

1 **Analyses of ovarian activity reveal repeated evolution of post-reproductive**
2 **lifespans in toothed whales**

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16

17 **Abstract**

18 In most species the reproductive system ages at the same rate as somatic tissue and individuals
19 continue reproducing until death. However, females of three species – humans, killer whales and
20 short-finned pilot whales – have been shown to display a markedly increased rate of reproductive
21 senescence relative to somatic ageing. In these species, a significant proportion of females live
22 beyond their reproductive lifespan: they have a post-reproductive lifespan. Research into this puzzling
23 life-history strategy is hindered by the difficulties of quantifying the rate of reproductive senescence
24 in wild populations. Here we present a method for measuring the relative rate of reproductive
25 senescence in toothed whales using published physiological data. Of the sixteen species for which
26 data are available (which does not include killer whales), we find that three have a significant post-
27 reproductive lifespan: short-finned pilot whales, beluga whales and narwhals. Phylogenetic
28 reconstruction suggests that female post-reproductive lifespans have evolved several times
29 independently in toothed whales. Our study is the first evidence of a significant post-reproductive
30 lifespan in beluga whales and narwhals which, when taken together with the evidence for post-
31 reproductive lifespan in killer whales, doubles the number of non-human mammals known to exhibit
32 post-reproductive lifespans in the wild.

33

34 **Introduction**

35 Why a female should cease reproducing before their expected end of life is a long-standing question
36 in evolutionary biology¹⁻³. The taxonomic scarcity of this strategy suggests that it requires unusual
37 selective pressures to evolve⁴. Comparative research has shown that females of only three species of
38 mammal - humans (*Homo sapien*), killer whales (*Orcinus orca*) and short-finned pilot whales
39 (*Globicephala macrorhynchus*) – are known to have a statistically significant post-reproductive
40 lifespan in the wild⁵. Recent work has also suggested that females of a third toothed whale species,
41 false killer whales (*Pseudorca crassidens*), may also have a post-reproductive lifespan⁶. Here we
42 define post-reproductive lifespans as common and prolonged female survival after the cessation of
43 reproduction, such that a female entering the adult population can expect to live a substantial period of
44 her life post-reproductive^{5,7}. We differentiate post-reproductive lifespans from non-adaptive brief and
45 rare survival past last reproduction resulting from the usual processes of senescence⁷.

46 Given the logistical difficulties inherent in studying a predominantly oceanic taxon such as the
47 toothed whales (*Odontoceti*) it is somewhat surprising that all but one of the species known to have
48 post-reproductive lifespans are in this group. Recent research has suggested that the demographic
49 consequences of certain social structures are important in life-history evolution⁸, and the evolution of
50 post-reproductive lifespans in particular^{4,9}. Toothed whales show a remarkable diversity of social and
51 reproductive strategies^{10,11}. The diversity of social structures and reproductive strategies in the toothed
52 whales makes them an important target group to understand the evolution of post-reproductive
53 lifespans.

54 Distinguishing post-reproductive lifespans from general declines in fecundity with age requires
55 detailed data on reproduction and survival rates of the females in a population over their lifetime¹².
56 The difficulties of studying long-lived marine taxa mean that data meeting this requirement are rare
57 for cetaceans. However, physiological data exist for many species: a consequence of mass mortality
58 events and a tradition of using physiological data to infer life-history traits for parameterising
59 conservation and management models¹³. In this study, we use these published physiological data to
60 infer the rate and timing of reproductive senescence in female cetaceans. Using these data we analyse

61 the rates of reproductive senescence as a population level trait and reveal the prevalence of post-
62 reproductive life history in the toothed whales.

63 **Results**

64 *Quantifying reproductive senescence*

65 In cetaceans, female reproductive history can be inferred from anatomical examination of the
66 ovaries¹⁴. After ovulation, the Graffian follicle, in which the ovum develops, degenerates first into a
67 corpus luteum, and then into a corpus albicans^{15,16}. In most Cetacea, these corpora remain present in
68 the ovary and can therefore be used as an individual measure of past ovulation history. A decline in
69 ovarian activity with age will result in slower formation of new corpora in older individuals (Fig. 1).
70 The null expectation is that rate of corpora formation is constant throughout life, whereas a decrease
71 in the rate of corpora formation with age indicates decreasing rates of ovulation as females get older:
72 reproductive senescence.

73 We used published data of age-specific corpora counts to infer the timings and rate of reproductive
74 senescence. These data are generated from anatomical examination of deceased whales (see methods).
75 In a systematic search for age-specific corpora data in all 72 species of toothed whale we found
76 sixteen species with age-specific corpora count data suitable for analysis: (see methods;
77 supplementary 1).

78 In ten of the sixteen species, a second degree polynomial best explained the relationship between
79 corpora count and age showing that age-specific ovarian activity declined with age (e.g. Fig. 1; Table
80 1). The rate of reproductive senescence relative to the rate of somatic senescence in these ten species
81 was inferred by comparing the standardised age-specific ovarian activity to standardised age (see
82 methods; Table 1). Four species showed a rate of reproductive senescence greater than the rate of
83 somatic senescence: beluga whale *Delphinapterus leucas* (relative rate of reproductive senescence =
84 1.69), narwhal *Monodon monoceros* (relative rate = 1.48), northern right-whale dolphin *Lissodelphis*
85 *borealis* (relative rate = 1.14) and short-finned pilot whales (relative rate = 1.38). After the removal of
86 an outlier the northern right-whale dolphin rate dropped to below one (relative rate = 0.75: this outlier

87 is not removed for the calculation of population-level metrics, see below), but the other species results
88 are qualitatively robust to the removal of outlying data.

89 In three species a linear relationship between corpora count and age suggests that there is no decrease
90 in reproductive effort with age and therefore no reproductive senescence (Table 1). For three other
91 species, we found no correlation between the number of corpora and age ($\text{adj-R}^2 \leq 0.1$; see
92 supplementary 1), suggesting that ovarian corpora are not a good measure of reproductive senescence
93 in the species.

94 *Quantifying post-reproductive lifespans*

95 Post-reproductive representation (PrR) is a population-level metric which calculates the proportion of
96 adult female years in the population being lived by post-reproductive females. For example, in
97 humans (without modern medical care) approximately 40% of adult female years are being lived by
98 post-reproductive females ($\text{PrR} = 0.443$)⁵. PrR is typically performed on observational data, but here
99 we calculate PrR in toothed whales from our physiological measures of rates of reproductive
100 senescence (Phys-PrR). Assumptions around population growth rates (see methods) mean that the
101 Phys-PrR is reported for a static population, a shrinking population and a growing population (as:
102 static [shrinking - growing]).

103 Of the ten species that show a decline in reproductive activity with age (Table 1) in three a significant
104 proportion of adult female years are being lived by post-reproductive females (Fig. 2): beluga whales
105 ($\text{Phys-PrR} = 0.27$ [0.19-.33], $p < 0.001$ [<0.001 , <0.001]), narwhals ($\text{Phys-PrR} = 0.24$ [0.19-0.29], $p <$
106 0.001 [<0.001 , <0.001]) and short-finned pilot whales ($\text{Phys-PrR} = 0.15$ [0.08-0.22], $p < 0.001$). For all
107 other species, the proportion of post-reproductive adult females is not significantly different from 0
108 (Fig. 2). For three species, short-finned and long-finned pilot whales and false killer whales age-
109 specific pregnancy data are also available, allowing us to validate our method (Fig. 1; supplementary
110 2).

111 PrR calculated from observations of births or pregnancy data is comparable to Phys-PrR in both
112 species of pilot whale and false killer whales (long-finned pilot whales, $\text{Phys-PrR} = 0.02$ [0.00,0.02],

113 PrR=0.01, Fig. 1c; short-finned pilot whales, Phys-PrR=0.15[0.08-0.22], PrR=0.28), Fig. 1d; false
114 killer whales – see supplementary 2). This similarity demonstrates that our physiological measure
115 reflects observed age-specific changes in reproductive activity. Moreover, using simulation
116 approaches we demonstrate that our results are robust to potential errors in the estimation of whale
117 ages (supplementary 3).

118 We combined the physiological data on ovarian activity with other sources of information about
119 toothed whale life-history to examine the evolution of post-reproductive lifespans in this clade.
120 Phylogenetic ancestral state reconstruction reveals only one node, the common ancestor of the beluga
121 and narwhal, with substantial support (proportional probability = 0.95) for the presence of post-
122 reproductive lifespans in any ancestral species of any toothed whales. All the other nodes show very
123 strong support (proportional probability>0.9) for a lack of post-reproductive lifespans in ancestral
124 species. Our results suggest that post-reproductive lifespans have evolved independently three times
125 in the toothed whales: once at some point before the separation of the beluga and narwhal lineages,
126 once in the lineage leading to short-finned pilot whales, and once in the lineage leading to killer
127 whales (Fig. 3; supplementary 4).

128 **Discussion**

129 Using physiological data, we have found evidence of post-reproductive lifespans in three species of
130 toothed whale: beluga whales, narwhals and short-finned pilot whales. To our knowledge this is the
131 first record of population-level post-reproductive lifespans in beluga whales and narwhals, and
132 supports previous suggestions of significant post-reproductive lifespans in short-finned pilot
133 whales^{5,17}. When taken together with the evidence for post-reproductive lifespans in killer whales
134 from long-term individual based studies^{5,18–20} and non-invasive physiological studies²¹ our new
135 findings effectively double the number of non-human mammals known to exhibit this unusual life-
136 history strategy. Further, we found that post-reproductive lifespans are likely to result from at least
137 three independent evolutionary transitions in the toothed whale lineage.

138 Recent work suggests that the evolution of post-reproductive lifespans in humans and killer whales is
139 driven by changes in local relatedness across the lifespan^{20,22}. In resident-ecotype killer whales (a
140 salmon-eating killer whale population inhabiting NE Pacific ocean), neither males or females disperse
141 from their natal group: though males mate outside the group²³. In ancestral humans dispersal is
142 thought to have been female biased^{24,25}. Under these demographic conditions selection will favour
143 young females to invest resources in their own reproduction at the cost of reproduction in other group
144 members^{9,20}. Older females on the other hand can increase their inclusive fitness by aiding other group
145 members to reproduce through grandmother and mother benefits^{9,26}. Having a post-reproductive
146 lifespan can be the optimal strategy when the inclusive fitness costs of reproductive conflict are
147 combined with the inclusive fitness benefits of late-life helping^{9,20}. Benefits to late-life helping and
148 costs of reproductive conflict have been found in both humans and killer whales^{20,22,26-28}. We predict
149 that the two new species with a post-reproductive lifespan reported here will have demography that
150 increases female within group relatedness as a function of age: either bisexual social philopatry with
151 non-local mating or female dispersal with local mating⁹. Comparing the social structures of cetacean
152 species with and without a significant female post-reproductive lifespan provides a unique
153 opportunity to test the generality of demographic processes that are predicted to select for the
154 evolution of post-reproductive lifespans^{9,29}.

155 The limited information available on social structure in short-finned pilot whales, beluga and narwhal
156 suggest that the population social structure may be based on bisexual philopatry. For example, genetic
157 studies and observations at stranding events suggest that short-finned pilot whales live in mixed sex
158 groups with males mating outside the group^{30,31}. Similarly, both male and female beluga whales
159 show high fidelity to natal summering feeding areas³², and both female and male (especially young
160 males) are regularly found in association with close kin³³. Narwhal societies appear to be focussed
161 around matrilineal while migrating to summer feeding grounds^{34,35}. Thus, in all three species current
162 evidence suggests patterns of demography, that may lead to an increase in females local relatedness
163 to their group with age, much like in resident killer whales and ancestral humans^{8,9}. Further work

164 based on individual based longitudinal studies and or population genetic studies are needed to confirm
165 these findings.

166 The social structures of toothed whales without a significant post-reproductive lifespan are varied
167 (supplementary 5). For example, female sperm whales live do not disperse and remain with their
168 matrilineal unit throughout their life¹⁰. The males, in contrast, disperse at sexual maturity and are
169 largely solitary, roving between female groups in search of mating opportunities¹⁰. This male-biased
170 dispersal does not lead to the relatedness dynamics predicted to promote selection for female post-
171 reproductive lifespans⁹. However, it is important to note that female relatedness to her group
172 increasing with age does not presuppose the evolution of post-reproductive lifespans. For example,
173 the available evidence suggests that long-finned pilot whales exhibit bisexual philopatry⁴⁰ - much like
174 short-finned pilot whales – and yet they do not have a significant post-reproductive lifespan. This
175 highlights that it is not only demographic structures but also the balance of the costs of harming and
176 the benefits of helping that may lead to the evolution of post-reproductive lifespans. Even within
177 species there is considerable variation in social structure. Transient-ecotype killer whales (a mammal-
178 eating population in the NE Pacific), for example, form much smaller groups than resident-ecotype
179 killer whales, and some males disperse from their natal group⁴¹. This would lead to very different
180 relatedness structures in transient compared to resident-ecotype killer whale societies. It is unknown if
181 transient-ecotype killer whales exhibit significant post-reproductive lifespans. Overall, there is a
182 considerable amount still to be discovered about toothed whale social structure and life-history. Our
183 results highlight the importance of the taxa for understanding the interplay between social behaviour
184 and life history evolution.

185 In this study we use corpora count as a measure of fecundity. An advantage of using this
186 physiological measure of fecundity is that the species in which ovarian activity ceases before the end
187 of life are physiologically incapable of bearing in offspring (though this does not necessarily preclude
188 them from lactating and nursing calves³⁰). However, for many species females may stop reproduction
189 prior to complete physiological reproductive senescence (measured via ovarian activity). For example,
190 in rural Bangladesh women have their last child, on average, a decade before reproductive

191 cessation⁴². Detailed age-specific pregnancy data are rare for cetaceans, but do exist for short-finned
192 pilot whales where, much like humans, the post-reproductive lifespan measured via pregnancy data is
193 longer than the post-reproductive lifespan measured via ovarian activity (Fig. 1). This difference
194 between a physiological measurement of reproduction and the direct observation of pregnancy may be
195 a reason why our results differ from a recent analysis investigating the presence of post-reproductive
196 lifespans in false killer whales⁶ (discussed in more detail: supplementary 2). Our results are
197 conservative in that the data captures age at last possible reproduction, rather than of last
198 reproduction, and it is possible that detailed studies on age-specific pregnancy rates will reveal further
199 cetacean species that exhibit a prolonged post-reproductive lifespan.

200 Studying the evolution of female post-reproductive life is hindered by its taxonomic rarity. Our
201 physiological analyses gives new insight into life-history variation in cetaceans, and double the
202 number of non-human mammals known to experience post-reproductive lifespans. This provides new
203 opportunities to test the evolutionary origins and maintenance of post-reproductive lifespans in
204 humans and toothed whales.

205 **Materials and Methods**

206 *Data*

207 We used published age-specific corpora counts to quantify the rate of reproductive senescence in
208 female toothed whales. In Cetaceans, reproductive history can be inferred from anatomical
209 examination of the ovaries¹⁴. After ovulation, the Graafian follicle, in which the ovum is develops,
210 degenerates first into a corpus luteum, and then into a corpus albicans (hereafter collectively corpora)
211 which persists in the ovary⁴³. Corpora counts have been used to infer ovulation rate and other
212 reproductive characteristics in a variety of Cetacean species (e.g.^{30,43,44}). Here we use corpora counts
213 as a measure of ovarian activity and not to estimate pregnancy rates which may differ from the
214 corpora count^{15,45,46}. In earlier studies corpora albicans and corpora atretica may not always have been
215 properly distinguished⁴³, however, as we are measuring ovarian activity, not ovulations *per se* this
216 will not bias our results.

217 We undertook a thorough literature search for age-specific corpora count data on all 72 recognised
218 species of Odontocetes⁴⁷. Our criteria for data inclusion were: each female studied had a count of
219 corpora and an independent estimate of age; female age structure was well represented; and that the
220 data is presented in a clear format to be accurately obtained. Independent estimates of age were based
221 on examination of dentine cemental layers in all species except narwhals, where the racemization of
222 aspartic acid in the eye was used^{48,49}. Recent research has shown that beluga whales deposit growth
223 layer groups annually^{50,51}. We therefore use growth layer group counts as our estimate of beluga
224 whale age- though we note that as PrR is calculated as a proportion systematic age, estimation errors
225 (doubled or halved for example) would not affect our conclusions. Appropriate data was found for
226 sixteen species: Atlantic white-sided dolphin *Lagenorhynchus acutus*⁵², Baird's beaked whale
227 *Berardius bairdii*⁵³, beluga whale *Delphinapterus leucas*⁵⁴, common bottlenose dolphin *Tursiops*
228 *truncatus*^{55,56}, false killer whale *Pseudorca crassidens*⁵⁷, harbour porpoise *Phocoena phocoena*⁵⁸,
229 long-finned pilot whale *Globicephala melas*⁴⁴, melon-headed whale *Peponocephala electra*⁵⁹, narwhal
230 *Monodon monoceros*⁴⁹, Northern right-whale dolphin *Lissodelphis borealis*⁶⁰, Pantropical spotted
231 dolphin *Stenella attenuata*⁶¹, short-beaked common dolphin *Delphinus delphis*¹⁵, short-finned pilot
232 whale *Globicephala macrorhynchus*³⁰, sperm whale *Physeter macrocephalus*⁶², spinner dolphin
233 *Stenella longirostris*⁶³ and striped dolphin *Stenella coeruleoalba*⁶¹. Previous work in resident killer
234 whales (*Orcinus orca*) has documented significant post-reproductive lifespans using long term
235 individual based observations^{5,18-20} and the post reproductive period has been confirmed using non-
236 invasive hormonal samples²¹. Currently however, to our knowledge there are no published corpora
237 count data on killer whales of a sufficiently large sample size for a robust test of the rate of
238 reproductive senescence and a calculation of physiological PrR (see⁶⁴). Killer whales are not,
239 therefore, included in our analysis of ovarian activity. Data were restricted to include only data from
240 the age of first ovulation, i.e. the age with the first non-zero corpora count. All analysis was
241 performed in R⁶⁵ with the ggplot2 package used for producing the figures⁶⁶.

242 It is important to note that throughout this study we refer to species, but our data is only based (with
243 one exception) on a single population. For one species, the common bottlenose dolphin, data were

244 available from three geographically distinct populations which we analyse independently. Data are
245 also available from two false killer whale populations⁵⁷, however we only use data from one
246 population (Japan) as the second population (South Africa) may have been reproductively
247 compromised⁵⁷.

248 Our analysis is based on the assumption that corpora counts are a reliable measure of ovarian activity
249 across the lifespan, which is supported by detailed examination of ovaries across a range of cetacean
250 species^{57,62,67}. For some species of cetacean however, there is evidence to suggest corpora may
251 regress, and not persist indefinitely¹⁵ and in some cases there may be multiple eggs released at a single
252 ovulation event¹⁵. However, there is no evidence of age-related changes in either poly-ovulation or
253 regression of corpora, which could otherwise affect our analysis of age-dependent changes in ovarian
254 activity. Indeed, for three species (short- and long-finned pilot whales, false killer whales) both
255 pregnancy and corpora data are available and in both cases changes in pregnancy rate show a
256 strikingly similar age-related pattern to changes in corpora deposition (Fig. 1 c and d; supplementary
257 2), validating our approach that ovarian activity (corpora count) can be used as a reliable measure of
258 fecundity. To our knowledge this is the first population level examination of the relationship between
259 corpora count and pregnancy rate.

260 *Quantifying reproductive senescence*

261 A physiological decrease in fecundity with age in toothed whales will result in a lower rate of
262 ovulation in older individuals. In populations with decreasing fecundity with age we therefore expect
263 a second order relationship between ovarian activity and age, as older individuals are producing fewer
264 new corpora per unit time. Reproductive senescence will be accompanied by a declining rate of
265 ovarian activity with age. We fitted second order polynomials (which, inversed, decline in rate
266 towards a peak) to each of the sixteen species to investigate this declining ovarian activity (e.g. Fig.
267 1). The change in ovarian activity with age is described by the slope of the fitted curve. A negative
268 change in ovarian activity is an artefact of fitting a quadratic curve and was therefore treated as 0. We
269 normalised both age and change in ovulation activity to between 0 and 1 to facilitate interspecies
270 comparison.

271 We used AIC model comparison to investigate if the relationship between corpora count and age were
272 best described by a 2nd order polynomial or linear relationship. A linear relationship is our null
273 assumption as it suggests that there is no decline in physiological reproductive activity through life.

274 We found a relationship between corpora count and age in thirteen of the sixteen species (detailed fit
275 information; supplementary 1). For three species we found no correlation between the number of
276 corpora and age ($\text{adj-R}^2 \leq 0.1$), suggesting that either the data are too sparse or that ovarian corpora
277 are not a good measure of reproductive senescence in the species. These three species are: Atlantic
278 white-sided dolphin ($\text{adj-R}^2 = -0.02$), harbour porpoise ($\text{adj-R}^2 = 0.07$) and the short-beaked common
279 dolphin ($\text{adj-R}^2 = 0.10$). No further analysis was performed on these species.

280 *Calculating post-reproductive lifespans*

281 For species with a decline in fecundity with age we then calculated their physiological post-
282 reproductive representation (Phys-PrR). Post-reproductive representation is a population level
283 measure describing the proportion of adult females years in the population that are being lived by
284 post-reproductive females¹². As our data are based on ovarian activity we measured the presence of
285 physiologically post-reproductive females in the population (i.e. the proportion of females not
286 ovulating).

287 The calculation of PrR is based on age-specific measures of survival and fecundity. We calculate age-
288 specific survival from age-cohorts constructed from the original corpora data. Age-cohorts were
289 constructed by making variable bin-widths starting at the oldest female in the study. We used these
290 variable bin widths to construct monotonically decreasing age-cohorts, a pre-requisite for calculating
291 survival from age-cohorts⁶⁸. Bin widths were calculated in reverse: from the oldest individual. The
292 oldest bin contains only the oldest female in the sample. The lower limit of the next bin was then
293 selected to contain more than one whale, i.e. a greater number of females than the next oldest bin.
294 This process continued until all females were assigned to a bin. In some cases, to fit the assumption
295 of monotonically decreasing age cohorts the first age (youngest) bin for some species had to be
296 smoothed to match the second youngest bin. This method will tend to underestimate late life survival,

297 and therefore underestimate post-reproductive representation. Survival was then calculated from these
298 age cohorts with survival assumed to be evenly spread through each age represented in a cohort. It
299 should be noted that due to the low probability of sampling ‘rare’ ages of individuals, older whales are
300 likely to be underrepresented in our data, further underestimating survival and the significance of the
301 post-reproductive lifespan.

302 Calculating survival from age-cohort data assumes a stable population. If the population is not at
303 equilibrium then calculation of survival, and therefore PrR, will be inaccurate. For example, in a
304 growing population younger individuals will be overrepresented, underestimating late-life survival,
305 and *vice versa*⁶⁸. In the absence of detailed population growth parameters for most cetacean species,
306 we model three population change scenarios in our calculation of Phys-PrR. Firstly, we assume a
307 population at equilibrium, where population growth (r)=0⁶⁸. Secondly we assume a population in
308 serious decline, $r=-0.1$, where the total population shrinks by 10% each year. We model the largest
309 possible population growth scenario for each species, up to $r=0.1$, given the age-structure of the
310 data⁶⁸. These values are comparable to the estimated population growth rates of cetacean populations.
311 For example, at the peak of the modern sperm whale fishery between 1945 and 1975 the best estimate
312 of global sperm whale population decline averaged approximately 2.67% ($r=-0.027$) per year
313 (calculated from¹³). In contrast, North Atlantic humpback whales (*Megaptera novaeangliae*) may be
314 recovering from very severe whaling at annual growth rate of 0.073-0.086⁶⁹.

315 We used our measure of age-specific ovarian activity as a measure of fecundity. PrR is the summed
316 life-expectancy in years after 95% of population fecundity has been completed (age M). Age M is
317 independent of population change and therefore remains unchanged in the different growth scenarios.
318 Because our data begin from maturity, age B (usually the age at which 5% of lifetime fecundity has
319 been realised) is equal to the first age present in our data. We calculated Phys-PrR for each population
320 change scenario for all ten species with evidence of reproductive senescence.

321 The significance of our PrR values was calculated by simulating the life-history of individuals based
322 on the real survival and fecundity data. We calculate the estimated Phys-PrR of 1000 populations of
323 1000 individuals with reproductive senescence equal to somatic senescence¹². The reported p values

324 are the number of these simulated populations with a higher Phys-PrR than the real Phys-PrR.

325 Significance is reported as the result of a two-tailed test.

326 It should be noted that these calculations are based on a stable and representative age structure. For
327 some species (notably in this study sperm whales¹³ and beluga whales⁷⁰) hunting pressures may have
328 changed the demographics, with a bias to removing large (old) individuals from the population. For
329 these species, this will lead to an underestimation of the frequency of post-reproductive females in the
330 population, and therefore an underestimation of Phys-PrR.

331 *Phylogenetic ancestral state reconstruction*

332 We combined the results of our Phys-PrR analysis with other published data on late-life reproduction
333 to infer when post-reproductive lifespans have evolved in this clade using phylogenetic comparative
334 methods. For this study we used a consensus tree created from the Bayesian posterior sample of
335 10,000 trees of the inferred phylogenetic relationships between cetacean species from the 10k tree
336 project⁷¹. This tree was pruned to leave only those species for which we have either physiological
337 measures (n=13) or other suitable records of reproduction in older females (n=12; Fig. 3;
338 supplementary 4), resulting in a phylogenetic tree containing 25 species.

339 We used a continuous-time Markov chain method⁷² to model the evolution of post-reproductive
340 lifespans as involving transitions between two states (post-reproductive lifespans present, and post-
341 reproductive lifespans absent). This model has a single parameter, the instantaneous rate of change
342 between these two states (transitions to and from post-reproductive lifespans are fixed to take the
343 same value). We used the ancestral state estimation function in the R package “ape”⁷³ in order to
344 estimate the value for this rate parameter using maximum likelihood estimation. This approach allows
345 us to infer the likely state of post-reproductive lifespans at ancestral nodes in the phylogeny given this
346 model of evolution. These inferences are given as proportional probabilities (range: 0 to 1) and
347 indicate whether ancestral species are likely to have had the trait under consideration.

348 *Ethics Statement*

349 All data used in this study are from published corpora counts from dissection of whale corpses. The
350 corpses from each study come from a variety of sources (supplementary 6). Some are from accidental
351 deaths; five species data are from mass stranding events and four from by-catch in fisheries. Other
352 data are from deliberate killing of whales; two species data are from aboriginal subsistence hunts, one
353 from historical commercial whaling (sperm whales) and six from drive hunts in Japan and the Faroe
354 Islands. The authors wish to state, in the strongest terms, that we in no way condone whaling as a data
355 collection method. The data used here are from historical sources, collected by scientists working
356 alongside commercial operations and no data were used from scientific whaling. We emphasise that
357 terminal sampling is not the best way to collect data on reproductive senescence in cetaceans. Short,
358 but especially long-term detailed demographic studies give much richer data for studying the relative
359 rates of reproductive senescence, social structures and post-reproductive lifespans (e.g. killer whales
360 in the Salish Sea^{18,23,28,74}). In the absence of such published data for cetaceans we have made use of
361 this historical physiological data, but highlight the need for, and value of, detailed individual based
362 longitudinal demographic data in the future.

363 **Data Availability**

364 All data used in this study are available in the publications referenced.

365

366 **Competing Interests**

367

368 The authors declare no competing interests.

369

370 **Author Contributions**

371 SE and DPC conceived the project in discussion with MAC and DWF. SE and DPC searched the

372 literature to find the raw data for the analysis with assistance from DG and KB. SE extracted and

373 analysed the data in discussion with DPC, DWF, SN, TC and MAC. TC ran the phylogenetic analysis.

374 SE and TC drafted the figures. SE wrote the first draft of the paper with input from DPC, all authors

375 provided input on subsequent drafts.

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383

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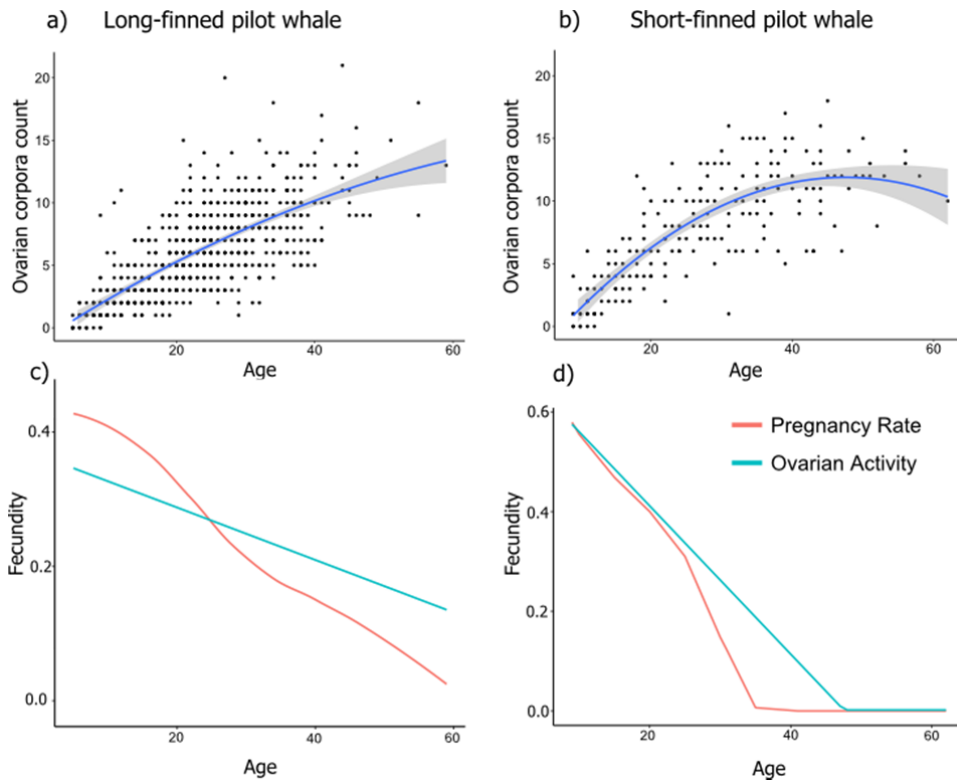
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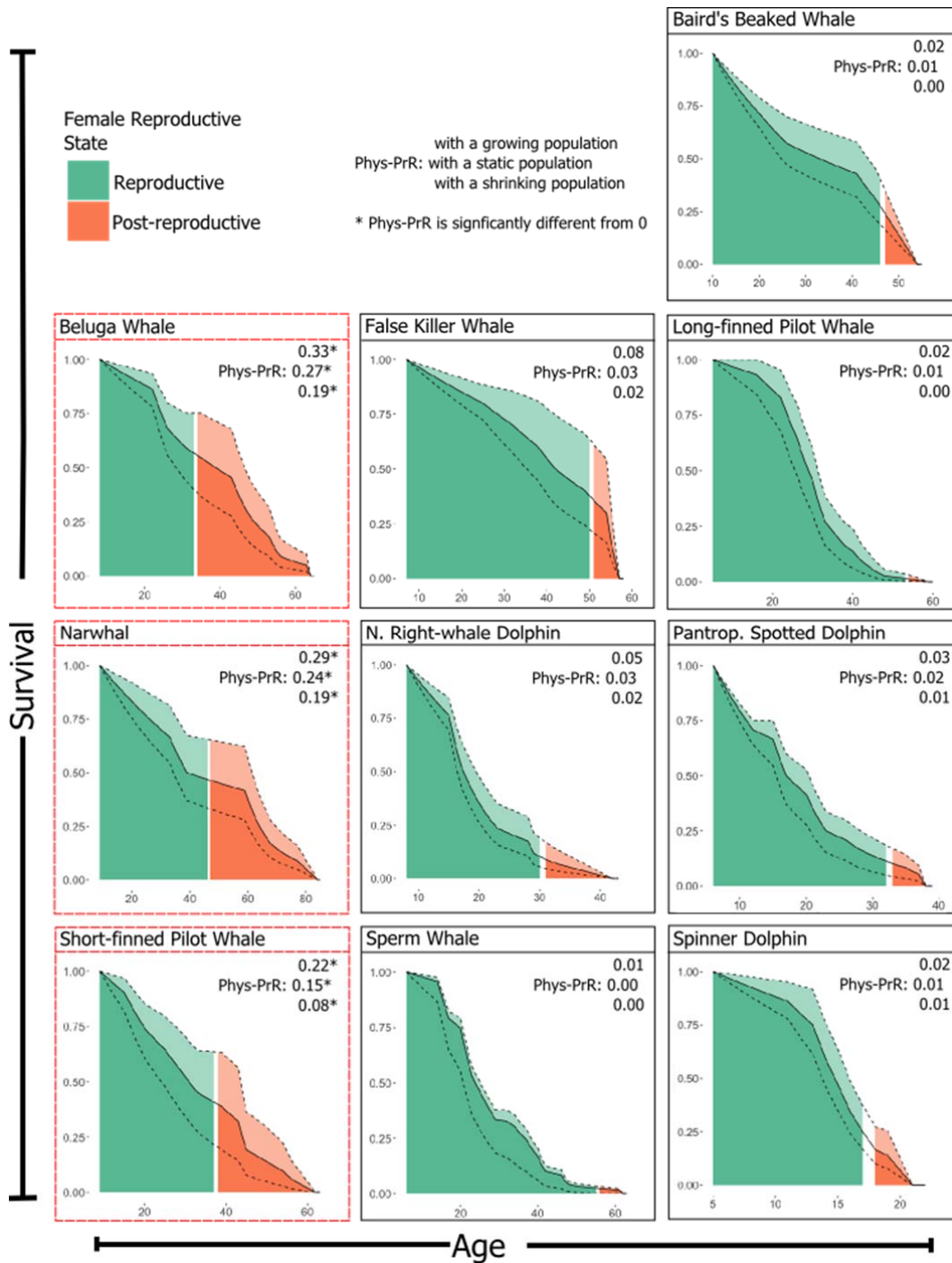
568 **Fig. 1.** Calculation of age-specific fecundity for long-finned (a and c) and short-finned (b and
569 d) pilot whales. Calculations for other species are shown in supplementary 1. a) and b) Age-
570 specific corpora counts in long-finned and short-finned pilot whales. Lines show fitted
571 second order polynomial (with confidence intervals). Curves show that ovarian activity
572 declines with age in both species, but that the decline is more pronounced in short-finned
573 pilot whales than long-finned pilot whales. c) and d) Age-specific fecundity for long- and
574 short- finned pilot whales calculated both from ovarian activity (the slope of the fitted
575 polynomial (a and b)- blue line) and pregnancy rate (smoothed- red line). Both species show
576 a decline in fecundity with age by both measures, however whereas short-finned pilot whale
577 fecundity reaches 0 before the end of life, long-finned pilot whale fecundity does not. This is
578 reflected in calculations of post-reproductive representation (a measure of post-reproductive
579 lifespan, see text). Calculated from pregnancy rate short-finned pilot whales have a

580 significant post-reproductive lifespan ($\text{PrR} = 0.28$,⁴) whereas long-finned pilot whales do not
581 ($\text{PrR} = 0.02$, calculated from:^{44,75}).

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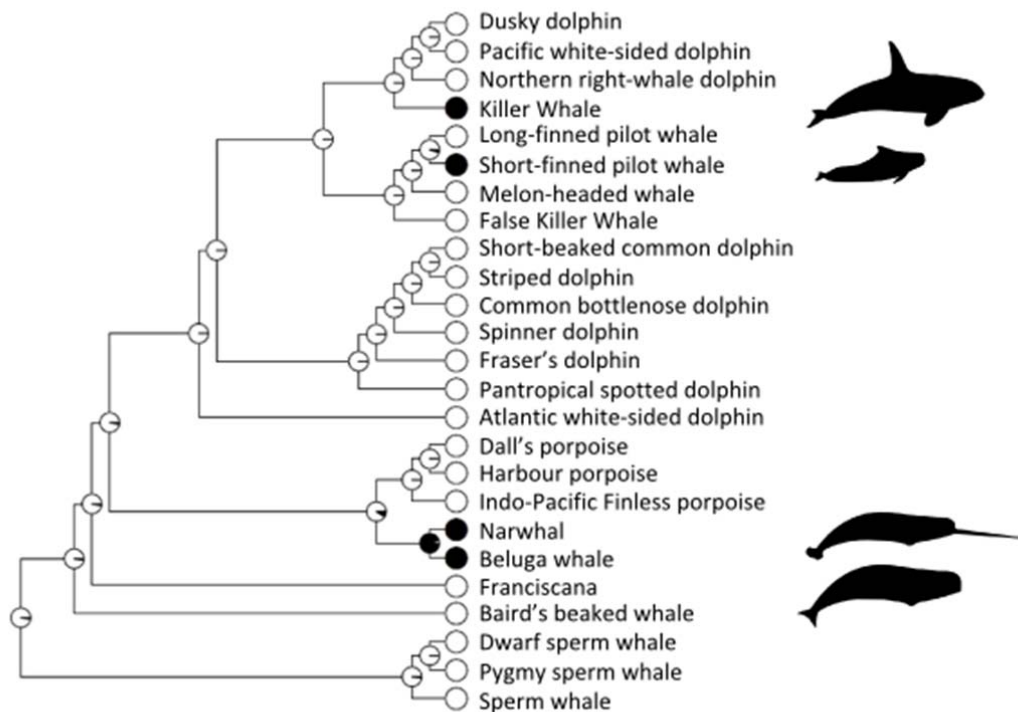
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587 **Fig. 2.** Female survival curves showing the predicted reproductive state of ten species of
 588 toothed whale. Females of three species: beluga whales, narwhals and short-finned pilot
 589 whale spend a significant proportion of their life post-reproductive. The age at which
 590 individuals become post-reproductive is defined based on the age at which 95% of population
 591 fecundity (measured as ovarian activity) has been completed. Green areas show when the

592 females in the population are reproductively active, orange show when individuals are no
593 longer reproductively active and therefore post-reproductive. The three curves represent
594 different population change scenarios, the highest dashed curve represents a growing
595 population, the middle solid curve a static population and the lowest dashed curve a shrinking
596 population (see methods for details). Physiological post-reproductive representation (Phys-
597 PrR) is calculated based on age-specific ovarian activity, values denoted with an asterisk (*)
598 are significantly different from 0, indicating that the species experiences post-reproductive
599 lifespans.

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604 **Fig. 3.** Phylogeny showing the evolution of post-reproductive lifespans in toothed whales
 605 (black; post-reproductive lifespans present, white; post-reproductive lifespans absent) for
 606 species in which data on the presence or absence of prolonged female post-reproductive
 607 lifespans are available. Pie charts at the nodes represent proportional probability that post-
 608 reproductive lifespans were present in ancestral species. Phylogenetic comparative methods
 609 (see methods) suggest that post-reproductive lifespans have evolved at least three times
 610 independently in Odontocete cetaceans. Species included are the 13 that show age-related
 611 changes in ovarian activity in this study and resident type killer whales which are well known
 612 to have a post-reproductive lifespan¹⁷ and 11 other species with records of reproduction in
 613 very old females (Table S2). Branch lengths are proportional to molecular change. Whale
 614 diagrams are adapted (cropped and the outline filled) from images by C Huh⁷⁶⁻⁷⁹ published

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616 (<https://creativecommons.org/licenses/by-sa/3.0/>).

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Common name	Species name	Age vs Corpora relationship	Relative rate of reproductive senescence	Phys-PrR stable population [shrinking population – growing population]	Conclusion
Beluga whale	<i>Delphinapterus leucas</i>	Polynomial	1.69	0.27* [0.19*-0.33*]	Reproductive senescence and post-reproductive lifespans
Narwhal	<i>Monodon monoceros</i>	Polynomial	1.48	0.24* [0.19*-0.29*]	Reproductive senescence and post-reproductive lifespans
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	Polynomial	1.38	0.15* [0.08*-0.22*]	Reproductive senescence and post-reproductive lifespans
Baird's beaked whale	<i>Berardius bairdii</i>	Polynomial	0.87	0.01 [0.00-0.02]	Reproductive senescence
False killer whale	<i>Pseudorca crassidens</i>	Polynomial	0.77	0.03 [0.02-0.08]	Reproductive senescence
Long-finned pilot whale	<i>Globicephala melas</i>	Polynomial	0.62	0.01 [0.00-0.02]	Reproductive senescence
Northern right-whale dolphin	<i>Lissodelphis borealis</i>	Polynomial	1.14 (0.75)	0.03 [0.02-0.05]	Reproductive senescence
Pantropical spotted dolphin	<i>Stenella attenuata</i>	Polynomial	0.84	0.02 [0.01-0.03]	Reproductive senescence
Sperm whale	<i>Physeter macrocephalus</i>	Polynomial	0.64	0.00 [0.00-0.01]	Reproductive senescence
Spinner dolphin	<i>Stenella longirostris</i>	Polynomial	0.89	0.01 [0.01-0.02]	Reproductive senescence
Common bottlenose dolphin	<i>Tursiops truncatus</i>	1. Linear 2. Linear 3. Linear	n/a	n/a	No reproductive senescence
Melon-headed whale	<i>Peponocephala electra</i>	Linear	n/a	n/a	No reproductive senescence
Striped dolphin	<i>Stenella coeruleoalba</i>	Linear	n/a	n/a	No reproductive senescence
Atlantic white-sided dolphin	<i>Lagenorhynchus acutus</i>	No correlation	n/a	n/a	Corpora are not a good measure of ovarian activity.
Harbour porpoise	<i>Phocoena phocoena</i>	No correlation	n/a	n/a	Corpora are not a good measure of ovarian activity.
Short-beaked common dolphin	<i>Delphinus delphis</i>	No correlation	n/a	n/a	Corpora are not a good measure of ovarian activity.

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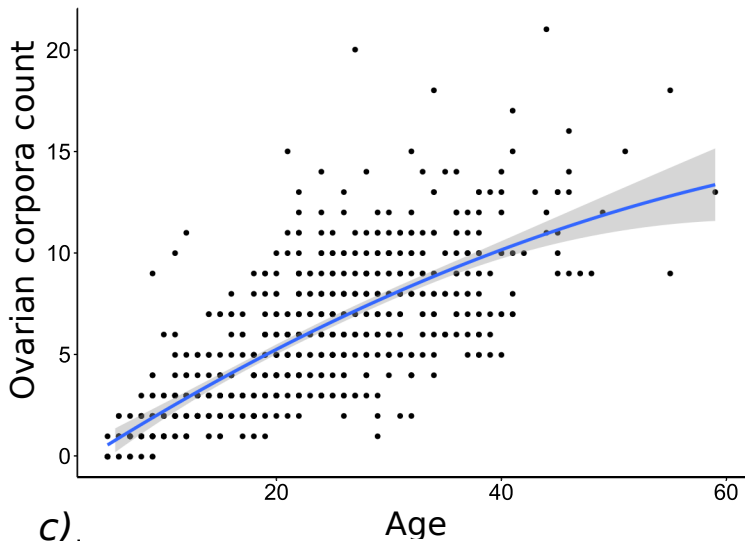
620 **Table 1.** Reproductive senescence in toothed whales inferred from physiological analysis.

621 The relative rate of reproductive senescence is calculated relative to somatic senescence using

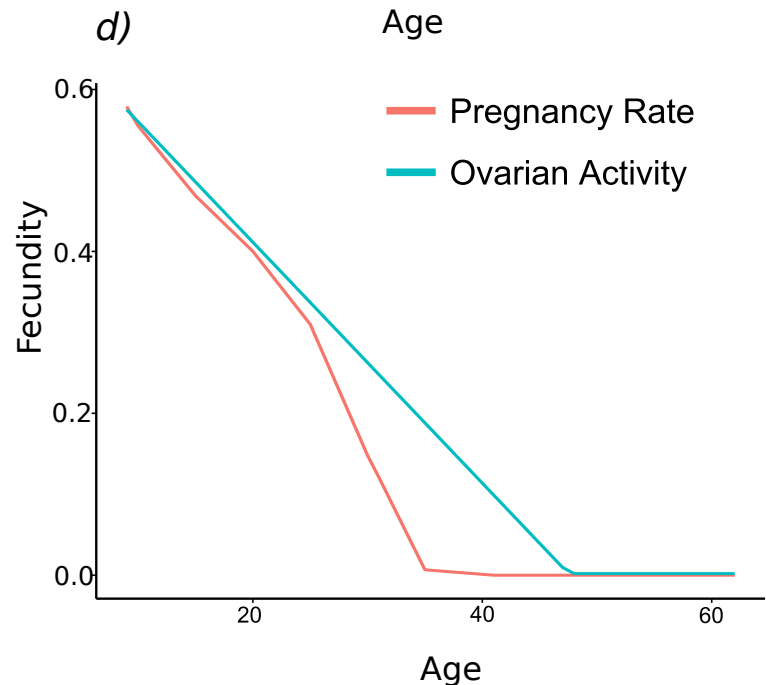
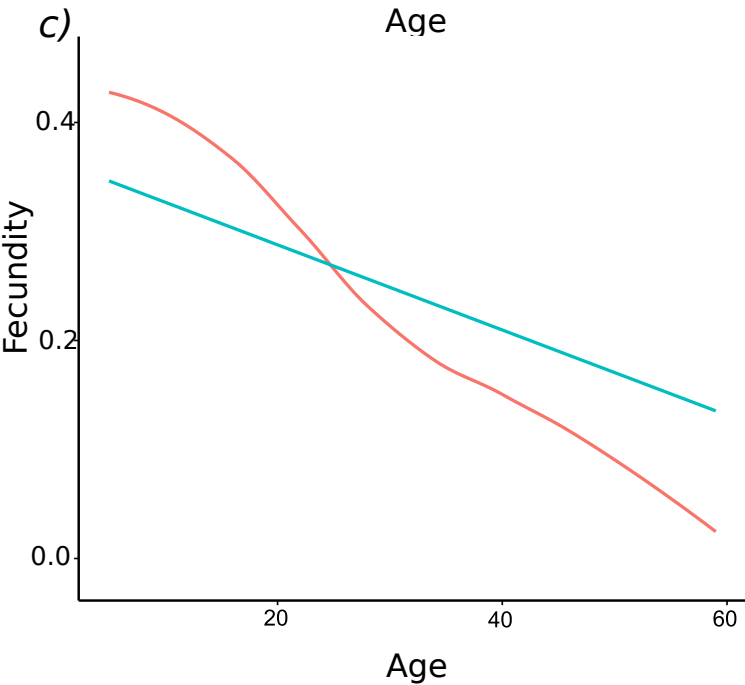
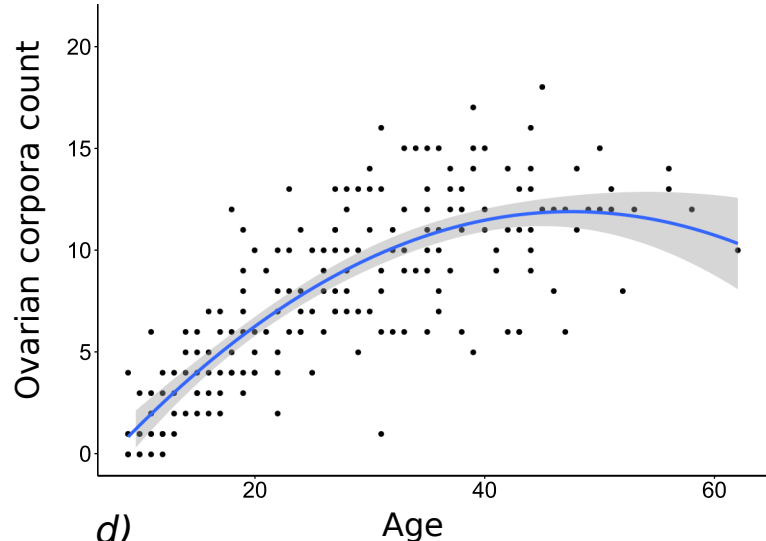
622 normalised data. A rate of exactly 1 would mean that ovarian activity is declining linearly

623 with age. A rate of greater than 1 implies that ovarian activity is declining more slowly than
624 somatic senescence. Rate in parentheses is the rate without a single outlying older individual.
625 Phys-PrR (physiological post-reproductive representation) is the proportion of female years
626 being lived by post-reproductive females in the population (those marked with an * are
627 significantly different from 0).

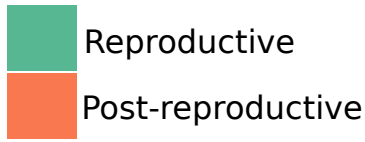
a) **Long-finned pilot whale**



b) **Short-finned pilot whale**

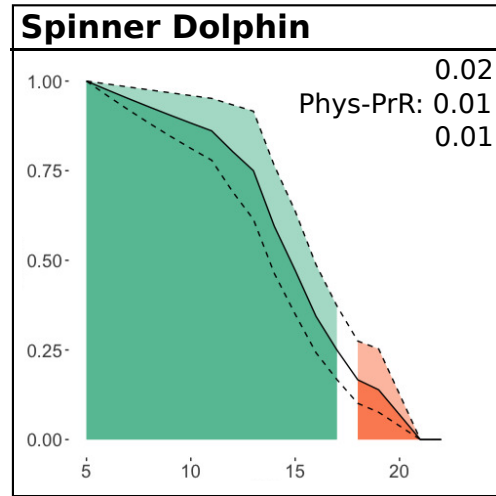
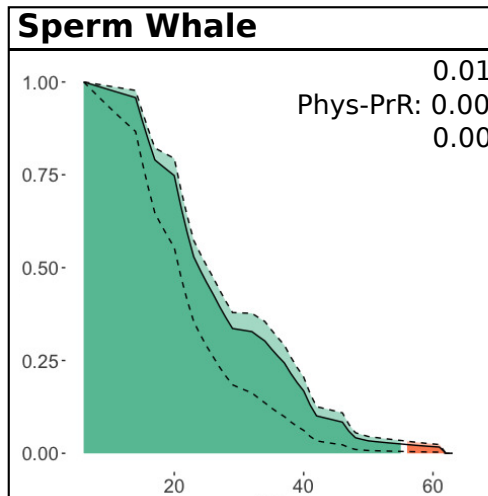
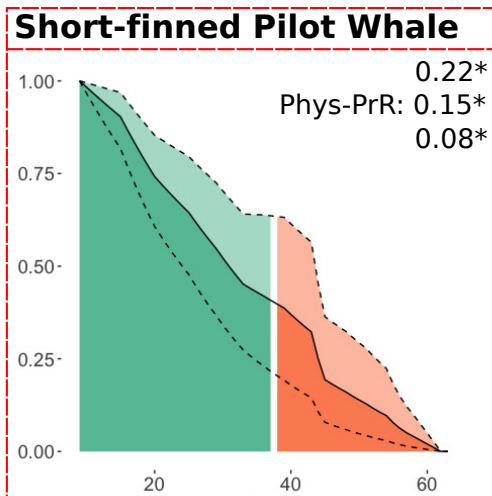
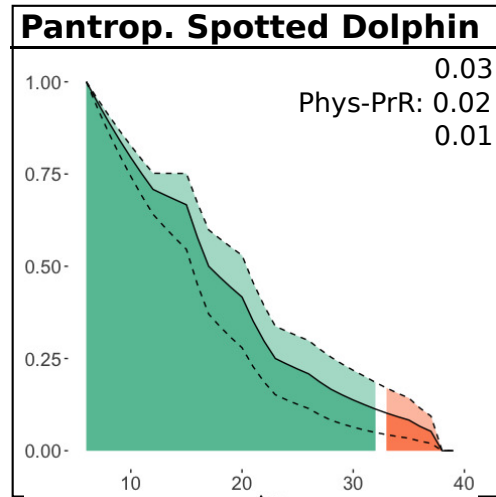
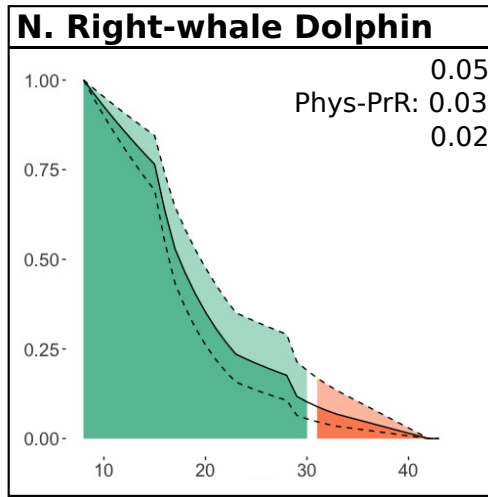
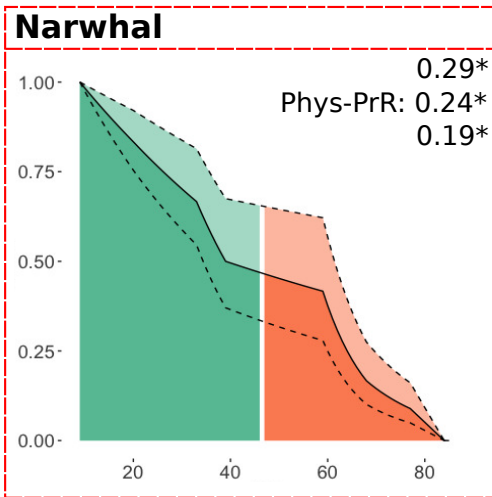
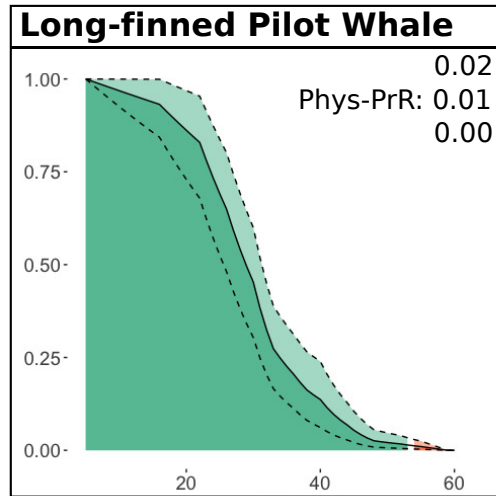
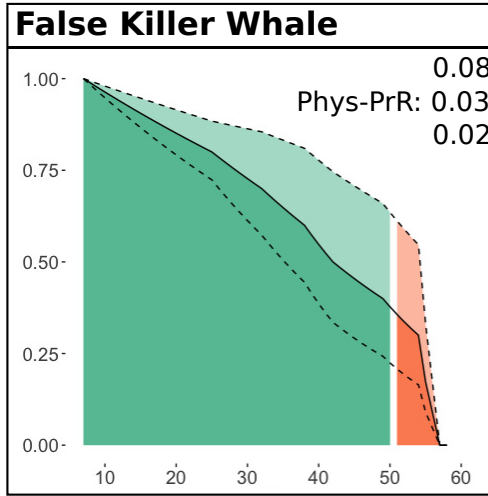
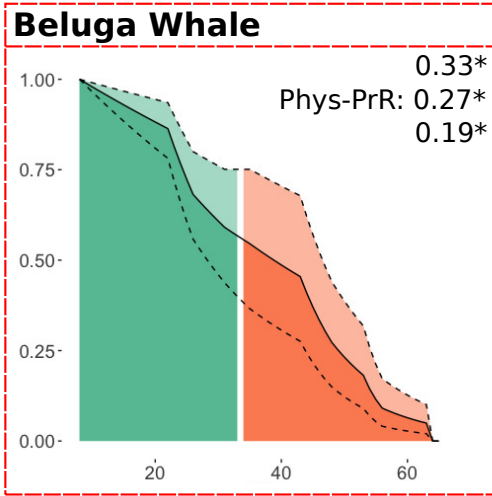
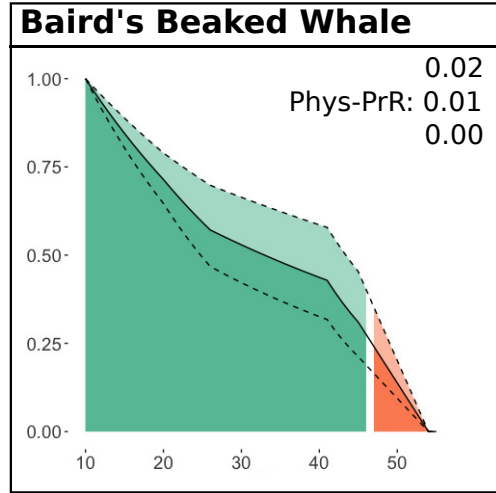


Female Reproductive State



with a growing population
Phys-PrR: with a static population
with a shrinking population

* Phys-PrR is significantly different from 0



Age

