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Temporal trends and phenology in grey seal (*Halichoerus grypus*) pup counts at Skomer, Wales

James C Bull[1], Luca Börger[1], Novella Franconi[1], Roma Banga[1], Kate M Lock[2], Ceri W Morris[3], Philip B Newman[2], Thomas B Stringell[3]

1. Department of Biosciences, Swansea University, Swansea, SA2 8PP
2. Skomer Marine Conservation Zone, Natural Resources Wales, Fisherman's Cottage, Martins Haven, Haverfordwest, Pembrokeshire, SA62 3BJ
3. Natural Resources Wales, Maes y Ffynnon, Bangor, Gwynedd LL57 2DW

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Contents

1. Crynodeb Gweithredol

Mae'r morlo llwyd (*Halichoerus grypus*) wedi'i nodi yn Atodiad II o Gyfarwyddeb Cynefinoedd yr UE ac mae'n nodwedd gymwys o dair Ardal Cadwraeth Arbennig yng Nghymru. Mae gan gytrefi Sir Benfro'r boblogaeth fridio fwyaf yn ne-orllewin Prydain. Nod yr astudiaeth hon oedd darparu tystiolaeth ar statws niferoedd y morloi llwyd bychain o amgylch Ynys Skomer, Sir Benfro, ar sail dros 30 o flynyddoedd o ddata arolwg a gasglwyd rhwng 1983 a 2015.

Y prif amcanion oedd: 1) Meintoli'r twf diweddar yn y boblogaeth. 2) Dadansoddi amseru'r tymor esgor. 3) Darparu argymhellion ar gyfer dyfodol yr arolwg hwn.

1) Cynyddodd niferoedd y morloi bychain ar Ynys Skomer 8.9% y flwyddyn ar gyfartaledd rhwng 1983 a 1993. Mae hyn yn gyflymach na'r Penrhyn Marloes cyfagos (6.2%) ond o fewn yr amrediad ar gyfer morloi ledled y DU (3–15%). Wedi hyn, gwnaeth niferoedd y morloi bychain sefydlogi am ryw reswm neu'i gilydd, cyn y gwelwyd ail gyfnod o dwf yn y boblogaeth, cynnydd o 10.2% y flwyddyn, rhwng 2011 a 2015.

2) Mae morloi bychain yn dechrau cael eu geni ym mis Awst, ond gydag amrywiant amlwg tymhorol (oddeutu tair wythnos). Ymddengys fod hwn wedi dilyn patrwm cylchol, gan gychwyn ar ddechrau mis Awst o amgylch 1993, 2003 a 2013, ac yn hwyrach yn y blynyddoedd rhwng y rhain. Gwelwyd pwynt canol y tymor (pan fydd genedigaethau morloi bychain ar eu cyflymaf) yng nghanol mis Hydref ar ddechrau'r 1990au a dechrau'r 2010au, ond yng nghanol mis Medi ar ddechrau'r 2000au.

3) Cyflwynir cyfres o argymhellion, gan gynnwys parhau â'r arolwg o leiaf tan fydd nifer y morloi bychain yn sefydlogi, ymchwilio i'r sbardunau amgylcheddol sy'n ennyn llwyddiant o ran esgor morloi bychain, a chyfuno data Skomer gyda data eraill ar forloi yng Nghymru er mwyn llywio cynllunio gofodol morol.

2. Executive Summary

The grey seal (*Halichoerus grypus*) is listed in Annex II of the EU Habitats Directive and is a qualifying feature of three Special Areas of Conservation in Wales. Pembrokeshire colonies represent the largest breeding population in southwest Britain. The aim of this study was to provide evidence on the status of grey seal pup numbers around the Island of Skomer, Pembrokeshire, based on over 30 years of survey data collected from 1983-2015.

Key objectives were: 1) Quantify recent population growth. 2) Analyze the timing of the pupping season. 3) Provide recommendations for the future of this survey.

1) Skomer pup counts increased by an average of 8.9% per year from 1983 – 1993. This is faster than the adjacent Marloes peninsula (6.2%) but within the range for seals around the UK (3 – 15%). After this, pup numbers stabilized for unknown reasons, before a second population growth phase of 10.2% per year was observed from 2011 – 2015.

2) Pupping starts in August but with marked temporal variation (c. 3 weeks). This appears to have followed a cyclical pattern, starting at the beginning of August around 1993, 2003, and 2013, and later in the intervening years. The midpoint of the season (where pup accumulation is fastest) occurred in mid-October in the early 1990s and early 2010s but in mid-September in the early 2000s.

3) A series of recommendations are presented, including continuation of the survey at least until pup counts stabilize, investigation of environmental drivers of pupping success, and combining Skomer data with other Welsh seal data to inform marine spatial planning.

3. Introduction

3.1. Grey seal population status

Quantifying the abundance and distribution of a species is fundamental to understanding its population dynamics, as well as predicting likely responses to future change; this is particularly important for species of conservation concern, such as marine mammals. The grey seal (*Halichoerus grypus*) of the northeast Atlantic and Baltic Sea is a species listed in Annex II of the EU Habitats Directive (Council Directive 92/43EEC). Consequently, considerable local, national and international efforts have been made to assess the status of grey seal populations across Europe.

In Wales, grey seals are qualifying features of three SACs (Figure 1): Pembrokeshire Marine / Sir Benfro Forol SAC in the southwest, Cardigan Bay / Bae Ceredigion SAC in the west and Lleyn Peninsula and the Sarns / Pen Llŷn a'r Sarnau SAC in the north. One of the responsibilities of Natural Resources Wales (NRW) is to monitor the number of grey seal pups born in these SACs (Stringell *et al*., 2014).

Seal numbers can be hard to quantify, due to their elusive and highly mobile nature. In terms of overall population size, it has recently been estimated that 44% of the global total is resident in the UK, based on an extrapolation from pup production (57,000 out of 129,000. Table 3 of SCOS, 2015). 88% of the UK population breed at large colonies in Scotland (SCOS, 2015). Of the remainder, around 4% breed in Wales, where most are found in Pembrokeshire (Duck, 2009). The Pembrokeshire colonies represent the largest breeding population in southwest Britain and the Irish Sea (Baines *et al*., 1995; Strong *et al*., 2006; Duck & Thompson, 2007).

3.2. Grey seal phenology

Phenology is the investigation of annual life cycle events, such as breeding and migration (Edwards & Richardson, 2004). The study of phenology can provide sensitive indicators of the effects of climate change (from global warming; or regionally, e.g., the El Niño / La Niña cycle; or more locally, e.g., The North Atlantic Oscillation) on ecosystem status and function (Hughes, 2000). In particular, mismatches in seasonal events, for example between predator and prey populations or flowering plants and their pollinators, can decouple biological communities and lead to critical transitions in population structure, biological regime shifts and even collapse of ecosystem services (Kudo & Ida, 2013; Conversi *et al*., 2015; Stevenson *et al*., 2015).

Marine mammal phenology has been cited as evidence of a major system shift in the Indian Ocean and parts of the Southern Ocean (Weimerskirch *et al*., 2003) and climate-driven changes in seasonal timing are predicted to have substantial negative effects on marine mammal populations themselves (Learmonth *et al*., 2006). There are now observable changes in the timing of seal life history in the northeast Atlantic (Osinga *et al*., 2012). This makes it vitally important that the UK continues to develop a robust evidence-base for grey seal population status, remaining vigilant for early warning signs of changes in life history timing.

3.3. Aims and objectives

The aim of this study was to provide evidence on the status of grey seal pup numbers around the island of Skomer, Pembrokeshire, based on intensive survey data collected by Wildlife Trust South and West Wales (and its precursors) from 1983-2015 and under contract since 1990 to Natural Resources Wales (and its precursor agency, Countryside Council for Wales).

The following objectives were explored:

1. Quantify temporal trends from thirty-three years of annual pup surveys, highlighting the shape of population growth and provide an estimate of the annual rate of change where consistent year-on-year increases were evident.

2. Develop a model to provide robust estimates of the length of the pupping season, that is relatively insensitive to chance events at the tails of the season. Analyse changes in the start date, as well as estimated mid-point and length, of the pupping season through the years (phenology).

3. Relate findings to equivalent population growth rate estimates from around the UK, providing recommendations for the future of this survey.

4. Methods

4.1. Study site

The Island of Skomer forms a component of the Skomer Marine Conservation Zone (SMCZ) area in Pembrokeshire, south Wales (51° 43′ 55.2″ N, 5° 16′ 33.6″ W) (Figure 1). Adult female grey seals haul out on sheltered beaches or in caves throughout this area to give birth and nurse pups until weaning.

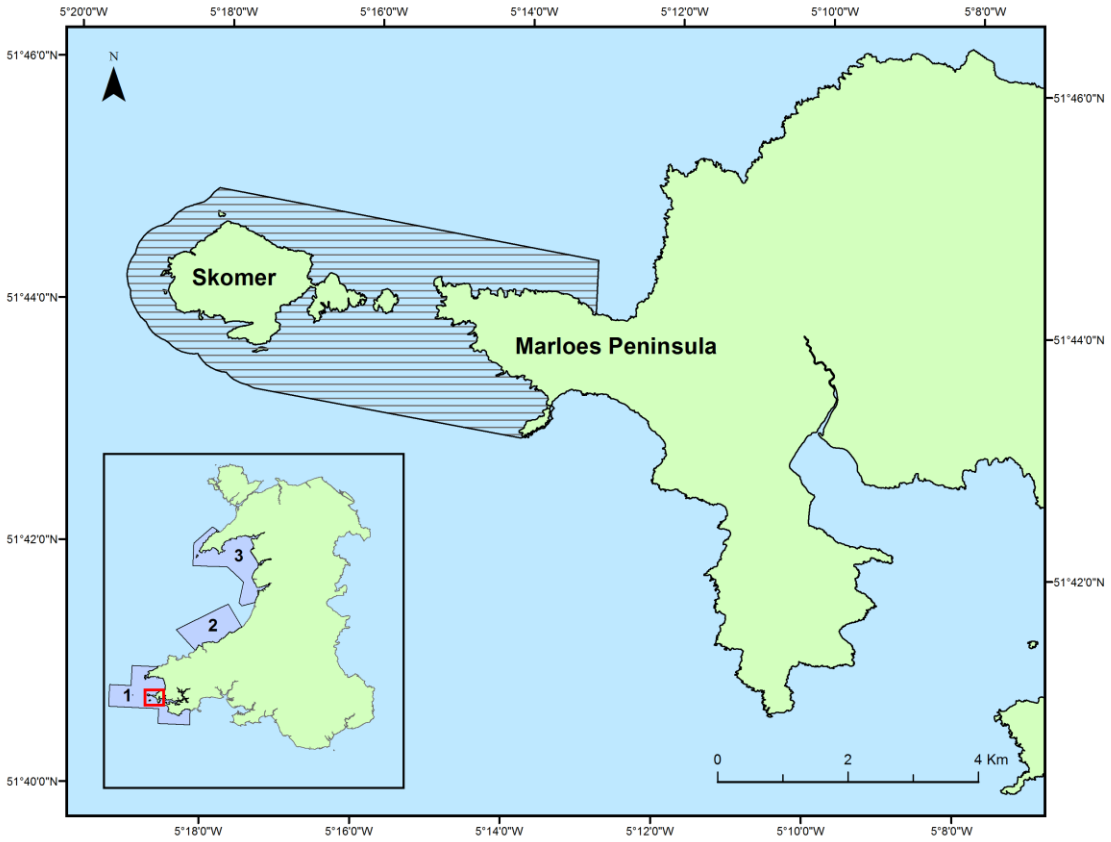

Figure 1. Marloes peninsula and Skomer Island within the Skomer Marine Conservation Zone (hatched area), Southwest Pembrokeshire, Wales. Inset shows extent rectangle (red) for main map and Pembrokeshire Marine / Sir Benfro Forol (1), Cardigan Bay / Bae Ceredigion (2) and Lleyn Peninsula and the Sarns / Pen Llŷn a'r Sarnau (3) Special Areas of Conservation.

4.2. Data collection and processing

Each year trained staff carried out a survey of all the main grey seal pupping sites on Skomer Island. The beach sites were checked every 1-2 days from the cliff tops. Beaches with difficult access were visited when females were observed in the area. Cave sites were accessed whenever conditions allowed (based on weather, tides, adult seal activity); they were not entered if a cow remained inside with her pup, avoiding disturbance.

Individual records were kept of each pup's progress from birth to moult following a standardized protocol (e.g., Büche & Stubbings, 2015). Details included a unique numerical pup identifier, the location (beach name) and date of first observation, and the developmental stage (1-5) of the pup (Smith, 1966). A

qualitative assessment was made of the body condition of each pup when last seen, classified on a five point scale:

1. Very small: Assumed not to survive long after moult.
2. Small but healthy: In good condition; reasonable chance of survival.
3. Good size: Most should survive.
4. Very good size: All should survive.
5. Super moulter: An exceptional sized pup.

Sites were visited once a week and pups marked with a unique pattern (using coloured aerosol sheep fleece marker sprays) to help monitor each individual.

Records were maintained in field note books and transferred to recording sheets and spreadsheets (see Data Archive). Annual reports have been produced each year, from which the data in this study have been collated (e.g., Büche & Stubbings, 2015). These are available from NRW on request.

4.3. Statistical analysis

Spatially aggregated (annual totals for the whole island of Skomer) counts of pup numbers were analyzed in this report (Appendix 1). Trends in population abundance were quantified by fitting a Generalized Additive Model (GAM) to the time series of annual pup counts (Crawley, 2012). This approach indicated that the time series could be usefully separated into phases where consistent population growth was evident over a number of years, and a phase where no net population growth was evident. This splitting of the time series was subjective but shifting the split by +/-1 year made little difference to overall findings.

During the phases where consistent population growth was evident, we estimated average annual population growth by fitting a log-linear regression model to these data. The 'gradient' parameter estimated by these models, on a log-scale, provides a measure of this average annual growth, here expressed as a percentage. Over these growth phases, we did not quantify temporal autocorrelation, as it is more biologically informative to do this where no net growth is evident (cf. Bull *et al*., 2017, where only exponential growth was observed) (see below).

During the phase where pup counts showed no net change over a series of years (here, 1993 – 2011), we assessed evidence of temporal correlation using autocorrelation (ACF) and partial autocorrelation (Partial ACF) functions. In particular, a statistically significant negative correlation between one year and its previous year ('Lag 1', assessed by Partial ACF to remove the effects of serial correlation through the years) is regarded as preliminary evidence of population regulation around the environment's carrying capacity (Dennis & Taper, 1994) – i.e. equilibrium. While this test is relatively weak and open to alternative interpretation, where no negative lag 1 autocorrelation is evident, there is little justification to pursue alternative statistical inference methods.

From 1992 onwards (1992 – 2015), detailed within-season pup records are available from NRW (Büche & Stubbings, 2015, and references to earlier reports therein). These allowed us to analyse the cumulative increase in pup counts throughout the pupping season for each year and any phenological changes in these distributions. We analysed three measures of the pupping season: the date of the first pup observed, the mid-point of the season, and the length of the season. The first measure was taken from the empirical data. However, since the end of the observing season was dictated more by logistical constraints than the date of the last pup around Skomer, we developed a model to estimate both the mid-point and length of the pupping season that was insensitive to random fluctuations in the tails of the season.

Since empirical cumulative counts of pups were seen to closely follow a sigmoid shape each year (Appendix 2), we fitted three parameter logistic curves to cumulative pup counts, separately for each year, using non-linear mixed-effects models with 'year' as a random variable (Pinheiro & Bates, 2006). The three parameters that describe these curves are: the asymptotic maximum number of pups, the 'point of inflection' of the fitted sigmoid curve, and a 'scale parameter'. The point of inflection provides a robust estimate of the mid-point of the season (the date where 50% of pups have been counted). The scale parameter provides a measure of the length of the pupping season, where six times the scale parameter is a robust estimate of the length of time for the central 95% of the counted pups to accrue (Börger, 2011).

Subsequently, GAMS were used to test whether the pupping season start, mid-point and length had changed over time during the period 1992 – 2015.

All statistical analysis was undertaken using R v3.2.1 (R Core Team, 2015). GAMS were fitted using the 'gam' function in the 'mgcv' package. Non-linear models were fitted using the 'nlme' function in the 'nlme' package. Other analyses used base functions within R.

5. Results and discussion

5.1. Population abundance trends

Annual pup counts around the island of Skomer showed marked variation in temporal trends throughout the years assessed (Figure 2, Appendix 1). Pup counts were increasing at an average rate of 8.9% (S.E. = 1.2%, $t = 6.9$, $p < 0.01$) per year from 1983 (73 pups) to 1993 (178 pups). For the purposes of this study, we define 1983 – 1993 as the 'early population growth phase'. After this, pup counts appeared to show no net change (1993 – 2011, $t = 1.6$, $p = 0.13$), which we define here as the 'no net population growth phase'. In the final years of the current study there has been another marked increase in pup counts, averaging 10.2% (S.E. = 1.5%, $t = 6.6$, $p < 0.01$) per year from 2011 (157 pups) to 2015 (240 pups), which we define here as the 'recent population growth phase'.

The two 'population growth phases' we identified in this study were slightly faster than annual increases elsewhere in the Skomer Marine Conservation Zone, with pup counts on the adjacent Marloes peninsula showing a consistent annual

increase of 6.2% from 1992 – 2013 (Bull *et al*., 2017). Skomer increases are also faster than estimated population growth around the UK of 6-7% through the 1960s and 1970s (Summer, 1978). However, they are comparable to more recent estimates around Orkney and the Hebrides of 6-10% per year between 2010 and 2012 (SCOS, 2015). Elsewhere around the UK, grey seals have been increasing in recent years, with annual population growth rates of between 3% and 15% reported, although there is evidence that many Scottish colonies in particular are now stabilizing (Table 2 of SCOS, 2015).

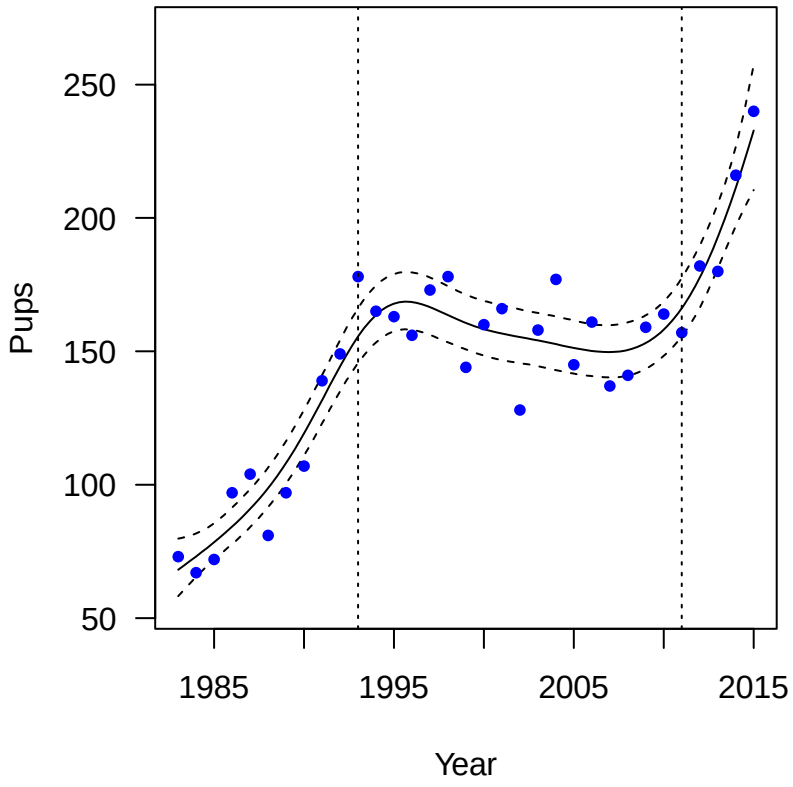

Figure 2. Time series of annual pup counts from the island of Skomer (blue dots). Solid line shows fitted trend line. Dashed lines show 95% confidence intervals of the fit. Vertical dotted lines divide the time series into three phases: early population growth (1983 – 1993), no net population growth (1993 – 2011), and recent population growth (2011, 2015).

We quantified temporal autocorrelation during the 'no net population growth' phase (1993 – 2011) using autocorrelation functions (ACF) and partial autocorrelation functions (Partial ACF). The latter in particular is used as an initial test for density dependence operating in population abundance time series. It is notoriously difficult to infer underlying processes and mechanisms from statistical patterns (since more than one process might result in the same pattern). However, a significant negative partial autocorrelation at 'lag 1' is predicted to be seen in populations that are in equilibrium, at a level set by the carrying capacity of the environment for that species (Dennis & Taper, 1994). Here, we found no statistically significant time-lagged correlations (Figure 3). This statistical probe showed no evidence that the grey seal population had

reached a level determined by the carrying capacity during the period 1993 – 2011.

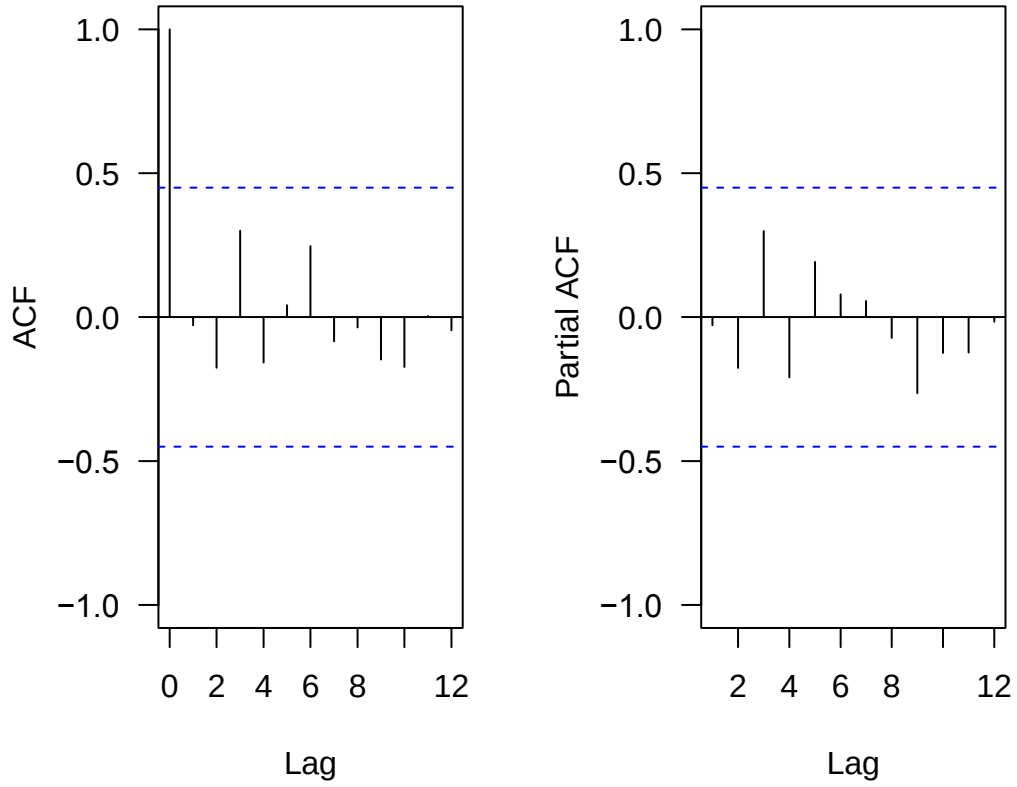

Figure 3. Temporal autocorrelation analysis of annual pup count time series for the 'no net population growth' phase (1993 – 2011) around the Island of Skomer. Left panel shows autocorrelations (ACF). Right panel shows partial autocorrelations (Partial ACF). Dashed blue lines indicate significance at the 0.05 level. No time-lagged correlations are statistically significant.

5.2. Phenology

The pupping season began in the month of August throughout the study period, 1992 – 2015, but with marked variation through the years (Figure 4, Appendix 1). The drivers of this variation are unknown and a planned analysis of local and regional climatic drivers is beyond the scope of the current study.

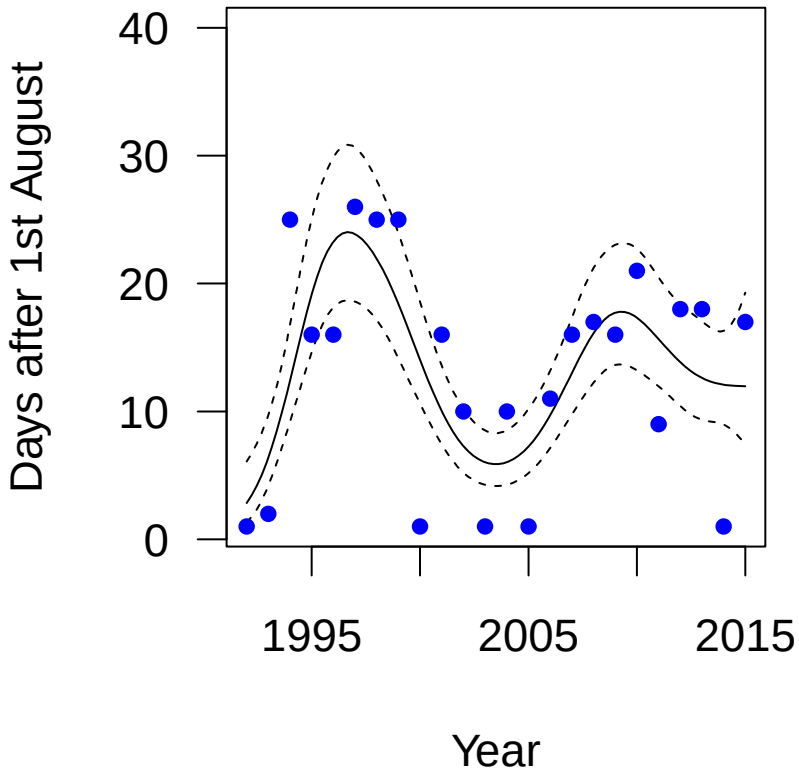

Figure 4. Phenological trends in the start of the grey seal pupping season (first pup observed) from the island of Skomer, 1992 – 2015. Blue dots show data points. Solid line shows fitted trend line. Dashed lines show 95% confidence intervals.

In addition to quantifying changes in the start of the pupping season, we also analyzed changes to the mid-point and length of the pupping season around the island of Skomer from 1992 – 2015 (Figures 5 & 6, Appendix 3). Estimates of both these quantities were derived from three parameter logistic models fitted to the data, to reduce the influence of uncertainties in the tails of the season. Both the estimated mid-point and length of the season showed substantial variation (mid-point SD = 7.3 days, season length SD = 14.8 days) but no consistent trend was identified.

The causes of the change in the timing of the mid-point and length of the season are unknown but further analysis relating this to local, regional and global climatic indicators is planned and beyond the scope of this report. The observation that the season is not getting consistently longer, while pup counts have approximately tripled over thirty years, suggests that there is little capacity for behavioural changes in the timing of pupping (spreading across a longer season) in response to greater competition brought about through population

growth. Interestingly, we see substantially different phenological changes at Skomer, compared to the neighbouring Marloes Peninsula seals (Bull *et al*., 2017). These two areas are adjacent and only separated by a narrow strait, which is easily crossed by seals (Figure 1). The reasons for the differences are currently unknown but these findings emphasise the importance of selecting a spatial scale for monitoring, analysis, and management that is relevant to the biology of the focal species or ecosystem. There is also a need to develop approaches such as tagging and photo ID to understand movement patterns between these, and other, seal pupping sites.

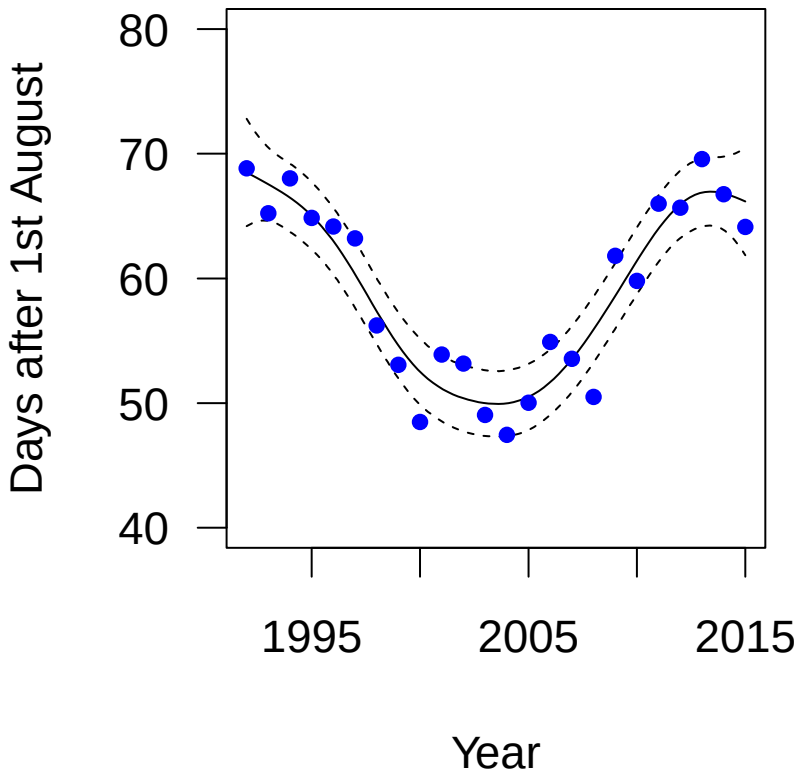

Figure 5. Phenological trends in the mid-point of the grey seal pupping season from the island of Skomer, 1992 – 2015. Blue dots show data points. Solid line shows fitted trend line. Dashed lines show 95% confidence intervals.

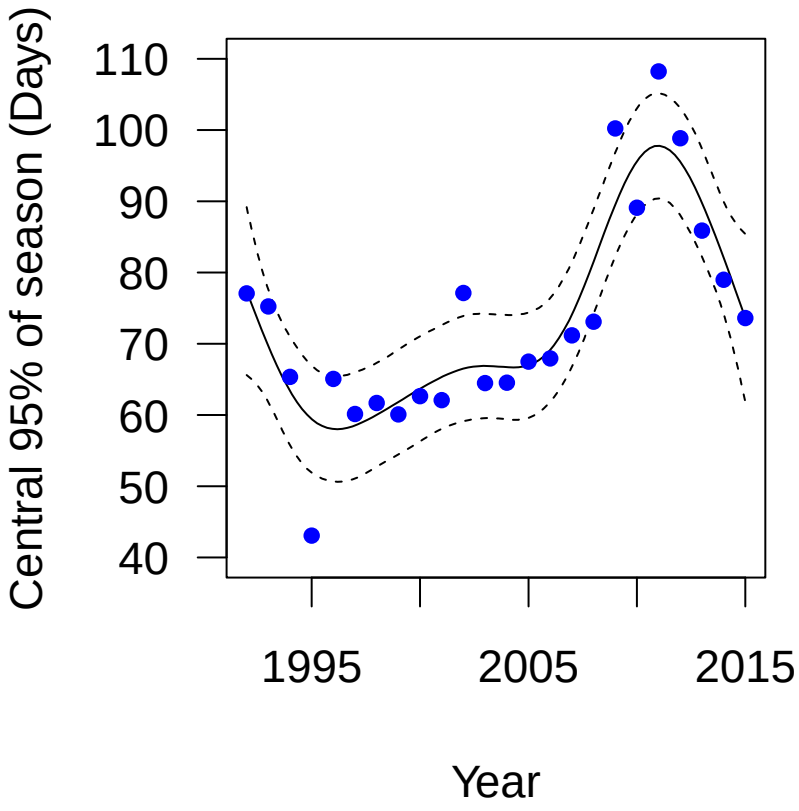

Figure 6. Phenological trends in the length of the grey seal pupping season from the island of Skomer, 1992 – 2015. Blue dots show data points. Solid line shows fitted trend line. Dashed lines show 95% confidence intervals.

6. Conclusions and recommendations

The island of Skomer, Pembrokeshire, is one of the most intensively surveyed grey seal breeding sites in Wales. Moreover, the consistency of methodology and effort, combined with the continuity of monitoring over many years, makes this area an internationally important study site. This dataset has captured the rapid expansion of a population. Following an annual increase of 8.9%, it appeared that this population growth rate slowed and it might be assumed that the area had reached its carrying capacity. A deceleration in population growth has been observed elsewhere in the UK, particularly Scotland (SCOS, 2015). However, there is no evidence that the period of no net population growth was underpinned by density regulation, so observations are inconsistent with the hypothesis that carrying capacity was limiting further growth around Skomer. Furthermore, in the last four years of the dataset, there has been a rapid increase in pup counts (10.2% per year), at a rate similar to the fastest expansions seen elsewhere in the UK (Table 2 of SCOS, 2015). As the local grey seal population grows, its ecological importance will also increase, making it essential to consider these changes in any management strategy. In order to move from quantifying observed patterns to understanding ecological processes, with a view to informing evidence-based management, it is crucially important to:

- Relate pup counts to appropriate environmental (e.g., climatic) factors, to identify abiotic drivers. This analysis is on-going, as a collaborative project between NRW and Swansea University.

- Continue current seal pup monitoring at least until the Skomer population reaches a stable equilibrium level, to quantify intrinsic biotic drivers (e.g., density dependence underpinned by intraspecific competition). The rate at which population growth approaches equilibrium is a key component in the construction of a predictive framework for population dynamics.

- Combine pup data from the island of Skomer with equivalent data from other major grey seal breeding colonies in Wales (e.g., Marloes peninsula and Ramsey in Pembrokeshire, as well as other breeding colonies in North Wales, such as Bardsey). This analysis is on-going, as a collaborative project between NRW and Swansea University.

- Integrate pup counts within a wider programme of adult seal censuses, to develop a full understanding of grey seal life history and local population viability.

- Develop techniques (e.g., using photo ID and tagging) to quantify movement between seal colonies, to assess spatial population turnover and regional population viability (metapopulation dynamics).

Encouragingly, many of these elements are already in place around Wales, thanks to long-term ecological monitoring carried out by NRW (and its predecessors) and collaborators. This study improves the understanding of this iconic species, which underpins NRW's evidence-based advice.

7. Acknowledgements

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Many others helped collect data over the years and are acknowledged in the annual Skomer seal reports, eg see Büche & Stubbings (2015) for recent example.

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9. Appendices

9.1. Appendix 1. Summary data used in this report.

Table A1. Total grey seal pup count from the island of Skomer, 1983 – 2015.

Year	Count	Year	Count	Year	Count
1983	73	1994	165	2005	145
1984	67	1995	163	2006	161
1985	72	1996	156	2007	137
1986	97	1997	173	2008	141
1987	104	1998	178	2009	159
1988	81	1999	144	2010	164
1989	97	2000	160	2011	157
1990	107	2001	166	2012	182
1991	139	2002	128	2013	180
1992	149	2003	158	2014	216
1993	178	2004	177	2015	240

Table A2. Date of first grey seal pup sighting from the island of Skomer, 1992 – 2015.

Year	Date	Year	Date	Year	Date
1992	01-Aug	2000	01-Aug	2008	17-Aug
1993	02-Aug	2001	16-Aug	2009	16-Aug
1994	25-Aug	2002	10-Aug	2010	21-Aug
1995	16-Aug	2003	01-Aug	2011	09-Aug
1996	16-Aug	2004	10-Aug	2012	18-Aug
1997	26-Aug	2005	01-Aug	2013	18-Aug
1998	25-Aug	2006	11-Aug	2014	01-Aug
1999	25-Aug	2007	16-Aug	2015	17-Aug

9.2. Appendix 2. Cumulative grey seal pup counts.

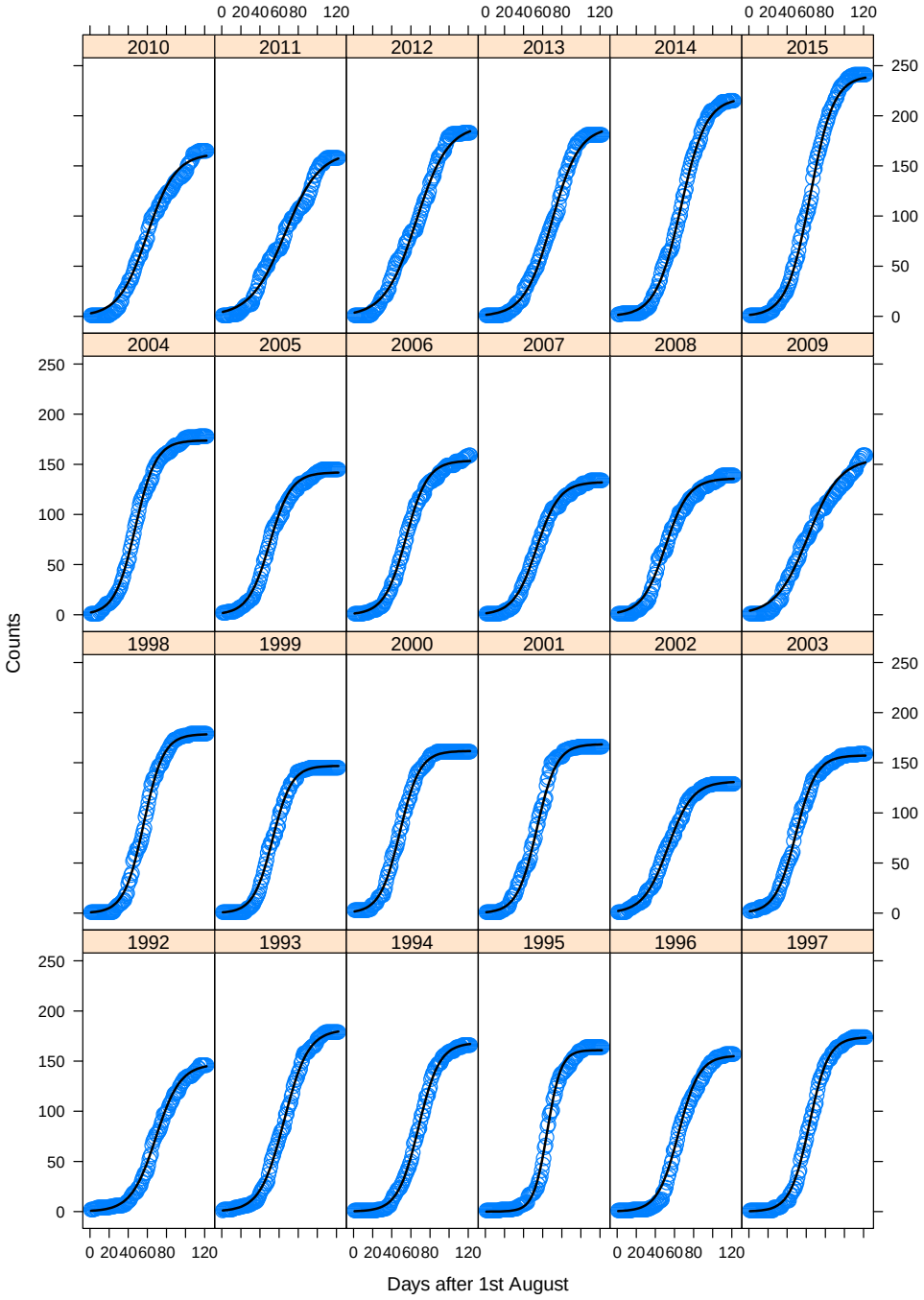

Figure A1. Cumulative grey seal pup counts. Blue circles show raw data (available from NRW), black lines show fitted three parameter logistic curves.

9.3. Appendix 3. Estimated grey seal season parameters (three parameter logistic fit).

Table A3. Estimated date of the grey seal pupping season mid-point from the island of Skomer, 1992 – 2015 (shown as days after 1st August to nearest integer).

Year	Date	Year	Date	Year	Date
1992	69	2000	48	2008	50
1993	65	2001	54	2009	62
1994	68	2002	53	2010	60
1995	65	2003	49	2011	66
1996	64	2004	47	2012	66
1997	63	2005	50	2013	70
1998	56	2006	55	2014	68
1999	53	2007	54	2015	64

Table A4. Estimated length of the grey seal pupping season at the Marloes peninsula (number of days to the nearest integer when the central 95% of pups were counted).

Year	Days	Year	Days	Year	Days
1992	77	2000	63	2008	73
1993	75	2001	62	2009	100
1994	65	2002	77	2010	89
1995	43	2003	64	2011	108
1996	65	2004	65	2012	99
1997	60	2005	67	2013	86
1998	61	2006	68	2014	79
1999	60	2007	71	2015	74

10. Data Archive Appendix

Data outputs associated with this project are archived at Project 478, media 1555 on server–based storage at Natural Resources Wales.

The data archive contains:

The final report in Microsoft Word and Adobe PDF formats.

A spreadsheet named Data_Skomer.xls with metadata described in a file called Data_Skomer_Notes.xls.

A spreadsheet named Skomer_daily_births.csv

An R software statistical analysis script named skomer analysis.R

Metadata for this project is publicly accessible through Natural Resources Wales' Library Catalogue http://libcat.naturalresources.wales/webview/ (English Version) and http://libcat.naturalresources.wales/cnc/ (Welsh Version) by searching 'Dataset Titles'. The metadata is held as record no 119129

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