The status of harbour seals (*Phoca vitulina*) in the United Kingdom

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ABSTRACT

1. Estimates of population size and trends are essential for effective conservation and management of wildlife populations. For harbour seals (*Phoca vitulina*), these data are required to fulfil statutory reporting obligations under national and international regulations.
2. Aerial survey counts of harbour seals hauled-out during their annual moult were used to estimate population sizes and trends at UK, regional (Seal Management Unit; SMU) and local (Special Area of Conservation; SAC) scales.
3. Results indicate that the current UK harbour seal population is similar to estimates from the late 1990s, but there were significant declines in some sub-populations and increases in others.
4. Fitted trends suggest that the UK harbour seal population can be divided into three geographically coherent groups: Southeast populations (Southeast and Northeast England SMUs) have shown continuous increases punctuated by Phocine Distemper Virus (PDV) epidemics in 1988 and 2002; Northeast populations (East Scotland, Moray Firth, North Coast & Orkney, and Shetland SMUs) have declined since the late 1990s; Northwest populations (West Scotland, Western Isles, and Southwest Scotland SMUs) have remained stable or increased. Similar geographical population substructure is evident in recent population genetics results.
5. Trends within SACs generally match SMU trends since 2002. Of the nine SACs designated for harbour seals, four declined (in East Scotland, Moray Firth and North coast & Orkney SMUs), four remained stable (in Shetland and West Scotland SMUs), and one increased (in Southeast England SMU).
6. Large changes in relative abundance have resulted from differences in regional trends: e.g. in 1996-1997 the West Scotland and North coast & Orkney SMUs each held c.27% of the GB population but now hold c.50% and c.4% respectively; in 1980, the Southeast England SMU population was c50% that of the Wadden Sea population but by 2016 was equivalent to <20% of the Wadden Sea count.

1. **INTRODUCTION**

Marine predators have been proposed as potential indicators of environmental health (Boyd, Wanless, & Camphuysen, 2006), but their utility has been limited by lack of population data and information on the drivers of changes in abundance at suitable temporal and spatial scales. The wide distribution and the existence of almost range wide monitoring programmes for harbour seals (Bjorge, Desportes, Waring, & Rosing-Asvid, 2010) means that the status of their populations could provide useful comparative indicators of environmental status. Indeed, within Europe, harbour seals have been selected as a key indicator species under the Marine Strategy Framework Directive and a series of ecological quality indicators (EcoQOs) have been defined based on the status of harbour seal populations within management regions in the member states (OSPAR, 2005).

Harbour seals (*Phoca vitulina*) are widely distributed marine predators, occurring in temperate and sub-polar seas throughout the northern hemisphere. Throughout their range, regularly monitored populations of harbour seals have shown widely contrasting trends. For example in the Pacific sub-species (P.v. richardii), depleted populations in California, Oregon and Washington increased and appear to have reached carrying capacity sometime in the early 1990s while in Alaska, the 12 identified stocks (O'Corry-Crowe, Martien, & Taylor, 2003) have variously experienced rapid increases, rapid declines or stable populations (Muto et al., 2018). The eastern North Atlantic subspecies (P.v.vitulina), that includes the UK populations, has also shown widely contrasting regional dynamics since the 1970s; populations in the southern North Sea have shown rapid, continuous growth (punctuated by two discrete disease events that caused 50% reductions in 1988 and 2202) (Galatius et al., 2017), while over the same period, populations in Iceland have declined continuously (Þorbjörnsson, Hauksson, Sigurðsson, & Granquist, 2017)

The conservation legislation and management regimes relevant to harbour seals operate at various spatial and temporal scales. Harbour seals are listed in Annex II of the EU Habitats Directive (Council of the European Communities, 1992), which requires that specific areas in Member States be designated as Special Areas of Conservation (SACs) to help maintain populations in a favourable conservation status. In the UK, harbour seals were the primary feature of designation for nine SACs, and a qualifying feature for a further three. The six-yearly SAC reporting cycle requires formal status assessments for these sites, with the next review due in 2019. At present, all SACs designated for seals are based on terrestrial haulout sites, so population estimates and information on trends of harbour seals at those haulout sites is a minimum requirement for the SAC assessments.

In the UK, harbour seals are also protected by the Conservation of Seals Act 1970 in England and Wales, the Marine (Scotland) Act 2010 and The Wildlife (Northern Ireland) Order 1985. For management purposes, the UK harbour seal population is subdivided into Seal Management Units (SMUs) (sometimes referred to as Seal Management Areas in Scotland) (Figure 1) that were defined on the basis of the spatial distribution of haulout sites; e.g. existence of clear separations between groups of haulout sites and/or pragmatic factors such as ability to conduct synoptic surveys within a single survey window and recognition of national boundaries to simplify reporting to various stakeholder.

The Conservation of Seals Act allows the taking of seals in England and Wales except during a defined, closed period over the breeding season, but does allow seals to be shot for protection of fishing operations at any time under the so-called netsman's defence (Gov.UK, 2015). In Scotland, seals may only be taken under a licence issued for a specific reason, usually for protection of fisheries or aquaculture operations (Scottish Government, 2018). The Conservation of Seals Act and The Marine (Scotland) Act allow for specific Conservation Orders to ban any takes of seals in specific management units in order to protect vulnerable populations. Such orders were established after the 1988 and 2002 Phocine Distemper Virus (PDV) epidemics (SCOS, 2017), which caused a dramatic reduction in the populations in the Southern North Sea, Baltic Sea and Wadden Sea (Härkönen et al., 2006).

Three such orders were established after the 2002 PDV epidemic (SCOS, 2017), providing year round protection to harbour seals along the east coasts of England and Scotland and throughout the Outer Hebrides, Shetland and Orkney. In Scotland, the conservation orders were superseded by the designation of seal conservation areas under the provisions of the Marine (Scotland) Act 2010; these areas provide the same effective protection and cover the same sections of coast. The conservation orders are under annual review (SCOS, 2017) and assessing the effectiveness and continuing requirement for these conservation actions again requires reliable and regular estimates of population status.

In addition to providing supporting information for these statutory management requirements, there are often additional requirements for population census data to support management of specific interactions between seals and human activities. For example, many countries have set ambitious targets for marine renewable energy generation, in response to demands for low carbon energy generation. In Scotland in particular, this has led to proposals to install tidal stream energy converters (tidal turbines) in tidally energetic inshore sites (Callaghan, 2010; Lewis et al., 2011) that are frequented by harbour seals. Concerns over potential lethal collisions between seals and the moving parts of tidal turbines means that the potential population level consequences of resulting mortalities have to be considered when permitting tidal energy developments. The fact that these developments are likely to occur in areas with recorded population declines (Lonergan et al., 2007) means that detailed, accurate and up to date information on population size and status is required at spatial scales of relevance to managing impacts of localised developments/disturbances.

Although many of the potential threats to populations occur at sea, seals are notoriously difficult to see and count in the water. Harbour seals do, however, haul out on land for a significant proportion of their time, meaning that a proportion of the population is then available to count. The wide geographical spread of haulout sites and their general inaccessibility means that aerial surveys of haulouts provide the only practical method for obtaining reliable indices of abundance over large parts of their range. Ideally, multiple surveys would be carried out each year (Teilmann, Riget, & Härkönen, 2010; Thompson et al., 1997) but in practice, the limited resources available mean that it is not possible to carry out synoptic, range-wide surveys at such intensities. Aerial surveys of the UK harbour seal population have been carried out regularly since the late 1980s with some irregular and sparse monitoring in south-east England as far back as the late 1960s (Lonergan et al., 2007; Thompson, Lonergan, & Duck, 2005, 2010). Lonergan et al. (2007) presented UK wide results of surveys up to 2005. These showed the effects of the two Phocine Distemper Virus (PDV) epidemics in the southern North Sea that dramatically reduced the south-east English population by approximately 50% and 30% in 1988 and 2002 respectively (Lonergan et al., 2007; Thompson et al., 2005). Lonergan et al. (2007) also noted that by 2006 the population in south-east England was still in a decline initiated by the 2002 epidemic. This contrasts with the rapid, 12% p.a. post 2002 epidemic increase recorded in the large Wadden Sea population (Brasseur et al., 2018), and the relatively rapid recovery in the southeast England population following the 1988 epidemic (Thompson et al., 2005). Although the 2002 PDV epidemic did not appear to have had any noticeable impact on harbour seal populations around Scotland, Lonergan et al. (2007) reported population declines in Orkney and Shetland of 40% (95% CI: 30–50%) between 2001 and 2006, indicating that harbour seals in these areas experienced substantially increased mortality and/or very low recruitment over this period. More recently, Hanson, Thompson, Duck, Baxter and Lonergan (2015) reported a continuing 19.9% p.a. decline in the local harbour seal population in the Tay and Eden SAC, producing a decrease of approximately 94% between 2000 and 2013.

This paper reports the results of recent surveys of harbour seals around the UK and combines these with the previously reported survey results to describe the current status of the UK harbour seal population and to identify and quantify the trends in sub-populations at both regional (SMU) and smaller (SACs) scales. These trends are then compared to population estimates and trends in adjacent populations within Europe and the wider North Atlantic.

2. METHODS

2.1. Survey methods

All surveys were conducted during the annual harbour seal moult in August. Survey were conducted using aerial photography of seals at haulout sites, with the exception of sites in the Tees estuary (Figure 1) that were counted on land, by the Industry Nature Conservation Association(INCA) (Bond, 2018). The aerial survey methods used varied depending on the location and physical characteristics of the haulout sites.

Surveys of east coast estuaries: Seals are relatively easy to detect on sandbanks and in tidal creeks and channels. Fixed-wing aircraft and conventional photography, either vertical with a large format camera (prior to 2000) or oblique with a hand-held digital SLR camera, were used to survey the estuarine haulout sites on the east coast of England and in eastern Scotland (in the Firth of Tay and the Moray Firth); see Thompson et al. (2005) for detailed methodology.

Surveys of rocky shores: Harbour seals hauling out on rocky or seaweed covered shores are more difficult to detect. Surveys of Orkney, Shetland, West Scotland, and rocky shores on the east coast of Scotland were therefore carried out by helicopter (operating at an altitude of 150-250m and at a distance of 300-500m offshore) using a thermal imaging camera (Barr and Stroud IR18) that can detect the infra-red signature of groups of seals at distances of over 3km (depending on weather conditions). The thermal imager was mounted on a pan and tilt head and operated out of the helicopter window. Simultaneous oblique photographs were obtained of seal groups using a hand-held camera equipped with an image-stabilized zoom lens. Both harbour and grey seals were digitally photographed and the images used to classify species composition of groups of seals. The technique enables rapid and thorough surveying of seals inhabiting complex coastlines allowing synoptic censuses of areas that would not be possible by any other method; see Cronin et al. (2007) for detailed methodology.

In 2016, this system was replaced by a custom-built, 3-camera system, based on Trakka System's SWE-400 comprising a gyro-stabilized gimbal containing thermal imaging, HD video and digital still cameras and a laser range finder. Video and still images are recorded on laptops that display a moving map, highlighting areas that have already been surveyed during the flight.

Seasonal timing: Historical information from the Wash (Thompson et al., 2005) suggested that counts are high and consistent during the first 3 weeks of August, when harbour seals are moulting (Thompson & Harwood, 1990; Thompson & Rothery, 1987). Earlier surveys in England had been carried out in the early part of August since the 1970s. In order to ensure that the current data are consistent with earlier data, surveys were restricted to the month of August.

Counts of harbour seals during the moult may not be fully representative of their distribution at other times of the year. However, surveys during the breeding season in both the Moray Firth (Cordes & Thompson, 2015) and The Wash and Southeast England (SCOS, 2017) show that the breeding season distribution is similar to that of the moult. The purpose of the monitoring programme is to track population trajectories to assess their status. Local redistributions will not affect the population indices for SMUs.

Time of day: There is evidence for a slight temporal effect on numbers of seals hauled out, with higher numbers associated with low tides occurring in the afternoon (Thompson & Harwood, 1990; Russell et al., 2015). Although these studies did not cover the harbour seal moult, the surveys were further restricted to low tides occurring in the afternoon. This restriction was occasionally relaxed for the English east coast and Moray Firth surveys where a large proportion of the haulout sites are within military restricted airspace that can only be accessed at weekends.

Tidal state: Haulout patterns relative to local tidal times in the Moray Firth and telemetry data from seals in Orkney and West Scotland, during the August moult period (Lonergan, Duck, Moss, Morris, & Thompson, 2013; Thompson et al., 2005), showed that the number of seals on individual haulout sites exceeded 90% of the maximum count for approximately 1.5 hours before low water until at least two hours after low water. Similar haulout patterns have been described for Moray Firth harbour seals during the pupping season in June and July (Thompson et al., 1997). The surveys described here were carried out within the period from two hours before to two hours after the predicted times of local low tides (derived from POLTIPS, National Oceanographic Centre, NERC).

Weather: Surveys were carried out only during periods of good visibility and with light to moderate winds. Surveys were not carried out in heavy or persistent rain because the probability of detecting hauled out seals with the thermal imager is reduced in rain. Light rain is not thought to have a significant effect on haulout numbers; although Grellier, Thompson, & Corpe (1996) counted significantly fewer seals on days with precipitation the effect size was small and did not cover the moult and in other studies, e.g. Granquist & Hauksson, (2016), no effect of precipitation was detected.

Extent and frequency of Surveys: Based on previous boat-based surveys and reports from wildlife conservation and naturalist groups around the UK it is clear that harbour seals are effectively absent from the UK coast line between Dover and the Solway Firth, with the exception of a small group that haul out in Chichester Harbour on the south coast and occasional sightings of individuals or small groups of seals in Cornwall and the Dee estuary in North Wales (SCOS, 2017). SMUs 10, 11, 12 and 13 (Figure 1) were not regularly surveyed for harbour seals and are not included in this study.

The frequency and spatial extent of surveys was determined by both practical and financial constraint; it is not possible to survey the entire UK population in a single season with available resources. As far as possible, entire SMUs are surveyed within one year (August). In order to provide both national population estimates and finer temporal resolution data for areas where rapid population changes were thought to be occurring, the survey effort was stratified. Southeast England, Moray Firth and East Scotland SMUs were areas of particular historical interest because of seal hunting (Vaughan, 1978) or seal/fishery conflict (Butler, Middlemas, Graham, & Harris, 2011). These are all areas where seals haul out on sand banks, mud flats and tidal creeks, and can be surveyed at relatively low cost. They have, for the most part, been surveyed annually, with one to three surveys each year from 1988 to 2016.

Areas requiring helicopter mounted thermal imagery take longer to cover and surveys are substantially more expensive. As the primary aim of the survey programme was to provide a UK wide estimate approximately every five years, the SMUs in Scotland and Northern Ireland were surveyed more sporadically (Duck, 2006). However, surveys in 2006 indicated a major decline occurring within the Orkney population, so more intensive survey effort was applied to that management region as a consequence.

2.2 Population estimates

The count data represent an index of population size, as not all animals are hauled out during the survey. Population estimates presented are derived from scaling the counts by estimates of the proportion of harbour seals hauled out during the survey period. The probability of a seal being hauled out during the survey window was estimated using flipper tag mounted satellite telemetry transmitters that continued to transmit through the moult (Lonergan et al., 2013). The probability of being hauled out during the survey window was higher for tagged females (0.84; 95% CI: 0.63–0.99) than males (0.61; 95% CI: 0.34–0.86). However, as the aerial survey images do not provide sex ratio information, an averaged proportion of 0.72 (95% CI: 0.54-0.88) was used to convert seal counts to total population. The conversion factor used here, was close to the middle of the range (0.6 to 0.8) of values estimated for other populations in Europe and North America (e.g. Harvey and Goley, 2011; Huber, Jeffries, Brown, DeLong, & VanBlaricom, 2001; Simpkins, Withrow, Cesarone, & Boveng, 2003; Reis, Hiby, & Reijnders, 1998). UK wide and regional population estimates were generated by scaling the most recent counts summed across all areas.

2.3 Trends in count data

Trends in moult counts were estimated, where possible, for each SMU and SAC in which harbour seals were a primary reason for designation (Figures 1 & 2). The starting dates of the time series varied between regions, with regular surveys beginning in the late 1980s or early 1990s in most SMUs (Table 2). In some regions, primarily the estuarine sites on the East coast, frequent surveys (usually at least one per year) have been carried out, but in rocky shore habitats surveys were carried out at approximately five yearly intervals. Where possible entire SMUs were surveyed synoptically (i.e. within a single August survey season). However, in some cases it was not possible to survey an entire SMU in one season and counts had to be combined across multiple years – the resulting count was assigned to the year that encompassed the majority of the total (focal year). In most of these cases over 95% of the count was from the focal year and combining across years would likely have little effect on the resulting trend. However, the large size of West Scotland SMU meant that it was rarely surveyed in a single year. For this SMU, the focal year accounted ≥64% of the combined count, and together with the two surrounding years accounted for a ≥90% of the count.

Similarly, in the large central sub-region, for two years (1989 and 2007), the focal year accounted for only 90% of the count (≥ 95% when including the two surrounding years). The necessary combining of data across years in these two regions likely led to a reduced power to detect trends.

Where the limited number of years with counts prohibited robust model fitting for a particular SMU, the largest subset of sites within it (i.e. the subset of haulout sites with the largest proportion of the SMU total), for which the monitoring was frequent enough to allow model fitting, was used as a proxy for the SMU. The relationship between the SMU and subset counts in years when the whole area was surveyed can be used to assess how representative the subset trends are of the regional trends.

All models were fitted within R (R Core Team, 2017). Following Lonergan et al. (2007), counts were modelled as a function of year assuming negative binomial errors. Generalised linear models (GLMs) with negative binomial errors were fitted using the function glm.nb in the MASS library (Venables & Ripley, 2002). For some datasets, the limited number of data points resulted in problems estimating the theta parameter for the negative binomial distribution. In these cases, a Poisson distribution was assumed; examination of the residual plots confirmed that use of a Poisson error distribution was appropriate for these datasets. Generalised additive models (GAMs) were fitted within mgcv (Wood, 2011). Model selection by AICc was used to select a final model.

The model formulations fitted during model selection were dependent on the SMU/SAC. For all datasets, at least three models were fitted: an intercept only GLM (null model), a linear year effect within a GLM, and a non-linear smooth year effect within a GAM. Additional models were fitted to the datasets from the north and east coasts. For the Northeast and Southeast England SMUs trends were punctuated by sudden falls in abundance following the PDV epidemics; such trends may not be captured within a GLM with a single trend or even using a GAM. SMUs of the east and north coasts of Scotland (East Scotland, Moray Firth, North Coast & Orkney, and Shetland SMUs), also showed a potential change in trend coincident with 2002 (the year of the second PDV epidemic). Thus for these datasets, individual trends were fitted (constant, linear or smooth) prior to, and following, the PDV epidemics (1988 and 2002). For SMUs with clear drops in abundance following PDV epidemics (Northeast and Southeast England), a step change in abundance coincident with the PDV epidemics was also offered. For datasets for which there was a gap in data around this time (2002 to 2005; Shetland SMU, North Coast & Orkney SMU, Sanday SAC), trends were fitted either side of the data gap; i.e. no trend was modelled within the gap. In each time series, all linear trends were fitted within one GLM, which allowed selection by AICc to be used to determine if the trend was the same before and after step changes associated with the PDV epidemics. Any trends that were identified as being non-linear were fitted separately within a GAM. AICc was then used to select the most appropriate model for that part of the time series.

3 RESULTS

3.1. Total UK harbour seal population size

The most recent composite count for the entire UK was 31,300 based on counts from surveys carried out mostly between 2014 and 2016 (2011 in the Western Isles and Northern Ireland) (Table 1). Scaling this count by the probability of being hauled out (0.72 (95% CI: 0.54 - 0.88); Lonergan et al., 2013) produces a total UK population estimate of 43,450 (95% CI: 35,550 - 57,900). Approximately 80% of the total were recorded in Scotland, 17% in England and 3% in Northern Ireland.

No survey data were available for Northern Ireland before 2002, but the harbour seal population of Great Britain (GB, i.e. the UK minus Northern Ireland) was surveyed in 1996-97. The composite count in GB in 1996-97 (Table 1) produced a total population estimate of 45,550 (95% CI: 37,250 - 60,700). Although this earlier estimate was 7.5% higher than the most recent estimate (42,100; 95% CI: 34,500 - 52,300) it is not significantly different.

3.2 UK harbour seal distribution

The distribution and relative abundance of harbour seals around the UK during the annual moult is shown in Figure 3. The data are presented as numbers of hauled out seals counted per 10km grid square and represent composites of the counts from surveys carried out in 1996 and 1997 (Figure 3a) and 2014 to 2016 (2011 in the Western Isles and Northern Ireland) (Figure 3b).

The overall distribution, in terms of occupancy, has remained constant since the earliest synoptic aerial surveys, comprising counts from 1996 and 1997 (Figure 3a) (N.B. as no counts were available for Northern Ireland in 1996-1997 this comparison applies to the GB totals). However, there have been large changes in relative abundance (Figure 4) driven by dramatic differences in regional population trends. For example, in the 1996-1997 counts the West Scotland and the North coast & Orkney SMUs each held 27% of the GB population. In the most recent counts, they held 50% and 4% respectively.

3.3 Seal Management Unit trends

Based on AICc selection criteria all SMUs, sub-units and SACs were best fitted with GLMs, with one exception; the time series of counts after 2002 in The Wash were best fit by a GAM. A detailed list of estimated growth rates and associated confidence intervals for each SMU and various sub units and the SACs within them are presented in Table 2 and briefly described below.

Southeast England Seal Management Unit

The Southeast England SMU encompasses five geographically distinct haulout groups: Donna Nook, The Wash, Blakeney Point, Scroby Sands, and the Greater Thames Estuary (Figure 1). The Wash encompasses approximately 65% of the count in this unit and is within The Wash and North Norfolk Coast SAC - the only SAC in England for which harbour seals were a reason for designation. The Wash has been surveyed since 1968, whereas Donna Nook, Blakeney Point, and Scroby Sands were not included in the survey programme until immediately before the 1988 PDV epidemic. Sites in the greater Thames Estuary region have only been sporadically surveyed until recently; a recent series of surveys of the Thames have been completed by the Zoological Society of London (ZSL) and will be presented elsewhere, but are not included in this analysis. Consequently, there are few complete, synoptic surveys of the entire Southeast England SMU. The regional trends are therefore represented by the trends in the combined counts from Donna Nook, The Wash, and Blakeney Point. These combined counts represent over 90% of the total for the unit.

The combined counts for The Wash, Donna Nook and Blakeney Point, assumed here to represent the Southeast England SMU, are available from 1988 to 2017 (Figure 5a). The 1989 count was approximately 50% lower than the pre-epidemic count in 1988. The selected model for the combined counts incorporated two periods of exponential increase; 6.6% p.a. (95% CIs: 5.3, 7.9) between 1989 and 2002 and 2.8% p.a. (95% CIs: 1.3, 4.3) between 2003 and 2017. These periods of exponential increase were separated by a step change decrease of approximately 30% between 2002 and 2003 coincident with the second PDV epidemic. For the period 2003-2017, though a GLM was marginally preferred by model selection (ΔAICc = 2), there was an indication of a non-linear trend with a constant abundance followed by an increase and finally a levelling off in recent years.

Trends were also examined separately for The Wash and North Norfolk Coast SAC which comprises the haulout sites in The Wash and at Blakeney Point. The Wash accounts for >85% of the SAC population, and time series for The Wash began earlier (1968) than elsewhere, thus trends were examined for The Wash as well for the SAC as a whole. The selected model for The Wash and North Norfolk Coast SAC was similar to the overall SMU model, with similar growth rates and a similar negative step change coincident with the 2002 PDV epidemic.

The best fitting model for the long time series of counts for The Wash included three distinct trajectories (Figure 5b). From 1968 until 1988, the moult counts increased exponentially at 3.5% p.a. (95% CIs: 2.3, 4.76) reaching an estimated maximum count of c.3000 (95% CIs: 2500, 3500) in 1988. The counts then fell by approximately 50% between 1988 and 1989 as a result of a PDV epidemic. This collapse was followed by a second period of exponential increase, but at a higher rate of 6.0% p.a. (95% CIs: 4.2, 7.8), with counts reaching c.3100 (95% CIs: 2800, 3350) by 2002 before a recurrence of the PDV epidemic caused another decrease. The counts from 2003 to 2017 are best described by a GAM that initially estimates a decreasing trend until around 2006, increases rapidly until around 2010 and then levels off, suggesting that the population is approaching an asymptote. The selection for the GAM here but not in the other two Southeast England datasets may be a result of the higher sample size of 24 for The Wash 2003 and 2017, compared to 19 for the other two datasets. The recent counts for The Wash are similar to the levels in 1988 and 2002 immediately before the two PDV epidemics.

Northeast England Seal Management Unit

The small population of harbour seals in the Northeast England SMU is split between Lindisfarne in Northumberland where sporadic counts suggest between 6 and 20 seals regularly haul out and the Tees estuary where a breeding group was re-established in the late 1980s. Counts in the Tees have increased at approximately 7.4% p.a. (95% CIs: 6.07, 8.80) since 1989 (Figure 5c) punctuated by a drop of c. 40% between 2001 and 2003.

East coast of Scotland Seal Management Unit

In the East Scotland SMU the population is mainly concentrated in the Firth of Tay and Eden Estuary SAC and in the Firth of Forth. Small groups are also present in the Montrose Basin and at coastal sites in Aberdeenshire. Counts in the Firth of Forth have been sporadic and therefore trends were only fitted to counts within the SAC. The selected model indicates that counts in the SAC remained stable between 1990 and 2002, at which time they represented approximately 85% of the total management region count. From 2002 to 2017 the counts in the SAC declined rapidly and monotonically at approximately 18.6% p.a. (95% CIs: 17.1, 20.0) (Figure 6a, Table 2); over the 15 year period counts fell from approximately 680 to less than 40, representing a 95% decline. By 2016 the SAC counts represented only approximately 15% of the SMU total.

Moray Firth Seal Management Unit

The Moray Firth SMU encompasses the stretch of coast from Duncansby Head (north-east point of Scotland) to Fraserburgh. Counts between 2005 and 2016, showed no clear trend, and were variable around a mean of c.900 (Figure 6b). The only count of the entire region prior to this was in 1995 and was c.40% higher than the 2005 to 2016 mean. The majority of the seals counted in the SMU wide surveys are at haulout sites between Loch Fleet and Findhorn (c. 90% in 2016); this area has been surveyed more regularly than the region as a whole and is presented here as a proxy for the SMU. The selected model for this area shows that counts were decreasing at a rate of 5.6% p.a. (95% CIs: 2.5, 8.5) between 1994 and 2000, followed by a step change with a drop of c.28% occurring between 2000 and 2003 and no significant trend in counts thereafter (Figure 6b, Table 2). Counts of harbour seals within the Dornoch Firth and Morrich More SAC site have shown a monotonic decline of c. 8.0% p.a. (95% CIs: 6.3, 9.7) from the first surveys in 1992 to 2017.

North Coast & Orkney Seal Management Unit

The selected model for the North Coast & Orkney SMU indicates that counts were stable until 2001, that the next count in 2006 showed a decline of 46% (Figure 6c) and that from 2006 onwards, there was a continued decline of 10.4% p.a. (95% CIs: 9.3, 11.5) (Table 2). Overall, the composite counts for the North Coast & Orkney SMU have declined from approximately 8800 in the mid-1990s to 1350 by 2016 (Table 1) representing an 85% decrease in what was the largest single SMU population in the UK. The counts for the Sanday SAC show a similar trend, with a step change between 2001 and 2006 and a continuing declining at 17.8% p.a. (95% CIs: 13.3, 22.0) since 2006.

Shetland Seal Management Unit

The selected model for counts for the whole of Shetland incorporated a step change involving a drop of approximately 40% occurring between 2001 and 2005 (Figure 6d). Counts either side of the step change (1991-2001 and 2006-2015) do not show any obvious trend, though in both cases the sample size was limited (n=4 and 3, respectively).

Counts at the two Shetland SACs show different trajectories. The Mousa SAC counts show a monotonic exponential decline at an average rate of 11.1% p.a. (95% CIs: 8.7, 13.5) between 1991 and 2015 (Table 2). In contrast, an intercept only model was selected to fit the counts (1991-2015) of the Yell Sound SAC. However, including only counts between 1995 and 2015 (i.e. excluding 1991 and 1993), the selected model showed a decline of 5.3% p.a. (95% CIs: 2.6, 7.9).

West Scotland, Southwest Scotland and Western Isles Seal Management Units

Intercept only models were selected to fit the counts of the West Scotland, Southwest Scotland, and Western Isles SMUs (Figure 7, Table 2). This may have been in part due to the small sample sizes as only five or six counts were available for the 25 year period, and for the West Scotland these counts were largely a result of combining counts across multiple years (see Methods). Counts for the most recent surveys in each of the West Scotland, Southwest Scotland and Western Isles SMUs are the highest counts obtained since the start of surveys (Figure 7); in the West Scotland SMU, currently the largest SMU population in the UK (Table 1), the 2014 count was approximately double the 1990 count and, in the Southwest Scotland SMU the 2015 count was approximately three times the 1989 count.

Although the West Scotland region is defined as a single SMU, it is very large geographically in terms of total coastline and contains a large proportion of the UK harbour seal population, i.e. 49% of the 2016 estimate of UK total count (Table 1). The trajectories of counts within north, central and south sub-divisions (Figure 2) of this large region are shown in Figure 8. In both the north sub-unit (Cape Wrath to Loch Ewe) and the central sub-unit (Loch Ewe to Ardnamurchan), the selected models indicate that counts have increased since the early 1990s, by 4.86% p.a. (95% CI: 4.02, 5.70) and 4.0% p.a. (95% CIs: 3.1, 5.0) respectively (Figure 8a & 8b). The selected model for the Ascrib, Isay and Dunvegan SAC which is situated in the central sub-region was an intercept only model indicating no trend.

In the south sub-region (Ardnamurchan to Scarba) an intercept only model was selected, indicating that the overall population has remained stable since the early 1990s (Figure 8c). Intercept only models were selected for both the Southeast Islay Skerries and the Lismore SACs, though for Southeast Islay skerries a constant count was only marginally preferred over an increasing trend (ΔAICc = 2) of 2.67% p.a. (95% CIs: 1.31, 4.04).

Northern Ireland Seal Management Unit

Only two synoptic surveys have been carried out of the entire harbour seal population in Northern Ireland. However, a subset of the population from Carlingford Lough to Copeland Islands has been monitored more frequently from 2002 to 2011 (Figure 6d). This area contained 80-85% of the total in the two years with complete coverage. This subset of the population has declined slowly over the period at an average rate of 2.7% p.a. (95% CIs: 1.8, 3.5).

4 DISCUSSION

4.1 Geographical patterns

Previous studies have reported indications of a general decline in several of the large harbour seal populations in SMUs around Scotland (Lonergan et al., 2007) as well as dramatic declines in some important populations in SACs (Hanson et al., 2017; Thompson, Van Parijs, & Kovacs, 2001). The more extensive time series of survey results presented here have allowed a more robust analysis of these trends. Although there are significant declines in some important components of the UK harbour seal population, the picture of a general decline no longer holds true.

Significant numbers of harbour seals are present in ten SMUs; seven in Scotland, one in Northern Ireland, and two that cover the English east coast. The trends differ between SMUs, but there appears to be a strong geographical component determining, or at least associated with, the patterns. Based on the recorded trends it is possible to divide the UK harbour seal population into three geographically coherent groups with contrasting dynamics:

Populations along the English East coast, from Kent to the Scottish border have generally increased year on year, with those increases punctuated by major declines associated with two major PDV epidemics in 1988 and 2002. Recent trends, i.e. those that incorporate the last 10 years (2006 to 2016) show significant growth in both SMUs (Figure 5).

Populations along the East coast of Scotland and in the Northern Isles have generally declined. The recorded declines have differed in intensity but in all areas the current population size is at least 40 % below the pre-2002 level. Populations in North coast & Orkney, and East Scotland SMUs are continuing to decline. Although continued declines are not evident in Shetland or the Moray Firth, there is no indication of recovery (Figure 6).

Populations in western UK are either stable or increasing. Counts in the central section of the large West Scotland management region have been increasing since the 1990s and in all other areas they have remained stable, with the exception of Northern Ireland which appears to have declined slowly throughout (Figure 7).

A similar geographical population substructure is also evident in recent population genetics results. Olsen et al. (2017) analysed DNA samples from approximately 300 harbour seals from sites throughout the UK and the Wadden Sea. Their results suggested two distinct groups, one in northern UK, and the other in southern UK and mainland Europe. The northern UK group was further divided into a north-western cluster equivalent to the West Scotland, Southwest Scotland and Western Isles SMUs and a north-eastern cluster equivalent to Shetland, North Coast & Orkney, Moray Firth, and East Scotland SMUs. The southern UK and mainland Europe group encompasses the Southeast England SMU and the Wadden Sea. The three groups of SMUs exhibiting different population dynamics therefore correspond with the groups identified by the genetic differences. The geographical pattern in SMU population trends suggests that at least some of the factors driving the differences in population dynamics may be acting on a larger scale than the individual SMUs. This highlights the importance of considering possible impacts across these larger population units when developing management actions for individual SMUs.

Apart from the clear impacts of the 1988 and 2002 PDV epidemics in the English SMUs, there is at present no clear explanation for the different dynamics in these three areas. The declines recorded in the Northern Isles and along the East coast of Scotland must ultimately be due to reduced fecundity or increased mortality. Lonergan et al. (2007) and Hanson et al. (2017) suggested that the observed declines in the North coast and Orkney SMU and the Tay and Eden Estuary SAC could not be due purely to reduced reproduction; even repeated complete reproductive failure would be unlikely to produce the sustained rapid rates of decline suggesting that the declines, that have now persisted now for over 15 years, must be due in part to loss of adults as well as pups.

4.2 Changes in Abundance

Here we have used counts of seals hauled out during the annual moult as an index of population size in order to track population status. Various management actions, e.g. setting management targets such as Potential Biological Removals (PBR) or estimating predation pressure on fish stocks, require estimates of total population size. Here we have used a correction factor for proportion of seals hauled out based on a study of haulout behaviour of a sample of telemetry tagged seals in Orkney and the Inner Hebrides (Lonergan et al., 2013) to scale the counts to total population size.

Different sex and age classes are thought to haulout at different times during the moult; it has been shown that juvenile harbour seals tend to moult earliest and adult males latest (Cronin, Gregory, & Rogan, 2014; Daniel, Jemison, Pendleton, & Crowley, 2003; Thompson & Rothery, 1987). The age structure of the population may therefore influence the proportion of the total population that are counted during the surveys. At present, we do not know the sex and age composition of the seals counted during the surveys. However, it is clear that changes in population trajectories must ultimately be due to changes in demographic rates; e.g. increased pup mortality and reduced fecundity were identified as the most likely factors driving the recorded declines in the Moray Firth SMU population (Matthiopoulos et al., 2014). Such changes in demographic rates would have direct effects on the population age structure. If there were large changes in the sex and/or age structure (Härkönen, Harding & Lunneryd, 1999) or the timing of the moult, the counts might no longer represent a constant proportion of the population. This could affect both the observed trends and the count to total population scaling factor.

Significant changes in timing of the pupping season have been reported in the Wadden Sea (Reijnders, Brasseur, & Meesters, 2010) and these may imply similar changes in timing of the moult. Cronin et al. (2014) have shown that the timings of the moult differ between Ireland, Scotland and the Wadden Sea, so it is possible that the timing of the moult varies throughout the UK. It is therefore possible that the scaling factor between counts and total population size may have changed over time and/or may differ between SMUs.

We do not have independent estimates of the timing of the moult in different SMUs within our survey areas nor any information on temporal trends in the timing, so cannot rule out the possibility of regional differences or temporal changes in scaling factors. However, it is unlikely that the proportion of the population being counted would change in such a way as to produce the observed range of patterns from rapid increases, to step changes, static populations and rapid declines.

4.3 OSPAR convention compliance.

The OSPAR Convention EcoQO's for harbour seals have defined criteria for triggering management action, i.e. that harbour seal population size in defined sub-units should not decline by more than 10% over a five-year period (OSPAR, 2010) and in the longer term should not decline by more than 25% relative to the baseline, in this case defined as the population in the early 1990s. The SMUs considered here are synonymous with the defined harbour seal EcoQO sub units.

The trends presented here show that the East Scotland and North Coast & Orkney SMUs fall below the short term criteria as they both declined by more than 10% over the last 5 years of data collection and all four of the EcoQO subunits along the east coast of Scotland and in the Northern Isles fail the long term criterion, having declined by more than 25% from the reference population in the 1990s. Conversely, the sites on the east coast of England and in the west of Scotland would all pass against both short and long-term criteria.

The OSPAR convention requires management actions to be applied in the event that an EcoQO indicates a problem. In Scotland a targeted research programme to investigate the proximate and ultimate causes of local population declines has been initiated (Arso-Civil et al., 2018). In addition, the East Scotland, Moray Firth, North coast and Orkney, Shetland, and Western Isles SMUs have been designated as Conservation Areas for harbour seals and a bespoke Seal Management Plan has been developed and operated to manage conflicts between harbour seals and salmon fisheries in the Moray Firth (Butler, Middlemas, Graham, & Harris, 2011). PBR calculations for these SMUs use minimum values for the recovery factor (F_r) to ensure minimal impact of anthropogenic takes (SCOS 2017). These actions have reduced directed takes of harbour seals to very low levels (Scottish Government, 2018), but have not so far prevented the continued rapid declines in the north and east of Scotland.

4.4 SAC monitoring

One of the main drivers for counting harbour seal populations in Europe is the provision of population status information needed to fulfil the reporting requirements for SACs designated for seals under the EU Habitats Directive regulations. Assessing conservation status depends on regular monitoring to determine population trends within SACs. With the limited resources available for population monitoring, an unintended consequence of this requirement will be a bias towards monitoring populations within SACs. SACs are therefore likely to become de facto indicators of overall population status.

The survey programme presented here has produced extensive data for the nine SACs in the UK where harbour seals are the primary feature, allowing the UK to fulfil its responsibilities under the Habitats Directive. It has also produced similar data for larger SMUs that encompass the SACs, allowing us to assess the effectiveness of SACs as population status indicators. In both the Southeast England and East Scotland SMUs the single SACs include a large proportion of the population, so the SAC and regional trends are similar. However, in the East Scotland SMU the SAC is declining more rapidly than the overall SMU. In other SMUs the SACs include smaller proportions of the overall population. Of the remaining seven SACs, five have trends that are similar to the regional trend. However, the Mousa SAC in Shetland reports an exponential decline whereas the SMU reports a stable population after a step change in 2002 and the Ascrib, Isay and Dunvegan SAC in West Scotland central region reports a static population whereas the wider population is increasing exponentially. These comparisons suggest that SACs for harbour seals provide a reasonable indication of wider population trends in most cases, including regions with increasing, stable and decreasing populations. In the two cases where SAC and regional trends diverged, both reported lower growth than the regions and were, in these cases, conservative indicators of regional trends. However, the fact that there is substantial local variation in trends highlights the potential risk of using SACs as de-facto indicator sites.

4.5 Robustness of trends

The results of the monitoring programme have allowed estimation of trends in harbour seal populations at spatial scales appropriate to the statutory monitoring requirements. However, while they generally address the requirements, there are clear differences in our ability to assess trends in different SMUs.

Most of the UK east coast has been surveyed at least annually, providing rich data sets, with between 25 and 57 data points. These data enable robust estimation of the effects of the PDV epidemics and the intervening population trends. Even with these data, despite similar patterns (Figure 5) between 2002 and 2017 across datasets within the Southeast SMU, using AICc model selection criteria, GLMs were marginally preferred for the Southeast England, and The Wash and North Norfolk coast SAC datasets over than the more flexible GAM that was fitted to The Wash data. This was likely due to the lower sample sizes for these time series (19 versus 24 in The Wash). Thompson et al. (1997) examined the effect of survey frequency on the power to detect trends in the Moray Firth harbour seal population and concluded that detecting trends of the magnitude reported here, in the short term, would require multiple surveys each year. However in the longer term, e.g. over the 19 to 36 year datasets for east coast sites presented here, there was clearly sufficient power to both detect and quantify trends as well as catastrophic step changes when only one survey is carried out in most years.

The sampling frequency for SMUs and SACs in the Northern Isles and Western Scotland was much lower, with only 5 to 11 surveys carried out between the early 1990s and 2017. In the Northern Isles these sparse data (n=7 to 11) still allowed detection of the rapid population declines and/or large step changes that occurred between 2001 and 2006. For the three SMUs in western Scotland (n=5 to 7) the selected models all suggested no significant trend over the study period, although in the north and central sub regions of West Scotland, even moderate trends (c. 4-5% p.a.) were detected with a similar sample size (n=6).

Counts in the West Scotland, Western Isles and Southwest Scotland SMUs have been variable and although counts are now higher than at the start of the time series, there was not a monotonic increase in counts across the time series. It possible that the variability in counts represents more complex trends but such models (i.e. GAMs) could not be supported by the limited data. For West Scotland (n=5), any trend may have been masked by the combining of data across years (see Methods). Because multiple surveys are required to identify a trend, the current survey frequency means that even rapid decreases would not be detectable for a prolonged period of time. Further stratification of survey effort may need to be considered to provide more sensitive metrics for the large and widely dispersed populations around Scotland.

4.5 Possible reasons for declines

4.5.1 Grey seal competition

One putative explanation for the regional harbour seal population declines is competition with grey seals. There are significant overlaps in both diet (Wilson & Hammond, This Issue) and at-sea distributions (Russell, Jones, & Morris, 2017) so there is the potential for competition for prey resources to occur. Grey seals are now known to be direct predators of harbour seals (Brownlow, Onoufriou, Bishop, Davison, & Thompson, 2016; van Neer, Jensen, & Siebert, 2015).

The populations of grey seals in the three broad geographical areas show different dynamics to those of harbour seals (Russell et al., This issue, Thomas et al., This issue). Both pup production and population estimates for grey seals in the West Scotland and the Western Isles SMUs were increasing until the mid-1990s and have been stable since. In Orkney the grey seal population increased until around 2000 and has been relatively stable since. In contrast, the grey seal population in the North Sea continues to increase exponentially. The levelling off of some regional grey seal populations is evidence of density dependence which is most likely mediated through processes at sea (Russell et al., This Issue; Thomas et al., This issue) and probably related to prey resources which would likely lead to increased competition with harbour seals.

Harbour seal populations are apparently stable or locally increasing in the west, where grey seals have been at their carrying capacity since harbour seal surveys began; they are increasing in the southern North Sea where grey seal populations are growing at close to their theoretical maximum; they are suffering serious declines in the northern North Sea (Moray Firth and East Scotland SMUs) and Northern Isles (North Coast & Orkney and Shetland SMUs) over a period when grey seals have approached their carrying capacity. There is therefore no simple/clear link between the status of grey and harbour seal populations.

However, the lack of a simple relationship does not necessarily rule out a competition effect. Density dependent effects would presumably be operating as the populations approach their carrying capacities. Assuming little change in the carrying capacity, any such density dependence would have been fully operational before harbour seal surveys began in the west of Scotland and therefore, competition from grey seals would have been relatively constant throughout. The relatively stable harbour seal populations could represent the steady state populations under that level of competition.

The rapid harbour seal declines in the northern North Sea and Northern Isles have occurred over a period when the regional grey seal population has appeared to approach carrying capacity (Russell et al. This issue; Thomas et al., This issue), a period where density dependent effects could have led to increasing levels of interspecific competition. Observed declines could therefore represent the effects of increasing levels of competition with grey seals. Wilson and Hammond (This issue) have shown that in eastern Scotland and the Northern Isles, where harbour seals have declined, a large proportion of their diet comprises sandeels, and that declines in sandeel abundance may be a contributing factor driving harbour seal declines. Sandeels are also important in grey seal diet in this area and increased consumption by grey seals may further reduce sandeel availability to harbour seals.

The increasing trends in both species in the central and southern North Sea could simply indicate that density dependent effects have not yet become evident. Recent reports from the Wadden Sea (Galatius et al., 2017) suggest that the moult counts of harbour seals have remained constant for the past five years, following a 15 year period of rapid increase. This apparent stabilization of the Wadden Sea population has occurred at the same time as The Wash counts appear to be levelling off. This may be an early indication that the rapidly increasing grey seal population in the southern North Sea is beginning to influence harbour seal populations.

4.5.2 Predation

4.5.2.1 Grey seal predation

Recent reports of grey seals as major predators of harbour porpoises, grey seal pups and adult harbour seals (Brownlow et al., 2016; Haelters, Kerckhof, Jauniaux, & Degraer, 2012;

Leopold et al., 2014; Van Neer et al., 2015) have highlighted the potential involvement of grey seal predation in the harbour seal declines. To date none of these studies has quantified the level of predation.

The relative patterns of grey and harbour seal population changes suggest that predation by grey seals on harbour seals is not likely to be a routine behaviour pattern, shared by a large proportion of the grey seal population. If a significant proportion of grey seals are acting as predators, the rapid increases in grey seal numbers in the Southeast England region would have been expected to have led to increased predation. Recent summer counts of grey seals suggest that up to a third of the UK's grey seal population is using haulout sites along the east coast of England during the summer (SCOS, 2017). This is substantially more than are found in Orkney at the same time of year and the Orkney grey seal counts have been stable since the late 1990s (SCOS, 2017). In the late 1990s the Orkney harbour seal population was around 12,000 and has fallen by approximately 85% since 2000. If that decline was due to predation by the local grey seal population it seems unlikely that a much smaller harbour seal population in south-east England could have been able to increase if subjected to similar or greater predation pressure from the rapidly expanding local grey seal population.

This does not, however, exclude the possibility that predation by grey seals is a major contributory factor in some declines. Hanson et al. (2017) pointed out that the observed levels of mortality due to grey seal predation in the Firth of Tay and Eden SAC was unsustainable and sufficient to account for the continuing decline there.

In the North Coast & Orkney SMU, the harbour seal counts have declined by approximately 6,500 since 2000, assuming that the counts represent approximately 70% of the total population (Lonergan et al., 2013), this is equivalent to the removal of ~9,000 seals over 15 years or ~600 p.a. Counts of grey seals hauled out during the August harbour seal surveys have remained relatively stable over that period, and suggest a summer population of approximately 42,000 grey seals centred on Orkney (SCOS 2017). Assuming a sex ratio of 0.7♂:1♀ and an average survival rate of 0.95 for age 1+ animals (Thomas et al., This issue) c.10,000 of these would be adult males. Observations at Blakeney Point in south-east

England and at Helgoland in Germany suggest that small numbers, possibly even individual male grey seals can kill large numbers of harbour seals over short periods of time (Bexton et al., 2012; Van Neer et al., 2015). The relative sizes of the populations of grey and harbour seals in Orkney means that just 1% of adult male grey seals each taking six harbour seals per year would be sufficient to account for the observed decline.

4.5.2.2 Killer whale predation.

Killer whales are known predators of harbour seals over most of their range in both the North Atlantic and North Pacific (Bolt, Harvey, Mandleberg, & Foote, 2009; Deecke, Nykanen, Foote, & Janik, 2011; Ford et al., 1998; Jourdain, Vongraven, Bisther, & Karoliussen, 2017). Bolt et al. (2009) used sightings of killer whales in Shetland and estimates of field metabolic rates to estimate the total energy requirement of the local population during the harbour seal breeding season. They showed that a small number of whales relying on harbour seals as prey would be sufficient to account for the reported declines in Shetland, but it was not possible to confirm the proportion of the diet made up of harbour seals in Shetland. There are no data on rates of predation by killer whales on harbour seals in other areas and it is therefore not possible to assess the likelihood of such predation being a contributing factor to declines in Orkney or East Scotland SMUs.

4.5.3 Effects of PDV epidemics

The 1988 PDV epidemic removed approximately 50% of the harbour seal populations in the southern North Sea. This was followed by a period of sustained growth. The patterns of decrease and recovery in the Southeast England SMU population were similar to those in the only other major population in the southern North Sea, the Wadden Sea population. A second PDV epidemic spread through the populations in the southern North Sea in late summer and autumn 2002. However, despite the epidemic in The Wash starting at the same time of year and with the population being effectively the same size as in 1988, the trajectory of the population after the 2002 epidemic was different to that following the 1988 epidemic.

The GAM fitted to the detailed data set for The Wash after 2002 indicated that the counts declined until 2006, falling by approximately 50% overall, before a period of rapid recovery and eventual levelling off after 2010. In contrast, in the Wadden Sea, the pattern of decline and recovery was similar to that seen after the 1988 epidemic with an initial drop of c50% followed by a rapid increase at around 12% p.a. from 2003.

These two populations have been diverging since the 1970s. The growth rates in The Wash before and after the 1988 epidemic were substantially lower than those estimated in the Wadden Sea (Thompson et al., 2005). Although both populations suffered a dramatic 50% decrease in 1988 and then both increased exponentially until 2001, the growth rate in the Wadden Sea from 1989 to 2001 was approximately 12% p.a. compared to 7.9% p.a. in the Southeast England SMU (Brasseur et al., 2018; Galatius et al., 2017).

In the early 1980s the Wadden Sea population was approximately twice the size of The Wash population (no counts were available for other parts of the Southeast England SMU before 1988). As a consequence of these differing growth rates, although the Southeast England population is currently close to its pre-epidemic level in 1988, the Wadden Sea population is now approximately eight times larger than The Wash population (Figure 8) (Brasseur et al., 2018; Galatius et al., 2017). This represents a large shift in the relative importance of these two populations.

At present there is no clear explanation for the different population responses to the 2002 epidemic or for the substantially lower growth rates in the English harbour seal populations throughout the time series. The continued decline between 2002 and 2006 is not thought to have been due to direct mortality related to PDV as there is no indication that live virus persisted in the population after 2002 (Härkönen et al., 2006). Differential sex or age linked mortality may have contributed to an apparent decline, but pup counts for the Wash population (SCOS 2017) did not show the same decline after the epidemic suggesting that the number of breeding adult females at least did not decrease over that period. It is possible the continued decline simply reflected a change in the proportion of the population choosing to moult in the area, effectively a temporary emigration to alternative moulting sites. If this did occur, the lack of a coincident increase in the counts at Blakeney and Donna Nook suggests that any such movement must have been to sites outside the study area.

Interestingly the 2002 counts at all three sites in Southeast England SMU were lower than the 2000 and 2001 counts. This may be coincidental, but could also indicate that the epidemic was already influencing haulout behaviour of a proportion of the population some weeks before the first mortalities were observed along the coast of south-east England. This difference could be due to simple variability in seal counts, but could also be the result of weather and currents keeping carcasses away from the shore before the moult surveys. Alternatively, if a proportion of the seals destined to moult in the Wash forage close to the European coast or haul out there, they could have become infected earlier and been included in the mortality totals in mainland Europe. Despite large scale tracking studies in both populations, there have, to date, been no records of telemetry tagged seals moving directly between the Wadden Sea and The Wash in either direction. Unfortunately the timing of tagging studies in which tags are usually applied post moult or early spring and usually fall off prior to the breeding season, means that there is little information on movements during the short period between breeding and moulting.

Although the effect of the 2002 PDV epidemic was most apparent in south-east England, allowing models to fit different trajectories before and after the 2002 epidemic indicates evidence of concurrent declines in all other SMUs on the east and north coasts. There are no indications of a downturn in any of the SMUs or SACs in the west.

Few PDV cases were reported from the East Scotland or the Northern Isles in 2002, although some sero-positive animals were recorded in East Scotland (Härkönen et al., 2006) indicating that part of the population was exposed to PDV at the time. It is not clear how low level exposure to a PDV epidemic could lead to a continual decline over a prolonged period. The wide-spread change from stable to declining populations coincident with the 2002 epidemic is unexpected, especially in areas that did not experience large scale mortality at the time. There are no indications that PDV caused any direct mortality in the years following either the 1988 or 2002 epidemics (Härkönen et al., 2006) so it is unlikely that the declines observed in eastern and northern Scotland were due to direct infection mortality. If the declines are related to the PDV epidemics it seems likely to be due to some change in geographical patterns of recruitment of juveniles and/or migration of adult seals to the southern North Sea or western Scottish SMUs. Other than occasional movements between adjacent SMUs the available telemetry data do not indicate large scale, long distance movement of adult harbour seals and there are few data on movements of juveniles. There is therefore no independent evidence of movement of harbour seals out of the region of decline in the east and north of Scotland.

4.5.4 Other diseases

In addition to PDV, an outbreak of avian influenza in 2014, killed at least 1600 harbour seals in the Wadden Sea (Common Wadden Sea Secretariat, 2014) and 580 in the Kattegat-Skagerrak (Krog et al., 2014; Zohari, Neimanis, Härkönen, Moraeus, & Valarcher, 2014). No cases were reported in UK waters, but the fact that grey seals have been identified as a possible wild reservoir for influenza-A (Puryear et al., 2016) means that there is clear potential for such an outbreak in future and the possibility that such outbreaks could have occurred and gone unreported in areas of decline.

Brucella infection is widespread in UK harbour seals; Kershaw et al. (2017) found that 16% of a sample of 490 harbour seals tested positive for *Brucella* although there were no pathological signs of infection. However, there was no evidence of higher sero-prevalence, or circulating antibody levels in animals in the areas with the greatest declines. *Brucella* infection is therefore unlikely to be a major contributing factor to recent declines.

4.5.5. Algal toxins

Algal toxins, have been proposed as potential causes or contributors to the regional declines in harbour seals. Jensen et al. (2015) showed that harbour seals around Scotland are exposed to both domoic acid (DA) and saxitoxins (STXs) at potentially lethal levels in their diet. The proportion of positive samples and the toxin levels measured in the excreta were significantly higher in areas where harbour seal abundance is in decline suggesting that algal toxins may be factors in the regional harbour seal declines. Unfortunately there is insufficient historical information on patterns of occurrence to relate changes in frequency of harmful algal blooms to the start of local harbour seal declines.

4.6 Conclusions

This paper presents the results of a long-term monitoring programme designed to provide periodic estimates of the UK harbour seal population and to provide trend information through more frequent surveys of regional and local populations. The analyses demonstrate the importance of carefully targeting survey effort to provide long-term population monitoring at different temporal resolutions, for specific areas depending on the intended use of the results.

These results represent the current knowledge of one of the most intensively studied large mammal populations in Europe, and the trend analyses provide the necessary information to adequately fulfil reporting requirements under the current management and conservation legislation. However, to some extent that is a fortunate state of affairs. While probably representing the best use of available resources it is clear that the current survey regime's ability to detect or quantify quite large, short-term changes or more gradual, long-term changes is limited by the low frequency of surveys in some important populations. The ability to detect chronic impacts of future anthropogenic activities may require a re-assessment of the monitoring strategy and a more focused application of survey resources.

The apparent geographical structure of the UK harbour seal population may have significant implications for future population management. If the drivers of population trajectories are acting at scales larger than individual SMUs it may be possible and necessary, in some circumstances, to manage populations at these larger scales.

The fitted trends show that despite the imposition of conservation orders along the entire east coast of the UK, the harbour seal populations in some SMUs are continuing to decline. With the continuing rapid development of offshore activities this failure to recover despite strong conservation action is clearly a cause for concern.

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Table 1. The most recent August counts of harbour seals at haul-out sites in Britain and Northern Ireland by Seal Management Area, compiled from surveys in 2014 to 2016 and 2011 in Northern Ireland and the Western Isles. Similar compilation counts are presented for three previous periods: 2007 to 2009, 2000 to 2006 and 1996 to 1997.

Seal Management Unit / Country		Harbour seal counts			
		2011-2016	**2007-2009**	**2000-2006**	**1996-1997**
1	Southwest Scotland	1,200	923	623	929
2	West Scotland	15,184	10,626	11,666	8,811
3	Western Isles	2,739	1,804	1,981	2,820
4	North Coast & Orkney	1,349	2,979	4,384	8,787
5	Shetland	3,369	3,039	3,038	5,994
6	Moray Firth	940	776	1,028	1,409
7	East Scotland	368	283	667	764
SCOTLAND TOTAL		**25,149**	**20,430**	**23,391**	**29,514**
8	Northeast England	86	58	62	54
9	Southeast England	5,061	3,952	2,964	3,222
10	South England	23	15	13	5
11	Southwest England	0	0	0	0
12	Wales	5	5	4	2
13	Northwest England	10	5	5	2
ENGLAND & WALES TOTAL		**5,185**	**4,035**	**3,048**	**3,280**
GREAT BRITAIN TOTAL		**30,334**	**24,462**	**26,471**	**32,794**
NORTHERN IRELAND TOTAL		**948**	**1,101**	**1,176**	
UK TOTAL		**31,282**	**25,563**	**27,618**	

Table 2. Model estimated growth rates and associated confidence intervals for each Seal Management Unit, and various sub-units and the SACs within them. The number of years in which surveys occurred is shown, and for east coast sites where multiple surveys occurred in some years, the total number of survey counts (n) used in the analyses is shown. Trend values are average annual percentage change in counts of seals hauled out during the annual moult in August. All estimates were derived from GLMs fitted to counts over the periods indicated. See text for details of models fitted to the data and model selection criteria.

Seal Management Unit	sub-unit	years (n)	first trend: years trend % (95% C.I.)	second trend: years trend % (95% C.I.)	third trend: years selected model
Southeast England	Donna Nook, The Wash & Blakeney Point	27 (34)	1989-2002: +6.61 (5.35, 7.89)	2003-2017: +2.82 (1.34,4.31)	
	Wash & North Norfolk Coast SAC	27 (35)	1989-2002: +6.41 (5.11,7.73)	2003-2017:+3.06 (1.54, 4.61)	
	The Wash	36 (57)	1968-1988: +3.51 (2.28, 4.76)	1989-2002: +5.99 (4.24,7.77)	2003-2017: GAM
Northeast England	The Tees	29	1989-2002: +7.43 (6.07, 8.80)	2002-2017: +7.43 (6.07,8.80)	
East Scotland	Firth of Tay & Eden Estuary SAC	22 (25)	1990-2002: constant	2002-2017: -18.58 (17.25, 19.88)	
Moray Firth	Loch Fleet to Findhorn	19 (25)	1994-2002: -5.55 (2.47, 8.53)	2002-2017: constant	
Moray Firth	Dornoch Firth & Morrich More SAC	20 (26)	1992-2017: -8.00 (6.30, 9.66)		
North Coast & Orkney		9	1993-2001: constant	2006-2016: -10.41 (9.29,11.52)	
	Sanday SAC	11	1993-2001: constant	2006-2016: -17.75 (13.29,21.99)	
Shetland		7	1991-2001: constant	2006-2015: constant	
	Mousa SAC	7	1991-2015: -11.13 (8.69,13.5)		
	Yell Sound Coast SAC	7	1991-2015: constant		
Western Isles		7	1992-2017: constant		
West Scotland		5	1990-2014: constant		
West Scotland; North		6	1991-2017: +4.86 (4.02, 5.70)		
West Scotland; Central		6	1989-2014: +4.02 (3.08, 4.97)		
	Ascrib, Isay and Dunvegan SAC	11	1990-2017: constant		
West Scotland; South		5	1990-2014: constant		
	Eileanan agus Sgeiran Lios mor SAC	9	1990-2014: constant		
	South-East Islay Skerries SAC	6	1990-2015: constant		
Southwest Scotland		5	1989-2015: constant		
Northern Ireland	Carlingford Lough to Copeland Islands	6	2002-2011: -2.66 (1.79, 3.52)		

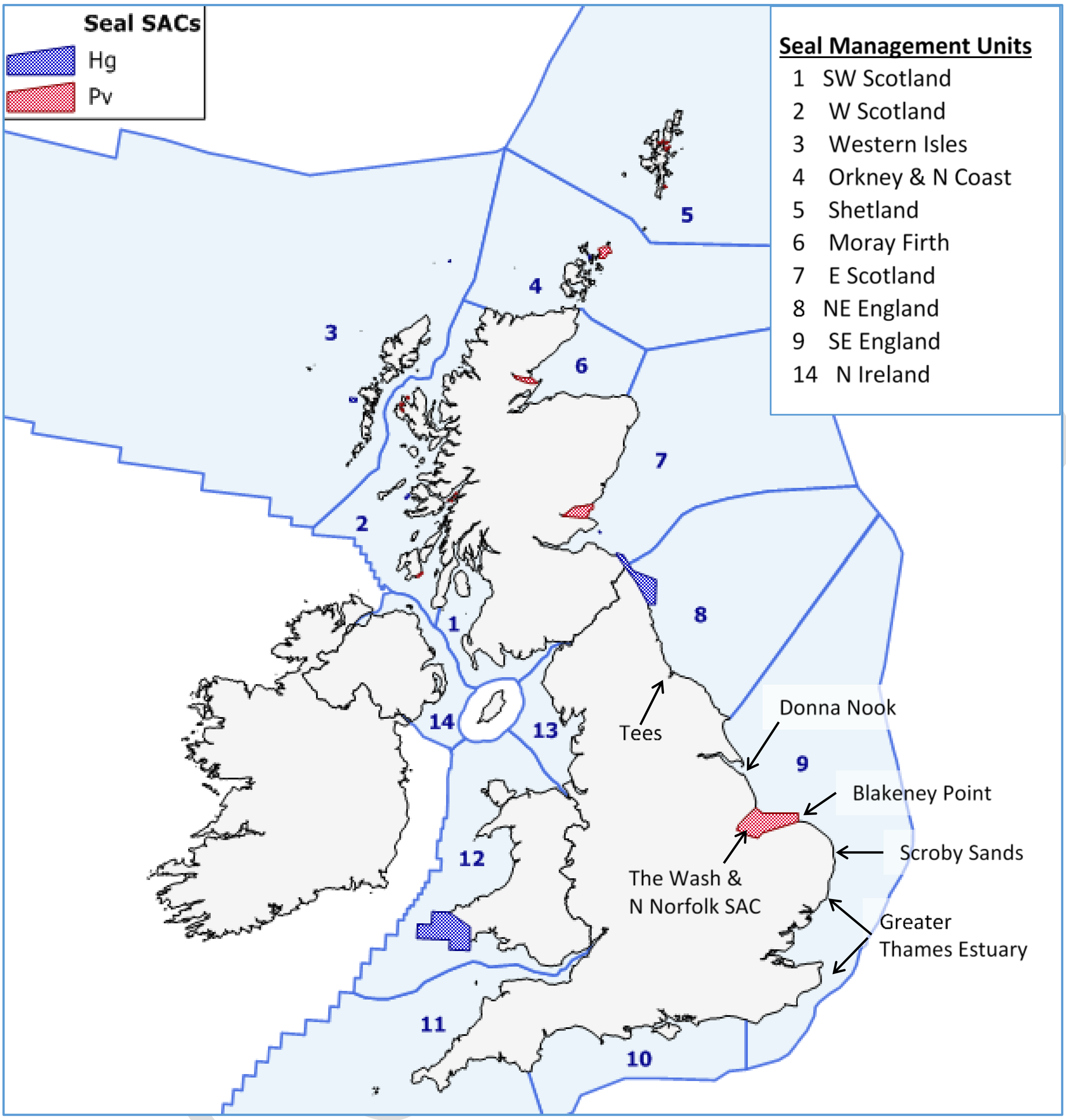

Figure 1 Map showing the Seal Management Units (SMUs) in the UK. Geographical locations mentioned in the text and locations of Special Areas of Conservation (SACs), where seals were a primary feature for designation, are also shown. SAC sites in Scotland are detailed in Figure 2 below.

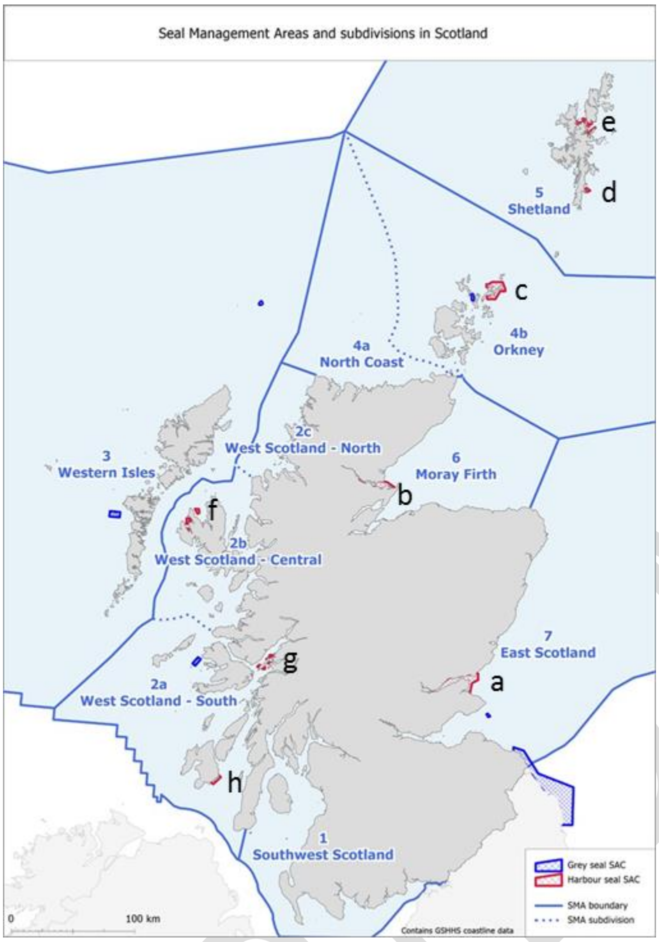

Figure 2 Map showing the Seal Management Units, West Scotland sub-units and the locations of SACs in Scotland where harbour seals are identified as a main qualifying feature. SAC locations identified by black letters are a) Firth of Tay and Eden Estuary; b) Dornoch Firth and Morrich More, c) Sanday, d) Mousa, e) Yell Sound, f) Ascrib, Isay and Dunvegan, g) Eileanan agus Sgeiran Lios mor, h) South-East Islay Skerries.

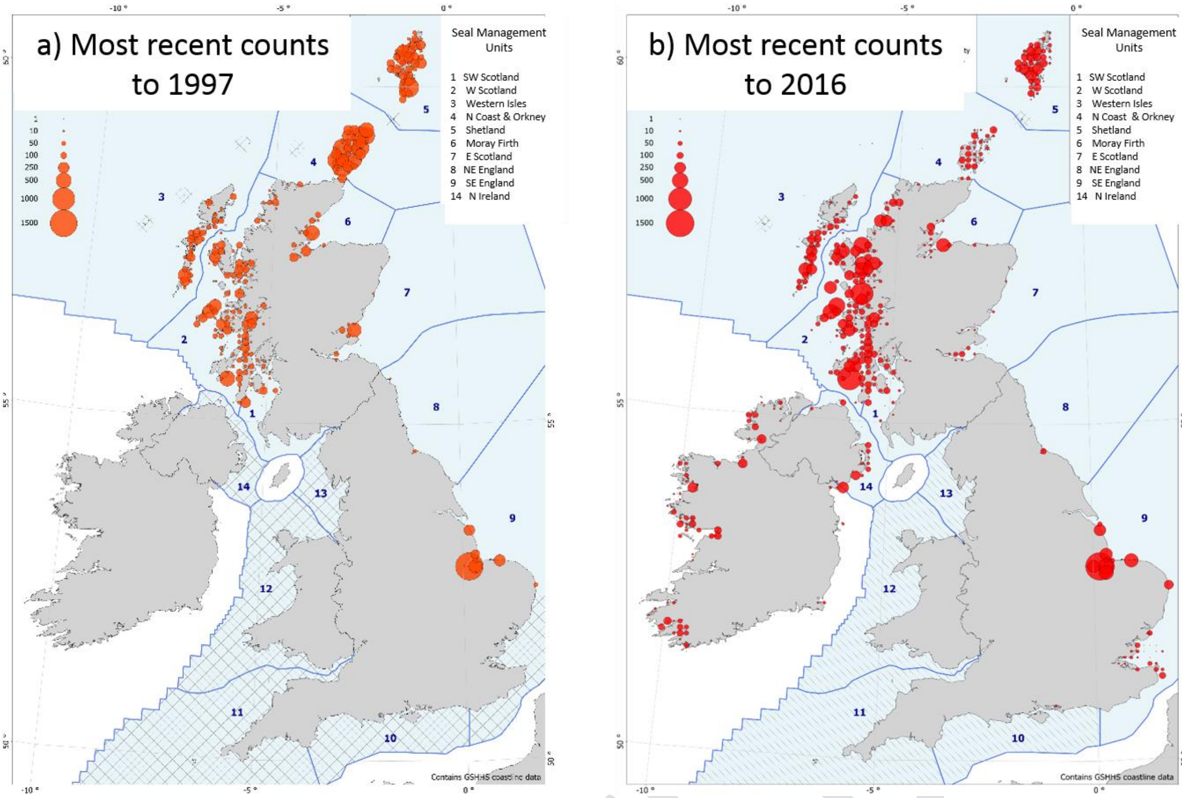

Figure 3 Distribution of harbour seals on haulout sites in August around the British Isles: a) Surveys carried out in 1996-1997; b) Surveys carried out in between 2014 and 2016 (2011 for Northern Ireland and Outer Hebrides). Small numbers of harbour seals (<20) are anecdotally but increasingly reported for the South-West England & Wales management unit, but are not included on this map.

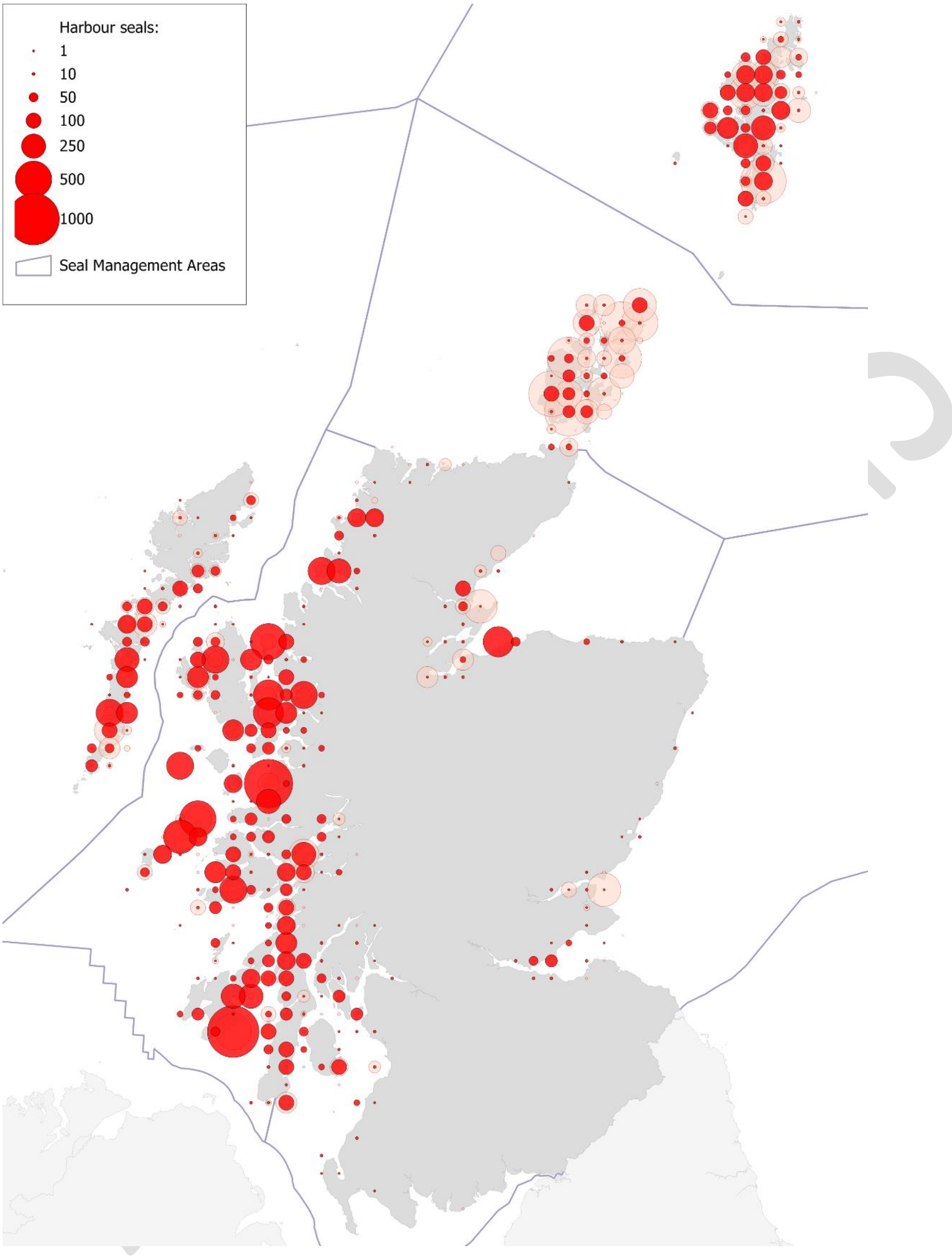

Figure 4 Distribution of harbour seals on haulout sites in August at sites around Scotland. Counts from the most recent survey round (2011-2016, dark red circles) are shown superimposed on the counts from the first synoptic survey round (1996-1997, faint red circles). Size of circle (area) indicates the magnitude of the count. Seal management region boundaries are shown; see figure 1 for region names.

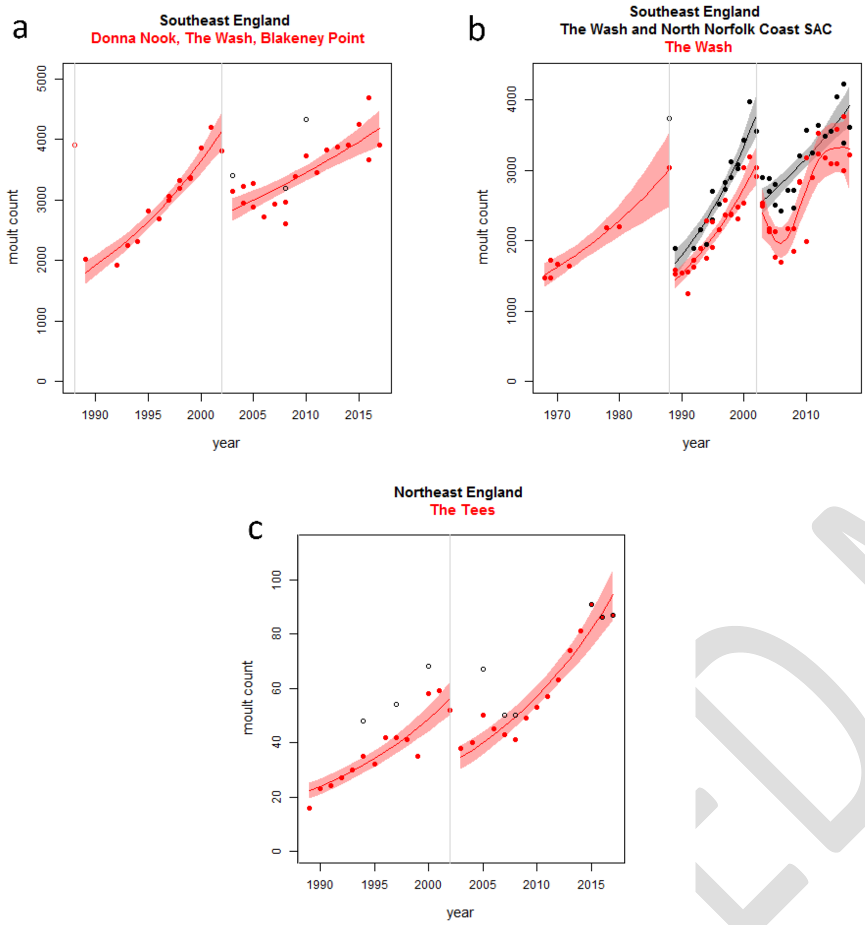

Figure 5 Survey counts and fitted trends for different seal management units and sub-units of the English harbour seal population. Counts and fits for each SMU or sub-unit are shown in black. Counts not used in model fits are shown as open dots. Where a robust model could not be fitted to the overall SMU, the counts and model fit for a subset of the region is shown in red: a) The combined South East England region (1988-2017); b) The Wash and North Norfolk SAC (1988 – 2017) and The Wash (1967 – 2017); c) North East England SMU and the Tees SAC (1990-2017).

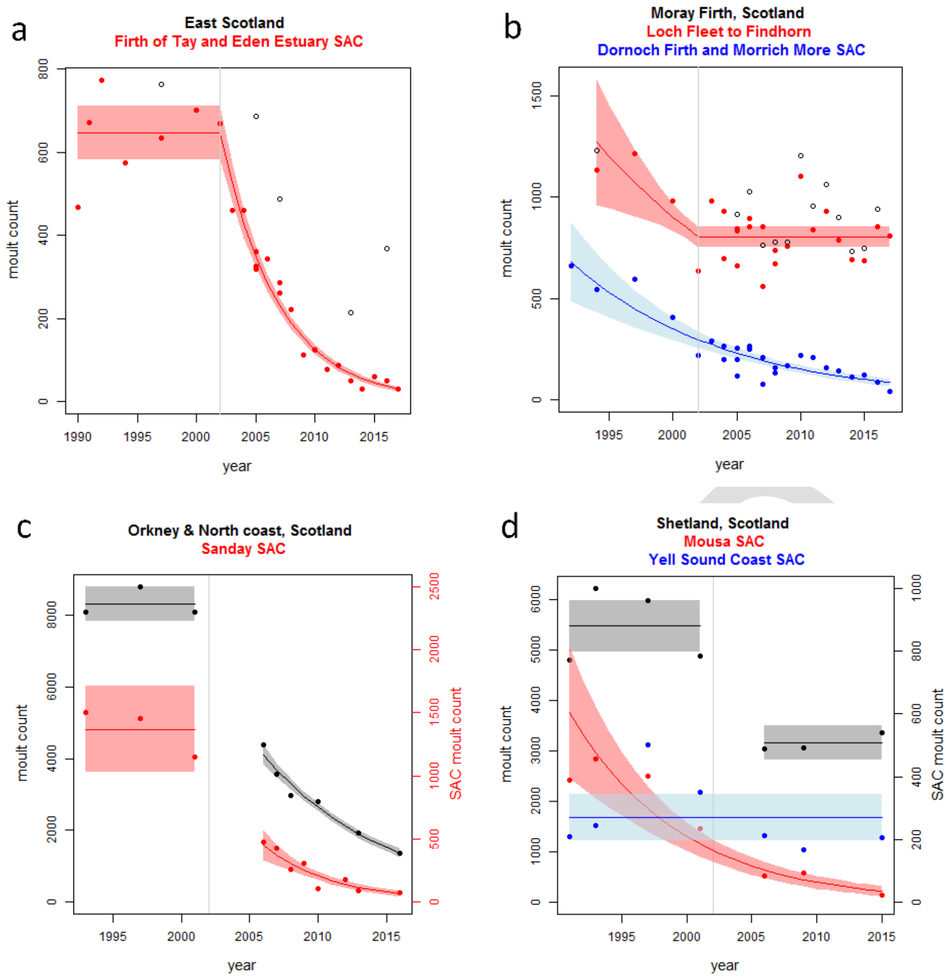

Figure 6 Survey counts and fitted trends for different seal management units and sub-units of the Scottish harbour seal population on the East coast and Northern Isles. Counts and fits for each SMU or sub-unit are shown in black. Counts not used in model fits are shown as open dots. Where a robust model could not be fitted to the overall SMU, the counts and model fits for subsets of the region are shown in red and blue: a) The combined East Scotland SMU and the Firth of Tay and Eden estuary SAC (1990-2017); b) The Moray Firth SMU, Inner Moray Firth and the Dornoch Firth and Morrich More SAC (1993 – 2017); c) Orkney and North Coast SMU and the Sanday SAC (1993 – 2016); d) Shetland SMU and the Mousa and Yell Sound SACs (1993-2015).

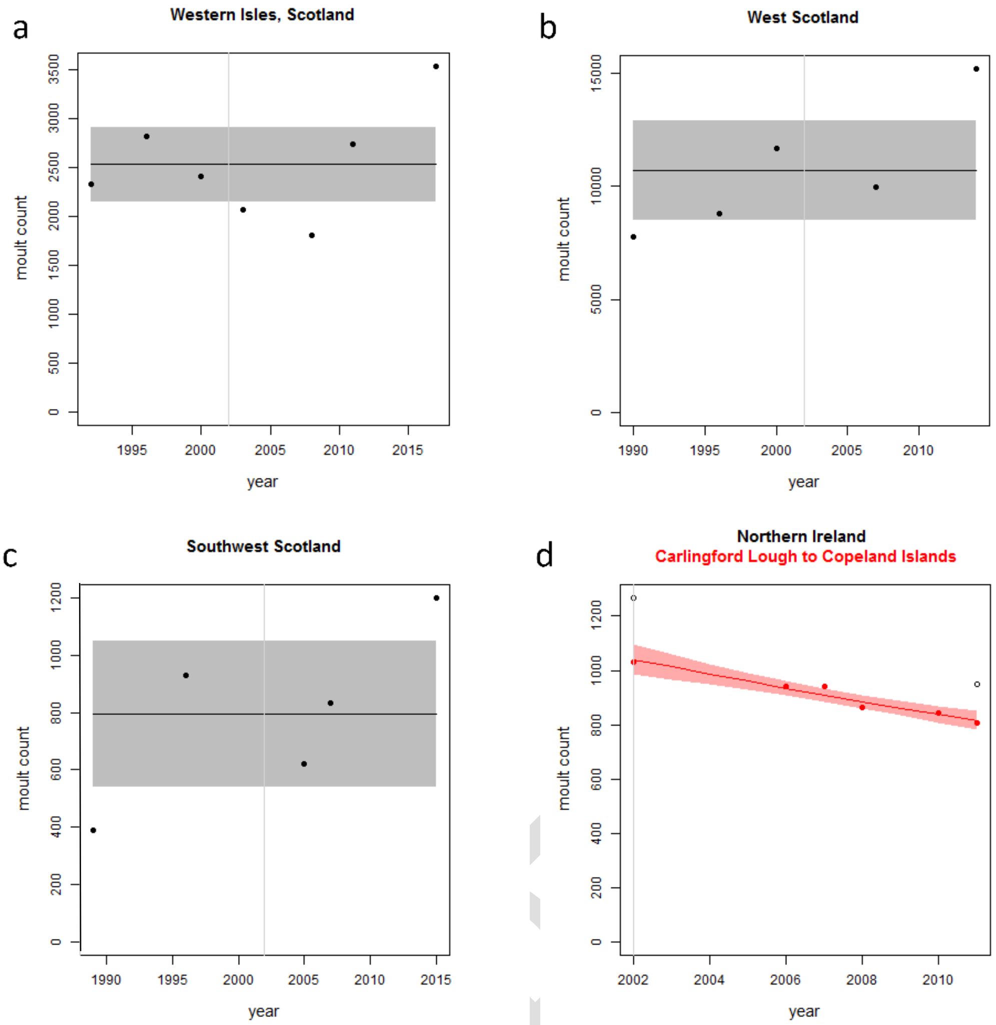

Figure 7 Survey counts and fitted trends for different seal management units of the harbour seal populations on the Scottish West coast and in Northern Ireland. Counts and fits for each SMU are shown in black. Counts not used in model fits are shown as open dots. The counts and model fits for subsets of the region are shown in red: a) The West Scotland SMU (1990-2014); b) The Western Isles (Outer Hebrides) SMU (1992 - 2017); c) South-West Scotland SMU (1989 - 2015); d) Northern Ireland SMU (2002 - 2011).

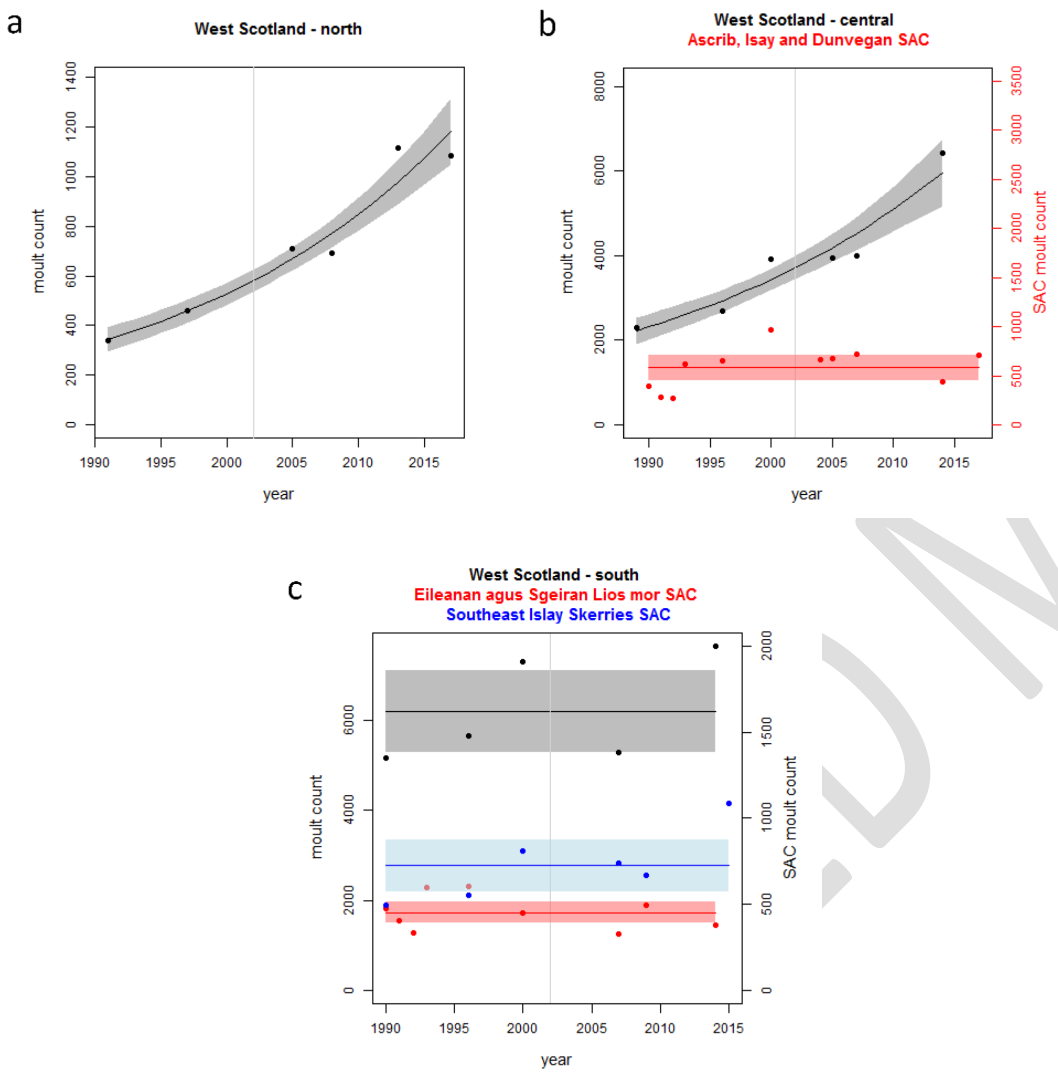

Figure 8 Survey counts and fitted trends for sub-sections of the harbour seal population in the West Scotland SMU (see Figure 1 for section boundaries). Counts and fits for each sub-region are shown in black. Where a robust model could not be fitted to the overall region, the counts and model fits for subsets of the region are shown in red and blue: a) West Scotland north (1992-2017); b) West Scotland central and the Ascrib, Islay and Dunvegan SACs (1989 – 2016)); c) West Scotland south and the Lismore and S.E. Islay Skerries SACs with a single model fit to the entire time series (1990 – 2015).

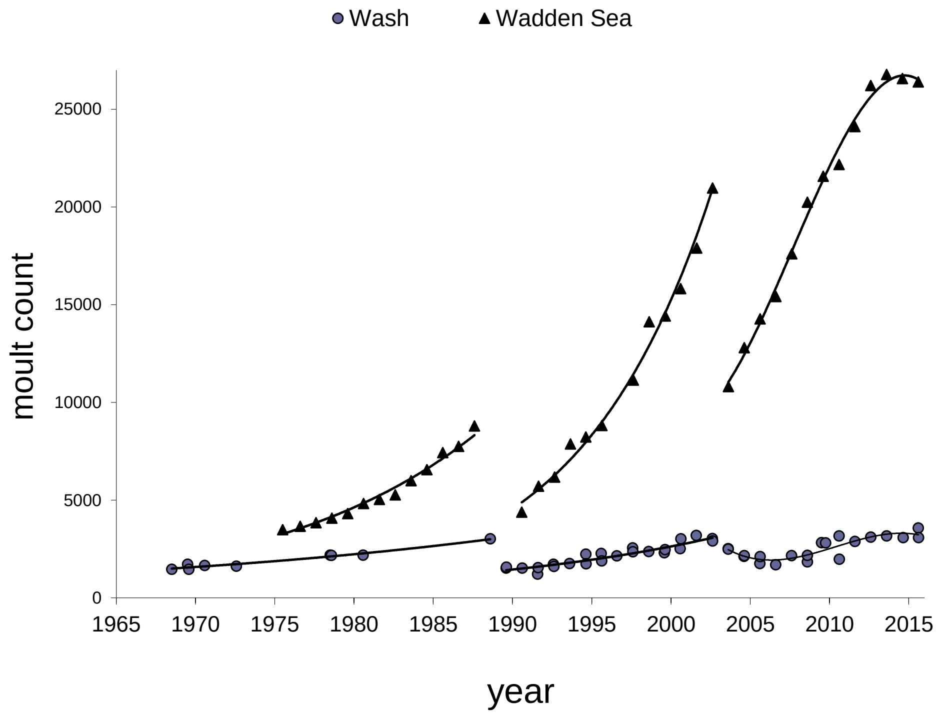

Figure 9 Comparison of moult counts for the harbour seal population in The Wash, and the Wadden Sea from 1968 to 2016. (Wadden Sea data from Galatius et al., 2017).