whitecoat class had it survived. Under the first scenario there would clearly be a downward bias. Under the second and third scenario, the magnitude of impact is dependent on timing; specifically whether a pup would have been surveyed as a moulted pup had it survived. Although less substantial than under scenario one, there would still be a downward bias under the second scenario if surveys were still being conducted once the carcass was no longer visible. Under the third scenario, there would be an upward bias if the pup was erroneously counted as whitecoat. Which scenario is most likely is dependent on both the age at which pups die and how long carcasses remain visible.

Information on age at which pups die is available from systematic searches for dead pups carried out at the end of season on the Isle of May (North Sea; Figure 1) in 2008, 2012 and 2013 (Quaggiotto et al., 2018). Over the 75% of carcasses were classed into one of five stages; the rest were starvelings or too decomposed to stage. Relating the frequency of pups in each stage to the mean age of pups in each stage (Kovacs & Levinge, 1986) resulted in an estimated mean age of death of between 5 and 7 days old (Quaggiotto et al., 2018). The total number of dead pups counted near to the end of the season on the Isle of May in 2008 was 223 (Quaggiotto et al., 2018). Only a small proportion of pupping at this colony occurs on beaches, from which dead pups can be lost into the sea, thus it is likely that this value is close to the total mortality. On aerial photographs, whether a pup is dead is judged by shape and posture, blood-stained pelage and scavenging by gulls. Clearly dead pups are unlikely to remain visible across all aerial surveys; the number of dead pups counted from aerial photographs taken in 2008 during five surveys at approximately ten-day intervals was 1, 15, 78, 164, and 145 resulting in a total of 403. Interestingly, summing the dead pups across the third and fifth (78 & 145) aerial surveys, 20 days apart results in the same number of dead pups as reported from the ground census. This allows us to speculate that at least for that year and colony, dead pups would have been visible for approximately the same time as they would have remained in the whitecoat class had they survived. However, this conclusion is predicated on the assumption that, on the aerial photographs, live pups are not misclassified as dead. Twiss, Duck, and Pomeroy (2003) estimated at North Rona, that carcasses remained visible for an average of 10 days. The duration that carcasses remain visible will be dependent on their proximity to the sea, and on levels of scavenging, habitat and weather, but the above studies suggest that dead whitecoats will not remain visible longer than they would have remained in the whitecoat class had they survived (Scenario 3). It follows that any bias in pup production estimates, resulting from mortality, will likely be in the downward direction. Levels of mortality are variable and can be high (e.g. c.14.5% at North Rona) but do not appear to be related to colony density (Twiss et al., 2003).

The above discussion indicates that the pup production estimates should be treated with caution. For aerially surveyed colonies, the sensitivity of the estimates to TTL suggests that under the current parametrisation, any bias in pup production estimates is likely to be upward (despite any mortality-related bias acting in the opposite direction). Nevertheless, trends in pup production are likely to be robust as there is no evidence that the life-history parameters (TTL and TTM), mortality rates or detection probabilities (PCorrectMoult and PCount) that are set in the model will have shown directional change through time or with colony numbers. The model presented here allows estimation of pup production from a limited number of surveys (three or more) for colonies with differing birth curves. Current research is ongoing to improve the parametrisation of this model, and thus the reliability of the pup production estimates.

4.2 Overall trends in pup production

Notwithstanding the caveats discussed above, the best estimate for UK pup production (regularly monitored colonies and other colonies; Baines, Earl, Pierpoint, & Poole, 1995; Boyle, 2010; Sayer, Hockley, & Witt, 2012; Strong et al., 2015; Westcott, 2008; Westcott & Stringell, 2003) in 2010 was around 45,000. The pup production in three of the four study regions, and as a consequence in the UK as a whole, has shown a decreased growth rate since the mid-1990s (Figure 4). This indicates that population dynamics are being driven by density-dependent processes and that the populations are at or nearing carrying capacity (Thomas et al., This Issue). In theory, density dependence could be acting on emigration, fecundity, or survival; though here emigration alone could not be responsible for such trends. How pup production and its trends relate to estimates of population size and trajectories is dependent on levels of fecundity and age-sex-specific survival, and changes therein. Combining this pup production time-series with an independent estimate of population size (Lonergan, Duck, Thompson, Moss, & Mcconnell, 2011; Russell, Duck, Morris, & Thompson, 2016), within an age-structured population model, has revealed that the main density dependent effect is likely acting through increased pup mortality (Thomas et al., This Issue). Similar mechanisms appear to be underlie the slowing down of the growth rate of the Sable Island colony; pup survival has dropped from 0.74 for the cohorts of the 1980s to 0.33 in recent cohorts (den Heyer, Bowen, & Mcmillan, 2014). Pup survival increases with weight and length at weaning (Bowen, den Heyer, Mcmillan, & Iverson, 2015; Hall, Mcconnell, & Barker, 2001), and mass at weaning is related to female mass (Pomeroy et al., 1999). So pup survival may still be driven by density dependent processes acting on females, as well as those acting directly on pups. At sea, density dependent processes may act on pups through competitive exclusion, by older individuals, from the highest quality foraging areas (Breed, Bowen, & Leonard, 2013). Regional population trends are discussed in Thomas et al. (This Issue).

The two subregions of the North Sea considered here, central and south, show markedly differing rates of increase. The exponential rate of increase in grey seal pup production in the southern North Sea must, in part, be driven by recruitment of females born elsewhere. It is unknown whether such immigration is solely from within the region (emigration from central to south) or whether it also a result of emigration from Orkney, which may be related to the density dependence. Until recently, the proportion of the UK grey seal population foraging in the southern North Sea was larger than the proportion breeding there, indicating that some females were foraging in the southern North Sea but returning to the north to breed (Russell et al., 2013). Although grey seals exhibit natal philopatry to a degree, they show higher breeding site fidelity once they have recruited into a breeding population (Pomeroy, Twiss, & Redman, 2000). It seems likely that pups from further north travel to the southern North Sea and the Wadden Sea (Brasseur, van Polanen Petel, Gerrodette, Meesters, Reijnders, & Aarts, 2015) in search of favourable foraging conditions and then stay to pup (in an area which has higher pup survival than their natal region; Thomas et al., This Issue). Foraging conditions seem comparatively favourable in the southern North Sea (compared to the northern North Sea and Orkney) for other marine mammals. Surveys conducted in 1994 detected the highest densities of harbour porpoise in the central and northern North Sea, whereas equivalent surveys conducted in 2005 and 2016 showed the highest densities in the southern North Sea (Hammond et al., 2013, 2017). Harbour seal populations are also performing better in the southern North Sea compared to the central or northern North Sea (Thompson et al., This Issue).

4.3 Local trends in pup production

There is a lack of understanding as to the underlying drivers of colony-specific dynamics within metapopulations (Breton, Diamond, & Kress, 2006). As well as populations being driven by density dependent processes (Thomas et al., This Issue) that are likely acting at-sea, at least on a local scale, trends in pup production are in part driven by processes acting at the colony level. For the Inner Hebrides and the two subregions of the North Sea, the regional trends are largely reflected in the encompassed colonies. In contrast, the colony-specific trends in the Outer Hebrides and Orkney are variable. In the Outer Hebrides, the regional asymptotic trend was driven by the Monach Isles which accounted for c. 80% of the region’s pup production in 2010. In contrast, colonies which historically produced the majority of the region’s pups have shown sustained declines (including North Rona SAC); some of which started before the regional growth rate had slowed. Other, more recently formed colonies in the south of the region were increasing. In Orkney, although pup production at many colonies peaked at the same time as the regional pup production reached an asymptote (c. 2000), most have subsequently declined. Others reached their peak earlier or later than the regional trend; Linga Holm, the biggest colony in Orkney (c. 4,000 pups produced in 2010), only appeared to have started levelling off in recent years. Other, often newer, colonies (especially in southern Orkney) were still increasing rapidly in 2010. Indeed, pup production in southern Orkney, which has traditionally represented a small proportion of production (<20% in 2000) in Orkney, accounted for around a third in 2010. This raises interesting questions: why would some colonies decline rapidly when the regional pup production is stable or increasing, and why would some colonies continue to grow rapidly in areas where density dependence has apparently reduced the growth rate in that region to zero?

There are various potential explanations for such trends: differing local trends in fecundity, survival, or recruitment. Differential fecundity or female (pup or adult) survival outwith the breeding season is unlikely to be responsible for these trends because grey seals are wide-ranging and individuals from different breeding colonies, and even different breeding regions, will forage in the same area (Russell et al., 2013), often several hundred kilometres from their breeding sites. Even when pups first leave the pupping colony, they do not spend a prolonged period at sea in the vicinity of the colony (Carter et al., 2017), and thus conditions (in terms of prey availability) surrounding individual colonies would be unlikely to result in colony specific differences in pup survival. Similarly, although pup mortality rates on the colony are variable, they do not appear to show temporal trends or relate to density (Pomeroy, Twiss & Duck, 2000; Twiss et al., 2003). It seems likely that the observed trends are driven by differential recruitment. Such trends can arise under population level density dependent regulation in species with high site fidelity (Matthipopulos, Harwood, & Thomas 2005).

For grey seals, on a local scale, rates of recruitment may depend on two interacting factors affecting colony attractiveness: habitat quality and conspecifics. Good habitat quality is associated with access to the sea or pools (Stephenson, Matthiopoulos, & Harwood, 2007; Twiss, Caudron, Pomeroy, Thomas, & Mills, 2000; Twiss, Thomas, & Pomeroy, 2001). Part of the reason for the decline in pup production at historic colonies in the Outer Hebrides may have been caused by colonies of superior habitat quality becoming available. These historic colonies are topographically similar in that, for the most part, pupping sites are on the grassy tops of steep sided islands with limited access to the sea. In contrast, the Monach Isles are low-lying islands with extensive beach areas and wide unrestricted access to the sea. Thus it may be that the observed distribution of breeding colonies pre 1960 was constrained by the pattern of human habitation and farming. Once human habitation and farming ceased on the Monach Isles, pup production increased exponentially, initially driven by preferential recruitment of females from these traditional colonies. As a result of the recruitment to the Monach Isles, traditional colonies were predominantly made up of established females (Pomeroy, Smout, Moss, Twiss, & King, 2010). As well as a lack of recruiters, these declining colonies may also have lost established females to other colonies; even early in the decline of the historic Outer Hebrides colonies, the rates of decline were higher than estimated adult mortality (Thomas et al., The Issue).

As colonial species, the attractiveness of a breeding site also depends on the presence of conspecifics. The conspecific-attraction hypothesis (Serrano & Tella, 2003; Stamps, 1988) predicts that attractiveness increases with density. This may explain why some colonies remained relatively stable at low sizes for a prolonged period before increasing rapidly. However, the trends observed here indicate that increasing colony size may be associated with high attractiveness (high natal recruitment) only up to a point after which recruitment decreases (e.g. Kim, Torres, & Drummond, 2009), potentially because recruiting females may be unable to compete for space, or the space still available is sub-optimal (i.e. far from water; Pomeroy, Twiss & Duck, 2000). Indeed, combining genetic data with a subset of the trends presented here, Gaggiotti, Jones, Lee, Amos, Harwood & Nichols (2002), found evidence of density-dependent dispersal; compared to other colonies of a similar size that were still growing, colonies for which pup production had reached an asymptote contributed relatively more recruits to newly established colonies. Such a mechanism would lead to production levelling off, or oscillations, which may be indistinguishable from levelling off in the trends presented here. To explain the sustained declines observed at some colonies, we propose that colony attractiveness may in part be driven by the levels of recruitment rather than density *per se* (recruiter-attraction hypothesis). In this process, a stochastic event would lead to a high level of recruitment to a colony; the presence of young breeders may be used as cue of colony quality and thus make a colony more attractive to prospecting seals. Colony size would increase until recruitment necessarily declines due to space restrictions. Even once space becomes available, there may be little recruitment (natal or from elsewhere) until another stochastic event results in high levels of recruitment. The relative importance of site fidelity, habitat quality, and presence of conspecifics will likely determine the future of historic Hebridean colonies, such as North Rona.

These colony level processes are unlikely to be independent from the regional level processes acting on the metapopulation. Ultimately, if not first regulated by density dependent processes at sea, regional pup production would be limited by available pupping space. Even currently, the recruitment into the North Sea and Wadden Sea, of grey seals born further north may not be (solely) driven by a drive to breed near to comparatively favourable foraging conditions at sea, but may also be driven by the presence of relatively attractive colonies. Dispersing individuals do appear to preferentially recruit near to their natal colonies (Gaggiotti et al., 2002) which may explain why individual colonies are increasing rapidly in southern Orkney. Nevertheless, it is feasible that a decrease in the relative attractiveness of the traditional sites in Orkney may have, in part, driven immigration into the breeding population of the southern North Sea. Colonies with such rapid growth rates towards the edge of a species range can quickly become source colonies (Santoro, Green, & Figuerola, 2016) facilitating range expansion. Thus, such rapid growth may bolster the population at the southern limit of their range (N.W. France), or even extend the range further south, if appropriate pupping habitat is available.

4.4 Implications

The within-region variation in trends of grey seal pup production highlights the importance of large-scale monitoring programs. Although use of a set of indicator sites for monitoring metapopulations could reduce costs, the contrasting dynamics of colonies within relatively small geographical areas means that such a monitoring programme may not capture the trends. Estimating total pup production on the basis of fixed subset of colonies requires a stable conversion factor. Indeed here, imposing indicator site trends onto a region-wide baseline could not only dramatically under or over-estimate pup production but also result in misleading trajectories. Declines in well-monitored colonies, such as SACs, taken out of context of regional trends, could result in the instigation of unnecessary and ineffective management strategies. Furthermore, our results suggest that historically relatively large colonies (e.g. North Rona SAC) may not represent optimal habitat but instead represent marginal but available habitatsThis has potential implications for the optimal conservation strategy for species with depleted populations (e.g. monk seals; *Monachus monachus, Neomonachus schauinslandi)*. As well as protecting the current population centres of such species, it may be as, if not more, important to protect small increasing colonies or other areas of suitable habitat. . Indeed, in species with high natal fidelity, all suitable sites may not be colonised even when local occupied colonies are nearing carrying capacity (Matthiopoulos et al., 2005). The dataset presented here provides a rare opportunity to investigate the drivers of local distribution in a species that exhibits a degree of natal site fidelity.

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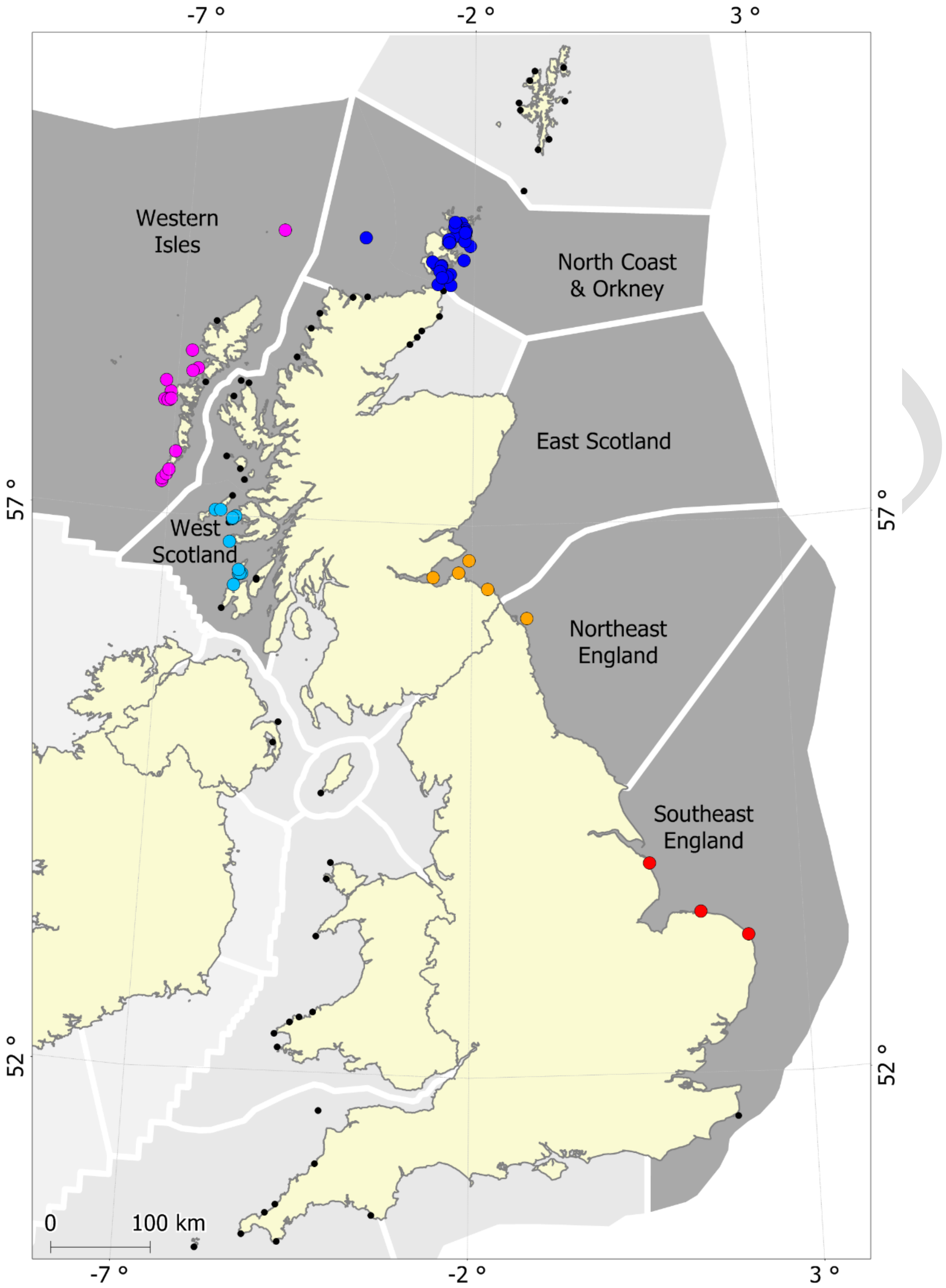

Figure 1. Map of UK and Isle of Man Seal Management Units showing the location of all grey seal colonies. Regularly monitored colonies are colour coded by survey region: Inner Hebrides (cyan), Outer Hebrides (pink), Orkney (blue), North Sea - central (orange), and North Sea - south (red), and the associated Seal Management Unit labelled.

(a)

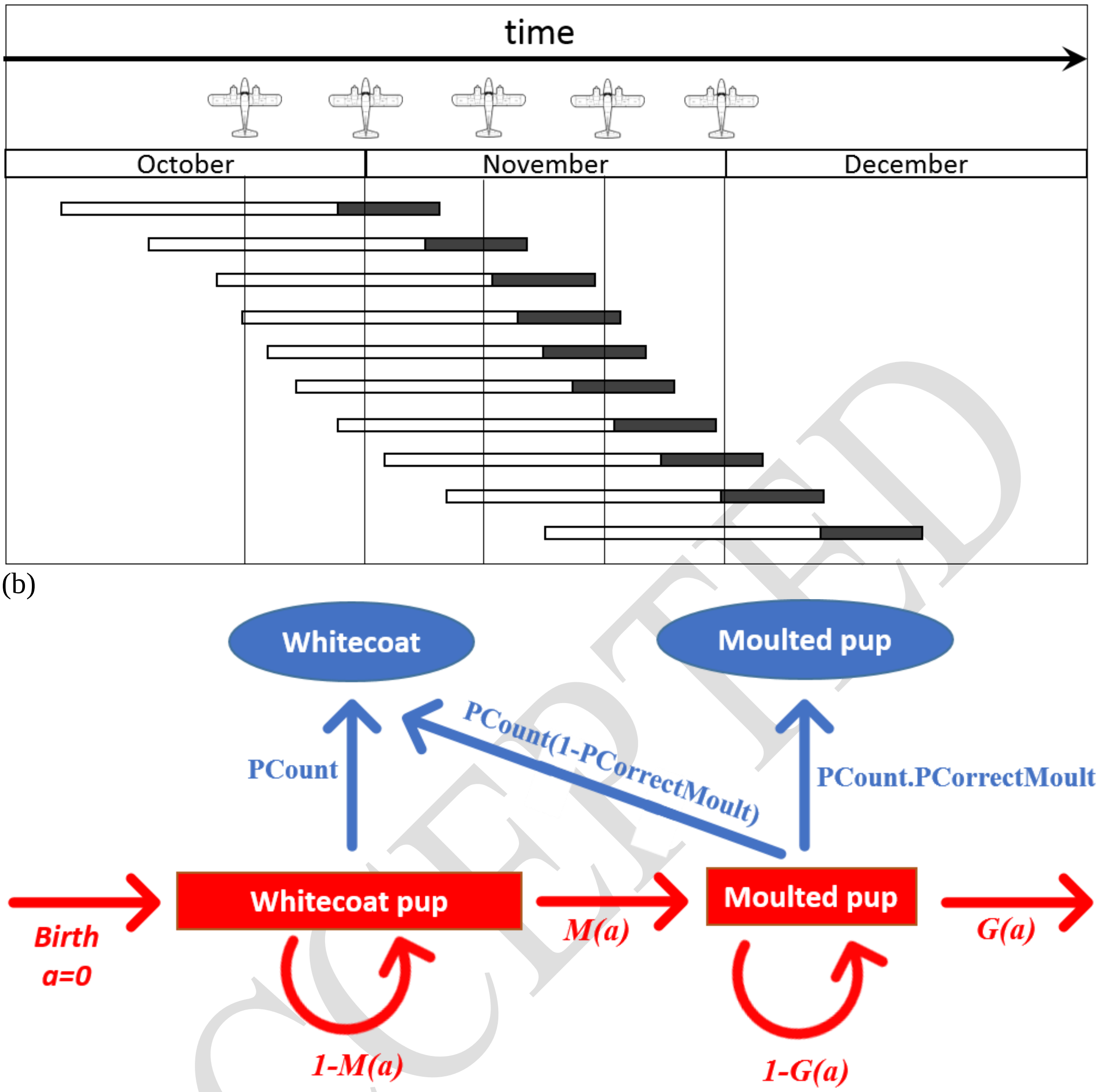

Figure 2. The relationship between the modelled process in which pups are born, moult and finally leave the colony and the observations. In (a) a hypothetical colony in which 10 pups (each horizontal bar) recruit into the whitecoat class (white fill), and then into the moulted class (grey fill) at 23 days (mean TTM), before finally leaving at 31.5 days (mean TTL). The plane symbols indicate when five aerial surveys would be conducted, none of which would capture all pups born. In (b) a graphic illustration of the process for a single pup is shown (red) given age, *a*, along with observation (blue ovals) from an air survey observation. The blue arrows show the relationship between the process and the observations.

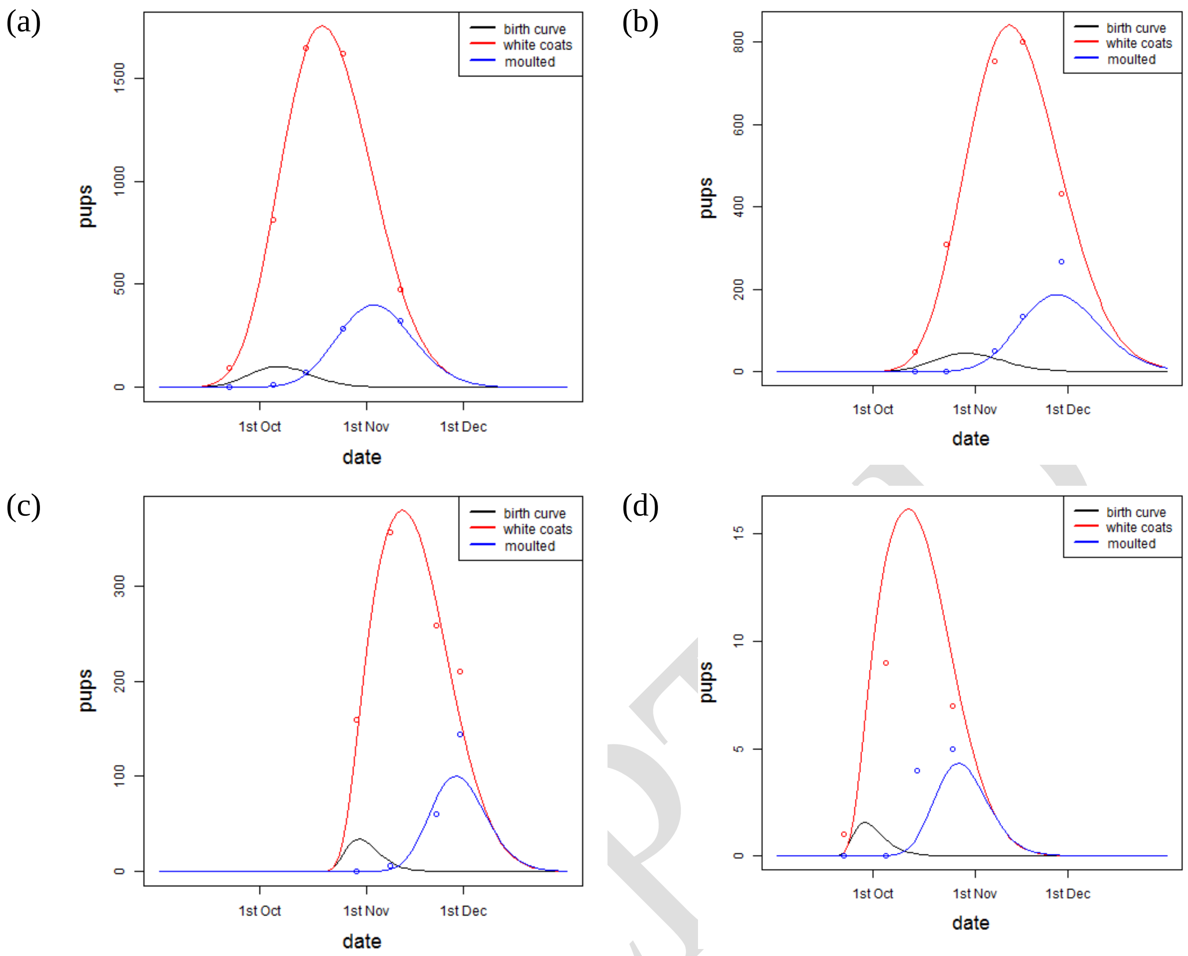

Figure 3. Examples of good (a) to poor model fits (d), with CVs of 0.012 (a), 0.035 (b), 0.092 (c), and 0.203 (d). Shown are the predicted curves of births/10, observed whitecoats and observed moulted pups, according to the pup production model. The observed numbers of whitecoats (red) and moulted pups (blue) are also shown.

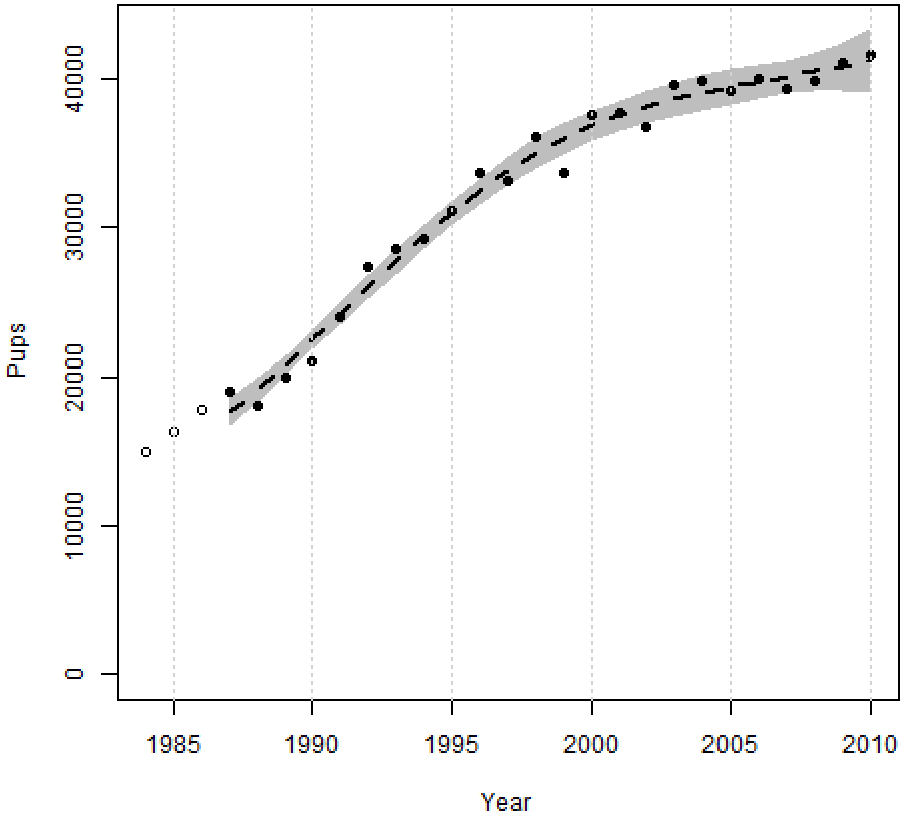

Figure 4. Estimated pup production of regularly monitored colonies (Figure 1). Estimates used to fit GAM are shown as filled dots. The shaded area indicates the 95% CIs around the trend. Estimates using different methodology than described in the paper are shown as open dots.

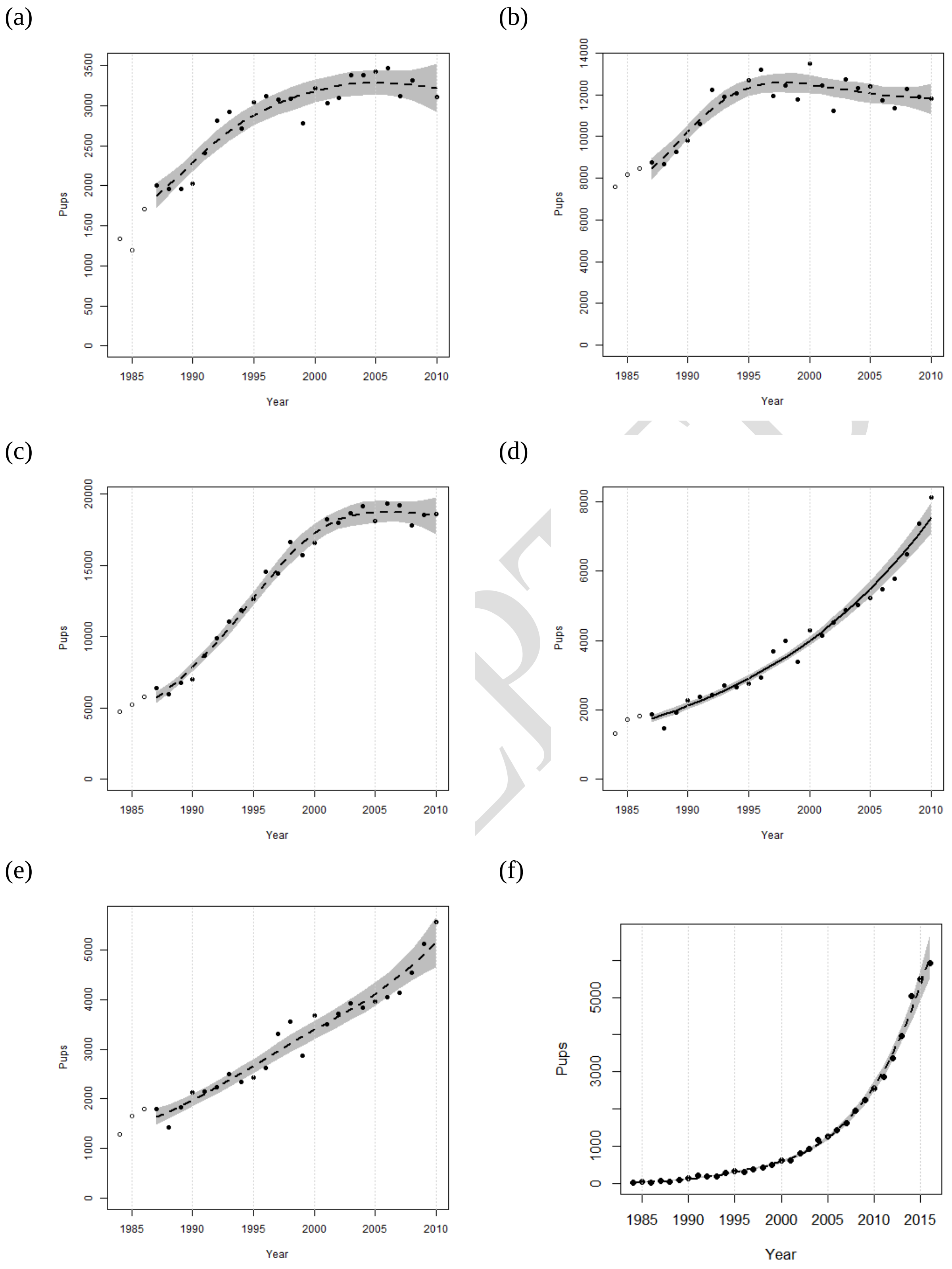

Figure 5. Estimated pup production of regularly monitored colonies in the Inner Hebrides (a), Outer Hebrides (b), Orkney (c), North Sea (d), North Sea – central (e), and North Sea- south (f). Trends are fitted using estimates (filled dots) up to 2010 (2016 for North Sea – south). Mean predictions are shown from the best fitting model (GLM: solid line, GAM: dashed line). The shaded areas indicate the 95% CIs around the trends. Estimates using different methodology than described in the paper are shown as open dots.

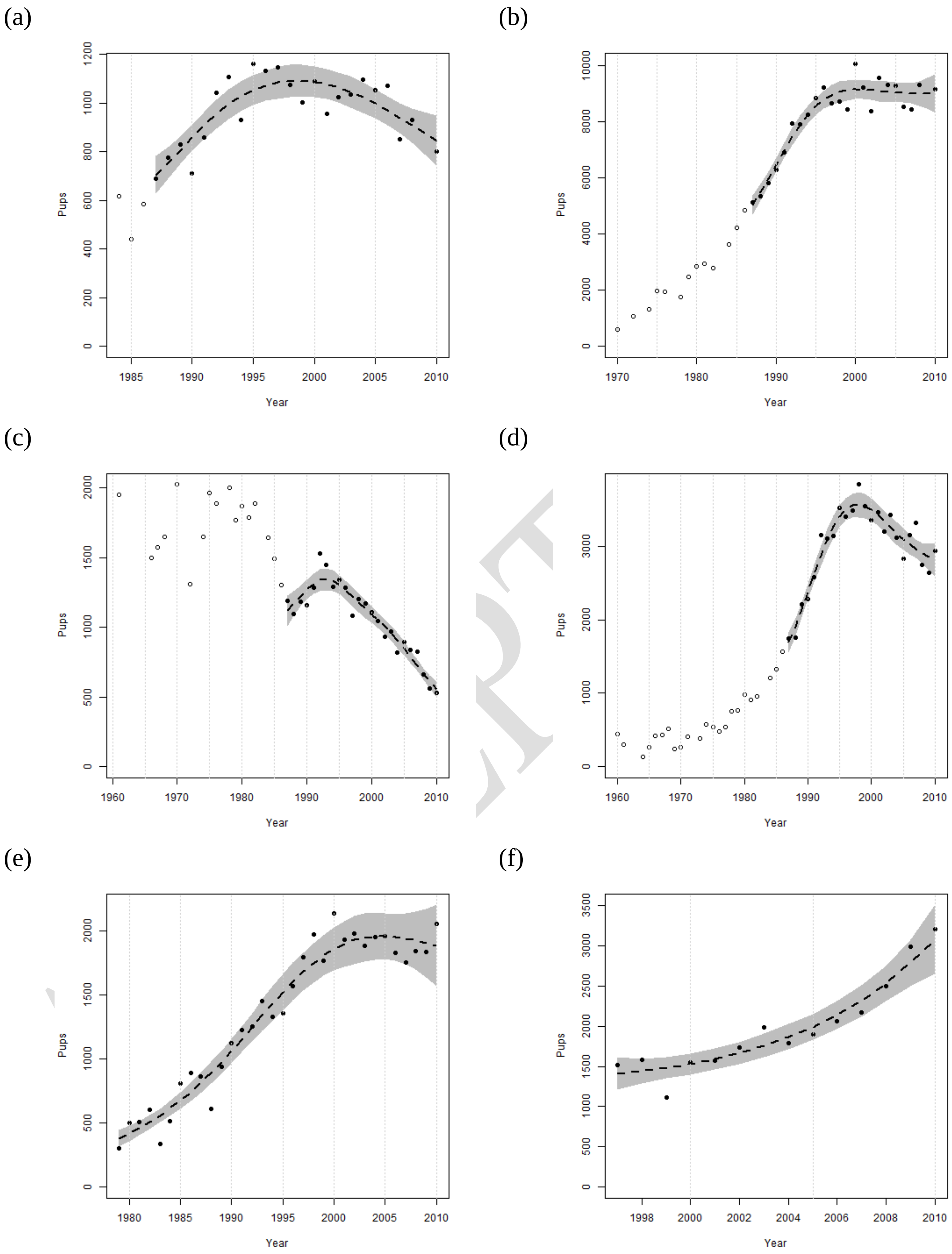

Figure 6. Estimated pup production at Special Areas of Conservation in the Inner Hebrides: Treshnish Isles SAC (a); Outer Hebrides: Monach Islands SAC (b), Rona SAC (c); Orkney: Faray & Holm of Faray SAC (d); North Sea– central: Isle of May SAC (e), Berwickshire & North Northumberland Coast SAC (f). Trends are fitted using estimates (filled dots) up to 2010. Mean predictions are shown from the best fitting model. The shaded areas indicate the 95% CIs around the trend. Estimates using different methodology than described in the paper are shown as open dots.