| 1 | Moulting phenology of the harbour seal in southwest Ireland |
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| 3 | Cronin, M ¹ , S. Gregory ² and E. Rogan ³ . |
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| 5 | ¹ Coastal and Marine Research Centre, University College Cork, Naval Base, Haulbowline, |
| 6 | Cobh. Co. Cork, Ireland. |
| 7 | |
| 8 | ² British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 OET, UK. |
| 9 | |
| 10 | ³ School of Biological, Earth and Environmental Sciences, University College Cork, |
| 11 | Distillery Field, North Mall, Cork, Ireland. |
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| 33 | Running head: Moulting phenology of the harbour seal in Ireland |
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35 Abstract

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37 Studies on the phenology of harbour seal moult have been carried out in the Atlantic and 38 Pacific, however there has been no research into this process in the Republic of Ireland, at 39 the southern edge of the species range in the NE Atlantic. Population estimates of harbour 40 seals are derived by counts primarily during the moulting seasons. In the absence of 41 information on the moult phenology planning the optimal timing of such surveys is 42 impossible. Furthermore, changes in moult phenology may reflect changes in resource 43 availability or competition, or demographic changes. The phenology of the harbour seal 44 moult was investigated in southwest Ireland in this study. Timing of the moult differed 45 among all cohorts, yearlings began moulting first following by adult females and finally 46 adult males. The number of seals hauled out was generally positively related to the 47 proportion of seals in active moult. The timing of the moult period was different to other 48 parts of the species' range and should be considered in determining optimal timing of future 49 surveys for assessing populations abundance and trends in Ireland.

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52 Key words: harbour seal, phenology, moulting, population estimate, Ireland

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54 Correspondance

Correspondance should be addressed to: Michelle Cronin, Coastal and Marine Research
Centre, University College Cork, Naval Base, Haulbowline, Cobh. Co. Cork, Ireland.

- 57 Email: michelle.cronin@ucc.ie
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61 Large-scale surveys of harbour seal (Phoca vitulina vitulina) populations occurring in rocky-62 shore habitats in the northeast Atlantic are generally conducted during the annual moult (e.g. 63 Reijnders et al., 1997; Duck et al., 2005; Cronin et al., 2007). Thompson & Harwood (1990) 64 suggested that the physiological constraints placed on seals during the moult period may make haul-out frequency likely to remain constant between years, thereby allowing a degree 65 66 of comparability between moult population estimates. Studies on harbour seal moult have 67 been carried out in Scotland (Thompson & Rothery, 1987) and in Alaska (Daniel et al., 2003) however there has been no dedicated research into the process in the Republic of 68 69 Ireland. The timing of harbour seal population assessment surveys in Ireland to date has been 70 based on best estimates of the peak moulting period in the nearby UK (Cronin et al., 2007). 71 As the timing of moult is known to vary depending on the location of the population (Boulva 72 & McLaren, 1979; Daniel et al., 2003) it is crucial that work is carried out to identify the 73 phenology of moulting in Ireland and identify optimal timing of population assessment 74 surveys. Previous studies on moult phenology in seals are based on direct observations of 75 individuals in the field. This is only possible at select haul-out sites that afford good vantage 76 points to observers and unobstructed views of a relatively large group or significant fraction 77 of a population e.g. Tugidak Island, Alaska (Daniel et al., 2003) and the Moray Firth, 78 Scotland (Thompson & Rothery, 1987). In the absence of such sites, it may be possible to 79 use photogrammetric analysis to investigate the timing of the moult in harbour seals. This 80 was explored in the present study with a view to identifying the phenology of the moult and 81 the optimum date when surveys should be conducted in Ireland, to ensure the most accurate 82 estimates of population size can be made.

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The objectives of the study therefore are (i) to establish the timing of the peak moult period of the harbour seal using a novel approach involving photogrammetric analysis and (ii) to examine changes in abundance of harbour seals at haul-out sites in southwest Ireland in relation to moulting.

- 89 METHODS
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91 Study area

Harbour seal haul-out distribution along the Irish coastline is predominantly along the northwest, west and southwest coasts, in sheltered bays and estuaries (Cronin *et al.* 2007). The study area comprised a bay in southwest Ireland, Bantry Bay, Co. Cork (51° 36'N, 9° 50'W) where up to 360 harbour seals haul-out during the moulting season, approximately 10% of the national minimum population estimate (Cronin *et al.*, 2007) Haul-out substrate is exclusively rocky and haul-out sites are generally on skerries or islands located adjacent to the mainland shore and relatively accessible by boat for counting/photographing.

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100 Surveys and image capture

101 Surveys of harbour seal haul-out sites in Bantry Bay were carried out in between 2003-2008 102 in a Tornado 5.8m Rigid Inflatable Boat (RIB) on at least a weekly basis between June 2003 103 and October 2005 and on at least a monthly basis between June 2006 and October 2008 and 104 more frequently when weather permitted. Surveys were scheduled to occur within two hours 105 before and after low tide, during daylight hours and not above wind force 4 on the Beaufort 106 scale. The numbers of seals at haul-out sites (Figure 1) were counted using Leica 10 x 42 107 binoculars and recorded on a Sony Dictaphone. Counts of seals at each haul-out site were 108 carried out independently and simultaneously by two observers and repeated if necessary 109 until consensus was agreed. Counts were initially obtained from a distance of approximately 110 200m from the haul-out site and at progressively closer ranges whilst preventing disturbance 111 to the seals.

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113 Where possible the RIB was manoeuvred close enough to allow the photographer to take 114 photographs of individual seals without causing disturbance, this effort was mainly 115 concentrated at Garnish Island in inner Bantry Bay. Images were obtained using a digital 116 SLR camera (Canon EOS-IDS) with a 600mm telephoto auto-focus image stabilising lens (Canon 600mm f/4L EF IS USM lens). The telephoto lens was mounted on a specialized 117 118 tripod head with a gimbal-type design (WH-101 Wimberley Inc [©]) for easier manipulation 119 of the large lens and to compensate for the movement of the boat. The aim was to take 120 photographs of the head, flanks and ventrums of all individuals at a site, ideally completely 121 un-obscured by rocks or other animals.

123 Moult phenology

124 Image analysis

125 Over 8500 photographs of individuals were obtained during the survey period 2003-2008. 126 Before any of the raw images could be analysed it was necessary to winnow down the photo 127 catalogue into usable pictures. Each individual photograph was viewed and only those 128 containing dry seals, where at least 80% of the body was visible at an angle giving a clear 129 view of the head and flank, were selected. When photographing the seals multiple passes of 130 haul-out sites were made to ensure clear images of the maximum number of animals were 131 captured, therefore photographs taken on the same day had to be double checked to ensure 132 there was no duplication of the same animal between pictures. This was done visually by 133 comparing pelage patterns and the position of the seal on the shore in relation to 134 distinguishable rock formations, areas of seaweed and other animals. No attempt was made 135 to identify individual seals in photographs taken on different days as each sample was 136 considered an independent random sample of the population available for photographing on 137 that day. A total of 829 photographs of seals were deemed suitable and analysed for moult 138 stage.

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140 Moult staging technique

141 Three main stages of moult were identified – premoult, active moult, and postmoult, (Table 142 1, Plate 1) and the moult status of each individual was recorded. For those in active moult the pattern of hair replacement across the body was noted by recording when hair was 143 144 shedding in five distinct regions (i) head and neck; (ii) the fore and hind flippers and tail; 145 (iii) ventrum; (iv) dorsum and (v) sides. The recognised pattern of hair replacement is that 146 initial shedding of hair first occurs on the head and flippers followed by the ventrum, then 147 the dorsum, with the sides being the last areas to moult (Stutz, 1967; Daniel et al., 2003). In 148 cases where this pattern was not observed and the head and flippers were the last areas to 149 shed, this was recorded as 'reverse moult'.

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151 Age and sex determination

Categorising a seal by age and sex purely from an individual photograph proved difficult. Close up images of individuals removed a sense of scale to judge the size of an animal and as most seals were photographed lying on their ventrum very few displayed genitalia. During the pupping season it was possible to identify adult females as those seals that had pups in attendance. Adult males often exhibit wounds and scars around the neck resulting from 157 fights during the breeding season (Thompson & Rothery, 1987); when visible these were 158 used to identify male seals. Individuals without these distinguishing features were classed as 159 being of unknown sex. To distinguish age categories a simple division between adults and 160 yearlings based on Thompson & Rothery (1987) was used, whereby yearlings were 161 identified by their paler, unpatterned pelage which is retained until their first moult. 162 Immature seals over one year were included in the adult category. It was not possible to 163 differentiate between immature and mature adults.

164

165 Data Analysis

166 Images were combined into bi-weekly periods in order to give adequate sample sizes while 167 still allowing relatively fine scale comparisons of timing. Inter-annual comparisons were not 168 possible between all years due to uneven spread of effort across the entire study period; 169 therefore the images from all years were combined into one large dataset, subdivided into the 170 eleven bi-weekly periods. The proportion of seals in the three moult stages were calculated 171 for each bi-weekly period. These results were plotted to illustrate the progression of moult 172 and used to calculate the duration of the moult process and the time period when the peak of 173 moulting occurred.

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175 The start of moult was defined as the earliest date a seal was observed in active moult. The 176 completion of moult was defined using the same criterion as Thompson & Rothery (1987), 177 the time at which 50% of seals were fully moulted. A non-linear, 3-parameter sigmoid 178 regression equation was used to fit a curve to the postmoult data and this was used to 179 estimate the date of moult completion. The peak moult date was defined as the time when 180 the highest proportion of seals were in active moult, the same definition used by Daniel et al. 181 (2003). By using the same criteria as the two other key harbour seal moult studies to define 182 the peak moult and completion dates, direct comparisons could be made between the timing 183 of these events at the different sites.

184

A comparison of the timing of the three moult stages between yearlings and adults was carried out using Wilcoxons signed rank tests to assess if there were differences in the timing of premoult, active moult and postmoult between the age classes. Sample sizes were insufficient to reliably compare the timing of moult between males and females. Counts of the numbers of seals hauled out for the entire Bantry Bay area were collected during surveys and, based on the theory that the proportion of seals in active moult in the photographed

191 sample was representative of the wider population, a linear regression was carried out to 192 investigate the relationship between the proportion of seals (Arcsin transformed) in active 193 moult and the numbers of seals hauled out.

194

The proportion of seals in active moult that showed a reverse pattern of hair replacement was calculated using data on the shedding of hair from distinct body regions. These data were examined to determine if this pattern was constant for all bi-weekly periods or changed during the moult season.

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200 Environmental Data

201 Water temperatures from two sites within Bantry Bay (Figure 1) were supplied by the Irish 202 Marine Institute who maintain a network of temperature probes (Onset Stowaway TidBit 203 sensors) around Ireland that provide water temperature readings every hour at multiple 204 depths. Maximum and minimum daily air temperatures and rainfall statistics for Glengarriff 205 (Figure 1) for the duration of the study period were supplied by Met Éireann (the Irish 206 Meteorological Service). Astronomical measurements giving the length of day (the time of 207 actual sunset minus the time of actual sunrise) were supplied by the online meteorological service Weather Underground. Readings were taken from Valentia Observatory (51° 56'N. 208 209 10° 14'W), the closest monitoring site to the study area located approximately 70km 210 northwest of Bantry. Based on the outputs of a Generalised additive model (GAM) that 211 examined the influence of environmental factors on the progression of the moult, 212 astronomical data on day lengths from the two other key harbour seal moult study sites, 213 Tugidak, Alaska (Daniel et al., 2003), and Orkney, Scotland (Thompson & Rothery, 1987), 214 were obtained for comparative purposes.

215

Generalised Additive Models (GAMs) were used to examine the relationship between the proportion of seals in active moult, and environmental variables, air and water temperature, rainfall and photoperiod. Month and year were included as nominal variables. A GAM using the binomial distribution and logistic link function was used to examine the relationship between the response variable (proportion of seals in active moult) and the explanatory variables. Stepwise model selection was used to exclude/include variables, and the Akaike Information Criteria (AIC) statistic was used to select the best model.

224 RESULTS

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226 Moult phenology

Seals in active moult were identified between 1 June and 1 November (Figure 2). The earliest instance was observed on 7 June and moult completion occurred in weeks 38/39 (mean date 27 September). The duration of the harbour seal moult period in southwest Ireland therefore was 16-17 weeks. The peak moult was determined as the time when the highest proportion of seals were in active moult status. This criterion identifies the peak moult time in weeks 36/37 (mean date 13 September).

233

234 For the first six weeks of the study the only seals observed in active moult were yearlings. 235 The first incidence of active moult in an adult was not observed until weeks 28/29 (mean 236 date 16 July). 87% of yearlings (n = 38) were in postmoult status by weeks 34/35 (mean date 237 30 August); however occasional yearlings were still observed to be shedding hair as late as 238 the end of October. There was a significant difference in the timing of premoult between 239 adults and yearlings (P < 0.05), however there was no significant difference between the two age classes for active moult or postmoult (P > 0.05). The first observed incidence of active 240 241 moult in a female occurred during weeks 28/29 (mean date 19 July) whereas the first 242 observed incidence of active moult in a male did not occur until weeks 32/33 (mean date 16 243 August).

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245 Relationship between numbers hauled out and progression of moult

Peak haul-out counts of seals of all ages in Bantry Bay is September 1st. A linear regression on the proportion of seals in active moult and numbers of seals at haul-out sites showed a significant positive relationship (P < 0.01, $R^2 = 0.25$) (Figure 3).

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250 Incidence of reverse pattern moulting

Reverse pattern moulting, whereby the head and flippers were the last areas to moult as opposed to the first, was observed in 96 seals, over half the number of those observed in active moult. The frequency of reverse moulting does not appear to be consistent throughout the moult period, with peak occurrence in mid Sept where almost 70% of seals in active moult showed a reverse moult pattern (Figure 4).

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258 *Potential influences on the phenology of the moult*

259 The full GAM model contained explanatory variables air and water temperature, rainfall and 260 photoperiod. Stepwise removal of explanatory variables, comparing deviances of full and 261 nested models using F tests suggested that the optimal GAM model for the proportion of 262 seals in active moult contains smoothing functions for daily maximum air temperature and 263 photoperiod (or daylength). This resulted in a model with a lower AIC and more of the 264 deviance explained (81.5%). Only photoperiod was significant (P < 0.001) in explaining the 265 proportion of seals in active moult, active moult peaking with daylength of 12.5 hours (mid 266 September).

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As the only significant explanatory variable was photoperiod, astronomical data were collated for the three moult study locations. The higher latitudes of the Scottish and Alaskan studies mean that both these sites experience longer periods of visible light during the summer months compared to Ireland, however by October all three sites have approximately the same photoperiod, and between November and April the length of day in Ireland is longer than the more northerly regions (Figure 5).

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275 DISCUSSION

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The duration of the harbour seal moult period in southwest Ireland was 17 weeks from the first observed incidence in early June until the mean estimated completion date in late September. Comparisons with data collected in Orkney, Scotland, the closest population where moult timing has been studied, showed that the duration of the moult in Ireland was longer than the 13 weeks recorded in Scotland (Thompson & Rothery, 1987). In both studies, the first observed incidence of moult occurred on June 7, but in Scotland the mean estimated completion date was August 23, more than 4 weeks prior to completion in Ireland. 284

Peak moult date was defined as the time at which the highest proportion of seals were in active moult, following approach of Daniel *et al.* (2003) and in southwest Ireland this occurred during weeks 36/37 (mean date September 13). In Tugidak, Alaska, harbour seals peak moult occurred during late August/early September, earlier than in southwest Ireland. There is no estimate for peak moult date for seals in Scotland however as completion of moult was observed in August (Thompson & Rothery, 1987) it is likely peak moult occurs much sooner than observed in southwest Ireland. In both the Scottish and Irish populations' yearlings were the first age class to moult with the adult moult starting later. In Ireland, the adult moult commenced approximately 9 days later than in Scotland (July 16 and July 7 respectively) (Thompson & Rothery, 1987). In Alaska, active moult of yearlings began about a month later than in Ireland or Scotland however the dates of onset of moult in adult seals in Alaska was more similar to Ireland (Daniel *et al.* 2003).

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299 The first observed incidence of active moult in a female in southwest Ireland occurred on 300 July 19 whereas the first observed incidence of active moult in a male did not occur until 301 almost a month later. This suggests that females are commencing the moult earlier than 302 males and while the small sample sizes may affect the level of confidence in such an 303 inference, it is supported by other studies of pinniped moult where females have been 304 observed starting to shed hair earlier than males from the same population (Thompson & 305 Rothery, 1987; Daniel et al., 2003; Badosa et al., 2006). Age and sex related differences in 306 the timing of the moult are reflected in heterogeneity in haul-out behaviour amongst 307 different age and sex classes, which in populations with non-stable age structure, can lead to severe biases in population estimates (Harkonen et al., 1999), suggesting research on 308 309 harbour seal population structure and haul-out behaviour at key haul-out sites in Ireland 310 across the moult period would also be worthwhile.

311

Overall the moulting phenology of harbour seals in southwest Ireland appears to follow the pattern of differences between age and sex classes identified by previous studies, however the actual timing of the moult period is noticeably different. The extent of the moult period is longer (4 weeks), the completion of moult is later (more than 4 weeks) than that recorded in Scotland and Alaska and the peak date is also later than recorded in Alaska.

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318 The latitudinal gradient between the three sites may explain the differences in moult timing, 319 as the only variable which had a significant effect on the proportion of seals in active moult 320 was day length. In Scotland and Alaska the length of day in July is up to two hours longer 321 than in Ireland. Photoperiodism is recognised as the most important synchroniser of seasonal 322 functions in mammals (Hoffman, 2004). Given the importance of epidermal temperature on 323 hair replacement it is possible that at higher latitudes where the summer period has longer 324 day lengths for a relatively short time the moult process would occur over a shorter time 325 period than at lower latitudes where the duration of summer is longer.

327 The pelage cycle is closely related to the annual cycle with respect to environmental factors 328 but also life processes particularly reproduction (Ling, 1970; Ashwell-Erickson *et al.*, 1986). 329 In mammals which undergo a suspended embryonic development, there appears to be a close 330 relationship between blastocyst implantation and moulting *e.g.* weasels (*Mustela erminea*), 331 mink (Mustela vison) and muledeer (Odocoileus hemionus) (Dolnick, 1959; Wright, 1963). 332 In most seal species, females moult approximately one month after mating, whereas in males 333 the delay is more variable (Ling 1970), the exception being the subtropical Hawaiian monk 334 seal (Monachus schauinslandi) in which breeding and moulting overlap (Ling, 1972). The 335 later timing of the peak and completion of the moult in harbour seals in Ireland compared to 336 other parts of their range could be linked to potential geographical related differences in 337 pupping phenology (e.g. Temte et al., 1991). Indeed recent evidence suggests later pupping 338 in harbour seals in Ireland (Cronin unpublished) compared to other parts of their European 339 range (e.g. Gjerta & Borset, 1992; Thompson & Wheeler, 2008; Reijnders et al., 2010) and 340 is being explored further.

341

342 By recording the progression of shedding hair pattern across the body, this study has 343 discovered an interesting phenomenon whereby a large proportion of the seals in southwest 344 Ireland showed a reverse pattern of hair replacement. The recognised pattern of hair 345 replacement for most pinnipeds, including harbour seals, has been recorded as starting on the 346 head and flippers, then on the ventrum followed by the dorsum, with the sides being the last 347 areas to moult (Stutz 1967; Daniel et al. 2003), yet this study observed the head and flippers 348 as being the last areas to moult in 48% of the seals in active moult. Daniel et al. (2003) 349 observed, although did not quantify, several cases of reverse moulting patterns for all cohorts 350 of harbour seals in Tugidak, Alaska. Reverse moult has been recorded in starving grey (H. 351 grypus) and harp (*Pagophilus groenlanicus*) seal pups in the Gulf of St. Lawrence and has 352 been associated with poor nutritional condition (Lydersen et al., 2000). The seals observed in 353 reverse moult in southwest Ireland however showed no evident physical signs of being 354 nutritionally compromised, however, a dedicated study on body condition using ultrasound 355 measurements of blubber thickness and/or labelled water dilution techniques (e.g. Reilly & 356 Fedak, 1990) would be worthwhile.

357

358 Photogrammetric techniques were shown to be effective in identifying stages of moult in 359 individual harbour seals and with sufficient photographic effort across the moult period can

360 enable the phenology of the moult to be established. Field measurements of the progression of the moult are labour intensive and often difficult to conduct, with in-situ subjective 361 362 classification of individuals (from a distance) into pre-defined categories invariably leading 363 to sampling bias. Our approach of capturing images of individuals across the moult period 364 with subsequent analysis in the laboratory is an approach that provides more opportunity for 365 quality control over the subsequent categorisation process. Photo catalogues of harbour seals 366 exist across parts of the species range resulting from mark recapture studies (e.g. Hastings et 367 al., 2001; Cunningham et al., 2009) and could retrospectively be utilised to examine 368 potential changes in the timing of the moult in these regions. As temporal changes in the 369 timing of the harbour seal moult have been observed (e.g. Daniel et al., 2003) ideally sample 370 effort would be high enough to allow between year comparisons, changes in moult 371 phenology may reflect changes in resource availability or demographic changes.

372

373 Accurate information on the timing of moult is of importance to the increasing numbers of 374 researchers using remote sensing devices deployed on animals to track movement and 375 behaviour (e.g. Cronin & McConnell, 2008). Expensive radio and satellite tags are 376 traditionally glued to the pelage of animals and lost when the fur is shed. A greater 377 understanding of the timing of moult would allow researchers to determine the optimal time 378 for instrument attachment, thus reducing potential time loss through capturing unsuitable 379 animals, maximising the data collection period and also reducing the potential loss of 380 equipment.

381

382 Fundamentally this study has shown that the assumption that the annual moult for seals in 383 Ireland occurs from late July to mid-August (Cronin et al., 2007), the same time as those in 384 the UK (Bonner, 1972) is incorrect; the peak in moult occurs in early September, with actual 385 completion being considerably later in mid-October. The significant relationship between 386 haul-out counts and the proportion of seals in active moult suggests that the timing of moult 387 influences haul-out behaviour, and therefore will influence the numbers of seals ashore for 388 estimates of population size. A long-term harbour seal monitoring program is currently 389 under development in Ireland (no census of the species has been conducted since 2003) and 390 it is critical that such information is integrated into this process to identify optimal survey 391 timing based on phenology of the moult in Ireland as opposed to elsewhere across the 392 species range, as was the case during the 2003 harbour seal census (Cronin et al., 2007).

When the timing of once-off surveys to establish population estimates is based on suchinformation, it can have significant consequences for the accuracy of population estimates.

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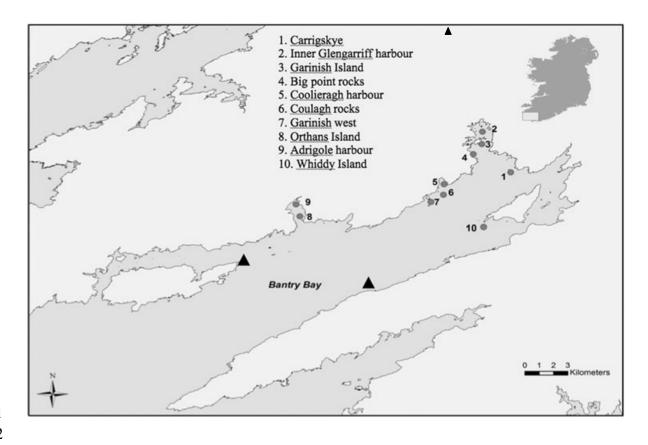
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- 516 Plate 1: Harbour seals in the three main defined moult stages (a) premoult; (b) active moult;
- 517 (c) postmoult





523 Fig. 1. Harbour seal haul-out sites and environmental monitoring sites in Bantry Bay, Co. Ireland,524 Ireland

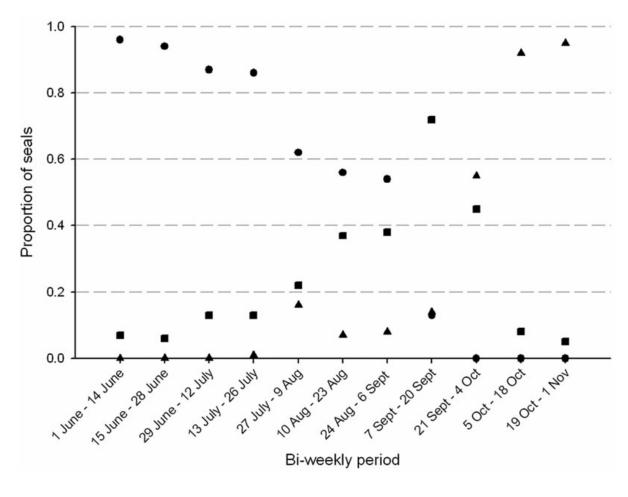
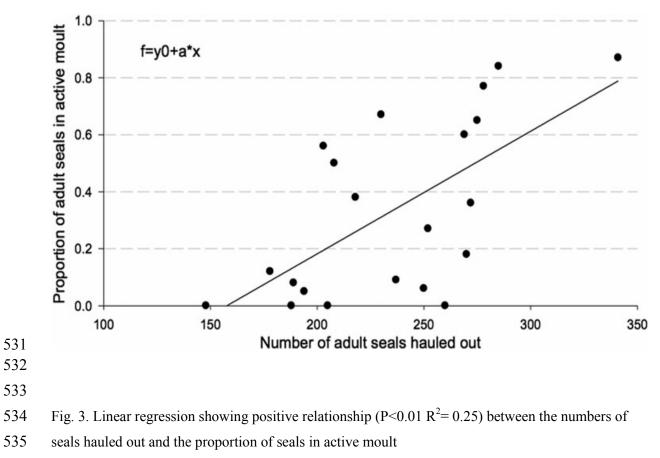
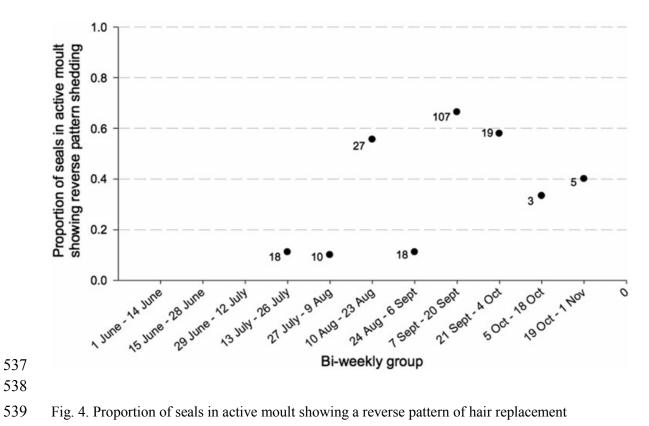
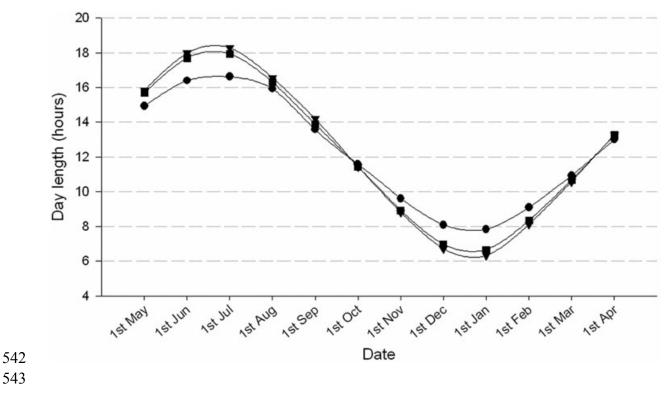


Fig. 2. Changes in the progression of moult status for all seals: premoult (circles), active moult(squares), and postmoult (triangles)





- 540 (datapoint label = sample size)



544 Fig. 5. Comparison of day lengths at Valentia, southwest Ireland (circles), Kirkwall, Orkney,
545 Scotland (triangles) and Kodiak, Alaska (squares)

Table 1: Classification criteria used to determine moult status of harbour seals in southwest

548 Ireland (adapted from Allen *et al.*, 1993; Stutz, 1967)

| Moult Stage | Sub-category | Description |
|--------------|--------------|--|
| Premoult | Pre-premoult | No indication of hair replacement having been initiated, |
| | | although pelage may look slightly shabby. |
| | Actual | Hair visibly degenerating. Coat has visibly changed |
| | premoult | colour to a dull brown, tawny, sepia or cinnamon colour |
| | | and pelage patterns have started to fade. |
| Active moult | - | Obvious hair loss with patches of new hair visible |
| | | through old pelage. |
| Postmoult | - | No old hair remaining, complete 'clean' new coat. |