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Age-length relationships in UK harbour seals during a period of population decline

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ABSTRACT

1. The abundance of harbour seals (*Phoca vitulina*) in the UK as a whole has increased over the past 10 years, after a 30% decline during the preceding 10 years and two major viral epidemics. However, population trends vary greatly among regions, with those on the east coast of Scotland and in the Northern Isles experiencing dramatic declines since the early 2000s and populations on the west coast being either stable or increasing. The reasons for these differences in population dynamics are unknown.

2. Determining whether there has been a change in somatic growth among populations can assist in assessing potential causes for abundance declines, as shifts in juvenile growth rates or maximum length at maturity may indicate changes in environmental conditions. Resource limitations are likely to result in slower growth and later age at sexual maturity, whereas causes of acute mortality could have the opposite effect.

3. Here, analysis of the most comprehensive length-at-age dataset for UK harbour seals found no evidence for major differences, or changes over time, in asymptotic length or growth parameters from fitted von Bertalanffy growth curves, across all regions, with the exception of one pairwise comparison; males from East Scotland were significantly shorter than males from all other areas by an average of almost 9 cm. However, the power to detect small changes was limited by measurement uncertainty and differences in spatial and temporal sampling effort.

4. Asymptotic lengths at maturity across all regions were slightly lower than published lengths for harbour seal populations in Europe, the Arctic and Canada, with females being on average 140.5 cm (95% CI, 139.4, 141.6) and males 149.4 cm (147.8, 151.1) at adulthood.

5. Reliable estimates of changes in growth over time are important for understanding environmental constraints on a population but knowledge of the underlying drivers of change is essential for the design of robust conservation and mitigation plans.

INTRODUCTION

Length-at-age relationships among marine mammals can provide important insights into the growth rate and condition of individuals and populations (Grandi, Dans, Garcia, & Crespo, 2010; Harding, Salmon, Teilmann, Dietz, & Härkönen, 2018; Krafft, Kovacs, Frie, Haug, & Lydersen, 2006; McLaren, 1993). Comparing morphometric measures, such as maximum body length and juvenile growth rates can therefore assist in understanding how nutritional and food related constraints may be impacting populations. In addition, estimates of age at sexual maturity (Gibbens & Arnould, 2009; Hutchings, Myers, Garcia, Lucifora, & Kuparinen, 2012) and longevity (Lynch & Fagan, 2009) are key parameters required for modelling population dynamics and extinction risk. Indeed, for pinniped species with polygynous breeding systems and large degrees of sexual dimorphism, attaining maximum body length may be particularly important for males where size is related to mating success (Lidgard, Bowen, & Boness, 2012). Thus age-length relationships and changes in growth curves are often used to investigate the impact of changes in habitat, population density or abundance on mammalian somatic growth and physiological condition. Here, differences among the age-length relationships for UK harbour seals (*Phoca vitulina*) from seven of the 13 harbour seal Management Units (MUs) are explored.

Management Units are spatially discrete regions or populations that have been established to enable stakeholders responsible for the conservation and management of marine mammals to achieve the best conservation outcomes for a species. In Scotland, the Units for seals are referred to as Management Areas and, for harbour seals, were adopted following the introduction of the Marine Scotland Act (2010). They were defined based on available information on harbour seals ecology, and now underpin regional assessments undertaken by Marine Scotland when issuing seal licences. Across the UK seal Management Units have been endorsed by the Joint Nature Conservation Council and the relevant Statutory Nature Conservation Bodies. Further details of their spatial extent and the long-term population trends within each Unit can be found in Thompson, Duck, Morris, & Russell (2019). The genetic distinctiveness of the harbour seal Management Units and thus the structure of the UK harbour seal as a metapopulation has recently been explored by Olsen et al. (2017). They found that the spatial designation of the MUs was largely in agreement with the genetic population structure results, supporting the spatial basis for managing harbour seals in the UK within these regional boundaries.

Some populations of harbour seals within the Management Units around the Scottish coast are currently in decline, particularly those in the Northern Isles and on the east coast (Lonergan et al., 2007; SCOS, 2017). For example, the abundance of harbour seals in Orkney has declined by 10% per annum since 1997. In the Firth of Tay and Eden Estuary Special Area of Conservation, the number of seals counted during their annual moult in August 2016 represented a 90% decrease from the mean number recorded between 1990 and 2002 (SCOS, 2017). Thus, although these recent abundance data suggest this trend is continuing for some populations, others, such as those in the West Scotland and the Western Isles Management Units, have been stable or increasing over the same time period (SCOS, 2017). The reasons for these declines are not clear but potential factors include increased competition for food by sympatric grey seals (*Halichoerus grypus*) and other top piscivorous predators, changes in prey availability or prey quality, increased predation (Brownlow, Onoufriou, Bishop, Davison, & Thompson, 2016), interactions with vessels (Jones et al., 2017) and exposure to biotoxins produced by harmful algae (Hall & Frame, 2010).

Widespread and dramatic declines in abundance may have impacts on population age structure (Holmes & York, 2003), which may also affect timing of breeding (Lunn, Boyd, & Croxall, 1994) and population recovery. For example, following the 1988 phocine distemper virus epidemic among harbour seals in Northern Europe the rate of increase in the population in the Wadden Sea was significantly higher after the outbreak (1989-1994 average annual rate 16%) than it was during the pre-epidemic period (1976-1987 average annual rate 9%), probably as a result of selective mortality during the epidemic (Reijnders et al., 1997). In UK waters whilst the epidemic caused approximately a 50% decline in the abundance of animals in Southeast England (Thompson et al., 2019; Thompson & Hall, 1993), populations in Scotland were affected to a much lesser extent (Hall, Pomeroy, & Harwood, 1992). Nevertheless, such differential mortality factors could result in a population with a skewed or truncated age distribution, a pattern which may also provide information on the drivers of changing population dynamics. More recently Harding et al. (2018) found that harbour seals in the Skagerrak had become significantly shorter over a 14-year period. They suggest that this could be an early signal of density dependence in this region and aerial surveys for abundance confirmed declining rates of population increase in the same area. Similar drivers may therefore also be affecting growth in UK harbour seals where populations have stabilized. Thompson et al. (2019) explore the variation in population trends for harbour seals throughout the UK in detail. Temporal and spatially explicit length-at-age data for harbour seals may therefore assist in understanding changes in the various population trajectories if they manifest as changes in somatic growth and morphology. Here, the aim is to examine age-length relationships for harbour seals among MUs and, where sufficient data are available, relate differences in growth parameters to changes in population abundance spanning similar timescales.

The objectives of this study were therefore to: (1) investigate spatial differences in age at maximum length and age-length growth functions across UK harbour seal Management Units for which data were available, and (2) to investigate temporal changes in growth parameters by year of capture and year of birth during the period of harbour seal decline in abundance. Significant variations in these parameters may provide insights into the reasons for the decline. However, the direction of any change is difficult to predict since lower abundance may result in a reduced pressure on remaining resources and consequent increases in growth. Alternatively, if nutritional stress or factors affecting growth and maturation were a cause of the decline then animals may suffer slower growth and be shorter for a given age.

Changes in growth parameters over time and by Management Unit were investigated by fitting Von Bertalanffy age-length curves. Harbour seals have been captured, sampled and released around the UK since the late 1980s for various studies relating to their biology and their ages have been estimated from counting the growth layer groups (GLGs, one layer is equivalent to one year of age) in the incisor teeth (Dietz, Heide-Jorgensen, Härkönen, Teilmann, & Valentin, 1991). In addition, the length of the captured animals was measured.

MATERIALS AND METHODS

Live captures and collection of harbour seal teeth

Adult and juvenile seals were captured in nets and pups were manually restrained in bags and, where necessary, were sedated with Zoletil 100 (Virbac, France) at a dose rate of 1ml/100kg body weight intramuscular or 0.5ml/100kg body weight intravenous. Animals were weighed, measured, sexed and an incisor tooth removed for aging. A 0.1ml dose of local anaesthetic (Lignocaine 2%w/v, Lignol, Mass Pharma (Pvt) Ltd., Pakistan) was also administered into the gum. The tooth was removed from the lower jaw using a dental elevator and stored at -20^{o}C until processing. All length measurements were standard nose-tail lengths. Over the 30-year period spanning this study, all sampling was carried out under a series of Home Office Licences issued to the University of St Andrews and the University of Aberdeen under the Animal (Scientific Procedures) Act 1986 (PPL numbers 60/3303, 60/4009 and 192CBD9F), following approval by their respective Animal Welfare and Ethics Committees. Licences to capture and release animals in the wild for research was also granted by Marine Scotland Licensing and the Scottish Office.

Age estimation from growth layer groups in incisor teeth

Growth layer groups (GLGs) in the cementum of the incisor teeth from the live animals were counted from decalcified, stained sections (Dietz et al., 1991) using a light microscope at 10x magnification and photomicrographs enhanced by Adobe Photoshop where necessary.

The von Bertalanffy growth function (von Bertalanffy, 1951) has been used to investigate growth in many mammalian species, including seals (Childerhouse, Dawson, Fletcher, Slooten, & Chilvers, 2010) and age-length curves were thus fitted to the data for each group of harbour seals as follows:

$$E[L|t] = L_\infty(1 - e^{-K(t - t_0)})$$

Where L_∞ is the asymptote for the model of average length-at-age, K is the 'Brody' growth rate parameter (units are yr^{-1}), or the rate at which L_∞ is approached, and t_0 is the age of the animal at zero length if it had always grown in a manner described by the equation. The model was fitted using the *nls* function in the programme R (R Core Team, 2013). The 95% confidence limits were calculated from 1000 bootstrapped resampling of the data. Comparisons between the three parameters from the von Bertalanffy growth curves (L_∞, K and t_0) were carried out using likelihood ratio tests (LRT) (Kimura, 1980).

RESULTS

Overall age-length relationships by sex

A total of 658 harbour seals with age and length data were included in this analysis, 294 males and 364 females caught between 1988 and 2017 (Table 1). The frequency distribution of all the aged animals by year of capture is shown in Figure 1. The bimodal distributions reflect the variation in capture effort. The first set of samples was obtained from captures during a six-year study of the ecology of harbour seals in the Moray Firth (Thompson, Mackay, Tollit, Enderby, & Hammond, 1998; Thompson, Tollit, Corpe, Reid, & Ross, 1997) which followed the1988 phocine distemper epidemic (Thompson, Thompson, & Hall, 2002). More recently studies have been carried out to investigate the movements, dive behaviour, health and the genetic population structure of harbour seals all around the UK, resulting in a variable number of animals being captured in different regions and years. Despite this additional effort, the largest regional contributor remained the Moray Firth.

Growth models were fitted separately to the data for males and females. Table 2 shows the estimates for the three model parameters and their asymptotic 95% confidence intervals. The asymptotic length (L_∞) for the males was 149.4 cm (95% CI 147.8, 151.1) and the Brody growth parameter (K) was 0.327 yr^{-1} (95% CI 0.285, 0.370, Figure 2a, Table 2). For females the asymptotic length was approximately 9 cm less at 140.5 cm (95% CI 139.4, 141.6) whilst the growth parameter was 0.114 yr^{-1} higher at 0.441 yr^{-1} (95% CI 0.395, 0.488, Figure 2b, Table 2). This indicates that, in general, the early growth for all females is higher than for males whilst overall length at maturity is lower. Males reached 90% of their asymptotic length (an indication of age at maturity, (Laws, 1956)) by the age of 4.26 yr. In females, 90% asymptotic length was reached by the age of 3.20 yr.

Differences in growth among Management Units

There were insufficient data to fit a curve to the male data for the North Coast and Orkney Management Unit. Although there were 38 animals with age-length information, these were all adults (Table 1). The mean length for these males was 148.6 cm (95% CI 146.6, 150.6). For Northern Ireland there were only seven males in total (mean length 143.8 cm, 95% CI 138.4, 149.3). Similarly, for the females, there were insufficient data to fit curves for Northern Ireland (all adults, mean length 132.0 cm, 95% CI 109.3, 154.8) and East Scotland (all adults 132.9 cm, 95% CI 128.4, 137.3) and the dataset for females in Shetland was based on only four data points (Table 1).

Males from the Moray Firth and Southeast England reached similar asymptotic lengths which were generally slightly longer than males from the other Management Units, but their growth rates were slower and age at zero length (t_0) was lower (Table 2). However, results of the LRT comparisons for the growth model parameters among the different MUs for which there were sufficient data indicated these differences were not significant (see Supporting Information, Table S1). The only pairwise comparison that was significant was the males from the East Scotland MU were significantly shorter than animals from the Moray Firth and West Scotland ($p=0.001$ and $p=0.004$ respectively). The conservative use of Bonferroni adjustment for multiple comparisons increased the significance level to $p=0.008$ so although the results indicated the East Scotland animals were also shorter than males from Shetland and Southeast England, they were not significant ($p>0.008$). However, Rothman (1990) has contested the need for adjustments due to multiple comparisons because the cost of this is to increase the frequency of finding no statistical relationship. Therefore, taking the standard approach of significance at $p<0.05$ indicates that east coast males are now shorter (by approximately 9 cm) than harbour seals from elsewhere in the UK. Males from the east coast also had a significantly higher Brody growth parameter and age at zero length than the animals from the Moray Firth but not any other regions. For the females there was no significant difference in the growth parameters among the regions (see Supporting Information, Table S1). Unfortunately, there were insufficient data to fit growth curves by region and year of birth to investigate changes that could be related to differences in seal density due to the 1988 and 2002 seal epidemics (see Harding et al., 2018). Indeed, samples from Southeast England, where the epidemic-related effects of change in density may have been most pronounced, did not contain any individuals born before 2002. When combining the data across all Management Units, there was no relationship between the residuals around the age-length relationships by year of capture or year of birth, for either males or females (data not shown).

Growth in harbour seals in the Moray Firth compared to other Management Units.

Harbour seals captured in the Moray Firth contributed the largest (n=309) and longest time series (1988 – 2017). A comparison between these data and growth curves from the other individual

Management Units was unfortunately not possible because there were insufficient data to make a robust comparison. However, it was possible to compare the Moray Firth with all other MUs as combined they produced a similar size dataset (n=349). Since only one group (East Scotland males) were found to be different in the pairwise comparisons, it was possible to amalgamate these data. The parameter estimates from the fitted von Bertalanffy growth models for the Moray Firth males and females compared to all the other regions combined across all years are shown in Table 3. There was no significant difference in the asymptotic lengths but there was a significant difference in the Brody growth parameter (K) with Moray Firth males being lower than other regions (Moray Firth = 0.259, Other Regions = 0.441, LRT p=0.020) and age at zero length (t_0) parameter (Moray Firth = -3.53, Other Regions = -2.00, LRT p=0.020). Thus, early growth was lower for Moray Firth males indicating it took longer for them to reach the asymptotic length compared to the other regions. Among the females, there was no significant difference about the growth parameters.

The samples obtained from the harbour seals in Moray Firth MU spanned a period of 29 years, making it possible to explore temporal variation in growth parameters. Figure 3a shows the residuals around the von Bertalanffy growth function fitted to the Moray Firth male data, by two-year categories, noting that animals were not captured every year. There was no observable trend in the residuals over time, except that the animals captured in 1990-1991 were significantly larger (linear model without an intercept to determine which year categories are significantly different from zero, p=0.003) for their age. By contrast those captured in 2012-2013 were significantly smaller (linear model, p=0.0002, Figure 3a). A similar relationship was explored among the females from the Moray Firth and again no observable trend was found, with the exception that females were larger for their age captured in 1994-1995 (Figure 3b, p=0.038). These temporal variations did not correlate with any observed changes in the population trends (Thompson et al., 2019).

DISCUSSION

This study comprises the most comprehensive analysis of harbour seal age-length data from live captured and released animals from the UK to date. Age was estimated from counts of growth layer groups in the incisor teeth which is a well-established method for phocid seals (Bernt et al., 1996; Blundell & Pendleton, 2008; Lydersen & Kovaks, 2005).

In general, male harbour seals were approximately 9 cm longer at maturity than females and reached 90% of their asymptotic length almost one year later than females. Härkönen and Heide-Jorgensen (1990) found that females in East Atlantic populations reached sexual maturity at 87% of their asymptotic length. Boulva & McClaren, (1979) reported this to be 93% for the harbour seals in Eastern Canada, and Laws (1956) suggested that in general seals mature at between 80 and 90% of their asymptotic length. Independent information on sexual maturity for the UK harbour seals was not available, but our results also match with Gardiner, Boyd, Racey, Reijnders, and Thompson (1996) who suggested a length of 125 cm for mature females, which is 89% of the overall estimated asymptotic length of 140 cm for all the females in this study. Other studies of harbour seal populations in Europe, the Arctic, Canada and Alaska reported slightly greater asymptotic lengths with the exception of harbour seals in the Skagerrak and Svalbard (asymptotic lengths: 139 cm in the Skagerrak; 145 cm in the Kattegat, 137 cm in Limfjorden, and 150 cm in the Western Baltic (Harding et al., 2018); 147 cm in Norway (Markussen, Bjorge, & Oritsland, 1989), 140 cm in Svalbard (Lydersen & Kovacs, 2005), 143 cm in Eastern Canada (Boulva & McClaren, 1979), 148 cm in British Columbia (Bigg, 1969), and 148 cm in Alaska (Hutchinson, Atkinson, & Hoover-Miller, 2016)).

Similarly, asymptotic lengths reported for male harbour seals in the same regions (except Alaska where only females were studied) were longer than the overall estimate for UK males of 149 cm with the exception of the Skagerrak and Limfjorden where male asymptotic lengths were also estimated at 149 cm (Harding et al., 2018) (Kattegat 160cm, Western Baltic 167 cm, (Harding et al., 2018) Norway 155 cm (Markussen et al., 1989), Svalbard 153 cm (Lydersen & Kovacs, 2005), Eastern Canada 154 cm (Boulva & McClaren, 1979) and British Columbia 161 cm (Bigg, 1969)). Some of this variation may be due to measurement differences obtained from live-captured compared to dead animals. All of the studies referred to above obtained their measurements from carcasses (hunted or dead stranded) with the exception of those in Svalbard. Thus, due to the sexual dimorphism, regional and temporal patterns in growth, size needs to be considered separately for each sex.

Although there were a few regional differences among the sex-specific age-length von Bertalanffy growth parameters, only one was statistically significant. Over all age classes, males were significantly shorter for their age in the East Scotland MU compared to the seals sampled from the other MUs. This is the harbour seal MU where the population abundance has declined most rapidly (Lonergan et al., 2007; SCOS, 2017; Thompson et al., 2019). Unfortunately, it was not possible to investigate any trends over the time spanning the identified decline period (since around 2000 to the present), as the animals were largely captured in two years, 2008 and 2012. It may well be that animals in the East Scotland MU had reduced somatic growth during the period of decline, which could indicate reduced prey intake or reduced prey quality affecting the intake of important nutrients (Calkins et al., 1998), particularly protein required for robust skeletal growth (Carreira et al., 2014; Gat-Yablonski & De Luca, 2017). This is in line with ecological theory, which suggests that population declines driven by bottom-up processes such as resource limitations, would result in slower growth and a delayed mean age at sexual maturity (Stearns, 1976). However, we cannot rule out the possibility that observed differences in male size were related to unknown levels of regional variation in the intensity of sexual selection.

Harbour seals in the Moray Firth have been studied since the late 1980s (Thompson & Miller, 1990) and this region contributed the largest temporal age-length dataset. Interestingly, despite large fluctuations in the population size during this time, due to a combination of factors (Matthiopoulos et al., 2014; Thompson, Mackey, Barton, Duck, & Butler, 2007), the length-at-age data did not show any substantial or biologically significant variation in the residuals around the growth function over time. This would suggest, at least for the captured individuals, the observed changes in population dynamics and abundance were not associated with changes in growth. Similarly, Cordes, and Thompson (2013) concluded that an advance in pupping date during a period of decline was likely to be related to top down (direct removals) rather than bottom up processes.

In the past, information on length-at-age was often restricted to populations which had been harvested (Blundell & Pendleton, 2008; Boulva & McClaren, 1979) or subject to major disease outbreaks (Härkönen & Heide-Jorgensen, 1990). This often constrains temporal and regional comparison of growth patterns, especially for those populations which are of conservation concern. There are no previously published age-at-length curve data for UK harbour seals, and such information exists for only a few other north-east Atlantic populations (Harkonen & Heide Jorgensen, 1990; Lydersen & Kovacs, 2005; Markussen et al., 1989). The most detailed study in European waters recently investigated changes in the growth of harbour seals in Danish and Swedish waters (Harding et al., 2018), and found evidence for density dependent phenotypic changes. Seals born in cohorts during periods of lower abundance were longer at adulthood. However, their study included a very large sample of over 1,400 individuals which indicates the magnitude of the dataset required to detect such changes.

Errors associated with the age estimates, due to indistinct layers in some teeth, were not included in this analysis. Whilst this can be an important source of measurement error, Blundell and Pendleton’s (2008) comparison of age estimates from paired incisors and canines found no bias associated with including lower certainty estimates. It should also be recognized that measurement error associated with the standard nose-tail length measurements of these live seals was not formally included, and the results presented here should be interpreted recognizing that these sources of uncertainty have not been taken into account.

There were insufficient data to fully explore changes in somatic growth with respect to the major variations in population dynamics that UK harbour seals have experienced over the last 30 years. Nevertheless, for Management Units where acute population declines have been observed, particularly

Southeast England following PDV outbreaks (see Thompson et al., 2019), increases in asymptotic length may have been expected (Harding et al., 2018). However, this effect may not be observed if the disease predominantly affects adults, as was suspected to be the case in Southeast England (Hall et al., 1992). Although harbour seal populations in Scotland were much less affected by PDV, they have seen major changes in their populations (Thompson et al., 2019). Longer-term declines in abundance may also result in changes in growth depending on the drivers. For example, lack of prey may affect juvenile growth through nutritional stress. However, reductions in population density may result in the opposite effect. Unfortunately, there were insufficient data to explore these competing hypotheses. Nevertheless, evidence of significantly shorter male seals in the East Scotland Management Unit indicate either that bottom up impacts are driving the 18.5% p.a. decline observed between 2000 and 2017 (SCOS, 2017) or that differential mortality has resulted in smaller animals remaining in the population.

Intensive live-capture release efforts to study harbour seal biology have provided an extensive dataset for this study. Nevertheless, there was limited power to make direct comparisons among populations due to variation in sample sizes between years, and spatial and temporal differences in sampling effort. In future, the development of remote photogrammetric methods have the potential to provide more systematic comparisons of population size structure (Sweeney, Shertzer, Fritz, & Read, 2014) and condition (Fearnbach, Durban, Ellifrit, & Balcomb, 2018; Krause, Hinke, Perryman, Goebel, & LeRoi, 2017) which may provide additional insights into regional drivers of population change that are impacting population age structure and growth. However, whilst this would indicate gross changes, specific information on age would still be required because animals could only be assigned to age classes from photographs. Determining if there has been a shift in growth or structural parameters across regions would help to narrow down the potential causes for the observed declines in abundance. Evidence from Harding et al. (2018) suggests that a time-series of asymptotic length data may indicate when populations have reached carrying capacity and can provide a more general indicator of nutritional stress. Such reductions in growth may result from variation in the abundance or quality of prey, or through changes in competition either within or between species. Whilst these data provide important evidence for the stakeholders developing conservation strategies for different regions, the underlying causes of reduced growth would also need to be identified to assess whether effective management measures can be developed.

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REFERENCES

Bernt, K.E., Hammill, M.O., & Kovacs, K.M. (1996). Age estimation of grey seals (*Halichoerus grypus*) using incisors. *Marine Mammal Science,* 12, 476-482.

Bigg, M. A. (1969). The harbour seal in British Columbia. *Bulletin of the Fisheries Research Board of Canada,* 172, 1-33.

Brownlow, A., Onoufriou, J., Bishop, A., Davison, N., & Thompson, D. (2016). Corkscrew Seals: Grey Seal (*Halichoerus grypus*) Infanticide and Cannibalism May Indicate the Cause of Spiral Lacerations in Seals. *PLoS ONE,* 11, e0156464. doi.org/10.1371/journal.pone.0156464

Blundell, G. M., & Pendleton, G. W. (2008). Estimating age of harbor seals (*Phoca vitulina*) with incisor teeth and morphometrics. *Marine Mammal Science,* 24, 577-590. doi:10.1111/j.1748-7692.2008.00194.x

Boulva, J., & McClaren, I. A. (1979). Biology of the harbor seal, Phoca vitulina, in Eastern Canada. *Bulletin of the Fisheries Research Board of Canada,* 200, 1-24.

Calkins, D.G., Becker, E.F., & Pitcher, K.W. (1998). Reduces body size of female Stellar sea liuons from a declining population in the GFulf of Alaska. *Marine Mammal Science,* 14, 232-244. doi: 10.1111/j.1748-7692.1998.tb00713.x

Carreira, A. C., Lojudice, F. H., Halcsik, E., Navarro, R. D., Sogayar, M. C., & Granjeiro, J. M. (2014). Bone Morphogenetic Proteins Facts, Challenges, and Future Perspectives. *Journal of Dental Research,* 93, 335-345. doi:10.1177/0022034513518561

Childerhouse, S. J., Dawson, S. M., Fletcher, D. J., Slooten, E., & Chilvers, B. L. (2010). Growth and reproduction of female New Zealand sea lions. *Journal of Mammalogy,* 91, 165-176. doi:10.1644/09-mamm-a-110r.1

Cordes, L. S., & Thompson, P. M. (2013). Variation in breeding phenology provides insights into drivers of long-term population change in harbour seals. *Proceedings of the Royal Society B-Biological Sciences,* 280. doi:ARTN 20130847 10.1098/rspb.2013.0847

Dietz, R., Heide-Jorgensen, M. P., Härkönen, T., Teilmann, J., & Valentin, N. (1991). Age-Determination of European Harbor Seal, *Phoca vitulina* L. *SARSIA,* 76, 17-21.

Fearnbach, H., Durban, J. W., Ellifrit, D. K., & Balcomb, K. C. (2018). Using aerial photogrammetry to detect changes in body condition of endangered southern resident killer whales. *Endangered Species Research,* 35, 175-180.

Gardiner, K. J., Boyd, I. L., Racey, P. A., Reijnders, P. J. H., & Thompson, P. M. (1996). Plasma progesterone concentrations measured using an enzyme-linked immunosorbent assay useful for diagnosing pregnancy in harbor seals (*Phoca vitulina*). *Marine Mammal Science,* 12, 265-273.

Gat-Yablonski, G., & De Luca, F. (2017). Effect of Nutrition on Statural Growth. *Hormone Research in Paediatrics,* 88, 46-62. doi:10.1159/000456547

Gibbens, J., & Arnould, J. P. Y. (2009). Age-specific growth, survival, and population dynamics of female Australian fur seals. *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* 87, 902-911. doi:10.1139/z09-080

Grandi, M. F., Dans, S. L., Garcia, N. A., & Crespo, E. A. (2010). Growth and age at sexual maturity of South American sea lions. *Mammalian Biology,* 75, 427-436. doi:10.1016/j.mambio.2009.09.007

Hall, A. J., Pomeroy, P., & Harwood, J. (1992). The descriptive epizootiology of phocine distemper in the UK during 1988/89. *Science of the Total Environment,* 115, 31-44.

Hall, A. J., & Frame, E. (2010). Evidence of domoic acid exposure in harbour seals from Scotland: A potential factor in the decline in abundance? *Harmful Algae,* 9, 489-493.

Härkönen, T., & Heide-Jorgensen, M.-P. (1990). Comparative life histories of east Atlantic and other harbour seal populations. *Ophelia,* 32, 211-235.

Harding, K., Salmon, M., Teilmann, J., Dietz, R., & Härkönen, T. (2018). Population Wide Decline in Somatic Growth in Harbor Seals—Early Signs of Density Dependence. *Frontiers in Ecology and Evolution*, 6, 59. doi: 10.3389/fevo.2018.00059.

Holmes, E. E., & York, A. E. (2003). Using Age Structure to Detect Impacts on Threatened Populations: a Case Study with Steller Sea Lions. *Conservation Biology,* 17, 1794-1806. doi:doi:10.1111/j.1523-1739.2003.00191.x

Hutchings, J. A., Myers, R. A., Garcia, V. B., Lucifora, L. O., & Kuparinen, A. (2012). Life-history correlates of extinction risk and recovery potential. *Ecological Applications,* 22, 1061-1067.

Hutchinson, E., Atkinson, S., & Hoover-Miller, A. (2016). Growth and reproductive tracts from fetal to adult harbor seals in the Gulf of Alaska. *Marine Ecology Progress Series,* 557, 277-288. doi:10.3354/meps11832

Jones, E. L., Hastie, G. D., Smout, S., Onoufriou, J., Merchant, N. D., Brookes, K., & Thompson, D. (2017). Seals and shipping: quantifying population risk and individual exposure to vessel noise. *Journal of Applied Ecology*, 54, 1930-1940. doi:10.1111/1365-2664.12911

Kimura, D. K. (1980). Likelihood Methods for the Vonbertalanffy Growth Curve. *Fishery Bulletin,* 77, 765-776.

Krafft, B. A., Kovacs, K. M., Frie, A. K., Haug, T., & Lydersen, C. (2006). Growth and population parameters of ringed seals (*Pusa hispida*) from Svalbard, Norway, 2002-2004. *ICES Journal of Marine Science,* 63, 1136-1144. doi:10.1016/j.icesjms.2006.04.001

Krause, D. J., Hinke, J. T., Perryman, W. L., Goebel, M. E., & LeRoi, D. J. (2017). An accurate and adaptable photogrammetric approach for estimating the mass and body condition of pinnipeds using an unmanned aerial system. *PLoS ONE,* 12, e0187465. doi:10.1371/lournal.pone.0187465

Laws, R. M. (1956). Growth and sexual maturity in aquatic mammals. *Nature,* 178, 193-194. doi:10.1038/178193a0

Lidgard, D. C., Bowen, W. D., & Boness, D. J. (2012). Longitudinal changes and consistency in male physical and behavioural traits have implications for mating success in the grey seal (*Halichoerus grypus*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* 90, 849-860. doi:10.1139/z2012-053

Lonergan, M., Duck, C. D., Thompson, D., Mackey, B. L., Cunningham, L., & Boyd, I. L. (2007). Using sparse survey data to investigate the declining abundance of British harbour seals. *Journal of Zoology,* 271, 261-269. doi:10.1111/j.1469-7998.2007.00311.x

Lunn, N. J., Boyd, I. L., & Croxall, J. P. (1994). Reproductive-Performance of Female Antarctic Fur Seals - the Influence of Age, Breeding Experience, Environmental Variation and Individual Quality. *Journal of Animal Ecology,* 63, 827-840. doi:10.2307/5260

Lydersen, C., & Kovacs, K. M. (2005). Growth and population parameters of the world's northernmost harbour seals *Phoca vitulina* residing in Svalbard, Norway. *Polar Biology,* 28, 156-163. doi:10.1007/s00300-004-0656-7

Lynch, H. J., & Fagan, W. F. (2009). Survivorship curves and their impact on the estimation of maximum population growth rates. *Ecology,* 90, 1116-1124. doi:10.1890/08-0286.1

Markussen, N. H., Bjorge, A., & Oritsland, N. A. (1989). Growth in harbour seals (*Phoca vitulina*) on the Norwegian coast. *Journal of Zoology,* 219, 433-440.

Matthiopoulos, J., Cordes, L., Mackey, B., Thompson, D., Duck, C., Smout, S., . . . Thompson, P. (2014). State-space modelling reveals proximate causes of harbour seal population declines. *Oecologia,* 174, 151-162. doi:10.1007/s00442-013-2764-y

McLaren, I. A. (1993). Growth in Pinnipeds. *Biological Reviews of the Cambridge Philosophical Society,* 68, 1-79.

Olsen, M. T., Islas, V., Graves, J. A., Onoufriou, A., Vincent, C., Brasseur, S., . . . Hall, A. J. (2017). Genetic population structure of harbour seals in the United Kingdom and neighbouring waters. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 27, 839-845. doi:10.1002/aqc.2760

R Core Team. (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reijnders, P. J. H., Ries, E. H., Tougaard, S., Nørgaard, N., Heidemann, G., Schwarz, J., . . . Traut, I. M. (1997). Population development of harbour seals Phoca vitulina in the Wadden Sea after the 1988 virus epizootic. *Journal of Sea Research,* 38, 161-168. doi:http://dx.doi.org/10.1016/S1385-1101(97)00031-2

Rothman KJ (1990) No adjustments are neede for multiple comparisons. *Epidemiology*, 1, 43-46

SCOS. (2017). *Special Committee on Seals: Scientific Advice on Matters Related to the Management of Seal Populations 2017.* Sea Mammal Research Unit, University of St Andrews, St Andrews, 144pp.

Stearns, S. C. (1976). Life-history tactics: a review of the ideas. *The Quarterly Review of Biology,* 51, 3-47.

Sweeney, K. L., Shertzer, K. W., Fritz, L. W., & Read, A. J. (2014). A novel approach to compare pinniped populations across a broad geographic range. *Canadian Journal of Fisheries and Aquatic Sciences,* 72, 175-185. doi:10.1139/cjfas-2014-0070.

Thompson, D., Duck, C., Morris, C. & Russell, D.J.F. (2019). The status of harbour seals (*Phoca vitulina*) in the United Kingdom. *Aquatic Conservation: Marine and Freshwater Ecosystems*.

Thompson, P. M., & Hall, A. J. (1993). Seals and Epizootics - What Factors Might Affect the Severity of Mass Mortalities. *Mammal Review,* 23, 149-154. doi:DOI 10.1111/j.1365-2907.1993.tb00427.x

Thompson, P. M., Mackay, A., Tollit, D. J., Enderby, S., & Hammond, P. S. (1998). The influence of body size and sex on the characteristics of harbour seal foraging trips. *Canadian Journal of Zoology,* 76, 1044-1053. doi:DOI 10.1139/cjz-76-6-1044

Thompson, P. M., Mackey, B., Barton, T. R., Duck, C., & Butler, J. R. A. (2007). Assessing the potential impact of salmon fisheries management on the conservation status of harbour seals (*Phoca vitulina*) in north-east Scotland. *Animal Conservation,* 10, 48-56. doi:10.1111/j.1469-1795.2006.00066.x

Thompson, P. M., & Miller, D. (1990). Summer Foraging Activity and Movements of Radio-Tagged Common Seals (*Phoca vitulina* L) in the Moray Firth, Scotland. *Journal of Applied Ecology,* 27, 492-501.

Thompson, P. M., Thompson, H., & Hall, A. J. (2002). Prevalence of morbillivirus antibodies in Scottish harbour seals. *Veterinary Record,* 151, 609-610. doi:10.1136/vr.151.20.609

Thompson, P. M., Tollit, D. J., Corpe, H. M., Reid, R. J., & Ross, H. M. (1997). Changes in haematological parameters in relation to prey switching in a wild population of harbour seals. *Functional Ecology,* 11, 743-750.

Von Bertalanffy, L. (1951). *Theoretische Biologie*. Bern, Switzerland: A Francke AG Verlag.

Vaughan, R. W. (1978). A study of common seals in the Wash. *Mammal Review,* 8, 25-34.

Commented [MOU1]: Add details when available

Table 1. Number of harbour seals captured and sampled by Management Unit, sex and year.

Region **Year classes**	East Scotland		Moray Firth		North Coast and Orkney		Northern Ireland		Shetland		Southeast England		West Scotland		
Sex	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**F**	**M**	**Total**
1988-1989	0	0	8	5	0	0	0	0	0	0	0	0	0	0	13
1990-1991	0	0	23	24	0	0	0	0	0	0	0	0	0	0	47
1992-1993	0	0	68	39	0	0	0	0	0	0	0	0	0	0	107
1994-1995	0	0	31	22	0	0	0	0	0	0	0	0	0	0	53
1996-1997	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1998-1999	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2
2000-2001	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2
2002-2003	2	1	9	0	0	0	0	0	0	0	0	0	1	0	13
2004-2005	0	0	0	0	0	0	0	0	0	0	2	4	0	0	6
2006-2007	0	0	0	0	25	0	0	0	0	0	0	0	24	0	49
2008-2009	8	14	16	3	18	15	0	0	0	0	0	0	12	15	101
2010-2011	1	4	0	0	2	7	5	7	4	11	0	0	4	10	55
2012-2013	1	11	0	8	5	11	0	0	0	0	15	14	12	13	90
2014-2015	1	3	9	14	0	0	0	0	0	0	0	0	6	2	35
2016-2017	0	0	12	18	26	5	0	0	0	0	0	0	13	11	85
	14	36	176	133	76	38	5	7	4	11	17	18	72	51	658

Table 2. Parameter estimates from the von Bertalanffy growth curves fitted to harbour seal age-length data by sex and regional group.

Group	**L_∞**	**K**	**t_0**
Males			
East Scotland	142.5 (138.6, 146.3)	0.557 (0.202, 0.912)	-1.26 (-2.37, -0.14)
Moray Firth	151.8 (148.1, 155.6)	0.259 (0.210, 0.308)	-3.53 (-4.21, -2.86)
North coast and Orkney	-	-	-
Shetland	151.4 (143.9, 159.0)	0.384 (-0.241, 1.00)	-0.389 (-8.34, 7.56)
Southeast England	152.3 (143.1, 161.6)	0.262 (0.092, 0.432)	-3.82 (-6.64, -1.00)
West Scotland	150.1 (147.4, 152.8)	0.423 (0.254, 0.593)	-2.16 (-3.08, -1.25)
All Males	**149.4 (147.8, 151.1)**	**0.327 (0.285, 0.370)**	**-2.77 (-3.19, -2.35)**
Females			
East Scotland	-	-	-
Moray Firth	138.8 (136.7, 140.9)	0.411 (0,344, 0.476)	-2.39 (-2.82, -1.96)
North Coast and Orkney	142.7 (140.8, 144.6)	0.530 (0.337, 0.722)	-1.56 (-2.19, -0.935)
Shetland[1]	150.1 (148.8, 151.3)	0.233 (0.207, 0.260)	-4.55 (-5.04, -4.06)
Southeast England	142.8 (138.8, 146.8)	0.396 (0.153, 0.640)	-2.73 (-4.81, -0.652)
West Scotland	141.7 (139.1, 144.3)	0.407 (0.302, 0.512)	-1.98 (-2.50, -1.46)
All Females	**140.5 (139.4, 141.6)**	**0.441 (0.395, 0.488)**	**-2.02 (-2.27, -1.78)**

[1] Note : This relationship is based on only four data points.

Table 3. Comparison between the growth parameters for the Moray Firth compared to the other MUs. The overall comparison tests are $L\infty_{mf} = L\infty_{o}$, $K_{mf}=K_o$ and $t_{0mf}=t_{0o}$ where subscripts mf and o represent Moray Firth and Other MUs respectively.

Group	**Asymptote ($L\infty$) (95% confidence interval)**	*p*	***K* (95% confidence interval)**	*p*	**t_0 (95% confidence interval)**	*p*	Overall
Males							
Moray Firth	151.8 (148.1, 155.6)	0.065	0.259 (0.210, 0.308)	**0.020**	-3.53 (-4.21, -2.86)	**0.020**	0.104
Other Regions	148.1 (146.5, 149.8)		0.441 (0.339, 0.544)		-2.00 (-2.58, -1.42)		
Females							
Moray Firth	138.8 (136.7, 140.9)	0.300	0.411 (0,344, 0.476)	0.313	-2.39 (-2.82, -1.96)	0.330	0.126
Other Regions	141.4 (140.0, 142.8)		0.459 (0.372, 0.546)		-1.82 (-2.19, -1.45)		

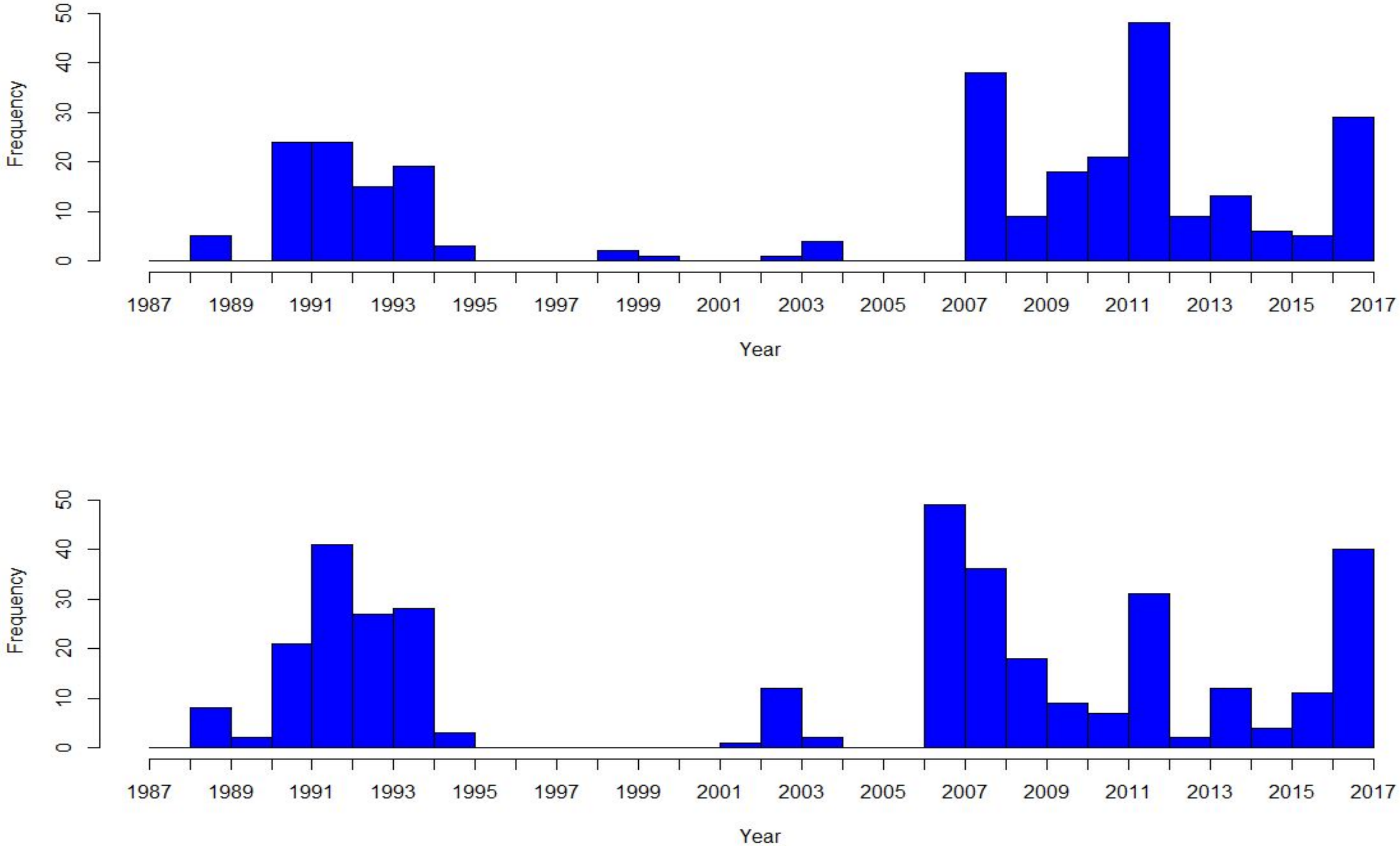


Figure 1. Frequency distributions by year of capture for aged (a) male n= 294 and (b) female n= 364 UK harbour seals.

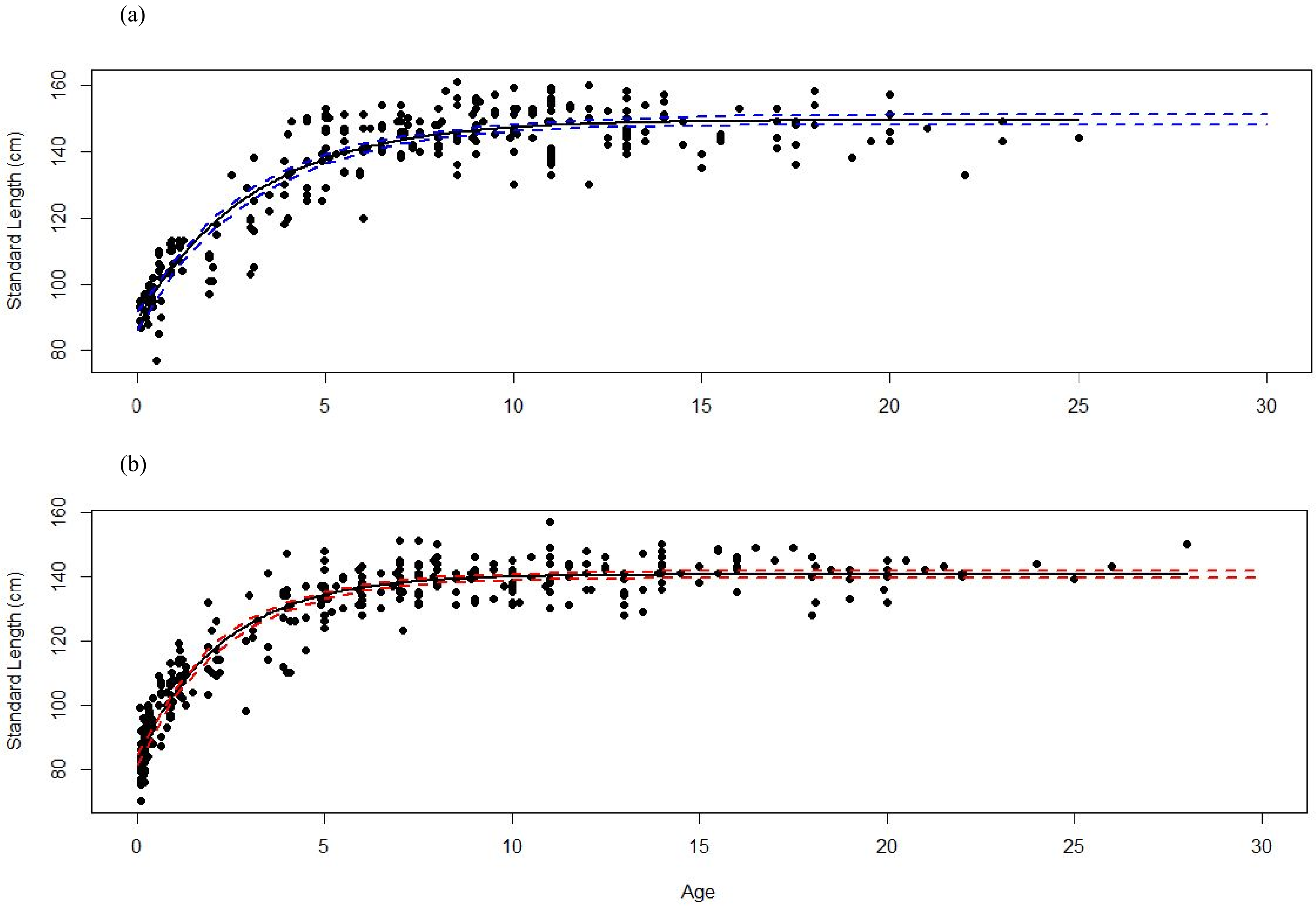
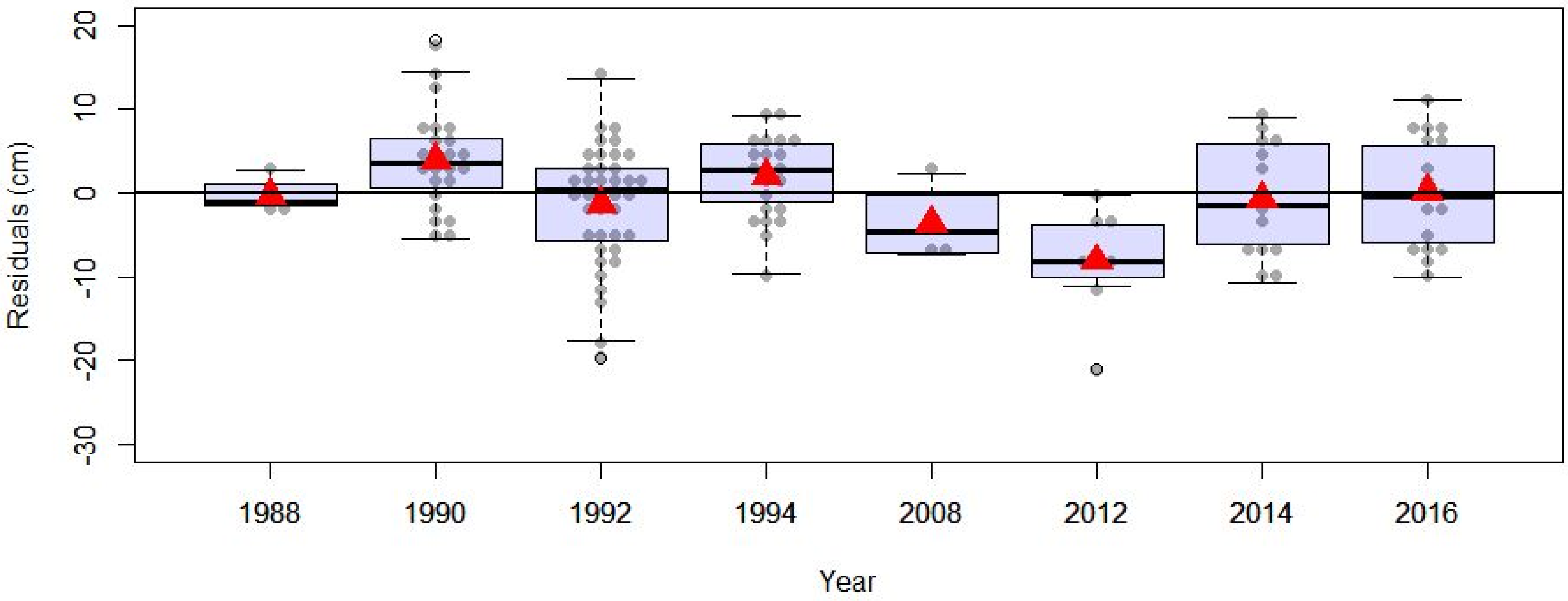


Figure 2. Von Bertalanffy fitted growth curves for (a) male and (b) female harbour seals.

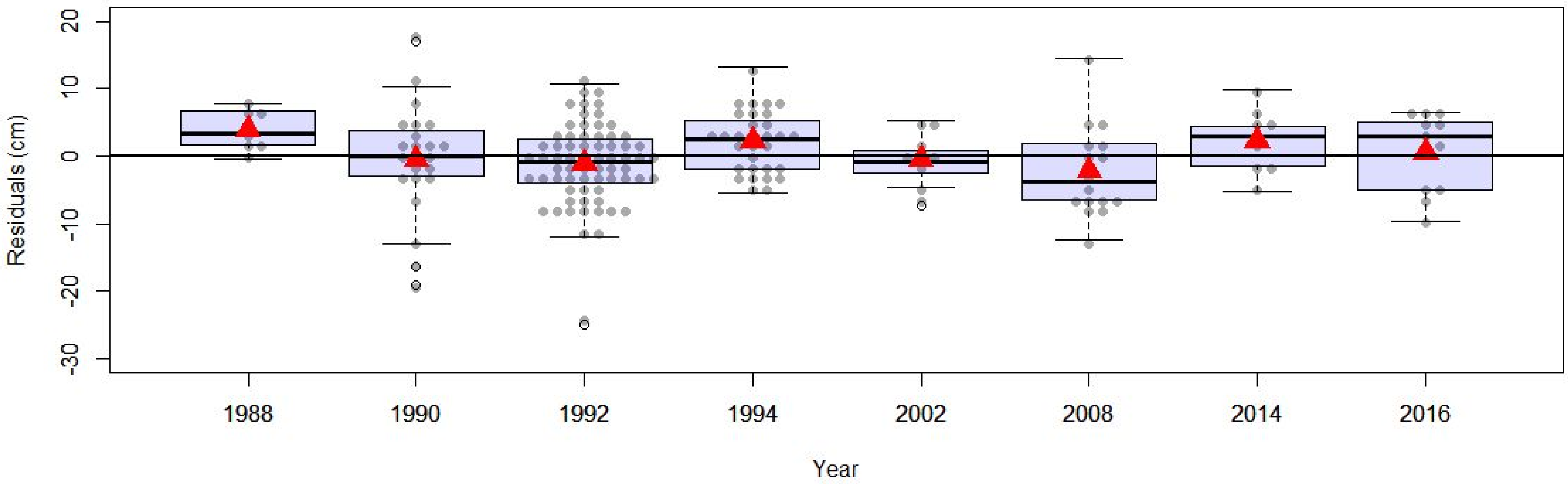
(a)



n = 4 24 39 22 4 8 14 18

Figure 3a. Residuals around the Von Bertalanffy growth function for the male harbour seals captured in the Moray Firth by year of capture. The boxplots show the median and quartiles, grey points are the data and the red triangles are the mean residuals by two year classes. Note that animals were not captured every year.

(b)



n = 8 23 68 31 9 16 9 12

Figure 3b. Residuals around the Von Bertalanffy growth function for the female harbour seals captured in the Moray Firth by year of capture. The boxplots show the median and quartiles, grey points are the data and the red triangles are the mean residuals by two year classes. Note that animals were not captured every year.

Figure 1. Frequency distributions by year of capture for aged (a) male n= 294 and (b) female n= 364 UK harbour seals.

Figure 2. Von Bertalanffy fitted growth curves for (a) male and (b) female harbour seals.

Figure 3. Residuals around the Von Bertalanffy growth function for the male harbour seals captured in the Moray Firth by year of capture. The boxplots show the median and quartiles, grey points are the data and the red triangles are the mean residuals by two year classes. Note that animals were not captured every year.