

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

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21

22 **ABSTRACT**

23 1. The abundance of harbour seals (*Phoca vitulina*) in the UK as a whole has increased over the past  
24 10 years, after a 30% decline during the preceding 10 years and two major viral epidemics. However,  
25 population trends vary greatly among regions, with those on the east coast of Scotland and in the  
26 northern isles experiencing dramatic declines since the early 2000s and populations on the west coast  
27 being either stable or increasing. The reasons for these differences in population dynamics are  
28 unknown.

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

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

40 4. Asymptotic lengths at maturity across all regions were slightly lower than published lengths for  
41 harbour seal populations in Europe, the Arctic and Canada, with females being on average 140.5 cm  
42 (95% CI, 139.4, 141.6) and males 149.4 cm (147.8, 151.1) at adulthood.

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

46

## 47 INTRODUCTION

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

63

64 Management Units are spatially discrete regions or populations that have been established to enable  
65 stakeholders responsible for the conservation and management of marine mammals to achieve the best  
66 conservation outcomes for a species. In Scotland, the Units for seals are referred to as Management  
67 Areas and, for harbour seals, were adopted following the introduction of the Marine Scotland Act  
68 (2010). They were defined based on available information on harbour seals ecology, and now  
69 underpin regional assessments undertaken by Marine Scotland when issuing seal licences. Across the  
70 UK seal Management Units have been endorsed by the Joint Nature Conservation Council and the  
71 relevant Statutory Nature Conservation Bodies. Further details of their spatial extent and the long-  
72 term population trends within each Unit can be found in Thompson, Duck, Morris, & Russell  
73 (submitted). The genetic distinctiveness of the harbour seal Management Units and thus the structure  
74 of the UK harbour seal as a metapopulation has recently been explored by Olsen et al., (2017). They  
75 found that the spatial designation of the MUs was largely in agreement with the genetic population  
76 structure results, supporting the spatial basis for managing harbour seals in the UK within these  
77 regional boundaries.

78

79 Some populations of harbour seals with the Management Units around the Scottish coast are currently  
80 in decline, particularly those in the northern isles and on the east coast (Lonergan et al., 2007; SCOS,  
81 2017). For example, the abundance of harbour seals in Orkney has declined by 10% per annum since  
82 1997. In the Firth of Tay and Eden Estuary Special Area of Conservation, the number of seals counted

83 during their annual moult in August, 2016 represented a 90% decrease from the mean number  
84 recorded between 1990 and 2002 (SCOS, 2017). Thus, although these recent abundance data suggests  
85 this trend is continuing for some populations, others, such as those in the West Scotland and the  
86 Western Isles Management Units, have been stable or increasing over the same time period (SCOS,  
87 2017). The reasons for these declines are not clear but potential factors include increased competition  
88 for food by sympatric grey seals (*Halichoerus grypus*) and other top piscivorous predators, changes in  
89 prey availability or prey quality, increased predation (Brownlow, Onoufriou, Bishop, Davison, &  
90 Thompson, 2016), interactions with vessels (Jones, Hastie, Smout, Onoufriou, Merchant, Brookes &  
91 Thompson, 2017) and exposure to biotoxins produced by harmful algae (Hall & Frame, 2010).

92  
93 Widespread and dramatic declines in abundance may have impacts on population age structure  
94 (Holmes & York, 2003), which may also affect timing of breeding (Lunn, Boyd, & Croxall, 1994) and  
95 population recovery. For example, following the 1988 phocine distemper virus epidemic among  
96 harbour seals in Northern Europe the rate of increase in the population in the Wadden Sea was  
97 significantly higher after the outbreak (1989-1994 average annual rate 16%) than it was during the  
98 pre-epidemic period (1976-1987 average annual rate 9%), probably as a result of selective mortality  
99 during the epidemic (Reijnders et al., 1997). In UK waters whilst the epidemic caused approximately  
100 a 50% decline in the abundance of animals in Southeast England (Thompson et al., submitted;  
101 Thompson & Hall, 1993), populations in Scotland were affected to a much lesser extent (Hall,  
102 Pomeroy & Harwood, 1992). Nevertheless, such differential mortality factors could result in a  
103 population with a skewed or truncated age distribution, a pattern which may also provide information  
104 on the drivers of changing population dynamics. More recently Harding et al., (2018) found that  
105 harbour seals in the Skagerrak had become significantly shorter over a 14 year period. They suggest  
106 that this could be an early signal of density dependence in this region and aerial surveys for abundance  
107 confirmed declining rates of population increase in the same area. Similar drivers may therefore also  
108 be affecting growth in UK harbour seals where populations have stabilised. Thompson et al.  
109 (submitted) explore the variation in population trends for harbour seals throughout the UK in detail.  
110 Temporal and spatially explicit length-at-age data for harbour seals may therefore assist in  
111 understanding changes in the various population trajectories if they manifest as changes in somatic  
112 growth and morphology. Here, the aim is to examine age-length relationships for harbour seals among  
113 MUs and, where sufficient data are available, relate differences in growth parameters to changes in  
114 population abundance spanning similar timescales.

115  
116 The objectives of this study were therefore to (1) investigate spatial differences in age at maximum  
117 length and age-length growth functions across UK harbour seal Management Units for which data  
118 were available and (2) to investigate temporal changes in growth parameters by year of capture and  
119 year of birth during the period of harbour seal decline in abundance. Significant variations in these

120 parameters may provide insights into the reasons for the decline. However, the direction of any  
121 change is difficult to predict since lower abundance may result in a reduced pressure on remaining  
122 resources and consequent increases in growth. Alternatively if nutritional stress or factors affecting  
123 growth and maturation were a cause of the decline then animals may suffer slower growth and be  
124 shorter for a given age.

125

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

132

### 133 **MATERIALS AND METHODS**

#### 134 *Live captures and collection of harbour seal teeth*

135 Adult and juvenile seals were captured in nets and pups were manually restrained in bags and, where  
136 necessary, were sedated with Zoletil 100 (Virbac, France) at a dose rate of 1ml/100kg body weight  
137 intramuscular or 0.5ml/100kg body weight intravenous. Animals were weighed, measured, sexed and  
138 an incisor tooth removed for aging. A 0.1ml dose of local anaesthetic (Lignocaine 2%w/v, Lignol,  
139 Mass Pharma (Pvt) Ltd., Pakistan) was also administered into the gum. The tooth was removed from  
140 the lower jaw using a dental elevator and stored at -20°C until processing. All lengths measurements  
141 were standard nose-tail lengths. Over the 30 year period spanning this study, all sampling was carried  
142 out under a series of Home Office Licences issued to the University of St Andrews and the University  
143 of Aberdeen under the Animal (Scientific Procedures) Act 1986 (PPL numbers 60/3303, 60/4009 and  
144 192CBD9F), following approval by their respective Animal Welfare and Ethics Committees.

145 Licences to capture and release animals in the wild for research was also granted by Marine Scotland  
146 Licensing and the Scottish Office.

147

#### 148 *Age estimation from growth layer groups in incisor teeth*

149 Growth layer groups (GLGs) in the cementum of the incisor teeth from the live animals were counted  
150 from decalcified, stained sections (Dietz, Heide Jorgensen, Härkönen, Teilmann, & Valentin, 1991)  
151 using a light microscope at 10x magnification and photomicrographs enhanced by Adobe Photoshop  
152 where necessary.

153

154 The von Bertalanffy growth function (von Bertalanffy, 1951) has been used to investigate growth in  
155 many mammalian species, including seals (Childerhouse, Dawson, Fletcher, Slooten, & Chilvers,  
156 2010) and age-length curves were thus fitted to the data for each group of harbour seals as follows:

157

$$158 \quad E[L|t] = L_{\infty}(1 - e^{-K(t-t_0)})$$

159

160

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

168

## 169 **RESULTS**

### 170 *Overall age-length relationships by sex*

171 A total of 658 harbour seals with age and length data were included in this analysis, 294 males and  
172 364 females caught between 1988 and 2017 (Table 1). The frequency distribution of all the aged  
173 animals by year of capture is shown in Fig. 1. The bimodal distributions reflect the variation in  
174 capture effort. The first set of samples was obtained from captures during a six year study of the  
175 ecology of harbour seals in the Moray Firth (Thompson, Mackay, Tollit, Enderby, & Hammond, 1998;  
176 Thompson, Tollit, Corpe, Reid, & Ross, 1997) which followed the 1988 phocine distemper epidemic  
177 (Thompson, Thompson, & Hall, 2002). More recently studies have been carried out to investigate the  
178 movements, dive behaviour, health and the genetic population structure of harbour seals all around the  
179 UK, resulting in a variable number of animals being captured in different regions and years. Despite  
180 this additional effort, the largest regional contributor remained the Moray Firth.

181

182 Growth models were fitted separately to the data for males and females. Table 2 shows the estimates  
183 for the three model parameters and their asymptotic 95% confidence intervals. The asymptotic length  
184 ( $L_{\infty}$ ) for the males was 149.4 cm (95% CI 147.8, 151.1) and the Brody growth parameter ( $K$ ) was  
185  $0.327 \text{ yr}^{-1}$  (95% CI 0.285, 0.370, Fig. 2a, Table 2). For females the asymptotic length was  
186 approximately 9 cm less at 140.5 cm (95% CI 139.4, 141.6) whilst the growth parameter was  $0.114 \text{ yr}^{-1}$   
187 higher at  $0.441 \text{ yr}^{-1}$  (95% CI 0.395, 0.488, Fig. 2b, Table 2). This indicates that, in general, the early  
188 growth for all females is higher than for males whilst overall length at maturity is lower. Males

189 reached 90% of their asymptotic length (an indication of age at maturity, (Laws, 1956)) by the age of  
190 4.26 yr. In females, 90% asymptotic length was reached by the age of 3.20 yr.

191

### 192 *Differences in growth among Management Units*

193 There were insufficient data to fit a curve to the male data for the North Coast and Orkney  
194 Management Unit. Although there were 38 animals with age-length information, these were all adults  
195 (Table 1). The mean length for these males was 148.6 cm (95% CI 146.6, 150.6). For Northern  
196 Ireland there were only 7 males in total (mean length 143.8 cm, 95% CI 138.4, 149.3). Similarly for  
197 the females, there were insufficient data to fit curves for Northern Ireland (all adults, mean length  
198 132.0 cm, 95% CI 109.3, 154.8) and East Scotland (all adults 132.9 cm, 95% CI 128.4, 137.3) and the  
199 dataset for females in Shetland was based on only four data points (Table 1).

200

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

224

225 *Growth in harbour seals in the Moray Firth compared to other Management Units.*  
226 Harbour seals captured in the Moray Firth contributed the largest (n=309) and longest time series  
227 (1988 – 2017). A comparison between these data and growth curves from the other individual  
228 Management Units was unfortunately not possible because there were insufficient data to make a  
229 robust comparison. However, it was possible to compare the Moray Firth with all other MUs as  
230 combined they produced a similar size dataset (n=349). Since only one group (East Scotland males)  
231 were found to be different in the pairwise comparisons, it was possible to amalgamate these data. The  
232 parameter estimates from the fitted von Bertalanffy growth models for the Moray Firth males and  
233 females compared to all the other regions combined across all years are shown in Table 3. There was  
234 no significant difference in the asymptotic lengths but there was a significant difference in the Brody  
235 growth parameter (K) with Moray Firth males being lower than other regions (Moray Firth = 0.259,  
236 Other Regions = 0.441, LRT p=0.020) and age at zero length ( $t_0$ ) parameter (Moray Firth = -3.53,  
237 Other Regions = -2.00 , LRT p=0.020). Thus, early growth was lower for Moray Firth males  
238 indicating it took longer for them to reach the asymptotic length compared to the other regions.  
239 Among the females, there was no significant difference about the growth parameters.

240  
241 The samples obtained from the harbour seals in Moray Firth MU spanned a period of 29 years,  
242 making it possible to explore temporal variation in growth parameters. Fig. 3a shows the residuals  
243 around the von Bertalanffy growth function fitted to the Moray Firth male data, by two-year  
244 categories, noting that animals were not captured every year. There was no observable trend in the  
245 residuals over time, except that the animals captured in 1990-1991 were significantly larger (linear  
246 model without an intercept to determine which year categories are significantly different from zero,  
247 p=0.003) for their age. By contrast those captured in 2012-2013 were significantly smaller (linear  
248 model, p=0.0002, Fig. 3a). A similar relationship was explored among the females from the Moray  
249 Firth and again no observable trend was found, with the exception that females were larger for their  
250 age captured in 1994-1995 (Fig. 3b, p=0.038). These temporal variations did not correlate with any  
251 observed changes in the population trends (Thompson et al., submitted).

252

## 253 **DISCUSSION**

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

258

259 In general, male harbour seals were approximately 9 cm longer at maturity than females and reached  
260 90% of their asymptotic length almost one year later than females. Härkönen & Heide-Jorgensen,



261 (1990) found that females in East Atlantic populations reached sexual maturity at 87% of their  
262 asymptotic length. Boulva & McClaren, (1979) reported this to be 93% for the harbour seals in  
263 Eastern Canada and Laws (1959) suggested that in general seals mature at between 80 and 90% of  
264 their asymptotic length. Independent information on sexual maturity for the UK harbour seals was not  
265 available, but our results also match with Gardiner, Boyd, Racey, Reijnders, & Thompson, (1996)  
266 who suggested a length of 125 cm for mature females, which is 89% of the overall estimated  
267 asymptotic length of 140 cm for all the females in this study. Other studies of harbour seal populations  
268 in Europe, the Arctic, Canada and Alaska reported slightly longer asymptotic lengths with the  
269 exception of harbour seals in the Skagerrak and Svalbard (asymptotic lengths; 139 cm in the  
270 Skagerrak; 145 cm in the Kattegat, 137 cm in Limfjorden and 150 cm in the Western Baltic (Harding  
271 et al., 2018); 147 cm in Norway (Markussen, Bjorge, & Oritsland, 1989), 140 cm in Svalbard  
272 (Lydersen & Kovacs, 2005), 143 cm in Eastern Canada (Boulva & McClaren, 1979), 148 cm in  
273 British Columbia (Bigg, 1969) and 148 cm in Alaska (Hutchinson, Atkinson, & Hoover-Miller,  
274 2016)).

275  
276 Similarly, asymptotic lengths reported for male harbour seals in the same regions (except Alaska  
277 where only females were studied) were longer than the overall estimate for UK males of 149 cm with  
278 the exception of the Skagerrak and Limfjorden where male asymptotic lengths were also estimated at  
279 149 cm (Harding et al., 2018) (Kattegat 160cm, Western Baltic 167 cm, (Harding et al., 2018) Norway  
280 155 cm (Markussen et al., 1989), Svalbard 153 cm (Lydersen & Kovacs, 2005), Eastern Canada 154  
281 cm (Boulva & McClaren, 1979) and British Columbia 161 cm (Bigg, 1969)). Some of this variation  
282 may be due to measurement differences obtained from live-captured compared to dead animals. All  
283 of the studies referred to above obtained their measurements from carcasses (hunted or dead stranded)  
284 with the exception of those in Svalbard. Thus, due to the sexual dimorphism, regional and temporal  
285 patterns in growth, size needs to be considered separately for each sex.

286  
287 Although there were a few regional differences among the sex-specific age-length von Bertalanffy  
288 growth parameters, only one was statistically significant. Over all age classes, males were  
289 significantly shorter for their age in the East Scotland MU compared to the seals sampled from the  
290 other MUs. This is the harbour seal MU where the population abundance has declined most rapidly  
291 (Lonergan et al., 2007; SCOS, 2017; Thompson et al., submitted). Unfortunately, it was not possible  
292 to investigate any trends over the time spanning the identified decline period (since around 2000 to the  
293 present), as the animals were largely captured in two years, 2008 and 2012. It may well be that  
294 animals in the East Scotland MU had reduced somatic growth during the period of decline, which  
295 could indicate reduced prey intake or reduced prey quality affecting the intake of important nutrients  
296 (Calkins et al., 1998), particularly protein required for robust skeletal growth (Carreira et al., 2014;  
297 Gat-Yablonski & De Luca, 2017). This is in line with ecological theory, which suggests that

298 population declines driven by bottom-up processes such as resource limitations, would result in slower  
299 growth and a delayed mean age at sexual maturity (Stearns, 1976). However, we cannot rule out the  
300 possibility that observed differences in male size were related to unknown levels of regional variation  
301 in the intensity of sexual selection.

302

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

312

313 In the past, information on length-at-age was often restricted to populations which had been harvested  
314 (Blundell & Pendleton, 2008; Boulva & McClaren, 1979) or subject to major disease outbreaks  
315 (Härkönen & Heide-Jorgensen, 1990). This often constrains temporal and regional comparison of  
316 growth patterns, especially for those populations which are of conservation concern. There are no  
317 previously published age-at-length curve data for UK harbour seals, and such information exists for  
318 only a few other northeast Atlantic populations (Lydersen & Kovacs, 2005; Markussen et al., 1989;  
319 Harkonen & Heide Jorgensen, 1990). The most detailed study in European waters recently  
320 investigated changes in the growth of harbour seals in Danish and Swedish waters (Harding et al.,  
321 2018), and found evidence for density dependant phenotypic changes. Seals born in cohorts during  
322 periods of lower abundance were longer at adulthood. However, their study included a very large  
323 sample of over 1,400 individuals which indicates the magnitude of the dataset required to detect such  
324 changes.

325

326 Errors associated with the age estimates, due to indistinct layers in some teeth, were not included in  
327 this analysis. Whilst this can be an important source of measurement error, Blundell and Pendleton's  
328 (2008) comparison of age estimates from paired incisors and canines found no bias associated with  
329 including lower certainty estimates. It should also be recognised that measurement error associated  
330 with the standard nose-tail length measurements of these live seals was not formally included, and the  
331 results presented here should be interpreted recognising that these sources of uncertainty have not  
332 been taken into account.

333

334 There were insufficient data to fully explore changes in somatic growth with respect to the major  
335 variations in population dynamics that UK harbour seals have experienced over the last 30 years.  
336 Nevertheless, for Management Units where acute population declines have been observed, particularly  
337 Southeast England following PDV outbreaks (see Thompson et al., submitted), increases in  
338 asymptotic length may have been expected (Harding et al., 2018). However, this effect may not be  
339 observed if the disease predominantly affects adults, as was suspected to be the case in Southeast  
340 England (Hall et al., 1992). Although harbour seal populations in Scotland were much less affected by  
341 PDV, they have seen major changes in their populations (Thompson et al., submitted). Longer-term  
342 declines in abundance may also result in changes in growth depending on the drivers. For example,  
343 lack of prey may affect juvenile growth through nutritional stress. However, reductions in population  
344 density may result in the opposite effect. Unfortunately there were insufficient data to explore these  
345 competing hypotheses. Nevertheless, evidence of significantly shorter male seals in the East Scotland  
346 Management Unit indicate either that bottom up impacts are driving the 18.5% p.a. decline observed  
347 between 2000 and 2017 (SCOS, 2017) or that differential mortality has resulted in smaller animals  
348 remaining in the population.

349

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

368

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374

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

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512

Region  Year classes	East Scotland		Moray Firth		North Coast and Orkney		Northern Ireland		Shetland		Southeast England		West Scotland		Total
	F	M	F	M	F	M	F	M	F	M	F	M	F	M	
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

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514



515 Table 2. Parameter estimates from the von Bertalanffy growth curves fitted to harbour seal age-length  
 516 data by sex and regional group.  
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 518  
 519

<b>Group</b>	<b>L<sub>∞</sub></b>	<b>K</b>	<b>t<sub>0</sub></b>
<b>Males</b>			
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)
<b>All Males</b>	<b>149.4 (147.8, 151.1)</b>	<b>0.327 (0.285, 0.370)</b>	<b>-2.77 (-3.19, -2.35)</b>
<b>Females</b>			
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 <sup>1</sup>	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)
<b>All Females</b>	<b>140.5 (139.4, 141.6)</b>	<b>0.441 (0.395, 0.488)</b>	<b>-2.02 (-2.27, -1.78)</b>

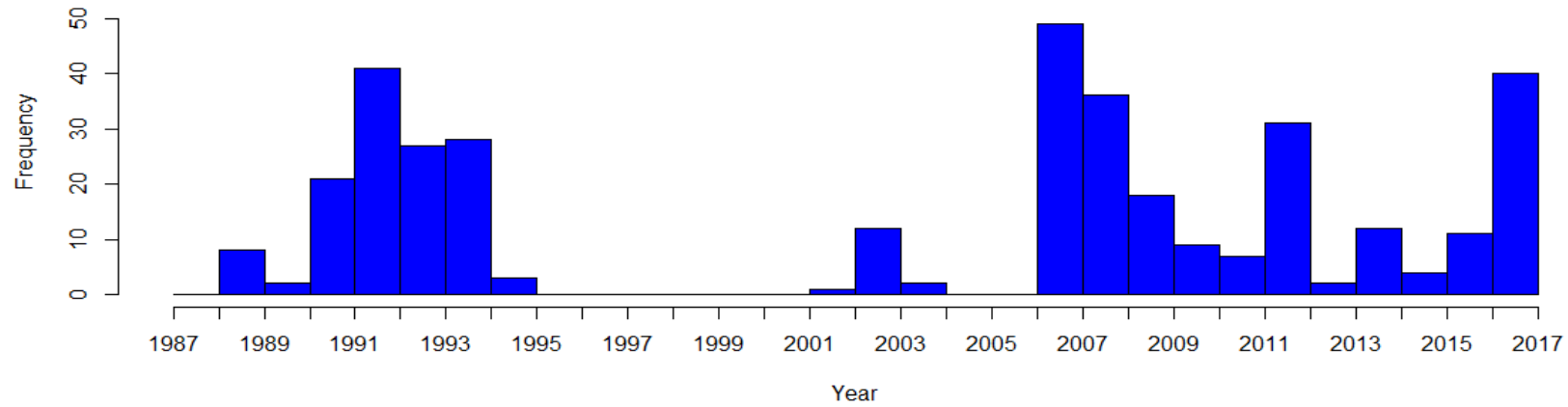
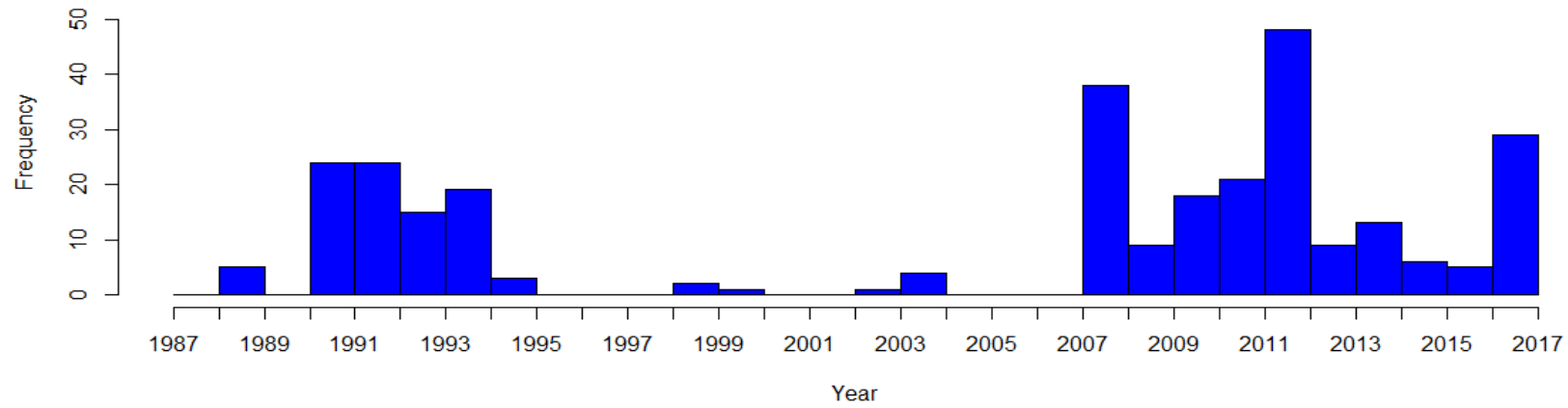
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 521 <sup>1</sup> Note : This relationship is based on only four data points.  
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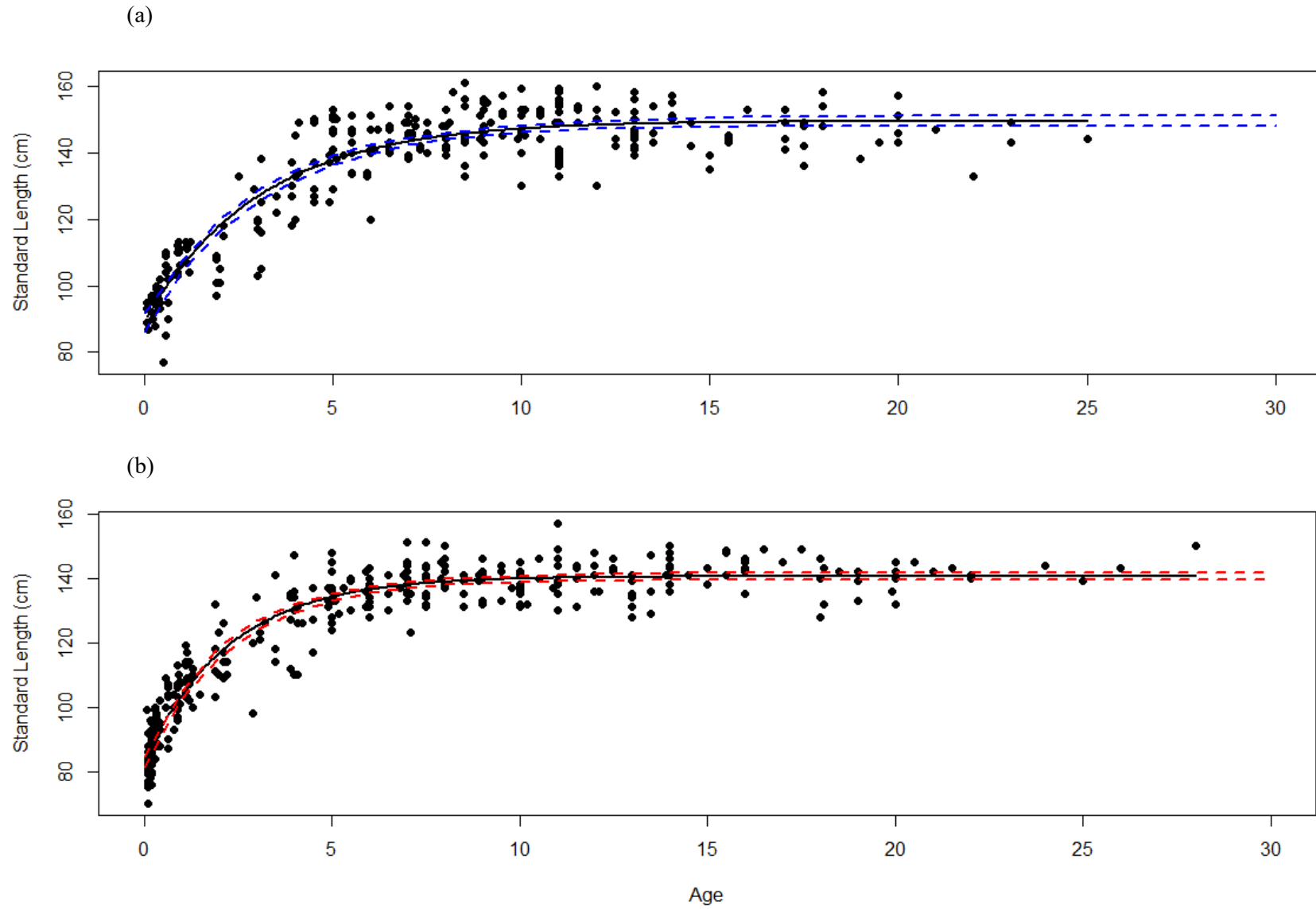
Table 3. Comparison between the growth parameters for the Moray Firth compared to the other MUs. The overall comparison tests are  $L_{\infty mf} = L_{\infty o}$ ,  $K_{mf} = K_o$  and  $t_{0mf} = t_{0o}$  where subscripts mf and o represent Moray Firth and Other MUs respectively.

Group	Asymptote ( $L_{\infty}$ ) (95% confidence interval)	$p$	$K$ (95% confidence interval)	$p$	$t_0$ (95% confidence interval)	$p$	Overall
<b>Males</b>							
Moray Firth	151.8 (148.1, 155.6)	0.065	0.259 (0.210, 0.308)	<b>0.020</b>	-3.53 (-4.21, -2.86)	<b>0.020</b>	0.104
Other Regions	148.1 (146.5, 149.8)		0.441 (0.339, 0.544)		-2.00 (-2.58, -1.42)		
<b>Females</b>							
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)		

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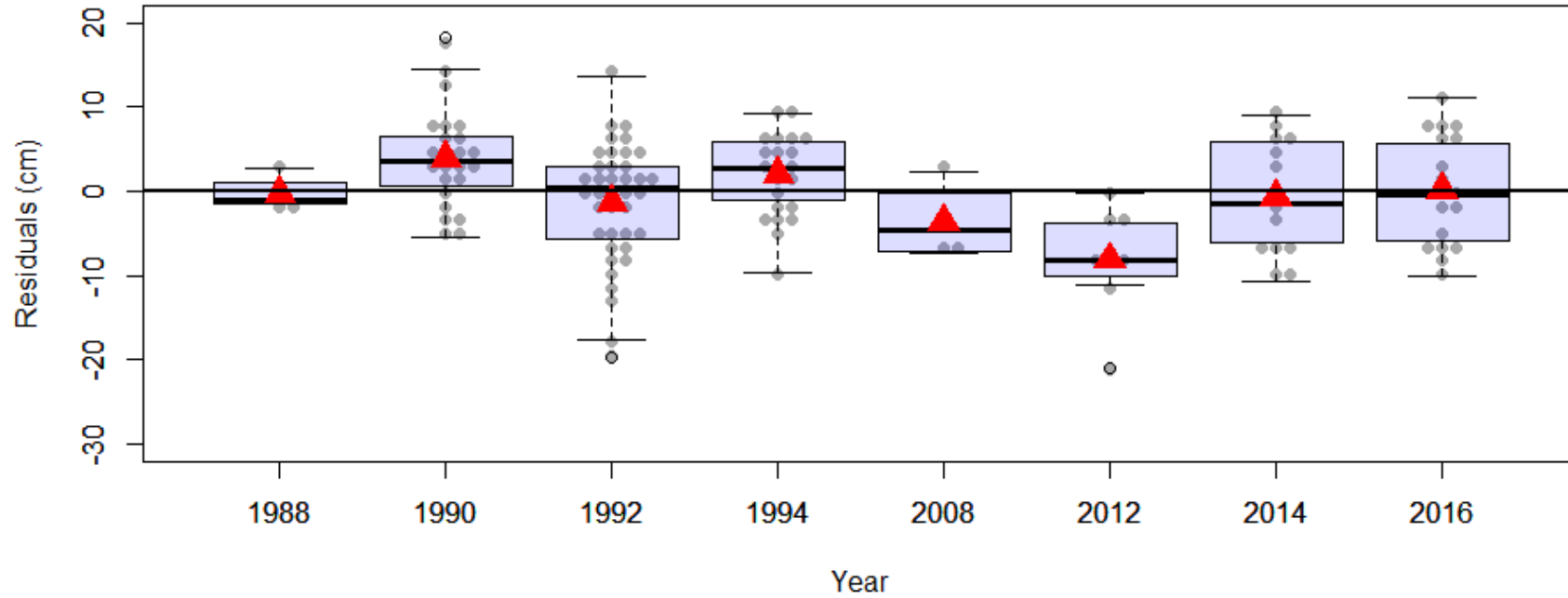


532 Figure 1. Frequency distributions by year of capture for aged (a) male  $n=294$  and (b) female  $n=364$  UK harbour seals.



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

534 (a)



535 n =                    4                    24                    39                    22                    4                    8                    14                    18

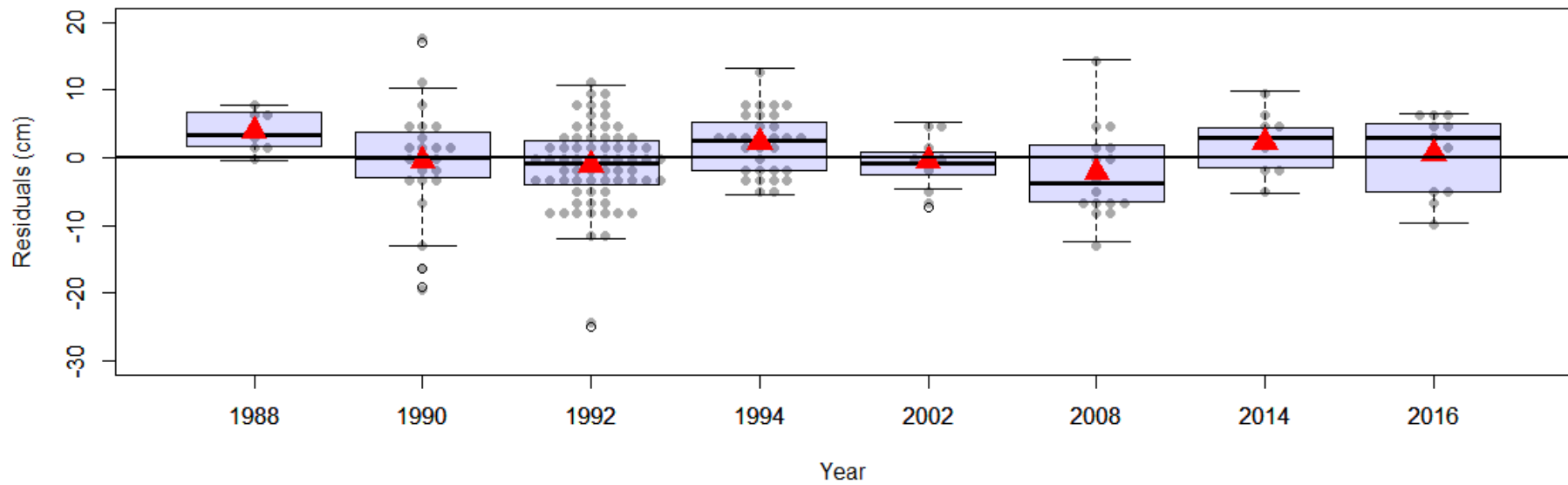
536

537 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  
538 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  
539 every year.

540

541 (b)

542



543

n =            8            23            68            31            9            16            9            12

544

545 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  
546 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  
547 every year.

548

549 **Supplementary information**

550

551 Table S1. Likelihood ratio test pairwise comparisons for differences between parameters from the von Bertalanffy growth curves. Significant differences are  
 552 shown in bold type using Bonferroni adjustment for multiple comparisons with a significance level  $p=0.0083$ . Those in italics are the additional  
 553 comparisons that were significant at  $p<0.05$ .

<b>Males</b>	East Scotland			Moray Firth			North Coast and Orkney			Shetland			Southeast England			West Scotland		
	$L_{\infty}$	K	$t_0$	$L_{\infty}$	K	$t_0$	$L_{\infty}$	K	$t_0$	$L_{\infty}$	K	$t_0$	$L_{\infty}$	K	$t_0$	$L_{\infty}$	K	$t_0$
East Scotland				<b>0.001</b>	<b>0.006</b>	<b>0.003</b>	-	-	-	<i>0.012</i>	0.699	0.764	<i>0.012</i>	0.085	0.110	<b>0.004</b>	1.000	0.663
Moray Firth							-	-	-	1.000	0.572	0.403	0.729	0.920	0.823	0.431	<i>0.029</i>	0.062
North Coast and Orkney													-	-	-	-	-	-
Shetland													0.862	0.680	0.539	0.507	0.663	0.597
Southeast England																0.396	0.126	0.284
West Scotland																		
<b>Females</b>																		
East Scotland				-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Moray Firth							0.060	0.446	0.265	-	-	-	0.073	0.888	0.680	0.151	0.777	0.862
North Coast and Orkney										-	-	-	0.689	0.532	0.303	1.00	0.435	0.322
Shetland													-	-	-	-	-	-
Southeast England																0.752	1.00	0.806
West Scotland																		

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